

Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies

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Abstract

The understory light environment is a key determinant of vegetation pattern and ecosystem processes, and varies spatially perhaps more than any resource used by plants. Understory light varies along gradients of vegetation structure that range from grassland with no woody canopy cover to forest with nearly complete woody canopy cover. Spatial variability in understory light is largely determined by several characteristics of overstory plants — spatial pattern, height, and cover — which vary concurrently along the grassland/forest continuum. Using a spatially-explicit ray-tracing model, we quantified trends in mean and variance of understory light along the continuum. We modeled understory light over a growing season for two types of plots: (1) generated plots in which cover, spatial pattern, and height of trees were varied systematically, and (2) three actual plots using stand data from piñon-juniper woodland sites for which cover, spatial pattern and height varied concurrently. Mean understory light decreased with increasing canopy cover and was sensitive to changes in height, as expected, but was not sensitive to spatial pattern. Variance in understory light was maximum at an intermediate value of cover that was dependent on both spatial pattern and cover — maximum variance occurred at lower values of cover as height increased and as spatial pattern progressed from regular to random to aggregated. These trends in the overall patterns of understory light were also examined with respect to changes in understory light in canopy and intercanopy locations. Variance in understory light for intercanopy locations was less than that for canopy locations at low canopy cover, but exceeded that for canopy locations as canopy cover increased. The value of canopy cover at which variance in intercanopy locations exceeded that in canopy locations was sensitive to variation in height but not in spatial pattern. The distributions of understory light for the actual plots were generally similar to those for corresponding generated plots, with dissimilarities attributable to differences in cover and height. The general trends highlighted by our simulations are broadly applicable to sites along the grassland/forest continuum. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Canopy microclimate; Photosynthetically active radiation; Ray tracing; Savanna; Shading; Solar radiation

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1. Introduction

The understory light environment is a key determinant of vegetation pattern and ecosystem processes, and varies spatially perhaps more than any resource used by plants (Bazzaz, 1996). Spatial patterns of understory light are determined by several overstory characteristics, particularly spatial pattern, height, and cover of woody plants. These overstory characteristics vary concurrently along vegetation gradients and may produce complex patterns of understory light across vegetation gradients because the spatial pattern and height of trees can change with increases in woody-plant cover (Padien and Lajtha, 1992). These gradients of vegetation structure can be viewed as a continuum that ranges from grassland with no woody canopy cover to forest with nearly complete woody canopy cover (Belsky and Canham, 1994; Breshears and Barnes, 1999). Many extensive semi-arid shrublands and woodlands span substantial portions of the grassland/forest continuum. For example, piñon-juniper woodlands, which are the most extensive ecosystem type in the western USA, can span a large proportion of this continuum (West, 1988; Padien and Lajtha, 1992; Milne et al., 1996). The understory light environment is important in these woodlands because of its effects on microclimate (e.g. solar radiation, soil temperature, leaf temperature, soil evaporation), which is strikingly different in canopy patches (i.e. directly below tree crowns) than in intercanopy patches (Breshears et al., 1997b, 1998). The center portions of canopy patches receive 40% less near-ground solar radiation than intercanopies through the year, and > 50% less during much of the growing season (Breshears et al., 1997b). Consequently, soil temperatures in intercanopy patches can exceed those in canopy patches by > 10°C in summer, which in turn results in increased soil evaporation rates in intercanopy patches (Breshears et al., 1998). Further, microclimate affects plant processes such as seedling establishment, germination, facilitation, and growth (Floyd, 1983;

Padien and Lajtha, 1992; Martens et al., 1997), as evident in the differences in distributions of understory plants in canopy and intercanopy patches (Arnold, 1964; Lohstroh and Van Auken, 1987; Armentrout and Pieper, 1988; Van Auken and Lohstroh 1990; Ludwig et al., 1997). Hence, the spatial distribution of understory light—and in particular the difference between canopy and intercanopy patches — can have a large influence on vegetation dynamics for sites along the grassland/forest continuum.

Several studies have quantified heterogeneity of understory light at an individual site along the grassland/forest continuum — in piñon-juniper woodlands (Lin et al., 1992; Breshears et al., 1997b) as well as other systems (see reviews in Scholes and Archer (1997) and McPherson (1997)). However, a systematic analysis is lacking of how understory light patterns vary along the grassland/forest continuum with changing stand characteristics (spatial pattern, height, and cover). Our first objective was to evaluate the relative importance of changes in canopy structural characteristics (cover, spatial pattern, and height) in the understory light environment for sites along the grassland/forest continuum. To address this objective we systematically varied these three structural characteristics independently to generate plots with differing overstories. Along the grassland/forest continuum, however, spatial pattern, height, and cover vary concurrently and may not be independent (Padien and Lajtha, 1992). Consequently, our second objective was to quantify the spatial pattern in the understory light environment in three actual woodland sites along an elevational gradient for which cover, spatial pattern, and height of overstory trees changed simultaneously. The sites were piñon-juniper woodlands in northern New Mexico, USA. We addressed these objectives using a ray-tracing model to estimate the understory light. Our results quantify how changes in canopy structural characteristics produce complex patterns of understory light. The trends we found are broadly applicable to other sites along the grassland/forest continuum.

2. Methods

2.1. Understory light modeling

We constructed a computer simulation model that depicts tree crowns as three-dimensional ellipsoids and calculates transmitted direct beam photosynthetically active radiation (PAR) after attenuation by the crowns. It is similar in concept to other models (Norman and Welles, 1983; Kuluvainen and Pukkala, 1989; Oker-Blom et al., 1989; Wang and Jarvis, 1990; Pukkala et al., 1991, 1993; Cescatti, 1997a,b; Brunner, 1998 de Castro and Fetcher, 1998; Lappi and Stenberg, 1998). Pukkala et al. (1993) found good agreement between model predictions and the overall pattern of understory light. Our model differs in that it uses a general-purpose ray-tracing approach (Glassner, 1989) to calculate the intersections of the solar beam with the ellipsoidal objects.

