BIOTROPICA
THE JOURNAL OF TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 40(6): 676–685 2008 10.1111/j.1744-7429.2008.00431.x

Modelling Direct Radiation and Canopy Gap Regimes in Tropical Forests

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ABSTRACT

Spatial and temporal variation in the below-canopy light environment of tropical forests is not well known and its measurement is technically challenging. Distributions of gap and understory areas in forests are likewise little known because of the resource requirements of forest structural censuses and a lack of consensus over how gaps should be defined. A basic model of forest structure, based on tree allometries from the 50 ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panama, and a solar positioning algorithm were used to predict spatial and temporal variation in the distribution of direct light at the forest floor. Predicted duration of direct sunlight was then compared with the distribution of gap and understory areas, delimited according to four standard gap definitions, giving predictions for the correspondence between direct light regimes and forest structure. At least 36 percent of the areas of gaps of all sizes was predicted to receive < 1 h of direct sunlight per day, and the understory to receive direct sunlight for ≥ 1 h per day in up to 15 percent of its area, even when not in proximity to gaps. The predicted distribution of light changed over the course of the year with the greatest spread of light throughout the forest floor coinciding with the months when maximum daily solar elevation peaked. These predictions suggest a partial decoupling of light regimes from canopy structure, with implications for gap definitions, patch models of forest development and current understanding of tree seedling recruitment patterns.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: field gap definitions; forest dynamics; gap models; habitat partitioning; Panama; patch models; treefall gaps.

Canopy gaps have long been considered a driving force behind the regeneration of tropical forests (Runkle 1985, Yamamoto 1992). The local disturbance that creates a canopy gap alters the microclimatic variables and light in the gap area, and thereby alters germination and growing conditions. For the seeds, seedlings and trees that survive gap formation, and for seeds that subsequently disperse into the gap, a successional sequence called 'gap-phase regeneration' then begins, culminating in one or more of them taking the place of the fallen canopy trees (Whitmore 1978, 1982; Orians 1982). The gap concept has been highly successful in explaining some of the patterns of species distribution in tropical forests (Brokaw 1985b, Hubbell & Foster 1986, Brokaw & Busing 2000) and is the background to much current research on the maintenance of tree species richness (*e.g.*, Hubbell 2004, Poorter 2005). Surprisingly, however, gaps have seldom been sampled exhaustively and delimited in a systematic way in large (> 20 ha) areas of tropical forest (but see Sanford *et al.* 1986, Popma *et al.* 1988, Jans *et al.* 1993, Green 1996).

The below-canopy light environment of a tropical forest is spatially heterogeneous (Turnbull & Yates 1993, Capers & Chazdon 2004). High-light areas (*e.g.*, central areas of large gaps) contrast with areas of low light (*e.g.*, clumps of tall trees in the understory), but there are many intermediate zones (Brown 1993, Montgomery & Chazdon 2002) and the light distribution varies over both days and seasons because of changes in sun angle (Canham 1988). Furthermore, spatial and temporal changes in photon flux density do not simply correlate with changes in other aspects of the light regime (Chazdon & Fetcher 1984, Machado & Reich 1999, Capers & Chazdon 2004). Although relatively well studied in temperate forests (Monteith & Unsworth 1990, Machado & Reich 1999), the radiation regime of a tropical forest has, like the gap distribution, seldom been characterized systematically across a large area or over a long period (but see Yoda 1974, Smith *et al.* 1992, Brown 1993, Turnbull & Yates 1993, Clark *et al.* 1996, Nicotra *et al.* 1999). It remains debatable to what extent gap and understory areas within a forest coincide with areas of high and low light availability.

The initial concept of a forest canopy 'gap' was as an area of disturbance created by a single treefall (Runkle 1985, Yamamoto 1992; *e.g.*, Fig. 1). The term gradually widened to include large branchfalls and multiple treefalls (Whitmore 1978, Brokaw 1982a, Orians 1982), spaces at different levels of the canopy (Hubbell & Foster 1986, Connell *et al.* 1997), and clearings formed by large disturbances (Brokaw 1985b, Whitmore & Burslem 1996). Both Runkle (1981, 1982) and Brokaw (1982a) recognized the need for a practical, field-based definition and gave two different procedures for delimiting 'canopy holes', which have been widely used, debated, and modified (see Table 1). However, no consensus yet exists among forest ecologists on which definition to use (for earlier reviews see Brokaw 1985b, Clark 1990, Jans *et al.* 1993).

The first gap definitions involved an assessment of aboveground vegetation structure only, which gave them the great advantage that they could be applied quickly and consistently in any forest. However, these definitions were quickly criticized as 'superficial' and not 'ecologically meaningful' (Swaine *et al.* 1987, Popma *et al.* 1988, Clark 1990) because they delimited areas much smaller than the ground-level physical environment modified by the canopy hole. To characterize this modified area requires an assessment of the light regime of the forest at a wide array of points and over a long period of time, which has seldom been undertaken (Turnbull & Yates 1993, Brown & Jennings 1996, Capers & Chazdon

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Received 20 December 2007; revision accepted 2 April 2008.

