



Restoring tropical biodiversity: Leaf traits predict growth and survival of late-successional trees in early-successional environments

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Abstract

Natural succession after abandonment of degraded land often results in a low-diversity secondary forest that persists for decades. Planting late-successional species in early-successional environments may help to bypass this low-diversity stage by overcoming dispersal limitation. To identify which late-successional species perform best in early-successional environments, we tested growth and survival of species with different expressions of leaf traits over 4 years. We measured the intraspecific variation in leaf mass per unit area (SLM) and in leaf density of 24 non-pioneer tropical tree species with different maximum mature heights near the Los Tuxtlas Biological Station in Veracruz, southeast Mexico. Growth and survival increased with increased variation in SLM in the entire sample (R^2 up to 0.44), with mid-canopy species (>11–25 m) closely reflecting variation in SLM (R^2 up to 0.88). A lesser but statistically significant relationship existed for leaf density. Intraspecific variation in SLM enables identification of flexible species with potentially higher growth rates and survival across the microhabitats of early-successional environments, providing an especially powerful tool for selecting mid-canopy species.

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1. Introduction

Large areas of tropical forest are now being lost to agriculture or cattle ranching, while remaining forest fragments lose biodiversity to random local extinctions (Turner, 1996). At the same time, tens of thousands of hectares of denuded land are abandoned

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annually to forest succession (Moran et al., 1994). Early-successional environments derived from intensive agriculture or cattle ranching progress back to forest very slowly because tree seeds arrive slowly, substantially reducing rates of plant colonization (Whitmore, 1989; Finegan, 1996; Boucher et al., 2001). In many places, dispersal limitation rather than soil compaction, nutrient limitation and competition from grasses, may be the primary factor that precludes colonization of open ground by late-successional trees. In large deforested areas, seeds of trees and shrubs that do arrive on their own are those of early-successional pioneers.

To speed succession, commercial tree plantations are increasingly used as synthetic forest matrices (Lugo, 1997; Lamb, 1998; Parrotta and Knowles, 1999). The input of seeds of native species in plantations is higher than in pastures or agricultural lands; many seeds germinate and establish in the understories of plantations, eventually increasing canopy biodiversity at sites where colonists are allowed to mature (Lugo, 1992, 1997). Benefits of these practices for stopping degradation of ecosystem functions are clear; the usual practice of establishing plantations of one or a very few species, almost all wind-dispersed, stops erosion and helps retain nutrients and water. However, these low-diversity plant communities do not resemble the former forest for many years, if ever. An alternative is establishment of mixed assemblages, using species that have characteristics likely to predict high survival, and when animal-dispersed, are likely to catalyze colonization of additional animal-dispersed species.

The rate of forest regeneration depends largely on the growth rates and survival of native species that are planted or arrive on their own. Where time is at a premium, native or exotic early-successional trees with high growth rates are often used (e.g. 5 m per year, Gómez-Pompa and Vazquez-Yanes, 1981; Whitmore, 1989; D'Antonio and Meyerson, 2002). In the tropics, if native pioneers are planted, such plantations may cover large areas of land with a small proportion (<1–20%) of forest biota that usually arrives by passive dissemination anyway (e.g. Martínez-Garza and González-Montagut, 1999). The use of exotic pioneers may prevent the establishment of some native species, will not contribute to the return of the native plant–animal interactions, and may or

may not facilitate regeneration of native species in the understory (Keenan et al., 1997; D'Antonio and Meyerson, 2002). Much slower to recruit are late-successional species that provide much of the structural diversity in the mature forest, as well as food resources for fruit- and seed-eating animals (Welden et al., 1991; Martínez-Ramos, 1994). Planting dispersal-limited late-successional species that provide a variety of food resources for animals is a preferable reforestation tactic than reliance on a low-diversity pioneer matrix (Wunderle, 1997; Martínez-Garza and Howe, 2003). In theory, acceleration of development of a species-rich and structurally diverse forest in early-successional habitats is a valuable option. However, it is unknown which late-successional species are best able to endure the variable, and sometimes severely xeric, abiotic conditions of early-successional environments.

Existing evidence suggests that many late-successional species grow and survive well in early-successional habitats if they get there (i.e., abandoned pastures; Montagnini et al., 1995; Haggard et al., 1998; Loik and Holl, 1999; Leopold et al., 2001; Hooper et al., 2002). A challenge is to determine characteristics of species that are best suited to reforestation management. Given the high biodiversity of tropical ecosystems, it is impractical to test more than a small fraction of individual species on regenerating agricultural lands. One approach is to determine plant characteristics associated with tree growth and survival under the stressful conditions of abandoned pastures or croplands, and then use those characteristics as criteria for species selection to enrich forest restoration.

Morphological and functional leaf characteristics that change with environmental conditions affect growth rates. Within a species, plants growing in low light have larger leaves with lower dry leaf weight for unit leaf area (specific leaf mass; SLM), leaf density and water content than plants in high-light environments, which in contrast have smaller leaves with high SLM (e.g. Parkhurst and Loucks, 1972; Percy and Sims, 1994). It is likely that these traits minimize water loss and maximize photosynthesis; individuals under different environmental conditions may maintain similar growth rates. Between species, the key distinction is between effects of mean and variance in SLM under controlled and natural environments. Mean SLM is negatively related to

growth rates for many species in greenhouse studies under controlled light, water and nutrients (e.g., Grime et al., 1997; Westoby, 1998; Reich et al., 1999). In general, those species with large leaves and low SLM have higher growth rates than species with high SLM and small leaves. Therefore under homogeneous light conditions, growth rates of species are related to leaf mass per unit area. In far more dynamic early-successional environments, the high turnover of fast-growing pioneer species generates a highly heterogeneous light environment. Given this environmental heterogeneity that develops in the normal course of succession, we reason that a measure of the variability of leaf traits known to change in response to light and water availability may reflect the capacity of species to adjust leaf morphology to different microhabitats.