A reverse ray-tracing algorithm was used in which the path of a ray was calculated from the point of interest on the ground along the solar beam. Solar position can be described by solar zenith angle, θ , and solar azimuth angle, α . The solar position was estimated as a function of latitude, time of year, and time of day using the equations of Walraven (Walraven, 1978, 1979). The ray origin can be described by the vector, $\mathbf{R}_o = [X_o, Y_o, Z_o]$ and the ray direction by $\mathbf{R}_d = [X_d, Y_d, Z_d]$. The ray direction vector \mathbf{R}_d is normalized so that $X_d^2 + Y_d^2 + Z_d^2 = 1$. The direction vector is defined by solar position as:

$$X_d = \sin \theta \cos \alpha$$

$$Y_d = \sin \theta \sin \alpha$$

$$Z_d = \cos \theta$$

The ray can then be described by a parametric line equation:

$$\mathbf{R}(t) = \mathbf{R}_d t + \mathbf{R}_o \quad \text{where } t > 0$$

An ellipsoid, representing a tree crown, can be described by two vectors that define the center and the radii of the ellipsoid. The center vector is

$$\mathbf{E}_c = [X_c, Y_c, Z_c]$$

which defines the center point of the ellipsoid. The radius vector is

$$\mathbf{E}_r = [X_r, Y_r, Z_r]$$

which defines the radii along the x , y , and z axes, respectively. Each radius is expressed relative to the maximum radius, $m_r = \text{maximum of } (X_r, Y_r, Z_r)$, to define \mathbf{E}_{rm} by using:

$$X_{rm} = (X_r - X_c)/m_r$$

$$Y_{rm} = (Y_r - Y_c)/m_r$$

$$Z_{rm} = (Z_r - Z_c)/m_r$$

The surface of an ellipsoid can be expressed as the quadric equation:

$$Ax^2 + By^2 + Cz^2 + Gx + Hy + Iz + J = 0$$

where, for an ellipsoid defined by \mathbf{E}_c and \mathbf{E}_{rm} :

$$A = m_r/X_r^2$$

$$B = m_r/Y_r^2$$

$$C = m_r/Z_r^2$$

$$G = -2AX_c$$

$$H = -2BY_c$$

$$I = -2CZ_c$$

$$J = AX_c^2 + BY_c^2 + CZ_c^2 - m_r$$

Substituting the parametric equation of the ray into the quadric equation for the ellipsoid yields:

$$A_c t^2 + B_c t + C_c = 0$$

where:

$$A_c = AX_d^2 + BY_d^2 + CZ_d^2$$

$$B_c = 2AX_o X_d + 2BY_o Y_d + 2CZ_o Z_d + GX_d + HY_d + IZ_d$$

$$C_c = AX_o^2 + BY_o^2 + CZ_o^2 + GX_o + HY_o + IZ_o + J$$

To determine if the ray and ellipsoid intersect, the discriminant, D , is calculated (Haines, 1989; Lindley, 1992):

$$D = \sqrt{(B_c^2 - 4A_c C_c)}$$

If $D^2 < 0$, then no intersection of ray and ellipsoid occurs. If $D^2 \geq 0$, then the roots are calculated:

$$t_1 = (-B_c - D)/(2A_c)$$

$$t_2 = (-B_c + D)/(2A_c)$$

The values of t are used to calculate the intersection points of the ray and ellipsoid. An intersection point P_i is:

$$P_i = [X_i, Y_i, Z_i] = [X_o + X_d t, Y_o + Y_d t, Z_o + Z_d t]$$

The path length of the ray through the ellipsoid is calculated as the Euclidean distance between the intersections points calculated with t_1 and t_2 .

The instantaneous PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at the top of the canopy was calculated using (Britton and Dodd, 1976; Weiss and Norman, 1985; Pukkala et al., 1993):

$$I_o = 2700 e^{-(0.185/\cos \theta)} \cos \theta$$

The amount of PAR transmitted through the ellipsoid decreases exponentially as a function of path length, L , and foliage density, F , using Beer's Law:

$$I_b = I_o e^{-LF}$$

In addition, we assumed a spherical distribution of foliage elements and hence attenuation within the crown does not depend on solar zenith angle. We ignored reflectance and transmittance, and assumed foliage to be optically black for PAR.

Our model, then, accounts for the attenuation of direct beam radiation through stands of tree crowns, thereby producing spatially-explicit predictions of understory light. Note that diffuse radiation is not considered in our model. In semiarid environments, incident solar radiation is dominated by the direct beam component. For example, for Albuquerque, NM, USA, direct beam radiation accounts for >70% of total solar radiation for any month during the growing season (April through October). Including diffuse radiation from the sky, scattering of radiation from surrounding foliage or soil, or assuming overcast or cloudy sky conditions, would all yield a decrease in the variances reported here. Indeed, at the extreme of a heavily overcast sky, transmitted radiation would have a

very low mean and variance. Thus, our model simulations represent the high extreme of variance to be expected; real conditions are likely to result in lower variances.

We parameterized the model assuming a foliage density of $1.1 \text{ m}^2 \text{ m}^{-3}$ for all trees. This value was estimated for *Pinus edulis* using crown measurements from our high elevation study plot (TA-51, see Section 2.3 below) and reported relationships (crown data from conversion of diameter-at-base to foliar biomass from Garcia (1977) and foliar biomass to foliar area from Barnes (1986)). Our calculations were not highly sensitive to changes in foliage density (a 100% increase in foliage density produced a decrease in mean PAR for a plot of <6.4%, and a 50% decrease in foliage density produced an increase in mean PAR for a plot of <17%).

