The Influence of Overstory Structure on Understory Light Availability in a Longleaf Pine (*Pinus palustris Mill.)* Forest

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(ABSTRACT)

Understory light environments are inherently heterogeneous and therefore difficult to characterize. Numerous methods to measure understory light have been assessed in closed-canopied forests; however, the reliability of these methods has not been addressed for open-canopied forests. Therefore, the first objective of this study, presented in Chapter 3, was to test the accuracy and precision of various light measurement techniques at different time scales and sky conditions. The methods assessed performed differently depending on the sky condition and time of year when the sample was taken. To estimate annual photosynthetic photon flux density transmittance (annual %PPFD), the use of a 10-minute average of PPFD measured on an overcast day (%$\text{PPFD}_{\text{overcast}}$) was effective, but accuracy decreased with decreasing solar altitude (*ie* season change). Hemispherical photographs used to estimate weighted canopy openness and gap fraction were effective methods, but gap light index (GLI) also derived from hemispherical photographs performed better. Accuracy of daily %PPFD estimates using %$\text{PPFD}_{\text{overcast}}$, weighted canopy openness, and gap fraction were strongly affected by solar altitude and sky condition. Gap light index was very effective in estimating daily %PPFD for all sky conditions and time periods. The second objective of this study, presented in Chapter 4, was to characterize the relationship between canopy structure and spatial distribution of light by using three replicates of one uncut treatment and three harvest treatments: single tree, small gap (0.1 ha), and large gap (0.2 ha). Each harvest retained similar residual basal area but with different spatial patterns of the residuals, ranging from uniformly dispersed (single tree) to different degrees of aggregation (small and large gap). Average stand level light availability increased 12-22% when the same residual basal area of trees was distributed in clusters versus a uniform distribution. The variation of light availability increased as stands became more aggregated and larger amounts of the variation was explained by the spatial pattern of the canopy structure. Spatial autocorrelation range was twice as large in the small gap harvest then the other harvest treatments. It is suggested that seedling growth response to these differences in spatial patterns of light may differ between the different harvests.

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Chapter I: INTRODUCTION

Study Rationale

In forest ecosystems, light is a key resource for seedling establishment and growth. Therefore, understanding how a canopy structure influences understory light environment is important. The forest understory can be described as a mosaic of shade and sun. This heterogeneity of light patterns is a result of the interaction of canopy structure and the solar elevation. Although light is a key resource to seedling regeneration, natural forests have continued to regenerate under such heterogeneous light environments. Many silvicultural practices attempt to emulate the canopy structure of natural forests to regenerate specified tree species with a variety of techniques. For example, the structure of the longleaf pine (*Pinus palustris* Mill.) forest system has been characterized as an open, park-like forest composed of mosaics of multi-aged patches of longleaf pine trees with a diverse understory of grasses and herbs (Landers *et al* 1995, Johnson and Gjerstad 1998). The use of shelterwood with reserves has been proposed to maintain this type of forest structure. This technique retains a portion of the overstory for one or more rotations, creating two or more cohort age structures (Smith *et al.* 1997). The retention of the residual basal area can be manipulated to form different spatial patterns. Not only can different spatial patterns of the residual overstory create patterns of understory light, it can also change the stand structure of the future forest via different stand level regeneration patterns. To further complicate matters, patterns of light in the understory change if the predominant light changes from direct to diffuse, but in unknown ways. Understanding heterogeneity of light and the effects it has on the regeneration, survival, and growth of the longleaf pine seedlings is an important issue that needs to be investigated. However, classification of the light environment in any forest is a very complex endeavor.

