

CHAPTER III

A Comparison of Light Transmittance Estimation Methods in an Open- Canopied Coniferous Forest

ABSTRACT

The reliability of different indirect measurements of light transmittance has been documented extensively for closed canopy forests, yet limited research has focused on the accuracy and precision of these methods in open canopied forests. In this study, five methods for estimating mean annual percent photosynthetic photon flux density (PPFD) were compared to continuous measurements of PPFD throughout the growing season within a mature longleaf pine (*Pinus palustris* Mill.) forest. Effectiveness of these methods to estimate daily %PPFD was examined under different sky conditions at different times of the year. Methods evaluated were (i) 10-minute averages recorded by photodiodes during overcast sky conditions were used for as a surrogate values for a method that uses 10-minute average percent above canopy $\text{PPFD}_{\text{overcast}}$, (ii) weighted canopy openness, (iii) gap fraction, (iv) Gap Light Index (GLI), and (v) calibrated Gap Light Index. Measured PPFD was recorded continuously as 20-minute averages from June until December using gallium arsenide phosphide photodiodes in the understory and a Li-Cor quantum sensor (LI-190SA) in an open field. Photodiodes were placed at 1 meter above the ground within plots that spanned a gradient of overstory density. Hemispherical photographs were taken at each location at the same height. I found that the different methods tested performed differently depending on the sky condition and time of year the sample was taken. The 10-minute average %PPFD_{overcast} was an efficient method but the precision and accuracy decreased when solar altitude was at its maximum and minimum (eg. June and December). Both weighted canopy openness and gap fraction were efficient methods in the estimation of mean annual %PPFD, but gap light index performed better than these hemispherical photograph estimates. Accuracy of daily %PPFD was strongly affected by solar altitude and sky condition for the 10-minute average %PPFD_{overcast}, weighted canopy openness, and gap fraction. The 10-minute average %PPFD_{overcast} method estimated %PPFD on overcast days well, but its accuracy decreased when estimation of clear day transmittance was needed, especially during days will lower solar altitudes. Weighted canopy openness and gap fraction performed best on overcast days, but had lower accuracy when clear day transmittance was estimated. Gap light index was shown to be very effective in estimating %PPFD for all sky conditions and time periods. The moderate r^2 values for all the estimates, especially on clear days,

suggest that beam enrichment is an important component in the understory light environment in a longleaf pine forest.

INTRODUCTION

In forested ecosystems, light is a key resource in the regulation of seedling establishment, persistence, and growth; thus, understanding how canopy structure regulates the spatial and temporal variation in light quantity is important to elucidating patterns in stand dynamics. While variation in canopy structure and its effect on light has been studied in closed-canopied forests, the manner in which trees in open canopied forests regulate light quantity and seedling response has not been extensively investigated.

The manner that overstory canopies influence quantity of light varies depending upon the extent that the light environment is dominated by direct versus diffuse radiation. The intensity of direct light beam radiation is dependent upon the changing position of the daily solar track and the solar altitude throughout the year (Hutchison and Matt 1977). Penetration of direct light to the understory is dependent upon the location of a canopy opening, the size of the opening, canopy height, and cloudiness (Anderson 1970, Canham *et al* 1990, Baldocchi and Collineau 1994). Diffuse light emanates from the entire hemisphere of the sky and penetrates the forest canopy from all directions uniformly (Parent and Messier 1996). Thus, both direct light and diffuse light are spatially and temporally variable in the forest understory, but in different ways depending on the characteristics of the canopy structure.

Endler (1993) classifies closed-canopied forests as forest shade light habitats characterized as having very small or few gaps in which most of the incident light is either reflected from or transmitted through the vegetation. Although some direct light can reach the understory through the small gaps that are present in the canopy, it is in limited quantities. Thus, the understory light environment in the forest shade light habitat is composed of diffuse light with limited quantities of direct light.

The light environment of the open-canopied forests differs vastly from those of the forest shade light habitat. Open-canopied forests are classified as woodland light

habitats, in which there are two types of light environments: woodland shade and large gap (Endler 1993). Woodland shade receives a significant fraction of incident light from the sky but with no direct light from the sun. Light in the large gap is mostly from direct sunlight and open sky. Thus, the understory light environment of a woodland habitat is composed of a mosaic of direct and diffuse light.

As a result of changes in sun altitude and sky conditions throughout a growing season, this mosaic of direct and diffuse light changes temporally and spatially and is difficult to quantify (Baldocchi and Collineau 1994). To adequately describe the spatial and temporal light characteristics of an understory environment at spatial scales relevant to tree regeneration and seedling growth, measurements need to be taken over a long period of time at many microsites. Multi-channelled dataloggers and gallium arsenide phosphide (GASP) photodiodes have been used to directly measure temporal and spatial variability in the understory light environment over long periods of time (days to weeks) and under varied sky conditions (Chazdon and Fetcher 1984, Chazdon and Field 1987, Rich *et al* 1993, Easter and Spies 1994, Gendron *et al* 1998). However, this technique is expensive, time consuming, and has inherent limits for multiple microsite sampling (*i.e.* length of wires connecting light sensor to datalogger). More often, indirect measurements of light transmittance have been utilized to characterize understory light environments.

Recently, a method proposed by Messier and Puttonen (1995) has been utilized by many investigators to estimate light transmittance (Parent and Messier 1996, Comeau *et al* 1998, Gendron *et al* 1998). Messier and Puttonen (1995) proposed light transmittance is stable throughout an overcast day, thus an instantaneous measurement of light on an overcast day would be representative of the mean daily %PPFD (photosynthetic photon flux density). Parent and Messier (1996) confirmed this proposal reporting a strong linear relationship ($r^2=0.969$) between three instantaneous measurements of %PPFD on an overcast day and mean daily %PPFD measured continuously on an overcast day. In addition, they also reported a strong linear relationship ($r^2=0.862$) between mean daily %PPFD measured on an overcast day and a clear day (Parent and Messier 1996). Based

on these findings, they suggest that instantaneous measures of %PPFD obtained under completely overcast sky conditions are representative of the mean daily %PPFD for both sky conditions.

This method has been subjected to criticism for a variety of reasons (Stadt et al 1997). One of the requirements for this method is that the solar disk is obscured and the sky condition homogeneously overcast, limiting the practicality of the measurement, particularly in locations that rarely receive this type of sky condition. Another concern is that this method implies that the spatial distribution of the canopy openness is trivial (Stadt et al 1997). However, the interaction of the distribution of canopy openness and solar path influence the amount, variation, and type of light available in the understory. Canham et al (1999) reported that the majority of solar radiation that penetrated the canopy at their study site (55° N) occurred between solar angles of 35°-60° and that stand-level canopy openness for several coniferous species increased linearly from the horizon to directly overhead. Canopy openness at the summer solstice (65°) was 20-45%, at the equinox (41°) it was 10-30%, and at the winter solstice (18°) it was 3-15%. Because canopy openness differed at these time periods and the probability of direct sunlight penetrating the canopy increases with greater canopy openness and higher solar angles, the amount of light that reaches the understory would differ for these different time periods. Therefore, an instantaneous light measurement taken at the summer solstice intended to estimate annual transmittance might overestimate while measurements taken at the winter solstice might underestimate.

Instantaneous measurements of %PPFD on overcast days may be acceptable for closed-canopied forests, which have a uniform distribution of foliage and branches and low percentages of direct light penetration, but are likely to be more problematic for other forested systems that have clumped distributions or heterogeneous canopies (Stadt et al 1997) that receive large amounts of direct light. Gendron et al (1998) reported that when this method was used in areas of heterogeneous canopies (defined as gaps 30-74% open), there was a decrease in the strength of the relationship between instantaneous %PPFD

and growing season %PPFD and that hemispherical photographs performed slightly better under these conditions.

Hemispherical photography is a technique used quite frequently to characterize the spatial and temporal characteristics of understory light (Anderson 1964, Chazdon and Field 1987, Pearcy 1989, Canham *et al* 1990, Rich *et al* 1993, Whitmore *et al* 1993, Palik *et al* 1997, Comeau *et al* 1998, Gendron *et al* 1998). Hemispherical photography incorporates the spatial distribution of the canopy structure to estimate light transmittance. Commonly used estimates derived from hemispherical photography include weighted canopy openness, gap fraction, and gap light index. Weighted canopy openness is a measure of the sum of the proportion of visible sky in a given sky sector. Openings that are closer to the zenith are weighted heavier than those near the horizon. Gap fraction is a measure of the sum of the proportion of the visible sky in the entire hemisphere. Both weighted canopy openness and gap fraction ignore the contribution of beam-enriched light and the interaction of the solar path with the canopy structure. Therefore, these estimates would be better predictors when the understory is dominated by diffuse light than direct light. Although gap light index ignores beam enrichment, it takes into consideration the changing solar altitude, canopy structure, and the path of the sun over an entire year in the calculation of light transmittance. This method has been shown to yield strong correlation between direct sensor measurements and photograph estimation of PPFD for periods ranging from minutes to weeks have been reported for a number of closed-canopied forest types (Chazdon and Field 1987, Becker 1989, Rich *et al* 1993, Whitmore *et al* 1993, Easter and Spies 1994, Comeau *et al* 1998).

Based on the difference in light attenuation among different forest types, the conclusions based on studies of the accuracy of different light measurement methods performed in the forest shade light habitats can not be carelessly applied to open-canopied systems. The canopy structure of the longleaf pine (*Pinus palustris* Mill.) ecosystem has been characterized as an open, park-like savanna forest composed of mosaics of multi-aged patches of longleaf pine trees with a diverse understory of grasses and herbs (Schwarz 1907). Typical canopy closure averages only 50% in second-growth

stands (Palik *et al* 1997) and has been reported as low as 20-30% in old-growth stands (Penfound and Watkins 1937 cited in Palik *et al* 1997). Using Endler (1993) classification of light habitats, the longleaf pine forest falls within the woodland category in which most of the crowns are separated leaving large gaps in the canopy. The combination of the simple two-layered vegetative strata and the “openness” of the intact canopy in the longleaf pine ecosystem provides for a convenient setting for comparing different light measurement methods in an open-canopied system.

