Early understory succession following catastrophic wind damage in a deciduous forest

Jeff P. Castelli, Brenda B. Casper, Jon J. Sullivan, and Roger Earl Latham

Abstract: Early succession was followed in a 2.5-ha gap created by a severe wind storm in a 5.5-ha fragment of eastern North American deciduous forest. Understory vegetation cover by species, light, soil moisture, and levels of several major nutrients were measured in 1 × 2 m census plots 3 years prior to the disturbance. Coincidentally, the storm felled 50–55% of the trees over a portion of these plots. Vegetation cover by species was again measured in all plots 3 years following the disturbance. Species were grouped by growth form, and group cover values used to examine changes in the composition of the vegetation and to determine whether these changes were correlated with any measured predisturbance environmental variables. Given the size of the gap, shade-intolerant tree species were expected to increase but did not, most likely because of repression by the shrub layer. The main response to the disturbance appeared to occur through reorganization of existing vegetation. The value of predisturbance species cover data and limitations of our sample sizes are discussed.

Résumé : Les auteurs ont suivi le début de la succession dans une ouverture de 2,5 ha, créée par de forts vents, dans un fragment de 5,5 ha de forêt décidue de l'est de l'Amérique du Nord. Le recouvrement des espèces végétales du sous-étage, la lumière, l'humidité du sous-sol et la teneur en plusieurs éléments nutritifs majeurs ont été mesurés dans des placettes de recensement de 1 × 2 m, 3 ans avant la perturbation. Par coïncidence, la tempête a abattu, dans une partie des placettes, de 50 à 55% des arbres. Le recouvrement des espèces végétales a été remesuré dans toutes les placettes 3 ans après la perturbation. Les espèces ont été regroupées en fonction de leur forme de croissance et les valeurs de recouvrement des groupes ont été utilisées pour examiner les changements dans la composition de la végétation et pour déterminer si ces changements étaient corrélés avec une quelconque variable environnementale mesurée avant la perturbation. Compte tenu de la dimension de l'ouverture, on s'attendait à ce que la proportion d'espèces intolérantes à l'ombre augmente, mais cela ne s'est pas produit, très probablement à cause de leur répression par la strate arbustive. La principale réaction à la perturbation semblait être la réorganisation de la végétation existante. Les auteurs discutent de la valeur des données de recouvrement des espèces d'avant la perturbation et des limitations dues à la dimension des échantillons.

[Traduit par la Rédaction]

Introduction

A synthesis of the factors driving the course of forest succession can only come after studying changes following many disturbance events in a variety of forest types. Current conceptual models addressing the progress of forest succession in gaps take into account forest age and size, gap location and size, or some combination of these factors. Forest age and time since last disturbance should affect the dominant tree species and the temporal development or decay of the seed bank (Marks 1974; Peterson and Carson 1996), while the area occupied by the forest and the proximity of the disturbance to a pre-existing forest edge influence immigrant seed dispersal by pioneer species (Peterson and Carson 1996). Gap size may affect the relative success of tree species with different shade tolerances. Larger gaps generally favor shade-intolerant species (Dunn et al. 1983; Brokaw 1985; Whitmore 1989; Everham 1996); however, they also may favor competing shrub species (Ghent et al. 1957; Kneeshaw and Bergeron 1996).

Some attention has also been given to how plant performance responds to spatial heterogeneity in soil characteristics within gaps (Collins and Wein 1998, Kneeshaw and Bergeron 1998). Obvious causes of spatial heterogeneity include exposure of mineral soil through formation of tree fall pits and mounds (Putz 1983), and accumulation of litter (Yih et al. 1991; Molofsky and Augspurger 1992) or organic matter resulting from decay of woody material (Putz 1983; Vitousek and Denslow 1986; Gray and Spies 1997).

We report vegetation changes in a 2.5-ha gap within a fragment of eastern North American deciduous forest. Unlike the majority of studies describing vegetation changes after natural disturbance (but see Dunn et al. 1983), our description is not based solely on differences between intact forest and the disturbed area following the storm. Coincidentally, 2 years prior to the disturbance we collected data on vegetation cover and environmental variables from sampling plots

Received February 19, 1999. Accepted August 9, 1999.

