Int. J. Plant Sci. 163(6):991–1000. 2002.
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1058-5893/2002/16306-0012$15.00

EFFECTS OF *RHODODENDRON MAXIMUM* THICKETS ON TREE SEED DISPERSAL, SEEDLING MORPHOLOGY, AND SURVIVORSHIP

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In the southern Appalachian forests, the regeneration of canopy trees is severely inhibited by *Rhododendron maximum* L., an evergreen understory shrub producing dense thickets. While light availability is a major cause, other factors may also contribute to the absence of tree seedlings under *R. maximum*. We examined the effects of *R. maximum* on several life history stages of tree species, including seed dispersal, seed bank germination, seedling growth, and survivorship. We found no significant effect of *R. maximum* on seed reaching the forest floor for *Acer rubrum*, *Liriodendron tulipifera*, *Quercus rubra*, *Quercus prinus*, *Carya* spp., and *Nyssa sylvatica*. This indicates that either seed output of maternal trees rooted within the thicket were unaffected by *R. maximum* or seed dispersal from surrounding areas into thickets compensated for a lower seed production of canopy trees rooted in the thickets. Germination of tree seeds (*A. rubrum*, *L. tulipifera*, *Q. rubra*, and *Betula lenta*) from the seed bank also was not reduced by leaves and substrates within the thickets. Seedling mortality of all species (*Q. rubra*, *Prunus serotina*, and *Tsuga canadensis*) planted in our experimental plots was up to fivefold higher in thickets of *R. maximum* compared with those outside the thickets. The order of mortality under the *R. maximum* thickets, *Prunus* > *Quercus* > *Tsuga*, was consistent with the shade tolerance ranking of these species. Loss of *Tsuga* seedlings was attributed to burial by litter rather than shade. Surviving seedlings of *Quercus* and *Prunus* in *R. maximum* thickets were taller than those outside the thickets, but the seedlings in *R. maximum* thickets produced significantly fewer leaves, smaller total leaf area, leaf mass, and stem mass. Leaf N (%) was significantly higher in *Quercus* seedlings in *R. maximum* thickets compared with seedlings outside the thickets. Moreover, no difference was found in leaf N (%) between forest types for *Prunus* and *Tsuga*, indicating that seedlings in *R. maximum* thickets were not N limited. Rather, light limitation, herbivory, and litter fall contributed to the lack of tree regeneration under *R. maximum* thickets.

Keywords: *Quercus rubra*, *Prunus serotina*, *Tsuga canadensis*, recruitment limitation, shrub understories, shade adaptation, southern Appalachian forest.

Introduction

The replacement of canopy trees by seedlings under an intact canopy is a major determinant of forest community dynamics. While seedling establishment is often assessed with reference to canopy disturbance (Canham 1985, 1988; Runkle 1990), environmental variation near the forest floor could be equally important (Cross 1981; Horsley 1993; Johnson-Maynard et al. 1998; George and Bazzaz 1999*a*, 1999*b*). Advanced regeneration (seedlings present on the forest floor before release by disturbance) can be an important component of canopy tree replacement during disturbance. Seedling establishment is dependent upon a succession of life history stages, including seed rain, seed germination, seedling establishment, and seedling growth and survival. Therefore, any factor that alters seed rain or microhabitat conditions on the forest floor may have a strong impact on the presence of advanced regeneration seedlings.

For instance, very few tree seedlings are found in the southern Appalachian forest when a thicket of the evergreen *Rhododendron maximum* L. shrub is present. In this region, *R. maximum* forms extensive thickets largely in cove forests and on north-facing slopes (Monk and Day 1985; Lipscomb and Nilsen 1990; Dobbs 1995). There has been a steady increase in the coverage of *R. maximum* in this region (Dobbs 1995) that coincided with the decline of the American chestnut (*Castanea dentata*; Anagnostakis and Hillman 1992). *Rhododendron maximum* grows more vigorously in disturbed sites, such as that created by the death of a chestnut in the canopy. Once established, *R. maximum* can aggressively expand into adjacent forest through root sprouting and branch layering forming a persistent thicket.

Along with *R. maximum*, several other ericaceous shrubs also have been found to inhibit forest regeneration (e.g., *Kalmia angustifolia*, Inderjit and Mallik 1996; *Kalmia latifolia*, Monk et al. 1985; *Rhododendron ponticum*, Cross 1981). A major cause of seedling mortality appears to be reduced light availability as exemplified by *R. ponticum* thickets in the oakwoods of Ireland (Cross 1981). Shade alone, however, did not explain the mortality of red maple seedlings under *R. maximum* (Clinton and Vose 1996). In addition to light limitation,

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Manuscript received October 2001; revised manuscript received June 2002.

seedling establishment under an intact forest may be affected by competition for soil moisture and nutrients, allelopathy, lack of appropriate mycorrhizae, predation, and pathogens (Augspurger 1984; Molofsky and Fisher 1993; Lorimer et al. 1994; Walters and Reich 1996; Canham et al. 1999; George and Bazzaz 1999*a*, 1999*b*). However, Nilsen et al. (1999) found no evidence for interference by allelopathy in the substrate of *R. maximum*. Under *R. maximum*, the availability of several resources is reduced relative to areas outside the thickets. These resources include light, cation concentrations, N mineralization rate, soil moisture, and mycorrhizae (Clinton et al. 1994; Clinton and Vose 1996; Walker et al. 1999; Nilsen et al. 2001). Lower belowground resources, possibly from sequestering of available nutrients by *R. maximum* roots (Monk et al. 1985), could affect both seedlings and adult trees. It is not known whether lower seed production in canopy trees rooted in *R. maximum* thickets may be the first factor contributing to the lack of seedlings. Even if seed dispersal into *R. maximum* is not reduced, the number of seedlings established may not necessarily be proportional to that of seed dispersed (Clark et al. 1998). The thick, slowly decomposing litter found under *R. maximum*, for example, may prevent germinating seedling radicles from reaching the soil, causing seedling death (Romancier 1971). The effect of forest litter on regeneration will be examined.