Only a few studies have investigated the influence of canopy structure on understory light availability in the longleaf pine system (Palik *et al* 1997, Brockway and Outcalt 1998, McGuire *et al* 1999). Results are conflicting, possibly because the sampling techniques employed may not adequately capture the spatial and temporal heterogeneity of light in the understory. However, none of these studies addressed the reliability in techniques used for measuring light transmittance in an open canopied system.

Because the movement in solar path and decrease in zenith angle differs depending on the latitude of the site and different forest types influence the amount of direct and diffuse light present in the understory, methods used to estimate light transmittance at different latitudes for specific time periods might have dissimilar success rates. The purpose of this study was to evaluate the effectiveness of different light transmittance measurement techniques in an open-canopied longleaf pine forest. Using direct measures with photodiodes as a standard, we investigated the accuracy and precision of (i) 10-minute averages recorded by photodiodes during overcast sky conditions, (ii) weighted canopy openness, (iii) gap fraction, (iv) Gap Light Index, and (v) calibrated Gap Light Index. The objectives were to determine which method most accurately estimated mean annual %PPFD. Furthermore, we also want to determine which method has the best estimation of mean daily %PPFD for different sky conditions at different times of the year.

Study area

The study was conducted at the Joseph W. Jones Ecological Research Center in southwestern Georgia, U.S.A (31°N, 84°W) from August 1998 to July 1999. It was part of a larger study investigating the role of overstory structure on regeneration processes in longleaf pine ecosystems. Measurements were taken in a 60-80 year old second-growth forest. The mean height of all trees >4 cm dbh was 20.87 ± 5.77 meters. Topography is gently sloped (1-5% slope) with some sinkholes present. The climate is humid subtropical (Christensen 1981) with an average annual precipitation of 131 cm which is evenly distributed throughout the year. Mean daily temperatures range between 21-34°C in summer and 5-17°C in winter. The soils are classified as excessively drained sites of the Orangeburg and Wagram series. The vegetation is maintained with prescribed fire with intervals ranging from 1 to 5 years, depending on moisture conditions and fuel accumulation. The understory is dominated by the perennial grass *Aristida stricta* Michx. with many other species of perennial grasses and forbs (Goebel et al. 1997).

METHODS

Site selection

As part of the larger study, three replicates of four overstory manipulation treatments were used to determine the effects of spatially variable overstory light competition on longleaf pine seedlings. The four treatments were randomly assigned and consisted of 1) an uncut control, 2) basal area reduction through thinning of widely spaced individual trees, 3) basal area reduction through small gap harvesting (~0.10 hectare gap), and 4) basal area reduction through large gap harvesting (~0.20 hectare gap). For the three cut treatments, residual basal area was similar (10-15 m²/ha, Table 3.1), but the residual overstory was spatially varied.

For each plot, a complete survey of tree height (m), dbh (cm), and GPS location was performed. The location of each individual tree was entered into a GIS database and maps were drawn for each plot. A 5x5 m grid was superimposed on the map to determine a competition index, overstory abundance index (OAI), for each grid point.

OAI was calculated by summing the trees' basal areas within 5m (BA5), 10m (BA10), and 15m (BA15) from the point, dividing each value by the distance, and adding these three values together (Equation 1).

$$\text{OAI} = \text{sum} ((\text{BA5})/5) + \text{sum} ((\text{BA10})/10) + \text{sum} ((\text{BA15})/15) \quad (1)$$

This allowed a tree's size to be weighted by its distance from the point. A tree closer to the point is weighted more heavily than one 15 meters away. Once OAI was calculated for each grid point, a frequency distribution of OAI based on 20% intervals for each plot was calculated. Out of each interval class for each plot, five points were randomly selected to represent a measurement station. Thus, twenty-five stations were assigned to each plot for measurement.

Above and below canopy light measurement equipment

A Li-Cor Li-190SA quantum sensor (Li-Cor, Lincoln, NE) attached to a data logger (Li-Cor 1000, Li-Cor, Lincoln, NE) was placed 1 meter above the ground in an open field adjacent to the study to obtain above-canopy light measurements. Below-canopy light quantity was measured using calibrated gallium arsenide phosphide (Gasp) photodiodes (G1118, Hamamatsu Corporation Bridgewater, N.J.). Each photodiode was attached to a 70-meter wire plugged into a multiplexer data acquisition system (Easylogger 900, Wescor, Logan, UT). Gasp sensors were ideal for this experiment due to their low cost and good quantum response between 300 and 680nm (Percy 1989). Photodiodes were placed 1 m above the ground in the middle of each station within a treatment. Due to the size and shapes of the treatment plots (2.2 ha), a few stations were beyond reach, but at least half of the stations per plot were measured (sample size varied with light measurement technique; see below). Photodiodes were placed within the plots to span the gradient of overstory abundance.

Table 3.1: Residual basal area (m²/ha) of the longleaf pine stands that were used to measure light intensity.

PLOT	BLOCK	TREATMENT	AREA (ha)	NUMBER OF TREES	STAND BASAL AREA (m ² /ha)
1	1	CONTROL	2.40	578	15.16
2	1	SINGLE TREE	2.10	234	11.11
3	1	SMALL GAP	2.04	509	9.84
4	1	LARGE GAP	2.15	230	11.24
5	2	CONTROL	2.13	538	14.80
6	2	SINGLE TREE	2.03	282	13.92
7	2	SMALL GAP	2.45	549	13.76
8	2	LARGE GAP	2.36	416	12.76
9	3	CONTROL	2.16	448	18.44
10	3	SINGLE TREE	2.14	260	12.84
11	3	SMALL GAP	2.18	305	13.28
12	3	LARGE GAP	2.11	504	15.38

Calibration of below canopy photodiodes

All Gasp photodiodes were calibrated by using a Li-Cor Li-190 SA quantum sensor. Calibration of the Gasp photodiodes occurred in September 1998 and June 1999. Two calibrations were required due to the replacement of all Gasp photodiodes for the 1999 measurements. Before each calibration, both the quantum sensor and the photodiodes were leveled. In September, Gasp sensors were calibrated under clear sky conditions during the midday. Various intensities of shade cloth (0% to 100%) were used to lower light intensities. For each shade intensity, measurements were made every minute for at least 20 minutes. For the June calibration, an approach used by Gendron *et al* (1998) was used. With this technique, the sensors measured light intensity over several days to capture a wide range of solar angles and sky conditions.

Linear regression analysis between each sensor and the quantum sensor was established to generate a conversion factor from the output of the photodiode (millivolt) to the output of the Licor quantum sensor (PPFD in $\mu\text{mol s}^{-1} \text{m}^{-2}$). At low light intensities, the relationship between millivolt and PPFD was linear, however, at higher intensities, the relationship became quadratic. With a strictly quadratic fit, the lower light intensities tended to be overestimated. With a strictly simple fit, the higher light intensities tended to be underestimated. To remedy this, we applied the two different relationships to the section of data that corresponded with both situations by using an iterative process. The relationships between the photodiodes and quantum sensor for both sections of the relationship were very strong for both the September ($r^2 > 0.99$, $n = 92$ of 95) and June ($r^2 > 0.97$, $n = 73$ of 80) calibrations.

PPFD measurements and calculation of light transmittance

Below and above canopy PPFD was measured for 10 seconds and stored as 1-min averages each day for sun angles $> 15^\circ$. Solar angles $< 15^\circ$ were not used due to the lowered accuracy of the quantum sensor at those angles (Biggs 1986). Throughout the day, (especially partly cloudy days) there were times that light levels were greater in the understory than in the open. This was due to the distance (1.25 km) of the open sensor to the below-canopy sensors. For instance, on a partly cloudy day, the sensor in the open

maybe shaded by the cloud while at the same time direct light is penetrating the canopy at a location in the understory (or vice versa). This would lead to great errors in the calculation of transmittance. To compensate for these situations, light values for both the open and understory sites were calculated with a moving average of 20 minutes. For instance, a light value reported at 12:00 would really be the average light level from 11:50 to 12:10. Therefore, a light value reported at 12:01 would be the average light level from 11:51 to 12:11. Although this technique decreases the variability at fine temporal scales (minute), the integrated value over the entire day is an acceptable estimate of light transmittance. Other studies report light values using 10-minute averages, 30-minute averages, or with hourly averages (Anderson 1964, Comeau *et al* 1998, Gendron *et al* 1998, Macado *et al* 1999).

The daily sum of below canopy PPF_D recorded for each station was divided by the sum of the above canopy PPF_D to calculate daily transmittance (%PPFD). A total of 56 days were measured during the entire experiment. For each measurement period, a different block consisting of the 4 treatments was measured. Block 1 was measured in November (7 to 10 days), December (5 to 7 days), and June (6 days) while block 2 was measured in August (4 to 8 days), September (4 to 13 days), and July (7 days). Block 3 was only measured in October (8 to 11 days). For each station, annual %PPFD was calculated by averaging the daily transmittance for all of the days that were measured for a specific location. A total of 133 stations were measured throughout the experiment to assess annual %PPFD.

Clear and overcast day transmittance

Three representative clear (June 19, 1999; September 14, 1998; and December 2, 1998) and three overcast days (June 27, 1999; September 11, 1998; and December 8, 1998) were chosen from the complete data set (Figures 3.1 a-c). These dates approximately overlap the full range of sun declination angle throughout the year (23.5° to 0°). For each station, the mean daily %PPFD measured by the photodiodes was calculated.

Instantaneous light transmission on overcast days

Usually this method measures an instantaneous light transmittance on an overcast day. However, I utilized the method Gendron et al (1998) used to assess the reliability of light transmittance on an overcast day in which 10-minute average was used as a surrogate for the instantaneous measurement on an overcast day. This method was shown to yield similar results to the instantaneous method. The three representative overcast days mentioned in the last section were used to test the reliability of a 10 minute-average %PPFD for estimation of daily %PPFD and annual %PPFD. For each day, I calculated the 10-minute average for three time periods (10:00-10:09, 14:30-14:39, and 16:30-16:39) that correspond to the times used by Parent and Messier (1996). For the December measurement, only the first two periods were used due to the shortened length of day. Within a day, the %PPFD for the separate time periods was not significantly different indicating that %PPFD was stable over time within an overcast day (Anderson 1970, Messier and Puttonen 1995).

