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AN INDEX FOR UNDERSTORY LIGHT LEVELS IN AND AROUND CANOPY GAPS¹

Charles D. Canham²

The importance of canopy gaps for the reproduction, growth, and survival of canopy and understory species has been widely documented (e.g., Pickett and White 1985). The responses of plants to canopy openings are usually attributed to an increase in resource availability and/or a decrease in resource competition following the death of an overstory tree. While there is uncertainty about whether the availability of water and soil nutrients increases in a gap (e.g., Vitousek and Denslow 1986), there is an obvious enhancement of understory light levels following the creation of an opening (Canham 1984, Chazdon and Fetcher 1984).

Although enhancement of understory light levels in gaps is readily apparent, it has been difficult to quantify the actual effects of an opening. Large diurnal and seasonal changes in the position of the sun produce dramatic changes in the amount of direct beam radiation received at a point in or around a gap. Thus, instantaneous or even integrated daily measurements of photosynthetically active radiation (PAR) have limited usefulness as indices of seasonal total light levels. Moreover, there is substantial spatial variation in understory light levels as a result of the geometry of shading by canopy trees adjacent to a gap, so that gap size is inadequate as an index of the amount of light received by plants at different locations in or around a gap.

Despite the often dramatic spatial and temporal variation in understory light levels, there are several predictable relationships between the geometry (size and shape) of a gap and the transmission of diffuse and direct PAR to any particular point in or around an opening (Canham 1984). Here these relationships are used to derive a gap light index (GLI) that specifies the percentage of incident PAR transmitted through a gap to any particular point in the understory over the course of a growing season. The gap light index was tested using data from two different gaps, and the application of the index is discussed using calculations from idealized openings.

Derivation and Test of a Seasonal Gap Light Index
The gap light index (GLI) is of the form

$$GLI = [(T_{diffuse} P_{diffuse}) + (T_{beam} P_{beam})] \cdot 100.0, \quad (1)$$

where $P_{diffuse}$ and P_{beam} are the proportions of incident seasonal PAR received at the top of the canopy as either diffuse sky radiation or direct beam radiation respectively $(P_{diffuse} = 1 - P_{beam})$, and $T_{diffuse}$ and T_{beam} are the proportions of diffuse and beam radiation, respectively, that are transmitted through the gap to a point in the understory. The index ranges form 0, when there is no clearly defined gap visible in the canopy, to 100 for a site in the open. Thus, the index specifies the contribution of the gap to the light regime at any given point in the understory, measured as a percent of the PAR received at an open site. The total amount of PAR received will, of course, also include light that penetrates through the canopy surrounding the gap. For the purposes of the derivation, a gap is described in terms of the spherical coordinates of the outline of the gap (i.e., the angle from vertical to the edge of the gap in each compass direction), with the coordinate system centered at a specified point in the understory. Thus, for any particular gap, there will be a unique set of gap coordinates for each point of interest in the understory.

If detailed records of diffuse and direct solar radiation are available for a nearby open site, $P_{diffuse}$ and P_{beam} can be calculated empirically. On the other hand, these terms depend on general features of climate, so that data from a single weather station should provide reasonable estimates for any location with a similar climate. Where direct measurements of P_{beam} and $P_{diffuse}$ are not available, there are a number of approaches for estimating these terms from more widely available meteorological data. A number of the techniques assume standard or idealized patterns of atmospheric scattering and the distribution of sky brightness (e.g., Hooper and Brunger 1980) and are unsuitable for integration over a wide range of cloud conditions. The most promising approach for estimation of seasonal values of P_{beam} and $P_{diffuse}$ is based on an empirical relationship between P_{beam} and atmospheric transmission coefficients (K_T) (i.e., K_T = the proportion of incident solar radiation above the atmosphere that is transmitted to the earth's surface; see Spitters et al. 1986). In general, the relationship is nonlinear, with P_{beam} for hourly or daily measurements falling to 0 when the sun is obscured by clouds and K_T is correspondingly low (i.e., <0.3). As K_T increases (i.e., more of potential solar radiation is transmitted by the atmosphere), P_{beam} increases rapidly and roughly linearly until both parameters reach maximum values in the range from 0.7 to 0.8 (Spitters et al. 1986). Daily and seasonal K_T values are available for weather stations throughout the United States (e.g., Knapp et al. 1980). Equations of the form given by Spitters et al. (1986) can then be used to calculate the overall seasonal values of $P_{diffuse}$ and P_{beam} from daily data for K_T by integrating over the growing season. As a much simpler approximation, mean regional K_T values for all but extremely cloudy climates will be very close to seasonal values for P_{beam} given the roughly linear relationship between K_T and P_{beam} over a wide range of atmospheric conditions.