Techniques used to characterize heterogeneous understory light environment range from direct measurements of light with single instantaneous measurements to longer-term studies that measure light continuously from days to months. Parent and Messier (1996) demonstrated that an instantaneous measure of %PPFD (photosynthetic photon flux density) on an overcast day is a useful method for estimating mean daily %PPFD. Other studies have shown that this method is also useful for estimating growing season transmittance (Comeau et al 1998, Gendron et al 1998, Machado and Reich 1999). This method measures diffuse light that penetrates the canopy openings as well as transmitted, reflected, and beam enriched light. However, the method ignores the contribution of direct light and implies that the spatial distribution of the canopy structure is trivial (Stadt et al 1997). Indirect methods such as hemispherical photography incorporate 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 then 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. Gap light index accounts for the interaction of the spatial distribution of canopy openings and the solar path throughout the year. However, this method ignores beam enrichment.

Modification of the light environment due to the presence or absence of an overstory has been studied with the above techniques 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 Beers law (exponential decrease of light with increasing leaf area index). The attenuation of light in open canopied forests where foliage is clustered and distributed, such as the longleaf pine forest, may be quite different than closed-canopied forests, yet little work in open-canopied woodlands has been published.

Typical canopy closure in the longleaf pine ecosystem averages only 50% in second-growth stands (Palik *et al* 1997) and 20-30% in old-growth stands (Penfound and Watkins 1937 cited in Palik *et al* 1997). The combination of the simple two-layered vegetative strata and the "openness" of the canopy in the longleaf pine ecosystem allows for a unique investigation of the role of overstory interception of light and its effect on the light availability at the regeneration layer. To date, only a few studies have investigated the influence canopy structure has on understory light availability in the longleaf pine system (Palik *et al* 1997, Brockway and Outcalt 1998, McGuire *et al* 2000). These studies lack agreement concerning effects of overstory density on light conditions, partly due to the use of sampling techniques that may not capture the heterogeneity of light in the understory. These studies have only briefly addressed the light environment with limited direct measurements (Brockway and Outcalt 1998) or measurements with hemispherical photography (Palik *et al* 1997, McGuire *et al* 2000).

Objectives and Hypotheses

This study was initiated to investigate the relationship between residual overstory structures on light patterns in a longleaf pine forest where understory light is important for regeneration of this shade intolerant species. Although many studies have confirmed the accuracy of several light measurement techniques in closed-canopied forests, the issue of reliability of these techniques in open-canopied forests has not been addressed. Therefore, the first objective in this study was to evaluate the effectiveness of different light transmittance measurement techniques in the longleaf pine forest on an annual basis. In addition, we also want to determine which method resulted in the best estimation of mean daily %PPFD for different sky conditions at different times of the year. My hypotheses were:

1. **Agreement between the direct continuous light measurements and the indirect light measurement methods that estimate annual transmittance will vary according to the sampling time.**

   a) The estimates of the %PPFD$_{overcast}$ method will vary according to the sampling period with the strongest agreement occurring at the equinox, which corresponds, to the average trajectory of the solar path at the study site's latitude.
   b) Since the hemispherical photographs estimate transmittance based on the amount of canopy openness, estimates should be in good agreement with direct measurements, but at various degrees. Gap light index will give better estimates than weighted canopy openness and gap fraction because it takes into consideration the changing solar path and location of the canopy openings.
2. **Estimates of daily %PPFD on a clear and overcast day will vary according to the method and sampling period.**
   a) The %PPFD$_{overcast}$ will be a strong predictor of daily %PPFD on an overcast day, but will be a weaker predictor on clear days. The strength of the clear day prediction will decrease as maximum zenith angle decreases.
   b) Unweighted canopy openness and gap fraction will be stronger predictors for overcast day transmittance than clear days. However, relationship strength will decrease as maximum zenith angle decreases.
   c) Gap Light Index will be a strong predictor of both clear and overcast days for all time periods due to the consideration of the changing solar path, the location of canopy openings, and the ability to define the proportion of above canopy direct and diffuse light within the calculation.

