Forest Ecology and Management 279 (2012) 66–76

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Understory light regimes following silvicultural treatments in central hardwood forests in Kentucky, USA

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ARTICLE INFO

Article history:
Received 28 March 2012
Received in revised form 12 May 2012
Accepted 14 May 2012

Keywords:
Light
PAR
Canopy
Variability
Thinning
Shelterwood

ABSTRACT

Manipulation of the light regime is a primary goal of many silvicultural treatments, but the specific light conditions created remain poorly documented for many forest types and geographic locations. To help quantify effects of silvicultural treatments on light conditions, measurements of basal area, canopy cover, and photosynthetically active radiation (PAR), measured both instantaneously and across time, were collected in central hardwood forests in Kentucky, USA following silvicultural treatments. These measurements were used to: (1) Investigate the magnitudes of differences in understory percent ambient PAR following implementation of shelterwood with reserves and thinning treatments; (2) document the spatial and temporal distribution and variability of understory percent ambient PAR in shelterwood with reserves treatments (mean residual basal area = 5.2 m^2/ha), thinning treatments (18.5 m^2/ha), and untreated controls (27.1 m^2/ha); and (3) examine relationships between: basal area and canopy cover; basal area and measured percent ambient PAR; and canopy cover and measured percent ambient PAR.

Mean light levels from instantaneous measurements were 78% of ambient in the shelterwood with reserves, 33% of ambient in the thinning and 9% of ambient in the control. Similarly, only 1.3% of the approximately 140 h of PAR measurements in the controls indicated high light conditions (>60% of ambient), 15.9% in the thinning treatment and 65.4% in the shelterwood with reserves treatment. There were only 32 periods of high light found across all plots in the control, 176 periods of high light in the thinning treatment, and 441 periods of high light in the shelterwood with reserves treatment. Indexes of variability in light across time and among sampling locations within a stand did not differ statistically between the shelterwood with reserves and thinning treatments but both treatments were statistically more spatially and temporally variable than the uncut control. Simple linear regression relationships were observed between stand basal area and mean relative PAR (r^2 = 0.8784 for instantaneous measurements, r^2 = 0.9697 for continuous measurements), and basal area and canopy cover (r^2 = 0.8479). Such relationships provide a means for including light management in forest planning and application of silvicultural treatments. The results for the distribution of light also suggest, however, that treated stands may have similar mean light levels, but differ substantially in the spatial and temporal distribution of light.

1. Introduction

Forest resource managers have no control over amounts of incoming PAR above the canopy (Smith et al., 1997), but can profoundly influence the abundance and distribution of PAR in forest understories by implementing appropriate silvicultural practices. The amount and structure of residual canopy after harvesting can be adjusted to provide enough PAR to enable establishment of desired tree species, and simultaneously limit undesirable competitors and temperature extremes (Loftis, 1990; Lieffers et al., 1999). Further, for a given residual basal area, the arrangement and structure of overstory trees can affect not only the amount of light reaching understory vegetation, but also how that light is distributed in space and time. Spatial arrangements of residual trees can be manipulated to affect the response and productivity of the

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http://dx.doi.org/10.1016/j.foreco.2012.05.017

understory, and limit or enhance regeneration of desired species (Baldocchi and Collineau, 1994; Nicotra et al., 1999; Battaglia et al., 2002; Palik et al., 2003).

Although it is intuitive that increases in PAR will accompany various levels of canopy removal, *specific* amounts of PAR resulting from different silvicultural treatments and PAR requirements for establishment, growth, and survival of many tree species have not been precisely determined. Studies involving quantification of understory PAR regimes and the rate of change of PAR availability during regeneration and subsequent stand development have been conducted (Clark and Clark, 1992; Clark et al., 1996; Beaudet and Messier, 2002; Beaudet et al., 2004), but relationships between different silvicultural treatments and PAR remain poorly understood for many forest types, geographic regions, and site types. Information on species–specific PAR requirements and responses to various levels of light is also incomplete, but has increased in recent years through physiological and eco-physiological research. Examples include studies of PAR interception efficiency and foliar physiological responses to PAR (Ashton and Berlyn, 1994; Delagrange et al., 2006) and investigations of canopy light transmission and its relationship to the growth and spread of understory competition (e.g., Lieffers and Stadt, 1994). Efficiency of capture and utilization of PAR for photosynthesis have been shown to depend on the intensity and duration of available PAR (Pearcy, 1990; Chazdon and Pearcy, 1991). The intensity of light and duration of full sunlight required to initiate photosynthesis have also been studied and differences have been discovered in the response time of woody and herbaceous species to increased light (Knapp and Smith, 1990). Once the requirements of many species and their physiological responses to different PAR levels have been determined, it should be possible to identify the range, spatial distribution and temporal distribution of understory PAR most appropriate for growth and survival of desired species. Such targets would enable managers to consistently and more efficiently achieve their management goals (Lieffers et al., 1999).

Implementation of specific targets will require reliable methods of equating a given desired light level to variables such as basal area that are more easily measured in the field. Previous research (e.g., Comeau et al., 1998; Buckley et al., 1999; Hale, 2003; Balandier et al., 2006) suggests that reasonable relationships between understory PAR and basal area can exist. As a result, continued research on this relationship in additional forest types would be useful. The relevance of relationships between commonly measured silvicultural variables and PAR is increasing as researchers and forestry practitioners continue to explore alternative shelterwood methods for regenerating oak species (Loftis, 1990; Brose et al., 1999), and other methods that involve retention of various components of canopy structure for at least a portion of the rotation (Franklin et al., 1997; Palik et al., 2003; Miller et al., 2006).

To establish the effects of overstory silvicultural treatments implemented in upland central hardwood forests on the characteristics of understory light regimes, the objectives of this research were to: (1) Investigate the magnitudes of differences in understory percent ambient PAR among shelterwoods with reserves, thinnings, and uncut controls; (2) document the spatial and temporal distribution and variability of understory percent ambient PAR in shelterwoods with reserves, thinnings, and uncut controls; and (3) examine relationships between: basal area and canopy cover, basal area and measured percent ambient PAR, and canopy cover and measured percent ambient PAR.