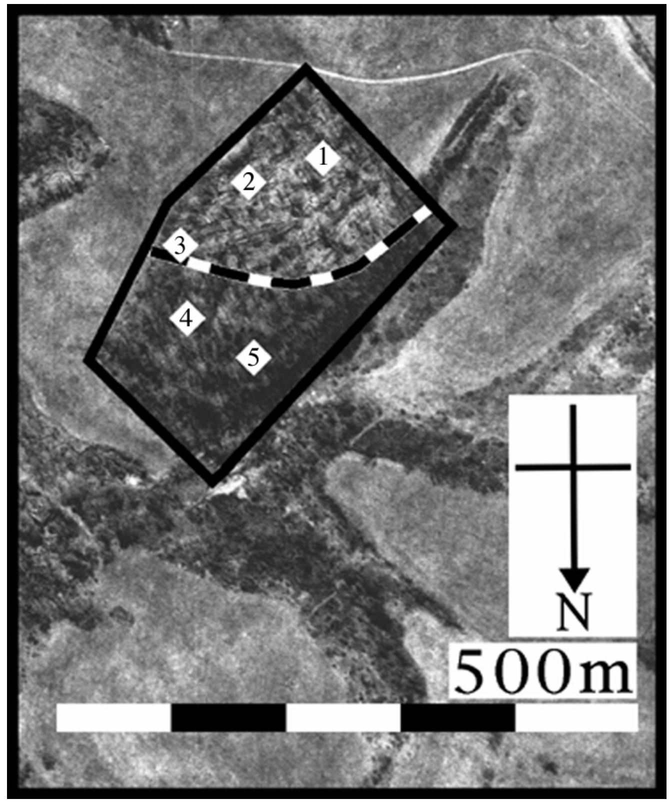
J.P. Castelli,[1] B.B. Casper, and J.J. Sullivan. Department of Biology, University of Pennsylvania, Philadelphia, PA, 19104, U.S.A. e-mails: jpcastel@sas.upenn.edu, bcasper@sas.upenn.edu, and jjsulliv@sas.upenn.edu
R.E. Latham. Department of Biology, Swarthmore College, Swarthmore, PA 19081-1397, U.S.A.
e-mail: rlatham1@swarthmore.edu

[1]Corresponding author.

that were to be located in both areas, and we obtained post-disturbance cover data for these same plots.

Based on both the large gap size (Dunn et al. 1983; Brokaw 1985; Whitmore 1989; Everham 1996) and high mortality among canopy trees (Putz and Appanah 1987; Peterson and Pickett 1991; Everham 1996) we expected pioneer species to become an important component of early successional response. We used our repeated censuses of vegetation cover and our predisturbance measurements of environmental variables to (*i*) describe vegetation changes in the 3 years after the disturbance while taking pre-existing spatial variation in species distributions into account, (*ii*) determine whether spatial variation in environmental variables could explain the spatial patterns of vegetation cover before the disturbance, and (*iii*) determine whether predisturbance spatial variation in environmental variables explained any of the spatial variation in species cover following disturbance, which presumably removed light limitations imposed by the canopy.

Fig. 1. An aerial image of the Laurels forest fragment (center), taken in 1990 one year after the severe storm damage, with surrounding hayfields and abandoned fields. The forest above the broken line was heavily affected by the 1989 storm, with approximately half of the trees >15 cm DBH being felled, while most trees remained standing in the area of forest below the broken line. The five experimental blocks are shown as white squares numbered 1 through 5 consecutively counterclockwise from the highest block.



Methods

The study took place in a 5.5-ha forest fragment located in the "The Laurels," a 300-ha preserve owned by the Brandywine Conservancy in the Piedmont Uplands of southeastern Pennsylvania. The forest occupies a nearly flat hilltop grading to a 20–30% north–northwest slope and is surrounded by hayfields and abandoned old fields (Fig.1). The site was never cultivated, and timber had not been harvested for several decades. Before the disturbance, 17 canopy species and four sub-canopy species occurred within or overtopped the sampling plots, with *Acer rubrum* L., *Fagus grandifolia* Ehrh., *Quercus alba* L., and *Quercus coccinea* Lam. being the most common. Common understory species included *Arisaema triphyllum* (L.) Schott, *Aster divaricatus* L., *Carex pensylvanica* Lam., *Podophyllum peltatum* L., and *Viburnum acerifolium* L.