Hemispherical canopy photographs method

Hemispherical photographs were taken at all stations (n=133) during July and August 1998 on calm, cloudless mornings at sunrise and evenings prior to sunset. It was assumed that canopy openings in the coniferous forests do not change significantly throughout the year (Rich 1990). Photographs were taken on Kodak t-400 black and white film with a Nikon 35mm camera with an attached 180-degree equidistant fisheye lens (Sigma 8mm). The lens was placed at the location of the Gasp sensors 1.5 m above the ground on a tripod. The camera was oriented north and leveled for each photograph.

Negatives were scanned into a computer and examined by using Adobe PhotoShop (version 5.0, Adobe, San Jose, CA). In Adobe PhotoShop, pictures were edited to increase the contrast between the foliage and the visible sky. A threshold gray level was determined for each photograph to distinguish between the foliage and visible sky. In order to minimize observer error all photographs were taken, scanned, edited, and analyzed by the same person. Each photograph was analyzed using the image analysis program Hemiview (version 2.1, Delta-T, UK). This program yields two estimates

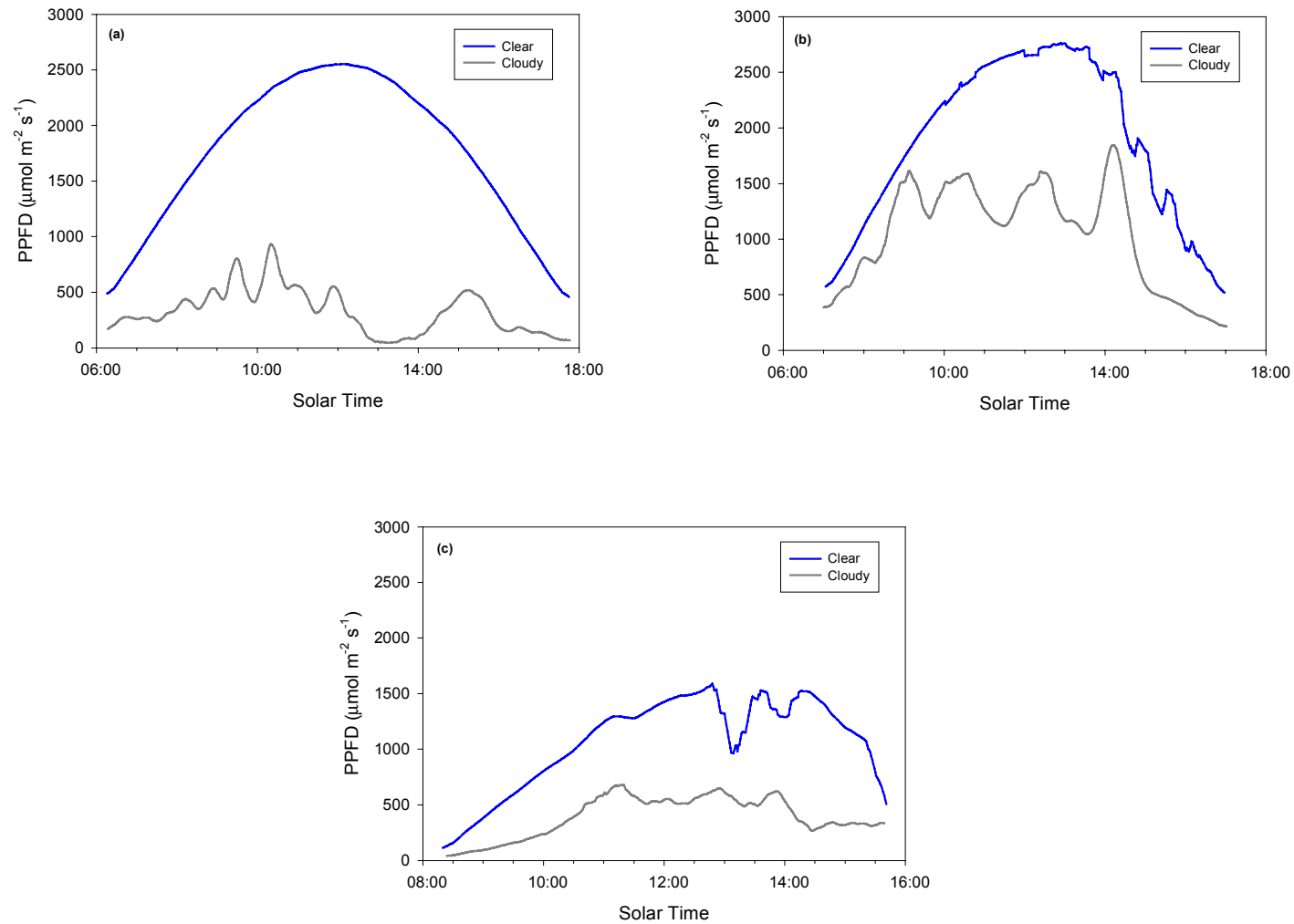


Figure 3.1: Smoothed daily course of average PPFD above the canopy for a clear and overcast day in: (a) June, (b) September, and (c) December. The black line represents the clear day and the gray line represents the overcast day. A 10-minute moving average was used to reduce noise in all smoothed curves.

of canopy density; unweighted canopy openness (Gap Fraction) and weighted canopy openness (VisSky). For each calculation, the hemisphere was divided into sectors with an azimuth and a zenith resolution of 20.

Calculation of Gap Light Index

Hemiview was also used to calculate the amount of light transmittance to the understory based on canopy openness by accounting for the location of canopy elements, the diurnal path of the sun, and seasonal changes in sun angle. Parameters used for the estimates of direct transmission factor (T_{beam}) were transmissivity=0.65, beam fraction=0.50 and solar constant=2510 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Diffuse transmission factor (T_{diffuse}) was estimated using the Standard Overcast Sky (SOC) assumption (Anderson 1964) in which the brightness of a point in the sky at zenith angle is three times as bright as that near the horizon. With the estimates of direct and diffuse transmission factors, gap light indices (Canham 1988) were calculated. The gap light index (GLI) specifies the percentage of incident PAR transmitted through a gap to a point in the understory. GLI is calculated using the equation below (Canham 1988):

$$\text{GLI}=[(T_{\text{diffuse}} * P_{\text{diffuse}}) + (T_{\text{beam}} * P_{\text{beam}})]*100 \quad (2)$$

where P_{diffuse} and P_{beam} are the proportions of incident seasonal PAR received at the top of the canopy as either diffuse sky radiation or direct-beam radiation, respectively. T_{diffuse} and T_{beam} are the proportions of diffuse and direct-beam radiation that are transmitted through the canopy to the understory, respectively. A GLI of 0 indicates that there is no light in the understory, while a GLI of 100 indicates a totally open site.

Calculation of P_{diffuse} and P_{beam}

For the calculation of GLI, the parameters P_{diffuse} and P_{beam} must be provided. Most authors assume that each estimate is 0.5 (Machado and Reich 1999, Comeau *et al* 1998, Gendron *et al* 1998, Canham *et al* 1990) for an entire growing season. However, if estimation of light transmittance is required on a finer time scale (day, week, or month) these parameters might lead to less accurate predictions, especially for different sky conditions. Both parameters can be measured directly or estimated indirectly (Rich *et al* 1993, Easter and Spies 1994, Clearwater *et al* 1999). Since there were no values

currently available for our study site, we chose to estimate the parameters indirectly. Instead of assuming a single value (ie. $P_{\text{diffuse}}=0.5$ and $P_{\text{beam}}=0.5$), we varied P_{diffuse} and P_{beam} between 0.0 and 1 to calculate GLI as done by other studies (Rich *et al* 1993, Easter and Spies 1994, Clearwater *et al* 1999). GLI was calculated for an annual basis and for the specific sky condition days. For each GLI calculation, the P_{diffuse} and P_{beam} were varied to find the estimates that maximized the coefficient of determination for the linear relationship between %PPFD (dependent variable) and GLI (independent variable).

DATA ANALYSIS

Sample size for each analysis differed due to the size and shapes of the treatment plots (2.2 ha). In addition, problems with the photodiodes and data loggers resulted in various days for which data are missing from at least one plot. Linear regression analysis (PROC REG; SAS Institute 1999) was performed to examine the relationship between direct measurements of annual %PPFD by photodiodes (the dependent variable) and the indirect light transmittance estimates (Gap Fraction $n=133$; weighted canopy openness $n=133$; gap light index $n=133$; and 10-minute average overcast %PPFD; June $n=53$, September $n=47$, December $n=58$). For the specific clear and overcast days, linear regression analysis (PROC REG; SAS Institute 1999) was performed to examine the relationship between mean daily %PPFD on a clear day (June $n=61$, September $n=56$, December $n=43$) and mean daily %PPFD on an overcast day (June $n=53$, September $n=48$, December $n=58$) for gap fraction, weighted canopy openness, and gap light index. In addition, linear regression analysis was performed on the relationship of 10-minute average %PPFD on an overcast day to both mean daily %PPFD on a clear day and mean daily %PPFD on an overcast day for June (overcast $n=53$), September (clear $n=47$, overcast $n=47$) and December (clear $n=43$, overcast $n=58$). In June, different microsites were measured among the clear and overcast days and a comparison between the 10-minute average %PPFD on an overcast day to mean daily %PPFD on a clear day was not available.

For each regression analysis, normality (Kolmogorov-Smirnov) and homogeneity of variances (Leven Median test) were tested on the residuals using Sigma Plot (v. 4.01,

SPSS Inc, IL). Methods with higher coefficients of determination (r^2) were considered the better estimators of %PPFD. Confidence intervals (95%) were used to determine if 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 used to compare slopes for the two forms of GLI calculations and between clear and overcast days.

