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Using hemispherical photography for estimating photosynthetic photon flux density under canopies and in gaps in Douglas-fir forests of the Pacific Northwest

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Our primary objective in this study was to determine if hemispherical (fish-eye) photographs could be used to estimate photosynthetic photon flux density (PPFD) in mature and old-growth *Pseudotsuga–Tsuga* forests in the Oregon and Washington Cascade Range. LI-COR quantum sensors sampled PPFD at 10-s intervals at six points in each of two old-growth stands from January to December of 1991. Direct measures of PPFD were also made with photodiodes, which were calibrated against quantum sensors. They were used to sample PPFD for 6- to 14-day periods during the summer at 15 points in each of four stands, two mature and two old growth. Hemispherical photographs were taken at these sample points and were digitized and analyzed using the program CANOPY. The software predicts overall site openness and openness along the sun path. Regression models were developed based upon those parameters. The models predicted the mean daily PPFD for each month of the year. Two major factors were found that influenced regression models: stand age–structure (mature vs. old growth) and sky conditions (dry vs. wet seasons). Canopies in mature stands were more open than old growth stands, and their PPFD models were more heavily influenced by overall site openness. Conversely, PPFD models for old-growth canopies were more heavily influenced by openness along the sun path. Wet-season models were dominated by diffuse PPFD (overall site openness), and dry-season models were dominated by direct flux (openness along the sun path). Combining data sets from stands of comparable age–structure and seasons considerably increased regression R^2-values.

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L'objectif principal de cette étude consistait à déterminer si les photographies hémisphériques (panoramiques) pourraient être utilisées pour estimer la densité du flux de photons photosynthétiques dans les forêts matures et les vieilles forêts de *Pseudotsuga–Tsuga* croissant dans les Cascades des états de Washington et de l'Orégon. Des capteurs quantiques LI-COR mesuraient la densité du flux photonique à intervalle de 10 s à six endroits dans chacun des deux vieux peuplements du mois de janvier au mois de décembre 1991. Des mesures directes de la densité du flux photonique furent aussi effectuées avec des diodes photosensibles calibrées à partir des capteurs quantiques. Les diodes furent utilisées pour mesure la densité du flux photonique pour des périodes de 6 à 14 jours pendant l'été à 15 endroits dans chacun des quatre peuplements suivants : deux peuplements matures et deux vieux peuplements. Les photographies hémisphériques furent prises à ces endroits d'échantillonnage et furent digitalisées et analysées avec le programme CANOPY. Ce logiciel prédit l'ouverture générale du site et l'ouverture dans le trajet des rayons du soleil. Des modèles de régression basés sur ces paramètres furent développés. Les modèles prédisaient la densité moyenne du flux photonique pour chacun des mois de l'année. Deux facteurs qui ont beaucoup d'influence sur les modèles de régression furent mis en évidence : la relation âge–structure du peuplement (mature vs vieux) et les conditions atmosphériques (saison sèche vs humide). Dans les peuplements matures, le couvert était plus ouvert que dans les vieux peuplements et leurs modèles de densité du flux photonique étaient plus fortement influencés par l'ouverture générale du site. De la même façon, les modèles de densité du flux photonique des vieux peuplements étaient plus fortement influencés par l'ouverture dans le trajet des rayons du soleil. Les modèles de la saison humide étaient dominés par le rayonnement diffus (ouverture générale du site) alors que les modèles de la saison sèche étaient dominés par le rayonnement direct (ouverture dans le trajet des rayons du soleil). La combinaison des groupes de données des peuplements dont la relation âge–structure était comparable et pour une même saison a considérablement augmenté les valeurs de R^2 des régressions.

[Traduit par la Rédaction]

Introduction

Light environments underneath forest canopies are highly variable in time, space, and spectral quality. Characterizing this heterogeneous resource typically has required long-term direct measurements of either total radiation or photosynthetic photon flux density (PPFD) at many points using relatively expensive sensors. Hemispherical canopy photography is a potentially less expensive and time-consuming technique that directly measures canopy openness and indirectly estimates light levels (Chazdon and Field 1987; Rich 1989; Rich et al. 1993). This method has become popular for characterizing light environments because a canopy photograph taken at a single point in time can be used to estimate light penetration for different times of the year, and many photographs can be relatively easily taken and analyzed.

