

Linking light attenuation, sunflecks, and canopy architecture in mesic shrub thickets

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Abstract Expansion of shrubs into grasslands is often accompanied by a reduction in understory light and an associated reduction of shade-intolerant species. However, effects of specific canopy architectural characteristics on the light environment under shrub thickets are unknown. Our objective was to determine what characteristics of canopy architecture most influence understory light in mono-specific shrub thickets. We quantified understory light and canopy architecture for five shrub species in the eastern United States that have a history of expansion, and we used multiple regression to determine which canopy characteristics best predicted light attenuation and relative contribution of sunflecks. Measurements included leaf angle, leaf azimuth, branch bifurcation ratio, leaf area index (LAI), canopy depth (the vertical distance from the bottommost leaf to the top of the canopy), and leaf area density (LAD) as well as understory photosynthetic photon flux density (PPFD). The best predictor of light attenuation and the occurrence of sunflecks for all species was canopy depth. Multiple leaf and plant-level traits were correlated with canopy depth but not with LAI or LAD. The invasive shrub *Elaeagnus umbellata* had the lowest understory light levels of the species examined although LAI values

for *Morella cerifera* and *Rhododendron maximum* were higher. Branch bifurcation ratios for *E. umbellata* were significantly higher than for other species and this likely contributed to the differences in light attenuation and suppression of sunflecks. The potential of shrubs to intercept light is primarily dependent on vertical distribution of leaves in the canopy which is itself correlated with fine-scale, species-specific variations in leaf display.

Keywords Woody encroachment · Leaf orientation · Branch bifurcation ratios · Plant architecture · Leaf area index · Beer–Lambert law

Introduction

Expansion of both native and non-native woody plants, especially shrubs, has been identified as an important component of global change in the past century (Archer 1989; Wessman et al. 2004; Briggs et al. 2005; Sturm et al. 2005; Knapp et al. 2008). Changes in ecosystem services that accompany woody plant expansion include altered ecosystem hydrology, increased rates of nutrient cycling and storage, and changes in herbaceous diversity and cover (Wessman et al. 2004; Briggs et al. 2005; Knapp et al. 2008; Brantley and Young 2008).

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Woody encroachment may also result in a substantial increase in ecosystem annual net primary production (ANPP), especially in mesic systems where apical meristems give shrubs an advantage over grasses. According to Knapp et al. (2008), the basal meristem of grasses limits canopy density, light interception, and plant growth, even when the soil moisture is abundant. The reduced meristem limitation after shrub encroachment results in a substantial increase in LAI (Lett and Knapp 2003; Brantley and Young 2007; Knapp et al. 2008). For example, in tallgrass prairie in Kansas, USA, expansion of *Cornus drummondii* has resulted in dense patches of shrubs with LAI of ~ 11 (Lett and Knapp 2003) and on the Virginia, USA coast, LAI of *Morella cerifera* exceeded 12 in recently established thickets (Brantley and Young 2007). By comparison, LAI in temperate deciduous forest typically reaches a maximum of ~ 6 (Bolstad et al. 2000; Norby et al. 2003). On the Virginia coast, the high LAI has resulted in $<1\%$ of available light reaching the understory in newly established shrub thickets and the very low understory light has been associated with a substantial decline in herbaceous cover and diversity in the understory (Brantley and Young 2007, 2009).

In forests, variation in leaf orientation, branching patterns, and related structural characteristics below the stand level are major factors influencing interception of radiation by a stand with a given LAI (Teh et al. 2000). Similar studies comparing canopy architecture among shrub species and linking canopy architecture to understory light beneath shrubs have not been published. Knapp et al. (2008) proposed that mesic shrub thickets could maintain high LAI through a “dense and even” display of leaves. Growth characteristics of terminal shoots and biomass allocation (i.e., leaf vs. support structure) are important in optimizing light capture because these traits affect distribution of leaves in canopy space, thereby increasing light interception while preventing self-shading (Nicola and Pickett 1983; Takenaka et al. 2001; Kitajima et al. 2005). Branching strategies at the plant level that optimize light capture through an even leaf dispersion (versus a clumped leaf distribution) can be effectively summarized and compared using bifurcation ratios (Whitney 1976; Kempf and Pickett 1981). In plants, the branch bifurcation ratio is a measure of the number of smaller branches that derive from the next larger size

branch (Whitney 1976; Kempf and Pickett 1981; Valladares and Pugnaire 1999). A low bifurcation ratio results from a relatively uniform division of a larger branch into two or three smaller branches. For example, a dichotomous branching pattern would have a bifurcation ratio of two. In contrast, higher bifurcation ratios usually result from many smaller branches growing along the axis of the same larger branch (Whitney 1976). Generally, lower bifurcation ratios are associated with a non-random monolayer canopy as is commonly found in low light environments, whereas higher bifurcation ratios result in a multilayered canopy and are common in woody plants exposed to high light environments (Whitney 1976; Steingraeber et al. 1979). At the leaf level, foliage orientation (i.e., leaf angle and leaf azimuth) is also important. Increased leaf angles prevent self-shading in dense canopies and increase daily whole-canopy radiation capture through optimal interception of light earlier and later in the day (Sands 1995; Drouet and Mouliat 1997; Wirth et al. 2001; Niinemets and Fleck 2002; Falster and Westoby 2003).