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FIGURE 1. A treefall gap (reproduced with permission from Hallé *et al.* 1978: Fig. 109), generally described as an 'inverted cone' (Hubbell & Foster 1986). Although approximately true for small gaps, the nonconvex spatial extent of most large gap areas complicates this simple picture (*q.v.* Fig. 2; a convex area is one where all curved edges and corners point outwards; Kreyszig 1978). Delimiting the gap area is not straight-forward: even in this idealized gap the horizontal position of the base of the gap-creating tree does not coincide with the center of vegetation disturbance on the ground (*cf.* Riéra 1982), the center of where there are no large standing trees (*e.g.*, ≥ 250 mm dbh, Runkle 1981) or the center of the canopy hole (*q.v.* canopy height thresholds in Table 1).

TABLE 1. *Four canopy gap definitions. The 'expanded gap' of Runkle (1981, 1982) was used in the form as modified by van der Meer et al. (1994)* (i.e., *without assuming all gaps are elliptical). Extended gap definitions that include an area of understory modified by the gap* (e.g., *the total affected area of Popma* et al. *1988, the penumbral areas of Chazdon 1988, Brown 1993, Whitmore 1996, the species expanded gap of Dubé* et al. *2001) were not used because they do not allow direct comparisons between different forests and different times*[*]. *Gap definitions based on a straight vertical projection of low canopy areas* (e.g., *< 10 m canopy; Welden* et al. *1991; or < 5 m; Dalling* et al. *1998, Hubbell* et al. *1999, Schnitzer* et al. *2000; the closest analogue to the gaps in patch models, Bugmann 2001) were not used because of their low resolution (e.g., gap areas multiples of 25 m^2) and their requirement for a substantial forest canopy census (available only in a very few sites in the tropics). The 'chablis' concept (Riéra 1982) was not used because of the difficulty of discerning in the field what disturbed vegetation is due to gap formation (van der Meer et al. 1994). Gaps have also been assessed by above-canopy techniques (Sanford* et al. *1986) and by hemispherical photography (canopy openness; Kennedy & Swaine 1992, Brown 1993), but these methods were not tractable using the simulation approach adopted here.*

	Method for delineating gap perimeter and measuring size[†], given a starting point away from overhead canopy with vegetation < 2 m (= the 'debris height threshold' implicit in Brokaw 1982a, taken to be common to all definitions)
BROKAW	Walk to the gap edge in the eight cardinal directions, where 'edge' means any vegetation[**] ≥ 2 m tall (= the canopy height threshold), join up the edge points[††], and calculate the area by summing triangle areas (Brokaw 1982a)
MODIFIED-RUNKLE (MR)	Walk to the gap edge in 16 directions, using a canopy height threshold of 20 m, and then walk to the base of the canopy tree found, join up the base points (there may be < 16 of them), and calculate the area by summing triangles (van der Meer *et al.* 1994)
GREEN	Proceed as for Brokaw, but using 16 directions rather than eight and a canopy height threshold of 3 m (Green 1996)
VAN DER MEER (VDM)	Proceed as for Brokaw, but using a canopy height threshold of 20 m (van der Meer & Bongers 1996b)

[*] Popma *et al.* (1988) used the distribution of pioneer species to define their 'total affected areas', but this is not applicable in forests containing cryptic pioneers (Hawthorne 1993) or long-lived pioneers (Finegan 1996), which can occur in the understory, and, additionally, make gap size dependent on recruitment levels of the species concerned, which vary between years. Penumbral areas are defined according to the light distribution, which varies both within and between years.

[†] A specific number of directions must be used: Brokaw's procedure specified at least eight (taken here to mean exactly eight, following van der Meer *et al.* 1994, Green 1996), and for the MR procedure 16 directions was found to be sufficient to encounter all surrounding canopy (> 20 m) trees.

[**] Do not ignore debris (unless below the canopy height threshold). It is difficult to assess whether some species of plant are alive or dead, especially shortly after gap formation when even detached stems and branches still retain green foliage (T. R. Marthews, pers. obs.), and much gap debris includes liana tangles up to 10 m high where individual stems may be rooted far from the point of assessment despite no obvious sign of growth (Schnitzer *et al.* 2000). Debris that has begun to decompose is certainly dead, but this refers to only a small fraction of gap debris and assessing decomposition in the field is also imprecise. Although Brokaw (1982a) did not mention whether debris should be ignored, his 'hole in the forest extending through all levels' is understood to mean an empty area through which above-canopy light penetrates, devoid of either living or dead vegetation.

[††] Note that if vegetation extends into the gap between two cardinal directions it will be included in the gap area (*e.g.*, vegetation ≥ 2 m is possible in a gap delimited by Brokaw's procedure).

2004). Such assessments are important because they allow models of understory light regimes, which are used to drive tree growth in many forest models (reviewed in Bugmann 2001), to be calibrated correctly.

In this study, four definitions of canopy gap were selected and used to describe forest structure (Table 1). The light regime of the forest was described in terms of the direct component of sky light only (*i.e.*, coming directly from the sun's disk and unmodified by transmission through foliage or leaf litter), which accounts for the majority of incident light intensity (Monteith & Unsworth 1990; *n.b.* in this study 'direct light' does not include sunflecks, which were too brief (duration < 1 h; Chazdon 1988) to be calculated using this method). Using a modeling approach, a 5-ha area of tropical forest was analyzed after calibration of the model using data from Panama and comparisons with other tropical forests. Thus, the gap-understory environment was characterized over a large area, over the course of a year and according to four different gap definitions, and was compared to direct sunlight availability calculated at each point, which would have been impractical in a field-based study. The following questions were addressed: (1) What is the predicted distribution of direct sunlight in this forest and how closely does it correspond to areas of gap and understory? (2) What are the consequences of these predictions for gap definitions and patch models of forest growth?