2. Methodology

2.1. Study area description

This research was conducted in conjunction with a large, collaborative research project described in Schweitzer et al. (2011) entitled "Maintaining Habitat Diversity, Sustaining Oak Systems, and Reducing Risk of Mortality from Gypsy Moth and Oak Decline on the Daniel Boone National Forest: Silvicultural Approaches and Their Operational Dimensions". This project was established in upland central hardwood forest during the summer of 2006 by the United States Forest Service (USFS) near London in Laurel County, Kentucky, USA, on the London Ranger District of the Daniel Boone National Forest, (37° 3′ 41″ N, 84° 11′ 10″ W). The forest type on the study sites is predominantly comprised of white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), black oak (*Quercus velutina* Lam.), and red maple (*Acer rubrum* L.). Soils on the study sites are predominantly silt loams belonging to the Latham, Shelocta, and Whitley soil series (Ross et al., 1981). Site indices for upland oaks are 19.8–24.4 m on sub-mesic sites and 15.2–19.8 m on subxeric sites (Smalley, 1986; McNab et al., 2002). All stands studied were located on broad ridges and were at least 70 years old (Schweitzer et al., 2011). Stand slopes, elevation, and pre-treatment densities and basal areas were comparable (Table 1). The histories of the individual stands incorporated in this study are incomplete, but all have been impacted to some extent by past forest management practices implemented since their incorporation within the Daniel Boone National Forest. All stands were considered fully stocked prior to the application of treatments in 2006 (Schweitzer et al., 2011).

2.2. Silvicultural treatments and study design

The treatments incorporated in the light regime study described here included shelterwood with reserves with 5.2 m^2/ha residual basal area retained (Miller et al., 2006), thinning to the B-level of

Table 1
Pre- and post-treatment characteristics of stands studied.

Stand number	Pre-treatment density (Trees/ha)	Post-treatment density (Trees/ha)	Pre-treatment basal area (m^2/ha)	Post-treatment basal area (m^2/ha)	Slope (%)	Elevation (m)
Control						
13	417.6	416.4	27.2	28.9	3–14	369–381
26	415.1	411.4	25.6	27.2	2–10	372–395
34	338.5	338.5	23.6	25.1	2–12	366–381
Thinning						
11	338.5	122.3	30.1	20.2	3–21	362–379
18	373.1	137.1	26.5	18.8	1–15	361–383
33	369.4	134.7	26.9	16.4	3–17	367–379
Shelterwood with reserves						
12	402.8	27.2	25.9	4.1	3–22	373–381
16	389.2	49.4	24.2	5.8	5–19	367–379
35	369.4	33.4	25.4	5.7	2–23	356–374

the Gingrich (1967) stocking chart (resulting in a residual basal area of 18.5 m^2/ha), and uncut controls with an average basal area of 27.1 m^2/ha (Schweitzer et al., 2011). Residual trees within the shelterwood with reserves treatment were selected to promote increased forest health and to improve habitat for wildlife and plant species that benefit from open, low basal area conditions. Oak species were favored. Expectations are that a new stand will regenerate beneath the reserve trees and eventually lead to a two-aged structure (Schweitzer et al., 2011). Marking for the thinnings was based on tree vigor and crown class, and marking guides were developed by consulting the SILVAH model (Ernst and Stout, 1991). The primary rationale for the thinning treatment is that reductions in tree density will allow residual trees to benefit from improved growing conditions. Outcomes should include increased tree vigor, larger crown diameters, continued or enhanced diameter growth, and increased capacity to survive defoliation (Schweitzer et al., 2011).

The measurements described below were collected in nine stands with three replicates randomly assigned to each treatment. Each stand contained 20 0.04 ha vegetation measurement plots systematically arranged on a nominal 40 m grid adjusted to accommodate the size, shape, and terrain of each stand. These plots were established by USFS crews prior to treatment implementation (Schweitzer et al., 2011). All measurements for the investigation described here were completed during the first full growing season after completion of silvicultural treatments. Basal area, canopy cover, and the amount of light reaching the understory at a given instant in time were measured on all plots. To facilitate assessment of the temporal distribution of understory light, continuous light measurements were collected for a subset of plots.

2.3. Basal area and density

All trees 11.7 cm and greater in diameter on 0.04 ha plots were tallied and measured for diameter at breast height (1.4 m above ground) to determine density and basal area (Schweitzer et al., 2011). Basal area was determined for each tree using the measured diameter, with tree basal areas summed for each plot and expanded to a per hectare value. Stand basal area and density were calculated for each of the nine stands by averaging over the twenty measured plots.

2.4. Canopy cover measurements

Digital plant canopy imagery was collected at each 0.04 ha plot center in all stands sampled, using a CI-110 Digital Plant Canopy Imager (CID Bio-Science, Inc., Camas, WA, USA), and a laptop computer running CID's CI110 image analysis software (Version 3.0.2.0, 16 August 2002). A single digital plant canopy image was acquired at the center of each of the 20 plot locations in each stand. The imaging device was mounted on a tripod, leveled, oriented south (with a compass), and positioned approximately 1 m above plot center. Canopy imagery was acquired during August and September of 2008 and 2009. Images were collected at various times during the day in an effort to reduce unfavorable imaging effects such as glare, vignetting, and overexposure. These problems were encountered most often in the shelterwood with reserves treatment. Imagery was analyzed, and canopy cover estimates generated with the image analysis software. Percent canopy cover represented the area above the digital plant canopy imager that was not open sky.

2.5. Instantaneous understory light measurements

For the purpose of this study, understory light was estimated as the percent of above canopy PAR reaching the understory light sensor. It was not possible to place sensors above the canopy so comparable ambient PAR measurements were collected with a Li-COR Li-1400 Data Logger (Li-Cor, Inc., Lincoln, NE) linked to a Li-COR Li-190 Quantum Sensor, mounted on a tripod. The tripod-mounted quantum sensor and logger assembly was placed in either of two hayfields that were proximate to the treated stands, leveled, and in a location that was exposed to maximum available ambient sunlight (ambient PAR). The sensor was never shaded by trees or other obstructions during logging of ambient PAR data. The instrument was set up early in the mornings, and data collection started automatically at a programmed time (typically 9 AM Eastern Daylight Savings Time). The Li-1400 Data Logger and was synchronized with Decagon Ceptometers (Decagon Devices, Inc., Pullman, WA) used for understory PAR measurement each morning prior to data collection. This ensured that a minute by minute comparison of understory and ambient PAR data would be possible during data analysis. Percent ambient PAR values for treatment and control sample locations were calculated by dividing ambient PAR values by understory par values recorded at the same minute of the day. This ratio provided an estimate of the photosynthetically available light in the understory, and also provided an index of canopy light interception by the overstory.

All instantaneous understory PAR measurements were collected with four Ceptometers. The Ceptometers measured PAR in micromoles per square meter per second (μmol m^{-2} s^{-1}). Measurements were obtained at the plot centers of the 20 forest inventory plots, in each of the three replicate stands per each of the three treatments ($n = 3$ treatments × 3 replicates per treatment × 20 plots per replicate = 180 measurements). Measurements were collected during the summers of 2008 and 2009. The twenty plots in each stand were measured once. A single instantaneous understory PAR reading was recorded at each sample location. To minimize the effects of sun angle, measurements were typically collected within 1 h preceding and following solar noon. This period allowed time for travel between plots. The Ceptometer was held level at waist height (approximately 1 m above the ground), with the PAR sensor array centered over the sample plot. The Ceptometer was pointed south, (oriented by compass), and leveled for each measurement.