Once the most effective measurement technique for this system was established, the second objective of this study was to use this method to investigate the effect different arrangements of residual overstory on the average, frequency distribution, variation, and spatial pattern of understory light environments. I hypothesized:

1. **Light availability and variation will increase as residual basal area becomes more aggregated.**
2. **The occurrence of higher light availability will increase as residual basal area becomes more aggregated, but will have different distributions.**

3. **Stands with aggregation of trees will have a coarse-grained patch structure of light availability, while stands with uniformly dispersed residual trees will have a fine-grained patch structure.**

Chapter II: LITERATURE REVIEW

Background on light characteristics

As solar radiation passes through the earth's atmosphere, it is altered in quantity and quality as a result of scattering and absorption by aerosols, water vapor, and clouds. Once this alteration occurs, light is referred to as the total or global radiation (Monteith and Unsworth 1990). Global radiation can be divided into two categories: direct and diffuse light. Direct radiation comes directly from the sun and is bright in intensity. Diffuse radiation is the scattered solar radiation from the entire hemisphere of the sky and clouds.

The wavelengths of global radiation between 400-700 nm, known as photosynthetically active radiation (PAR), are important for plant survival, growth, and regeneration. PAR is typically expressed as an amount per unit area or the photosynthetic photon flux density (PPFD) (Biggs 1986). For the rest of this paper, *light* will refer to the amount of radiation within the 400-700 nm wavelength.

The amount of light that transmits through the earth's atmosphere changes with time of day, season, and sky condition. Within a day, the sun travels across the sky with a change in its altitude from sunrise to sunset. The intensity and spectrum of direct sunlight depend strongly on the path length of the beam and on the solar angle (Monteith and Unsworth 1990). The intensity of light increases from sunrise to the sun's zenith and then decreases. When the sun's angle is below 10^o, the increased path length leads to increased absorption and scattering resulting in spectra rich in blue (470 nm) and far-red (730 nm) wavelengths (Smith 1982). Once the sun's angle is above 10^o, the spectrum is relatively constant with direct sunlight rich in red (630 nm) wavelengths (Endler 1993).

As the earth rotates around the sun, the angle to which it faces the sun changes. This angle is known as the sun declination angle and changes from day to day within a year. As a result of this change in declination angle and combined with the latitude of a site on the earth's surface, the path of the sun in the sky changes everyday. In mid-latitudes, the sun's angle in winter is lower in the horizon, than it is during summer when the angle is almost directly above. This has dramatic influences on light availability during each season due to the path length that a beam of light must travel.

The effect of prevailing sky conditions also influences the quantity of light that reaches the earth's surface. In the Netherlands, Spitters *et al* (1986) reported that the proportion of total light that is diffuse is about 23% on a clear day. On days with some cloud cover, diffuse light proportions increase due to the forward scattering of light as it strikes the water vapor in the atmosphere (Monteith and Unsworth 1990). On these days, total radiation can surpass the amount of radiation on a clear day by 5-10% (Monteith and Unsworth 1990). On days that are completely overcast, the quantity of light is reduced from that of a clear day because of the absorption and back-reflection of radiation by and from the cloud cover.

Effect of canopy structure on components of light

When the direct and diffuse components of light intercept a tree canopy, a fraction of both components is reflected back to the sky and a portion is absorbed within the canopy. The light that reaches the forest floor is divided into several components. Direct light can pass unimpeded through openings in the canopy and reach the forest floor. Penetration depends on the intensity of the incident light, and upon the number, size, and spatial distribution of canopy openings (Anderson 1964, Reifsnyder *et al* 1971, Hutchinson and Matt 1977). On the other hand, diffuse light depends on the distribution and amount of sky brightness, the number, the size and the space distribution of canopy openings, and the geometry, space distribution and optical characteristics of the overstory trees openings (Anderson 1964, Reifsnyder *et al* 1971, Hutchinson and Matt 1977).

