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Differential Effects of Understory and Overstory Gaps on Tree Regeneration

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Citation Details

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BECKAGE, B. (Department of Plant Biology, University of Vermont, Marsh Life Science Building, Burlington, VT, USA 05405), B. D. KLOEPPEL (Odum School of Ecology, University of Georgia, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, North Carolina USA 28763), J. A. YEAKLEY (Environmental Science and Management, Portland State University, Portland, Oregon, USA 97207), S. F. TAYLOR (Odum School of Ecology, University of Georgia, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, North Carolina USA 28763), AND D. C. COLEMAN (Odum School of Ecology, University of Georgia, Athens, Georgia, USA 30602). Differential effects of understory and overstory gaps on tree regeneration. J. Torrey Bot. Soc. 135: 1–11. 2008.—Gaps in the forest canopy can increase the diversity of tree regeneration. Understory shrubs also compete with tree seedlings for limited resources and may depress tree recruitment. We compared effects of shrub removal and canopy windthrow gaps on seedling recruitment and understory resource levels. Shrub removal, with the canopy left intact, was associated with increased levels of understory light and soil moisture and coincided with increased species richness and diversity of tree regeneration compared to both control plots and canopy gaps. Canopy windthrow gaps, however, resulted in a more than 500 fold increase in soil nitrate concentrations, and seedling growth rates that were twice as high as that observed with shrub removal. Our results suggest that gaps in the understory shrub layer and the overstory canopy may have complementary effects on resource availability with corresponding benefits to seedling establishment and growth.

Key words: canopy gaps, *Rhododendron*, shrubs, species richness, tree seedling, understory gaps.

Low light levels beneath the forest canopy can limit tree regeneration to species that are tolerant of deep shade (e.g., Canham 1988, Pacala et al. 1994). The diversity of tree species observed in the forest overstory, which includes shade intolerant species, may result from elevated levels of light and other resources that are found beneath gaps in the forest canopy (e.g., Pickett and White 1985, Whitmore 1989). Canopy gaps result from disturbances such as windstorms, drought, insect outbreaks, or pathogens that remove overstory trees, creating openings in the forest canopy. Canopy gaps can provide recruitment opportunities for tree seedlings, increasing the diversity of tree regeneration, and have figured prominently in empirical and theoretical investigations of mechanisms that promote forest diversity (e.g., Shugart 1984, Platt and Strong 1989, Busing and White 1997). The empirical evidence supporting the role of gaps in forest regeneration, however, has been equivocal with studies both supporting (Barden 1980, Runkle 1981, Kneeshaw and Bergeron 1998, Lusk and Smith 1998) and

questioning the importance of canopy gaps in promoting the diversity of the forest overstory (Brewer and Merritt 1978, Hibbs 1982, Cho and Boerner 1991, Hubbell et al. 1999, Webb and Scanga 2001). Ambiguous evidence in support of the role of gaps in forest regeneration may result from differences in the density of understory vegetation as well as from variability in gap characteristics such as their size and mode of creation (Putz et al. 1983, Canham et al. 1990, Beckage et al. 2000).

Understory vegetation can mediate tree regeneration in forests through their influence on resource levels at the forest floor (Connell et al. 1997). Dense forest understories compete with tree seedlings for resources, limiting tree recruitment (Lorimer et al. 1994, Baker and Van Lear 1998, George and Bazzaz 1999, Beckage et al. 2000). Understory shrubs also usurp resources made available by canopy gaps, reducing tree regeneration (Phillips and Murdy 1985, Nakashizuka 1989, Clinton et al. 1994, Beckage et al. 2000). Understory gaps may be functionally similar to canopy gaps, elevating resource levels at the forest floor and increasing tree regeneration (Connell et al. 1997), but we are aware of few studies that compare canopy and understory gap effects on both abiotic conditions and tree regeneration (e.g., Pecot et al. 2007). We used the serendipitous occurrence of windthrown canopy trees within an existing shrub removal experiment to compare the effects of understory and canopy gaps on the species richness and diversity of tree regeneration in a temperate deciduous forest. The windthrow occurred within a control plot adjacent to a treatment plot where the understory shrub *Rhododendron maximum* L. had just been removed. Soil moisture and nutrient levels had been monitored for the prior year in both plots providing a unique opportunity to relate seedling recruitment to environmental responses. We subsequently established two additional control plots and monitored seedling recruitment over four years while continuing to monitor nutrients and soil moisture and also measuring light levels. While the unplanned nature of this experiment limited us to an unreplicated study, our results are suggestive of differential responses to these two modes of disturbance (overstory windthrow vs. shrub removal) and are reported in order to be subject to further exploration and testing.