The November 1989 disturbance occurred in the form of a severe wind downburst that felled 50–55% of the trees >15 cm diameter at breast height (DBH) from a 2.5-ha area. Most trees were uprooted, although some stems of *Nyssa sylvatica* Marshall, snapped off several meters aboveground. Stems of downed trees averaged 32 cm DBH with maximum DBH of 82 cm (B.B. Casper and R.E. Latham, unpublished data). Storm damage was restricted to the hilltop and to wooded areas on nearby hills.

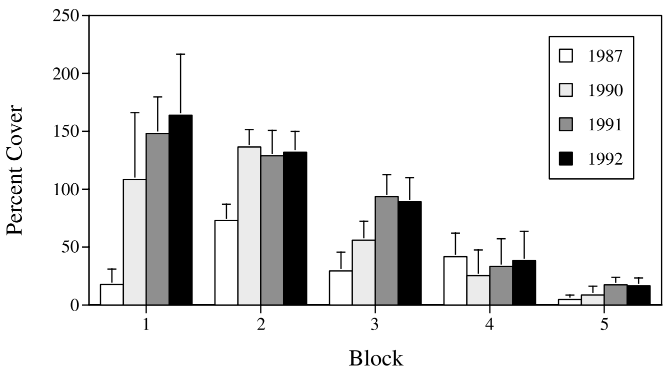
Sampling plots were established in late spring 1987 for a different study (Latham 1990). Plots were clustered in five blocks of five plots situated around single tree fall or tree limb gaps, no larger than 1000 m^2, to encompass small-scale heterogeneity in soil resources and light. Each plot consisted of two 1 × 1 m subplots aligned east and west. Blocks of plots ranged from 6 m to 19 m maximum radius and were separated by at least 22 m. Plot locations were chosen to exclude areas with dense shrubs, thickly deposited leaf litter, exposed bedrock, or boles of canopy trees. By the 1990 census the original gaps had closed considerably and were not readily apparent. The 1989 storm opened the tree canopy over some blocks of plots but not others. The forest remained intact in the vicinity of blocks 4 and 5 (Fig. 1). Blocks 1 and 2 were completely within the disturbed area. Block 3 was located in the forest edge, but was close enough to the blowdown to experience considerably increased solar radiation.

Soil nutrients, pH, and moisture were measured in all plots during the 1987 growing season. Soil samples were collected from 10 points spaced at least 10 cm apart within a 600 cm^2 area in the center of each subplot. Samples were taken to a depth of 25 cm using a 19-mm tubular soil sampler. The 10 cores from each subplot were mixed, air-dried, and forced through a 2-mm sieve. The fraction <2 mm was used for nutrient and pH analyses following procedures described in Latham (1990). Relative soil moisture was measured weekly from April to October as electrical resistance using gypsum blocks buried to a depth of 20 cm in the center of each subplot.

Understory vegetation censuses were conducted in early summer 1987 and again in August 1990, 1991, and 1992, following the November 1989 disturbance. Plant cover by species was measured in each subplot by dividing the 1 × 1 m area into 10 × 10 cm squares using a string grid and estimating cover to the nearest 10% in each square. The 1987 and 1990 censuses included only the herbaceous species and woody members of the understory <1.0 m in height, but in 1991 and 1992, as this layer of vegetation grew in height, we no longer applied the height criterion. Instead, we relied on data from previous censuses to eliminate plants that would have been taller than the understory (>1.0 m) at the 1990 census. Perimeter squares were excluded to minimize edge. Soil and vegetation data from each pair of subplots were combined and reported on a per-plot basis. The August census dates may have biased cover estimates for spring ephemerals.