RESULTS

Annual Transmittance

All 5 indices showed a linear relationship with mean annual %PPFD (Figure 3.2 a-g) but with various precision and accuracy. The 10-minute average %PPFD on an overcast day in September yielded the most precise estimate of annual %PPFD ($r^2=0.88$), although it slightly underestimated %PPFD (Figure 3.2b). The 10-minute average %PPFD on an overcast day in June, $GLI_{\text{calibrated}}$, gap fraction, and $GLI_{0.5, 0.5}$ showed moderate relationships (Table 3.2). Both estimates of GLI showed good agreement between the observed and estimated values (Figure 3.2 f and g). The June 10-minute average measurement overestimated %PPFD (Figure 3.2a) while gap fraction slightly underestimated %PPFD (Figure 3.2e). The lowest relationships were obtained by using 10-minute average %PPFD on an overcast day in December, which overestimated %PPFD (Figure 3.2c) and weighted canopy openness (Table 3.2), which underestimated %PPFD (Figure 3.2d).

Effect of sky condition on measuring method accuracy

A 10-minute average measurement of %PPFD made on an overcast day in June, September, and December was shown to have a strong relationship ($r^2>0.93$, $P=0.0001$) to the average integrated daily overcast %PPFD for the respective month (Figure 3.3 a-c). Slopes for June and September were close to 1, while December measurements slightly overestimated mean daily overcast %PPFD (Figure 3.3 a-c).

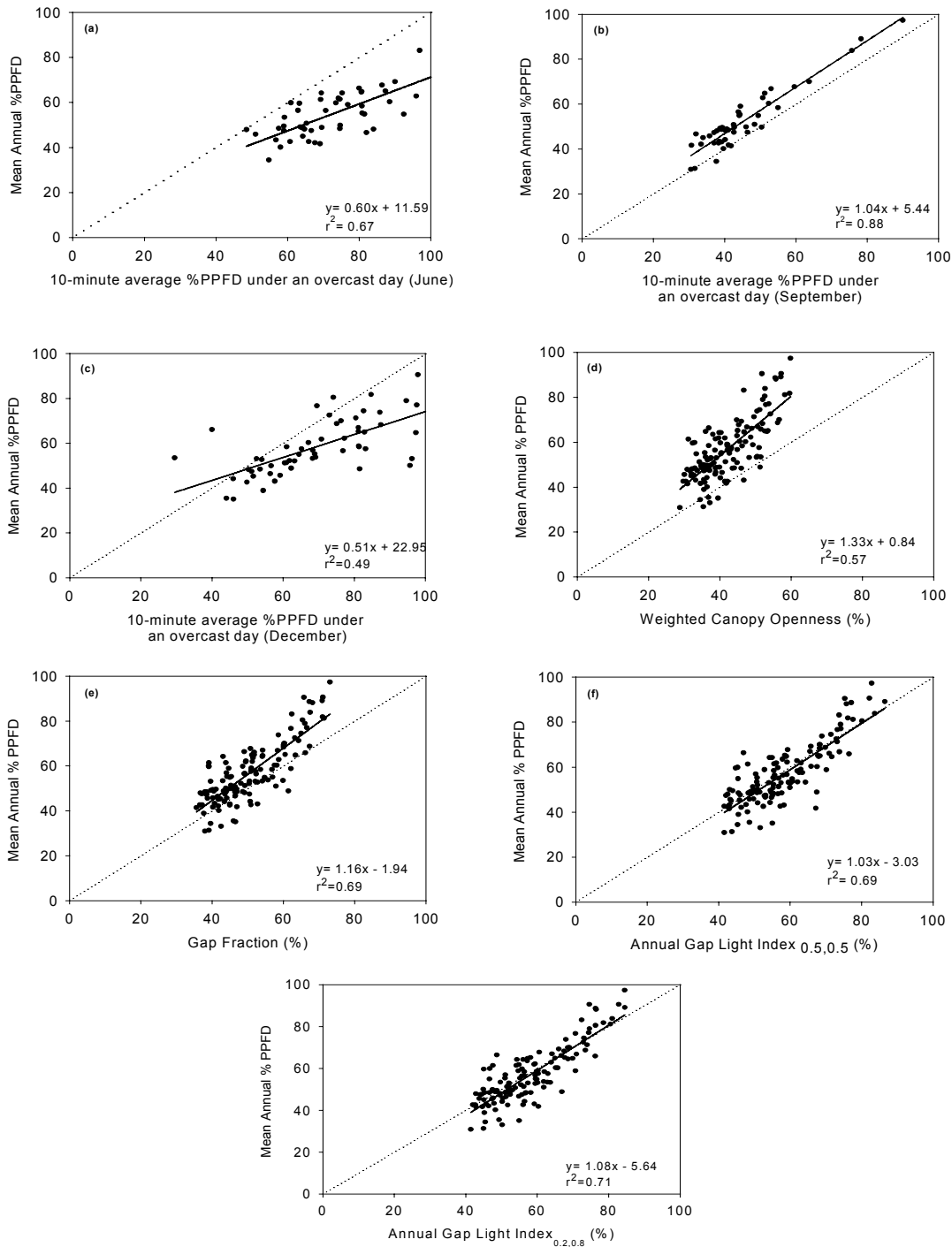


Figure 3.2: Relationships between the mean annual %PPFD measured with photodiodes and the light transmittance estimated using different methods: (a) 10-minute average %PPFD_{June} (n=53), (b) 10-minute average %PPFD_{September} (n=47), (c) 10-minute average %PPFD_{December} (n=58), (d) weighted canopy openness (n=133), (e) gap fraction (n=133), (f) GLI_{0.5,0.5}, (n=133) and (g) GLI_{0.2,0.8} (n=133). The dotted lines show a 1:1 relationship.

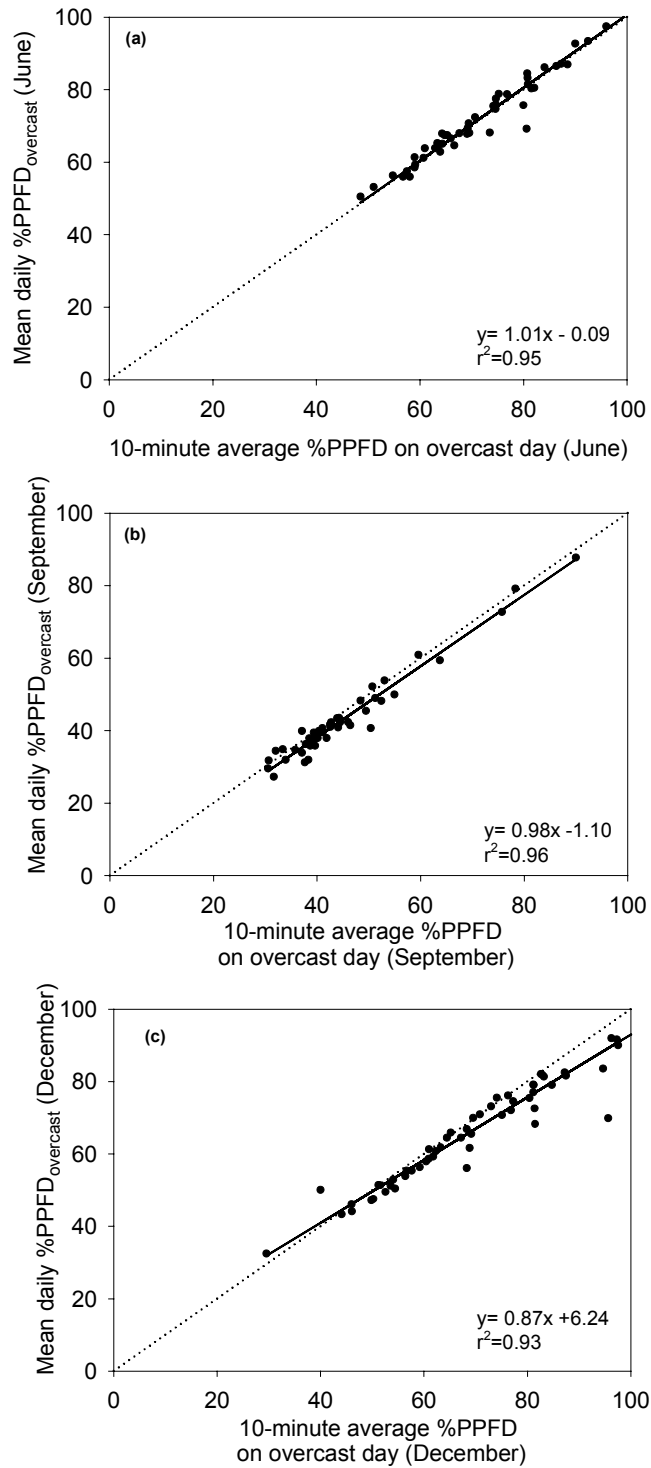


Figure 3.3: Relationships between 10-minute average %PPFD_{Overcast} and mean daily %PPFD_{Overcast} for (a) June (n=53), (b) September (n=47), and (c) December (n=58). The solid line is the linear regression. The dotted lines show a 1:1 relationship.

The same predictability was not observed when 10-minute average overcast %PPFD was compared to the average integrated daily %PPFD on a clear day in September and December. Although the slope for the September measurement was close to one, the r^2 (0.68) was much lower compared to the overcast day ($r^2=0.96$). For December, there was a much weaker relationship ($r^2=0.23$, $p=0.0001$) and %PPFD was overestimated greatly (Figure 3.4b).

Comparisons of the relationship between the integrated %PPFD on an overcast day to the integrated %PPFD on a clear day for both September and December showed the same pattern. September's measurement was slightly stronger ($r^2=0.72$) with a slope of 1 (Figure 3.5a). December's r^2 increased to 0.32 but still overestimated clear day %PPFD (Figure 3.5b).

