Chapter 6

Canopy Openness, Understory Light Environments, and Oak Regeneration

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Abstract

Understory light environments were evaluated in four mixed-oak forests in southern Ohio using hemispherical photography. Within each forest, plots were divided into nine treatment combinations based on three pretreatment fire categories and three Integrated Moisture Index (IMI) categories. For each of 108 photographs we determined the percentage of open sky, direct beam, and diffuse radiation; the latter two variables were combined to produce an estimate of the percentage of global radiation reaching the regeneration layer (1.5 m). Global light ranged from less than 1 to 23 percent and averaged 5.5 to 8.3 percent across treatment combinations; it did not differ significantly as a function of study area, treatment unit, or IMI. Xeric sites had a significantly greater percentage of open sky, but this influenced primarily the amount of diffuse radiation rather than direct beam radiation. Nearly 75 percent of the variance in global radiation could be predicted from open sky. The relationship between in situ light availability and IMI was evaluated with respect to oak regeneration in the seedling, pole, and sapling size classes. There was no strong relationship between the amount of ambient light or IMI and the amount of oak regeneration. Under ambient conditions in mature mixed oak forest, light and moisture may not be the primary determinants of establishment and early survival.

Introduction

Forest canopy structure is a complex and dynamic outcome of years of evolution and ecological interactions between vegetation and the environment (Norman and Campbell 1991). Canopy structure varies at a variety of spatial and temporal scales (Hutchison and Matt 1977). Variability in the overstory translates directly to altered microenvironments in the understory (Minckler et al. 1973; Vitousek and Denslow 1986), with the most obvious effects being changes in ground layer light environments. The quality and quantity of the light that reaches the forest floor are determined by ambient abiotic conditions, biological features, and disturbance regimes (Endler 1993).

The radiation environment within forests is primarily a function of simple sun-earth geometry, topography, canopy architecture, optical properties of the vegetation, and the ratio between direct and diffuse radiation (Ross 1981; Baldocchi et al. 1984). Abiotic conditions and site-quality factors including soil parent material, soil texture and structure, ion availability, and hydrology influence the distribution, abundance, and structure of overstory tree species within the forest (Martin 1975; Anderson and Vankat 1978; Muller 1982; McCarthy et al. 1984, 1987; Chapter 3). In turn, the constituent overstory species with their respective leaf morphologies, densities, reflectivity, and crown characteristics are the primary biological determinants of light quality and quantity reaching the forest floor (Endler 1993). Branchfalls, treefalls, defoliations, diebacks, and other disturbances in the canopy add to these biological features to create a unique canopy architecture (Chazdon and Pearcy 1991). In natural systems, this architecture often is spatially and temporally diverse, leading to heterogeneous understory light environments (Chazdon 1988).

Although considerable microenvironmental information is available for intensively managed agricultural and forest monocultures (Ross 1981), natural systems with their attendant heterogeneity have been less well studied. Among forest ecosystems, forest understories have been studied most intensively in tropical vegetation (Pearcy 1983; Chazdon and Fetcher 1984; Chazdon and Pearcy 1986) and coniferous vegetation (Reifsnyder et al. 1971; Tajchman 1972; Norman and Jarvis 1974, 1975; Sinclair and Knoerr 1982). Temperate deciduous forests have been reasonably well studied (Anderson 1964 a,b; Miller 1969; Horn 1971; March and Skeen 1976; Hutchison and Matt 1977; Canham 1988; Chason et al. 1991), but data still are limited because certain vegetation types have been neglected or the scope of research was too narrow and/or the techniques or sensors used were inappropriate (Baldocchi et al. 1984). Few data are available for mixed-oak forests using modern techniques of data acquisition and analysis (Baldocchi et al. 1984; Chason et al. 1991). The quantification of understory light environments is critical if we are to correctly parameterize forest growth models, understand light effects on regeneration ecology, and elucidate forest ecosystem processes.

The importance of canopy heterogeneity to understory light environments and microclimate in natural mixed-species systems has been recognized for many years (Weaver and Clements 1938; Daubenmire 1947; Oosting 1948). Light measurements in the forest have become more accurate and precise in recent years due to technological advancements (Pearcy 1991). Yet, there are relatively few methods with which to determine the amount of light that reaches the forest floor (Smith and Somers 1991). The method used depends on the goals of the study, the level of precision and accuracy desired, spatial scale (centimeters, meters, hectares), temporal scale (seconds, hours, months, years), and amount of resources available (time and money).