Our idea is that the variability in leaf traits, required during the development from a seedling to a tree, is already measurable in juvenile trees that are distributed over a range of environments. Variability in leaf traits, and therefore ecological performance, is then expected to correlate with tree stature because of the light gradient that occurs from the bottom to the top of the forest. Tall species may experience low light levels as seedlings or juveniles inhabiting the forest floor, but higher light levels as they gain height. Therefore, they show leaves with traits related to high-light environments (i.e., high mean SLM and leaf density), while short-statured trees show leaves with traits of low-light environments (low mean SLM; Thomas and Bazzaz, 1999). In addition, tall species experience higher heterogeneity in light levels within their crowns than shorter species that spend most of their lives under lower light levels (Thomas and Bazzaz, 1999; Martínez-Garza and Howe, 2005). For tall tree species, labile leaf characteristics could provide the functional means of adjusting easily to the changing environmental conditions of early-successional environments.

We asked whether: (1) the growth and survival of late-successional species growing in pastures, edges and secondary forests is related to intraspecific variation of SLM and leaf density, (2) growth and survival and leaf traits of late-successional trees are related to the maximum mature height of species, and (3) if those late-successional species that grow faster survive better in early-successional environments.

2. Methods

2.1. Study site

This study was conducted in a large experimental planting in the Cooperative of Lázaro Cardenas at approximately 6 km from Los Tuxtlas Biological Station (LTBS) in the state of Veracruz, southeast Mexico (18°30' and 18°40'N, 95°03' and 95°10'W). LTBS lies within a reserve of 640 ha of northernmost rain forest in the Neotropics. This lowland rain forest has a closed canopy about 40 m high. *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 mid-canopy and understory, respectively (Bongers et al., 1988). Sandy loams are classified as vitric andosols (FAO/UN 1975 in Soto-Esparza, 1976). Mean annual temperature and mean annual rainfall are 27 °C and 4900 mm, respectively. A dry season (<150 mm/month) extends from March to May, rains from June to February.

2.2. Land use history and experimental planting

The study area is located within a 25 ha parcel of former forest land that was deforested in 1968, used as crop land for 4 years and for cattle ranching for 15 years. It has undergone natural regeneration since abandonment in 1987. This early-successional environment has three distinct microhabitats: (1) secondary forest with a 15 m tall canopy of pioneer species: *Cecropia obtusifolia* Bertol. (Moraceae), *Heliocarpus appendiculatus* Turcz. (Tiliaceae), *Bursera simaruba* (L.) Sarg. (Burseraceae) and *Cedrela odorata* L. (Meliaceae); (2) open area of approximately 3 ha remains covered with the exotic grass *Cynodon plectostachyus* (K. Schum.) Pilg. up to 1.5 m tall in the wet season; and (3) low and broken tree canopy of 2–4 m of the same pioneer species that occur in the secondary forest. A general description of the site is in Ricker et al. (2000).

The general procedure was to germinate seeds collected from the LTBS in a shaded nursery, and transplant seedlings to three microhabitats in the field. In August–December 1996, seeds of 45 species of pioneer and late-successional trees, palms and lianas

were collected from the LTBS and germinated under shade in a nursery (100 individuals per species, on average; total of $N = 5000$ individuals). Seeds were collected from more than three maternal individuals to ensure genetic diversity. During January–March 1997, we marked a grid of 5000 $2\text{ m} \times 2\text{ m}$ squares covering the field, including each of the above-designated microhabitats. Seedlings of the 45 species approximately 4 months old were planted in mixed stands, one seedling in the middle of each square. The microhabitat that each experimental individual inhabited was described with respect to crown illumination index in 2001 (Table 1; Dawkins and Field, 1978 in Clark and Clark, 1992). This index ranges from 1 to 5, with 1 representing the dark understory of the secondary forest (no direct light reaching individuals) and 5 representing sunny pasture (individuals totally exposed to light). To characterize the physical environment in the five different levels of crown illumination index, we measured photon-flux density (PFD), gravimetric soil moisture, and bulk density in a sub-sample of individuals during the dry season. PFD was measured with a Light Meter (Li-cor LI-189 quantum sensor). Gravimetric soil moisture and bulk density were measured following Chapman (1976), bulk density was used as an estimate of soil compaction. Individuals of all species were exposed to significantly different photon-flux densities (Kruskal–Wallis $_{(4,495)} = 115.41$, $P < 0.0001$) and gravimetric soil moisture ($F_{(4,115)} = 4.02$, $P < 0.005$) at the different levels of crown illumination index. Individuals experienced similar bulk densities at all levels of the index ($F_{(4,115)} = 0.04$, $P > 0.5$; Table 1).

Twenty-four tree species from 15 families were used to represent the variety of fruit types and maximum mature heights of late-successional trees in the area (Table 2). Maximum mature height was considered to

be the tallest published height for adults of a given species at LTBS (Ibarra-Manríquez and Sinaca, 1995, 1996a, 1996b). To calculate seedling and juvenile growth rates, heights and diameters at the stem base were measured in April 1998, October 1998, April 1999 and April 2001. Grasses and herbs were removed within a radius of 25 cm around individuals at the time of measurement, but neighboring plants above each experimental plant were left untouched. Increments in height ($\text{height}_{t_2} - \text{height}_{t_1}/\text{time}$) and in basal stem diameter were calculated for the three periods between censuses. The survival percentage for each species was calculated as the number of individuals surviving from 1997 to 2001, divided by the number of individuals present in 1997. Seven species that experienced some losses of seedlings during a small accidental fire in 1998 were omitted from the analysis of survival, leaving 17 species for that analysis.

To determine intraspecific variation in leaf traits, three leaves from one individual per species in each microhabitat were measured for a total of five individuals per species ($N = 115$ individuals). For those species with compound leaves, one leaflet at the same position was sampled from three leaves. Leaves were sampled from different branches just behind the new leaves to select for similar leaf ages. For those species with few leaves, individuals selected were those with enough leaves to be sampled; when all individuals of a species had many leaves, individuals were chosen at random. Leaves were measured in a leaf area meter (Ci-202, CID, Inc. Camas, WA, USA; leaf size, LS) and weighed to the nearest 0.1 g (fresh weight, FW) within 2 h of collection (Balance Pocket Pro 250-B). Leaves were oven dried to constant mass at $100\text{ }^{\circ}\text{C}$ and weighed to the nearest 0.001 g (Balance Mettler PM 1200; dry weight, DW). With these data, leaf mass per unit area [$\text{SLM} = (\text{DW}/\text{LS})$] and leaf

Table 1
Physical environmental variables of an experimental planting in Los Tuxtlas, Veracruz, Mexico

Crown illumination index	PFD ($\mu\text{mol m}^{-2}\text{ s}^{-1}$)	Soil moisture (ml g^{-1})	Bulk density (g cm^{-3})
No direct light	20	0.45 ± 0.01 a	0.67 ± 0.02
Illumination from the side	25	0.45 ± 0.02 a	0.66 ± 0.01
Partial vertical illumination (10–90%)	33	0.42 ± 0.01 ab	0.67 ± 0.02
Full vertical illumination	80	0.44 ± 0.01 ab	0.67 ± 0.01
Crown fully exposed	1730	0.40 ± 0.01 b	0.66 ± 0.01

Photon-flux density (PFD; median, $N = 500$), gravimetric soil moisture, and bulk density (mean \pm S.E., $N = 120$) are given for each level of crown illumination index. Different letters after mean \pm S.E. indicate significant differences at $P < 0.05$ tested with a post hoc Tukey test.