Weighted canopy openness showed stronger relationships to mean daily %PPFD on overcast days than on clear days in the three months used for the analysis (Figure 3.6 a, d, f). On overcast days, June and September mean daily %PPFD on an overcast day had stronger relationships to weighted canopy openness than the December measurement (Table 3.2). Estimation of mean daily %PPFD from weighted canopy openness on clear days had lower strengths for all three months compared to the overcast day, but were similar among the months (Table 3.2). The use of weighted canopy openness underestimated daily %PPFD for both clear and overcast sky conditions for each measurement period, except for December, which overestimated daily %PPFD on a clear day (Figure 3.6 a, d, and g). June had a significantly steeper slope on an overcast day ($p=0.025$) (Table 3.2). The mean square error was highest for this method compared to the other hemispherical photograph estimates (Table 3.2, Table 3.3, and Table 3.4).

Gap Fraction showed stronger relationships to daily %PPFD of both overcast and clear days than did unweighted canopy openness (Table 3.3 vs. Table 3.2). The relationships to %PPFD on overcast days are stronger than that of clear days for all months measured (Table 3.3). In addition, relationship strength decreased as maximum solar elevation decreased (e.g. June to December). A substantially higher r^2 occurred for

the daily June overcast %PPFD ($r^2=0.82$) and clear day %PPFD ($r^2=0.65$) than was seen for the other months' measurements (Table 3.3 vs. Table 3.2). However, gap fraction underestimated %PPFD for both sky conditions on a June day (Figure 3.6b). Gap fraction had good agreement with observed %PPFD for both a clear and overcast day in September (Figure 3.6e). The relationship in December was slightly stronger to the %PPFD overcast day, but much weaker ($r^2=0.21$) to the %PPFD clear day (Table 3.3). Gap fraction underestimated %PPFD (Figure 3.6h) on an overcast day and overestimated %PPFD on a clear day in December (Figure 3.6h). Slope comparisons for the June and December days showed a significant steeper slope on an overcast day ($p=0.10$ for June; $p=0.05$ for December) (Figure 3.6 b and h).

$GLI_{\text{calibrated}}$ had the strongest relationships to %PPFD on both overcast and clear days (Table 3.4). Relationship strength decreased as maximum solar elevation decreased (e.g. June to December) (Table 3.4), but were consistent between the different sky conditions within the time period measured (Figure 3.6 i-j). In contrast to the other methods used to estimate %PPFD on a December clear day, $GLI_{\text{calibrated}}$ showed a considerable improvement in model strength (Table 3.4). Although model strength was strongest for this method, $GLI_{\text{calibrated}}$ underestimated %PPFD under both sky conditions in June (Figure 3.6c) and overestimated it in September (Figure 3.6f). In December, $GLI_{\text{calibrated}}$ underestimated %PPFD was underestimated on the overcast day and overestimated it on the clear day (Figure 3.6i). Mean square error was lowest in all months for this method compared to all the other hemispherical methods (Table 3.2-3.4). Slope comparisons between clear and overcast days for each month showed a significant higher slope for the overcast day for June ($p=0.025$) and December ($p=0.01$).

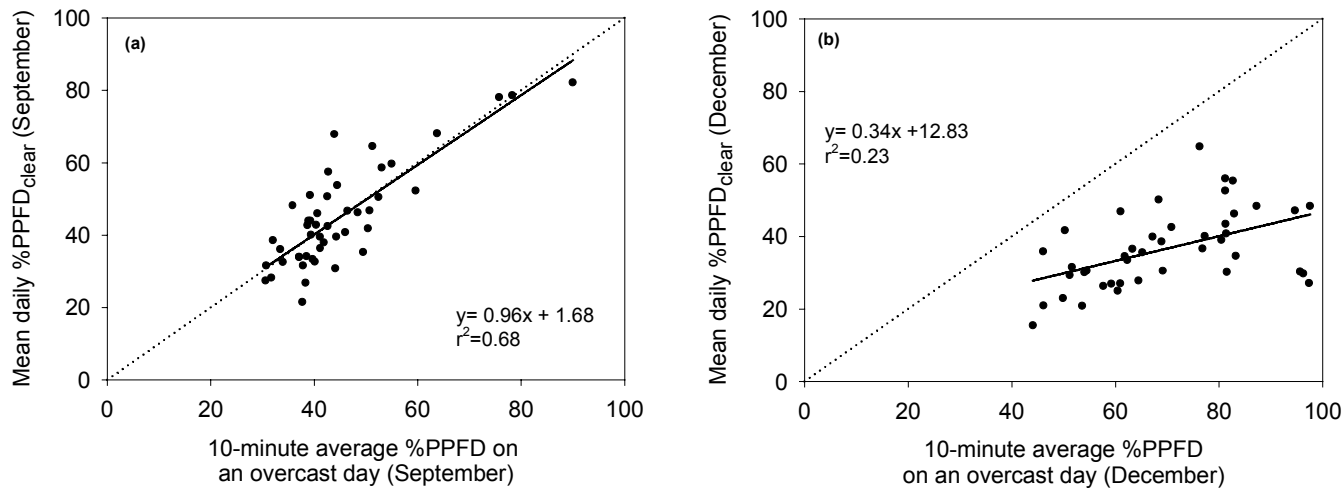


Figure 3.4: Relationships between 10-minute average %PPFD_{overcast} and mean daily %PPFD_{clear} for (a) September (n=47) and (b) December (n=43). The solid line is the linear regression. The dotted lines show a 1:1 relationship.

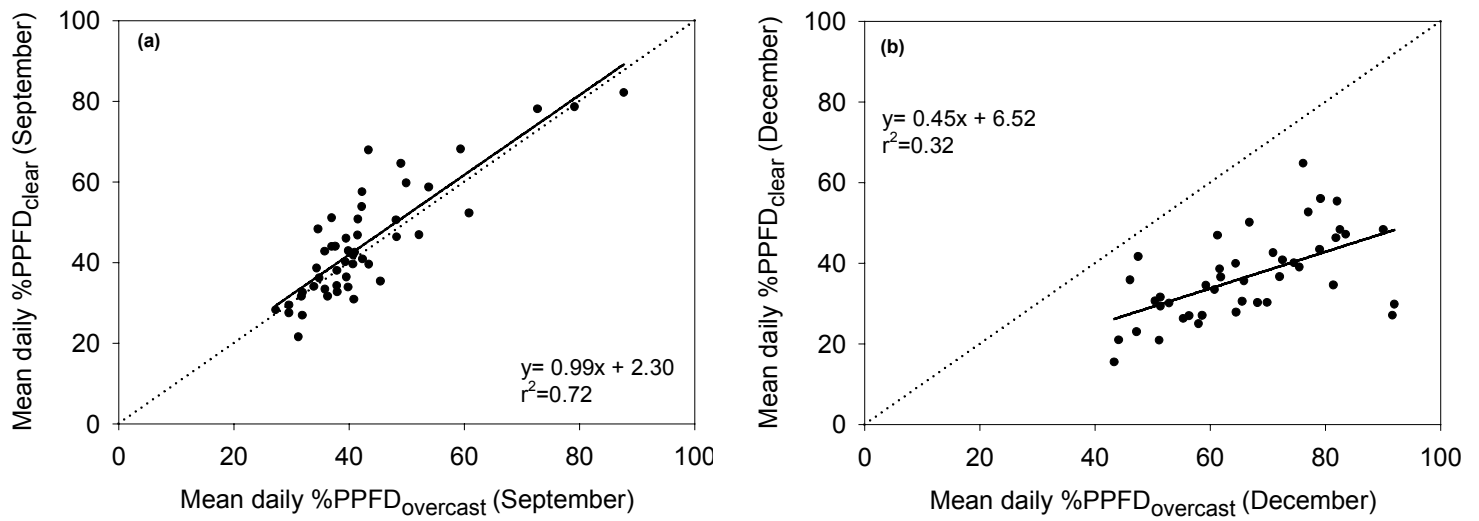


Figure 3.5: Relationships between mean daily %PPFD_{overcast} and mean daily %PPFD_{clear} for (a) September (n=47) and (b) December (n=43). The solid line is the linear regression. The dotted lines show a 1:1 relationship.

