Allometry of emergent tree species from saplings to above-canopy adults in a Costa Rican rain forest

David A. King[*,1] and Deborah A. Clark[†,‡]

* Biological and Ecological Engineering, Oregon State University, Corvallis, OR 97331 USA
† University of Missouri-St. Louis, St Lous, MO 63121–4400 USA
‡ La Selva Biological Station, Puerto Viejo de Sarapiqui, Costa Rica
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Abstract: Relations between crown width and tree height and trunk diameter and tree height were measured for trees of all sizes of six large emergent species (*Balizia elegans*, *Dipteryx panamensis*, *Hieronyma alchorneoides*, *Hymenolobium mesoamericanum*, *Lecythis ampla* and *Terminalia oblonga*) in the lowland tropical wet forest at La Selva, Costa Rica. Thirty to 45 individuals were chosen per species to provide a relatively even height distribution from 1 m up to the maximum encountered height. Among small juveniles, the crown widths of the two species with the smallest leaves and horizontally spreading branches were greater than those of the four large-leaved species. On reaching and exceeding the canopy, all but one species showed pronounced increases in crown width with increasing height. These patterns are linked to leaf size and first branching height in small juveniles and low densities of emergent trees at La Selva and other tropical forests, where crown expansion in all directions enhances light interception under the equatorial sun in trees that are not crowded by neighbours of similar height.

Key Words: *Balizia elegans*, Costa Rica, *Dipteryx panamensis*, emergent tree, *Hieronyma alchorneoides*, *Hymenolobium mesoamericanum*, leaf size, *Lecythis ampla*, *Terminalia oblonga*, tree allometry, tropical rain forest

INTRODUCTION

Trees show substantial variation in allometry – in the way in which crown dimensions vary with height, as they grow from seedlings to adults. Allometry is ecologically important, as it influences the amount of light that can be intercepted by a tree of given biomass and, along with wood properties, affects susceptibility to damage from storm winds and falling debris. Forest trees face trade-offs between elevating the crown, thereby increasing its exposure to light and lateral expansion that enhances light interception by increasing crown area. Tall trees also face greater water stress associated with longer hydraulic pathways and gravitational potentials (Domec *et al.* 2008) and greater risks of damage from storm winds and lightning. Trees exhibit substantial plasticity in crown shape and trunk thickness in response to local crowding and exposure to light and wind (Holbrook & Putz 1989, Lawton 1982), but also show species-specific allometries that have been related to adult stature, degree

of shade tolerance and leaf size (Bohlman & O'Brien 2006, King 1998, Osunkoya *et al.* 2007, Poorter *et al.* 2003, Thomas 1996). Interspecific variation in adult size and light requirements and associated allometric differences is one of many proposed mechanisms for species coexistence in diverse tropical forests (King *et al.* 2006, Kohyama 1993, Kohyama *et al.* 2003, Poorter *et al.* 2003).

Within forests, juveniles of large-statured species tend to have smaller crowns and thinner stems than adult understorey species of similar height, a difference that decreases the structural cost of height growth in the former (King 1981, 1996; Osunkoya *et al.* 2007). Nonetheless, there is substantial allometric variation among species of similar adult size and one can easily find examples where juveniles of a canopy species are broader crowned than similar-sized adults of an understorey species (King 1996, Poorter *et al.* 2003).

Leaf size is a second potential axis of allometric differentiation, albeit less studied. King (1998) found that across species, the height at which juveniles initiate

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[1] Corresponding author. Email dkingaz@yahoo.com

their first branch increases substantially with leaf size. As unbranched juveniles tend to have narrower crowns than branched ones, crown width may vary inversely with leaf size for tree heights at which a mix of branched and unbranched species are found (King 1998). However, the above study lumped species of all adult statures together making the generality of the crown width-leaf size relation across trees of differing stature uncertain.

Of particular interest is the allometry of the largest and tallest trees, the emergent class. In wet tropical forests, trees of emergent species often bear their crowns completely above the surrounding canopy. These species experience large changes in degree of shading and lateral crowding in growing from seedlings to maturity and may therefore be expected to show pronounced developmental shifts in allometry. Although low in numbers, such very large trees contain a substantial fraction of the live forest biomass (Clark & Clark 1996) and cast varying amounts of shade on the trees below them. For two co-occurring emergents, *Dipteryx panamensis* and *Lecythis ampla*, King (1996) found that both showed pronounced crown enlargement after exceeding the height of the surrounding canopy. The large-leaved species (*D. panamensis* was substantially narrower crowned in the sapling stage than small-leaved *L. ampla* in accordance with the general trend (King 1998, Sterck *et al*. 1999). Here we assess the generality of these patterns with allometric measurements of four additional emergent species at the same site; thereby further testing the hypothesis that sapling crown proportions are related to leaf size.

