Light and the Phenology of Tropical Trees

S. Joseph Wright, Carel P. van Schaik

American Naturalist, Volume 143, Issue 1 (Jan., 1994), 192-199.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at http://www.jstor.org/about/terms.html, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

American Naturalist is published by University of Chicago Press. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/ucpress.html.

American Naturalist
©1994 University of Chicago Press

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

http://www.jstor.org/
Thu Aug 23 13:48:31 2001

Vol. 143, No. 1 The American Naturalist January 1994

LIGHT AND THE PHENOLOGY OF TROPICAL TREES

S. JOSEPH WRIGHT* AND CAREL P. VAN SCHAIK†

*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, U.S.A., or Apartado 2072, Balboa, Republic of Panama; †Department of Biological Anthropology and Anatomy, Duke University, 3705 B Erwin Road, Durham, North Carolina 27705

Submitted March 18, 1992; Revised June 23, 1992; Accepted June 26, 1992

Abstract.—Tree phenologies from eight disparate tropical forests are consistent with the hypothesis that leaf and flower production have been selected to coincide with seasonal peaks of irradiance.

Plants that produce new organs when irradiance is maximal will realize two advantages. First, assimilation is greatest for a crop of new leaves before herbivory and senescence reduce leaf area and photosynthetic potential (Larcher 1973; Field 1987). Second, it is most efficient to transfer assimilates directly into growing organs rather than store them in different tissues first and mobilize and translocate them later (Chapin et al. 1990). Strong phenological selection results for light-limited understory plants, and in many deciduous forests understory plants produce leaves and flowers when the overstory is deciduous and understory irradiance is maximal (Janzen 1972). Seasonal variation in irradiance also occurs above forest canopies because of changes in cloud cover, day length, and solar angle. The effect on the phenologies of taller forest plants is unexplored. This article evaluates this effect for tropical forest trees.

Light-limited trees are predicted to produce new leaves and flowers during the season of maximal irradiance. Seed dispersal is not considered because its timing is confounded by selection for germination and seedling survival. Where rainfall seasonality is pronounced, dry-season drought constrains phenologies (Reich and Borchert 1984). Predictions are therefore evaluated separately for forests with strong rainfall seasonality. Tropical insect seasonality also increases with rainfall seasonality (Wolda 1988). Minimal insect activity and maximal irradiance often co-occur in the drier season, and the alternative hypothesis that reduced pest pressure selects for dry-season production is evaluated. First, however, two requisites for phenological selection are considered.

IRRADIANCE IN TROPICAL FOREST CANOPIES

Phenological selection requires predictable temporal variation in a limiting environmental factor. Correlations between plant performance and irradiance suggest

Am. Nat. 1994. Vol. 143, pp. 192–199.
© 1994 by The University of Chicago. 0003-0147/94/4301-0008$02.00. All rights reserved.

that light limits many tropical forest trees. Seed set increases with irradiance in Borneo (Wycherley 1973), the likelihood of a mast flowering increases with irradiance in peninsular Malaysia (van Schaik 1986), and trunk radial growth increases with irradiance in Surinam (Schulz 1960) and possibly Costa Rica (D. A. Clark and D. B. Clark, personal communication). These correlations are consistent with light limitation; however, co-varying environmental factors cannot be discounted.

Photosynthetic measurements also suggest that light limits many tropical forest trees. Photosynthesis by in situ canopy leaves becomes saturated with light at photosynthetic photon flux densities (PPFD) of 450–600 μmol m^{-2} s^{-1} for a wide variety of tropical forest trees (Oberbauer and Strain 1986; Pearcy 1987; K. Hogan, A. Smith, K. Winter, and G. Zotz, personal communication). Lower PPFD will limit photosynthesis. Radiant energy is extinguished exponentially with distance beneath forest canopies. Photosynthetically active radiation was reduced by 94% just 5 m into the canopy of a Puerto Rican wet forest (Johnson and Atwood 1970), and global radiation was reduced by 53% just 6 m into the canopy of a Malaysian rain forest (Yoda 1974; Aoki et al. 1975). More than 70% of PPFD measurements made for canopy leaves in tropical forests in Costa Rica and Australia were less than 400 μmol m^{-2} s^{-1} (Oberbauer and Strain 1986; Doley et al. 1987), and low PPFD associated with heavy cloud cover frequently limited wet-season photosynthesis by the canopy emergent *Ceiba pentandra* in central Panama (G. Zotz and K. Winter, personal communication). Self-shading, lateral shading by neighbors, and shading by lianas limit all but the uppermost leaves in tropical forests, and light interception by clouds can limit all leaves.