Quantum light sensors are generally used for short experiments involving the response of individual plants to abrupt changes in the amount of light received, i.e., sunflecks (Chazdon 1988). Photochemical sensors such as photosensitive sepia paper are used to evaluate the total amount of light received at a point over several day periods but the ability to resolve smaller changes in light intensity is sacrificed (Friend 1961). Data-collection techniques that include the use of photography have been described as being objective, accurate, and rapid ways of analyzing vegetation (Bonham 1989). Hemispherical photography is useful for estimating openness in forest overstories in a variety of environments (Hill 1924; Evans and Coombe 1959; Anderson 1964 a,b; Lin et al. 1992; Rich et al. 1993; Robison and McCarthy 1999).

Digital image analysis has greatly enhanced the precision and accuracy of hemispherical photography in determining understory light environments and allows a detailed analysis of light penetration through forest canopies (Rich 1990; Canham et al. 1990; Rich et al. 1993; Canham and Burbank 1994). This technique is relatively inexpensive, easily transported, can be replicated consistently over many years, and is desirable for comparative studies (Robison and McCarthy 1999). Hemispherical photographs have been used to indirectly estimate the percentage of solar radiation reaching the point where the photo was taken. Data collected include percentages of open sky, diffuse, direct, and global solar radiation (Smith and Somers 1994). A single photograph can be used to estimate the percentage of full-sun seasonal radiation at a particular site (Pearcy 1991).

The purpose of our study was to examine the ground-layer light environment in four oak-hickory forests in southeastern Ohio using hemispherical photography, and to evaluate the relationship between in situ oak regeneration and ambient light environments. Also, this study will provide baseline data that will be useful in examining the effects of prescribed fires on light regimes.

Methods

Study Areas and Experimental Design

The study areas and experimental design are described in detail in Chapter 1. Here a brief overview is provided. The four 75-90 ha study areas are located in Vinton County (Arch Rock and Watch Rock) and Lawrence County (Young's Branch and Bluegrass Ridge). The study areas are within in the Southern Unglaciated Allegheny Plateau, which is characterized by high hills, sharp ridges, and narrow valleys. Sandstones and shales are principle bedrocks. Forests are oak-dominated and the current overstory originated in the late-1800s, after the cessation of clearcutting for the charcoal iron industry.

In each study area, three prescribed fire treatments were established, a control unit (CONT), an infrequent burn unit (INFR), and a frequent burn unit (FREQ). To account for variation in soil moisture and vegetation, a GIS-derived integrated moisture index (IMI) was applied across the dissected landscapes of the study areas (Chapter 3). From the calculated IMI scores, each 30 x 30 m pixel was assigned to one of three soil moisture classes: xeric, intermediate, or mesic. Thus to examine the effects of prescribed fire and account for environmental heterogeneity, a split-plot experimental design was established. The four study areas are replicate blocks, fire treatment units are whole plots, and IMI classes are subplots. The 50 x 25 m vegetation plots (N= 108 total) were established as pseudoreplicates in each IMI class within each fire treatment unit (Chapter 1).

Field and Laboratory Methods

All 108 permanent plots (25 by 50 m) were used for the canopy analysis. A hemispherical photograph was taken at the exact center of each plot with a 35mm camera (Nikon FG-20) equipped with a Sigma 8mm fisheye lens mounted on a tripod. The height of the tripod was adjusted so the plane of the film surface was 1.5 m above the ground.

The camera body was leveled to a zero zenith angle using a bidirectional bubble level attached to the flash mount. From this position, three photos were taken at three consecutive f-stop settings to ensure proper exposure and contrast. For each photo, a sighting rod was placed nearby the camera so it could be seen through the viewfinder. The plot's identification code, the orientation (azimuth) of the sighting rod relative to the center of the lens, and the numbers associated with the exposures taken and roll of film used were recorded for each plot.

