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Reviewed work(s):
Source: *Functional Ecology*, Vol. 17, No. 2 (Apr., 2003), pp. 194-200
Published by: British Ecological Society
Stable URL: http://www.jstor.org/stable/3599175
Accessed: 03/10/2012 14:46

Functional Ecology 2003
17, 194–200

The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest

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Summary

1. Many studies discuss the adaptive value of plant architecture, but few have actually measured architectural effects on plant growth and survival. In this study, sapling growth and survival are related to crown traits for two tree species, *Trophis mexicana* (Liebm.) Bur. and *Pseudolmedia oxyphyllaria* Donn. Sm., in the Los Tuxtlas lowland rainforest of Mexico. The traits investigated were crown width, crown depth, number of leaves, number of leaves per unit crown area (horizontal self-shading), and number of leaves per unit silhouette area (vertical self-shading).

2. Self-shading indices decreased with crown size, but were unaffected by the number of leaves per tree. Larger crowns thus had more diffuse foliage, with less self-shading.

3. The number of leaves had positive effects on growth and survival, while self-shading indices had no effect. This indicates that shaded leaves do not necessarily have negative carbon balances.

4. Negative effects of crown width on horizontal crown growth, and positive effects on vertical crown growth, suggest that saplings tend to grow towards a shape intermediate between the narrow and wide crown extremes.

5. Survival was positively correlated with crown width in *Pseudolmedia*, and with the number of leaves in *Trophis*. Apparently, dependence of survival on crown traits differed among species.

6. Crown traits affected plant growth and survival, but the hypothesis emerging from light-limited carbon acquisition was confounded by other factors, such as tree size and the inherent branching patterns.

7. Crown traits are good and rather simple predictors of future sapling growth and survival, and may help foresters to select potential crop trees.

Key-words: Canopy architecture, morphology, path analysis, performance, *Pseudolmedia oxyphyllaria*, *Trophis mexicana*

Functional Ecology (2003) **17**, 194–200

Introduction

Tropical rainforest saplings live in weak but variable irradiance (Chazdon & Fetcher 1984). Their physiological and morphological traits, and their flexibility in these traits, are associated with growth and survival in such an environment (Kitajima 1996; Veneklaas & Poorter 1998). Most species show the same acclimation responses to light, including increases in crown size, total leaf area, and self-shading at high light (King 1994; Sterck, Bongers & Newbery 2001). Such responses largely account for the morphological differences among individuals of the same species in a forest (Sterck 1999). To date, little attention has been paid to the consequences of intraspecific morphological differences for the future growth and survival of trees. Strikingly, foresters aim at selecting trees with good future growth and survival prospects using simple morphological criteria, but the consequences of selection criteria are hardly ever tested. In the present study we develop general hypotheses on the consequences of simple morphological crown traits for survival and growth of tree saplings living in a forest, and test these hypotheses for two Mexican rainforest species.

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We focus on three morphological traits at the whole-plant level: total leaf area; leaf spread; and crown size. For successful growth and survival, saplings need to produce sufficient leaf area (King 1994) and spread their leaves to reduce self-shading. Leaf spreading may be horizontal to avoid mutual shading of a (mainly) vertical light source (Leopold 1971; Warren Wilson 1981), or vertical to reduce penumbra effects (Horn 1971; Terborgh 1985). Minimization of self-shading maximizes light interception in trees (Honda & Fisher 1979). At low light, self-shading is reduced mainly by slow leaf production rates, reducing the amounts of leaves and leaf area in the crown at any given time (Poorter & Werger 1999; Sterck, Bongers & Newbery 2001). Under these conditions, greater crown size increment cannot reduce self-shading because few resources are left for growth. At high light, however, more resources may result in more rapid crown growth, greater leaf production and accumulation of carbon reserves, thus having a positive effect on future growth and survival (Poorter 2001). We translated these findings into hypotheses on crown trait consequences for growth and survival. Such hypotheses apply *a priori* to saplings of any species in a forest, reflecting the idea that different species function similarly in terms of light interception (Valladares, Stillman & Pearcy 2002); stability (Sterck & Bongers 1998); and hydraulic architecture (West, Brown & Enquist 1997), despite large morphological differences among species (Hallé, Oldeman & Tomlinson 1978).

