

DEVELOPMENTAL AND PHYSIOLOGICAL CORRELATES OF LEAF SIZE IN *HYERONIMA ALCHORNEOIDES* (EUPHORBIACEAE)¹

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The tropical emergent tree *Hyeronima alchorneoides* has large decreases in leaf size with tree age: 1200 cm² at 1 yr, 900 cm² at 3 yr, 200 cm² at 11 yr, and 80 cm² in old (>30 yr) individuals. We tracked leaf growth and physiological attributes on trees of three different ages (1, 3, and 11 yr) to determine the developmental basis and functional consequences of this variation. Leaves on young trees grew faster and sustained maximum rates of leaf expansion longer than leaves on older trees. Leaf mass per area (LMA) did not differ among age classes. Maximum photosynthetic rates reflected differences in leaf nitrogen concentration, in which leaves from the lower crown of younger trees outperformed those at a comparable crown position in older trees. One-year-old trees had the lowest stomatal conductance and the greatest instantaneous water use efficiency. Ontogenetic plasticity in mature leaf size, structure, and physiology may be a balance between the advantages conferred by rapid height growth when trees are young and the benefits derived from producing branches that increase light harvesting ability as trees reach the canopy.

Key words: *Hyeronima alchorneoides*; leaf growth; leaf size; ontogenetic plasticity.

A number of fast-growing tropical tree species, such as *Hyeronima alchorneoides* Allemao (Euphorbiaceae) and *Ochroma pyramidale* Sw. (Bombacaceae), undergo dramatic changes in mature leaf size as the tree itself ages and grows. This pattern raises a number of questions about potential shifts in physiological capacity associated with changes in leaf size, as well as the underlying developmental mechanisms. Most studies on the consequences of different sized leaves have focused on interspecific trends (Kohyama and Hotta, 1990; King, 1991), while intraspecific studies have been largely restricted to a consideration of variation in leaf size due to environmental factors such as illumination (Thomas and Ickes, 1995). Although several researchers suggest that most tropical tree species undergo ontogenetic shifts in leaf size (e.g., Alvarez-Buylla and Martinez-Ramos, 1992; Thomas and Ickes, 1995), few studies have examined the changes in leaf traits directly correlated with this pattern.

The production of large leaves is thought to minimize investment in support per leaf area while trees are rapidly growing taller (Givnish, 1978). This may explain why many fast-growing, heliophyllic trees produce large leaves but remain monopodial while they rapidly grow toward the canopy. However, as these trees grow larger, the need to support more and more leaves along a single axis tends to intensify the degree of self-shading and ultimately to limit the total photosynthetic output. Longer petioles decrease self-shading among larger leaves (Takenaka, 1994), and due to the increased light inter-

ception capacity, longer petioles are thought to result in an increase in the overall height at which the first branches are produced by a young tree with large leaves (King, 1998). Trees that have an ontogenetic shift in leaf size are likely to reach a certain height at which light interception capacity by large leaves and long petioles is less effective than that by many smaller leaves arrayed along multiple branches.

One consequence of producing large leaves is that leaf boundary layer conductances (g^{bl}) are greatly reduced, thereby reducing photosynthetic gas exchange, water loss, and probably elevating leaf temperatures. This reduction in g^{bl} is most pronounced near the ground where wind speeds are lowest (Woodward and Sheehy, 1983; Niklas and Speck, 2001). However, as the tree grows into the canopy (and higher wind speeds), larger leaves present a greater mechanical drag to the supporting branches than do smaller leaves. Thus, increases in mechanical drag might also help to explain why trees begin to branch and produce smaller mature leaves well before their crowns reach the canopy.

The finite life span of leaves combined with the construction costs of providing hydraulic and mechanical support to the entire leaf surface may well be a major constraint on maximum leaf size. Larger leaves require a greater absolute investment in biomass for both support and supply, although how this scales with leaf area is not known. Corner (1949) described the relation between leaf size and plant architecture in terms of two principles. The first of these describes the correlation between the diameter of a branch or stem and the size (and complexity) of its appendages, while the second states that increasing ramification is associated with a decrease in the size of both the branches and their appendages (Hallé et al., 1978). When a number of mature tropical tree species were compared, they complied with Corner's Rules (Hallé et al., 1978). Changes in leaf size in *H. alchorneoides* also comply with Corner's Rules in that the largest leaves occur on monopodial saplings, with decreases in leaf size occurring on