Predictable irradiance seasonality occurs throughout the tropics. Near the equator seasonal changes in cloud cover are a more important cause than seasonal changes in day length and solar angle (Miller and Feddes 1971; Hastenroth 1985). In central Panama, for example, global radiation averages 31% greater on the March equinox than on the September equinox because of seasonal changes in cloud cover (Windsor 1990). Global radiation averaged 50% greater in the highest than in the lowest month in a pantropical survey of 24 sites where forest is the potential vegetation (annual rainfall of more than 1,000 mm; compiled from Müller 1982). Irradiance seasonality controls seasonal variation in net primary production in tropical evergreen forests (Raich et al. 1991) and should be a strong selective pressure on phenology.

WEAKLY SEASONAL FORESTS

Weakly seasonal forests were defined to have minimum mean monthly rainfall of more than 60 mm. This criterion is widely used to identify tropical forests where seasonal water stress is unimportant (Schulz 1960; Nieuwolt 1977; Whitmore 1984) and is close to Walter's (1971) criterion of twice the average temperature. The null hypothesis that 25% of tree species center production in the three sunniest months was tested for four weakly seasonal forests for which species-level phenologies have been published. For the Ducke Forest Reserve in Brazil and Itabuna, Brazil, numbers of individuals with new organs were presented by month (Alvim and Alvim 1978; Alencar et al. 1979), and the the angle of the mean

vector was calculated. For La Selva, Costa Rica, and Piste St. Elie, French Guyana, the population-level presence or absence of new organs was presented by month (Frankie et al. 1974; Opler et al. 1980; Sabatier 1985), and the month on which production centered was calculated. These estimates of central tendency are problematical when production occurs in disjunct peaks and, for presence-absence data, when production continues for many months (arbitrarily set at more than 6 mo). Analyses were performed with and without these problematical cases. The 3-mo period with highest irradiance at Ducke, Piste St. Elie, and Itabuna was estimated from hours of sunshine for nearby weather stations at Manaus, Cayenne, and Salvador, respectively (Müller 1982). For La Selva, the assessment of Breitsprecher and Bethel (1990), which agreed with sunshine data for the three nearest weather stations (Coen 1983), was used.

The number of species that centered phenological activity during the 3 mo of peak sunshine was 1.35–2.88 times greater than expected, and the null hypothesis was invariably rejected (table 1). The effect became even stronger when the problematical cases defined above were included (not shown).

STRONGLY SEASONAL FORESTS

A strong contrast is expected between drought-sensitive and drought-tolerant species when irradiance is maximal during the dry season. Leaf and flower production are predicted to occur during the wet season for drought-sensitive species (Reich and Borchert 1984) and during the dry-season irradiance peak for drought-tolerant species. Rooting depths often separate drought-sensitive and drought-tolerant species. Rooting depths and phenologies have been documented in East Java and Venezuela at forested sites where irradiance is maximal during a 4- or 5-mo dry season. In East Java, species with shallow roots (less than 1.5 m) produced leaves in the wet season only (three species), while species with deeper roots produced leaves in the dry season only (six), year-round (two), or in the wet season only (two) (Coster 1923, 1932, 1933; Braak 1929). In Venezuela, deciduous species had shallow roots and produced leaves in the wet season only (eight) while evergreen species had deeper roots and produced leaves in the dry season only (three) or in the wet season only (one) (Monasterio and Sarmiento 1976; Sobrado and Cuenca 1979; Sobrado 1986). The null hypothesis that rooting depth and season of leaf production are independent is rejected ($G_{adjusted} = 6.75$, df = 1, $P < 0.01$; year-round and wet-season-only conservatively combined). Deeply rooted species tended to produce leaves during the dry-season irradiance peak.