Although hemispherical photography has been widely used in many ecological studies (Evans and Coombe 1959;

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TABLE 1. Characteristics of the four research sites

Site	Age (years)	Slope (degrees)	Aspect	Elev. (m)	Dominant overstory		Dominant shrubs	
					Vegetation	LAI	Vegetation	% cover
Martha Creek	92	5–10	S–SW	460	*Pseudotsuga menziesii*	4.60	*Acer circinatum*	40
					Other conifer spp.	0.04		
					Other deciduous spp.	0.24		
Total LAI						4.88		
McRae Creek	~475–525	5–10	W	850	*Pseudotsuga menziesii*	2.73	*Acer circinatum*	2
					Tsuga heterophylla	6.42	*Tsuga heterophylla*	1
					Thuja plicata	0.66		
					Other conifer spp.	0.09		
Total LAI						9.90		
Panther Creek	~145	0–15	W–SW	850	*Pseudotsuga menziesii*	3.76	*Acer circinatum*	27
					Other conifer spp.	0.10	*Cornus nuttallii*	4
					Other deciduous spp.	0.07		
Total LAI						3.93		
Trout Creek	~475–525	0–3	na	460	*Pseudotsuga menziesii*	1.43	*Vaccinium* spp.	9
					Tsuga heterophylla	6.31	*Abies amabilis*	4
					Abies amabilis	1.31		
					Other conifer spp.	0.07		
Total LAI						9.12		

NOTE: Stand ages in the McRae, Panther, and Trout Creek sites were estimated from cut stumps. The Martha Creek stand is dated to the Siouxon–Yacolt burn of 1902 (Gray 1990). Leaf area indices (LAI) were calculated from various sources (BIOPAK software, cf. Means et al. 1994), using measured sapwood area from trees that were cut and regressions of sapwood area to diameter 1.4 m above ground for perimeter trees that were left standing.

Anderson 1964; Hutchinson et al. 1980; Pearcy 1983; Chazdon 1985; Oberbauer and Strain 1986; Chazdon and Field 1987; Oberbauer et al. 1988; Canham et al. 1990; Rich et al. 1993; Whitmore 1993), relatively few investigators have reported the relationship between the indirect measures of global radiation from fish-eye analysis and direct measures of PPFD measured with quantum sensors (Rich et al. 1993; Whitmore 1993). A good relationship between the two measures is expected; however, it is not known how that relationship varies as a function of canopy age, structure, and composition, or sky conditions. Our overall objective in this study was to determine the relationship between canopy openness (proportion of global radiation under a canopy relative to a totally open site) as measured by analysis of canopy photographs and PPFD as measured by quantum sensors in coniferous forests. Secondarily, we examined the effect of canopy structure and sky conditions on this relationship.

Materials and methods

Study sites

Our four research sites were located within the Western Hemlock Zone on the western slopes of the Cascade Range (Franklin and Dyrness 1973). The sites include (1) McRae Creek, an old-growth Douglas-fir – western hemlock – western red cedar stand (*Pseudotsuga menziesii* (Mirb.) Franco – *Tsuga heterophylla* (Sarg. – *Thuja plicata* Donn) initiated ~475–525 years ago; (2) Trout Creek, an old-growth Douglas-fir – western hemlock stand initiated ~475–525 years ago; (3) Martha Creek, a mature stand of Douglas-fir initiated 92 years ago (Gray 1990); and (4) Panther Creek, a mature stand of Douglas-fir initiated ~145 years ago. We define a mature stand as a forest of uniform age with relatively uniform canopy height and structure and an old-growth stand as an ancient forest with multiple age cohorts present and a mixed, complex canopy structure. All four stands were initiated by fire. The McRae Creek stand is located in the H.J. Andrews Experimental Forest, in the Willamette National Forest near Blue River, Oregon. The other three stands are located in the Wind River Experimental Forest, Gifford Pinchot National Forest, near Carson, Washington. Experimental gaps were cut as part of a gap dynamics study in the fall of 1990 (Spies et al. 1990). Stand descriptions (Table 1) were developed from vegetation measurements taken in 1990 and 1991. Shrub cover (%) was estimated from 3.14-m^2 microplots superimposed on a 4-m interval grid in the gaps. Tree heights and crown condition (as percent of all trees within the site) were measured. Sapwood area was measured on all felled trees to characterize leaf area index (LAI). We developed sapwood taper regressions from a subset of the harvested trees to estimate sapwood area at the base of live tree crowns and then used equations developed by Waring et al. (1982) to estimate leaf area for each site. All trees greater than 5 cm DBH were harvested in each gap, and LAI estimates are based upon a 100% sample of those trees, using the measured sapwood area on each tree.

Canopy structure and composition differ substantially between the two stand types (Table 1, Fig. 1). The mature stand canopies are monolayers of *P. menziesii* with a few scattered shade-tolerant conifers and hardwoods in the lower story, and a well-developed deciduous shrub layer. In contrast, the old-growth stands consist of emergent *P. menziesii* overstories with shade-tolerant western hemlock and western red cedar forming the dominant canopy layer in the midstory. These shade-tolerant conifers contribute most of the LAI in the old-growth stands (Table 1, Fig. 1).

