

Effects of Understory Foliage on Patterns of Light Attenuation near the Forest Floor¹

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ABSTRACT

Understory light availability is an important component of the environment for canopy tree seedlings. Understanding what generates variation in understory light availability represents one step in understanding processes regulating seedling banks, the beginning capital of regeneration in tropical forests. Near the forest floor, variation in light availability may be strongly influenced by the structure and composition of the understory. I examined abundance of understory foliage and patterns of light attenuation in five Neotropical forests (La Selva Biological Station, Costa Rica = LS; Barro Colorado Nature Monument, Panama = BCI; Cocha Cashu Biological Station, Manu National Park, Peru = CC; Kilometer 41, Manaus, Brazil = KM41; and Nouragues, French Guiana = NG). I used hemispherical canopy photos to estimate light availability at two heights (0.65 and 1.7 m) above the forest floor and counted foliage between these heights. Light availability differed significantly among sites, and site rankings depended on measurement height. At 0.65 m, NG had significantly lower mean light availability than CC, with KM41, LS, and BCI equivalent and intermediate. At 1.7 m, light availability was still lowest at NG, and highest at CC, but LS had levels similar to CC while KM41 and BCI remained intermediate. Across sites, light attenuation was positively related to foliage density. LS had the most understory foliage and the highest light attenuation between 0.65 and 1.7 m. KM41, NG and CC had intermediate amounts of foliage and intermediate light attenuation. BCI had the lowest density of understory foliage and no difference between light at the two measurement heights. My results show significant effects of understory foliage on understory light and indicate that the selective environment of canopy tree seedlings differs among sites.

RESUMEN

Las condiciones lumínicas en el sotobosque son un componente importante del ambiente selectivo de las plántulas de árboles del dosel. Entender los factores que regulan la variación en la cantidad de luz que llega a un punto dado del sotobosque representa un paso en la comprensión de los procesos que regulan la regeneración avanzada en bosques tropicales. Cerca del suelo del bosque, la variación en el ambiente lumínico puede verse afectado más por la estructura y la composición del sotobosque que por el dosel. Para evaluar esta hipótesis, examiné la abundancia del follaje del sotobosque y los patrones de la atenuación de luz en cinco bosques neotrópicos (Estación Biológica La Selva, Costa Rica = LS; Monumento Natural de Barro Colorado, Panamá = BCI; Estación Biológica Cocha Cashu, Parque Nacional Manu, Perú = CC; Kilómetro 41, Manaus, Brasil = KM41; y Nouragues, French Guiana = NG). Estimé la disponibilidad de luz con fotos hemisféricas (lente “ojo de pez”) tomados en dos alturas (0.65 y 1.7 m desde el suelo). Medí un perfil de follaje entre las alturas focales. Los sitios difirieron significativamente en la cantidad de luz. Además, el orden de los sitios en cuanto a condiciones lumínicas varió con la altura de la medida. A 0.65 m, NG mostró la menor disponibilidad de luz seguido por KM41, LS, y BCI (similares) y finalmente CC. A 1.7 m, NG todavía mostró la menor disponibilidad de luz seguido por KM41 y BCI, y ambos fueron más bajos que LS o CC (similares y las mayores cantidades). La atenuación de luz se relacionó positivamente con la densidad del follaje en el sotobosque. En LS observé la mayor cantidad del follaje del sotobosque y la mayor atenuación de luz entre alturas de medida. En KM41, CC, y NG observé cantidades intermedios del follaje y atenuación de la luz. BCI mostró las menores cantidades del follaje del sotobosque y ninguna diferencia entre la luz en las dos alturas medidas. Mis resultados muestran los efectos fuertes de la vegetación del sotobosque por el ambiente lumínico y indican que el ambiente selectivo de las plántulas de los árboles del dosel puede diferir entre sitios.

Key words: Brazil; Costa Rica; French Guiana; hemispherical photographs; light availability; Panama; Peru; shrub layer; tropical rain forest; understory.

