A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories

Brian Beckage, James S. Clark, Barton D. Clinton, and Bruce L. Haines

Abstract: We examined the importance of intermediate-sized gaps and a dense shrub layer on tree seedling recruitment in a southern Appalachian deciduous forest. We created 12 canopy gaps under two contrasting understory conditions: 6 gaps were dominated by the dense, shade-producing shrub, *Rhododendron maximum* L., while the remaining gaps were relatively open. Density of first-year and >first-year seedlings was monitored for 5 years in transects extending from adjacent undisturbed forest through the experimental gaps. We concurrently measured the understory light environment, soil moisture, litter biomass, and seed rain. Neither species diversity nor richness consistently increased following gap formation. *Acer rubrum* L. responded consistently to canopy gaps with increased seedling densities while most other species, including both shade-tolerant and shade-intolerant species, did not. Seedling densities were especially low and unresponsive to gap formation in areas dominated by *R. maximum*. Understory light levels were consistently low beneath *R. maximum* and did not increase with canopy gap formation. Our results suggest that dense shrub cover can neutralize recruitment opportunities in canopy gaps, that seed rain often limits recruitment in gaps, and that canopy gaps that are larger or include understory disturbance are needed to maintain diversity in these forests.

Résumé : Les auteurs ont examiné l'importance des ouvertures de taille intermédiaire et d'une strate arbustive dense sur le recrutement des semis d'arbres dans une forêt décidue des Appalaches méridionales. Ils ont créé dans le couvert 12 ouvertures avec deux types différents de sous-étage. Six ouvertures étaient dominées par *Rhododendron maximum* L., un arbuste dense produisant de l'ombre, tandis que les autres étaient relativement vides. La densité des semis âgés d'un an et de plus d'un an a été suivie durant 5 ans dans des transects qui s'étendaient de la forêt adjacente non perturbée à travers les ouvertures expérimentales. On a aussi mesuré, concurremment, l'intensité lumineuse en sous-étage, l'humidité du sol, la biomasse de la litière et la pluie de graines. Ni la diversité, ni la richesse spécifiques ne se sont accrues de façon régulière après la formation des ouvertures. Seul *Acer rubrum* L. a répondu régulièrement aux ouvertures du couvert en présentant une densité accrue de semis, alors que la plupart des autres espèces, autant tolérantes qu'intolérantes à l'ombre, n'y ont pas répondu. La densité des semis était particulièrement faible et indifférente à la formation des ouvertures dans les aires dominées par *R. maximum*. De la même façon, le niveau de luminosité en sous-étage était régulièrement bas sous *R. maximum* et il ne s'est pas accru avec la formation des ouvertures dans le couvert forestier. Les résultats obtenus suggèrent qu'un couvert arbustif dense peut neutraliser les possibilités de recrutement dans les ouvertures du couvert, que la pluie de graines limite souvent le recrutement dans ces dernières et que, pour maintenir la diversité dans ces forêts, on a besoin de plus grandes ouvertures dans le couvert ou d'ouvertures avec un sous-étage qui a subi une perturbation.

[Traduit par la Rédaction]

Introduction

With awareness that competition limits diversity in constant environments (MacArthur and Levins 1967; Tilman 1982), ecologists have searched for mechanisms that promote variability and, thus, coexistence on a few limiting resources. In forest understories, light is a limiting resource with tree establishment and growth linked to its availability (Canham 1988; Denslow et al. 1990; Pacala et al. 1994; Pearcy 1983). Canopy gaps provide the transient increases in light that many species require to reach the canopy (Bormann and Likens 1979; Brokaw and Scheiner 1989; Pickett and White 1985; Shugart 1984; Whitmore 1989). The spatial and temporal heterogeneity resulting from the deaths of individual trees might promote higher forest diversity than could be maintained in a constant environment (Chesson 1982; Chesson and Warner 1981; Comins and Noble 1985; Huston 1979; Pacala and Tilman 1994; Tilman and Pacala 1993).

While the importance of gap-phase replacement has long been recognized in forest dynamics (Bormann and Likens 1979; Botkin 1993; Shugart 1984; Watt 1947), the role of intermediate-sized canopy gaps in maintaining diversity is less certain despite their high abundance. We consider

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intermediate-sized gaps to be those created by the death of one to several canopy trees, as opposed to small gaps resulting from the partial death of canopy trees (e.g., loss of a branch, etc.) or large gaps formed by the death of many contiguous trees (e.g., large windthrows). Based on this definition, ≥80% of gaps in temperate deciduous forests would be considered intermediate sized (Cho and Boerner 1991; Dahir and Lorimer 1996; Runkle 1990). Alternatively, we can base a definition of intermediate-sized gaps on the 25th and 75th quantiles of the distribution of gap area. For eastern mesic forests, intermediate-sized gaps would then be gaps with expanded areas between 150 and 400 m^2, respectively (based on data from Runkle 1982); this definition largely intersects the first definition. Some studies have emphasized the importance of intermediate sized gaps (Barden 1979, 1980, 1981, 1983; Drobyshev 1999; Kneeshaw and Bergeron 1998; Lorimer 1980; Runkle 1981; Williamson 1975), while others have questioned their efficacy (Brewer and Merritt 1978; Cho and Boerner 1991; Della-Bianca and Beck 1985; Hibbs 1982). Most of these studies have been observational in nature; few have created gaps and gauged effects against pretreatment data, or have monitored variation in factors likely to impact recruitment such as seed rain. Others did not measure recruitment in intact canopies for comparison to that in gaps, making an assessment of gap effects difficult. Experiments that create replicated gaps and that concurrently monitor factors that impact seedling establishment, e.g., seed rain, light availability, etc., would circumvent some of these limitations and, perhaps, help clarify the role of intermediate-sized gaps in forest dynamics.

While interference from forest understories can inhibit seedling recruitment beneath intact canopies (George and Bazzaz 1999*a*, 1999*b*; Lorimer et al. 1994; Maguire and Forman 1983), few studies have explicitly investigated the interaction between understory shrubs and seedling establishment in gaps. Enhanced recruitment following gap formation depends on increased availability of limiting resources. Many forests support dense understories that buffer the forest floor against canopy changes that affect light, moisture, and nutrients (Clinton et al. 1994; Dolling 1996; Ehrenfeld 1980; Harmon and Franklin 1989; Huenneke 1983; Nakashizuka 1989; Veblen 1982, 1989; Yamamoto et al. 1995), so that understory shrubs might neutralize recruitment opportunities for tree seedlings in gaps. Some studies have associated low seedling densities with dense understories (Ehrenfeld 1980; Huenneke 1983; Nakashizuka 1989; Yamamoto et al. 1995), but we are unaware of studies explicitly examining how understory shrubs interfere with the gap-phase paradigm.

To investigate the impact of canopy gaps and shrub understories on forest dynamics, we created replicated experimental gaps and followed responses of environmental variables and seedling recruitment for 5 years. Our study design included gaps with both dense understories of *Rhododendron maximum* L., and gaps with open understories. Our artificial canopy gaps emulated those formed during droughts in the southern Appalachians (Clinton et al. 1993): the gap makers are standing dead and the gap area approximates that of a typical drought-induced gap. We measured the understory light environment, soil moisture, litter biomass, seed rain, and seedling densities (including pretreatment densities) to address the following questions. (*i*) Which tree species have increased seedling densities in intermediate-sized gaps? (*ii*) Does species diversity of tree seedlings increase in gaps? (*iii*) What effect does the understory shrub *R. maximum* have on seedling recruitment in gaps?

Study area

We conducted our study in second-growth forests at the Coweeta Hydrologic Laboratory (35°03′N, 83°27′W), located near Franklin, N.C., in the Blue Ridge Physiographic Providence of the southern Appalachians. Elevation in the 1626-ha Coweeta Basin ranges from 675 to 1592 m. Average monthly temperatures range from 3°C in January to 19°C in July. Average annual precipitation is 1800 mm and is distributed evenly throughout the year. Precipitation increases and temperatures decline with elevation at rates of 0.7 $mm \cdot m^{-1}$ and $0.0055°C \cdot m^{-1}$, respectively. Bedrock consists of granite–gneiss and mica–schist with overlying colluvium in valley bottoms. Soils are immature Inceptisols and older, developed Ultisols. Our 12 experimental canopy gaps were clustered at two sites, a low elevation site on a Cowee–Evard gravely loam series within the Hapludults (Ultisols) and a high elevation site on a Chandler gravely loam series within the Dystrochrepts (Inceptisols) (Swank and Crossley 1988).

Forests at the Coweeta Hydrologic Laboratory, as throughout the southern Appalachians, have been heavily impacted by human activities (Douglass and Hoover 1988). The Cherokee Indians regularly burned the forest understory prior to their removal in the 1830s. Early European settlers continued this practice and also grazed livestock in the basin until bought out by timber interests around the turn of the century. The basin was logged in the early part of this century before being purchased by the U.S. Department of Agriculture during the 1920s. The only significant disturbance following logging was the chestnut blight that, by 1940, had killed most chestnut trees (*Castanea dentata* (Marsh.) Borkh.) in the basin.

Whittaker (1956) described the regional vegetation in relation to elevation and moisture, including mixed oak forest, which is the most widespread forest type in the southern Appalachians and the focus of our analysis. Mixed oak is found at mid elevations and at moisture levels intermediate between those of cove hardwoods and oak–pine. *Castanea dentata* was abundant in mixed oak communities before the chestnut blight. Today, the mixed oak forest at our study sites type is composed of *Quercus prinus* L. (32%), *Quercus rubra* L. (22%), *Acer rubrum* L. (24%), *Oxydendrum arboreum* (L.) DC (10%), with *Nyssa sylvatica* Marsh., *Liriodendron tulipifera* L., *Robinia pseudoacacia* L., *Betula lenta* L., *Carya* spp., and *Tsuga canadensis* (L.) Carr. individually comprising ≤5% of canopy basal area.

Much of the forest understory at Coweeta is dominated by *R. maximum*, an ericaceous, evergreen shrub, that occurs at all elevations in the Coweeta basin (Swank and Crossley 1988). *Rhododendron maximum* forms a dense subcanopy layer 3–7 m in height, with stem densities between 5000 and 17 000 per hectare (Baker and Van Lear 1998), and leaf area indices (LAI) ranging from approximately 4.8 to 6.6 (Janneke HilleRisLambers, unpublished data). Stem densities in our gap plots are approximately 8900 per hectare (B. Beckage, unpublished data) with diameters most frequently ranging from 4 to 7 cm DBH (diameter at breast height) but sometimes greater than 10 cm DBH (B. Beckage, unpublished data). *Rhododendron maximum* has expanded in areal coverage this century as a result of chestnut decline and fire suppression (Baker and Van Lear 1998; Dobbs 1995; Monk et al. 1985; Phillips and Murdy 1985; Woods and Shanks 1959, but see McGee and Smith 1967). In the Coweeta basin, the area occupied by *R. maximum* doubled from approximately 15% in 1976 to nearly 32% by 1993

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(Dobbs 1995). *Gaylussaccia baccata* (Wang.) K. Koch, a short-statured ericaceous shrub, typically under 1 m in height, is common in areas lacking *R. maximum*. *Gaylussaccia baccata* averaged 48% coverage in 120, 1 m^2 quadrats outside *R. maximum* (B. Beckage, unpublished data). Beneath *R. maximum, G. baccata*'s average coverage was 0.8%. The next most abundant understory species was *Medeola virginiana* L. with 5.2% coverage outside versus 2.2% beneath *R. maximum*.