Species were classified into groups by growth form according to Gleason and Cronquist (1991): annuals, herbaceous perennials, shrubs and trees. Tree species were first examined as a group but then further separated into three shade-tolerance categories, modified from

Fig. 2. Average plot percent cover of all species in each block in 1987, 1990, 1991, and 1992 (n = 5 plots: error bars are 1 SE). The blowdown occurred in 1989. Blocks 1 and 2 were located completely in the blowdown, block 3 was located on the edge of the blowdown, and blocks 4 and 5 were located completely within the undisturbed forest.



ratings used by Baker (1949). The two most abundant post-disturbance species based on frequency and cover, *Rubus allegheniensis* Porter (a shrub) and *Phytolacca americana* L. (an herbaceous perennial), hereinafter referred to as *Rubus* and *Phytolacca*, were examined separately to avoid potential biasing of growth form group responses. Combined group cover data were used to compare mean percent cover per plot for each of the five blocks in all four census years.

To determine if vegetation differences existed in 1987 between blocks that were to remain fully within the forest (4 and 5) and blocks that would fall completely in the blowdown (1 and 2), mean percent cover values of vegetation groups were compared using ANOVA. Plot mean values were nested within block (random effect), and area (blowdown or intact forest) was treated as a fixed effect. When data were not normally distributed after arcsine transformation, percent cover was ranked among plots and ANOVA performed on the ranks. Percent cover of annuals were compared using a Mann–Whitney U test because even ranked data could not be normalized, thereby eliminating block as a factor in this analysis.

The percent cover of each vegetation group in postdisturbance years was compared between these same plots using ANCOVA with predisturbance cover values as a covariate. This procedure identified vegetation differences that developed between the intact forest and blowdown independent of pre-existing differences. Analysis of the covariate examined whether postdisturbance cover of a group was related to its abundance in 1987. Data were transformed as for the 1987 analysis, with a Mann–Whitney U test again being used for annuals. Separate analyses were conducted for the 1990, 1991, and 1992 census years. All statistical analyses were performed using Statistica for the Macintosh (StatSoft 1984–1997). A Dunn–Sidák correction was applied where appropriate to correct the type I error rate for multiple analyses, i.e., the nine different species groups. (For α = 0.05, α' = 0.006 when n = 9.)

To examine if predisturbance composition of vegetation was related to environmental conditions, Pearson's product moment correlations were calculated between levels of environmental variables and percent cover of the different vegetation groups in 1987. Because we were also interested in whether environmental conditions before the disturbance were related to the composition of the vegetation after the disturbance, we performed partial correlation analyses between levels of environmental variables in 1987 and percent cover of the different species or species groups each year after the disturbance. Partial correlation analyses included data from plots in blocks 1, 2, and 3 located within or near the blowdown. Since results for all three postdisturbance years are similar, only results for the first and last years, 1990 and 1992, are reported here. The use of partial correlations essentially removes the effects of any correlations between environmental variables and vegetation cover already existing in 1987. We felt that spatial autocorrelation due to blocks could be ignored in these analyses because of lower variation among blocks than within blocks in one-way ANCOVAs analyzing the effect of block on the coverage of each species group with the environmental variables as covariates. A Dunn–Sidák correction was again applied to correct the type I error for multiple analyses.

Results

By far the largest increases in percent cover between the 1987 and 1990 censuses occurred in blocks 1 and 2 located fully within the blowdown. The smallest increases occurred in blocks 4 and 5, still fully within the intact forest (Fig. 2). At the 1987 census, mean cover per plot had been low in block 1 (17.7%) but relatively high in block 2 (72.8%). Cover again increased in 1991 in blocks 1 and 2 but not as much as between 1987 and 1990, while cover in the other three blocks remained about the same. Between 1991 and 1992, percent cover changed little for any block although vegetation continued to grow in height