METHODS

The study was conducted at La Selva Biological Station in the Atlantic lowlands of Costa Rica (10°26′N, 84°00′W; 37–150 m asl). The mean annual rainfall is approximately 4000 mm and all months average at least 100 mm (Clark & Clark 2001).

The species studied were *Balizia elegans* (Ducke) Barneby & J. W. Grimes (syn. *Pithecellobium pedicellare*; Fabaceae), *Dipteryx panamensis* (Pittier) Record & Mell (Fabaceae), *Hieronyma alchorneoides* Allemão (Euphorbiaceae), *Hymenolobium mesoamericanum* H. C. Lima (Fabaceae), *Lecythis ampla* Miers (Lecythidaceae) and *Terminalia oblonga* (Ruiz & Pav.) Steud. (Combretaceae). These species' spatial distributions partially overlap each other at La Selva. *Terminalia oblonga* occurs on recent alluvium along rivers and creeks, *D. panamensis* occurs primarily on old alluvium, somewhat more removed from watercourses, *B. elegans* is most common on upland sites and *H. alchorneoides*, *H. mesoamericanum* and *L. ampla* occur on a range of soils (Clark *et al*. 1998). For the first five species, we examined subsets of individuals from the

long-term demographic studies of Clark & Clark (1992, 2001, 2006). Separate searches were made for *T. oblonga*.

For each study species we excluded individuals with heavy climber loads, substantial crown damage or with stems that were leaning more than 30° from the vertical or that were recovering from past breakage, as indicated by abrupt diameter reductions along the stem of > 25%. From 30 to 45 individuals were measured per species (37 on average) chosen to provide a relatively even height distribution from 1 m up to the maximum encountered height of 44–53 m per species.

The following measurements were made of each tree: height to the highest leaf, crown width projected onto the horizontal plane in two perpendicular directions including the widest projection and trunk diameter at 0.1 times total height for trees < 25 to 30 m tall. For taller trees of all species except *T. oblonga*, we used diameters measured above the buttresses (measurement protocols described in Clark & Clark 2006). Diameters were not measured for the larger *T. oblonga* trees, which often have buttresses or irregular trunk cross-sections to heights exceeding 5 m. Trees were measured in 1988–1990 for most individuals of *D. panamensis*, *L. ampla* and *T. oblonga* and in 2009 for the other species and the tallest trees of the former species.

Heights of trees < 4 m tall were measured with an extensible folding rule. Taller trees were measured by rangefinder and clinometer to determine the vertical distances from the sighting point up to the highest point and down to the tree base. For the large adults, 30 min or more was spent per tree searching for the highest point from multiple viewpoints. Heights above 4 m were measured with optical rangefinders in 1988–1990 (King 1996) and for 4–12-m-tall trees in 2009. Trees >12 m tall were measured by laser rangefinder in 2009. The rangefinders were initially calibrated against tape-measured distances and rechecked weekly.

Average leaf blade lengths and petiole lengths were determined for three to six 1- to 4-m-tall saplings per species, excluding severely suppressed saplings, which tend to have smaller than average leaves. For the three compound-leaved species (*B. elegans*, *D. panamensis* and *H. mesoamericanum*), blade length was defined as the distance from the bases of the proximal leaflets to the tip of the distal leaflet, measured parallel to the leaf rachis, and petiole length was the distance from the point of attachment to the stem to the point of attachment of the proximal leaflets.

Most of the species showed pronounced changes in the slope of crown width vs. tree height for large vs. small individuals. We therefore computed separate slopes for trees ≤ 25 m tall and trees > 25 m tall, the approximate height at which the shift in slopes was most evident. As neither covariate is strictly dependent on the other in allometric relations, we computed standardized major axis (SMA) regression slopes and tested for differences

using SMATR (Warton *et al.* 2006). This approach minimizes the variance perpendicular to the regression line and the resulting slope is equal to the standard regression slope divided by the Pearson correlation coefficient r. To compare crown widths for trees of specified heights we used standard regression, as is appropriate for predicting y given x.

