CHANGES IN SOUTHERN APPALACHIAN CANOPY TREE GAPS SAMPLED THRICE

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Abstract. Species responses to disturbance (mortality of dominant individuals within a community) influence many aspects of that ecological community. To trace the responses of vegetation to one particular type of disturbance, I sampled vegetation in 250 canopy gaps in 1976/1977, 1983, and 1990/1991. These gaps were located in three sites in the southern Appalachians of eastern North America: Great Smoky Mountains National Park, Walker Cove Research Natural Area, and Joyce Kilmer Wilderness Area. Each gap was sampled thrice for sapling composition (stems ≥1 cm in diameter at breast height). Additional measurements included the extension growth of border trees into the gap, recent mortality rates of border trees, deterioration rates of gap makers that had been standing dead in earlier samples, and the composition of understory plots.

The mean extension (branch) growth of border trees was 12 cm/yr, with slower growth by longer branches. Gap makers that had been tall stumps tended to deteriorate, although 35% stayed intact over the 14 yr of the study. Border-tree mortality averaged 0.60%/yr, with higher rates for larger stems and with much interspecific variation.

Stem density of saplings in gaps increased during the first sampling interval and decreased during the second as self-thinning counteracted increased establishment. Basal area increased during both sampling intervals. The death of border trees increased basal area per unit gap area.

The four main species (*Acer saccharum, Tsuga canadensis, Fagus grandifolia,* and *Halesia carolina*) showed different patterns of correlation to gap size and age. Species in general showed more correlations with gap age for the first sample than afterwards; gap size was more consistently related to species importance. Species patterns also were affected by the presence or absence of border-tree mortality. The stands studied seem nearly at equilibrium. Some small changes are likely to occur, but the species present dominated all size classes: gap saplings, border trees, other canopy trees not related to gaps, and understory saplings. Species differed in their relative growth rates in the understory and in gaps of different sizes. Species also differed in their survival rates in the understory and in the canopy.

Key words: Acer saccharum; *border trees; canopy gaps;* Fagus grandifolia; Halesia carolina; *long-term studies; old-growth forests; repeated disturbance, impacts on vegetation/species; southern Appalachians (USA); tree species, relative growth and survival;* Tsuga canadensis.

INTRODUCTION

Many studies have documented the response of species to gaps formed in the forest canopy by the death of a large branch, a whole tree, or a small group of trees (Watt 1947, Bray 1956, Denslow 1980, Brokaw 1985, Runkle 1985, Canham 1988, Stewart et al. 1991, Brown and Whitmore 1992, McClure and Lee 1993, Hiura 1995, Orwig and Abrams 1995, Lertzman et al. 1996, Ogden et al. 1996, van der Maarel 1996, Goldblum 1997). Only a few studies have followed changes in such gaps over time (Runkle 1984, 1990*a*, Young and Perkocha 1994, Kupfer and Runkle 1996, Poulson and Platt 1996, Valverde and Silvertown 1997). Sapling composition and population structure change after gap formation but it is not known how long those changes

persist. It also is not known how a new disturbance near the former gap affects the sapling layer.

In this paper I summarize changes occurring in 250 gaps sampled thrice. I initially sampled the gaps in 1976 and 1977 in old-growth stands of Great Smoky Mountains National Park of Tennessee and North Carolina, Joyce Kilmer Wilderness Area of western North Carolina, and Walker Cove Research Natural Area near Asheville, North Carolina (Runkle 1981, 1982). Most of these gaps were resampled in 1983 (Yetter and Runkle 1986, Runkle and Yetter 1987). In 1990 I resampled gaps from the Great Smoky Mountains National Park and Joyce Kilmer. In 1991 I resampled Walker Cove.

The goal of the 1990/1991 resample was to quantify several aspects of gap dynamics. (1) Changes in lengths of canopy tree branches extending into the gap were used to refine previous estimates of this mechanism of gap closure. (2) I estimated the deterioration rates of gap makers and the death and injury rates of trees bor-

dering gaps. (3) I measured changes in vegetation in gaps. The number, basal area, and species composition of saplings were related to gap size and age. (4) The impact of repeat disturbance (border tree mortality some time after initial gap formation) was determined for gap vegetation in general and for individual species. (5) Differences in species composition among saplings in gaps, trees bordering gaps, stems creating gaps, and the background vegetation were used to estimate changes likely to occur in the forests and to identify characteristics responsible for the relative success of important tree species.