Light measurements

PPFD was measured using calibrated LI-COR quantum sensors at 1.5 m above the ground at six points in each of the old-growth stands between January and December of 1991, sampled by data loggers at 10-s intervals and stored as 2-h means. In each of the two stands, three of the quantum sensors were located at points 25 m apart along a north–south transect through the center of a control plot. The other three sensors were installed at the north edge, center, and south edge of 50 m diameter circular gaps created in the same stand as part of the gap experiment. At least 50 m of closed-canopy forest separated each of the

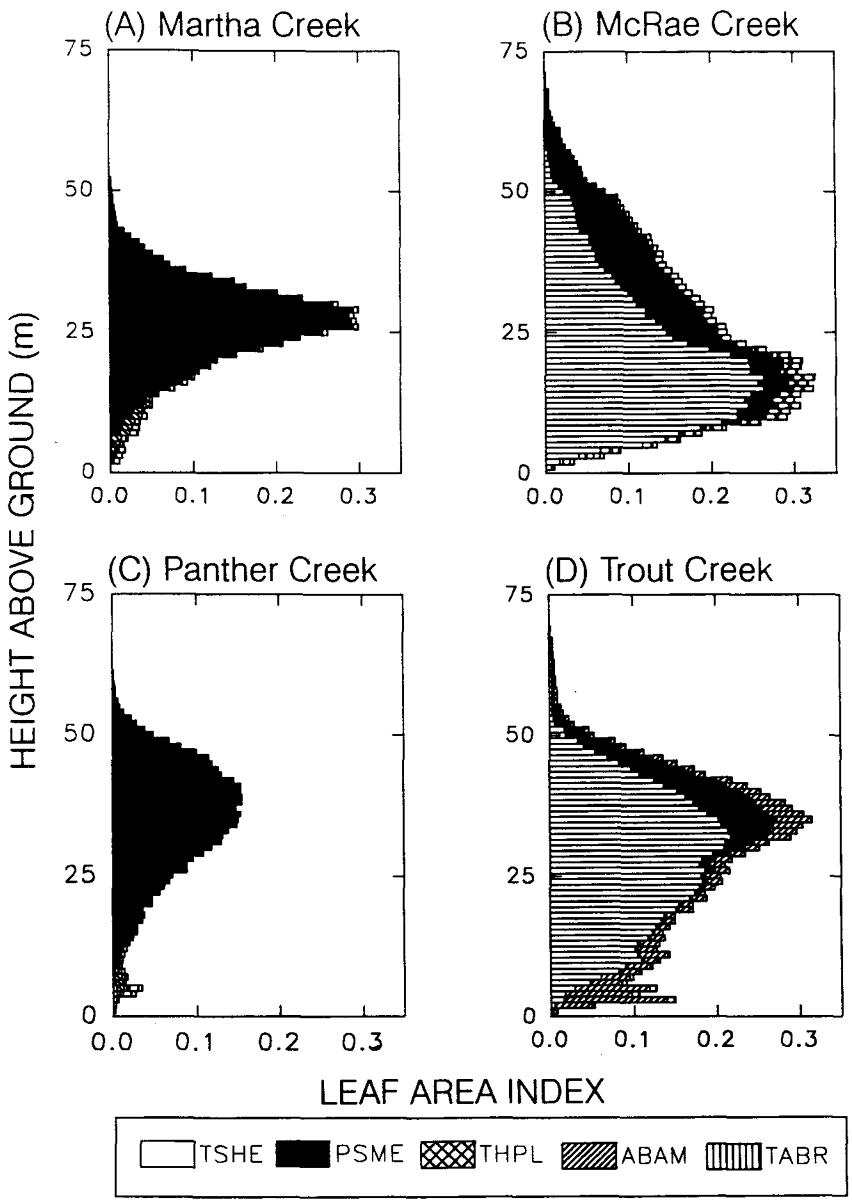

FIG. 1. Leaf area index as a function of height above ground for the five major conifer tree species present in the four stands: TSHE, *Tsuga heterophylla*; PSME, *Pseudotsuga menziesii*; THPL, *Thuja plicata*; ABAM, *Abies amabilis*; TABR, *Taxus brevifolia*.

gaps. Canopies ranged from 95–97% closed in the controls to ~50% closed at the gap center. The transect was oriented north to south to measure flux along the strongest PPFD intensity gradient.

Comparisons of mature and old-growth stands were made from photographs taken in the summer of 1990, prior to creating the gaps. The following summer, Gallium arsenide photodiodes (Hammamatsu Corporation G1738, Bridgewater, N.J.) were used to sample mature stands and additional sites in old-growth stands because of their low cost (Gutschick et al. 1985; Chazdon and Field 1987; Oberbauer et al. 1988; Rich et al. 1993). The photodiodes were calibrated side by side with quantum sensors over a 72-h period. Linear regressions of instantaneous readings were developed ($R^2 > 0.97$, $p < 0.0001$) for all sensors. In the mature stands, photodiodes were placed at the north edge, center, and south edge of experimental gaps equal to 0.2, 0.4, 0.6, and 1.0 gap-size ratios[2] in diameter, and in control (undisturbed) plots along north–south transects at intervals equal to one-half the mean canopy height. In the old-growth stands, photodiodes were added to experimental gaps of size 0.2, 0.4, and 0.6 to supplement the data already being collected with quantum sensors in the control and 1.0 gaps. The photodiodes were sampled at the same intervals as the permanent quantum sensors installed in the old-growth stands. The samples were collected at 6- to 14-day intervals during July, August, or early September in the four stands (Table 2).