Table 2

Family, fruit type, and published range of maximum mature heights of 24 late-successional tropical tree species growing in an experimental planting in Los Tuxtlas, Veracruz, Mexico

Species	Family	Fruit type ^a	Height ^a (m)
<i>Ampelocera hottlei</i> (Standl.) Standl.	Ulmaceae	Green drupes	15–30
<i>Amphitecna tuxtliensis</i> A.H. Gentry	Bignoniaceae	Green berry	3–10
<i>Calophyllum brasiliense</i> Cambess.	Clusiaceae	Green drupes	20–30
<i>Ceiba petandra</i> (L.) Gaertn.	Bombacaceae	Brown capsules	20–40
<i>Chrysophyllum venezuelanense</i> (Pierre) T.D. Penn	Sapotaceae	Brown spherical berry	5–20
<i>Cajoba arborea</i> (L.) Britton et Rose	Mimosaceae	Red legume	15–25
<i>Cordia megalantha</i> S. F. Blake	Boraginaceae	Brown drupes	20–35
<i>Cordia stellifera</i> I.M. Johnston	Boraginaceae	Red drupes	10–25
<i>Couepia polyandra</i> (Kunth) Rose	Chrysobalanaceae	Orange drupes	15–25
<i>Eugenia inirebensis</i> P.E. Sánchez	Myrtaceae	Yellow drupes	8–15
<i>Guarea grandifolia</i> A. DC.	Meliaceae	Brown or orange capsule	20–30
<i>Hirtella triandra</i> Sw. subsp. <i>media</i> (Standl.) Prance	Chrysobalanaceae	Purple berries	15–20
<i>Inga sinacae</i> M. Sousa et Ibarra-Manríquez	Mimosaceae	Hairy brown legume	6–20
<i>Licaria velutina</i> van der Werff	Lauraceae	Black drupes, red cap	10–15
<i>Lonchocarpus cruentus</i> Lundell	Fabaceae	Black legume	15–25
<i>Nectandra ambigens</i> (S.F. Blake) C.K. Allen	Lauraceae	Black drupes, red cap	20–40
<i>Persea schiedeana</i> Nees	Lauraceae	Green drupes	12–20
<i>Pimenta dioica</i> (L.) Merr.	Myrtaceae	Black berry	8–30
<i>Poulsenia armata</i> (Miq.) Standl.	Moraceae	Brown greenish multifruit	20–40
<i>Pouteria rhynchocarpa</i> T.D. Penn.	Sapotaceae	Yellow drupes	3–8
<i>Rhedia edulis</i> (Seems.) Planch. & Triana (<i>Garcinia</i>)	Clusiaceae	Yellow berry	5–15
<i>Sapindus saponaria</i> L.	Sapindaceae	Green berry	20–30
<i>Trichilia havanensis</i> Jacq.	Meliaceae	Green capsule	6–10
<i>Virola guatemalensis</i> (Helmsl.) Warb.	Myristicaceae	Brown capsule with arillate seed	20–30

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

density [leaf density = FW/DW] were calculated. Leaf density, as measured in this study, reflects the amount of cytoplasm versus hemicellulose and cellulose in plant tissues (Rascio et al., 1990; Garnier and Laurent, 1994). Intraspecific variation for each leaf trait is reported as its coefficient of variation (hereafter CV) = (standard deviation of given leaf trait) × (100)/ (mean of leaf trait across all microhabitats), corrected for sample size (Sokal and Rohlf, 2003).

2.3. Data analysis

Natural processes of succession left different numbers of individuals per species in the various microhabitats. Therefore, two estimators of increments in diameter and height were calculated: (1) with all individuals per species irrespective of the number of individuals found in each microhabitat, and (2) with one individual per microhabitat, the same sampled for leaf traits ($N = 5$). These estimators of growth increments are highly correlated (Pearson correlation

$r = 0.91$, $P < 0.0001$ for increments in height, and 0.80 , $P < 0.0001$ for increments in diameter). Regressions calculated with all individuals per species (estimator 1) were significant when regressions with the sample of five individuals per species (estimator 2) were significant. Because R^2 was lower with estimator 1, only results from estimator 2 are shown in the results.

Median final sizes were calculated with all individuals alive in 2001. Maximum height and diameter refer to the individual with the greatest size among all alive in 2001; the microhabitat where that was found is indicated by the crown illumination index. Linear regressions were performed for the intraspecific variation in leaf traits (CV of leaf traits) with survival and increments in height and in diameter. Intraspecific variations in leaf area and leaf water content were also evaluated but they were not related to growth rates and survival (Martínez-Garza, 2003). Mean increments in height and diameter for each species for the three periods of time between censuses

and across all habitats were used for regressions. Multiple regressions with both leaf traits together are undesirable because they are highly correlated (Pearson correlation = 0.70, $P < 0.001$). Linear regressions were partitioned by maximum mature height in canopy (>30 m, $N = 10$), and mid-canopy status (>11 m up to 25 m, $N = 10$). Regressions were not performed separately with three understory species, and one outlier mid-canopy species was excluded (*Lonchocarpus*, below). Increments were \log_2 transformed to satisfy regression assumptions; means shown for increments were back transformed. Species are referred to by genus, except for *Cordia* spp. Means are accompanied by standard errors throughout the paper. Except for the *F*-test, which was done by hand, statistical analyses were performed in Systat 9.0.