Throughout July 1995, photos were taken early or late in the day or under overcast conditions to avoid the definition-reducing "hot spot" caused by the solar disk (Smith and Somers 1991; Canham and Burbank 1994). Color slide film (Ektachrome 200, Kodak, Inc.) was used to increase the resolution between blue sky, clouds, foliage, tree trunks, branches, etc.

Following development, individual slides were scanned via an Agfa Arcus Plus flatbed scanner. FotoLook (v. 2.07b) interface and image-editing software was set to capture and crop the images (2.3 cm^2) at a resolution of 1,000 DPI in RGB format. The images were scaled to 50 percent before capture to reduce the size of the digitized slides to approximately 2.3 megabytes. The scanned images were edited using Adobe Photoshop (v. 2.5 for Windows). The east and west edges of the circular images were marked with green and red dots, respectively, based on the placement of the sighting rod. This software also was used to correct occasional flaws in images due to inclusion of the solar disk. These images, including the green and red east-west headings, were saved as *.bmp (bitmap) files and stored on compact disk using a write-to-CD unit (Pinnacle 1000 RCD). The original slides were archived in protective plastic sleeves.

Data Analysis

The digitized images were analyzed by Windows-based GLI/C (v. 3.1), a computer program designed by Dr. Charles Canham of the Institute of Ecosystem Studies, Millbrook, NY. The program superimposes the sun's path across the photo as it would normally move across the sky. The program repeats this process for as many days as the user defines. The regional dates for average last spring frost and first fall frost were used as the representative growing season (April 29 - October 8; 163d). The orientation of the photo (east-west headings) were entered according to the green and red markings on the images. The latitude of each plot was included in the analysis to ensure proper azimuth angle for the solar pathway.

Percentages are calculated for: open sky, beam radiation, diffuse radiation, and global radiation. Open sky is the percentage of sky that is visible through openings in the canopy; beam radiation is the percentage of radiation transmitted directly through openings in the canopy; diffuse radiation is the percentage of diffuse radiation that penetrates canopy openings; and global radiation is the combined percentage of diffuse and direct beam total seasonal radiation. The latter variable is equivalent to the Gap Light Index described in Canham (1988) and is arguably the best overall cumulative measure of light availability in the understory.

The statistical model for this project was classified as a mixed-effects, split plot with the main plots arranged in a crossed-effects block design. Study area served as the block and was treated as a random effect. Fire treatment and IMI (main effects) were treated as fixed effects. All data were analyzed using SAS v. 6.11 (SAS Inst. 1990). Data for the four variables were evaluated using the PROC MIXED procedure (SAS Inst. 1996). The MIXED procedure is a generalization of the GLM procedure and provides for more flexibility in modeling mixed effects. However, because it employs a modified estimation scheme it does not directly provide sum of squares; rather, variance components are estimated via a method known as residual maximum likelihood (REML). The fixed effects are tested using Type-III estimable functions; a containment approximation is used for the denominator degrees of freedom. *A posteriori* comparisons of main effects were made following Bonferroni corrections of the p-values for the lsmean differences.

We also examined the relationship between the number of stems in the oak regeneration size classes vs. global radiation (%) using ordinary least-squares regression. These analyses were performed by the regression procedure of NCSS (Hintze 1995). To meet the assumptions of normality and homogeneity of residuals, data were $\log_{10}$ transformed as appropriate. Regression diagnostics (Belsley et al. 1980) were used to increase the quality of the fit. As a result, several points were omitted from the analysis because of undue leverage or influence. Seedling (ht < 30 cm) data (N = 1003 stems) were available for all 108 plots while pole (d.b.h. < 2.5 and ht >30 cm; N = 56) and sapling (d.b.h. 2.5 to 9.9 cm; N =7) data were available only for 54 plots. Because of the low sample size in the sapling data set, saplings and poles were combined for analysis. The regeneration sampling methods are described in Chapter 8.