WITHIN FORESTED ECOSYSTEMS, VARIATION IN VEGETATION COMPOSITION AND STRUCTURE creates light environments that change in space and time (Chaz-

don & Fetcher 1984, Smith *et al.* 1992, Clark *et al.* 1996, Nicotra *et al.* 1999). Temporal variation in light occurs on many scales, from brief sunflecks (seconds, minutes, hours) to seasonal changes in insolation (months) to gap opening and closure (years). Gradients in vegetation composition, anthropogenic land use and disturbance (*e.g.*, branch fall, treefall, fire) influence spatial heterogeneity at

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a variety of scales. The magnitude and pattern of light attenuation from canopy to forest floor depends on the amount and vertical distribution of foliage in a forest (Anderson 1966, Terborgh 1985, Norman & Campbell 1989, Brown & Parker 1994, Montgomery & Chazdon 2001) and can also depend on characteristics of canopy species (Canham *et al.* 1994, Kabakoff & Chazdon 1996). Although patterns of light heterogeneity can be quantified, understanding of the causes of variation in light availability can be difficult. Most studies that have explored determinants of light heterogeneity in forested ecosystems focused on trees, examining stand density, basal area, tree species, or canopy height (Terborgh & Petren 1991, Brown & Parker 1994, Kabakoff & Chazdon 1996, Montgomery & Chazdon 2001).

In old-growth and second-growth forests of Costa Rica, variation in tree height, basal area, and density of stems 10 cm diameter at breast height (DBH) or greater failed to predict variation in light availability near the forest floor (10 × 10 m sampling plots; Montgomery & Chazdon 2001). The only predictor of light availability near the forest floor was the density of woody plants in small size classes (≥1 m tall and < 5 cm DBH). These results suggest that understory vegetation (including saplings of canopy trees) may uncouple variation in light availability from variation in local density of trees. While trees strongly decrease available light near the forest floor, variation in light availability may also be strongly affected by the structure and composition of the understory itself. The effects of understory vegetation on light availability near the forest floor have not been well studied despite their potential to critically impact canopy tree seedling regeneration (Maguire & Forman 1983; Chazdon 1986; Denslow *et al.* 1991; Smith & Vankat 1991; Conway *et al.* 1997; George & Bazzaz 1999a,b). In a lowland forest of Costa Rica, Chazdon (1986) found decreases in light availability between 1.5 and 0.5 m and argued that this attenuation was related to the abundance of short-statured palms in that forest (Chazdon 1986). In temperate forests, the establishment of a dense shrub layer can decrease light availability by 80 percent and arrest succession from old fields to hardwood forests (Putz & Canham 1992).

Understanding the environment in which canopy trees regenerate is essential to unravel the mechanisms that generate and maintain tropical tree diversity. The forest understory is the birthplace of all but epiphytic and hemi-epiphytic components of a forest. Many species of diverse

life-forms inhabit the forest understory, and canopy tree seedlings are but one component of a diverse community. Across Neotropical forests, the density and composition of the understory vegetation vary drastically (Gentry & Emmons 1987). A tree seedling's light environment will be determined in part by its neighbors, which can be anything from small forbs to canopy emergents. In a New England forest, patches of clonal understory ferns decrease light availability and selectively affect seedlings of particular species (George & Bazzaz 1999a). In tropical forests, a few studies suggest that the understory vegetation may have important consequences for local light availability and tree seedling establishment, survival, and growth (Brokaw 1983, Chazdon 1986, Taylor & Zisheng 1988, Denslow *et al.* 1991, Connell *et al.* 1997). To understand how understory vegetation influences light attenuation, I measured light at two focal heights above the forest floor and also measured the abundance and composition of vegetation between those heights. I examined five Neotropical forests that differ strongly in apparent understory structure and diversity. I hypothesized that forests with more understory foliage would have a steeper vertical gradient of light near the forest floor. I asked the following specific questions: How do the understory foliage density and light availability near the forest floor differ among five Neotropical lowland forest sites?; and What is the contribution of understory foliage to light attenuation near the forest floor? A related paper examines the relationships among understory resource availability and seedling abundance in these forests (Harms *et al.*, 2004).

