Light Transmittance Estimates in a Longleaf Pine Woodland

Michael A. Battaglia, Robert J. Mitchell, Paul P. Mou, and Stephen D. Pecot

ABSTRACT. While the importance of canopy structure in open woodlands and savannas on regulating the flow of energy and matter is well known, few studies have investigated how variation in overstory abundance influences canopy light transmission and the extent that estimates vary in their ability to characterize the light environment in these ecosystems. Canopy light transmittance (% photosynthetic photon flux density, or %PPFD) was measured with gallium arsenide phosphide (GaAsP) photodiodes and was monitored throughout the growing season in an open-canopy longleaf pine (*Pinus palustris* Mill.) woodland across an overstory abundance gradient. Several estimates of canopy light transmittance were also measured, including 10 minute averages of %PPFD under clear and overcast sky conditions during summer, fall, and winter, as well as light estimates derived from hemispherical photographs (gap fraction, GF: gap light index, GLI; and weighted canopy openness, WCO). Linear and curvilinear regression were used to analyze the relationship between (1) light measurements and canopy structure and (2) light estimates and growing-season % PPFD measured by light diodes. Of all light measurements in this study, ten-minute average % PPFD measurements during clear days were the most variable: only a small proportion in the 10-minute average of light reaching the understory was correlated to either overstory structure or growing-season canopy transmittance. While measures on overcast days improved the correlations, they tended to overestimate transmittance. Gap fraction (GF) and gap light index (GLI) were strongly correlated with % PPFD and overstory structure, and the relationship between GLI and % PPFD was improved by using a direct light setting of 60%. In addition to strong correlation, hemispherical photographic estimates of light fell along a 1:1 line with % growing-season PPFD; thus, estimates were relatively unbiased. Measures of light in this ecosystem need to incorporate the large spatial and temporal variation in light transmittance that is characteristic of this ecosystem if investigators are to understand the relationship between open-canopy woodlands and their light environments. FOR. SCI. 49(5):752–762.

Key Words: Beam enrichment, canopy gaps, direct light, diffuse light, foliar clumping, forest regeneration, hemispherical photographs, *Pinus palustris*, savanna.

PLANT–PLANT INTERACTIONS between the overstory and understory, while not extensively studied, are known to regulate the structure and function of savannas (Scholes and Archer 1997). Specifically, the mediation of light reaching the understory by the overstory is particularly critical in determining the frequency, distribution, and pro-

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ductivity of understory plant communities (Belsky et al. 1989, Jackson et al. 1990, Belsky et al. 1993, Palik et al. 1997, McGuire et al. 2001). Modification of the light environment due to the presence or absence of an overstory has been extensively studied in coniferous forests (Gay et al. 1971, Reifsnyder et al. 1971, Canham et al. 1990, Easter and Spies 1994), closed-canopied hardwood forests (Reifsnyder et al. 1971, Messier and Bellefleur 1988, Canham et al. 1990), mixed hardwood-conifer forests (Constabel and Lieffers 1996, Parent and Messier 1996, Comeau et al. 1998), and tropical forests (Pearcy 1983, Chazdon and Fetcher 1984, Chazdon and Field 1987, Canham et al. 1990, Rich et al. 1993, Whitmore et al. 1993). The canopy structure of the forests in these studies is typically dense with many strata and canopy openings of various sizes and generally follows the Beer-Lambert law (exponential decrease of light transmittance with increasing leaf area index). However, the attenuation of light in open-canopied forests where foliage is typically clustered may be quite different from that of closed-canopied forests (Kucharik et al. 1999, Law et al. 2001a).

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 to 30% in old-growth stands (Penfound and Watkins 1937, cited in Palik et al. 1997). Using Endler's (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 and a mosaic of direct and diffuse light. As a result of changes in solar elevation and sky conditions throughout a day and growing season, this mosaic of direct and diffuse light varies temporally and spatially (Baldocchi and Collineau 1994).

The manner in which overstory structure influences light reaching the understory and how to best quantify light with respect to the high levels of temporal and spatial variability characteristic of open-canopied systems (Palik et al.) has yet to be adequately addressed (McGuire et al. 2001). Several studies have investigated the influence of canopy structure on understory light availability in the longleaf pine ecosystem (Palik et al. 1997, Brockway and Outcalt 1998, McGuire et al. 2001). However, these studies reported conflicting results, possibly due to the use of sampling techniques that may not capture the heterogeneity of light in the understory. Both Palik et al. (1997) and McGuire et al. (2001) utilized hemispherical photography to estimate light transmittance, while Brockway and Outcalt (1998) utilized instantaneous transmittance measurements from 12:00 to 16:00 on a clear day in December. Although these methods have been tested in closed-canopied forests, it is unclear whether these or other techniques used in closed-canopied systems would have the same reliability for estimating light transmittance in an open-canopied system.

The Beer-Lambert law, derived for homogeneous, broad-leaved, forest canopies in which foliage is randomly distributed is often used to describe the negative exponential relationship between the penetration of light transmittance and leaf area density. The appropriateness of using this relationship in open-canopied forests has come into question (Law et al. 2001a). Open-canopied coniferous forests are highly organized at the shoot, branch, whirl, and crown level. This organization results in a canopy gap fraction that is larger than that of a random canopy (Law et al. 2001b) resulting in a clumped foliage distribution that increases light transmittance over that of a canopy with randomly distributed foliage (Baldocchi and Collineau 1994, Law et al. 2001a, Norman and Jarvis 1975, Whitehead et al. 1990). Clumped foliage makes light penetration relatively insensitive to changes in leaf area (Gholz et al. 1991), and ignoring the clustering of a canopy leads to overestimation of leaf area index (Law et al. 2001*b*). Furthermore, errors associated with the estimation of light transmittance in a canopy with clumped foliage using the assumption of randomly distributed foliage are often greatest on a clear day (Whitehead et al. 1990).

Based on the possible differences in light attenuation among forest types, the suitability of different light measurement methods used in closed-canopied forests cannot necessarily be applied to open-canopied systems with the same result. Because different forest types influence the amount of direct and diffuse light present in the understory, methods used to estimate light transmittance in one system may vary in precision for systems that are structurally distinct. This article addresses the manner that overstory density in an open-canopied longleaf ecosystem regulates the amount of light reaching the understory. Furthermore, the precision of different methods of light measurement was evaluated in order to provide validated indices of light transmittance for this temperate savanna.

