

Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests

CHARLES D. CANHAM

Institute of Ecosystem Studies, New York Botanical Garden, Mary Flagler Cary Arboretum, Box AB, Millbrook, NY 12545, U.S.A.

JULIE S. DENSLOW

Department of Biology, Tulane University, New Orleans, LA 70118, U.S.A.

WILLIAM J. PLATT

Department of Botany, Louisiana State University, Baton Rouge, LA 70803, U.S.A.

JAMES R. RUNKLE

Department of Biological Sciences, Wright State University, Dayton, OH 45435, U.S.A.

TOM A. SPIES

USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, OR 97331, U.S.A.

AND

PETER S. WHITE

Department of Biology, University of North Carolina, Chapel Hill, NC 27524, U.S.A.

CANHAM, C. D., DENSLOW, J. S., PLATT, W. J., RUNKLE, J. R., SPIES, T. A., and WHITE, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**: 620-631.

Light regimes beneath closed canopies and tree-fall gaps are compared for five temperate and tropical forests using fish-eye photography of intact forest canopies and a model for calculating light penetration through idealized gaps. Beneath intact canopies, analyses of canopy photographs indicate that sunflecks potentially contribute 37-68% of seasonal total photosynthetically active radiation. In all of the forests, potential sunfleck duration is brief (4-6 min), but the frequency distributions of potential sunfleck duration vary because of differences in canopy geometry and recent disturbance history. Analysis of the photographs reveals that incidence angles for photosynthetically active radiation beneath closed canopies are not generally vertical for any of the forests, but there was considerable variation both among and within sites in the contribution of overhead versus low-angle lighting. Calculations of light penetration through idealized single-tree gaps in old growth Douglas-fir - hemlock forests indicate that such gaps have little effect on understory light regimes because of the high ratio of canopy height to gap diameter. However, single-tree gaps in the other four forest types produce significant overall increases in understory light levels. There is also significant spatial variation in seasonal total radiation in and around single-tree gaps. Our results demonstrate that there can be significant penetration of light into the understory adjacent to a gap, particularly at high latitudes. As gap size increases, both the mean and the range of light levels within the gap increases, but even in large gaps (ca. 1000 m²) the potential duration of direct sunlight is generally brief (<4 h). The major differences in gap light regimes of the five forests are largely a function of canopy height and latitude. The effects of latitude should also result in differences in gap light regimes across the geographic range of individual forest types.

CANHAM, C. D., DENSLOW, J. S., PLATT, W. J., RUNKLE, J. R., SPIES, T. A., et WHITE, P. S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20** : 620-631.

Les régimes lumineux sous couvert fermé et dans des trouées dues à la chute des arbres dans cinq forêts tempérées et tropicales ont été comparés à l'aide de la photographie panoramique des couverts forestiers intacts et d'un modèle pour calculer la pénétration de la lumière à travers des ouvertures idéales. Sous couvert intact, l'analyse des photos indique que les petites percées de lumière représentent jusqu'à 37 à 68% du rayonnement saisonnier total utile pour la photosynthèse. Dans toutes les forêts, la durée potentielle des petites percées de lumière est courte (4 à 6 min), mais les distributions de fréquence de la durée potentielle de ces percées varient à cause des différences dans la géométrie du couvert et l'histoire des perturbations récentes. L'analyse des photos révèle aussi que l'angle d'incidence du rayonnement utile pour la photosynthèse sous couvert fermé n'est généralement pas vertical pour aucune des forêts, mais il y avait des variations considérables, à la fois entre et dans les stations, dans la proportion du rayonnement vertical par rapport au rayonnement à faible angle d'incidence. Les calculs de pénétration de la lumière par des trouées idéales créées par l'absence d'un seul arbre, dans une vieille forêt de Sapin de Douglas et de Pruche, indiquent que ces trouées ont peu d'effet sur le régime lumineux en sous-étage, à cause du rapport élevé entre la hauteur du couvert et le diamètre de ces trouées. Dans les quatre autres types de forêt cependant, les trouées causées par l'absence d'un arbre entraînaient une augmentation générale des niveaux de lumière en sous-étage. Il y a aussi une variation spatiale importante du rayonnement saisonnier total dans et autour de ces trouées. Nos résultats démontrent qu'il peut y avoir une pénétration importante de lumière en sous-étage à proximité d'une trouée, particulièrement aux latitudes élevées. À mesure que la dimension d'une trouée augmente, la moyenne et l'étendue des niveaux de lumière dans la trouée augmente, mais même dans les grandes trouées (environ 1000 m²), la durée potentielle d'ensoleillement direct est généralement brève (<4 h). Les principales différences dans le régime lumineux des trouées entre les cinq types de forêt sont en grande partie fonctions de la hauteur du couvert et de la latitude. De plus, les effets de la latitude devraient provoquer différents régimes lumineux dans un même type de forêt selon son étendue géographique.

[Traduit par la revue]

Introduction

The importance of canopy gaps for the dynamics of forest ecosystems has been widely documented (e.g., Brokaw 1985; Runkle 1985). While canopy gaps may alter many features of understory microenvironments (e.g., Minckler et al. 1973; Vitousek and Denslow 1986), their most obvious effects are on understory light regimes. There has been a great deal of research on both canopy disturbance regimes and the responses of individual species to gaps; however, there has been remarkably little research on the nature of forest light regimes in and around gaps in comparison with light regimes beneath closed canopies (March and Skeen 1976; Pearcy 1983; Chazdon and Fetcher 1984; Canham 1984, 1988b). It is clear that there can be significant spatial and temporal heterogeneity in gap light regimes (Canham 1988b). However, the lack of quantitative, comparative studies has limited our ability to evaluate the importance of this heterogeneity.

Advancements in the measurement of photosynthetically active radiation (PAR) have made it feasible to conduct detailed studies of temporal and spatial heterogeneity in understory light regimes on time scales of seconds–days (e.g., Pearcy 1983; Chazdon and Fetcher 1984). However, for comparative autecological studies, longer term studies of variation over entire growing seasons are necessary. Given the dependence of instantaneous light measurements on conditions unique to the time of measurement (i.e., cloud conditions and solar position), results from short-term studies cannot be readily used for interpretation of seasonal patterns. However, there are a number of indirect techniques for evaluating the transmission of PAR through either a closed forest canopy or a discrete gap over the course of a growing season (e.g., Chazdon and Field 1987; Canham 1988b).

In this paper, we present the results of a comparative study of understory light regimes in five temperate and tropical forests. We use fish-eye photography of intact forest canopies and a model for calculating light penetration through idealized gaps to examine spatial and temporal variation in understory light levels in response to canopy structure, gap geometry, topography, and latitude.

Methods

Study areas

Our study areas are (i) an old-growth Douglas-fir – hemlock forest at the H.J. Andrews Experimental Forest in the Cascade Mountains of the northwestern United States, (ii) Hueston Woods, an old-growth northern hardwood forest in southwestern Ohio, (iii) a montane red spruce – balsam fir forest in Great Smoky Mountain National Park of the Appalachian Mountains of the eastern United States, (iv) Woodyard Hammock, an old-growth mixed southern hardwood forest at the Tall Timbers Research Station in the southeastern United States, and (v) a tropical rain forest at the LaSelva Biological Station in the Atlantic lowlands of Costa Rica (Fig. 1).

The Douglas-fir – hemlock site is dominated by emergent Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a uniform subcanopy of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). The northern hardwood site is dominated by a uniform canopy of beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.), whereas the spruce–fir site is dominated by a more patchy canopy of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.). The southern hardwood site is

characterized by a canopy of magnolia (*Magnolia grandiflora* L.) and beech. The tropical rain forest site is typically diverse (ca. 350 tree species), with *Pentaclethra macroloba* (Willd.) O. Ktze. (Leguminosae) as the canopy dominant. The sites range from 10 to 44°N latitude (Table 1). Average canopy heights in mature stands range from 25 to 70 m, and the length of the growing season ranges from 137 to 365 days (Table 1). Both the spruce–fir and southern hardwood sites were subject to widespread but diffuse disturbance prior to this study. Infestation by the balsam wooly adelgid has caused significant mortality among canopy balsam fir in spruce–fir forests of the southern Appalachian Mountains, and a hurricane in 1985 removed 10–15% of the overstory trees at the Woodyard Hammock site. The sites are described in more detail by Platt and Hermann (1986), Denslow and Gomez Diaz (1990), Runkle (1990), and Spies et al. (1990).