METHODS

I conducted my research between September 2001 and November 2002 at five sites in Central and South America. La Selva Biological Station (LS) and Barro Colorado Island (BCI) were visited during the middle of the wet season (2001), whereas Cocha Cashu Biological Station (CC) and the Kilometer 41 (KM41) field station of the Biological Dynamics of Forest Fragments project were visited at the end of the dry season (2001). Nouragues was visited in the middle of the dry season (2002). For detailed site descriptions, see Gentry (1990), Bongers *et al.* (2001), and Powers (2004).

I sampled light availability along six 50 m transects per site, except at NG, where I sampled two 152 m transects. Fifty-meter transects were laid in mature forest in areas that had canopy heights greater than 15 m. I avoided large gaps, steep slopes, and

swamps to minimize the variance in the small sample area. At NG, longer transects made it impossible to completely avoid canopy gaps; however, transects were laid on level upland terrain in mature forest. I took hemispherical photographs at 0.65 m above the forest floor every 2 m (25 per transect) and at 1.7 m every 4 m (13 per transect) using a Nikon Coolpix 990 with fisheye adaptor mounted on a tripod. At NG, photos were taken in discontinuous 1 m² quadrats that were distributed at distances that varied from 1 to 5 m between nearest pairs of quadrats (53 per transect, 106 total). The top of the camera was oriented north and the camera leveled using a bubble level placed on the lens cap. At sampling points where photos were taken at both heights, I measured a foliage profile between 0.65 and 1.7 m height. Life-form (*e.g.*, woody dicot, palms [Arecaceae], ferns [Pteridophyta], broadleaved herbaceous monocot taxa [Araceae, Heliconiaceae, Marantaceae, and Zingiberaceae]) was recorded for each leaf touching a vertical pole (1 cm diam) within the 105 cm range between the photo heights. Hemispherical photographs were analyzed using HemiView ver. 2.0 (Delta-T Devices Ltd). In all analyses, I used the value for visible sky derived from photographs. This value was correlated to the direct, diffuse, and global site factors but did not make assumptions about how far the vegetation was away from the photograph. Values of visible sky vary from 0 to 1, with 1 being completely open and 0 being completely closed. When multiplied by 100, visible sky becomes percent canopy openness ($\text{visible sky} \times 100 = \% \text{ canopy openness}$). In the rest of the paper, I refer to this metric as canopy openness. To quantify light attenuation, I calculated the difference in canopy openness at 0.65 and 1.7 m for each sampling point where both an upper and lower photo were taken. To relate these data to understory foliage, I categorized each foliage sampling point into points with zero, one, or two or more leaves in the profile.

Ecological data are notorious for spatial autocorrelation. Such autocorrelation violates the assumption of independence in parametric statistics and must be addressed in data interpretation. To avoid problems associated with spatially autocorrelated data, all but one of my analyses used transects as the level of replication ($N = 6$ except NG, $N = 2$). A related manuscript (Harms *et al.* 2004) examines spatial structure in light availability and the understory vegetation community. In a single analysis, I examined the relationship between number of leaves in the profile and light attenuation within sites. This analysis used individual plot data as the level of replication. Before conducting this

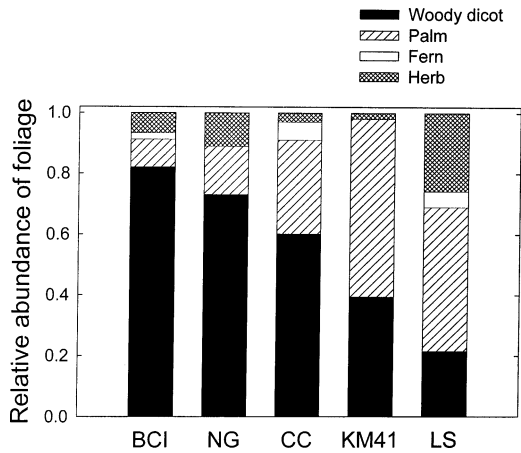


FIGURE 1. Relative abundance of foliage for each life-form (woody dicot, palm, fern, broadleaved herbaceous monocot) encountered in a vertical line transect between 0.65 and 1.7 m at five Neotropical forest sites. LS = La Selva Biological Station, Costa Rica; BCI = Barro Colorado Nature Monument, Panama; CC = Cocha Cashu Biological Station, Peru; KM41 = KM 41 field camp, Manaus, Brazil; NG = Nouragues, French Guiana; $N = 6$ at all sites except NG, where $N = 2$.