Plots of tree height vs. trunk diameter were compared to the relation for critical height above which buckling would occur for a cylindrical wooden column fixed at base, calculated as (Greenhill 1881, King *et al.* 2009)

$$H_{crit} = 0.792(E/G\rho_g)^{1/3}D^{2/3}$$

where E is Young's modulus of elasticity for green (freshly cut) wood, G is the gravitational force per unit mass at Earth's surface (9.8 N kg^{-1}), ρ_g is the density of green wood including the water within, and D is column diameter. For *Hieronyma* spp. and *Hymenolobium excelsum* mean E = 13.2 × 10^9 N m^{-2} (USDA 1999) and ρ_g was estimated to be 1077 kg m^{-3}, derived from a mean base wood density (dry mass/green wood volume) of 640 kg m^{-3} for the above two taxa (USDA 1999) and a moisture content–wood density relation derived from the data of Suzuki (1999) for 284 Bornean species. Based on these values, H$_{crit}$ = 85.3 D$^{2/3}$ where both H and D are expressed in m, or H$_{crit}$ = 3.96 D$^{2/3}$ for the usual convention of specifying tree height in m and trunk diameter in cm. Actual critical buckling heights will differ somewhat from this relationship due to species-specific differences in wood properties, stem taper and relative crown weight (King *et al.* 2009, Niklas 1994).

RESULTS

The species differed substantially in leaf size and petiole length (Table 1). The three compound-leaved species had large leaves with long petioles, as did one of the simple-leaved species, *Hieronyma alchorneoides* – as measured on saplings. (The leaves of adult *H. alchorneoides* trees are substantially smaller, though they are still relatively long-petioled; Reich *et al.* 2004.) The other two simple-leaved species had small leaves with short petioles. The four large-leaved species all bear their leaves in a spiral arrangement on ascending twigs (orthotropic branching), whereas the two small-leaved species bear planar sprays of foliage (plagiotropic branching). Of the small-leaved species, *L. ampla* bears its leaves in a two-ranked arrangement on arched branches (Troll's model of Hallé *et al.* 1978). *Terminalia oblonga* bears its leaves in successively upturned rosettes on planar branches, as is typical of this genus.

The two small-leaved plagiotropic species had wider crowns than each of the larger leaved species, as assessed

for 3-m-tall saplings, significantly so for five of the eight pairwise comparisons between large- and small-leaved species (Table 1). These small-leaved species also had the largest SMA regression slopes of crown width vs. tree height for 1–25-m-tall trees (Table 1).

However, larger trees showed quite different crown allometries for five of the six species (Figure 1). For trees >25 m tall, crown width-tree height regression slopes were much larger than for 1–25-m-tall trees for all species except *T. oblonga*, which showed a lesser, albeit significant increase in slope (Table 1, Figure 1). For 44-m-tall trees (the greatest height measured across all species), *T. oblonga* had a significantly narrower crown than each of the other species (Bonferroni P < 0.01). Whereas *T. oblonga* had a crown width to tree height ratio of 0.49 for trees of this height, the other emergent species had a mean ratio of 0.72, i.e. double the crown area of the former species. Furthermore, *L. ampla* was one of the widest-crowned species at this height (Table 1).

The relation between tree height and trunk diameter is shown in Figure 2, as compared with the height at which buckling due to elastic instability would occur for a wooden cylinder with the average green wood properties of two of the study genera. The illustrated relationship shows that 10–20-m-tall trees have small margins of safety with respect to gravitationally induced buckling as compared with smaller saplings and larger trees. Note that the height–diameter relation for *T. oblonga* is only shown for trees with trunk diameters < 45 cm, due to difficulties in measuring above-buttress diameters on larger trees.

DISCUSSION

The observation of wide crowns in the sapling stage for the two small-leaved species is consistent with the negative correlation between sapling crown width and leaf size reported by King (1998) for species of varying adult stature. The contrast between plagiotropic branches in small-leaved, short-petioled species and ascending orthotropic branches in large-leaved, long-petioled species occurs throughout the wet tropics and results from a coordination of branching and leaf dimensions that reduces self shading within crowns (King & MainDonald 1999).

