

TEMPORAL VARIATION IN PHOTOSYNTHETICALLY ACTIVE RADIATION (PAR)
IN MESIC SOUTHERN APPALACHIAN HARDWOOD FORESTS
WITH AND WITHOUT *RHODODENDRON* UNDERSTORIES

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Abstract: Understanding spatial and temporal variation in the understory light regime of southern Appalachian forests is central to understanding regeneration patterns of overstory species. One of the important contributors to this variability is the distribution of evergreen shrub species, primarily *Rhododendron maximum* L. We measured photosynthetically active radiation (PAR) in the understory of closed forest canopies in areas with and without *R. maximum*. Measurements were taken from March through November 1993 with a frequency of approximately 3 weeks. In 1994 measurements resumed from March through May. PAR under sub-canopies of *R. maximum* averaged 77% (e.g., 14 vs. 65 $\mu\text{mol m}^{-2}\text{s}^{-1}$) lower than in areas without *R. maximum* during the growing season, and 70% (e.g., 179 vs. 641 $\mu\text{mol m}^{-2}\text{s}^{-1}$) lower in the dormant season. Variation in PAR during the growing season ranged from 73% to 86% lower in *R. maximum* versus non-*R. maximum* understories. During the growing season, light levels beneath *Rhododendron* were observed to be < 2% of full sun. Low-light environments associated with *R. maximum* understories are extremely limiting with respect to regeneration of important hardwood species.

INTRODUCTION

The structure of forest canopies is extremely heterogeneous and the spatial distribution of light at the forest floor is a consequence of this heterogeneity (Pukkala and others, 1991). Although soil nitrogen availability commonly limits productivity in most temperate forests (Vitousek and others, 1982), light is typically the most limiting resource under closed canopies in southern Appalachian forests (Wayne and Bazzaz, 1993).

The quantity of light in the understory is a function of the rate of light extinction through the canopy. Utilization efficiency of the residual radiant energy in the understory depends upon the understory tolerance levels of woody plant species and determines their ability to survive and develop under light-limited conditions. It is this difference in understory tolerance among species which determines the compositional and structural characteristics of forests in the southern Appalachians.

The evergreen shrub *Rhododendron maximum* L. is an important component of mesic forest sites in the central and southern Appalachians. This species has been recognized for its influence on microclimatic conditions (Romancier, 1971) and understory composition (Clinton and others, 1994; Monk and others, 1985; Phillips and Murdy, 1985). Even though the mechanisms (e.g., competition for water and nutrients, allelopathy, litter depth and quality, light extinction) of its influence on above and belowground conditions are not completely understood, there is little doubt that this species impacts the light environment beneath it. The purpose of this paper is to present data on the temporal variation in the light environments of open versus *Rhododendron* occupied understories in mesic southern Appalachian forests.

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Study Design

Sampling was conducted in mature stands of mixed-hardwoods at the Coweeta Hydrologic Laboratory located in the Southern Appalachian physiographic province of western North Carolina. Basal area of these stands is approximately $25 \text{ m}^2 \text{ ha}^{-1}$ most of which is accounted for by *Quercus prinus*, *Q. coccinea*, and *Acer rubrum*. The basal area of *Rhododendron* is approximately $2 \text{ m}^2 \text{ ha}^{-1}$. All plots are mid-elevation (800 - 1100 m) and generally have a northerly aspect. Photosynthetically active radiation (PAR) was measured on sunny days between the hours of 1030 and 1330 in open understories and in understories containing continuous *Rhododendron* sub-canopies. Measurements were made on each of 8 plots (6 non-*Rhododendron* and 2 *Rhododendron* plots). Plots were approximately 300 m^2 each containing a permanently marked transect. Along each transect were permanently marked measurement points approximately 2 m apart. Using a portable light meter (Sunfleck Ceptometer, Decagon Devices, Pullman, WA, USA), four measurements of PAR (400 - 700 nm) taken approximately 1 m above the forest floor were averaged and recorded at each point. Measures of full-sun were taken before and after each set of measurements and averaged. Measurements were made at approximate 3-week intervals beginning early in the growing season of 1993 and continuing into the spring of 1994.

Data Analysis

Comparisons were made for PAR between the two understory conditions using PROC ANOVA (SAS, 1987). Significant differences were evaluated at the 0.05 level.