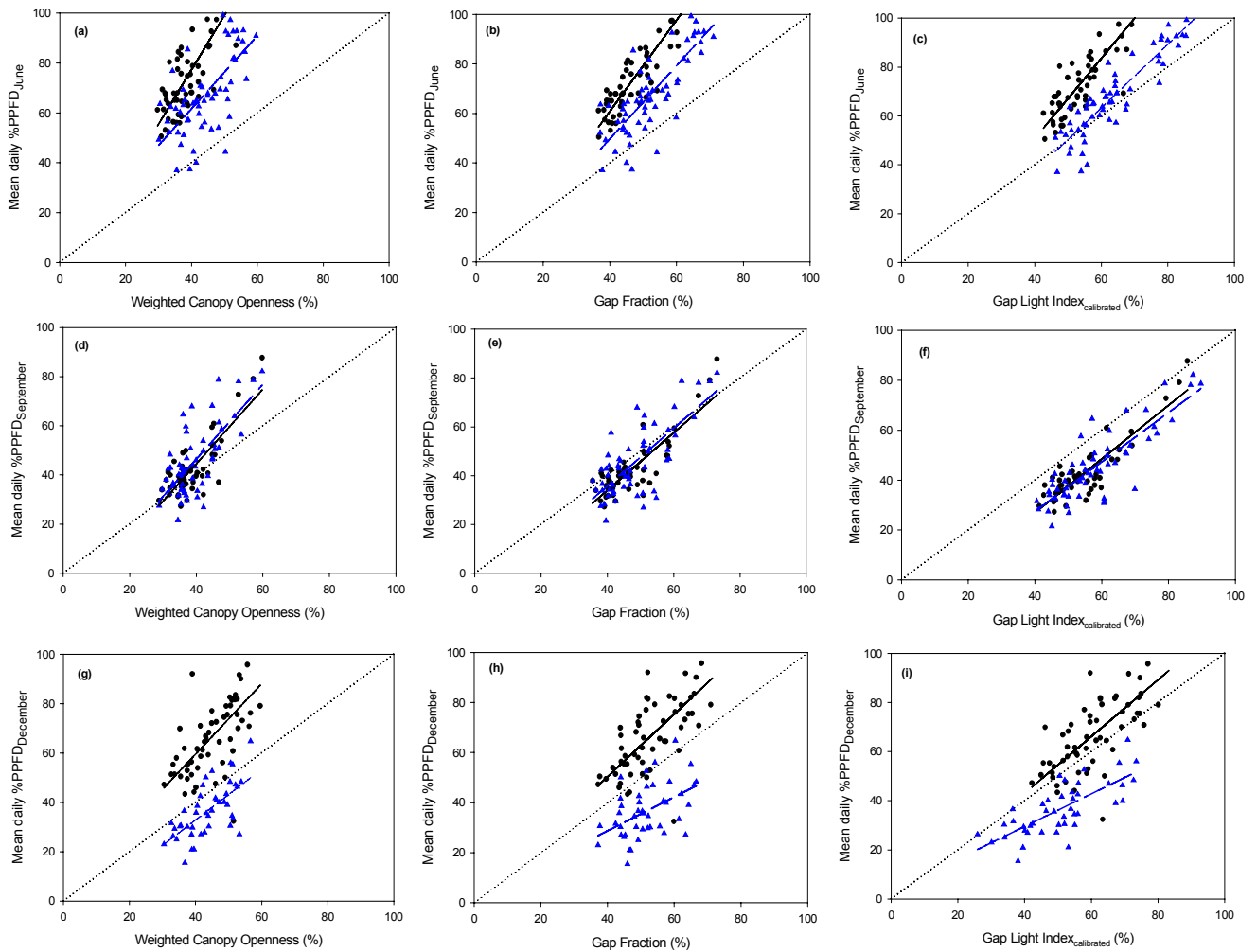


Figure 3.6: Relationships between %PPFD for June (a-c), September (d-f), and December (g-i) measured by photodiodes under clear and overcast sky conditions to the light transmittance estimated by different methods: weighted canopy openness (a,g,d), gap fraction (b,e,h), and gap light index (c,f,i). Circles represent overcast day transmittance. Triangles represent clear day transmittance. Solid lines represent the linear regression for overcast day transmittance. Dashed lines represent the linear regression for clear day transmittance. The dotted lines show a 1:1 relationship. See Table 3.4 for weighted canopy openness regression coefficients. See Table 3.5 for gap fraction regression coefficients. See Table 3.6 for Gap Light Index regression coefficients.

Table 3.4: Linear relationship coefficients (standard deviation in parentheses) between mean daily %PPFD measured continuously on a clear and overcast day to weighted canopy openness for June, September, and December.

TIME PERIOD	SKY CONDITION	INTERCEPT	SLOPE	r ²	ROOT MEAN SQUARE ERROR	N
JUNE	OVERCAST	-10.21 ns (8.59)	2.19 (0.22)	0.66	10.35	53
JUNE	CLEAR	2.92 ns (9.71)	1.47 (0.21)	0.43	12.67	61
SEPTEMBER	OVERCAST	-16.34 (6.24)	1.52 (0.16)	0.66	7.10	48
SEPTEMBER	CLEAR	-14.40 ns (8.20)	1.52 (0.20)	0.50	10.25	56
DECEMBER	OVERCAST	2.57 ns (9.91)	1.42 (0.21)	0.43	12.22	58
DECEMBER	CLEAR	-8.28 ns (8.17)	1.03 ns (0.19)	0.42	8.14	43

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). The general equation is $y = b + mx$.

Table 3.5: Linear relationship coefficients (standard deviation in parentheses) between mean daily %PPFD measured continuously on a clear and overcast day to gap fraction for June, September, and December.

TIME PERIOD	SKY CONDITION	INTERCEPT	SLOPE	r ²	ROOT MEAN SQUARE ERROR	N
JUNE	OVERCAST	-13.01 (5.83)	1.85 (0.12)	0.82	7.54	53
JUNE	CLEAR	-9.55 ns (7.46)	1.48 (0.14)	0.65	9.95	61
SEPTEMBER	OVERCAST	-13.41 (5.16)	1.18 (0.11)	0.72	6.42	48
SEPTEMBER	CLEAR	-11.57 ns (7.21)	1.18 (0.15)	0.54	9.81	56
DECEMBER	OVERCAST	0.211 ns (9.19)	1.25 (0.17)	0.49	11.6	58
DECEMBER	CLEAR	1.58 ns (10.04)	0.68 (0.19)	0.21	9.45	43

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). The general equation is $y = b + mx$.

Table 3.6: Linear regression coefficients (standard deviation in parentheses) for comparison of Gap Light Index with P_{beam} and P_{diff} calibrated (independent variables) used to estimate %PPFD (dependent variable) on a clear and overcast day for June, September, and December. Calibration of P_{beam} and P_{diff} is representative of the sky conditions during the measurement period.

TIME PERIOD	SKY CONDITION	P_{BEAM}	P_{DIFF}	INTERCEPT	SLOPE	r^2	ROOT MEAN SQUARE ERROR	N
JUNE	OVERCAST	0	1	-14.68 (5.90)	1.64 (0.11)	0.82	7.50	53
JUNE	CLEAR	0.6	0.4	-14.68 (4.97)	1.30 (0.08)	0.83	6.98	61
SEPTEMBER	OVERCAST	0	1	-16.27 (4.64)	1.08 ns (0.08)	0.78	5.72	48
SEPTEMBER	CLEAR	0.5	0.5	-12.09 (5.23)	0.99 ns (0.09)	0.7	7.95	56
DECEMBER	OVERCAST	0	1	-3.11 ns (8.93)	1.15 ns (0.14)	0.53	11.15	58
DECEMBER	CLEAR	0.7	0.3	2.94 ns (4.84)	0.66 (0.09)	0.54	7.20	43

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). The general equation is $y = b + mx$.

DISCUSSION

Accuracy of annual %PPFD

The distribution of canopy openness along the sun's path at different times of the year lead to varied strengths for the different methods used to determine light availability. On an annual scale, the strongest relationship ($r^2=0.88$) and lowest mean square error was found for the 10-minute average overcast %PPFD_{September} method. Moderate relationships ($r^2 \geq 0.67$) were found for GLI_{calibrated}, gap fraction, GLI_{0.5, 0.5}, and 10-minute average overcast %PPFD_{June}. In this system, the use of the 10-minute average %PPFD_{overcast} measurement for mean annual %PPFD was constrained by the interaction of the distribution of canopy openness and sun altitude. Studies that have utilized this method with great accuracy have been predominantly at latitudes above 46°N with measurements limited to summer months in which solar altitude is between 40° and 60° at maximum zenith (Messier and Puttonen 1995, Parent and Messier 1996, Gendron *et al* 1998, Macado *et al* 1999). Our coefficients of determination were comparable to Comeau *et al* (1998) ($r^2=0.98;n=12$) and Gendron *et al* (1998) ($r^2=0.92;n=52$), however, we found that the strength of the relationship was dependent on the time of year the sample was taken. September yielded the strongest relationship, while June and December had lower r^2 . At my study site, September has a maximum zenith angle of 60° (Figure 3.7), which corresponds to the angles that other studies have utilized this method. Measurements taken in June or December overestimated mean annual %PPFD, suggesting that solar altitude has a major effect on the accuracy of this method.

Another factor that influences the accuracy of this method is the density of canopy structure. The investigation by Gendron *et al* (1998) combined three types of light environments, which incorporated a full range of growing season %PPFD (4.6% to 97.8%). When these three light environments were separated into closed, canopy gap, and open canopy, the efficiency of the 10-minute average overcast %PPFD method decreased. In our system, %PPFD ranged from 30-80% for the mean annual %PPFD, which corresponds to their 'canopy gap' environment. For this light environment, Gendron *et al* (1998) found a similar relationship ($r^2= 0.62;n=21$) in July as we did for

our June measurement. In their study, measurements made during that period underestimated mean annual %PPFD (Gendron et al 1998), while our study overestimated %PPFD. At our study site, the maximum zenith angle in June is 82°. Because the solar path during this time period is at its maximum (Figure 3.7) and the longleaf pine canopy is more open at these angles, more light can reach the understory at this time period and thus annual %PPFD is overestimated.

The influence of solar altitude on estimates of mean annual %PPFD also affected the accuracy of two of the hemispherical photograph estimates. For instance, weighted canopy openness rendered the lowest r^2 (0.57) to mean annual %PPFD. Weighted canopy openness is a measure of the sum of the proportion of visible sky in a given sky sector, relative to the entire hemisphere of sky direction (Rich *et al* 1999). Therefore, gap openings closer to the zenith (90°) of the photograph are more heavily weighted than those near the horizon. At our study site, zenith angles range from 40° to 80°, so for limited times of the year (summer), this measure might be appropriate but would still have unexplained variation. This method may be more appropriate to estimate mean annual %PPFD at latitudes where the majority of maximum zenith angles are close to 90° throughout the year and/or when diffuse light is the main component of understory light.

In contrast to the weighted canopy openness, gap fraction integrates the total number of open points for the entire hemisphere without any weighting. Nicotra *et al* (1999) stated that gap fraction (MDIR in their study) was a better estimate of diffuse light penetration (and perhaps overall light availability) than weighted canopy openness. This was confirmed in our study. For the mean annual %PPFD, gap fraction explained 69% of the variation, compared to 57% of the variation explained by weighted canopy openness. Because gap fraction ignores the directional aspect of solar radiation and the understory of this system receives a large amount of direct light, this method underestimated mean annual %PPFD.