At the stand level, the Beer–Lambert law has been used to explain differences in light attenuation based on LAI and an extinction coefficient, termed k (Monsi and Saeki 1953; Campbell and Norman 1989; Gower et al. 1999). While this model of light attenuation is useful to make rapid estimates of LAI, it has several limitations. The model is most accurate under sky conditions that exhibit uniformity in diffuse light and little or no direct sunlight, which can be problematic under all but the heaviest cloud cover (Rosenberg 1974). Perhaps the most significant limitation of the Beer–Lambert equation is that it does not account for the influence of brief periods of direct light, or sunflecks, on understory microclimate characteristics that affect plant distribution and growth. Sunflecks are defined here as periods of direct light lasting less than 10 min (Smith et al. 1989), although the great majority of sunflecks under a closed canopy are far shorter (Brantley and Young 2009). Despite the brief duration, the ecological importance of sunflecks to understory communities is well-established (Chazdon 1988; Neufeld and Young 2003). Sunflecks create a heterogeneous environment in forest understories that is important in maintaining understory diversity, but heterogeneity varies with canopy architecture (Ustin et al. 1984; Montgomery and Chazdon 2001; Montgomery 2004; Lei et al. 2006; Brantley and Young

2009). Brantley and Young (2009) concluded that sunfleck frequency, length, and intensity were all reduced in mesic shrub thickets compared to temperate forests, although diffuse light was often similar. They hypothesized that the differences in heterogeneity of understory light among communities was related to stand-level differences in canopy architecture, such as stem density and leaf area density (LAD), that affect size and distribution of canopy gaps. Differences in canopy height alone could also explain the relative lack of sunflecks in shrub thickets compared to forests. Smith et al. (1989) demonstrated that size and maximum intensity of sunflecks were related to both gap size and distance from the gap to the incident surface. Differences in canopy height between shrubs and trees, or even among shrubs, may help explain variations in the size, length, and intensity of sunflecks at the surface, even if LAI and other canopy architectural characteristics are similar.

Our objective was to compare understory light and canopy architecture across a variety of shrub species with a history of expansion. Our primary goal was to determine what characteristics of canopy architecture drive attenuation of diffuse understory light and the contribution of sunflecks. We hypothesized that LAD would be the best predictor of understory light because it reduces the size of gaps, thus inhibiting penetration of diffuse light and sunflecks. A second goal was to compare canopy architectural characteristics across three levels of organization within the canopy (leaf, plant, and stand level) and determine which characteristics were related to high LAI values previously observed in mesic shrub thickets. We hypothesized that higher bifurcation ratios would result in increased light attenuation by optimizing the

dispersion of leaves in the canopy. Furthermore, species with dense canopies should display vertically oriented leaves to avoid self-shading and optimize whole-plant carbon gain. Therefore, our final hypothesis was that leaf angles would be positively correlated with LAI and LAD. Our results should provide valuable insight into how shrubs are able to optimize light capture for carbon gain and exclude shade-intolerant grassland species through competition.

Materials and methods

Study sites

Field work was conducted in five communities dominated by shrub species forming dense monospecific thickets. General site descriptions are provided in Table 1. Each species has a history of expansion or invasion and all have the potential to substantially alter the ecosystem's structure and function (Petranka and McPherson 1979; Beier et al. 2005; Baer et al. 2006; Owens et al. 2007; Young et al. 2007). Two communities were located on Hog Island, a barrier island located ~10 km east of the Delmarva Peninsula, Virginia, USA. The island is a part of the Virginia Coast Reserve, an NSF-funded long-term ecological research site owned by the Nature Conservancy. Thickets of *Morella cerifera* (L.) Small (Myricaceae), a native, evergreen, nitrogen-fixing shrub, are located in mesic interdunal swales in the upland portion of the island (Young et al. 1995). Stands of *Iva frutescens* L. (Asteraceae), a native, salt-tolerant shrub, occur at the upland edge of salt marsh (Young et al. 1994). Stands of *Rhus copallina* L. (Anacardiaceae), a native shrub or small tree are

Table 1 Site, habitat, and climate summary for five mesic shrub communities in Virginia, USA

Species	Location	Elevation (m above mean sea level)	Habitat type	Mean annual temperature ^a (°C)	Mean annual precipitation ^a (mm)
<i>Morella cerifera</i>	37.449° N, 75.667° W	1–3	Interdunal swale	14.2	1065
<i>Iva frutescens</i>	37.452° N, 75.673° W	<2	High salt marsh	14.2	1065
<i>Rhus copallina</i>	37.134° N, 75.960° W	4	Old field	14.7	1035
<i>Elaeagnus umbellata</i>	38.093° N, 77.335° W	64	Old field	13.6	1167
<i>Rhododendron maximum</i>	36.652° N, 81.511° W	1530	Grassy Bald	11.9	1212

