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Effects of *Rhododendron maximum* L. on *Acer rubrum* L. Seedling Establishment

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ABSTRACT

Rhododendron maximum L. restricts regeneration of overstory species; however, the mechanisms are poorly understood. Three treatments were used to examine the effects of *R.* maximum germination success and survival of *Acer rubrum* L. under a closed overstory canopy: (1) *R. maximum* understory, (2) open understory, and (3) open understory with shadecloth. Shadecloth treatments mimicked the low light conditions beneath *R. maximum* (<5 % full sun) while controlling for *R. maximum* forest floor influences. Soil moisture was significantly lower under *R. maximum* than under open or shadecloth treatments. Initially, *Acer rubrum* survival was similar for open understory and shadecloth treatments, while germination and survival in *R. maximum* plots were low. After approximately 20 d, mortality in the shadecloth treatment increased and survival rates were less than 5% by the end of the sampling period. Survival in the open understory treatment stabilized at >2× that observed under shadecloth, while percent germination and survival in *R.* maximum plots were lower than in either of the other treatments throughout the sampling period. These results suggest that in addition to the light limitation associated with *R. maximum*, edaphic effects such as low soil moisture or allelopathic compounds may inhibit *Acer rubrum* success.

INTRODUCTION

Tree replacement after small scale disturbances in the southern Appalachians depends on successful seed germination and seedling establishment. Woody seedlings and saplings present in the understory before disturbance have an advantage over species attempting to colonize after a disturbance. The ability of understory-tolerant and intermediately tolerant species to become established under a continuous overstory canopy is basic to this process. However, beneath dense understories of the evergreen shrub L., germination and establishment of even the most understory-tolerant species is limited (Phillips and Murdy 1985) and inversely related to ***R. maximum*** abundance (Baker 1994).

Fire and grazing, common in the southern Appalachians before the 1920's, probably prevented ***R. maximum*** from becoming an important competitor (Hertzler 1936, Douglass and Hoover 1988). Monk et al. (1985) found that few ***R. maximum*** stems in the Coweeta Basin date back to the mid-1920's. Coincident with increasing public ownership in the Appalachians during the 1920's, fire suppression, limited livestock grazing, and the chestnut blight may have contributed to increased dominance in the understory (Woods and Shanks 1959). Recent surveys at the Coweeta Hydrologic Laboratory (Coweeta) located in western North Carolina show that ***R. maximum*** currently occupies 20% of the land area (M. Dobbs, pers. comm.) and forms pure stands in some areas.

The influence of ***R. maximum*** on tree replacement processes (Minckler 1941, Phillips and Murdy 1985) and microclimatic conditions (Romancier 1971) has long been recognized. Where timber production is the objective, silvicultural treatments are commonly prescribed to reduce the competitive influence of ***R. maximum*** and other evergreen shrubs (Clinton et al. 1993, Vose and Swank 1993). However, even though qualitative information on impacts of ***R. maximum*** is substantial, mechanisms associated with the influence of ***R. maximum*** on germination, establishment, and the physiological processes that ultimately determine tree seedling fitness are poorly understood.

Several hypotheses have been advanced to explain these mechanisms; low light levels, litter depth and quality, competition for water and nutrients, and allelopathy. Because the crown of ***R. maximum*** is dense, limited light penetration is the most obvious explanation. At Coweeta, the levels of incident photosynthetically active radiation (PAR; 400-700 nm) under ***R. maximum*** sub-canopies are 14-34% of those observed in the surrounding non-R. ***maximum*** forests (Clinton 1995), which are ≈15% of full sun. Forest floor characteristics also differ substantially between ***R. maximum*** and non-R. ***maximum*** areas. Because its foliage is sclerophyllous (Monk et al. 1985), ***R. maximum*** litter decomposes slowly and a thick (≈ 10 cm) litter layer develops. This thick litter layer dries out quickly and may induce moisture stress, act as a physical barrier preventing seeds from reaching mineral soil, or both, thus reducing the potential for seed germination (Plocher and Carvell 1987). ***Rhododendron maximum*** produce allelopathic compounds, which can inhibit germination and establishment of tree species (Yang and Wang 1978, Pittillo 1980, Nielson 1980, Wang and Yang 1981). These compounds have at least four potential sources: 1) litter decomposition, 2) root decomposition 3) root exudates, and 4) leaf exudates.