3. Results

3.1. Final sizes, increments, survival and maximum mature height

3.1.1. Height

Mean final height over all species after 4 years was 130.3 ± 17.5 cm, measured for five individuals of each of 24 species (120 plants) with a mean increment of 1.4 ± 1.3 cm month⁻¹. The tallest individual was the mid-canopy *Lonchocarpus* at 740 cm (70 mm diameter at breast height [DBH]) growing in gap conditions (crown illumination index 4; Table 3); this species had the highest mean growth increment in height of 9.6 ± 5.9 cm month⁻¹. *Ampelocera*, a canopy tree, had the lowest increment in height (0.94 ± 0.51 cm month⁻¹). Those species with higher

Table 3

Final size after 4 years and monthly increments in height and diameter for 24 late-successional tropical tree species growing in an experimental planting in Los Tuxtlas, Veracruz, Mexico

Species	Final size						Increments			
	Height	Max Hgt	CII	Diameter	Max Dia	CII	All individuals		Five individuals	
							Height	Diameter	Height	Diameter
<i>Ampelocera</i>	30	183	3	6.0	68	5	0.59 ± 0.60	0.10 ± 0.10	0.94 ± 0.51	0.11 ± 0.08
<i>Amphitecna</i>	47	145	3	9.5	19	4	1.24 ± 1.60	0.21 ± 0.11	3.92 ± 6.0	0.17 ± 0.08
<i>Calophyllum</i>	75	306	3	7.0	20	3	1.73 ± 1.34	0.24 ± 0.22	1.25 ± 0.47	0.17 ± 0.08
<i>Ceiba</i>	223	500	4	57.0	132	4	6.44 ± 4.14	1.5 ± 1.1	7.32 ± 4.70	1.8 ± 1.1
<i>Chrysophyllum</i>	115	367	4	15.0	60	3	1.78 ± 2.1	0.58 ± 0.18	1.62 ± 1.30	0.22 ± 0.16
<i>Cojoba</i>	196	525	3	50.0	120	3	5.47 ± 3.48	1.25 ± 0.90	5.40 ± 4.40	0.75 ± 0.58
<i>C. megalantha</i>	64	310	3	16.0	73	4	1.71 ± 1.69	0.49 ± 0.46	2.52 ± 2.10	0.58 ± 0.48
<i>C. stellifera</i>	78	283	4	14.5	69	4	2.54 ± 1.92	0.54 ± 0.40	4.55 ± 2.26	0.69 ± 0.32
<i>Couepia</i>	85	264	4	11.0	30	4	2.20 ± 1.44	0.27 ± 0.12	3.42 ± 1.75	0.43 ± 0.16
<i>Eugenia</i>	50	110	2	5.5	12	2	0.66 ± 0.77	0.04 ± 0.15	1.08 ± 0.91	0.10 ± 0.03
<i>Guarea</i>	74	200	3	15.0	35	3	1.51 ± 0.83	0.36 ± 0.15	2.17 ± 1.14	0.47 ± 0.14
<i>Hirtella</i>	110	265	3	16.0	35	3	1.32 ± 1.34	0.10 ± 0.24	1.41 ± 1.22	0.21 ± 0.34
<i>Inga</i>	250	735	5	33.5	150	5	5.79 ± 4.50	0.92 ± 0.81	4.0 ± 3.86	0.72 ± 0.38
<i>Licaria</i>	141	363	5	15.0	34	3	3.32 ± 1.83	0.30 ± 0.12	3.92 ± 1.10	0.32 ± 0.11
<i>Lonchocarpus</i>	351	740	4	43.0	123	5	9.53 ± 5.5	1.2 ± 0.8	9.60 ± 5.90	1.17 ± 0.96
<i>Nectandra</i>	70	350	5	8.0	44	5	1.78 ± 1.56	0.27 ± 0.36	3.19 ± 2.45	0.75 ± 1.10
<i>Persea</i>	220	474	4	32.0	64	4	5.26 ± 2.63	0.66 ± 0.40	4.69 ± 1.10	0.60 ± 0.36
<i>Pimenta</i>	82	210	4	7.0	35	4	1.78 ± 1.26	0.20 ± 0.21	2.19 ± 1.01	0.20 ± 0.15
<i>Poulsenia</i>	107	167	3	21.5	31	4	2.33 ± 0.82	0.48 ± 0.23	2.61 ± 0.66	0.48 ± 0.07
<i>Pouteria</i>	70	170	4	12	24	3	1.45 ± 0.92	0.10 ± 1.9	1.72 ± 1.12	0.34 ± 0.09
<i>Rheedia</i> (Garcinia)	50	90	3	7.0	16	3	0.55 ± 0.77	0.16 ± 0.17	1.12 ± 0.50	0.15 ± 0.02
<i>Sapindus</i>	98	384	4	13.0	142	4	2.73 ± 1.86	0.39 ± 0.32	3.41 ± 2.80	0.48 ± 0.34
<i>Trichilia</i>	289	456	3	37.0	82	3	6.52 ± 2.94	0.87 ± 0.46	5.10 ± 2.84	0.52 ± 0.22
<i>Virola</i>	204	374	3	24.0	78	3	2.56 ± 2.00	0.36 ± 3.10	2.50 ± 0.82	0.44 ± 0.10

Final size: median of final height (Height, cm) and diameter (Diameter, mm), level of the crown illumination index (CII) where the individual with the maximal height (Max Hgt, cm) and maximal diameter (Max Dia, mm) was found. Increments: increments in height (cm month⁻¹) and in diameter (mm month⁻¹) calculated with: (1) all individuals per species irrespective of the number of individuals in each microhabitat and (2) five individuals per species, those used to evaluate leaf traits.

increments in height measured across all microhabitats of early-successional environments showed higher final individual height (Pearson correlation $r = 0.93$, $P < 0.0001$) and maximal height ($r = 0.85$, $P < 0.0001$). For 12 species, the largest individuals were in gap or open conditions (crown illumination index 4 or 5, respectively); for 11 species, the largest individuals were in sites with partial vertical illumination (crown illumination index 3). The largest individual of one species (*Eugenia*) was found in sites with illumination from the side (crown illumination index 2; Table 3).