[2]Gap-size ratio = (mean gap diameter)/(mean canopy height). Mean diameter was calculated from the diagonal distance between canopy edges across the gap, through the gap center. Mean height was calculated from the heights of dominant overstory trees.

Hemispherical photography

Our protocols follow those of Rich (1989) with some modifications, described below. Photographs were taken with a Canon 7.5-mm hemispherical lens on a Canon AE-1 body. Kodak PX-125 film was used for all photographs. A red filter was used in cloudy weather and a blue filter in cloudless weather to increase contrast between sky and canopy images in the photographs. The camera body was positioned on a jig that held a small tungsten lamp mounted perpendicular to the plane of the lens, to indicate true south and mark the correct rotation for sun-track simulations. A compass was attached to the jig to ensure correct north–south

TABLE 2. Experimental design for the study

Stand	Gap-size ratio[a]	No. and type of sensors	No. of months sampled	n
Martha Creek	0.0 (control)	3 photodiodes	1 (Aug. 1–7)	3
	0.2	1 photodiode	1 (Aug. 1–7)	1
	0.4	3 photodiodes	1 (Aug. 1–7)	3
	0.6	3 photodiodes	1 (Aug. 1–7)	3
	1.0	3 photodiodes	1 (Aug. 1–7)	3
Total				13
McRae Creek	0.0 (control)	3 quantum sensors	11 (Feb.–Dec.)	33
	0.2	3 photodiodes	1 (Aug. 17–31)	3
	0.4	3 photodiodes	1 (Aug. 17–31)	3
	0.6	3 photodiodes	1 (Aug. 17–31)	3
	1.0	3 quantum sensors	11 (Feb.–Dec.)	33
Total				75
Panther Creek	0.0 (control)	3 photodiodes	1 (July 25–30)	3
	0.2	3 photodiodes	1 (July 25–30)	3
	0.4	3 photodiodes	1 (July 25–30)	3
	0.6	3 photodiodes	1 (July 25–30)	3
	1.0	3 photodiodes	1 (July 25–30)	3
Total				15
Trout Creek	0.0 (control)	3 quantum sensors	11 (Jan.–Dec.)	36
	0.2	3 photodiodes	1 (July 11–23)	3
	0.4	3 photodiodes	1 (July 11–23)	3
	0.6	3 photodiodes	1 (July 11–23)	3
	1.0	3 quantum sensors	12 (Jan.–Dec.)	36
Total				81

NOTE: n refers to the sample points used in the regression analysis. Dates are from 1991.
[a]Location of sensor.

orientation. All photographs were taken with the apex of the lens at the same point in space as the sensing surface of the quantum sensor or photodiode. Photographs were usually taken on uniformly cloudy days, but from June to September 1991 they were taken during twilight before sunrise or after sunset. We found it difficult to distinguish between sunlit crowns and canopy openings in black and white photographs, hence we photographed only during evenly lit (diffuse) sky light conditions.

We analyzed the photographs using CANOPY image analysis software. Images were digitized from photograph negatives with a Cohu 4815-2000 monochrome video camera. Analysis was performed using an Imaging Technology ImagePlus frame grabber installed on a 486-based IBM-compatible personal computer. Digitized hemispherical images were viewed and edited on a Sony Corp. PVM-1342Q monitor. The program CANOPY was configured for lens and cosine correction, and analysis was performed based on the uniform overcast day (UOC) flux distribution model.

A subjective assignment of image threshold levels by the user is required in the analysis, through which the software separates portions of the photograph that are open sky and those that are canopy. To minimize this subjective element, a single operator analyzed all photographs four times, repeating a standardized protocol for each photograph. The mean indirect sky factor (ISF) and direct sky factor (DSF) from these four analyses for each photograph were used in the regressions. ISF is the overall angular openness weighted by the UOC model, and DSF is the angular openness along the sun track weighted by the UOC model.

Statistical analysis

Canopy structure effects were analyzed using regression equations relating measured PPFD to ISF and DSF figures derived from the program CANOPY. These equations were developed using a model for PPFD levels in forest ecosystems (Anderson 1964; Rich 1989; Canham et al. 1990; Rich et al. 1993), as follows:

$$[1]\quad \mathrm{GSF} = (T_{\mathrm{dif}}P_{\mathrm{dif}}) + (T_{\mathrm{dir}}P_{\mathrm{dir}})$$

where GSF is global site factor (a measure of openness), T_{dif} and T_{dir} are the respective proportions of diffuse and direct PPFD received above the canopy, and P_{dif} and P_{dir} are the respective proportions that are transmitted through the canopy. The term $T_{\mathrm{dif}}P_{\mathrm{dif}}$ is the diffuse PPFD portion received under the canopy (hereafter referred to as the diffuse flux term). $T_{\mathrm{dir}}P_{\mathrm{dir}}$ is the direct portion (hereafter referred to as the direct flux term). We substituted the mean daily measured quanta (Q_{t}, by month) for GSF, ISF for P_{dif}, and DSF for P_{dir} in eq. 1 at each of the sample points, so that the modified model reads

$$[2]\quad Q_{\mathrm{t}} = (T_{\mathrm{dif}}\ \mathrm{ISF}) + (T_{\mathrm{dir}}\ \mathrm{DSF})$$

We solved the equation for the missing parameters (T_{dif} and T_{dir}) using stepwise regression with maximum R^2 and zero intercept. The mean daily PPFD for each month of the year were compared with the corresponding ISF values, the monthly DSF values, and the values in the regression model (Table 3A). Statistically significant ($p < 0.01$) models were developed for all stands (Tables 3A and 3B).

