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Stem architecture of shade tolerant species in a low-stature tropical rain forest in Mexico

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Abstract

The relationship of diameter and height of the stem is an architectural feature that is related to shade tolerance of the trees, as well as mechanical resistance to stem buckling. Theoretically it is postulated a high value of this coefficient for shade-tolerant species. The tropical rain forest of Los Tuxtlas, Mexico is a low-stature forest with higher light levels in the understory, in comparison with other forests in the world. It was estimated the value of the diameter/height coefficient for 275 tree saplings (100-300 cm) of three shade-tolerant species and compared with the theoretically proposed values of stem buckling limit in trees. Particularly for this forest and contrary to general assumptions, we expect to find a low coefficient value due to increased height growth in comparison to diameter growth caused by high light levels in the understory. Indeed the three species showed a low coefficient of 0.492 for *Guamia* sp., 0.745 for *Pseudolmedia oxyphyllaira*, and 1.15 for *Trophis mexicana*. This may suggest that the height-diameter coefficient value of the stem for these species is in relation to the high levels of light in this forest in particular.

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Introduction

Tree architecture varies among tropical rain forest trees, both within and between species. This variation may be related to microsite (e.g., Bongers and Popma, 1988; Clark and Clark, 1992; Horn, 1971), ontogeny (e.g., O'Brien *et al.*, 1995; Rich *et al.*, 1986), tree stature at maturity (King, 1991, 1996), shade tolerance of the species (Shukla and Ramakrishnan, 1986; Kohyama and Hotta, 1990), and forest type (King, 1991; Ennos, 1996). (Et al must be italics all through the manuscript).

Biomass allocation and wood density are important features for the Resistance and construction, and thus for survival of the trees. Regarding the stem particularly, biomass increase in stem and branches affects the balance between its mechanical stress and resistance during tree growth (Bongers and Sterck 1998). Safety factors for buckling and bending are important determinants of the risk of mechanical failure (Putz *et al*., 1983), tree architecture (Poorter *et al*., 2003; Sterck *et al*., 2001), and the efficiency and rate at which trees grow towards the canopy (King *et al*., 2005; Poorter *et al*., 2003). For example, trees exposed to mechanical stress caused by supporting lianas or epiphyte, invest more in the thickness of the trunk (Bongers and Sterck 1998).

Based on stem height and diameter, three coefficients have been proposed to determine the stem buckling limit for trees (Norberg, 1988, b = 1.0; geometric similarity; McMahon 1973, b = 1.5; elastic similarity; Dean and Long, 1986, b = 2.0). From these, the value of b = 2.0 offers a higher safety margin, and b = 1.0 offers the lowest safety margin. The higher the coefficient b (estimate value of the slope of the linear model of the stem diameter/height relationship), the greater the diameter of the stem, the safety margin, and therefore, the height a tree can reach at a given diameter.

Differences in the stem buckling limit in tropical trees of different successional stage and height have been found (Clausen and Maycock, 1995). Dean and Long (1986) in particular have suggested that shade-tolerant species show a high coefficient value or safety margin for stem buckling (a greater force to break the stem is required). Sterck and Bongers (1998) found shade-tolerant species with higher safety margins than the shade-intolerant species. The pioneer species seem to have a lower limit than the canopy species against stem buckling (Rich *et al*., 1986). As well, in general, the coefficient decreases with height or age of the tree making it more susceptible to stem buckling (Clausen and Maycock 1995).

Also, it has been found that shade-tolerant species experience higher damage rates than light-demanding species owing to trees and branch falls (Gartner, 1989; Paciorek et al., 2000; Putz and Brokaw, 1989). Trees and branch falls in the tropical rain forests may act as a selecting force in tree species populations since they cause sapling mortality (Clark and Clark 1991). Something similar happens in animal activity. Some understorey species have been found to show relative thick trunks (high safety margins against stem buckling), which are likely to enhance survival (King, 1990; Kohyama and Hotta, 1990), because, unlike the pioneer species, they spend more time in the understory owing to their slow growth.