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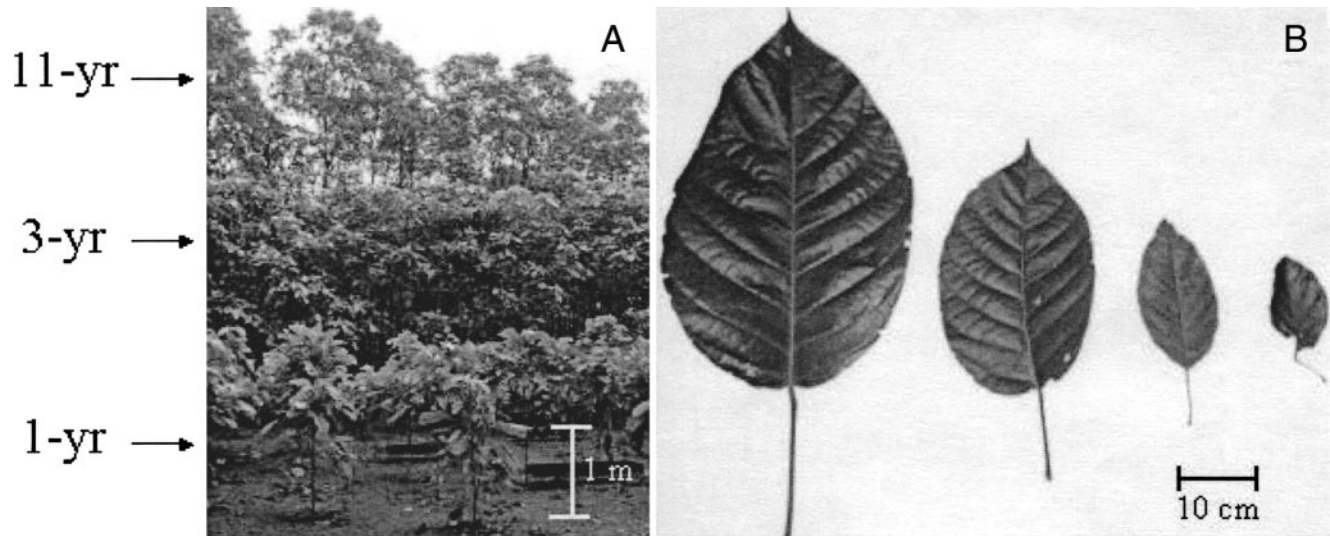


Fig. 1. *Hyeronima alchorneoides* at La Selva Biological Station, Costa Rica. (A) The experimental plantations. One-year-old trees are in the foreground, 3-yr-old trees in the center, and 11-yr-old trees are seen above in the background. (B) Mature leaves of 1-, 3-, 11-, and >30-yr-old trees (left to right).

larger, branched individuals. However, the extent to which leaf size in different aged *H. alchorneoides* trees is limited by mechanical constraints is not known.

The goal of this study was to examine the developmental and physiological correlates of leaf size in *H. alchorneoides*. In a plantation setting, where the confounding effects of variable soil characteristics are negligible, (Hagger and Ewel, 1995), we asked (1) what are the growth patterns responsible for the differences in size and (2) do leaf traits differ with tree age, or do they scale with leaf size? To address these questions, we examined leaf development as a function of bud size, rates of leaf expansion, leaf allometry and support biomechanics, leaf nutrient content, maximum rates of photosynthesis, and instantaneous water use efficiency from three age classes of *H. alchorneoides*.

MATERIALS AND METHODS

This study took place in 1-, 3-, and 11-yr-old plantations of *H. alchorneoides* (Fig. 1A) between March 2001 and August 2002 at La Selva Biological Station (10°26' N, 84°01' W; 35 m asl), a rainforest site in Costa Rica. With an average annual rainfall of nearly 4000 mm, the region is classified as a tropical wet forest (Holdridge, 1967). The plantation, underlain by fertile alluvium, is on a peninsula formed by the confluence of the Sarapiquí and Puerto Viejo rivers. *Hyeronima alchorneoides*, whose saplings and subcanopy trees are strongly associated with gaps (Clark and Clark, 2001), occurs in rainforests throughout central and south America and is an emergent evergreen tree with dense heartwood that is commercially valuable. Following an initial monopodial phase, growth in *H. alchorneoides* is sympodial, with orthotropic branches and simple leaves forming a dense crown. Saplings are very fast-growing (Hagger and Ewel, 1995), but trees may take 100–300 yr to reach full size (Clark and Clark, 1992), which at this site has been measured at 187 cm in diameter above the buttresses (Clark and Clark, 2001). In the experimental plantations used in this study, each age class is replicated three times in a randomized block design (Hagger and Ewel, 1995). The trees were planted for experimental purposes at high density (2887 trees/ha) and, in plots with trees older than 1 yr, were periodically thinned to avoid stand stagnation (Hagger and Ewel, 1997). Each tree is 2 m from all neighboring trees. Trees in the plantation become reproductive in approximately 8–12 yr.

The mature leaves of 1-yr-old saplings of *H. alchorneoides* are generally >50 cm long and can be 1200 cm² in surface area. As these trees age, new

leaves mature to smaller maximum sizes; mature leaves of 30-yr-old trees are approximately 10 cm long and less than 100 cm² in surface area (Fig. 1B). *Hyeronima alchorneoides* is evergreen at all ages and has a relatively constant rate of leaf turnover. All trees used in this study were growing in full sun. Access to crown tops and efforts to standardize for the effect of crown position on leaf traits (Rijkers et al., 2000) required that we sample from the lower quadrant of the crowns of 3-yr-old and 11-yr-old trees. The monopodial growth of 1-yr-old trees required that we sample from the upper half of the stem. All leaves sampled were unshaded.

Leaf production and expansion—Leaf and bud size were quantified from material (10 branch tips × three blocks per age class) collected in the field and immediately transported back to the laboratory in sealed plastic bags. The diameter of terminal buds, defined here as the dome of developing tissue within the two leaves yet unseparated from the bud, was measured with calipers under a dissecting microscope. Maximum leaf length (length of the central longitudinal axis) per branch was also recorded from these branches.

