The influence of canopy, sky condition, and solar angle on light quality in a longleaf pine woodland

Stephen D. Pecot, Stephen B. Horsley, Michael A. Battaglia, and Robert J. Mitchell

Abstract: Light transmittance estimates under open, heterogeneous woodland canopies such as those of longleaf pine (*Pinus palustris* Mill.) forests report high spatial and temporal variation in the quantity of the light environment. In addition, light quality, that is, the ratio of red to far-red light (R:FR), regulates important aspects of plant development including stem extension, specific leaf area, and seed germination. We conducted two experiments to document sources of variation in R:FR (using a LI-COR 1800 portable spectroradiometer with a cosine-corrected light sensor) in a 70- to 90-year-old natural longleaf pine woodland in southwest Georgia, USA. The first experiment compared instantaneous measurements of R:FR over a 3-day period (March) with annual estimates of canopy transmittance (using gallium arsenide phosphide photodiodes) across the range of observed overstory abundance. The second experiment examined the effect of wiregrass cover (above or below), sky condition (blue sky or overcast), and solar angle (four sampling periods between October and March) on R:FR using a multifactorial repeated measures design. We found that (1) R:FR was significantly ($p < 0.0001$) and strongly ($R^2 = 0.72$) related to annual estimates of canopy transmittance (percent photosynthetic photon flux density, %PPFD); (2) R:FR and %PPFD showed significant negative relationships with increasing overstory stocking ($R^2 = 0.20$, $p = 0.028$ for R:FR, and $R^2 = 0.87$, $p < 0.0001$ for %PPFD); and (3) R:FR decreased with increasing solar angle from maximum zenith for the study site under blue skies, was greater under overcast skies (0.84 blue sky vs. 1.18 overcast sky), and decreased under wiregrass (*Aristida stricta* Michx.) canopies (1.10 above vs. 0.98 below).

Résumé : Les estimations de la transmission de la lumière sous un couvert arborescent clairsemé et hétérogène comme celui des forêts de pin des marais (*Pinus palustris* Mill.) sont caractérisées par de fortes variations spatiales et temporelles dans la quantité de la lumière. De plus, la qualité de la lumière, c.-à-d., le rapport entre le rouge et rouge lointain (R:RL), régit d'importants processus végétaux comme l'élongation de la tige, la surface foliaire spécifique et la germination des graines. Les auteurs ont mené deux expériences pour décrire les sources de variation du rapport R:RL (en utilisant un spectroradiomètre portatif LI-COR 1800 muni d'un capteur de lumière à correction de cosinus) dans un peuplement naturel de pin des marais de 70 à 90 ans dans le sud-ouest de la Géorgie, aux États-Unis. La première expérience a comparé les mesures instantanées du rapport R:RL pendant une période de trois jours en mars aux estimations annuelles de transmittance du couvert (à l'aide de gallium arsenide phosphide photodiodes) pour toute la gamme observée de densité du couvert. La deuxième expérience visait à étudier l'effet d'un couvert herbacé (au-dessus et en dessous), de l'état du ciel (dégagé ou nuageux) et de l'angle solaire (quatre périodes d'échantillonnage entre les mois d'octobre et mars) sur le rapport R:RL en utilisant un dispositif multifactoriel à mesures répétées. Ils ont trouvé que (1) le rapport R:RL était significativement ($p < 0{,}0001$) et fortement ($R^2 = 0{,}72$) relié aux estimations annuelles de transmittance du couvert (densité du flux des photons photosynthétiques, %PPFD); 2) le rapport R:RL et le %PPFD étaient significativement et négativement reliés à la densité du couvert dominant ($R^2 = 0{,}20$, $p = 0{,}028$ pour R:RL et $R^2 = 0{,}87$, $p < 0{,}0001$ pour %PPFD); et (3) le rapport R:RL diminuait proportionnellement à l'augmentation de l'angle solaire par rapport au zénith maximal de la station à l'étude sous un ciel dégagé, était plus grand sous un ciel couvert (0,84 sous un ciel dégagé et 1,18 sous un ciel couvert) et diminuait sous le couvert d'une plante herbacée (*Aristida stricta* Michx.) (1,10 au-dessus et 0,98 en dessous).

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Introduction

The quantity and quality of solar radiation serve as sources of energy and information about the external environment to plants (Jennings et al. 1996; Lieffers et al. 1999). Several critical ecological processes are controlled through changes in the light environment, including regeneration and establishment, competitive responses, and physiological processes relating to productivity (Endler 1993). Many wavebands within the light spectrum are of biological significance, including photosynthetically active radiation (PAR) (400–700 nm) for photosynthesis and UVA/UVB (350–500) for stomatal opening and induction of phototropism (Smith 1982; Grant 1997; Hart 1998). The ratio of red (660) to far-red (730) light (R:FR) is important for the detection of competition (Casal et al. 1987; Ballaré et al. 1990) and regulation of seed dormancy and germination (Lee et al. 1996; Orozco-Segovia et al. 2000), stem elongation and leaf area expansion (Morgan 1981), apical dominance (Morgan and Smith 1981), and internode expansion (Morgan and Smith 1978*a*; Ballaré et al. 1990; Grant 1997). Generally, plants respond to a decrease in R:FR by increasing leaf area and internode length in an effort to access more available light (Morgan and Smith 1978*b*; Smith 1981, 1982). Plants have extremely sensitive environmental cues that can be used to gain competitive advantage over neighbors. Light, therefore, serves as a critical resource for carbon acquisition to plants but also as a photosensory cue (Jennings et al. 1996).