Acer rubrum L. is an important component of southern Appalachian forests. It currently occupies 10% of the basal area in the Coweeta Basin, has the highest density among canopy trees (Clinton 1989), and has widespread distribution. In addition, *Acer rubrum* has a high germinative capacity (85–91%; McDermott 1953). This study examines differences in seed germination and seedling densities of *Acer rubrum* beneath closed understories of ***R. maximum*** and in open understories. and relates these differences to the microenvironment.

METHODS

Site Description

This study was conducted at Coweeta (35°03′N, 83°25′W), located in the Blue Ridge physiographic province of the southern Appalachians near Franklin, North Carolina. The soils are primarily Ultisols (Typic and Humic Hapludults) and Inceptisols (Umbric and Typic Dystrochrepts and Typic Haplumbrepts;

Velbel 1988). Mean annual precipitation ranges from 178 cm at low elevations (670 m) to over 250 cm at high elevations (1,600 m), with less than 5% falling as snow or ice. Precipitation is usually distributed evenly throughout the year. Mean annual temperature is approximately 13°C and ranges from -18°C in January to 24°C in July (Swift et al. 1988). The study site is located in an upper cove at an elevation of 1,020 m, has an approximate SE aspect, and is moderately sloping (≈ 25”). The overstory canopy is closed and primarily comprised of *Quercus prinus* L. (chestnut oak), *Q. rubra* L. (northern red oak), *Liriodendron tulipifera* L. (yellow poplar), and *Acer rubrum* (red maple).

Experimental Design

Three replicates of three treatments were used: 1) dense *Rhododendron maximum* cover, 2) open understory, and 3) open understory with shadecloth. Shadecloth type was selected based on its ability to reduce light by 78% and allow precipitation to pass through. Shadecloth was intended to duplicate the light conditions (i.e., photosynthetically active radiation; 400-700 nm) found beneath *R. maximum* understories. Furthermore, shadecloth provided the means to separate responses due to edaphic and allelopathic influences from responses due to low light. We did not test for differences in light quality among treatments; however, we recognize that light quality might be an additional variable influencing seedling physiology.

Seeds from mature *A. rubrum* were collected during the spring of 1994. Because no pre-germination treatment is required for *A. rubrum* seeds (Schopmeyer 1974), collected seeds were planted immediately (i.e., late may 1994). *Acer rubrum* germination extends from April through July (Schopmeyer 1974). For each treatment, 6 seeds were planted directly into the forest floor/soil matrix at a depth of 0.5 cm on an approximate l-m spacing at nine locations within each of three replicates. In addition, a known number of seeds were broadcast in two, 1-m^2 patches in open and *R. maximum* understories to determine germination success without physically planting the seeds. Two additional “blank” 1-m^2 plots in open and *R. maximum* understories were used to assess *A. rubrum* germination rates from surrounding seed sources. Plots were inventoried at 2- to 5-d intervals from early June through late August. During each inventory, seedlings in each plot were counted. No attempts were made to assess germination or survivorship of specific individuals. Thus, net seedling densities reflect the combined effects of germination, mortality, and seed predation.

To characterize the microenvironment, soil moisture was measured (4 pairs TDR rods at 15-cm depth on each *R. maximum* and non-R. *maximum* site) with time domain reflectometry (TRASE®, Soil Moisture Equipment, Inc.‘). Incident photosynthetically active radiation (PAR; 400-700 nm; Decagon Sunfleck Ceptometer,[1] Pullman, Washington) was quantified at the terminal of each seedling by taking the average of several readings, and soil temperature (upper 5 cm) was determined using a digital soil temperature probe. Microenviromental measure-

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[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Table 1. Means of photosynthetically active radiation (PAR; μmol $m^{-2}sec^{-1}$), soil temperature (°C at 5 cm depth), and soil moisture (% < 15 cm depth) with associated test statistics. Means within rows with the same superscript are not significantly different. Values in parentheses are standard errors

	Rhodo	**Open**	**Shade**	**P > F**
PAR	11.8’ (1.60)	123.9^b (22.3)	32.8’ (3.30)	0.006
Soil Temperature	16.7’ (0.05)	18.7” (0.18)	17.9^c (0.24)	0.001
Soil Moisture	22.2’ (1.17)	35.7^b (2.16)	31.7^b (3.70)	0.014

ments were made when seeds were planted and periodically during the seedling census period.