Methods

Study Area

The study was conducted at the Joseph W. Jones Ecological Research Center in southwestern Georgia (31°N, 84°W) from August 1998 to June 1999. Measurements were taken in a 60- to 80-yr-old second-growth longleaf pine forest. These forests are typically dominated by longleaf pine in the overstory with infrequent midstory hardwood species such as bluejack oak (*Quercus incana* Bartr.), sand post oak (*Quercus margaretta* Ashe), and turkey oak (*Quercus laevis* Walt.) (Mitchell et al. 1999). Mean diameter at breast height (dbh) and total height (± 1 SE) of all longleaf pine trees >4 cm dbh (n = 4853) was 27.81 cm ± 0.18 cm and 20.87 m ± 0.13 m, respectively. The understory is dominated by wiregrass (*Aristida stricta* Michx.) with many other species of perennial grasses and forbs (Kirkman et al. 2001). Topography is gently sloped (1–5 % slope) with some limestone 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 soils of the Orangeburg and Wagram series. The vegetation is maintained with prescribed fire between February and May with intervals ranging from 1 to 3 yr, depending on moisture conditions and fuel accumulation.

Three replicates of four overstory manipulation treatments (approximately 2 ha in size) were used to determine the effects of spatially variable overstory structure on light reaching the understory of longleaf pine ecosystems. The four treatments were randomly assigned to each of three replicates including: (1) an uncut control; (2) basal area reduction through thinning of widely spaced individual trees, i.e., single tree selection; (3) basal area reduction through small gap harvesting (~0.10 ha gap); and (4) basal area reduction through large gap harvesting (~0.20 ha gap). Basal area in the control plots averaged 17.3 m^2/ha. For the three cut treatments, mean residual basal areas after harvesting were similar (mean of 12.3 m^2/ha in the single tree and small gap treatments and 11.9 m^2/ha in the large gap treatment), but varied spatially, i.e., more evenly spaced in single tree selection and more aggregated as gap size increased (Palik et al. 2003, Jones et al. 2003).

We undertook a complete survey of every tree in the study area in November 1997, recording tree height (m) and dbh (cm). Exact geographical location of all trees and plot boundaries was accomplished by (1) recording relative location of all trees and plot boundaries with a laser transit system (Sokkisha Model 3DM3F, Sokkia Corporation, Olathe, KS), (2) recording plot boundaries and a small subset of trees in each plot using a GPS datalogger, and (3) overlaying the two datasets using GIS software to convert laser transit data to UTM (Universal Transverse Mercator) space. The accuracy of the laser transit was approximately 0.1 m, and the accuracy of the GPS datalogger was <1 m; therefore, we felt that this method adequately assessed individual tree locations. We overlaid all possible 5 m by 5 m grid points (the approximate subplot size) and determined a measure of overstory competitor abundance with the equation

$$OAI = \sum_{i=1}^{n} (A / d) \quad (1)$$

where *OAI* = overstory abundance index (typically expressed as a dimensionless value), A = cross-sectional area of tree i (cm^2), and d = distance (m) of tree i from the grid point. This formula was applied within a 15 m radius (706 m^2 area) circle from the grid point (Stoll et al. 1994). The number of grid points among plots varied, ranging from 444 to 533. Twenty-five subplots were chosen that span the range of overstory competitor abundance (*OAI*). Further details of subplot selection are given in Jones et al. (2002).

Light Measurements Using Photodiodes and Quantum Sensors

The relative percent of photosynthetic photon flux density (%PPFD) was measured across an entire growing season from December 1998 to November 1999. %PPFD was defined as the daily sum of below-canopy (above understory) PPFD (μmol s^{-1} m^{-2}) divided by the daily sum of above-canopy PPFD. Below-canopy light quantity was measured using gallium arsenide phosphide (GaAsP) photodiodes (model G1118, Hamamatsu Corporation, Bridgewater, NJ). GaAsP photodiodes were ideal for this experiment due to their low cost and good spectral response between wavelengths of 300 and 680 nm (Pearcy 1989, Pontailler 1990, Fielder and Comeau 2000). Each photodiode was soldered to a 70 m wire attached to a multiplexer data acquisition system (Easylogger 900, Wescor, Inc., Logan, UT). The photodiodes were protected from adverse weather conditions using putty and shrink tubing. A quantum sensor (LI-COR Li-190SA, LI-COR, Inc., Lincoln, NE), calibrated at the beginning and end of this study, was attached to a data logger (LI-COR 1000) and placed 1 m above the ground in a large, open field less than 1 km distance from the study area to obtain 1 min. values for solar constant and the surrogate measure of above-canopy light measurements.

All GaAsP photodiodes were calibrated against a LI-190 quantum sensor in September 1998 and again in June 1999 in the same field where above-canopy light quantity measurements were taken. Before each calibration, the quantum sensor and the photodiodes were carefully leveled so that the photodiodes surrounded the LI-190 sensor in the space of approximately 0.25m^2. For the September 1998 calibration, GaAsP sensors were calibrated under clear sky conditions during midday. Various intensities of shade cloth resulting in approximately 0 to 100% occlusion were used to vary light intensities. For every change in shade cloth, measurements with the photodiodes and the LI-190 sensor were made every minute for at least 20 min. For the June 1999 calibration, we utilized the approach performed by Gendron et al. (1998) in which the sensors measured light intensity for several days to capture a wide range of solar angles.

Regression analysis between each GaAsP sensor and the quantum sensor was established to generate a conversion factor to convert millivolt output of the photodiode to photosynthetic photon flux density (PPFD; μmol s^{-1} m^{-2}). At low light intensities, the relationship between millivolt and PPFD was linear; however, at higher intensities, the relationship became quadratic. To remedy this, we applied a simple linear fit to low light intensities and a quadratic fit to higher light levels. An iterative process using nonlinear regression determined the point between the simple linear and quadratic fit. The relationships, expressed as fit index (FI), between the photodiodes and quantum sensor for both sections of the relationship were very strong for the September (FI > 0.99, n = 92 of 95) and June (FI > 0.97, n = 73 of 80) calibrations. While our GaAsP photodiodes were not cosine-corrected, several precautions were taken to minimize potential problems with using these sensors: (1) they were calibrated with cosine-corrected sensors; (2) we omitted data >75° from zenith because of lower accuracy of both sensors at these levels (Biggs 1986, Fielder and Comeau 2000); and (3) photodiodes were randomly distributed across space and time. Finally, the relationship between millivolt (photodiode) and PPFD (quantum sensor) was consistent across all sensors; therefore, any error was evenly distributed across all sampled points.