METHODS

Barro Colorado Island (BCI; 9°09′ N, 79°51′ W) is a 15.6 km^2 island in the Canal Zone of Panama administered by the Smithsonian Tropical Research Institute, and this area was used as the basis for model development. BCI supports a Tropical Moist Forest (Holdridge Life-Zone System, Holdridge *et al.* 1971) with a canopy 24.6 ± 9.5 m high (Fig. 2), approximately half of which has been undisturbed since at least *ca* 1600 (Foster & Brokaw 1982). Annual rainfall is 2644 ± 443 mm (mean ± SD; 1925–2005 data; T-ESP 2006). There are two seasons, a dry season (21 Dec to 4 May; mean dates 1954–2005; T-ESP 2006), when rainfall averages 2.1 mm/day, and a wet season, with rainfall 10.1 mm/day (1925–2005 data; T-ESP 2006).

FOREST SIMULATION.—A model called *FORLIGHT* (version 1.7) was written for this project using R (a GNU® freeware programming language, R Development Core Team 2006). *FORLIGHT* was designed to simulate a forest based on 2000 census data from BCI and used the *SolPos* algorithm (Rymes 1998) to calculate solar position, from which the below-canopy radiation regime (*i.e.*, above litter and herbs, but below trees) was calculated.

FORLIGHT used a square grid of 1-m^2 cells to simulate a 5-ha area of BCI, the cell size being an estimate of the area of ground where, from an average input of seeds, there would be only one eventual recruit of 10 mm dbh (Harms *et al.* 2000, Comita *et al.* 2007). On each run, a fresh simulated one-species forest was generated on the grid by placing trees of random dbh in the cells (0 or 1 per cell, *i.e.*, assuming that two stems of $\geq$ 10 mm dbh never occur in a 1-m^2 area on BCI). Diameter at breast height values were sampled directly from the distribution for all trees on the 50-ha Forest Dynamics Plot on BCI (four censuses 1985–2000; Condit *et al.* 2005). Trees were assumed to occur in each cell with a probability of 47.5 percent (over 1985–2000, there were a mean of 4752.7 stems $\geq$ 10 mm dbh per ha on the 50-ha plot). Note that this method did not simulate nonrandom variation in stem density within the simulation grid (*e.g.*, clumping), because, although individual species are often clumped on BCI, the forest as a whole is dominated by common, uniformly distributed species (Condit *et al.* 2000).

Tree height (stems assumed vertical), crown radius (crowns assumed cylindrical) and canopy depth (tree height minus height of lowest branch) were assumed to be functions of dbh according

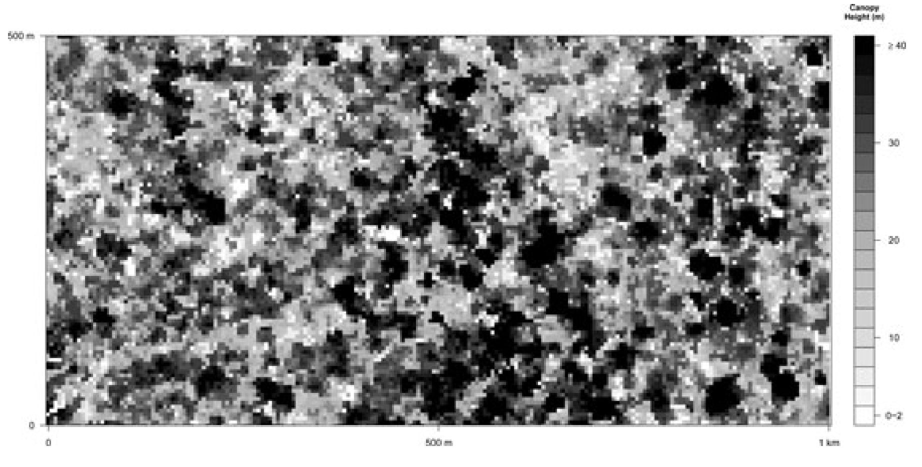

FIGURE 2. Canopy height on the 50 ha Forest Dynamics Plot on BCI in 2000 (Hubbell & Foster 1986; S. Hubbell, L. Comita & R. Condit, pers. comm.) showing the prevalence of irregular, nonconvex gaps on BCI (complex gaps *sensu* van der Meer *et al.* 1994). The mean ± SD height was 24.6 ± 9.5 m taking the $\geq$ 40 m class as 40 m (*i.e.*, an underestimate), with the principal mode at 29.5 m.

to allometric regressions derived from 1552 trees of 90 species on the BCI Forest Dynamics Plot (Chave *et al.* 2003; R. Condit, pers. comm.), with tree heights uniformly increased by 51 percent to bring the generated mean canopy height in line with measured values (Fig. 2):

$$(\textit{tree height in m}) = 68.1 \times (1 - \exp(-0.009D^{0.742}))$$

$$(\textit{crown radius in m}) = 24.8 \times (1 - \exp(-0.003D^{0.673}))$$

$$(\textit{canopy depth in m}) = 8.4 \times (1 - \exp(-0.008D^{0.944}))$$

($D =$ dbh in mm, parameters are abundance-weighted means over all species). This height increase corrects for the biases associated with tree leaning (crown plasticity *sensu* Purves *et al.* 2007; Strigul *et al.* in press) and local variation in these allometries, which remain unquantified on BCI. In a model of crown plasticity, Strigul *et al.* (in press) found that the standard deviation of crown join heights was reduced by 50 percent even when the maximum angle of lean was only 5° from vertical. Even a few leaning trees may have a large effect on mean canopy height, so this height correction was accepted as reasonable.