Our model simulations integrated transmitted PAR from 1 April through 31 October, a period corresponding to the growing season for our actual plots (described below in Section 2.3). We calculated seasonally integrated totals for transmitted PAR from estimates of daily totals for every 10 days; the daily totals were estimated using a 2 h time step within days. Decreasing the time step within days from 2 to 0.1 h changed the integrated daily irradiance by less than 0.3%, and decreasing the seasonal time step from 10 days to 1 day changed seasonally integrated irradiance by 2.4%.

Each simulation encompassed a $50 \times 50 \text{ m}$ plot which contained a set of tree crowns. We calculated understory light at 1600 points spaced 1 m apart in the x and y directions over a $40 \times 40 \text{ m}$ grid. The grid was centered in the plot, providing a 5 m buffer on each side. This width was sufficient to minimize the edge effects. At lower solar elevation angles the model may overestimate the ability of rays to penetrate the grid through the buffer, dependent on the spatial distribution of the trees actually outside the buffer. However, these rays would be of very low energy. For example, incident radiation at sun elevations less than 45° accounts for at most 9% of the total incident radiation from all sun elevations (see the equation for I_o above).

2.2. Systematic variation of canopy structural characteristics

We systematically varied the canopy structural characteristics to evaluate the understory light environment along the grassland/forest continuum. We evaluated the independent influences of cover, height, and the spatial pattern of trees for generated sets of crowns with specified characteristics. To evaluate the effects of the canopy cover we calculated the understory light for plots with randomly distributed trees ranging from 0 to 81% canopy cover. The random Poisson distribution of tree positions was generated by selecting x and y coordinates from independent uniform random distributions. We created 50×50 m plots with various sets of trees at several intervals of canopy cover along the grassland/forest continuum. The sets of trees were obtained by sampling the tree crown ellipsoids from data for an actual piñon-juniper stand (the high-elevation plot, TA-51, see Section 2.3 below) until the desired percent canopy cover was achieved.

To evaluate the effects of the spatial pattern, we generated additional 50×50 m plots as above but varied the spatial pattern to produce a set of plots with regularly spaced trees and a set with aggregated trees. The plots with regularly spaced trees were generated by placing the trees on a grid (aligned in the cardinal directions), the spacing of which varied with the density of the trees. The plots with aggregated trees were generated using a Poisson cluster process (Diggle, 1983). All aggregated plots had a Hopkins index (Hopkins, 1954) greater than 2.0 ($P < 0.05$). To evaluate the effects of height, we used the set of plots with randomly distributed trees and changed the height of each tree to 200% of its original height in one case, and to 50% in another.

We summarized the results with respect to mean and variance for the grid overall, for points directly under tree crowns (canopy locations), and for points between tree crowns (intercanopy locations). We also used contour plots based on the map of 1600 points and histograms for all points, for canopy locations, and for intercanopy locations.

2.3. Understory light environment for measured woodland stands

Our study plots were located within three piñon-juniper woodland (*P. edulis* and *Juniperus monosperma*) stands located at Los Alamos National Laboratory, NM, USA. The sites were part of a grassland/forest continuum along an elevational gradient of increasing precipitation and decreasing mean annual temperature (Bowen, 1990). The plots coincided with three of those used by Padien and Lajtha (1992) (TA-33, White Rock, and TA-51) and were along an elevational gradient studied by Barnes (1986). The highest elevation plot (TA-51; latitude 34.30° N, longitude 106.27° W) receives about 400 mm annual precipitation. This site is the location of long-term studies focusing on hydrological (Wilcox, 1994; Wilcox and Breshears, 1995; Davenport et al., 1996, 1998; Reid et al., 1999) and ecological (Lajtha and Barnes, 1991; Lin et al., 1992; Lajtha and Getz, 1993; Breshears et al., 1997a,b; Martens et al., 1997; Breshears et al., 1998) processes.

We mapped and measured the tree crowns at each of the three 50×50 m plots previously marked by Padien and Lajtha (1992). Measurements of height, maximum crown radius, and radius perpendicular to the maximum crown radius were obtained for all trees > 1 m high in each plot. We estimated canopy volume (V) as an ellipsoid: $V = (4/3) \times \pi \times \text{radius}^2 \times (\text{height}/2)$, where radius is the mean of the two measured radii per tree. All plots had slopes $< 7\%$. The stand characteristics for each plot were summarized with respect to canopy cover (non-overlapping; the proportion of area covered by tree canopy), overlapping cover (sum of the tree crown areas; may exceed 100% of the ground surface area), height, and density. The Hopkins index (Hopkins, 1954) was used to assess the spatial pattern of the trees (regular, random, or aggregated).

For each of our three study plots, we calculated the understory light using our measurements of canopy structural characteristics and summarized the results as for the generated plots.

3. Results

3.1. Systematic variation of canopy structural characteristics

Simulations based on the generated plots enabled us to evaluate the independent effects of cover, spatial pattern, and height on the understory light along the grassland/forest continuum. The percent canopy cover for the grassland/forest continuum ranged from 0 to 81%, over which mean understory light for a plot decreased with increasing canopy cover in a nearly linear fashion (Fig. 1A). Furthermore, different spatial patterns (regular, random, aggregated) produced nearly equivalent mean understory light for a plot at all values of cover. Variance in the mean understory light was a curvilinear function of cover such that the variance was highest at intermediate values of canopy cover (Fig. 1B), and in contrast to the mean, was dependent on the spatial pattern. The variance for aggregated patterns was greater than that for random ones, which in turn was greater than that for regular ones.