Methods

We studied recruitment in 12 experimental gaps, half of which contained a natural *R. maximum* understory. We monitored seedling recruitment in the artificial gaps and adjacent canopy controls prior to and for four years following gap creation. We concurrently measured factors that were likely to affect recruitment, including light, soil moisture, litter biomass, and seed rain.

Our clusters of experimental gaps were located in two mixed oak stands that bracket the elevation range of this community, hereafter referred to as "low elevation" (850 m) and "high elevation" (1100 m) sites. Sites had a northeast aspect and slopes ranged from 30 to 50% (high elevation) and from 45 to 70% (low elevation). At both sites, we established six plots (12 plots total), each corresponding to a single experimental gap. Three of the six plots at each elevation had a dense *R. maximum* understory, while three plots lacked *R. maximum*. *Rhododendron maximum* has a patchy distribution at these sites, permitting us to locate experimental gaps (with and without *R. maximum*) in close proximity, thus allowing for consistent overstory composition, slope, soils, and microclimate. Locations for experimental gaps were selected in 1991, and canopy trees were marked for girdling to produce gaps of approximately 300 m^2 (expanded gap definition, Runkle 1981) with a gap diameter to canopy height ratio of approximately 0.95. Up to five trees from a variety of species were girdled to create each gap. A transect, comprised of 40 contiguous 1 m^2 quadrats, was established across each planned gap. Transects were generally oriented in a north–south direction. Transects included 20 central quadrats exposed to gap conditions and 20 outer quadrats subtended by the surrounding canopy. There were a few exceptions to this layout, due to topographic considerations or patchiness of the *R. maximum*. In these cases, transects deviated from a north–south orientation or were interrupted to maintain consistent understory conditions (e.g., with or without *R. maximum*). Following collection of pretreatment data in 1993, we produced experimental canopy gaps by girdling trees in late summer of the same year. The herbicide Garlon was applied to trees that leafed out the following spring. Girdled trees remained standing for the duration of our study, although large branches began to fall in the 4th year.

We quantified the understory light environment using hemispherical photographs taken in the center and at both ends of each transect. Photographs were taken at a height of 1 m in the summer of all years from 1992 and 1997, except 1993 (due to logistical problems). Photography for a given sample period was completed for all transects on one or two consecutive days. Photographs were taken using a fish-eye Nikkor 8 mm f2.8 lens (180° field of view) with Kodak Tri-X film and a self-leveling gimbal. All photographs were taken using a red filter (to increase the contrast between sky and foliage) with magnetic north at the top of the image. This allowed superposition of the solar track onto the photograph. Photographs were digitized using a Polaroid slide scanner and analyzed using Hemiview canopy analysis software (Delta-T Devices, Cambridge, U.K.). The software estimates direct and indirect site factors (ISFs and DSFs), which are defined as the proportion of direct and diffuse radiation received below the canopy as a fraction of that received above the canopy (Rich 1989). Site factors range from 0 (open sky) to 1 (complete obstruction). Cosine corrected direct and indirect site factors were combined into a global site factor (GSF) using weighting factors that represent the proportion of diffuse vs. direct light at our study site. Weighting factors were calculated based on meteorological data collected at the Coweeta basin (Bonan 1989; Nikolov and Zeller 1992). The GSFs from both ends of each transect were averaged into one value representative of canopy conditions for comparison to the GSF of the transect center. While the steep slopes and different aspects of our two sites (i.e., low and high elevation) would be expected to effect light levels in the gaps, the canopy photographs and their subsequent analyses accounted for these considerations in the final estimated site factors.

To determine how soil moisture might be affected by gap creation and understory characteristics, we estimated volumetric soil moisture content (%Water Content) in the upper 15 cm along transects. Because microclimatic conditions beneath *R. maximum* are less variable (Clinton 1995), we obtained measurements along only one of the three *R. maximum* transects but in all three transects without *R. maximum* at each elevation (resulting in data for 8 of 12 transects). Estimates of percent water content were made using time domain reflectometry (TDR; TRASE, Soil Moisture Equipment, Inc., Santa Barbara, Calif.) (Topp 1993). Measurements were made at 11 positions along each transect, including nine at 2-m intervals extending outward from the gap center and two near the ends of each transect. Measurements were made at 3-week intervals during the growing season and at 4-week intervals during the non-growing season beginning on 21 May 1993 and continuing through 21 August 1996. We include in this analysis only those measurements taken from June through the end of September because these dates represent growing season conditions.

To determine how litter may affect recruitment, we collected two samples of litter biomass from each plot (one from gap and one from canopy) at four different times from November 1996 to December 1997 (96 samples in total). We removed all litter within a 35 × 35 cm area of the forest floor selected at random until only unidentifiable organic detritus remained. Litter was placed in paper bags and dried at 60°C to constant weight.

Seed rain was monitored continuously at two mixed oak stands near (within 200 m of) our experimental gaps as part of a larger study of forest dynamics in the Coweeta basin (Clark et al. 1998). We compared seed rain data from the mixed oak sites to seedling recruitment in our experimental gaps. Twenty 0.42 × 0.42 m seed traps were arrayed 5 m apart along two 20 m long transects at each site. Trap contents were collected two to four times annually and whole seeds were sorted to the lowest possible taxonomic unit. In the case of *O. arboreum*, seed capsules were counted instead of actual seeds. We estimated that there were 25 seeds per capsule based on a subsample of capsules, but this estimate is likely to be conservative as the capsules had already partially opened. Viable seed rain (henceforth we mean viable seed rain when we refer to "seed rain") was obtained by multiplying number of whole seeds by estimates of seed viability. Viability estimates for our taxa were taken from the literature (Burns and Honkala 1990; Schopmeyer 1974; Young and Young 1992) or from our own data. Estimated viabilities were 0.91 for *A. rubrum*, 0.54 for *Amelanchier arborea* (Michx. f.) Fern., 0.43 for *B. lenta*, 0.6 for *Carya* spp, 0.54 for *Fraxinus* spp, 0.1 for *L. tulipifera*, 0.55 for *Magnolia acuminata* L., 0.6 for *N. sylvatica*, 0.19 for *O. arboreum*, 0.9 for *Q. prinus*, 0.9 for *Q. rubra*, and 0.9 for *R. pseudoacacia*.

We censused tree seedlings along all transects annually in July or August from 1993 to 1997. We identified all seedlings and saplings <2 m tall to genus or species (for *A. rubrum*, *L. tulipifera*, and *Q. prinus*). Seedlings classified as *Betula* spp were likely *B. lenta*, because *B. allegheniensis* is restricted to the highest elevations at Coweeta. We were unable to confidently differentiate all seedlings of *Q. velutina*, *Q. coccinea*, and *Q. rubra*, so these were grouped as *Q. rubra* type.

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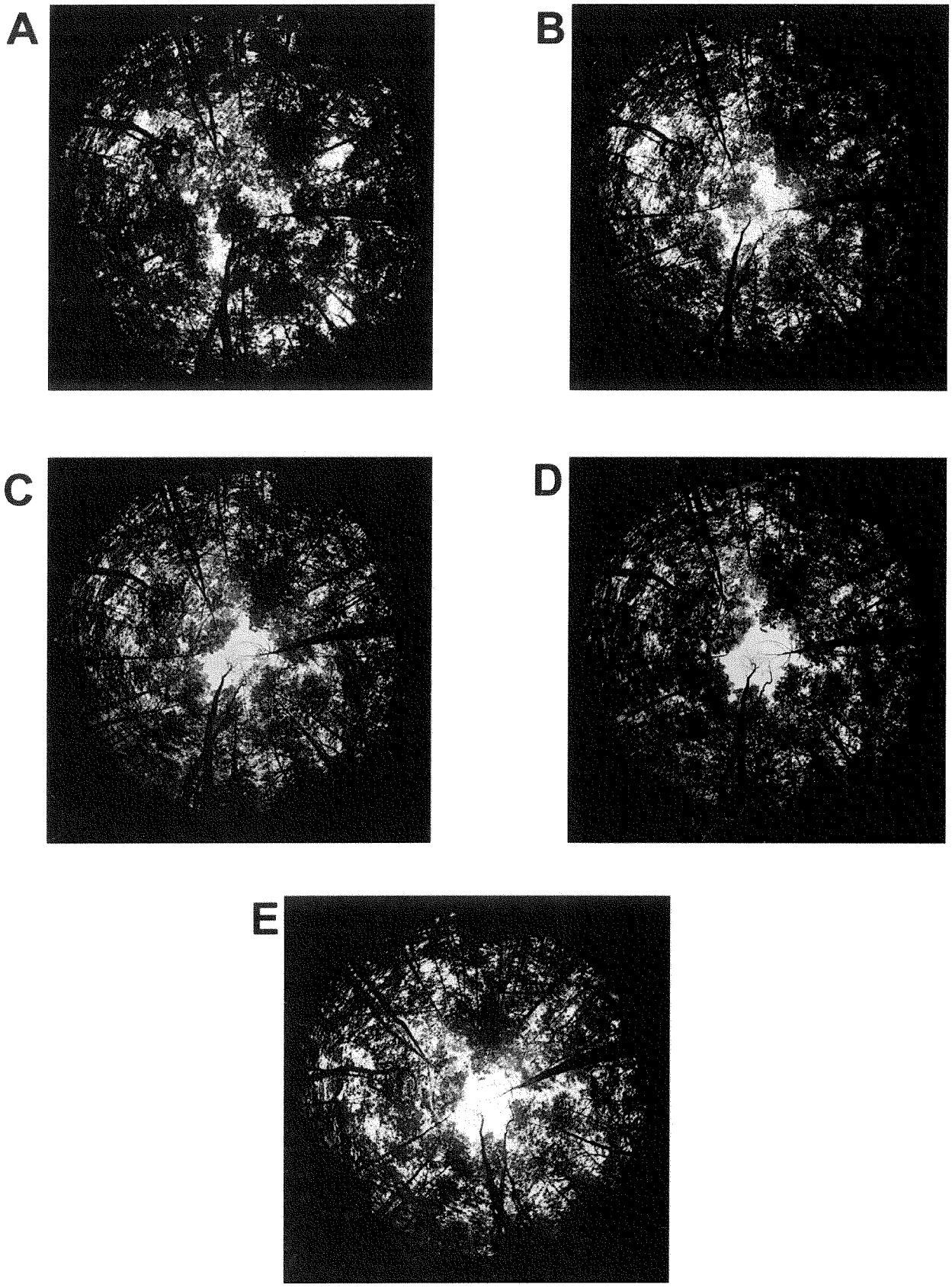
Fig. 1. Time course of gap formation showing (*a*) canopy prior to creation of canopy gap and the canopy gap (*b*) 1 year, (*c*) 2 years, (*d*) 3 years, and (*e*) 4 years following girdling of trees.