METHODS

Field methods

All of the areas studied were mid-elevation sites (766–1236 m elevation, latitude 35–36° N) chosen to avoid obvious human impacts. Dominant species included sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), American beech (*Fagus grandifolia*), mountain silverbell (*Halesia carolina*), white basswood (*Tilia heterophylla*), yellow buckeye (*Aesculus octandra*), and yellow birch (*Betula allegheniensis*). Fires were rare to absent. Most wind damage in the study areas was localized with relatively few stems being affected by any one event. I avoided areas in which rhododendron (*Rhododendron maximum*) formed a dense shrub layer and areas in which American chestnut (*Castanea dentata*) had been abundant and which therefore still were recovering from the chestnut blight. Several diseases and pests are likely to increase tree mortality in the future but have not influenced my results: dogwood anthracnose was not reported in the region before 1988, beech bark disease was not reported in the Great Smoky Mountains National Park before 1993, the European gypsy moth and hemlock woolly adelgid have not yet arrived in my study areas (SAMAB 1996). Further site details are given in Runkle (1981, 1982, 1985) and Runkle and Yetter (1987).

For some analyses I subdivided my data into the same three relatively homogeneous groups as in Runkle (1981). Roaring Fork is a mid-elevation cove (mean 929 m) in the Great Smoky Mountains with much hemlock. Albright Grove–Kalanu Prong are mid-elevation coves (mean 985 m) in the Great Smoky Mountains with substantially less hemlock. Walker Cove is a high elevation cove (mean 1213 m) with no hemlock or silverbell.

Gaps were relocated using my original field notes as described in Runkle and Yetter (1987). Some gaps were not relocated, usually because the small coves in which they were found were not adequately described in the field notes. If the starting point for a transect was well described usually all gaps on that transect were relocated. Size or other characteristics of individual gaps did not influence whether a gap would be resampled.

The extension growth of canopy-tree branches into gaps was measured as follows. In 1976 I measured the diameter at breast height (dbh; 1.4 m) and extension into the gap of 384 border trees, usually recording the information along lines between pairs of trees found on opposite sides of the gap. In 1983 I relocated 247 trees and in 1990 I relocated 274 trees, using the previously recorded information to identify them, and again measured their dbh and extension into the gap along the same lines. Differences were used to calculate extension growth over the 7-yr or 14-yr periods. I excluded from the analysis differences that seemed likely to be in error—much higher or lower than other readings. Such results could have occurred if I measured the wrong trees or measured distances along the wrong lines. The values obtained were of net lateral growth, i.e., the total horizontal spread of the branches, not the total branch length from beginning to end.

Gap makers (stems whose death or injury created the gap studied in 1976/1977) were reevaluated for injury class and stump height. The following injury classes were recognized: living but injured, snag (standing dead), tall stump (broken with height ≥2.5 m), low stump (height <2.5 m), partly uprooted, and uprooted.

The canopy trees bordering each gap originally were recorded only as the number of stems of different species for most gaps, with dbh or other characteristics sometimes noted. In 1983 I recorded the death of trees originally by the gap, presumably among trees originally recorded as border trees. In 1990–1991 I recorded the dbh, approximate position around the gap, and injury status (same as for gap makers, with an additional class of no injury) of each stem, matching the species composition as closely as possible to my original notes. For some analyses gaps were divided into four groups determined by their history of border-tree mortality. For the first group border-tree mortality was not recorded either for 1983 or for 1990/1991. For the second group border-tree mortality was recorded only in 1983. By 1990/1991 the mortality recorded for this group was no longer obvious. For the third group mortality was recorded in both resamples. This group includes gaps in which two or more episodes of mortality had occurred and gaps affected by a single episode of mortality which had occurred before 1983 and was still obvious in 1990/1991. For the fourth group border-tree mortality was recorded only in 1990/1991.