RESULTS

Variability for a given measurement period within each understory condition was low, particularly within *Rhododendron* understories (Fig. 1). However, considerable variability exists between the two understory conditions (Table 1). For each measurement date, total PAR was significantly higher in the non-*Rhododendron* understory (Table 1; Fig. 1). Maximum PAR was observed during the spring before full leafout when non-*Rhododendron* areas had PAR fluxes from $600 - 900 \mu\text{m m}^{-2} \text{ s}^{-1}$ (Table 1). *Rhododendron* areas showed maxima during the same period, but PAR was considerably less ($125 - 200 \mu\text{m m}^{-2} \text{ s}^{-1}$) (Table 1). Light levels were most similar, both in terms of PAR and percent full sun during the months of September and November (Table 1; Fig. 1 and 2), and the highest degree of variability occurred during the month of July as evidenced by the high C.V. for those dates (Table 1). Over the entire sampling period, PAR in *Rhododendron* areas ranged from 12% - 33% of observed PAR in non-*Rhododendron* areas. Throughout the growing season, light levels in non-*Rhododendron* areas were observed to be <10% full sun (Fig. 2). Furthermore, levels under *Rhododendron* sub-canopies were less than 2% of full sun (Fig. 2). PAR levels early in the growing season (Fig. 1) may be sufficient for a limited number of species to germinate during that period.

Table 1. Means and associated test statistics for PAR in rhododendron versus non-rhododendron understories by measurement date. Values in parentheses represent the fraction of full-sun.

Date	PAR($\mu\text{moles}/\text{m}^2/\text{s}$)		F	P>F	C.V.
	non-Rhodo	Rhodo			
Apr 16	613.7 (0.393)	206.4 (0.131)	35.07	0.0001	59.32
Apr 4	663.7 (0.440)	169.7 (0.148)	41.88	0.0001	62.4
Jun 2	85.2 (0.052)	12.2 (0.007)	12.06	0.0006	135.56
Jun 22	55.3 (0.043)	14.0 (0.011)	10.99	0.0017	86.51
Jul 6	92.7 (0.060)	13.9 (0.011)	4.46	0.0398	159.81
Jul 21	87.0 (0.076)	23.4 (0.016)	6.64	0.0114	153.38
Aug 16	39.8 (0.031)	10.8 (0.007)	22.67	0.0001	82.70
Sep 1	37.7 (0.027)	10.1 (0.007)	21.95	0.0001	84.44
Nov 22	189.9 (0.324)	22.2 (0.028)	47.43	0.0001	72.65
Mar 4	463.2 (0.392)	127.5 (0.103)	45.18	0.0001	58.15
Apr 1	734.6 (0.496)	191.2 (0.133)	76.8	0.0001	45.73
Apr 18	789.0 (0.539)	126.6 (0.103)	139.8	0.0001	39.68
May 2	396.4 (0.220)	55.2 (0.043)	33.56	0.0001	83.60