Results

Analysis of variance (Table 1) indicated that neither the pretreatment identity (assigned burn regime) nor the IMI significantly affected global light levels (all $P > 0.05$). Global light averaged 5.5 to 8.3 percent across treatment units (Fig. 1). Global light can be decomposed into beam radiation and diffuse radiation. Upon doing this, it became clear that direct beam radiation was not influenced by pretreatment units or IMI (all $P > 0.05$; Table 1). However, diffuse beam radiation differed significantly among pretreatment units ($P = 0.0556$; Table 1) and IMI ($P = 0.0209$; Table 1). These differences were driven largely by the increased diffuse light on xeric plots in the control and infrequent units (Fig. 1). Direct beam radiation averaged 6.1 to 9.7 percent vs. 4.7 to 7.5 percent for diffuse beam radiation. The amount of open sky (3.2 to 5.7 percent) showed a similar pattern with respect to the diffuse beam radiation, i.e., strong effects of treatment unit ($P = 0.0592$) and IMI ($P = 0.0041$; Table 1). There were no significant interactions between treatment units and IMI for any dependent variables (Table 1). Study area was treated as a random effect and was not tested in the mixed-model analysis. A separate GLM procedure indicated no significant differences among the four study areas (all $P > 0.10$).

To determine whether the percentage of open sky can be used to indirectly assess overall understory light conditions, we conducted a separate regression analysis of open sky vs. global radiation. The overall regression was highly significant ($P < 0.0001$), with a y-intercept indistinguishable ($P < 0.003$) from zero. The coefficient of determination ($R^2 = 0.636$) and power (1.000) were sufficiently high to conclude that the percentage of open sky is a reasonably good predictor of global radiation (Fig. 2).

Histograms were produced to summarize the amount of oak (*Quercus* spp.) regeneration in the 108 plots. Data were tallied at the genus level, so all species were combined for these analyses. Because pole and sapling data were available only for half of the plots, these data were scaled by a factor of two to make them comparable to the seedling data. Seedlings were found in all but two sample plots and occurred as >5 individuals per plot in 60 of the samples, the modal category (Fig. 3). The modal category for poles was one to two poles per plot. The modal category for saplings was zero (80 plots) with one to two stems in 28 plots. As expected, the data indicate a steady decline in abundance across size classes from seedlings to saplings (Fig. 3).

Regression analyses were conducted to evaluate the relationship between number of stems in a size class for each sample plot and the ambient global light percent for that plot (Fig. 4). The seedling class yielded a nonsignificant regression with very poor fit and weak power, as did the combined pole and sapling data (Fig. 4). There did not appear to be a relationship between light and ambient oak reproduction, at least under the range of ambient light environments encountered in these mature mixed oak forests.

Discussion

Hemispherical photography can provide an accurate measure of understory light conditions as there apparently is a strong relationship between photosynthetically active radiation (PAR) and canopy openness. Becker et al. (1989) and Rich et al. (1993) found excellent agreement between hemispherical canopy photographs and actual photosynthetic photon flux densities measured via sensors.

Using hemispherical photography, we determined that the average grand mean of global radiation (across all treatment combinations) was 6.6 percent. This value is considerably greater than those for relative transmittance measured in other North American temperate deciduous forests. Horn (1971) observed transmittance of 2.9 percent in a New Jersey

Table 1.—Analysis of variance for two-way randomized block design using unbalanced mixed-effects model; study areas treated as random effects and Integrated Moisture Index: treated as fixed effects.

Variable	Source	Num. dfdf	Den. dfdf	F	P
Open sky	Treatment	2	6	4.70	0.0592
	IMI	2	18	7.58	0.0041
	Trt * IMI	4	18	1.14	0.3714
Beam	Treatment	2	6	1.92	0.2264
	IMI	2	18	0.18	0.8381
	Trt * IMI	4	18	0.61	0.6599
Diffuse	Treatment	2	6	4.86	0.0556
	IMI	2	18	4.84	0.0209
	Trt * IMI	4	18	1.11	0.3814
Global	Treatment	2	6	2.77	0.1407
	IMI	2	18	0.74	0.4930
	Trt * IMI	4	18	0.75	0.5719