All species except *E. umbellata*, an invasive, are native to Virginia

^a Source: National Climatic Data Center (2004)

located in an old field at the Eastern Shore National Wildlife Refuge, VA and developed after a prescribed burn (personal observation). Thickets of *Elaeagnus umbellata* Thunb. (Elaeagnaceae), an invasive, nitrogen-fixing shrub that forms dense thickets in open fields, along roadsides, and forest edges (Baer et al. 2006) are located at Fort A.P. Hill, VA. *Rhododendron maximum* L. (Ericaceae), a native, evergreen shrub, forms dense thickets in mountain forest understories and around the edge of high-elevation grassy balds (Schafale and Weakley 1990). Sites are located adjacent to grassy balds along Wilburn Ridge in the Mount Rogers National Recreation Area, Jefferson National Forest, VA. Sampling of each species, except *M. cerifera*, was done over 3–4 consecutive days. Measurements for *M. cerifera* were taken during 3 days over a 2-week period. All sampling was done during the summer of 2008.

Stand-level measurements

Canopy depth (D), stem density (d_s), stem basal area, leaf area index (LAI), leaf area density (LAD) and light (PPFD) were quantified for six plots in each community. Canopy height and solar angle interact to determine the size of the canopy area that affects understory light, and it would be inappropriate to establish large plots for smaller shrubs. For example, the canopy of *I. frutescens*, 2 horizontal meters away from a light sensor would only affect light readings for that sensor at extremely low solar angles but not at midday. Therefore, plot size was based on approximate canopy height for each species. Plot sizes were 1×1 m for *I. frutescens*, 2×2 m for *Rhus copallina*, and 5×5 m for *M. cerifera*, *E. umbellata*, and *R. maximum*. Canopy height was also used to establish the minimum distance between the plot edge and the thicket edge, i.e., a plot in *R. copallina* was at least 2 m from the thicket edge and a plot in *M. cerifera* was at least 5 m from the thickets edge. Canopy height and height to the canopy bottom were measured using a telescoping pole marked in 0.1 m increments. Mean canopy depth (D) for each plot was measured as the mean difference between canopy height and height to the bottommost leaf along five vertical transects in each plot. Stem density and basal area were measured at 0.7 m height for all species. LAI was estimated using allometric models developed for each species relating

stem diameter and leaf mass and converted to leaf area using specific leaf area (SLA) (see Brantley and Young 2007). LAD was calculated as $\text{LAI} \times D^{-1}$ and is expressed as $\text{m}^2 \text{ leaf area} \times \text{m}^{-3} \text{ canopy space}$ (Campbell and Norman 1989).

Leaf and plant-level measurements

For each species, leaf angle (θ) and leaf azimuth (A) were measured for >200 canopy sun leaves located on at least 20 different branches distributed evenly among the six plots. Leaf angle was measured with respect to the horizontal (0°) to the nearest 5° from 0° to 90° using a clinometer. Leaf azimuth was measured as the direction that the leaf surface was facing to the nearest 5° using a lensatic compass. Specific leaf area was measured for 20 leaves for each species (Brantley and Young 2007). Plant bifurcation ratios were measured for 20 stems exhibiting terminal shoots exposed to full sunlight. Branch bifurcation ratios were then calculated using the equation:

$$R_b = \frac{N - 1}{N - N_1}$$

where N is the total number of branches of all branch orders on the stem and N_1 is the total number of first order branches (Steingraeber et al. 1979). Branch ordering follows the same logic used in stream ordering (Horton 1945), i.e., the first and smallest branches on the outer edge of the plant are first order and the order increases as one moves toward the larger branches eventually ending at the main stem or stems. Only live branches were included in the measurements.

Light measurements

Understory photosynthetic photon flux density (PPFD) was sampled in each plot using three Li-Cor 190S quantum sensors attached to an LI-1400 data logger (Li-Cor Biosciences, Lincoln, Nebraska, USA). Sensors were placed at ground level and spaced 0.25–1.0 m apart. For each sensor, PPFD was measured and logged every 1 s for ~ 1 h during midday (within 2 h of solar noon) resulting in ~ 3600 measurements per sensor and ~ 10800 measurements per plot. Sampling occurred on cloudless days when possible, so that sunfleck characteristics could be

included in the analyses (see Brantley and Young 2009). Above-canopy PPFD was measured immediately before and after each sampling period and a mean above-canopy PPFD value was interpolated from those readings. For each sampling period, total understory PPFD (Q_b) was calculated as the percentage of above-canopy light. Intensity of diffuse light and sunflecks for a given community, or even for different plots within a community, vary considerably and the criterion for what is a sunfleck cannot be defined arbitrarily using an absolute value of PPFD (Chazdon 1988; Smith et al. 1989; Brantley and Young 2009). Therefore, a threshold that represented the maximum observed value for diffuse PPFD was assigned and for a given PPFD value, the portion of that PPFD value that exceeded the diffuse PPFD threshold was classified as deriving from a sunfleck. Thresholds between diffuse PPFD and sunflecks were estimated individually for each plot by visually analyzing a time-series of each sample and assigning a threshold value for maximum diffuse light at the nearest $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ increment. Thresholds ranged from $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ in five of the *M. cerifera* plots to $375 \mu\text{mol m}^{-2} \text{s}^{-1}$ in two plots of *R. copallina*. No recorded sunfleck lasted longer than the sampling period. Sunfleck frequency was calculated as the percentage of all readings that exceeded the threshold for sunflecks for each sensor and averaged across sensors for each plot. Cumulative PPFD from sunflecks ($\text{mol m}^{-2} \text{h}^{-1}$) was then calculated for each sensor as the difference between total PPFD during the sampling period and total diffuse PPFD (i.e., all values below the threshold for a sunfleck plus the maximum value of diffuse light that occurred during sunflecks) and averaged across sensors for each plot.