Materials and Methods. STUDY AREA. Our study was conducted at Coweeta Hydrologic Laboratory, near Otto, North Carolina in the southern Appalachian Mountains (35°03′ N, 83°25′ W). Elevations in the Coweeta Basin range from 675 m to 1592 m and encompass a drainage area of 1626 ha. Mean annual precipitation is 1770 mm at the Coweeta base climate station. Vegetation in the lower elevations at Coweeta consists of second-growth mixed oak-hickory (*Quercus-Carya*) forest often with an understory of the evergreen ericaceous shrub *Rhododendron maximum* (Swank and Crossley 1988). *Rhododendron* can form a dense subcanopy (Baker and Van Lear 1998) with leaf area indices in the range of 4.8 to 6.6 and can have strong effects on the understory light environment (Beckage et al. 2000). Low light levels beneath *Rhododendron* subcanopies can have a dramatic impact on seedling regeneration, precluding nearly all seedling establishment (Beckage et al. 2000, Lei et al. 2002).

Our study resulted from the serendipitous occurrence of windthrown canopy trees in a study of the effect of *Rhododendron* removal on biogeochemical cycling. The original experiment examined watershed differences in nutrient fluxes due to shrub removal. We employed a watershed level experimental design (i.e., one treatment vs. one reference watershed), which is commonly used because of the high cost of watershed level studies, that relies on pre- and post-treatment data in a randomized intervention analysis that compares changes in temporal signals (Yeakley et al. 2003). Originally, two study sites, located within 100 m of each other were instrumented for the collection of data on nutrient fluxes and one year of pre-treatment data was collected prior to the removal of the *Rhododendron* understory layer in one of the sites (Yeakley et al. 2003). At the end of August 1995, the aboveground portions of all *Rhododendron* stems within a 10 m by 30 m area of one site were manually removed and the herbicide Roundup (Monsanto, Luling, LA) was applied once to the top of cut stumps. Sixty-five stems of *Rhododendron* were removed, representing approximately 30% of total above-ground woody biomass. This plot is referred to as the shrub removal treatment. On 4 October 1995, Hurricane Opal blew down 9 canopy trees in the adjacent site, which was originally intended as a control plot, while

not damaging the shrub removal plot. We subsequently designated a 10 m by 30 m area within this blowdown site as the canopy removal plot. There was minimal damage to the shrub layer in the canopy removal plot, with forty-five intact stems of *Rhododendron* present. Undisturbed reference plots were located adjacent to both the shrub and canopy removal treatments, to maximize similarity between paired treatment and controls, and are referred to as the shrub and canopy controls, respectively. All four plots had similar pre-treatment overstory composition and *Rhododendron* density as well as aspect, topography, and soils (Yeakley et al. 2003).

We subsequently began monitoring the species richness and diversity of tree regeneration as well as the growth and survivorship of individual seedlings in all four of these plots. Our nomenclature follows Wofford (1989). Seedling censuses were conducted in ten 1 m by 1 m quadrats that were randomly located in each of the four plots and that were permanently marked with PVC corner posts. The height and species of all tree seedlings present in the quadrats were recorded during censuses conducted in the growing season of four consecutive years (1997–2000), and each seedling that was recorded in a prior census was scored as alive or dead in subsequent censuses. Species richness and the Shannon-Wiener index of species diversity (H') were calculated for each quadrat in every census year using the seedling counts. We calculated the relative growth rates (RGR) for species with seedlings that survived three years; i.e., from the first census in 1997 to the final census in 2000, in two or more treatment plots. RGR was calculated as $\log\left(\frac{H_T}{H_0}\right)\Big/T$ where H_T was the final height of the seedling in the 2000 census, H_0 was the initial height of the seedling in the 1997 census, and T was the elapsed time in years (i.e., 3 years; Beckage and Clark 2003).

The availability of light, soil moisture, and soil nutrients was measured across sites. Photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}) was measured at a height of 1 m over each quadrat during overcast days in the 1998 growing season using a sunfleck ceptometer (Decagon Devices, Pullman, Washington). Soil moisture in each of the seedling quadrats was measured six times from early June to late September 1998 using time domain reflectometry (TDR), with 3 mm dia-

meter stainless steel rods inserted vertically 5 cm apart to a depth of 20 cm, following established methods (Topp et al. 1985, Yeakley et al. 1998). Eight lysimeters were installed at a depth of 20–25 cm (BA horizon) in both the canopy removal and shrub removal plots (16 lysimeters total), with four lysimeters installed in the BA horizon in the shrub control plot (Yeakley et al. 2003). Soil water samples were taken weekly and composited monthly for laboratory analysis of nutrient concentrations, including NO_3, NH_4, PO_4, SO_4, K, Na, Ca, and Mg (Yeakley et al. 2003). Soil water samples were measured beginning one year prior to the removal of the canopy and shrub vegetation in 1994 and continuing through 2000. We present results for NO_3 (nitrate), averaged over the growing season (May–Sep) of each year, as nitrate had the largest response to disturbance (Yeakley et al. 2003).