analysis, I examined spatial dependence in the total number of leaves in the profile and the difference in canopy openness between heights using the GS+ statistical package (Gamma Design Software, Plainwell, Michigan). I found no spatial structure in these variables at any site and proceeded with a parametric approach. One-way analyses of variance (ANOVAs) were conducted with STATISTICA (StatSoft, Inc., Tulsa, Oklahoma). *Post hoc* Tukey HSD tests examined pairwise differences among sites, and values of $P < 0.05$ were considered significant.

RESULTS

Sites differed significantly in understory foliage density (Fig. 1; $F_{4, 21} = 7.43$, $P < 0.001$). LS had more foliage between 0.65 and 1.7 m (1.18 ± 0.091 SE) than CC (0.860 ± 0.053), KM41 (0.943 ± 0.084), or NG (0.849 ± 0.038), which had more than BCI (0.543 ± 0.104). In addition, relative abundance of different understory life-forms differed among sites (Fig. 1). There were relatively fewer woody dicots in the foliage profile at LS compared to other sites ($F_{4, 21} = 13.49$, $P = 0.0001$). Relative abundance of palms differed significantly among sites ($F_{4, 21} = 8.58$, $P < 0.001$). BCI had significantly fewer palms in the profile than KM41 and LS (Tukey's HSD, $P < 0.05$). NG

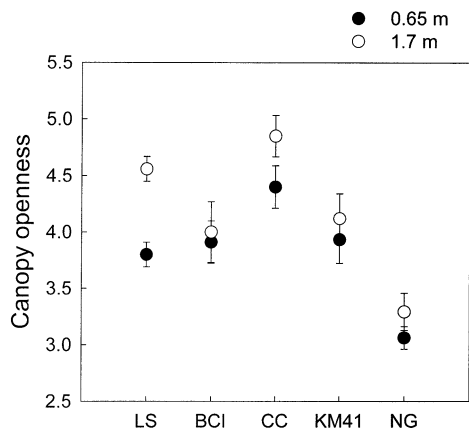


FIGURE 2. Canopy openness (\pm SE) calculated from hemispherical photographs taken at 0.65 and 1.7 m above the forest floor at five Neotropical forest sites. Each point is a mean for a single site. $N = 6$ at all sites except NG, where $N = 2$. Site codes follow those in Figure 1.

and CC were intermediate. Although KM41 and LS did not differ in relative abundance of palms in the profile, these sites did differ in the leaf morphology of the understory palm layer (Montgomery, per. obs.). LS had many bifid-leaved geonomid palms, whereas pinnate-leaved palms such as *Bactris elegans* dominated the KM41 understory (A. Oliveira, pers. comm.). LS had significantly higher relative abundance of herbs in the profile compared to other sites ($F_{4, 21} = 3.67$, $P < 0.05$; Tukey's HSD, $P < 0.05$). In general, ferns made up a small to nonexistent component of the profile at all sites. These data concur with a larger dataset of understory compositional differences among these five forests (Harms *et al.* 2004).

Sites differed significantly in light availability at both heights; however, ranking of sites changed with height (Fig. 2). At 0.65 m, NG had significantly lower light than CC, with LS, KM41, and BCI intermediate ($F_{4, 21} = 4.19$, $P < 0.05$). At 1.7 m, ranking changed; CC and LS had the highest light followed by KM41, BCI, and finally NG. In part, change in rank reflected the magnitude of decrease in light with height at each site. For LS, light decreased 16 percent between 1.7 and 0.65 m, 9 percent at CC, and only 2 percent at BCI ($F_{2, 41} = 4.23$, $P < 0.05$). These results differ somewhat from those presented by Harms *et al.* (2004) because that analysis did not include NG.