Plant canopies act as selective light filters, continuously altering the spectral distribution of light below them (Endler 1993; Grant 1997). R light is largely absorbed by chlorophyll and other leaf pigments in the vegetative canopy, while most FR is transmitted or reflected (Larcher 1995); therefore, R:FR decreases with increasing canopy cover under blue-sky conditions (Holmes and Smith 1977; Smith 1981; Ballaré et al. 1987; Messier et al. 1989). The extent to which R:FR impacts plant development has been studied in several plant systems of the world, including agricultural areas (Sattin et al. 1994), grass swards (Child et al. 1981; Morgan et al. 1981; Bain and Attridge 1988), boreal (Messier et al. 1989), temperate deciduous (Horsley 1993; Lei et al. 1996), and tropical deciduous forests (Kwesiga and Grace 1986; Turnbull 1991; Lee et al. 1996; Capers and Chazdon 2004). These studies suggest that light quality may be a critical ecological variable in woodlands (Tasker and Smith 1977).

Canopy morphology affects light quality partially through the shape and orientation of its leaves. Generally, broader and horizontally oriented leaves absorb more R light than narrow, upright-facing leaves, resulting in lower PAR and R:FR below their canopies. The magnitude of the decline in R:FR below deciduous tree canopies is greater than that of coniferous canopies as a result of more selective transmission of light (Federer and Tanner 1966) and greater R absorption by leaves (Ross et al. 1986; Messier et al. 1998; Lieffers et al. 1999). Messier et al. (1989) found that R:FR declined in western redcedar – western hemlock stands to 0.30 (0.3% full sunlight), while Lee (1987) reported that R:FR values declined to 0.13 in tropical deciduous forests (1.23% full sunlight) and as low as 0.003 directly under the leaves of the evergreen perennial shrub *Calotropis procera* R. Br. (Lee 1986). Horizontal and vertical variation in the understory can further reduce R:FR in similar ways as in the overstory (Tang and Washitani 1995; Skálová et al. 1999). Hay-scented fern (*Dennstaedtia punctilobula* Michx.) growing in temperate deciduous forests reduced R:FR to as low as 0.04 below its leaves (Horsley 1993), and the understory plant salal (*Gaultheria shallon* Pursh) reduced R:FR to 0.13 in western redcedar – western hemlock forests (Messier et al. 1989). A grass understory, however, attenuates R:FR less than does a broadleaved understory because of its more upright growth form and the tendency to have more interstitial spaces between plants. In one study comparing R:FR in mountain grasslands, Skálová et al. (1999) found that vertical profiles of R:FR among three communities differed greatly and could be explained by the growth behavior of the dominant grass in each community. The wide, horizontal leaves of *Anthoxanthum alpinum* lowered R:FR (from 1.05 to ~0.55) more than that of the narrow-leaved, generally upright foliage of *Nardus stricta* (1.05 to ~0.85).

Plant canopies interact with sky condition and solar angle to vary R:FR in complex ways (Endler 1993). Clouds interact with canopy cover by minimizing the influence of direct solar radiation and increasing the influence of diffuse radiation that is relatively low in FR light (Holmes and Smith 1977; Lee and Downum 1991). As a result the slope of the decline in R:FR with increasing canopy cover is less under overcast skies (Holmes and Smith 1977; Messier et al. 1989), and R:FR is higher on overcast days (Lee and Downum 1991). Endler (1993) described how mean R:FR declined with increasing canopy cover under sunny conditions, and under overcast skies R:FR in the forest shade light habitat increased four-fold (relative to the blue-sky condition). Though Endler (1993) stated that the woodland light environment is especially sensitive to clouds because of the greater role of direct light than in forest shade (Federer and Tanner 1966), only data showing the effects of clouds on R:FR in forest shade were presented.

Solar angle and canopy cover also interact by altering the solar path length through the canopy and the proportions of direct and diffuse light (Anderson 1964; Holmes and Smith 1977; Ross et al. 1986). This is dependent on canopy type, but only under sunny sky conditions (Holmes and Smith 1977; Ross et al. 1986). After a spike in R:FR at sunrise due to atmospheric absorption of FR at 728 nm, R:FR above the canopy is relatively constant throughout the day until sunset (Smith and Morgan 1981; Lee and Downum 1991). R:FR varies with changes in the solar zenith angle, i.e., across seasons, as well as leaf morphology. In high-latitude forests, for example, boreal systems, deciduous forests show a decrease in R:FR values as leaf area accrues, then begins to increase with leaf senescence, while R:FR in coniferous canopies generally declines across the growing season (Ross et al. 1986).

While recent work has described the role of overstory structure on canopy light transmittance in temperate coniferous woodlands (Palik et al. 1997; McGuire et al. 2001; Battaglia et al. 2002, 2003; Palik et al. 2003), information is lacking on how R:FR varies in these systems. Understanding how R:FR varies across space and time is crucial for gaining insight into the function of an ecosystem and for interpretation of experimental results that investigate phenotypic plant responses (Murphy and Briske 1994; Dudley and Schmitt 1995; Batlla et al. 2000).

The objective of this work was to describe how light quality varies in a temperate coniferous woodland across space and time. Specifically, we were interested in the degree to which the canopy (overstory and understory), sky condition, and solar angle control R:FR. Two experiments were conducted. In the first experiment, we investigated the relationship between overstory stocking and R:FR under clear skies. The second experiment described how R:FR varied with sky condition, solar angle, and the presence of a bunchgrass understory.

