



Short communication

# Landscape variations in understory PAR for a mixed deciduous forest in New England, USA

Matthew M. Fladeland, Mark S. Ashton\*, Xuhui Lee

*School of Forestry and Environmental Studies, Yale University, 360 Prospect Street, New Haven, CT 06511, USA*

Received 5 July 2002; received in revised form 13 March 2003; accepted 26 March 2003

## Abstract

Information from horizontal quantum sensor arrays and data on forest structure was used to measure photosynthetically active radiation (PAR). Forest sites with stands of similar age and land-use history were blocked into three valley, three mid-slope, and three ridge topographic positions. Analysis of forest structure and light measurements demonstrate: (1) canopy height and leaf area index decreased on progressing from valley to ridge; (2) total understory radiation increases on progressing from the valley to ridge; (3) sunflecks contribute a disproportionate amount of photosynthetic photon flux (PPF) on sunny days (40–80%) with number and duration of sunfleck periods increasing from valley to ridge.

© 2003 Elsevier Science B.V. All rights reserved.

*Keywords:* Advance regeneration; Photosynthetically active radiation; Photosynthetic photon flux; Oak-hardwood; Topography; Understory

## 1. Introduction

Prior to forest canopy disturbance, the resource that appears to most limit survivorship and growth of advance regeneration in the forest understory of moist forests is light (Chazdon and Pearcy, 1991; Canham et al., 1994).

In the forests of southern New England the degree to which the canopy is opened during disturbance events changes not only light levels, but other micro-environmental attributes such as groundstorey temperatures (Chen et al., 1999) and soil moisture regimes (Breshears et al., 1997). This information, while difficult to gather (see Reifsnyder et al., 1971), has proven to be useful in modeling important ecosystem functions such as net primary productivity (Hutchison and Matt, 1976, 1977), net exchange of

CO<sub>2</sub> and other greenhouse gases (Wofsy et al., 1993). However, relatively little is known with respect to how light levels change across larger environmental scales of gently undulating landscapes (ridge–valley topography) beneath closed canopied forest (Swanson et al., 1988; Xu et al., 1997).

Recent studies in southern New England have shown that gradients exist in soil nutrient concentrations and soil moisture across topographic positions (Ashton and Larson, 1996; Ashton et al., 1998). Gradients in understory light availability would suggest differential survival of regeneration; more shade-tolerant tree species enduring darker understory environments than those species that were more shade-intolerant.

The objective of this study was to examine if understory gradients in availability of light exist across the gently undulating topography of closed canopied forest in southern New England during the growing season.

\* Corresponding author. Tel.: +1-203-432-9835.

E-mail address: [mark.ashton@yale.edu](mailto:mark.ashton@yale.edu) (M.S. Ashton).

## 2. Site description

The experiment was conducted at the 7840 acre Yale Myers Forest, located at 41°57'N, 72°07'W, in northeastern Connecticut, USA (Meyer and Plusnin, 1945). It is classified as a mixed deciduous–coniferous forest with a tree canopy comprised primarily of *Quercus rubra* L., *Acer saccharum* Marsh, *Betula lenta* L., and *Tsuga canadensis* Sarg. The mean annual precipitation is 110 cm with approximately equal distribution throughout the year (Ashton and Larson, 1996).

Land in the region was incorporated in the late 1700s and consisted of a mosaic of farmland, pastureland, woodlots and wetlands. Since agricultural abandonment in the 1850s much of the land has regenerated into forestland. The stands sampled in this study were all closed canopy forests ranging between 80 and 100 years having regenerated beneath old-field pine at the turn of last century (1900). The forest ridge–valley topography is undulating, aligned in a southwest–northeast direction, and of ancient metamorphic origin (schist and gneiss—Meyer and Plusnin, 1945). Mean elevation differences between ridge and valley (mean elevation 200 m amsl) were 50 m, with mean distances of 500 m between ridge crest and valley trough.

## 3. Methods

### 3.1. Experimental design

The nine forest stands selected for this study were chosen within mixed deciduous forests of similar land-use history and age. Forest stands were stratified equally into three valley, three mid-slope, and three ridge topographic positions. Sites were all gently sloping or flat given the nature of the rolling topography of southern New England. A 30 m × 30 m plot (aligned east–west, north–south) was demarcated in which stems larger than 1 cm were mapped and canopy projections in the four cardinal directions were taken to estimate canopy cover. Species were identified and stem diameter was measured from which species basal areas were calculated (Table 1). Canopy heights and live crown ratios were measured along a 10 × 30 strip (aligned north–south) down the center of the plot (east–west) to assess canopy height and depth. Within each of the nine 30 m × 30 m plots, six random points were selected for sampling understory radiation conditions using radiation sensors. At each of the six radiation sampling points ocular estimates of leaf area index (LAI) were also estimated. We used the 90° angle of a clinometer vernier eyepiece to insure accuracy. The vernier allowed measurement

Table 1

Descriptive measures made in June 2001 of stand structure and composition across topographic positions (valley, mid-slope, ridge)<sup>a</sup>

