

SHORT COMMUNICATION

Inferring growth rates from leaf display in tropical forest saplings

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In temperate trees, the extension growth history of stems and branches is easily inferred from the positions of the rings of over-wintering bud-scale scars, allowing one to assess environmental responses from surveys of saplings (Beaudet & Messier 1998, Canham 1988, King 2001). But tropical trees rarely show such distinct demarcations of growth flushes. Furthermore, the frequency of flushing may vary with tree size and environment, and a number of tropical species, often light demanding, show continuous leaf production and extension growth throughout the year (Coley 1983).

However, stem extension rates may also be correlated with leaf internode length (King 1993, 1994) and with the total length of the leaf display from the axis tip to the lowest leaf directly attached to it, i.e. the leaved stem length. (Note that 'leaved stem length' as used here differs from 'crown depth', defined as the vertical distance from the lowest to highest leaf over all axes, though the two measures may be correlated.) For a species with a leaf life span of precisely 1 y, the extension growth over the past year will be equal to the current leaved stem length. On the other hand, variation in leaf life span and past extension rates would reduce the correlation between these two variates. This paper examines the relationship between height growth rate and leaved stem length for saplings of three tree species of a wet tropical forest (La Selva, Costa Rica) and one species of a more seasonal tropical forest (Barro Colorado Island, Panama) to assess the utility of this potential measure of growth.

Saplings were studied primarily in old-growth forests at the two study sites. The La Selva Biological Station of the Atlantic lowlands of Costa Rica (10°26'N, 84°00'W;

elevation 37–150 m) receives a mean annual average of 4000 mm of rain and all months average > 100 mm (McDade *et al.* 1994). Barro Colorado Island (BCI), Panama in Lake Gatun of the Panama Canal (9°9'N, 79°51'W; elevation 27–170 m) receives a mean annual average of 2600 mm of rain, with a pronounced dry season of about 4 mo duration, typically from mid-December to April (Leigh 1999). The study species were all more or less shade tolerant, in that the saplings were mostly found under closed canopies (Clark & Clark 1992, King 1994).

The saplings assessed at La Selva were part of a long-term demographic study of emergent and canopy trees (Clark & Clark 1992, 2001). Of the chosen species, *Simarouba amara* saplings were erect and generally unbranched over the studied size range, with compound leaves, while *Minquartia guianensis* saplings were erect with a continuous distribution of plagiotropic lateral branches. In contrast, saplings of *Lecythis ampla* were arched and spreading with all axes more or less plagiotropic. During each year, the total height of each sapling was measured, as part of the annual tree census. Height was measured from the stem base to the base of the highest meristem on saplings < 1.5 m tall and to the highest leaf on saplings > 1.5 m tall. For *Lecythis*, height was measured to the base of the highest meristem in all cases (Clark & Clark 2001). In 2001, height was measured during the period of February–April for most of the saplings at La Selva. From 16 February to 5 March 2002, the leaved stem length was measured as the distance along the stem from the tip of the terminal leader to the petiole base of the lowest leaf attached to the leader. Height was measured to the same position (highest leaf or meristem base) as in the previous year's census. Most saplings in the 0.9–3 m height range were measured, as well as a few which had grown somewhat larger by the time of the final measurement.