The amount of direct light penetrating the understory is highly variable due to the change in solar elevation angle throughout a year. This is compounded by the variable distribution of canopy openings in the forest canopy. When the position of the sun and a canopy opening synchronize, direct light reaches the understory unimpeded. This type of light is known as a sunfleck under a closed canopy forest (Chazdon 1988). Sunflecks are heterogeneous on the forest floor both spatially and temporally due to the directional aspect of direct light. The amount and variation of a sunfleck occurring depends on the arrangement of canopy openings and the sun's path. The penetration of diffuse light is not constricted to the strict influences of direct light. When compared to direct light, diffuse light in the understory is more homogeneous, both spatially and temporally.

Light environments in the understory of different forest types

The interaction of canopy structure and understory light condition has been studied extensively from tropical to boreal forests. Each study has shown varied results due to the characteristics of the forest studied. The influence a canopy has on light reaching the understory depends on the location of openings, geometry, and light transmission characteristics (Canham *et al* 1994, Messier 1996). Different forest ecosystems, particularly those with different structures, regulate light differently. Thus, each needs to be examined and interpreted separately to understand the role a canopy plays in transmitting light.

Temperate Coniferous Forests

Many light environment studies in coniferous forests have been limited to ones with homogeneous canopies (Gay *et al* 1971, Reifsnyder *et al* 1971, Vales and Bunnell 1988, Gholz *et al* 1991). These studies measured the proportions of direct and diffuse light that reached the forest understory at different temporal scales ranging from days to seasons.

In a 36-year old red pine (*Pinus resinosa*) plantation, Reifsnyder *et al* (1971) found that on a direct light dominated day, the canopy acted as a uniformly scattering medium in which penetration of direct beam accounted for 53% of the understory radiation and diffuse light accounted for 32%. Sunflecks contributed up to 25% of the direct radiation at the forest floor and were characterized as large and bright patches. Reflectance of light from foliage, stems, and branches contributed the rest.

Other studies have investigated the influence of the interaction of canopy structure and varied sky conditions on understory light availability. In a 32-year old loblolly pine (*Pinus taeda*) plantation, Gay *et al* (1971) recorded a mean transmittance of 17% for an eight-day period of varied sky conditions. On a clear day, 46% of the understory light was diffuse radiation, compared to the 15% of above canopy light as diffuse. Vales and Bunnell (1988) also recorded greater diffuse light proportions in the understory then above the canopy diffuse light. In young Douglas fir (*Pseudotsuga menziesii*) forests as crown closure increased from 30% to 90%, the proportion of direct light to global radiation transmitted decreased from 43% to 5% (Vales and Bunnell 1988). However, the proportion of diffuse light transmitted increased substantially in the understory of the denser canopies. The increase of diffuse light in the understory of more open canopy was a result of reflection and scattering of direct beam radiation (Hutchinson and Matt 1976) off the foliage. The importance of direct light to beam enrichment, the scattering of the direct light that transmitted through the canopy changing to diffuse light, in the more open Douglas fir canopies was evident on days with increased cloudiness, when beam enrichment decreased (Vales and Bunnell 1988).

Seasonal variations in light transmittance for temperate coniferous forests have been less studied. Light transmission tends to increase as the sun approaches its zenith around the summer solstice. With the sun reaching its maximum zenith, the path through the gaps between trees is shortened allowing direct sunlight to reach the understory. This change in transmittance was observed in a study performed in a slash pine plantation that reported an increase in transmittance between early winter (18%) to early summer (42%) (Gholz 1991).

Temperate Deciduous Hardwood

Most studies of transmittance in hardwood forests have focused on the summer months when leaf area is greatest. In the summer, transmittance is much lower in hardwood forests then that reported for coniferous forests. This is attributed to the much denser and multi-layered canopies of the hardwood forests. Typical summer transmittances range from 1-3.7% (Hutchinson and Matt 1977, Canham *et al* 1990, Brown and Parker 1994).