The relation between phenology, irradiance, and drought sensitivity can be evaluated in greater detail for trees from Barro Colorado Island (BCI), Panama (9°9′N, 79°51′W). Minimum midday leaf water potentials (ψ_{min}) have been determined in the final month of the dry season for nine BCI tree species (Rundel and Becker 1987; Wright and Cornejo 1990; S. J. Wright, unpublished data) and are used to evaluate drought sensitivity. Comparisons of ψ_{min} are limited to subcanopy (at most 20 m tall) and canopy (30 m tall or taller) trees to minimize complications associated with vertical gradients in vapor pressure deficits and gravitational potentials. New leaves were scored as present or absent in 208 weekly censuses of

TABLE 1

OBSERVED AND EXPECTED NUMBERS OF TREE SPECIES THAT CENTER LEAF FLUSH AND FLOWERING IN THE 3-MO PERIOD OF MAXIMUM SUNSHINE FOR FOUR WEAKLY SEASONAL TROPICAL FORESTS

	Leaf Flush			Flowering		
Site	Observed	Expected	χ^{2a}	Observed	Expected	χ^{2a}
Ducke	14	6.75	10.4**	13	6.75	7.7*
La Selva[b]	54	18.75	89.3***	65	48.25	10.1**
Itabuna	. . .	. . .	. . .	12	6.5	6.2*
Piste St. Elie[b]	. . .	. . .	. . .	54	26.25	39.1***

NOTE.—Ellipses indicate that there are no data.

[a] For each contingency analysis, sample size is the expected value multiplied by four. Observed and expected values for the 9 mo of lower insolation equal the sample size minus the appropriate values from this table.

[b] Species with year-round production are excluded because the central tendency is arbitrary for population-level presence-absence data.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

focal trees (N = 8–46 tree-years), and flowers were scored as present or absent in 208 weekly censuses of 200 0.5-m^2 litter traps. Most lowland tropical trees open flowers for just 1 d, so anthesis and flower fall coincide closely (Primack 1985). Barro Colorado Island has a single dry season, and the transitions between seasons almost always occur in December and April–May (Windsor 1990). Daily photosynthetically active radiation (PAR) averages 48% greater in the dry season than in the wet season (fig. 1). Drought-tolerant species are predicted to produce leaves and flowers early in the dry-season PAR peak.

Observed and predicted phenologies agree closely (fig. 1). The canopy trees *Beilschmiedia pendula* and *Jacaranda copaia* and the subcanopy tree *Heisteria concinna* had the most favorable dry-season water status (largest ψ_{min}). Both leaf flush and flowering peaked between December and March for these species. The canopy trees *Dipteryx panamensis, Trichilia cipo,* and *Quararibea asterolepis* and the subcanopy tree *Faramea occidentalis* had the smallest ψ_{min} for their strata. Flowering occurred early in the wet season for all four species. Leaf flush was either largely restricted to the wet season (*D. panamensis, F. occidentalis*) or bimodal with peaks early in both seasons (*T. cipo, Q. asterolepis*). The soil dries slowly over the first half of the dry season on BCI (Windsor 1990; Wright 1991), and water stress may limit *T. cipo* and *Q. asterolepis* only late in the dry season (Rundel and Becker 1987). The canopy (*Prioria copaifera;* −2.19 MPa) and subcanopy (*Hirtella triandra;* −1.36 MPa) trees with intermediate ψ_{min} flushed leaves year-round and flowered in 11 or 12 mo (data not shown).