3.1.2. Diameter

Mean final diameter after 4 years was 19.8 ± 15 mm with a mean increment of 0.23 ± 1.07 mm month⁻¹. The individual with the largest basal diameter was an *Inga* with 150 mm; this individual growing in pastures (crown illumination index 5) had 62 mm DBH and 375 cm in height; this species showed a mean growth increment in diameter of 0.72 ± 0.38 mm month⁻¹ (Table 3). *Eugenia* had the lowest growth increment in diameter, while the canopy tree *Ceiba* had the highest (Table 3). Those species with higher growth increments in diameter measured across all microhabitats of early-successional environments showed higher final diameters (Pearson correlations $r = 0.95$, $P < 0.0001$) and maximal diameters ($r = 0.77$, $P < 0.0001$). For 13 species, the largest individuals were in gap or open conditions (crown illumination index 4 or 5, respectively); for 10 species, the largest individuals were in sites with partial vertical illumination (crown illumination index 3). The individual with the largest basal diameter of one species (*Eugenia*) was found in sites with illumination from the side (crown illumination index 2; Table 3).

The outlier species *Lonchocarpus* was removed from analyses. Regressions including this species were significant, but the slopes were uncharacteristically steep due to a remarkably high growth rate in height and diameter (Table 3).

3.1.3. Survival

The mean percent survival over 4 years for the 16 species analyzed with at least 60 individuals (without the outlier *Lonchocarpus*, see above) was $74.4 \pm 5.5\%$. *Eugenia*, a mid-canopy tree, had the

lowest survival (32.2%) while *Sapindus*, a canopy tree, had the highest (96.8%).

3.1.4. Maximum mature height

The mean maximum mature height of the 24 species from the literature was 25 ± 2 m, ranging from 8 m for *Pouteria* to 40 m for *Poulsenia* and *Nectandra*.

3.2. Regressions

3.2.1. Increments and leaf traits

Mean CV of SLM was $17.6 \pm 1.8\%$ and mean CV of leaf density was $13.3 \pm 1.5\%$ (Appendix A). The increment in height was positively related to CV of SLM, as expected (Table 4). Partitioning by maximum mature height category (mid-canopy versus canopy or taller) showed that the regression of increments in height on CV of SLM for mid-canopy species (Fig. 1a) was far stronger than the one including all species or only canopy species. The increment in height was not related to CV of leaf density for the entire sample of 23 species, nor were increments in height associated with CV of leaf density for canopy and mid-canopy species considered separately (Table 4).

Increment in diameter was related to CV of SLM (Table 4). As predicted, those species with higher intraspecific variability in SLM showed higher growth rates in diameter. The increment in diameter was not related to CV of leaf density. Partitioning by maximum mature height category again showed a much stronger regression of the increments in diameter on the CV of SLM of mid-canopy species (Fig. 1b, Table 4). Regression of increments in diameter on the CV of leaf density for mid-canopy species was not significant. The increment in diameter was not related to CV of SLM or CV of leaf density for canopy species, analyzed separately (Table 4).

3.2.2. Survival and leaf traits

As expected, 4-year survivorship was positively associated with CV of SLM (Table 4) and CV of leaf density (Fig. 2a, Table 4) for 16 late-successional tree species growing in the various microhabitats of an early-successional ecosystem. Partition of species by maximum mature height showed that this overall relationship of 4-year survivorship was due to the mid-canopy species for CV of SLM (Fig. 2b, Table 4); as yet there is no evidence that 4-year survivorship of

Table 4

Regression equations, R^2 and probabilities of incremental growth and survival on the CV of SLM and CV of leaf density of 23 late-successional tree species growing in an experimental planting in Los Tuxtlas, Veracruz, Mexico

	CVSLM		CV leaf density
Increment in height			
All species $N = 23$	Increment height = $-0.06 + 0.06CV\ SLM$	$R^2 = 0.48^{****}$	ns
Canopy sp. $N = 10$	Increment height = $-0.1 + 0.06CV\ SLM$	$R^2 = 0.30^*$	ns
Mid-canopy $N = 10$	Increment height = $-0.2 + 0.08CV\ SLM$	$R^2 = 0.81^{****}$	ns
Increment in diameter			
All species	Increment diameter = $-2.0 + 0.04CV\ SLM$	$R^2 = 0.44^{****}$	ns
Canopy sp.	ns		ns
Mid-canopy	Increment diameter = $-2.1 + 0.04CV\ SLM$	$R^2 = 0.88^{****}$	ns
Survival			
All species $N = 16$	4-Year survivorship% = $47.0 + 1.6CV\ SLM$	$R^2 = 0.24^*$	4-Year survivorship% = $52.1 + 1.6CV\ density, R^2 = 0.25^*$
Canopy sp. $N = 6$	ns		0.45^\dagger
Mid-canopy $N = 8$	4-Year survivorship% = $29.2 + 2.5CV\ SLM$	$R^2 = 0.64^{**}$	ns

Equations are shown for regressions with significant R^2 values. ns: not significant.

$^\dagger P < 0.1$.

* $P < 0.05$.

** $P < 0.01$.

**** $P < 0.0005$.

canopy species is related to CV of SLM or CV of leaf density. Survival of canopy species weakly reflected CV of leaf density ($P < 0.08$; Table 4).

3.2.3. Maximum mature height, leaf traits and increments

As expected, CV of SLM was related to maximum mature height but contrary to expectation CV of leaf density was not (Table 5). Partition by maximum mature height category suggested a stronger regression of maximum mature height on CV of SLM for mid-canopy species than for canopy or all species (Table 5). Variance for 10 canopy species in CV of SLM is 56.34; for 10 mid-canopy species is 80.03 ($F_{9,9} = 1.42, P > 0.5$), which although not significant, gives the regression less variation to work with. Maximum mature height was related to CV of leaf density only for mid-canopy species (Table 5).

Increments in height and diameter, as contrasted with CV of each character, showed a somewhat different relationship to maximum mature height. Growth increments in height were not related to maximum mature height (Table 6). Maximum mature height was related to increments in diameter for all species pooled, for canopy species, and for mid-canopy species (Table 6). Tall species showed higher

growth rates in diameter than short species; again the strongest relationship was for mid-canopy species.

3.2.4. Increments and survival

Increments in height and diameter were related to 4-year survivorship (Table 7). Mid-canopy species with higher growth rates in height showed higher 4-year survivorship (Fig. 3a) while species with higher growth rates in diameter suggested or showed higher 4-year survivorship for both canopy and mid-canopy species (Fig. 3b). Partition by maximum mature height category again suggested a stronger relationship for mid-canopy species than for all species. The relationship between 4-year survivorship and increment in height is not strictly a regression, because slow-growing and fast-growing species cluster (the line connects two diffuse “points”). The cluster of fast-growing species does appear to have substantially higher survival.