We hypothesize that (i) leaf self-shading increases with increasing number of leaves and decreases with increasing crown depth and crown width; and (ii) number of leaves, crown depth and crown width have positive effects on crown growth and sapling survival, and self-shading has a negative effect on growth and survival (Fig. 1).

The predictions were tested for two shade-tolerant tree species of the Moraceae family in a Mexican lowland rainforest (González-Soriano, Dirzo & Vogt 1997). We used path analysis to unravel correlation into direct effects of predictors on growth and survival (causal relationship) and indirect effects – the effects of predictors through correlation with other predictor(s) (Fig. 1; Sokal & Rohlf 1995).

Methods

SITE 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 South-eastern 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 & Vogt 1997).

The Moraceae is the second most species-rich family at Los Tuxtlas. For this study we selected two abundant, shade-tolerant Moraceae species, *Trophis mexicana* (Liebm.) Bur. and *Pseudolmedia oxyphyllaria* Donn. Sm. Both species have a monopodically, continuously growing trunk and plagiotropic branches, and conform to the architectural model of Roux (cf. Hallé, Oldeman & Tomlinson 1978). Their leaves are simple and measure *c.* 10 cm long by 3 cm wide. *Trophis* attains a maximum height of 15 m and *Pseudolmedia* 25 m (González-Soriano, Dirzo & Vogt 1997).

FIELD MEASUREMENTS

Two hundred 10 m^2 plots were established in a 20 × 20 m grid in a 2 ha area in the Los Tuxtlas rainforest in 1990.

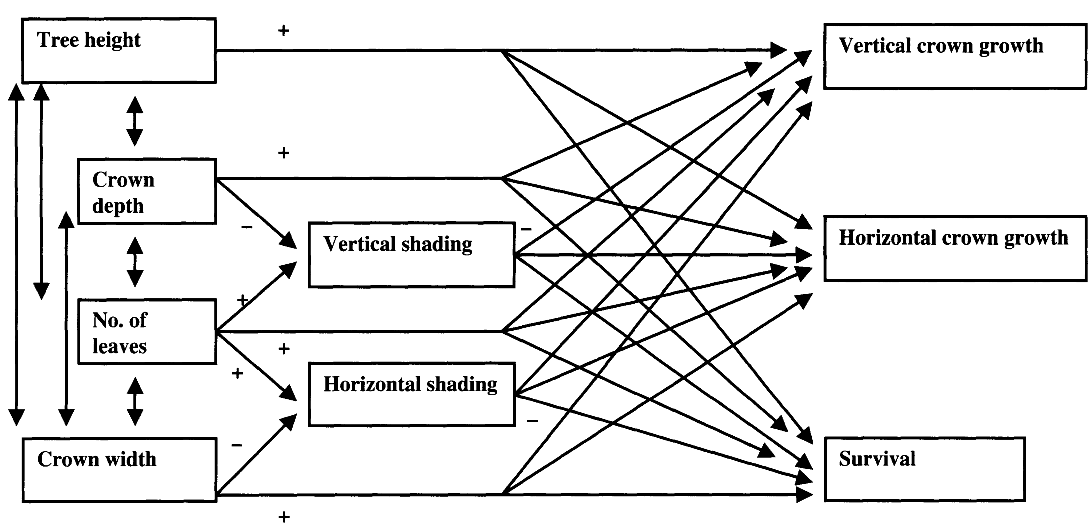

Fig. 1. The path diagram shows the expected relationships between crown traits and growth and survival. Plus signs refer to positive effects, minus signs to negative effects, and apply to all adjacent arrow branches. Single-headed arrows refer to causal relationships; double-headed arrows to correlations. See text for further explanation.

All 0·5–2·0 m tall individuals of the two Moraceae species were inventoried (*Pseudolmedia*, $N = 313$; *Trophis*, $N = 328$). These saplings were exposed to the dominant low irradiance of the forest (M.M.-R., unpublished data). Plant height, height to lowest leaf, and two perpendicular crown widths were measured with a measuring tape (precision ~1 cm), and the number of leaves was counted. The number of leaves appeared to be a good predictor of total leaf area in saplings of these species (Popma & Bongers 1988; Bongers & Popma 1990) and others (Sterck, Bongers & Newbery 2001). Mean crown width and crown depth were calculated from these data. In addition, two self-shading indices were calculated: number of leaves per unit crown area (horizontal self-shading); and number of leaves per unit silhouette area (vertical self-shading). Crown area was calculated as an ellipse: $0{\cdot}25\pi D_1 D_2$ (Bongers *et al.* 1988), where D_1 and D_2 represent the two perpendicular crown widths. Silhouette area was calculated with the same formula, but replacing D_1 by the average crown width and D_2 by crown depth. Saplings with recent stem breakage were excluded from further analysis. One year after the first census, all trees were checked for their survival, and vertical and horizontal crown dimensions were re-measured for the surviving individuals (*Pseudolmedia*, $N = 259$; *Trophis*, $N = 279$). From these dimensions we calculated absolute vertical crown growth and absolute horizontal crown growth (m).