For calculating the Modified Runkle (MR) gap definition (Table 1), not only the canopy height had to be recorded over each cell, but also the co-ordinates of the stem base of the tree that produced the highest foliage, which is why actual heights from the BCI canopy census (Fig. 2) could not be used in the simulations. *FORLIGHT* included no gap creation subroutine because large-scale disturbances are infrequent on BCI (T-ESP 2006): gaps were simply an emergent feature of the tree placement procedure. *FORLIGHT* did not include any changes in topography over the simulation area because the BCI Forest Dynamics Plot varies only ± 20 m in altitude over 50 ha and the terrain varies gently over nearly all of this area. Gap shape and orientation were also not controlled so that the results could be taken as an average over all possible gap geometries.

IDENTIFYING GAPS AND SIMULATING THE LIGHT ENVIRONMENT.—A forest was simulated for each month in 2000. Gap centers in the simulation were identified using an algorithm that maximized mean distance from center to edge (radius) in each gap (Appendix S1), which was assumed to be approximately how Brokaw (1982a) chose 'a central point within the gap' by eye. Gaps were recorded from largest to smallest (≥ 4 m^2) separately for each gap definition (Table 1). For each hour from mean (over 2000) sunrise to mean sunset (0619–1820 h; Rymes 1998), the azimuth and angle of elevation of the sun were then calculated for each cell in the simulation grid and the hours of direct sunlight received by each cell over the simulation day (*i.e.*, not blocked by vegetation) were summed.

To produce a representative mean for all outputs, all simulations were repeated 10 times with different simulated forests. The simulation area was surrounded with a 25 m 'buffer' of extra forest to remove edge effects (= the mean height of the BCI canopy, Fig. 2; the buffer did not contribute to the output statistics). The 5-ha simulation area (plus 2.5 ha buffer), 1-h time step, and 10 repeats were dictated by memory constraints and the time available for simulation runs.

For each simulation of each month in 2000, and for each gap definition, the area A_{hk} was defined to be the area predicted to receive h hours of direct sunlight ($0 \leq h \leq 12$) within gaps of size class k ($0 \leq k \leq 4$ with $k = 0$ indicating understory and $k > 0$ the four gap size classes 4–20 m^2, 20–100 m^2, 200–400 m^2 and ≥ 400 m^2; *q.v.* Table 2), summed over all the gaps in that size class. These areas were then converted to percentages $P_{hk} = 100 \times \frac{A_{hk}}{B_k}$ of the area B_{k} ($= \sum_h A_{hk}$) of the simulation covered by gap class k (*n.b.* $\sum_k B_k = 5$ ha for each gap definition in each simulation). Assuming P_{hk} to be an exponential function of h at ground level (Yoda 1974; *i.e.*, P_{hk} follows an exponential probability distribution for h), the slope, m, and intercept, c, of a regression of $\log_{10}(P_{\mathrm{hk}})$ against h were then calculated, applying the constraint that each regression fit must give predicted areas that sum to the correct area B_{k} (the regression that satisfied the constraint with highest R^2 was chosen). This constraint meant that m and c could be written in terms of a single variable, S_{k}, defined as the percentage of B_{k} predicted to receive ≥ 1 h direct sunlight during the simulated day ($c = \log_{10}(100 - S_k)$ and $m = \log_{10}(\frac{S_k}{100})$ since $10^{13\mathrm{m}} << 1$). Taking the mean of S_{k} over the 10 regression fits for each month produced a measure of how illuminated the gaps of size class k were predicted to be.

In the results presented below, a *t*-test was used to compare the results of one month's $N = 10$ simulation runs with another unless the variances were dissimilar, in which case the nonparametric Wilcoxon test was employed to compare the two medians. Multiple pairwise tests that were *t*-tests or Wilcoxon tests depending on the variances are reported below as paired *t* or Wilcoxon tests.

MODEL EVALUATION.—Overall, the simulated gaps covered 1.3–1.5 percent of the forest area (Brokaw's definition), which corresponds well with field measurements from a range of tropical forests (Table 2). Simulated gaps were slightly smaller in size than measured gaps (Table 2), but some of these studies did not sample their forest areas exhaustively (*e.g.*, van der Meer *et al.* 1994, Green 1996), implying that representative gaps were chosen, and some applied a minimum gap size threshold of 20 m^2 rather than 4 m^2 (*e.g.*, Brokaw 1982a, Green 1996), which would also have excluded many small gaps (Table 2). Given the wide geographical spread and differences between the forests used for evaluation, the simulations provide an acceptable approximation of gap sizes and coverage, especially for gaps defined according to Brokaw's (1982a) method (Table 2).

The mean simulated basal area of trees ≥ 10 mm dbh was 32.0 m^2/ha and the mean dbh of all stems ≥ 1 cm dbh was 46.5 mm, which matched acceptably the actual basal area of 29.1 ± 1.7 m^2/ha and dbh of 45.0 ± 0.8 mm, respectively (mean ± SE; four censuses 1985–2000, Condit *et al.* 2005). Published turnover times (*e.g.*, Brokaw 1982a, b; Clark 1990; Hartshorn 1990), and their implied spatial coverage of gap, were not used to validate the model because rates of gap formation and closure are still unknown on BCI (Denslow 1987, van der Meer & Bongers 1996a, Fraver *et al.* 1998, Schnitzer *et al.* 2000).