Rates of leaf production were quantified for 5 mo, spanning the dry and wet seasons in 2002 (February–June), by marking one leaf per shoot with plastic-coated wire immediately after bud break. The number of leaves produced subsequent to that leaf was recorded every 2 wk, and the mean number of leaves produced per month in each age class was calculated. Twenty-five shoots were monitored in each of three blocks, resulting in a total of 75 buds per age class.

The leaves monitored to estimate leaf production were also used to determine leaf expansion rates in the three age classes. We randomly selected 10 such leaves from each block, resulting in a total of 30 leaves per age class. Petiole length and diameter and leaf blade length were recorded weekly for 5 mo (February–June). Petiole length was measured as the distance from the petiole scar on the shoot to the base of the leaf (where the petiole attaches), and petiole diameter was measured midway along the petiole. Leaf length was measured from the distal tip to the point at which the petiole attaches, and leaf width was measured at the leaf length midpoint. Five leaves were randomly collected from each age class and each block, then immediately transported to the laboratory in sealed plastic bags. Leaf surface area was recorded using a digital area meter (LI-COR 3100, LI-COR, Lincoln, Nebraska, USA).

Analysis of variance was used to test for differences among blocks and age classes. This and, unless otherwise noted, all further statistical analyses were carried out using Systat 10.0 (SPSS, Chicago, Illinois, USA).

Allometry—The size and shape of the youngest fully expanded leaves from trees of each age class (five leaves × three age classes × three blocks) were

measured as described earlier during the early wet season (April–July) of 2002. The number of secondary veins was counted, and the distance between the second and third basal secondary veins was measured. Secondary veins were taken to be the large, conspicuous veins branching off the midvein. The diameter of the second-most proximal secondary vein was measured adjacent to the midvein, and the length from the midvein to the point at which this secondary vein becomes the diameter of a tertiary vein also was recorded.

The primary and secondary veins were dissected from the leaf blade, and the surface area of the blade was recorded. Petioles, blades, and veins were dried to constant mass at 70°C and weighed. Leaf area and mass (with and without the excised vascular tissue) were then used to calculate leaf mass per unit area.

The relation between leaf size and the cross-sectional area of the subtending stem or branch (Corner's principle of "axial conformity") was examined both within and between different age classes. The cross-sectional area of each stem was calculated from the branch diameter 5 cm from the base. Because the 1-yr-old trees are unbranched, basal diameter of the trunk was used for the stem basal diameter. Ten branches per block were examined, resulting in 30 branches per tree age class.

Leaf orientation in *H. alchorneoides* varies from nearly vertically oriented petioles when the leaves are first produced to more horizontally supported structures as the leaves age and are displaced from the shoot apex. We examined the relationships between leaf size and two estimates of the mechanical support provided by the petiole: an index of the flexural stiffness of a vertical column (the Euler buckling index) and an index of the vertical tip deflection of an end-loaded horizontal beam (the cantilever deflection index). We calculated the Euler buckling index from the equation that estimates the critical buckling load (P_{cr}) for a vertical column (Niklas, 1992):

$$P_{cr} = \frac{\pi^2 EI}{4l_p^2} \quad (1)$$

where E is the elastic modulus of the material, l_p is the length of the petiole and because the petioles of *H. alchorneoides* are cylindrical, the second moment of area of a cross-section, $I = \pi r^4/4$. The second moment of area (I) describes mass distribution around a given center of mass. Assuming E remains constant for all mature leaves regardless of tree age class, P_{cr} is proportional to the Euler buckling index, r^4/l_p^2 . To use this index, the mass of the petiole is assumed negligible, and it is assumed that the petiole has a uniform cross-sectional geometry throughout its length (Timoschenko and Gere, 1961; Niklas, 1992).

The cantilever deflection index is calculated from the equation:

$$\delta = \frac{P_m l_p^3}{3EI} \quad (2)$$

where P_m is the load (mass) of the leaf lamina and δ is the deflection distance (Niklas, 1992). Once again, if E remains constant and I is equal to that of a cylinder, δ of a horizontal petiole is proportional to $P_m l_p^3/r^4$. We can rearrange this relationship to estimate the critical load, P_{cr} , required to cause a certain deflection from horizontal, δ . The cantilever deflection index is proportional to P_m , or $\delta r^4/l_p^3$. With δ equal to an absolute value, we see that P_m for a cantilevered beam is proportional to r^4/l_p^3 . The mass of the petiole is again assumed negligible, and it is assumed that the petiole has a uniform cross sectional geometry throughout its length (Niklas, 1992).