Results and discussion

Prior to analyzing the effects of canopy structure and weather conditions on the regression models, we first developed separate models based upon site, stand age (old vs. mature), and season (dry vs. wet). We compared the slopes of the models using analysis of variance, and found that the slopes of the regressions were all statistically different ($p < 0.05$). Hence, we have a statistical basis upon which to evaluate biophysical differences and similarities between the stands.

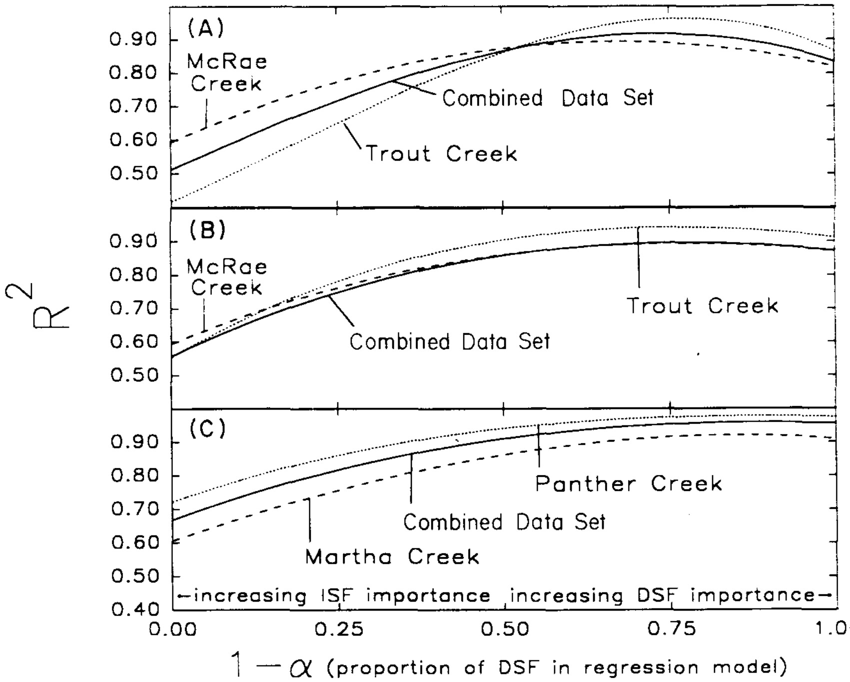

FIG. 2. Regression R^2 as a function of relative ISF and DSF proportions in the regression models. The R^2 was calculated from the following regression model: Quanta = {[ISF(α)] + [DSF(1 − α)]} T_r. Quanta is the measured mean daily flux for the month, ISF is the indirect site factor, DSF is the direct site factor for the month, α is the weighting factor, and T_r is the regression parameter. (A) Old growth, wet season. (B) Old growth, dry season. (C) Mature, dry season.

We believe it is potentially misleading to compare actual regression parameters gained from the analysis. The sites were separated by 16–320 km (10–200 mi) and up to 400 m elevation, which can result in substantial differences in the global radiation received by the forest canopies. We based most of the following analysis upon the ratio of the regression parameters (T_{dif}/T_{dir}), and the R^2 of the regressions.

Stand structure effects

Differences were found when we stratified the regressions by stand age. We first calculated separate, statistically significant ($p < 0.0001$) equations for each stand for the dry season (we had no wet-season data for the mature stands) and found that T_{dif}/T_{dir} was similar among stand types (0.13–0.19 for mature, 0.30–0.55 for old growth). To further understand the relationship between the regression parameters, we calculated R^2 as a function of a weighted combination of ISF and DSF (Fig. 2). The mature age-class yielded regressions dominated by the direct flux term, whereas the diffuse flux term was more important in the old growth.

Based upon these similarities, we combined the data sets by age-class, yielding statistically significant equations ($p < 0.0001$), with corresponding degradations in the R^2-value of less than 5%. However, when we combined the data from all stands into one regression, the R^2-value decreased over 50%. Hence, we believe that the differences in the regressions within age-classes are small enough to be considered negligible for the purposes of comparison, whereas differences between age-classes are substantial enough to warrant calculating separate regressions.

We were concerned that the period during which PPFD was measured at the temporary sites (6–14 days) did not accurately represent the mean daily PPFD received during that month. To investigate this, we created a subset of the PPFD data collected at the six sensors in the control and size 1.0 gaps in McRae Creek for July and August. We calculated separate regression models for coincident 7-day periods from July and August. The parameter estimates in these models were very similar to those calculated for the dry-season models from the full data set, and the slopes of the regressions were not significantly different ($p > 0.05$).

