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Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests

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Abstract

Five methods for estimating the mean growing season percent photosynthetic photon flux density (PPFD) were compared to continuous measurements of PPFD throughout the growing season within a young bigleaf maple stand on Vancouver Island (Canada). Measured PPFD was recorded continuously as 10-min averages over the growing season (May 18–October 14, 1996) using 52 gallium arsenide phosphide photodiodes in the understory and a LI-COR quantum sensor (LI-190SA) in the open. Photodiodes were randomly located on a systematic grid of points and represented a wide range of above canopy openings which were classified into three different types of light environments: closed canopy, gaps of various sizes, and open canopy. Objectives of this study were to compare different methods for estimating the growing season %PPFD and to determine the efficiency of these methods in the three light environments. At each photodiode location, instantaneous light measurements using a Ceptometer on sunny days around noon and a LAI-2000 Plant Canopy Analyzer were made and hemispherical canopy photographs were taken. 10-min averages recorded by the photodiodes during completely overcast sky conditions were used as surrogate values for a method that uses instantaneous measurements on overcast days. Finally, a new light model (LITE) developed to estimate growing season %PPFD in a deciduous canopy was tested. All these five methods provided estimates of growing season %PPFD and are much less time consuming than continuous measurements of %PPFD using photodiodes. The three most accurate (r^2>0.89) methods to estimate the growing season %PPFD were the 10 min averages on overcast days, the diffuse non-interceptance calculated using the LAI-2000, and the gap light index (GLI) calculated from the hemispherical canopy photographs. These three methods performed similarly in each type of light environment. Although the relationship between the LITE model and the growing season %PPFD was good (r^2=0.79), the model systematically underestimated light transmission. The instantaneous sunny days around noon method was the least efficient method (r^2=0.68) for estimating the growing season %PPFD, although replacing instantaneous measures with the mean of two 10-min averages improved r^2 to 0.84. Estimates on sunny days tended to be low in low light and high in high light. Practical considerations such as equipment availability, cost, sampling and processing time, sky conditions, and the number of microsites to be sampled should be taken into account in the selection of the suitable method for a particular study.

Keywords: Light transmission; LAI-2000; Hemispherical photographs; Light sensor; Photodiodes; Light environments

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1. Introduction

Because of its role in photosynthesis and other plant processes, solar radiation between 400 and 700 nm (photosynthetically active radiation or PAR) is one of the most important resources for plants. Photosynthetic photon flux density in the corresponding waveband is the most commonly used unit to characterize this light quantity (Shibles, 1976) and is hereafter referred to simply as light. Light measurements have been used to characterize plant growth and morphology (Schoettle and Smith, 1991; Carter and Klinka, 1992; Lieffers and Stadt, 1994; Ackerly and Bazzaz, 1995; Parent and Messier, 1995), to estimate plant competition (DeLong, 1991; Cannell and Grace, 1993; Comeau et al., 1993), and to assess plant interactions (Aphalo and Ballaré, 1995). Light measurements are also useful to calculate leaf area index from canopy light transmission (Pierce and Running, 1988; Martens et al., 1993; Chen, 1996) and to document temporal changes in canopy structures (Hutchison and Matt, 1977a; Baldocchi et al., 1984; Rich et al., 1993).

Characterization of light in forest understories can be difficult due to spatial and temporal variability (Baldocchi and Collineau, 1994). Underneath a canopy, a single point receives both direct and diffuse light. Direct light comes from the solar disc and is highly variable in both space and time. Its availability at the forest floor is determined by the position of the solar track, location within gaps, gap size, canopy height, cloudiness, leaf phenology, and foliage movement due to wind (Anderson, 1970; Canham et al., 1990; Baldocchi and Collineau, 1994). Amounts of direct light penetrating to the forest floor also vary with time of day and year as solar altitude changes (Hutchison and Matt, 1977b). Conversely, diffuse light comes from all parts of the sky and is much more spatially (Anderson, 1964; Reifsnyder et al., 1971) and temporally (Messier and Puttonen, 1995) uniform than direct light under a forest canopy. Under completely overcast sky conditions light is 100% diffuse. The proportion of total light that is diffuse decreases with decreasing cloudiness to a minimum of 23% on clear days (Spitters et al., 1986). Light in the understory is also composed of direct light reflected or transmitted by vegetation (beam enrichment) (Hutchison and Matt, 1976; Vales and Bunnell, 1988) as well as reflected and transmitted diffuse light (Reifsnyder et al., 1971).

Various methods have been used to quantify this complex light environment in the understory. Ideally, light should be measured continuously for several days in order to sample the spatial and temporal complexity of the light environment. However, this is not practical for most research since it is time consuming, expensive, and limits the number of microsites that can be sampled. Consequently, several methods, which are less time consuming, have been proposed as a way to estimate the overall growing season light transmission. Most of these methods use percent of incident radiation in order to compare light availability under different conditions.

Characterizing the light environment via instantaneous measurement of light transmission on sunny days around noon has been very popular (DeLong, 1991; Carter and Klinka, 1992; Comeau et al., 1993; Brown and Parker, 1994; Smith and Riitters, 1994; Wünsche et al., 1995). Many points can be measured in the understory during this period assuming that sky irradiance above the canopy is similar for all measurements. More recently, hemispherical canopy photographs have been used to estimate the percentage of incident photosynthetic photon flux density (PPFD) transmitted through gaps to any particular point in the understory measured as percent of PPFD received in the open (Canham, 1988; Canham et al., 1990; Rich et al., 1993; Easter and Spies, 1994; Wünsche et al., 1995). Light transmission can be integrated for any specified period (daily, growing season etc.). Both diffuse and direct light components that are transmitted through the canopy to the point in the understory where the photographs were taken are also estimated. This method assumes that there are no significant seasonal changes in the canopy throughout the growing season (Pearcy, 1989). Messier and Puttonen (1995) proposed a new method to estimate light environments in the understory: instantaneous diffuse light transmission on overcast days. This method is based on the fact that under overcast sky %PPFD in any particular microsite is very stable throughout the day (Messier and Puttonen, 1995) and is representative of the mean daily %PPFD found under all sky conditions (Messier and Puttonen, 1995; Parent and Messier, 1996). Light transmission can also be estimated using a LAI-2000 Plant Canopy

Analyzer (Li-Cor, Lincoln NE, USA) since the diffuse non-interceptance (DIFN) calculated by this instrument is conceptually similar to the instantaneous diffuse light transmission obtained on overcast days. According to a recent paper, intercepted PAR estimated from DIFN values closely simulated daily temporal variations of light (Hanan and Bégué, 1995). Physically based models can also be used to estimate understory light using crown structure data (Norman and Welles, 1983; Grace et al., 1987; Pukkala et al., 1993). The LITE model (Comeau and MacDonald, 1998; Comeau et al., 1998) has been developed recently to estimate light transmission under deciduous canopy stands.