Some post-processing of the collected data was necessary to minimize outliers and ensure accurate assessments and comparisons of treatments. Data from 175 of 180 plots were utilized for analysis. Outliers, defined as understory PAR measurements that were equal to, or greater than, 110% of ambient PAR were deleted from the data set. It was also found that even when placed under identical light conditions there were minor differences among the measured PAR values obtained with the four different Ceptometers used for understory PAR and the sensor used for ambient PAR. Correction factors were generated for each Ceptometer to normalize comparisons of understory PAR measurements collected with different Ceptometers. The correction factors were generated after side by side simultaneous PAR collection with all instruments, beneath two layers of 50% shade cloth, and ambient (uncovered) conditions during Octobers of 2008 and 2009, following completion of fieldwork on the Daniel Boone National Forest. The correction factor assessment measurements were conducted at Fulton Bottoms Rugby Field, on the campus of the University of Tennessee, Knoxville in October, 2008, and in October, 2009 at the University of Tennessee Arboretum in Oak Ridge, Tennessee and Agricultural Research and Education Center in Knoxville, TN. Microsoft Excel 2007 and Access 2007 (Microsoft, Inc. Redmond, WA) were utilized to compile and match all data, and to generate regression lines and equations for PAR measurements, basal area, and canopy cover. Correction factors for the Ceptometers ranged from approximately −3% to +15%, with the mean being an adjustment of +10% to minimize the bias of each understory unit relative to the ambient sensor.

2.6. Continuous understory light measurements

Continuous PAR measurements were collected at 7–8 plots in each stand (data from a total of 69 plots across all stands and treatments were utilized in this analysis). Collection of continuous PAR measurements at 8 plots per stand was planned, but equipment malfunction reduced the number of plots that were sampled. The plots for continuous PAR measurements were a selected subset of the plots where instantaneous PAR was also measured. Ceptometers were placed at the plot centers on tripods, oriented south (with a handheld compass), leveled and centered above the plot center. For analysis, continuous PAR measurements were truncated to a 400 min period, 200 min either side of solar noon, which corresponded to the maximum continuous block of measurements captured by all Ceptometers. Both the unattended understory Ceptometers and the ambient censor recorded PAR measurements once each minute during the collection period. A subset of eight plot centers were selected for continuous PAR measurement from among the 20 possible plot centers in each stand sampled. Plot centers were selected that were at least 20 m from stand boundaries and, where possible, were not adjacent to other selected plot centers in an attempt to obtain a sample representative of the entire stand.

Ambient PAR was obtained in the same manner used for instantaneous understory light measurements, with the ambient measurements obtained every minute over the data collection period. The understory percentage of ambient PAR was calculated for each minute by matching the time stamps from the ambient and understory sensors. Following the same post-processing methods used with the instantaneous measurements 965 of 27,484 total measurements (approximately 3.5%) were discarded before analysis.

2.7. Analysis

Amounts of stand-level light and canopy cover were estimated as the mean of plot measurements of canopy cover, instantaneous percent of ambient PAR, and continuous percent of ambient PAR within a given stand. For canopy cover and instantaneous percent ambient PAR, these means were calculated from single measurements taken at each of the plots. For the continuous percent ambient PAR measurements, it was necessary to first obtain a plot-level estimate by averaging the nominally 400 measurements taken at each plot and then average these plot-level estimates to obtain a stand-level mean.

Comparisons of spatial variability in light and canopy cover were conducted for each of the three variables. As with the means, it was possible to use the standard deviation of the individual plot measures of canopy cover or instantaneous percent ambient PAR as estimates of stand-level spatial variability.

The collection of continuous measurements allowed for estimation of indices of temporal variability as well. However, the implications of temporal variability can vary by scale so indices of temporal variability were calculated for time periods from 5 to 120 min in length in 5 min increments. For each plot the temporal variability index was the average of the standard deviation of percent ambient PAR over all possible time periods of the desired length in minutes as follows.

$$tv_{ij} = \sum_{p=1}^{m_{ij}-l} \sqrt{\frac{\sum_{t=p}^{l+p}\left(x_{tij} - \frac{\sum_{t=p}^{l+p} x_{tij}}{l}\right)^2}{l-1}} \Bigg/ m_{ij} - l \qquad (1)$$

where tv_{ij} is the temporal variability index for plot i in stand j, l is the length of time of interest (i.e. 5 to 120 min in 5 min increments for separate indexes), p is the index of period of time being measured, and t is the index of minute the measurement was taken. Additionally, m_{ij} is the number of minutes recorded for that plot and x_{tij} is the percent of ambient par recorded at a given minute for a given plot. Due to the post processing of data, there were periods in which not all of the measured minutes were available for analysis. If fewer than 80% of the minutes in a given period were not included in the dataset then that period was not included in the calculation of tv_{ij}.

Differences among the treatments in the amount and spatial variability of canopy cover, instantaneous percent ambient PAR, and continuous percent ambient were assessed using a one-way analysis of variance (ANOVA). Differences among the treatments in the index of temporal variability from the continuous percent ambient PAR were evaluated similarly. All data analyses were conducted in SAS 9.2 (SAS Institute Inc., Cary, NC, USA.). One-way ANOVA, conducted with the General Linear Models Procedure was utilized to analyze differences among treatments in mean values for canopy cover, instantaneous percent ambient PAR, and continuous percent ambient PAR, and also differences among treatments in sample standard deviations calculated for these variables. ANOVA models appropriate for a completely randomized design were utilized. The Univariate Procedure was used to examine model assumptions, and no transformations were necessary. Tukey's Honestly Significant Difference (HSD) was used for all pairwise comparisons.

A number of summary statistics were calculated to determine how often and how long the continuous PAR measurements indicated periods of high light. High light conditions were considered to be those where understory PAR was at least 60% of ambient. This 60% threshold represents the third quartile of all PAR measurements collected during the study across all plots and treatments.

Mean stand-level canopy cover, instantaneous percent ambient PAR, and continuous percent ambient PAR were used in regression analyses conducted to determine whether these measured variables could be related to basal area, a common forest inventory variable. These three simple linear regressions were conducted with the Regression Procedure in SAS 9.2. Model diagnostics, such as residual plots, were conducted for all regressions, and no transformations were necessary. Alpha was set to 0.05 for all statistical tests. Identical regression analyses were also performed to investigate how canopy cover was related to stand-level instantaneous percent ambient PAR and continuous percent ambient PAR.

3. Results

3.1. Treatment effects on structure

The thinning and shelterwood with reserves treatments resulted in approximately three- and ten-fold reductions in the number of trees per hectare, respectively, and concomitant decreases in basal area (Table 1). Diameter distributions among treatments were comparable prior to treatment implementation and changed most following implementation of the shelterwood with reserves treatment (Fig. 1).

