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Does Rhododendron maximum L. (Ericaceae) Reduce the Availability of Resources Above and Belowground for Canopy Tree Seedlings?

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ABSTRACT.—Subcanopy shrubs and perennial herbs inhibit recruitment of canopy trees in forests around the world. Although this phenomenon is widespread, and can have significant effects on community dynamics, the mechanisms of inhibition are not well understood. In the southern Appalachian region, *Rhododendron maximum* inhibits the recruitment of canopy trees in forests of northern red oak (*Quercus rubra*). We have shown, in previous research, that processes occurring before canopy tree seed germination are not responsible for this inhibition. Therefore, post-germination processes, such as competition for resources are most important. In this study we show that the presence of a thicket of *R maximum* in the understory reduced the availability of light by 80%, the frequency and duration of sunflecks by 96%, the availability of water by 20% and the availability of several soil nutrients (particularly cations) by variable amounts. Moreover, the survival of *Q. rubra* seedlings in the understory over 3 y was significantly reduced (by about 40%) in the presence of a *R maximum* thicket compared with forest without a thicket. Seedling survival was positively associated with light availability, but the slope and intercept of that relationship was different in forest with or without *R maximum.* Therefore, belowground processes are involved in reduced seedling survival under the *R maximum* thicket The resources most associated with survival of Q. *rubra* seedlings were water and light. Although many soil nutrients were significantly lower in forest with *R. maximum* than in forest without *R maximum,* no individual nutrient was a significant covariate with *Q. rubra* survivorship. Our data indicate that competition for resources both above- and belowground is an important mechanism for inhibition of canopy tree recruitment by *R* maximum. Light is important to seedling survival, but is not the only important factor. Water availability and the ability to accumulate soil nutrients are equally or more important than light to survival of canopy tree seedlings in the presence of a subcanopy thicket of *R maximum.*

INTRODUCTION

Subcanopy evergreen shrubs and grasses inhibit canopy tree recruitment in many temperate and tropical forests worldwide. For example, *Galtheria shalon* Pursh., growing in the subcanopy of coniferous forests in the northwestern United States, can interfere with seedling survival (Klinka et *al.*, 1989; Messier, 1993). In Chile and Costa Rica (Veblen, 1982; Widmer, 1998) species of dwarf bamboo (*Chusquea* sp.) inhibit regeneration of southern beech (*Nothofagus* sp.) and oak (*Quercus* sp.). Other species of dwarf bamboo (*Sasa* sp.) in the temperate deciduous forest of SW China and Japan inhibit regeneration of *Abies* sp., *Betula* sp. and most other canopy tree seedlings (Nakashizuka and Numata, 1982; Taylor and Qin, 1992). Broad leaf palms inhibit canopy tree seedling recruitment in Costa Rican

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rain forest (Denslow et al., 1991). The invasive species Rhododendron *ponticum* L., inhibits regeneration of canopy trees in the United Kingdom (Fuller and Boorman, 1977; Cross, 1981; Mitchell et *al.*, 1997). The best examples of this phenomenon in eastern North America are *Rhododendron maximum* L. in the southern Appalachian Mountains and *Kalmia angustifolia* (Small) Fernald. in northeastern Canada (Clinton *et al.*, 1994; Mallik, 1995; Baker and van Lear, 1998; Nilsen *et al.*, 1999; Walker et *al.*, 1999).

Rhododendron maximum is a particularly important example of this inhibition pattern because of its significance to ecosystem processes, succession and forest management. The extent of ***R*** maximum thickets has been estimated at 0.5 million ha of the southern Appalachian Mountains (Wahlenberg, 1950), and has been increasing over the past three decades (Dobbs, 1995; Baker and Van Lear, 1998). These ***R*** *maximum* thickets are commonly located in riparian zones along streams, in coves or on north slopes all prime sites for forest productivity. Forest scientists have recognized the inhibitory effect of ***R maximum*** on forest productivity for more than four decades. This has led to many studies on how ***R*** maximum could be eradicated or suppressed on high quality hardwood production sites (Wahlenberg and Doolittle, 1950; Yawney, 1962; Hooper, 1969; Romancier, 1971). The high relative abundance of *R. maximum* in southern Appalachian forests, and its suppression of productivity and forest development in prime forest sites, make the interaction between ***R*** maximum and canopy tree seedlings the most important shrub-tree interaction in Appalachian forests.

The evidence that evergreen subcanopy shrubs inhibit canopy tree recruitment is indisputable, and the importance of the inhibition to forest processes is unequivocal, but the mechanisms by which the inhibition occurs have only occasionally been tested (for example; Denslow et *al.*, 1991; Walters and Reich, 1996). It is commonly thought that light is the primary regulator of seedling performance on the forest floor (Pacala *et al.*, 1996), but the importance of nutrients and water to seedling survival below a forest canopy remain poorly defined (Coomes and Grubb, 2000). In previous research we have shown that there is no significant effect of *R.* maximum thickets on pregermination processes of several dominant tree species (Nilsen et al., 1999; Semones, 1999). Therefore, the mechanisms by which ***R*** *maximum* inhibits seedling recruitment must relate to the effects of this shrub on seedling survivorship following dispersal and germination. However, it is important to note that in one field trial there was some evidence that germination of *Acer rubrum* L. may be inhibited by the presence of ***R. maximum*** (Clinton and Vose, 1996). In previous research we also have shown that there is no ecologically significant allelopathic effect of ***R*** maximum on tree seed'germination and seedling growth (Nilsen *et al.*, 1999). Therefore, soil toxicity can be **ruled** out as an important factor influencing seedling survival in forests with ***R maxi***mum. Belowground resource availability may influence seedling performance because there is some evidence that ***R*** maximum influences some belowground resources (Monk *et* al., 1985; Boettcher and Kalisz, 1990; Clinton and Vose, 1996). Therefore, this'study focuses on above- and belowground resource availability and the consequences for competition between canopy tree seedlings and ***R* maximum** plants.

To determine the potential competitive effects of Rhododendron *maximum* on canopy tree seedlings we evaluated the spatial and temporal availability of resources in a uniform forest containing a mosaic of ***R*** maximum thickets. In particular, we asked five questions: (1) Is the presence of a thicket of ***R*** *maximum* associated with lower light availability for seedlings compared to forest sites without the thicket as indicated by total daily PPFD, weighted canopy openness and the amount of light from sunflecks? (2) Is water availability for seedlings significantly lower in a forest when a thicket of ***R*** maximum is present? (3) Are the availabilities of nutrients in mineral soil for seedlings significantly lower in a forest when a thicket of *R.* maximum is present? (4) Which resources are most associated with *Quercus rubra* L. seedling survivorship? (5) Does the presence of a thicket of *R.* maximum have a significant effect on the associations between resources and *Q. rubra* seedling survivorship?