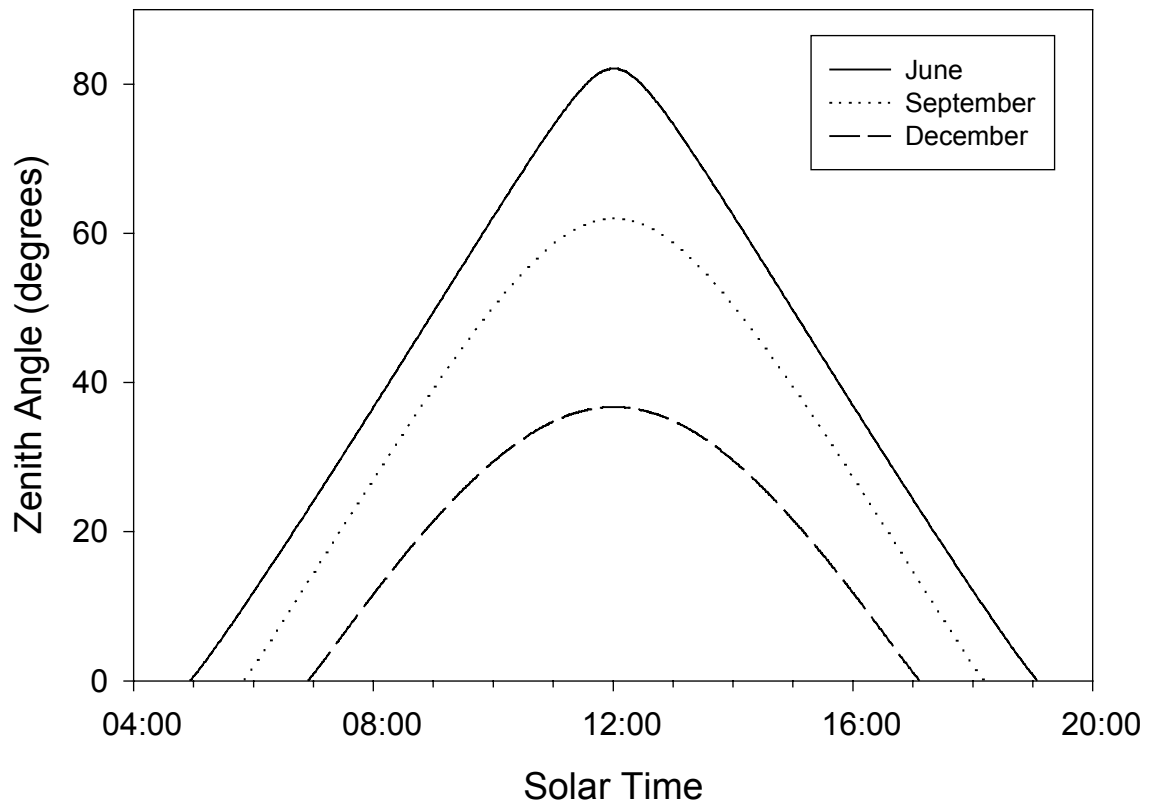


Figure 3.7: Solar altitude over the course of a day for different times of the year for our study site (31°N, 84°W). Solid line represents the summer solstice in June. Dotted line represents the autumn equinox in September. Dashed line represents the winter solstice in December.

In the calculation of gap light index, consideration for the changing solar altitude and its interaction with the canopy structure allows this estimate from hemispherical photography to have greater accuracy of light transmittance. Over an entire year, $GLI_{0.5,0.5}$ was similar in precision as the gap fraction estimate. Even with the calibrated values of P_{beam} and P_{diffuse} , $GLI_{\text{calibrated}}$ estimation was slightly higher in precision. However, the slopes between $GLI_{0.5,0.5}$ and $GLI_{\text{calibrated}}$ were not significantly different and observed and estimated values were similar, indicating they are more accurate in their estimated values than gap fraction. Still, there was a significant amount of variation unexplained by GLI. This may be due to the influence of beam enrichment in which hemispherical photograph estimates ignore. Beam enrichment has been shown to be important in other coniferous and deciduous forests because it accounts for a significant portion of the understory light environment (Hutchinson and Matt 1976, Hutchinson and Matt 1977, Vales and Bunnell 1988, Canham *et al* 1994, Lieffers *et al* 1999). Therefore, although beam enrichment has not been addressed in open-canopied forests, we believe that the influence of beam enrichment in this system may be an important understory light component and should be studied further.

Estimation on a daily basis

On overcast days, diffuse light penetrates the forest canopy from all directions uniformly and is spatially and temporally homogeneous in the understory (Messier and Puttonen 1995, Parent and Messier 1996). Based on this assumption, light transmittance on an overcast day is a function of canopy openness and methods that utilize canopy openness to estimate light transmittance should be acceptable surrogates for estimation. Although this assumption has been tested in closed-canopied forests in which diffuse light is the prominent component of the understory light environment this has not been addressed in open-canopied environments that receive a large amount of direct light. In this study, a strong relationship ($r^2 \geq 0.93$) between the 10-minute average $\%PPFD_{\text{overcast}}$ and mean daily $\%PPFD_{\text{overcast}}$ for June, September, and December was found. This suggests that 10-minute average $\%PPFD$ on an overcast day is an acceptable estimator of daily $\%PPFD$ on an overcast day for the specific time period measured.

All three hemispherical photograph methods utilize canopy openness in the estimation of light transmittance, but in different ways. Weighted canopy openness weights canopy openness as a function of the location an opening occurs in the entire canopy. Gap fraction estimates light transmittance based on total openness. Gap light index estimates direct and diffuse light transmittance separately in its calculation. Diffuse light transmittance is based on total canopy openness, but direct light transmittance is based on the location of the canopy opening within the solar path. However, on an overcast day, gap light index ignores the direct light component and is similar to the gap fraction method. Comparisons of these three methods on overcast days show that weighting the location of the opening decreases the precision of the estimation of %PPFD on an overcast day.

Parent and Messier (1995) suggest that transmittance on an overcast day and clear day are similar and that measurements made on an overcast day can be used to characterize light environments. This assumption is based on a study performed in a forest at high latitude in which direct light penetration is not the dominant component of the understory light environment. In this study, light transmittance on an overcast day and clear day was similar only for the September measurement. Each method used to estimate clear day transmittance indicated that light transmittance on an overcast day is twice as high than on a clear day in December. As a result of this trend, measurements taken on an overcast day in December overestimated %PPFD on a clear day (Figure 3.3c and 3.4b).

Methods that ignore the interaction of the solar altitude and the distribution of canopy openness can profoundly alter the accuracy and precision of the estimation of %PPFD on a clear day. On a clear day, understory light is composed of direct and diffuse light. Diffuse light can be separated into two components: skylight and beam enriched light. The amount of skylight is based on the openness of the canopy. Direct light can reach the understory unimpeded if the sun overlaps a canopy opening. However, if the sun overlaps an area with foliage, the direct light is absorbed and scattered by the foliage and converted to diffuse light. Therefore, the probability of the presence of direct and

beam enriched light is dependent on the interaction of the canopy structure and the solar path.

Examination of the distribution of angular openness as a function of solar angle shows that canopy openness in our system is greater than 50% for solar angles larger than 30° (Figure 3.8). Therefore, direct light can penetrate more readily throughout a day with solar angles greater than 30°, increasing the proportion of direct light in the understory. At the latitude of this study (31°N), the majority of solar angles for June (summer solstice) and September (autumn equinox) are above the 30° threshold, but for December (winter solstice), only a small portion is above this threshold (Figure 3.7). Therefore, as solar path decreases from summer to winter, the interaction with canopy openness will increase, thus increasing the proportion of beam enrichment.

Methods that account for the directional aspect of direct light and the probability of beam enrichment should have higher precision in their estimations of clear day %PPFD. None of the methods used in this study account for direct light beam enrichment. Therefore, precision of the estimates will depend solely on whether or not the method incorporates the change in solar path. The 10-minute average on an overcast day, weighted canopy openness, and gap fraction do not incorporate solar path to calculate transmittance. As a result, these methods had higher precision on overcast days than clear days. In addition, as the probability of beam enrichment increased, the precision of the estimates decreased for clear days.

Gap light index takes into consideration the changing solar altitude, canopy structure, and the path of the sun. Within the calculation of GLI, the user must assign specific P_{beam} and P_{diffuse} values to aid in the estimation. Although, the importance of assigning the correct P_{beam} and P_{diffuse} over an entire year was shown to matter slightly in the explanation of variation, the user must estimate the P_{beam} and P_{diffuse} values for the specific day, otherwise the estimated light transmittance will be the same for a clear and overcast day. With calibrated P_{beam} and P_{diffuse} values, $GLI_{\text{calibrated}}$ was shown to estimate light transmittance on overcast and clear days with similar strength. However, the

precision of the method decreased as the solar altitude decreased. This was the result of neglecting the contribution of beam enrichment, especially in December.

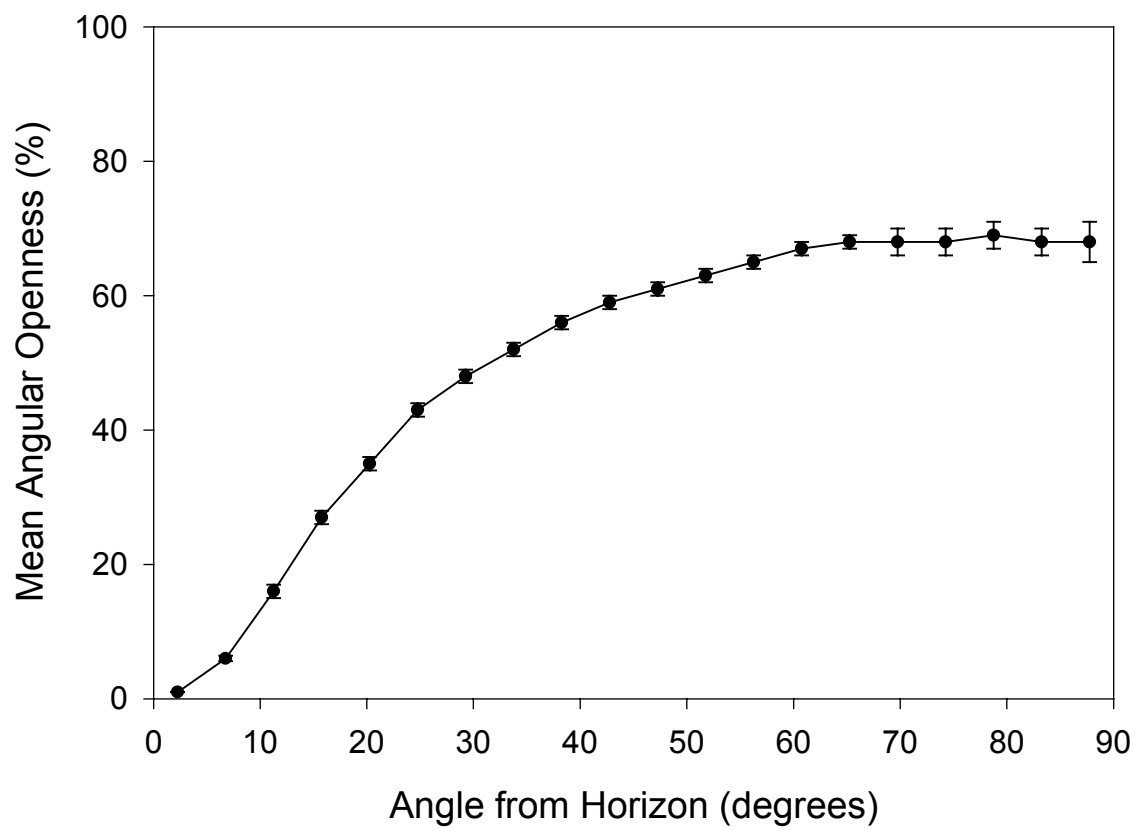


Figure 3.8: Distributed angular openness as a function of solar angle in hemispherical photographs from our study sites. Data are presented as mean \pm SE. The n for each mean is 133.