In 1987, herbaceous perennials (excluding *Phytolacca*) were the most common vegetation group followed by annuals, shrubs, and shade-tolerant trees (Table 1). Only plots located in the area that would become the blowdown contained any annuals. The two most common species in the blowdown, *Rubus* and *Phytolacca* were present in 7 and 11 of the 15 plots, respectively, before the disturbance occurred. Each species occupied a maximum of 12 blowdown plots in the years afterwards. Both were uncommon in the plots that were to remain in the forest, occurring in only one (*Rubus*) and two plots (*Phytolacca*) in 1987. The ANOVA conducted on the 1987 data (Table 1) showed that those plots that would be located within the blowdown had higher percent cover of tree seedlings (when all categories of tree species were combined; $p < 0.03$) than did plots in the intact forest, but the difference was not significant with the Dunn–Sidák correction. The blowdown plots also tended toward higher percent cover of shade-tolerant tree seedlings, shade-intolerant tree seedlings, annuals, and *Rubus* ($0.05 < p < 0.09$). The lack of significant difference in cover of annuals, despite their absence from the forest, is undoubtedly due to the small number of plots in which they occurred.

The disturbance resulted in percent cover increases for several vegetation groups (Table 1). In 1990, the first season after the disturbance, percent cover of annuals, *Phytolacca*, *Rubus*, other shrubs, and shade-intolerant tree seedlings all increased in the blowdown plots, with *Rubus* and *Phytolacca* eventually dominating. Annuals declined in 1991 and further still in 1992, while cover of *Phytolacca* continued to increase in 1991 but declined the next year. Shrubs, shade-tolerant tree seedlings, and *Rubus* continued to increase through 1992.

The ANCOVA conducted on post disturbance (1990–1992) data (Table 1) showed that the percent cover of most vegetation groups increased in the blowdown plots. In 1990, shade-intolerant tree seedlings, annuals, and *Rubus* tended toward higher percent cover in the blowdown than in the intact forest ($p < 0.05$), but none was significant with the

Table 1. Mean percent cover and standard error of vegetation groups in plots located fully within the blowdown (blocks 1 and 2) compared with plots located within the intact forest (blocks 4 and 5) in 1987, 1990, 1991, and 1992.

Vegetation group	Year	Blowdown	Forest	*F* or *U* statistic	*p*	Covariate *p*
Annuals[a]	1987	1.12 (1.08)	0.00 (0.00)	35.00	0.068	na
	1990	13.35 (7.98)	0.00 (0.00)	30.00	**0.031**	na
	1991	3.43 (3.21)	0.05 (0.05)	39.50	0.256	na
	1992	0.14 (0.10)	0.13 (0.13)	46.00	0.627	na
Perennials[b]	1987	16.84 (5.19)	6.99 (2.99)	0.19	0.707	na
	1990	15.05 (7.18)	1.96 (0.57)	2.26	0.272	0.722
	1991	7.82 (7.66)	4.08 (1.14)	0.13	0.757	0.472
	1992	15.05 (8.65)	3.75 (2.35)	73.10	**0.013**	0.603
Shrubs[b]	1987	5.62 (1.94)	2.34 (1.05)	2.40	0.262	na
	1990	15.44 (5.89)	4.19 (2.49)	0.10	0.448	**0.000 003**
	1991	21.20 (7.84)	5.00 (2.47)	199.20	**0.006**	0.063
	1992	25.15 (10.62)	5.52 (2.52)	2.70	0.234	0.123
All trees[b]	1987	7.18 (1.82)	3.13 (1.06)	34.84	**0.028**	na
	1990	17.42 (4.70)	3.33 (1.80)	2.50	0.272	0.160
	1991	25.85 (8.37)	6.34 (2.30)	3.57	0.194	0.524
	1992	37.71 (15.64)	6.33 (1.95)	1.44	0.354	0.235
ST trees[c]	1987	6.24 (1.95)	1.28 (0.51)	10.19	0.087	na
	1990	7.50 (3.76)	1.68 (1.31)	0.61	0.516	0.688
	1991	11.30 (6.49)	3.48 (1.76)	0.21	0.695	0.311
	1992	26.22 (14.22)	3.02 (1.36)	0.13	0.754	0.085
SIT trees[b]	1987	0.52 (0.34)	0.78 (0.44)	9.53	0.091	na
	1990	9.65 (3.64)	0.80 (0.43)	38.10	**0.024**	0.937
	1991	14.30 (4.43)	1.37 (0.68)	23.15	**0.042**	0.394
	1992	10.59 (3.50)	1.74 (0.83)	2.21	0.277	0.840
MST trees[c]	1987	0.41 (0.15)	0.98 (0.53)	3.02	0.224	na
	1990	0.27 (0.19)	0.73 (0.32)	881.80	**0.001**	**0.005**
	1991	0.25 (0.17)	1.49 (0.70)	1461.67	**0.0006**	0.228
	1992	0.21 (0.21)	1.56 (0.68)	12.21	0.073	**0.011**
Rubus[c]	1987	1.34 (0.70)	0.01 (0.01)	18.06	0.051	na
	1990	28.92 (9.49)	0.00 (0.00)	70.96	**0.014**	**0.029**
	1991	37.10 (8.71)	0.03 (0.03)	31.24	**0.031**	0.067
	1992	48.40 (12.60)	0.05 (0.05)	28.09	**0.034**	0.064
Phytolacca[c]	1987	1.58 (0.79)	0.48 (0.47)	4.95	0.156	na
	1990	23.80 (6.35)	0.80 (0.54)	3.20	0.216	**0.044**
	1991	35.63 (8.31)	1.06 (0.60)	9.02	0.095	0.094
	1992	18.65 (7.31)	1.43 (0.92)	2.07	0.287	0.053

