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 d’un an et plus d’un an a été suivie durant 5 ans dans les transects qui s’étendaient de la forêt adjacente non perturbée à travers les ouvertures expérimentales. On a aussi mesuré, concrétionnément, 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.

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; Pearya 1983). Canopy gaps provide the transient increases in light that many species require to reach the canopy (Bormann and Likens 1979, 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...
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, 20% to 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 m², 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 1999a, 1999b; 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 (Clintion 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*, and gaps with open understories. Our 12 experimental canopy gaps were clustered at two sites, a low elevation site on a Cowee-Évard gravelly loam series within the Hapludults (Ultisols) and a high elevation site on a Chandler gravelly loam series within the Dystric hreptps (Inceptisols) (Swank and Crossley 1988).

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**Study area**

We conducted our study in second-growth forests at the Cowee Hydrologic Laboratory (35°03’N, 83°27’W), located near Franklin, N.C., in the Blue Ridge Physiographic Province of the southern Appalachians. Elevation in the 1626-ha Cowee 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·m⁻¹ and 0.005°C·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-Évard gravelly loam series within the Hapludults (Ultisols) and a high elevation site on a Chandler gravelly loam series within the Dystric hreptps (Inceptisols) (Swank and Crossley 1988).

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 is composed of *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 Cowee is dominated by *R. maximum*, an ericaceous, evergreen shrub, that occurs at all elevations in the Cowee 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 Hille RisLambers, 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 area 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 Murray 1985; Woode and Sharno 1967). In the Cowee basin, the area occupied by *R. maximum* doubled from approximately 15% in 1976 to nearly 32% by 1993.
Gaylussacia baccata (Wang.) K. Koch, a short-statured ericaceous shrub, typically under 1 m in height, is common in areas lacking R. maximum. Gaylussacia baccata covered 48% coverage in 120, 1 m² 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 understory, while three R. maximum 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 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 & 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 Uter 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 x 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 x 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 using a camera 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 0.01 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 Q. arboresum, 0.9 for Q. prunus, 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. prunus). 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. cocinea, and Q. rubra, so these were grouped as Q. rubra type.
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.
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–Wiener diversity index. Nomenclature follows Wofford (1989).

Analysis

Global site factors (GSF), Uitter, 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 Institute 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, NC, personal communication). We then analyzed mean seedling densities of the 16 subplots assuming Gaussian error. To achieve normality, seedling densities were transformed to \( \text{ln}(\text{seedling density} + 1) \) 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. (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 other 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 la 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. 1b and 1c). By the third year following gap creation (i.e., 1996), the canopy gaps were formed by three standing dead trees (Fig. 1d). By 1997 (Fig. 1e), 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. 2a; gap x R. maximum interaction, \( P < 0.0001 \); gap x R. maximum x 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 vs. P < 0.0001) but were unchanged in gaps with R. maximum (contrast of 1994–1997 vs. 1993 in G + R vs. 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. 2a) resulted from branches falling from dead trees and further opening the understory.

Soil moisture increased in all treatments following gap creation (Fig. 2b). Precipitation was especially low during the summer of 1993 relative to subsequent summers (Fig. 2v), 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 of the canopy conditions.
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 * 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.

Litter biomass was 20% higher in sites with than in sites without R. maximum (R+ = 508.2 vs. R- = 423.8 g/m², P = 0.0002), but litter was not affected by gaps (G+ = 462.1 vs. G- = 469.9 g/m², 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. 3d). Betula lenta and O. arboreum were notable in that they had low seedling densities despite relatively high seed rain (Fig. 3b). 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,
Fig. 4. Seed rain (right-hand y axis of a and e) and seedling densities of the shade-tolerant *A. rubran*. 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 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).*

*M. acuminata, Fraxinus spp., and R. pseudoacacia* were consistent with low seed rain. *Acer rubran* was the most responsive species to gap formation, benefiting from abundant, well-dispersed seed at both elevations (Figs. 4a and 4e) 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. rubran* 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. 5a and 5e). 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
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).