We sampled forest floor litter components in February 2000 using ten 30×30 cm (0.09 m^2) quadrats in each of our four treatment plots. Material within each quadrat was separated into three components: litter (Oi), a combined fermentation and humus component (Oe + Oa), and the total organic layer (Oi + Oe + Oa). Small wood (< 7.5 cm diameter) within the 30×30 cm sampling frame was cut using pruning shears, and forest floor material was removed by component (i.e., Oi, Oe + Oa, Oi + Oe + Oa) after cutting along the inside of the sampling frame. Forest floor materials were placed in a paper bag and transported to the laboratory where they were dried at 60°C to a constant mass.

Statistical Analysis. Our analyses of species richness, diversity, seedling survival, and abiotic responses are intended to be exploratory in nature because of the limitations of our data. Our study lacked true replication across spatial units because of its opportunistic nature. Sampling units were located within a single site that experienced the same canopy disturbance or shrub removal treatment (Hurlbert 1984). The seedling recruitment portion of our study benefited from four years of sampling as well as from measurements of abiotic resources including nutrient responses to disturbance.

We estimate seedling regeneration and abiotic responses in our plots using Bayesian

methods (Gelman et al. 2003): the posterior distributions calculated in this study will provide prior distributions for more extensive studies of the relative importance of *Rhododendron* removal vs. canopy removal. The resulting posterior distributions also provide an estimate of the within–plot variability relative to plot effects. We report if the estimated posterior distributions of treatment effects differ with a probability greater than 0.95. We constructed likelihood functions to estimate the underlying responses while accounting for autocorrelation among repeated sampling periods and year effects, while also using the most appropriate error distribution. Seedling survival was modeled as a Bernoulli process with an annual survival probability that is a function of treatment, and year, and also includes a random effect that captures seedling to seedling variability (e.g., Lavine et al. 2002, Beckage et al. 2005). Species richness was estimated using a Poisson likelihood that adjusted for year effects and for serial autocorrelation across repeated censuses of seedling quadrats using an autoregressive (AR) term of order 1 (Beckage and Stout 2000, Beckage and Platt 2003). We used a similar model for the species diversity data except that the errors were normally distributed (Beckage and Stout 2000). The PAR measurements and soil moisture data were analyzed using a normal likelihood. Our likelihood function accounted for sequential measurement periods in the soil moisture sampling intervals. Models were fit using Bayesian methods and either the winBugs (www. mrc-bsu.cam.ac.uk) or R (www.r-project.org) software. We include the complete descriptions of our statistical models, posterior parameter estimates, and associated statistics in an appendix. Actual code for these procedures can be found at www.uvm.edu/~bbeckage/reprints.html.

Results. Light levels in the forest understory were extremely variable across quadrats (Fig. 1a), with median PAR values of 150, 42, 25, and 3 μmol m^{-2} s^{-1} in the shrub removal, canopy removal, shrub control, and canopy control plots, respectively. PAR levels were significantly higher in the canopy and shrub removal plots compared to controls ($P \geq 0.95$) as well as in the shrub removal compared to the canopy removal plots ($P \geq 0.95$). Soil moisture was also higher in the

shrub removal plot compared to the canopy removal or shrub control plots ($P \geq 0.95$) (Fig. 1b). Canopy removal was not associated with significantly greater soil moisture compared to its control ($P < 0.95$). Concentrations of several nutrients changed in response to the blowdown (Yeakley et al. 2003), but the most pronounced soil water nutrient change occurred for NO_3. Nitrate concentrations increased by a factor of > 500 at depths of both 20–25 cm and 40–45 cm in the canopy removal plot in the post-hurricane period relative to the pre-treatment period, compared to increases 6 y a factor of 1.3 and 3.3 in the shrub removal plot over the same period. The concentration of nitrate was 770 times greater in the canopy removal treatment compared to shrub removal in the 1997 growing season (Fig. 1c). Increases in nitrate lasted approximately 5 years in our study.