Photodiodes were placed 1 m above the ground in the middle of each subplot. Daily checks were made at all locations to ensure lens clarity and that the diode was level (using a bubble level). An average (± 1 SD) of 15 ± 6 subplots was used in each plot to measure below-canopy light quan-

tity. All sample locations were randomly selected from a stratified list to encompass the range of overstory abundance indices observed in this study. A total of 51 days were measured during the entire experiment. For each measurement period, a different block consisting of the four treatments was measured. Block 1 was measured in December 1997 (5 to 8 days), February 1998 (1 day), and June 1998 (6 days); block 2 was measured in July (7 days), August (4 to 8 days), and September (4 to 13 days) (all 1998); and block 3 was measured in October (1 to 4 days) and November (7 to 10 days) (all 1998). Months were defined using the time periods documented in the HemiView® 2.1 user manual (Rich et al. 1999). Below- and above-canopy PPFD was measured every 10 sec and stored as 1 min averages each day for sun angles >15° from the horizon. The daily sum of below-canopy PPFD recorded for each subplot was divided by the sum of the above-canopy PPFD to estimate daily transmittance (%PPFD).

A subset of the photodiode data from three representative clear days (June 19, 1999, $n = 68$; September 14, 1998, $n = 55$; and December 2, 1998, $n = 43$) was used to test the clear day light assessment approach utilized by Carter and Klinka (1992) and tested by Gendron et al. (1998) to estimate annual %PPFD. The mean light transmittance values for 10 min averages from 10:00–10:10 and from 14:00–14:10 were used to calculate $\%PPFD_{clear}$. We also utilized the method of Gendron et al. (1998) to assess the reliability of light transmittance on an overcast day in which a 10 min 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 (Gendron et al. 1998). Three representative overcast days (June 27, 1999, $n = 53$; September 10, 1998, $n = 47$; and December 8, 1998, $n = 58$) were used to test the reliability of a 10 minute average %PPFD for estimation of annual %PPFD. These days represented sampling dates closest to the summer solstice, autumnal equinox, and the winter solstice, respectively. For each of the days, we calculated the 10 min average transmittance around solar noon (11:56–12:05).

Light Measurements Using Hemispherical Photographs

Hemispherical photographs were taken at all subplots ($n = 300$) during July and August 1998 on calm, cloudless mornings at sunrise and evenings prior to sunset. It was assumed that canopy openings in 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 35 mm camera with an attached 180° equidistant fisheye lens (Sigma 8 mm). The lens was placed at the location of the GaAsP 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. 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 Devices, Ltd., 128 Low Road, Burwell, Cambridge CB5 0EJ UK). This program yields estimates of gap fraction (GF) and weighted canopy openness (WCO). For each calculation, the hemisphere was divided into sectors with an azimuth and a zenith resolution of 20.

HemiView© v.2.1 software 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. Gap light index (GLI) is a value that estimates the percentage of incident PAR transmitted through a gap to a point in the understory (Canham 1988). GLI is calculated using the equation below (Canham 1988):

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

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. For the calculation of $T_{diffuse}$, we chose to use the SOC (Standard Overcast Sky) model. T_{beam} was calculated with the solar constant set to 2510 μmol m^{-2} s^{-1}. SOC assumes diffuse light is three times brighter at the zenith angle than the horizon (Anderson 1964, Machado and Reich 1999).

For the calculation of GLI, the parameters $P_{diffuse}$ and P_{beam} must be provided. Most authors assume that estimate of $P_{diffuse}$ and P_{beam} is 0.5 for an entire growing season (Comeau et al. 1998, Gendron et al. 1998, Canham et al. 1990, Machado and Reich 1999); however, for finer time scales, e.g., day, week, or month, these parameters might lead to less accurate predictions given temporally variable 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 are no values currently available for our study site, we chose to estimate the parameters indirectly. Instead of assuming equal proportions of $P_{diffuse}$ and P_{beam}, we varied $P_{diffuse}$ and P_{beam} between 0.0 and 1.0 in increments of 0.10 to calculate GLI as done by other studies (Rich et al. 1993, Easter and Spies 1994, Clearwater et al. 1999) and then compared correlation of coefficients of GLI estimates with %PPFD measured with photodiodes.

Data Analysis

To obtain the annual %PPFD for each subplot, the sum of below canopy %PPFD for all days that a subplot was measured was calculated and divided by the sum of the above-canopy %PPFD for the corresponding days. Subplots within each block were then ranked from lowest to highest *OAI*. A subplot with a similar *OAI* value from each block was then randomly chosen to represent a separate *OAI* class ($n = 28$). For each *OAI* class, the *OAI* value and the corresponding annual% PPFD, WCO, GF, and GLI values for the three blocks were averaged to obtain the mean annual %PPFD, WCO, GF, and GLI for a specific *OAI* value. Linear regression analysis was performed to

examine the relationship between the mean annual %PPFD and the hemispherical photograph estimates WCO, GF, and GLI. A nonparametric model was fit to examine the relationship between the mean *OAI* class value and mean annual %PPFD. The equation obtained from this relationship was used to predict the mean annual %PPFD for subplots used in the analysis for the clear and overcast day method. Linear regression analysis was performed to examine the relationship between the predicted mean annual %PPFD and the clear day method transmittance for subplots measured in June, September, and December and the overcast day method transmittance for subplots measured in July, September, and December. The data analysis for this study was generated using SAS® software, Version 8.2 of the SAS System for UNIX.