Calculation of light penetration through canopy gaps

Seasonal changes in the sun's path produce dramatic seasonal changes in the amount of direct-beam radiation received at any point in or around a gap. Thus, instantaneous or even integrated daily measurements of PAR have very limited use as indices of seasonally integrated light levels in gaps. However, there are predictable relationships between the geometry of a canopy opening and the transmission of incident PAR to any point beneath the gap. A gap light index (GLI), which specifies that percentage of incident PAR transmitted through a gap to any particular point in the understory over the course of the growing season, can be computed as

$$[1] \quad GLI = [(T_d P_d) + (T_b P_b)]100.0$$

where P_d and P_b are the proportions of incident seasonal PAR received at the top of the canopy as either diffuse sky radiation or direct-beam radiation, respectively, and T_d and T_b are the proportions of diffuse and direct-beam radiation, respectively, that are transmitted through the gap to a point in the understory (for our purposes, understory refers to any location near the forest floor, without regard to whether there is a gap or a closed canopy directly overhead) (Canham 1988b). The index ranges from 0, when there is no clearly defined gap visible in the canopy, to 100 for a site in the open. Thus, the index calculates the contribution of a gap to the light regime for any given point in the understory, measured in units of the percent of PAR received in the open. For the purposes of the calculations, 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 location in the understory.

There are a number of approaches for calculating the terms in the equation for GLI. For our calculations, we have used the methods described in Canham (1988b). On the basis of published data on atmospheric transmission coefficients (Knapp et al. 1980), P_d and P_b were set equal to 0.5 for all sites (i.e., incident radiation was split evenly between diffuse and beam radiation). Individual sites and actual measurements in any given year will deviate slightly from this estimate. However it is the most reasonable estimate for long-term comparisons among the sites. T_d and T_b were calculated from equations given in Canham (1988b), with calculations for solar geometry iterated every 5 min each day during the growing season.

In effect, the calculation of the effect of a gap on understory light levels is reduced to the calculation of the percent of open-site PAR that originates from the portion of the sky hemisphere visible within the gap. This is a unique function of the geometry of the outline of the gap, latitude, and the time of the growing season. For the purposes of this study, we have used calculations of light penetration through idealized gaps. The hypothetical gaps consist of cylinders of a specified radius through canopies of a given height

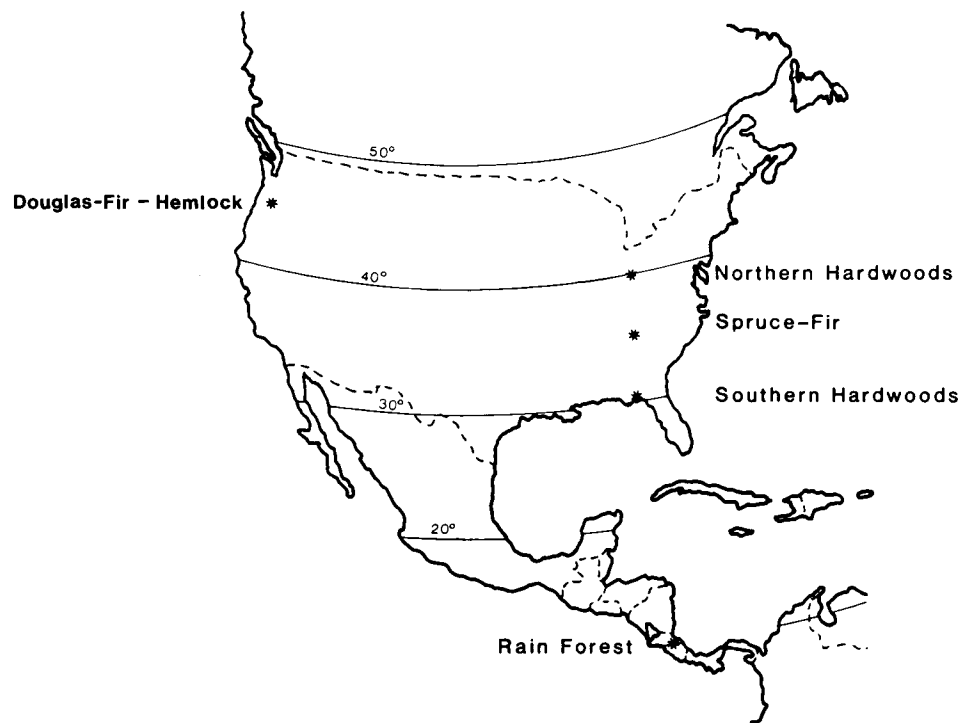


FIG. 1. Locations of the five study sites.

TABLE 1. Characteristics of the five sites used in this study

Site	Latitude (°N)	Canopy height (m)	Canopy depth (m)	Growing season (month-day)	Potential PAR (mol/m ²)
Douglas-fir - hemlock	44.3	70	45	5-15 to 10-15	10 079
Northern hardwoods	39.6	27	11	4-22 to 10-15	11 898
Spruce-fir	35.6	30	15	5-25 to 10-8	9 405
Southern hardwoods	30.7	25	10	2-28 to 11-27	17 182
Tropical rain forest	10.4	35	15	1-1 to 12-31	23 206

NOTE: The values in the first four columns were those used for calculating gap light index (GLI) values. See the text for a description of the specific study sites. Potential PAR is the potential insolation (i.e., above the atmosphere) over the entire growing season. It was calculated from the equation $PAR = \int I_0 \cos Z_t$, where I_0 is the solar constant ($2415 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and Z_t is the zenith angle of the sun at time t . Z_t was calculated from standard equations for solar geometry for 5-min intervals throughout the growing season.

and depth on a site with a given slope and aspect. The only other parameters required for the GLI calculations are latitude and the beginning and end of the growing season (Table 1).

Most of our analyses focus on the single-tree gaps that predominate in these forests in the absence of major storms. The average size (projected area) of a single-tree gap is remarkably similar ($75\text{--}100 \text{ m}^2$) among the five forest types (Platt and Hermann 1986; Denslow 1990; Runkle 1990; Spies et al. 1990), so we have chosen a standard radius of 5 m (projected area = 78 m^2) for our analysis of single-tree gaps. The forests differ significantly, however, in canopy height and depth (Table 1). Calculations were also done for 10 m radius gaps to provide an example of a larger, multitree gap.

It is clear that gaps occur in all shapes and sizes (Brokaw 1985; Runkle 1985). Our choice of cylindrical gaps simply facilitates comparison among the forest types. It should be noted that the calculations are designed to assess the potential effects of an opening in the canopy, not the penetration of light through whatever understory layers of trees, shrubs, lianas, or herbs may exist at a site. However, differences in understory vegetation among forests will have significant effects on the ecological consequences of canopy gaps.

Photographic analysis of closed-canopy light regimes

At each site, fish-eye (hemispherical) photographs (using an Olympus 8-mm lens, or a Minolta 7.5-mm lens at LaSelva) were taken at 10 randomly chosen locations beneath closed canopies. The photographs were taken at heights of approximately 1.5 m above the ground. The cameras were positioned horizontally, with markers within the field of view that allowed determination of true east and west. The photographs were taken either early or late in the day or under overcast conditions to minimize glare from direct sunlight. The negatives were exposed using a meter reading from a nearby open site. This helps standardize the brightness of sky in the resulting image and effectively underexposes the foliage to enhance the contrast between foliage and sky. For all exposures we used black and white medium grain film (Plux-X, Kodak Inc.).

The negatives were digitized using a computerized image analysis system (C2, Olympus Corp.) with a resolution of 512×512 pixels. A threshold grey level was determined for each negative to distinguish between visible sky and foliage. All of the negatives were analyzed by the same person (C.D.C.) to minimize observer error in the determination of the threshold.

Analysis of the digitized images involves calculating the penetration of both diffuse and direct-beam radiation through the small

TABLE 2. Mean percent transmission (range in parentheses) of diffuse, direct, and global (i.e., combined diffuse and direct) PAR through closed canopies for the five sites

Site	Diffuse transmission	Direct-beam transmission	Global PAR transmission
Douglas-fir - hemlock	0.5 (0.1-1.3)	0.6 (0.04-2.1)	0.6 (0.1-1.7)
Northern hardwoods	0.7 (0.3-1.8)	1.9 (0.3-5.8)	1.3 (0.3-3.8)
Spruce-fir	6.1 (2.3-9.0)	4.4 (0.9-10.5)	5.2 (1.6-9.7)
Southern hardwoods	1.1 (0.3-2.0)	1.4 (0.4-3.4)	1.3 (0.4-2.5)
Tropical rain forest	0.4 (0-0.9)	0.5 (0-0.9)	0.5 (0-0.9)
<i>F</i> -statistic (<i>p</i> -value)	32.56 (<0.001)	6.30 (<0.001)	14.89 (<0.001)

NOTE: *F*-statistics are given for one-way ANOVAS for variation among sites for the three variables. Pairwise comparisons among the sites using the Tukey-Kramer test (SAS 1987) indicate that the spruce-fir site is significantly greater than the other four sites for all three variables. *N* = 10 for all sites except spruce-fir, where *N* = 5.