The highest species richness and diversity of tree regeneration occurred in the shrub removal plot followed by canopy removal and controls (Fig. 2). Species richness and diversity were significantly greater in the shrub removal plot compared to the canopy removal plot ($P \geq 0.95$), and both treatment plots had higher species richness and diversity compared to their controls ($P \geq 0.95$). Mean species richness was 3.1 (SE = 0.13) and 2.4 (SE = 0.18) species m^{-2} with shrub and canopy removal, respectively, compared to 0.98 (SE = 0.084) and 1.4 (SE = 0.17) species m^{-2} for their controls. Similarly, mean species diversity was 0.77 (SE = 0.036) and 0.48 (SE = 0.059) with shrub and canopy removal, compared to 0.05 (SE = 0.022) and 0.31 (SE = 0.072) in the shrub and canopy controls, respectively. The maximum species richness of an individual quadrat was 5 and occurred in the shrub removal treatment, whereas the minimum species richness of a quadrat was 0 and occurred in the canopy removal, canopy control, and shrub control plots, but not in the shrub removal plot (Table 1). Species richness increased by a factor of 2.3 and 1.5 in the shrub and canopy removal plots compared to their controls when calculated within plots rather than within quadrats. Recruitment responses to canopy and shrub removal treatments resulted both from the occurrence of novel species, such as the shade intolerant species *Betula lenta* and *Liriodendron tulipifera*, and from increased abundance of species that occurred across all treatments (Table 1).
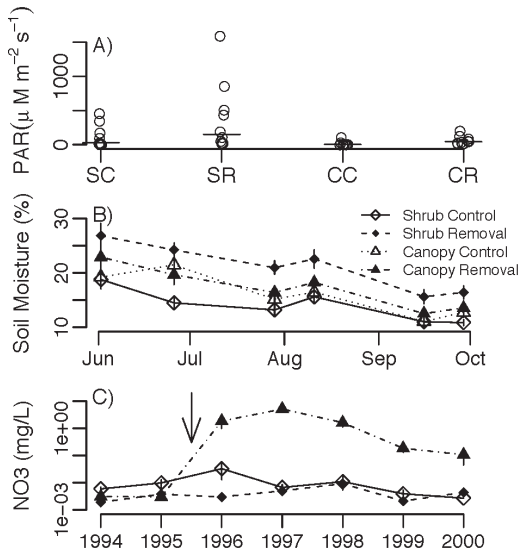
FIG. 1. Abiotic responses to shrub and canopy removal. A) Photosynthetically active radiation (PAR) measured over each quadrat during the 1998 growing season using a sunfleck ceptometer. One measurement was made at a height of 1 m over each quadrat on an overcast day for a total of 10 measurements per plot. SC corresponds to shrub control, SR to shrub removal, CC to canopy control, and CR to canopy removal. B) Volumetric soil moisture in the shrub removal, canopy removal, and control plots across the 1998 growing season measured using time domain reflectometry. One measurement was made for each quadrat six times across the 1998 growing season for a total of 10 measurements per plot. We show means and standard errors. C) Nitrate concentrations in the BA horizon (20–25 cm in depth) for the 1994–2000 growing seasons (May–Sep) in the shrub control, shrub removal, and canopy removal plots. Removal of the canopy and understory layers is indicated by the arrow. Data are based on eight lysimeters in both the canopy removal and shrub removal plots and four lysimeters in the shrub control plot. We report means and standard errors.

Comparisons of relative growth rates across treatments were limited to two species, *Acer rubrum* and *Liriodendron tulipifera*, and to the canopy and shrub removal plots, because of low seedling numbers of other species across treatments. More seedlings of the shade tolerant *A. rubrum* occurred in the canopy removal plot than did seedlings of the shade intolerant *L. tulipifera*, likely because *A. rubrum* could better tolerate the lower light levels in the understory of the canopy removal plot (Fig. 3). The seedlings that established in the canopy removal plot, however, had higher growth rates, which were associated with elevated nitrogen levels, compared to other
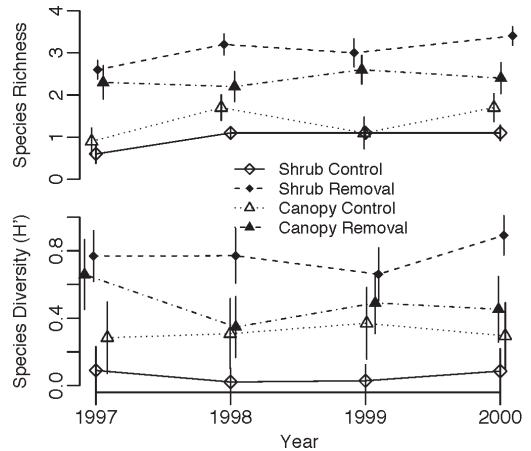

FIG. 2. Species richness and diversity of tree regeneration (mean and s.e.) following removal of shrub understory (shrub removal) in August 1995, or formation of windthrow gaps (canopy removal) in October 1995. Censuses of all quadrats were made in May and October 1997, May, June, and September 1998, June and September 1999, and June 2000, and were combined into a single measurement for each quadrat within a year. The means and s.e.'s are based on the combined yearly censuses for the 10 quadrats in each plot. The location of points along the x-axis have been offset slightly to better distinguish points.

plots (Fig. 3). Relative growth rates were nearly twice as great in the canopy removal compared to the shrub removal plots for both of these species ($P \geq 0.95$) (Fig. 3), although the precision of these estimates was limited by low numbers of seedlings in some treatments. *Betula lenta* seedlings also had very high growth rates in the canopy removal plot (mean RGR = 0.67) in areas of highly disturbed soils in windthrow tip-up mounds.