Light transmittances in the understory of closed canopy deciduous hardwood forests differ greatly depending on the season. In an extensive study of seasonal variation of light environment in the understory of a tulip poplar (*Lirodendron tulipifera*) forest in Tennessee, Hutchinson and Matt (1977) noted an increase in average light transmittance in the leafless forest from winter (16.5%) to early spring (45%) due to an increase in solar elevation. Although solar elevation continued to increase from spring to summer, the amount of solar radiation reaching the understory decreased sharply from 19.8% to 3.3% due to a leaf area index (LAI) increase from spring to summer.

The amount of diffuse and direct light in the understory of the tulip poplar forest changed according to season and sky condition (Hutchinson and Matt 1976). On a clear day in winter, it was found that the diffuse light was higher then the direct light for most of the day. However, when the solar elevation increased to its maximum zenith, more direct light was able to penetrate to the understory. This was not the case for the summer months. Although the solar elevation reaches its maximum during these months, direct light reaching the forest understory is almost non-existent due to the blockage by foliage. In contrast, the amount of diffuse light increased substantially in the summer as a result of beam enrichment (Hutchinson and Matt 1976).

On an overcast winter day, a greater proportion of total light penetrated the canopy then on a clear day. However, the amount of diffuse light in the understory was less on the overcast day then on a clear day. Hutchinson and Matt (1976) suggest that even in a leafless forest, beam enrichment (caused by scattering by branches and boles) on a clear day may significantly increase the amount of diffuse light in the understory. On an overcast summer day, the proportion of diffuse light underneath the canopy was lower than a clear day. In fact, the total amount of understory light on an overcast summer day was less than the amount of total diffuse light in the understory on a clear day. Again, this was attributed to the influence of beam enrichment from the direct light reflecting off the leaves (Hutchinson and Matt 1976, Hutchinson and Matt 1977).

Although hardwood forests have very low transmittance levels, sunflecks contribute a significant amount of light to the understory. Canham *et al* (1990) reported that between 46-80% of the growing season PAR in the understory of a northern hardwood forest was due to sunflecks with duration of 4 to 8 minutes. Southern hardwoods had similar values, ranging from 48-69% with duration's ranging from 4 to 11 minutes (Canham et al 1990).

Tropical evergreen forests

The canopy of a tropical evergreen forest is much denser then a temperate/boreal coniferous or hardwood forest. As a result, understory light levels are extremely low. Bjorkman and Ludlow (1972) reported a yearly average of 0.44% of the incident light that reached the forest floor in a Queensland, Australia forest. Pearcy (1983) reported a slightly higher transmittance of 2.4% in a Hawaiian forest. In a Costa Rican tropical premontane wet forest, Chazdon and Fetcher (1984) reported a 1-2% transmittance.

Although total light is lower on an overcast day compared to a clear day, it has been shown that diffuse light transmittance to the understory on an overcast day is greater (Bjorkman and Ludlow 1972, Chazdon and Fetcher 1984). On a clear day in Queensland, only 0.41% of the light transmitted through the canopy. Sunflecks contributed 61% while diffuse light contributed 39% of the light transmitted (Bjorkman and Ludlow 1972). On an overcast day, light transmittance to the understory increased to 1.1% due to the ability of diffuse light to penetrate the canopy from all directions.

Chazdon and Fetcher (1984) studied understory light transmittance of a lowland tropical rain forest in Costa Rica that experienced a wet and dry season. At their site, the dry season occurred from January to April, with a short period between September to October. The dry season has a less cloud cover resulting in greater direct light, in spite of the lower solar angles. The wet season has more cloud cover and higher solar angles, although the potential higher amount of light above the canopy is muted due to the clouds.

During the dry season, PPFD was 24% greater in the understory compared to the wet season. This was due to the lower frequency of cloud cover. Sunflecks contributed up to 77% of the total PPFD in the understory for the dry season. During the wet season, understory PPFD values increased, indicating higher diffuse radiation as a result of beam enrichment. Sunflecks during this period reached values between 100 and 500 μmol m^{-2} s^{-1}. Although these occurrences were low in frequency, they contributed up to 55% of the total understory daily PPFD during the wet season (Chazdon and Fetcher 1984).