These five methods were compared to the %PPFD measured continuously with photodiodes from May 18 to October 14. The five methods all share the same characteristic: they are much less time consuming in the field than the continuous measurements of %PPFD throughout the growing season. It should be emphasized that it was not our intent to explain canopy transmittance, which is a function of sun inclination angle, leaf area index, and wavelength (Norman and Jarvis, 1974). Our intent was to compare different methods in order to provide reliable indexes, which could be quickly obtained, of growing season %PPFD reaching microsites along a wide range of light transmission. The two objectives of this study were (1) to compare different methods to estimate the growing season %PPFD in a deciduous forest stand; and, (2) to determine the efficiency of these methods in three types of light environments: open canopy, gaps of various sizes, and closed canopy. Additionally, the main advantages and disadvantages of the three most efficient methods are summarized.

2. Methods

2.1. Study site

The study was conducted on a site located approximately 13 km northeast of Port Alberni (49°N, 125°W) on Vancouver Island in the Coastal Western Hemlock biogeoclimatic zone of British Columbia, Canada during the summer of 1996. Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) and bigleaf maple (*Acer macrophyllum* Pursh.) were clearcut in 1988, and planted with Douglas fir and grand fir (*Abies grandis* (Dougl.) Lindl.) in 1989. After logging, maple resprouted and by 1995 the area had approximately 400 bigleaf maple clumps per hectare that were relatively evenly spaced. As part of a study of the effects of maple density on growth of understory conifers, ten 30 m×30 m plots were established and spaced to create densities ranging from 0 to 400 resprouting clumps per hectare in February 1996 (Thomas and Comeau, 1997). In April 1996, six of these plots were selected to provide a wide range of maple densities and light conditions. Stand structures for these six plots are shown in Table 1. Leaf area index was estimated using a LAI-2000 to provide a rough estimation of canopy density. Mean crown radius is the mean of four crown radii for each clump measured with a steel ruler to the nearest cm in the four compass directions. Diameter at breast height of each stem in clumps was measured using calipers.

2.2. Below canopy light measurements

A systematic grid of points consisting of 25 points (6 m spacing between points) was established in each

Table 1
Stand structures for each of the six 30 m×30 m plots in the bigleaf maple forest

Maple density (coppices/ha)	Estimated mean LAI (m^2 m^{-2})	Mean height (m)	Mean crown radius (cm)	Mean number of stems/clump	Sum of stem area (cm^2)
0	–	–	–	–	–
33	0.59	9.41	273.21	24	1947
133	1.46	9.05	262.52	23	4719
167	1.54	8.67	261.75	22	5529
300	2.13	9.57	242.38	18	8772
400	3.03	10.01	237.74	21	9962

plot, and of these ten were randomly selected for installation of photodiodes 2 m above the ground to measure PPFD. Photodiodes were installed at 2 m so that they would not receive shade from understory Douglas firs or other vegetation and because the LITE model estimates light at 1 m intervals from the ground to the top of the canopy (Section 2.5.5). Gallium arsenide phosphide photodiodes (Hamamatsu, model G2711-01, Middlesex, NJ, USA) were chosen because of their low cost and good spectral response between 300 and 680 nm (Pearcy, 1989; Pontailler, 1990). Photodiodes were placed flush within a hole on a 10 cm×10 cm plexiglass plate on top of a 2 m stake, leveled and connected to a CR-10 datalogger (Campbell Scientific, Logan, UT, USA) installed in the middle of each plot. Dataloggers were sealed in plastic pelican boxes with a desiccant and earth grounded for lightning protection.

2.3. Calibration of the below canopy photodiodes

Photodiodes were calibrated against quantum sensors (model LI-190SA, LI-COR, Lincoln, NE, USA) in both early and late summer. Before each calibration, photodiodes and quantum sensors were leveled. During the first calibration, the quantum sensors were left during a complete day beside the photodiodes to cover a wide range of zenith angles. However, for the late summer calibration only half a day was used because results of the first calibration showed that the r^2 between the two types of radiation sensors did not increase once a half day of data was logged. Instead of 10-min averages, hourly averages were used for the second set of calibration to attempt to minimize effects of extreme variation in light levels caused by sunflecks. Photodiodes were usually calibrated once in each of the early and late summer calibrations, however if the r^2 was lower than 0.95, diodes were recalibrated.

Linear regression analyses without intercept on each calibration generated a multiplier (conversion factor) to convert millivolt output from each photodiode to PPFD (μmol m^{-2} s^{-1}). Linear relationships between photodiodes and quantum sensors were usually very strong (r^2>0.99, n=43/52). If multipliers changed <5% between the first and second calibration period, the first multiplier was used. If the difference between the two multipliers was between 5% and 20%, a linear relationship was assumed between the first and second readings, and multipliers were adjusted accordingly based on the date (i.e. time since first calibration). A linear function was selected because the multipliers of the three photodiodes in the open (Section 2.4) decreased linearly during the summer. If multipliers changed more than 20% between the two calibrations, the corresponding photodiodes were discarded from the analyses, resulting in the loss of 8 of the original 60 photodiodes for analysis of growing season %PPFD. This ensured that only the best photodiodes were used since the faulty ones were discarded.

2.4. Above canopy light measurements

A quantum sensor (LI-190SA, LI-COR, Lincoln, NE, USA) and three photodiodes were installed at the top of a 13-m tree to record above canopy light. These four sensors were connected to a CR-10 datalogger installed at the base of the tree. Only the readings recorded by the quantum sensor were used as above canopy light readings. Three photodiodes were installed at this location to evaluate their stability over time. Calibrations with the quantum sensor showed that one photodiode above the canopy did not change and two photodiodes changed linearly during the growing season. It is on this basis that a linear weighting was selected to correct the multiplier of the below canopy photodiodes when the difference between the two multipliers was between 5% and 20%.

Below and above canopy PPFD was measured every second and stored as 10-min averages. Continuous measurements were recorded from May 18 to October 14, 1996 between 400 and 2100 hours (Pacific Time Zone) at the beginning of the summer and between 600 and 1800 hours at the end of the summer. The sum of below canopy PPFD recorded by each photodiode was divided by the sum of above canopy PPFD to calculate the measured %PPFD for each photodiode location. Since the measured %PPFD was calculated from continuous measurements during five months in the growing part of the year, it will be referred as growing season %PPFD hereafter.