Leaf nutrients and physiology—Leaf blade nitrogen and phosphorus concentrations (as a percentage by mass) were determined after acid digestion with colorimetric assays (Setaro and Jones, 1989) and using inductively coupled plasma emission spectroscopy (Luh Huang and Schulte, 1985). The youngest fully expanded leaf of each of five randomly selected individuals was collected from each block and from each age class of trees, for a total of 15 leaves per age class. Equal amounts of photosynthetic tissue were excised from each leaf and combined to form one sample per block in each age class ($N = 3$). The tissue was dried to constant mass at 70°C and ground to a fine powder before being sent for analysis. Tissue nutrient concentration was converted to an area basis using the LMA values. Total standing crop of foliar N and P were calculated using a March 2001 estimate of the leaf area

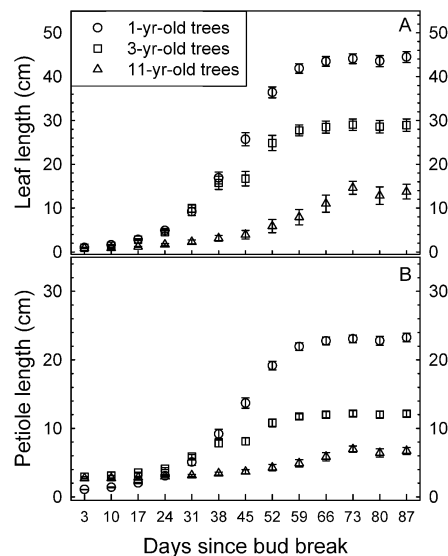


Fig. 2. Leaf growth in 1-, 3-, and 11-yr-old trees of *Hyeronima alchorneoides*. (A) Leaf expansion. (B) Petiole elongation. Each point is the mean of 30 measurements, and error bars represent one standard error of the mean.

index (LAI, as square meters of leaf area per square meter of ground) in these stands using methods described in Haggard and Ewel (1997), which was estimated with the measurement of diffuse light in the plots ($N = 3$) relative to ambient light using an LAI-2000 plant canopy analyzer (LI-COR).

Maximum rates of photosynthesis (CO_2 assimilation, A), stomatal conductance (g), and transpiration (E) were measured in the youngest fully expanded leaf on a randomly selected, sun-exposed branch in each age class ($n = 5$) between 1000 and 1130 hours (thereby avoiding any midday decline in stomatal conductance) using a portable photosynthesis system (LI-COR 6400). One leaf was measured per tree. Based on the leaf production and expansion data, we determined that these leaves were 8–10 wk old at the time of the measurements. Ambient temperature was 30°C, and relative humidity was 69%. We used the instrument's internal quantum source to expose the leaves to a saturating level of photosynthetically active radiation ($1200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and maintained a constant partial pressure of CO_2 equal to ambient (350 ppm). The leaf boundary layer conductance (g^{bl}) to water was determined by the LI-COR 6400 computer, which accounts for the leaf area and the fan speed within the 6 cm^2 chamber, as $2.84 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (LI-COR, 1998). We estimated intrinsic water use efficiency as the ratio of A to E in the leaf chamber.

Dimensional leaf boundary layer conductance can be estimated from the diffusion coefficient (D) of the moving substance (j); the size of the leaf, which is effectively approximated by the leaf length (l); and the ambient wind velocity v (Nobel, 1999):

$$g^{\text{bl}} = \frac{D_j}{4} \sqrt{\frac{v}{l}} \quad (3)$$

Wind speeds have been measured at this site at 0.1–1.0 m/s (Bigelow, 2001) with regional gusts up to 20 m/s (OTS, 2002). We assumed that 10.0 m/s is the mean maximum wind speed above a 30-m canopy at this site. In an effort to account for an underestimation of boundary layer conductances based on leaf length, we calculated dimensional leaf g^{bl} based on wind speeds of 0.1, 1.0, and 10.0 m/s. Substituting these values for v , and using D for water vapor at 30°C ($D_{\text{wv}} = 2.57 \times 10^{-5} \text{ m}^2/\text{s}$) and D for CO_2 at 30°C ($D_{\text{CO}_2} = 1.6 \times 10^{-5} \text{ m}^2/\text{s}$), we estimated the dimensional leaf g^{bl} for both water vapor and CO_2 .

RESULTS

Production and expansion—Maximum leaf size varied greatly among tree age classes (Fig. 2A); however, bud size

TABLE 1. Tree age, mean petiole diameter (d) at the initiation of leaf blade expansion, the change in petiole diameter before leaf blade expansion (Δd), and the rate of change in leaf area as a function of petiole diameter (m) with the correlation coefficient (r^2). *** denotes $P < 0.0001$.

Tree age (yr)	d (mm)	Δd (mm)	m (cm ² /mm)	r^2
1	2.9	0.7	282.4	0.89***
3	2.4	0.7	231.5	0.64***
11	1.9	0.4	241.6	0.74***

did not (2.4–2.7 mm; $df = 2$, $MS = 0.33$, $F = 1.64$, $P = 0.203$). Leaf production was highest in the 1-yr-old trees (4.0 ± 0.5 leaves per shoot per month), intermediate in the 3-yr-old trees (1.3 ± 0.3), and lowest in the 11-yr-old trees (0.5 ± 0.2 ; $df = 2$, $MS = 9.97$, $F = 25.78$, $P = 0.001$). Although all leaves were of similar size at the time of bud break, within 3 wk the expansion rate of leaves from the 11-yr-old trees slowed relative to those of the other age classes. Expansion rates in leaves from 1- and 3-yr-old trees were similar until week 6, after which time leaves on the 3-yr-old trees expanded at a slower rate. Leaves from the 1- and 3-yr-old trees were 50% fully expanded in 38–45 d, 95% fully expanded in 59 d, and fully expanded in 66 d. Leaves from the 11-yr-old trees were 50% fully expanded in 52–59 d, 95% fully expanded in 66–73 d, and fully expanded in 73 d (Fig. 2A).