Across sites, light attenuation in the understory was positively related to the amount of understory foliage (Fig. 3A). As the number of leaves in the foliage profile increased, the difference between

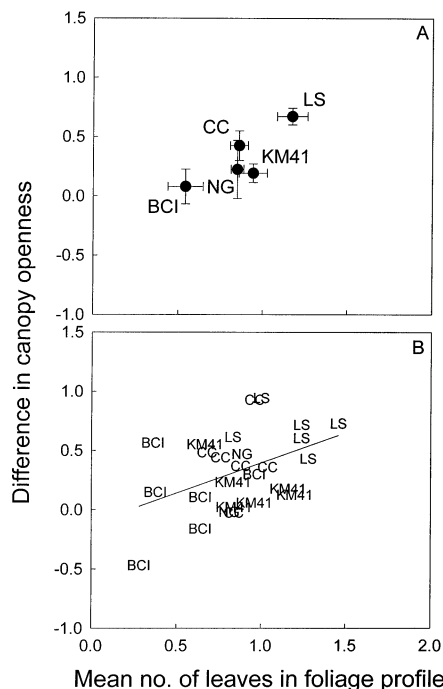


FIGURE 3. Relationship between mean number of leaves encountered in a vertical line transect between 0.65 and 1.7 m above the ground and light attenuation, measured as the difference in canopy openness between measurement heights. (A) Each point is a mean (\pm SE) for a site ($N = 6$ at all sites except NG, where $N = 2$). (B) Each point is a mean for a single transect ($N = 13$ per transect except NG, where $N = 53$). Site codes identify transects and follow Figure 1.

light availability at 0.65 and 1.7 m increased (Fig. 3B). When foliage profiles are categorized as no leaf, one leaf, or two or more leaves, there are significant negative effects of foliage on light within all sites ($F_{2, 433} = 9.64$, $P < 0.0001$). Across sites, sampling points with two or more foliage layers had significantly greater light attenuation than points with one or fewer layers ($P < 0.001$). Sites differed in patterns of light attenuation in all foliage categories (Fig. 4). At BCI there were significant differences between light at 0.65 and 1.7 m only at points with two or more foliage layers. At KM41, any point with one or more leaves in the profile had lower light than those without foliage. Interestingly, at LS and CC, all sampling points showed decreases in light from 1.7 to 0.65 m regardless of the number of foliage layers. This pattern may be related to the proportion of sampling points with zero, one, or two or more foliage layers, which differed among sites (Table 1). A greater per-

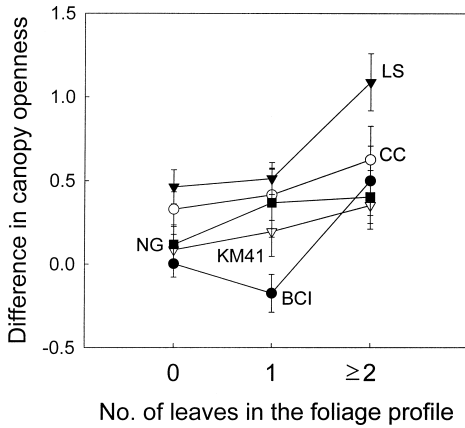


FIGURE 4. Light attenuation (difference in canopy openness between 0.65 and 1.7 m) as a function of sampling points that had none, one, or two or more foliage layers at five Neotropical forest sites. Each point is a mean light attenuation at a site and bars are SE. ($N = 78$ per site except NG, where $N = 106$). Site codes follow Figure 1.

centage of points had no foliage in the profile at BCI (66.4 %) than at the other sites (33.8–42.7%).