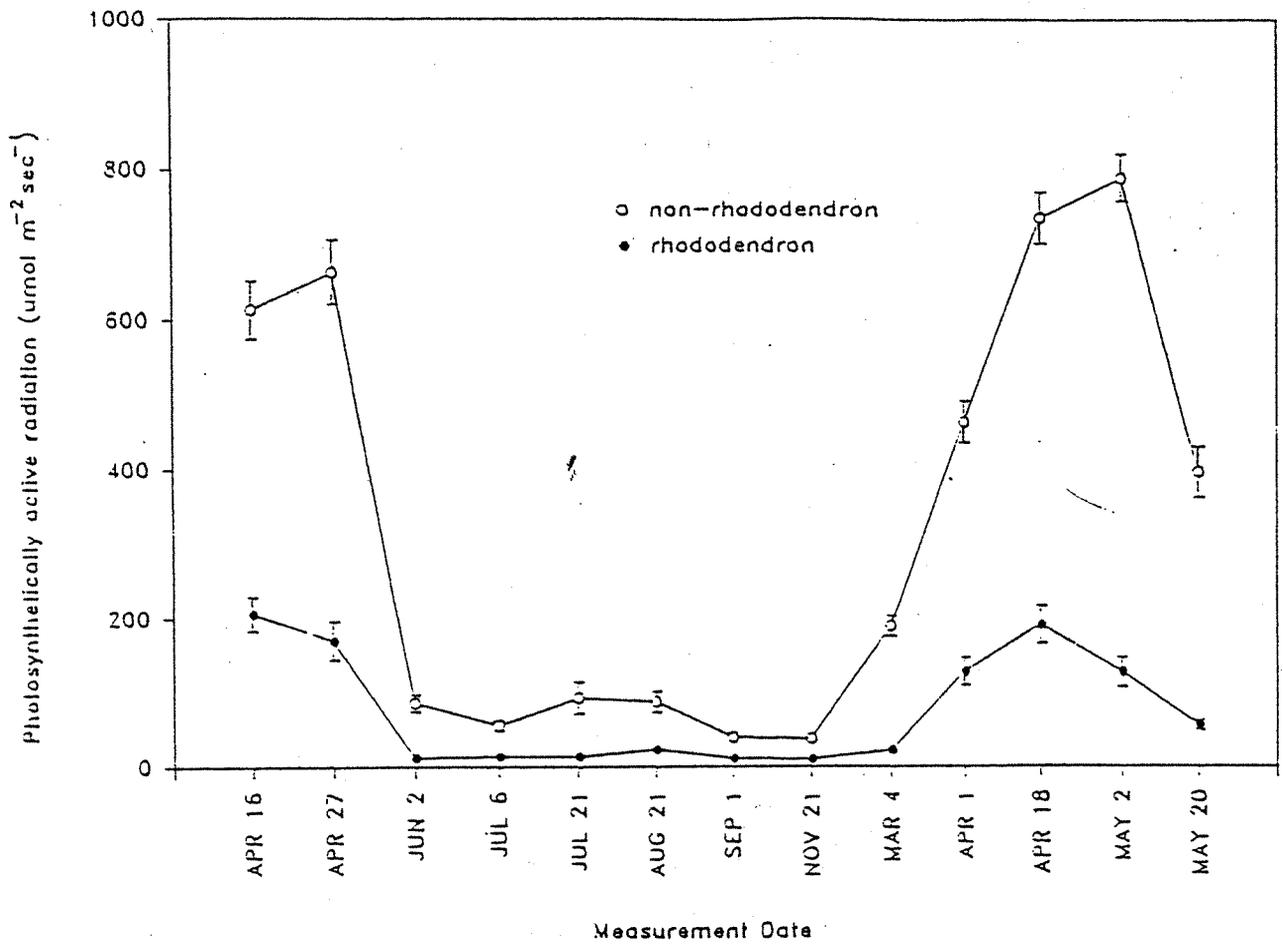


Figure 1. Measured photosynthetically active radiation (PAR) in *Rhododendron* versus non-*Rhododendron* understories. Error bars represent +/- 1 standard error.