Petiole elongation was complete after 59 d in the 1- and 3-yr-old trees, whereas elongation in those from the 11-yr-old trees was complete after 66 d (Fig. 2B). Initial petiole diameter was 2.2 mm in the 1-yr-old trees and 1.6 mm and 1.4 mm in the 3- and 11-yr-old trees, respectively. Petiole diameter in the 1- and 3-yr-old trees increased by 0.8–1.0 mm prior to the onset of leaf blade expansion. In the 11-yr-old trees petiole diameter increased by only 0.6 mm prior to leaf blade expansion (Table 1).

Allometry—Many of the parameters describing the size and shape of fully expanded leaves were strongly correlated with one another within and among tree age classes (leaf width with length [$r^2 = 0.98$], petiole length and diameter with leaf length [$r^2 = 0.82$ and $r^2 = 0.89$] or area [$r^2 = 0.98$ and $r^2 = 0.94$]). However, the relationships were always weaker in the 1-yr-old trees. Other leaf traits (i.e., secondary vein diameter with leaf length or area) scaled predictably among tree age classes ($r^2 = 0.69$ and $r^2 = 0.70$, respectively), but the relationship was weak within any given tree age class ($r^2 = 0.00$ – 0.29 in all

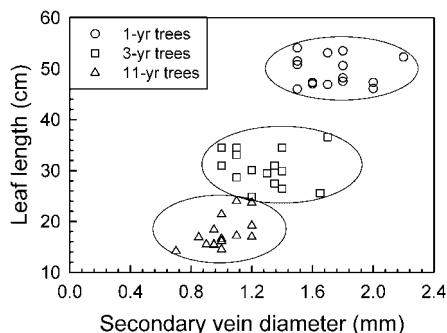


Fig. 3. Leaf length as a function of secondary vein diameter in 1-, 3-, and 11-yr-old trees of *Hyeronima alchorneoides*.

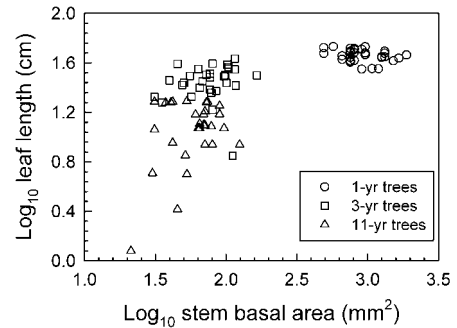


Fig. 4. Relationship between maximum leaf length and stem basal area in mature leaves from 1-, 3-, and 11-yr-old trees of *Hyeronima alchorneoides*.

cases; Fig. 3). Still other leaf traits, for example leaf mass per area, differed both within and among age classes ($df = 1$, $MS = 34507.5$, $F = 29.7$, $P < 0.0001$), though within the 11-yr-old trees there was no significant effect ($t = 0.41$, $P = 0.68$). The relationship of leaf length as a function of distance between secondary veins was very weak both within ($r^2 = 0.15$ – 0.22) and among tree age classes ($r^2 = 0.48$).

When all age classes are compared, the architecture of *H. alchorneoides* is consistent with Corner's Rules. When age classes were considered separately, there was no relation between stem basal area and leaf length in younger trees (1- and 3-yr-old), with only a weak relation between these two parameters in the 11-yr-old trees (Fig. 4). Neither the Euler buckling index for a vertical petiole (Fig. 5A), nor the cantilever deflection index for a horizontal petiole (Fig. 5B) was a good predictor of leaf size in general ($r^2 = 0.41$ and $r^2 = 0.51$, respectively). However, if we consider only the 3- and 11-yr-old trees, 34% of the variation in leaf size can be explained by the vertical support (Euler buckling index; $r^2 = 0.34$, $P = 0.0004$).

To examine the combined influence of the seven allometric and two biomechanical variables on leaf size, we first created multivariate variables through a principal components analysis (SAS Institute, Cary, North Carolina, USA). The first principal component axis, which accounted for 72.6% of the variability in leaf size, primarily comprised allometric variables (vein mass; petiole diameter, length, and mass; shoot basal area; and secondary vein diameter). Principal component axes two and three reflected the importance of biomechanical traits (LMA,

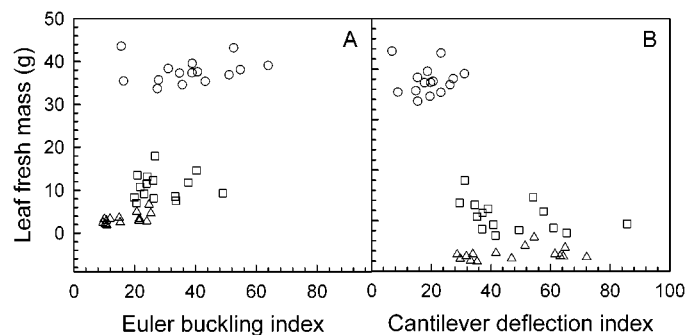


Fig. 5. Relationship between leaf fresh mass and petiole support mechanics, estimated as (A) the Euler buckling index (r^4/l^2_p ; m²), and (B) the cantilever deflection index (r^4/l^3_p ; m), in mature leaves from 1-, 3-, and 11-yr-old trees of *Hyeronima alchorneoides* (circles, squares, and triangles, respectively).