ANALYSIS

We used a path analysis (Wright 1934; Sokal & Rohlf 1995) to evaluate the effects of various crown traits (predictors) on growth and survival (criterion variables, Fig. 1). Tree height was included to correct for size effects on these relationships. Path analysis shows direct (or causal) effects as standardized partial regression coefficients or path coefficients. We expected positive direct effects of crown size on growth and survival, and negative direct effects of self-shading indices (single-headed arrows in Fig. 1). Relations without causal effect are calculated as Pearson's product moment correlation coefficients, and were expected among sapling size variables (double-headed arrows in Fig. 1). An indirect effect occurs when a predictor (size variable) is correlated with growth or survival through its correlation with a predictor that has a direct effect, and is calculated as the product of corresponding correlation and path coefficients. Both direct and indirect effects indicate the change in a criterion variable (expressed in standard deviation units) as a result of a change of one standard deviation in its predictor.

The effects of crown traits on survival were quantified with a logistic regression model, with a binomial error for the criterion variable. Here the effects were expressed as odds ratios. These ratios are not equivalent to path coefficients, as they quantify the increase in the odds of survival with an increase of one in the unit of the predictor (Sokal & Rohlf 1995). As the data did not deviate from a normal distribution, they were not transformed for the path analysis.

Results

The two species were characterized by similar crown sizes, self-shading indices, growth rates and survival probabilities, and exhibited large variation in these variables (Table 1). The low values of horizontal shading compared with vertical shading may reflect the relatively horizontal orientation of leaves in the crown. Comparisons between vertical and horizontal shading within and among species are inappropriate, as leaf orientation was not measured in this study. Vertical crown growth exceeded horizontal crown growth in both species.

Table 1. Plant traits for tree saplings of *Pseudolmedia oxyphyllaria* ($N = 259$) and *Trophis mexicana* ($N = 279$), both Moraceae, in the Los Tuxtlas forest of Mexico

		Pseudolmedia		*Trophis*	
	Units	Mean	SD	Mean	SD
Size					
Sapling height	10^{-2} m	91·9	43·2	95·8	40·0
Crown width	10^{-2} m	69·3	30·8	56·9	25·0
Crown depth	10^{-2} m	40·7	26·5	34·3	32·6
Number of leaves		4·2	1·1	3·4	1·2
Self-shading index					
Number of leaves/crown area*	m^{-2}	15·8	14·4	18·1	12·0
Number of leaves/silhouette area†	m^{-2}	32·8	47·8	50·2	66·8
Performance					
Horizontal crown growth	10^{-2} m year^{-1}	0·2	15·5	0·3	13·9
Vertical crown growth	10^{-2} m year^{-1}	2·7	18·5	4·0	18·9
Sapling survival	year^{-1}	0·83‡		0·86‡	

*Horizontal shading.
†Vertical shading.
‡Proportion of survivors per year.