Once a seedling germinates, its ability to persist in a closed forest understory depends on a suite of traits associated with improving light interception and efficient resource use in the shade (Bjorkman 1981; Givnish 1988; Lei and Lechowicz 1998; Walters and Reich 1999). Differences in these traits among species can determine which are capable of regenerating in forest shade and which are not (Kobe et al. 1995). Adaptive changes in plant characters can range from the configuration of thylakoids to leaf morphology and whole plant architecture (Wild 1979; Björkman 1981; Corré 1983; Givnish 1988). It is expected that survivorship in increasing shade would be enhanced for those species with greater morphological acclimation. While the long-term failure of canopy tree seedlings to survive under *R. maximum* is known, we are interested in identifying the mechanisms for that failure and the adaptive limits of common temperate forest tree seedlings to severe resource limitation.

The aim of this study was to evaluate possible mechanisms by which *R. maximum* interferes with several life history stages from seed dispersal to seedling survival of three common southern Appalachian forest trees: *Quercus rubra* L., *Prunus serotina* Ehrhart, and *Tsuga canadensis* (L.) Carr. The following hypotheses were addressed: (1) seed dispersal into *R. maximum* thickets is lower than that outside the thickets; (2) there is a smaller seed bank of tree species under *R. maximum* thicket than in forest free of *R. maximum*; (3) seedlings growing under the thickets of *R. maximum* will show greater shade acclimation traits; (4) mortality of seedlings is correlated with light availability and with established shade tolerance among species. In order to address these hypotheses, we sampled leaf and whole plant properties of the three tree species with differing shade tolerance and examined the association between these characters and seedling survival in forest plots with and without *R. maximum* thickets over a 3-yr period.

Material and Methods

Site Description

This study was conducted in a mature mixed-hardwood forest at the Coweeta Hydrologic Laboratory located in the Nantahala Mountains of western North Carolina (35°02′N, 83°27′W). The site was on a north-facing slope (60%) at an elevation of 1000 m a.s.l. with extensive patches of *Rhododendron maximum* in the understory (fig. 1). The overstory canopy was approximately 25–30 m above the ground and the *R. maximum* canopy at 3–4 m. The soil type at the experimental site was a deep, well-drained coarse loam of the Edneyville series (Thomas 1996). The regional climate is classified as marine, humid with cool summers, mild winters, and adequate rainfall (averaging 1800 mm annually) across all seasons (Swank and Crossley 1988).

There were 14 common overstory species (>12 cm dbh) present in the vicinity (within 10 m) of the experimental plots. They were, in order of abundance, *Acer rubrum* L. (41%), *Quercus prinus* L. (22%), *Carya* spp. Nutall (7%), *Quercus rubra* L. (7%), *Nyssa sylvatica* Marshall (6%), *Oxydendrum arboreum* (L.) DC. (6%) and, less than 6%, *Betula lenta* L., *Tsuga canadensis* (L.) Carr., *Robinia pseudo-acacia* L., *Quercus coccinea* Muenchh., *P. serotina* Ehrhart, *Q. velutina* Lam., *Magnolia fraseri* Walter, *M. accuminata* L., and *Acer pensylvanicum* L. Edaphic conditions are affected by *R. maximum* where soil moisture content was 20% lower within the thickets. Also, concentration of cations such as nitrate, potassium, and calcium were significantly lower in the mineral soil under the shrub compared with the rest of the forest (Nilsen et al. 2001).

Seed Recruitment

Seed fall was determined using circular fine-mesh seed traps of 1 m^2 (ca. 1 m above the forest floor) placed in the vicinity of the experimental plots at five locations 200–500 m apart. At each location, three traps (3–5 m apart) were placed under *R. maximum* and another three in adjacent forest outside the thicket. The traps were placed without regard to location of overstory species. From May 11, 1996, to December 1, 1997, contents of the seed traps (seed and litter) were collected monthly. Total seed count was made for all tree species except *Betula lenta* L., where seed number per trap was estimated by applying the number of seeds per dry weight in three subsamples of the fine-sieved fraction to the total weight of the fine fraction.

Paired seed bank samples (in and out of *R. maximum*) were collected from the same locations as the seed traps in April 1997. Care was taken to maintain the substrate structure (litter, organic, and top mineral layer) as samples were placed in trays. Samples were incubated in a greenhouse at 50% full sun, 25°C, and kept moist. The samples were maintained for 6 mo to allow for full germination of viable seeds before a total seedling count by species was made.

Seed/Seedling Planting

A total of six one-quarter ha blocks were randomly located within and outside of the thickets (fig. 1). The number and