DISCUSSION

Tree phenologies from seven widely disparate tropical forests are consistent with the hypothesis that leaf and flower production have been selected to coincide

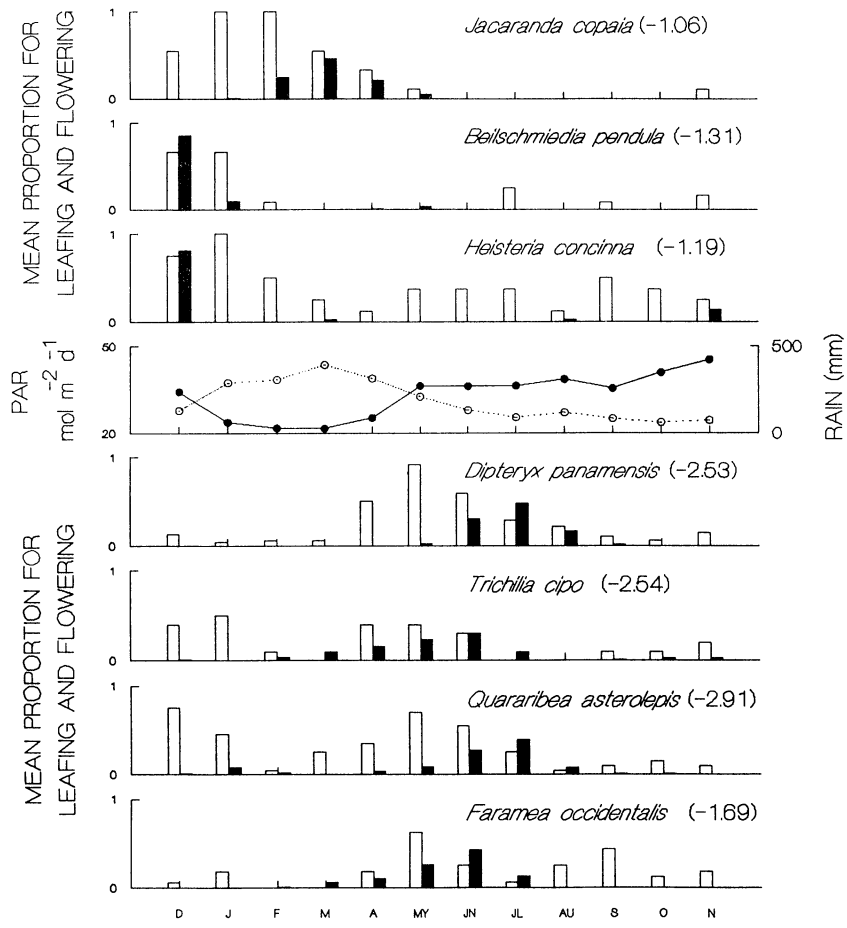

FIG. 1.—Tree phenologies, rainfall (*closed circles*), and PAR (*open circles*) for BCI. *Open histograms* represent the mean proportion of census individuals that flushed leaves (N = 4 yr). *Solid histograms* represent the mean proportion of annual trap records for flowers (N = 4 yr). *Numbers in parentheses* after species names are mean leaf water potentials (MPa) recorded at midday in the last month of the dry season ($N \geq 4$ individuals). The top three species had the largest values for their respective strata, the bottom four the smallest.

with peak irradiance when water is available. In each of these forests, however, peak irradiance occurs during the drier season, when the activities of most tropical insects are much reduced (Wolda 1988). The alternative hypothesis that leaf production and flower production have been selected to coincide with minimal insect pest levels must be considered (Lieberman 1982; Aide 1988).

The two hypotheses can be evaluated for forests where peak irradiance and peak insect activities coincide. This is the case at Makokou, Gabon, where the long dry season is cloudy and the number of sunshine hours and insect biomass average 2.1 and 3.9 times greater during the wetter months, respectively (Hladik 1973; Charles-Dominique 1977). Community-wide flowering and leaf production

by 33 of 34 tree species were also concentrated in the wet season (Hladik 1973, 1978). It is unlikely that water stress limits plants during the long dry season at Makokou because heavy cloud cover reduces evapotranspiration to its annual low, and leaf fall is also at its annual low (Hladik 1973, 1978). Selection on plant phenologies by insect pests is well established. Nevertheless, Makokou phenologies suggest a more important role for irradiance. Data are needed from additional forests where insect and irradiance seasonalities coincide to evaluate this possibility.