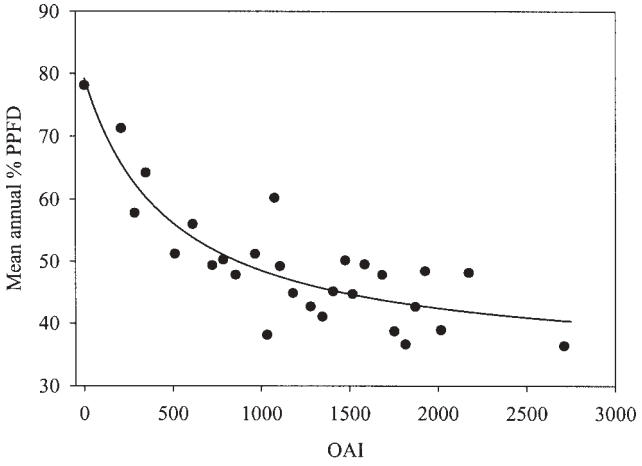

Figure 1. Mean annual %PPFD as estimated by photodiodes in relation to overstory abundance index for a 60- to 80-yr-old longleaf pine forest, Baker County, Georgia. The fitted line is $y = 33.31 + 45.87/(1 + 0.00202*OAI)$ ($FI = 0.76$).

Results

Overstory Abundance and Light Transmittance

The relationship between *OAI* and light reaching the understory depended on the method used to quantify canopy transmittance. Annual transmittance measured by photodiodes ranged from 40% to 78% (Figure 1). Approximately 76% of the variation in light reaching the understory was explained by a curvilinear relationship with *OAI* (Figure 1). However, the relationship between overstory abundance and canopy transmittance varied with the method and time that light transmittance was recorded (Figure 2). Measuring light with 10 min averages during clear days tended to have a lower correlation with overstory abundance and ranges in %PPFD

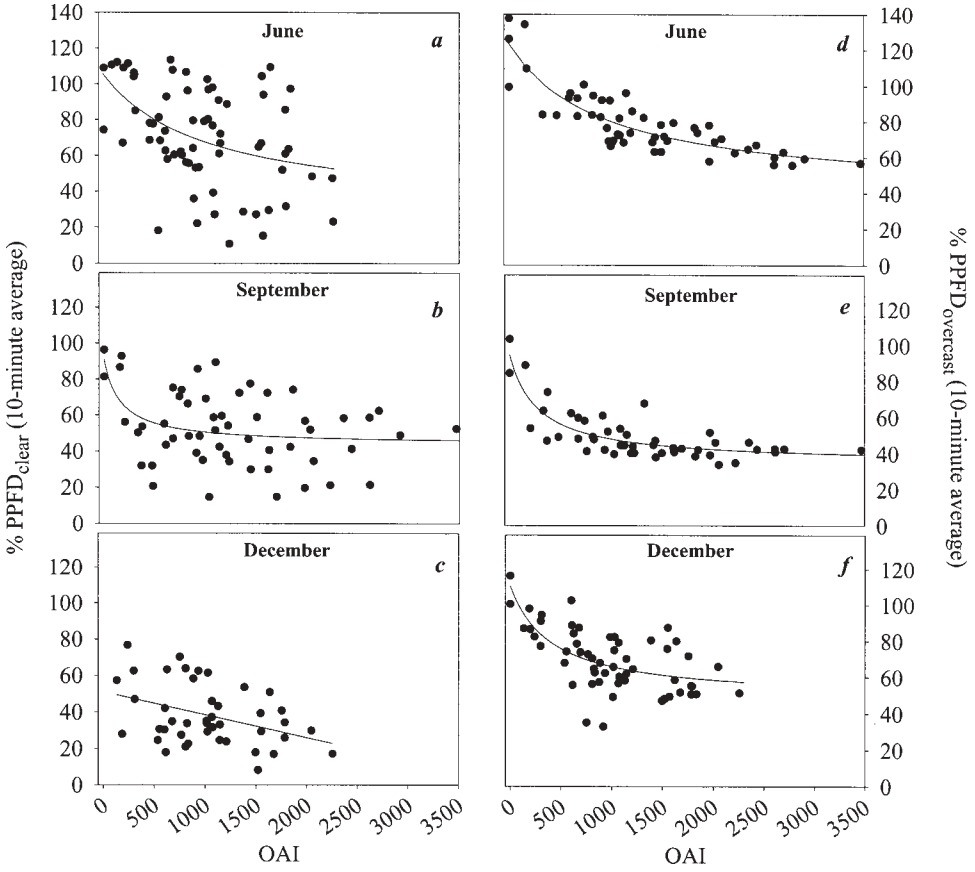

Figure 2. Ten-minute averages of %PPFD for clear days (a, b, c) and overcast days (d, e, f) during June, September, and December in relation to overstory abundance index for a 60- to 80-yr-old longleaf pine forest, Baker County, Georgia. [Ten-minute averages are from 10:00–10:09 and 14:00–14:09 for clear days and from 11:56–12:05 for overcast days. The equations (*a–f*, respectively) are $\%PPFD = 29.35 + 75.64/(1 + 0.00099*OAI)$ ($FI = 0.20$); $\%PPFD = 43.97 + 46.77/(1 + 0.00622*OAI)$ ($FI = 0.19$); $\%PPFD = 51.00 - 0.013*OAI$ ($P = 0.01$, $r^2 = 0.15$); $\%PPFD = 40.06 + 83.16/(1 + 0.00107*OAI)$ ($FI = 0.75$); $\%PPFD = 35.20 + 59.41/(1 + 0.00367*OAI)$ ($FI = 0.71$); $\%PPFD = 48.12 + 62.21/(1 + 0.00250*OAI)$ ($FI = 0.51$).

values that varied more than annual measures of light transmittance. For instance, 10 min averages of light transmittance during June varied from greater than 100% to less than 20%, while only 20% of the variation in %PPFD on a clear day was related to overstory abundance (Figure 2). While clear day measurements varied seasonally, all times were poorly correlated with *OAI*.

Mean 10 min light transmittance on overcast days was much more strongly correlated to overstory abundance than measurements recorded on clear days (Figure 2). Similar to the clear day measurements, overcast day 10 min transmittance measurements tended to show a greater range in values than that observed for annual measurement with photodiodes (Figure 2). The three hemispherical photographic estimates of light transmittance were well correlated to overstory structure. WCO was least correlated to *OAI* (FI = 0.74; Figure 3*a*), and GF was most correlated to *OAI* (FI = 0.86; Figure 3*b*). Correlation of GLI and *OAI* was between that observed with WCO and GF (FI = 0.82; Figure 3*c*).