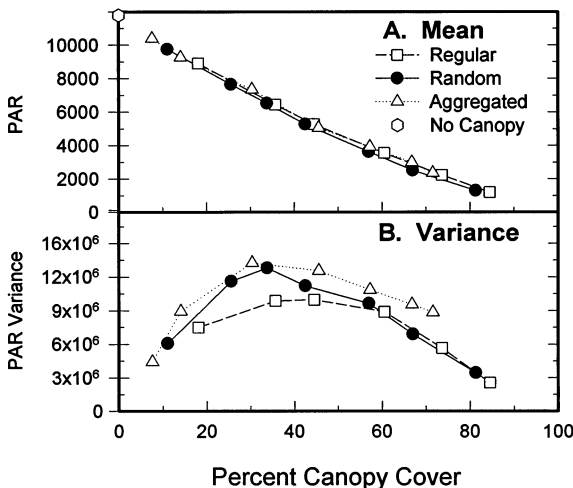


Fig. 1. The effect of spatial pattern on transmitted photosynthetically active radiation (PAR; 1 April–31 October; mol m⁻²) for generated plots of increasing percent canopy cover along a grassland/forest continuum. Estimates are for patterns of regular, random, and aggregated trees; also single estimate for no canopy: (A) means, and (B) variances.

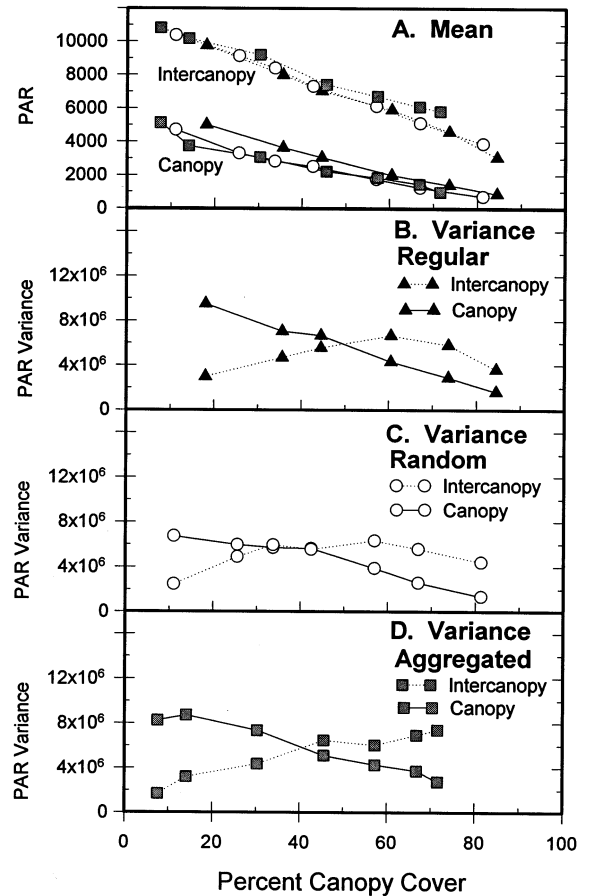


Fig. 2. Differences between intercanopy and canopy locations resulting from effects of spatial pattern on transmitted photosynthetically active radiation (PAR; 1 April–31 October; mol m⁻²) for generated plots of increasing percent canopy cover along a grassland/forest continuum. Estimates are for means (A) and variances of three spatial patterns of trees: (B) regular, (C) random, and (D) aggregated.

The understory light for a plot overall was decomposed into components for the canopy and the intercanopy locations. For all three spatial patterns, the mean understory light for the canopy and for the intercanopy locations decreased with increasing canopy cover (Fig. 2A). For the intercanopy locations, the mean understory light for the plot overall was greatest for aggregated spatial patterns, whereas for canopy locations the understory light was greatest for regular spatial patterns. Regardless of the spatial

pattern, the variance in canopy locations decreased with increasing canopy cover (Fig. 2B–D). At low cover the variance was greater in the canopy locations than the intercanopy locations, whereas at high cover the converse was true (producing an ‘x’-like pattern in Fig. 2B–D). The variance within the two components was slightly modified by the spatial pattern.

The changes in crown height that we generated affected the mean and variance of the understory light for a plot overall. The mean understory light for a plot decreased with increasing cover for all three heights (Fig. 3A). As the tree height increased, the mean understory light for a plot decreased for all values of cover. The relationship between the mean understory light for a plot and the cover was nearly linear at the lowest height and became increasingly non-linear with increasing height. The variance in understory light for a plot was a curvilinear function of cover for all three heights such that the variance was highest at intermediate cover values (Fig. 3B). At low cover the variance in understory light for a plot increased with increasing tree height, whereas at

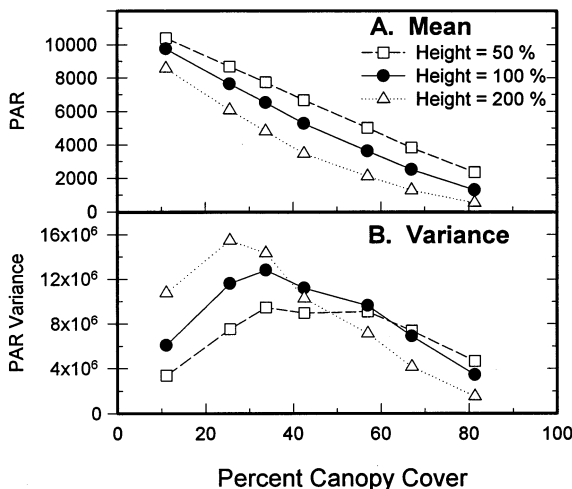


Fig. 3. The effect of height on transmitted photosynthetically active radiation (PAR; 1 April–31 October; mol m^{-2}) for generated plots of increasing percent canopy cover along a grassland/forest continuum. Estimates are for heights of 50, 100 and 200% of measured tree heights: (A) means, and (B) variances.