TABLE 2. *Gaps found by FORLIGHT in 120 simulated forests of 5 ha each, and the land area covered by understory and gaps, compared to measurements from tropical forests (4–20 m^2 gaps included or excluded as appropriate for each field study). Gap size distributions[*] are given as (the % of gaps < 100 m^2 in size, % of gaps ≥ 400 m^2 in size) and coverages[*] are given as (the % of surveyed area in a gap [above the minimum size], % of surveyed area in gaps < 100 m^2 [but still $>$ the minimum size], % of surveyed area in gaps ≥ 400 m^2) (means over* N = *120 simulations).*

		Simulated		Measured	
Gap definition (Table 1)	Minimum gap size (m^2)	Gaps	Coverages	Gaps	Coverages
BROKAW	20	4.9 /ha (100%, 0%)	[1.3%, 1.3%, 0%]	4.9 /ha (73%, 0%)[a]	[4.2%, 1.8%[†], 0%][a]
				3.2 /ha (74%, 0%)[b]	[2.8%, 1.1%[†], 0%][b]
				3.8 /ha[†] (76%[†], 3%[†])[c]	[1.2%[†], 0.5%[†], 0.2%[†]][c]
	10	No model output		2.1 /ha (93%, 0%)[d]	[0.8%, 0.6%[†], 0%][d]
	5	No model output		18.0 /ha[†] (95%[†], 0.7%[†])[c]	[1.5%[†], 0.9%[†], 0.2%[†]][c]
	4	5.5 /ha (100%, 0%)	[1.5%, 1.5%, 0%]	0.9 /ha (78%, 0%)[e]	[0.5%, 0.2%, 0%][e]
				6.2 /ha (100%, 0%)[f]	[1.2%[†], 1.2%[†], 0%][f]
MODIFIED-RUNKLE (MR)	20	44.0 /ha (61%, 7%)	[71.4%, 16.4%, 22.5%]	No field results	
	4	45.3 /ha (62%, 7%)	[71.7%, 16.6%, 22.5%]	0.9 /ha (0%, 33%)[e]	[3.0%, 0%, 1.7%][e]
				6.2 /ha (19%, 14%)[f]	[15.2%[†], 0.6%[†], 5.7%[†]][f]
GREEN	20	12.7 /ha (100%, 0%)	[3.2%, 3.2%, 0%]	1.2 /ha (77%, 2%)[g]	[1.0%[†], 0.5%[†], 0.1%][g]
	4	19.1 /ha (100%, 0%)	[4.3%, 4.3%, 0%]	No field results	
VAN DER MEER (VDM)	20	33.8 /ha (70%, 5%)	[39.5%, 11.6%, 9.8%]	No field results	
	4	38.1 /ha (74%, 4%)	[40.3%, 12.4%, 9.8%]	2.6 /ha (61%, 3%)[f]	[3.3%[†], 0.7%[†], 0.4%[†]][f]

[*] Division into size classes is based on 100 m^2, the size below which the first year growth of pioneer plants is not significantly different from growth in the understory, and 400 m^2, above which not significantly different from open space (Brokaw 1985a, 1987; Dalling *et al.* 1998; but see Kennedy & Swaine 1992, Brown & Jennings 1996, Brokaw & Busing 2000). Use of the terms 'small' and 'large' is variable, *e.g.*, $>$ 150 m^2 gaps were large for Brokaw and Scheiner (1989) but $<$ 400 m^2 was small for Hartshorn (1980).

[†] Values estimated from data presented in the sources quoted (in Murray 1988, using the unbiased gap-size distribution).

[a] On BCI, August 1975–April 1980 (Brokaw 1982a).

[b] On BCI, August 1976–October 1978 (Brokaw 1982b).

[c] At Monteverde, Costa Rica, March 1982–March 1984 (Murray 1988).

[d] At Taï, Ivory Coast, July–September 1990 (Jans *et al.* 1993).

[e] At Nouragues, French Guiana (van der Meer *et al.* 1994).

[f] At Nouragues, April 1991 for Brokaw and MR, April 1991–December 1993 for VDM (van der Meer & Bongers 1996a).

[g] On Christmas Island, Indian Ocean, July 1988 (Green 1996).

RESULTS

The relationship between the predicted percentage of gap area illuminated and period of direct sunlight per day was a close fit to a negative exponential in every month of the year (4 gap procedures × 4 gap sizes × 12 mo × 10 simulations = 1920 constrained exponential regression fits: $R^2 > 0.67$ for gaps found using Brokaw's procedure, $R^2 > 0.68$ for MR, $R^2 > 0.53$ for Green's and $R^2 > 0.68$ for VDM), although the distribution showed some divergence from exponential during April and September as the area receiving 1 h direct sunlight widened to almost the area receiving 0 h. This model fit was sufficient to allow the analysis to proceed in terms of percentage area receiving direct sunlight (S values) calculated as described above.

MODEL PREDICTIONS.—The proportion of gap area predicted to be in shade ($<$ 1 h direct sunlight per day) differed according to the gap definition used and gap size. However, irrespective of the definition used, at least 36 percent of the area within gaps was in the shade (Fig. 3A, April) and, in all but 2 mo, more than 50 percent of the area within gaps was in the shade (Fig. 3). No matter which gap definition was considered, the understory was predicted to receive some direct sunlight during all months of the year except December–January, with up to 11–14 percent and 13–15 percent of understory points receiving $\geq$ 1 h direct sunlight in April and September, respectively (Fig. 3).