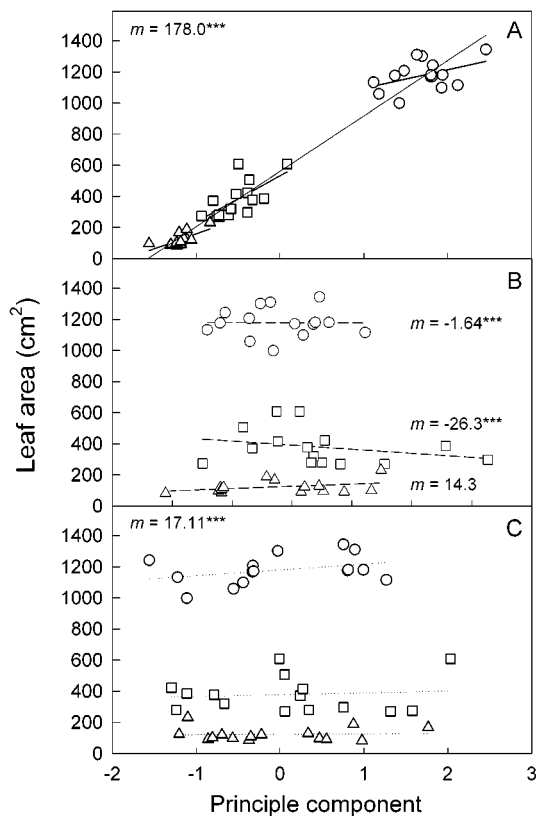


Fig. 6. Regressions of leaf area as a function of principal component axis (PCA) 1 (A), PCA 2 (B), and PCA 3 (C). Vein mass; petiole diameter, length, and mass; shoot basal area; and secondary vein diameter comprise PCA 1, listed here in order of eigenvector value (ranging from 0.347 to 0.388). Leaf mass per area, cantilever deflection index, and Euler buckling index comprised PCAs 2 and 3 (rank ordered with eigenvectors ranging from 0.506 to 0.602). The slopes of the regression lines (m) are noted in each panel. *** denotes slopes significantly different from zero, with $P < 0.000$.

cantilever deflection index, and Euler buckling index). We then conducted a regression with leaf size as the dependent variable, the first three principal component axes as the independent variables and age class as a dummy variable. The first three principal components accounted for 94.5% of the variation in leaf size (Fig. 6). We tested the interaction between the independent variables and age class, but removed the interaction term when not significant. Each of the three principal components was significantly associated with leaf size ($P = 0.0003$). In addition, the second principal component axis interacted significantly with tree age class ($df = 2$, $MS = 47578$, $F = 18.11$, $P < 0.0001$), which means that the relationship between the biomechanical traits and leaf size varied across age class. Overall, age class was not significant.

Leaf nutrients and physiology—Nitrogen content was higher in leaves from 1-yr-old trees (1.75 ± 0.10 g/m²) than in leaves from 3-yr-old (1.68 ± 0.09 g/m²) and 11-yr-old trees (1.34 ± 0.10 g/m²; $df = 2$, $MS = 0.74$, $F = 16.47$, $P < 0.0001$). One-year-old stands had an LAI of 0.7, whereas 3-yr-old stands had an LAI of 4.3, and 11-yr-old stands had an LAI of 2.58. Because of the high LAI and relatively high foliar N content in the 3-yr-old trees, the standing crop of foliar N

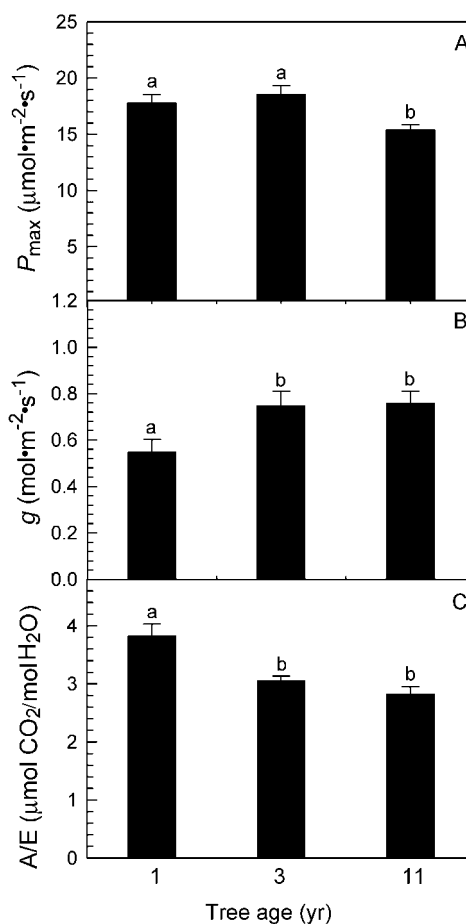


Fig. 7. Physiological traits of mature leaves from 1-yr-old (circle), 3-yr-old (square), and 11-yr-old (triangle) trees of *Hyeronima alchorneoides* ($n = 5$). (A) Maximum photosynthesis. (B) Stomatal conductance. (C) Instantaneous water use efficiency (ratio of photosynthesis over transpiration). Error bars represent one standard error of the mean. Lowercase letters indicate significant differences in photosynthesis ($df = 2$, $MS = 16.90$, $F = 5.96$, $P = 0.012$), stomatal conductance ($df = 2$, $MS = 0.09$, $F = 4.87$, $P = 0.022$), and water use efficiency ($df = 2$, $MS = 1.89$, $F = 11.41$, $P = 0.001$).