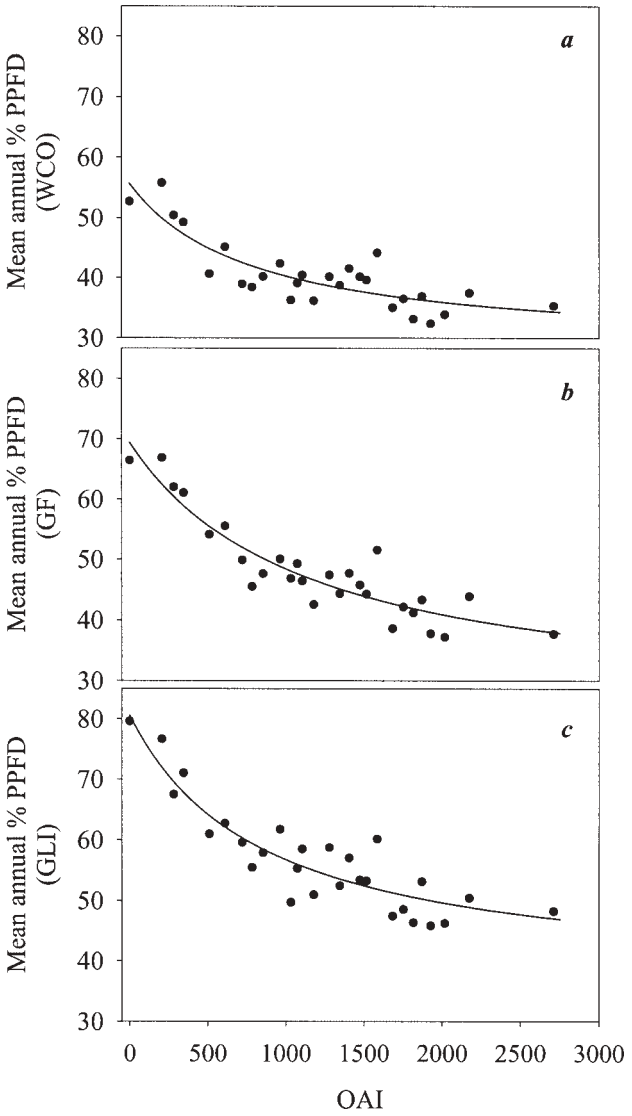

Figure 3. Mean annual %PPFD as estimated by WCO (a), GF (b), and GLI (60:40 direct:diffuse light ratio) (c) in relation to overstory abundance index for a 60- to 80-yr-old longleaf pine forest, Baker County, Georgia. [Equations are *WCO* = 28.23 + 27.44/(1 + 0.00128OAI*) (FI = 0.74), *GF* = 25.11 + 44.28/(1 + 0.00090* *OAI*) (*FI* = 0.86), and *GLI* = 36.63 + 43.98/(1+0.00119**OAI*) (FI = 0.82), respectively.]**

Precision of Light Estimates

The 10 min average %PPFD on clear and overcast days for time periods proximal to the summer solstice, autumnal equinox, and the winter solstice were regressed against annual % transmittance estimates of light. The 10 min average %PPFD on a clear day was the least precise technique to estimate mean annual transmittance (Figure 4 a–c). Although a statistically significant relationship was detected, the amount of variability explained was low for all time periods. Further-

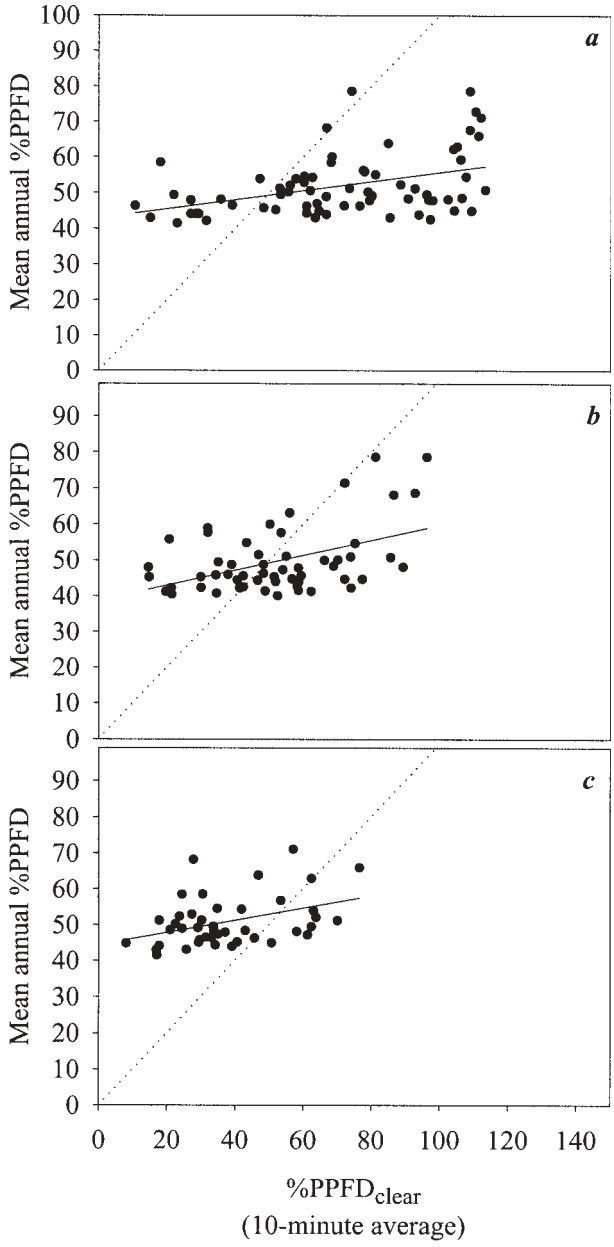

Figure 4. Mean annual %PPFD measured with photodiodes in relation to mean light transmittance from 10:00–10:09 and 14:00–14:09 on a clear day in June (a; *n* = 68), September (b; *n* = 55), and December (c; *n* = 43) for a 60- to 80-yr-old longleaf pine forest, Baker County, Georgia. The dotted lines show a 1:1 relationship. [Equations are *y* = 44.17 + 0.1201PPFD* (r^2 = 0.18), *y* = 39.95 + 0.1703**PPFD* (r^2 = 0.14), and *y* = 45.564 + 0.1588**PPFD* (r^2 = 0.13), respectively. Slopes for all relationships were significantly different from 1 (*P* < 0.05).]**