No matter which gap definition was used, gaps were predicted to receive significantly more light than the understory, but not in all months. The following P values refer to 192 paired t or Wilcoxon tests ($N = 10$ simulations), comparing log transformed S (percentage of simulation area predicted to receive $>$ 1 h of direct sunlight per day) between the gaps and the understory. As expected, more direct sunlight was predicted to be received in the 20–100 m^2 Brokaw and Green gaps than the understory all year

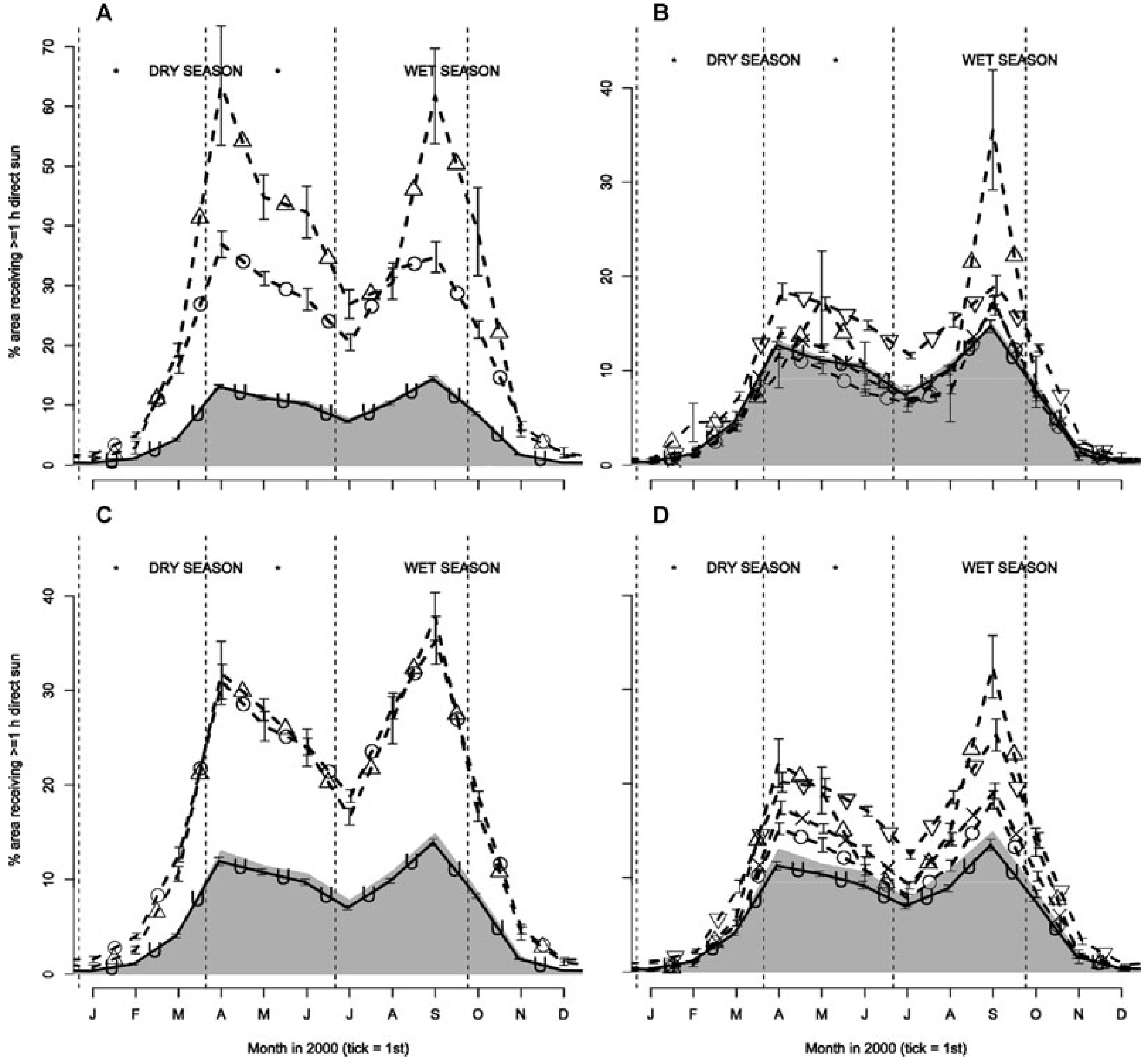

FIGURE 3. The percentage of area in the understory (U), 4–20 m^2 gaps (Δ), 20–100 m^2 gaps (O), 100–400 m^2 gaps (X) and ≥ 400 m^2 gaps (∇) predicted to receive ≥ 1 h direct sunlight during the first day of each month (mean ± SE; = S_k in text) when using the: (A) Brokaw; (B) Modified Runkle (MR); (C) Green; and (D) Van Der Meer (VDM) procedures (Table 1), with the percentage of total forest area shaded. For clarity, points are shown only by error bars and the symbols are placed on the lines between points, and all are slightly offset horizontally. Note the different vertical scale in (A). For reference, the vertical lines indicate the equinoxes (20 Mar, 23 Sep) and solstices (20 Jun, 21 Dec) for 2000 (Rymes 1998) and stars indicate the beginnings of the dry and wet seasons in 2000 on BCI (17 Jan and 10 May, T-ESP 2006).

round ($P < 0.004$ and $P < 0.002$, respectively, throughout the year), but in the same size class of MR or VDM gaps the model only predicted more direct sunlight in September (MR, $P < 0.001$) or during April–June and August–September (VDM, $P < 0.02$). In 100–400 m^2 gaps, significantly more direct sunlight than in the understory was predicted during April–May for MR gaps ($P < 0.05$) and March–October for VDM gaps ($P < 0.006$). For ≥ 400 m^2 gaps more direct sunlight was predicted than the understory all year except November for MR gaps ($P < 0.049$) and all year-round for VDM gaps ($P < 0.006$). The predictions for 4–20 m^2 gaps found by all gap procedures yielded no significant results.