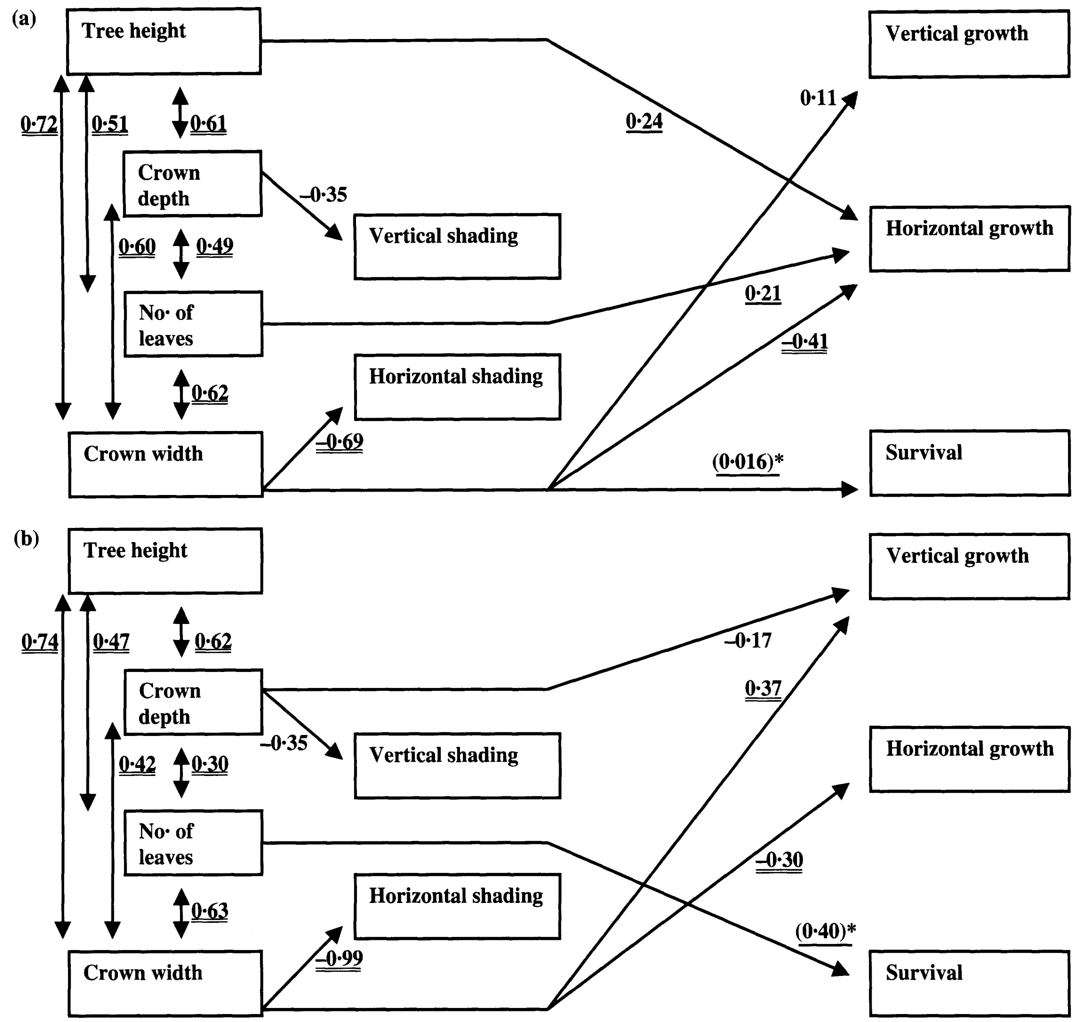

Fig. 2. Path diagrams show the relationships between crown traits and growth and survival for saplings of (a) *Pseudolmedia oxyphyllaria* and (b) *Trophis mexicana*. Significant relationships are shown ($P < 0{\cdot}05$ plain type, $P < 0{\cdot}01$ underlined, $P < 0{\cdot}001$ double underlined). Single-headed arrows represent direct effects (causal relationships); double-headed arrows, correlations. Values along single-headed arrows are path coefficients, except for the effects on survival (odds ratios). These odds ratios reflect the increase in survival probability with an increase in crown width of 1 cm (*Pseudolmedia oxyphyllaria*), or an increase in leaf number of 1 (*Trophis mexicana*).

Table 2. Pearson's correlations among plant traits for saplings of *Pseudolmedia oxyphyllaria* ($N = 259$) and *Trophis mexicana* ($N = 279$), Moraceae, Los Tuxtlas, Mexico

	Pseudolmedia						
	Crown depth	Crown width	Number of leaves	Horizontal self-shading	Vertical self-shading	Horizontal crown growth	Vertical crown growth
Trophis							
Crown depth		0·60**	0·49**	−0·28**	−0·39**	NS	NS
Crown width	0·42**		0·62**	−0·59**	−0·31**	−0·10*	0·10*
Number of leaves	0·30**	0·63**		−0·31**	−0·15*	NS	NS
Horizontal self-shading	−0·21**	−0·70**	−0·18**		0·32**	0·13*	NS
Vertical self-shading	−0·41**	−0·32**	−0·13**	0·35**		NS	NS
Horizontal crown growth	NS	−0·26**	NS	0·25**	0·13*		0·40**
Vertical crown growth	−0·11*	0·18**	0·13*	−0·12*	NS	0·23**	

NS if $P > 0{\cdot}05$; * if $P < 0{\cdot}05$; ** if $P < 0{\cdot}01$.