3.2. Effects of changes in canopy cover

The typical effects of the treatments on canopy cover are visible in Fig. 2. From the continuous percent ambient PAR data summarized in Fig. 3, it is apparent that for a given minute of the measurement period the interquartile ranges, an indication of the variability of the measured variable within the treatment, is smallest for the control, but comparable between the thinning and the shelterwood with reserves treatments. As expected, canopy cover decreased with treatment intensity and light increased with treatment intensity (Figs. 3 and 4).

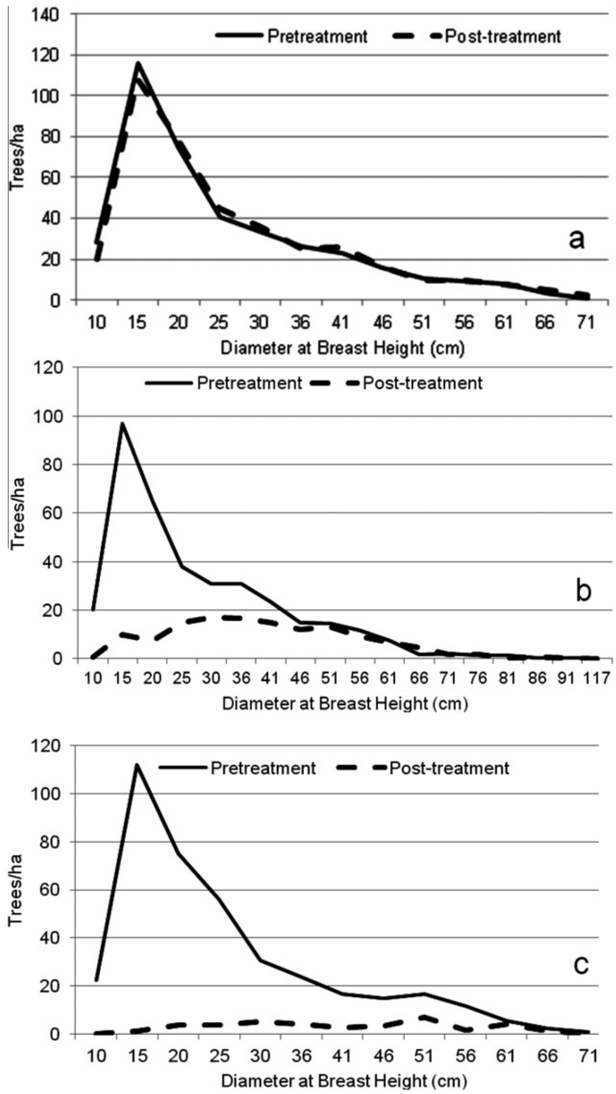

Fig. 1. Pre- and post-treatment diameter distributions in (a) control stands, (b) thinning treatments, and (c) shelterwood with reserves treatments.

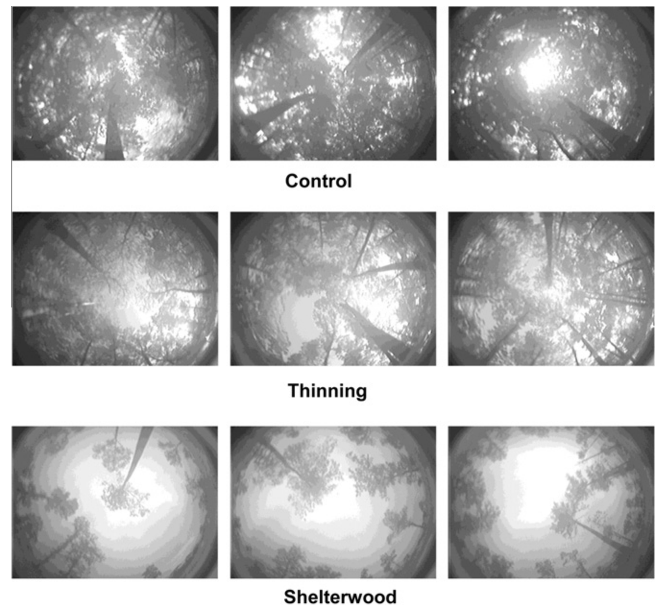

Fig. 2. Representative canopy images obtained with digital plant canopy imager at three plot locations within stands receiving the indicated treatment.

Results of ANOVA indicated average percent canopy cover differed ($P < 0.0001$) among treatments and controls (Table 2, Fig. 2). Mean canopy cover in the controls was approximately two times greater than that in the shelterwood with reserves (Table 2). However, ANOVA results suggested no difference in spatial variability index among treatments and control ($P = 0.2246$, Table 2).

3.3. Instantaneous light measurements

Based on the results of ANOVA, mean instantaneous percent ambient PAR values differed ($P < 0.0001$) among treatments and controls (Table 3). Measured mean percent ambient PAR was approximately four times greater in thinnings than in controls, and approximately eight times greater in shelterwoods with reserves than in controls (Table 3). ANOVA results indicated the spatial variability index of instantaneous percent ambient PAR differed ($P = 0.0006$) between treatments and controls, but did not differ between the two treatments (Table 3). The spatial variability index of instantaneous percent ambient PAR was more than four times greater in the treatments than in the controls (Table 3).

3.4. Continuous light measurements

Results of ANOVA suggested mean continuous percent ambient PAR differed ($P < 0.0001$) among treatments and controls. Measured mean values and magnitudes of differences in continuous mean percent ambient PAR across treatments (Table 4) were comparable to those for instantaneous percent ambient PAR (Table 3). However, in contrast to the instantaneous measurements, ANOVA results suggested that the spatial variability index of continuous percent ambient PAR did not differ ($P = 0.1392$) among treatments and controls (Table 4). In the controls, there was no practical difference between the instantaneous and continuous measurement techniques. However, differences between the techniques did increase with treatment intensity. Instantaneous percent ambient PAR was 4.27 greater than continuous in the thinning treatment and 10.07 greater in the shelterwood with reserves treatment (Tables 3 and 4). The indexes of temporal variability increased with the length of time over which the variability was calculated (Fig. 5). Results for the ANOVA procedure indicated differences among treatments for all lengths of time used to calculate temporal variability ($P < 0.0001$ for all, with df ranging from 64 to 66, with the lower df corresponding to stands with plots having high numbers of outliers that were removed in post processing). The Tukey's HSD procedure further revealed that for periods of 5 and 10 min, the treatments differed both from each other and the control. In contrast, for all longer time lengths, there was no difference in the temporal light variability between the thinning and shelterwood with reserves treatments, but both were different from the control.