ACKNOWLEDGMENTS

We have benefited from discussions with J. Denslow, A. Herre, J. Karr, and J. Terborgh. O. Calderon and B. DeLeon conducted phenology censuses on BCI. Grants from the Environmental Sciences and Scholarly Studies programs of the Smithsonian Institution supported fieldwork on BCI.

LITERATURE CITED

Aide T. M. 1988. Herbivory as a selective agent on the timing of leaf production in a tropical understory community. Nature (London) 336:574–575.

Alencar, J. da C., R. A. de Almeida, and N. P. Fernandes. 1979. Fenologia de especies florestais em floresta tropical umida de terra firme na Amazonia Central. Acta Amazonica 9:163–198.

Alvim, P. de T., and R. Alvim. 1978. Relation of climate to growth periodicity in tropical trees. Pages 445–464 *in* P. B. Tomlinson and M. H. Zimmermann, eds. Tropical trees as living systems. Cambridge University Press, London.

Aoki, M., K. Yabuki, and H. Koyama. 1975. Micrometeorology and assessment of primary production of a tropical rain forest in West Malaysia. Journal of Agricultural Meteorology 31:115–124.

Braack, C. 1929. Het klimaat van Nederlandsch-Indie. I. Algemene hoofdstukken. Koninklijke Magnetisch en Meteorologisch Observatorium Batavia, Verhandelingen no. 8. Observatorium Batavia (Jakarta), Indonesia.

Breitsprecher, A., and J. S. Bethel. 1990. Stem-growth periodicity of trees in a tropical wet forest in Costa Rica. Ecology 71:1156–1164.

Chapin, F. S., III, E.-D. Schulze, and H. A. Mooney. 1990. The ecology and economics of storage in plants. Annual Review of Ecology and Systematics 21:423–447.

Charles-Dominique, P. 1977. Ecology and behaviour of nocturnal primates. Columbia University Press, New York.

Coen, E. 1983. Climate. Pages 35–46 *in* D. H. Janzen, ed. Costa Rican natural history. University of Chicago Press, Chicago.

Coster, C. 1923. Lauberneuerung und andere periodische Lebensprozesse in dem trockenen Monsun-Gebiet Ost-Javas. Annales du Jardin Botanique de Buitenzorg 33:117–189.

———. 1932. Wortelstudien in de tropen. I. De jeugdontwikkeling van een zeventigtal boomen en groenbemesters. Tectona 25:828–872.

———. 1933. Wortelstudien in de tropen. II. Het wortelstelsel op ouderen leeftijd. Korte Mededeelingen Boschbouwproefstation Buitenzorg, no. 31. Boschbouwproefstation, Buitenzorg (Bogor), Indonesia.

Doley, D., D. J. Yates, and G. L. Unwin. 1987. Photosynthesis in an Australian rainforest tree, *Argyrodendron peralatum,* during the rapid development and relief of water deficits in the dry season. Oecologia (Berlin) 74:441–449.

Field, C. 1987. Leaf-age effects on stomatal conductance. Pages 367–384 *in* E. Zeiger, G. D. Farquhar, and I. R. Cowan, eds. Stomatal function. Stanford University Press, Stanford, Calif.

Frankie, G. W., H. G. Baker, and P. A. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62:881–919.

Hastenroth, S. 1985. Climate and circulation of the tropics. Reidel, Dordrecht.

Hladik, A. 1978. Phenology of leaf production in rain forest of Gabon: distribution and composition of food for folivores. Pages 51–72 *in* G. G. Montgomery, ed. The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C.