The fraction of diffuse PAR transmitted by a gap $(T_{diffuse})$ is equivalent to the proportion of diffuse PAR that originates from the portion of the sky hemisphere visible within the gap. In general, the intensity of diffuse radiation is highly variable across the sky hemisphere at any given time (Iqbal 1983). Thus, instantaneous measurements of light levels beneath gaps can vary significantly over time depending on the brightness of the sky visible in the gap. There are a number of models for the distribution of sky brightness under standard, idealized conditions (Iqbal 1983) and a number of different approaches to modeling the penetration of diffuse radiation through forest canopies (e.g., Anderson 1964, Hutchison et al. 1980); however, there are no currently accepted models that specify integrated totals for diffuse radiation received from different areas of the sky hemisphere over the course of a growing season. Anderson (1964) used the standard overcast sky (SOC) approximation of Moon and Spencer (1942) in her early work on the penetration of diffuse radiation through forest canopies. That model assumed that the sky is brightest at the zenith, with sky brightness at the horizon dropping to roughly one-third of the zenith intensity. However, for periods of time when the sun is not near the zenith, the zenith can actually be the darkest portion of the sky hemisphere (Iqbal 1983). Thus, until a more accurate model for the seasonal distribution of sky brightness is available, it appears to be more reasonable to assume that the intensity of diffuse PAR is isotropic (uniform) across the sky hemipshere.

Even with the assumption of an isotropic distribution of diffuse radiation, the amount of diffuse radiation incident on a horizontal surface from any particular point in the sky hemisphere will depend on the cosine of the angle of the point from vertical (i.e., the cosine law). Thus, $T_{diffuse}$ can be estimated for any point in the understory as

$$T_{\text{diffuse}} = \sum_{i=a}^{b} \cos(A_i) / \sum_{i=1}^{N} \cos(A_i), \qquad (2)$$

where A_i is the angle to the center of a unit area of the sky hemisphere, and i = a..b are the areas inside the gap and i = 1..N represents the entire area of the sky hemisphere.

The final parameter required for the gap light index is T_{beam} , the proportion of direct beam radiation that penetrates through the gap, i.e.,

$$T_{beam} = (\%BEAM_{gap} \ GLOBAL_{gap}) /$$

$$(\%BEAM_{total} \ GLOBAL_{total}), \tag{3}$$

where $GLOBAL_{gap}$ and $GLOBAL_{total}$ are seasonal global radiation (combined diffuse and beam radiation) during times when the sun is either within the outline of the gap or for the total growing season, respectively, and $\%BEAM_{gap}$ and $\%BEAM_{total}$ are the percent of global radiation received as beam radiation during the two time periods respectively. In principle, T_{beam} can be calculated directly for any set of gap coordinates if beam radiation data are recorded on a short time interval (i.e., every 5-10 min) at a nearby monitoring station by comparing beam radiation totals during time periods when the sun is within the outline of the gap with beam radiation totals for the entire growing season. Such data, however, are rarely available, particularly near field sites. However, only two simple assumptions are required to calculate T_{beam} solely from gap coordinates. The first assumption is that $\%BEAM_{gap}$ is approximately equal to $\%BEAM_{total}$. This requires that the times of the day when the sun is within the outline of the gap have approximately the same degree of cloudiness and haziness as the day in general. While this is not generally true for any given day, it is much more reasonable for the entire growing season, particularly since gaps generally occur near the zenith. On this basis, T_{beam} is equivalent to $GLOBAL_{gap}$ GLOBALtotal Global radiation for any given time period (t = a..b) is approximately equal to

GLOBAL RADIATION =
$$I_o K_T \sum_{t=a}^{b} \cos(Z_t)$$
, (4)

where I_o is the solar constant for that integrated time period, K_T is the overall atmospheric transmission coefficient for the time period, and $\cos(Z_t)$ is the cosine of the zenith angle of the sun at time t. This leads to the second assumption, namely that the atmospheric transmission coefficient (K_T) for times when the sun is within the outline of the gap is approximately equal to the transmission coefficient for the whole growing season. Given the relationship between K_T and P_{beam} described above, the first and second assumptions are functionally equivalent. Thus, T_{beam} can be estimated

$$T_{beam} = \sum_{t=a}^{b} \cos(Z_t) / \sum_{t=1}^{N} \cos(Z_t),$$
 (5)

where t = a..b are the time periods (e.g., 5-min intervals) when the sun is within the gap, and N is the number of those intervals during the daylight hours of the growing season. Given the spherical coordinates of a gap, T_{beam} can be calculated using a microcomputer and standard equations for solar geometry.

