

CHANGING THE GAP DYNAMICS PARADIGM: VEGETATIVE REGENERATION CONTROL ON FOREST RESPONSE TO DISTURBANCE

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Abstract. Understanding the manner in which changes in disturbance regimes will affect forest biodiversity is an important goal of global change research. Prevailing theories of recruitment after disturbance center on the role of pioneer species; predictions of forest biodiversity focus almost exclusively on dispersal and shade tolerance while vegetative reproduction is virtually omitted from models and serious discussions of the topic. However, the persistence of live damaged trees increases understory shade, generates fine-scale environmental heterogeneity, and moderates ecosystem responses to damage, while the sprouting of damaged trees offers a shortcut to reestablishment of the canopy. While a number of studies document snapshots of post-disturbance vegetative reproduction, we lack an understanding of the underlying demographic processes needed in order to both comprehend and predict observed patterns. In this study we quantify the abundance, competitive ability, and interspecific variability of vegetative reproduction in 18 replicated experimental gaps in the southern Appalachians and Carolina Piedmont, USA, in order to assess the potential role of sprouting in driving gap dynamics. Annual rates of damaged adult survival, sprout initiation, growth, and mortality were monitored over four years and compared to the performance of gap-regenerating saplings. Recruitment from sprouts was found to constitute 26–87% of early gap regeneration and forms the dominant pathway of regeneration for some species. Sprouts from recently damaged trees also grow significantly faster than the saplings with which they compete. For all measured demographic rates (damaged tree survival, sprout initiation, number, growth, and survival) differences among species are large and consistent across sites, suggesting that vegetative reproduction is an important and non-neutral process in shaping community composition. Sprouting ability does not correlate strongly with other life-history trade-offs, thus sprouting potentially provides an alternate trait axis in promoting diversity.

Key words: Bayesian statistics; damaged trees; demography; individual effects; Piedmont, USA; recruitment limitation; southern Appalachians, USA; sprouting; succession; vegetative reproduction.

INTRODUCTION

The response of forest biodiversity to global change will greatly depend on regeneration following disturbance. Increases in severe storms (Overpeck et al. 1990, Knutson et al. 1998, Emanuel 2005), fire (Clark 1988, Westerling et al. 2006), and drought (IPCC 2001, Breshears et al. 2005) will modify the mosaic of stand ages and may also cause widespread tree mortality and rapid ecosystem shifts. For much of the world's forests, particularly those areas with long fire return intervals, natural disturbance cycles are thought to be dominated by regeneration in canopy gaps. Traditional gap theory assumes that shade-intolerant species, which have

profuse seed production and rapid seedling growth, are best adapted to exploit the high-light environment in gaps. Increased disturbance is expected to cause a shift to early successional species, with an overall net loss of shade-tolerant species (Connell and Slayter 1977, Huston and Smith 1987).

Although ecologists have long recognized that post-disturbance recruitment can originate from both seed and a range of vegetative mechanisms, the complexity of vegetative responses and lack of quantification means that non-seed regeneration rarely enters theoretical discussions (Clark 1991, Bellingham and Sparrow 2000, Loehle 2000, Bond and Midgley 2001) or models of forest response to contemporary global change (de Groot et al. 2003). In fact, treefall gaps in most ecosystems are not dominated by shade-intolerant species (Webb 1999, Brokaw and Busing 2000). While there is growing recognition of the role of advanced regeneration, recruitment coming from seedlings and saplings that survive disturbance (Runkle 1990, Hubbell

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et al. 1999, Platt and Connell 2003), there remains a potentially large role for damaged trees and sprouts in gap dynamics.

Sprouts have access to substantial energy reserves and may rapidly reenter the canopy following disturbance. In fire-dominated ecosystems it is well known that many species recover rapidly from fire by resprouting (Clark 1996, Keeley et al. 1999, Lloret et al. 2005). In forest gaps, a number of observational studies have documented high rates of damaged tree survival and/or sprouting following natural windthrow (e.g., Glitzenstein and Harcombe 1988, Webb 1989, DeCoster 1996, Peterson 2000). However, most research on forest gap dynamics does not address the capacity of species to persist in a damaged state and recover by vegetative reproduction.

The overemphasis on regeneration by seed stems from the challenges of large-scale and long-term experiments and from the limitations of observational research. Except in the case of fortuitous damage to monitored stands (e.g., Batista and Platt 2003), observational gap studies rarely include "pretreatment" data, which is critical for distinguishing whether individuals originate from seed, sprout, or advanced regeneration, and more often provide only a "snapshot" of the community some time after disturbance. Observational data do not provide the replication, stratification by factors responsible for change, and randomization over uncontrollable variables needed for strong inference.

Experimental gaps allow for these design considerations, but require substantial effort, planning, and long-term commitment. Unfortunately, for logistical reasons, most experimental gaps are created by cutting trees, thus precluding a damaged-tree response. A notable exception, the Harvard Forest hurricane experiment, which involved creation and monitoring of damaged individuals rather than cutting and removing canopy trees, may be unique (Cooper-Ellis et al. 1999). Even this ambitious study did not extend to replication, stratification, and randomization and was restricted to examining the community pattern of damaged trees and sprouts rather than their underlying demographic rates. While experimental gaps created by cutting often show a strong sprout response (Phillips and Shure 1990, Thompson et al. 1998, Shure et al. 2006), as do many logging studies (e.g., Boring et al. 1981), it is unclear how this response applies to natural disturbance. Overall, the role of sprouting in gap regeneration is potentially large, but remains poorly understood.

Here we assess the importance of sprouting to gap regeneration in experimental gaps in the southeastern United States. This study combines the advantages of a carefully designed long-term experiment with model-based inference, in which models follow individual demography nested within populations (Clark 2005). The experimental design took advantage of stratification by site and gap size, randomization within sites, non-gap controls, and detailed longitudinal data on resources

and individual-level responses annually and across landscapes over six years. We hypothesized that vegetative reproduction may be the dominant mode of gap regeneration and that the early trajectory of regeneration by sprouts produces dynamics different from those expected under seed recruitment. Our assessment involves four criteria. First, we evaluate whether the contribution of damaged tree survival and sprouting to gap recruitment occurs in sufficient numbers relative to other sources of recruits, such as advanced regeneration and seedling germination, that it be considered an important pathway for recruitment rather than a chance occurrence. Second, we assess whether sprouts have rates of growth and mortality that would permit them to reach the canopy ahead of other recruits. Together these two tests can demonstrate that sprouts are likely components of the future community, but not that they would alter the overall diversity. Additionally, we assess whether demographic rates vary among species. Finally, we determine whether interspecific variation in demographic rates merely reinforces existing trade-offs among species or it introduces new ones.

The basis for our analysis is estimates of demographic rates of damaged trees (mortality, sprouting, number of sprouts, size and growth rate of sprouts, and sprout survival) for the first four years of an experimental gap study replicated in the southern Appalachians and Carolina Piedmont, USA. We quantify the overall pattern of recruitment for stems >2 m tall and examine the pathways by which different species recruit. These analyses demonstrate that for both study sites, sprouts occur in large numbers, show large variation among species, grow faster than saplings, and have comparable mortality rates. Our results have profound implications for biodiversity and demonstrate that vegetative reproduction needs to be incorporated into theory and models involving life-history trade-offs, patch dynamics, and forest responses to global change.

METHODS

The gap experiment entails a time series intervention design with two years pretreatment observation, four years of post-gap observation, and replicates for each of two gap sizes within each of two sites (Piedmont and southern Appalachians). However, instead of a standard ANOVA based on these design considerations, we analyze individual demographic responses using model-based inference (Clark 2007). In this section we discuss field methods and data, the overall demographic and statistical framework, and models used for estimation of demographic rates and community change.

Site description and field work

Experiments were implemented in the Blackwood Division of the Duke Forest, Chapel Hill, North Carolina, and the Coweeta Long-Term Ecological



PLATE 1. Snapped and uprooted trees immediately after gap creation in the Duke Forest, Chapel Hill, North Carolina, USA. Photo credit: M. Dietze.

Research (LTER) site, Otto, North Carolina. The Duke Forest Experimental Gap site (35°85' N, 79°05' W) is a 4.5-ha mapped stand in the Carolina Piedmont, with approximately half the site consisting of mature, secondary oak–hickory forest of unknown age and the other half being ~80-yr-old loblolly pine (*Pinus taeda*) with a mixed-hardwood understory. Both halves of the site show clear evidence of former agricultural use, as is characteristic of the region. The stand had an initial (pre-gap) stem density of 2030 stems/ha and a basal area of 36.7 m²/ha. Mean annual precipitation is 1140 mm and mean annual temperature is 15.5°C. Soils are a clayey loam. A thorough description of the study site is *available online*.⁴

The Coweeta Long Term Ecological Research (LTER) Experimental Gaps (35°03' N, 83°27' W) include two similar, mapped stands of mature, secondary mixed oak totaling 4.8 ha in southern Appalachian hardwood forest. The Coweeta basin was logged around 1900, though the exact impact on our study plot is unknown, and then underwent significant structural change with the chestnut blight of the mid-1930s. The stands had an initial stem density of 1090 stems/ha and a basal area of 34.9 m²/ha. Mean annual precipitation and temperature are 2200 mm and 13°C, respectively. Soils are primarily Ultisols and Inceptisols. Further site information is *available online*.⁵

Information on the natural disturbance regimes at both sites is incomplete, but wind damage is a primary

agent for generating large disturbances for both locations (Runkle 1985, 1990). Large wind disturbance events at both sites are primarily due to hurricanes, which occur mostly in the autumn. For example, Hurricanes Fran (September 1996) and Opal (October 1995) created large damaged areas in Duke Forest and Coweeta, respectively. Estimates of the historical role of fire in both ecosystems vary widely (Frost 1998; J. Lynch, *personal communication*), but the contemporary role of fire is very limited in both systems.