Woody vegetation within gaps was resampled using the same techniques as earlier (Runkle 1981, 1982, Runkle and Yetter 1987). The dbh, number, and species of all woody stems ≥1 cm dbh were recorded for the ground area extending outward to the bases of canopy trees bordering the gap. In some cases it was difficult to know whether stems near gap borders had been measured previously or not. Where possible, questionable stems were checked against earlier field notes, looking for potential matches based on size and species identification.

TABLE 1. Diameter growth and lateral crown growth of stems bordering gaps between sample years in three mid-elevation old-growth southern Appalachian canopy-tree gaps.

Parameter	Time period	Mean	1 SD	No. of trees
Annual diameter growth (mm)	1976–1983	2.7	3.2	249
	1983–1990	3.9	4.0	205
	1976–1990	3.2	2.6	290
Annual lateral crown growth (cm)	1976–1983	18	14	247
	1983–1990	5	20	158
	1976–1990	12	11	274

For each gap I identified four ''potential successors'' (cf. Stewart et al. 1991), defined as the tallest under-story stem in each quarter of the gap. The species, dbh, and approximate height of these stems were recorded.

To estimate the species and size-class composition of the forest in general I used strip transects (10 m wide by 90–350 m long) in which I recorded all stems ≥ 1 cm dbh. Most of these transects were sampled in 1983; one was sampled in 1990. In 1983 I also sampled a 600-m^2 plot along Ekaneetlee Creek in the Great Smoky Mountains National Park in an area where a tornado had occurred ~1975.

The point-centered quarter method had been used to quantify canopy composition of transects in 1976/1977. Trees ≥ 25 cm dbh were sampled along the same transects used to sample gaps. The relative density values of those canopy trees were compared to other estimates of species composition (saplings in and out of gaps, border trees, gap makers).

Species nomenclature follows Little (1979).

Analytical methods

Most statistical tests were done using the SAS statistical package (Joyner 1985). The significance level for statistical tests was set at $P \leq 0.05$, unless otherwise noted. The values for r^2 in Fig. 2 come from the Cricket Graph computer package (version: CA-Cricket; Computer Associates International, Malvern, Pennsylvania, USA); the fits were based on averages values for each year. The original estimate of gap size (expanded gap, based on the distance to the bases of trees bordering the gap, Runkle 1982) was used for statistical analyses

TABLE 2. Lateral growth of border trees into gaps by species, based on data from 1976 through 1990.

Species	No. of stems	Lateral growth (cm/yr)	
		Mean	1 SD
Acer rubrum	8	18	15
Liriodendron tulipifera	8	17	11
Halesia carolina	58	14	12
Acer saccharum	45	13	15
Fagus grandifolia	27	11	7
Aesculus octandra	15	11	11
Tilia heterophylla	11	10	9
Tsuga canadensis	74	10	9
Betula alleghaniensis	12	10	9
Magnolia acuminata	8	10	12

involving gap size. Gap size is not constant: it increases if border trees die and decreases if their branches grow into the gap. However, I used the original area for several reasons. It should be correlated with later gap area in the absence of border-tree mortality so the significance of relationships involving either value of area should be similar. It also is of interest how long gap processes are likely to be affected by the gap area measured at one time. ''Gap age'' was the age in 1976/1977 plus the additional number of years to the later sampling periods. Age in 1976/1977 was estimated using sapling extension-growth rates, the condition of the canopy tree whose death made the gap, the number of years that had passed since saplings were bent by the fallen gap maker, etc. (Runkle 1982, 1992).

Mortality rates were calculated as exponential decays:

$$\text{Average annual mortality rate} = 1 - (S/N_0)^{(1/y)}$$

where S = number of survivors, N_0 = original number of stems, and y = number of years between samples (Runkle 1990b, Sheil et al. 1995).

Species compositions were compared using percentage similarity, defined as

$$\text{PS} = \sum \min(p_a \text{ or } p_b)$$

where PS is the percentage similarity value, p_a and p_b are the relative densities (as percentages) for a given species in the two samples, a and b, being compared, and the summation is over all species (Whittaker 1975).