We estimated the effect of treatments on seedling survival of *Acer rubrum* using 823 newly germinated seedlings that were widely distributed across plots, i.e., 237 (shrub removal), 305 (canopy removal), 171 (shrub control), and 110 (canopy control) seedlings. Seedling survival was highest in the shrub removal treatment compared to the canopy removal ($P \geq 0.95$) or its control plot ($P \geq 0.95$). Seedling survival was also higher in the canopy removal plot compared to its control plot ($P \geq 0.95$), but the shrub and canopy control plots were not significantly different ($P < 0.95$). The mean annual survival probabilities of *A. rubrum* seedlings were 0.86 (shrub removal), 0.82 (canopy removal), 0.59 (shrub control), and 0.60 (canopy control). Year to

Table 1. Mean density (SE) per m² and frequency of tree seedlings over four years[a].

Species	Shrub control		Shrub removal		Canopy control		Canopy removal	
	Density	Freq.	Density	Freq.	Density	Freq.	Density	Freq.
Acer pennsylvanicum	0	0	0	0	0	0	0.10 (0.32)	1
Acer rubrum	17.4 (2.2)	10	24.8 (4.0)	10	11.4 (3.3)	10	31.4 (5.9)	10
Amelanchier arboreum	0	0	0	0	0	0	0.10 (0.32)	1
Betula lenta	0	0	20.7 (6.0)	10	0.50 (0.49)	3	6.2 (3.9)	7
Cornus florida	0	0	0.10 (0.32)	1	0	0	0	0
Liriodendron tulipifera	0	0	7.1 (1.4)	10	0	0	1.5 (0.78)	6
Pinus strobus	0	0	0.10 (0.32)	1	0.30 (0.28)	3	0.40 (0.40)	3
Quercus prinus	0.10 (0.32)	1	0	0	0.20 (0.30)	2	0.10 (0.32)	1
Quercus species	0	0	0	0	0	0	0.10 (0.32)	1
Sassafras albidum	0	0	1.0 (0.43)	6	0	0	0	0
Unknown species	0.10 (0.32)	1	0.10 (0.32)	1	0.10 (0.32)	1	0.10 (0.32)	1
Species richness of quadrats								
Minimum	0		2		0		0	
Maximum	2		5		4		4	
Mode	1		3		1		3	

[a] Each treatment or control plot had ten 1 m² quadrats. An individual stem was counted only once even if it survived across all four years. Frequency is the number of quadrats (out of 10) in which seedlings of the given species occurred. The minimum, maximum, and mode number of species found within individual quadrats within a treatment are also reported.

year variation in seedling survival was estimated at 3.6 (median on logit scale), which was much larger than the variance associated with individual seedlings (0.095, median on logit scale).

The soil organic layer was reduced in the shrub removal plot compared to the other

Fig. 3. Relative growth rate in height for *Acer rubrum* and *Liriodendron tulipifera* seedlings over the period from 1997 to 2000. The sample means are indicated by horizontal lines and are based on sample sizes of 17, 42, 24, and 4 seedlings from left to right in the panel, respectively.

treatments, primarily due to decreased amounts of humus (Table 2).

Discussion. Our limited study suggests that canopy and understory gaps may have complementary effects on resource availability and patterns of seedling recruitment. While both canopy and shrub removal were associated with increased seedling recruitment compared to controls, the greatest diversity and highest survivorship of seedlings coincided with shrub removal while the highest seedling growth rates occurred with canopy removal. The initial establishment of tree seedlings may benefit from the environmental conditions more strongly associated with the removal of understory shrubs, including higher levels of light and soil moisture: shrub removal coincided with seedling regeneration that was 1.3 times more species rich and 1.6 times more diverse than in the canopy removal plot. The understory shrub *Rhododendron* does not inhibit tree regeneration through allelopathy, modification of seed rain, or through increased predation (Nilsen et al. 1999, Lei et al. 2002, Beckage and Clark 2005), suggesting that the higher diversity of tree seedlings in the shrub removal plot was likely related to elevated levels of light and soil moisture. In addition, seedling establishment may have been facilitated by a > 43% reduction in the
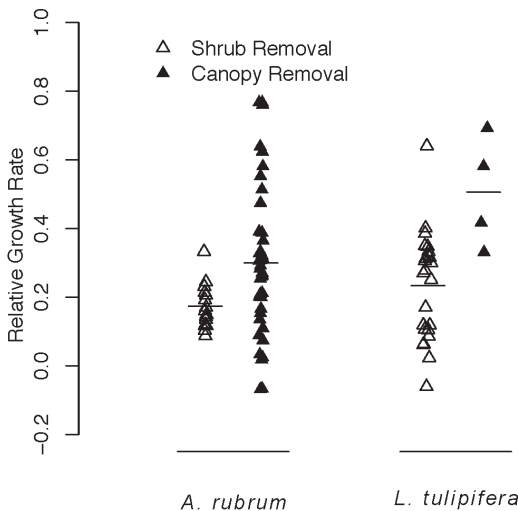
Table 2.   Litter, humus, and total organic layer components of the forest floor[a].