Materials and methods

Study area

The study was conducted in a 70- to 90-year-old second-growth longleaf pine (*Pinus palustris* Mill.) forest at the Joseph W. Jones Ecological Research Center in southwestern Georgia, USA (31°N, 84°W). The landscape is gently sloped (1%–5%) karst topography. The climate is humid subtropical (Christensen 1981), with an average annual precipitation of 131 cm evenly distributed throughout the year. Mean daily temperatures range between 21 and 34 °C in summer and between 5 and 17 °C in winter. Soils are in the excessively drained Orangeburg and Wagram series, which are Psammentic Kandiudults and Grossarenic Kandiudults (loamy sands over sandy loams). The study site is located within the Plains and Wiregrass Plains subsections of the Lower Coastal Plain and Flatwoods section (McNab and Avers 1994). The longleaf pine forests at this site have been managed with low-intensity, primarily dormant-season prescribed fires, with a return interval of 1–3 years. The understory is dominated by wiregrass (*Aristida stricta* Michx.) but also contains high numbers of endemic perennial grasses and forbs (Kirkman et al. 2001).

Experiment 1: relation of overstory stocking to R:FR

Sample design

We measured light quality and quantity across a range of overstory abundance, which was provided by a larger study investigating spatial distribution of overstory retention (Battaglia et al. 2003; Jones et al. 2003; Palik et al. 2003). Stand measurements are presented in Table 1. Twelve treatment areas totaling 24 ha were established within a 120-ha tract of land on the property. Basal areas were reduced by approximately 30% in all harvested treatments, but we altered the spatial distribution of residual trees by cutting progressively larger and fewer openings from dispersed retention to small- and large-aggregate retention. All trees greater than 5 cm diameter at breast height in the study area were mapped into Universal Transverse Mercator (UTM) space using a laser transit system and a global positioning system datalogger. To quantify overstory competition, we calculated an overstory abundance index (OAI) at the center of each plot. OAI is a distance-weighted measurement of basal area within a circumscribed area (Stoll et al. 1994; Jones et al. 2003; Palik et al. 2003):

$$[1] \qquad \mathrm{OAI} = \sum_{i=1}^{n} A / d$$

where OAI is overstory abundance index (cm^2/m), A is cross-sectional area of tree i (cm^2), and d is distance (m) of tree i from the grid point. The point to tree distance (d) was constrained to be no less than 1 m to prevent giving undue weight to trees in close proximity (i.e., <<1 m) to the sample point. We chose 15 m as the radius for our circumscribed area, since most overstory effects of longleaf pine on plant responses are observed within that distance (Brockway and Outcalt 1998; McGuire et al. 2001). OAI is a better index of overstory competitor abundance than basal area because it gives greatest weight to trees most likely to preempt resources from a target plant, that is, larger trees and trees closest to the measurement point (Stoll et al. 1994). Conversely, small trees located far from a target plant will contribute very little to OAI, reflecting their limited ability to preempt resources from the target plant. Thirty-five plots were randomly chosen to encompass the range of OAI in the study area.

Table 1. Description of study sites in a 70- to 90-year-old, second-growth longleaf pine forest in Baker County, Georgia, USA.

	Mean	SE	Range
Experiment 1			
DBH (cm)	27.81	0.18	4.2–64.0
Height (m)	20.81	0.13	2.9–30.7
Basal area (m^2/ha)	13.50	0.83	9.9–20.3
Experiment 2			
DBH (cm)	34.77	0.99	11.0–50.4
Height (m)	23.97	0.42	10.5–33.3
Basal area (m^2/ha)	13.90	0.41	5.70–21.8

Light quality and quantity

Three days representative of clear-sky conditions (7 March 1998, 8 March 1998, and 10 March 1998) were selected to sample light-quality measures. For each plot, we measured light quality for three periods of the day (0800–1100, 1100–1400, and 1400–1700) and averaged these values to obtain a single value for comparison. We were restricted from taking more measurements because of limited access to sampling equipment. The order of sampling (across plots as well as through time) was randomized prior to arrival in the field. For each sample, a LI-COR LI-1800 portable spectroradiometer (LI-COR, Inc., Lincoln, Nebraska) equipped with a remote cosine receptor was placed on the ground. The receptor was leveled and a measurement recorded. Two measures of light were calculated from the data set. PPFD was estimated by summing the total irradiance from 400 to 700 nm. R:FR was estimated by dividing the total irradiance of red light (R; 660 nm ± 6 nm wavelength) by the total irradiance of far-red light (FR; 730 nm ± 6 nm wavelength).

Canopy transmittance (%PPFD) was measured for a total of 51 days scattered over an entire growing season from December 1998 to November 1999 in 22 of the 35 study plots. Below-canopy light quantity was measured every 10 s and stored as 1-min averages (for sun angles > 15° from the horizon) using gallium arsenide phosphide (GaAsP) photodiodes (model G1118, Hamamatsu Corporation, Bridgewater, New Jersey). The photodiodes were placed 1 m above the ground in the middle of the plot. Daily checks were made at all locations to ensure lens clarity and that the diode was level (using a bubble level).

All GaAsP photodiodes were calibrated against a LI-190 quantum sensor in September 1998 and again in June 1999 in the same location where above-canopy light quantity measurements were taken (Battaglia et al. 2002, 2003). 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 0.25 m^2. For the September 1998 calibration, GaAsP sensors were calibrated under clear-sky conditions during midday. Various amounts of shade cloth, resulting in approximately 0% to nearly 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 used 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 GaAsP photodiode to PPFD. At low light intensities the relationship between millivolt and PPFD was linear; however, at higher light 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. Fit index is analogous to a correlation coefficient (r^2) but is appropriate for nonlinear regression. 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. %PPFD was defined as the daily sum of below-canopy (but above the understory) PPFD ($\mu mol \cdot m^{-2} \cdot s^{-1}$) divided by the daily sum of above-canopy PPFD (measured in an open field less than 1 km away from the study site using a LI-COR 190 quantum sensor).