METHODS

SITE DESCRIPTION AND SAMPLING DESIGN

This study was conducted in a mature mixed-hardwood forest at Coweeta Hydrologic Laboratory in the Nantahala Mountains of western North Carolina (35°02′29″N, 83°27′16″W). The site was a north-facing slope (60%) at an elevation of 1000 m (ASL) dominated by *Quercus rubra* forest with thickets of *Rhododendron maximum* in the subcanopy of part of the site. The *R. maximum* thickets had their leaf area distributed at 3-4 m aboveground, whereas the forest canopy was approximately 12 to 15 m aboveground. The soil type at the experimental site was a well drained coarse-loam of the Edneyville series (Thomas, 1996). The regional climate was classified as maritime, humid with cool summers, mild winters and adequate rainfall during all seasons (Swank and Crossley, 1988).

The site was surveyed for uniformity in elevation, aspect, position and slope. The selected area had a midslope position, a northerly aspect, a slope of 60° and an elevation between 1000 and 1010 m. Within this area three locations were in forest without a subcanopy of *Rhododendron maximum*. Three other locations were in forest with a subcanopy of *R. maximum*. Fifteen plots (2 X 2 m) were positioned within each of these locations in a regular grid with a buffer of at least 2 m on all sides of each of the plots. Resources were expected to be highly variable from plot to plot so we treated the 2 X 2 plots as experimental units. However, we recognize that location may also influence resource availability because resources may be patchy in forests at a variety of scales. The presence ("+Rm") or absence ("−Rm") of a subcanopy of *R.* maximum are referred to as "forest types."

MEASUREMENT OF RESOURCE AVAILABILITY

Temporal availability.—Microclimatic conditions were evaluated in 1996 and 1997 in or near two of the six main locations (one of the +Rm locations and one of the −Rm locations) using permanently installed instrumentation in weather stations. Each installation contained: (1) a light sensor to determine the amount of photosynthetically active radiation (PAR) (LICOR Inc. model 190s Quantum sensor, Lincoln, Nebraska), (2) copper-constantan thermocouples to determine air temperature at 20 cm height and (3) a shielded relative humidity sensor (Campbell Scientific, Inc., model 217, Logan, Utah). Data from all sensors were recorded every minute and the minimum, maximum and average for every 10-min interval were computed and stored (Campbell Scientific, Inc., model 21 X microdatalogger). These data were used to evaluate seasonal changes in weather factors. In order to determine if our single installation was typical of light conditions of a wider area, eight gallium-arsenide photo-diodes equally spaced within a 7.2 m diameter circle were placed 50 cm above the ground surface in + Rm and -Rm forest types. The photo-diodes were calibrated against a LI-190s quantum sensor and the signal was corrected for each individual diode. Light intensity was recorded over 24 h periods. This was repeated 10 times with the diode arrays in different forest locations. Results were compared with the quantum sensors positioned at the permanent installation. In a similar manner, the spatial heterogeneity of air temperature was determined by placing eight shaded thermocouples in a similar configuration as that for the photo-diodes. Air temperatures were also recorded simultaneously in the two forest types (+Rm and −Rm) over 24 h periods. The arrays were compared with the air temperature recording at the permanent locations. Short-term variation (min) in light availability was evaluated by calculating the number of sunflecks and the total minutes of sunfleck light during day cycle measurements made by the photodiodes. A sunfleck was defined as occurring when light intensity was greater than 100 $\mu mol\ m^{-2}\ s^{-1}$. Seasonal variation in soil water availability was determined monthly in 1996, at a depth of O-15 cm, in the center of every plot by Time Domain Reflectometry (Tektronix model 1502C TDR cable tester, Heerenveen, The Netherlands).

Spatial variation.—All measurements used to evaluate spatial variation of resource availability were recorded in all 90 2 X 2 m plots. Soil samples were taken in June at a depth of 10 cm for nutrient analysis. Soil was removed from the tips of an isosceles triangle (50 cm sides) centered in each plot. The three samples were pooled for nutrient analysis. Soil pH and concentration of cations were determined by the Soil Testing Laboratory at Virginia Tech using inductively coupled plasma mass spectroscopy (Thermo Jarrell Ash Corp., model ICAP 61, Franklin, MA). Carbon and nitrogen content of the soils were determined with a CHN analyzer (Perk&Elmer model 2400 CHN elemental analyzer, Norwalk, Connecticut). Nitrogen mineralization was determined by a 2S-d in situ ‘incubation (Adams and Attiwill, 1986) in July in every plot. Two cores (PVC pipe 4.3 cm diam and 15 cm long) were driven into each plot to a depth of 10 cm. When the cores were installed ($t = 0$) one core was collected from each plot and one core was left in situ. The soil from the extracted core was kept cool, returned to the laboratory, stored at 4 C and processed within 48 h. Samples were sieved to <6 mm. Five grams of fresh soil were shaken for 1 h in 2 M KCL (1:4 soil/extractant ratio) and centrifuged at 3715 X G (6000 rpm) for 15 min. Concentrations of NO_3 and NH, in the extractions were determined on an autoanalyzer (Technicon Instruments Corp., Tarrytown, NY) using a cadmium column (Franson, 1985a) and alkaline phenol (Franson, 1985b) methods, respectively. After 28 d ($t = 1$) the in situ cores were collected and processed in the same fashion. Net N-mineralization was determined by taking the difference in NO_3-N and NH,-N between $t = 0$ and $t = 1$. We use the July values for soil volumetric water content as’an indication of spatial variation in water availability.

Canopy hemispherical photographs of each plot were taken during the period of maximum seedling growth (July). The images were made on Kodak Tri-X film with a Nikon FM2 camera fitted with an 8 mm fisheye lens (Niion, Tokyo). The camera was positioned over the center marker of the plot (same location as soil and water samples), and the top of the lens was 80 cm above the forest floor. The images were analysed using a software program (FEW 4.0) developed by M. Ishizuka (pers. comm.). Indices of light availability derived by FEW 4.0 from these hemispherical photographs were: (1) Weighted canopy openness WCO = ratio of unobstructed sky to the whole hemisphere. Weighted canopy openness takes into account the unevenness of brightness in openings from the zenith to the horizon using the method described for indirect radiation. (2) Indirect Site Factor ISF = The flux of indirect radiation available at the height of the canopy photograph in mol $m^2\ mon^1$. Total radiation flux above the canopy (direct and diffuse) is calculated using the standard overcast sky equation (SOC) that assumes the zenith to be three times brighter than the horizon. ISF is determined by summing the diffuse light level (derived from SOC) for each open pixel along -the solar track specified by the month under consideration. (3) Direct site factor DSF = direct radiation which has penetrated the canopy at the height of the canopy photograph. DSF is calculated as ISF but the direct radiation is summed rather than diffuse radiation.