As described in the deciduous hardwood forests, sunflecks contribute a significant amount of the light in the understory of tropical forests. However, the contribution differs for the different tropical forests due to their canopy densities. In the Hawaiian forest, which was not as dense as the Queensland forest, 40% of the total light in the understory was due to sunflecks (Pearcy 1983) compared to the 0.25% of the Queensland forest. In a lowland rainforest in Mexico, Chazdon and Pearcy (1991) reported 52% of the total light was contributed by sunflecks.

Light conditions in canopy gaps

Forests are subject to many disturbances that create canopy gaps. Disturbances can be classified into two categories: coarse-scale and fine-scale (Spies and Franklin 1989). Coarse-scale events include wildfire, wind, and volcanic eruptions. These events typically create gaps of 0.1 to >100,000 ha in the forest (Spies and Franklin 1989). Fine-scale events include single tree death, windthrow, and lightning strikes and create openings of less then 0.1 ha.

There has been an increasing interest in the use of uneven-aged management that mimics canopy structure after a natural disturbance. With uneven-aged management, residual trees are left to maintain structural diversity and areas within the canopy are cut to form gaps or thinned to lower densities. Studies focused on the role that different overstory densities have on light transmittance have shown that as density increased, light transmittance decreased (Holbo *et al* 1985, Vales and Bunnell 1988, Lieffers and Stadt 1994, Rich *et al* 1993, Palik *et al* 1997, Comeau *et al* 1998, Gendron *et al* 1998). The response was dependent on the overstory tree species, age of the overstory trees, depth of the canopy, and density of the overstory.

Many studies have compared gap vs non-gap light environments (Chazdon and Fetcher 1984, Canham *et al* 1990, Whitmore *et al* 1993, Denslow *et al* 1998, McGuire *et al* 2000, Van Pelt and Franklin 1999). Canopy gaps increase the light availability for regenerating seedlings (Canham and Marks 1985). The amount of light received depends on the size, shape, and orientation of the gap (Brokaw 1985), as well as the height of the surrounding trees. Coates and Burton (1997) found that light received in the gaps was reduced from 75% to 50% and to 25% of full light as the gap diameter was reduced from 50 m, to 25m and to less then 10 m, respectively. Large gaps receive direct light from early morning to late afternoon, while smaller gaps receive direct light in the middle of the day. Denslow and Hartshorn (1994) determined that heterogeneity of available light was the dominant component influencing successful seedling regeneration in Neotropical rainforests.

Light is not evenly distributed within a gap. At different positions in a gap, the amount of direct light changes according to the time of day and season (Bazzaz and Wayne 1994). In the Northern Hemisphere, the northern portions of a gap receive more light then southern portions. Northeastern areas of a gap will receive light 2-2.5 hours later then the northwestern area of a gap (Bazzaz and Wayne 1994). Seedlings on western edges of a gap will receive sunlight earlier in the day then those on the eastern side (Wayne and Bazzaz 1993). Although the western and eastern edges of the gap may receive similar light peak intensities, the timing of the peaks is different. This will have significant impact on seedling response to light conditions as weather changes during a day. Wayne and Bazzaz (1993) found that seedlings grown on the western side of gap had greater carbon gain then eastern plants and this difference was greater with increasing water stress.

Light measurement techniques

Studies of light transmittance have ranged temporally from continuous seasonal measurements to a single instantaneous measurement. The quantum sensors can measure photosynthetically active radiation (PAR) temporal scales ranging from instantaneous to years. Ideally light would be measured continuously for to characterize the spatial and temporal light environment in any understory. However for long-term scales, this is unrealistic due to the expense and effort needed to measure just one point. Hemispherical photography can estimate light with less effort. The photograph records the canopy structure at one point in time and the sun's path throughout a growing season is projected on the photograph to estimate mean light levels.