DISCUSSION

The understory vegetation of forests plays an important role determining local light environments through effects on the amount and pattern of light attenuation (Fig. 3; Conway *et al.* 1997; George & Bazzaz 1999a,b). Across five Neotropical forests, the amount of foliage between 1.7 and 0.65 m significantly decreased light availability at 0.65 m. The magnitude of decrease in light availability ranged from 2 percent at BCI (low foliage density) to 16 percent at LS (high foliage density). The declines within some sites were similar in magnitude to among-site differences at a single height. At 1.7 m, NG (lowest light site) had 32 percent lower light levels compared to CC (highest light site), despite the fact that the NG transects traversed canopy gaps. These data highlight the importance of studying the vertical distribution of light within forests. The rank order of sites based on light availability changed depending on measurement height. The light attenuation curves for individual sites crossed, and this difference in vertical distribution of light was related to understory foliage density. The gradient between 0.65 and 1.7 m was steepest at LS, whereas at BCI there was no gradient. Similarly, in a series of Florida sand pine scrub stands,

TABLE 1. Proportion of foliage profile sampling points that had zero, one, and two or more foliage layers at five Neotropical forest sites (La Selva Biological Station, Costa Rica = LS; Barro Colorado Island, Panama = BCI; Cocha Cashu Biological Station, Peru = CC; Kilometer 41 field camp, Brazil = KM41; $N = 149$ at each site; Nouragues, French Guiana = NG; $N = 106$).

Site	Foliage layers ^a		
	0	1	≥2
LS	33.8	32.4	33.8
BCI	66.4	18.8	14.8
CC	42.7	33.3	24
NG	59.4	15.1	25.5
KM41	35.1	39.9	25

^a Between 0.65 and 1.7.

shrub layer density was significantly negatively related to light availability at 0.5 m and the site with the sparsest shrub cover had the highest tree regeneration (Conway *et al.* 1997). Previous studies at LS showed significant decreases in light availability moving from 5 to 3 to 0.5 m above the forest floor (Chazdon 1986; Clark *et al.* 1996; Capers & Chazdon, in press) but no concurrent measures of vegetation were made. Chazdon (1986) argued that differences in light availability above and below 1.5 m were related to the high abundance of palms, many of which have crowns between 1 and 1.5 m. My results support her argument.

Site differences in light attenuation may have important implications for the selective environment of small tree seedlings. The steepness of the vertical light gradient near the forest floor could influence height growth strategies, seedling carbon balance, allocation patterns, and ultimately, patterns of long-term tree seedling demography. By acting as selective ecological filters, understory plants may influence spatial structure of seedling communities. In a New England forest, fern-free areas were dominated by *Betula alleghaniensis*, and recruitment under ferns was dominated by *Acer rubrum* and *Fraxinus americana* (George & Bazzaz 1999a). In addition, seedlings of some species were more abundant and had higher survivorship in fern-free areas (George & Bazzaz 1999a). In this study, the site with the steepest vertical gradient of light in the understory, LS, had significantly lower seedling densities than the other five sites (Harms *et al.* 2004).

The vertical gradient of light can also depend on the composition of the understory. The amount

of local shading near the ground may depend on the morphology of the foliage above the site. Smaller differences between light at different heights at KM41, despite similar density of foliage compared to LS, may result from the dominance of *Bactris* and other pinnate-leaved palms. In contrast, strong differences between heights at LS may be related to the abundance of bifid-leaved geomid palms. In Florida sand pine scrub, abundant palmettos (*Serenoa repens* [Bartram] Small and *Sabal etonia* Swingle ex. Nash) were associated with lower light availability near the forest floor (Conway *et al.* 1997).

Horizontally, spatial variation in the density of understory plants affects patterns of light availability. My results suggest that the light environment that a seedling experiences is related to the density of neighboring foliage. At LS and CC, and to a lesser extent at KM41, sampling points with no foliage still had significant differences in light between heights (Fig. 4). This pattern probably reflected dense foliage in the neighborhood of a sampling point. At LS, CC, or KM41, the chance that a point with no foliage had a neighboring point with intervening foliage was 60–65 percent. In contrast, at BCI the chance that the adjacent sampling point had foliage was only 30 percent.

