Journal of Tropical Ecology (2006) **22**:223–226. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467405002968 Printed in the United Kingdom

SHORT COMMUNICATION

Juvenile tree growth in relation to light availability in second-growth tropical rain forests

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(*Accepted 28 August 2005*)

Key Words: increment growth, red:far-red ratio, shade tolerance, succession, tropical wet forest

Light is a key environmental factor limiting growth and survival of trees in the subcanopy of wet tropical forests (Davies 2001, Thomas 1996). Light availability varies both vertically and horizontally and affects tree height, crown shape and tree architecture (Bongers & Sterck 1998, Sterck & Bongers 2001, Sterck *et al*. 1999) in addition to growth and survival (Clark & Clark 1992, 2001). Although many studies of tree seedlings and saplings have shown that growth varies significantly with light availability in tropical wet forests (Clark *et al*. 1993, Iriarte & Chazdon 2005, King 1991, Kohyama 1991, Montgomery & Chazdon 2002, Oberbauer *et al*. 1988, 1993; Poorter & Werger 1999, Sterck *et al*. 1999, Welden *et al*. 1991), few studies have examined these relationships in size classes above 5 cm dbh (Sterck 1999). King *et al*. (2005) found that annual increment growth of trees in the 8–20-cm dbh size class in two Asian forests was positively dependent on an index of crown light interception, but no direct measurements of light availability were taken in this study. Due to logistical challenges, few direct measurements of light environments above tree crowns have been made in tropical forests (Sterck & Bongers 2001). To our knowledge, no measurements have been made in second-growth forests.

We examined variation in growth rates and crown sizes of trees in the 5–9.9-cm dbh size class in response to variation in light availability above crowns of three species in two second-growth, 1-ha plots at La Selva Biological Station in north-eastern Costa Rica (Chazdon *et al*. 2005). Trees in this size class establish beneath the pioneer successional canopy and represent the future generation of canopy tree species. Gaps are infrequent in young secondary forests of this region (Montgomery & Chazdon 2001, Nicotra *et al*. 1999) and tree recruitment into the subcanopy and canopy occurs in the absence of gaps through continuous vertical growth through the understorey and subcanopy. The natural vegetation in the area is classified as Tropical Wet Forest (*sensu* Holdridge *et al*. 1971).

Both plots are on ultisols derived from weathered volcanic deposits (Sanford *et al*. 1994). Stands developed on abandoned cattle pastures. In 2004, LEP was 27 y old and LSUR was 19 y old; stand age was documented by aerial photographs and personal accounts. In 2004, basal area of trees $\geq$ 10 cm dbh was greater in the older LEP stand than in the LSUR stand (27.2 and 22.0 m^2 ha^{-1}, respectively).

We studied three shade-tolerant tree species that were present in both sites and that were 5–9.9 cm dbh in 2003, with a maximum crown height of 10 m; *Ocotea leucoxylon* (Sw.) Laness. (Lauraceae), *Pentaclethra macroloba* (Willd.) Kuntze (Fabaceae) and *Virola sebifera* Aubl. (Myristicaceae). These were the most abundant tree species in this size class in the two study plots. *Ocotea leucoxylon* is a subcanopy tree, whereas the other two species are canopy trees (Hartshorn & Hammel 1994). This study is part of a long-term project to monitor vegetation dynamics in second-growth tropical forests in north-eastern Costa Rica (Chazdon *et al*. 2005).

In 2004, we sampled light availability for all trees present in the 5–9.9-cm dbh size class in 2003, with the exception of 10 *Pentaclethra* trees in LSUR that were omitted due to equipment failure. In total, 91 trees were measured (10 of *O. leucoxylon*, 64 of *P. macroloba* and 17 of *V. sebifera*). We used a red:far-red (R:FR) sensor to evaluate light availability above individual tree crowns, based on the rapid assessment technique of

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Table 1. Red:far-red ratio, tree size, and annual increment growth data for trees 5–10-cm dbh in two second-growth forests in 2004 (mean ± 1 SD) and results of two-way ANOVA. Analyses are based on log-transformed variables. Different lower case letters indicate significant differences among species based on two-way ANOVA *post-hoc* tests ($P < 0.05$).