4. Discussion

Planting late-successional species in early-successional environments helps enrich low-diversity forests colonized by pioneers that arrive by unassisted

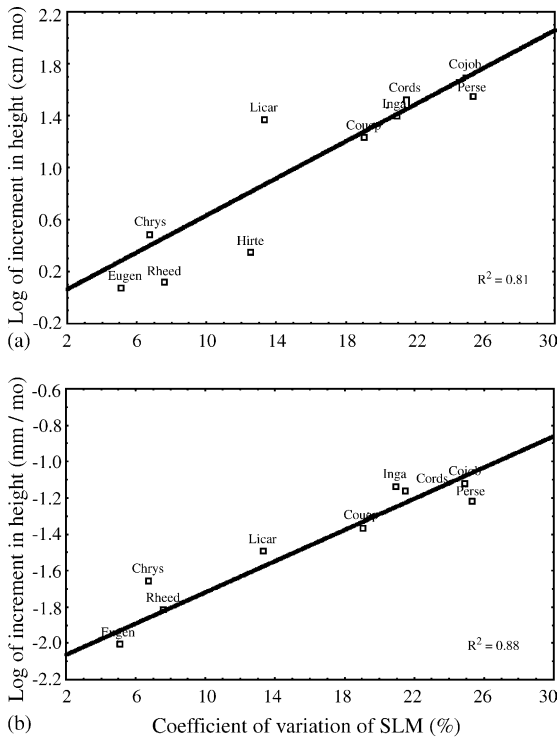


Fig. 1. Relationships of the (a) log of increment in height and (b) log of the incremental growth in basal diameter on the coefficient of variation of SLM of 10 mid-canopy late-successional species growing in an experimental planting in the Cooperative of Lázaro Cardenas, Los Tuxtlas, Mexico. Incremental growth refers to one mean for three periods (of 6, 6 and 24 months) of growth from 1998 to 2001 calculated for those individuals used to evaluate leaf traits ($N = 5$ per species). Species acronyms refer to the first five letters of the genus; additional regression details are in Table 4.

dispersal (“pioneer desert” of Martínez-Garza and Howe, 2003). To select late-successional species to enrich early-successional environments, we relate plant traits to ecological performance. Maximum mature height and variation in leaf traits are associated with survival or growth rates of late successional species planted in early-successional environments. Mid-canopy species with higher intraspecific variation in SLM show higher growth rates and survival, as expected. Also, taller species show higher growth increments in diameter, but not in height. Finally, those species with higher growth rates experience higher survival. All relationships between measured growth rates are strongest for mid-canopy species ($R^2 \geq 0.6-0.8$), and may only consistently exist with

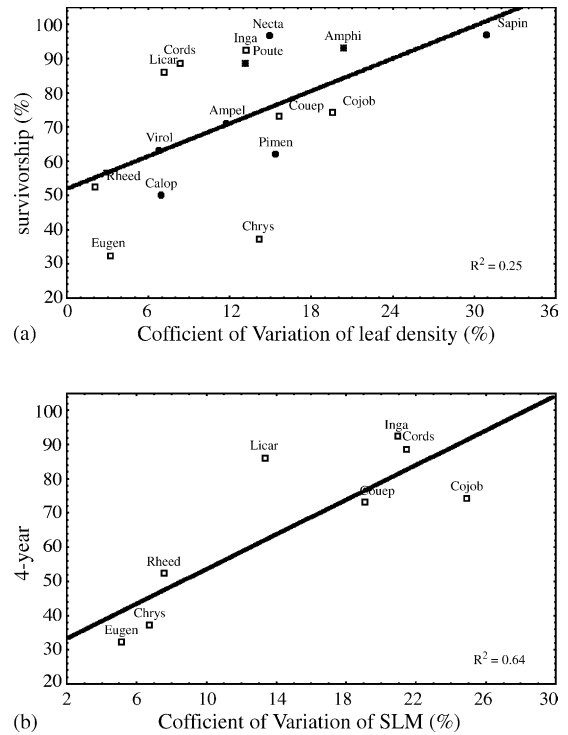


Fig. 2. Relationship of 4-year survivorship on (a) the coefficient of variation of leaf density for 16 late-successional tree species, and (b) the coefficient of variation of SLM for eight mid-canopy late-successional species growing in an experimental planting in the Cooperative of Lázaro Cardenas, Los Tuxtlas, Mexico. Filled circles correspond to canopy and emergent species (>30 m), squares to mid-canopy species (>11 m up to 25 m) and stars to understorey species (<10 m). Species acronyms refer to the first five letter of the genus; additional regression details are in Table 3.

them. Among canopy species, growth rate is the best predictor of survival ($R^2 > 0.45$). It should be noted that survival of canopy and mid-canopy species is generally high and similar (canopy $73.25 \pm 19.36\%$, $N = 6$; mid-canopy $66.96 \pm 23.52\%$, $N = 8$). It may be that this sample of six canopy species is insufficient to show clear differences with so little variation in key variables, or that other factors are at play with canopy as compared with mid-canopy species.

The successful contribution is an easy-to-measure plant trait that predicts growth and survival of mid-canopy trees; a strong positive relationship exists between variation in SLM and growth and survival of this segment of the forest community. There are good reasons why variation in leaf traits should be a good

Table 5

Regression equations, R^2 and probabilities of regression of the CV of SLM and CV of leaf density on maximum mature height (T Height) of 23 late-successional tree species growing in an experimental plantation in Los Tuxtlas, Veracruz, Mexico

	Maximum mature tree height		
	All species	Canopy sp.	Mid-canopy
CV SLM	CV SLM = $8.64 + 0.32$ T Height, $R^2 = 0.18^*$	CV SLM = $-11.7 + 0.9$ T Height, $R^2 = 0.36^*$	CV SLM = $-11.3 + 1.4$ T Height, $R^2 = 0.43^*$
CV leaf density	ns	ns	CV leaf density = $9.32 + 1.0$ T Height, $R^2 = 0.46^{***}$

Equations are shown for regressions with significant R^2 values. ns: not significant.

* $P < 0.05$.