SEEDLING SURVIVORSHIP

Five germinating red oak (*Quercus rubra*) acorns were collected in 1996 from the immediate region (surrounding each plot) and placed in the center and four corners of a square located 20 cm in from all edges of each plot (total of 450 acorns). All planted seedlings were labeled individually in order to distinguish them from other acorns germinating in the plots. Survivorship of the marked seedlings was followed montbly over three growing seasons. Here we use the percentage survivorship at the end of 3 y as an index of the plots suitability for seedling persistence.

STATISTICAL ANALYSES

The test for significant effects of forest type on temporal variation in soil moisture did not conform to conditions required for repeated measure ANOVA (Huynh-Feldt value < 1) ; therefore, repeated measure MANOVA was used as suggested by Potvin et al. (1990). Significant effects of forest type on seasonal patterns in climatic characters (total daily PPFD), temperature (daily mean) and relative humidity (daily mean) were also evaluated with MANOVA. All statistical tests were performed with SAS (SAS 1988).

Effects of forest type (+Rm and −Rm) on spatial resource availability (soil nutrient concentrations, nitrogen mineralization, pH, light indices, 'water availability) were assessed by analysis of variance (ANOVA) using a nested design (Sokal and Rohlf, 1995). The observational units were the plots (90) nested within locations (6) within forest types (2). We tested for the effect of forest type (df = 1) and location within forest type (df = 4). If the null hypothesis was rejected ($\alpha < 0.01$) then there was a significant difference in resource availability between forest types or between locations within types. Correlations among resources were evaluated with Pearson correlation coefficients using all 90 plots.

Analysis of covariance (ANCOVA) was used to determine if there was a significant effect of forest type on the relationship between the survivorship of *Quercus rubra* seedlings and resource availability. Also, best-fit linear regression models (with 1, 2, 3 and 4 resource variables) and stepwise multiple regression (steps l-4). were used to determine which variables were most associated with *Q. rubra* seedling survivorship.

RESULTS

TEMPORAL VARIATION IN RESOURCES

Diurnal variation.-The amount of diffuse photosynthetic photon flux density (PPFD), as indicated by the permanently installed quantum sensors, was higher at all daylight hours in the sampled −Rm site than the sampled +Rm site (Fig. 1A). These values of PPFD from our sampled locations are similar to those measured by the photo-diode arrays in this study.

Air temperature at seedling height in −Rm locations was within one degree of that in +Rm sites throughout the day on all days measured (Fig. 1B). In addition, air temperatures recorded by the thermocouple arrays were similar to those collected by the weather stations on the same days. On some dates the +Rm location had a higher relative humidity than the −Rm location during the midday hours (11:00–16:00), but this was not consistent among dates (Fig. 1C).

Total accumulated PPFD and maximum PPFD during a 24 h period'in July, as indicated by the photo-diodes, was 80% less in +Rm compared with −Rm (Table 1). In the +Rm forest sites the mean number of light events greater than 100 μmol m^{-2} s^{-1} was approximately 96% less than that of the −Rm measurements (Table 1) and the mean length of time when PPFD was greater than 100 μmol m^{-2} s^{-1} was 3 h in −Rm measurements, while that of +Rm was only 8 min (data not presented). Comparisons between the results from the photodiodes and the permanently installed sensors show that the quantum sensors positioned at the weather stations were within the range of variation of the diodes located at various positions within each forest type (Table 1). Thus, measurements recorded by the quantum sensors can be used to represent the temporal pattern of light in both forest types.

Both forest types had occasional sunflecks (sudden, short-term increases in light inten-

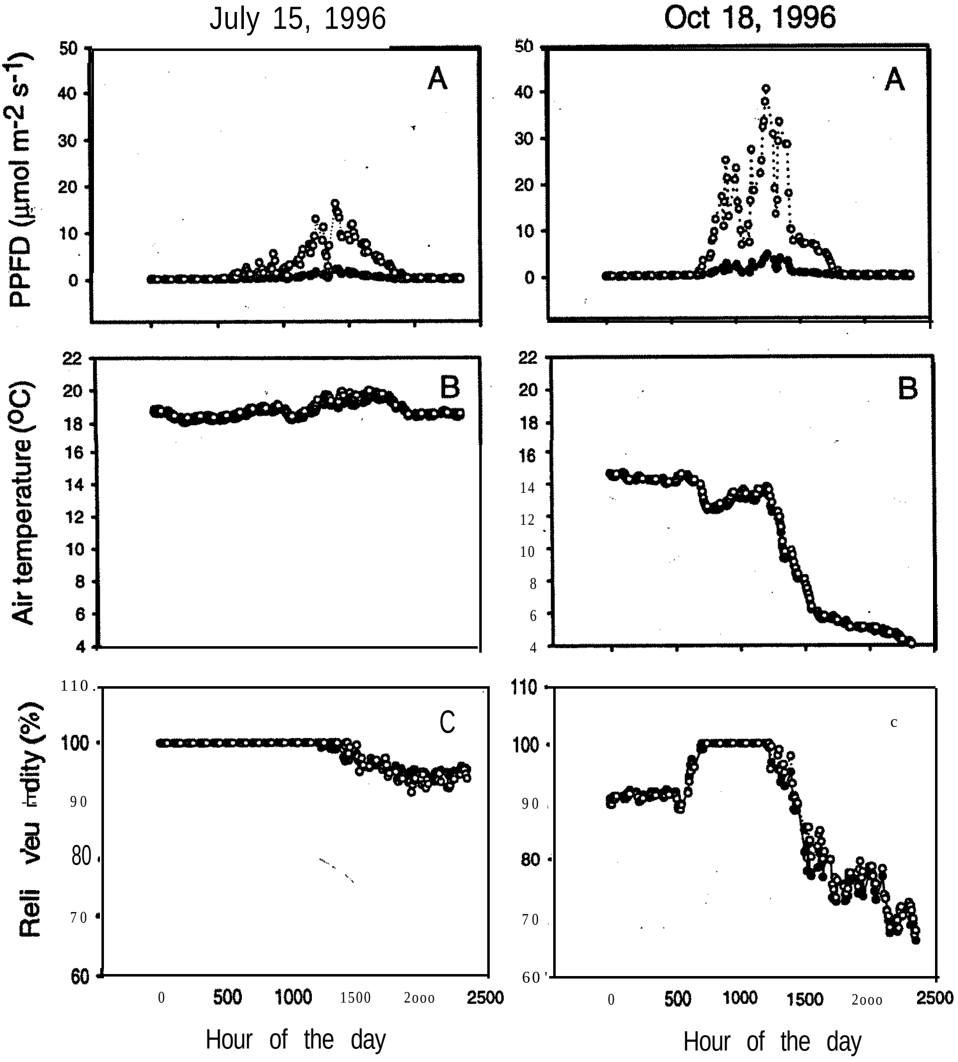

FIG. 1.—Two representative diurnal cycles in summer and autumn show photosynthetic photon flux density (A), air temperature (B) and relative humidity (C) in the subcanopy of a southern Appalachian forest. Each point represents a mean of measurements taken each minute over a 10 min period in sites with (closed symbols) or without (open symbols) a thicket of *Rhododendron maximum*