Statistical analyses

Differences among species for each parameter were analyzed using ANOVA for all individual characteristics of canopy architecture and light, except leaf angle and leaf azimuth. Leaf angles for three species exhibited non-normal distributions and were analyzed using non-parametric tests (Kruskal–Wallis) to detect significant differences. To describe leaf azimuth, A and length of the mean vector were calculated based on Zar (1999). Length of the mean vector (z) is analogous to a correlation coefficient, as it ranges from 0 to 1 with 0 representing no directionality and

1 representing an instance where all measurements are in a single direction. Significance of z in relation to a uniform directionality (i.e., $z = 0$) was tested using the Rayleigh test (Zar 1999). A and z were then combined into a common metric, termed here A_s for southern leaf bias, with a range of 0 to 1 by scaling A to equal 1 at 180° (i.e., facing due south), 0.5 at 90° or 270° and 0 at 0° and multiplying A by z . All parameters were entered into a stepwise multiple linear regression to determine which, if any, characteristics of canopy architecture (independent variables) could predict sunfleck frequency and total light attenuation (dependent variables). Independent variables were then analyzed using a cross-correlation matrix to detect interactions between canopy structural characteristics within and among the levels of canopy organization. When appropriate, a curve-fit estimation was used to describe relationships between individual independent and dependent variables. All statistics were performed in SPSS 15.0 (SPSS Inc., Chicago, IL, USA) unless otherwise noted.

Results

Above-canopy light on clear days ranged from 1710 to $1970 \mu\text{mol m}^{-2} \text{s}^{-1}$. Above-canopy light during our sampling of *R. maximum* ranged between 340 and $365 \mu\text{mol m}^{-2} \text{s}^{-1}$, and we were not able to include sunfleck data for *R. maximum* because of persistent cloud cover. Additionally, only three plots for *I. frutescens* were included in the sunfleck analysis due to cloud cover during part of that sampling period. Total understory light, Q_b , expressed as a percentage of above-canopy PPFD, varied significantly by species ($F = 12.048$, $P < 0.001$) (Fig. 1). Thresholds between sunflecks and diffuse light, estimated individually for each plot, were generally similar within species with some notable variation for species with lower LAI. For example, thresholds for *M. cerifera* plots were either 25 or $50 \mu\text{mol m}^{-2} \text{s}^{-1}$, but thresholds for plots of *R. copallina* varied from 100 to $375 \mu\text{mol m}^{-2} \text{s}^{-1}$. The relationship between total understory light and understory light from sunflecks was strong and positive ($r^2 = 0.90$, $P < 0.001$) (Fig. 2). Sites with more frequent and longer sunflecks tended to have higher levels of understory PPFD from both sunflecks and diffuse PPFD.

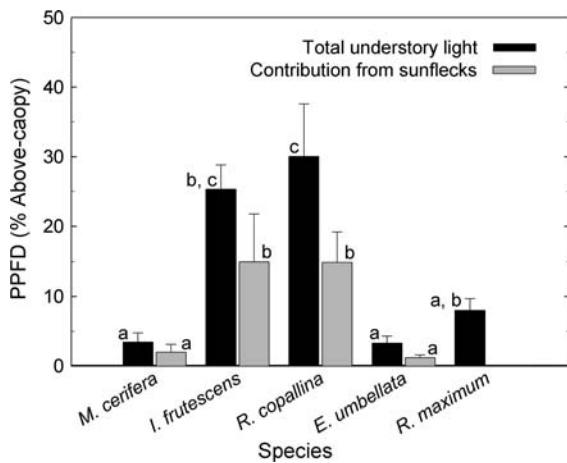


Fig. 1 Total understory light (PPFD) and total light from sunflecks (mean ± 1 standard error) for five mesic shrub communities (total light from sunflecks for *R. maximum* could not be determined because of persistent cloud cover). Significant differences between species are noted with lower-case letters

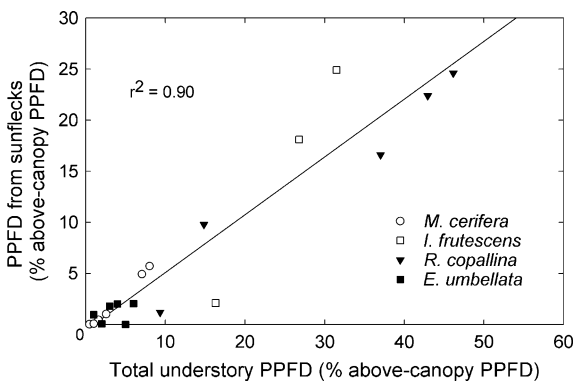


Fig. 2 Relationship of PPFD from sunflecks to total understory PPFD for 20 plots located in mesic shrub thickets. Coefficient of determination (r^2) was determined by least squares regression