CONCLUSIONS

As the sun altitude changes throughout the year, its interaction with the distribution of canopy openness from the horizon to the zenith changes the proportion of direct and diffuse light and thus the ability to accurately predict light transmittance. In our study, we found that the different methods tested performed differently depending on the sky condition and time of year the sample was taken. The 10-minute average %PPFD_{overcast} method showed the strongest relationship to mean annual %PPFD, but the solar altitude affected its accuracy and precision. The hemispherical estimates were also shown to be useful methods for estimation of mean annual %PPFD, with gap light index performing the best. The assumption that P_{beam} and P_{diffuse} are equal to 0.5 was shown to be acceptable for annual predictions by gap light index. On a daily scale, 10-minute average %PPFD_{overcast} estimated light transmittance on an overcast day well, but its accuracy decreased when estimation of clear day transmittance was needed, especially at lower solar angles. Weighted canopy openness and gap fraction were shown to be better predictors of light transmittance when solar angles were at maximum, but accuracy and precision decreased as solar angle decreased toward its minimum. Weighted canopy openness and gap fraction performed best on overcast days, but had lower precision when clear day transmittance was estimated. Gap light index was shown to perform the best of all hemispherical estimates, and estimated light transmittance similarly on both overcast and clear days due to the ability of the user to input the proportions of direct and diffuse light above the canopy. The moderate r^2 values for the hemispherical photograph estimates suggest that beam enrichment, a parameter which hemispherical photographs ignore, is an important component in the understory light environment of the longleaf pine forest.

It has been shown in many studies that all these methods are appropriate measures to estimate light transmittance in closed canopy forests. This study shows that these methods can also be used in an open canopied system, such as the longleaf pine forest. However, it should be understood that the accuracy and precision will not be as great as

that found in closed canopy forest, most likely due to the contribution to the understory light environment by beam enrichment.

To date, only three studies have measured understory light environment in a longleaf pine forest. Both Palik *et al* (1997) and McGuire *et al* (1999) utilized gap light index to estimate light transmittance and we feel confident that these measures accurately depict the mean annual %PPFD. However, Brockway and Outcalt (1997) measured light transmittance on a clear day in December and found no difference in light transmittance from gap edge to gap center. Based on our study, we found that light transmittance on a clear day in December is lower than the light transmittance on an overcast day. In addition, we found that %PPFD on a clear day in December overestimates mean annual %PPFD and conclude that %PPFD on a clear day is a poor estimator of light transmittance for the longleaf pine system.

LITERATURE CITED

Anderson, M.C. 1964. Studies of the woodland light climate. II. Seasonal variation in the light climate. *Journal of Ecology* **52**: 643-663.

Anderson, M.C. 1970. Interpreting the fraction of solar radiation available in forest. *Agricultural Meteorology* **7**: 19-28.

Baldocchi, D., and Collineau, S. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. *In* Exploitation of environmental heterogeneity by plants; Ecophysiological processes above and below ground. *Edited by* M.M. Caldwell and R.W. Pearcy. Academic Press, New York. pp.21-71.

Becker, P., Erhart, D.W. and A.P. Smith. 1989. Analysis of forest light environments 1. Computerized estimation of solar radiation from hemispherical canopy photographs. *Agricultural and forest meteorology* **44**: 217-232.

Biggs, W. 1986. Radiation Measurement. *In* Advanced Agricultural Instrumentation : Design and Use. *Edited by* Gensler, W.G. The University of Arizona.

Brockway, D.G. and K.W. Outcalt. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. *Forest Ecology and Management* **106**: 125-139

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

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A. and P.S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**: 620-631.

- Canham, C.D., A.C. Finzi, S.W. Pacala, and D.H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can J. For. Res.* **24**: 337-348.
- Chazdon, R.L. and Fetcher N. 1984. Photosynthetic light environments in a lowland tropical rainforest in Costa Rica. *Journal of Ecology* **72**: 553-564.
- Chazdon, R.L. and C.B. Field. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* **73**: 525-532.
- Christensen, N.L. 1981. Fire regimes in southeastern ecosystems. In: H.A. Monney, T.M. Bonnicksen, N.L. Christensen, J.E. Lotan, and W.A. Reiners (eds). Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26. Pp. 112-136.
- Clearwater, M.J., T. Nifinluri, and P.R. van Gardingen. 1999. Forest fire smoke and a test of hemispherical photography for predicting understory light in Bornean tropical rain forest. *Agricultural and Forest Meteorology* **97**: 129-139.
- Comeau, P.G., F. Gendron, and T. Letchford. 1998. A comparison of several methods for estimating light under a paper birch mixedwood stand. *Can. J. For. Res.* **28**: 1843-1850.
- Easter, M.J. and T.A. Spies. 1994. Using hemispherical photography for estimating photosynthetic photon flux density under canopies and in gaps in Douglas-fir forests of the Pacific Northwest. *Can. J. For. Res.* **24**: 2050-2058.
- Endler, J.A. 1993. The color of light in forests and its implications. *Ecol. Mono.* **63**: 1-27.

Gay, L.W., Knoerr, K.R. and M.O. Braaten. 1971. Solar radiation variability on the floor of a pine plantation. *Agr. Meteorol.* **8**: 39-50.

Gendron, F., C. Messier, and P.G. Comeau. 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forests. *Agricultural and Forest Meteorology* **92**: 55-70.

Goebel, P.C., B.J. Palik, L.K. Kirkman, and L. West. 1997. Field guide: landscape ecosystem types of Ichauway, Technical Report 97-1. Joseph W. Jones Ecological Research Center at Ichauway, Newton, GA.

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

Hutchinson, B.A., and Matt, D.R. 1977. The distribution of solar radiation with a deciduous forest. *Ecol. Monogr.* **47**: 185-207.

Lieffers, V.J., C. Messier, K.J. Stadt, F. Gendron, and P.G. Comeau. 1999. Predicting and managing light in the understory of boreal forests. *Can. J. For. Res.* **29**: 796-811.

Machado, J. and P.B. Reich. 1999. Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory. *Can. J. For. Res.* **29**: 1438-1444.

McGuire *et al* 2000. Canopy gaps in Savannas. *Submitted to Ecological Applications*.

McPherson, G.R. 1997. Ecology and management of North American savannas. The University of Arizona Press. Tucson, AZ.

- Messier, C., and Puttonen, P. 1995. Spatial and temporal variation in the light environment of developing Scots pine stands: the basis for quick and efficient method of characterizing light. *Can. J. For. Res.* **25**: 343-354.
- Nicotra, A.B., R.L. Chazdon, and S.V.B. Iriarte. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80(6): 1908-1926.
- Palik, B.J., R. Mitchell, G. Houseal, and N. Pederson. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. *Can. J. For. Res.* 27:1458-1464.
- Parent, S. and C. Messier. 1996. A simple and efficient method to estimate microsite light availability under a forest canopy. *Can. J. For. Res.* **26**: 151-154.
- Pearcy, R.W. 1989. Radiation and light measurements. In: R.W. Pearcy, J.R. Ehleringer, H.A. Mooney, and P.W. Rundel, *Plant Physiological Ecology: Field methods and instrumentation..* Chapman & Hall, London, pp. 95-116.
- Penfound, W.T. and A.G. Watkins. 1937. Phytosociological studies in the pinelands of southeastern Louisiana. *Am. Midl. Nat.***18**: 661-682.
- Rich, P.M. 1990. Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews* **5(1)** : 13-29.
- Rich, P.M., D.B. Clark, D.A. Clark, and S.F. Oberbauer. 1993. Long-term study of solar radiation regimes in a tropical wet forest using quantum sensors and hemispherical photography. *Agricultural and Forest Meteorology* **65**: 107-127.
- Rich, P.M., J. Wood, D.A. Vieglais, K. Burek and N. Webb. 1999. Hemiview User Manual.

SAS Institute. 1999. SAS/STAT and Base SAS. Release 8 edition. SAS Institute Incorporated. Cary, North Carolina, USA.

Schwartz, G.F. 1907. The longleaf pine in virgin forest. John Wiley and Sons, New York.

Stadt, K.J., Landhausser, S.M, and J.D.Stewart. 1997. Comment- the effects of direct-beam light on overcast-day estimates of light availability. *Can. J. For. Res.* **27**:272-274.

Vales, D.J. and F.L. Bunnell. 1988. Relationship between transmission of solar radiation and coniferous forest stand characteristics. *Agricultural and Forest Meteorology* **43**: 201-223.

Whitmore, T.C., N.D. Brown, M.D. Swaine, D. Kennedy, C.I. Goodwin-Bailey and W.K. Gong. 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *Journal of Tropical Ecology* **9**: 131-151.