TABLE 3. Mean sunfleck characteristics (range in parentheses) beneath closed canopies in the five sites

Site	% sunflecks ^a	Mean sunfleck duration (min)	Median sunfleck duration (min)	% of direct PAR in sunflecks < median sunfleck
Douglas-Fir - hemlock	47.0 (17-74)	6.0 (2-10)	4.8 (2-10)	36.5 (21-50)
Northern hardwoods	67.6 (46-80)	6.7 (4-8)	5.0 (2-8)	27.3 (17-39)
Spruce-fir	36.8 (29-54)	11.9 (6-24)	6.4 (4-8)	23.7 (9-35)
Southern hardwoods	55.7 (48-69)	7.1 (4-11)	5.4 (4-8)	31.3 (18-56)
Tropical rain forest	52.5 (0-68)	5.7 (0-8)	4.4 (0-6)	31.7 (0-56)
<i>F</i> -statistic (<i>p</i> -value)	4.30 (0.006)	3.79 (0.011)	ns	ns

NOTE: *F*-statistics are given for one-way ANOVAS for variation among sites for the four variables. *N* = 10 for all sites except spruce-fir, where *N* = 5.

^aThe percent of total seasonal PAR in the understory received as sunflecks (assuming that 50% of incident radiation above the canopy is received as direct-beam radiation).

but discrete openings visible between leaves. In effect, each minute opening is treated as a separate gap, and the overall percent transmission of incident radiation by the canopy is simply the sum of the GLI values for each opening. For the calculations, solar positions were calculated at 2-min intervals for each day of the growing season using standard equations for solar geometry (Iqbal 1983).

It should be noted that our analyses only consider light that penetrates directly through openings visible in the canopy. Light transmitted by leaves and beam radiation that is reflected downward by leaves and stems (beam enrichment, Hutchison and Matt 1976) also contribute to understory light levels. The relative importance of these additional sources of light may vary between forests as a function of leaf properties and canopy architecture; however, we do not address those factors in this study. Our methods also limit us to analyzing only light quantity, not quality. The effects of forest canopies on the spectral quality of understory light are fairly well known (e.g., Smith 1982). Since canopy openings allow an increase in the penetration of spectrally uniform open-site radiation, gaps should act to lessen the pronounced spectral shifts, particularly in red and far-red wavelengths, that are characteristic of sites beneath a closed forest canopy.

Results

Light regimes beneath closed canopies

With the exception of the spruce-fir site, an average of less than 2% of incident PAR penetrated directly through the discrete openings between leaves of intact canopies of the different forests (Table 2). Actual seasonal total PAR will be higher because of light transmitted and reflected downwards by leaves. The estimated proportion of total

growing season PAR received as sunflecks ranged from 37 to 68% of the total amount of light penetrating through canopy openings (Table 3). We have calculated histograms of potential sunfleck duration from the photographs, but these calculations are for comparative purposes only, since clouds and motion by leaves in wind will result in many sunflecks of much shorter duration. In all of the forests, potential sunfleck duration was very brief (median duration <7 min) (Table 3). The spruce-fir and southern hardwoods sites were both characterized by a greater contribution from prolonged sunflecks (Fig. 2). This is presumably a consequence of recent widespread but diffuse disturbances in each of these sites (Platt and Hermann 1986). Despite obvious differences in canopy structure, the Douglas-fir - hemlock forest and the tropical rain forest were the two sites most similar in total light penetration and sunfleck characteristics. The Douglas-fir - hemlock forest had the lowest mode for sunfleck duration of any of the five forest types (Table 3).

Incident radiation (above the canopy) at all five latitudes has a very broad peak of origin between 30 and 50° from the zenith, whereas light reaching the forest floor generally originated from a narrower portion of the sky hemisphere (Fig. 3). However, the five sites differed substantially in the portions of the canopy through which PAR penetrated. The two sites with histories of recent diffuse disturbance (spruce-fir and southern hardwood) had the greatest contribution from low-angle lighting. The Douglas-fir site would probably also have significant amounts of low-angle light

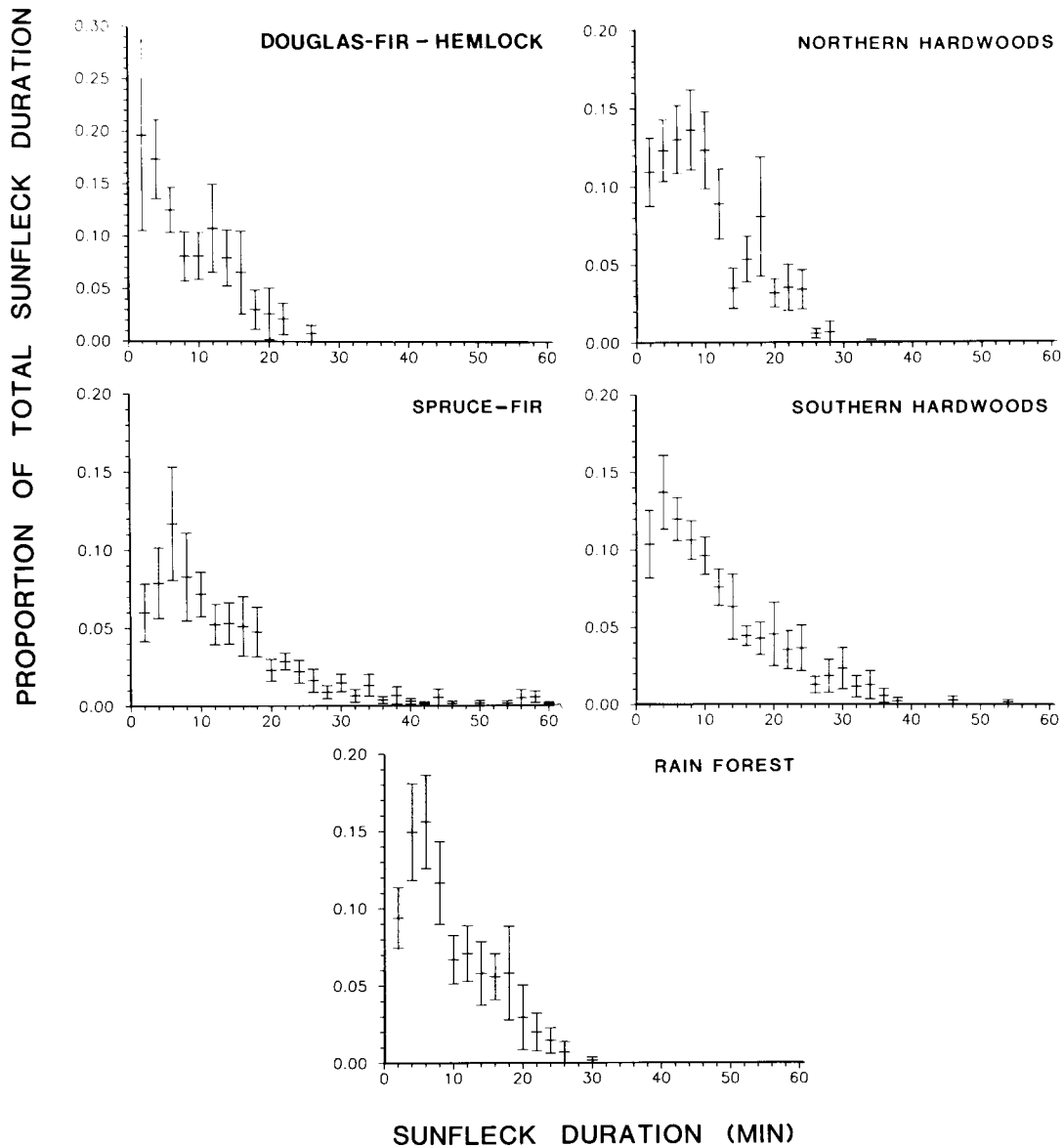


FIG. 2. Frequency distributions of potential sunfleck duration beneath closed canopies for the five sites. The bars are the means (± 1 SE) of the proportion of total sunfleck duration received. $N = 10$ for all sites except spruce-fir, where $N = 5$.

if the relatively uniform subcanopy of hemlock was not present. The Douglas-fir - hemlock and northern hardwood sites both had understory light regimes with distinct peaks of origin between 15 and 30° from the zenith, whereas the tropical site showed a bimodal distribution, with peaks between 15–20° and 35–40° from the zenith. The northern hardwood and tropical rain forest sites were the only forests where the understory received a greater percent of light from within 20° of the zenith than would a site in the open, although the differences were not statistically significant (Table 4). In contrast, locations beneath the Douglas-fir - hemlock canopy received less than 3% of total understory PAR from portions of the sky hemisphere within 20° of vertical. Even more striking was the variation within forests in the importance of overhead versus low-angle light (Table 4). For example, in the northern hardwood and tropical sites, the contribution of overhead light (i.e., light originating within 20° of vertical) for individual locations beneath a closed canopy ranged from 0 to over 50% of total understory PAR (Table 4).