However, the general shift in allometry on emerging above the canopy and the allometric divergence between the two small-leaved species, suggests that differences between sapling crown proportions that may be related to leaf size do not pertain as emergent trees approach full stature. Poorter *et al.* (2006) found an analogous shift in the relationship between crown dimensions and maximum adult height; large-statured species had narrower crowns than smaller-statured species when

Table 1. Sapling leaf dimensions (mean ± SD), crown widths of 3- and 44-m-tall trees and standardized major axis (SMA) regression slopes of crown width vs. tree height and associated coefficients of variation for 1–25- and >25-m-tall trees. Leaf blade length defined as the distance from the bases of the proximal leaflets to the tip of the distal leaflet for the three compound-leaved species (*B. elegans, D. panamensis* and *H. mesoamericanum*). Crown widths of 3-m- and 44-m-tall trees determined by standard regressions of crown width vs. tree height for 1–6- and > 25-m-tall trees, respectively. Dimensional values within a column not sharing a common superscript differ significantly (Bonferroni P < 0.05), as determined by pairwise t-tests of sapling leaf dimensions (df = 4–8) and pairwise t-tests of regression-based crown widths for 3-m-tall saplings (df = 4–29) and 44 m trees (df = 21–36). The SMATR test statistic for common SMA slopes (Warton *et al.* 2006) was used for the slope significance tests (df = 1 in all cases for this statistic).

Species	Leaf blade length (cm)	Petiole length (cm)	Crown width (H = 3 m) (m)	Crown width (H = 44 m) (m)	1–25-m trees		> 25-m trees	
					Slope	r^2	Slope	r^2
Balizia elegans	42.2[b] ± 5.8	7.9[c] ± 1.6	1.20[a]	31.9[bc]	0.32[abc]	0.96	1.78[bc]	0.65
Dipteryx panamensis	52.5[b] ± 6.0	13.6[cd] ± 3.3	0.90[a]	32.3[c]	0.33[abc]	0.93	1.52[bc]	0.86
Hieronyma alchorneoides	40.9[b] ± 3.5	23.3[d] ± 3.4	1.39[abc]	33.3[bc]	0.26[ab]	0.86	1.81[c]	0.90
Hymenolobium mesoamericanum	46.0[b] ± 3.6	7.8[d] ± 0.8	1.13[ab]	26.9[b]	0.25[a]	0.87	1.14[b]	0.83
Lecythis ampla	9.3[a] ± 2.5	0.12[a] ± 0.02	1.75[bc]	33.6[bc]	0.41[c]	0.89	1.59[bc]	0.81
Terminalia oblonga	14.3[a] ± 1.4	0.7[b] ± 0.15	1.61[c]	21.6[a]	0.37[bc]	0.89	0.63[a]	0.80

compared at heights <5 m, but wider crowns for comparison heights exceeding 15 m.

Caution is warranted in inferring differences in light interception from these interspecific differences in crown width, as crown density and crown depth were not measured, though there are some obvious differences among our study species. The heights of emergent *B. elegans* trees were easily measured from below, as they bear sparse planar monolayers of leaves that seldom overlap, so that much sky can be seen through
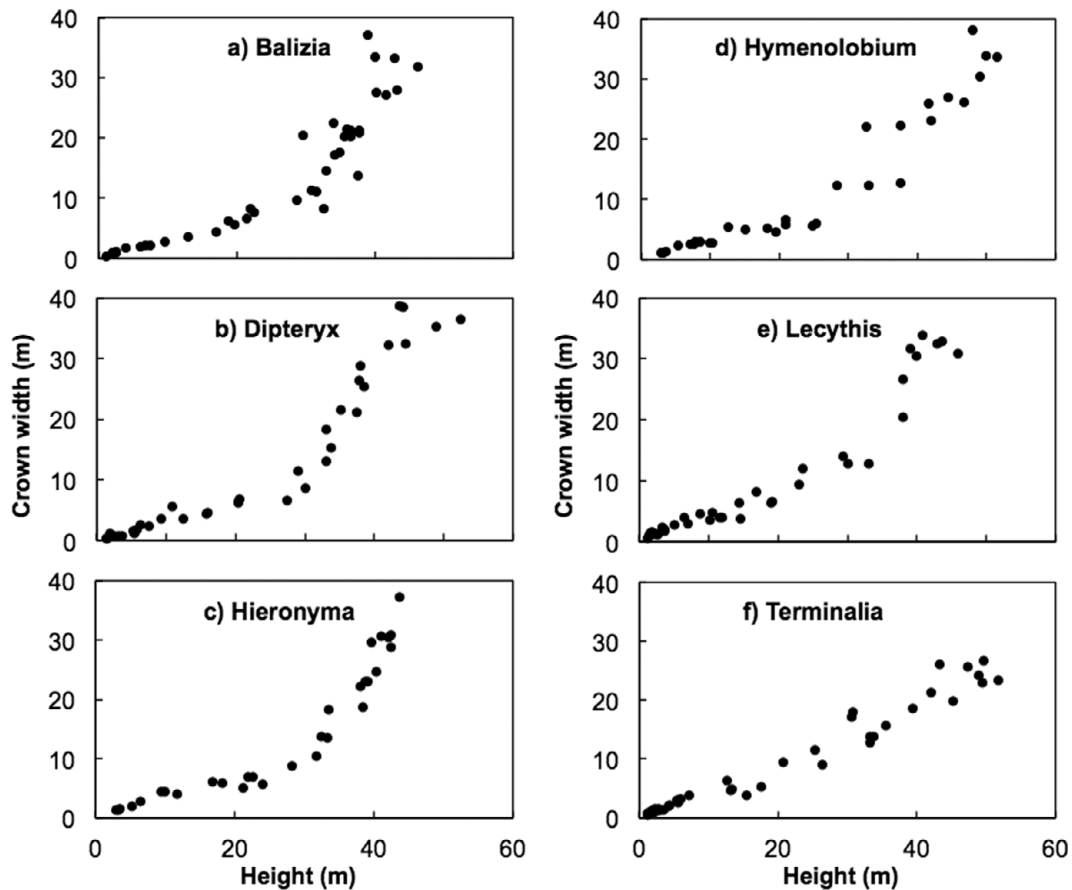