The forest of Los Tuxtlas has been described as a tropical rain forest based on its climate and structure. However, within the rain forests, is one of the lower-stature because it presents a canopy height of 35m with emerging trees up to 40m (Bongers et al., 1988), in comparison with the Lacandon forest in Chiapas, Mexico, or forests of the amazons or Asia with a taller canopy stratum. Also, by its proximity to the coast and influence of the northern winds, presents a remarkable open canopy due to a frequent fall of trees and branches. This relatively wide opening in the canopy, creates a greater light environment in the interior than in forests with taller trees and denser canopies, and in the understorey in particular. The availability of total light in the understorey of this forest is around 5% (Martinez-Sanchez et al., 2008), while in other forests like in Costa Rica is 0.5% (Canham, et al., 1990), 0.4% in Queensland, Australia (Bjorkman and Ludlow, 1972) and the Tai forest, Ivory Coast (Alexandre, 1982), 2% (Chazdon and Fetcher 1984), 2.4% in Hawaii (Pearcy 1983) and 3% in Malaysia (Aoki et al., 1978).

Presently, studies which relate values of coefficient b with light levels in the understorey are lacking. In this study we postulate that higher light environments in the understorey influence saplings stem architecture giving slender stems and a low coefficient b value.

The aim was to find the value of the coefficient b of the saplings stem of three shade-tolerant species in a high light-environment. The hypothesis was to find a low value of coefficient b in saplings of these shade-tolerant species living with high light-levels in the understorey.

Materials and methods

Study area and species. This study was carried out at the Los Tuxtlas Tropical Field Station (18° 35′ N, 95 °07′ W) owned by the National University of Mexico (UNAM), and located in Southeastern Mexico, in the state of Veracruz. Mean annual precipitation is around 4560 mm, mean annual temperature 23·7 °C, and altitude between 150 and 530 m. Soils are of volcanic origin, rich in nutrients (N, P, K) and organic matter. The dominant vegetation type is lowland tropical high evergreen rainforest (Bongers *et al*., 1988; González-Soriano, Dirzo and Vogt, 1997). The Moraceae is the second most species-rich family at Los Tuxtlas. For this study we selected three abundant, shade-tolerant species,*Trophis mexicana* (Liebm.) Bur. and *Pseudolmedia oxyphyllaria* Donn Sm. are Moraceae species and have a monopodically, continuously growing trunk and plagiotropic branches, and conform to the architectural model of Roux (cf. Hallé, Oldeman and Tomlinson, 1978). *Trophis* attains a maximum height of 15 m and *Pseudolmedia* 25 m (González-Soriano, Dirzo and Vogt, 1997). The third species was *Guamia* sp. (“colorado”) with heights about 3-7 (-10) m, an as yet undetermined and perhaps undescribed understorey species of the Annonaceae family, which was earlier erroneously reported as *Sapranthus microcarpus* (Donn.Sm.) R.E.Fr. (Murray 1993). The species exhibit orthrotopic and monopodial growth in the trunk, and plagiotropic and monopodial growth in the branches.

For all species, individuals measuring between 50 and 300 cm in height and without apparent physical damage were selected: 88 for *Guamia*, 100 for *Pseudolmedia*, and 87 for *Trophis*. For each individual total height and stem diameter at 30 cm height from the ground were measured.

Statistical analysis

The linear regressions of Log (stem height) *vs*. Log (stem diameter) of the three species were obtained and compared amongst and against the models proposed by Norberg (1988), McMahon (1973) and Dean and Long (1986). The linear regression of each theoretical model of stem buckling limit was obtained using the X values (sapling height) of every measured sapling of the three species and the proposed value of the coefficient b (slope) of each model. A theoretical Y value (stem diameter) was yielded and then the line of each regression model. Statgraphics Plus 4.0 was used to compare the six linear regression models.

Results

Intercepts and slopes of the six regression models (the three species and the three theoretical models) were different ($P < 0.00001$; Table 1). The coefficient value (slope) of the stem height-diameter relationship for *Guamia* sp. was 0.492, 0.745 for *P. oxyphyllaira*, and 1.15 for *T. mexicana*. The value of the slope of *Trophis*

(1.15) did not differ from the value of the model of geometric similarity (b = 1.0). It is notable that the value of the interception *Trophis* (-0.41) coincides exactly with the three proposed theoretical values (Table 1). The plotted lines of the six regression models are different (Fig. 1).