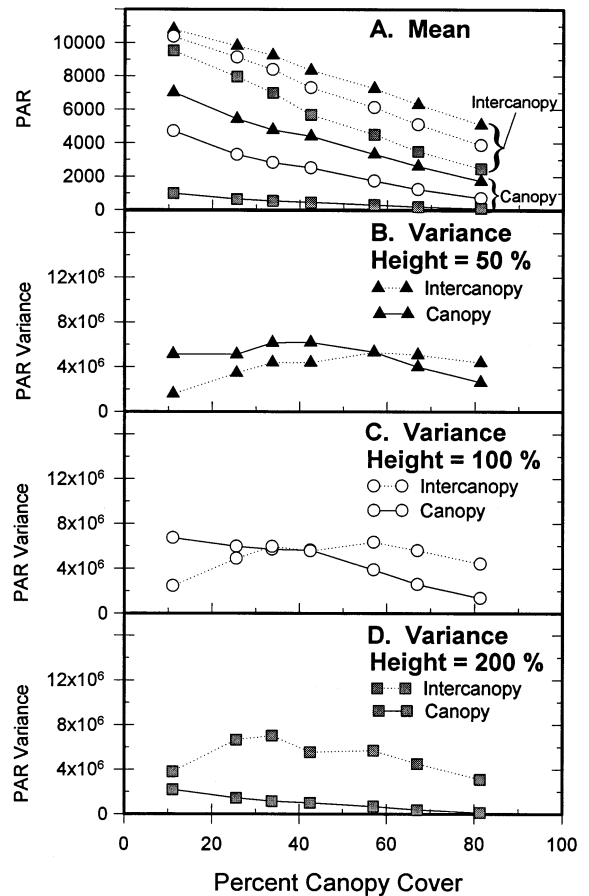


Fig. 4. Differences between intercanopy and canopy locations resulting from effects of height on transmitted photosynthetically active radiation (PAR; 1 April–31 October; mol m^{-2}) for generated plots of increasing percent canopy cover along a grassland/forest continuum. Estimates are for means (A) and variances of three percentages of measured tree heights: (B) 50, (C) 100, and (D) 200%.

high cover the variance was less sensitive to tree height (Fig. 3B).

Height differentially affected the distributions of understory light within the canopy and the intercanopy locations. For both location types the mean understory light was greatest when the trees were short (Fig. 4A). The mean understory light for the intercanopy locations was more sensitive to height at high cover, whereas that for the canopy locations was more sensitive to height at

low cover (Fig. 4A). At high cover the variance in understory light in the intercanopy was greater than the variance within the canopy for all heights (Fig. 4B–D). At the greatest tree height (200%) the variance for the intercanopy locations exceeded that for the canopy locations at all cover values (Fig. 4D).

The understory light was highly spatially variable within the plots, as illustrated by contour maps of understory light for generated plots with a percent cover of 26% (Fig. 5A), 34% (Fig. 5B), and 42% (Fig. 5C). The frequency distribution of understory light differed between the canopy and the intercanopy locations at each of the plots and changed substantially over this range of change in percent cover (Fig. 5D–F).

In the generated plots the regions of low understory light ($< 5000 \text{ mol m}^{-2}$), which reflect the locations of the tree crowns, increased in area as cover increased from 26 (Fig. 5A) to 42% (Fig. 5C). At the generated plot with 26% cover (Fig. 5A and D) a large proportion of the area received maximum understory light ($> 11\,000 \text{ mol m}^{-2}$), indicating that the effects of tree shading on the intercanopy areas were minor for much of this plot. At the generated plot with 42% cover (Fig. 5C and F) most of the intercanopy area was affected by tree shading (i.e. $\text{PAR} < 11\,000 \text{ mol m}^{-2}$), effectively reducing the contrast between the canopy and the intercanopy patches.

3.2. Understory light environment for measured woodland stands

Along the elevational gradient of the actual piñon-juniper woodland plots the tree density increased, nearly doubling between the low and high elevation plots (Table 1); similarly tree canopy volume increased by more than 4-fold. Canopy cover (non-overlapping) and overlapping cover also increased with elevation and more than doubled between the low and high elevation plots. Tree height increased with elevation, by almost 150%. The spatial pattern of the trees became increasingly aggregated with elevation as measured by the Hopkins index; the pattern at the low elevation plot was random whereas it was significantly aggregated at the mid and high elevation plots.

Understory PAR decreased with increasing cover for the plots for the canopy locations, the intercanopy locations, and overall (Fig. 6A). At the low-elevation plot (21% canopy cover), variance of understory PAR for the intercanopy locations was greater than for the canopy locations, whereas at the high elevation plot (43% canopy cover) the variance between the two location types was equal (Fig. 6B). The results from these actual plots are similar to the generated plots (Figs. 1 and 2).

At all three actual plots the understory light was highly spatially heterogeneous (Fig. 7 A–C).

Table 1
Plot characteristics along an elevational gradient of increasing canopy cover^a

	Low elevation (TA 33)	Mid elevation (White Rock)	High elevation (TA 51)
Elevation (m)	1960	1985	2140
Canopy cover, non-overlapping (%)	21	34	43
Overlapping cover (%)	23	40	56
Mean tree height (m)	2.6	3.1	3.8
Number of trees	87	157	171
Total tree volume (m ³) ^b	1170	2660	4970
Hopkins index	1.2	1.4*	2.3**
Spatial pattern	Random	Aggregated	Aggregated

^a Piñon-juniper woodland plots (50 × 50 m) for which actual tree data (locations and crown dimensions) were obtained. Hopkins index is a test for Poisson spatial randomness, distinguishing between random, aggregated, and regular spatial patterns.

^b Total volume of canopy ellipsoids on a plot.

* $P < 0.01$.