Note: Comparisons between blowdown and forest plots were analyzed by nested ANOVAs (df = 1, 2) in 1987. Comparisons in 1990–1992 were analyzed by nested ANCOVAs with 1987 cover values as covariates (df = 1, 2). Significant p values ($p < 0.05$) are given in boldface; Dunn–Sidák correction for nine analyses per year is $p < 0.0057$ for $p < 0.05$.). ST, shade tolerant; MST, intermediate shade tolerant; SIT, shade intolerant; *Rubus*, *Rubus allegheniensis*; *Phytolacca*, *Phytolacca americana*. na, not applicable.

[a]Annuals were analyzed by a Mann–Whitney U test between areas for each year.

[b]Values were arcsine transformed prior to analysis.

[c]Values were ranked and analysis performed on the ranks.

Dunn–Sidák correction for multiple analyses. In 1991, mean percent cover of shade-intolerant tree seedlings, shrubs and *Rubus* tended toward higher percent cover in the blowdown than in the intact forest ($p < 0.05$), but only the values for shrub cover ($p < 0.006$) met significance under the Dunn–Sidák correction. In 1992, mean percent cover of *Rubus* and perennials (excluding *Phytolacca*) tended toward higher percent cover in the blowdown than in the intact forest ($p < 0.05$) but, again, not significantly so when corrected for multiple analyses. However, tree seedlings of intermediate shade tolerance had lower percent cover in the blowdown plots than in the intact forest plots in 1990 and 1991 even after the correction ($p < 0.001$).

Few new species established after the disturbance. Of four species of annuals, only *Erechtites hieraciifolia* (L.) Raf. was absent from the study area before the disturbance, and it was unimportant afterwards, appearing in only one plot. Only 10 species first appeared in the 1990 census or later, and none was ever common. A few other species that first appeared in the blowdown plots after the disturbance were found in the forest plots before the disturbance but contributed little cover. Changes in the percent cover of shrubs in

1990, intermediate shade tolerant trees in 1990 and 1992, *Rubus* in 1990, and *Phytolacca* in 1990 were related ($p < 0.05$) to their initial 1987 covariate cover values (Table 1), but only shrubs and intermediate shade-tolerant trees in 1990 met significance under the Dunn–Sidák correction ($p < 0.0057$).

Environmental variables explained little of the variation in percent cover for different vegetation groups in 1987. To show trends in the data, we list correlations with $p < 0.02$ but recognize that none was significant with the Dunn–Sidák correction ($|r| > 0.703$ for $p < 0.005$ when $n = 9$). Percent cover of all tree seedlings (combining the shade-tolerance categories) was positively correlated with relative soil moisture ($r = 0.63$) and light ($r = 0.62$). Percent cover of shade-tolerant tree seedlings was correlated with light ($r = 0.70$), percent cover of shade-intolerant tree seedlings was correlated with mineralizable nitrogen ($r = 0.56$), and percent cover of annuals was correlated with extractable phosphorus ($r = 0.63$).