Stem leaf mass was predicted (all $r^2 \geq 0.90$, $P \leq 0.001$) by stem diameter for each species, demonstrating that the allometric models were a reliable means of estimating LAI (see Brantley and Young 2007 for *M. cerifera* results). LAI across all plots ranged from 0.4 (*I. frutescens*) to 14.0 (*M. cerifera*). Mean LAI varied significantly ($F = 14.721$, $P < 0.001$) by species from 0.9 to 10.0 (*I. frutescens* and *M. cerifera*, respectively) (Fig. 3). Canopy depth (D) also varied significantly by species ($F = 22.442$, $P < 0.001$) (Fig. 3) and was more correlated with leaf and plant-level characteristics than with other

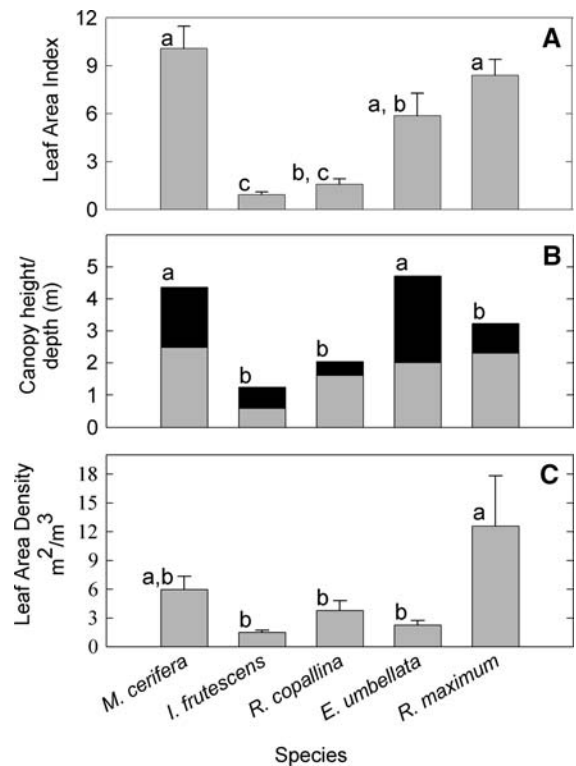


Fig. 3 Stand-level canopy characteristics (mean ± 1 standard error) for five mesic shrub communities. Bar height in **b** represents canopy height, while the black area represents space filled by foliage (canopy depth). Significant differences among species are noted with lower-case letters

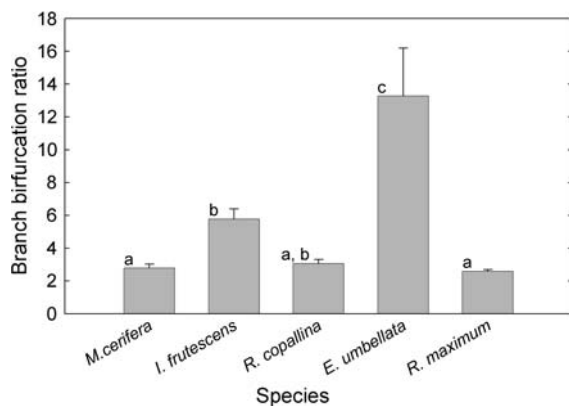
stand-level characteristics (Table 2). Leaf area density, a function of LAI and D , also varied significantly among species ($F = 4.817$, $P = 0.006$) (Fig. 3). Variations in LAD among all plots were better predicted by LAI ($r^2 = 0.33$, $P = 0.002$) than by D ($r^2 = 0.06$, $P = 0.23$) (data not shown).

Plant and leaf-level variations were also substantial among species. Bifurcation ratios (R_b) varied significantly among species ($F = 24.538$, $P < 0.001$). Mean R_b for *E. umbellata* was 13.3, more than twice the value for the next species, *I. frutescens*, and more than four times higher than the other species (Fig. 4). Leaf angle (θ) exhibited bimodal distributions for two species, *M. cerifera* and *I. frutescens*, while distribution of θ was skewed, though to differing degrees, toward higher angles for other species (Fig. 5). Leaf angle varied significantly among species ($P < 0.001$) according to non-parametric tests and median leaf angles ranged from 30 (*E. umbellata* and *R. copallina*) to 42.5 (*I. frutescens*)

Table 2 Correlation matrix for canopy characteristics for five shrub and small tree species that form monotypic stands