more, the models underestimated mean annual transmittance at microsites that received lower levels of light (<50% PPFD) and overestimated mean annual transmittance at microsites that received higher levels of light (>50% PPFD) (Figure 4). On overcast days, the fit between the 10 min average %PPFD and mean annual %PPFD was much greater than that of clear days (Figure 5). On overcast days in June, this relationship yielded the highest r^2 but tended to overestimate mean annual %PPFD (Figure 5a). The September measurement showed a lower r^2 and overestimation of mean annual %PPFD at microsites receiving greater than 50% PPFD (Figure 5b). The measurements in December showed a further decrease in precision as well as overestimation of mean annual %PPFD for the majority of the microsites (Figure 5c).

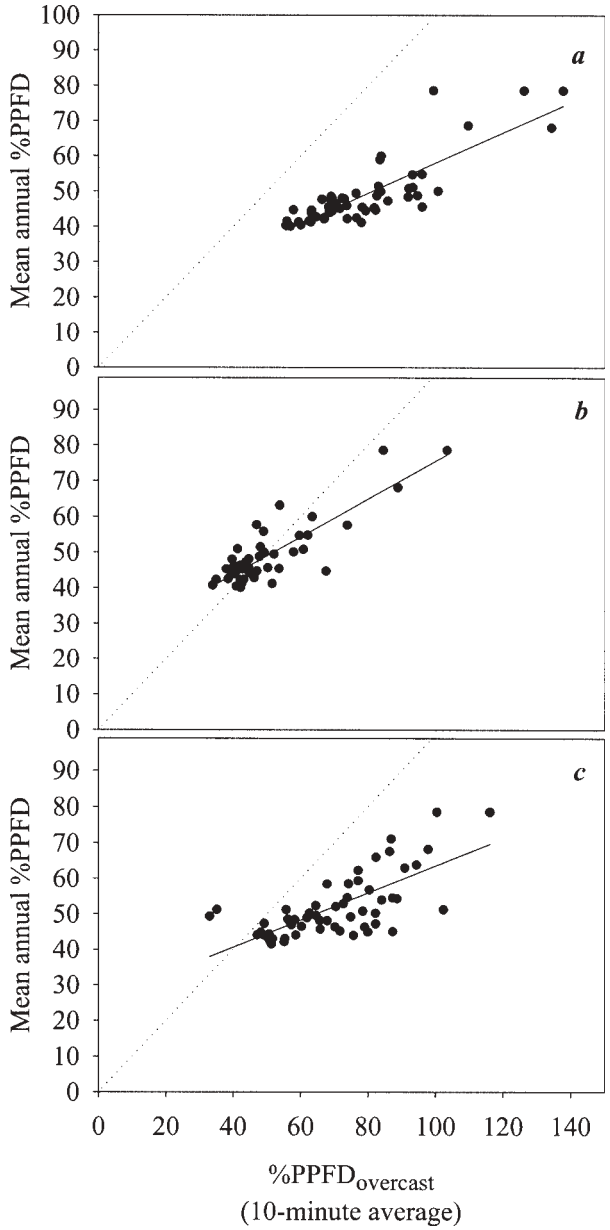

Figure 5. Mean annual % PPFD measured with photodiodes in relation to mean light transmittance from 11:56-12:05 on an overcast day in June (*a*; n=53), September (*b*; n=47), and December (*c*; n=58) for a (60 to 80) year-old longleaf pine forest, Baker County, Georgia, USA. The dotted lines show a 1:1 relationship. [Equations are $y = 15.797 + 0.414*PPFD$ ($r^2 = 0.70$), $y = 23.958 + 0.4904*PPFD$ ($r^2 = 0.57$), and $y = 30.152 + 0.3171*PPFD$ ($r^2 = 0.46$), respectively. Slopes for all relationships were significantly different from 1 ($P < 0.05$).]

For various estimates of light transmittance using hemispherical photographs, WCO underestimated mean annual %PPFD and yielded the weakest r^2 (Figure 6a). GF showed good agreement between the observed and estimated values (Figure 6b), as well as the highest precision of all methods. The estimate of GLI showed the second highest precision but slightly overestimated mean annual %PPFD (Figure 6c).