Site	Litter	Humus	Total organic layer
Shrub control	120.84	358.83	479.67
Shrub removal	110.8	117.45	228.67
Canopy control	102.42	353.71	456.13
Canopy removal	93.71	309.15	402.86

[a] Mean values from ten 30×30 cm quadrats in each treatment or control plot are reported in g m^{-2}.

soil organic layer that occurred following shrub removal (Table 2). Seedling growth rates, in contrast to seedling diversity, were highest in the canopy removal plot, which corresponded with very large increases (> 700 times greater) in soil nitrate levels. Elevated nitrate levels may be related to the high level of soil disturbance caused by the uprooting of trees in the canopy removal site (Schaetzl et al. 1989, Aber et al. 1998, Greenberg and McNab 1998), which did not occur in any of the other plots. Shrub removal that leaves the canopy relatively intact can occur naturally with low intensity fire (McGee and Smith 1967, Thaxton and Platt 2006, Waldrop et al. 2007) for instance, resulting in a much lower level of soil disturbance than canopy windthrows. Our results are consistent with previous studies finding that seedling establishment is sensitive to light conditions and soil moisture (Haeussler et al. 1995, Negi et al. 1996, Weisberg and Baker 1995) while seedling growth rates respond strongly to nutrient additions especially in conjunction with elevated light levels (Phares 1971, Walters and Reich 2000, Beckage and Clark 2003). Our limited study suggests the need for more extensive field studies of the influence of understory and overstory gaps on tree regeneration, including the potential for complementary effects on light, moisture, and nutrient resources with corresponding effects on seedling establishment, survival and growth (e.g., Beckage and Clark 2003).

Our results indicate that equivocal support for the role of canopy gaps in tree regeneration may stem, in part, from both the variable density of understory vegetation across forest stands and the propensity for different modes of canopy gap formation to create understory gaps. Canopy gaps created by drought or insect outbreaks produce standing dead trees with little damage to the forest understory (Clinton et al. 1993, Beckage et al. 2000), and catastrophic forest disturbance, such as results from large blowdowns or landslides, can lead to the elimination of both overstory and understory layers (Veblen and Ashton 1978, Rebertus et al. 1997). Forests with dense understories may require severe disturbance for successful tree regeneration (Veblen 1982, Nakashizuka 1989, Veblen 1989). Forests of the southern Appalachians, for example, have areas with extensive understories of *Rhododendron*, *Kalmia*, and *Gaylussacia*, and canopy gaps created by standing dead trees have failed to increase tree regeneration (Clinton et al. 1994, Beckage et al. 2000). Dense understory layers occur in forests worldwide (e.g., Niering and Egler 1955, Nakashizuka 1989, Veblen 1989, Dolling 1996) and the differential effects of disturbance on overerstory and understory gaps could play a significant role in determining patterns of forest regeneration.

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Appendix

A. *Model of species diversity*. Our statistical model of species diversity was

$$y_t \sim Normal\left(\mu_t, \boldsymbol{I}\sigma_e^2\right)$$

$$\mu_t \sim \mathbf{X}\boldsymbol{\beta}_{trt} + \mathbf{Y}\boldsymbol{\beta}_{quad} + \mathbf{Z}\boldsymbol{\beta}_{year} + \phi y_{t-1}$$

where the $\mathbf{X}$, $\mathbf{Y}$, and $\mathbf{Z}$ represent the design matrices for the particular components of the model. Each component of the vectors $\boldsymbol{\beta}_{quad}$ and $\boldsymbol{\beta}_{year}$ were distributed as $\beta_{quad} \sim Normal(0, \tau_{quad})$ and $\beta_{year}^j \sim Normal(0, \tau_{year})$, where $\sigma_{quad}^2 = \frac{1}{\tau_{quad}}$; $\sigma_{year}^2 = \frac{1}{\tau_{year}}$.