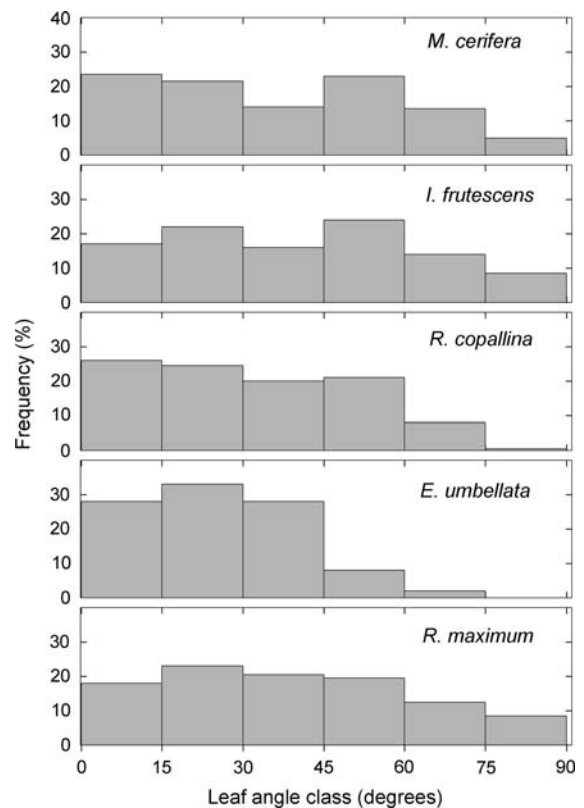
	LAI (leaf area index)	<i>D</i> (canopy depth)	LAD (leaf area density)	<i>R_b</i> (bifurcation ratio)	θ (mean leaf angle)	<i>A_s</i> (southern leaf bias)
LAI	–					
<i>D</i>	0.426**	–				
LAD	0.577 [†]	–0.237 [†]	–			
<i>R_b</i>	–0.103	0.633**	–0.368	–		
θ	–0.056	–0.519**	0.083	–0.685**	–	
<i>A_s</i>	0.315	0.502**	0.242	0.584**	–0.581**	–

Correlations with values are [†]related methodologically and **significant at $P = 0.05$

**Fig. 4** Branch bifurcation ratios (mean \pm 1 standard error) for five mesic shrub species. Significant differences among species are noted with lowercase letters

(Fig. 5). Leaf *A* also varied among species (Fig. 6). Leaf *A* for two species, *M. cerifera* and *R. copallina*, was calculated but the distribution did not deviate from random ($P = 0.056$ and 0.966 , respectively). Of the remaining species, *I. frutescens* ($P = 0.004$) displayed a mean *A* of $\sim 300^\circ$ and z of 0.13 (on a 0 to 1 scale). *E. umbellata* ($P < 0.001$) and *R. maximum* ($P < 0.001$) both demonstrated a south-facing bias with a mean *A* of $\sim 170^\circ$ and the greatest z values (i.e., directionality was greatest) at 0.27 and 0.28 , respectively.

Multiple regression analysis indicated that the best model to predict total understory light included variables *D* and LAI ($R^2 = 0.53$, $F = 13.714$, $P < 0.001$). However, LAI and canopy depth were collinear ($r = 0.43$, $P = 0.027$). Removing LAI from the model resulted in a linear model with *D* as the single independent variable ($r^2 = 0.42$). The predictive power of *D* was improved using a non-linear model (Fig. 7). A curve-fit analysis indicated that Q_b

**Fig. 5** Frequency distributions of leaf angles for five mesic shrub species. Distributions are divided into 15° classes. Mean leaf angle (± 1 standard error) for each species is shown in parentheses. All leaves were located on terminal shoots in the outermost canopy

could be best related to *D* through a power function ($r^2 = 0.58$) given by the equation:

$$Q_b = 7.54(D)^{-1.30}$$

Results were similar when understory PPFD from sunflecks was analyzed by multiple regression but contribution of sunflecks was slightly more difficult

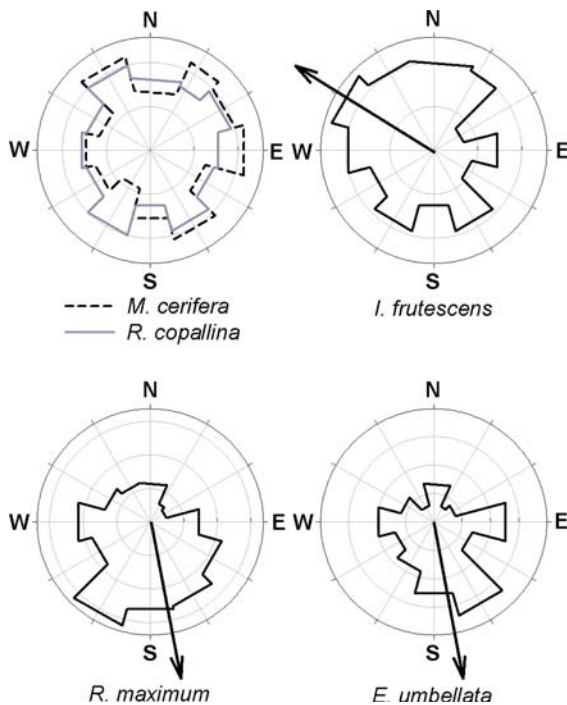


Fig. 6 Radial distribution of leaf surface azimuths for five mesic shrub species shown in relation to cardinal direction. Leaf azimuths of *M. cerifera* and *R. copallina* did not deviate from a random radial distribution ($P > 0.05$). Mean azimuths for other species are represented with arrows