(72.86 ± 4.34 kg/ha) was substantially higher than that of both the 1-yr-old (12.19 ± 0.70 kg/ha) and the 11-yr-old trees (34.57 ± 2.32 kg/ha). Foliar P content was highest in the 3-yr-old trees (0.14 ± 0.01 g/m²), but not significantly so ($df = 2$, $MS = 0.001$, $F = 3.69$, $P = 0.067$). The standing crop of foliar P was highest in the 11-yr-old trees (2.58 ± 0.25 kg/ha), followed by the 1-yr-old (0.91 ± 0.07 kg/ha) and the 3-yr-old trees (0.61 ± 0.43 kg/ha).

Carbon assimilation in *H. alchorneoides* paralleled foliar N concentration. Leaves from 1- and 3-yr-old trees had equivalent photosynthetic rates, while those of the 11-yr-old trees were significantly lower (Fig. 7A). Leaves from 1-yr-old trees had lower stomatal conductance and higher instantaneous water use efficiency than both the 3- and 11-yr-old trees (Fig. 7B and C, respectively).

Estimated dimensional leaf g^{bl} for water vapor (1.15 – 20.98 mol · m⁻² · s⁻¹) and for CO₂ (0.72 – 1.30 mol · m⁻² · s⁻¹) increased dramatically with wind speed and to a lesser extent with decreasing leaf size (Table 2). The changes in dimensional g^{bl} associated with decreasing leaf size (and increasing tree age) and increasing wind speed results in even greater

TABLE 2. Tree age and height, mature leaf length, and the estimated dimensional leaf boundary layer conductance for water vapor (g_{wv}^{bl}) and CO_2 ($g_{CO_2}^{bl}$) calculated for different wind speeds (v).

Tree age (yr)	Tree height (m)	Leaf length (m)	v (m/s)	g_{wv}^{bl} ($mol \cdot m^{-2} \cdot s^{-1}$)	$g_{CO_2}^{bl}$ ($mol \cdot m^{-2} \cdot s^{-1}$)
1	1.5	0.5	0.1	1.15	0.715
			1.0	3.63	2.26
			10.0	11.49	7.15
3	5	0.28	0.1	1.54	0.96
			1.0	4.86	3.02
			10.0	15.36	9.56
11	25	0.15	0.1	2.09	1.31
			1.0	6.64	4.13
			10.0	20.98	13.06

differences in A and E among tree ages than those reported in Fig. 7, but the overall pattern observed using the g^{bl} in the LI-6400 cuvette does not change.

DISCUSSION

There are two basic ways in which some leaves can become larger than other leaves: either they can grow at the same rate, but for a longer period of time, or they can grow for the same amount of time, but at higher rates. In *H. alchorneoides*, leaves from younger trees expanded at rates much greater than those from older trees, and the period of maximum leaf elongation in 1- and 3-yr-old trees (Fig. 2, 17–59 d) was approximately 7 d longer than in the 11-yr-old trees (Fig. 2, 52–73 d). This is consistent with leaf expansion characteristics from 51 species in Australia (Moles and Westoby, 2000). However, it is important to note that the entire period of leaf expansion was longer in the older trees than in the younger trees. The measured lag in leaf elongation after petiole diameter growth supports the notion that there are functional constraints, either hydraulic or mechanical, operating during leaf development. Early allocation to leaf support tissues is widespread, as reported for *Lupinus arboreus* (Fabaceae), a coastal shrub of northern California (Reich et al., 2002). Once the hydraulic and mechanical infrastructure is established, the photosynthetic tissue scales predictably with petiole length. This kind of scaling relationship between leaf and petiole size has been reported in both tropical (Yamada and Suzuki, 1996) and temperate (Sack et al., 2003b) species.

Due to the large leaf size (and mass) in the 1-yr-old trees, we expected larger leaves would be the ones to scale most strongly with the mechanical support, but our results revealed a more complicated scenario. The relationship between leaf size and petiole diameter was very strong within and among tree age classes. However, the relationship between leaf size and stem basal area was strong only at the gross scale (tree age classes combined); it was weak in older trees and non-existent in the younger age classes (Fig. 4). Leaf size also tended to scale with the Euler buckling index of the supporting petiole in older trees but not in younger trees (Fig. 5A); it did not scale with the cantilever deflection index in any age class (Fig. 5B). The strong relationship of petiole diameter to leaf size coupled with the weak relationships of the mechanical indexes suggests that mechanical support does not dictate leaf size. It is possible that hydraulic architecture is a more important influence.