2.5. Methods of light measurements

2.5.1. Instantaneous light transmission on sunny days around noon

A Ceptometer (model SF-40, Decagon Devices, Pullman, WA, USA) was used for measuring below canopy PPFD on sunny days around noon (between 1000 and 1400 hours, July 9–10 and August 14). Since the photodiodes were at the top of 2-m stakes, a ladder was used by the operator who leveled and centered the probe of the Ceptometer beside the photodiode. Two consecutive north–south readings were recorded followed by two consecutive east–west measurements. The average of these four readings was stored in the datalogger. Concurrently, PPFD was recorded in the open every 5 s and stored as 1-min averages on a LI-1000 datalogger (LI-COR, Lincoln, NE, USA) by a quantum sensor installed in a clearing at 500 m from the study site. Clocks in both the Ceptometer and the LI-1000 datalogger were synchronized beforehand. To cross calibrate the Ceptometer and the quantum sensor, 1-min averages were recorded by both instruments in the clearing before and after below canopy measurements. The ratio between the quantum sensor and the Ceptometer was calculated to correct Ceptometer readings. Ratios of synchronized below and above canopy readings gave instantaneous %PPFD, which was then compared to the growing season %PPFD.

2.5.2. Instantaneous light transmission on overcast days

Usually, this method requires quantum sensors both below and above the canopy (Parent and Messier, 1996). However, in the present study the 10-min averages recorded by the photodiodes below the canopy and above canopy readings measured by the quantum sensor were used. There was actually no point in measuring these values with other quantum sensors again, since these data were already available. It is important to note that 10-min average (mean of 600 readings) does not exactly correspond to the instantaneous light transmission on overcast days method (only one instantaneous reading) developed by Messier and Puttonen (1995) and Parent and Messier (1996). However, diffuse light transmission underneath the canopy is stable over time on overcast days (Anderson, 1970; Messier and Puttonen, 1995) and showed little variation with period of averaging (Reifsnyder et al., 1971). Hence, 10-min average light transmissions on overcast sky conditions were chosen as a surrogate to instantaneous light transmissions and should not affect the conclusions about the instantaneous light transmission on overcast days method. Three 10-min averages were selected, at the beginning, middle, and end of the summer (June 23, July 9, and September 13, respectively) under completely overcast sky conditions. Selected below canopy 10-min averages of PPFD measured by the 52 photodiodes were divided by the above canopy 10-min average PPFD recorded at the same time in the open to calculate the instantaneous light transmission on overcast days.

2.5.3. Instantaneous DIFN using the LAI-2000 Plant Canopy Analyzer

The LAI-2000 has a nearly hemispherical (300° field of view) lens in front of a group of five concentric silicon ring detectors causing each of them to see five different zenith angles (7°, 23°, 38°, 53°, and 68°). A filter rejects radiation above 490 nm minimizing the contribution of radiation scattered by foliage and allowing the calculations of actual measured diffuse light penetration (LI-COR Inc., 1992). At each photodiode, readings with the LAI-2000 were done with two different sizes of view restrictor on the lens. During the first period of measurements, the readings were taking using a 90° view restrictor during days of variable sky conditions (July 9–10). Below canopy readings were recorded holding the sensor at 2 m above the ground beside each photodiode. Leveling of the sensor was possible with the leveling bubble beneath the sensor. The LAI-2000 readings were collected for each compass direction (N, S, E, W) separately, and care was taken to record light readings opposite to the sun direction, so no direct sunlight reached the lens. The average of the four calculated DIFN values (DIFN90; mean of four directions totaling 360°) was used for the comparisons with the growing season %PPFD. Measurements were collected on a second period on an overcast sky morning (August 15) with a 270° view restrictor on the lens (DIFN270), in one direction (W) only. During both measurement periods, a synchronized LAI-2000 unit with the same size of view restrictor as the below canopy unit was mounted in the open to collect above canopy readings every 30 s. The orientation of the above canopy sensor was changed to match the orientation of the below canopy sensor for each set of measurements. Cross calibration of all the LAI-2000 units was done at the beginning of each session as outlined in the LAI-2000 Plant Canopy Analyzer instruction manual (LI-COR Inc., 1992), except that we reversed the roles of below and above canopy units.

2.5.4. Hemispherical canopy photographs method

Hemispherical canopy photographs were taken at each photodiode location on July 9, 1996, with a Nikon F601 camera equipped with a Nikorr 8 mm f/2.8 fisheye lens. The camera was mounted with the top to the north on a tripod at 150 cm above the forest floor and installed 15–30 cm from the south side of the photodiode stakes. Photographs were taken in the morning (725–1045 hours) to improve contrast and to minimize glare from direct sunlight (Canham, 1988; Easter and Spies, 1994). Even with this precaution 14 photos were retaken on September 5, 1996 because of insufficient contrast between sky and foliage.

After processing, negatives (Kodak® TMAX 100 black and white film) were scanned using a Sprint Scan 35 (Polaroid®, Santa Ana, CA, USA) with the Adobe Photoshop® program (version 2.5 for Windows®, Adobe Systems, San Jose, CA, USA). Since the tripod was shorter than the stakes, portions of the stakes could be seen in scanned photos. Stakes were erased from the photos with Photoshop® tools if there was no vegetation behind them, but remained in the picture if it was not clear whether it was sky or foliage in the background. When it was difficult to determine the photo perimeter, brightness was temporarily maximized using Photoshop® to identify pixels that had received light and were therefore part of the photo. Once this boundary was determined, two small white dots were placed at the outer east and west sides. To increase the distinction between vegetation and sky, most of the photos were modified with ‘brightness’ and ‘contrast’ functions in Photoshop®. Scanned photos were then analyzed to calculate the gap light index (GLI) using image analysis software developed by Canham (1995). The GLI ranges from 0, when there is no clearly defined gap visible in the canopy, to 100 for a site in the open (Canham, 1988). As suggested by Canham (1995), beam fraction and clear sky transmission were set at 0.5 and 0.65 and the hemisphere was divided in sectors with an azimuth and an altitude resolution of 30 and 20, respectively. The user-selected growing season length (May 1–October 31) was slightly longer than the one measured by the photodiodes. Each photo was analyzed twice by the same person to decrease subjectivity of the thresholding process. The average value of each photo was used for further calculations comparing the GLI to the measured growing season %PPFD.