to predict. A linear model that included only D had an r^2 of 0.41. No other independent variable, including LAI, was significant in predicting PPFD from sunflecks in the multiple regression analysis. The predictive power of D was not improved substantially by using a non-linear model. For example, a power function as used previously resulted in an r^2 of 0.39 (Fig. 7). Sunfleck frequency was also best predicted by D , but the results of linear regression were less definitive ($r^2 = 0.31$, $F = 7.953$, $P = 0.001$) and did not improve with non-linear models. LAD was a poor predictor of total understory PPFD ($r^2 = 0.007$, $F = 0.187$, $P = 0.669$), PPFD from sunflecks ($r^2 = 0.001$, $F = 0.063$, $P = 0.805$) and sunfleck frequency ($r^2 = 0.02$, $F = 0.422$, $P = 0.524$) and was not included in any of the models.

A correlation matrix of the independent variables revealed several significant relationships across levels of canopy architecture. Perhaps most important in the context of the above relationships, there were significant correlations ($P < 0.01$) between D , R_b , θ and A_s . (Table 2). For example, there was a negative

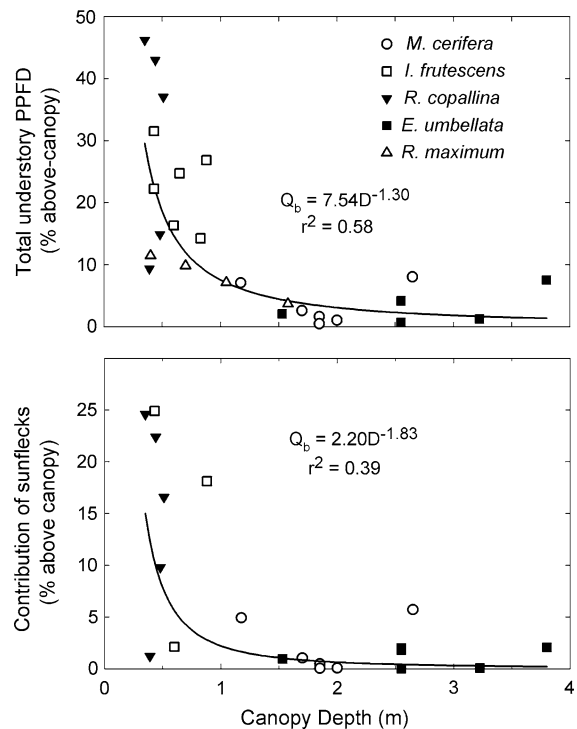


Fig. 7 Curve estimation for the relationship of total understory PPFD (top figure) and total PPFD from sunflecks (bottom figure). The top figure represents 27 plots among five shrub species while the bottom figure represents 20 plots among four shrub species. Curves, equations, r^2 values represent the best-fit relationship for a power function

correlation between D and θ ($r = -0.519$, $P = 0.005$) indicating that lower leaf angles were associated with deeper canopies. Deeper canopies also had higher levels of branching ($r = 0.633$, $P < 0.001$) and leaf azimuths with greater bias towards a southerly direction ($r = 0.502$, $P = 0.008$). Additional significant correlations were often the result of interdependence due to methodology and such relationships were omitted from consideration. For instance, LAI and basal area were highly correlated because both LAI and basal area values were calculated from the same stem diameter measurements.

Discussion

Stand-level characteristics remain the best predictors of understory light. However, we failed to support our hypothesis that LAD could predict understory light due to a suppression of sunflecks. LAD was a poor

predictor of understory PPFD either from diffuse light or from sunflecks. The effects of high LAD on light attenuation may be negated by lack of branching that creates a high level of leaf clumping. Canopy depth was the single best stand-level structural parameter to predict total light attenuation, sunfleck frequency, and contribution of sunflecks. LAI was also a significant predictor of total understory light (but not sunflecks). However, LAI and canopy depth were collinear. A positive relationship between LAI and D seems intuitive, as a canopy with greater depth would necessarily require a higher LAI, at least for low LAI values. The conclusion that canopy depth would greatly influence sunflecks and light attenuation is not completely novel. Smith et al. (1989) postulated that the likelihood of a sunfleck being rapidly eclipsed as solar position changed would increase as canopy depth increased. The same principle may apply to indirect light as well. Although canopy depth predicted some variation in sunfleck occurrence, diffuse light was actually more predictable.