Statistical Analysis

Differences in mean seed germination, seedling survival rates, and microclimatic variables among treatments were evaluated with analysis of variance (PROC ANOVA; SAS 1987). Where significant differences were found, Duncan’s multiple range tests (SAS 1987) were used to separate means.

RESULTS

Microclimate

Significant differences were observed for all microclimatic measurements (Table 1). Incident PAR was significantly lower in shadecloth and *Rhododendron maximum* treatments than in the open understory treatment. Soil temperature was significantly different across all treatments (open > shadecloth > *R. maximum),* and the greatest difference was found between *R. maximum* and open understory (Table 1). No difference in soil moisture was found between open and shadecloth treatments; however, soil moisture was substantially lower in the *R. maximum* treatment than in the other two treatments.

Seedling Density

Germination of seeds planted in the mineral soil began in mid-June. No germination of *A. rubrum* from surrounding natural seed sources occurred in the blank plots; therefore, adjustment for germination of planted seeds was not necessary. In addition, seeds broadcast on top of the forest floor did not germinate. Initial seedling density was significantly lower in the *R. maximum* compared to the open and shadecloth treatments (Figure 1). The number of seedlings increased with time in the open and shadecloth treatments, but declined immediately under *R. maximum,* where it remained lower for the remainder of the sampling period. The numbers of seedlings in the open and shadecloth treatments were similar ($\approx$ 1 seedling m^{-2}) for approximately 3 wk, when the number of seedlings under shadecloth began to decline at a faster rate than in the open. By the end of the

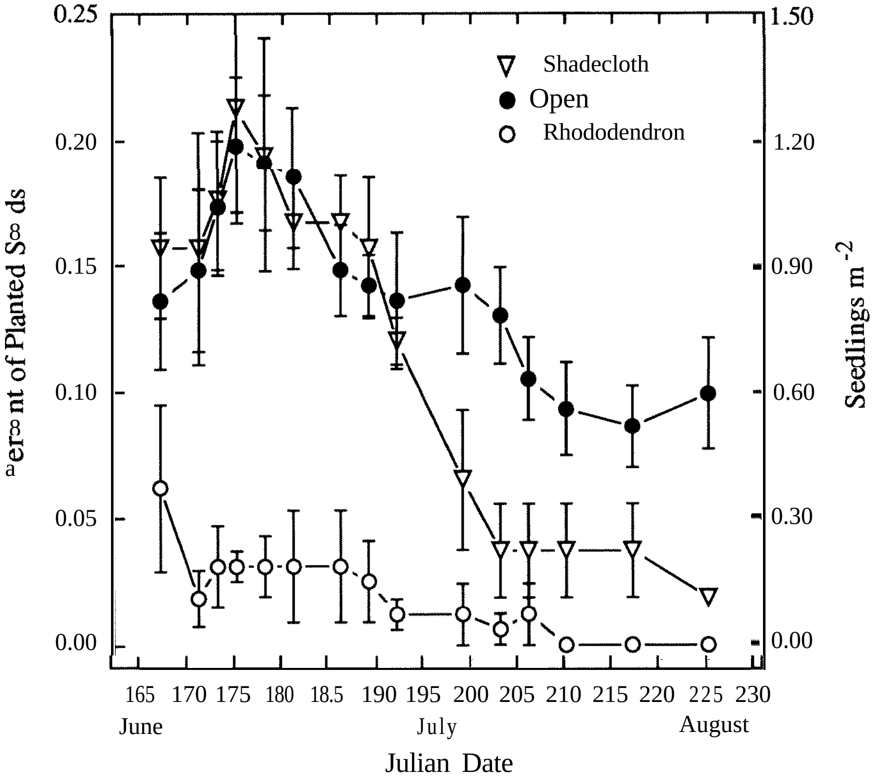

Figure 1. Survival of planted seeds (%) and equivalent seedling density (stems m^{-2}) by sample date for shadecloth, open, and *Rhododendron* maximum treatments. Error bars represent one standard error.

sampling period, seedling density under shadecloth had reached levels comparable to those under *R. maximum*. By mid-August, seedling density in the open treatment had declined but was still significantly greater than shadecloth or *R. maximum* plots.