sity), but sunflecks were more abundant and of higher intensity in the −Rm plot than the +Rm plot (Fig. 2). The number of discernable sunflecks varied from 2 to 45 per day over the growing season for the −Rm site and 0 to 10 per day in the +Rm site. Hemispherical canopy photographs taken at seedling height in all plots also indicated that plots in the forest without *Rhododendron* maximum would receive more than five times as much light in sunflecks compared with forest that has a thicket of *R* maximum.

Seasonal *variation.*—During most of the growing season (June-September) the mean

TABLE 1.—Quantifiable characteristics for representative diurnal cycles of light intensity recorded by an array of 8 photo-diodes at 50 cm above the forest floor during a 24 h period in July 1997

Characteristic	Photo-diode number 1	2	3	4	5	6	7	8	Mean	±SE	Quantum sensor
Forest plots without *R.* maximum											
Total PPFD[2] (mmol m^{-2} day^{-1})	689	1034	632	647	7210	337	974	310	729*	114	794
Max PPFD (μmol m^{-2} s^{-1})	40	103	62	48	93	48	202	37	79.2*	19.5	65.8
# of events[3] > 100 μmol $m^{-2}s^{-1}$	21	37	14	13	43	3	13	2	18.3*	5.25	27
Forest plots with *R maximum*											
Total PPFD (mol m^{-2} day^{-1})	121	160	167	115	88	182	182	112	141	12.9	112
Max PPFD (μmol m^{-2} s^{-1})	3	4	39	6	2	13	42	22	16.4	5.74	6.2
# of events > 100 μmol m^{-2} s^{-1}	0	0	1	0	0	2	2	1	0.75	0.31	0

[1] Data recorded at one permanently installed quantum sensor; [2] PPFD = photosynthetic photon flux density; [3] event = mean value for a 10 minute period; * = significant difference between means of photo-diode data for the two forest types ($P < 0.01$)

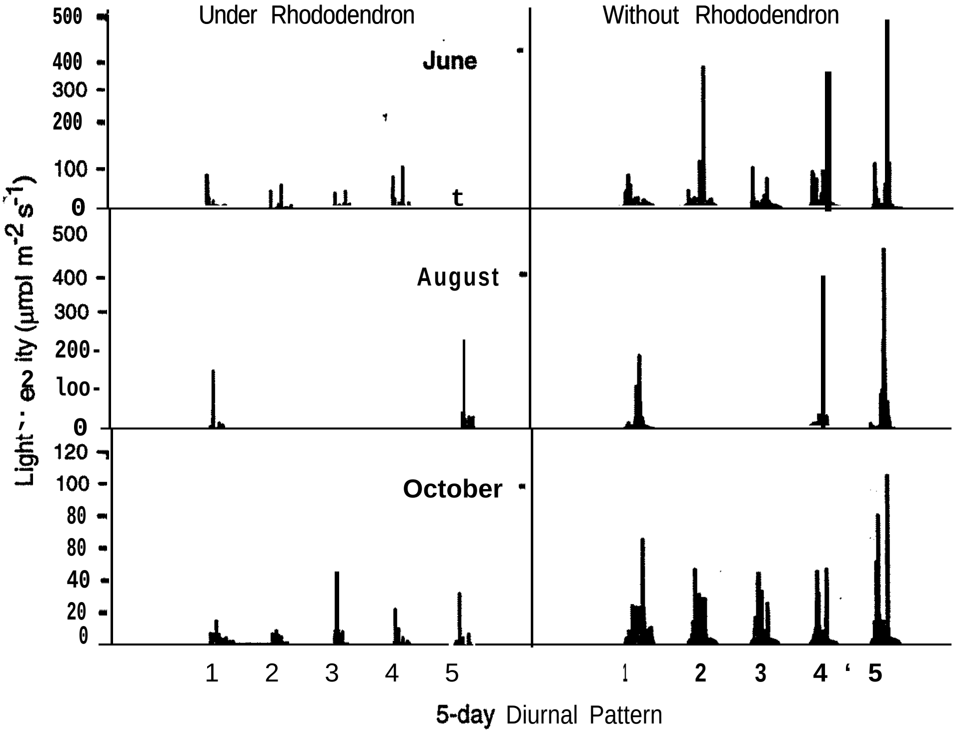

FIG. 2.-Representative variation in diurnal cycles of photosynthetically active radiation in the subcanopy of a southern Appalachian forest, Each horizontal pair of panels represents a 5 d period in June, August or October when light intensity was measured simultaneously at the two sites. Steep vertical spikes in the day cycles illustrate the frequency and intensity of sunflecks

maximum PPFD in the -Rm weather station was 10-15 µmol m^{-2} s^{-1}, while the mean maximum PPFD was 2–4 µmol m^{-2} s^{-1} in the +Rm weather station (Fig. 3A). During the winter and early spring (January-May) mean maximum PPFD increased to above 120 µmol m^{-2} s^{-1} at the -Rm weather station but remained below 30 µmol m^{-2} s^{-1} at the +Rm weather station. The monthly mean maximum PPFD was higher in the -Rm weather station compared with that of the +Rm weather station over all months measured. In contrast, there was no difference in the monthly mean minimum radiation between the two forest types during the summer.

The mean maximum relative humidity throughout the year varied from 95% in August to 70% in April, and the mean minimum relative humidity decreased to 63% in April, indicating a drier and more variable level of RH in the spring (when seed germination is occurring) compared with the summer and fall (Fig. 3B) regardless of forest type. There was no significant difference in maximum, minimum and mean relative humidities between the two forest types throughout the year. Mean monthly midday air temperature during the growing season varied from 21 C to 16.0 C (data not presented), and spring (March-May) mean monthly midday air temperatures ranged between 10 C and 14 C in both forest types. Moreover, there was no forest type effect on mean maximum or mean minimum monthly air temperature during all months sampled (Fig. 3C).