Likewise, no significant partial correlations were found between the environmental variables measured in 1987 and vegetation group cover values in 1990 when significance levels were corrected for multiple comparisons. The following are partial correlations with $p < 0.05$: percent cover of annuals in 1990 was negatively correlated with soil moisture ($r = -0.62$) and positively correlated with calcium ($r = 0.67$); percent cover of all tree species (combined across shade-tolerance categories) in 1990 was negatively correlated with pH ($r = -0.53$); percent cover of intermediate shade-tolerant tree seedlings in 1992 was positively correlated with mineralizable nitrogen levels ($r = 0.58$); and percent cover of *Rubus* in 1992 was negatively correlated with soil pH ($r = -0.52$) and extractable potassium ($r = -0.51$).

Discussion

Contrary to our expectations, the early response of this forest to the severe wind damage consisted predominantly of the reorganization of existing vegetation and not through the recruitment of early successional species (Marks 1974; Webb 1986). Our conclusion is based on several observations.

(1) Few new species established, and those that did were unimportant in percent cover. Three of the four species of annuals were already present with low percent cover prior to the disturbance.

(2) The two most abundant species throughout the blowdown, *Rubus* and *Phytolacca*, occurred in many census plots before the disturbance. While new seedlings of both species did appear, much of the increased cover came from vegetative growth of existing plants (including extensive clonal growth by *Rubus*).

(3) *Prunus pensylvanica* L.f., a common pioneer species in disturbed hardwood forests farther north and at higher elevations (Marks 1974), was absent from the blowdown plots entirely. The ecologically similar *P. serotina* Ehrh. was present but not abundant, occurring in nearly the same plots before the storm as afterwards.

(4) Based on the size and severity of the disturbance we also expected greater overall importance of shade-intolerant trees than was observed (Dunn et al. 1983; Brokaw 1985; Putz and Appanah 1987; Whitmore 1989; Peterson and Pickett 1991; Everham 1996). The trend toward shade-intolerant trees exhibiting greater cover in the blowdown than in the forest in 1990 and 1991 disappeared by 1992.

The results of our study do not fit neatly into any existing conceptual model of early forest succession. The forest could be considered an old forest, since it consisted of mature trees of uneven sizes. An advanced age would argue for a depleted seed bank of pioneer species (Peterson and Carson 1996). On the other hand, it is also a small forest embedded within a matrix of hayfields, small abandoned fields, and vegetated fence rows, which could serve as seed sources for annuals or longer lived pioneer species. Several factors may have contributed to the observed lack of recruitment.

(1) Litter may have been rearranged by the storm, but it was not disturbed as much as it would have been if the gap had resulted from fire or clear-cutting. Areas outside our census plots where mineral soil was exposed did display higher seedling densities of pioneer species, particularly *Phytolacca* (B.B. Casper, personal observation). Studies of seed rain at the site showed that seeds of some hayfield species did disperse into the edge of the blowdown, but they did not usually germinate, even in flats of potting soil (Hyatt 1996).

(2) Shading from the rapidly developing shrub layer, especially *Rubus*, may additionally have repressed recruitment, especially for shade-intolerant tree species (Ghent et al. 1957; Kneeshaw and Bergeron 1996).

(3) The location of our plots in areas that had been small gaps prior to the disturbance may have biased our findings of reorganization over recruitment by making our plots areas of high seedling density before the disturbance (Spurr 1956). However, such gaps are common in this and other mature forests.