Understory light regimes in and around canopy gaps

The gap created by the death of a single canopy tree in an old-growth Douglas-fir - hemlock forest has very little effect on understory light levels beneath the gap (Fig. 4). This is simply a consequence of the extremely high ratio of tree height to crown width in this forest. Given the differences in canopy heights (Table 1), it would take a gap radius of 13 m (e.g., a gap size of 528 m²) to create understory light levels comparable to those found in a 5 m radius gap in a northern hardwood forest at the same latitude.

For the four other forest types, our calculations show that even these small, single-tree gaps produce significant increases in understory PAR. Since light levels beneath closed canopies may often be as low as 1–2% of full sun (Table 2), seasonal total light levels will be more than doubled for large areas in and around these representative single-tree gaps (i.e., areas with GLI values > 1–2%) (Fig. 4).

Figure 4 illustrates two of the most prominent features of understory light regimes in and around canopy gaps. First

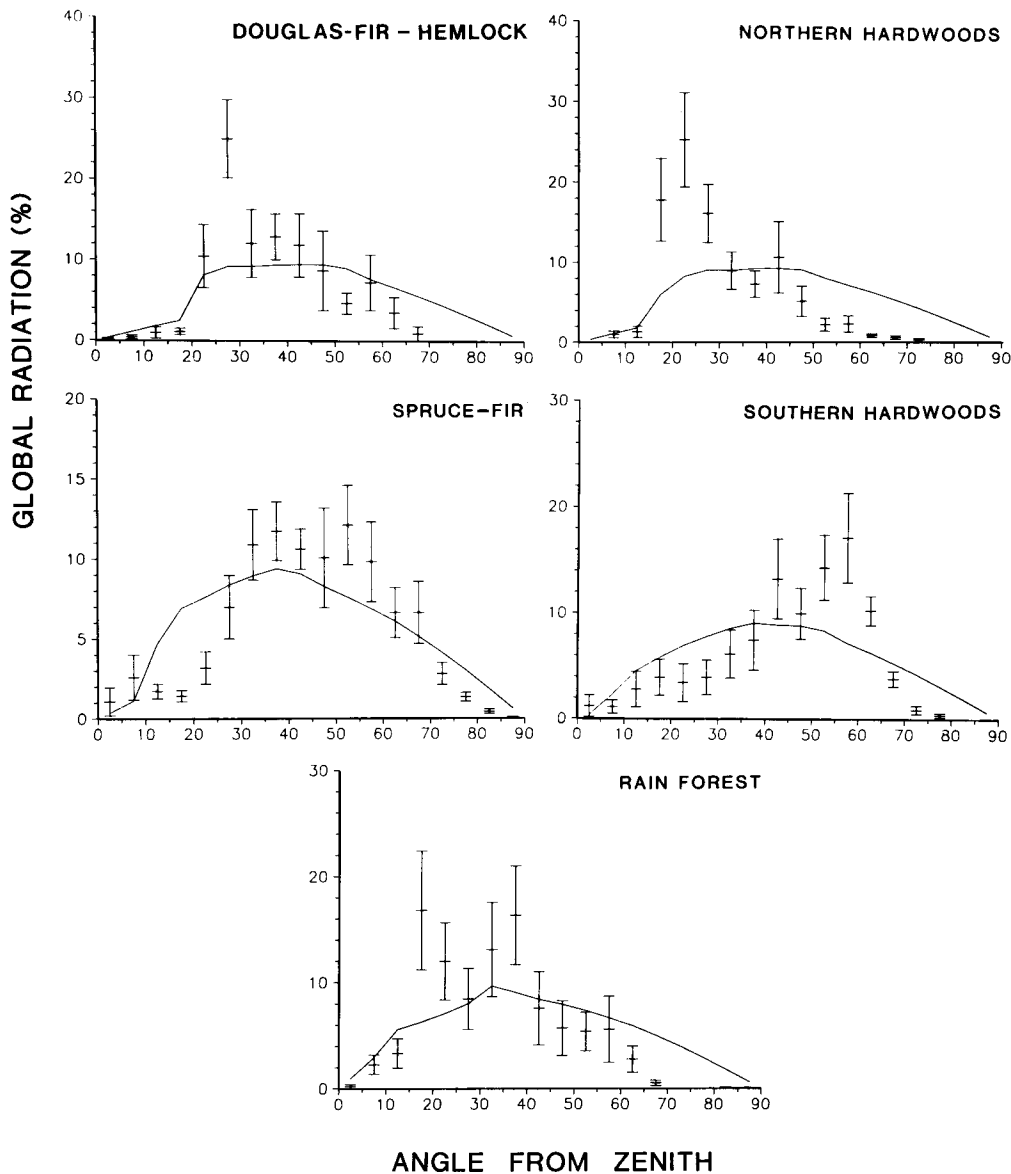


FIG. 3. Incident radiation versus zenith angle for the five sites. The solid line is the calculated incidence pattern for an open site. The bars are the means (± 1 SE) of the proportion of global radiation beneath a closed canopy that originates from 5° bands of the sky hemisphere.

TABLE 4. Percent of total seasonal PAR in open sites and beneath closed canopies that originated from portions of the sky within 20° of the zenith (i.e., vertical)

Site	Open (%)	Closed canopy (%)
Douglas-fir - hemlock	5.7	2.6 (0-11)
Northern hardwood	9.3	20.1 (1-57)
Spruce-fir	13.1	6.8 (0-16)
Southern hardwoods	13.0	9.0 (0-34)
Tropical rain forest	15.7	22.6 (0-55)

NOTE: Values for the closed canopy are means (range in parentheses). Open site values were taken from Fig. 3 and computed using latitudes and growing seasons given in Table 1. The Douglas-fir - hemlock site was the only location where the average closed-canopy value was significantly different from the open-site value (two-tailed t -test, $t = -2.963$, $df = 9$, $p < 0.05$). The high values for closed-canopy locations in the northern hardwood and tropical sites were due to light originating between 15 and 20° from vertical. $N = 10$ for all sites except spruce-fir, where $N = 5$.

is the often striking degree of spatial heterogeneity in seasonal total light levels. GLI values, particularly at the higher latitude sites, can vary significantly over a distance of only several meters. Although the role of sunflecks in producing extremely fine-scale spatial heterogeneity in instantaneous light levels has been widely documented (e.g., Evans 1956; Pearcy 1983), our results illustrate that gaps can produce significant spatial variation in seasonal total PAR.

The second salient feature is that the effects of the canopy gap can extend considerable distances beyond the projected outline of the gap. The GLI values illustrate only potential effects, since the calculations ignore shading by tree trunks and understory vegetation. However the results support the concept of the extended gap (Runkle 1982) rather than simply focusing on the projected gap area.