A number of summary statistics were calculated to further examine the temporal aspects of light availability (Table 5). Non-statistical comparisons of these summaries revealed that high light conditions were only encountered 1.3% of the time in the control treatments, but were more than tenfold more common in the thinning treatments and 50 times more common in the shelterwood with reserves treatments than in the controls. Further, the periods of nominally continuous high light occurred 5.5 times more frequently in the thinning treatments than in the controls and 2.5 times more frequently in the shelterwood with reserves treatments than in the thinning treatments. The length of high

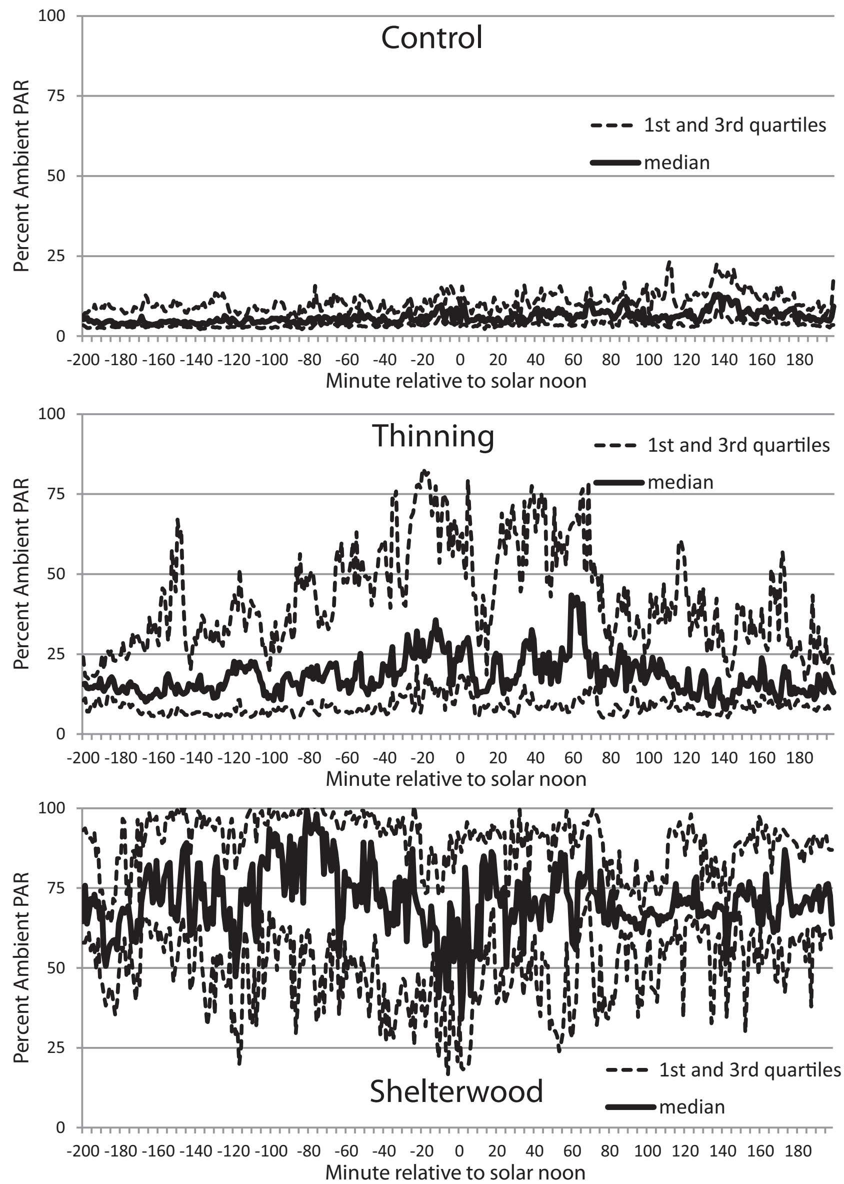

Fig. 3. Tracks of percent of ambient PAR across all measured plots in the indicated treatment for the indicated minute relative to solar noon. The median number of valid plot measurements available during each minute was 24 for the control, 23 for the thinning and 22 for the shelterwood with reserves treatment with a minimum of 12 plots.

light periods also typically increased with increasing overstory removal. However, these comparative differences were not as extreme suggesting that when high light conditions occurred, they occurred over short periods (1–3 min) in all treatments (Table 5).

3.5. Regression results

Simple linear regression analysis revealed a statistically significant relationship between the independent variable of basal area and each of the dependent variables: canopy cover, instantaneous mean percent ambient PAR and continuous percent ambient PAR. The relationship between instantaneous mean percent ambient PAR and basal area (Fig. 6) appeared strongly linear with increases in basal area resulting in decreased light availability at the forest floor ($P = 0.0002$). For the highest basal areas observed in this study (those in the uncut control), mean light levels were less than 15% of ambient, and as low as 8% in one stand. Regression analysis of continuous PAR data revealed a significant ($P < 0.0001$) relationship between mean continuous percent ambient PAR and basal area. Basal area explained 96.97% of the variation in average continuous percent ambient PAR (Fig. 6). Regression analysis revealed a significant ($P = 0.0004$) relationship between canopy cover and basal area. Basal area explained 84.79% of the variation in mean canopy cover (Fig. 6).

Further regression analysis revealed relationships between the independent variable of canopy cover and the dependent variables: instantaneous mean percent ambient PAR and continuous percent ambient PAR. Mean percent canopy cover explained 81.69% of the variation in instantaneous mean percent ambient PAR ($P = 0.0008$, Fig. 7). Regression analysis revealed a significant ($P = 0.0002$) relationship between continuous mean percent ambient PAR and mean percent canopy cover. Mean percent canopy cover explained 87.61% of the variation in continuous mean percent ambient PAR (Fig. 7).

4. Discussion and conclusions

All of the analyses conducted here indicated that increased intensity of silvicultural treatment resulted in decreased canopy

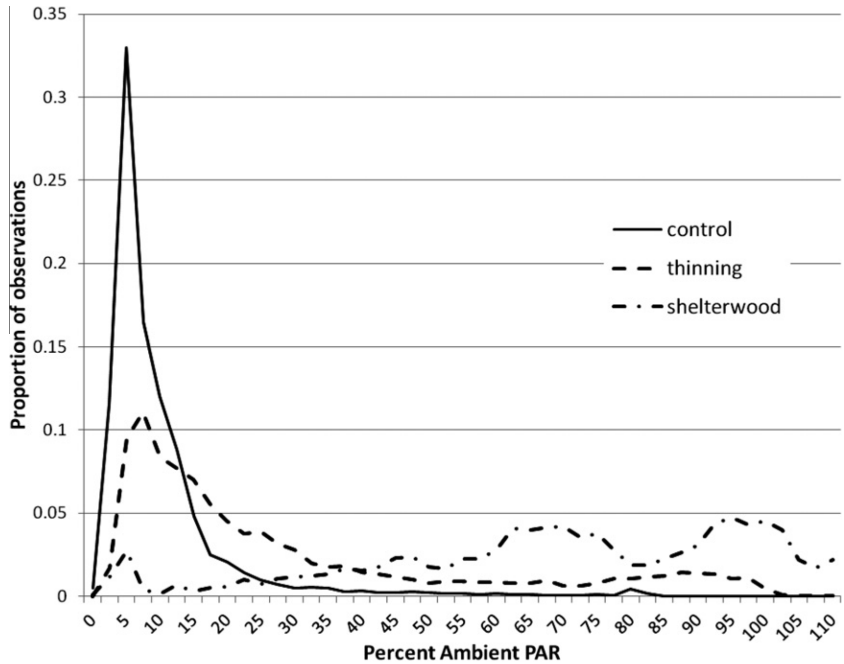

Fig. 4. Distribution of all the continuous measurements of percent ambient par for all the plots in each treatment and over all measured minutes.