Data analysis

We tested the relationship of instantaneous measures of %PPFD and R:FR as well as OAI and %PPFD by evaluating several regression models (linear and nonlinear) and compared them statistically with likelihood ratio tests. Ultimately, we predicted R:FR as a function of %PPFD using the equation

$$[2] \qquad \mathrm{R:FR} = B_0 e^{B_1 \, \%\mathrm{PPFD}}$$

where B_0 and B_1 are constants, and %PPFD and OAI using the equation

$$[3] \qquad \%\mathrm{PPFD} = \frac{B_0 + B_1}{(1 + B_2 \mathrm{OAI})}$$

where B_0, B_1, and B_2 are constants. To test the relationship between instantaneous measures of R:FR and OAI we used eq. 2. Significant relationships were noted at $\alpha < 0.05$.

Experiment 2: relation of sky condition, solar angle, and wiregrass cover to R:FR

Study design

Light quantity and quality measurements were taken in a 70- to 90-year-old second-growth longleaf pine forest. The overstory canopy is dominated by longleaf pine with tree crowns widely spaced (leaf area index ranges from 0.6 to 1.4; S. Pecot, unpublished data). The 107-ha study area had been burned the previous year in January 1996 and was not burned again until the spring of 1998 after completion of the experiment. Overstory basal area was within the range of most naturally regenerated second-growth longleaf pine stands (Boyer 1990). Summary statistics for the study site are presented in Table 1.

Nine plots were established to encompass the range of overstory basal area found in natural second-growth longleaf pine forests. Plots with only longleaf pine as the overstory and midstory species were selected for measurements. Within each plot we established two transects running northeast to southwest and southeast to northwest. The intersection of these two transects was subplot number 1. Four additional subplots were established along each transect 10 m apart for a total of nine subplots per plot. Overstory basal area was estimated using a one-factor wedge prism. Subplots were marked with a 10 cm × 10 cm wooden square placed on the ground below the entire understory, leveled, and secured with a spike countersunk through its center. This allowed us to make repeated measurements through time in the same location.

Four sampling periods were chosen to collect light quality data under two sky conditions and at two locations in the wiregrass canopy (Table 2). All sampling for this experiment occurred after leaf senescence, that is, the loss of deciduous leaves in the understory and second-year needles in pines (October), but before the new foliage growth the following spring (April). Though we sampled sky conditions at different times of the year, we standardized these sampling periods using the solar angle from maximum zenith as an analog for time (Table 2). The second and fourth sampling periods coincided closely with the equinoxes (autumnal and vernal) and the winter solstice, respectively. The first and third sampling periods were selected between these periods. During the experiment we assumed that overstory and wiregrass leaf area did not vary significantly. The first sky condition, blue sky, is typical of the first few days after the arrival of a high barometric pressure front and is also considered a direct-light-dominated day. The second sky condition, overcast, represented a diffuse-light-dominated day, with the solar disc not visible. Measurements were classified as either blue or overcast sky if these conditions were present only during the measurement period for that day. We randomized data collection across and within plots for each sampling period.

Light measurements

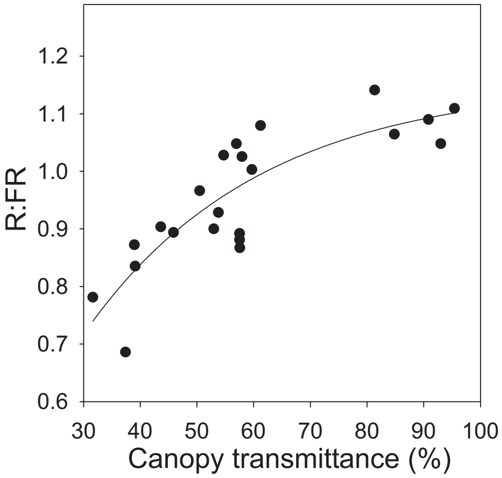
A LI-COR 1800 spectroradiometer equipped with a remote cosine receptor was used to scan the radiant spectra between 400 and 750 nm wavelength at each subplot directly above the wiregrass and at ground level below the wiregrass

Table 2. Sampling dates used to measure differences in light quantity and quality in a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA.

Sampling period	Direct-light-dominated day (blue sky)	Diffuse-light-dominated day (overcast)	Mean solar angle (range) (°)[a]
1	27 March	24 March	17.3 (16.7–17.9)
2	17 and 22 March	22 September	20.8 (19.7–21.8)
3	24 February	16 October	28.7 (28.6–28.8)
4	16 December	13 January	41.9 (40.9–42.9)

[a] Degrees from maximum solar zenith of 78.4° for the study site.

Fig. 1. For the first experiment, light quality (red : far red, R:FR) during three clear-sky days (0800–1700) in March increased with increasing annual estimates of canopy transmittance in a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. The equation for the fitted line is $\mathrm{R:FR} = 1.154(1 - e^{0.032\%\mathrm{PPFD}})$ ($R^2 = 0.72$, $p < 0.0001$, $n = 22$).