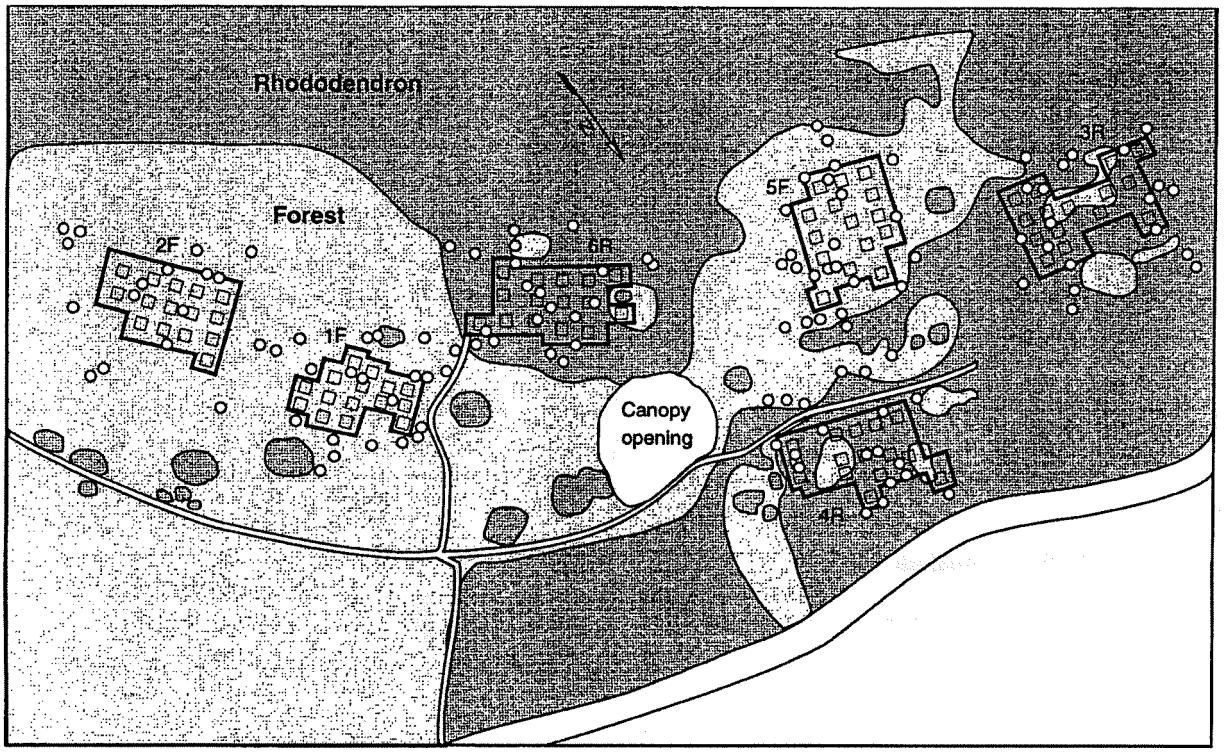

Fig. 1 Map of the experimental plot layout with reference to the *Rhododendron maximum* thickets (dark gray) and canopy trees (white circles, >15 cm dbh) at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains. The six main plots located in (e.g., *6R*) and out (e.g., *1F*) of the thickets are ca. 20 × 20 m. Small squares represent substrate manipulation plots.

species of overstory trees associated with each block (within and 10 m beyond the block) was similar, at 17–24 individuals. Fifteen 2 × 2-m plots were established in each block, totaling 90 plots: 45 inside the thickets and 45 in forest free of *R. maximum*. The experimental plots were allowed to stabilize over winter before seeds or seedlings were planted the following spring.

Seedlings of three tree species—black cherry (*Prunus serotina*), northern red oak (*Quercus rubra*), and hemlock (*Tsuga canadensis*)—were planted in the plots to follow their morphological development and survivorship over 3 yr. These species were chosen because of their contrasting shade tolerance and because they are known to form ectomycorrhizae. The effect of mycorrhizae on seedling growth and survival was examined in another study (Walker et al. 1999). *Quercus rubra* acorns were collected in the vicinity of the experimental plots in March and April 1996 and planted in mid-April 1996. The naturally stratified acorns (some had already begun radical extension) were planted at a density of 16 acorns per plot. *Prunus serotina* seeds of local provenance (Cherokee Seed, Murphy, N.C.) were soaked in concentrated H_2SO_4 for 30 min, stratified in two separate lots of forest and *R. maximum* organic substrate at 4°C for 4 mo, and planted at a density of 16 seeds per plot. Because of their low germination *in situ*, hemlock (*T. canadensis*) seeds were stratified in separate forest and *R. maximum* organic substrates at 4°C for 2 mo in greenhouse flats. Seedlings were maintained under shade cloth (10% full sunlight to promote moderate growth and size gain) for 1 mo before they were transplanted at nine seedlings per plot in early June 1996. Acorns, seeds, or seedlings were planted at the intersection points of a grid in the plot. The species planted at each intersection point was randomly assigned.

Seedling Properties

One randomly selected seedling per species was harvested from the plots on September 15, 1996, September 6, 1997, and September 14, 1998. *Quercus rubra* and *T. canadensis* were sampled in all 3 yr, while *P. serotina* seedlings were sampled in the second and third year only. Each plant was lifted with a largely intact root system, put in a zip-lock bag, placed on ice, and transported to the lab, where leaf area, plant height, and stem basal diameter were recorded for each seedling. The root was separated from the stem and kept frozen for later evaluation of mycorrhizal formation (Walker et al. 1999) before drying. Leaf area was measured (LI-3200 leaf area meter; LI-COR, Lincoln, Nebr.) then dried together with stems at 72°C to a constant weight. Specific leaf area was calculated as the fraction of total leaf dry weight divided by leaf area. Leaves and stems of individual seedlings were ground separately in a Wiley mill and analyzed for percentage nitrogen on a dry weight basis using a CHN elemental analyzer (Perkin-Elmer 2400, Norwalk, Conn.).

Seedling Survivorship

Survival of *P. serotina*, *Q. rubra*, and *T. canadensis* over the 3-yr period was recorded by counting the number of planted seedlings within each plot at the start and the end of each growing season.

Light Environment Measurements

To evaluate seedling response to the light environment at the plot level, canopy hemispherical photographs of each plot were taken in July 1996. The images were made on Kodak Tri-X film with a Nikon FM2 camera fitted with an 8-mm fish-eye lens (Nikon, Tokyo). The camera was positioned over the center marker of the plot, and the top of the lens was 80 cm from the forest floor. Film was developed with Microdol-X developer. The images were analyzed using a software program (FEW 4.0) developed by M. Ishizuka (personal communication). Direct and diffuse site factors were derived for each plot.

Statistical Analysis

Of the six randomly selected, noncontiguous blocks (three inside the *Rhododendron maximum* thickets and three where *R. maximum* was absent; fig. 1), we found no systematic bias of edaphic and environmental characteristics among blocks within each canopy type (*R. maximum* present or absent), hence the blocks were treated as replicates of the main effect in the analysis of variance. Because the two factors in the main effect (i.e., with and without *R. maximum*) are not strictly experimental treatments but naturally occurring heterogeneity in the forest environment, the main effects of canopy type on plant traits were determined using the following sums of square (SS of Type III ANOVA, Proc ANOVA; SAS Institute 1988) ratio to calculate the F statistic with df = 1, 4:

$$F = \frac{\text{SS canopy type/1}}{\text{SS main plot(canopy type)/4}}.$$

Survivorship under the two canopy types was compared for each species using survival analysis and an exponential survival distribution (JMP version 4). Relationships between light environment parameters and seedling mortality were examined using logistic regression and maximum likelihood estimation (Proc CATMOD; SAS Institute 1998) with individual plots within each block as the experimental unit.

Results

Seed Rain

Seed trap data for most of the six canopy tree species collected over two growing seasons were not significantly different (t-test $P > 0.05$) in forest areas with or without *R. maximum* (fig. 2). For *Acer rubrum*, peak seed dispersal occurred between late April and mid-May. The total number of viable *A. rubrum* seeds dispersed in 1997 was not different (t-test $P > 0.05$) between sites with *R. maximum* (+*Rm*; 233 ± 27 m^{-2}) and without *R. maximum* (−*Rm*; 254 ± 30 m^{-2}). There tended to be more *Liriodendron* seed dispersing into the thickets than outside in both years. In Coweeta, *Quercus rubra* masted in 1995 and produced few acorns in the subsequent 2 yr. Regardless of the total acorns produced, *R. maximum* sites always tended to have a higher number of acorns than sites without *R. maximum*, but this difference was not significant (t-test $P > 0.05$). *Betula lenta*, with its small seed, varied among sites, particularly outside the thickets, but no significant difference (t-test $P > 0.05$) between forest types was found. Seed production for *Carya* and *Nyssa* was low in both years (0.5–7 m^{-2}) with a slightly greater number (t-test $P < 0.05$) of *Nyssa* seed in *R. maximum* sites in 1997 (fig. 2).