To further understand the differences in canopy architecture and how it might affect the regression equations, we examined the distribution of openings in the photographs (Fig. 3). Maximum openness occurred between zenith angles of 15 and 45° in all four stands. The relative angular openness was substantially higher in the mature stands. We believe this is a function of lower LAI in the mature stands. The dense western hemlock midstory found in the old-growth stands appears to substantially affect canopy openness, as measured from 1.5 m above ground.

One would expect to find a direct relationship between the measured canopy openness and PPFD, regardless of canopy structure. A single relationship might then be calculated for all age-classes that links PPFD with ISF and DSF parameters, rather than the separate regressions discussed above. We speculate that the differences in the models may be related to differences in fine-scale canopy geometry. The significance of fine-scale "microgaps" has been documented in tropical and temperate deciduous canopies (Chazdon 1988; Chazdon and Pearcy 1991), and we believe they may be a factor in these coniferous forests as well. Small openings along the sun path, on the scale of the size of conifer needles (approximately 1–10 cm), may produce brief but significant sunflecks with associated penumbral effects (Smith et al. 1989), with intensities disproportionately large compared with the size of the opening. These openings may be so small that they are mistaken for closed canopy when photographed and digitized into pixels for analysis. For example, the SOLARCALC program by Chazdon and Field (1987)

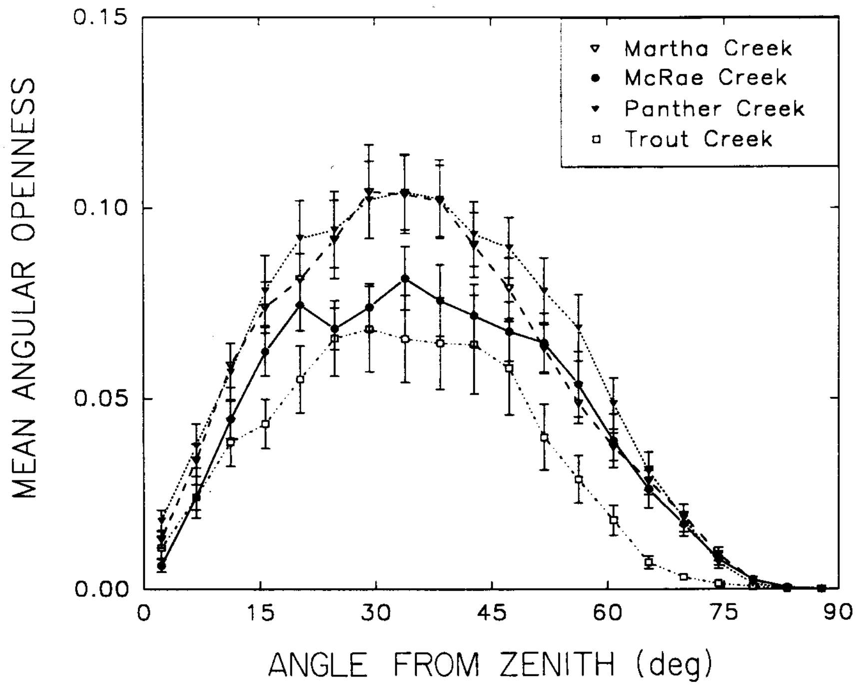

FIG. 3. Distributed angular openness as a function of zenith angle in hemispherical photographs from the four sites. Data are presented as mean ± 1 SE. The *n* for each mean is 23. Data were determined from canopy photographs taken at all measurement sites prior to creating the gaps.

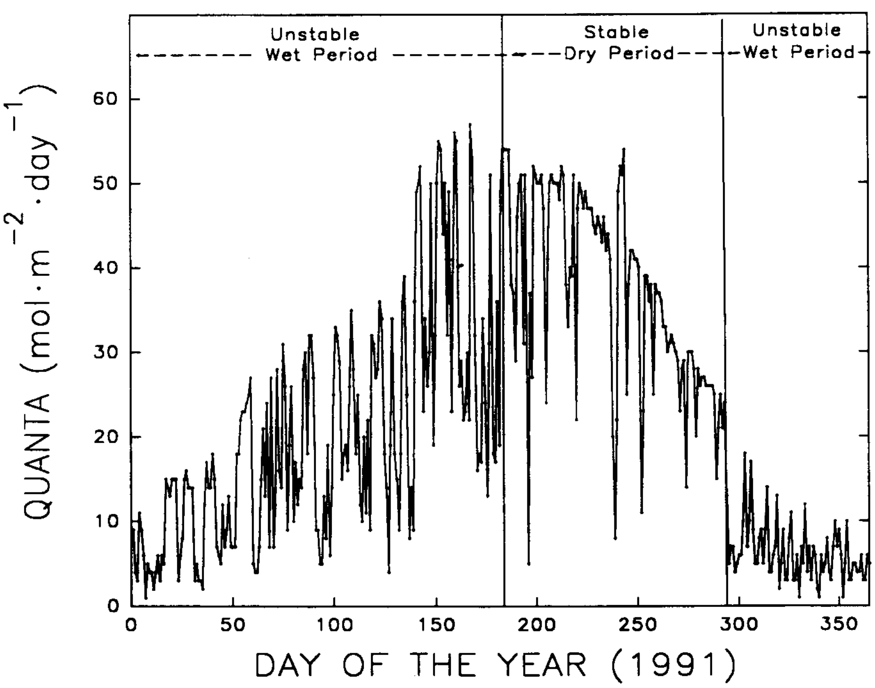

FIG. 4. Total daily flux measured in a large opening near the Wind River sites. Quanta were measured with a LI-COR LI-190 quantum sensor sampled at 60-s intervals.