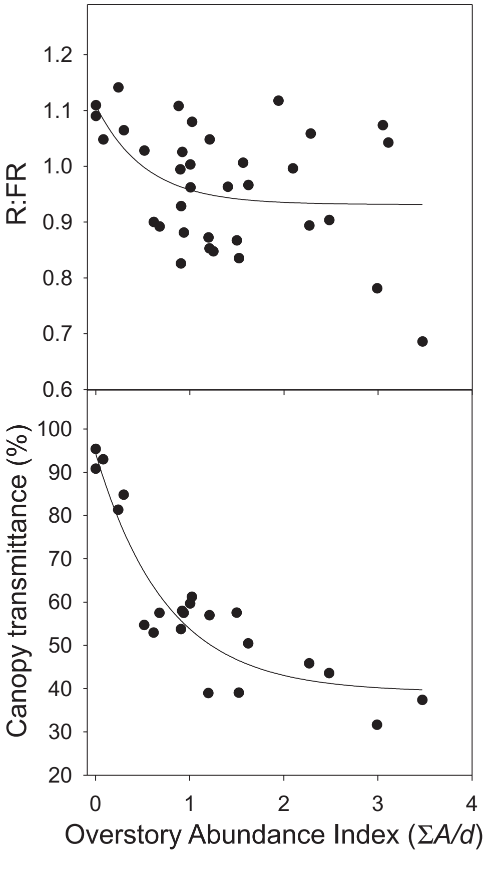


canopy. PPFD and R:FR were calculated in the same way as in experiment 1. To ensure repeatability of measurements, the instrument was calibrated using a LI-COR LI-1802 optical radiation calibrator prior to each sampling period.

Data analysis

A nonlinear equation of R:FR as a function of PPFD was fit for each sample period, sky condition, and wiregrass cover condition. When statistical differences between the covariates sky condition and wiregrass cover were not significant ($p > 0.05$ using ANCOVA), data were pooled and a new equation was fit. We used a mixed-model repeated measures approach (Littell et al. 1996) to test for significant differences in light quality with respect to solar angle from maximum zenith, sky condition, and wiregrass cover (H_0: there are no differences). Since sampling intervals were not equally spaced through time, orthogonal polynomial coefficients were calculated using the Interactive Matrix Language or PROC IML (SAS® version 8.2) to generate coefficients for these unequally spaced contrasts of interactions. Overstory basal area was tested as a possible covariate to explain differences in R:FR; however, this variable was not significant ($p = 0.104$) and was omitted from the analysis. Main effects and their interactions were tested for differences ($\alpha = 0.05$), and where significant interactions were present simple contrasts (slices) were performed to test specific relationships. The data analysis for this paper was conducted using SAS version 8.2 for UNIX (SAS Institute Inc. 2001).

Fig. 2. For the first experiment, light quality (red : far red, R:FR) during three clear-sky days (0800–1700) in March (*a*) and annual estimates of canopy transmittance (*b*) both decreased with greater overstory stocking in a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. The fitted line for (*a*) is $\mathrm{R:FR} = 0.931 + 0.178e^{(-1.907\mathrm{OAI})}$ ($R^2 = 0.20$, $p = 0.028$, $n = 35$), and for (*b*) the line is $\%\mathrm{PPFD} = 39.18 + 55.25e^{(-1.329\mathrm{OAI})}$ ($R^2 = 0.87$, $p < 0.0001$, $n = 22$).



Results

Experiment 1: relation of overstory stocking to R:FR

R:FR was significantly related to canopy transmittance (%PPFD), with more than 70% of the variation explained ($R^2 = 0.72$, $p < 0.0001$) (Fig. 1). Because of constraints from the larger study (Battaglia et al. 2003), only 22 of the 35 plots were used for comparison between %PPFD and R:FR.

Table 3. Regression coefficients (±1 SE) of the relationship between R:FR and PPFD presented in Fig. 3.[a]

Sampling period (solar angle from max. zenith)	b_0	b_1	b_2	F	$p > F$	F.I.[b]
Period 1 (17.3°)						
Blue sky (n = 150)	1.21 (0.014)	–0.016 (0.002)	–40.84 (7.236)	332.07	<0.0001	0.82
Overcast sky (n = 72)[c]	—	—	—		—	—
Period 2 (20.8°)						
Blue sky (n = 172)	1.20 (0.015)	–0.024 (0.003)	–26.43 (6.660)	195.14	<0.0001	0.70
Overcast sky (n = 108)	1.25 (0.012)	–0.047 (0.011)	–3.60 (0.853)	25.13	<0.0001	0.33
Period 3 (28.7°)						
Blue sky (n = 140)	1.14 (0.016)	–0.011 (0.001)	–36.17 (7.828)	355.22	<0.0001	0.84
Overcast sky (n = 162)	1.29 (0.035)	–0.012 (0.004)	–110.77 (33.775)	62.24	<0.0001	0.44
Period 4 (41.9°)						
Blue sky (n = 318)	1.08 (0.011)	–0.007 (0.001)	–58.43 (5.757)	1273.21	<0.0001	0.89
Overcast sky (n = 108)[c]	—	—	—		—	—