The autoregressive coefficient ϕ was assigned a stationary prior: $\varphi \sim Beta(a, b)$; $\phi = 2*\varphi - 1$

Noninformative priors were used for each component of $\boldsymbol{\beta}_{trt}$:

$\beta_{trt}^k \sim Normal(0, \sigma_{trt}^2)$ where σ_{trt}^2 was assigned a very large value (e.g., 1000).

$\tau_{quad} \sim Gamma(\alpha, \beta)$; $\tau_{plot} \sim Gamma(\alpha, \beta)$

$\sigma_e^2 = \frac{1}{\tau_e}$ where $\tau_e \sim Gamma(\alpha, \beta)$ where (α, β) were chosen to be uninformative, e.g., (0.0001, 0.0001).

This regression model, with minor variations, was also used to estimate abiotic responses to our treatments.

Our Markov Chain Monte Carlo (MCMC) simulation had a burn in of 1000 samples; 100,000 samples were subsequently generated and these were thinned to 1 in 20 for a total of 5,000 samples. The fitted parameters and uncertainty are given in the table below. β_{cc}, β_{cr}, β_{sc}, and β_{sr} refer to the four components of the vector $\boldsymbol{\beta}_{trt}$, and correspond to the canopy control, the canopy removal plot, the shrub control plot, and the shrub removal plot. The shrub contrast compares the shrub removal to the shrub control plot, while the canopy contrast compares the canopy removal to the canopy control plot. The control contrast compares the shrub and canopy control plots, while the removal contrast compares the shrub removal to the canopy removal plot.

Parameter	Mean	sd	MC error	2.50%	Median	97.50%
β_{cc}	0.259	0.312	0.026	−0.450	0.279	0.867
β_{cr}	0.438	0.310	0.026	−0.282	0.458	1.019
β_{sc}	0.037	0.314	0.026	−0.654	0.058	0.639
β_{sr}	0.750	0.314	0.027	0.039	0.778	1.344
ϕ	0.020	0.005	0.000	0.010	0.020	0.031
σ^2	0.034	0.005	0.000	0.025	0.034	0.046
σ^2 Quadrat	0.071	0.021	0.000	0.039	0.067	0.123
σ^2 Year	0.366	0.436	0.016	0.033	0.234	1.488
Shrub contrast	0.713	0.129	0.003	0.463	0.711	0.975
Control contrast	−0.223	0.127	0.002	−0.481	−0.222	0.025
Canopy contrast	0.178	0.128	0.003	−0.077	0.178	0.432
Removal contrast	0.312	0.128	0.003	0.051	0.312	0.570

B. *Model of species richness.* Our statistical model of species richness was

$$y_t \sim Poisson(\lambda_t)$$

$$\log(\lambda_t) \sim \mathbf{X}\boldsymbol{\beta}_{trt} + \mathbf{Y}\boldsymbol{\beta}_{quad} + \mathbf{Z}\boldsymbol{\beta}_{year} + \phi\log(\boldsymbol{y}_{t-1})$$

where the **X**, **Y**, and **Z** represent the design matrices for the particular components of the model. Each component of the vectors $\boldsymbol{\beta}_{quad}$ and $\boldsymbol{\beta}_{year}$ were distributed as $\beta_{quad}{}^i \sim Normal(0, \tau_{quad})$ and $\beta_{year}{}^j \sim Normal(0, \tau_{year})$, where $\sigma^2_{quad} \sim \frac{1}{\tau_{quad}}$; $\sigma^2_{year} \sim \frac{1}{\tau_{year}}$.

The autoregressive coefficient ϕ was assigned a stationary prior: $\varphi \sim Beta(a, b)$; $\phi = 2*\varphi - 1$.

Noninformative priors were used for each component of $\boldsymbol{\beta}_{trt}$:

$\beta_{trt}{}^k \sim Normal(0, \sigma_{trt}{}^2)$ where $\sigma_{trt}{}^2$ was assigned a very large value (e.g., 1000).

$\tau_{quad} \sim Gamma(\alpha, \beta)$; $\tau_{plot} \sim Gamma(\alpha, \beta)$ with (α, β) chosen to be uninformative, e.g., (0.0001, 0.0001).

Our MCMC simulation had a burn in of 11,000 samples; 90,000 samples were subsequently generated and these were thinned to 1 in 20 for a total of 4,550 samples. The fitted parameters and uncertainty are given in the table below. β_{cc}, β_{cr}, β_{sc}, and β_{sr} refer to the four components of the vector β_{trt}, and correspond to the canopy control, the canopy removal plot, the shrub control plot, and the shrub removal plot. The shrub contrast compares the shrub removal to the shrub control plot, while the canopy contrast compares the canopy removal to the canopy control plot. The control contrast compares the shrub and canopy control plots, while the removal contrast compares the shrub removal to the canopy removal plot.