The two species showed similar patterns for the correlations and effects among plant traits (correlations in Table 2; effects in Fig. 2). Crown size variables were positively correlated with one another. Self-shading indices were negatively correlated with crown width, crown depth and leaf number, but were only directly negatively affected with increasing crown width and crown depth (see direct effects, Fig. 2). Large crowns thus had more diffuse foliage, with less self-shading.

Most of the correlations (Table 2) between crown

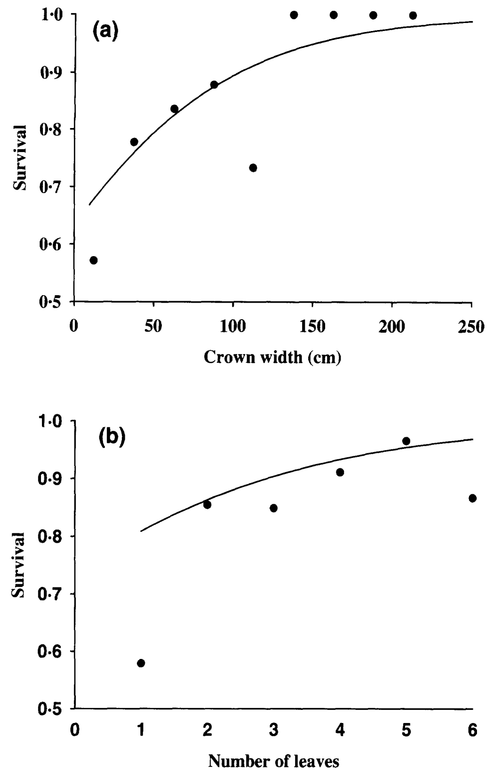

Fig. 3. Effects of size variables on survival using a logistic regression model with the probability of survival as the independent variable *P* and a size or shading variable as independent variables *X* $\left(P = \frac{e^{\alpha+\beta x}}{1 + e^{\alpha+\beta x}}\right)$. (a) Influence of crown width in *Pseudolmedia oxyphyllaria* ($\alpha = 0{\cdot}549$, $\beta = 0{\cdot}016$, $P = 0{\cdot}016$, Nagelkerke $R^2 = 0{\cdot}04$). Survival means for the 25 cm classes are shown as dots. (b) Influence of number of leaves in *Trophis mexicana* ($\alpha = 1{\cdot}042$, $\beta = 0{\cdot}400$, $P = 0{\cdot}010$, Nagelkerke $R^2 = 0{\cdot}10$). Survival means per leaf number are shown as dots.

size variables and growth reflect direct effects (Fig. 2). In both species, crown width affected horizontal crown growth negatively and vertical crown growth positively. In *Pseudolmedia*, number of leaves and tree height affected horizontal crown growth positively. In *Trophis*, crown depth negatively affected vertical crown growth. Self-shading was correlated with horizontal and vertical crown growth in some cases, but there were no significant direct effects of self-shading on growth.

The two species differed in their relationship between crown traits and survival. Survival increased with crown width in *Pseudolmedia*, and with number of leaves in *Trophis* (Figs 2 and 3). In both species, survival was unaffected by self-shading indices. Many of the other expected relationships with survival were not found.

Discussion

ARCHITECTURE AND SELF-SHADING

We predicted positive effects of leaf number on self-shading, and negative effects of crown size on self-shading. Self-shading was indeed reduced with increasing crown width and crown depth, but was unaffected by the number of leaves. This result implies that saplings with smaller crowns risk greater self-shading. The unexpected impact of the crown dimension alone (and not of leaf number) in both species may result from the inherited developmental pattern, described for both species by the Roux model. This pattern is characterized by a vertical (orthotropic) main axis, with horizontal branches arranged spirally at successive nodes along the main axis (e.g. Hallé *et al.* 1978). The inhibition or stimulation of branch growth causes large variations in crown dimension among small saplings (Sterck 1997), and probably accounted for the negative correlations with self-shading in our individuals. Our results, however, contrast with those of a study on Dipterocarpaceae and Euphorbiaceae species of Malaysian rainforest (Sterck, Bongers & Newbery 2001). Six of the eight species in that study had branching patterns similar to *Trophis* and *Pseudolmedia*, but their (horizontal) self-shading index correlated positively with crown size variables. Those trees were, however, much bigger (5–20 m) than our 1 m tall saplings, and therefore were less flexible than small saplings in their (relative) crown dimensions. In the large trees, variation in leaf production and mortality appeared to be the major factor driving underlying variation in self-shading. In our small saplings, crown size, probably driven by the variation in plagiotropic branch growth, caused the variation in self-shading among individuals. These results suggest that self-shading mechanisms differ among trees of different size, as well as among species with different inherited developmental patterns.