Figure 1. Crown width vs. tree height for *Balizia elegans* (a), *Dipteryx panamensis* (b), *Hieronyma alchorneoides* (c), *Hymenolobium mesoamericanum* (d), *Lecythis ampla* (e) and *Terminalia oblonga* (f) at La Selva, Costa Rica.
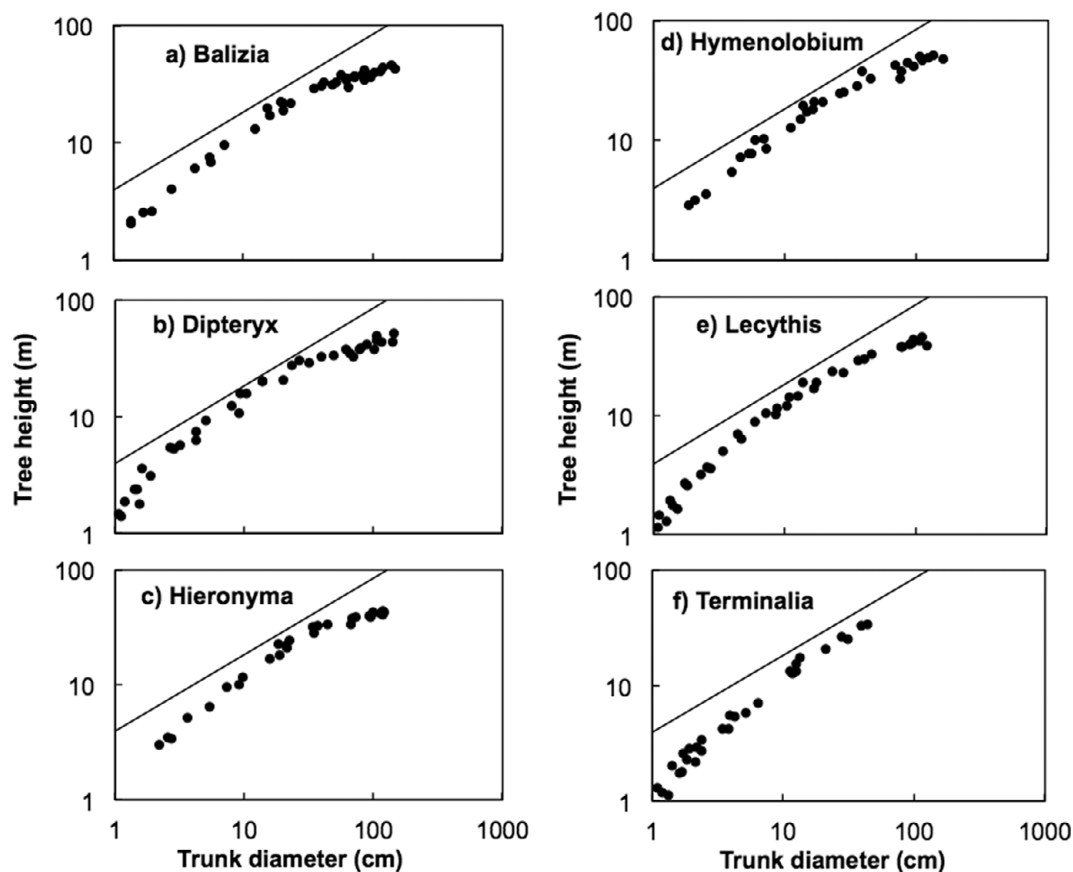
Figure 2. Tree height vs. trunk diameter at 0.1 × tree height or above buttresses on larger trees for *Balizia elegans* (a), *Dipteryx panamensis* (b), *Hieronyma alchorneoides* (c), *Hymenolobium mesoamericanum* (d), *Lecythis ampla* (e) and *Terminalia oblonga* (f) at La Selva, Costa Rica, plotted on a log–log scale. The line indicates the height–diameter relation for a wooden column at the critical buckling height calculated for average green wood properties for *Hieronyma* spp. and *Hymenolobium excelsum*. Relationship shown for diameters < 45 cm for *T. oblonga*, due to difficulties in measuring above-buttress diameters on larger trees of this species.