Stands were initially censused at both sites in 2000. All live trees >2 m in height were identified, tagged, measured for diameter breast height (dbh, measured at 1.45 m above the ground surface), and mapped relative to a 10-m grid established using a Topcon GTS-300 Total Station survey unit (Topcon Positioning Systems, Livermore, California, USA). In March 2002, following two years of pretreatment data collection, experimental gaps were created by pulling canopy trees with a winch until they were down (see Plate 1). All downed trees were left in place. Only individuals visually determined to be dominant or codominant in the canopy were pulled to mimic the effects of wind damage, which selectively culls the largest individuals (*sensu* Cooper-Ellis et al. 1999). Trees were selected to create gaps 20 m (“small,” $n = 8$ gaps) or 40 m (“large,” $n = 10$ gaps) in diameter. There were four large and four small gaps at the Duke Forest site and six large and four small gaps at the Coweeta site. Small gaps required pulling 5–12 trees, while large gaps required pulling 25–40 trees. Maps depicting plot locations, gap sizes, and mean treefall direction are given in the Appendix, along with detailed information on gap creation methods.

⁴ <http://www.env.duke.edu/forest>

⁵ <http://coweeta.ecology.uga.edu>

All mapped stands were censused again in the first (May–June 2002) and third (April–May 2004) year after gap creation for growth, survival, ingrowth, and damage class. Damaged trees were classified as leaning, bent, downed, snapped, or uprooted. A tree was considered leaning if the trunk departed substantially from vertical but the top was always angled upward, while trees were classified as bent if the top of the tree was horizontal or bent downward. Trees classified as “down” had their trunks or major branches supported by the ground. Uprooted trees had exposed root systems. Snapped trees included both trees having the trunk completely severed and trees that experienced mechanical failure but had upper and lower portions the trunk still attached. From the 2002 census, all trees >10 cm dbh that had been damaged by gap creation were marked for further study. These trees were censused in September 2002, 2003, 2004, and 2005 for survival and basal sprouting. A stem was considered alive if it had any live foliage on the trunk or branches, including epicormic sprouting. Basal sprouting was defined independent of stem survival as growth from the base of the trunk, tip-up mound, or major roots and thus excluded epicormic sprouting and long-distance root suckering. In the fall 2004 census the number of sprouts were counted and, for the largest sprout of each tree, we measured basal diameter, dbh, height to the apically dominant meristem (measured along the stem), and the height of all observable bud scars on the dominant leader in order to estimate growth over the past one to three seasons.

In the census, and throughout this manuscript, sprouting refers to new vegetative reproduction that occurred in response to gap formation; sprouts that occurred prior to gap formation were tallied as additional adult stems (>2 m) or saplings (0.5–2 m), depending on height. This definition of sprout arises primarily because our primary hypotheses are about sprouting in response to gap formation, not sprouting in general, but also because it is not practical to distinguish stems originating from seed vs. sprouting except for those few species that do not sprout (conifers) and for *Castanea dentata*, which only originates from sprouts. For all other species, dieback and resprouting of seedling and saplings in the understory is a common and continuous process, with resprouts accounting for 58–79% of the total population (Del Tredici 2001, Dietze 2006). However, this is a qualitatively different process from resprouting by large individuals in response to disturbance, so we do not feel that this complicates our results or interpretation. For *C. dentata* the relevant analyses were repeated, excluding this group as noted in the following.

For the analysis of community change we make use of two other data sets: sprouts from stems >2 m tall but <10 cm dbh and sapling advanced regeneration. While the demography of sprouts was not specifically tracked for smaller stems, the addition of new stems from previously tagged individuals was recorded during the

mapped stand census (2002 and 2004). Rates of ingrowth of saplings was determined by the addition of new stems reaching 2 m in height in 2002 and 2004 that did not come from already tagged individuals. Based on sapling plot measurements it is estimated that >95% of this ingrowth came from advanced regeneration at least 50 cm tall at the time of gap creation (M. C. Dietze, unpublished data) rather than seed or seedlings.

For the comparison of the demography of saplings to sprouts we make use of 34 annually measured 10 × 10 m sapling plots, 20 in the 10 southern Appalachian gaps and 14 in the eight Piedmont gaps, established to measure the gap response of advanced regeneration (Dietze 2006). In 2001 all stems >50 cm tall but not already tagged in the stem map (<2 m tall) were tagged, mapped, and measured for basal diameter (5 cm height), dbh when applicable, total height, and bud scar height. Sapling plots were censused again in late August 2002, 2003, 2004, and 2005 for new ingrowth, survival, growth in diameter and height, physical damage from gap creation, and dieback (loss of height) from any other agent.

For the demographic analysis some species were aggregated due to small sample sizes and/or taxonomic uncertainty. These included hickories (*Carya* spp.) and red oaks (*Quercus* section *Lobatae*: *Quercus marilandica*, *Q. falcata*, *Q. rubrum*, and *Q. velutina* at Duke Forest; *Q. coccinia*, *Q. rubrum*, and *Q. velutina* at Coweeta) at both sites. At Duke Forest white oaks (*Quercus* section *Quercus*: *Q. alba* and *Q. stellata*), pines (*Pinus echinata* and *P. taeda*), and elms (*Ulmus alata* and *U. americana*) were analyzed together. Remaining species with small sample sizes were as follows: Coweeta, *Acer pensylvanicum*, *Castanea dentata*, and *Robinia pseudoacacia*; Duke Forest, *Cercis canadensis*, *Morus rubra*, and *Nyssa sylvatica*. For the community analysis at Coweeta, we considered *Acer pensylvanicum*, *Castanea dentata*, and *Robinia pseudoacacia* independently because of their greater representation among saplings and sprouts off small trees, but lumped *Magnolia fraseri*, *Nyssa sylvatica*, and *Quercus montana*. Taxonomic classification follows Radford et al. (1968), with the exception of *Q. montana* (chestnut oak, formerly *Q. prinus*).

Statistical methods

To assess the demographic processes behind the pattern of vegetation change following gap creation, four sequential demographic processes were modeled: the survival of damaged trees, formation of sprouts, growth of sprouts, and survival of sprouts. Within each of these four processes, annual demographic rates are modeled conditioned on the previous state. For example, survival in 2004 is modeled conditioned on being alive in 2003; individuals that died before 2003 are removed from the analysis for 2004. It is expected that the four demographic processes are correlated, and therefore to account for these interrelations the analysis is treated as one large model. However, by making

assumptions about the causal direction of these relationships (e.g., assuming adult survival affects sprout initiation, growth, and survival rather than the other way around) we are able to unwind the fitting of the model into a set of sequential steps rather than fitting the whole model at once.

In addition to the ecological relationships among demographic processes, there are additional modeling considerations associated with missing data. While the amount of missing data is not unusual in this data set, the time series nature of the data is such that under a conventional analysis one year of missing data for one process could necessitate throwing out a whole individual for all processes. For example, if an adult tree is alive in 2003, missed in 2004, and dead in 2005, we cannot say exactly when it died. This loss of information would then cascade through the analysis, since sprout formation, growth, and survival are modeled with adult survival as a covariate. Fortunately Bayesian Markov chain/Monte Carlo (MCMC) methods allow missing data to be accounted for in a formal, integrated manner that propagates uncertainty (Gelman et al. 1995). Instead of removing missing data, we iteratively impute missing states based on the current parameter values and then update parameters conditioned on the current states using MCMC.

Statistical analyses are done in a Bayesian framework using standard MCMC computational methods such as Gibbs sampling and Metropolis sampling (Gelman et al. 1995). All analyses are done using the R statistical language (R Development Core Team 2005). Unless otherwise stated each MCMC was run for 100 000 steps with a burn-in of 20 000 steps and thinning to one in four values to reduce autocorrelation. Model selection was done using a squared-error predictive loss metric (Gelfand and Ghosh 1998), with variables sequentially removed from the full model using a backward elimination procedure.

Damaged tree and sprout demography

Annual survival of damaged tree i in year t , $Y_{i,t}$, given that it was alive in year $t - 1$, was modeled as a logistic regression in a generalized linear model (GLM):

$$p(Y_{i,t}|Y_{i,t-1} = 1) = \text{logit}^{-1}(\mathbf{X}_i\boldsymbol{\beta}) \quad (1)$$

where the design vector \mathbf{X}_i is [1, species, damage class, dbh] and $\boldsymbol{\beta}$ is the fit parameter vector. Throughout these analyses species, damage class, year, and age are all categorical variables represented with indicator variables. Logistic regression was chosen due to the Boolean nature of survival data.

Sprouting involves a two-part analysis, considering whether or not a stem sprouts and, if so, the number of sprouts for that stem. The annual initiation of sprouting is modeled as a logistic regression $Z_{i,t}$ conditional on not having sprouted yet: $p(Z_{i,t}|Z_{i,t-1} = 0) = \text{logit}^{-1}(\mathbf{W}_{i,t}\boldsymbol{\alpha})$, where $\mathbf{W}_{i,t} = [\text{species, damage classes, dbh, year, adult survival}]$ and $\boldsymbol{\alpha}$ is the parameter vector. Additional

sprouting from the same stem is not considered a new sprouting event.