Measurements on clear days

Some studies have characterized light environments by measuring light two hours before and after solar noon under clear sky conditions (Morgan *et al* 1985, Messier *et al* 1989). This type of characterization is questionable due to the high variability of light (Gay *et al* 1971, Rich 1993) as a result of seasonal shifts in the sun elevation and gap location (Rich *et al* 1993, Comeau *et al* 1998). In addition, some studies have shown that this technique could lead to overestimation of %PPFD for the site (Messier and Puttonen 1995, Parent and Messier 1996).

Measurements on overcast days

Many studies have shown that transmittance measurements taken near midday on a clear day showed more variability and lower correlation to growing season transmittance then those taken under overcast conditions (Messier and Puttonen 1995, Parent and Messier 1996, Comeau *et al* 1998). 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 on an overcast day is stable throughout the day, and therefore an instantaneous measurement taken at almost any time 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).

Instantaneous measurements on an overcast day have been criticized 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, a condition which may be rare in some locations. Another concern is that this method implies that the spatial distribution of the canopy openness is trivial (Stadt *et al* 1997). However, two microsites can have similar canopy openness and dissimilar transmittance due to the direction in which this openness occurs. This directional aspect is important on a clear day in which direct light penetration is highly affected by the distribution of canopy openness. Thus, the instantanteous measurement on an overcast day may be acceptable for closed canopy forests, which have a uniform distribution of foliage and branches, but may be more problematic for other forested systems that have clumped distributions or heterogeneous canopies (Stadt *et al* 1997). 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 and that hemispherical photographs performed slightly better under these conditions. Another criticism is that this technique is inadequate to describe the spatial and temporal characteristics of light in a stand (Gay *et al* 1971).

Continuous seasonal measurements

Many studies have used multi-channeled dataloggers and gallium arsenide phosphide photodiodes to make continuous measures of the understory light environment (Chazdon and Fetcher 1984, Chazdon and Field 1987, Rich *et al* 1993, Easter and Spies 1994, Gendron *et al* 1998). This technique allows both the temporal and spatial characterization of the light environment to be measured. Measurements can be made over long periods of time (days to weeks) and under varied sky conditions. Longer periods of measurements can aid in characterizing a site's light environment. Comeau *et al* (1998) showed that with increased measurement periods (from 1-h period to 6-h period), the correlation between %PPFD for the time period measured and the %PPFD of a growing season increased and root mean square error declined. The cost of the equipment and the number of sampling locations that can be reached, are limitations to this approach.

Hemispherical photography

Another technique used quite frequently in characterizing the spatial and temporal characteristics of understory light is hemispherical photography (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 photographs allow direct measurement of canopy structure and an estimation of transmitted solar radiation. Estimation of light is based on the assumption that canopy openings will allow unobstructed penetration of solar radiation and that foliage completely blocks radiation. However, the analysis neglects scattering, reflecting, or transmission through leaves.

The analysis of the photographs yields two parameters used to estimate light transmittance. These two factors are the direct site factor (DSF) and the indirect site factor (ISF), which are the direct radiation and diffuse radiation under the canopy relative to above the canopy, respectively. DSF and ISF values are based on clear sky conditions and only consider radiation that penetrates the canopy (Rich 1996). Assumptions of the contribution of above canopy direct and diffuse light are needed to estimate the values of ISF and DSF (Rich 1996). Becker (1987) has empirically derived these assumptions by measuring the transmissivity or atmospheric clearness (global radiation/extraterrestrial radiation) at several study sites. With a transmissivity of 0.3 (hazy), the proportion of radiation that is direct (P_{beam}) is approximately 0.2-0.4, and diffuse radiation ($P_{diffuse}$) is 0.6-0.8. If transmissivity is 0.65, P_{beam} is around 0.7-0.9 and $P_{diffuse}$ is approximately 0.1-0.3 (Rich 1996).