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Seedlings were censused in two age-classes: first-year and >first-year. First-year seedlings were new seedlings that had germinated in the current year (or since the previous summer's census). They were recognized by the presence of cotyledons and lack of terminal bud scale scars. All older seedlings were classified as >first-year seedlings, although this group may include vegetative reproduction for *A. rubrum* and *N. sylvatica*. We found these age-classes useful because the first-year seedling class provided information on seed arrival and germination, while the >first-year class provided information on the pool of surviving seedlings. The census data were used to calculate species richness, abundance, and the Shannon–Weiner diversity index. Nomenclature follows Wofford (1989).

Analysis

Global site factors (GSF), litter, and seedling data were analyzed using analysis of variance (ANOVA). Because soil moisture measurements were unbalanced, we tested gap–canopy differences using one-sided *t*-tests. GSF values, which range from 0 to 1, were arcsine square root transformed (Steel et al. 1997) to achieve normality and analyzed as a split-split plot, mixed model ANOVA (PROC MIXED; SAS Institute Inc. 1995). Transects were considered whole-plot units (random effect) with gap–canopy being the first split and year being the second split. Main effects were decomposed into single-degree-of-freedom contrasts to test specific hypotheses. Litter data were not transformed, because they were normally distributed (PROC UNIVARIATE; SAS Insitute Inc. 1995).

To compare recruitment in the gap center with that in the understory, we compared tree species richness, diversity, and seedling counts in the inner 16 quadrats with those of the outer 16 quadrats of the same transects, omitting a 4-m transitional area at the two gap edges. We used a symmetric transitional area (vs. one offset to the north), because not all transects were oriented in a north–south direction. We refer to these subsets as "gap" and "canopy," respectively. Tree species richness and diversity indices were calculated in two manners. Data were summed across quadrats within gap and canopy treatments to examine changes within these treatments but were summed across all 32 quadrats within transects for comparison of total species richness and diversity (including gap and canopy conditions together) pre- and post-gap formation. Seedling counts were initially analyzed assuming a Poisson distribution using the GLIMMIX macro (Littell et al. 1996). However, GLIMMIX had difficulty converging for most species in our data set. This is a common problem with the GLIMMIX macro particularly when there are many 0 values or a small data set (D. Higdon, Duke University, Durham, N.C., personal communication). We then analyzed mean seedling densities of the 16 subplots assuming Gaussian error. To achieve normality, seedling densities were transformed as ln(seedling density + 1) and analyzed using the mixed model ANOVA described above. Results of this analysis were similar to those obtained using the GLIMMIX macro (in the cases where convergence was achieved). Only the results using Gaussian error are reported. Within the ANOVA model, treatment effects were examined in two ways. First, we compared responses of treatments to their respective controls. Second, we compared pre- to post-treatment densities (intervention analysis). We did this by examining both main effects and appropriate single degree of freedom contrasts. We adopt the notation of referring to gap conditions as G^+ (vs. canopy ~G^-), the presence of *R. maximum* as R^+ (vs. no *R. maximum* ~R^-), and treatments combinations such as gap conditions with *R. maximum* as $G^+ + R^+$.

We conducted an analysis of covariance (ANCOVA) to test the effects of gap and *R. maximum* on *A. rubrum* seedling densities after adjusting for understory light conditions. We used *A. rubrum* seedling densities, because it was the most widespread and abundant taxon across our transects and was most responsive to gap and *R. maximum* treatments. Arcsine square root transformed GSF values from the canopy photographs were used as covariates representing understory light conditions. Because we lacked canopy photographs for 1993, we paired the 1992 canopy photographs with the 1993 seedling censuses (for the effect of light on seedling recruitment). This pairing is sensible, because the 1993 seedling censuses were conducted before the trees were girdled, and, thus, their light environment was similar to that in the 1992 canopy photographs.

We also conducted an ANCOVA using *Q. rubra* to test for seed rain limitations on recruitment. We specifically tested whether the elevation effect was, in fact, a seed availability effect by determining whether there was an elevation effect after adjusting for seed rain differences. We estimated (viable) seed input into each gap–canopy subplot by multiplying canopy tree basal area by yearly estimates of fecundity (seeds per unit of basal area). Fecundity estimates were derived from the seed rain data from adjacent low- and high-elevation mixed oak sites (described above). Basal area estimates were calculated for an approximately 20 m radius surrounding each gap–canopy subplot. We limited our analysis to *Q. rubra*, because most seed is dispersed short distances; estimates of seed input from species having longer dispersal (i.e., >20 m) would likely be poor. These seed rain estimates for each gap–canopy replicate were used as covariates with transformed first-year seedling densities.

Results

The experimental gaps

An example of gap formation in a treatment without *R. maximum* is shown in Fig. 1. Figure 1*a* shows the closed canopy in 1992 before the experiment began. The 2 years following gap formation (i.e., 1994 and 1995) showed reduced leaf area in canopy trees that were girdled (Fig 1*b* and 1*c*). By the third year following gap creation (i.e., 1996), the canopy gaps were formed by three standing dead trees (Fig. 1*d*). By 1997 (Fig. 1*e*), branches had begun to fall from standing dead trees and reduced understory leaf area in many gaps.

Environmental responses

The effect of gap creation on light levels at 1 m above the ground depended on the presence of *R. maximum* (Fig. 2*a*; gap × *R. maximum* interaction, $P < 0.0001$; gap × *R. maximum* × year, $P = 0.0003$). The proportion of light above the canopy reaching the understory (GSF value) increased following gap creation in gaps without *R. maximum* (contrast of 1994–1997 vs. 1993 in $G^+ + R^-$, $P < 0.0001$) but were unchanged in gaps with *R. maximum* (contrast of 1994–1997 vs. 1993 in $G^+ + R^+$, $P = 0.09$). The GSF values did not increase beneath canopy controls. The GSF value was 0.023 beneath *R. maximum* (R^+), 0.052 beneath the canopy outside *R. maximum* ($G^- + R^-$), and 0.119 in gaps outside *R. maximum* ($G^+ + R^-$). The rise in GSF values in 1997 in gaps outside of *R. maximum* ($G^+ + R^-$; Fig. 2*a*) resulted from branches falling from dead trees and further opening the understory.

Soil moisture increased in all treatments following gap creation (Fig. 2*b*). Precipitation was especially low during the summer of 1993 relative to subsequent summers (Fig. 2*b*), accounting for the increased soil moisture content (percent water content) for all treatments after 1993. However, percent water content was consistently higher in gaps than beneath the canopy following gap creation, regardless

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Fig. 2. Abiotic factors following gap creation in late summer 1993. (*a*) Light availability represented by global site factors from canopy photographs (n = 6, mean + SE). (*b*) Soil moisture from TDR rods as percent water content (n = 6 for R^-, n = 2 for R^+, means), and monthly total precipitation measured at low- and high-elevation sites within the Coweeta basin. (*c*) Soil moisture differences between gap–canopy pairs as percent water content (n = 6 for R^-, n = 2 for R^+; mean + SE). We refer to gap conditions as G^+ (vs. canopy, G^-) and to the presence of *R. maximum* as R^+ (vs. no *R. maximum*, R^-) so that treatment combinations are defined as follows: $G^+ + R^-$, gap with no *R. maximum*; $G^- + R^-$, canopy with no *R. maximum*; $G^+ + R^+$, gap with *R. maximum*; $G^- + R^+$, canopy with *R. maximum*. One-sided t tests under the null hypothesis that gap–canopy differences were 0 yielded P values of 0.077, 0.056, 0.031, 0.047 for R^- in 1993 through 1996, respectively, and 0.69, 0.35, 0.016, 0.072 for R^+ in 1993 through 1996.

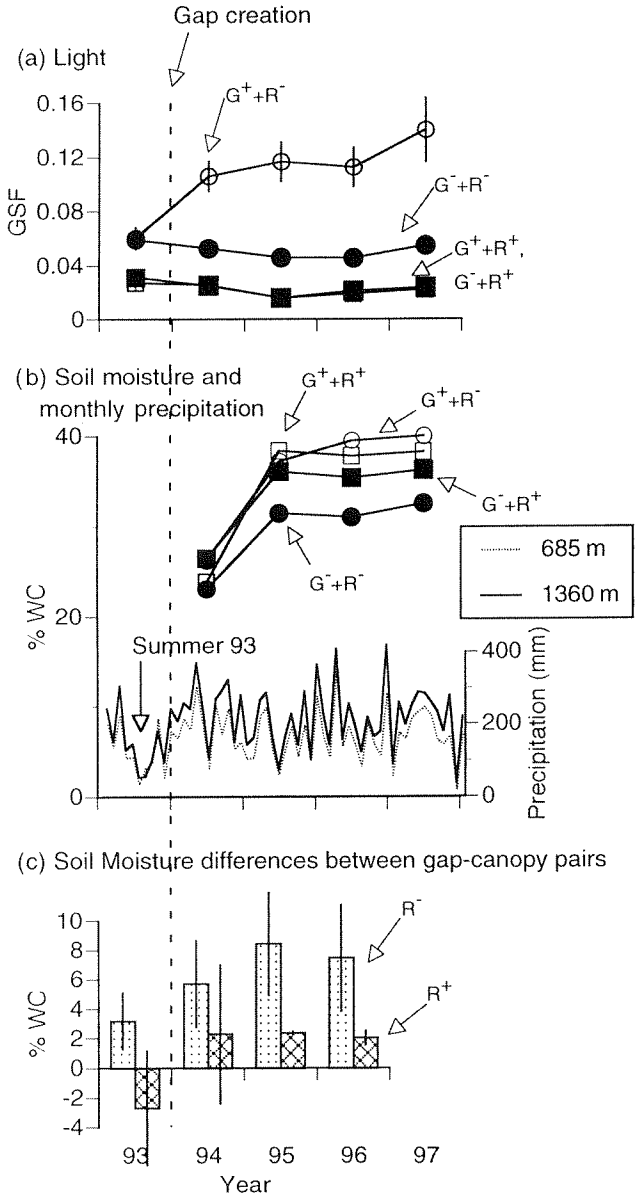
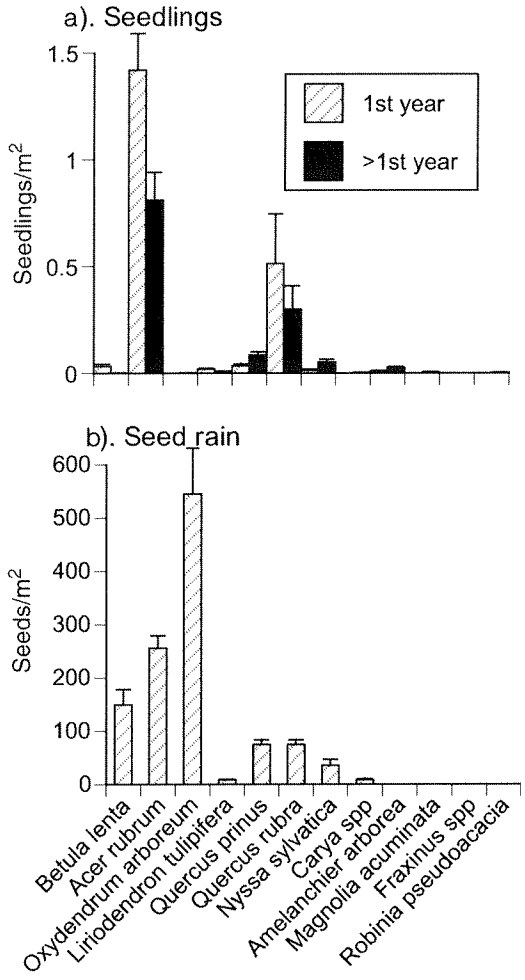