The annual survival rate of sprouts is a logistic regression of sprout status (alive vs. dead), $p(Z_{i,t}|Z_{i,t-1} = 1) = \text{logit}^{-1}(\mathbf{T}_{i,t}\boldsymbol{\kappa})$, where $\mathbf{T}_{i,t} = [1, \text{species, damage, dbh, adult survival } (Y_{i,t}), \text{lag adult survival } (Y_{i,t-1}), \text{year, age}]$.

We specified Gaussian priors on $\boldsymbol{\beta}$, $\boldsymbol{\alpha}$, and $\boldsymbol{\kappa}$ with mean zero and variance 100. The MCMC simulations were conducted using a Metropolis step with Gaussian jump distributions having variances of 0.05, 0.075, and 0.05, respectively.

For a small fraction of trees, survival data are missing in some years (for damaged trees, 2.6% and 2.3% missing data at Duke Forest and Coweeta, respectively; for sprout initiation/mortality, 17.5% and 16.6% missing data at Duke Forest and Coweeta, respectively, with most [90% and 84%] of the missing data in the first census due to a protocol error; for sprout growth, 3.1% and 1.4% missing data). Missing data were modeled in each time step based on the current imputed parameter values for each variable:

$$Y_t^{(m)} \sim \text{Bernoulli}(\text{logit}^{-1}(\mathbf{X}\boldsymbol{\beta}_g))$$

$$Z_t^{(m)} \sim \text{Bernoulli}(\text{logit}^{-1}(\mathbf{W}_t\boldsymbol{\alpha}_g))$$

$$Z_t^{(m)} \sim \text{Bernoulli}(\text{logit}^{-1}(\mathbf{T}_t\boldsymbol{\kappa}_g))$$

where (m) designates a missing value whose provisional value is drawn based on the g th iteration of the MCMC. In this way missing data are “averaged over” based on the observed data with an essentially “flat” prior on the missing data. Imputed values of Z were used to recalculate sprout age at each iteration of the MCMC.

Unfortunately, growth could not be included as a covariate in estimating sprout survival because growth was only measured in 2004 and thus we have no information on growth for individuals that died from 2002 to 2004. Personal observation does suggest the individuals experiencing early mortality were growing slower than those that survived.

Sprout height growth rate ($\Delta H_{i,t}$, in meters per year) is modeled as a log linear regression with random individual effects:

$$\log(\Delta H_{i,t}) = \mathbf{S}_{i,t}\boldsymbol{\eta} + \zeta_i + \varepsilon_{i,t} \quad (2)$$

$$\varepsilon_{i,t} \sim \mathcal{N}(0, \sigma^2)$$

$$\zeta_i \sim \mathcal{N}(0, v^2)$$

where subscripts i and t denote individual and time, $\mathbf{S}_{i,t} = [1, \text{species, damage, year, age, adult survival } (Y_{i,t})]$, $\boldsymbol{\eta}$ is a vector of fixed effects, ζ_i is the random individual effect, and $\varepsilon_{i,t}$ is residual error. Priors are taken to be $\sigma^2 \sim \text{IG}(\alpha_s, \gamma_s)$, $v^2 \sim \text{IG}(\alpha_n, \gamma_n)$ (where IG indicates an

inverse Gaussian distribution), and $\eta_i \sim \mathcal{N}(H_0, V_0)$ with prior parameter values set at $\alpha_s = \alpha_n = 0.1$, $\gamma_s = \gamma_n = 0.1$, $H_0 = 0$, and $V_0 = 100$, which are essentially flat on a log scale since growth is only expected to vary over a few orders of magnitude.

Since we could not follow the bud scars on every sprout back to the base, we modeled missing heights using the growth model conditioned on the previous and next heights:

$$\begin{aligned} \Pr[H_t = h | H_{t-1}, H_{t+1}, \dots] \\ \propto N(\log(H_{t+1} - h) | \mathbf{S}\boldsymbol{\eta} + \zeta_i, \sigma^2) \\ \times N(\log(h - H_{t-1}) | \mathbf{S}\boldsymbol{\eta} + \zeta_i, \sigma^2). \end{aligned}$$

Missing heights were sampled using a Metropolis algorithm using a reflected normal jump distribution with standard deviation of 100. Since sprouts originated after the gaps were created, we were able to confidently assign ages to sprouts missing their initial height values, thus fixing the initial height at zero for the year before the individual sprouted. Missing adult survival data (Y_t) for the set of covariates were drawn from the posteriors above. Due to the smaller number of individuals remaining alive in some taxa, and thus available for growth estimation, we adjusted the previous species groupings, treating *Carya glabra*, *C. tomentosa*, and *Morus rubra* individually at Duke Forest and *Quercus coccinea*, *Q. rubra*, and *Robinia pseudoacacia* individually at Coweeta.

The number of sprouts per adult stem in 2004, conditioned on the stem having sprouts, was modeled as a zero-truncated Poisson because all individuals in the sample have at least one sprout:

$$\text{ZTP}(r|\lambda) = \frac{e^{-\lambda}\lambda^r}{r![1 - e^{-\lambda}]}.$$

When combined with the previous analysis on sprout initiation, this can be viewed as a two-part Poisson mixture model of overall abundance (LaDeau and Clark 2001, Clark et al. 2004, Cunningham and Lindenmayer 2005). We model λ using a log link, $\log(\lambda_i) = \mathbf{U}_i\boldsymbol{\gamma}$, where $\mathbf{U}_i = [\text{species, damage, dbh}]$ and $\boldsymbol{\gamma}$ is the parameter vector. The value of predictive loss calculated for model selection was performed using the correction that $E[\text{ZTP}] = \lambda/(1 - e^{-\lambda})$ rather than simply λ , as is the case for a standard Poisson.

Sapling demography

The comparison of the growth rates of saplings and sprouts is done based on the empirical distribution of observed individual growth rates. The comparison of mortality rates, on the other hand, is done based on the distribution of individual mortality probabilities from the logistic survival analysis. The Bayesian logistic survival analysis for saplings, which followed the same methods as the sprout analysis above, included height

growth (ln-transformed), dieback, damage class, and species as covariates but found that there were few that were significant. In the southern Appalachians, none of the covariates were selected, while in the Piedmont, damage type and growth were included. The full analysis of the sapling data is reported elsewhere (Dietze 2006; M. C. Dietze and J. S. Clark, *unpublished manuscript*).

Community pattern

To assess the importance of sprouting as a pathway for regeneration, we tallied the number of new stems in the adult stem map (stems >2 m tall) in 2004 that entered either as sprouts or as ingrowth from the sapling layer. We estimated the proportion of new recruits that came from sprouts, p , using a beta-binomial model with a flat priors ($\alpha = \beta = 1$):

$$\begin{aligned} \Pr[p|x, n, \alpha, \beta] &= \text{Beta}(p|x + \alpha, n - x + \beta) \\ &\propto \text{Binomial}(x|n, p)\text{Beta}(p|\alpha, \beta) \end{aligned}$$

where n is the total number of recruits and x is the number that are from sprouts. The beta-binomial model is based upon a beta prior on p and a binomial likelihood and, unlike many Bayesian models, has an analytical solution for the posterior. Sprout recruitment was further subdivided into two categories, sprouts from adults (stems >10 cm dbh) vs. sprouts from smaller poles (<10 cm dbh but >2 m tall). The ingrowth from the sapling layer is not distinguished by origin and could include individuals that started the experiment as saplings, individuals that recruited from below that stage, and sprouts from saplings.

RESULTS

Damaged tree and sprout demography

Overall, the growth rates of sprouts were considerably higher than the growth rates of preexisting saplings (Fig. 1a, b). In the southern Appalachians sprout height growth averaged 65.1 ± 2.8 cm/yr (mean \pm SE) while saplings averaged 21.5 ± 0.3 cm/yr. Growth rates in the Piedmont were slightly lower for both saplings and sprouts, with sprouts averaging 49.7 ± 3.2 cm/yr and saplings averaging 13.8 ± 0.5 cm/yr. Sprout growth also showed large differences among individuals within a species; at both sites individual variability (ζ_i) is in a similar range as residual variance (ϵ_{it}) (Eq. 2; Table 3). For mortality, sprouts show much greater variability than saplings (Fig. 1c, d), with some groups experiencing rapid mortality while others persisted. On average, median sprout annual survival at Duke Forest (0.968) was actually higher than median sapling survival (0.953), while at Coweeta sapling survival was slightly greater (0.986) compared to sprouts (0.945), but for both sites, sapling survival rate was within the 95% credible interval of sprout survival rate.