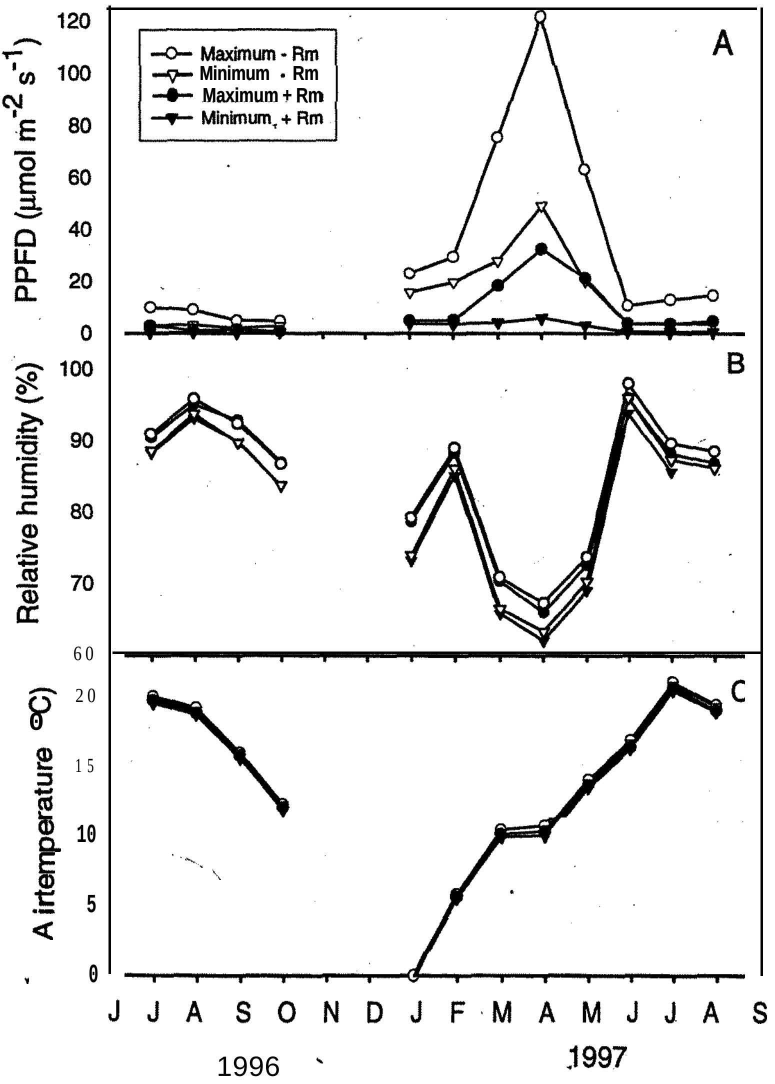

FIG. S.-Daily maximum and minimum PPFD (A), relative humidity (B) and air temperature (C) averaged by month in southern Appalachian forest sites with (closed symbols) or without (open symbols) a thicket of *Rhododendron* maximum

Soil moisture decreased from its highest value at the beginning of the growing season in April to its lowest value in July in both forest types (Fig. 4). Following the low point in July soil moisture increased through the rest of the growing season. There was a significant temporal variation in soil moisture (Pillai's trace = 0.94, $P < 0.001$). The temporal variation between forest and Rhododendron maximum sites also was significant (Pillai's Trace = 0.15, $P = 0.01$), but the interaction term between season and forest type was not significant. These statistical results verify that soil moisture in the +Rm forest plots was significantly lower than that of the −Rm forest plots throughout the growing season.

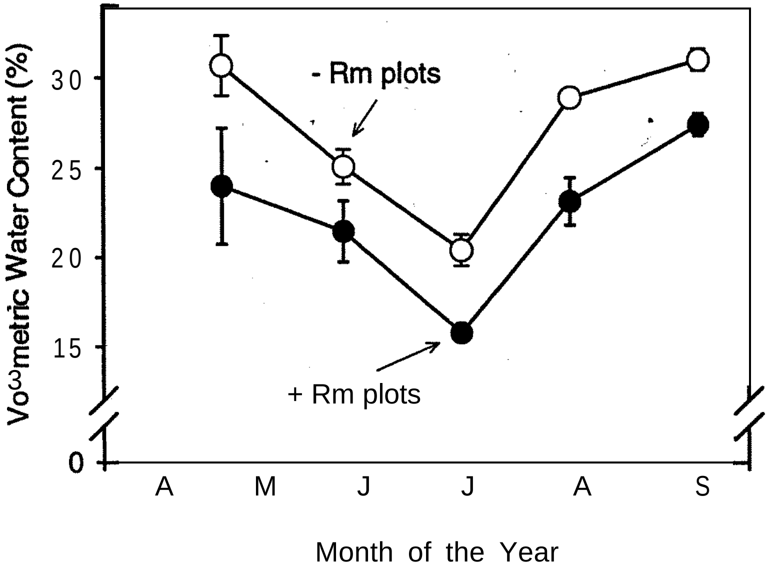

FIG. 4.—Soil moisture content at a depth of 0-15 cm in southern Appalachian forest sites with (+Rm) or without (−Rm) a thicket of *Rhododendron maximum*. Each point refers to a mean of 45 samples. Error bars refer to one standard deviation

SPATIAL VARIATION IN RESOURCES

All indices of canopy openness derived from canopy photographs were significantly different between forest types and among locations (Table 2). Moreover, the means of all light indices were lower in +Rm plots. However, there was a large overlap in the range of values for light indices between forest types. In fact, 8 of the 30 brightest plots were +Rm plots and 11 of the dimmest 30 plots 'were -Rm plots. Therefore, microsites for seedlings under *Rhododendron maximum* thickets are significantly, but not universally, shadier than forest outside the thickets.

Mean volumetric soil moisture was significantly lower in +Rm plots compared with −Rm plots and there were no location effects on moisture availability (Table 2). The difference of 4.5% in volumetric soil moisture between forest types in July is similar to the difference in soil moisture between forest types found throughout the growing season (Fig. 4). Therefore, the water availability values obtained in July can be used to represent the entire growing season.

All soil samples were acidic with pH ranging between 4.5 and 5.2. There'was a significant difference in soil pH between forest types and among locations, but that difference was small on the log scale (Table 2). These soils were characterized by high extractable aluminum and iron averaging 630 and 40 ppm, respectively, as is true of many other acidic soils. Among heavy metal species only Cu, Zn and Mn had significantly different concentrations in the two forest types (Table 2). Copper content of the soil was higher whereas Mn and Zn concentrations were lower in +Rm plots compared with -Rm plots. All heavy metals measured in this study except boron showed significant effects of location.