Whereas numerous studies have examined the light environment of tropical forests (Chazdon & Fetcher 1984; Clark *et al.* 1996; Grove *et al.* 2000; Rijkers *et al.* 2000; Smith *et al.* 1992; Terborgh & Mathews 1999; Whitmore *et al.* 1993; Capers & Chazdon, in press), studies have varied in the height of measurement, the measure chosen to represent light availability, and the programs used for analyses. Furthermore, the observer bias inherent in the analysis of canopy photos makes evaluation across studies difficult. My estimates of light availability derived from hemispherical canopy photos appear to be higher than those of previous studies (Clark *et al.* 1996, Smith *et al.* 1992) reflecting a

combination of observer bias and a difference in photographic method employed. Digital images, as in this study, consistently give higher estimates of light than film images (Englund *et al.* 2000, Frazer *et al.* 2001). Nevertheless, to my knowledge, this study represents the first cross-site attempt in the tropics to quantify light availability using a standard method and a single observer. Thus, results are directly comparable among sites.

In summary, understory foliage density strongly influences light availability near the forest floor. Dense foliage can create vertical gradients in light availability near the forest floor and has the potential to significantly influence growth and survival of tree seedlings. These vertical gradients differ among sites and may influence the structure and composition of the seedling banks in these forests. Data presented here support work in temperate forests and point to the general ecological importance of the understory in forested ecosystems. Future studies of forest light environments need to address the impact of the understory, especially when trying to understand determinants of patterns in the abundance and density of canopy tree seedlings.

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LITERATURE CITED

- ANDERSON, M. C. 1966. Stand structure and light penetration. II. A theoretical analysis. *J. Appl. Ecol.* 3: 41–54.
- BONGERS, F., P. CHARLES-DOMINIQUE, P.-M. FORGET, AND M. THÉRY. 2001. Nouragues. Dynamics and plant–animal interactions in a Neotropical rainforest. Kluwer Academic, Dordrecht, The Netherlands.
- BROKAW, N. V. L. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. *Trop. Ecol.* 24: 194–200.
- BROWN, M. J., AND G. G. PARKER. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. For. Res.* 24: 1694–1703.
- CANHAM, C. D., A. C. FINZI, S. W. PACALA, AND D. H. BURBANK. 1994. Causes and consequences of resource heterogeneity in forests: Interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24: 337–349.