Demographic rates varied among species at both the Piedmont (Duke Forest) and southern Appalachian

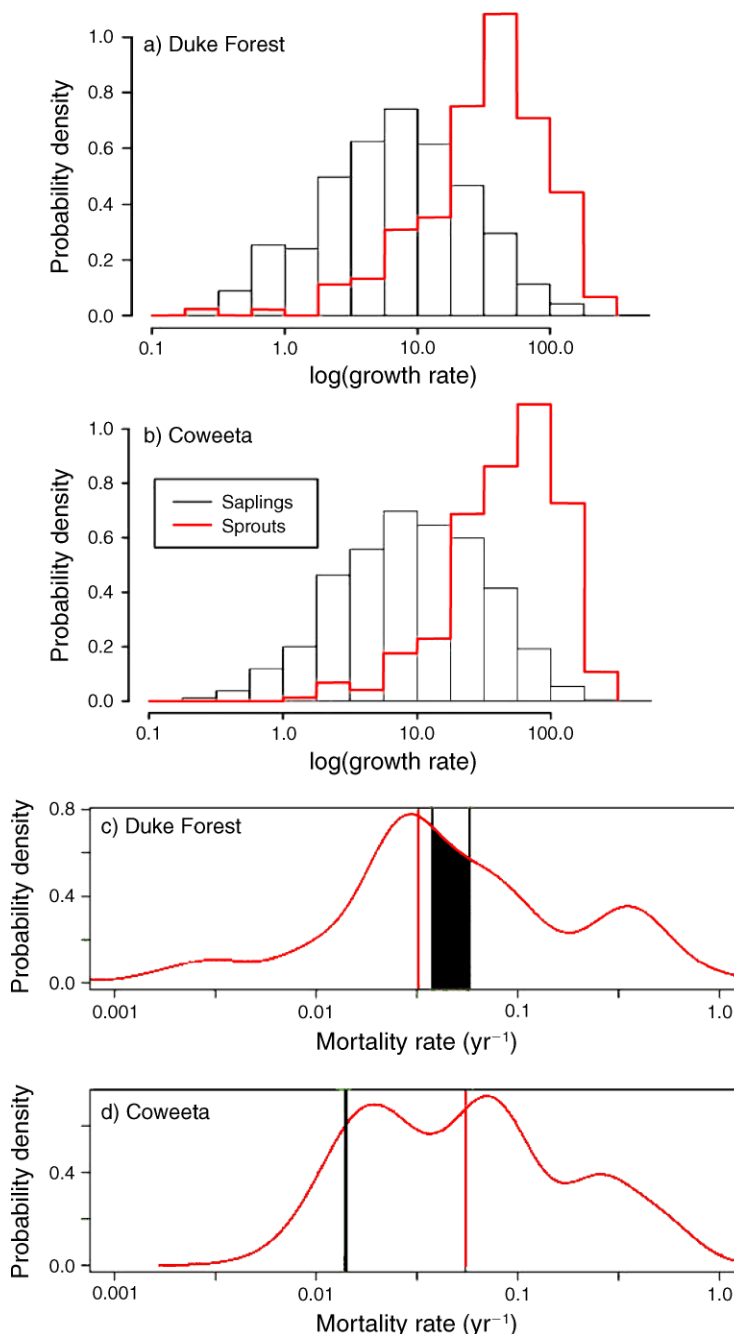


FIG. 1. Sprout and sapling log height growth distributions for (a) Piedmont (Duke Forest), USA, and (b) southern Appalachians (Coweeta), USA, show the large difference between these two recruitment pathways. Growth rate, log-transformed prior to analyses, was measured in cm/yr. For the Piedmont, $N = 181$ sprouts, $N = 1931$ saplings; for the southern Appalachians, $N = 297$ sprouts, $N = 5617$ saplings. The distributions of mortality probability for (c) the Piedmont and (d) southern Appalachians show considerable variation among sprouts (red curve). However, the median sprout mortality probability (vertical red line) is comparable to that for saplings (vertical black bar), where bar width indicates the range of sapling mortality probabilities.

(Coweeta) sites (Tables 1–3, Fig. 2). Across both sites and demographic stages there were clear trends in species performance that are consistent with previous studies. Of the species that occurred in both study regions, *Oxydendrum arboreum*, *Liriodendron tulipifera*,

and *Acer rubrum* had consistently high adult survival and sprouting. *Cornus florida* also had high adult survival and sprouting at Duke Forest but did less well at Coweeta, possibly due to the higher prevalence of the fungal pathogen dogwood anthracnose (*Discula destruc-*

TABLE 1. Results of the demographic analysis for the Piedmont, USA.

Parameter	Adult survival		Sprouting		Sprout survival	
	Mean	Credible interval	Mean	Credible interval	Mean	Credible interval
Intercept	4.36	2.87 to 5.98	3.71	-3.05 to 13.40
Species and code						
<i>Carya</i>	-2.15	-3.15 to -1.24	-1.76	-4.43 to 0.98	0.48	-1.59 to 2.54
<i>Cornus florida</i> (COfl)	-1.81	-3.33 to -0.32	1.93	-2.42 to 7.30	1.29	-0.74 to 3.56
<i>Fraxinus americana</i> (FRam)	-0.80	-2.15 to 0.55	0.33	-2.96 to 3.99	0.10	-2.22 to 2.43
<i>Juniperus virginiana</i> (JUvi)	-1.35	-3.17 to 0.79	-9.55	-22.14 to 1.29
<i>Liquidambar styraciflua</i> (LIst)	-1.41	-2.47 to -0.45	1.44	-1.41 to 4.74	0.60	-0.93 to 2.27
<i>Liriodendron tulipifera</i> (LItu)	0.017	-1.20 to 1.23	0.55	-2.46 to 3.85	0.15	-1.62 to 2.18
<i>Oxydendrum arboreum</i> (OXar)	0.54	-1.77 to 4.77	-1.35	-4.14 to 1.41	8.33	0.89 to 19.53
<i>Pinus</i>	-4.67	-5.94 to -3.57	-3.61	-7.30 to -0.35	-1.28	-5.66 to 3.09
<i>Quercus</i> sec. <i>Quercus</i> (QUwt)	-3.30	-4.41 to -2.31	-3.21	-6.79 to 0.77	0.04	-2.701 to 2.65
<i>Quercus</i> sec. <i>Lobatae</i> (QUrd)	-3.43	-4.78 to -2.12	-11.57	-20.38 to -4.55
<i>Ulmus</i>	-1.02	-2.30 to 0.31	-2.22	-7.64 to 3.89	5.22	-2.60 to 16.42
Other species	-1.98	-3.42 to -0.50	2.89	-1.37 to 6.79	-4.73	-14.51 to 0.63
Damage						
Bent	1.33	-0.81 to 3.52	0.72	-3.89 to 5.28	-5.07	-15.03 to 1.98
Down	-1.08	-2.59 to 0.39	0.50	-3.10 to 4.64	-4.23	-14.18 to 2.33
Snap	-0.73	-2.15 to 0.69	1.08	-1.98 to 4.28	-2.89	-13.61 to 3.85
Uproot	-1.61	-2.98 to -0.27	2.04	-1.40 to 5.78	-4.97	-15.04 to 1.16
Other damage	0.82	-0.77 to 2.47	-0.67	-3.82 to 2.46	-5.66	-15.60 to 0.47
Adult parameter						
Adult dbh	-0.49	-1.24 to 0.25	-0.62	-3.50 to 2.34	1.74	-0.42 to 4.03
Adult survival	2.17	-0.012 to 4.45	2.90	1.50 to 4.47
Adult survival lag	0.47	-0.92 to 1.92
Year						
2002	1.20	-2.99 to 5.50
2003	-1.66	-5.79 to 2.89
2004	-7.20	-11.56 to -2.28
2005	-7.54	-11.94 to -2.64

Notes: Parameter means and 95% credible intervals for logistic regression of damaged tree survival, sprout initiation, and sprout survival (values are proportions) and zero-truncated Poisson/log-link regression of the number of sprouts per tree are given. These values are summary statistics of the fit parameters of the statistical models (Bayesian variants of general linear models) and thus are synonymously regression coefficients. Covariates are species, damage type, adult dbh, adult survival, and year. Species abbreviations used in figures appear in parentheses. Positive coefficients represent greater adult survival, sprouting, sprout survival, and number of sprouts, respectively. Ellipses indicate parameters that were not included in the most parsimonious model based on a predictive loss metric or species with insufficient sample size at a given demographic stage. The species *Acer rubrum* (ACru; $n = 41$) is used as the omitted reference species for the species effects and thus is defined as 0, and all species coefficients are scaled relative to this one. The sample size, n , is by species and damage class for adult survival and sprouting.

tiva) in the southern Appalachians. *Quercus* spp. and *Carya* spp. were consistently poor sprouters, though damaged tree survival was appreciably higher for *Carya* spp. than for *Quercus* spp., while established sprouts have intermediate growth and survival for both. Conifers consistently had poor sprout performance. For damaged trees, eastern pine species have particularly low survival, while *Tsuga canadensis* and *Juniperus virginiana* are intermediate. The remaining species tend to fall out in intermediate positions both overall and for specific demographic rates. *Nyssa sylvatica* was an exception, having high damaged tree survival at Coweeta, but having low rates of sprout formation and sprout survival. The number of sprouts produced by each stem varied considerably among species: *Acer rubrum*, *Oxydendrum arboreum*, *Cornus florida*, and *Fraxinus americana* were prolific sprouters; *Liquidambar styraciflua* and *Quercus* spp. were intermediate; and *Carya* spp., *Liriodendron tulipifera*, and *Ulmus* spp. tended to produce a single dominant sprout. With the

exception of a lack of conifer sprouting, there was no obvious explanation for differences among species in damaged tree survival and sprouting. There was no clear pattern among shade tolerance classes, as defined by rankings in Baker (1948) and Burns and Honkola (1990). Additionally, there was no obvious pattern in survival or sprouting ability as a function of mechanical constraints, such as wood strength, though the greater flexibility of smaller stems may explain their higher survival rates.