2.5.5. LITE model

Directional LAI-2000 measurements were taken at each point in the systematic grid of points to provide data for calibration of the LITE model, version 1.6b (Comeau and MacDonald, 1998; Comeau et al., 1998). One reading was taken in each of the four cardinal compass directions with a 90° view restrictor on the lens. The model used this information to calculate leaf area contained in each cubic meter of space and map the distribution of leaf area in the simulated canopy. Field measurements such as height to crown base and canopy top height were entered in the model for each point of the sampling grid. Other input information included the azimuth reading of the orientation of each plot from true North (175° in this study) and coordinates of each point in the systematic grid. Hourly averages of above canopy PPFD recorded using the quantum sensor (Section 2.4) were used and partitioned into diffuse and direct components (Spitters et al., 1986) in the model. In the model, direct light penetration to the understory was determined from the location of the sun and was transmitted through the cubes that were affected by the canopy. Diffuse light was divided evenly among 480 segments of the sky (uniform overcast sky), and its transmission was summed over these 480 segments. For both direct and diffuse light, the amount of PPFD that reached a specific point beneath the canopy (Q_i) was determined with the application of Beers’ law:

$$Q_i = Q_0 \mathrm{e}^{-K\mathrm{LAI}} \qquad (1)$$

(Q_0) was light (direct or diffuse) above the canopy recorded using the quantum sensor. As suggested in the user’s manual (Comeau and MacDonald, 1998), the extinction coefficient (K) was set to 0.64 for bigleaf maple canopy and the leaf area (LAI) was calculated for each cubic meter of interest from the LAI-2000 measurements. The LITE model assumes that foliage is randomly distributed in each cubic meter of canopy space and randomly oriented. It is then reasonable to assume a constant K value and to estimate the penetration of light from each sector of the sky using the Beers' Law. This approach was utilised by Norman and Welles (1983) and by Grace et al. (1987). Growing season (May 18–October 14) total (direct plus diffuse) light transmission calculated at each photodiode location was compared with the measured growing season %PPFD. Photodiodes were installed on 2-m stakes because LITE estimates light transmission at the top of the cubic meter units used in the model and 2 m was high enough to read light above the understory vegetation (including planted conifers).

2.6. *Types of light environments*

To classify the light environment of the 52 photodiodes, canopy PPFD intercepted by the photodiodes over one day was plotted over time for a completely clear day (July 14, 1996). Graphs were categorized as closed canopy, gaps of various sizes, or open canopy light environments. The closed canopy light environment showed very low light levels during most of the day and received direct light (>1000 μmol m^{-2} s^{-1}) for less than 2 h. Measured growing season %PPFD varied from 5% to 29% in the closed canopy light environment. Open canopy light environments were those that had a pattern of daily light similar to the one in the open. Measured growing season %PPFD varied from 74% to 98% PPFD. Canopy gap light environments were those that could not be classified as either closed or open and received between 33% and 73% PPFD.

2.7. *Statistical analyses*

Linear regression analysis was performed to examine the relationship between the growing season %PPFD measured by photodiodes (dependent variable) and the light transmission estimated using the different methods (independent variable). Methods of light transmission with higher coefficients of determination were considered better estimators of the growing season %PPFD. To test if the slope of the linear regression of a particular method was significantly different from 1 (a slope of 1 results when estimates and observed values are identical), F tests were performed (SAS Institute Inc., 1990). In the case of the growing season light transmission estimated by LITE, a linearised form of the logarithmic function was used in the regression analysis (Sit and Poulin-Costello, 1994). For the overcast days method, an analysis of covariance (SAS Institute Inc., 1990) was performed on the three selected 10-min averages for each period (beginning, middle, and end of the summer) to determine if they were significantly different from each other. The linear relationship between the measured growing season %PPFD and the DIFN estimated using the LAI-2000 with the 270° view restrictor was done using data from only 50 photodiodes. Two data points were discarded because a test of influence performed during the linear regression analysis indicated that these photodiode locations had a strong influence on the slope and the residuals were not within the 95% interval confidence (SAS Institute Inc., 1990). To compare the coefficients of determination between methods within the same type of light environment, a comparison of variances (F test) was done on untransformed variables. The variables were left untransformed even though some did not have their residuals normally distributed to remain consistent among comparisons.

3. Results

3.1. *Comparison of methods*

Growing season %PPFD measured by the 52 photodiodes varied from 4.6% to 97.8%. Mean daily %PPFD was fairly stable over the growing season (Fig. 1), but was most variable at the beginning and end of the growing season (before day 170 and after day 250). At the start of the summer, the mean daily %PPFD was over 70 and decreased continually until reaching 54 (day 160). After day 160, mean daily %PPFD remained constant at about 54 with little fluctuation during mid summer, but large fluctuations after day 260.

Among comparisons between estimated growing season %PPFD and observed growing season %PPFD, the weakest relationship (r^2=0.68, P=0.0001) was obtained with the instantaneous light transmission calculated from ceptometer measurements on sunny

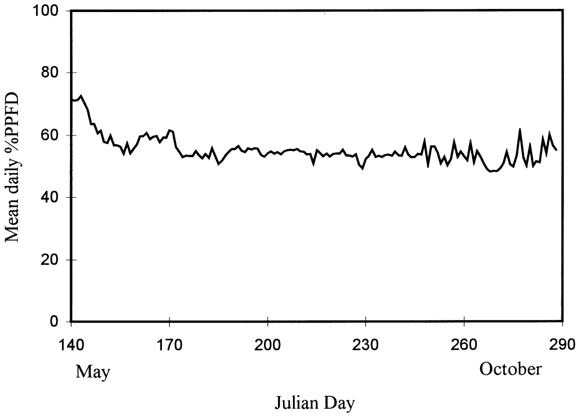

Fig. 1. Mean daily %PPFD measured using 52 photodiodes over the growing season (May 18–October 14, 1996) at 2 m above the ground in a bigleaf maple canopy understory.

days around noon (Table 2; Fig. 2(a)). This method underestimated %PPFD at low light levels (<50 %PPFD), but overestimated it at high light levels. Most of the estimated light transmission values calculated with this method were concentrated below 30% and above 80% PPFD (Fig. 2(a)). Standard errors of the intercept and slope were the highest among all methods. Since one instantaneous measurement of light transmission was poorly correlated with the growing season %PPFD, we also tested the approach used by Carter and Klinka (1992) to use the average of two 10-min light transmissions recorded using the photodiodes at 1000 and 1400 hours on a completely clear day (July 14). The relationship was improved (r^2=0.84, P=0.0001), but the slope was still significantly different from 1 and the intercept different from 0 (Table 2, Fig. 2(b)).