Most of the spatial heterogeneity in GLI values in and around gaps is due to variation in the amount of direct-beam radiation. The contribution of diffuse radiation to the GLI drops off uniformly with increasing distance from the center of the gap. Direct-beam radiation, however, shows striking

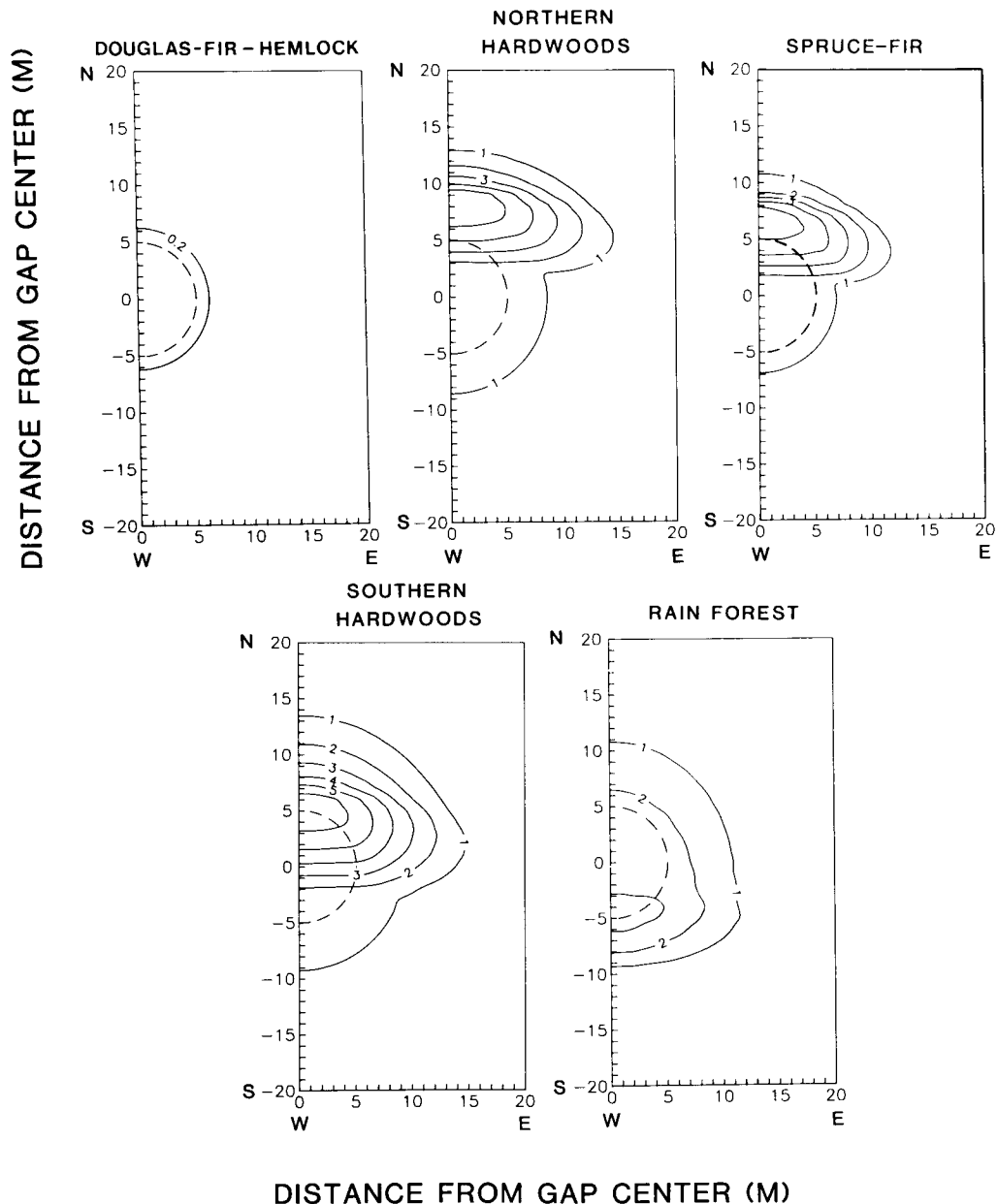


FIG. 4. Contours of gap light index (GLI) values in and around 5 m radius gaps at the five sites. The projected outline of the gap is indicated with a broken line. The figures show only the eastern half of each gap since the patterns are symmetrical about the north-south axis. Note that the contour intervals for Douglas-fir - hemlock differ from intervals for the other four sites. See Table 1 for the parameters used for GLI calculations.

spatial variation that is a direct function of solar geometry and the geometry of the perimeter of the gap (Fig. 5). The average duration of direct-beam radiation received through the gap (for days during the growing season when a point receives at least some direct sun through the gap) can vary from 0 to over 1 h within a distance of only 5 m even in these single-tree gaps (Fig. 5).

Given the relatively similar canopy heights and depths for all of the sites except Douglas-fir - hemlock, most of the differences illustrated in Fig. 4 are simply due to latitude (Fig. 6). For instance, at 44°N, maximum GLI values are displaced well to the north of the projected edge of the single-tree gaps. In fact, at both 44 and 40°N, no direct-beam radiation reaches the forest floor within the projected outline of the gap (Fig. 6). For sites at progressively lower

latitudes, the area of greatest enhancement of understory light levels shifts to the south of the gap. With the exception of the southern hardwood forests, the geographic ranges of the remaining four forests extend across as much as 10° of latitude. As a result, the latitudinal differences illustrated in Fig. 6 also apply to geographic differences in gap light regimes within individual forest types. The tropical site (10°N) has the least north-south asymmetry in understory light levels, the lowest maximum GLI values, and the lowest degree of spatial heterogeneity in total growing season light levels (as indicated by the steepness of GLI contours) of the five sites. This is a consequence of the year-long growing season and the large portion of the sky through which the sun passes during the year at this latitude. GLI values for shorter periods of the year (particularly winter versus sum-

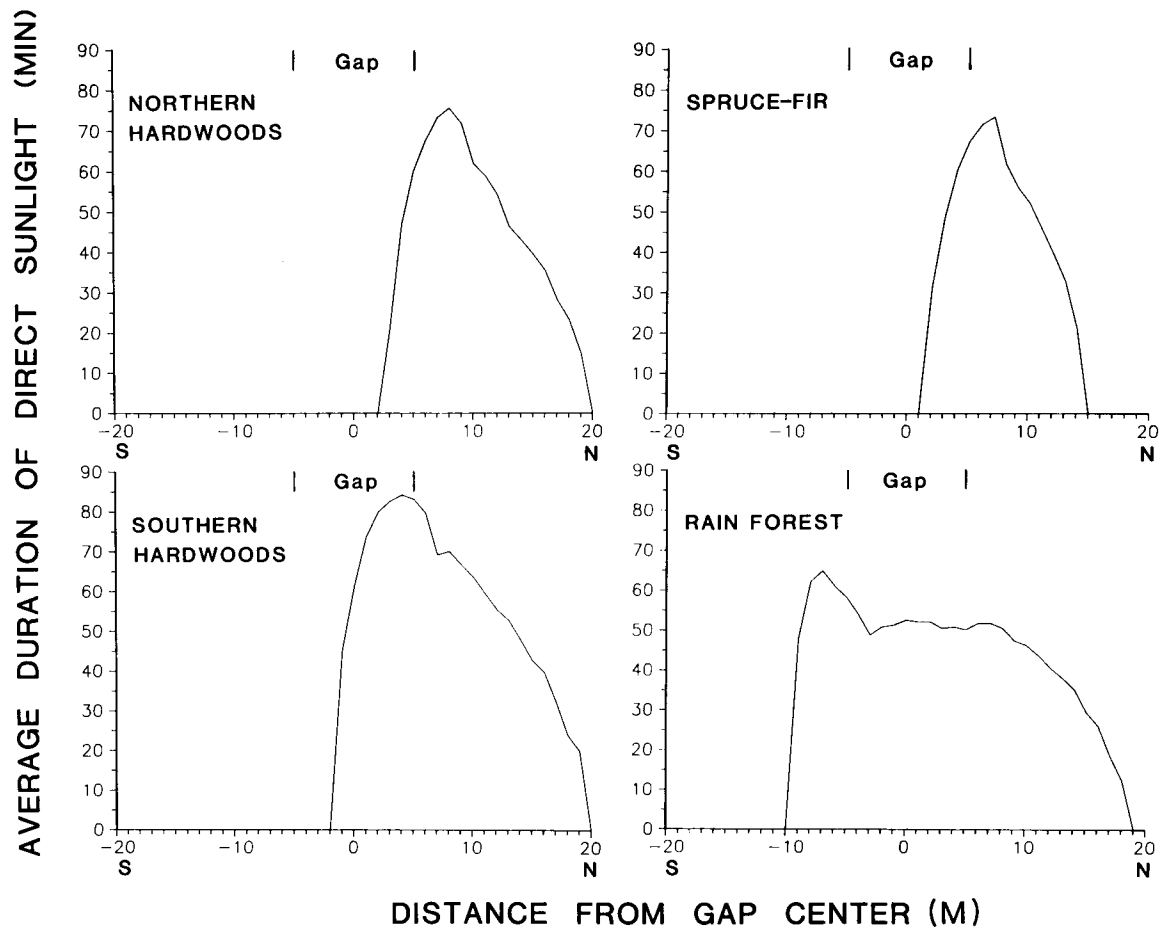


FIG. 5. Average potential daily duration of direct-beam radiation along north-south transects through the centers of 5 m radius gaps in four of the forest types. The calculations ignore obstruction of the sun by clouds.

mer) would show slightly higher degrees of spatial heterogeneity because of the narrower range of sun paths involved.