DISCUSSION AND CONCLUSIONS

The lack of germination in the plots with seeds distributed on top of the forest floor suggests that *Acer rubrum* requires physical contact with the mineral soil, or that predators consumed exposed seeds before they could germinate, or both. If the former is true, then *A. rubrum* seedling establishment would most likely occur in areas with exposed mineral soil or after burial by animals. The thick litter layer beneath *Rhododendron maximum* adds an additional barrier to contact with the mineral soil (Plocher and Carvell 1987). Because no data on seed consumption by animals were collected, the importance of seed predation in regulating *A. rubrum* regeneration in these systems is unknown.

Because the shadecloth treatment maintained light levels comparable to those found beneath the effects of light can be separated from other factors. Although a three-fold (but not statistically significant) difference in PAR between ***R. maximum*** and shadecloth plots was found (12 and 33 μmoles m^{-2} sec^{-1}, respectively), this difference probably does not affect seedling survivorship. We base this conclusion on the results of a related study on similar sites (K.J. Elliott, pers. comm.), which showed no significant difference in ***A.*** *rubrum* seedling photosynthetic rates under light conditions comparable to the ***R. maximum*** and shadecloth treatments. The ten-fold difference in light levels between the ***R. maximum*** and open treatment plots is significant and indicates that light is a potentially important regulating mechanism in ***A.*** *rubrum* germination and survival. McDermott (1953) found no difference in ***A.*** *rubrum* seed germination under low and high light conditions, indicating that light does not affect the germination process for this species. Hence, the low initial seedling density in ***R. maximum*** (Figure 1) plots suggests that something other than light was responsible for the lack of germination in those plots. The small number of seeds that did germinate beneath ***R. maximum*** were unable to become established due to the combined effects of low-light levels and other potential above and belowground sources of inhibition.

Mortality under ***R. maximum*** began approximately 1 week after germination, while seedling survival patterns for open understory and shadecloth treatments were similar and did not show high mortality until approximately 3 weeks after germination. The divergence in seedling density between shadecloth and open treatments after the initial 3 wk may indicate accelerated mortality due to the cumulative effects of low light.

Differences in soil temperature between ***R. maximum*** and open understory plots did not likely influence germination. Soil temperatures observed in this study were higher than the average soil temperature (11.3%) beneath ***R. maximum*** in April observed in a separate study (Clinton, unpubl. data). Thus, although the temperature difference was statistically significant, the direct impacts on seedling germination were probably minimal because soil temperatures were well above those observed in April when ***A.*** *rubrum* seeds begin to germinate.

Differences in soil moisture between ***R. maximum*** and both the open and shadecloth treatments may explain low germination and survivorship beneath ***R. maximum.*** The porous humus layer beneath ***R. maximum*** contributes to low litter moisture and evapotranspirational losses (especially high interception) associated with ***R. maximum*** probably causes low soil moisture. Seedling establishment is limited under these conditions possibly because young seedlings desiccate before root systems become sufficiently developed.

Our results substantiate qualitative descriptions of restricted regeneration beneath ***R. maximum.*** Germination was extremely low (i.e., maximum of 0.35 seedlings m^{-2}) and by the end of the study, all seedlings had died. Results from the shadecloth treatment indicate that multiple factors may be responsible for the lack of seedling establishment. First, the extremely low seedling density in June beneath ***R. maximum*** relative to the shadecloth and open treatments indicates that germination may be restricted by factors other than or in addition to light. Low soil moisture beneath ***R. maximum*** is a potential regulating mechanism, but allelopathy, nutrient limitations, or both are equally plausible mechanisms. Future studies should separate the effects of moisture, nutrients, and allelopathy on germination and establishment.

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