Fig. 3. Seedling and seed rain abundance for all tree species observed in our seedling transects; (*a*) seedling means and standard errors over all years and treatments and (*b*) seed rain observed in mixed oak communities adjacent to our experimental gaps averaged over years (mean + SE).



of *R. maximum*. Paired gap–canopy differences reflect this pattern, with moisture differences increasing disproportionately in gaps (Fig. 2*c*).

Litter biomass was 20% higher in sites with than in sites without *R. maximum* (R^+ = 508.2 vs. R^- = 423.8 g/m^2, P = 0.0002), but litter was not affected by gaps (G^+ = 462.1 vs. G^- = 469.9 g/m^2, P = 0.72). *Rhododendron maximum* affected litter character as well; *R. maximum* leaves are thicker, more sclerophyllous, and of lower nutrient quality than deciduous leaves (B. Beckage, personal observation; Monk et al. 1985).

Recruitment responses

Twelve tree seedling taxa occurred in our censuses, with most taxa present at very low densities (Fig. 3*a*). *Betula lenta* and *O. arboreum* were notable in that they had low seedling densities despite relatively high seed rain (Fig. 3*b*). *Acer rubrum* was the most common species, corresponding with its high seed rain. *Quercus rubra* had the next most abundant seedlings despite only moderate seed rain. The low seedling densities of *L. tulipifera, Carya* spp., *A. arborea*,

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Fig. 4. Seed rain (right-hand *y* axis of *a* and *e*) and seedling densities of the shade-tolerant *A. rubrum*. Seedling densities (mean + SE) beneath gaps and canopy controls by year for the (*a–d*) high- and (*e–h*) low-elevation sites. Plots in the right-hand column contain *R. maximum*. Seedling densities are shown for two age-classes, first-year seedlings (*a*, *b*, *e*, *f*) and >first-year seedlings (*c*, *d*, *g*, *h*).

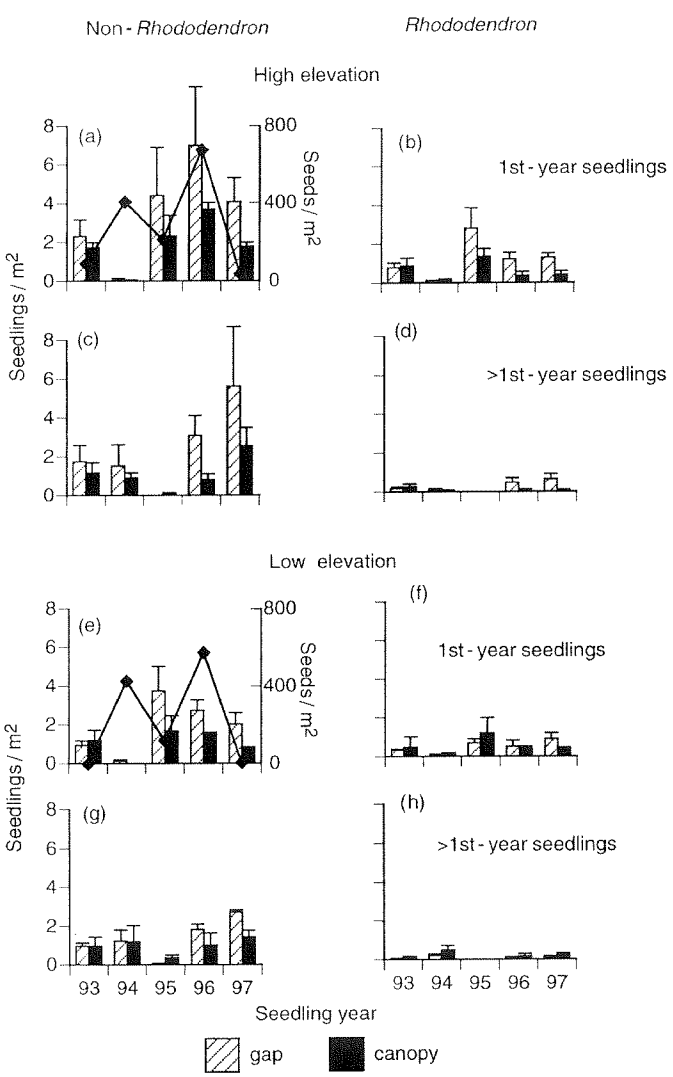
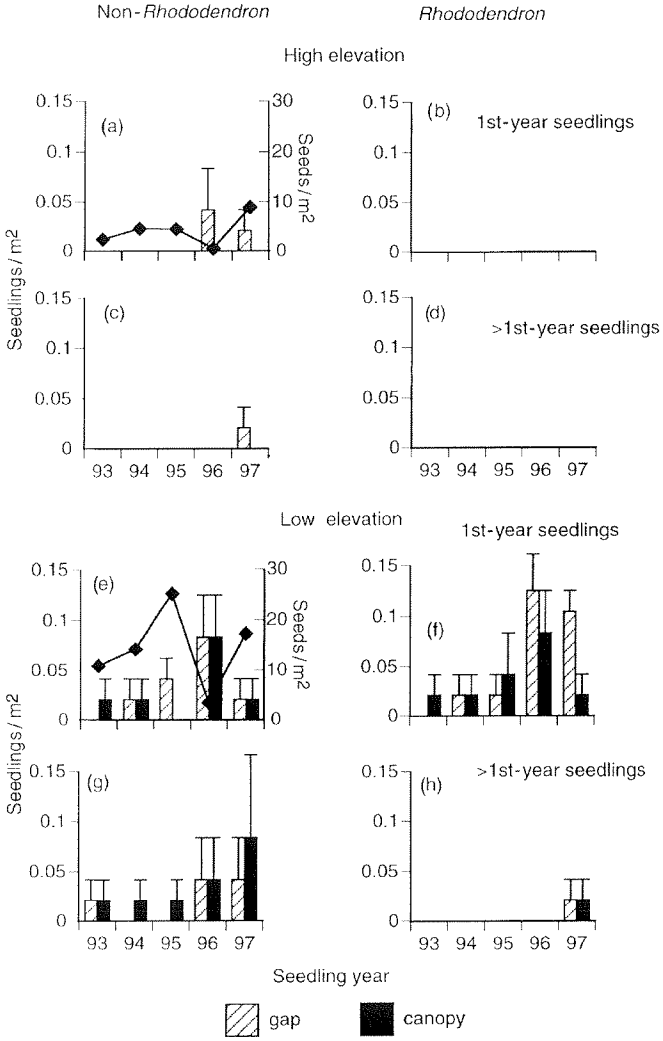


Fig. 5. Seed rain (right-hand *y* axis of *a* and *e*) and seedling densities of the shade-intolerant *L. tulipifera*. Seedling densities (mean + SE) beneath gaps and canopy controls by year for the (*a–d*) high- and (*e–h*) low-elevation sties. Plots in the right-hand column contain *R. maximum*. Seedling densities are shown for two age-classes, first-year seedlings (*a*, *b*, *e*, *f*) and >first-year seedlings (*c*, *d*, *g*, *h*).



M. acuminata, *Fraxinus* spp., and *R. pseudoacacia* were consistent with low seed rain.

Acer rubrum was the most responsive species to gap formation, benefiting from abundant, well-dispersed seed at both elevations (Figs. 4*a* and 4*e*) and shade tolerance. First-year and >first-year seedling densities were greater in gaps but only outside *R. maximum* (G^+ vs. G^- contrasts in R^- for 1994–1997 were $P = 0.018$ and $P = 0.015$ for first-year and >first-year seedlings, respectively; G^+ vs. G^- contrasts in R^+ for 1994–1997 were $P = 0.19$ and $P = 0.61$ for first-year and >first-year seedlings, respectively). *Rhododendron maximum* resulted in lowered seedling densities of both first-year and >first-year *A. rubrum* seedlings ($P = 0.0053$, $P = 0.0020$).