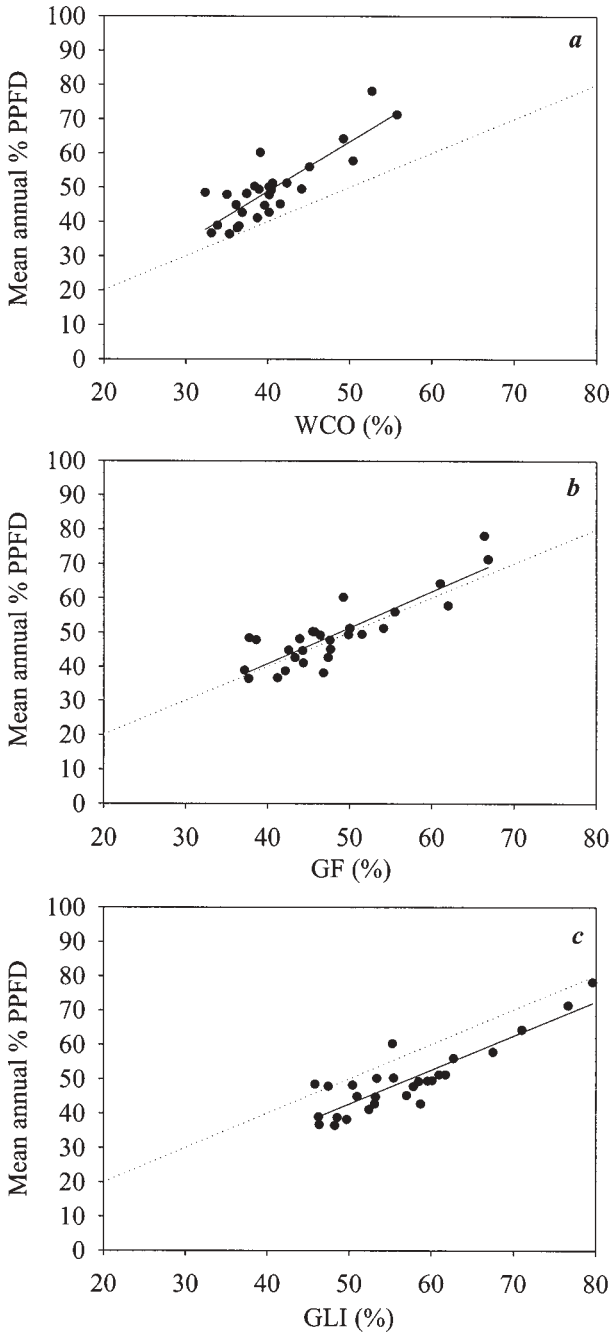

Figure 6. Mean annual % PPFD measured with photodiodes in relation to WCO (*a*), GF (*b*), and GLI 60:40 direct:diffuse light ratio) (*c*) for a (60 to 80) year-old longleaf pine forest, Baker County, Georgia, USA. The dotted lines show a 1:1 relationship. [Equations are $\%PPFD = -9.44 + 1.45*WCO$ ($r^2 = 0.72$), $\%PPFD = -1.29 + 1.05*GF$ ($r^2 = 0.74$), and $y = --7.43 + 1.00*GLI$ ($r^2 = 0.77$), respectively. The slope for *a* was significantly different from 1 ($P < 0.05$), while the slopes for *b* and *c* were not significantly different from 1 ($P > 0.05$).]

Varying the proportion of direct and diffuse light in the calculation of GLI only made modest differences in the slope or the amount of variation in annual %PPFD explained (Figure 7). When the ratio of direct to diffuse light was set at 60%:40% and regressed with annual %PPFD measured with photodiodes, the slope of the regression line was 1.00, and r^2 was 0.77. We believed that since there were very small differences in the variation explained we would use the ratio that had the least statistical bias, i.e., a 1:1 line, between hemispherical and photodiode estimates of annual %PPFD (Figure 7).

Discussion

The amount of light transmitted to the understory of the longleaf pine forest investigated in this study (38–80%) was substantially higher than that typically reported for other forest types. For example, typical summer transmittance values in temperate hardwood forests range from 1–3.7% (Hutchinson and Matt 1977, Canham et al. 1990, Brown and Parker 1994). Studies in tropical evergreen forests have reported low transmittance values ranging from 0.44% (Bjorkman and Ludlow 1972) to 2.4% (Pearcy 1983). Boreal coniferous forests have reported light transmittance values ranging from 14–30% (Canham et al. 1999).

The large difference in light transmittance between closed-canopy forests and the present study is largely due to the differences in forest canopy structure. For instance, a study performed in northern British Columbia (55˚N) investigated the transmittance and canopy architecture of several coniferous (*Tsuga heterophylla* [Raf.] Sarg., *Pinus contorta* var. *latifolia* Engelm., *Picea glauca* [Moench] Voss) and broad-leaved (*Betula papyrifera* Marsh.) tree species (Canham et al. 1999). Average canopy openness was much lower for these species (6%–14%) than that noted in this study. At 55°N, the majority of incident light occurs at solar angles between 35° and 60° (Canham et al. 1999), where canopy openness ranges between 10–35% depending on the species and light transmittance is low (14–30%). In longleaf pine forests canopy openness was greater than 50% at similar solar angles.

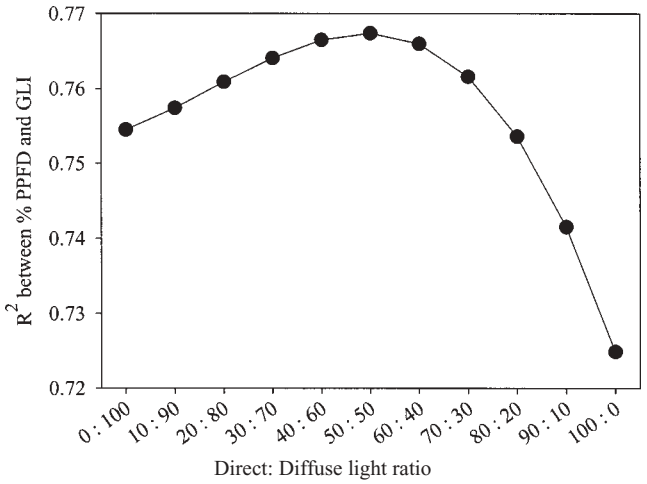

Figure 7. Statistical fit of mean annual %PPFD (measured using photodiodes) and GLI (measured using hemispherical photographs) as a function of direct:diffuse light ratios for a 60- to 80-yr-old longleaf pine forest, Baker County, Georgia.

Though canopy structural features across forested communities are complex, Endler (1993) suggests that forest light could be classified into four major environments: forest shade, small gap, woodland shade, and large gap, each with specific structural features. While most light studies have been conducted in forest shade and small gaps, longleaf pine woodlands are largely characterized by woodland shade and large gaps. While the open-canopy structure of longleaf pine woodlands allows for relatively more light to reach the understory, the heterogeneous canopy structure as well as the diurnally and seasonally variable sun angle creates spatially and temporally variable light environments. Variation in the extent of canopy openness and the proportion of direct and diffuse light has been suggested as critical factors in the reliability of various light measures in different forest habitats. While few light measurements have been reported for longleaf pine forests, those that have used different approaches have come to diametrically opposed conclusions of how overstory regulates light and regeneration responses (Palik et al. 1997, Brockway and Outcalt 1998, McGuire et al. 2001).