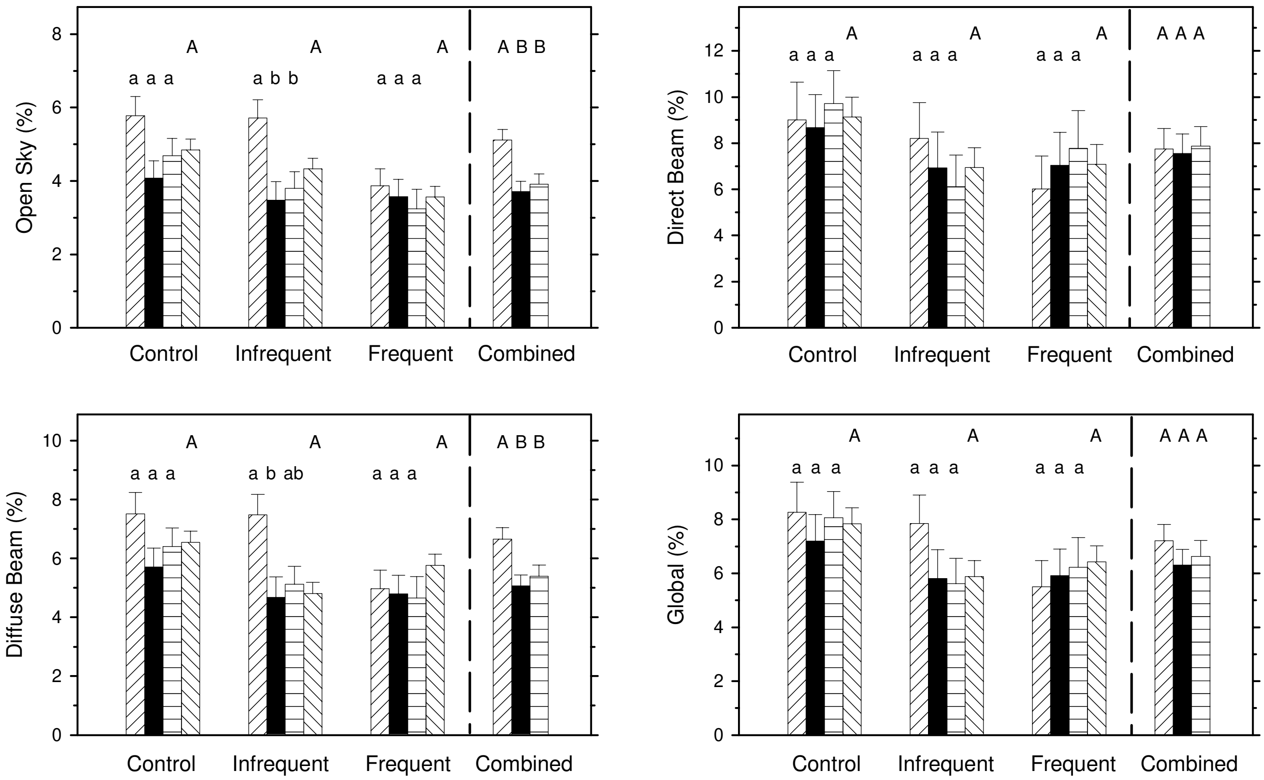

Figure 1.— Least squares means (±SE) for the four light environment variables (%): open sky, direct beam, diffuse beam, and total global radiation. Control, infrequent, and frequent refer to treatment designations. Fill colors designate the integrated moisture index (IMI) level: rising-right hatch = xeric, filled = intermediate, horizontal hatch = mesic, rising-left hatch is the overall mean for that burn regime. Data to the right of the dashed line within a panel are overall means for the IMI's. Letters are used to designate adjusted Bonferroni comparisons. Means with the same case letter within a line of a panel are not significantly different from each other (P > 0.05).

Piedmont forest, March and Skeen (1976) found that global radiation was about 3 percent beneath a Georgia hardwood-pine forest and Hutchison and Matt (1977) observed transmittance of 2.2 percent in 50-yr-old yellow-polar stands in Tennessee. Floyd et al. (1978) measured PAR above and below a mixed-oak forest during several phenological stages. They reported that 98 percent of incident PAR was attenuated by the forest canopy following foliar development. Baldocchi et al. (1984, 1986) recorded similar results (PAR below 3 percent) in an uneven-aged oak-hickory stand in Tennessee. In southwestern Wisconsin, Lorimer et al. (1994) recorded light levels as low as 1 percent in closed-canopy forests dominated by red and white oak.