Seed rain appeared to limit recruitment of *L. tulipifera* at high elevation; seedling densities were particularly low at the high-elevation site compared with the low-elevation site ($P = 0.0022$) corresponding to disparities in seed rain (Figs. 5*a* and 5*e*). But even at low elevations, seedlings of the shade-intolerant *L. tulipifera* occurred at low densities regardless of gap or *R. maximum* treatment. First-year *L. tulipifera* seedling densities were greater in gaps than beneath canopy, regardless of *R. maximum*, but only at the

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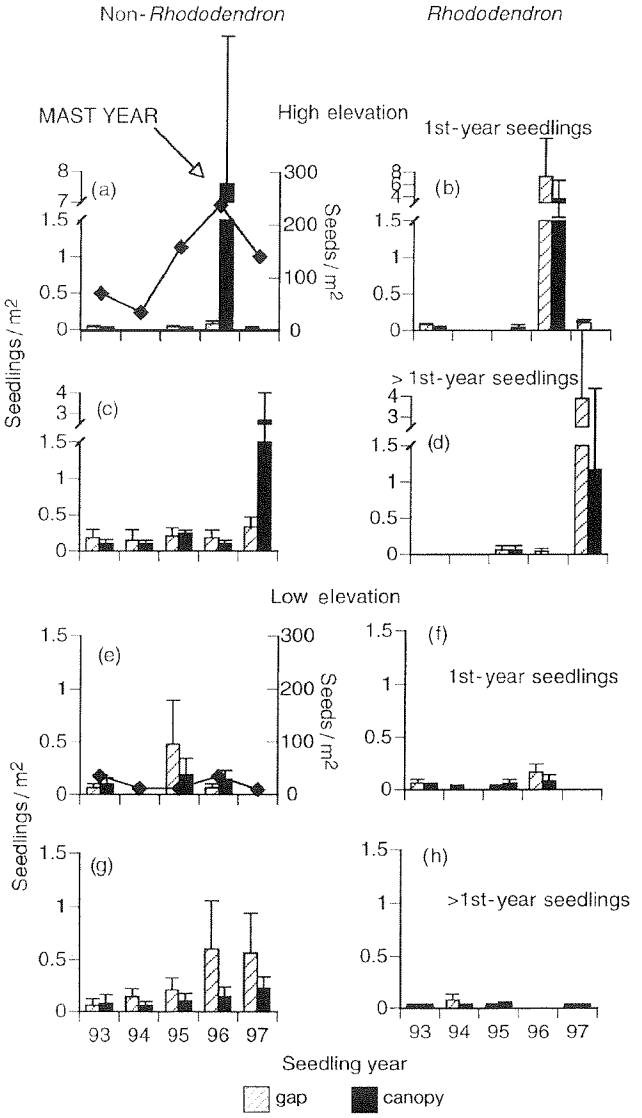
Fig. 6. Seed rain (right-hand *y* axis of *a* and *e*) and seedling densities of the intermediately shade-tolerant *Q. rubra*. Seedling densities (mean + SE) beneath gaps and canopy controls by year for the (*a–d*) high and (*e–h*) low elevation sites. Plots in the right-hand column contain *R. maximum*. Seedling densities are shown for two age-classes, first-year seedlings (*a*, *b*, *e*, *f*) and >first-year seedlings (*c*, *d*, *g*, *h*).



low-elevation sites (Figs. 5*e* and 5*f*; intervention analysis; the contrast for 1994–1997 vs. 1993 in $G^+ + R^-$ and $G^+ + R^+$ at low elevation were $P = 0.020$ and $P = 0.0003$, respectively). This is partly the result of lower seedling densities in the gaps (compared with canopy) in the pretreatment year of 1993. The higher densities of first-year seedlings in gaps did not result in higher densities of >first-year seedlings in subsequent years, indicating that seedling survivorship was low. While the effect of *R. maximum* on *L. tulipifera* was not significant ($P = 0.68$ and $P = 0.28$ for first-year and >first-year seedlings, respectively), there were more >first-year seedlings outside *R. maximum* (Fig. 5*g* vs. 5*h*).

Another shade-intolerant species, *B. lenta* (Burns and Honkala 1990), had higher first-year seedling densities in gaps (contrast of G^+ vs. G^- in 1994–1997, $P = 0.019$). This resulted in increased >first-year seedlings only in high elevation gaps outside *R. maximum* (contrast of $G^+ + R^-$ vs. $G^- + R^-$ in high elevation in 1994–1997 for >first-year seedlings, $P = 0.029$). No >first-year *B. lenta* seedlings occurred beneath *R. maximum*.

Recruitment patterns for the intermediately shade-tolerant *Q. rubra* were dominated by the 1995 mast year (Figs. 6*a* and 6*e*), which produced a large 1996 cohort at the high-elevation site (Figs. 6*a* and 6*b*; elevation × year for first-year seedlings, $P < 0.0001$). *Quercus* fecundity (seed production per basal area) at the high elevation was six times greater than at the low elevation in the mast year. The mast event produced a large cohort of seedlings concentrated beneath and downslope of parent trees, regardless of gap or *R. maximum* treatment. Although mortality of these seedlings was high, this cohort (>first-year) was still abundant in the high-elevation stand in 1997 (Figs. 6*c* and 6*d*). In contrast, densities of >first-year seedlings in the low elevation plots, which did not experience a mast event, were higher outside *R. maximum* (Figs. 6*e* and 6*g* vs. 6*f* and 6*h*) and higher in gaps than beneath the canopy in areas without *R. maximum* (Fig. 6*g*).

The effect of gaps and *R. maximum* for all species (averaged across years) is shown in Fig. 7. While most species had higher seedling densities in gaps compared with intact canopy, the increases were only significant for *A. rubrum* and first-year *B. lenta* as already described above (Fig. 7*a*). Similarly, seedling densities of most species were decreased beneath *R. maximum*, but only *A. rubrum* (described above) and *Q. prinus* (>first-year $P = 0.043$) were significantly different (Fig. 7*b*).

To determine whether seedling densities beneath *R. maximum* were low in response to reduced light levels, we conducted an ANCOVA on first-year and >first-year seedlings of our most abundant species, *A. rubrum*, with light (GSF values) as a covariate. Light × treatment interactions were not significant for either seedling age-class indicating that homogeneity-of-slopes criteria were met. With light as a covariate, the gap and *R. maximum* effects were not significant for first-year *A. rubrum*. For >first-year seedlings, the gap effect was not significant, but the *R. maximum* effect was still significant ($P = 0.0079$). This suggests that *R. maximum* suppressed >first-year seedlings beyond its influence on light availability.

We also conducted an ANCOVA on first-year *Q. rubra* seedlings with seed rain (see Methods) as a covariate to ascertain whether differences in seedling densities between high- and low-elevation sites correspond to disparities in available seed. Homogeneity of slopes criteria were met for treatment groups. In the ANOVA model without the seed rain covariate, the effect of elevation was marginally significant ($P = 0.050$). With seed rain in the model, the effect of elevation was not significant ($P = 0.11$). This suggests that the difference in first-year seedling densities between the high- and low-elevation sites was due to differences in seed rain.

Species richness and diversity of seedling regeneration

Rhododendron maximum had more impact on species richness, species diversity, and density of seedling regeneration than did canopy gaps. Species richness was greater

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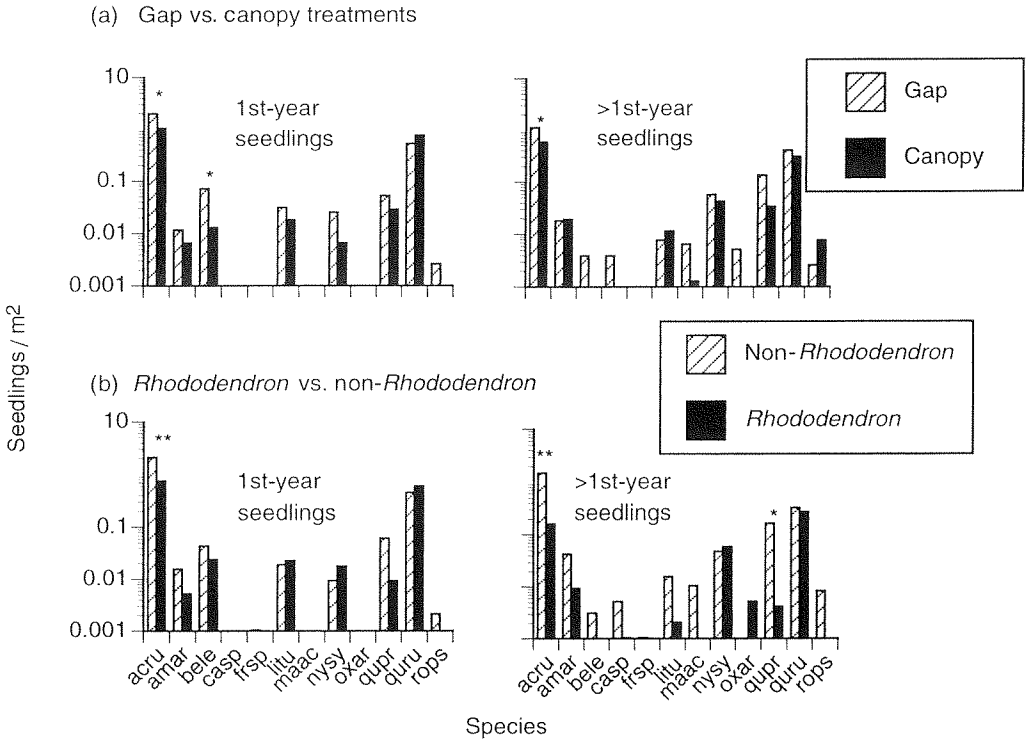
Fig. 7. Overall responses of individual species to treatments (*a*) Seedling densities in gaps versus canopy controls for first-year and >first-year seedlings, respectively. (*b*) Seedling densities in areas with or without *R. maximum* for first- and >first-year seedlings. Values in Fig. 7*a* are means over years following gap creation, while values in Fig. 7*b* includes pre-gap years as well. *, $P < 0.05$; **, $P < 0.01$. acru, *Acer rubrum*; amar, *Amelanchier arborea*; besp, *Betula* spp.; casp, *Carya* spp; frsp, *Fraxinus* spp.; litu, *Liriodendron tulipifera*; maac, *Magnolia acuminata*; nysy, *Nyssa sylvatica*; oxar, *Oxydendrum arboreum*; qupr, *Quercus prinus*; quru, *Quercus rubra*; rops, *Robinia psuedoacacia*.



outside *R. maximum* (Fig. 8*a*, 4.28 in R^- vs. 2.52 in R^+, $P = 0.017$) but was not significantly higher in gaps (3.75 in G^+, 3.06 in G^-; contrast of G^+ vs. G^- canopy in 1994–1997, $P = 0.055$) nor was the gap × *R. maximum* interaction significant ($P = 0.60$; gap × *R. maximum* × year, $P = 0.37$). Species richness did not increase following canopy gap formation in any gap × *R. maximum* treatment combination (intervention analysis, P values ranged from 0.47 to 0.84). Species richness in transects (gap + canopy portions of transect) was not greater following gap formation compared with pre-treatment levels (Fig. 8*a*, 1993 vs. 1994–1997 in R^- and R^+, $P = 0.51$ and 0.91, respectively). The Shannon–Weiner diversity index was not significantly higher outside *R. maximum* (Fig. 8*b*, 0.60 in R^- vs. 0.43 in R^+, $P = 0.10$) except in 1994 and 1995 ($P = 0.045$, $P = 0.0047$). Diversity was not significantly higher in gaps (0.54 in G^+, 0.48 in G^-; contrast of G^+ vs. G^- canopy in 1994–1997, $P = 0.33$), did not increase in any gap × *R. maximum* treatment combination following gap creation (intervention analysis, P values ranged from 0.09 to 0.84) nor was the gap × *R. maximum* interaction significant ($P = 0.25$; gap × *R. maximum* × year, $P = 0.26$). Diversity in transects (gap + canopy portions of transect) did not increase following gap formation compared with pre-treatment levels (1993 vs. 1994–1997 in R^- and R^+, $P = 0.92$ and 0.66). Total seedling densities were higher beneath gaps, but the difference was not significant for either first-year or >first-year seedlings ($P = 0.061$, $P = 0.16$, Fig. 9*a*). *Rhododendron maximum* appeared to inhibit seedling establishment; seedling densities were significantly lower beneath *R. maximum* for both seedling age-classes ($P = 0.010$, $P = 0.0016$, Fig. 9*b*). Neither the gap × *R. maximum* nor the gap × *R. maximum* × year interactions were significant for either age-class ($P = 0.85$ and 0.42 for first-year seedlings and $P = 0.37$ and 0.60 for >first-year seedlings, respectively).