Damage type affected adult survival, with lightly damaged trees (lean, bent) showing higher survival than snapped and uprooted stems. The effects of damage type on sprout demographic rates were less clear but taken as a whole suggest that sprouting is most successful at intermediate levels of damage, with light damage not inducing a strong response and severely damaged stems less likely to sprout. Both sites show a decrease in adult survival and sprout formation with tree size. Sprout survival represents the only demographic rate having

TABLE 1. Extended.

Sprout number (no. sprouts/tree)		
Mean	Credible interval	<i>n</i>
2.11	1.74 to 2.46	
-1.81	-2.51 to -1.21	30
-1.22	-1.59 to -0.89	7
-0.30	-0.60 to -0.01	11
...	...	6
-1.31	-1.67 to -0.96	29
-0.98	-1.26 to -0.70	20
-1.51	-2.04 to -1.01	7
...	...	80
-0.84	-1.42 to -0.30	36
...	...	14
-17.31	-27.66 to -9.46	
-1.06	-2.07 to -0.28	7
-0.019	-0.60 to 0.57	11
1.63	1.22 to 2.04	26
0.62	0.23 to 1.03	43
0.58	0.20 to 1.00	113
0.30	-0.15 to 0.77	69
...	...	
...	...	
...	...	
...	...	
...	...	
...	...	
...	...	

size effects that differed between study regions, increasing with parent tree dbh at Duke Forest but decreasing with dbh at Coweeta. Sprout formation showed consistently strong year effects, with sprouting highest in the first year, intermediate in the second, and tailing off to negligible levels in the third and fourth years. Likewise, the year effects at Coweeta and the year \times age interaction in Duke Forest both suggest a decline in growth rates in the third year. This observation is consistent with the expectation that growth slows over time as the subsidy sprouts receive from the parent tree declines. Similarly, adult survival increased both sprout formation and sprout survival. For sprout survival there was a significant one-year lag effect of adult survival that suggests sprout survival continues to decline at Duke Forest in the years after the adult dies, but that survival rebounds at Coweeta.

Community pattern

Sprouts constituted a substantial fraction of new stems at both sites. At Coweeta, sprouts were 60% (95% credible interval = 0.53–0.66) of the stems in the large gaps and 45% (95% credible interval = 0.28–0.63) in the small gaps, while in Duke Forest sprouts were 26% (95% credible interval = 0.21–0.33) of the stems in the large gaps and 55% (95% credible interval = 0.34–0.74) in the

small gaps. A large fraction of sprouting at Coweeta came from *Castanea dentata*, now an obligate sprouter due to chestnut blight (*Endothia parasitica*); however, even with *C. dentata* removed, the overall contribution of sprouting at Coweeta was 68% (95% credible interval = 0.59–0.75) compared to 29% at Duke Forest (95% credible interval = 0.23–0.35). The diversity of recruits was also much greater in Coweeta (12 species) than in Duke Forest (four species: *Acer rubrum*, *Cornus florida*, *Liquidambar styraciflua*, and *Liriodendron tulipifera*), though for Coweeta we only discuss the seven species represented by at least five individuals. Three sources of recruits were considered in this analysis: ingrowth from saplings, ingrowth from sprouts of trees <10 cm dbh (pole sprouts), and ingrowth from sprouts of trees >10 cm dbh (adult sprouts). For each site and gap size we considered recruitment from the perspectives of the composition (Fig. 3) and the importance of each pathway to species recruitment (Fig. 4).

The importance of sprouting for recruitment varied substantially among species. In the Duke Forest large gaps, *A. rubrum* accounted for 36% of the recruits and was equally represented in all three pools. *Liriodendron tulipifera*, which contributes 5% to overall recruitment, increased substantially in relative abundance from sapling to pole sprout to adult sprout. In contrast, *L. styraciflua*, which constitutes 48% of recruitment, declined over the same stages such that only 22% of recruits came from sprouts. *Cornus florida* increased in representation from sapling (11%) to pole sprouts (36%), but was absent among adult sprouts. The composition of the recruit pool in Duke Forest small gaps was more straightforward: *A. rubrum* and *L. tulipifera*, which accounted for 45% and 10% of the recruit pool, only recruited from sprouts; *L. styraciflua* and *C. florida*, which accounted for 20% and 25% of recruits, only recruited from saplings.

A substantial portion of the recruitment in the Coweeta large gaps consisted of *C. dentata* stems (42%), which are split evenly between the sapling and pole sprout pools. Of the remaining species, *A. rubrum* dominated the adult sprout pool and the non-chestnut portion of the pole sprout pool, accounting for 26% of recruits, 91% of which were sprouts. *Oxydendrum arboreum* is also dominated by sprouts (100% sprouts, 2% of recruits), while *Acer pensylvanicum* (22% sprouts, 12% recruits) and *Quercus* (red; 20% sprouts, 2% recruits) were dominated by sapling recruitment. *Liriodendron tulipifera* (45% sprouts, 10% of recruits) and *Robinia pseudoacacia* (50% sprouts, 2% of recruits) were evenly split between sprouts and saplings. Recruitment in small gaps at Coweeta was again simpler than the large gaps and was likewise largely *C. dentata* (29% sprouts, 59% recruits) and *A. rubrum* (67% sprouts, 20% recruits). The remainder of the recruitment in small gaps was made up of only a few individuals of each species in question but the pattern is consistent with their contributions to the large gaps.

TABLE 2. Results of the demographic analysis for the southern Appalachians, USA.

Parameter	Adult survival		Sprouting		Sprout survival	
	Mean	Credible interval	Mean	Credible interval	Mean	Credible interval
Intercept	6.94	4.77 to 9.07	4.71	3.33 to 6.31
Species						
<i>Carya</i>	-0.66	-1.44 to 0.14	-2.04	-3.81 to -0.36	-1.77	-2.82 to -0.70
<i>Cornus florida</i> (COfl)	-3.58	-5.70 to -1.59	-2.48	-5.94 to 0.68	-1.55	-3.99 to 2.11
<i>Liriodendron tulipifera</i> (LItu)	-0.40	-1.05 to 0.25	0.36	-0.96 to 1.78	0.62	-0.61 to 2.04
<i>Nyssa sylvatica</i> (NYsy)	1.72	0.24 to 3.73	-1.75	-3.44 to -0.22	-2.93	-3.96 to -1.85
<i>Oxydendrum arboreum</i> (OXar)	0.68	-0.28 to 1.80	0.09	-1.40 to 1.49	-1.58	-2.58 to -0.50
<i>Quercus montana</i> (QUmo)	-1.54	-2.08 to -1.01	-2.02	-3.50 to -0.47	-0.41	-1.57 to 0.81
<i>Quercus</i> sec. <i>Lobatae</i> (QUrd)	-2.01	-2.61 to -1.41	-1.55	-3.24 to 0.10	-0.68	-2.07 to 0.73
<i>Tsuga canadensis</i> (TSca)	0.089	-1.35 to 2.31	-14.78	-28.58 to -4.01
Other species	6.87	0.94 to 14.10	-1.35	-4.19 to 1.64	0.07	-2.01 to 2.89
Damage						
Bent	-2.91	-5.33 to -0.49	1.12	-1.04 to 3.44
Down	-4.28	-6.48 to -2.04	1.55	-0.88 to 4.07
Snap	-4.93	-7.07 to -2.73	-0.82	-2.79 to 1.51
Uproot	-3.97	-6.13 to -1.76	0.20	-1.68 to 2.31
Other damage	-4.03	-6.32 to -1.77	1.33	-0.90 to 3.81
Adult parameters						
Adult dbh	-0.44	-0.80 to -0.052	-0.12	-0.99 to 0.80	-1.13	-1.68 to -0.57
Adult survival	0.96	-0.05 to 2.08	1.17	0.29 to 2.02
Adult survival lag	-1.29	-2.59 to -0.12
Year						
2002	2.78	0.21 to 5.12
2003	-0.16	-2.76 to 2.12
2004	-2.80	-5.31 to -0.67	-1.21	-1.96 to -0.50
2005	-2.60	-4.93 to -0.61	0.41	-0.59 to 1.49

Notes: Parameter means and 95% credible intervals for logistic regression of damaged tree survival, sprout initiation, sprout survival, and zero truncated Poisson/log-link regression of number of sprouts. Covariates are species, damage type, adult dbh, adult survival, and year. Positive coefficients represent greater adult survival, sprouting, sprout survival, and number of sprouts, respectively. Ellipses indicate parameters that were not included in the most parsimonious model based on a predictive loss metric or species with insufficient sample size at a given demographic stage. The species *Acer rubrum* (ACru; $n = 103$) is used as the omitted reference species for the species effects and thus is defined as 0, and all species coefficients are scaled relative to this one. The sample size, n , is by species and damage class for adult survival and sprouting.