Table 2
Mean percent canopy cover by treatment (n = 180, df = 177), mean of standard deviations (a metric of variability in canopy cover) by treatment (n = 9, df = 6), and mean percent cover by stand. Means with the same letters are not significantly different based on Tukey's Honestly Significant Difference (HSD) (alpha = .05). Standard deviations in parentheses.

Treatment	Treatment means		Treatment variability		Stand means		
	% Canopy cover	Tukey's HSD	Mean standard deviation of % canopy cover	Tukey's HSD	Stand number	% Canopy cover	Plots
					13	54.03 (15.55)	20
Control	60.31 (8.72)	A	15.62 (1.88)	A	26	70.27 (17.29)	20
					34	56.63 (13.59)	20
					11	48.72 (8.73)	20
Thinning	46.31 (2.15)	B	10.06 (1.62)	A	18	45.59 (11.87)	20
					33	44.6 (9.59)	20
					12	29.69 (10.74)	20
Shelterwood	31.12 (4.87)	C	12.15 (5.52)	A	16	27.12 (8.75)	20
					35	36.55 (18.04)	20

Table 3
Mean instantaneous percent ambient PAR by treatment (n = 170, df = 167), mean of standard deviations (a metric of variability) in instantaneous percent ambient PAR (n = 9, df = 6), and mean instantaneous percent ambient PAR by stand. Means with the same letters are not significantly different based on Tukey's Honestly Significant Difference (HSD) (alpha = .05). Standard deviations in parentheses.

Treatment	Treatment means		Treatment variability		Stand means		
	% Full ambient PAR	Tukey's HSD	Mean standard deviation of % full ambient PAR	Tukey's HSD	Stand number	% Full ambient PAR	Plots
					13	12.8 (9.03)	19
Control	9.06 (3.77)	A	6.17 (3.22)	A	26	9.12 (6.79)	20
					34	5.26 (2.69)	20
					11	33.55 (38.03)	20
Thinning	32.77 (0.99)	B	33.91 (5.28)	B	18	31.66 (35.75)	20
					33	33.09 (27.96)	19
					12	69.19 (23.05)	17
Shelterwood	78.34 (13.17)	C	28.23 (4.72)	B	16	93.43 (29.39)	15
					35	72.4 (32.27)	20

cover and increased understory light. However, treatment intensity had a less consistent impact on the spatial and temporal variability of the light environment. Measurements of both instantaneous and continuous PAR provided an opportunity to compare and contrast patterns in each measure across treatments. Control, thinning, and shelterwood with reserves treatments exhibited comparable measured means and magnitudes of differences across treatments in instantaneous and continuous PAR, although the differences between the measurement techniques did increase with decreasing canopy cover, suggesting that they

Table 4
Mean continuous percent ambient PAR by treatment ($n = 69$, df = 66), mean of standard deviations (a metric of variability) in continuous percent ambient PAR ($n = 9$, df = 6), and mean continuous percent ambient PAR by stand. Means with the same letters are not significantly different based on Tukey's Honestly Significant Difference (HSD) (alpha = .05). Standard deviations in parentheses.

Treatment	Treatment means		Treatment variability		Stand means		
	% Full ambient PAR	Tukey's HSD	Mean standard deviation of % full ambient PAR	Tukey's HSD	Stand number	% Full ambient PAR	Plots
					13	10.61 (5.29)	8
Control	9.09 (1.47)	A	4.04 (1.60)	A	26	7.68 (2.24)	8
					34	8.99 (4.59)	8
					11	25.67 (12.49)	8
Thinning	28.5(8.16)	B	13.22 (6.13)	A	18	22.13 (7.49)	8
					33	37.69(19.68)	7
					12	70.83 (20.44)	7
Shelterwood	68.27 (2.55)	C	17.98 (11.04)	A	16	68.26 (5.91)	8
					35	65.73 (27.59)	7

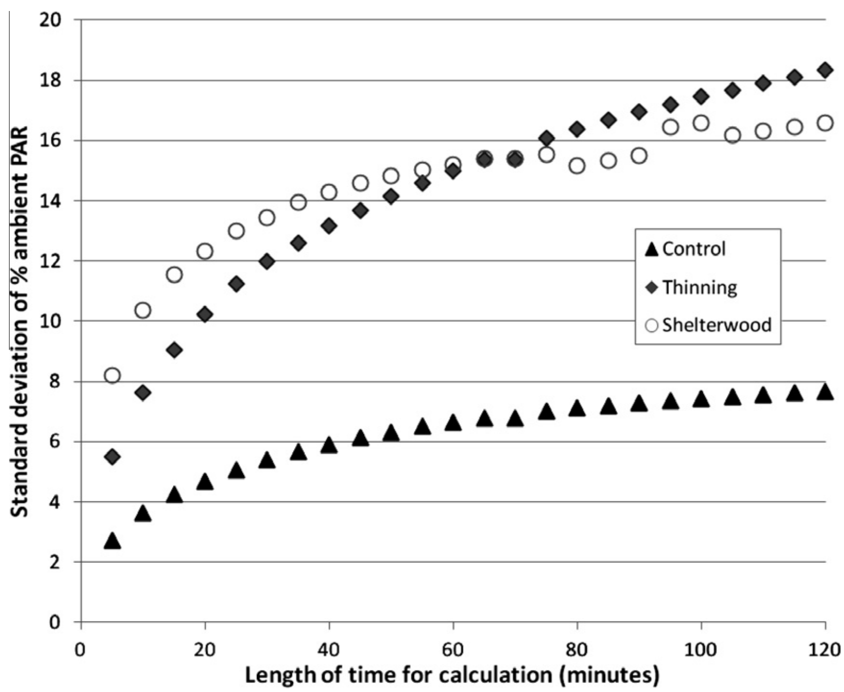

Fig. 5. Plot indicating the mean value of index of temporal variability for each treatment. The index was calculated using Eq. (1) using each of the indicated time period lengths from 5 to 120 min in 5 min increments.