DISCUSSION

SPATIAL VARIATION IN THE LIGHT REGIME.—Gaps are not uniformly illuminated (Canham *et al.* 1990). Even the gaps predicted to be the most brightly illuminated had more than 36 percent of their area out of the sun (< 1 h direct sunlight) in the brightest month (September) and the area of shade was usually over 50 percent. These within-gap gradients in the light environment are some of the known causes of gap partitioning among plant species (reviewed in Dalling *et al.* 1998, Brokaw & Busing 2000). The pattern of light availability in gaps is generally asymmetric (*e.g.*, Canham 1988), because it is dependent on latitude, and modified by variation in surrounding canopy height (Whitmore 1996), within-gap saplings and debris (Uhl *et al.* 1988, Brokaw & Busing 2000), and the nonconvexity of the gap itself (Turnbull & Yates 1993).

Understory areas are not uniformly shaded. The proportion by area of the understory predicted by this study to receive ≥ 1 h of direct sunlight in September was 13–15 percent, which was broadly in line with the measurements of Nicotra *et al.* (1999) for La Selva, Costa Rica (*cf.* 20–25 percent at Okomu, Nigeria, attributed to 'sunflecks' (all areas of direct sunlight) around midday; Evans 1956). Therefore, since the understory was predicted to cover up to 98.7 percent of the forest area (Brokaw's definition; Table 2), the majority of well-lit areas in the forest were predicted, unexpectedly, to occur outside gaps. Despite the 'closed' canopy, direct sunlight may enter the understory through infiltration, either by oblique 'sidelight' from gap areas nearby (Canham 1988, Brown 1993, Whitmore 1996, Brokaw & Busing 2000) or through spaces between treecrowns (*e.g.*, where a low canopy area is adjacent to a high canopy area, Clark *et al.* 1996, Terborgh & Mathews 1999). Lighter areas of the understory caused by infiltration from gaps may be distributed around the gaps themselves (*e.g.*, the 'penumbral' areas of Chazdon 1988, Brown 1993, Whitmore 1996), but illuminated areas created by canopy height differences would rather be concentrated in areas of high spatial variability in canopy height or, possibly, in areas of low stem density, which both occur throughout the understory (Fig. 2; Condit *et al.* 2000). Heterogeneity in within-understory direct sunlight regimes is a possible alternative explanation for the observed ecological partitioning of the understory by plant species (Brokaw & Scheiner 1989, Connell *et al.* 1997, Terborgh & Mathews 1999, Montgomery & Chazdon 2002).

TEMPORAL VARIATION IN THE LIGHT REGIME.—Direct sunlight received below the canopy was predicted to vary through the year. In December–January, both gaps and understory received low amounts of direct light and the difference between them was not significant. In April and September, the understory became slightly illuminated and the gaps significantly more so. These model predictions correspond to the 'moving window' of light availability (Nicotra *et al.* 1999) whereby the daily area of illumination tracks over different patches of the forest floor as solar position changes seasonally.

On BCI, maximum daily solar elevation is greatest (overhead) in April and September (minima of 75° and 57° in June and December; Rymes 1998) so the duration of direct sunlight penetrating the canopy and received at ground level is greatest during these months (Holmes 1981). Consequently, other factors aside, forest floors are most illuminated twice a year from the Equator toward the Tropics of Capricorn and Cancer (with peak illumination at the equinoxes on the Equator) and most illuminated only once beyond the tropics (at the summer solstice). This is consistent with the seasonal variation found by Turnbull and Yates (1993) at Gambubal, Australia (27°48′ S), where photon flux density in a gap site also correlated with solar elevation, showing a single annual maximum at the end of December.

CAVEATS.—This paper has used modeling to investigate the extent of coupling between canopy structure and direct light transmission to forest understories. Many factors have had to be excluded in order to make the computations tractable. For example, the effects on the understory light regime of species-specific light transmission through the canopy (Holmes 1981, Monteith & Unsworth 1990, Capers & Chazdon 2004), sunflecks (direct sunlight in the understory of duration generally < 1 h, Chazdon 1988, Canham *et al.* 1990), reflected and diffuse light (Holmes 1981, Canham 1988, Monteith & Unsworth 1990), debris and within-gap saplings ('advance regeneration'; Uhl *et al.* 1988, Brokaw & Busing 2000) and, specifically for BCI, deciduousness (Terborgh & Mathews 1999) and large-scale disturbances (Whitmore & Burslem 1996) were not included. Therefore, understory illumination may be even greater and more variable than predicted. Conversely, some species of tree can lean toward and obscure direct sunlight that would otherwise reach the forest floor (Purves *et al.* 2007; N. Strigul *et al.* in press) and the effects of cloud cover were not modeled (T-ESP 2006), so understory illumination may also be smaller and less variable than predicted. Analysis of these factors, and any effects of clumping and topography, await further model development and systematic surveys of understory light environments in sites where continuous records of solar radiation are available.