DISCUSSION

The primary goal of this paper was to assess four criteria related to the role that damaged tree survival and sprouting plays in forest gap regenerations. The first two criteria were aimed at assessing whether sprouts are an important pathway for regeneration. Specifically, sprouts must occur in sufficient numbers, compared to other forms of regeneration, and they must have competitive demographic rates. The second pair of criteria assess whether sprouting affects the competitive outcome among species. First and most obviously, there must be ecologically important differences among species in their demographic rates and abundances. Second, these differences must act in a manner that does not merely reinforce existing competitive differences and life-history trade-offs. For example, sprouting is an important pathway for regeneration if the first three criteria are met, but would result in the same composition if the species recruiting by sprouting are the same as those recruiting by seed and advanced regeneration. The results from this long-term and highly replicated experiment in two study regions clearly show that sprouts met all four criteria at both sites during early gap recovery and are likely to affect long-term gap dynamics.

Sprout abundance

The results of the analysis of community pattern clearly demonstrate the importance of the sprout pathway to overall recruitment and species differences. Sprouts constituted a large portion of the recruits at both sites and both gap sizes. Interestingly, there was not a clear gap size effect on the balance between sapling and sprout recruitment, with the large gaps at Duke Forest having a lower sprout percentage than the small gaps, while the large gaps at Coweeta were higher. Overall, sprouting appears to be more important at the Coweeta site. Part of this difference is likely due to the larger representation of non-sprouting (*Pinus*) or poorly sprouting (*Quercus*) species in Duke Forest, but it is unknown how much is also due to inherent differences in climate, soils, and other environmental factors.

In many ways this analysis underestimates the overall impact of sprouting on forest dynamics since it was focused on sprouting in direct response to gap creation and does not include individuals that were sprouts prior to gap formation. Sprouting is very common among saplings (Paciorek et al. 2000; M. C. Dietze and J. S. Clark, *unpublished manuscript*) and seedlings (Del Tredici 2001), with estimates of sprouts ranging from

TABLE 2. Extended.

Sprout number (no. sprouts/tree)		
Mean	Credible interval	<i>n</i>
0.834	0.61 to 1.14	
-1.54	-2.27 to -0.82	25
1.05	0.41 to 1.84	5
-1.26	-1.54 to -0.94	37
-1.39	-2.08 to -0.73	22
0.05	-0.22 to 0.28	22
-0.20	-0.43 to -0.03	56
-0.48	-0.80 to -0.25	38
...	...	6
-1.00	-1.41 to -0.57	7
1.81	1.47 to 2.07	20
0.76	0.47 to 1.06	24
1.57	1.29 to 1.82	61
0.99	0.69 to 1.30	183
0.73	0.40 to 1.08	25
0.009	0.0028 to 0.017	
...	...	
...	...	
...	...	
...	...	
...	...	
...	...	

58% to 79% of the total population. The extreme example of this is *C. dentata*, which has persisted for the last 80 years following chestnut blight (*E. parasitica*) by prolific sprouting (Paillet 1984, 1988; N. L. Christensen, *personal communication*). If one tallies all *C. dentata* ingrowth as belonging to the sprout category, then the estimates of sprout ingrowth at Coweeta jump to 82% and 87% for large and small gaps, respectively. Similarly, much of the sapling ingrowth at Duke Forest attributed to *C. florida* and, to a lesser extent, *L. styraciflua*, appears to have come from stems that originated as root sucker sprouts (M. C. Dietze, *personal observation*). At Duke Forest, 86% of *C. florida* seedlings-sized individuals come from root suckering rather than seed (I. Ibañez, *personal communication*).

The abundance of sprouts observed in this study vs. other ecosystems is dependent upon such factors as the composition and age of the stand; the size, severity, and type of disturbance; and the timing of the disturbance relative to seasonal cycles of nonstructural carbon storage. For example, damaged tree survival and sprouting decline with size and age, a result consistent with previous studies (Prager and Goldsmith 1977, DeCoster 1996, Bellingham and Sparrow 2000, Peterson 2000). Also, sprouting is most successful at intermediate levels of damage, which is consistent with Peterson's (2000) observation of much higher rates of survival and sprouting following a weak tornado than a severe one.

The relative contribution of sprouts also depends upon the presence and persistence of advanced regeneration, seed dispersal, and soil seed banks. In the present study the gaps were large enough that they could not close by lateral ingrowth of the canopy and the falling canopy trees inflicted substantial damage on understory trees, accounting for two-thirds of the stems damaged. In contrast, single-tree gaps often close due to lateral ingrowth; seedling recruitment is minimal (Beckage et al. 2000), and it may take multiple gap cycles for understory trees to reach the canopy (Runkle 1990). In such gaps sprouts are unlikely to recruit directly into canopy, though they may establish an advanced position in the understory.

Competitive ability

With respect to competitive ability, we showed that sprout growth rates are significantly higher than those of saplings while average mortality rates are comparable (Fig. 1). It remains to be seen whether sprout growth and mortality will reach an asymptote at rates equivalent to those seen in recruits from seed. The year and age effects on growth suggest that we are beginning to see a slowing of the rapid sprout growth rates. Critical to the potential of sprouts to establish in the canopy is that sprout mortality rates must remain comparable to undamaged stems as they age (Paciorek et al. 2000). Research from another set of experimental gaps in the southern Appalachians suggests that sprouts can indeed make this transition to long-term dominance, with sprouts dominating net primary productivity over a 17-year study across a large range of gap sizes (Shure et al. 2006). However, evidence from forestry manipulations suggests sprouts may eventually have higher mortality rates, often due to heart rot related to the decomposition of the parent stump (Del Tredici 2001), though it is unclear whether heart rot is as prevalent in natural gaps with uncut stems.

Species differences

Overall, the results of the demographic analysis support the hypothesis that there is sufficient variation among species in order for species to sort by sprouting ability (Fig. 1, Tables 1–3). Species differences were consistent both across sites and with previous research (Burns and Honkala 1990). For example, among the poor sprouters, DeCoster (1996) also observed low sprouting in *Quercus* and *Carya* in the Piedmont, while the higher survival of *Carya* was also seen at Harvard Forest (Cooper-Ellis et al. 1999). Interestingly, the poor sprouting of *Quercus* adults does contrast with the general observation of successful sprouting by seedlings following fire (Burns and Honkala 1990). Eastern pines consistently have low survival, with the interesting exception of *Pinus strobus* (Webb 1989, Cooper-Ellis et al. 1999), while *Nyssa sylvatica* was also observed to have high survival for two Texas sites (Glitzenstein and Harcombe 1988).

TABLE 3. Results of sprout height growth analysis: regression of log-transformed height increment as a function of species, damage class, year, and age for Piedmont and southern Appalachians.

Parameter	Piedmont			Southern Appalachians		
	Mean	Credible interval	<i>n</i>	Mean	Credible interval	<i>n</i>
Intercept	3.90	2.84 to 4.97		3.59	2.15 to 5.01	
Species						
<i>Acer rubrum</i> (ACru)	27	0.30	-1.07 to 1.65	52
<i>Carya glabra</i> (CAgl)	-0.93	-2.56 to 0.68	2	-1.17	-2.75 to 0.39	2
<i>Carya tomentosa</i> (CAto)	-2.12	-3.10 to -1.12	3	0
<i>Carya</i>	0	-0.64	-2.12 to 0.81	5
<i>Cornus florida</i> (COfl)	-0.65	1.46 to 0.15	5	-0.83	-2.76 to 1.10	1
<i>Fraxinus americana</i> (FRam)	-1.24	-1.97 to -0.51	6	0
<i>Liquidambar styraciflua</i> (LlSt)	-0.15	-0.72 to 0.43	11	0
<i>Liriodendron tulipifera</i> (LlTu)	0.52	-0.03 to 1.07	14	0.27	-1.11 to 1.63	20
<i>Morus rubra</i> (MORu)	-0.21	-2.47 to 2.04	1	0
<i>Nyssa sylvatica</i> (NYSy)	0	-0.21	-1.75 to 1.30	3
<i>Oxydendrum arboreum</i> (OXar)	-0.59	-1.35 to 0.18	5	0.46	-0.97 to 1.88	8
<i>Quercus alba</i> (QUal)	-0.79	-2.00 to 0.38	2	0
<i>Quercus coccinea</i> (QUco)	0	-0.48	-2.11 to 1.12	2
<i>Quercus montana</i> (QUmo)	0	-0.43	-1.84 to 0.95	13
<i>Quercus rubra</i> (QRu)	0	-0.52	-1.97 to 0.93	5
<i>Quercus</i> sec. Lobatae (QRld)	0	-1.32	-3.18 to 0.54	1
<i>Robinia pseudoacacia</i> (ROps)	0	-0.89	-2.52 to 0.73	2
<i>Ulmus</i>	-1.06	-2.70 to 0.56	1	0
Damage						
Down	0.12	-0.66 to 0.90		0.43	-0.13 to 0.99	
Snap	-0.01	-0.57 to 0.54		0.50	0.015 to 0.98	
Uproot	0.19	-0.32 to 0.70		0.19	-0.26 to 0.65	
Year						
2003	-0.39	-0.95 to 0.17		0.21	0.02 to 0.39	
2004	-0.37	-1.25 to 0.48		-0.08	-0.26 to 0.10	
Age						
First year	0.00	-0.88 to 0.85		
Second year	0.33	-0.24 to 0.90		
Individual variance	0.38	0.17 to 0.66		0.38	0.31 to 0.47	
Residual variance	0.71	0.55 to 0.92		0.28	0.17 to 0.42	

Notes: The miscellaneous taxa were used as the omitted reference species for the species effects and thus are defined as 0, and all species coefficients are scaled relative to these. Ellipses represent effects not significant by the predictive loss metric or taxa with a sample size that was too small or taxa that were present at one site but not the other.