** $P < 0.001$.

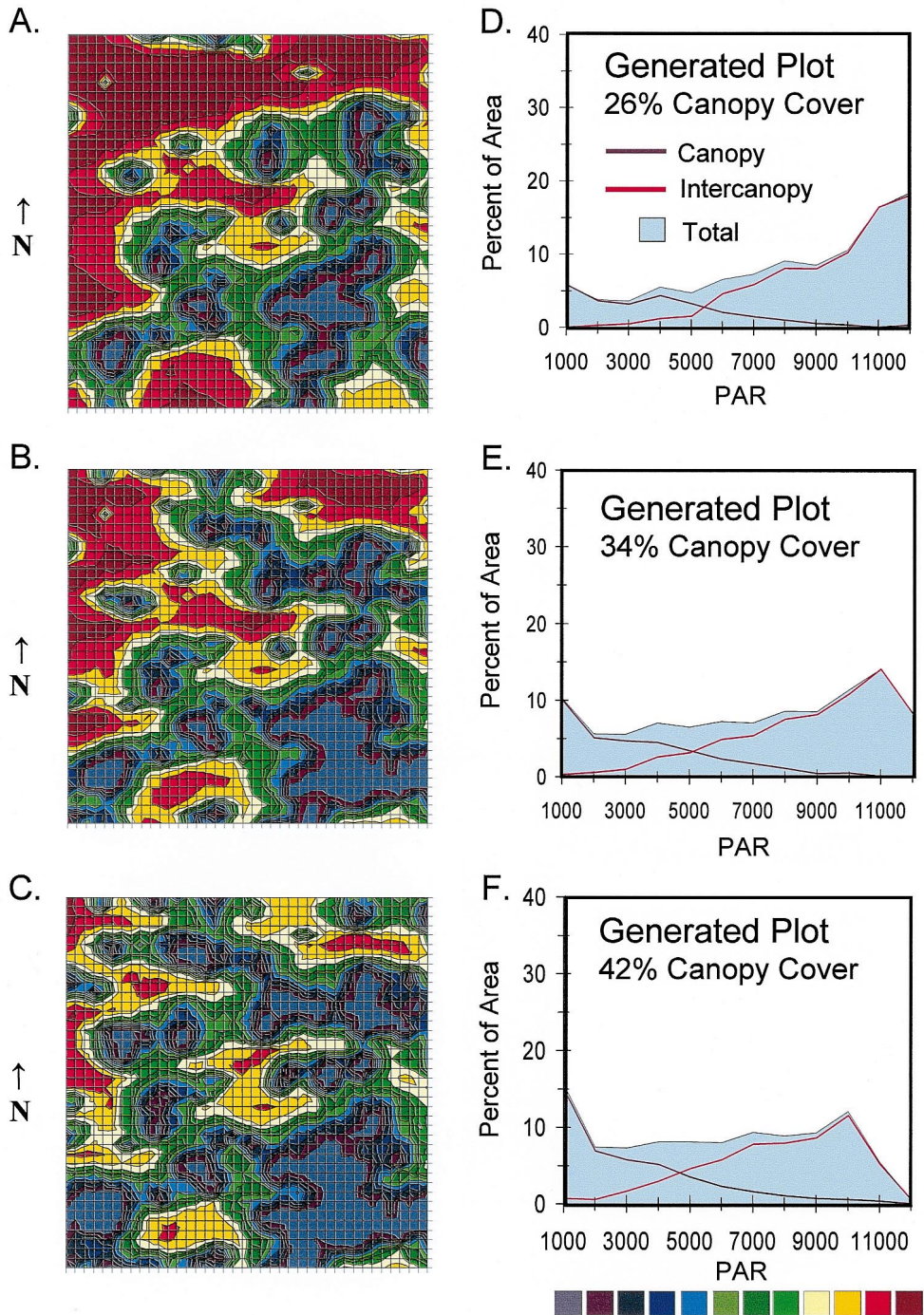


Fig. 5. Contour plots of spatial variation in transmitted photosynthetically active radiation (PAR; mol m^{-2}) integrated over 1 April–31 October for generated plots (40×40 m; grid cell = 1 m^2) with: (A) 11% canopy cover, (B) 42% canopy cover, and (C) 81% canopy cover. Arrows denote true north. Histograms of understory light for canopy locations, intercanopy locations, and total (overall for plot): (D) low elevation, (E) mid elevation, and (F) high elevation. Bin labels indicate bin upper limits. Bin labels in (F) also indicate color contour values for panels (A–C).

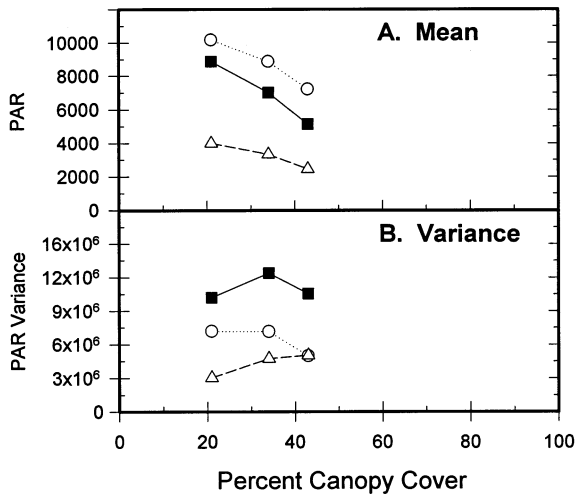


Fig. 6. The effect of spatial pattern on transmitted photosynthetically active radiation (PAR; 1 April–31 October; mol m^{-2}) for actual study plots along a grassland/forest continuum: (A) means, and (B) variances.

In addition, the frequency distribution of the understory light differed between the canopy and the intercanopy locations at each of the plots (Fig. 7D–F). These frequency distributions are similar to those for the generated plots with approximately the same percent canopy cover (Fig. 5D–F) — the difference in frequency of PAR $> 10\,000$ mol m^{-2} between the generated plot at 26% cover (Fig. 5D) and the actual plot at 21% cover (Fig. 7D) can be attributed to the differences in canopy cover and tree heights.