calculates the number of sunfleck events for each solar track and produces a frequency distribution of sunfleck lengths from hemispherical photographs, based upon 2-min interval changes in solar position. This level of resolution may be the current technological limit, owing to errors introduced by camera positioning, compass readings, etc. Many sunflecks are shorter than 2 min; hence, the net result may be an openness factor in the mature stands that is actually higher than that yielded by hemispherical analysis. Regression analysis may yield a higher DSF regression parameter to compensate for these differences.

Growing-season effects on old growth

Separate regressions were developed from the old-growth data set stratified by season (wet and dry). We defined the limits of the wet and dry season from data collected at the Wind River tree nursery near the Wind River Experimental Forest (Fig. 4). The dry season occurred as a period of relatively cloudless, stable weather during July, August, and September. The relatively unstable wet season occurred during the remainder of the year. We conducted our analysis in a manner similar to that for the age-class effects. Stratifying models by season reduced the variance (Tables 3A and 3B,

TABLE 3. Stepwise regression statistics

(A) Regression statistics for the four stands

Stand	Age-class	Season	Regression equation	T_{dif}/T_{dir}	Adj. R^2	F
Martha Creek	Mature	Dry	$Q_t = [(5.39 \times 10^6)$ ISF] + $[(2.98 \times 10^7)$ $DSF_m]$	0.18	0.912	68.3
Panther Creek	Mature	Dry	$Q_t = [(5.00 \times 10^6)$ ISF] + $[(3.63 \times 10^7)$ $DSF_m]$	0.14	0.973	250.9
McRae Creek	Old growth	Dry	$Q_t = [(6.42 \times 10^6)$ ISF] + $[(1.97 \times 10^7)$ $DSF_m]$	0.33	0.898	172.3
Trout Creek	Old growth	Dry	$Q_t = [(9.89 \times 10^6)$ ISF] + $[(2.74 \times 10^7)$ $DSF_m]$	0.36	0.949	354.1
McRae Creek	Old growth	Wet	$Q_t = [(7.56 \times 10^6)$ ISF] + $[(1.40 \times 10^7)$ $DSF_m]$	0.53	0.896	125.7
Trout Creek	Old growth	Wet	$Q_t = [(6.80 \times 10^6)$ ISF] + $[(1.97 \times 10^7)$ $DSF_m]$	0.34	0.964	541.4

(B) Regression statistics for the two age-classes, stratified by season

Age-class	Season	Regression equation	ISF/DSF	Adj. R^2	F
Mature	Dry	$Q_t = [(4.42 \times 10^6)$ ISF] + $[(3.47 \times 10^7)$ $DSF_m]$	0.13	0.955	287.2
Old growth	Dry	$Q_t = [(7.25 \times 10^6)$ ISF] + $[(2.36 \times 10^7)$ $DSF_m]$	0.31	0.903	357.7
Old growth	Wet	$Q_t = [(6.95 \times 10^6)$ ISF] + $[(1.64 \times 10^7)$ $DSF_m]$	0.42	0.917	387.1

NOTE: Regression equations are based upon eqs. 1 and 2, with regression parameters substituted for T_{dir} and T_{dif}. Q_t, mean total daily quanta per month; ISF, indirect site factor, which was uniform for all months of the year; DSF_m, direct site factor for the applicable month (regressions were calculated from monthly means). $p > F$ was 0.0001 for all regressions.

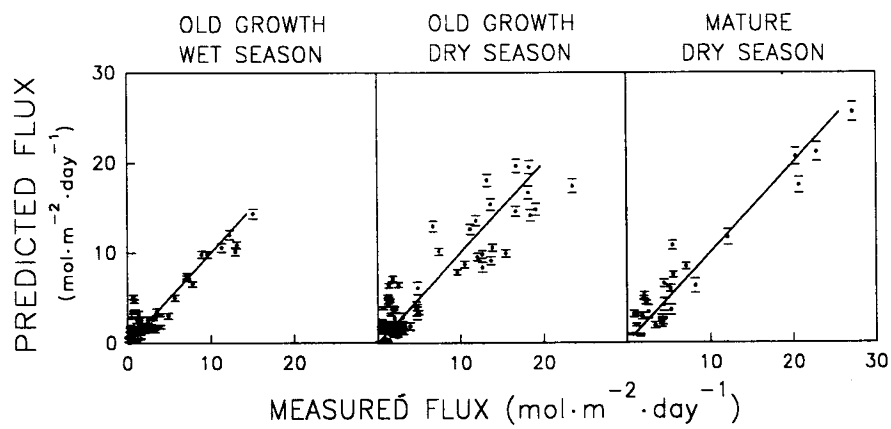

FIG. 5. Results of the regression analysis. Each data point represents the measured mean daily quanta for an individual month during the year compared with the flux predicted by the regression model and the standard error associated with that prediction.