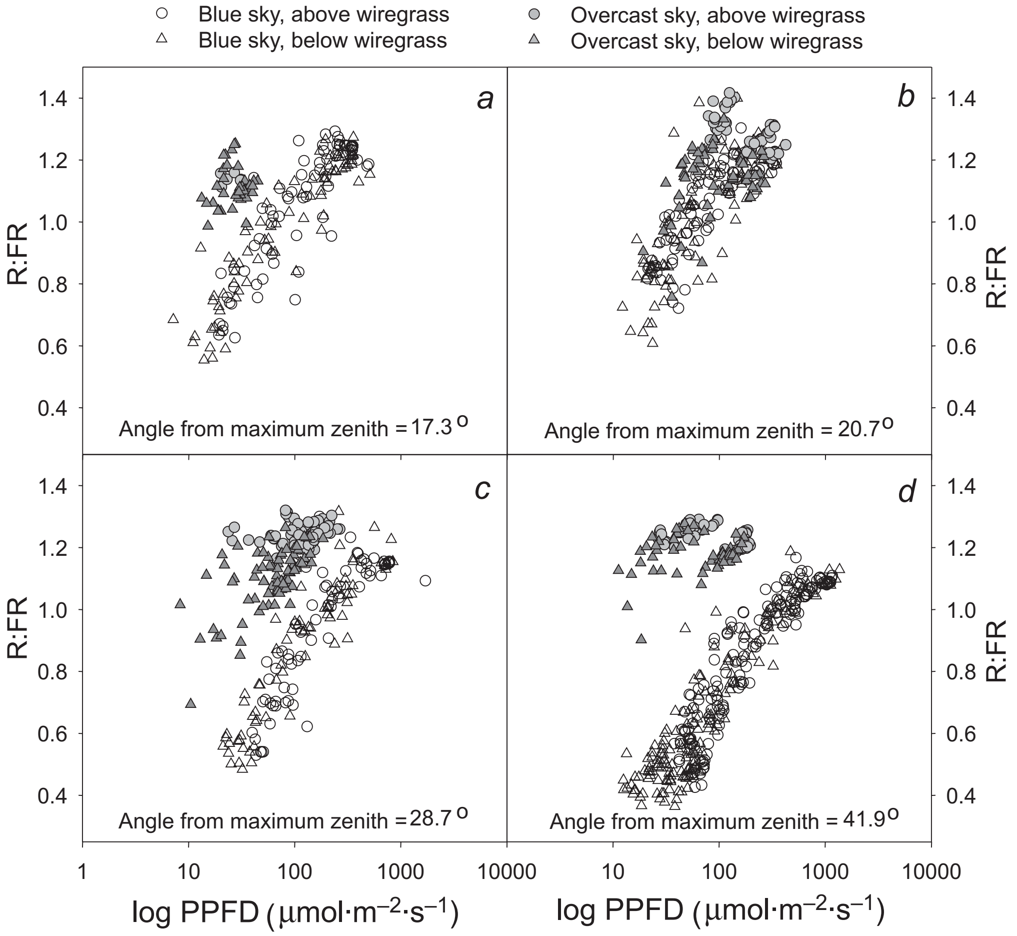
Note: Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. Data were collected during three time periods: morning (0800–1100), midday (1100–1400), and afternoon (1400–1700). Each equation includes the pooled above and below wiregrass condition.

[a] Equation fitted is of the form R:FR = $b_0[1 - e^{b1(\mathrm{PPFD} - b2)}]$.

[b] FI (fit index) is analogous to a correlation coefficient (r^2) but is appropriate for nonlinear equations.

[c] Model did not converge.

Fig. 3. For the second experiment, light quality (red : far red, R:FR) measured between the autumnal and vernal equinoxes increased with increasing light quantity (photosynthetic photon flux density, PPFD) over time (solar angle from zenith), between sky conditions (blue sky or overcast) and the presence of wiregrass (above or below). For clarity, the $\log_{10}$ scale is presented for the x-axis (PPFD). Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. Coefficients for fitted lines are presented in Table 3.



The range of observed R:FR values was 0.69–1.17. R:FR was significantly related to OAI, with R:FR values increasing only at OAI values <0.5; at OAI values >0.5, mean R:FR remained constant ($R^2 = 0.20$, $p = 0.028$) (Fig. 2*a*). Estimates of canopy transmittance were strongly related to OAI ($R^2 = 0.87$, $p < 0.0001$) (Fig. 2*b*).

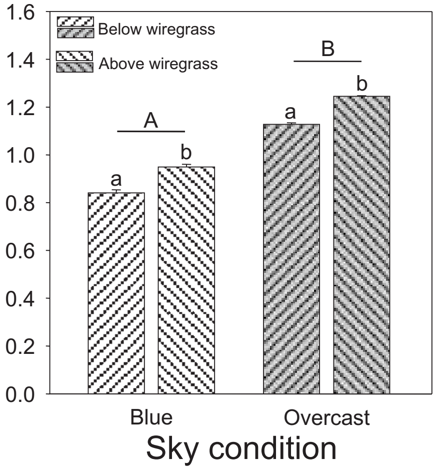
Experiment 2: relation of sky condition, solar angle, and wiregrass cover to R:FR

R:FR was significantly and positively related to PPFD between sky conditions and across solar angles except under overcast sky conditions during the first and fourth sample periods (near the vernal equinox) (Table 3). The range of individual R:FR values over all sampling periods was 0.36–1.42 (Fig. 3). Maximum R:FR (over all sampling periods) under the overstory canopy (but above the wiregrass canopy) during blue-sky conditions was 1.13 at a PPFD value of 886 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (approximately 40% full sunlight). We observed a much narrower range of PPFD and R:FR with overcast skies (Figs. 3*a*–3*d*). The largest R:FR value observed under overcast skies was 1.23 (at 208 $\mu mol \cdot m^{-2} \cdot s^{-1}$, or approximately 10% full sunlight).