The gap light index was tested using measurements of PAR over periods of 6–12 d at 30 points in and around two gaps and 12 points at random locations beneath the closed canopy of an old-growth oak-hem-

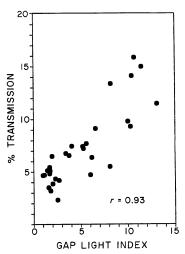


Fig. 1. Percent transmission of photosynthetically active radiation (PAR) to locations in and around canopy gaps vs. the gap light index (GLI) calculated for each point.

lock forest located at the Mary Flagler Cary Arboretum in southeastern New York (41°45' N, 73°44' W). The stand was located on a level stream terrace, and was dominated by hemlock (Tsuga canadensis [L.] Carr.), black birch (Betula lenta L.), and red oak (Quercus rubra L.). The 30 sample locations around the two gaps were chosen subjectively to cover the range of understory light levels in and around the gaps. Light levels were measured with quantum sensors (LI-190S, LI-COR) and monitored with data loggers (Model CR21X, Campbell Scientific). Open-site radiation was monitored with similar equipment 1000 m away in a large clearing. Atmospheric transmission coefficients (K_T) were computed by dividing open-site quantum flux by potential quantum flux above the atmosphere for the same time periods. The relationship between P_{beam} and K_T was examined by partitioning global PAR into diffuse and beam radiation using a shadow band with an appropriate correction factor (Drummond 1964).

On the assumption that most investigators will not have access to actual measurements of diffuse vs. beam radiation, K_T values were used as estimates of P_{beam} . Gap coordinates were digitized from fisheye photographs, and $T_{diffuse}$ and T_{beam} were calculated using Eqs. 2 and 5. The computed gap light index was then compared with the observed percent transmission of incident PAR using orthogonal regression (Sokal and Rohlf 1969).

For the 30 gap points, the functional relationship between observed light levels and the gap light index (Fig. 1) was

%
$$Transmission = 2.643 + 1.037 \ GLI$$

($r = 0.9294$). (6)

The slope of the line was not significantly different from 1.0 (95% CI = 0.899 - 1.196), and the intercept of the equation was not significantly different from the mean percent transmission of light to the 12 points randomly located beneath a closed canopy ($\bar{X} = 2.688, t = 0.139,$ P > .5). Thus, the percent of open-site PAR received in the understory was approximately equal to the percent transmission of PAR by a closed canopy plus the value of the GLI calculated on the basis of gap geometry. The gap light index thus provided a reasonably accurate index of the relative increase in understory light levels produced by the canopy gaps. The present derivation of GLI differs slightly from a previous derivation (Canham 1984), although the two formulations give almost identical results for a given set of gap coordinates.

Application and Implications of the Gap Light Index

The power of the gap light index lies in the ability to easily determine the contribution of a canopy opening to the seasonal light regime at any particular point in the understory. Its utility is generally limited to sites in which an intact canopy is uniform enough for discrete gaps to be recognized. Appropriate sites include any location, such as a stream corridor or forest clearing, where there are discrete openings in a plant canopy. By relying on relationships between light levels and canopy geometry, the index can be computed without recourse to the cumbersome (and expensive) task of measuring seasonally integrated light levels at many different locations in the understory. The gap coordinates required for the computation of the index can be recorded in several ways. The most accurate is through an appropriately oriented, 180° fisheye photograph. However, for relatively simple gaps, the coordinates can also be recorded through the use of a compass and a clinometer. Either technique allows an investigator to determine the gap light index for any desired location in or around a gap.