Hladik, C. M. 1973. Alimentation et activité d'un groupe de chimpanzés réintroduits en forêt Gabonaise. Terre et la Vie 27:343–413.

Janzen, D. H. 1972. *Jacquinia pungens,* a heliophile from the understory of tropical deciduous forest. Biotropica 2:112–119.

Johnson, P. L., and D. M. Atwood. 1970. Aerial sensing and photographic study of the El Verde rain forest. Pages B-63–B-78 *in* H. T. Odum, ed. A tropical rain forest. Division of Technical Information, U.S. Atomic Energy Commission, Washington, D.C.

Larcher, W. 1973. Ökologie der Planzen. Ulmer, Stuttgart.

Lieberman, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. Journal of Ecology 70:791–806.

Miller, D. B., and R. G. Feddes. 1971. Global atlas of relative cloud cover 1967–70. Department of Commerce, Washington, D.C.

Monasterio, M., and G. Sarmiento. 1976. Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest of the Venezuelan llanos. Journal of Biogeography 3:325–356.

Müller, M. J. 1982. Selected climate data for a global set of standard stations for vegetation science. Tasks for vegetation science, no. 5. Junk, The Hague.

Nieuwolt, S. 1977. Tropical climatology. Wiley, Chichester.

Oberbauer, S. F., and B. R. Strain. 1986. Effects of canopy position and irradiance on the leaf physiology and morphology of *Pentaclethra macroloba* (Mimosaceae). American Journal of Botany 73:409–416.

Opler, P. A., G. W. Frankie, and H. G. Baker. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 68:167–188.

Pearcy, R. W. 1987. Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. Functional Ecology 1:169–178.

Primack, R. B. 1985. Longevity of individual flowers. Annual Review of Ecology and Systematics 16:15–37.

Raich, J. W., E. B. Rastetter, J. M. Melillo, D. W. Kicklighter, P. A. Steudler, B. J. Peterson, A. L. Grace, B. Moore III, and C. J. Vorosmarty. 1991. Potential net primary production in South America. Ecological Applications 1:399–429.

Reich, P. B., and R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. Journal of Ecology 72:61–74.

Rundel, P. W., and P. F. Becker. 1987. Cambios estacionales en las relaciones hídricas y en la fenologia vegetativa de plantas del estrato bajo del bosque tropical de la Isla de Barro Colorado, Panama. Revista de Biologia Tropical 35(suppl. 1):71–84.

Sabatier, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. Terre et la Vie 40:289–320.

Schulz, J. P. 1960. Ecological studies in northern Suriname. North-Holland, Amsterdam.

Sobrado, M. A. 1986. Aspects of tissue water relations and seasonal changes of leaf water potential components of evergreen and deciduous species coexisting in tropical dry forests. Oecologia (Berlin) 68:413–416.

Sobrado, M. A., and G. Cuenca. 1979. Aspectos del uso de agua de especies deciduas y siempreverdes en un bosque seco tropical de Venezuela. Acta Científica Venezolana 30:302–308.

van Schaik, C. P. 1986. Phenological changes in a Sumatran rain forest. Journal of Tropical Ecology 2:327–347.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver & Boyd, Edinburgh.

Whitmore, T. C. 1984. The tropical rain forests of the Far East. Oxford University Press, Oxford.

Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: long-term records for Barro Colorado Island, Panama. Smithsonian Contributions to the Earth Sciences 29:1–145.
Wolda, H. 1988. Insect seasonality: why? Annual Review of Ecology and Systematics 19:1–18.
Wright, S. J. 1991. Seasonal drought and the phenology of shrubs in a tropical moist forest. Ecology 72:1643–1657.
Wright, S. J., and F. H. Cornejo. 1990. Seasonal drought and leaf fall in a tropical forest. Ecology 71:1165–1175.
Wycherley, P. R. 1973. The phenology of plants in the humid tropics. Micronesica 9:75–96.
Yoda, K. 1974. Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. Japanese Journal of Ecology 24:247–254.

Associate Editor: F. Stuart Chapin III