Species	n	R:FR	dbh (cm)	Crown height (m)	Crown area (m^2)	2003–2004 growth increment ($mm\ y^{-1}$)
Ocotea leucoxylon	10	0.61 ± 0.21^a	6.81 ± 1.27^a	8.30 ± 1.15^{ab}	6.27 ± 3.69^a	2.20 ± 0.34^a
Pentaclethra macroloba	64	0.52 ± 0.12^a	6.63 ± 1.02^a	8.36 ± 1.24^a	12.6 ± 5.83^b	2.00 ± 0.21^a
Virola sebifera	17	0.56 ± 0.12^a	6.26 ± 0.69^a	9.25 ± 0.34^b	8.85 ± 3.32^a	4.70 ± 0.36^b
P (species)		0.250	0.387	0.033	0.0002	0.00055
P (site)		0.178	0.297	0.494	0.048	0.0097
P (species × site)		0.048	0.569	0.672	0.015	0.295

Capers & Chazdon (2004). This method provides highly sensitive readings beneath dense forest canopies and does not require the use of paired sensors. We measured photon flux density ($\mu mol\ m^{-2}\ s^{-1}$) of red (660 nm) and far-red (730 nm) wavelengths using a Skye SKR 110 sensor. The sensor was factory-calibrated 1 y prior to our study. Measurements were recorded using a Campbell Scientific 23X data logger. Readings were taken during overcast or cloudy conditions when diffuse light was predominant, as required by this method. The SKR 110 sensor and a 15-m extension cable were mounted on a weighted gimbal to maintain a level orientation; the gimbal was then mounted on the end of an adjustable, telescoping aluminium pole (maximum extension, 10 m). Most readings were taken between 7 and 9 m height. A tripod was used to stabilize the pole on slopes or in muddy patches. Three, 1-min readings (the average of six 10-s averages) were taken approximately 120 degrees apart above the crown of each tree and averaged. Values of per cent diffuse transmittance of photon flux density (%T) were calculated from averaged R:FR data, based on the non-linear regression equations developed by Capers & Chazdon (2004).

We measured stem diameter at breast height (1.3 m) using a nylon diameter tape to the nearest mm. Crown height was assessed using an extendable fibreglass measuring pole to the nearest cm. Crown width to the nearest cm was measured using a metre tape in two dimensions at 90-degree angles and crown area was calculated using the formula for area of an ellipse. Comparisons of R:FR, tree size and annual increment growth across species and between sites were made using two-way ANOVA. Linear regressions were performed to quantify dependence of tree characteristics on light availability. To normalize the data we used a log $(x + 1)$ transformation for increment growth data as some trees had growth increments of zero; we applied simple log-transformations for all other variables examined.

Red:far-red ratio ranged from 0.31 to 1.05 (mean = 0.54) and %T ranged from 1.05 to 33.6 (mean = 3.27). Light availability (R:FR) did not differ significantly between sites ($P = 0.178$) or among species ($P = 0.250$; Table 1). Mean annual growth increments from 2003 to 2004 were significantly higher in the younger LSUR plot ($P = 0.0097$) and differed significantly among species ($P = 0.0005$), with no plot – species interaction ($P = 0.295$; Table 1). Despite similar light availability, diameter increments for *V. sebifera* were significantly greater than those for *O. leucoxylon* and *P. macroloba* (Tukey HSD test; Table 1). The species differed significantly in crown size variables; crown height was significantly greater for *V. sebifera* than *P. macroloba*, and crown area was significantly greater for *P. macroloba* compared with the other two species (Table 1).

For the entire sample of 91 trees, increment growth from 2003–2004 was significantly dependent on R:FR ($R^2 = 0.207$; $P = 0.00006$), although coefficients of determination were low (Figure 1). A multiple regression using R:FR and three tree size variables (crown area, crown height and dbh) was also highly significant ($R^2 = 0.256$; $P = 0.00004$), with R:FR the only variable significantly affecting increment growth ($P = 0.00001$).