	Valley	Mid-slope	Ridge
Basal area by species			
White oaks	–	1.75	3.29
Red oaks	5.95	14.93	8.99
Hickories	3.62	2.31	11.67
Sugar maple	6.06	1.16	–
Red maple	2.04	2.30	0.04
Birches	5.64	1.51	–
Eastern hemlock	1.08	–	1.51
Other hardwoods	11.57	1.02	0.37
Total basal area (m <sup>2</sup> ha <sup>-1</sup> )	35.96 a	24.98 b	25.87 b
Forest structure			
Canopy height (m)	29.72 (+ 3.83) a	26.00 (+2.16) ab	19.72 (+3.00) b
LAI	6.00 (+0.67) a	5.33 (+0.58) ab	4.66 (+0.95) b

<sup>a</sup> Letters qualitatively indicate significant differences among treatments ( $a > b > c$ ) according to Tukey's studentized range test ( $P < 0.05\%$ ).

of the number of times a leaf intersected an imagined vertical line from the eye to the top of the forest canopy. LAI can simply be defined as the amount of one-sided leaf surface area per unit of ground area.

### 3.2. Quantum sensor measurements

Continuous light measurements were made from two fully open sites using data loggers (LI-1000, Li Cor, Lincoln, NE) and light sensors (LI-190SA). Measurements were recorded as 10 min means to estimate total daily photosynthetic photon flux (PPF) received above the forest canopy during the growing season (1 May–30 September).

Measurements of photosynthetically active radiation (PAR) in the form of PPF for each of the nine stands were taken using quantum sensors (LI-190SA) that were simultaneously positioned on a balanced horizontal stand at the ground surface over each of the six sample points within the 30 m × 30 m plot. On any instance when groundstorey vegetation was immediately above a sensor it was removed. Sensors were connected to a data logger (LI-1000) and records made over several 48 h periods during the summer months of July–August 2001 (clear sunny days: 2–3 June, 24–26 June, 16–18 June; uniformly overcast days: 9–10 June, 3–5 July, 1–2 August). Data loggers were programmed to read every 10 s, from which 10 min mean values were calculated of PPF ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). These means were recorded and summed over the day to yield total daily PPF ( $\text{mol per day m}^{-2}$ ). The minimum and maximum PPF reading for each 10 min interval was also recorded. Summations of 10 min readings on overcast days were used to estimate ambient levels of indirect light (Gendron et al., 1998). Ten minute means on clear sunny days were then compared to measures of ambient indirect light levels to estimate sunfleck intensity, number per day, and duration. Estimates of sunfleck duration were then used to calculate relative contributions of direct versus indirect beam radiation to total daily PPF on clear sunny days.

### 3.3. Data analysis

Data was collected and summarized by forest structure measures (basal area, canopy height, LAI) and measures of understory light (radiation sensors).

One-way ANOVA tests were carried out for forest structure measures, total daily PPF between each point, as well as with respect to the different stands and topographic positions.

## 4. Results

### 4.1. Forest structure

There was a significant difference in basal area between the valley topographic position and those of the ridge and mid-slope. The mean basal area for all stands sampled was  $29.84 \text{ m}^2 \text{ ha}^{-1}$  (Table 1). Mean canopy height and LAI decreased significantly with increasing elevation on going from valley to ridge (Table 1).

### 4.2. Quantum sensors

PPF was continuously recorded at Yale Myers Forest from 1 May to 30 September in two open fields. Results showed that the mean PPF received each day was approximately two-thirds that received on completely clear days. During this period 32% of the days were clear.

Quantum sensor data of 10 min means of PPF on sunny days showed significant increases in available understory PPF from valley to ridge top positions (Table 2). Sunflecks were an important source of PPF on sunny days contributing as much as 80% of the total PPFD for the day. However, their duration was short (13–17 min) with no significant difference shown among slope positions. The number of sunfleck periods increased on progressing from valley (3.9 per day) to ridge top (13.0 per day) (Table 2).

## 5. Discussion

Our results conform to other estimates of deciduous forest light regimes with respect to measurements of total daily PPF reaching the understory (Canham et al., 1990; Ashton and Larson, 1996). However, to the best of our knowledge, no other study has demonstrated differences in light as a function of meso-topography. Clearly, our findings show important differences across the landscape (valley to ridge) in both total amount of PPF and the nature of proportional difference

Table 2

Comparisons in the various measures of understory light across topographic positions (valley, mid-slope, ridge) over June, July, and August 2001<sup>a</sup>

	Valley	Mid-slope	Ridge
Radiation sensors (based on three periods, totaling 7 overcast days)			
PPF (mol mol <sup>-2</sup> per day)	0.37 (±0.04) c	0.53 (±0.03) b	1.00 (±0.17) a
% PPF to full open	3.0% b	9.3% a	8.7% a
Radiation sensors (based on three periods, totaling sunny overcast days)			
PPF (mol m <sup>-2</sup> per day)	1.01 (±0.10) c	1.66 (±0.18) b	2.91 (±0.49) a
% of direct PPF	65–80	45–70	43–67
% PPF to full sun	1.6 b	3.2 ab	5.2 a
Mean duration of a single sunfleck (min)	13.6 a	16.4 a	16.9 a
Number of sunflecks per day	3.9 (±2.2) b	5.3 (±2.3) b	13.0 (±1.6) a
Total period of sunflecks (min per day)	48.9 c	87.6 b	219.8 a
Mean sunfleck intensity (μmol m <sup>-2</sup> per day)	225 a	151 a	285 a

<sup>a</sup> PPF is measured in mol m<sup>-2</sup> per day. Standard errors are shown in parentheses. Letters qualitatively indicate significant differences among treatments ( $a > b > c$ ) according to Tukey's studentized range test ( $P < 0.05\%$ ).

in direct versus indirect light received at the forest groundstorey beneath closed canopy forest.