Strong relationships were found between the 10-min averages on overcast days and growing season %PPFD for the three periods during the start, middle, and end of summer (r^2>0.89–0.92, P=0.0001) (Table 2). Moreover, the intercepts were near zero (P>0.0519) and the slopes did not differ significantly (P>0.16) from 1 for these three overcast sky periods, indicating good comparability between this method and growing season %PPFD. Analysis of covariance showed that intercepts and slopes were not significantly different (P>0.43) among the three overcast sky periods, so only the relationship between light transmission measured in the middle of the summer and the growing season %PPFD is shown in Fig. 2(c) (r^2=0.92). Estimates were more variable between 20% and 70% than at lower or higher values (Fig. 2(c)).

Table 2
Regression coefficients (standard error in parentheses) for comparison of the different methods (independent variables) used to estimate the growing season %PPFD (dependent variable)

Method	Intercept	Slope	r^2	Root mean square error	n
Sun$^{\text{inst}}$	21.92 (3.81)	0.586s (0.056)	0.68	0.1570	52
Sun$^{\text{10 h,14 h}}$	10.79 (3.14)	0.721s (0.044)	0.84	0.1127	52
Overcast$^{\text{b}}$	5.45ns (2.73)	0.935 (0.046)	0.89	0.0921	52
Overcast$^{\text{m}}$	4.47ns (2.38)	0.974 (0.040)	0.92	0.0798	52
Overcast$^{\text{e}}$	1.64ns (2.54)	0.960 (0.041)	0.91	0.0815	52
DIFN90	5.50 (2.42)	0.960 (0.041)	0.91	0.0825	52
DIFN270	6.26 (2.57)	0.869s (0.040)	0.91	0.0857	50
GLI	7.15 (1.74)	0.983 (0.031)	0.95	0.0618	52
LITE	93.16 (3.23)	0.313s (0.022)	0.79	0.1264	52

Sun$^{\text{inst}}$=instantaneous light transmission measured on sunny days between 1000 and 1400 hours; Sun$^{\text{10 h,14 h}}$=average of two 10-min light transmissions recorded using the photodiodes at 1000 and 1400 hours on a completely clear day; overcast$^{\text{b,m,e}}$=instantaneous light transmission (10-min averages) measured on three cloudy days at the beginning, the middle, and the end of the summer, respectively; DIFN90=diffuse non-interceptance measured using a 90° view restrictor on the LAI 2000 lens (average of four compass directions); DIFN270=diffuse non-interceptance measured using a 270° view restrictor on the LAI 2000 lens; GLI=gap light index calculated from analysis of hemispherical canopy photographs; LITE=growing season light transmission estimated from the light model. All intercepts are significantly different (P<0.05) from zero (except as noted, ns=non-significant). All slopes are not significantly different (P<0.05) from 1 (except as noted, s=significant). Note that the general equation for the methods is $y = a + bx$, except for the LITE model where $y = (a + b\ln(x/100)) \times 100$.

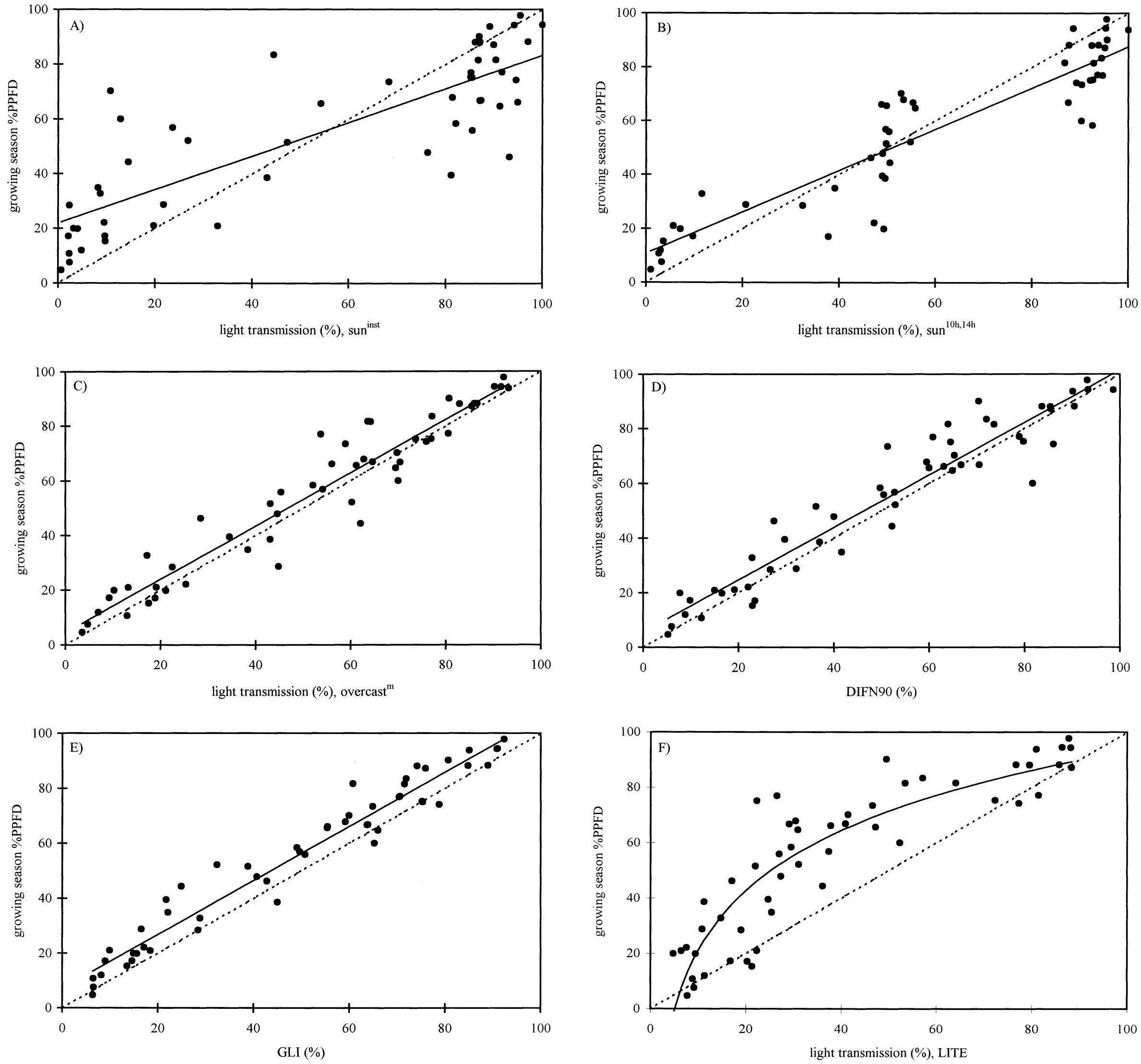

Fig. 2. Relationships between the growing season %PPFD measured with photodiodes and the light transmission estimated using different methods. See Table 2 for abbreviations and regression coefficients. The dashed lines show a 1:1 relationship.