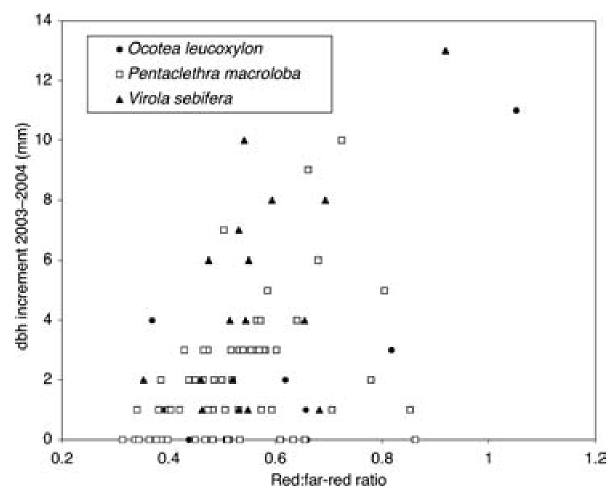

Figure 1. Annual diameter growth increment (mm) of juveniles of three tree species in second-growth forest understorey in relation to light availability measured directly above crowns. Regression statistics for all trees combined and for each species are provided in the text.

https://doi.org/10.1017/S0266467405002968 Published online by Cambridge University Press

Tree size variables of crown area, dbh and crown height showed no significant dependence on light availability for all trees overall ($P > 0.05$).

Species showed distinct responses in increment growth and size in relation to light availability. Increment growth showed a significant positive dependence on R:FR for the two canopy species, *P. macroloba*: ($R^2 = 0.18$; $P = 0.0004$) and *V. sebifera* ($R^2 = 0.270$; $P = 0.032$), but not for the subcanopy species *O. leucoxylon* ($P = 0.114$). *Ocotea leucoxylon*, on the other hand, was the only species that showed a significant positive dependence of crown area on R:FR ($R^2 = 0.753$; $P = 0.0011$). *Virola sebifera* was the only species that showed a significant negative dependence of crown height:dbh on R:FR, indicating that trees were more 'stout' under relatively brighter conditions ($R^2 = 0.383$; $P = 0.008$). A multiple regression including R:FR and tree size variables showed that crown height of *V. sebifera* was a significant determinant of increment growth ($P = 0.005$); when this variable was included, the effect of R:FR on increment growth was no longer significant ($P = 0.734$). Greater crown height was therefore the major determinant of increased diameter increments for small trees of this species.

The ability to adjust growth responses to variation in light availability beneath the canopy is an important determinant of tree recruitment in young second-growth forests where gaps are infrequent (Montgomery & Chazdon 2001, Nicotra *et al.* 1999). From 1997–2002, populations of trees ≥ 5 cm dbh of *Pentaclethra* and *Virola* in the younger site increased 1.6 and 8.5% y^{-1}, respectively, and no individuals in the 5–9.9-cm dbh size class died (Chazdon *et al.* 2005). In the older site, *Ocotea* and *Virola* populations increased an average of 1.45 and 2.64% y^{-1} and small trees of *Virola* and *Pentaclethra* showed mortality rates of 0 and 1.5% y^{-1}, respectively.

Our direct sensor measurements clearly showed that juvenile trees responded differentially to variation in light availability beneath the canopy in second-growth tropical wet forests. These responses are consistent with the successional behaviour and vertical distribution of these species. Within this small diameter class, species also demonstrated variation in tree shape, with higher crown areas in *P. macroloba*, and greater crown heights in *V. sebifera* (Table 1). Further studies on increments in crown size as well as diameter and height growth of a range of tree species will clarify the significance of these growth responses for long-term dynamics in successional tropical rain forests. Many shade-tolerant species establish populations early during tropical forest succession (Finegan 1996, Peña-Claros 2003) and their growth responses to light availability are likely to be key factors underlying their successful recruitment into the subcanopy and canopy within the first 30 y of secondary forest succession.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of Jeanette Paniagua, Hannah Alpert-Abrams, Marcos Molina, Juan Romero, Alvaro Redondo and Braulio Vilchez. The Organization for Tropical Studies and the staff of La Selva Biological Station provided logistical assistance and excellent research facilities. Funding was provided by the Andrew W. Mellon Foundation, the University of Connecticut Research Foundation and the Summer Undergraduate Research Fund.

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