As expected, potential GLI values increase as saplings increase in height within the projected outline of a gap (Fig. 7). However, a sapling that becomes established in the high light levels beneath the north edge of a gap at 40°N will experience declining GLI values as it increases in height (Fig. 7). Variation in topography also has predictable effects (Fig. 8), with gaps on south-facing slopes in the temperate forests generally receiving higher GLI values than gaps on north-facing slopes. The magnitude of the difference between north- and south-facing slopes increases with increasing latitude, but the spatial patterns for north- and south-facing slopes are qualitatively similar at each of the sites.

As gap size increases, GLI values increase correspondingly (Fig. 9). The quantity of diffuse radiation received through a 10 m radius gap is high enough in all except the Douglas-fir - hemlock site such that all locations inside the projected gap receive at least twice as much light as areas beneath a closed canopy, but there is still considerable spatial heterogeneity in seasonal total light levels even within these large gaps (Fig. 9). In addition, as gap size increases, light can penetrate even greater distances into the understory adjacent to the gap (Figs. 4 and 9). The average duration of direct sunlight at the center of a gap initially increases quite rapidly as gap size increases above a threshold (Fig. 10). However, the potential duration of direct sunlight is still low (i.e.,

3-4 h) even at the centers of gaps as large as 1000 m². In the Douglas-fir - hemlock forest, gaps of 1000 m² still are not large enough for the center of the gap to receive any direct sunlight through the gap.

Discussion

Our results suggest a number of qualitative differences between understory, gap, and open-site light regimes that apply to all five of the forest types. Over the course of the growing season, both total open-site PAR and total closed-canopy PAR are roughly evenly split between diffuse and direct radiation (Table 2), although the total amounts of PAR and durations of periods of direct-beam radiation are obviously vastly different for those two light environments. An individual gap, on the other hand, can produce a range of light regimes with considerable variation in the relative importance of diffuse versus direct radiation. As a result, understory locations may receive similar total photosynthetic photon flux density (PPFD) over a growing season, but with very different temporal patterns of light availability (e.g., moderate but consistent PPFD dominated by diffuse radiation on the south edge of a 10 m radius gap versus predominantly low PPFD but with brief daily periods of high PPFD from direct radiation on the north edge of a 5 m radius gap).

In gaps, periods of high light are produced on time scales of both minutes (by sunflecks when the sun is below the horizon of the gap), and hours (when the sun is visible within

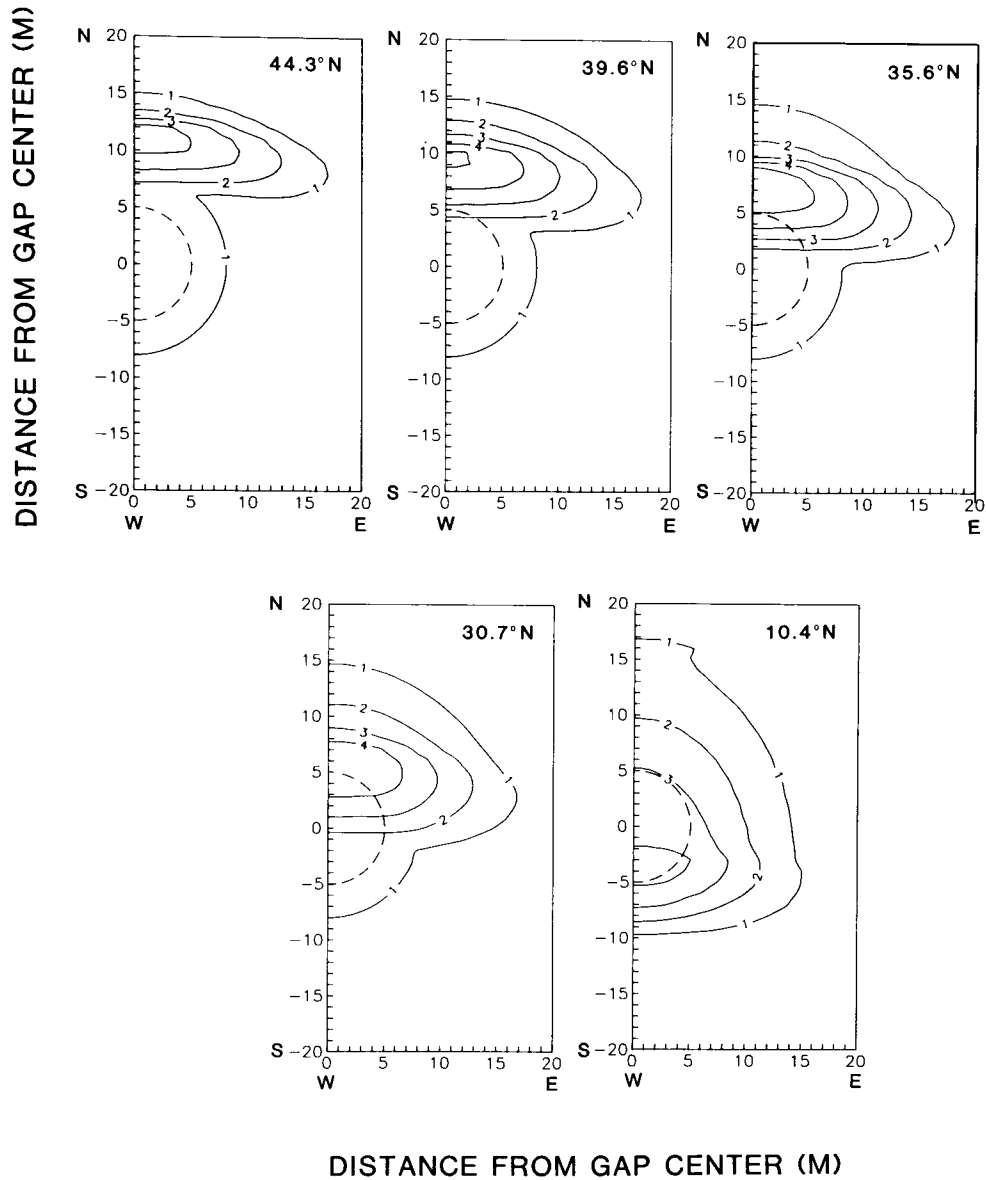


FIG. 6. The effects of latitude on spatial patterns in GLI values in and around single-tree gaps. All of the figures assume a 5 m radius gap, a 25 m tall canopy, a 10 m canopy depth, a level site, and the growing seasons listed in Table 1. The projected outline of the gap is indicated with a broken line.

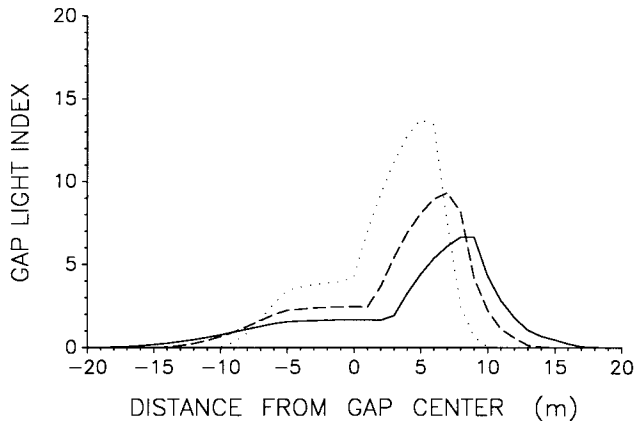


FIG. 7. GLI values along a north-south transect through the center of a 5 m radius gap in a northern hardwood forest at heights of 0 m (—), 5 m (---), and 10 m (····) above the ground. Negative distances indicate locations south of the center of the gap.

a gap on clear days). However, even in large gaps, the potential duration of high light levels from direct radiation is both relatively brief (Fig. 10) and limited to a much narrower range of incidence angles than at an open site. Thus, gaps place two different limitations on the effectiveness of adaptations to high light. First, the relatively brief duration of high light levels provides only a limited time of high potential carbon gain in which to recover the synthesis and maintenance costs of physiological and morphological acclimation to high light (Canham and Marks 1985). Second, many of the architectural responses to high light regimes at the level of whole plants function most effectively when direct radiation is received from a wide range of incidence angles (e.g., McMillen and McClendon 1975).