Discussion

Our results do not support the efficacy of intermediate-sized canopy gaps for maintaining diversity in second-growth forests. Canopy gaps did not increase seedling diversity or richness compared to pre-treatment levels (Fig. 8, intervention analysis in results). Seedlings of most species were rare, and, with the exception of *A. rubrum*, densities did not increase following gap formation (Fig. 7*a*, >first-year seedlings). Seedling densities were especially low (Figs. 7*b*, 9*b*) and unresponsive to gap formation beneath the understory shrub *R. maximum*. The weak recruitment response to experimental gaps of this size (~300 m^2) resulted not only from competition with the shrub understory but also because seed rain often limited recruitment.

Previous studies have lead to some uncertainty regarding the importance of intermediate-sized gaps in forest regeneration. This could derive from several causes. First, the effect of gaps may differ in second-growth versus old-growth forests (Clebsch and Busing 1989) as well as in forests of

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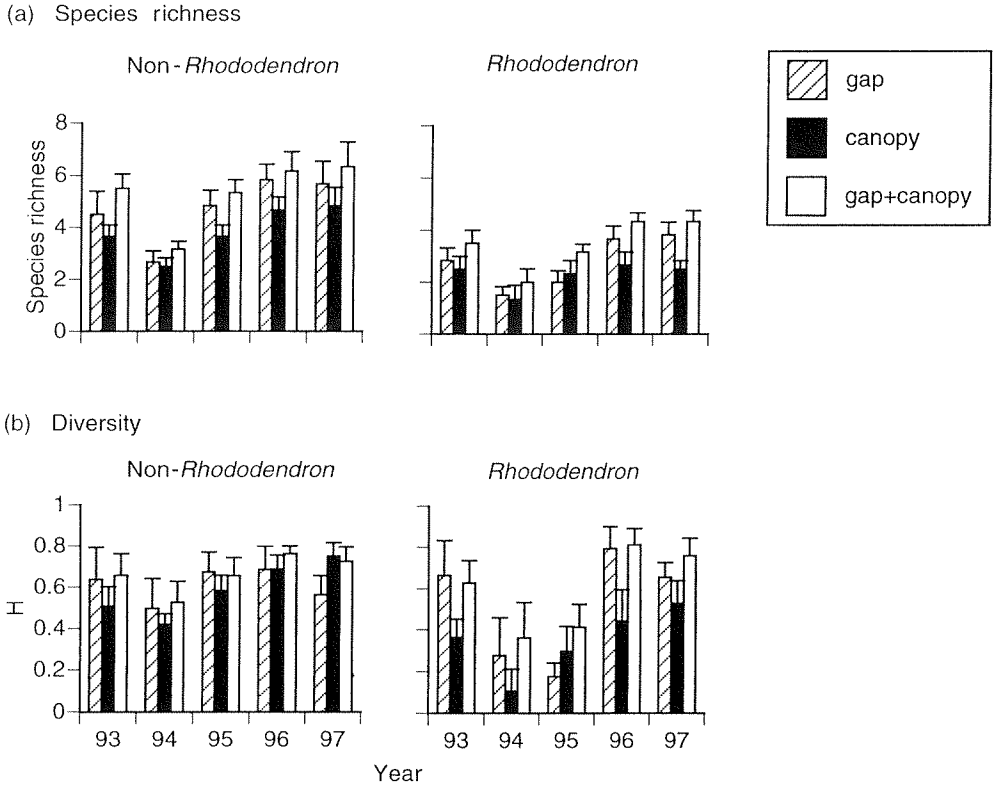
Fig. 8. Species richness (*a*) and Shannon–Weiner diversity (*b*) by year for gap and *R. maximum* treatments (mean + SE). Gap + canopy indicates species richness and diversity calculated over both treatments in each transect.



differing composition. Studies suggesting that intermediate-sized gaps maintain forest diversity often have been done in old-growth stands (Barden 1979, 1980, 1981; Busing 1994; Lorimer 1980; Runkle 1981; Williamson 1975), whereas studies that question the importance of such gaps mostly come from second-growth forests (Collins and Pickett 1987; Della-Bianca and Beck 1985; Hibbs 1982). Clebsch and Busing (1989) suggest that the physical structure of second-growth stands may minimize gap and canopy microsite differences, which is consistent with the results from other studies (Collins and Pickett 1987). In our study, light levels beneath intact canopy (outside of *R. maximum*) were, in fact, higher than would be expected beneath mesic forests (~1 vs. 5% in our study; Canham et al. 1990), blurring the distinction between gap and canopy conditions. However, differences between old-growth versus second-growth stands could simply be a function of gap size; trees are often larger in old-growth forests, and thus, their deaths result in more pronounced increases in resource levels. This possibility is difficult to evaluate because studies often do not report gap size. When gap size is reported, it is measured using one of two methods (expanded gap definition (Runkle 1981) or the projected area of the canopy opening) that are difficult to compare (Valverde and Silvertown 1997). Second, some studies that emphasized the importance of intermediate-sized gaps based their conclusions on the relative abundance of seedlings in gaps or on the frequency of "gap successors" relative to their abundance in the overstory (Barden 1979, 1980, 1981; Runkle 1981). In these studies, relative abundance beneath intact canopies is not measured for comparison with that in gaps; instead, there is an implicit assumption that gaps are important to regeneration. In fact, the relative abundances of >first-year seedlings in our experimental gaps did not differ from those beneath the closed canopy for any species in our study (Fig. 10, P values > 0.05 on arcsine square-root transformed data), a result similar to that found by Busing and White (1997). Therefore, Markov models based on relative abundances in either intermediate-sized gaps or beneath closed canopy would appear adequate to explain overstory abundance. In addition, calculation of future composition based only on relative abundance of juveniles in gaps can be inaccurate, because future composition also depends on absolute abundance. Seedling recruitment in our experimental gaps was too sparse to predict eventual canopy dominants. Given the seedling densities observed in our canopy gaps, annual survivorship would need to be ≥75% for a single individual (of any species) to survive 20 years in a typical gap, whereas we actually find much lower juvenile survivorship (B. Beckage and J.S. Clark, unpublished data).

Seed rain matters

Seedling recruitment was linked to seed availability. In general, species with low seed rain had few or no seedlings, e.g., *Amelanchier*, *Carya*, *Fraxinus*, *Liriodendron*, *Magnolia*, *Robinia* (Fig. 3). Elevation differences in *L. tulipifera* and *Q. rubra* seedling densities corresponded to differences in seed rain (Figs. 5 and 6, results of *Q. rubra* ANCOVA). Yearly fluctuations in seed rain were clearly apparent in seedling dynamics. For example, the single large *Q. rubra* cohort corresponded to a mast event in 1995 (Fig. 6). While masting can be widespread (e.g., Mencuccini et al. 1995;

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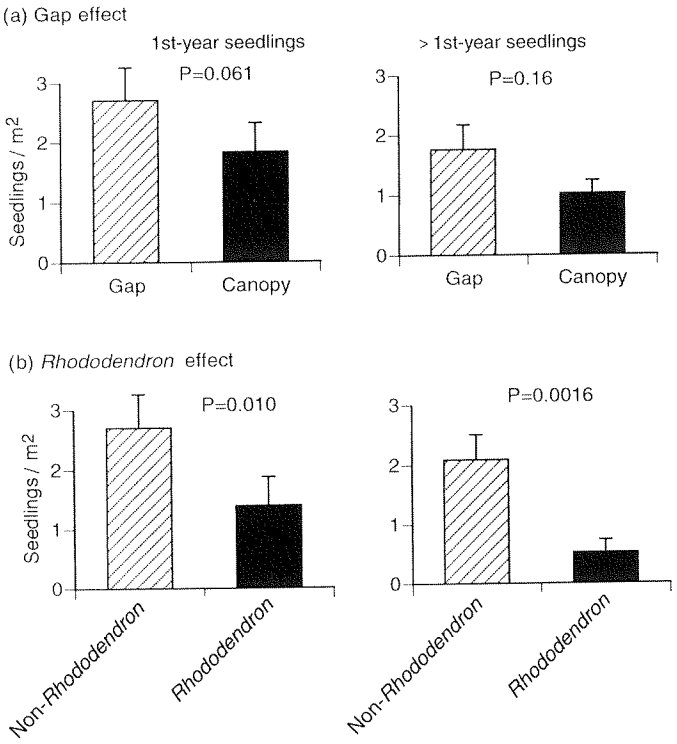
Fig. 9. Main effects of (*a*) gap creation and (*b*) *R. maximum* on first-year and >first-year seedlings (mean + SE). *P* values are for the null hypothesis that treatment means do not differ.

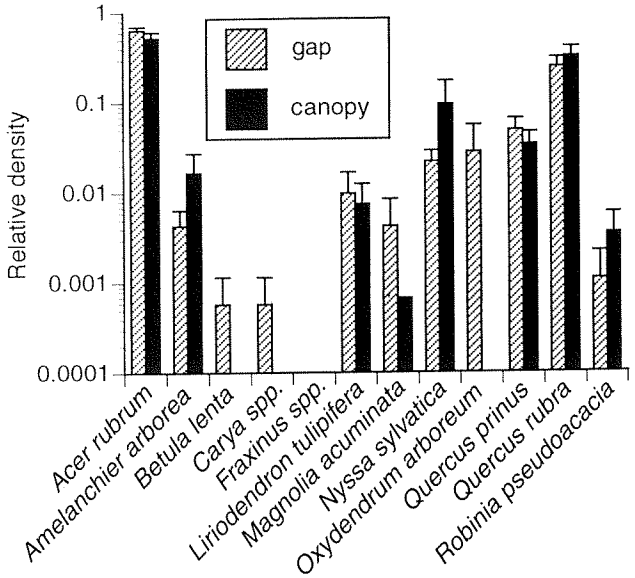


Rehfeldt et al. 1971), in this case the mast event was confined to high elevations (Figs. 6*a* and 6*e*). Although seed rain is often overlooked in recruitment studies, low seedling densities, even in gaps, may result from seed limitation (Clark et al. 1998; Dalling et al. 1998; Hubbell et al. 1999; Reader et al. 1995).