The discrepancy between the light environment descriptions in these studies and our study likely is due to a variety of biotic (species) and abiotic (site quality) factors. For example, Canham and Burbank (1994) found that light transmittance was closely correlated with the degree of shade tolerance of the dominant species. Hemlock and beech stands provided less than 1 percent light transmission to the understory, maple stands allowed 2.4 to 4.4 percent, and stands dominated by red oak and ash allowed 5.7 and 6.2 percent, respectively. Thus, the data obtained from our mixed-oak stands might be explained largely by species composition and attending foliar spectral qualities. The discrepancy between our data and those from other mixed-oak stands (i.e., Baldocchi et al. 1984, 1986) probably can be attributed to the increased length of growing season, different solar path, and higher site qualities in southern Appalachian than in central Appalachian forests. Site quality affects growth, density, and crown closure in most hardwood stands (Daniel et al. 1979). As a result, light transmission to the forest floor is directly affected by stand density, leaf-area index, tree spacing, crown closure, and basal area (Reifsnyder and Lull 1965).

Interestingly, Canham and Burbank (1994) did not find significant differences in light transmittance as a function of height within the range of 1.0 to 7.5 m above ground in any forest type they studied. Thus, the available light to seedlings, poles, and saplings in any given area should be similar on average. Our data are consistent with this observation in that we found no relationship between global light and any regeneration size class of oak.

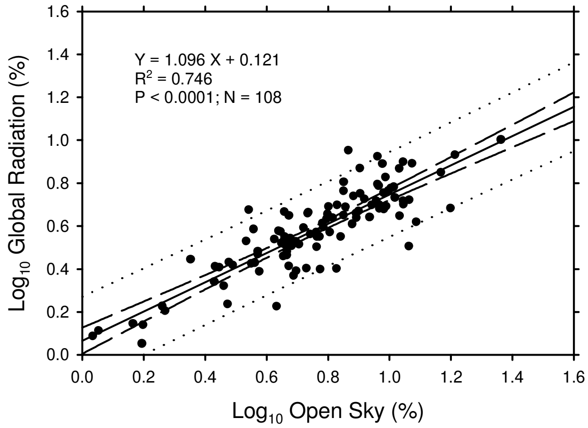

Figure 2.—Ordinary least-squares regression of open sky (percent) vs. total global radiation (percent). Data were $\log_{10}$ transformed to meet normality and homogeneity of variance assumptions. Solid line represents the best fit OLS line; dashed lines represent the upper and lower 95 percent confidence intervals, respectively; dotted lines represent the predication intervals. Approximately 75 percent of the global radiation can be predicted by open sky.

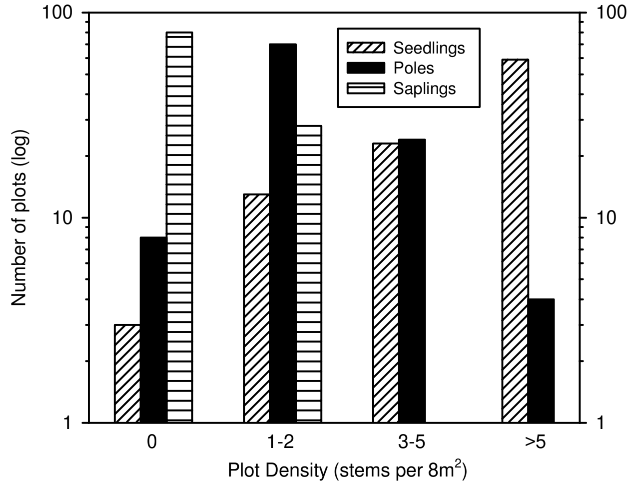

Figure 3.—Frequency histogram ($\log_{10}$ scale) for the distribution of seedlings (ht < 30 cm), poles (ht ³ 30 cm and d.b.h. < 2.5 cm), and saplings (d.b.h. 2.5-10.0 cm) in the 108 study plots.