There is also interesting variation in the qualities that make a species a good sprouter, such as the alternate strategies of prolific sprouting vs. a single dominant leader, and what is limiting species that are poor sprouters (e.g., low sprouting rate but average growth and survival in *Quercus*). Among the top sprouters, *O. arboreum* and *C. florida*, both understory species, had higher sprout survival but lower growth rates than *A. rubrum* and *L. tulipifera*, both canopy species, which is consistent with their different life-history strategies. In terms of overall numbers, species were shown to differ in their reliance on sprouting for regeneration, with sprouting being the dominant pathway for some taxa, such as *A. rubrum* and *O. arboreum* at Coweeta and *L. tulipifera* at Duke Forest, while others, such as *Quercus*, are dominated by sapling regeneration.

Life-history trade-offs

Variation among species in sprouting does not appear to be related to other life-history traits related to successional trade-offs. This is consistent with Paciorek

et al.'s (2000) suggestion that sprouting ability is poor for both the most shade-tolerant and shade-intolerant species at Barro Colorado Island, Panama, while species of intermediate shade tolerance had large variability in sprouting. In angiosperm trees, the development of suppressed buds in a collar around the base of the trunk appears to be the ancestral evolutionary state; angiosperms appear to be almost universally capable of sprouting, though this trait diminishes with age (Wells 1969, Del Tredici 2001, Bond and Midgley 2003). In contrast, conifers lack the dormant root collar buds found in angiosperms (Del Tredici 2001), which explains their poor sprouting regardless of successional status. While there is an expectation for suppressed seedlings and saplings that shade-tolerant species invest more in reserves and thus are more capable of sprouting than intolerant species (Kobe 1997), this does not seem to apply to the sprouts considered, which came from larger stems and were all able to draw on existing over-winter reserves. Based on work primarily in fire-dominated ecosystems, it has been suggested that "sprouters

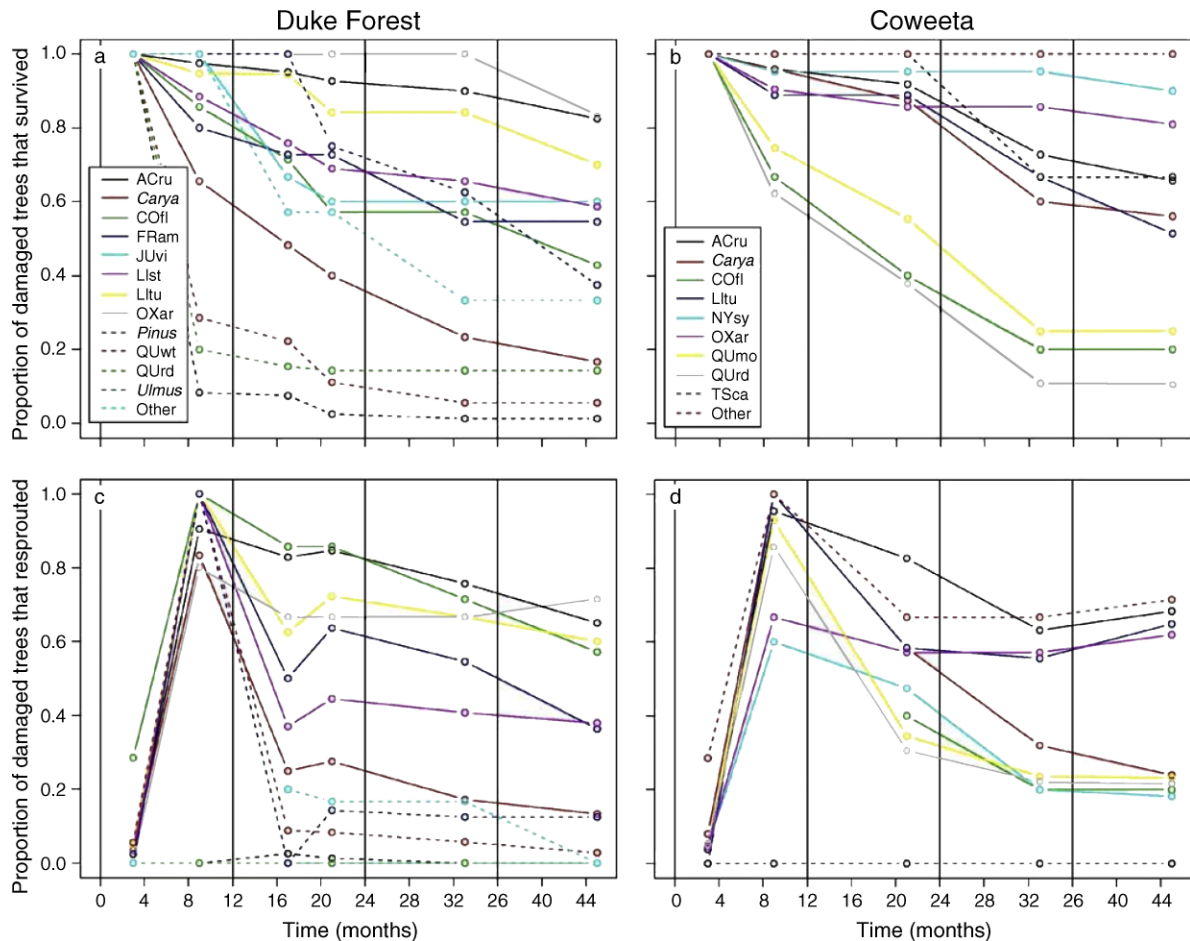


FIG. 2. (a, b) Survival of damaged trees and (c, d) sprout time series by species for (a, c) the Piedmont (Duke Forest) and (b, d) the southern Appalachians (Coweeta). At both sites there is large interspecific heterogeneity in demographic rates. However, the behavior of shared taxa is generally consistent across sites. Species abbreviations and sample sizes are given in Tables 1 and 2. Time is recorded as months since January 2002, the year the gaps were created.

generally have fewer seeds, smaller seedbanks, slower growth and maturation rates (from seeds) and almost always have fewer seedlings and poorer seedling survival than nonsprouters in matched species comparisons” (Bond and Midgley 2001:46). Among the top sprouters in this study the understory species *C. florida* and *O. arboreum* followed this pattern somewhat but *A. rubrum* and *L. tulipifera* clearly did not, both being common in the seed rain, seed bank, and seedling stages. Even though sprouting may be responsible for the majority of gap regeneration for some species, most sprouting in this study was from species that are not dedicated sprouters (i.e., species whose primary mode of regeneration is vegetative and have negligible recruitment from seed, e.g., *Populus tremuloides*). The possible exception to this may be *O. arboreum*, which had strong sprouting but no recruitment from seed at either site (I. Ibañez, *personal communication*) and produces very small seed that requires high light and bare mineral soil to germinate (Horn 1981). The trade-offs in sprouting vs. seed

observed in ecosystems subject to frequent fire, such as chaparral, do not appear to transfer simply to gap dynamics.

Future work

There remains a need to understand the long-term impact of sprouting on forest dynamics and the manner in which forests will respond to interacting changes in both climate and disturbance. In the Southeast in particular there is almost no information from traditional paleoecological studies to understand past responses of vegetation to climate. Furthermore, current forests are dominated by regeneration following agriculture and forestry that ceased 70–100 years ago with very little old-growth forest in which to directly observe long-term gap dynamics. Interestingly, a 75-year study of vegetation change in the Carolina Piedmont (McDonald et al. 2002) did show increases among good sprouters and declines among poor sprouters, though it is unclear whether this is a direct result of sprouting or an indirect