Table 1. Comparison of the regression lines of Log (height) *vs*. Log (diameter) in sapling stems (50 – 300 cm) of three shade-tolerant species and the theoretical buckling limits proposed for trees. Different superscript letters denote different slopes and intercepts ($P < 0.05$).

	Slope (b) Estimate	Intercept Estimate	*P* of Intercept	*P* of Slope
Guamia sp.	0.492 [a]	0.119 [a]	0.139	0.0001
Pseudolmedia oxyphyllaria	0.745 [b]	-0.05 [b]	0.594	0.000 0
Trophis mexicana	1.15 [c]	-0.41 [c]	0.02	0.0003
Norberg (1988) – geometric similarity	1.0 [c]	-0.41 [c]	-	-
MacMahon (1976) – elastic similarity	1.5 [d]	-0.41 [c]	-	-
Dean and Long (1986)	2.0 [e]	-0.41 [c]	-	-

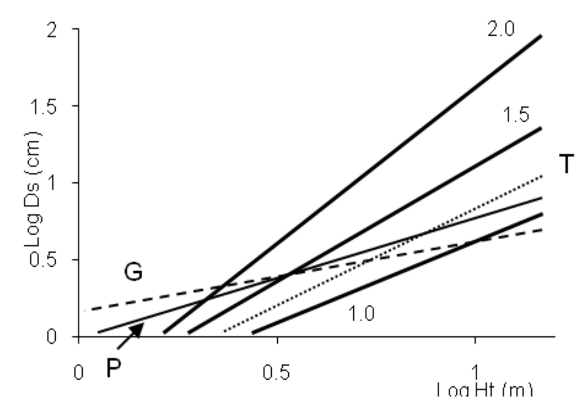

Fig. 1. Regression lines of the height – diameter relationship in sapling stems (50 – 300 cm) of three shade-tolerant species and those of the proposed models of Norberg (1988), b = 1.0, geometric similarity; McMahon (1973), b = 1.5, elastic similarity; Dean and Long (1986), b = 2.0.

Discussion

For young saplings in this stature range (0.5 – 3.0 m) the three species showed a low value of the coefficient b of the stem. Based on these results, *T. mexicana* would be the most tolerant species to shade and *Guamia* sp. the least tolerant. *P. oxyphyllaria*, lies somewhere in between.

The three species present a value of coefficient b below the limit value or safety margin proposed by Dean and Long (1986) and MacMahon (1973). Only *T. mexicana* presents a value equal to 1.0 that fits the model of geometric similarity proposed by Norberg (1988) which assumes that the stem increases the diameter proportionally to stem height. In the other two species there is proportionally greater growth in height than in diameter. This result indicates that the stem buckling limit for these species is low and far from being characteristic of shade tolerant species.

Usually the stem buckling limit is high when the trees are young and decreases as the tree grows (Clauseen and Maycock, 1995). The low coefficient value of these species indicates that these species indeed have a relatively small diameter that may confer some disadvantages for survival in the forest understorey (Gartner, 1989; Paciorek *et al*., 2000; Putz and Brokaw, 1989). This would apply particularly to Guamia sp. and *P. oxyphyllaria* which have a value below the theoretical coefficient value of 1.0.

According to Sterck *et al*. (1999) saplings require 1–3 y to establish a crown trait in response to light levels in the forest. Based on this, we can consider that these results are valid, as the trees of these species are usually taken 3 years to reach approximately 50 cm in height.

The result shows that individuals in the juvenile stage of these three species are growing fast and trying to reach greater heights. It is very likely that this increased growth in height than in diameter is due to high light levels in their environment. It is proven that shade tolerance involves a very limited or slow height growth of young trees, and a thicker stem (Kohyama 1991). In this case, it seems that there is not a strong light stress in the understory, which allows these trees grow faster. Species, although are shade tolerant in terms of its size and habit of life (Sterck and Bongers, 2005), have a relatively rapid growth in its juvenile stage without much light stress. Based on this result we can conclude that the higher light level in the understory of this forest is probably the factor that modifies the coefficient b of the stem of these shade-tolerant species and produce a low value.

As the height-diameter relationship of the stem in the trees is of great concern to the forest industry, this result may help foresters to know the stem morphological plasticity for these and close-related species in particular.

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