The strong relationship of petiole diameter to leaf size also suggests that leaf size in this younger age class has other con-

straints such as self-shading and perhaps the threat of leaf loss to herbivores (most notably leaf-cutting ants) before the leaf is functional. When we examined the diameters of the petiole and secondary veins from 1-yr-old *H. alchorneoides* as gauges of hydraulic support, we found that leaf size is well correlated with petiole diameter both within and among age classes. Leaf size also correlates with secondary vein diameter among age classes, but does not scale within any age class. We do not have a direct measure of the hydraulic capacity of the secondary veins, but our data suggest that if there are hydraulic constraints they are at the level of the minor veins. This information, in combination with the lack of scaling between leaf size and distance between secondary veins, raises some interesting questions about the role of leaf hydraulic supply and venation in determining leaf blade size (Plymale and Wylie, 1944; Zwieniecki et al., 2002; Sack et al., 2003a). Further information about the functional hydraulics in *H. alchorneoides* may help to explain the patterns of high water use efficiency and photosynthetic rates in younger trees.

The adaptive significance of an ontogenetic shift in leaf size is likely for maximal light interception (Williams et al., 1989) and to allocate biomass efficiently. The rainforest environment provides a steep gradient in light availability (Chazdon, 1986) and is therefore likely to apply a strong selective pressure on saplings of emergent trees. For pioneer trees growing in short-lived gaps, quick access to higher light is essential for growth and success (Whitmore, 1978; Sanford et al., 1986). These trees are therefore presented with a tradeoff in biomass allocation between producing more photosynthetic area to harvest more light and growing taller and branching more to access higher light levels. Ultimately, large-leaved saplings tend to maintain a monopodial growth form while growing to greater heights than smaller leaved trees (Hallé et al., 1978; White, 1983). Further, with more branching, light interception efficiency may increase and heat loading may decrease with decreasing leaf size (Van Der Meulen and Werger, 1984). Although young trees, such as the mangrove species *Rhizophora mangle*, have a variety of morphological and physiological traits that can be modified by changes in light levels (Farnsworth and Ellison, 1996), we found that with light remaining constant, there is an ontogenetic component to variation in such leaf traits. That our 1-yr-old trees produce massive leaves growing in full sun indicates that the control of leaf size in saplings is not directly attributable to ambient light levels during sapling development.

Evidence of a trade-off in biomass allocation is most notable in the 1-yr-old trees, where mature leaf size decreases with the onset of branching. As a monopodial sapling, the large leaves of *H. alchorneoides* eventually begin to shade the lower leaves. Branching both increases total leaf area and the incident light on the increased leaf surface area (Turner et al., 1995; King, 1998). The branches, being smaller in diameter, provide lower mechanical and hydraulic support, which in turn may constrain leaf expansion. We suggest that, under hydraulic and mechanical constraints, the trade-off between maximizing light harvesting and growth in *H. alchorneoides* results in smaller leaves in older trees, as observed in *Cecropia obtusifolia* (Alvarez-Buylla and Martinez-Ramos, 1992; King, 1998).

The maximum leaf size in *H. alchorneoides* occurs when trees are 1 to 2 yr old, several years before trees reach reproductive maturity. An important component of reproductive output is the number of meristems from which inflorescences

will develop. Because *H. alchorneoides* has terminal inflorescences, it follows that the onset of branching is necessary well before the trees reach reproductive age. It may be that the decrease in leaf size is ultimately driven by the necessity to prepare for future reproduction, and as a consequence, the onset of branching is accompanied by the production of progressively smaller leaves. This pattern is in contrast to those reported for *Cecropia obtusifolia* (Alvarez-Buylla and Martinez-Ramos, 1992), *Garcinia nervosa* and *G. malaccensis* (Thomas and Ickes, 1995), none of which bear terminal inflorescences. In these three species, maximum leaf size coincided with reproductive age.

Ontogenetic shifts in leaf size in *H. alchorneoides* are associated with changes in their physiology. For example, as the trees age and grow, nutrient storage in foliage is highest when tree age is intermediate. We measured high rates of photosynthesis in young trees and lower rates when trees were old enough to reach the canopy, which is in contrast to results from other studies on tropical evergreen trees, where little change was observed among size classes (Thomas and Winner, 2002). And finally, the efficiency with which the leaves use water shifts as a function of tree age. While this shift may be partially due to differences in leaf age (recall that measured leaves were 8–10 wk old), leaf size also must be playing an important role in the physiological changes documented here.

Several researchers have focused on improving our understanding of interspecific patterns in leaf form and function, including tissue nitrogen content, leaf mass per area, hydraulic conductance, photosynthetic rates, and water use efficiency (Grubb, 2002; Wright and Westoby, 2002; Sack et al., 2003b). Based on our results, we suggest that the patterns described among species are largely dependent on tree age and possibly life history stage. These findings contribute to our understanding of how plants carry out the building of leaf area and the deployment of nitrogen. We further suggest that the physiological differences in leaf traits associated with ontogenetic changes in leaf size translate into shifts in important functional roles in the local ecology of the individual trees. This developmental plasticity appears to be an important means of rapidly gaining access to the forest canopy.

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