The gap environment

Both the size and the character of gaps influence seedling recruitment (Brokaw and Scheiner 1989; Spies and Franklin 1989). We created gaps that emulated those created by a severe drought in the southern Appalachians in the 1980s (Clinton et al. 1993). These gaps formed gradually, had standing dead trees that resulted in minimal disturbance to the understory, and had little exposure of mineral soil, which contrasts with gaps formed suddenly by windthrow (Nakashizuka 1989; Putz et al. 1983; Schaetzl et al. 1989). However, consideration of gradual gaps formed by drought or disease is important as they may be much more abundant than sudden gaps (Krasny and Whitmore 1992). Our artificial gaps included up to five girdled trees and resulted in openings of 300 m^2 (expanded gap definition; Runkle 1981), which approximates the mean gap size produced by recent droughts in the southern Appalachians (Clinton et al. 1993). The low recruitment of some taxa, e.g., *B. lenta*, even with seed present (Fig. 3), may result from the absence of mineral soil in our standing dead gaps (Burns and Honkala 1990; Carlton and Bazzaz 1998; Godman and Krefting 1960), suggesting that the mode of disturbance may be as important as the size. Within standing dead gaps, litter removal can increase *B. allegheniensis* seedling recruitment by an order of magnitude (Hatcher 1966). S. Taylor and B. Beckage (unpublished data) observed prolific *B. lenta* and *L. tulipifera* regeneration in tree fall gaps (originating from windthrows) with exposed mineral soil.

Fig. 10. Seedling relative densities (e.g., seedlings of a species found in a given gap/total seedlings found in that gap) for gap and canopy treatments (mean + SE). None of the gap–canopy differences are significant for any species (*P* values ≥ 0.05).



Our small gaps resulted in modest increases in light (6%) and in soil moisture (7%) but only in areas lacking the understory shrub *R. maximum* (Fig. 2). These changes in light levels are consistent with results reported for small to mid-sized gaps (Denslow et al. 1990; Orwig and Abrams 1995; Whitmore and Brown 1996; Zhang and Liang 1995). Light levels beneath *R. maximum* were in the low range where even shade tolerant species may not regenerate (Emborg 1998). Although we found some evidence of increased soil moisture following gap formation, the results of previous studies are inconsistent with some finding no change (Orwig and Abrams 1995) or even decreased availability (Zhang and Liang 1995). The small increase in seedling densities for some species, e.g., *A. rubrum* (Fig. 4*b*) in *R. maximum* gaps may result, in part, from increased moisture.

Role of the shrub understory

Understory shrubs reduced seedling recruitment largely by attenuating light. Beneath intact canopy, light penetration was twice as high outside *R. maximum* as it was under *R. maximum* (Fig. 2*a*). Outside *R. maximum*, light levels increased twofold with gap formation; however, beneath *R. maximum*, light levels did not increase following gap creation. This corresponds to the low seedling densities beneath *R. maximum* and their failure to increase following gap formation. Analysis of covariance confirmed this pattern for first-year *A. rubrum* recruitment but suggested that additional factors may contribute to mortality of older *A. rubrum* seedlings beneath *R. maximum*. Of course, once a seedling has grown through the *R. maximum* layer, it may have a higher chance of successfully entering the canopy because of fewer potential competitors for canopy openings.

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While *R. maximum* limits tree establishment primarily by reducing light levels, other mechanisms may contribute to reduced seedling densities. The thick litter beneath *R. maximum* (see Results) may inhibit seedling establishment (Facelli 1991; Molofsky and Augspurger 1992; Romancier 1971). When newly germinated seedlings of small-seeded species (e.g., *A. rubrum* or *L. tulipifera*) were found beneath *R. maximum*, they preferentially occurred in microsites with mineral soil (B. Beckage, personal observation), suggesting that litter suppresses seedling recruitment. In fact, litter removal and seed predation experiments show that litter inhibits *A. rubrum* establishment and that seed predation rates are higher beneath *R. maximum* (B. Beckage, unpublished data). Experimental removal of *R. maximum* increases tree seedling densities to those found in areas without *R. maximum* (S. Taylor and B. Beckage, unpublished data), demonstrating that pre-existing soil characteristics of sites supporting *R. maximum* do not explain poor tree recruitment. While soil moisture was not adversely affected by *R. maximum* in our study (Fig. 2*b*), this may not always be the case (E.T. Nilsen, unpublished data). *Rhododendron maximum* may have no effect (C. Wright, unpublished data) or reduce (E.T. Nilsen, unpublished data) nitrogen mineralization rates. Finally, *R. maximum* does not appear to have allelopathic effects on tree seedlings (Nilsen et al. 1999; Romancier 1971).

Understory interference with seedling recruitment in canopy gaps may be a widespread phenomenon. Many forests support dense shrub understories that include dwarf bamboo (*Sasa* spp.) in Japan (Nakashizuka 1989; Yamamoto et al. 1995), *Chusquea* bamboo in Chile (Veblen 1982, 1989), *Corylus* in the upper Midwest (Clark 1990; Kurmis and Sucoff 1989), and perennial species in the northeastern and northwestern United States (Ehrenfeld 1980; Harmon and Franklin 1989; Huenneke 1983; Neiring and Egler 1955). In these forests, light penetration to the forest floor increases only when gaps occur in both the canopy and shrub layers. Because windthrows can produce gaps that penetrate to the forest floor, windthrows versus drought-created gaps are expected to have different consequences for tree recruitment where shrub layers are well developed. Neither resource levels nor heterogeneity increase with formation of standing dead gaps in areas with dense shrub understories, potentially offsetting any tendency for gaps to increase forest diversity (Pacala and Tilman 1994).

Seed characteristics, such as size and dispersal distance, affected the immediacy and strength of *R. maximum* and gap effects on seedlings. For example, *Q. rubra* seeds have short dispersal distances (Clark et al. 1998) in the absence of animal vectors but are provided with large energy reserves enabling them to survive for a limited time in unfavorable light environments. Thus, while most seeds remain concentrated beneath parent trees with few reaching canopy gaps, they are able to temporarily survive in low light environments. Therefore, first-year *Q. rubra* seedling distributions were little affected by gap and *R. maximum* treatments but, rather, reflect their seed shadow. As energy reserves in *Q. rubra* seeds are exhausted after the first year (Long and Jones 1996), the distribution of *Q. rubra* seedlings may begin to reflect their microsite environment (Figs. 6*g* and 6*h*). In fact, the vigor of seedlings from the 1995 mast cohort was poor beneath *R. maximum* after their first year, with high mortality in their second year (Beckage, unpublished data). In contrast, we expect the distribution of small-seeded, widely dispersed species with little energy reserves to reflect the microsite environment in the first year. This was the case for the small seeded, widely dispersed *A. rubrum*. Densities of first-year seedlings were greater in higher light levels outside *R. maximum* and within canopy gaps (Fig. 4).

Implications for forest dynamics

Our 5-year experimental study demonstrates that intermediate-sized gaps, created by standing dead trees, are not effective at promoting diversity in second-growth forests in the southern Appalachians. This failure was due to only modest increases in resource availability compared with intact canopy, competition with the understory shrub *R. maximum*, and limited availability of seed. Canopy gaps that result in concomitant disturbance to the understory, e.g., windthrows, or that are larger in area appear to be necessary for the persistence of many species in these forests. Understory disturbance also appears to be important in other forested systems with dense understories (Veblen 1982; Yamamoto et al. 1995). Other studies have shown that species diversity in gaps increases with increasing gap size (Barden 1981; Busing and White 1997; Clinton et al. 1994; Phillips and Shure 1990; Runkle 1982). We demonstrate that intermediate-sized gaps, representing a size and mode of formation typical for these forests, appear inadequate to maintain diversity of tree species, and, in fact, do not promote seedling regeneration of most tree species, whether shade tolerant or intolerant.

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References

Baker, T.T., and Van Lear, D.H. 1998. Relations between density of rhododendron thickets and diversity of riparian forests. For. Ecol. Manage. **109**: 21–32.

Barden, L.S. 1979. Tree replacement in small canopy gaps of a *Tsuga canadensis* forest in the southern Appalachians, Tennessee. Oecologia, **44**: 141–142.

Barden, L.S. 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. Oikos, **35**: 16–19.

Barden, L.S. 1981. Forest development in canopy gaps of a diverse hardwood forest of the southern Appalachian Mountains. Oikos, **37**: 205–209.

Barden, L.S. 1983. Size, age, and growth rate of trees in canopy gaps of a cove hardwood forest in the southern Appalachians. Castanea, **48**: 19–23.

Bonan, G.B. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecol. Modell. **45**: 25–306.

Bormann, F.H., and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York.

© 2000 NRC Canada

Botkin, D.B. 1993. Forest dynamics: an ecological model. Oxford University Press, Oxford, New York.

Brewer, R., and Merritt, P.G. 1978. Windthrow and tree replacement in a climax beech–maple forest. Oikos, **30**: 149–152.

Brokaw, N.V.L., and Scheiner, S.M. 1989. Species composition in gaps and structure of a tropical forest. Ecology, **70**: 538–541.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Vol. 2. Hardwoods. U.S. Dep. Agric. Agric. Bull. 654.

Busing, R.T. 1994. Canopy cover and tree regeneration in old-growth cove forests of the Appalachian Mountains. Vegetatio, **115**: 19–27.

Busing, R.T., and White, P.S. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. Oikos, **78**: 562–568.

Canham, C.D. 1988. Growth and canopy architecture of shade tolerant trees: the response of *Acer saccharum* and *Fagus grandifolia* to canopy gaps. Ecology, **69**: 786–795.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**: 620–631.

Carlton, G.C., and Bazzaz, F.A. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. Ecol. Monogr. **68**: 99–120.

Chesson, P.L. 1982. The stabilizing effect of a random environment. J. Math. Biol. **15**: 1–36.

Chesson, P.L., and Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. Am. Nat. **117**: 923–943.

Cho, D., and Boerner, R.E.J. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. Vegetatio, **93**: 9–18.

Clark, J.S. 1990. Landscape interactions among nitrogen mineralization, species composition, and long-term disturbance. Biogeochemisty, **11**: 1–22.

Clark, J.S., Macklin, E., and Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. Ecol. Monogr. **68**: 213–235.