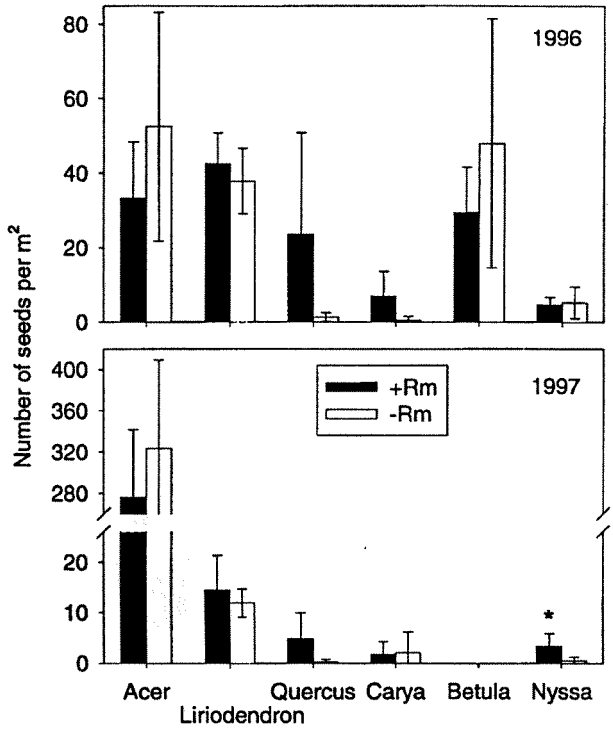

Fig. 2 Mean total number of seeds per square meter falling in seed traps located in forest with (+*Rm*) or without (−*Rm*) a subcanopy of *Rhododendron maximum* at Coweeta. The species quantified were *Acer rubrum*, *Liriodendron tulipifera*, *Quercus rubra*, *Carya* spp., *Betula lenta*, and *Nyssa sylvatica*. Error bars refer to 95% confidence limits of the mean.

Seed Bank

Rhododendron maximum thickets did not significantly affect the seed bank of four overstory species (fig. 3). Incubation of forest substrate collected from five locations produced very low numbers of *A. rubrum* seedlings in spite of the very high seed rain (fig. 2). This indicates that *A. rubrum* seeds quickly lose viability after dispersal. Naturally occurring first-year *A. rubrum* seedlings were common in all sites, but they rarely persist beyond the first year (T. T. Lei, personal observation). A large number of *Liriodendron tulipifera* seedlings emerged from the seed bank, compared with seed rain, indicating a longer seed viability than that of *A. rubrum*, but like *A. rubrum*, both *L. tulipifera* and *B. lenta* seedlings rarely survive

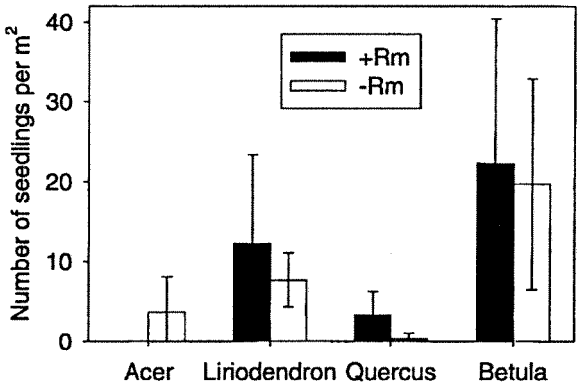

Fig. 3 Mean total number of seedlings per square meter emerging from seed bank samples taken from forest with (+*Rm*) or without (−*Rm*) a subcanopy of *Rhododendron maximum*. No other tree species germinated in the samples. Error bars refer to 95% confidence limits of the mean.

over winter *in situ* (T. T. Lei, personal observation). The low number of *Q. rubra* seedlings emerging from seed bank samples was consistent with the low seed number found in traps during the nonmasting years of this study. No seedlings of *N. sylvatica* or *Carya* sp. emerged from the substrate samples. A significant regression ($R^2 = 0.73, P = 0.002, n = 10$) between total seedling emerged from seed bank samples (collected in spring 1997) and total seed number collected in seed traps for 1996 indicates that potential seedling number is associated with the seed fall of the previous year.

Plant Characteristics

Quercus rubra seedlings in *R. maximum* had a significantly reduced total leaf area, leaf dry mass, and leaf number (3.1 vs. 4.0 in −*Rm* for 1997, $P < 0.01$; inset of fig. 4). Leaf area and weight of seedlings in +*Rm* were 60% smaller than those in −*Rm* during their first 3 yr. End of season leaf area and leaf mass declined from 1997 to 1998 for both canopy types, indicating no significant growth even in the absence of *R. maximum*. *Prunus serotina* seedlings, most of which germinated a year later, had a mean leaf number of 3.4 per seedling in +*Rm*, not significantly different from the 4.1 in −*Rm*. However, total leaf area and leaf mass of −*Rm* seedlings was 1.5–2 times greater ($P < 0.05$) in 1997 (fig. 4). Seedlings of *P. serotina* surviving to the autumn of 1998 were much reduced in leaf area and weight, particularly in −*Rm* sites. Relative to the other species, *Tsuga canadensis* seedlings were the smallest (fig. 4). Total leaf area of 2-yr-old *T. canadensis* seedlings (1997) outside the thickets was 65% higher than those inside. Unlike the other two species, *T. canadensis* seedlings surviving to 1998 showed an increase in leaf area and weight from the previous year. The relative differences (between +*Rm* and −*Rm*) in leaf area and weight in 1997 was *P. serotina* > *Q. rubra* > *T. canadensis*.