4. Discussion

4.1. Understory light along the grassland/forest continuum

Our results represent a landscape analysis of how concurrent changes in cover, spatial pattern, and height of trees affect understory light. We found that the mean understory light at a plot was most influenced by cover and was modified by height; spatial pattern had a negligible effect on the mean. Consequently, in situations where the mean for a plot is the issue of concern, cover and height may be sufficient parameters for pre-

dicting mean understory light for a plot; spatial pattern, which requires the most effort to obtain, has little effect on mean understory light for a plot.

For many ecological processes variance is as important as the mean in determining trends and responses. The response of the plot variance to the three canopy characteristics (cover, spatial pattern, and height) was more complex than that of the plot mean. The variance in understory light at a plot was largely influenced by cover such that it was greatest at values of intermediate cover (Fig. 1B). Height and cover interacted to determine variance such that at low cover, increasing height increased variance whereas at high cover increasing height decreased variance (Fig. 3B). Further, variance was sensitive to spatial pattern (Fig. 1B). Hence, cover, spatial pattern, and height all have an important effect on the variance in the understory light at a plot.

Our decomposition of these trends into canopy and intercanopy components (Figs. 2 and 4) explains how the two patch types determine the patterns for the overall plot mosaic (Figs. 1 and 3). For example, as the cover increased the influence of canopy patches on intercanopy patches increased such that the boundaries between the two became less distinct (Fig. 5A–C and Fig. 7A–C), resulting in a reduction of variance over this range of canopy cover (Fig. 1B).

The relationships that we quantified between canopy characteristics and understory light for the grassland/forest continuum extend the results of other studies that examined small portions of the continuum. Kuuluvainen and Pukkala (1987) found that for a single value of canopy cover the understory light for a plot was not sensitive to the spatial pattern of trees (random versus regular). Our study documents that this conclusion applies to a wide range of canopy cover (0–81%; Fig. 1A). In addition, Pukkala et al. (1991) found that within-plot variance in the understory light was not sensitive to changes in canopy cover (50 versus 80%). Our results are consistent with theirs, but also show that at lower values of canopy cover ($< 50\%$) variance is sensitive to spatial pattern (Fig. 1B). Furthermore, our results can be generalized to explain trends with respect to per-