them − where not obscured by understorey crowns. Emergent *H. alchorneoides* and *T. oblonga* crowns are much denser, requiring sightings from multiple vantage points to ascertain their full heights. Emergent *T. oblonga* crowns appear to be deeper than those of most of the other species, increasing their interception of lateral light. Thus, the deep, thickly foliated crowns of *T. oblonga* may compensate for their relative narrowness as compared with the other emergent species.

The increase in the buckling safety factor with tree height for trees > 25 m tall may be related to their greater exposure to wind above the forest canopy. The upper canopy height ranges from 15–30 m for most of the old-growth forest area at La Selva (Clark *et al*. 2008). Thus, emergent species have small safety margins as they approach this upper canopy (Figure 2), but are increasingly exposed to storm winds as they grow above 25 m. This increase in wind speed with increasing height is compounded by the large increase in crown area with height above 25 m. As a result, emergent trees are exposed to disproportionately large wind forces as compared

with subcanopy trees and the corresponding increase in buckling safety factors is not surprising. Regarding the greater stability of small saplings, these are at risk from falling debris from the canopy above (Clark & Clark 1991) and several were found pinned to the ground or bent over by debris falls and thus excluded from the study.

These conclusions apply to old-growth forests of the Atlantic lowlands of Costa Rica. As the study species grow over a wider range of Central and tropical South America, similar patterns may occur in some other wet lowland neotropical forests. However, the emergent habit becomes less pronounced with increasing elevation or duration and severity of drought stress (Whitmore 1984). Emergent trees grow taller in the lowland forests of South-East Asia that are dominated by the Dipterocarpaceae (Ashton 1964, King *et al*. 2009). Forest profile diagrams (Ashton & Hall 1992, Whitmore 1984) suggest that emergents of these forests have lower crown width to height ratios than the species studied here. King *et al*. (2009) reported a flattening of the relation between height and stem diameter for selected emergent species

of Malaysia, but this shift began at a greater height than for the Costa Rican emergents studied here.

The crowns of very tall trees (>60 m in height) are relatively narrow in the tallest eucalypt forests of South-East Australia and especially the conifer forests of the Pacific Northwest of North America (Van Pelt *et al.* 2004). These tall temperate forests often have even-aged canopies and much higher densities of large trees than at La Selva and most other tropical forests, which may limit crown spread. In a survey of old forest at La Selva (D.B. Clark, unpubl. data), only 7 trees ha^{-1} had stem diameters exceeding 70 cm and less than a quarter of these trees were classified as emergents (where an upward-facing cone enclosing the crown with sides angled $45°$ to the horizontal would include no foliage from other trees). Thus, large emergent trees are on average widely spaced at La Selva.

The predominance of lower sun angles at temperate latitudes, particularly in autumn, winter and spring when photosynthesis still occurs in tall evergreen maritime forests, may also favour deep narrow crowns over the broad spreading crowns observed in our study (Kuuluvainen 1992). Hence, the equatorial location, all-aged stand structure and low densities of emergent trees may select for the observed shift from relatively narrow to broad crowns as emergent species grow up through the crowded subcanopy and overtop their neighbours.

ACKNOWLEDGEMENTS

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