Given our restricted sample size we were not able to provide evidence that environmental parameters measured prior to the disturbance explained any significant amount of variation in vegetation composition after the disturbance. However, we feel that we were able to illustrate the importance of considering pre-existing vegetation structure. By knowing the composition of the understory prior to the disturbance we avoided incorrectly assigning some differences between the blowdown and the forest to the disturbance per se. The use of predisturbance cover values as a covariate in our statistical analyses generally reduced postdisturbance differences between the two areas. This was even true for *Phytolacca* and *Rubus*, the most common postdisturbance species, because they had existed as suppressed individuals in many blowdown plots, but were absent from nearly all plots that were to remain within intact forest. Likewise, three of the four annual species within the blowdown were already present and restricted to that area in 1987. Had that information not been available, colonization by dispersing seed or germination from a long-buried seedbank would have been likely interpretations. The fact that half of the vegetation groups in 1990 were related to predisturbance cover values in 1987 suggests that stand history may have restricted postdisturbance successional dynamics.

We realize that our ability to document pre-existing spatial heterogeneity in vegetation was fortuitous and that predisturbance data are not always possible to obtain. However, studies of forest gap succession should make some attempt to partition spatial differences in vegetation into that existing before the disturbance and that caused by the disturbance. Continued studies of vegetation structure before and after disturbance in a variety of forests are necessary if we wish to understand how forest gap successional processes are influenced by stand history.

Acknowledgements

We thank Jeff Shaman and Elizabeth Diener for technical assistance, Peter Petraitis and Warren Ewens for statistical advice, and the Brandywine Conservancy for access to the study site.

References

Baker, F.S. 1949. A revised tolerance table. J. For. **47**: 179–181.

Brokaw, N.V.L. 1985. Gap-phase regeneration in a tropical forest. Ecology, **66**: 682–687.

Collins, B., and Wein, G. 1998. Soil resource heterogeneity effects on early succession. Oikos, **82**: 238–245.

Dunn, C.P., Guntenspergen, G.R., and Dorney, J.R. 1983. Catastrophic wind disturbance in an old-growth hemlock–hardwood forest. Can. J. Bot. **61**: 211–217.

Everham, E.M., III. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. **62**(2) 113–185.

Ghent, A.W., Fraser, D.A., and Thomas, J.B. 1957. Studies of regeneration in forest stands devastated by the spruce budworm. For. Sci. **3**: 184–208.

Gleason, H.A., and Cronquist, A. 1991. Manual of vascular plants of the northeastern United States and adjacent Canada. New York Botanical Garden, Bronx.

Gray, A.N., and Spies, T.A. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology, **78**: 2458–2473.

Hyatt, L.A. 1996. Seed bank dynamics in a temperate deciduous forest. Ph.D. dissertation. University of Pennsylvania, Philadelphia.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888–898.

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

Latham, R.E. 1990. Co-occurring tree species change rank in seedling performance with small-scale resource variation. Ph.D. dissertation. University of Pennsylvania, Philadelphia.

Marks, P.L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monogr. **44**: 73–88.

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

Peterson, C.J., and Carson, W.P. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Can. J. For. Res. **26**: 45–52.

Peterson, C.J., and Pickett, S.T.A. 1991. Tree fall and resprouting following catastrophic windthrow in an old-growth hemlock–hardwoods forest. For. Ecol. Manage. **42**: 205–217.

Putz, F.E. 1983. Tree fall pits and mounds, buried seeds, and the importance of soil disturbanace to pioneer trees on Barro Colorado Island, Panama. Ecology, **64**: 1069–1074.

Putz, F.E., and Appanah S. 1987. Buried seeds, newly dispersed seeds, and the dynamics of a lowland forest in Malaysia. Biotropica, **19**: 326–333.

Spurr, S.H. 1956. Natural restocking of forests following the 1938 hurricane in central New England. Ecology, **37**: 443–451.

StatSoft. 1984–1997. Statistica for the Macintosh. StatSoft, Tulsa, Okla.

Vitousek, P.M., and Denslow, J.S. 1986. Nitrogen and phosphorus availability in tree fall gaps of lowland tropical rainforest. J. Ecol. **74**: 1167–1178.

Webb, S.L. 1986. Windstorms and the dynamics of two northern forests. Ph.D. thesis, University of Minnesota, Minneapolis.

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

Yih, K., Boucher, D.H., Vandermeer, J.H., and Zamora, N. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. Biotropica, **23**: 106–113.