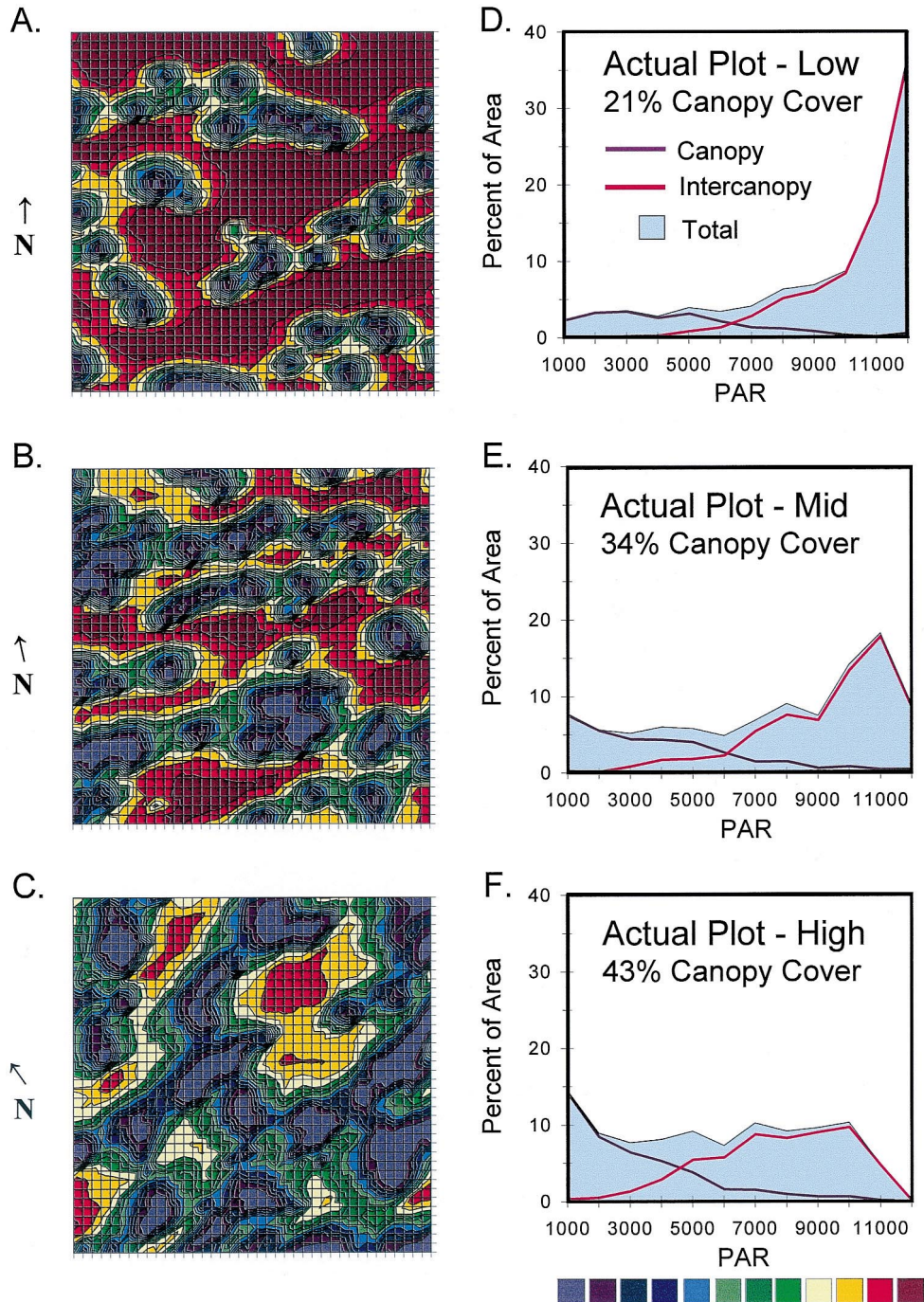


Fig. 7. Contour plots of spatial variation in transmitted photosynthetically active radiation (PAR; mol m^{-2}) integrated over 1 April–31 October at three actual plots (40×40 m; grid cell = 1 m^2): (A) low elevation (TA-33) with 21% canopy cover, (B) mid elevation (White Rock) with 34% canopy cover, and (C) high elevation (TA-51) with 43% canopy cover. Arrows denote true north. Histograms of understory light for canopy locations, intercanopy locations, and total (overall for plot): (D) low elevation, (E) mid elevation, and (F) high elevation. Bin labels indicate bin upper limits. Bin labels in (F) also indicate color contour values for panels (A–C).

cent canopy cover and tree height. Along elevational gradients, height and percent cover often increase concurrently, as observed at our three plots (Table 1). Under these conditions the general relationship between the mean understory light for a plot and percent canopy cover is sigmoid (Fig. 8A, solid line) rather than nearly linear as is the case when height is constant with increasing cover (Fig. 8A, dashed line). Furthermore, under these conditions of concurrent changes in height and percent cover the variance is reduced at low and high values of cover in comparison to plots for which mean tree height is constant (Fig. 8B).

Our results are relevant to shrubs as well as trees, to other latitudes, and to other seasonal periods of the year. First, our simulations were for trees, but in general our results are also applicable to gradients of increasing shrub cover, which are also extensive globally. We expect the same general types of responses for shrubs, which can be viewed as smaller ellipsoids, as documented for trees. Second, our results for approximately 35° latitude can be related to other latitudes based on the results of Pukkala et al. (1991). Their results showed that the mean and

variance for 30° latitude was greater than those at either 0 or 60° latitude. Maximum mean and variance should occur near 23.5° latitude, at the plane of the ecliptic where the solar zenith is maximum (Walraven 1978). We expect that this trend is also reflected in the heterogeneity in solar radiation between the canopy and intercanopy locations — that is, the contrast in understory light between the canopy and intercanopy locations is greatest near 23.5° latitude. Third, our estimates of understory light for the period April through October (roughly corresponding to the growing season) provide an indication of the trends along the grassland/forest continuum throughout the year. Although the mean and variance of the understory light should be lower during the winter period (November–March) than during the growing season, we expect that the effects of cover, spatial pattern, and height of trees on the understory light across plots are similar throughout the year.

4.2. Implications of understory light patterns for vegetation dynamics and ecosystem processes

Much of the terrestrial biosphere falls within the grassland/forest continuum. Previous studies have primarily contrasted the extremes of this continuum with respect to ecosystem processes (Coffin and Urban, 1993; Lauenroth et al., 1993). A few studies have evaluated ecosystem processes across these broad gradients with respect to shrubs (Aguilar et al., 1996; Schulze et al., 1996) although none have evaluated understory light, which is perhaps the most variable of resources from a phytocentric perspective (Bazzaz, 1996). Along the grassland/forest continuum the relative role of belowground versus aboveground resources is hypothesized to change with light becoming increasingly important with increasing canopy cover (Smith and Huston, 1989; Coffin and Urban, 1993; Holmgren et al., 1997). Although understory light decreases monotonically along the grassland/forest continuum (Fig. 1A) spatial variance in understory light, and hence habitat heterogeneity, is greatest in the intermediate portion of the continuum (Fig. 1B). Relationships developed for either extreme of the

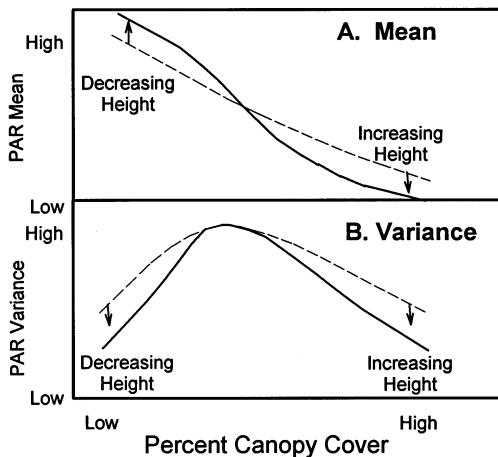


Fig. 8. Generalizations of the relationship between transmitted PAR and percent canopy cover. Predicted trend from generated plots with constant height (dashed line) and variation in trend for grassland/forest continuum in which height increases with increasing canopy cover (solid line): (A) mean, and (B) variance.

grassland/forest continuum may be poor predictors of system behavior for intermediate sites. Hence, it is important to quantify the relationships for ecosystem processes at intermediate sites (Belsky and Canham, 1994) as we have done here for understory light, and as Breshears and Barnes (1999) have discussed for soil water. Understanding ecosystem processes within these intermediate sites is important not only for site-specific assessments but is also crucial for regional-scale assessments.

In summary, we showed that understory light for sites within the grassland/forest continuum is dependent primarily on cover and can be substantially modified by height; spatial pattern of the tree canopy patches has a small influence on the site mean but does influence the variance. Our results quantify the relationships for understory light along the entire grassland/forest continuum and have important implications for a wide variety of ecosystem processes. We have demonstrated the utility of viewing ecosystems along the continuum as a mosaic of canopy and intercanopy patches for the prediction of understory light and its spatial distribution. More generally, these two patch types can be used to understand a wide variety of ecosystem processes within the grassland/forest continuum worldwide.

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