In all of the sites except the Douglas-fir - hemlock forests, single-tree gaps produce significant variation in total growing season light levels on the scale of 1-10 m. As a result, for a given disturbance regime, the effective return time for

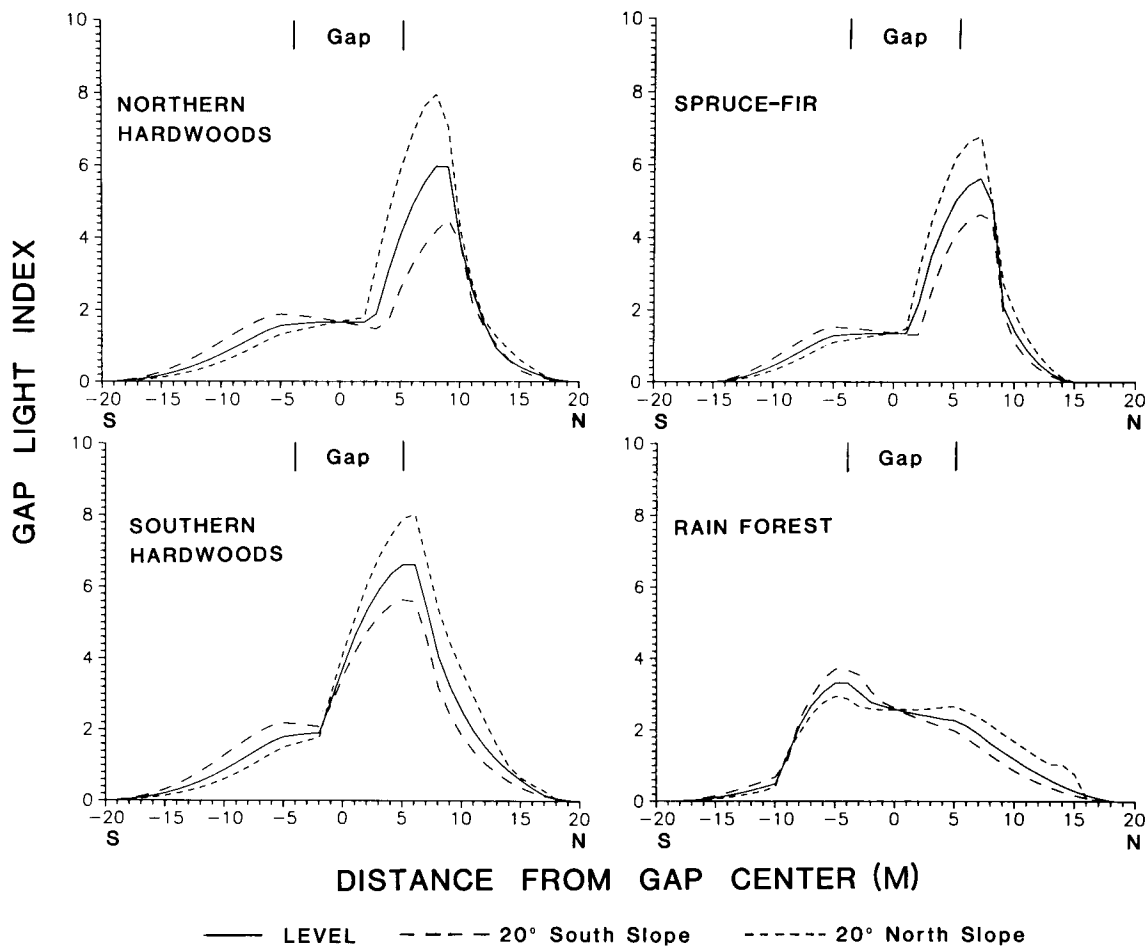


FIG. 8. GLI values along north-south transects through the centers of 5 m radius gaps on level sites, 20° south-facing slopes, and 20° north-facing slopes in four of the forest types.

conditions suitable for seedling establishment and growth will vary as a result of different minimum light requirements among species. As individuals reach sapling sizes, their canopies will begin to integrate over some of this heterogeneity, and individual plants may effectively forage for areas of high light through differential growth and shedding of lateral branches (Canham 1988a).

Our methods were chosen to provide a common basis for comparison among the forest types. For a variety of reasons, the actual pattern of light regimes in any single gap will depart from the patterns described here. In particular, understory strata can be expected to strongly modify horizontal and vertical gradients in PAR, particularly the penetration of light to closed canopy areas adjacent to gaps. There has been recent interest in understory plant response to vertical gradients in PAR in both gap and closed-canopy environments (e.g., Terborgh 1985; Chazdon 1986); however, there is still far too little data on vertical gradients to identify general patterns either within or among different forests. The incidence angles for light penetrating through a closed canopy varied among our five forest types, presumably in response to the recent disturbances in two of the forests. Canopy gaps provide an obvious source of vertical variation in light intensity. As a result, we expect that disturbance history will be an important determinant of variation in vertical patterns of light availability.

There have been a number of suggestions that there may be biologically significant differences in the shade cast by

different canopy species within particular forests, and that these differences might lead to predictable patterns of tree by tree replacement (e.g., Horn 1971; Fox 1977; Woods 1979; Woods and Whittaker 1981). However, the patterns of incidence angles for open-site and understory PAR documented in Table 4 and Fig. 3 indicate that even if consistent differences in light transmission characteristics of canopy species exist, there will be no simple relationships between the species of canopy tree directly overhead and the understory light regime beneath. Given the importance of low-angle PAR in all five of our forest types, the majority of light reaching any particular point in the understory will have passed through the foliage of a number of trees other than the tree directly overhead.

Despite major differences among our five forest types in species composition and foliar characteristics, there were few striking differences among the forests in either closed-canopy or gap light regimes. We attribute most of the observed differences in total light penetration, sunfleck characteristics, and incidence angles beneath closed canopies to the effects of recent disturbances in the spruce-fir and southern hardwood forests (e.g., a pest outbreak and a hurricane, respectively). The major difference in gap light regimes among the five forests was due to the very high ratio of canopy height to gap radius in the Douglas-fir - hemlock forests. As a result, single-tree and even larger multitree gaps of 300-500 m² in these forests have little effect on light levels at the forest floor. For the remaining four forest types, even