Since the gap light index is solely a function of the geometry of the opening above a particular point (given an appropriate value of P_{beam}), the index can be used to explore the effects of gap and solar geometry on understory light levels in and around hypothetical gaps. As an example, I have assumed a gap shaped as a cylinder of 5 m radius in a 25 m tall canopy, with a canopy thickness of 10 m. These values approximate the dimensions of an average-sized single-tree gap in an old-growth northern hardwood forest (Runkle 1982). Calculations were done for gaps of these dimensions of two latitudes (36° N, i.e., the southern Appalachians, and 44° N, i.e., the Adirondack Mountains of New York) and for three topographic positions (level, 15° north slope, and 15° south slope). A growing season from 1 May to 31 September and $P_{beam} = 0.5$ were used for both latitudes. The calculations ignore the effects of shading by understory trees and shrubs, and were done using a PASCAL program written for a microcomputer (Compaq).

The calculations illustrate that even a single-tree gap can have effects that extend well beyond the vertical projection of the gap (Fig. 2) and support Runkle's (1979, 1982) emphasis on the "extended" gap rather than simply the projected gap. For a 5 m radius gap (78.5 m² projected area), the area of the understory with light levels high enough for release of suppressed saplings of shade-tolerant species may be several times as large as the projected area of the gap (Fig. 2) (Canham 1984). In contrast, gap-phase or shade-intolerant species that require much higher light levels could be limited to an area that is actually smaller than the projected area of the gap. This implies that calculations of canopy turnover times based on projected gap size will not necessarily be appropriate as estimates of the interval of time between effective releases of saplings suppressed in the understory (Canham 1985).

The calculations also illustrate the potential for significant variation in seasonal total light levels across very short distances beneath even small gaps. For instance, assuming a 4% transmission of PAR through a closed canopy, the effects of a 5 m radius gap at 36° N could range from a 25 to 200% increase in total PAR (i.e., *GLI* values of 1–8) for locations within 5 m of each other (Fig. 2).

While differences in slope and aspect produced expected differences in the spatial pattern of GLI values, the variation between the three different topographic positions for a given latitude was not as striking as the overall variation due to differences in latitude (Fig. 2). These simple latitudinal differences in gap light regimes may explain the apparent latitudinal difference in the importance of small, single-tree gaps for the reproduction of yellow birch (Betula lutea Michx.), one of the common gap-phase species of northern hardwood forests. While yellow birch saplings appear to successfully colonize and fill single-tree gaps in old-growth forests of the southern Appalachians (36° N) (Barden 1979, Runkle 1979, 1982), they are very rare in comparably sized gaps in old-growth stands in the upper Midwest (46° N) or the Adirondack Mountains of New York (44° N) (C. Canham, personal observation). At these higher latitudes, yellow birch saplings that became established in the relatively high light regimes north of the projected gap would move out of the high light levels as they grew taller and into the more heavily shaded areas directly beneath canopy trees adjacent to the gap. In contrast, yellow birch saplings that became established in comparable light levels just south of the north edge of a small single-tree gap in the southern Appalachians would experience increasing light levels

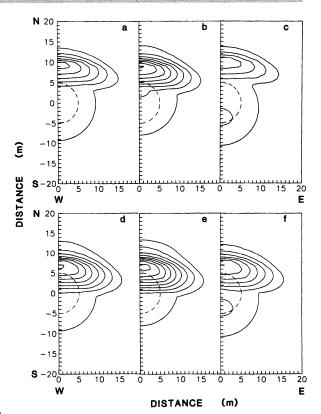


FIG. 2. Contour maps of *GLI* values (proportion of incident PAR) at the forest floor in and around 5 m radius gaps. The outline of the projected gap is shown with a dashed line. (a) 44° N, level slope; (b) 44° N, 15° south slope; (c) 44° N, 15° north slope; (d) 36° N, level slope; (e) 36° N, 15° south slope; (f) 36° N, 15° north slope. Only the eastern half of each gap is shown since the patterns are symmetrical around the north-south axis.

as they grew taller within the projected outline of the gap.

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- ¹ Manuscript received 8 September 1987; revised 20 December 1987; accepted 12 February 1988. ² Institute of Ecosystem Studies, New York Botanical Garden, Mary Flagler Cary Arboretum, Millbrook, New York 12545 USA.

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ERRATUM

In an article by F. Stuart Chapin III et al. ("Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing water," *Ecology* **69**(3):693–702) the first full sentence on page 694 should read:

An experimental decrease in soil water reduced the net carbon storage by intact cores of tundra vegetation and soil in laboratory microcosms (Billings et al. 1982).

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