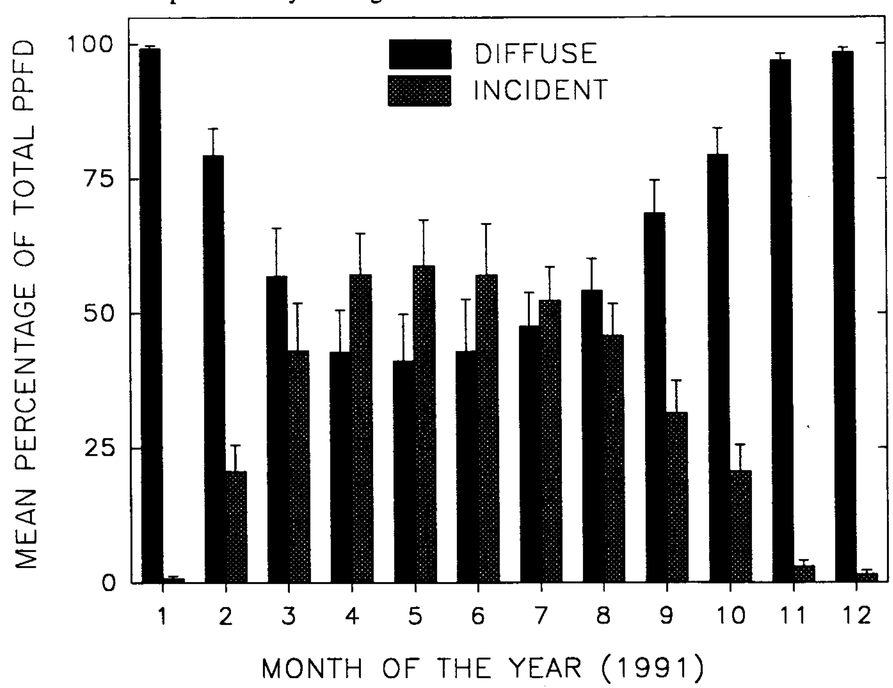

FIG. 6. Relative percentages of diffuse and direct flux in mean daily totals for the 12 months of the year. Means were derived from the two old-growth stands, using the respective wet and dry season models. Incident refers to direct-beam flux.

TABLE 4. Recommended weighting factors for flux estimates from hemispherical photograph analysis

Age-class	Season	Weighting factor	
		ISF	DSF
Old growth	Dry	0.23	0.77
	Wet	0.30	0.70
Mature	Dry	0.11	0.89

NOTE: These factors are recommended for within-stand or age-class comparisons only, based on the following equation: potential relative PPFD = [(weighting $factor_{ISF}$) ISF] + [(weighting $factor_{DSF}$) DSF].

Fig. 5). Regression equations calculated from the entire year's data set had an R^2 value 0.30–0.32 lower than the R^2 of those equations stratified by season.

We were concerned that the control and gap size 1.0 sites would dominate the old-growth dry-season regression models, since they contributed the majority of the data points. We calculated separate dry-season regression models stratified by sensor tye (permanent: control and gap size 1.0; temporary: gap size 0.2–0.6). The resulting parameters were very similar to each other, and differences in the slopes of the regression equations were not statistically significant.

Contributions of ISF and DSF parameters

PPFD under cloudy skies typically is dominated by diffuse radiation, whereas PPFD under a cloudless sky is dominated by direct radiation (Rosenberg 1983; Oke 1987; Lowry and Lowry 1989). It follows that eqs. 1 and 2 would be dominated by diffuse flux terms in cloudy weather and direct flux terms during clear weather. This is the case in our findings (Fig. 6). Although the magnitude of the estimates for T_{dif} (eq. 2 ISF parameters) are small compared with those for T_{dir} (eq. 2 DSF parameters) (Tables 3A and 3B), this appearance is misleading. Values for ISF are often larger than those for DSF, especially for the winter months, when sun angles are low.

Conclusions

Our results indicate that a close relationship exists for these forests between canopy openness, measured by hemispherical photographs, and measured PPFD. However, it is apparent that the effects of stand structure and composition and regional cloud cover must be considered by researchers working in multiple-aged forests experiencing variable weather.

Because weather variations produce great variability in the PPFD received by a forest canopy, those researchers and resource managers wishing to precisely estimate PPFD from hemispherical photographs should follow the techniques discussed above and calculate regressions that are specific to the site and time period desired. However, different sites or plots within stands or age-classes of interest may be compared by combining the ISF and DSF in a constant ratio (Table 4).

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