R:FR under overcast skies (1.18) was 32.6% higher than that of blue skies (0.89) ($F_{[1,30]} = 490.22$, $p < 0.0001$) (Fig. 4). The presence of a wiregrass understory decreased R:FR, though this effect was not as strong as that of sky condition: R:FR declined 10.6% from 1.10 above the wiregrass to 0.98 below the wiregrass canopy ($F_{[1,30]} = 75.75$, $p < 0.0001$) (Fig. 4). The interaction between sky condition and wiregrass cover was also significant ($F_{[1,30]} = 63.57$, $p < 0.0001$). Under blue skies, R:FR above the wiregrass canopy (0.94) was 11.6% greater than that directly below the wiregrass canopy (0.84) ($F_{[1,30]} = 35.21$, $p < 0.0001$). Under overcast skies, wiregrass canopies decreased R:FR 9.6% from 1.24 to 1.13 ($F_{[1,30]} = 40.65$, $p < 0.0001$) (Fig. 4).

Over time, significant differences in R:FR were detected with respect to the presence of wiregrass ($p < 0.0001$), sky condition ($p < 0.0001$), and solar angle ($p < 0.0001$) (Table 4). All but one interaction of the main effects was significant (wiregrass cover × solar angle, $p = 0.538$) (Table 4). R:FR significantly decreased with increasing solar angle from the zenith under the blue-sky condition from 1.07 to 0.83 above wiregrass ($R^2 = 0.95$, $p = 0.021$) and from 1.01 to 0.66 below wiregrass ($R^2 = 0.95$, $p = 0.024$), with the lowest R:FR (0.66) observed under the wiregrass canopy when the solar angle was largest (nearest to the winter solstice) (Fig. 5). Maximum R:FR under overcast sky conditions did not vary among solar angles ($p = 0.92$ above wiregrass, $p = 0.31$ below wiregrass), but was consistently higher than that of blue-sky conditions across all solar angles (Fig. 5).

Fig. 4. For the second experiment, light quality (red : far red, R:FR) measured between the autumnal and vernal equinoxes increased with cloud cover (relative to blue sky) and decreased below wiregrass canopies (relative to directly above the wiregrass canopy). Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. Uppercase letters denote significant differences ($p < 0.05$) between the blue- and overcast-sky conditions, and lowercase letters denote significant differences ($p < 0.05$) in R:FR above versus below wiregrass for each sky condition.



Discussion

Light quality and overstory stocking were weakly related in this study, though there was a strong relationship between canopy transmittance (i.e., light quantity) and overstory stocking. Significant relationships between R:FR and overstory stocking have been observed in other work (Federer and Tanner 1966; Lee 1987; Messier et al. 1989; Endler 1993). The high R:FR values and the poor fit between R:FR and overstory stocking in this coniferous woodland may be due to the open and spatially variable canopy. Canopy light transmittance is higher (and leaf area index lower) in longleaf pine forests than in other forest systems (Palik et al. 1997; McGuire et al. 2001; Battaglia et al. 2002, 2003; Palik et al. 2003). Longleaf pine woodlands typically consist of a single overstory species with high horizontal and vertical variation in size and age (Platt et al. 1988; Palik and Pederson 1996) as well as persistent light gaps (Palik et al. 1997, 2003). Stochastic disturbances of varying intensity (the most important being frequent, low-intensity fires) maintain the open woodland structure by suppressing hardwood populations (Glitzenstein et al. 1995; Jacqmain et al. 1999). Persistent light gaps and high canopy transmittance allowed for direct light to move across the forest floor such that R:FR was variable throughout a day. Only the largest openings (greater than 0.1 ha) experienced mean R:FR values greater than 1.0, but areas with the highest overstory stocking on average had an R:FR value slightly less than that of the gaps (0.96). The poor fit between R:FR and overstory stocking may also be a result of the sampling regime employed for this study. For the first experiment we sampled R:FR only under blue skies and at one point in time (March). Homogeneous light conditions (PAR) in longleaf pine woodlands have been reported with sampling at low solar angles under blue-sky conditions (Brockway and Outcalt 1998), though others have reported high variation in space, time, and sky condition (Battaglia et al. 2003).

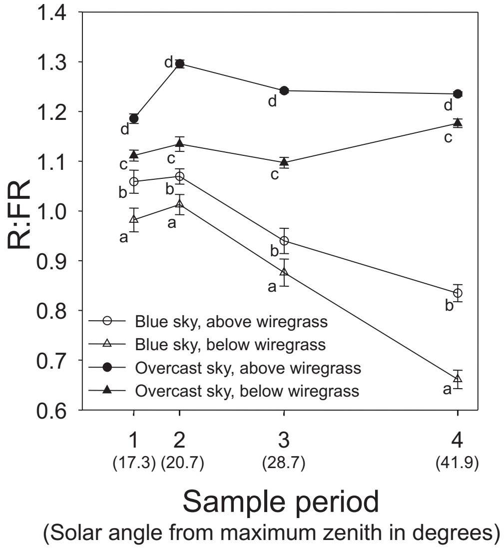
In this study, the understory reduced R:FR significantly but less than that reported for other systems. The small decrease in R:FR below wiregrass canopies (10.6%) may be partly explained by the growth form of the leaves. Canopies with leaf surfaces that are narrow and vertically presented

Table 4. Repeated measures, mixed-models output for differences in R:FR in a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA.

Main effect	ndf, ddf[a]	F	$p > F$
Wiregrass cover	1, 1215	118.37	<0.0001
Sky condition	1, 1215	670.26	<0.0001
Solar angle[b]	3, 1215	40.16	<0.0001
Wiregrass cover × sky condition	1, 1215	6.68	0.010
Wiregrass cover × solar angle	3, 1215	0.72	0.538
Sky condition × solar angle	3, 1215	49.03	<0.0001
Wiregrass cover × sky condition × solar angle	3, 1215	6.93	0.0001

[a] Numerator degrees of freedom, denominator degrees of freedom.
[b] Degrees from maximum solar zenith of 78.4° for the study site.