Clebsch, E.E.C., and Busing, R.T. 1989. Secondary succession, gap dynamics, and community structure in a southern Appalachian cove forest. Ecology, **70**: 728–735.

Clinton, B.D. 1995. Temporal variation in photosythetically active radiation (PAR) in mesic southern Appalachian hardwood forests with and without *Rhododendron* understories. *In* Proceedings, 10th Central Hardwood Forest Conference. *Edited by* Kurt W. Gottschalk and Sandra L.C. Fosbroke. USDA For. Serv. Gen. Tech. Rep. NE-197.

Clinton, B.D., Boring, L.R., and Swank, W.T. 1993. Canopy gap characteristics and drought influences of the Coweeta basin. Ecology, **74**: 1551–1558.

Clinton, B.D., Boring, L.R., and Swank, W.T. 1994. Regeneration patterns in canopy gaps, mixed-oak forests of the southern Appalachians: influences of topographic position and evergreen understory. Am. Midl. Nat. **132**: 308–319.

Collins, B.S., and Pickett, S.T.A. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. Vegetatio, **70**: 3–10.

Comins, H.N., and Noble, I.R. 1985. Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. Am. Nat. **126**: 706–723.

Dahir, S.E., and Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. Can. J. For. Res. **26**: 1875–1892.

Dalling, J.W., Hubbell, S.P., and Silvera, K. 1998. Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. J. Ecol. **86**: 674–689.

Della-Bianca, L., and Beck, D.E. 1985. Selection management in southern Appalachian hardwoods. South J. Appl. For. **9**: 191–197.

Denslow, J.S., Schultz, J.C., Vitousek, P.M., and Strain, B.R. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology, **71**: 165–179.

Dobbs, M.M. 1995. Spatial and temporal distribution of the evergreen understory in the Southern Appalachians. M.S. thesis, University of Georgia, Athens.

Dolling, A.H.U. 996. Interference of bracken with Scots pine and Norway spruce seedling establishment. For. Ecol. Manage. **88**: 227–235.

Douglass, J.E., and Hoover, M.D. 1988. History of Coweeta. *In* Forest hydrology and ecology at Coweeta. *Edited by* W.T. Swank and D.A. Crossley. Springer-Verlag, New York. pp. 17–31

Drobyshev, I.V. 1999. Regeneration of Norway spruce in canopy gaps in *Sphagnum–Myrtillus* old-growth forests. For. Ecol. Manage. **115**: 71–83.

Ehrenfeld, J.G. 1980. Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club, **107**: 29–41.

Emborg, Jens. 1998. Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. For. Ecol. Manage. **106**: 83–96.

Facelli, J.M. 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. **57**: 1–32.

George, L.O., and Bazzaz, F.A. 1999*a*. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology, **80**: 833–845.

George, L.O., and Bazzaz, F.A. 1999*b*. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology, **80**: 846–856.

Godman, R.M., and Krefting, L.W. 1960. Factors important to yellow birch establishment in Upper Michigan. Ecology, **41**: 18–28.

Harmon, M.E., and Franklin, J.F. 1989. Tree seedlings on logs in *Picea–Tsuga* forests of Oregon and Washington. Ecology, **70**: 48–59.

Hatcher, R.J. 1966. Yellow birch regeneration on scarified seedbeds under small canopy openings. For. Chron. **42**: 350–358.

Hibbs, D.E. 1982. Gap dynamics in a hemlock–hardwood forest. Can. J. For. Res. **12**: 522–527.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., and Loo de Lao, S. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science (Washington, D.C.), **283**: 554–557.

Huenneke, L.F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. Bull. Torrey Bot. Club, **110**: 170–175.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. **113**: 81–101.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology, **79**: 783–794.

Krasny, M.E., and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. Can. J. For. Res. **22**: 139–143.

Kurmis, V., and Sucoff, E. 1989. Population density and height distribution of *Corylus cornuta* in undisturbed forests of Minnesota: 1965–1984. Can. J. Bot. **67**: 2409–2413.

© 2000 NRC Canada

Littell, R.C., Milliken, G.A., Stroup, W.W., and Wolfinger, R.D. 1996. SAS system for mixed models. SAS Institute Inc., Cary, N.C.

Long, T.J., and Jones, R.H. 1996. Seedling growth strategies and seed size effects in fourteen oak species native to different soil moisture habitats. Trees, **11**: 1–8.

Lorimer, C.G. 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology, **61**: 1169–1184.

Lorimer, C.G., Chapman, J.W., and Lambert, W.D. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. J. Ecol. **82**: 227–237.

MacArthur, R., and Levins, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. **101**: 377–385.

Maguire, D.A., and Forman, R.T.T. 1983. Herb cover effects on tree seedling patterns in a mature hemlock–hardwood forest. Ecology, **64**: 1367–1380.

McGee, C.E., and Smith, R.C. 1967. Undisturbed rhododendron thickets are not spreading. J. For. **65**: 334–336.

Mencuccini, M., Piussi, P., and Sulli, A.Z. 1995. Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. For. Ecol. Manage. **76**: 109–125.

Molofsky, J., and Augspurger, C.K. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology, **73**: 68–77.

Monk, C.C., McGinty, D.T., and Day, F.P., Jr. 1985. The ecological importance of *Kalmia latifolia* and *Rhododendron maximum* in the deciduous forest of the southern Appalachians. Bull. Torrey Bot. Club, **12**: 187–193.

Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology, **70**: 1273–1278.

Neiring, W.A., and Egler, F.E. 1955. A shrub community of *Viburnum lentago*, stable for twenty-five years. Ecology, **36**: 356–360.

Nikolov, N.T., and Zeller, K.F. 1992. A solar radiation algorithm for ecosystem dynamic models. Ecol. Model. **61**: 149–168.

Nilsen, E.T., Walker, J.O., Miller, O.K., Semones, S.H., Lei, T.T., and Clinton, B.D. 1999. Inhibition of seedling survival under *Rhododendron maximum*: could allelopathy be a cause? Am. J. Bot. **86**(11): 1597–1605

Orwig, D.A., and Abrams, M.D. 1995. Dendroecological and ecophysiological analysis of gap environments in mixed-oak understoreys of northern Virginia. Funct. Ecol. **9**: 799–806.

Pacala, S.W., and Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am. Nat. **143**: 222–257.

Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24**: 2172–2183.

Pearcy, R.W. 1983. The light environment and growth of C3 and C4 tree species in the understory of a Hawaiian forest. Oecologia, **58**: 19–25.

Phillips, D.L., and Murdy, W.H. 1985. Effects of rhododendron (*Rhododendron maximum* L.) on regeneration of southern Appalachian hardwoods. For. Sci. **31**: 226–233.

Phillips, D.L., and Shure, D.J. 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology, **71**: 204–212.

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc. Orlando, Fla.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., and Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. For. Res. **13**: 1011–1020.

Reader, R.J., Bonser, S.P., Duralia, T.E., and Bricker, B.D. 1995. Interspecific variation in tree seedling establishment in canopy gaps in relation to tree density. J. Veg. Sci. **6**: 609–614.

Rehfeldt, G.F., Stage, A.R., and Bingham, R.T. 1971. Strobili development in western white pine: periodicity, prediction, and association with weather. For. Sci. **17**: 454–461.

Rich, P.M. 1989. A manual for analysis of hemispherical canopy photography. Los Alamos National Laboratory, Los Alamos, N.M. Publ. LA-11733-M.

Romancier, R. 1971. Ecology of seedling establishment of *Rhododendron maximum* in the southern Appalachians. Ph.D. dissertation, Duke University, Durham, N.C.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology, **62**: 1041–1051.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern north America. Ecology, **63**: 1533–1546.

Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer–Fagus* forest and speculations on the geography of disturbance. Can. J. For. Res. **20**: 632–641.

SAS Institute Inc. 1995. SAS proprietary software release, version 6.11 edition. SAS Institute Inc., Cary, N.C.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. Vegetatio, **79**: 165–176.

Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric. Agric. Handb. 450.

Shugart, H.H. 1984. A theory of forest dynamics: the ecological implications of forest succession models. Springer-Verlap, Berlin.

Spies, T.A., and Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology, **70**: 543–545.

Steel, R.G.D., Torrie, J.H., and Dickey, D.A. 1997. Principles and procedures of statistics, a biometrical approach. 3rd ed. McGraw-Hill Co., Inc., New York.

Swank, W.T., and Crossley, D.A. 1988. Introduction and site description. *In* Forest hydrology and ecology at Coweeta. *Edited by* W.T. Swank and D.A. Crossley. Springer-Verlag, New York. pp. 3–16

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.

Tilman, D., and Pacala, S. 1993. The maintenance of species richness in plant communities. *In* Species diversity in ecological communities. *Edited by* R.E. Ricklefs and D. Schluter. University of Chicago Press, Chicago and London. pp. 13–25

Topp, G.C. 1993. Soil water content. *In* Soil sampling and methods of analysis. *Edited by* M.R. Carter. Lewis Publishers, Boca Raton, Fla. pp. 541–557.

Valverde, T., and Silvertown, J. 1997. Canopy closure rate and forest structure. Ecology, **78**: 1555–1562.

Veblen, T.T. 1982. Growth patterns of Chusquea bamboos in the understory of Chilean *Nothofagus* forests and their influences in forest dynamics. Bull. Torrey Bot. Club, **109**: 474–487.

Veblen, T.T. 1989. Tree regeneration responses to gaps along a transandean gradient. Ecology, **70**: 541–543.

Watt, A.S. 1947. Pattern and process in the plant community. J. Ecol. **35**: 1–22.

Whitmore, T.C. 1989. Canopy gaps and the two major groups of forest trees. Ecology, **70**: 536–538.

Whitmore, T.C., and Brown, N.D. 1996. Dipterocarp seedling growth in rain forest canopy gaps during six and a half years. Philos. Trans. R. Soc. London B, **351**: 1195–1203.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. **26**: 1–80.

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Williamson, G.B. 1975. Pattern and seral composition in an old-growth beech–maple forest. Ecology, **56**: 727–731.

Wofford, B.E. 1989. Guide to the vascular plants of the Blue Ridge. University of Georgia Press, Athens.

Woods, F.W., and Shanks, R.E. 1959. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology, **40**: 349–361.

Yamamoto, S., Nishimura, N., and Matsui, K. 1995. Natural disturbance and tree species coexistence in an old-growth beech – dwarf bamboo forest, southwestern Japan. J. Veg. Sci. **6**: 875–886.

Young, J.A., and Young, C.G. 1992. Seeds of woody plants in North America. Dioscorides Press, Portland, Oreg.

Zhang, Q., and Liang, Y. 1995. Effects of gap size on nutrient release from plant litter decomposition in a natural forest ecosystem. Can. J. For. Res. **25**: 1627–1638.

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