*** $P < 0.005$.

Table 6

Regression equations, R^2 and probabilities of regression of the growth increments in height and diameter on maximum mature height (T Height) of 23 late-successional tree species growing in an experimental planting in Los Tuxtlas, Veracruz, Mexico

	Maximum mature tree height		
	All species	Canopy sp.	Mid-canopy
Increment in height	ns	ns	ns
Increment in diameter	Increment diameter = $-1.75 + 0.02$ T Height, $R^2 = 0.22^*$	Increment diameter = $-3.19 + 0.05$ T Height, $R^2 = 0.42^*$	Increment diameter = $-2.6 + 0.06$ T Height, $R^2 = 0.46^{**}$

Equations are shown for significant regressions. ns: not significant.

* $P < 0.05$.

** $P < 0.01$.

indicator of growth and survival under varied conditions. Leaf traits vary within a species when individuals grow under different environmental conditions. Plants exposed to high-light conditions have smaller leaves, with higher SLM and leaf density than plants in low-light environments (Parkhurst and Loucks, 1972; Bongers and Popma, 1988; Witkowski

and Lamont, 1991; Pearcy and Sims, 1994). The ability of species to develop leaves adapted to high- or low-light conditions explains, in part, differential growth rates under different light levels (King et al., 1997). Within-individual variation in leaf traits has previously been related to success of individuals exposed to heterogeneous environments, for example,

Table 7

Regression equations, R^2 and probabilities of survival on increments in height (Inc Hgt) and in diameter (Inc Diam) for 23 late-successional tree species growing in an experimental planting in Los Tuxtlas, Veracruz, Mexico

	Increment in height (cm month^{-1})	Increment in diameter (mm month^{-1})
Survival		
All species $N = 16$	4-Year survivorship = $49.8 + 25.7$ Inc Hgt, $R^2 = 0.45^{***}$	4-Year survivorship = $134.5 + 40.9$ Inc Diam, $R^2 = 0.44^{***}$
Canopy sp. $N = 6$	ns	0.63^\dagger
Mid-canopy $N = 8$	4-Year survivorship = $35.8 + 31.8$ Inc Hgt, $R^2 = 0.74^{***}$	4-Year survivorship = $155.9 + 60.4$ Inc Diam, $R^2 = 0.69^{**}$

ns: not significant.

† $P < 0.06$.

** $P < 0.01$.

*** $P < 0.005$.

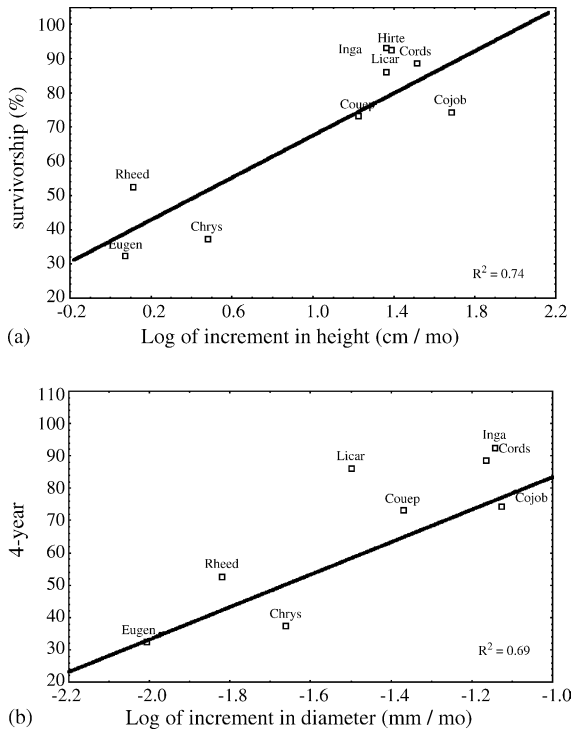


Fig. 3. Regressions of the 4-year survivorship on the (a) log of increment in height and (b) log of increment in diameter of eight mid-canopy late-successional tree species growing in an experimental planting in the Cooperative of Lázaro Cardenas, Los Tuxtlas, Mexico. Survival was calculated as the number of individuals present in 2001, divided by the number of individuals planted in 1997. Incremental growth refers to one mean for three periods (of 6, 6 and 24 months) of growth from 1998 to 2001 calculated for those individuals used to evaluate leaf traits ($N = 5$ per species). Species acronyms refer to the first five letter of the genus; additional regression details are in Table 7.

in vines (Lee and Richards, 1991), modular plants (ramets of a single genet; Pan and Price, 2002) and canopy trees (Popma et al., 1992). A higher intraspecific variation in leaf traits may be interpreted as a greater capacity to adjust to current environmental conditions of an early-successional environment, thereby predicting higher growth and survival of plants in these heterogeneous habitats.

Early-successional environments (pastures and edge conditions) have higher light levels, and lower availability of water, than the understory of the mature forest (Chazdon and Fetcher, 1984; Williams-Linera et al., 1998; Sanchez-Rios, 1999, but see Brown and

Lugo, 1990). Leaf density is expected to increase under water stress to enhance water-holding capacity of leaves (Rascio et al., 1990, Niinemets, 2001). However, in this study even when there is a correlation between CV of leaf density and CV of SLM (Pearson correlation = 0.70, $P < 0.001$), leaf density is less variable than SLM, this variation is only weakly related to survival, and it is not at all related to growth rates. Similar lack of response to situational shortages of water was found in seedlings of *Inga edulis* and *Ocotea withei* growing in pastures in Costa Rica with a dry season as long as the Los Tuxtlas season (ca. 3 months; Holl, 1999). Perhaps low intraspecific variation in the trait and low variation in water availability (Table 1) reduce the effectiveness of this character as a predictor of ecological performance. Both studies do show the tolerance of late-successional species to shortages of water, a characteristic that allows successful planting in deforested areas.

A gradient in light, temperature and relative humidity is found from the forest floor to the upper canopy (Chazdon and Fetcher, 1984). Higher light, temperature and relative humidity are found at the top of the canopy, where the highest temperatures remain for longer times (Freiberg, 1997) and the greatest fluctuations in relative humidity occur (Madigosky and Vatnick, 2000). It follows that the leaves of taller trees are exposed to higher light levels and higher fluctuation in environmental conditions than those of short species. Besides the environment, leaf traits are affected by height because the cost of foliar construction as tree size increases due to reduced water flow at the top of the canopy (Niinemets, 1996). Reduced water flow results in higher water stress for canopy leaves and limits maximum mature height (Koch et al., 2004). Therefore, tall trees show leaves with characteristics related to high-light levels and water stress (i.e., high specific leaf mass: Thomas and Bazzaz, 1999, for tropical trees; Koch et al., 2004, for redwoods). The interplay of adaptation to high-light and water stress may give canopy trees a different adaptive trajectory than mid-canopy species.