The DIFN90 calculated using the LAI-2000 was highly correlated (r^2=0.91, P=0.0001) with the growing season %PPFD. Although the intercept was higher than 0 (P=0.0275), the slope did not significantly differ from 1 (P=0.3393) (Table 2). As with the overcast days method, light estimates were more variable in the middle range of light transmission (Fig. 2(d)). The relationship between the DIFN270 and the measured growing season %PPFD was also strong (r^2=0.91, P=0.0001), but the intercept was significantly higher than 0 (P=0.0185) and the slope was significantly different from 1 (P=0.0020).

There was a strong relationship (r^2=0.95, P= 0.0001) between GLI and the growing season %PPFD (Table 2). GLI underestimated growing season %PPFD by about 7% (P=0.0001) in all light environments (Fig. 2(e)). GLI had the lowest standard error for its intercept and one of the lowest for its slope.

Table 3
Linear regression coefficients (standard error in parentheses) for comparison of the different methods (independent variables) used to estimate the growing season %PPFD (dependent variable) in three types of light environments. See Table 2 for abbreviations

Light environments	Intercept	Slope	r^2	Root mean square error	*n*
Closed					
Overcast^m	8.79 (2.24)	0.531 (0.116)	0.61	0.0442	14
DIFN90	6.77 (2.75)	0.660 (0.151)	0.58	0.0456	14
GLI	4.79ns (2.71)	0.959ns (0.186)	0.66	0.0410	14
Gaps					
Overcast^m	20.18 (6.29)	0.666 (0.115)	0.62	0.0763	21
DIFN90	23.06 (6.19)	0.629 (0.116)	0.59	0.0795	21
GLI	20.49 (4.41)	0.730 (0.089)	0.77	0.0593	21
LITE	29.28 (6.09)	0.826ns (0.184)	0.49	0.0883	21
Open					
Overcast^m	44.55 (9.70)	0.509 (0.121)	0.51	0.0534	17
DIFN90	49.33 (10.60)	0.444 (0.130)	0.40	0.0593	17
GLI	36.13 (12.10)	0.622 (0.153)	0.49	0.0544	17
LITE	71.15 (5.69)	0.202 (0.079)	0.26	0.0659	17

All intercepts are significantly different ($P<0.05$) from zero (except as noted, ns=non-significant). All slopes are significantly different ($P<0.05$) from 1 (except as noted, ns=non-significant). Coefficients of determination (r^2) in the same type of light environment are not significantly different according to a test of comparison of variances ($P=0.05$) except GLI that had a significantly higher r^2 than LITE in gaps light environment. Note that the general equation is $y = a + bx$.

The transmission estimated by the LITE model was correlated ($r^2=0.79$, $P=0.0001$) with the growing season %PPFD, but the relationship was curvilinear (Fig. 2(f)). The model underestimated light over most of the data range. The underestimation was most pronounced between 20% and 80% PPFD.

3.2. *Efficiency of methods in the three different types of light environments*

Relationships were not significant ($P>0.05$) for the sunny days around noon method within each of the three types of light environments and for the LITE model in the closed canopy light environment. For most of the methods, intercepts and slopes were significantly different from 0 and 1, respectively ($P<0.05$) (Table 3). Within each type of light environment, coefficients of determination were not significantly different among these methods (test F, $P>0.05$). The only exception was in the canopy gap light environment where the hemispherical canopy photographs method (GLI) gave better estimates of the growing season %PPFD than the LITE model ($r^2=0.77>r^2=0.49$, $P=0.05$). All methods tended to underestimate the growing season %PPFD (Fig. 3).

4. Discussion

4.1. *Theoretical considerations*

Mean daily %PPFD changes over the growing season were similar to the ones reported by Hutchison and Matt (1977b) and Baldocchi et al. (1984) in a deciduous canopy. They showed that light penetration in the canopy is higher in the spring because the new leaves are not fully expanded and then remains fairly stable throughout the summer as the canopy is rather static. At the beginning of the fall, light penetration increases because of leaf abscission and decreased canopy density. Day-to-day variations in the mean daily %PPFD were caused by sky conditions.

Five methods were tested in this study for estimating growing season %PPFD. 10-min average of light transmission on overcast days, LAI-2000 (DIFN90), and hemispherical canopy photographs were the three best methods because they had the highest coefficients of determination ($r^2 \geq 0.89$), their slopes were not significantly different from 1 and their intercepts were near 0 (Table 2). Relationships were not as good when data was compared among the three different types of light environment (Table 3), and no one method was clearly better than the others.

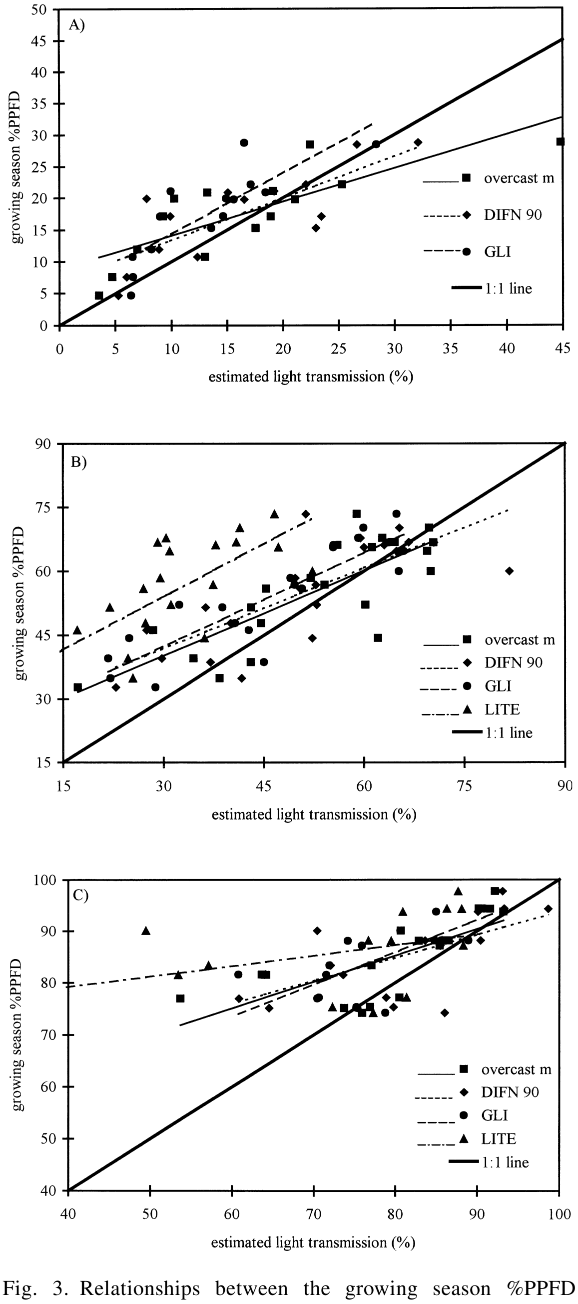

Fig. 3. Relationships between the growing season %PPFD measured with photodiodes and the light transmission estimated using different methods in closed canopy (A), gaps of various sizes (B), and open canopy light environments (C). See Table 2 for abbreviations and Table 3 for regression coefficients. The 1:1 lines show a linear relationship. Note that for the LITE model two points are not shown in the open canopy light environment.