There are two models used to calculate ISF, the Uniform Overcast Sky (UOC) and Standard Overcast Sky (SOC). UOC assumes diffuse radiation is the same from all sky directions. SOC assumes diffuse light is three times brighter at the zenith angle then the horizon (Machado and Reich 1999). It is widely accepted that these distributions do not adequately describe diffuse light distributions, but no current alternative is available (Rich 1990).

With the estimates of DSF and ISF and of P_{beam} and $P_{diffuse}$, gap light indices (Canham 1988) can be calculated. The gap light index (GLI) specifies the percentage of incident PAR transmitted through a gap to a point in the understory over a growing season. Assumptions of $P_{diffuse}$ in past studies have varied from 0.15 (Chazdon and Field 1987) to 0.5 (Canham *et al* 1990). Since $P_{diffuse}$ is site specific, Rich *et al* (1993) varied $P_{diffuse}$ between 0 and 1 and found that the maximum r^2 between hemispherical estimatation and direct light assessment occurred when $P_{diffuse}$ was 0.55. This relationship gave a slope close to 1 and an intercept near 0 (Rich *et al* 1993). The authors suggest that this type of analysis should be utilized when estimating light availability with hemispherical photography.

Studies have shown that there is good agreement between direct sensor measurements and photograph calculations of PPFD for periods ranging from minutes to weeks (Chazdon and Field 1987, Becker *et al* 1989, Rich *et al* 1993, Whitmore *et al* 1993, Easter and Spies 1994, Comeau *et al* 1998). However, Rich (1990) points out that long-term, detailed studies of light are required to better calibrate estimates of hemispherical photographs. This can be achieved by utilizing both the long-term light measurement and hemispherical photography techniques.

The study of light environments in longleaf pine forests

The comparison of canopy gaps to intact canopy in the open canopied longleaf pine forest has been only briefly addressed in the scientific literature. Palik *et al* (1997) investigated the role basal area had on understory light availability with use of hemispherical photography. The study was performed in an 80 year-old second-growth longleaf pine forest. In this study, hemispherical photographs were taken across gaps of 0.15 ha from the gap edge to the gap center along all cardinal directions and adjacent intact forests with no disturbance. The study found a curvilinear relationship between basal area and light availability, with increased light with decreasing basal area (Palik *et al* 1997).

The findings in Palik *et al* (1997) contrast with Brockway and Outcalt (1998) study of gap dynamics in the same forest type. Their study had similar gap size and sampling scheme. However, they measured PAR directly with a ceptometer. Measurements were made on clear days in late fall from noon until 16:00. They found that there was no significant difference in light from gap edge to gap center and that light was uniformly distributed across the transect. They attributed this uniformity to the characteristic open canopy of the longleaf pine, suggesting that light reached the understory laterally through the numerous holes in the sparse overstory.

A recent study of canopy gaps in the longleaf pine forest agrees with the findings of Palik *et al* (1997) (McGuire *et al* 2000). This study measured understory light availability of a 60-90 year-old longleaf pine forest with use of hemispherical photography in three experimental canopy gaps of 0.11, 0.41, and 1.63 ha in size and under an intact canopy. Light levels in the understory of the intact canopy were 48% of full sunlight (McGuire *et al* 2000). In contrast to the findings of Brockway and Outcalt (1998), understory light levels increased from the gap edge to the gap center with maximum light levels reported 36 m from the gap edge (McGuire *et al* 2000). In addition, light levels were greater in the northern part of the gaps and least in the southern portion of the gap. As gap size decreased, light levels in the northern part of the gap were concentrated. The author suggested that the limited light measurements in space and time for the Brockway and Outcalt study were not able to capture the heterogeneity of light within this system (McGuire *et al* 2000).

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