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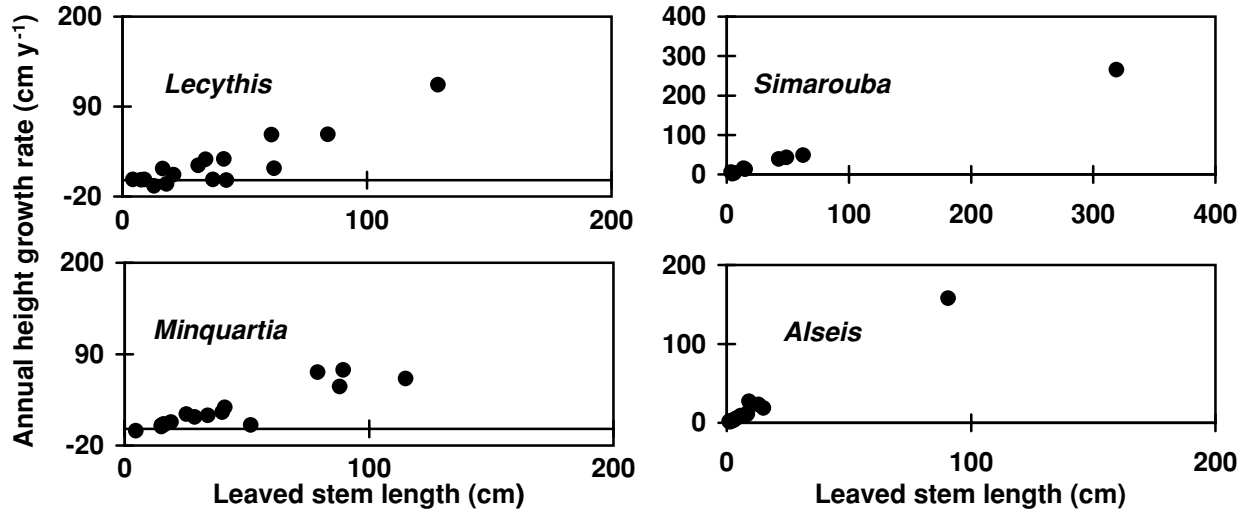


Figure 1. Annual height growth rate vs. leaved stem length for species of La Selva, Costa Rica and *Alseis blackiana* of Barro Colorado Island, Panama. The horizontal lines indicate height growth rates of 0 for *Lecythis* and *Miquartia*.

The Panamanian species was assessed during a study of the relationship between biomass partitioning and growth conducted August 1990–August 1991 (King 1994). Undamaged individuals were selected in gaps and understorey locations. Extension growth of the terminal leader of each sapling was determined over a 10–11-mo interval by measuring the distance from the apex to the uppermost painted ring on the stem (used to determine diameter growth) at the beginning and end of the study interval. As the saplings were all erect and mostly unbranched, height growth could be equated to extension growth (King 1994). The leaved stem length was measured at the end of the study.

At both sites saplings were omitted which had suffered severe herbivory, unusual loss of leaves compared with conspecifics, or had been bent or broken recently, as indicated by substantial diameter discontinuities along the upper stem. The leaved stem length was then related to the annual height growth rate, calculated as (height increment/number of days between measurements) × 365 for each sapling. Regression analyses were applied to logarithmically transformed variates, as this

procedure increased the normality of the distributions of the data points. Height growth rate was chosen as the dependent variable, as the objective of the paper is to evaluate how well leaved stem length predicts recent growth.

Leader extension growth rate was strongly related to leaved stem length for each of the three erect-stemmed species (Figure 1, Table 1). The relationship between log (height growth rate) and log (leaved stem length) was weaker for the arched species *Lecythis* ($r^2 = 0.69$) (Figure 1). The slope coefficients (b of Table 1) did not differ significantly among species, as determined by ANCOVA and were not significantly different from 1 for any of the species. Thus, height growth rate was directly proportional to leaved stem length, as might be expected. However, the b value was greatest for *Lecythis* and consideration of the three height growth rate values ≤ 0 , that were excluded from the analysis of log-transformed variates, suggests a curvilinear relation for this species, as illustrated in Figure 1. For *Lecythis* the angle to the horizontal of the terminal leader was positively correlated with leaved stem length ($r = 0.65$, $P = 0.007$),

Table 1. Regression coefficients (intercept (a) and slope (b)) relating log (height growth rate) to log (leaved stem length). The associated correlations were significant (two-tailed $P < 0.001$) in all cases. Height growth rates were determined for the geometric mean leaved stem length of 17 cm by back-transforming the associated values from the given regression relationships.