The carbon content in the soil of this forest ranged between 2.0 and '7.5%. There was no significant effect of location on % soil carbon or % soil nitrogen in either forest type. The mean carbon content of soil in +Rm forest type was significantly lower than that of

TABLE P.-Measurement of resource availability in forest types with a thicket of *R maximum* present (+Rm) and without (−Rm). Values are means of 15 plots in 3 locations in each forest type (n = 45 per forest type) ± standard deviation. Soil pH, volumetric water content and nutrient concentrations for mineral soil are measured at a depth of 10-15 cm. P values represent significance effect of forest type or location as evaluated by analysis of variance nested design (df, 1, 4). P values below 0.01 are considered significant

Resource	Units	Mean		P values	
		+Rm	−Rm	Forest type	Location
Weighted canopy openness	%	1.334 ± 0.19	1.786 ± 0.23	0.001	<0.0001
Indirect site factor	mol m^{-2} mon^{-1}	3.077 ± 0.41	4.119 ± 0.54	0.001	<0.0001
Direct site factor	mol m^{-2} mon^{-1}	9.26 ± 2.22	14.9 ± 4.16	0.006	0.001
Soil water	%	15.91. ± 0.92	20.51 ± 1.42	<0.0001	0.264
P H		4.75 ± 0.02	4.85 ± 0.05	0.001	<0.0001
Soil carbon	% of soil mass	3.55 ± 0.38	4.41 ± 0.32	0.001	0.031
Soil nitrogen	% of soil mass	0.16 ± 0.01	0.20 ± 0.02	0.0002	0.068
soil C/N ratio		22.2 ± 0.12	22.0 ± 0.15	0.820	<0.0001
Soil nitrate (NO,)	ppm	0.093 ± 0.078	0.0154 ± 0.022	0.035	0.619
Soil ammonium (NH_4)	ppm	1.43 ± 7.61	1.86 ± 6.60	0.103	0.451
N-mineralization	Mg N kg^{-1} soil	5.96 ± 5.05	8.61 ± 2.80	0.754	<0.0001
Soil phosphorus	ppm	0.01 ± 0.051	0.02 ± 0.130	0.167	0.463
Soil potassium	ppm	32.73 ± 2.24	43.42 ± 3.38	0.0001	0.580
soil calcium	ppm	32.80 ± 2.68	51.73 ± 6.24	<0.0001	<0.0001
Soil magnesium	ppm	13.08 ± 0.88	17.66 ± 1.04	<0.0001	0.002
Soil manganese	ppm	2.92 ± 0.42	5.65 ± 0.38	<0.0001	<0.0001
soil zinc	ppm	1.06 ± 0.08	1.54 ± 0.10	<0.0001	<0.0001
Soil aluminum	ppm	623.0 ± 33.0	640.6 ± 33.5	0.391	<0.0001
soil iron	ppm	40.92 ± 2.53	38.24 4 2.68	0.160	0.001
Soil copper	ppm	0.67 ± 0.05	0.56 ± 0.04	<0.0001	<0.0001
Soil boron	ppm	0.12 ± 0.01	0.13 ± 0.01	0.031	0.619

soil in -Rm forest type (Table 2). Soil nitrogen concentrations ranged from 0.1 to 0.34% and the mean N content of soil was lower in +Rm plots than that in −Rm plots. The mean carbon/nitrogen ratio (22.1) was consistent among samples (range was 21–22.5), and there was no significant effect of forest type. Extractable nitrate was often undetectable in soil samples while extractable ammonia ranged from 0.5 to 2.0 ppm. There was no significant difference between extractable nitrate or ammonium pools between forest types (Table 2). Nitrogen mineralization rates ranged between 3 and 10 mg N kg^{-1} soil and the average N mineralization rate was not significantly different in soil from +Rm plots compared with that from -Rm plots (Table 2), but there was a strong location effect on nitrogen mineralization rates. Extractable phosphorus (P) concentrations ranged from undetectable to 1.6 ppm. The mean concentration of P in the soil was close to zero in both forest types and not significantly different among locations or between forest types.

Extractable soil cation concentrations (K, Ca, Mg) were all significantly lower in +Rm plots than that in −Rm plots (Table 2). Differences in cation concentrations (considered as a group) between the two forest types were larger and more significant (lower P value) than that of any other group of plant nutrients.

SPATIAL CORRELATION AMONG RESOURCES

Many of the resources measured were significantly correlated with each other. We present only those resources that were significant to oak survivorship (Table 3). Weighted canopy

TABLE J.-Pearson correlation coefficients between resources measured in a southern Appalachian forest containing a subcanopy of Rhododendron maximum. The correlations are calculated based on data collected in +Rm plots and −Rm plots. Significant correlations are indicated by asterisks

	WCO[1]	ISF[2]	Water[3]	C	N	K	Ca	Mg	Zn	PH
WCO	1.000									
ISF	0.476***	1.000								
Water	-0.015	0.215	1.000							
C	0.118	0.164	0.292*	1.000						
N	0.163	-0.014								
K	0.037	-0.038	0.237*	0.217***	0.297*	1.000				
Ca	0.287*	0.220	0.131	0.291*	0.428***	0.431***	1.000			
Mg	0.055	0.115	0.314*	0.273*	0.400***	0.665***	0 649***	1.000		
Zn	0.137	0.200	0.377**	0.346**	0.316*	0.469***	0.394**	0.664***	1.000	
PH	0.240*	0.203	0.328**	0.197	0.237*	-0.067	0.313*	0.184	0.314*	1.000

[1] WCO = Weighted Canopy Openness calculated from a canopy photograph in July

[2] ISF = Indirect Site Factor calculated from a canopy photograph in July

[3] Water = Soil volumetric water content at 10-15 cm in July

* = $P < 0.05$, ** = $P < 0.01$, *** $P < 0.001$

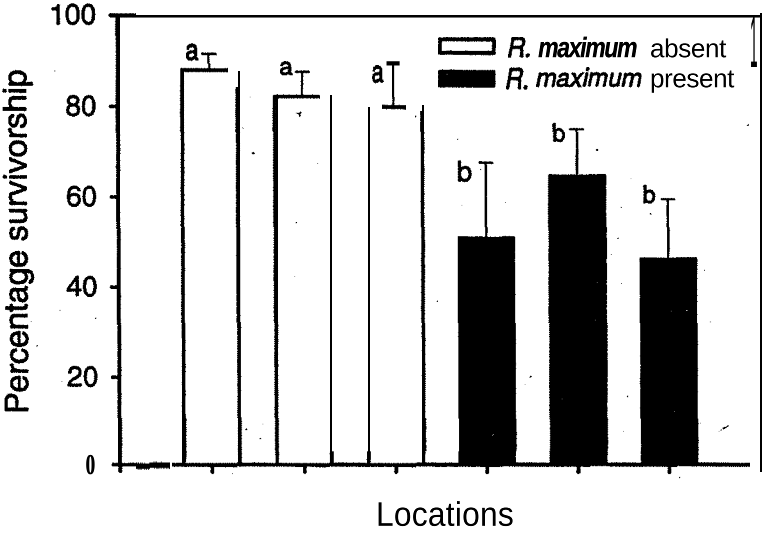

FIG. 5.—*Quercus rubra* seedling survivorship after 2 y of growth in southern Appalachian forest either with or without a thicket of *Rhododendron maximum.* Mean survivorship is calculated on the basis of five seedlings in each of 15 plots at each location. Significant differences among locations were determined by ANOVA with a nested design (degrees of freedom for location = 4) and $P < 0.01$