ARCHITECTURE AND GROWTH AND SURVIVAL

We predicted positive direct effects of numbers of leaves and crown size on growth and survival, and negative effects of self-shading indices on growth and survival. These hypotheses were not generally supported by the results.

First, self-shading did not significantly affect growth and survival. This seems surprising: the smallest crowns were most densely packed with leaves, and seem most sensitive to self-shading under the dominant low light conditions of the forest. Still, the effects of self-shading were negligible. The point of self-shading and its negative role in growth and survival has received much theoretical interest (Horn 1971; Warren Wilson 1981; Terborgh 1985), but little empirical evidence has been found so far in trees with complex branching patterns. Models, in combination with experimental data, showed convincingly that self-shading decreased the photosynthetic performance of shaded leaves in forest understorey trees (Pearcy & Yang 1996; Anten & Ackerly 2001). Yet, when shaded leaves contribute to the net carbon gain of the tree, the total number of leaves is expected to influence growth and survival positively, rather than self-shading having a negative effect (see also Ackerly 1999). Our results support this latter line of reasoning.

Second, horizontal crown growth was negatively affected by crown width. Jointly with the positive effect of crown width on vertical crown growth, and the negative effect of crown depth on vertical crown growth in *Trophis*, this suggests that crowns grow towards an intermediate shape. Wide-crowned saplings increase their crown width relatively less than narrow-crowned saplings and, conversely, narrow-crowned saplings increase their crown depth relatively less than wide-crowned individuals. When crown shape extremes (wide *vs* narrow crown) reflect responses to extreme (e.g. light) conditions in the past, the growth towards an intermediate shape in current light conditions may improve sapling functioning, for example in terms of optimal hydraulic or mechanical architecture (Niklas 1986; Farnsworth & Niklas 1995). It is beyond the scope of this study to speculate further on the factors driving this convergence towards an intermediate shape but, strikingly, the unexpected pattern was consistent for the two species studied.

Finally, survival was affected positively by crown width in *Pseudolmedia*, and positively by leaf number in *Trophis*. In other tree species, leaf area appeared to be the key variable driving survival (Zagt 1997; Sterck *et al.* 1999). It is unclear why the effect of leaf area did not appear in *Pseudolmedia*. This study suggests that the dependence of survival on crown traits may differ among species, contrasting with the general idea that different species show the same functional response (West, Brown & Enquist 1997; Valladares, Stillman & Pearcy 2002).

Thus, despite a number of significant expected effects, three observations contradict the general hypothesis of light-driven carbon acquisition and the resulting consequences of crown traits for tree growth and survival. First, the expected self-shading effects were not found. Second, the two species differed in at least some of their significant relationships (e.g. different effects on survival). Ultimately, crown width affected horizontal crown growth negatively instead of positively. We conclude that plant architecture seriously affected crown growth and sapling survival, but that the simple hypothesis emerging from light-driven carbon acquisition is flawed because of, for example, size effects, growth constraints other than light (water, stability), and inherited developmental patterns. At the species level, however, simple crown size variables may be good predictors of future sapling growth and survival, and thus provide useful information to forest managers aiming to select individuals with good potential as crop trees.

Acknowledgements

The Dirección General de Asuntos del Personal Académico of UNAM provided a postdoctoral grant to Frank Sterck at UNAM; WOTRO (NWO) provided a postdoctoral grant (W 01-53/BM 019) to Frank Sterck at Utrecht University.

References

Ackerly, D. (1999) Self-shading, carbon gain and leaf dynamics: a test of alternative optimality models. *Oecologia* **119**, 300–310.

Anten, N.P.R. & Ackerly, D.D. (2001) Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. *Functional Ecology* **15**, 252–262.