Parameter	Mean	sd	MC error	2.50%	median	97.50%
β_{cc}	0.413	0.259	0.025	−0.104	0.412	0.911
β_{cr}	0.984	0.248	0.026	0.495	0.981	1.471
β_{sc}	0.201	0.270	0.032	−0.329	0.210	0.710
β_{sr}	1.257	0.249	0.024	0.785	1.245	1.762
ϕ	0.000	0.001	0.000	−0.002	0.000	0.000
σ^2 Quadrat	0.124	0.060	0.003	0.039	0.113	0.269
σ^2 Year	0.375	0.425	0.017	0.044	0.245	1.526
Shrub contrast	1.057	0.220	0.018	0.617	1.059	1.505
Control contrast	−0.213	0.236	0.020	−0.662	−0.213	0.256
Canopy contrast	0.571	0.218	0.014	0.128	0.571	1.018
Removal contrast	0.273	0.201	0.011	−0.117	0.274	0.671

C. *Model of seedling survivorship.* Our statistical model of seedling survivorship was

$$\mathbf{s}_t \sim Bernoulli(\mathbf{p}_t)$$

$$\text{logit}(\mathbf{p}_t) \sim \mathbf{X}\boldsymbol{\beta}_{trt} + \mathbf{Y}\boldsymbol{\beta}_{individual} + \mathbf{Z}\boldsymbol{\beta}_{year}$$

where $\mathbf{s}_t$ is a vector of 1 and 0's indicating whether a given seedling was alive or dead and $\mathbf{p}_t$ is vector of annual survival probabilities for each seedling. The **X**, **Y**, and **Z** represent the design matrices for the particular components of the model: treatment effects, individual seedling to seedling variation, and year effects on annual survival probability. Each component of the vectors $\boldsymbol{\beta}_{individual}$ and $\boldsymbol{\beta}_{year}$ were distributed as $\beta_{individual}{}^i \sim Normal(0, \tau_{individual})$ and $\beta_{year}{}^j \sim Normal(0, \tau_{year})$, where $\sigma^2_{individual} \sim \frac{1}{\tau_{individual}}$; $\sigma^2_{year} \sim \frac{1}{\tau_{year}}$.

Noninformative priors were used for each component of $\boldsymbol{\beta}_{trt}$:

$\beta_{trt}{}^k \sim Normal(0, \sigma_{trt}{}^2)$ where $\sigma_{trt}{}^2$ was assigned a very large value (e.g., 1000).

$\sigma_{individual}{}^2 \sim Uniform(a, b)$; $\sigma_{year}{}^2 \sim Uniform(a, b)$ where (a, b) were chosen to be noninformative over a broad region of likely values of variance, e.g., (0, 100).

Our MCMC simulation had a burn in of 10,000 samples; 200,000 samples were subsequently generated and these were thinned to 1 in 10 for a total of 20,000 samples. The fitted parameters and uncertainty are given in the table below. β_{cc}, β_{cr}, β_{sc}, and β_{sr} refer to the four components of the vector β_{trt}, and correspond to the canopy control, the canopy removal plot (overstory removal), the shrub control plot, and the shrub removal plot. The shrub contrast compares the shrub removal to the shrub control plot, while the canopy contrast compares the canopy removal to the canopy control plot. The control contrast compares the shrub and canopy control plots, while the removal contrast compares the shrub removal to the canopy removal plot. We point out that while our estimates of individual regression coefficients are imprecise, we are able to estimate differences between regression coefficients with much greater confidence: this results from a high correlation between the MCMC chains for regression coefficients. The precision of our regression coefficient estimates would improve with increased MCMC sampling.

Parameter	Mean	sd	MC error	2.50%	median	97.50%
β_{cc}	−14.220	16.600	1.392	−53.930	−12.710	15.670
β_{cr}	−12.850	16.600	1.392	−52.540	−11.340	17.050
β_{sc}	−14.390	16.600	1.392	−54.090	−12.890	15.480
β_{sr}	−12.530	16.600	1.392	−52.190	−11.040	17.370
σ^2 Individual	0.114	0.085	0.006	0.006	0.095	0.325
σ^2 Year	5.824	7.390	0.223	1.125	3.661	24.150
Shrub contrast	1.856	0.196	0.001	1.475	1.855	2.246
Control contrast	−0.170	0.221	0.002	−0.603	−0.170	0.265
Canopy contrast	1.370	0.203	0.001	0.976	1.370	1.767
Removal contrast	0.317	0.170	0.001	−0.016	0.316	0.653
P (SR > SC)	1.000	0.000	0.000	1.000	1.000	1.000
P (SC > CC)	0.221	0.415	0.003	0.000	0.000	1.000
P (CR > CC)	1.000	0.000	0.000	1.000	1.000	1.000
P (SR > CR)	0.969	0.172	0.001	0.000	1.000	1.000