Fig. 5. For the second experiment, light quality (red : far red, R:FR) decreased with increasing solar angle (from the zenith) under blue skies but did not differ under overcast skies. R:FR values under overcast skies were consistently higher than that of the blue-sky condition. Data are from a 70- to 90-year-old second-growth longleaf pine forest in Baker County, Georgia, USA. Letters represent significant differences ($p < 0.05$) within a sample period using mixed-model analysis of variance.



attenuate R:FR less than those with broad, horizontally presented leaf surfaces (Lee 1987; Messier et al. 1989; Horsley 1993; Skálová et al. 1999). Skálová et al. (1999) found that *Nardus stricta* leaves (with narrow and upright foliage) lowered R:FR from approximately 1.05 to 0.85, which is similar to the decrease noted in our work (from 1.19 to 0.89). In contrast, a grassland community consisting mostly of *Polygonum bistorta* (wide and horizontally oriented leaves) lowered R:FR to approximately 0.6 (Skálová et al. 1999).

Frequent understory disturbance in longleaf pine woodlands may also explain the small reduction in R:FR under the wiregrass canopy compared to that observed in other work. The understory of longleaf pine woodlands historically burned on average every 1–3 years (Chapman 1932; Wahlenburg 1946), and present management attempts to maintain this return interval with prescribed burning operations (Boyer 1990). The low-intensity (<1 m height) fire removes a large part of the aboveground understory plant material and litter layer. Thus, the time between prescribed burns may not be long enough to allow for significant understory biomass accretion, which would significantly alter the light environment below the understory.

The understory plants in this temperate coniferous woodland may be similar in their phenotypic plasticity to that reported for other woodlands (Dudley and Schmitt 1995). In closed-canopy forests, plants orient their leaves to capture light with high R:FR (sunflecks) to maximize daily photosynthesis (Muraoka et al. 2003). Understory plants growing in woodlands, however, may be less responsive to changes in R:FR than understory plants in closed-canopy forests as there may be less competitive advantage to respond to changes in light quality by increasing height, leaf area, or internode length (Morgan and Smith 1979; Dudley and Schmitt 1995). We report high canopy transmittance (30%–80%) and mean R:FR values (>0.95) throughout the range of overstory stocking in our study site. Therefore, understory plants in these frequently burned woodlands may respond in similar ways to the response of understory plants noted in other woodlands. Future work should test plant responses to reduced R:FR for the major guilds of this woodland (e.g., grasses, legumes, and woody plants) to determine whether this is a valid supposition.

Clouds exerted a significant influence on R:FR in longleaf pine woodlands. Increases in R:FR with cloudy skies have been well documented (Federer and Tanner 1966; Holmes and Smith 1977; Messier et al. 1989; Lee and Downum 1991; Endler 1993). Under cloud cover there is a decrease in both the 400–600 and 700–800 nm wavelength bands and an increase in the 600–700 nm wavelength band (Holmes and Smith 1977). Endler (1993) noted a four-fold increase in R:FR in forest shade with cloud cover and hypothesized that with cloud cover R:FR in woodlands would be similar to that of open sky and large gaps. This was the case in our study: R:FR above the understory (but below the overstory) increased 40% with clouds to a value similar to that of open sky. R:FR on the forest floor, that is, below the wiregrass canopy, increased 32% with clouds. This has also been observed in other coniferous forests. Messier et al. (1989) found that R:FR under salal was two to three times greater with cloud cover. The greater impact of clouds on R:FR below the understory observed by Messier et al. (1989) may be attributed to low light levels observed in their study: canopy transmission in their study was <1%, while our study site ranged from 30% to 80% full sunlight. Thus, small absolute increments in canopy transmission can create large relative changes in PPFD and R:FR (Lee 1987; Messier et al. 1989).

R:FR decreased with increasing solar angle but only under clear-sky conditions. We observed a steady decline with increasing solar angle from maximum zenith under blue-sky condition, but no significant variation in R:FR with increasing solar angle was observed under overcast skies. Under cloudy skies, R:FR was uniformly high across all solar angles, even below the wiregrass canopy. This has been observed in wheat canopies (Holmes and Smith 1977) and is most likely due to a rise in R:FR with diffuse radiation, which is low in FR light.

Many deficiencies in our understanding remain as to how light quality impacts plants in field settings, including regeneration processes, competition, and physiology (Lee et al. 1996; Grant 1997; Lieffers et al. 1999). Canopies are complex arrangements of overstory, midstory, and understory plants that vary horizontally and vertically (Montgomery and Chazdon 2001). Plant materials interact with the solar path as well as clouds, making an understanding of the light environment of natural stands difficult (Grant 1997; Lieffers et al. 1999). In this work we have attempted to describe the primary sources of variation in light quality for a temperate coniferous woodland. While plant cover does significantly lower R:FR values, sky condition and solar path may be the most significant sources of variation for R:FR in frequently burned longleaf pine woodlands. The light environment in fire-maintained woodlands may be quite different from woodlands where disturbances, for example, fire, are less frequent or have been excluded. Comparative studies of R:FR across space and time with fire exclusion may provide valuable information on feedbacks between fire, vegetation, and successional gradients in longleaf pine ecosystems. Measuring R:FR over the entire range of solar angles observed at this site is also important for understanding connections between the light environment and plant morphology and phenology. Finally, whether the observed range of R:FR is of a magnitude to illicit strong physiological responses in these woodlands awaits further study.

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