Recruitment patterns for the intermediately shade-tolerant Q. rubra were dominated by the 1995 mast year (Figs. 6a and 6e), which produced a large 1996 cohort at the high-elevation site (Figs. 6a and 6b; elevation x year for first-year seedlings, P < 0.0001). Quercus femur (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 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. 6c and 6d). 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. 6e and 6g vs. 6f and 6h) and higher in gaps than beneath the canopy in areas without R. maximum (Fig. 6g).

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. 7a). 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. 7b).

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 x 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...
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. 7a are means over years following gap creation, while values in Fig. 7b includes pre-gap years as well. *, P < 0.05; **, P < 0.01. acru, Acer rubrum; amar, Amelanchier arborea; besp, Betula spp.; caru, Carpinus spp.; frsp, Fraxinus spp.; litu, Liriodendron tulipifera; maac, Magnolia acuminata; nysy, Nyssa sylvatica; oxar, Oxydendrum arboreum; qupr, Quercus prinus; quru, Quercus rubra; tops, Robinia pseudoacacia.

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. 8a). Seedling densities were not significantly higher outside R. maximum (Fig. 8a, 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 x R. maximum interaction significant (P = 0.60; gap x R. maximum x year, P = 0.37). Species richness did not increase following canopy gap formation in any gap x 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. 8a, 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. 8b, 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 x R. maximum treatment combination following gap creation (intervention analysis, P values ranged from 0.09 to 0.84) nor was the gap x R. maximum interaction significant (P = 0.25; gap x R. maximum x 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. 9a). 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. 9b). Neither the gap x R. maximum nor the gap x R. maximum x 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).
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.

(a) Species richness

(b) Diversity

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;
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.

(a) Gap effect

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seedlings/m²</th>
<th>1st-year seedlings</th>
<th>&gt;1st-year seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gap</td>
<td>3.0</td>
<td>0.9 ± 0.1</td>
<td>1.8 ± 0.2</td>
</tr>
<tr>
<td>Canopy</td>
<td>2.5</td>
<td>1.2 ± 0.3</td>
<td>1.5 ± 0.2</td>
</tr>
</tbody>
</table>

(b) *Rhododendron* effect

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Seedlings/m²</th>
<th>1st-year seedlings</th>
<th>&gt;1st-year seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-<em>Rhododendron</em></td>
<td>2.5</td>
<td>1.2 ± 0.3</td>
<td>1.5 ± 0.2</td>
</tr>
<tr>
<td><em>Rhododendron</em></td>
<td>3.5</td>
<td>2.4 ± 0.4</td>
<td>2.1 ± 0.3</td>
</tr>
</tbody>
</table>

Rehfeldt et al. (1971), in this case the mast event was confined to high elevations (Figs. 6a and 6e). 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 that resulted in minimal disturbance to the understory, and had little exposure of mineral soil, which is consistent 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 that resulted in minimal disturbance to the understory, and had little exposure of mineral soil, which is consistent with gaps formed suddenly by windthrow (Nakashizuka 1989; Putz et al. 1983; Schaetzl et al. 1989).

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Published data (Clark et al. 1998; Balling et al. 1998; Hubbell et al. 1999; Reader et al. 1995) suggest that the mode of disturbance may be as important as the size. Within standing dead gaps, Utter 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.

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 (Einflog 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. 4b) 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. 2a). 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.
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, Utter removal and seed predation experiments show that Utter 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. 2b), 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, Ught 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 Ught environments. Thus, while most seeds remain concentrated beneath parent trees with few reaching canopy gaps, they are able to temporarily survive in low Ught 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. 6g and 6h). 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 Ught 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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![Graph showing seedlings per m² for gap and canopy treatments](image)

(b) *Rhododendron* effect

![Graph showing seedlings per m² for non-rhododendron and rhododendron treatments](image)

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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).

![Graph showing seedling relative densities](image)

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