Bongers, F. & Popma, J. (1990) Leaf dynamics of seedlings of rain forest species in relation to canopy gaps. *Oecologia* **82**, 122–127.

Bongers, F., Popma, J., Meave del Castillo, J. & Carabias, J. (1988) Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. *Vegetatio* **74**, 55–80.

Chazdon, R.L. & Fetcher, N. (1984) Light environments of tropical forests. *Physiological Ecology of Plants of the Wet Tropics* (eds E. Medina, H.A. Mooney & C. Vasquez-Yanes), pp. 27–36. Dr W. Junk, The Hague.

Farnsworth, K.D. & Niklas, K.J. (1995) Theories of optimization, form and function in branching architecture in plants. *Functional Ecology* **9**, 355–363.

González-Soriano, E., Dirzo, R. & Vogt, R.C. (1997) *Historia Natural de Los Tuxtlas*. National University of Mexico, Mexico.

Hallé, F., Oldeman, R.A.A. & Tomlinson, P.B. (1978) *Tropical Trees and Forests: An Architectural Analysis*. Springer Verlag, Berlin.

Honda, H. & Fisher, J.B. (1979) Tree branch angle: maximizing effective leaf area. *Science* **199**, 888–890.

Horn, H.S. (1971) *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, NJ.

King, D.A. (1994) Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**, 948–957.

Kitajima, K. (1996) Ecophysiology of tropical tree seedlings. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 559–596. Chapman & Hall, New York.

Leopold, L.B. (1971) Trees and streams: the efficiency of branching patterns. *Journal of Theoretical Biology* **31**, 339–354.

Niklas, K. (1986) Computer simulations of branching-patterns and their implications on the evolution in plants. *Lectures on Mathematics in the Life Sciencies* **18**, 1–50.

Pearcy, R.W. & Yang, W. (1996) A three-dimensional crown architecture model for assessment of light capture and carbon gain by understorey plants. *Oecologia* **108**, 1–12.

Poorter, L. (2001) Light-dependent changes in allocation and their effects on the growth of rain forest tree species. *Functional Ecology* **15**, 113–123.

Poorter, L. & Werger, M.J.A. (1999) Light environment, sapling architecture and leaf display in six rain forest tree species. *American Journal of Botany* **86**, 1464–1473.

Popma, J. & Bongers, F. (1988) The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* **75**, 625–632.

Sokal, R.R. & Rohlf, F. (1995) *Biometry: The Principles and Practice of Statistics in Biology Research*. W.H. Freeman, San Francisco, CA.

Sterck, F.J. (1997) *Trees and light: tree development and morphology in relation to light availability in a tropical rain forest in French Guiana*. PhD thesis, Wageningen Agricultural University, Wageningen.

Sterck, F.J. (1999) Crown development in gaps and understorey. *Plant Ecology* **143**, 89–98.

Sterck, F.J. & Bongers, F. (1998) Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany* **85**, 266–272.

Sterck, F.J., Clark, D.B., Clark, D.A. & Bongers, F. (1999) Light fluctuations, crown traits, and response delays for tree saplings in a Costa Rican lowland rain forest. *Journal of Tropical Ecology* **15**, 83–95.

Sterck, F.J., Bongers, F. & Newbery, D.M. (2001) Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology* **153**, 279–292.

Terborgh, J. (1985) The vertical component of plant species diversity in temperate and tropical forests. *American Naturalist* **126**, 760–776.

Valladares, F., Stillman, J.B. & Pearcy, R.W. (2002) Convergence in light capture efficiencies among tropical forest understorey plants with contrasting crown architectures: a case of morphological compensation. *American Journal of Botany* **89**, 1275–1284.

Veneklaas, E.J. & Poorter, L. (1998) Growth and carbon partitioning of tropical tree seedlings growing in contrasting light environments. *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences* (eds H. Lambers, H. Poorter & M.M. van Vuuren), pp. 337–361. Backhuys, Leiden.

Warren Wilson, J. (1981) Analysis of light interception by single plant. *Annals of Botany* **48**, 501–505.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.

Wright, S. (1934) The method of path coefficients. *Annals of Mathematics and Statistics* **5**, 161–215.

Zagt, R.J. (1997) *Tree demography in the tropical rain forest of Guyana*. PhD thesis. *Tropenbos–Guyana* Series 3. Georgetown, Guyana.

Received 3 May 2002; revised 27 September 2002; accepted 7 October 2002