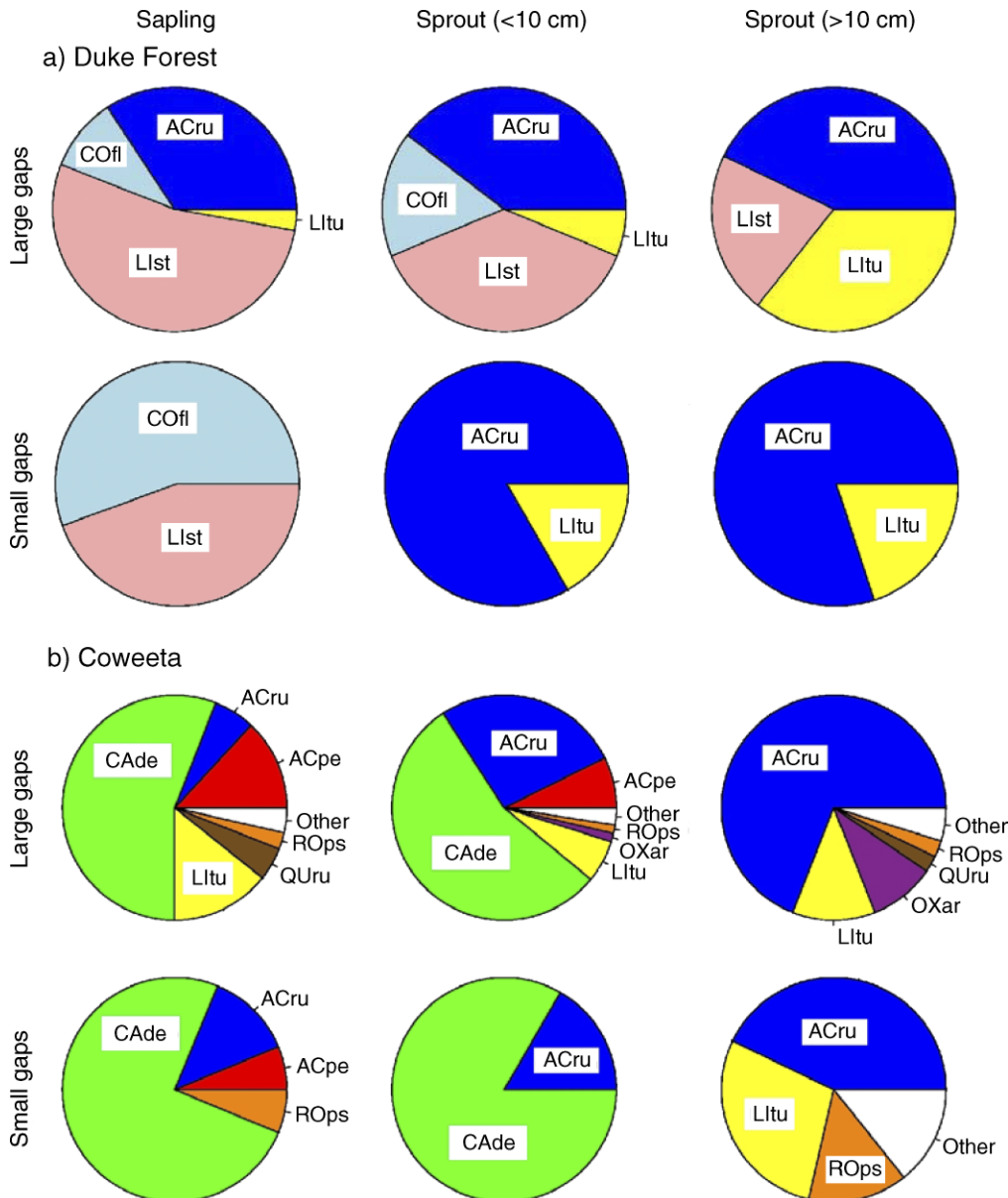


FIG. 3. Relative contribution of species to sapling and sprout recruitment for large (40 m diameter) and small (20 m diameter) gaps in (a) the Piedmont (Duke Forest) and (b) the southern Appalachians (Coweeta). The sprout pool is further subdivided into sprouts off of pole-sized (<10 cm dbh) individuals and adults (>10 cm dbh). At both sites there is a systematic change in the species that are recruiting from each pool. For example, when going from saplings to sprouts off of adults, *Liquidambar styraciflua* decreases while *Liriodendron tulipifera* increases in the Piedmont, while *Acer rubrum* increases in the southern Appalachians. Recruit diversity is much higher in the southern Appalachians. See Tables 1 and 2 for species abbreviations, except for *Castanea dentata* (CAde) and *Acer pensylvanicum* (ACpe).

effect due to other life-history characteristics (e.g., fire or browsing susceptibility). Likewise, such changes may be a part of long-term recovery from agricultural land use legacies or a novel response to climate and land use change.

The best way to answer such questions and to anticipate future change is through the synthesis of detailed demographic studies such as this one. Work is in progress to assess the role of sprouting in both the

long-term trajectory of forest gaps and their sensitivity to initial conditions using an advanced Bayesian forest simulator, scalable landscape inference and prediction (SLIP; Govindarajan et al. 2004). Moreover, increased allocation to storage and belowground processes in response to CO₂ fertilization (Moorcroft 2006) may further favor vegetative regeneration, as has been demonstrated in simple chamber experiments (Hoffmann et al. 2000). Vegetative reproduction may also be

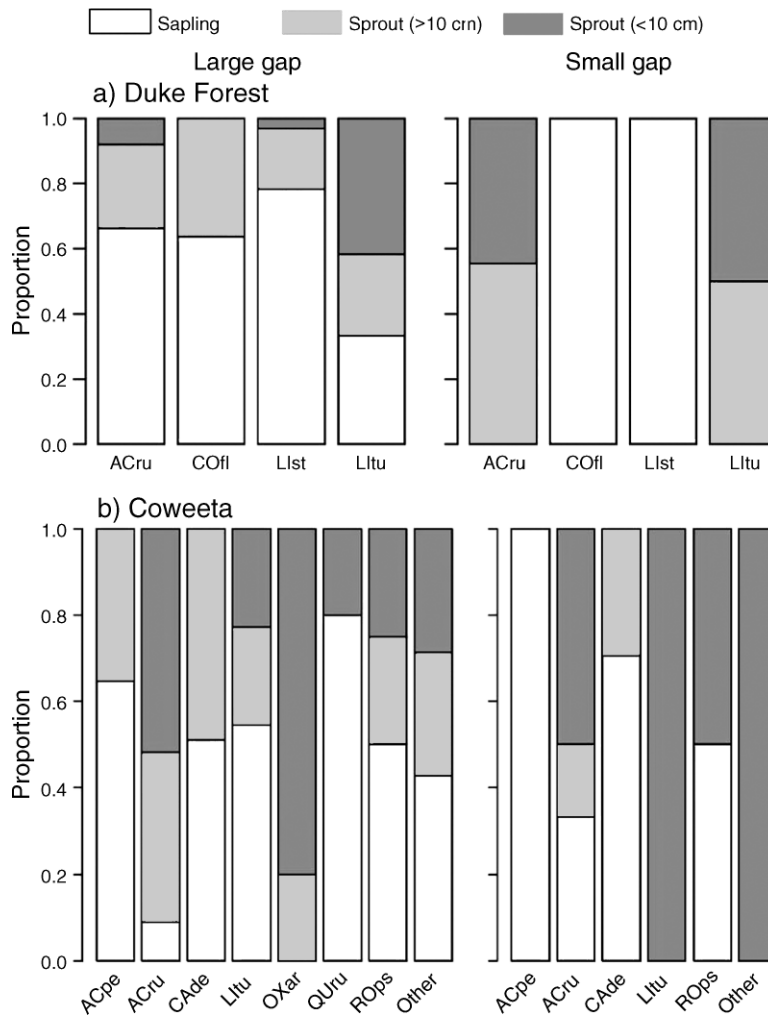


FIG. 4. Proportion of recruitment for each species by gap size that come from each of the three pools of recruits (sprouts off stems <10 cm dbh, sprouts off stems >10 cm dbh, and saplings) for (a) the Piedmont (Duke Forest) and (b) the southern Appalachians (Coweeta). Gaps are either 40 m diameter (large) or 20 m diameter (small). All species except *Oxydendrum arboreum* recruit from both sprout and sapling rather than having a single dedicated recruitment strategy, though the relative importance of sprouting vs. advance regeneration varies among species.

critical for the persistence of species when climate is no longer favorable for regeneration by seed. For example, general circulation models project conditions for the Southeast that may be particularly limiting for seedlings, both among resident species and potential migrants, due to drought mortality (Ibañez et al. 2008).

Conclusions

Traditional gap theory has mostly focused on the role of shade-intolerant species and the potential for disturbance to maintain diversity through a mosaic of patch ages and sizes. However, a growing body of literature suggests that gaps are generally dominated by residual vegetation, such as sprouts and advanced regeneration (Webb 1999, Brokaw and Busing 2000). This has led to some speculation that gap regeneration is merely a reflection of pre-gap conditions and therefore

plays a neutral role in the maintenance of diversity (Hubbell et al. 1999). This view may result, in part, from the practical difficulties in assessing the detailed dynamics of damaged vegetation. Our study not only supports the important role of residual vegetation in gap regeneration, but we also find a strong signal of interspecific differences that are consistent across our two study sites and with the literature. In addition to the direct effect of sprout recruitment, the shade cast by surviving damaged trees has a large impact on the gap light environment, producing much darker gaps and further reducing the opportunities for recruitment of shade-intolerant species (M. C. Dietze, S. Govindarajan, J. S. Clark, P. K. Agarwal, S. Chakraborty, I. Ibañez, S. LaDeau, and M. S. Wolosin, *unpublished manuscript*). Given that most tree species are recruitment limited (Clark et al. 1998, Hubbell et al. 1999), vegetative

reproduction may be an important pathway allowing species to persist and a mechanism for shaping community dynamics.

The combined role of sprouting and sapling regeneration heavily weighs toward a composition based on vegetation already in place at the time of disturbance. This establishes the potential for strong initial condition effects in which sprouting ability would act as a filter determining which species are likely to reach the canopy. This sensitive dependence on initial conditions suggests that regeneration in forest gaps, even if very predictable for an individual gap under known initial conditions, may be less predictable when viewed at the landscape level and easily misinterpreted as neutral. Likewise, even with regeneration influenced by initial composition, gap regeneration is not a lottery process (Hubbell et al. 1999, Brokaw and Busing 2000, Hubbell 2001) because of the differences among species in sprouting ability, as well as the differences in factors that favor recruitment by seed vs. sprout. At a local scale fitness is not equal among species. However, the spatial heterogeneity in the environment, the temporal heterogeneity in climate, and the interactive heterogeneity in disturbance create a complex mosaic that allows species with different life-history strategies to rise and fall in different times and places. Still, changes in disturbance in space and time will produce coherent changes in species composition over long time scales (Clark 1996, Clark and McLachlan 2003).

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APPENDIX

Detailed description of stand selection, plot layout, and experimental gap creation (*Ecological Archives* M078-012-A1).