Table 5
Statistics summarizing high light periods in which understory PAR measurements were >60% of ambient. The duration of periods with high light conditions were calculated as the number of consecutive measurements (1 measurement was obtained per minute) in which understory PAR was >60% of ambient. Statistics were calculated using the continuous understory light data.

Calculated statistic		Control	Treatment thinning	Shelterwood
Minutes in high light		128 (1.3%)	1427 (15.9%)	5091 (65.4%)
Minutes not in high light		9441 (98.7%)	7535 (83.8%)	2625 (33.7%)
Number of high light periods		32	176	441
Longest period of high light (min)		48	105	265
Length of high light period (min)	1st Quartile	1	1	1
	Median	2	2	3
	3rd Quartile	3	6	12
Number of plots		24	23	22
Total minutes measured		9569	8991	7789

may not be equivalent under higher light conditions (Tables 3 and 4). Long-term continuous measurements, however, are thought to be superior for estimating the seasonal light environment for a given point in a stand (Lieffers et al., 1999). Comeau et al. (1998) demonstrated greater strength in relationships between short-term averages and long-term averages calculated across the entire growing season as sampling periods increased from one to 3 h.

The amounts of PAR measured in controls and treated stands in this study represent a snapshot of PAR conditions in time relative to the periods of time required for stand development and

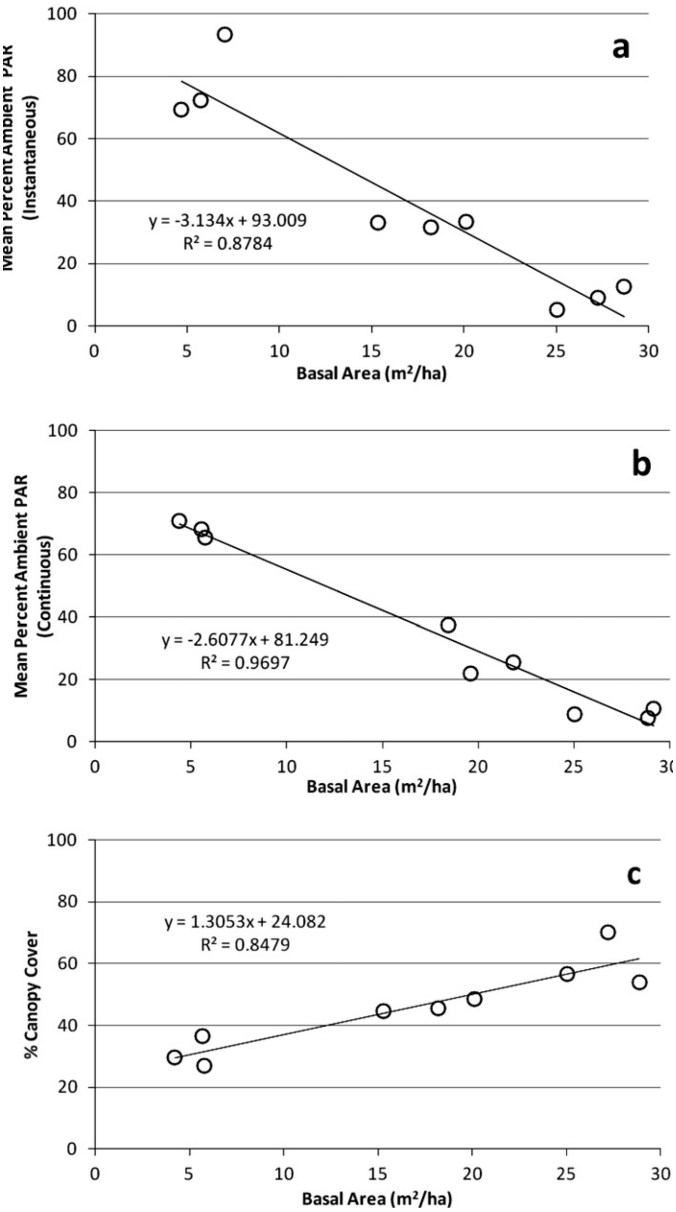

Fig. 6. Relationships between target stand-level variables (a) instantaneous percent ambient PAR, (b) continuous percent ambient PAR, and (c) percent canopy cover and the predictor variable stand basal area. Lines represent the results of simple linear regression with indicated equation and R^2. The relationships shown in graphs (a–c) had *p*-values of 0.0002, <0.0001, and 0.0004, respectively.

successional processes. Substantial changes in the amounts and distribution of PAR accompany the processes of stand development and succession (Beaudet et al., 2004). However, conditions in the first growing season following silvicultural treatments are important in determining the composition and success of regeneration, and setting the future course of succession. Amounts of instantaneous percent ambient PAR measured in shelterwood with reserves and thinning treatments in this study were approximately 1.3 times greater than those measured in northern red oak stands with comparable basal areas in northern Lower Michigan (Buckley et al., 1999). Differences in stand composition and latitude may have contributed to the differences in mean percent ambient PAR reported in these studies.

Standard deviation in plot-level PAR measurements within stands was used as an index of spatial variability in understory light within stands. There was no difference in the index of spatial variability of continuous PAR between treatments and controls (Table 4), but significant differences in spatial variability in instantaneous PAR existed between treatments and controls (Table 3). This result, along with the relatively high amounts of temporal variability evident in the shelterwood with reserves and thinning treatments (Fig. 3), suggests that the instantaneous measures may have inconsistently captured spatial variability because they were confounded with temporal variability introduced by the time required to move from one plot to another. Comparably, the continuous measurement technique smoothed out some of the spatial variability present at any one point in time by averaging over measurement periods of various lengths. Indeed, the length of the measurement period was likely the key driver of the differences among measurement techniques for spatial variability in understory light, as shown in Fig. 5.

Comparisons of variability in continuous PAR over time (using standard deviation of mean percent ambient PAR as a measure of variability) indicated results similar to those for instantaneous spatial variability, namely that treatments (which were not significantly different in variability from one another) were significantly more variable than controls. Characterization of the temporal variability of light environments is important because plants require particular periods of time to adjust to changes in light conditions over the course of a day, and photosynthetic responses to the temporal distribution of light vary considerably between species (Chazdon and Pearcy, 1991; Lei and Lechowicz, 1997; Hull, 2002; Schulte et al., 2003; Nilsen et al., 2009). While periods of high light were typically relatively short in all treatments, they were longer and more frequent in the shelterwood with reserves (Table 5). This information, along with the minimal amount of time high light conditions were recorded in the controls (1.3% of the measured time), suggests that it would be possible to create a desired temporal distribution of light by manipulating structure with silvicultural treatments. Temporal variability in light may affect survival and growth rates of different species. As a result, selection and design of silvicultural treatments to control not only the amount of light reaching the understory, but also the scale and amount of temporal variability in light, may be important (Figs. 3 and 5, Table 5). Continuous measurements provide a method to assess issues of temporal variability in understory light that cannot be detected with instantaneous methods alone (Figs. 3 and 5).