openness (WCO) was strongly correlated with indirect site factor (ISF) and was weakly correlated with soil calcium and soil pH. Indirect site factor was significantly correlated only with WCO. Soil water content was moderately correlated ($P > 0.001$) with Zn concentrations and soil pH and weakly correlated ($P > 0.01$) with a several other soil characteristics (C, N, IS, Mg). Total soil C and N were highly correlated ($P < 0.001$) with each other and moderately to weakly correlated with all other soil parameters. The concentrations of cations (Ca, IS, Mg,) were all highly correlated with each other and only weakly correlated with other soil nutrients. Soil heavy metals concentration (Mn, Fe, Cu, Al, Zn) were moderately correlated with each other (data not presented), and among those elements only Zn was correlated with many other resources (Table 3).

CLIMATIC VARIABLES AND SEEDLING SURVIVORSHIP

Mean seedling survivorship was 89% and 50% in -Rm and +Rm plots, respectively (Fig. 5) and was significantly different ($P < 0.0001$). Survivorship of *Quercus rubra* seedlings in all +Rm locations was significantly lower than that of the -Rm locations (Fig. 5). Based on a five variable best fit regression procedure (R-Square selection method), the resource variables most associated with the variance in oak seedling survivor-ship (in order of most to least important) were: weighted canopy openness, soil water availability, indirect site factor, soil zinc concentration and soil carbon or nitrogen concentration. Additionally, a stepwise regression selected water availability, indirect site factor, zinc concentration, soil carbon content and soil calcium availability (in order of importance) as the five most significant resource variables.

Analysis of covariance.—The resource variables identified by the best-fit and stepwise regression procedures were used in an analysis of covariance. ANCOVA was used to test if any resource variable had a significant regression with seedling survivorship, if that relationship

TABLE 4.—P values from ANCOVA for the effects of forest type (with or without a thicket of *Rhododendron maximum*) on the relationship between resource availability and *Quercus rubra* seedling survivorship. Only variables that were included in the best five variable models (maximizing R^2 method) for explaining the variance in *Q. rubra* survivorship are shown. P values less than or equal to 0.01 are considered significant

	Resource						
	ISF[1]	WCO[2]	water[3]	Zn	C	N	Ca
Effect of resource	0.001	0.001	0.013	0.206	0.277	0.200	0.008
Effect of forest type[4]	0.001	<0.001	0.003	0.003	0.301	0.485	0.652
Resource * Forest type	0.008	0.008	0.045	0.089	0.348	0.247	0.005

[1] ISF = Indirect Site Factor

[2] WCO = Weighted Canopy Openness

[3] Water = volumetric soil water content in July

[4] Forest type = forest site with or without a subcanopy thicket of *R. maximum*

was different in forest types and if the regressions were influenced by other resources. The results showed that weighted canopy openness, indirect site factor, water availability and soil calcium concentration had significant effects on seedling survivorship (Table 4). This result means that the regressions formulated between these site factors and *Quercus rubra* seedling survivorship (for each forest type) were significantly different from zero. In addition, forest type had a significant effect on *Q. rubra* survivorship response to weighted canopy openness, water availability, indirect site factor and soil zinc availability (Table 4). These results indicate that the y intercepts of the regressions formulated between these site factors and *Q. rubra* seedling survivorship are different between forest types. Moreover, the interaction term between site factor and forest type was significant for weighted canopy openness, indirect site factor, water availability and calcium availability (Table 4). These results indicate that the slopes of the two regressions (one for each forest type) for the listed site factors and *Q. rubra* seedling survivorship were significantly different. Therefore, in the case of three variables (weighted canopy openness, indirect site factor and water availability) their association with *Q. rubra* seedling survival is significant and the presence of the *Rhododendron maximum* thicket changes the slope and y intercept of the regressions. In the case of soil zinc concentration, there is no significant relationship with seedling survivorship, but there is a significant difference in zinc concentration in the soil of the two forest types. In the case of calcium, there is a significant relationship with seedling survival and the presence of a thicket of *R. maximum* changes the slopes (but not the y intercept) of the regressions. Neither carbon nor nitrogen in the soil had a significant regression with. *Q. rubra* seedling survivorship and there was no significant influence of *R. maximum* on those regressions.

DISCUSSION

RESOURCE AVAILABILITY

It is commonly held that reduced light availability is the overriding effect that subcanopy, evergreen thickets have on resource availability for seedlings of canopy trees. The results of this study showed that light was an important resource for tree seedlings growing in forest harboring *Rhododendron maximum,* but other resources such as soil water content may be equally or more important than light. Also, our results showed that during the growing season light intensity was commonly below 5 μmol m^{-2} s^{-1} (about 0.25% of full sunlight) during daylight under the *R. maximum* thickets. These intensities are characteristic of extremely low light availability and are below the light compensation point of photosynthesis for many woody seedlings of the eastern deciduous forest (Larcher, 1995; Semones, 1999). Diffuse radiation in the forest without a thicket of *R maximum* averaged only 40 µmol m^{-2} s^{-1} (about 2% of full sunlight) which is close to the light compensation point of many tree seedlings. Diffuse light availability in these forest sites without *R. maximum* is as low as the lowest treatments (2%) used in many studies of low light adaptation. Thus, most seedlings would not be able to attain adequate photosynthate for growth, without the use of sunfleck radiation in either forest type included in this study. The number of sunflecks, their intensity and their duration were higher in forest without a thicket of *R.* maximum. However, there were infrequent sunflecks below *R* maximum thickets that attamed values close to 200 µmol m^{-2} s^{-1} for a short time (from a few seconds to minutes). Although sunflecks are relatively less frequent in +Rm plots, use of sunfleck radiation is likely to be absolutely critical for seedling survival in the under a *R.* maximum thicket.