The conditions to which plants must respond change with ontogeny. These changes differ for canopy species of tall stature that eventually experience exposed canopy, as compared with mid-canopy species that experience full sun only intermittently, and shorter species that may never be exposed

to the sun. Canopy and mid-canopy species experience low-light levels early in their lives, but higher light levels as they grow to the canopy. They develop different leaves during ontogeny for this predictable increase in light levels (developmental changes in leaf traits, Winn, 1996; Thomas and Bazzaz, 1999; Martínez-Garza and Howe, 2005) and concomitant higher water stress as height increases (Koch et al., 2004). As adults, these species develop sun leaves at the top of the canopy and shade leaves at the bottom of the same crown (Popma et al., 1992; Oberbauer and Strain, 1986). Therefore, higher variability of leaf traits of canopy and mid-canopy species is anticipated and seems to arise in early ontogenetic stages.

The ability to develop various types of leaves likely helps these species accommodate suppression and release while growing to reach different levels in the canopy. Mean leaf traits may change during ontogeny, but the trees have the capacity to develop sun or shade leaves as required at any ontogenetic stages (Martínez-Garza and Howe, 2005). In mid-canopy, species variability in leaf traits may translate accurately in growth rates because they never experience full sun conditions, therefore, leaves within their canopy will show always different traits depending in environmental conditions. We can only speculate about the absence of response in canopy species. The possibility exists that a developmentally programmed response makes them less sensitive to minor changes in environmental light. Performance of canopy species may be fixed since they have a predictable future habitat: sun conditions in the canopy.

A positive relationship between growth rate and tree height appears to be general. The relationship holds in more than 50 tree species in Malaysian rainforest (Manokaran and Kochummen, 1987; Thomas, 1996), and 44 species in Costa Rica (Lieberman and Lieberman, 1987). This has implications for restoration that involves community-wide management of succession. In our study, relationships between tree height and growth rates differ when species are partitioned by their maximum mature height. The strength of the relationship found in this and other studies (up to $R^2 = 0.46$ for mid-canopy species) may not be enough to predict growth rates by tree height only, but it will be a useful tool to start selection of species before further testing is done. Short species, that are expected to show low growth

rates in most environments, may be introduced at later times to further enrich the forest.

Maximal growth of late-successional species primarily occurs in partial to full vertical illumination, suggesting that the absence of late-successional species in open areas is due to the lack of propagules and/or germination capacity instead of inability to grow in open conditions. Therefore, if planted for management or reforestation, late-successional species are not only able to cope with high-light levels and low water supply, they grow faster in early-successional conditions than under their more normal shaded seedling habitats (e.g., *Pouteria sapote* and *Diospyros digyna* in Ricker et al., 2000).

5. Conclusions

Late-successional tropical tree species represent >80% of rain forest tree species in undisturbed habitats, providing much of the structural diversity of the communities as well as food resources for fruit- and seed-eating animals. For places where natural regeneration is possible, but the species that are present in the old growth forest require many years to arrive by themselves (i.e. are dispersal-limited), the planting of late-successional species is a viable means of restoring diversity much more rapidly than natural regeneration (Martínez-Garza and Howe, 2003). Here we show that tree species with high intraspecific variability in SLM survive and grow better across different microhabitats of early-successional environments, with much the strongest relationships for mid-canopy species. The relationship for canopy species does not hold for this sample and remains to be confirmed. Based on our results, successful enrichments are likely to include mid-canopy species with high growth rates predicted by high variation of specific leaf mass (SLM), and canopy species with high growth rates predicted by maximum mature height. Use of variability in leaf traits and other indices (e.g., maximum mature height) that are related to performance may alleviate the need to individually screen large numbers of late-successional species for high growth rates and survival in restoration projects. Use of such easily assessed measures would free time and resources for evaluation of other criteria, such as economic value or dispersal attributes that influence

animal populations, for combinations of species that will generate desired restored forests. The range of variation in these traits may differ from one site to another, but in any particular forest mosaic the rankings of variation are likely to be consistent. Some of these traits may be measured in herbarium specimens. Mean values of SLM will be higher than those where leaf area is measured in fresh leaves (Martínez-Garza and Flores-Palacios, 2004). However, by measuring a large number of specimens it may be possible to capture the variation of SLM of the species evaluated. Secondary selections of species should be made taking into account those with the highest dispersal limitation (large seeds, low dispersal ability). Enrichment of early-successional environments that includes as many species as possible will maximize diversity and complexity of regenerating forests.

<i>Ceiba petandra</i>	26.66	8.3
<i>Chrysophyllum venezuelanense</i>	7.30	14.17
<i>Cajoba arbor ea</i>	27.30	19.61
<i>Cordia megalantha</i>	24.09	17.27
<i>Cordia stellifera</i>	29.47	8.35
<i>Couepia polyandra</i>	16.62	15.63
<i>Eugenia inirebensis</i>	6.57	3.22
<i>Guarea grandifolia</i>	15.48	11.64
<i>Hirtella triandra</i>	14.49	17.11
<i>Inga sinacae</i>	25.11	13.25
<i>Licaria velutina</i>	15.30	7.2
<i>Lonchocarpus cruentus</i>	51.49	30.56
<i>Nectandra ambigens</i>	20.0	14.93
<i>Persea schiedeana</i>	27.74	13.1
<i>Pimenta dioica</i>	21.08	15.4
<i>Poulsenia armata</i>	18.40	6.63
<i>Pouteria rhynchocarpa</i>	10.63	13.15
<i>Rheedia edulis</i> [<i>Garcinia intermedia</i>]	8.49	2.12
<i>Sapindus saponaria</i>	12.28	30.93
<i>Trichilia havanensis</i>	14.23	11.58
<i>Virola guatemalensis</i>	19.63	6.81

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Appendix A

CV of SLM and CV of leaf density of 24 late-successional tree species growing in an experimental planting in the Cooperative of Lázaro Cardenas, Los Tuxtlas, Mexico.

Species	CV SLM	CV leaf density
<i>Ampelocera hottlei</i>	6.82	11.76
<i>Amphitecna tuxtensis</i>	21.02	20.4
<i>Calophyllum brasiliense</i>	27.60	6.97

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