In the context of the practice of silviculture, mean PAR values may be suitable for an initial characterization of the understory PAR environment at the stand level, but are not necessarily indicative of the actual PAR environment at any specific location within the stand. Previous studies suggest patchiness associated with regeneration of oaks (e.g., Rozas, 2003; Loftis, 2004). Understanding this patchiness will enhance precision in creation of target PAR levels at specific locations within stands that are best suited for oak regeneration when planning overstory removal treatments. The spatial arrangement of residuals can have a profound effect on understory light at any specific location within the stand (Palik et al., 1997, 2003). Edge effects, variability in canopy strata, and differences in crown architecture among species will also contribute to patchiness in understory light. The primary implication of these sources of variability for silviculturists is that mean PAR values at the stand level must be interpreted with care. Stand-level mean understory PAR values, therefore, should be considered only as a general guideline when planning overstory removal treatments. Mean PAR values may not provide a sufficient level of detail regarding light levels at areas of stands where silvicultural treatments are most likely to achieve favorable results. For instance, the patchiness associated with oak regeneration (Loftis, 2004) suggests that increased precision with respect to creation of target light levels via silvicultural treatments would be warranted. In this

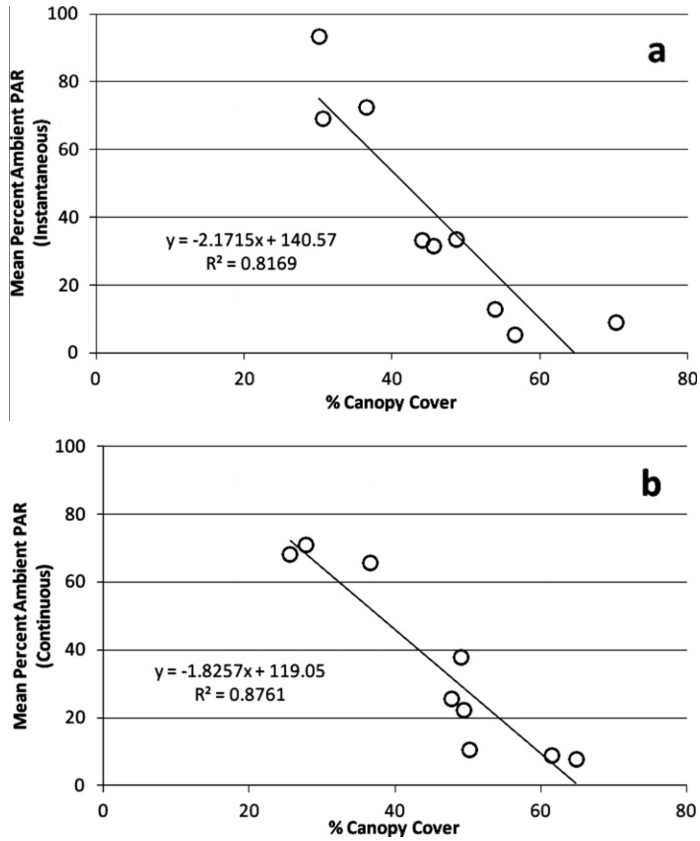

Fig. 7. Relationships between stand-level estimates of target variables (a) instantaneous percent ambient PAR and (b) continuous percent ambient PAR and predictor variable percent canopy cover. Lines represent the results of simple linear regression with indicated equation and R^2. The relationships shown in graphs (a and b) had *p*-values of 0.0008 and <0.0002, respectively.

study, mean understory PAR values did not capture the true PAR environment at specific locations within a stand, and PAR values ranging from very low intensities to very high intensities are to be expected at different points within stands, whether those stands are controls or stands that have undergone overstory removal treatments.

Regression results from this PAR regime study suggested that basal area was a better predictor of instantaneous and continuous percent ambient PAR than canopy cover. In contrast, Lhotka and Loewenstein (2006) found that canopy closure, estimated with hemispherical photography, was a better predictor of percent ambient PAR measured 1.25 m above the ground than basal area calculated from measurements of all stems >5 cm DBH in mixed-hardwood riparian forests in Georgia. Working in northern red oak (*Q. rubra* L.) stands in Michigan, Buckley et al. (1999) also found that canopy cover, measured with a spherical densiometer, was a better predictor of percent ambient PAR measured 1 m above the ground than basal area measured with a prism.

Some problems with the quality of digital plant canopy imagery used to determine canopy cover were observed and could have affected the accuracy of canopy cover measurements to some degree. Specifically, CID's digital plant canopy imager CI110 image analysis software program (Version 3.0.2.0, 16 August 2002) was unable to differentiate between darker clouds and actual canopy in some instances, and this was particularly common in imagery obtained within the shelterwood with reserves treatments. This tended to result in overestimations of canopy cover. Nonetheless, reasonably strong relationships were indicated between canopy cover estimates and percent ambient PAR, and between basal area and canopy cover estimates. The stronger relationships between continuous percent ambient PAR and basal area and between continuous percent ambient PAR and canopy cover than the relationships between instantaneous percent ambient PAR and these variables were likely due to the more precise estimates of percent ambient PAR obtained with the continuous measurement method.

Collectively, the regression results suggest that forestry practitioners could use the regression equations presented as a reasonable guide for achieving a given level of mean canopy cover or mean amount of percent ambient PAR in similar stands with similar treatments within the region. Different relationships would be needed for stands differing in composition, structure, and geographic location, as evidenced by differences in the relationships found in this study and those published previously for northern forest types by Buckley et al. (1999). Further, although the pre-treatment structure of the stands studied was reasonably comparable, density, diameter distributions, and basal area did vary between stands (Table 1, Fig. 1) within the relatively small geographic region encompassing the study area.

If documented more extensively over physiographic regions and forest types, mean understory PAR values could prove useful to resource managers. Specific understory PAR target levels could be used as guidelines for achieving post-treatment PAR levels that would be most likely to meet their specific silvicultural objectives. Managers who are attempting to alter PAR levels to favor a species or group of species over other competitors could use more precise PAR averages to assist in predicting the response of vegetation to disturbance. The results for the distribution of light also suggest, however, that treated stands may have similar mean light levels, but differ substantially in the spatial and temporal distribution of light. Further investigations of the response of plant species to these differences, and silvicultural techniques for manipulating them, are warranted.

Acknowledgments

This project was made possible through funding provided by the USDA Forest Service Southern Research Station under a Cooperative Agreement on Extramural Research. The authors wish to thank Stacy Clark, Research Forester, and all the other USDA Forest Service personnel from the Southern Research Station, Northern Research Station, and Daniel Boone National Forest who facilitated the completion of this research.

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