The lowest light conditions (including sunfleck light) were not universally found in +Rm sites and the highest light availabilities were not universally found in -Rm sites. The variation in light availability should have allowed some seedlings to survive in +Rm areas and have precluded some seedlings from surviving in −Rm sites. Therefore, subcanopy evergreen shrubs did not completely obliterate available light, and there were “safe sites” with higher potential radiation under the thickets. Light availability ought not’ to be thought of as the only factor inhibiting seedlings in forest containing Rhododendron *maximum* thickets.

There was no question that water availability was lower throughout the growing season under a thicket of *Rhododendron* ma&mum. The 6% difference in soil moisture that was found between forest types constitutes a 20% reduction in water availability for seedlings growing under *R maximum* thickets compared to those growing in forest without *R maximum.* This lower soil moisture in +Rm plots is most likely due to plant processes (increased evapotranspiration) rather than soil drainage processes because there was no difference in slope or soil texture between forest types.

The soil solution at this site was extremely low in available N (NO_3^-, NH_4^+) and P (PO,-). Since these nutrient resources are so low, it is likely that competition for these resources occurs between the *Rhododendron maximum* thicket and canopy tree seedlings. The amounts of these resources in the available soil solution were not significantly different between forest types, and nitrogen mineralization rates also were similar, indicating that forest with or without thickets of *R* maximum were drawing down the availability of these primary limiting resources in the mineral soil to a similar degree. However,‘ectomycorrhizae are important for optimal accumulation of N, and especially P, when these nutrients are at low availabilities. Our previous research has shown that ectomycorrhizal colonization of seedlings under thickets of *R* maximum is inhibited relative to seedlings in forest without *R maximum* (Walker et al., 1999). The low availability of major plant nutrients and the inhibition of mycorrhizal colonization make it likely that the presence of *R.* maximum reduces the ability of canopy tree seedlings to compete for soil nutrients.

Accumulation of other resources, such as cations, is not as dependent upon mycorrhizae as accumulation of nitrogen or phosphorus ions. Cation concentrations in soils in +Rm plots were particularly heavily depleted (relative to other nutrients) compared to -Rm plots. These results agree with data on nutrient accumulation by *Rhododendron maximum* collected in the same region as this study (Monk et al., 1985). The leaf mass of *R* maximum stores a large quantity of cations such as Ca and Mg but does not retain a large quantity of N and P (Monk et *al.*, 1985). Therefore, it is likely that the presence of a *R. maximum* thicket depletes the availability of cations in the mineral soil because of the retention of those nutrients in the shrub biomass.

RESOURCES MOST ASSOCIATED WITH *Q. RUBRA* SEEDLING SURVIVORSHIP

Survival of *Quercus rubra* seedlings was significantly correlated with light availability, but this relationship was not the same in forest with or without a thicket of *Rhododendron* maximum according to ANCOVA (Table 4). Therefore, some other factors must be involved in inhibiting seedling survivorship. Other aboveground factors (temperature and humidity) were not likely to be important because they did not differ significantly between forest types. In this study there were many belowground factors that differed between forest types, and these factors are, candidates for inhibition of seedling survivorship. Indices of light availability were not correlated with most soil nutrient traits or water, but many of those belowground traits were highly correlated with *Q. rubra* seedling survivorship. Thus, the belowground factors may act independently or synergistically with light availability on seedling survivorship.

It is well known that the response of species to belowground resources is dependent primarily upon light availability (see Robe *et al.*, 1995; Walters and Reich, 1997). For example, nitrogen amendment had *no* significant effects on seedling growth traits at 2% *or* 8% of maximum irradiation whereas the effect of light was highly significant (Walters and Reich, 1996). Results from many studies in forests and woodlands suggest that if light availability is below 2% of daylight, little response in tree seedling performance to belowground resources is expected (Coomes and Grubb, 2000). Based on the availability of diffuse radiation in our forest system (0.25% and 2% of daylight for sites with and without Rhododendron *maximum,* respectively) little to no response to belowground resources is expected. Yet, in our study, belowground factors did have a significant influence on seedling performance.

The second factor most associated with seedling survivorship in this study was water availability. Low soil moisture availability may limit the ability of subcanopy seedlings to keep stomata fully open during sunflecks (Knapp and Smith, 1990; Tinoco-Ojanguren and Pearcy, 1993), thereby reducing the ability of seedlings to maximize carbon gain during sunflecks. Consequently, lower soil moisture content under *Rhododendron* maximum thickets may exacerbate the effect of light limitation by reducing seedling effectiveness in using sunflecks. Additionally, Clinton and Vose (1996) implicated lower soil moisture conditions under *R. maximum* thickets in reduced seed germination and seedling survival of *Acer rubrum.* They concluded that higher porosity of the organic mat below *R.* maximum thickets (compared with other forest sites) resulted in faster dry-down periods following rain, resulting in des sication of seed radicals following emergence. An alternative hypothesis is that the evapotranspiration from the *R. maximum* leaf area increases water extraction from the soil compared to a forest without a thicket of *R. maximum.* As a result of either (or both) of these mechanisms, seedling establishment below *R.* maximum thickets could be inhibited by water stress during germination and during early seedling growth. This possibility is supported by our best two-factor regression model (WCO and water) and by the first two steps of the stepwise regression procedure (water and ISF). The association between seedling survivorship and water was also significantly affected by forest type. Therefore, limitation by water availability could not itself explain the difference in seedling survivorship in and out of *R.* maximum thickets.

The third most important factor associated with seedling survival was soil zinc availability. The zinc concentration of the soil was highly correlated with water availability so it is not surprising that zinc was highly associated with *Quercus rubra* seedling survival. Zinc concentration was also highly correlated with a number of other nutrients such as manganese, potassium, calcium and magnesium that were all significantly lower in plots containing

Rhododendron maximum than plots free of *R maximum.* Moreover, analysis of covariance showed that soil zinc concentration by itself was not significantly correlated with *Q. rubra* seedling survival. Therefore, the high correlation of zinc concentration in the soil with *Q. rubra* seedling survivorship could have represented a general cation effect, or a water effect, rather than a specific zinc effect.

This study has shown that both above- and belowground resource availability to tree seedlings is significantly reduced by Rhododendron maximum. Light availability was the aboveground factor that most influences the survivorship of *Quercus rubra* seedlings. However, the relationship between seedling survivorship and light was significantly different between sites ‘with or without a thicket of *R* maximum. Therefore, belowground processes related to the presence of *R* maximum were important to seedling survivorship. Water was one of those factors, and the combined effect of low cation availability may be another. Moreover, soil P limitation also may be important because P availability was zero and mycorrhizal synthesis is inhibited by *R maximum.* Therefore, this study supports the idea that *R maximum* inhibits forest regeneration by depleting light, water and cations in the microsites where canopy tree seedlings germinate.

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