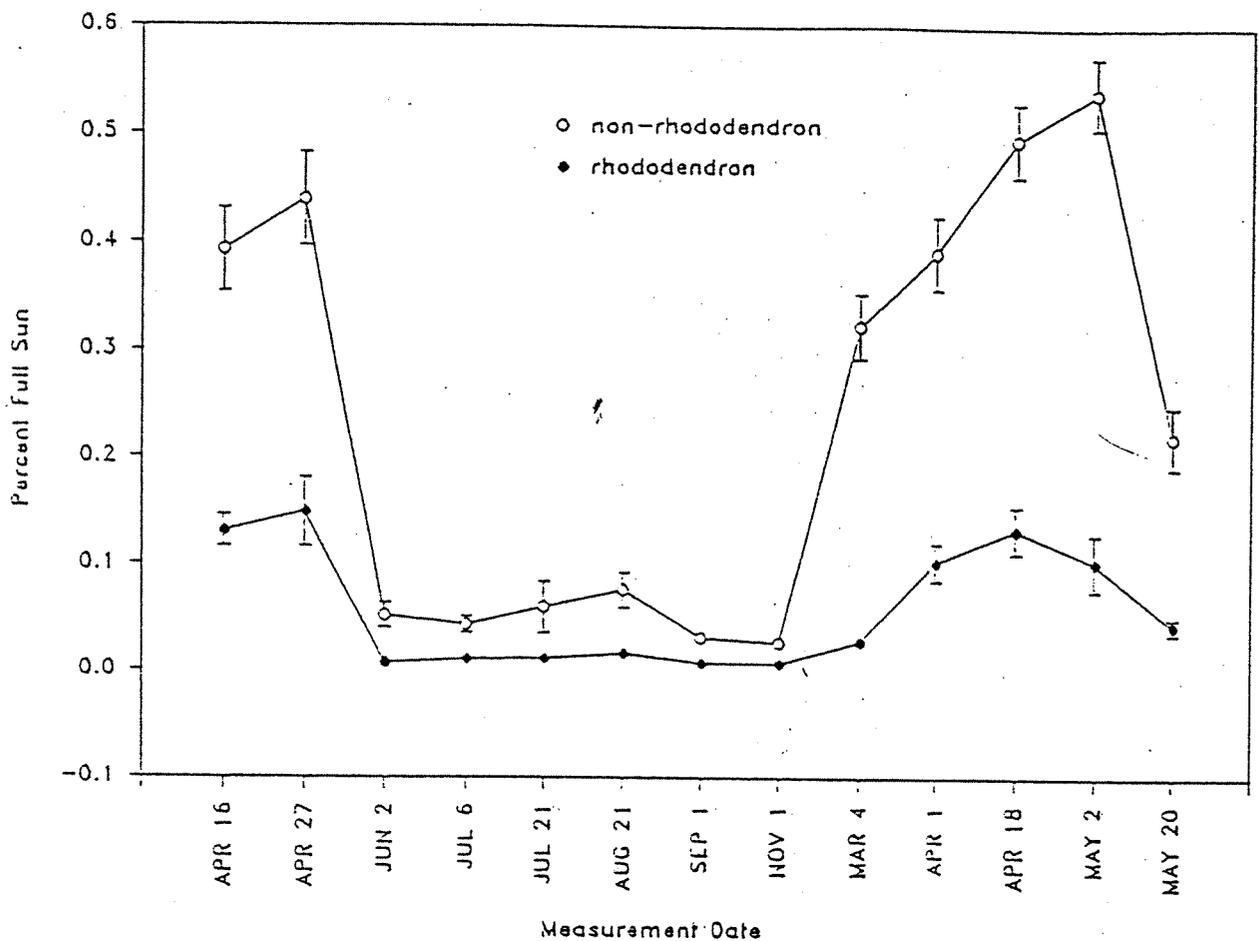


Figure 2. Percent full sun in *Rhododendron* versus non-*Rhododendron* understories. Error bars represent ± 1 standard error.

DISCUSSION

The light environment beneath *Rhododendron* sub-canopies was observed to be significantly different from non-*Rhododendron* understories throughout the sampling period. These differences may account for the general lack of hardwood regeneration in areas occupied by this species. The light compensation point for most woody species is usually about 2% full-sun (Salisbury and Ross, 1978) which was the level observed for *Rhododendron* areas during most of the growing season in this study. This result suggests that most woody species would simply be unable to become established in such light-limited environments. A few extremely shade tolerant species (e.g., *Acer saccharum* Marsh., *Tsuga canadensis* [L.] Carr.) have limited success in regenerating under *Rhododendron* (Clinton and others, 1994); however, they are not important components of mid-elevation southern Appalachian overstories (Day and others, 1988).

Phillips and Murdy (1985) found that tree regeneration on permanent plots at Coweeta was lower in areas containing heavy *Rhododendron* and that the difference in regeneration between *Rhododendron* and non-*Rhododendron* areas

increased with time. Clinton et al. (1994) observed hardwood seedling density to be significantly less in *Rhododendron* versus non-*Rhododendron* areas (0.5 vs. 2.1 stems m⁻²). In a germination experiment, Clinton and Vose (unpublished data) found that only 3% of planted *Acer rubrum* L. seed germinated under *Rhododendron* compared with 15% in non-*Rhododendron* areas. Although the low light levels observed under *Rhododendron* in this study may account for these differences, other sources of inhibition may also exist. For example, during the brief period in early spring preceding overstory foliar development, PAR may be adequate, but temperature requirements for germination of important oak species may not be satisfied.

SUMMARY

Rhododendron maximum is an important structural and functional component of southern Appalachian forests. The ecological implications associated with low light environments beneath *Rhododendron* are substantial. Its influence on tree replacement could impact overstory composition (Clinton and others, 1994; Phillips and Murdy, 1985), in addition to potential impacts on nutrient cycling processes. Most overstory species in the southern Appalachians are intolerant to intermediately tolerant to shade. Where loss of the overstory through natural mortality occurs in areas occupied by *Rhododendron*, what is the probability that the pre-mortality composition of the overstory will be replaced? Given the apparent influence of this species on tree regeneration either due to low light or other phenomena, and the recent observed increase in overstory mortality in the southern Appalachians (Clinton and others, 1993; Starkey and others, 1989; Tainter and others, 1984), it is not likely that overstory composition will be maintained in areas occupied by *Rhododendron*.

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