As reported by Messier and Puttonen (1995), one instantaneous measurement of light transmission on sunny days around noon is not a good method to estimate daily or growing season %PPFD. Direct light penetration to the understory is modified by vegetation cover that falls along the sun's path, and spatial variation in %PPFD between adjacent understory microsites on clear days is high for short-term observations, but decreases as the period of integration increases (Reifsnyder et al., 1971; Messier and Puttonen, 1995). We observed that values tend to be above the 1:1 relationship line at low light, below the line at high light, and very scattered in between. At low light, the photodiodes tended to be situated in direct shade from a maple clump, so that at noon few sunflecks reached the sensors, causing instantaneous light measurements that underestimate observed growing season %PPFD. In high light environments, photodiodes were in gaps, so that at noon they received direct light causing instantaneous values to overestimate the observed growing season %PPFD. However, the average of two 10-min light transmissions recorded using the photodiodes at 1000 and 1400 hours on a completely clear day gave better estimates of the growing season %PPFD. In comparison with instantaneous light transmission, this method decreases variations caused by sunflecks and movement of the sun on clear days (Carter and Klinka, 1992). However, the slope was significantly different from 1 and the intercept was significantly different from 0.

Parent and Messier (1996) reported that instantaneous measurements can be taken any time during the day if the sky is completely overcast. In this study, using 10-min averages instead of instantaneous estimates, we have shown that there is little difference among early, mid, or late summer measurements, as long as the deciduous canopy structure remains stable (from the end of June until the middle of September in these canopies). Ten-minute averages taken on overcast days using either quantum sensors or LAI-2000 record only diffuse light transmission and are both highly correlated to the growing season %PPFD. These results are consistent with the findings of Messier and Puttonen (1995) and Parent and Messier (1996) who reported that instantaneous light transmission recorded during overcast sky periods are representative of the mean daily %PPFD in any particular microsites. Moreover, diffuse light beneath the canopy is very uniform and measurements show very little variation when considering 5-min or full day averages (Reifsnyder et al., 1971). Although some concerns have been raised regarding the accuracy of the instantaneous light transmission on overcast days method in and around gaps (Stadt et al., 1997), this study demonstrates that this method is at least as good as hemispherical canopy photographs or LAI-2000 measurements (Table 3; Fig. 3).

Under spruce and birch canopies in the Swiss Alps, DIFN recorded on completely overcast days with the LAI-2000 (no view restrictor) was highly correlated to light transmission calculated with hemispherical canopy photographs (Thormann, 1997). In the present study, the LAI-2000 was better used with the 90° view restrictor (mean of four directions totaling 360°) than with the 270° view restrictor. Use of a 270° view restrictor is suggested when doing leaf area index measurements to mask off the portion of the sky where the sun or the operator is located (LI-COR Inc., 1992). However, the portion of the sky missed with this restrictor may have contributed to the slope being different from 1 and the intercept being higher than 0 in light transmission estimates. In practice, the DIFN (LAI-2000) method resembles that of the instantaneous light transmission on overcast days, except that the LAI-2000 measures only non-transmitted or reflected diffuse light. Consequently growing season %PPFD would tend to be underestimated, and therefore the intercept would be higher than zero, as was found in our study.

High accuracy in estimating growing season %PPFD with hemispherical canopy photographs agrees with other studies (Chazdon and Field, 1987; Rich et al., 1993; Easter and Spies, 1994; Wünsche et al., 1995). This method underestimated the growing season %PPFD because the tripod holding the camera was shorter than the stakes on which the photodiodes were installed. Thus, the portion of sky blocked with vegetation was greater than if the camera had been at the same height as the photodiodes. Additionally, portions of stakes were sometimes evident on the photos as discussed above. Consequently, the portion of visible sky on the photos, and therefore light transmission, may have been underestimated. Moreover, this method does not take into consideration beam enrichment (light reflected and transmitted by foliage).

Over most of the data range, the LITE model underestimated growing season %PPFD even though the r^2 was fairly high. There are several possible causes for this bias. The canopy model and data used may have not been able to recognize small gaps in the bigleaf maple canopy. The constant extinction coefficient of 0.64 used in the LITE model may have been too high. Little information is available on light penetration from different angles and on arrangement and orientation of leaves in maple or other canopies. Consequently, the use of a constant extinction coefficient in the LITE model is used as a first approximation since studies show that it changes with different canopy layers, sun inclination, sky conditions (Norman and Jarvis, 1974), stand age, and stand structure (Brown and Parker, 1994). Beers' law and LAI-2000 both assume randomness of foliage distribution in the canopy. This assumption is reasonable for individual cubic meter cells in the canopy, but is not valid for entire canopies (Myneni et al., 1986; Smith et al., 1993). Since LAI-2000 readings in the field were part of data acquisition to run the model, it would be better to use DIFN calculated using the LAI-2000 than the growing season light transmission estimated by the light model. However, the model has the advantage to estimate light transmission between light reading locations and at different canopy heights. It also provides a permanent record of the simulated canopy stand which is based on the leaf area index of each cubic meter of canopy. If LAI-2000 readings are done every year, the model may be useful for examining temporal variations in canopy structure such as variation of horizontal and vertical leaf area distribution.