In contrast to leaf area and mass, *Q. rubra* seedlings in +*Rm* were taller than those in −*Rm*, and the difference became larger with successive years (inset of fig. 5). But the taller seedlings in +*Rm* had lower stem dry mass, which together indicates a more slender shoot compared with seedlings in −*Rm* plots. Some oak seedlings were topped by rodents (T. T. Lei, personal observation). Clipped plants generally resprouted but with shorter shoots and smaller leaves than intact shoots. Given that oak seedlings are supported by hypogeal seed reserve for the first season and largely independent of abiotic conditions, we attribute the smaller stem size of first-year oak seedlings in +*Rm* solely to a higher occurrence of rodent damage in the thickets. Stem mass of *P. serotina* in *R. maximum* was significantly lower than in −*Rm* and declined from 1997 to 1998, but stem height showed a small annual increase in seedlings from both +*Rm* and −*Rm* plots and was only marginally shorter in +*Rm* in 1998. Main stem properties of *T. canadensis* was more similar between canopy types in 1997 than a year later when seedlings in −*Rm* plots increased in stem mass along with stem height, while those in +*Rm* plots decreased in stem mass (fig. 5).

Both leaves and stems of *Q. rubra* seedlings in +*Rm* had a consistently higher percentage of N in all 3 yr (fig. 6). However, when light availability (% canopy openness) was used as a covariate, no difference in leaf N ($P > 0.05$) was found between +*Rm* and −*Rm* sites for the 3 yr and only a marginal difference in the first 2 yr ($P = 0.036$ and 0.049, respectively) in stem N. Compared with −*Rm* seedlings, those in +*Rm* showed a larger annual decline in percent N of both leaves and stems. Measured only for 1998, the difference in tissue N between canopy types in *T. canadensis* and *P. serotina* were much smaller than that found in *Q. rubra*. However, total N in the aboveground tissue of *Q. rubra* in +*Rm* was significantly lower (5.6 ± 0.5 mg) than those in −*Rm* (8.9 ± 0.7 mg, $P < 0.01$), indicating a dilution effect of N in −*Rm* plants owing to their

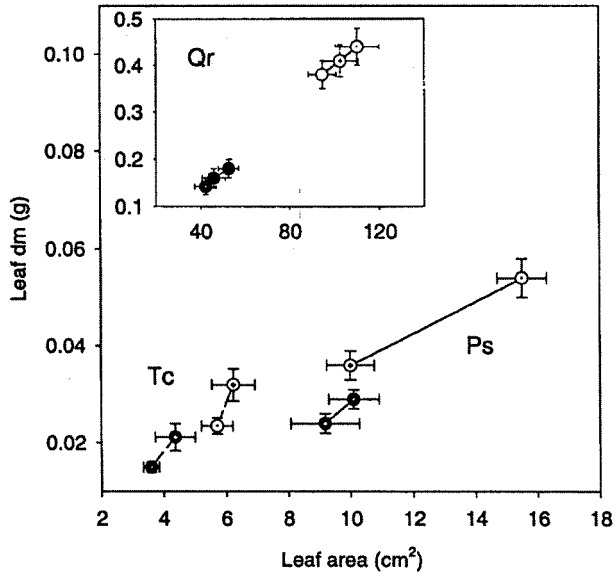

Fig. 4 Effect of *Rhododendron maximum* on leaf area and leaf mass at the end of 1996 (filled circle), 1997 (filled circle with dot), and 1998 (filled circle with cross) field seasons for *Quercus rubra* (*Qr*), *Tsuga canadensis* (*Tc*), and *Prunus serotina* (*Ps*) seedlings. Values were mean ± 1 SE under *R. maximum* (filled symbols) and in the absence of *R. maximum* (open symbols).

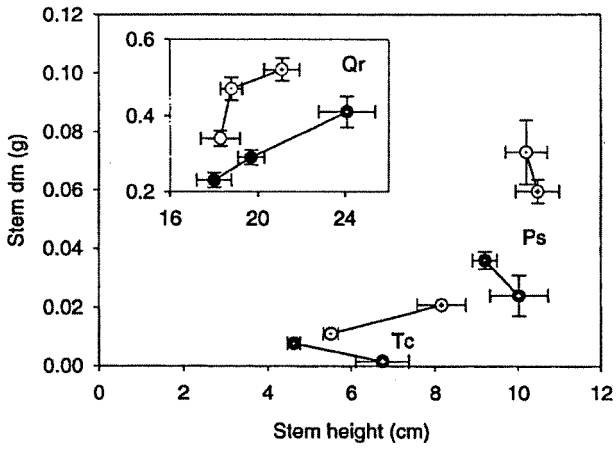

Fig. 5 Effect of *Rhododendron maximum* on stem height and stem dry mass of *Quercus rubra* (*Qr*), *Tsuga canadensis* (*Tc*), and *Prunus serotina* (*Ps*) seedlings at the end of 1996 (filled circle), 1997 (filled circle with dot), and 1998 (filled circle with cross) field seasons. Values were mean ±1 SE under *R. maximum* (filled symbols) and in forest absent of *R. maximum* (open symbols).

higher C accumulation and some increased uptake. The same effect is observed in the other two species but to a lesser extent ($P > 0.05$): *T. canadensis*, 0.7 ± 0.1 mg (−*Rm*) versus 0.5 ± 0.1 mg (+*Rm*); *P. serotina*, 1.1 ± 0.2 mg (−*Rm*) versus 0.7 ± 0.1 mg (+*Rm*).

Seedling Survivorship

Survival of seedlings established in the experimental plots was significantly lower under *R. maximum* (fig. 7). The number of *Q. rubra* seedlings increased from spring to the early summer of 1996 as seedlings emerged. In spite of the frequent rodent herbivory, mortality of *Q. rubra* seedlings in 1996 was relatively low. Many more *Q. rubra* seedlings died during the second growing season, and the trend continued into the spring of 1998. Overall survivorship was lower in +*Rm* ($\chi^2 = 71$, $P < 0.001$). Mortality of *T. canadensis*, transplanted to the plots as 1-mo-old seedlings, was also different between canopy types (fig. 7). Compared with *Q. rubra*, a greater loss of *T. canadensis* seedlings occurred during the winter, largely resulting from seedlings being buried under litter fall. Since litter collected in seed traps in +*Rm* plots was 30% higher in dry mass than that in −*Rm* plots, the significantly higher mortality of *T. canadensis* in +*Rm* ($\chi^2 = 42$, $P < 0.001$) is attributed to the shedding of *Rhododendron* leaves during winter months.