Species	Family	a	b	r^2	Height growth rate (17 cm) (cm y^{-1})	n
La Selva, Costa Rica						
<i>Lecythis ampla</i> ¹ Miers	Lecythidaceae	-1.266	1.529	0.69	4.1	13
<i>Miquartia guianensis</i> ¹ Aubl.	Olacaceae	-0.907	1.343	0.75	5.6	15
<i>Simarouba amara</i> Aubl.	Simaroubaceae	-0.148	1.023	0.93	12.9	12
BCI, Panama						
<i>Alseis blackiana</i> Hemsl.	Rubiaceae	0.045	1.133	0.96	27.4	15

¹ One *Miquartia* and three *Lecythis* saplings with height growth rates ≤ 0 were of necessity omitted from this analysis of log-transformed variates.

i.e. individuals with long leaved stem lengths tended to be more erect and might therefore show relatively greater height growth per unit leaved stem length than slow-growing individuals.

There were highly significant species effects ($P < 0.001$) among the three erect species as well as among all four species, i.e. the regression intercepts differed. This pattern is shown by the 5-fold range in height growth rate predicted for the geometric mean leaved stem length of 17 cm (Table 1). (The comparison of intercepts is most accurate at the mean value of \log (height growth rate), i.e. geometric mean of the untransformed variates, where the effects of errors in regression slopes are minimized.)

These results suggest that leaved stem length can be used as an approximate indicator of recent height growth rates of undamaged saplings, particularly in species with more-or-less erect saplings. As interspecific differences occurred in the relation between height growth rate and leaved stem length, likely due to differences in leaf life span (or differences in stem orientation in the case of *Lecythis*), the method is more appropriate for within-species comparisons.

The relationship between height growth and leaved stem length was weakest for *Lecythis*, the one species with arched, spreading crowns in the sapling phase. Variation among saplings in leader angle to the horizontal, which was in part correlated with growth rate for *Lecythis*, would be expected to weaken and/or alter the relationship between recent height growth and leaved stem length. However, leaved stem length may be a more reliable indicator of past leader extension growth, rather than height growth, as variation in the orientation of the leader would no longer be a direct factor influencing the measure of growth. Roughly 20% of the species of humid tropical forests have arched crowns conforming to the Troll model of Hallé *et al.* (1978); most of the rest are more erect (Hallé *et al.* 1978, King 2001, King *et al.* 1997, Millet *et al.* 1998).

Leaved stem length has been used here as an indicator of recent extension growth. However, leaved stem length may also be related to the mechanisms of growth, as it is likely correlated with total leaf area, particularly in unbranched saplings (King 1994). For saplings of similar size, growth is correlated with both total leaf area and irradiance, as expected given the photosynthetic function of leaves (Poorter 2001, Sterck *et al.* 1999). Additionally, larger, taller saplings may receive more light on average and therefore grow faster and have longer leaved stems than smaller saplings. Given these positive feedbacks between growth and leaved stem length, both height growth rate and leaved stem length may exhibit up to 100-fold variation in magnitude in saplings of gaps vs. understorey (Figure 1; Clark & Clark 2001, King 1993, 1994). This large variation in these covariates results in stronger correlations between them than would otherwise be the case.

Not surprisingly, the method is not as exact as the inference of growth histories from over-wintering bud scale scars or annual rings in temperate species. Nonetheless, the high correlations between the two variates imply that sapling characters, such as leaf size and crown shape, which may be correlated with growth rate (King 1994, King *et al.* 1997, Valladares *et al.* 2000) will also be correlated with leaved stem length. Thus, leaved stem length may be used to relate morphology to growth rate (King, unpubl. data), given the proviso that saplings with a wide range in leaved stem length are included in the study. Leaved stem length may be particularly useful in making qualitative assessments of growth in the overwhelming number of forests lacking studies of marked saplings. For example, one could quickly assess the vigour of primary forest species colonizing successional forests by noting their leaved stem lengths.

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