We compared four methods in three different types of light environment to determine if one method was better at estimating growing season %PPFD for any particular type. All the methods performed similarly in a given type of light environment. The only exception was GLI that gave better estimates than the LITE model in gaps. Compared to results obtained from analysis of the whole dataset over the full range of light transmission, the r^2 of each method using data from each of the three different types of light environment was low. It may be because of the low number of samples per light environment or to the fact that light measurements were only taken in a restricted range of light transmission. However, if one is interested in measuring light in a given type of light environment, the three best methods were equally effective at estimating growing season %PPFD. Hemispherical canopy photography is a popular method and is usually considered better than instantaneous light measurement methods because it takes into account shifts in solar elevation through the summer (Canham, 1988; Rich et al., 1993). However, in this study hemispherical canopy photography was not better at estimating growing season %PPFD than the two instantaneous methods that measure diffuse light for any given type of light environment. It is noteworthy that for validation of the GLI/C program, Canham (1988) used light measurement points in and around canopy gaps where the light transmission was below 20%. This situation is similar to the closed canopy light environment in this study (growing season %PPFD between 4 and 29) in which the intercept of the regression analysis was not significantly different from 0 (intercept=4.792, P=0.102) and the slope was not significantly different from 1 (slope=0.959, P=0.830). However, Canham's coefficient of determination was much higher (r^2=0.86) than the one found in this study for the closed canopy light environment (r^2=0.66).

The three best methods to estimate the growing season %PPFD differ in one important characteristic. Both GLI and DIFN calculated using the LAI-2000 read only light that comes unimpeded from the sky. GLI considers only light that penetrates directly through openings in the canopy (Canham et al., 1990) while the lens on the LAI-2000 has a filter that blocks light higher than 490 nm, which corresponds to the wavelengths where most of the scattering by the foliage occurs (LI-COR Inc., 1992). On the other hand, the instantaneous light transmission on overcast days method considers diffuse light that penetrates directly through openings in the canopy as well as transmitted light, reflected light, and beam enrichment. Beam enrichment, which is not measured by either the GLI or the LAI-2000 accounts for a significant portion of understory light in deciduous (Hutchison and Matt, 1976) and coniferous forests (Vales and Bunnell, 1988). Understories of shade tolerant canopies receive a fair amount of PAR in the form of beam enrichment (40% of total understory PAR) compared to locations beneath shade-intolerant species (around 15%) (Canham et al., 1994).

4.2. Practical considerations

In addition to examining the theoretical aspects, some practical considerations in the selection of methods are summarized in Table 4. Only three best methods (highest r^2) are presented. Martens et al. (1993) also discussed practical considerations related to the case of hemispherical canopy photography and LAI-2000 instruments.

Instantaneous measurements on overcast days has the lowest equipment cost of any method. Many light readings can be done quickly in the field by one person. Parent and Messier (1996) reported that more than 100 instantaneous measurements can easily be taken in 1 h. Data processing is simple and rapid. However, this method is not flexible regarding sky conditions because the solar disc has to be completely covered and the sky completely overcast with relatively little wind. Often time and effort are lost because of unsuitable conditions.

DIFN calculated using the LAI-2000 is the most expensive method, but has other uses such as measuring leaf area index, mean leaf angle, and the directionality of unimpeded sky light below 490 nm. When one unit is installed in the open to record above canopy readings, many below canopy readings can be quickly done in the understory. Since we used a 90° view restrictor on the lens, we could make measurements at any time during the day, regardless of sky conditions (except when raining). The only limitation during measurements was to direct the lens away from the sun location. For example, westward measurements were done in the morning when the sun was rising on the east side. Unfortunately, this also requires revisiting each sample point four times. In this study, the results showed that using a 270° view restrictor on the lens and doing only one set of measurements was not as effective as the averages of the four cardinal compass readings recorded with a 90° view restrictor (Table 2). A possible solution may be to use a 180° view restrictor and to do two sets of measurements in order to decrease sampling time. A 180° view restrictor would mask the sun so that light readings could be done on sunny or overcast days.

Equipment required for acquiring and analyzing hemispherical canopy photographs are fairly expensive, but the camera and the scanner also have other uses. Image analysis software is usually available free

Table 4
Practical considerations for light transmission measurements using the three methods that correlated the best with the growing season %PPFD

Consideration	Overcast days	LAI-2000 Plant Canopy Analyzer (DIFN)	Hemispherical canopy photographs (GLI)
Cost of instrument in US currency, LI-COR products as suggested in February 1998	\$2250 (total) Quantum sensors LI-190SA (2 units) 2×\$300=\$600 LI-COR dataloggers, LI-1000 (above)=\$1150, LI-250 (below)=\$500	\$9560 (total) LAI-2000 (2 units) 2×\$4780	\$6250 (total) fisheye lens (8 mm)=\$3100, camera=\$650, scanner/software=\$2500
Sampling time/Microsite	0.5 min	0.5 min×4, 1 set of readings for each compass direction	5 min
Processing considerations	Fast Uses Excel spreadsheet	Fast Uses software included with LAI-2000	Slow Must scan and analyze each negative (10 min/negative)
Sky conditions	Solar disc has to be completely invisible and sky completely overcast with little wind	Clear or overcast sky (must use view restrictor on clear days)	Overcast sky anytime Dawn or dusk on clear days
Information output	Instantaneous diffuse light	Instantaneous diffuse non-interceptance	Growing season gap light index
Other possibilities of instrument	Sunfleck contribution on clear days	Instantaneous diffuse light (<490 nm) transmission at five zenith angles Leaf area index Mean leaf angle	Direct and diffuse light transmission Percent of open sky Geometry of canopy Photo can be reanalyzed with other software

of charge. Markham and Mailly (1996) compared light transmission calculated from four popular hemispherical image analysis programs (GLI/C, Hemiphot, Solarcalc, and Sunshine) and concluded that these four programs gave similar results. Using hemispherical canopy photography is time consuming both in the field and during data analyses. Consequently, it may not be the most suitable method if large numbers of readings are required. When preparing scanned images users must maximize contrast between sky and foliage, which can be hampered if too much light reaches the film. Consequently, photographs must be taken on overcast days or at dawn and dusk when the sun is near the horizon. However, photographs provide a permanent record of the canopy and can be reanalyzed with different software to calculate new information such as direct and diffuse light transmission and percent of open sky (Rich et al., 1993; Canham, 1995), mean directionality of diffuse and direct light (Ackerly and Bazzaz, 1995), and sunfleck frequency distribution (Markham and Mailly, 1996).

5. Conclusions

Several quick methods can be used to estimate microsite growing season %PPFD with various levels of accuracy. The simplest method, instantaneous light transmission on sunny days around noon, was not found to predict growing season %PPFD with enough accuracy. The LITE model tended to underestimate growing season %PPFD in all light environments. The three other methods (10-min averages on overcast days, DIFN calculated using the LAI-2000, and hemispherical canopy photography) were equally good at estimating growing season %PPFD in all three light environments. When choosing an appropriate method one must consider factors such as equipment availability, cost, sampling and processing time, sky conditions, and the number of microsites to be sampled.

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