IMPLICATIONS FOR DEFINING GAPS.—The gap definitions used in this study (Table 1) all describe 'canopy holes' on BCI with reasonable success. However, the definitions of Brokaw and Green (Table 1) are difficult to apply in large gap areas because many of the plants that survive gap creation are > 2 m or > 3 m high. These procedures tend to either delimit an area of the gap that is much smaller than the canopy opening or divide the opening artificially into more than one gap. Additionally, the canopy height threshold of the MR and VDM definitions (Table 1) is too high to describe gaps in the forest of BCI because modal canopy height is not very much higher than 20 m (Fig. 2). From such a high viewpoint many gaps merge together to leave islands of emergent trees surrounded by a sea of 'gap' containing trees < 20 m tall.

In the absence of a comparative study between several tropical forests, the appropriate canopy height threshold to apply is difficult to judge. Presumably, a higher threshold would be suitable for higher-stature forests and a lower threshold for forests under edaphic constraint (*e.g.*, swamp forest), nutrient shortage (*e.g.*, heath forest), salt spray (*e.g.*, coastal dune forest), or a combination of inhibitory factors (*e.g.*, montane forest). A different canopy height threshold may even be required for different areas of the same forest, where, for example, contiguous riparian and nonriparian habitats have different mean canopy heights (Sanford *et al.* 1986).

Therefore, meaningful comparisons of gap regimes between forest types will only become possible when gaps are defined in relation to local estimates of mean canopy height.

Implications for patch models of forest growth.—Most models of forest growth take a 'patch' approach, dividing the simulated area into small spatial units with a uniform internal environment (reviewed in Bugmann 2001, Prentice *et al.* 2007; here called patch models rather than gap models to avoid confusion with field-based gap definitions). The 'Swiss cheese' nature of hard-edged patches has been noted many times (Lieberman *et al.* 1989, Publicover & Vogt 1991, Lieberman & Lieberman 1991) and it has proved difficult to model tree regeneration and migration adequately in patch models (Price *et al.* 2001), but the approach is widely used and has produced robust results (Prentice *et al.* 2007). As patch models achieve greater resolution (currently 100–1000 m^2; Bugmann 2001), however, the results of this study suggest that two complications arise:

1. When using field data from gaps for calibration and evaluation of patch models, it must be remembered that (a) 73–100 percent of natural gaps in tropical forests are $\leq$ 100 m^2 in size (Brokaw's definition; Table 2), so most gaps cannot yet be modeled realistically using patches, (b) larger gaps are almost always nonconvex (Fig. 2) unlike the gaps simulated in patch models, so larger gaps are modeled only approximately, and (c) in natural forests, gap definition heavily influences the shape and size of gaps found, which must be considered when using field data for model parameterization.
2. Most patch models assume that gaps are uniformly illuminated and the understory is uniformly shaded, or, at best, that understory illumination is restricted to a small area close to designated gaps (*e.g.*, Canham 1988). This study predicts that there are large areas of gap that do not receive direct sunlight on any day during the year (Canham *et al.* 1990), and also that there are areas throughout the understory that receive $\geq$ 1 h direct sunlight per day. Therefore, an improved characterization of light is required if natural gaps are to be modeled realistically in patch models.

Conclusions.—Using a basic forest canopy model and a solarpositioning algorithm, the likely temporal and spatial variation of light in an example tropical forest was calculated and compared to the gap distribution according to four standard definitions. Model predictions suggested that gaps are not uniformly illuminated (at least 36% by area in constant shade) and that the understory is not uniformly shaded (up to 15% in direct sunlight even when not in proximity to gaps). The temporal distribution of light depends on latitude, and varies, on BCI in Panama, from minimum illumination in December–January, when gap areas and understory areas are indistinguishable, to maxima in April and September, when solar elevation is at maximum. This partial uncoupling of gap and direct light regimes in time and space may account for frequent reports of the germination and emergence of seedlings of some pioneer species in tropical forest understories (*e.g.*, Hawthorne 1993, Brown & Jennings 1996, Finegan 1996).

Gap dynamics is still as much a 'leitmotif of research in both temperate and tropical forests' as it was 20 yr ago (Lieberman *et al.* 1989), but progress has been difficult, partly because of the lack of consensus on how to define gaps and the lack of systematic, field-based studies in tropical forests over a significant time period and spatial area. The spatial and temporal variability of tropical forest light regimes remains remarkably unknown, and there is a great need for further investigation. More precise characterizations of gap distributions and light variation in forests should lead to an improved understanding of gap-phase regeneration and, consequently, more realistic modeling of tropical forest environments.

ACKNOWLEDGMENTS

This research was supported by the Natural Environment Research Council (studentship to TRM and grant to DFRPB). We thank I. Perzia and the staff of the School of Biological Sciences at Aberdeen, especially B. Murray and N. Strachan for contributions to an earlier manifestation of *FORLIGHT* and M. Wattenbach for the use of his server. We thank the Smithsonian Tropical Research Institute staff and facilities on BCI, Panama, for support and J. Chave and two anonymous reviewers for comments on earlier drafts of this manuscript. Thanks to R. Condit for providing the BCI tree allometry data, to T. Toledo-Aceves, M. Swaine, B. Finegan, G. Murray and D. Purves for comments.

SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Appendix S1. Additional methods.

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