Even though *P. serotina* seed were already thermally stratified before sowing in the plots, very few seed planted in 1996 germinated that year. Significant seedling emergence occurred in the spring of 1997, peaking in late May to early June (fig. 7). The mean number of *P. serotina* seedlings per plot was initially greater under *R. maximum* than outside the thickets but seedling numbers declined more quickly in the thickets during the season. Very few *P. serotina* seedlings remained alive in plots under *R. maximum* in the following year. Overall survivorship was significantly lower in +*Rm* ($\chi^2 = 9.8$, $P = 0.002$). The relative survivorship from June 1997 to June 1998 was in the order of *Tsuga* > *Quercus* > *Prunus*.

To compare seedling survivorship in the experimental plots with those occurring naturally in the forest, we marked seedlings in randomly selected 1-m² quadrats in the vicinity of the experimental plots. Three paired quadrats (i.e., +*Rm* and −*Rm*) at five sites (total of 30 quadrats) were monitored. The total number of naturally emerged *Q. rubra* and *Q. prinus* seedlings under *R. maximum* declined by 81% from September 1996 (9.7 ± 3.9 m^{-2}) to June 1998 (1.8 ± 1.2 m^{-2}, $n = 9$), while quadrats outside the thickets began with fewer seedlings (2.5 ± 0.8 m^{-2}) but declined by only 28% during the same interval (1.8 ± 0.7 m^{-2}, $n = 6$).

Light Environment

Using hemispheric photographs, we derived the total available light (combining direct and diffuse radiation) to the seedlings and found that it is significantly correlated (rank correlation) with leaf mass of *Q. rubra* (both years, $r = 0.23$ and 0.23, $P = 0.046$ and 0.037, $n = 90$ and 84, respectively) and with specific leaf area of *Q. rubra* (both years, $r = -0.29$ and −0.24, $P = 0.005$ and 0.028, $n = 90$ and 83, respectively) and *P. serotina* (first-year $r = -0.26$, $P = 0.034$, $n = 69$). Across the 90 plots, the survivorship of both *Q. rubra* and *P. serotina* seedlings was significantly correlated with the local light environment and with each other (table 1). In contrast, the survivorship of *T. canadensis* was independent of the light parameters.

Discussion

Preemergence Factors

Seed dispersal into thickets of Rhododendron maximum. The first effect of *Rhododendron maximum* on forest regen-

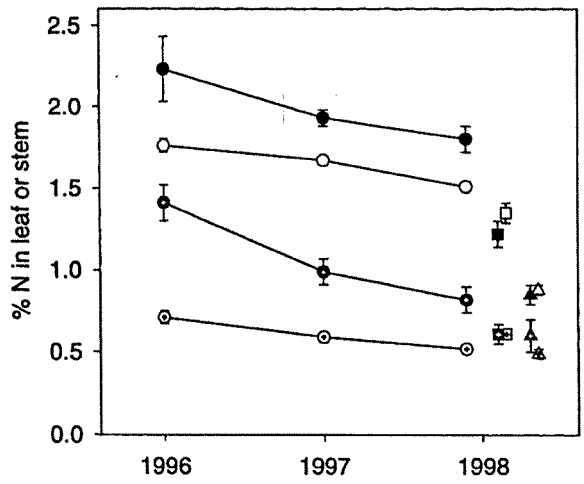

Fig. 6 Mean leaf N (% dry mass ±1 SE) of pooled leaves (circle, square, and triangle) and stem (circle, square, and triangle distinguished by an internal cross) per seedling at the end of three seasons in *Quercus rubra* (*Qr*) and for 1998 only in *Tsuga canadensis* (*Tc*) and *Prunus serotina* (*Ps*) seedlings. Filled symbols represent seedlings in +*Rm* and open symbols in −*Rm*.

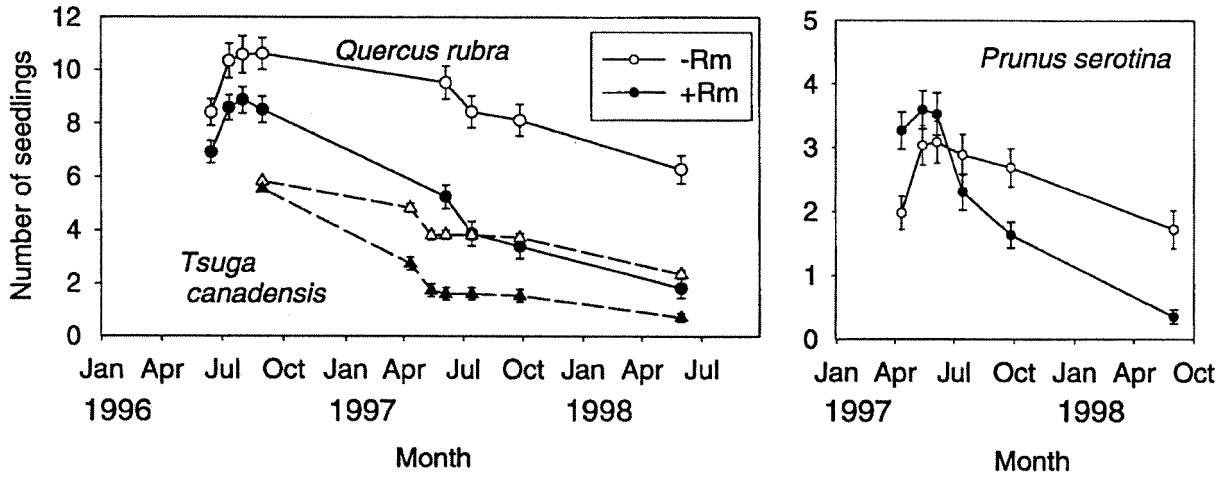

Fig. 7 Survivorship of *Quercus rubra*, *Tsuga canadensis*, and *Prunus serotina* seedlings in the experimental plots over a 3-yr period in forest with (*+Rm*) or without (*−Rm*) a subcanopy of *Rhododendron maximum*. *Prunus serotina* seedlings only began germinating in the spring of 1997. Error bars refer to ±1 SE of the mean.