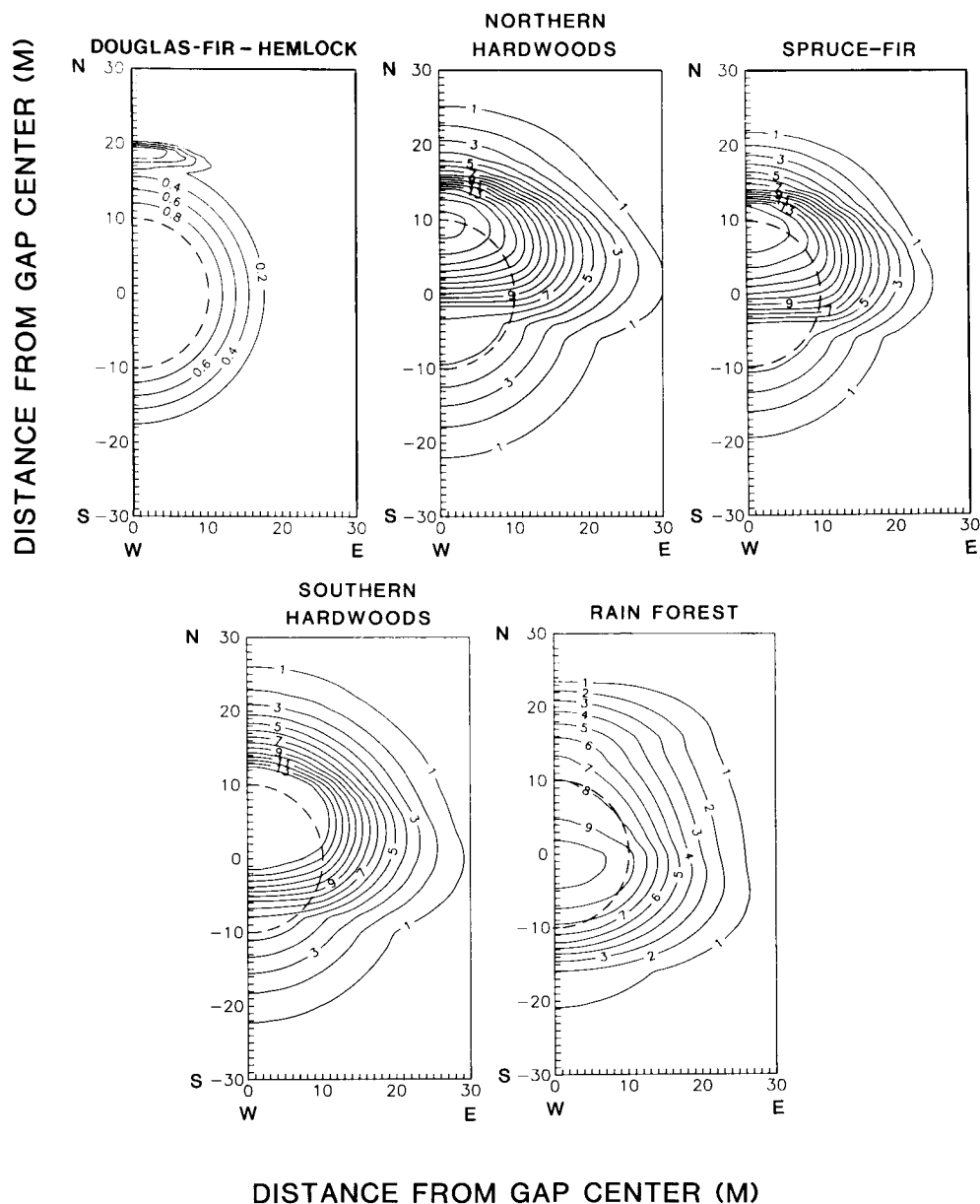


FIG. 9. Contours of gap light index (GLI) values in and around 10 m radius gaps at the five sites. The figures show only the eastern half of each gap since the patterns are symmetrical about the north-south axis. The projected outline of the gap is indicated with a broken line. Note that the contour intervals for Douglas-fir - hemlock differ from intervals for the other four sites. See Table 1 for the parameters used for GLI calculations.

small single-tree gaps can produce substantial increases in seasonal total PAR and significant spatial heterogeneity on spatial scales of 1-10 m.

Acknowledgements

This study is a contribution to the program of the Institute of Ecosystem Studies, The New York Botanical Garden. Financial support was provided by the Mary Flagler Cary Charitable Trust. We would like to thank Geoff Lloyd for his considerable help with the computer programs for image analysis. Computer programs for the image analysis procedures and gap light index calculations are available from the first author.

BROKAW, N. 1985. Treefalls, regrowth, and community structure in tropical forests. *In* The ecology of natural disturbance and

patch dynamics. *Edited by* S.T.A. Pickett and P. White. Academic Press, Orlando. pp. 53-69.

CANHAM, C.D. 1984. Canopy recruitment in shade tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy openings. Ph.D. thesis, Cornell University, Ithaca, NY.

_____. 1988a. Growth and canopy architecture of shade tolerant trees: response to canopy gaps. *Ecology*, **69**: 786-795.

_____. 1988b. An index for understory light levels in and around canopy gaps. *Ecology*, **69**: 1634-1638.

CANHAM, C.D., and MARKS, P.L. 1985. The response of woody plants to disturbance: patterns of establishment and growth. *In* The ecology of natural disturbance and patch dynamics. *Edited by* S.T.A. Pickett and P. White. Academic Press, Orlando. pp. 197-216.

CHAZDON, R.L. 1986. Light variation and carbon gain in rain forest understory palms. *J. Ecol.* **74**: 995-1012.

CHAZDON, R.L., and FETCHER, N. 1984. Photosynthetic light

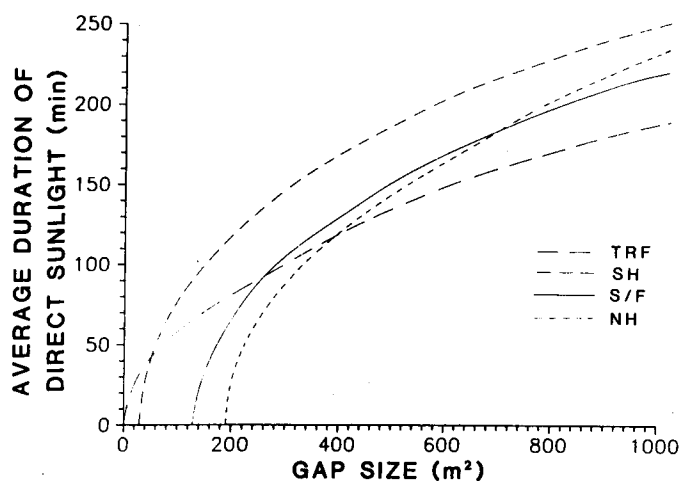


FIG. 10. Average potential daily duration of direct sunlight at the centers of circular gaps from 0 to 1000 m² in projected area for northern hardwood (NH), spruce-fir (S/F), southern hardwood (SH), and tropical rain forests (TRF).

environments in a lowland tropical rainforest in Costa Rica. *J. Ecol.* **72**: 553-564.

CHAZDON, R.L., and FIELD, C.B. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* (Berlin), **73**: 525-532.

DENSLOW, J.S., and GOMEZ DIAZ, A.E. 1990. Seed rain to tree-fall gaps in a neotropical rain forest. *Can. J. For. Res.* **20**: 642-648.

EVANS, G.G. 1956. An area survey method of investigating the distribution of light intensity in woodlands with particular reference to sunflecks. *J. Ecol.* **44**: 391-428.

FOX, J.F. 1977. Alternation and coexistence of tree species. *Am. Nat.* **111**: 69-89.

HORN, H.S. 1971. *The adaptive geometry of trees*. Princeton University Press, Princeton, NJ.

HUTCHISON, B.A., and MATT, D.R. 1976. Beam enrichment of diffuse radiation in a deciduous forest. *Agric. Meteorol.* **17**: 93-110.

IQBAL, M. 1983. *An introduction to solar radiation*. Academic Press, Ont.

KNAPP, C.L., STOFFEL, T.L., and WHITTAKER, S.D. 1980. *Insolation data manual: long term monthly averages of solar radiation, temperature, degree-days and global K_T for 248 National*

Weather Service stations. Solar Energy Research Institute, Washington, DC.

MARCH, W.J., and SKEEN, J.N. 1976. Global radiation beneath the canopy and in a clearing of a suburban hardwood forest. *Agric. Meteorol.* **16**: 321-327.

MCMILLEN, G.G., and MCCLENDON, J.H. 1975. Leaf angle: an adaptive feature of sun and shade leaves. *Ann. Bot. (London)*, **140**: 437-442.

MINCKLER, L.S., WOERHEIDE, J.D., and SCHLESINGER, R.C. 1973. Light, soil moisture and tree reproduction in hardwood forest openings. U.S. For. Serv. Res. Pap. NC-89.

PEARCY, R.W. 1983. The light environment and growth of C₃ and C₄ tree species in the understory of a Hawaiian forest. *Oecologia* (Berlin), **58**: 19-25.

PLATT, W.J., and HERMANN, S.M. 1986. Relationships between dispersal syndrome and characteristics of populations of trees in a mixed-species forest. *In* *Frugivores and seed dispersal*. Edited by A. Estrada and T.H. Fleming. Dr. W. Junk, Amsterdam, Netherlands. pp. 309-321.

RUNKLE, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology*, **63**: 1533-1546.

_____. 1985. Disturbance regimes in temperate forests. *In* *The ecology of natural disturbance and patch dynamics*. Edited by S.T.A. Pickett and P. White. Academic Press, Orlando. pp. 17-33.

_____. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest. *Can. J. For. Res.* **20**: 632-641.

SAS INSTITUTE INC. 1987. *SAS/STAT guide for personal computers*, version 6 edition. SAS Institute Inc., Cary NC.

SMITH, H. 1982. Light quality, photoperception, and plant strategy. *Annu. Rev. Plant Physiol.* **33**: 481-518.

SPIES, T., FRANKLIN, J.F., and KLOPSCH, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* **20**: 649-658.

TERBORGH, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. *Am. Nat.* **126**: 760-776.

VITOUSEK, P.M., and DENSLOW, J.S. 1986. Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *J. Ecol.* **74**: 1167-1178.

WOODS, K.D. 1979. Reciprocal replacement and the maintenance of codominance in a beech-maple forest. *Oikos*, **33**: 31-39.

WOODS, K.D., and WHITTAKER, R.H. 1981. Canopy-understory interaction and the internal dynamics of mature hardwood and hemlock-hardwood forests. *In* *Forest succession—concepts and application*. Edited by D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York.