There has been much discussion in the literature on the proper estimation of PPF in forest understories focusing specifically on differences between estimates made on cloudy versus sunny sky conditions (Gendron et al., 1998, 2000). Our study demonstrates the need to evaluate both sunny and cloudy conditions. Sunflecks can represent 40–50% of PPF on sunny clear days in the forest understory but their duration can be no more than 10 min (Ashton and Larson, 1996). In our study sunflecks on clear sunny days represented a range from 43 to 80% of total daily PPF across all topographic positions. Clearly the nature of this kind of light can play an important contributing role in maintaining seedling survival in light-limited forest understories. Our study suggests this is most likely to be in valleys and lower lying areas of the forest where canopy heights are taller, foliar stratification more complex, with higher leaf area indices than ridge and mid-slope forests.

Findings in this study elucidates this past work (Ashton and Larson, 1996) by suggesting that low seedling survival of canopy tree species in understories of valley sites may be due to limitations of light availability as compared to mid-slope and ridge sites.

## 6. Conclusions

The results of this study have direct implications for forest management. Silvicultural treatments that

remove some of the forest canopy to brighten the understory on valley sites may ensure regeneration survival of the more shade-intolerant species such as oak; this would not be necessary on mid-slope and ridge sites. Such treatments suggest more site-specific treatments for regeneration of oak species, implying that variations in the traditional shelterwood method used for securing oak.

## Acknowledgements

This study was made possible with fellowship funding from the Mellon Foundation. We also thank John McKenna for help in the stand structure measurements for each of the nine stands.

## References

- Ashton, P.M.S., Larson, B.C., 1996. Germination and seedling growth of *Quercus* (section *Erythrobalanus*) across openings in a mixed-deciduous forest of southern New England, USA. *For. Ecol. Manage.* 80, 81–94.
- Ashton, P.M.S., Harris, P.G., Thadani, R., 1998. Soil seed bank dynamics in relation to topographic position of a second-growth deciduous forest in southern New England, USA. *For. Ecol. Manage.* 111, 15–22.
- Breshears, D.D., Rich, P.M., Barnes, F.J., Campbell, K., 1997. Overstorey-imposed heterogeneity in solar radiation and soil moisture in a semi-arid woodland. *Ecol. Appl.* 7, 1201–1215.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and

- tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620–631.
- Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* 24, 337–349.
- Chazdon, R.L., Pearcy, R., 1991. The importance of sunflecks for forest understory plants. *BioScience* 41, 760–766.
- Chen, J., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F., 1999. Microclimate in forest ecosystem and landscape ecology. *BioScience* 49, 288–297.
- Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density of forests. *Agric. For. Meteorol.* 92, 55–70.
- Gendron, F., Messier, C., Comeau, P.G., 2000. Temporal variation in the understory photosynthetic photon flux density of a deciduous stand: the effects of canopy development, solar elevation and sky conditions. *Agric. For. Meteorol.* 106, 23–40.
- Hutchison, B.A., Matt, D.R., 1976. Beam enrichment of diffuse radiation in a deciduous forest. *Agric. Meteorol.* 17, 93–110.
- Hutchison, B.A., Matt, D.R., 1977. Distribution of solar radiation within a deciduous forest. *Ecol. Monogr.* 47, 185–207.
- Meyer, W.H., Plusnin, B., 1945. The Yale Forest in Tolland and Windham Counties. Yale School of Forestry and Environmental Studies Bulletin 55. Yale School of Forestry and Environmental Studies, New Haven, CT.
- Reifsnyder, G.M., Furnival, G., Horowitz, J.L., 1971. Spatial and temporal distribution of solar radiation beneath forest canopies. *Agric. Meteorol.* 17, 93–110.
- Swanson, F.J., Kratz, T.K., Caine, N., Wodmansee, R.G., 1988. Landform effects on ecosystem pattern and process. *BioScience* 38, 92–98.
- Wofsy, S.C., Golding, M., Munger, J.W., Fan, S.M., Bakwin, P.S., Daube, B.C., Bassow, S.L., Bazzaz, F.A., 1993. Net exchange of CO<sub>2</sub> in a mid-latitude forest. *Science* 260, 1314–1317.
- Xu, M., Chen, J.Q., Brookshire, B.L., 1997. Temperature and its variability in oak forests of the southeastern Missouri Ozarks. *Clim. Res.* 8, 209–223.