Midstory interference via tall saplings is a potentially important factor in the development of oak seedlings beneath mature oak stands. Lorimer et al. (1994) removed saplings of maple, hornbeam, and basswood for 5 years in a Wisconsin forest to form a park-like area that might be representative of a system characterized by repeated light fires (Abrams 1988). They found an enormous release effect as oak seedlings were able to recruit and grow significantly better on experimental removal plots compared to control plots. Lorimer et al. (1994) recorded radiation as low as 1 percent beneath closed-canopy controls and as high as 7 to 9 percent on experimental removal plots. Their experimental removal plots were similar to our 6.6-percent light environments with undisturbed midstories. However, we did not observe increased oak abundance in any structural layer (seedlings, poles, saplings) at global light of 10 to 25 percent.

Phares (1971) found that oak is photosynthetically saturated at 30 to 50 percent of full sunlight; oak can maintain optimal height growth in sunlight as low as 8 percent (Loach 1967; Hodges and Gardiner 1994). These data suggest that the ambient light found in our study areas in southern Ohio should be adequate for oak regeneration and that light may not be the “limiting” factor for establishment and growth.

Oak has ecological and physiological properties that limit its ability to respond to changing light environments. Small oak seedlings have been reported as poor competitors across a range of disturbance regimes from small canopy gaps to large overstory disturbances (Beck 1970; Ehrenfeld 1980; McGee 1984). Plants generally respond to low resource levels by favoring the growth of the organ responsible for capturing the most limiting resource (Fitter 1986). High root:shoot ratios have long been known as adaptations to drought (Levitt 1972), and oaks and hickories are well known for their high root:shoot ratios (Kozlowski et al. 1991) and adaptations to drought (Abrams 1990). This suggests that the limiting resource may well be a below-ground resource (moisture or fertility) rather than an above-ground resource (light). The relationship between root:shoot ratio and drought tolerance has been demonstrated for both oak (Kolb et al. 1990) and hickory (McCarthy and Bailey 1994). Thus, these plants would be classified as moderate stress tolerators (sensu Grime 1979) and their ecological strength should be greatest where resource levels allow them to compete with less stress-tolerant species (Kolb et al. 1990). This has been a partial explanation for why oak regeneration increases as site productivity decreases (McGee 1979).

Long-term studies of solar radiation can be effectively studied through the use of hemispherical photography, but they are quite rare (Rich et al. 1993). This study provides baseline data from which to examine the long-term effects of prescribed fire on understory light regimes in mixed oak forests. Long-term environmental monitoring of light and soil conditions under an experimental burn regime may provide increased insight into how these effects ultimately influence oak regeneration.

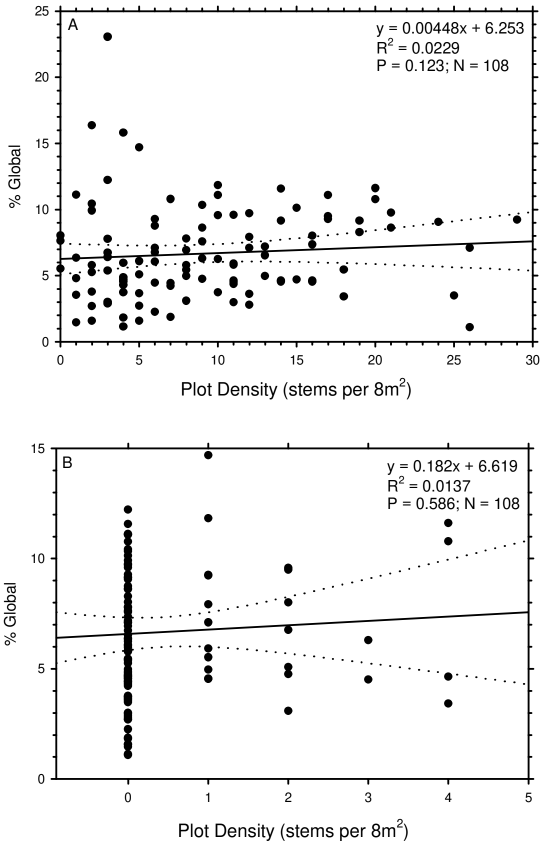

Figure 4.—Ordinary least-squares regression of number of stems vs. total global radiation (percent). Solid line represents the best fit OLS line, dashed lines represent the upper and lower 95 percent confidence intervals, respectively. (A) = seedlings; (B) = poles and saplings combined.

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