- CAPERS, R. S., AND R. L. CHAZDON. Rapid assessment of understory light availability in a wet tropical forest. *Ag. For. Meteorol.* (in press).
- CHAZDON, R. L. 1986. Light variation and carbon gain in rain forest understory palms. *J. Ecol.* 74: 995–1012.
- , AND N. FETCHER. 1984. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *J. Ecol.* 72: 553–564.
- CLARK, D. B., D. A. CLARK, P. M. RICH, S. WEISS, AND S. F. OBERBAUER. 1996. Landscape-scale evaluation of understory light and canopy structure: Methods and application in a Neotropical lowland rain forest. *Can. J. For. Res.* 26: 747–757.
- CONNELL, J. H., M. D. LOWMAN, AND I. R. NOBLE. 1997. Subcanopy gaps in temperate and tropical forests. *Aust. J. Ecol.* 22: 163–168.
- CONWAY, D. W., A. J. PARKER, AND K. C. PARKER. 1997. Understory light regime, shrub layer and sand pine (*Pinus clausa*) regeneration in four scrub stands. *Am. Midl. Nat.* 138: 84–96.
- DENSLow, J. S., E. NEWELL, AND A. M. ELLISON. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. *Biotropica* 23: 225–234.
- ENGLUND, S. R., J. J. O'BRIEN, AND D. B. CLARK. 2000. Evaluation of digital and film hemispherical photography and spherical densitometry for measuring forest structure. *Can. J. For. Res.* 30: 1999–2005.
- FRAZER, G. W., R. A. FOURNIER, J. A. TROFYMOW, AND R. J. HALL. 2001. A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. *Agric. For. Meteorol.* 109: 249–263.
- GENTRY, A. H. (Ed.). 1990. Four Neotropical rainforests. Yale University Press, New Haven, Connecticut.
- , AND L. H. EMMONS. 1987. Geographical variation in fertility, phenology, and composition of the understory of Neotropical forests. *Biotropica* 19: 216–227.
- GEORGE, L. O., AND F. A. BAZZAZ. 1999a. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. *Ecology* 80: 833–845.
- , AND ———. 1999b. The fern understory as an ecological filter: Growth and survival of canopy-tree seedlings. *Ecology* 80: 846–856.
- GROVE, S. J., S. M. TURTON, AND D. T. SIEGENTHALER. 2000. Mosaics of canopy openness induced by tropical cyclones in lowland rain forests with contrasting management histories in northeastern Australia. *J. Trop. Ecol.* 16: 883–894.
- HARMS, K. E., J. S. POWERS, AND R. A. MONTGOMERY. 2004. Variation in small sapling density, understory cover, and resource availability in four Neotropical forests. *Biotropica* 36: 40–51.
- KABAKOFF, R. P., AND R. L. CHAZDON. 1996. Effects of canopy species dominance on understory light availability in low-elevation secondary forest stands in Costa Rica. *J. Trop. Ecol.* 12: 779–788.
- MACGUIRE, D. A., AND R. T. T. FORMAN. 1983. Herb cover effect on tree seedling patterns in a mature hemlock–hardwood forest. *Ecology* 64: 1367–1380.
- MONTGOMERY, R. A., AND R. L. CHAZDON. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology* 82: 2707–2718.
- NICOTRA, A. B., R. L. CHAZDON, AND S. V. B. IRIARTE. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80: 1908–1926.
- NORMAN, J. M., AND G. S. CAMPBELL. 1989. Canopy structure. *In* R. W. Pearcy, H. A. Mooney, J. R. Ehleringer, and P. W. Rundel (Eds.). *Plant physiological ecology: Field methods and instrumentation*, pp. 301–325. Chapman and Hall, New York, New York.
- POWERS, J. S. 2004. New perspectives in comparative ecology of neotropical rain forests: Reflections on the past, present and future *Biotropica* 36: 2–6.
- PUTZ, F. E., AND C. D. CANHAM. 1992. Mechanisms of arrested succession in shrublands: Root and shoot competition between shrubs and tree seedlings. *For. Ecol. Manage.* 49: 267–275.
- RIJKERS, T., P. J. JAN DE VRIES, T. L. PONS, AND F. BONGERS. 2000. Photosynthetic induction in saplings of three shade-tolerant tree species: Comparing understory and gap habitats in a French Guiana rain forest. *Oecologia* 125: 331–340.
- SMITH, A. P., K. P. HOGAN, AND J. R. IDOL. 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24: 503–511.
- SMITH, L. L., AND J. L. VANKAT. 1991. Communities and tree seedling distribution in *Quercus rubra*- and *Prunus serotina*-dominated forest in southern Pennsylvania. *Am. Midl. Nat.* 126: 294–307.
- TAYLOR, A. H., AND Q. ZISHENG. 1988. Regeneration patterns in old-growth *Abies–Betula* forest in Wolong Natural Reserve, Sichuan, China. *J. Ecol.* 76: 1204–1218.
- TERBORGH, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* 126: 760–776.
- , AND J. MATHEWS. 1999. Partitioning of the understory light environment by two Amazonian treelets. *J. Trop. Ecol.* 15: 751–763.
- , AND K. PETREN. 1991. Development of habitat structure through succession in an Amazonian floodplain forest. *In* S. S. Bell, E. D. McCoy, and H. R. Mushinsky, (Eds.) *Habitat structure: The physical arrangements of objects in space*, pp. 28–46. Chapman and Hall, New York, New York.
- WHITMORE, T. C., N. D. BROWN, M. D. SWAINE, D. KENNEDY, C. I. GOODWINBAILEY, AND W. K. GONG. 1993. Use of hemispherical photographs in forest ecology—Measurement of gap size and radiation totals in a Bornean tropical rain-forest. *J. Trop. Ecol.* 9: 131–151.