eration might be a reduced seed rain. *Rhododendron maximum* could lower resources available to canopy trees by sequestering large quantities of available nutrients in its leaf pool, which has a slow turnover rate (Smith 1963; Romancier 1971; Martinez 1975; Monk et al. 1985; Elliott and Vose 1995), resulting in smaller seed crops in trees rooted in the *R. maximum* thicket. The *R. maximum* canopy and litter could also act as a physical barrier preventing seed from reaching the moist substrate and increasing the likelihood of seed desiccation. The seed trap data, however, indicate no such interference regardless of seed size, i.e., between the small-seeded *Betula*, *Tsuga*, *Acer*, and *Liriodendron* and the large-seeded *Prunus*, *Quercus*, and *Carya* (fig. 2). We infer from these findings that seed crop of trees rooted in *R. maximum* were not affected by belowground competition and/or that seed fall within the *R. maximum* is sustained by neighboring trees outside the tickets, particularly where steep hills and overhanging trees are present. This type of topography is common in cove forests where *R. maximum* proliferates. In this forest, seed dispersal of some species at distances greater than 20 m has been estimated by Clark et al. (1998). Therefore, even if canopy trees within the *R. maximum* thicket experience direct interference from *R. maximum*, sufficient seed dispersal from adjacent trees can occur, even for trees of shorter seed-dispersal range (e.g., *Quercus* and *Carya* species).

Seed banks in forest with or without Rhododendron maximum. Having reached the ground under the *R. maximum* thicket, seeds could be prevented from germinating by physical and chemical means. The coarse *R. maximum* litter and the drier soil under the thickets (Nilsen et al. 2001) could increase the rate of desiccation of seed and germinating seedlings. However, seed bank results indicated no reduction in the number of viable seed associated with the presence of *R. maximum*. The lack of seed desiccation by *R. maximum* is supported by a significant association between seed fall (1996) and seedling emergence in the following year (seed bank 1997). Even though seed bank samples were incubated under conditions of higher light and moisture than that of the forest floor (Brown 1992), estimates of viable seed were consistent with a survey of extant seedlings in the same forest. The absence of seedlings of small-seeded species such as *Betula* and *Oxydendrum* in field quadrats is likely attributable to their lack of sufficient seed reserve to support shoot emergence above the litter layer (Sydes and Grime 1981; Myster 1994). A detailed examination of the presence of allelochemicals in *R. maximum* found no evidence of inhibitory factors on the viability and germination potential of trees and bioassayed seeds (Nilsen et al. 1999). The larger number of *P. serotina* seeds that germinated in *R. maximum* plots (fig. 3) supports the lack of chemical inhibition in the *R. maximum* substrate. Since neither seed dispersal nor seed viability and persistence in the seed bank was affected by *R. maximum* thickets, we deduce that postemergence processes were responsible for the suppression of tree seedlings under *R. maximum*.

Postemergence Factors

Acclimation of seedlings to lower light under Rhododendron maximum. Starting in the first year of growth, seedlings of all three species in *+Rm* plots were less able to intercept light than those in *−Rm* plots because of a significantly reduced photosynthetic surface area (fig. 4). Among the traits measured, stem height was the least affected by *R. maximum*, particularly in the second and third year of growth (fig. 5). Accompanied by a significantly lower stem mass, it appears that the reduced light also led to a greater priority in height growth than diameter (i.e., wood strength). This is consistent with a phytochrome driven response if the R : FR ratio under *R. maximum* was lower (Smith 1982; Vásquez-Yanes et al. 1990; Schimpf and Danz 1999).

Compared with aboveground mass, root mass of *Q. rubra* and *T. canadensis* was more severely affected by the presence of *R. maximum* than *P. serotina* (data not shown). The preferential biomass allocation to leaves and shoot is consistent

Table 1

Association between Survivorship (%, June 1997 to June 1998) and the Light Environment (derived from Canopy Photographs Taken in July 1996) Expressed as χ^2, Using Logistical Regression

	Survivorship (%)								
	Quercus			*Prunus*			*Tsuga*		
Light environment	χ^2	*P*	*n*	χ^2	*P*	*n*	χ^2	*P*	*n*
Canopy openness (%)	670	<0.01	89	287	<0.01	85	0.02	0.89	59
Direct light	84	<0.01	89	84	<0.01	85	2.14	0.14	59
Light penetration (%)	148	<0.01	89	118	<0.01	85	1.96	0.16	59
Prunus survivorship (%)	621	<0.01	85						

Note. *P* is the significance value. Sample sizes (*n*) were less than the full 90 plots because some plots had no seedlings at the start of the census period (June 1997). The amount of direct light reaching the forest understory was daily PPFD values summed over the month of July, assuming clear skies. Light penetration was calculated as the ratio of total direct plus diffused light in the understory over that above the canopy.

with an adaptation to improve light capture under *R. maximum* (Marks 1975; Bloom et al. 1985; Cid-Benevento and Werner 1986). However, to maximize light interception, it is critical to enhance the proportion of leaf area to plant weight (LAR; Walters et al. 1993). We found only marginally higher LAR for *Q. rubra* seedlings in 1996: 86.2 ± 4.4 $cm^2\ g^{-1}$ in *+Rm*, compared with 77.5 ± 2.7 $cm^2\ g^{-1}$ in *−Rm* (*t*-test $t = -1.7$, $P = 0.09$, df = 82). It may be that under heavy shade, improving LAR contributes less to seedling growth and survival than adapting leaves to achieve greater net assimilation rate, as was found in Australian rain forest seedlings (Watling et al. 1997). We also found no increases in leaf display efficiency (leaf area to stem mass), which could improve assimilation performance of shaded seedlings (Chazdon 1985, 1986; Canham 1988; Lee 1988). These findings indicate that survival in deep shade may depend more on physiological than morphological or structural adjustments.

The higher percentage of N of stem and leaves of *Q. rubra* seedlings in *+Rm* is consistent with a concentration effect of N in smaller tissue biomass relative to those in *−Rm*. Since the percentage of N in stems and leaves of *Q. rubra* did not differ between canopy types when the light factor was removed as covariance, it is clear that edaphic factors, such as a lower in N mineralization rate in *R. maximum* (Nilsen et al. 2001), are not important determinants. Since 75% of leaf N is allocated to the photosynthetic apparatus (Chapin et al. 1987) and half of that in Rubisco (Evans 1989), greater leaf N would represents a high photosynthetic capacity. We have unpublished data showing marginally higher photosynthetic capacity of *Q. rubra* grown in *R. maximum*. But any potential benefit in carbon gain conferred by high leaf N is negated by the severe lack of light under *R. maximum*. We conclude that seedling survival under *R. maximum* of all three species did not result from N limitation (fig. 6) or lowered photosynthetic potential.