Several plant and leaf-level traits were related to canopy depth but none were strong enough alone to predict light attenuation. Therefore, the data do not directly support our second hypothesis that branch bifurcation ratios are positively correlated with light attenuation. However, branch bifurcation ratios were correlated with canopy depth. High levels of branching likely contributed to the relatively high light attenuation in the *E. umbellata* canopy compared with other species with higher LAI. Median leaf angle was not significantly correlated with either LAI or LAD. Therefore, we also failed to support our third hypothesis that individual leaf angles are positively related to leaf area of the stand. Early successional woody species, or any species exposed to full sunlight, often exhibit vertically oriented leaf and shoot angles that support a uniform distribution of leaves and improve efficiency of light capture for the whole canopy (Kitajima et al. 2005). Plants exposed to high light may also exhibit canopies with both erect and horizontal leaf angles with few leaves oriented at intermediate angles (de Wit 1965, as cited in Teh et al. 2000). Two of the species in our study, *M. cerifera* and *I. frutescens*, displayed a bimodal distribution of leaf angles that would indicate this type of leaf display. The bimodal distribution again appears unrelated to LAI, however, as these two

species had the highest and lowest LAI values of the species examined. Both LAI and median leaf angle for *E. umbellata* were significantly lower than for *M. cerifera* but understory light levels were similar.

Although we failed to support our initial hypotheses, the results of this study are revealing and show how little is known about the interaction of canopy architecture across scales. These data also illustrate that many canopy structural traits are not uniform in function across species. Rather, different species may use different strategies depending on environmental factors. Species such as *M. cerifera* appear to be very effective at intercepting light but only at the expense of a large investment in leaf biomass which can have other physiological consequences such as an increased water requirement. *Elaeagnus umbellata* was more structurally efficient at light interception (more light was intercepted per unit leaf area) through a combination of structural characteristics. High bifurcation ratios better dispersed leaves throughout the canopy, and leaf azimuths biased towards the south, and horizontal leaf angles allowed greater light attenuation at mid-day.

Although light is certainly an important resource, canopy structure may not necessarily be optimized only to maximizing light interception. *Iva frutescens* had the second highest bifurcation ratios but had relatively low LAI and the understory of *I. frutescens* thickets had very high light levels. Furthermore, *I. frutescens* and *E. umbellata* both exhibited erect asymmetrical branching as described by Whitney (1976), while other species demonstrated branching by symmetrical dichotomy (personal observation) resulting in lower bifurcation ratios. Perhaps the most distinguishing characteristic of *I. frutescens* was that the mean leaf azimuth was directed toward the west–north–west at $\sim 300^\circ$. Typically, leaf azimuths vary with respect to either optimizing photosynthesis, modulating energy balance or some combination of both (Sands 1995; Valladares and Pugnaire 1999; Falster and Westoby 2003; Kitajima et al. 2005). Our results for *R. maximum* and *E. umbellata* indicate that increasing capture of solar radiation may be most important for influencing leaf azimuths because they each demonstrated a southern bias. Under this assumption, one would expect that any non-uniform distribution would either reflect a bias toward the general direction of the sun or, in the case of full sun exposure and moderate temperature, orthogonal to

the sun to reduce radiation stress. While a 300° leaf azimuth, typified by *I. frutescens*, would certainly mitigate exposure to excess sunlight, leaf azimuth may also be influenced by other environmental factors, such as the prevailing wind observed in open sites on Hog Island. Effects of wind on leaf azimuths is poorly understood but Elmore et al. (2005) demonstrated that leaf azimuths of *Zea mays* could be changed experimentally by placing windbreaks against the prevailing wind direction during leaf development. Leaves of *I. frutescens* were arranged approximately perpendicularly to prevailing wind direction during the growing season (data not shown) indicating that stresses such as sea spray and leaf abrasion may also influence leaf azimuths in this community. Of the two Hog Island species, *I. frutescens* leaf azimuth exhibited a greater directional bias and these thickets were located in a much more exposed site than the *M. cerifera* thickets.

The shrub growth form is efficient at exploiting horizontal space by altering fine-scale leaf display through variations in branch length and branch angle that depend on sun exposure (Kempf and Pickett 1981). These characteristics, coupled with variations in leaf angle and azimuth, not only improve the overall plant carbon budget by maximizing light capture but they also improve competitive dominance through high attenuation of light (Sands 1995; Kitajima et al. 2005). Based on our results, the potential of shrubs to alter aboveground resource gradients and community structure is dependent on fine-scale, species-specific characteristics of canopy architecture that affect distribution of leaves in the canopy and enhance efficiency of light interception through leaf display. The order of magnitude variation in LAI values was somewhat surprising considering the similarity in climatic factors that existed among the communities examined. Nonetheless, the range of LAI values we observed represents the range of LAI values observed for shrub-dominated systems across North America (Knapp et al. 2008) and these results may be applicable to more arid systems as well. Our results may be confounded by extreme heterogeneity and complexity of canopy architecture and understory light at fine scales. However, to our knowledge, this is the first field study to link canopy depth directly to understory light availability in shrub thickets. Furthermore, the fact that differences can be significant within such a narrow range of variation in

canopy depth among these communities demonstrates the importance of this mechanism for light attenuation. This study represents only a first exploratory step in understanding interactions between canopy characteristics at different scales and the effect they have on understory light. Future research is needed to uncover the explicit causal relationships between canopy characteristics at different scales so that specific hypotheses can be tested through more robust statistical methods such as path analysis. Understanding the link between leaf, plant, and stand-level architectural characteristics of shrub canopies could provide valuable new insight into specific traits that facilitate woody expansion and control interactions between woody vegetation and grasses.

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