Several authors have suggested that arrays of photodiodes distributed across a range of forest conditions and measured throughout the day and seasons provide the most reliable measure of growing-season light transmittance by forest canopies (Rich et al. 1993, Comeau et al. 1998); however, these approaches are often limited by expense and logistics (Gendron et al. 1998). When annual measures of photodiodes were used across a range of tree abundance in longleaf pine woodlands, a strong curvilinear relationship between overstory structure and light reaching the understory was observed in our study similar to that reported by Palik et al. (1997). Ten-minute average light transmittance on clear days as reported by Brockway and Outcalt (1998), however, was much more variable. Increased variability and lower correlation with growing-season values for measurements of canopy transmittance using clear day measurements has been previously reported (Messier and Puttonen 1995, Parent and Messier 1996, Comeau et al. 1998). However, variability is decreased by averaging over longer time periods (Comeau et al. 1998). Thus, the 10 min averages we report here are likely to be less variable than the instantaneous measures reported by Brockway and Outcalt (1998). Not only did variance in canopy transmittance increase, and correlation between forest structure and canopy transmittance decrease, but systematic bias was observed in our clear day measurements (Figure 4). Furthermore, all other time periods and sky conditions, except December and clear sky, exhibited an exponential decay relationship between light transmission and *OAI*, while December/clear sky was linear (Figure 2*c*). This suggests that clear-day, instantaneous light measurements may not adequately assess light environments in these open-canopied forests.

Light estimates taken on overcast days have been shown to be an improvement over those measured on clear days in estimating growing-season transmittance values. However, these reports are largely for forests at latitudes above 46°N, and 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, Machado and Reich 1999). When overcast measures of light were regressed with growing-season light measures, r^2 values were less in our study (ranging from 0.46 to 0.70) than those reported by Comeau et al. (1998) (r^2 = 0.98) and Gendron et al. (1998) (r^2 = 0.92). However, we found that the strength of the relationship was dependent on the time of year the sample was taken, suggesting that solar altitude influences the precision of this method (Figure 5).

Another factor that may influence the precision of short time-scale, overcast measurements is canopy structure. Gendron et al. (1998) measured a range of growing-season %PPFD (4.6 to 97.8) and found overcast light transmittance to strongly predict growing-season transmittance. When these three light environments were separated into closed-canopy, canopy gap, and open-canopy, the precision of the 10 min average overcast %PPFD method decreased substantively. In our system, a mean annual %PPFD range of 30 to 80 most closely corresponds to their "canopy gap" environment. Gendron et al. (1998) found a similar relationship between overcast light transmittance and growing-season transmittance (r^2 = 0.62) in July, as we did in our study. In their study of a young bigleaf maple stand on Vancouver Island in Canada, measurements made during that period underestimated mean annual %PPFD; however, our study overestimated %PPFD. One reason for this dichotomy could arise from the difference in maximum zenith angle in June, which is 82° in our study but 49° in Gendron et al. (1998). Because the solar path during this time period is at its maximum and the longleaf pine canopy is more open at these angles, more light can reach the understory and, thus, annual %PPFD is overestimated.

Differences in canopy structure may also affect the appropriateness of the model used to estimate light transmission. Whitehead et al. (1990) reported an increase in the probability of direct light being transmitted through tree crowns of red pine with increasing solar zenith angle beyond 45˚ when a canopy is clumped. Thus, more variability would be observed on a clear day because of greater interception of direct beam by the crowns (Whitehead et al. 1990). In our study, the variability and bias of %PPFD during a clear day (Figure 4) was much greater than that of %PPFD on an overcast day (Figure 5), implying that the effect of canopy foliar clumping on light interception is more prevalent with relatively higher levels of direct light. While canopy light transmittance followed the Beer-Lambert law reasonably well in mature hardwood forests (Vose et al. 1995), multilayered stands and open canopies may require more detailed information on the spatial distribution of leaf area than stands with a simple architecture (Williams et al. 1996). Further work would be needed to elucidate some of the potential effects of using the Beer-Lambert Law to estimate canopy light transmission in open-canopy ecosystems such as longleaf pine and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws).

The influence of solar altitude on estimates of mean annual %PPFD also affected the precision of two of the hemispherical photograph estimates. For instance, WCO resulted in the lowest r^2 (0.72) with respect to mean annual %PPFD. WCO 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°; therefore for limited times of the year, e.g., summer, WCO as a hemispherical photograph measure might be appropriate. During other times of the year, however, WCO overestimates the amount of light. The use of WCO 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.

In contrast to the WCO, GF integrates the total number of open points for the entire hemisphere without any weighting. Nicotra et al. (1999) stated that GF (MDIR in their study) was a better estimate of diffuse light penetration (and perhaps overall light availability) than WCO. This was confirmed in our study: GF explained 74% of the variation of annual %PPFD, compared to 72% of the variation explained by WCO.

Gap light index (GLI) incorporates the changing solar altitude diurnally and seasonally and the interaction of solar angle with the canopy structure, often providing a more accurate estimate of growing-season light transmittance (Canham 1988). Light estimates from $GLI_{0.5,0.5}$ (direct beam and diffuse light as 50% each, a common assumption) were similar in precision to those provided by GF in our work. Varying the proportion of diffuse and direct light to both extremes, however, had only a minor influence on GLI estimates and only slightly improved fit (r^2 values ranged from 0.72 at 100% direct light to 0.77 at 50% direct light, with a 1:1 slope achieved at 60% direct light). Still, there was a significant amount of variation unexplained by GLI. This may be due to the influence of beam enrichment which hemispherical photograph estimates ignore. Beam enrichment, which is additional scattering of direct light off of leaves, stems, branches, etc., has been shown to be important in other coniferous and deciduous forests, accounting 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).

Conclusions

The open-canopy structure of longleaf pine woodlands results in increased amount and variation of light reaching the understory. Measuring light in these communities needs to account for the high degree of spatial and temporal variation, making instantaneous measures (particularly those on clear sky days) dubious. Contrary to Brockway and Outcalt (1998) but consistent with Palik et al. (1997) and McGuire et al. (2001), we found a strong curvilinear relationship between our index of overstory abundance and light reaching the understory. The reasons for the discrepancy in the literature are related to differences in the methods employed to assess light quantity. Light measurements (ten minute average)

during clear sky conditions showed greater variability, less correspondence to overstory structure (Figure 2), and greater bias (Figure 4). Measurements on uniform cloudy days (Figure 5) showed greater precision than that of clear days (Figure 4), but were inferior to hemispherical photographs that showed high r^2 with direct actual %PPFD measures and were unbiased (fell on or close to the 1:1 line) (Figure 6). Future work will include modeling light–overstory interactions with special attention to the effects of foliage distribution (Kucharik et al. 1999, Law et al. 2001a). Also, investigations into variable overstory retention, degree of aggregation, and seedling response will be addressed.

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