Mortality of seedlings. Seedlings of all species have a significantly lower survivorship under *R. maximum* thickets (fig. 7). While mortality between saplings of *P. serotina* and *Q. rubra* in deciduous forests free of *R. maximum* were similar (Kobe et al. 1995), we found higher mortality in *P. serotina* seedlings under *R. maximum* than that of *Q. rubra*. Under the additional shrub cover, the larger seed reserve of *Q. rubra* may have conferred a short-term survival advantage over *P. serotina* (Saverimuttu and Westoby 1996). But a larger respiratory demand associated with the larger oak seedling could also have contributed to its mortality once stored resources were exhausted. In contrast to seedlings of the two broadleaf species, survivorship of *T. canadensis* seedlings was high during the growing season, but many seedlings were lost during the winter months. We attribute this to the vulnerability of the small, nearly prostrate seedlings to burial by leaf litter. While litter production was higher and seedling burial more likely in the thickets, a sufficient amount of litter was produced annually in all locations to bury small seedlings. If we assume litter burial occurs regardless of the light environment, then the lack of correlation between *T. canadensis* mortality and light is expected (table 1). *Tsuga canadensis* was clearly more shade tolerant than the two broadleaf species, surviving well even under the deep shade of *R. maximum*. Based on its 0.2-mm stem diameter growth from 1996 to 1997 in *R. maximum* sites, *T. canadensis* is expected to survive well under the shade of *R. maximum* (Palmer 1987; Kobe et al. 1995), especially on mossy rocks where chances of litter burial is low (Palmer 1987; Collins 1990).

Light availability and seedling survivorship. Survivorship of *Q. rubra* and, to a lesser extent, *P. serotina*, was associated with light availability (table 1). In general, the presence of *R. maximum* canopy reduced direct light (i.e., sunflecks) by 20%–25% and diffuse light by 12%–29% during the growing season compared with *−Rm* sites. The amount of sunflecks (i.e., PAR > 10 mmol $m^{-2}\ s^{-1}$) during midday (1000–1400 h EST) was less than 20 min under the thickets compared with more than 100 min outside. These results are similar to the 70%–90% reduction in available PAR under *R. maximum* relative to forest floor without *R. maximum* (Clinton et al. 1994). Other than brief sunflecks, seedlings established under the thickets often experienced diffuse light below the compensation point for photosynthesis (S. W. Semones, unpublished data). This can lead to a seasonal carbon deficit where plant growth and survivorship are affected (Harper 1977). Importantly, some locations in forest without *R. maximum* were relatively more shaded than areas under the thickets. We attribute this to dense growth of low shrubs (such as *Gaylussaccia ursina*, which can reach 62 stems m^{-2}; T. T. Lei, unpublished data) and saplings (Lorimer et al. 1994) in the forest understory. Even under a dense sapling population, 30% of red oak seedlings survived to 5 yr (Lorimer et al. 1994), implying that the suppression imposed by *R. maximum* thickets is significantly greater.

While abiotic factors such as light may be a major cause of mortality in tree seedlings, the process may be exacerbated by predation (Molofsky and Fisher 1993; Canham et al. 1999). We observed higher rodent predation on oak seedlings in the thickets, which may be related to the more protected forest floor free of ground vegetation. Higher rates of seed removal also occurred under thickets of evergreen bamboo in a Japanese forest where tree regeneration was also severely restricted (Wada 1993). Although *Q. rubra* seedlings were able to recover from repeated herbivore damage (T. T. Lei, personal observation), there would have been a reduction in carbohydrate reserve. Increased mortality can be closely associated with a reduction in carbohydrate reserve in defoliated tree seedlings (Canham et al. 1999). The environment in *R. maximum* thickets may be one where seedling mortality resulting from low resource availability is compounded by greater herbivory.

Conclusions

Among the life history stages of the regenerating forest trees examined, we found no evidence that *Rhododendron maximum* prevented the arrival of seeds. Seeds dispersed into *R. maximum* thickets are as capable of germinating as those found outside the thickets. Tree seedlings are capable of some morphological and physiological adjustments to the deeper shade under *R. maximum* consistent with shade acclimation but that these adjustments were inadequate for seedlings to persist. We confirmed that *R. maximum* severely affects the persistence of seedlings, and seedling response to the presence of *R. maximum* was already evident in the first year, even while seed reserve was still available (for oak) to buffer against adverse conditions (Aizen and Woodcock 1996). Being more shade tolerant than the other two species, the expected lower mortality of *Tsuga canadensis* was supported. While some seedling characters of *T. canadensis* varied with the light environment, they were not correlated with its survival. Loss of *T. canadensis* seedlings occurred predominantly in the winter months as the result of burial under leaf litter. As *T. canadensis* are largely found to establish on litter-free mossy patches in the forest understory (Collins 1990), their survivorship may be regulated more by the presence of such safe sites (Palmer 1987) than the presence or absence of *R. maximum*. And last, evidence indicates that early seedling development is a greater function of light than nutrients or mycorrhizae. Other stress factors, such as reduced mycorrhizae and herbivory, while not sufficient to cause seedling death under *R. maximum* in the first year, may have contributed to a decline in seedling vigor that compounded their risk of mortality in subsequent years.

The persistence of *R. maximum* thickets will have an impact on the forest communities of the southern Appalachians. While our data indicate that the availability of tree seed under the thickets will not be affected, replacement seedlings will be rare from areas occupied by the thickets. Even under canopy gaps, regeneration is difficult within the thickets (Beckage et al. 2000), except where gaps within the thickets allow sufficient light penetration. But because *R. maximum* proliferates aggressively under canopy gaps, we predict that forest canopy of this region will become more patchy as adult trees within thickets die without replacement.

Acknowledgments

This study was funded by the USDA Forest/Range/Crop/Wetland Ecosystems Program, grant 95-37101-1902. Logistical assistance was provided by USDA Forest Service, Coweeta Hydrologic Laboratory. Sample processing was aided by H. Funkhousen, J. Radzio, E. Woodall, and S. Newton. We thank O. K. Miller, Jr., for his encouragement and valuable suggestions. C. Anderson-Cook provided advice on statistics. Canopy photographs were analyzed using FEW 4.0, a PC software developed by M. Ishizuka of Forestry and Forest Products Research Institute, Tsukuba, Japan.

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