RESULTS

Gap closure by lateral growth of border trees

The net lateral growth rate of trees bordering gaps was 12 cm/yr for 274 trees from 1976 to 1990 (Table 1). The observed growth rate decreased from 18 cm/yr between 1976 and 1983 to 5 cm/yr between 1983 and 1990. This decrease occurred despite an increase in mean diameter growth from 2.7 mm/yr between 1976 and 1983 to 3.9 mm/yr between 1983 and 1990. The mean extension growth rates for the most common species varied only from 10 to 18 cm/yr (Table 2); this variation was not significant (ANOVA, $P = 0.24$).

Net lateral growth from 1976 to 1990 (in centimeters) was negatively related to extension distance in 1976 (in meters):

TABLE 3. Injury-class transitions for gap makers.

	Injury class 1990/1991							
Injury class 1976/1977	1	2	3	4	5	6	Sum	%
1) Alive and injured	22	2	13	15	2	8	62	14
2) Snag (standing dead)	2	6	4	13	0	4	29	6
3) Stump, height ≥2.5 m	2	0	42	75	0	5	124	28
4) Stump, height <2.5 m	0	0	0	145	0	0	145	32
5) Partly uprooted	0	0	0	0	31	0	31	7
6) Uprooted	0	0	0	0	0	58	58	13
Sum	26	8	59	248	33	75	449	
%	6	2	13	55	7	17		

Extension growth 1976–1990

= 19.9 − 2.2 × Branch length in 1976

($R^2 = 0.13$, $P < 0.0001$, $n = 274$ trees). That is, longer branches grew more slowly than shorter branches, with each meter of length resulting in ~2.2 cm less extension growth per year.

The fates of gap makers and border trees

Gap makers deteriorated over the approximately 14-yr interval between the initial and latest sampling dates (Table 3). Living but injured stems died at a mean annual rate of 7%/yr, usually breaking but sometimes uprooting. This mortality rate is much higher than for canopy trees in general, most of which are not noticeably injured (Table 4). Most snags and tall stumps were reduced in height, although 35% stayed intact (i.e., had not broken off to <2.5 m and had not uprooted) even after 14 yr. Species differed in their rates of deterioration. The percentages of snags and tall stumps that did not deteriorate to smaller size categories were 42% for hemlock ($n = 45$ snags and tall stems), 39% for American beech ($n = 38$), 36% for sugar maple ($n = 14$), 26% for white basswood ($n = 19$), and 25% for mountain silverbell ($n = 24$). These species values

were not significantly different from each other ($\chi^2 = 0.83$, df = 4, $P = 0.93$).

Most trees bordering gaps in 1976 were healthy in 1990/1991 but ~8% had died to form stumps and "uproots" (Table 4). Mortality rates increased steadily with tree size, from 0.35%/yr for stems <25 cm dbh (diameter at breast height) to 1.41%/yr for stems ≥100 cm dbh. The fraction of trees dying and leaving tall stumps also increased with increased dbh. Mortality varied with species, from none for yellow-poplar and 0.10%/yr for yellow buckeye to 0.97%/yr for white basswood and 1.18%/yr for American beech. Border trees were significantly smaller than gap makers (Kolmogorov-Smirnov test, $n = 449$ for gap makers; critical difference = 0.077 for $P = 0.01$, observed difference = 0.096) (Fig. 1).

Changes in gap vegetation

Mean stem density in gaps increased from 1976/1977 to 1983 and then decreased through 1990/1991 (Table 5). Basal area steadily increased during both time intervals. All these changes were statistically significant. Larger gaps had significantly more stems but fewer stems per area than smaller gaps. Larger gaps also had significantly higher basal area per gap although basal

TABLE 4. Border-tree mortality and injury distribution.

	No.	Mean dbh (cm)	Percentage in injury class†						Mortality rate (%/yr)
			0	1	2	3	4	6	
Species									
Fagus grandifolia	288	47	85	0	<1	5	6	4	1.18
Tilia heterophylla	141	61	87	0	0	7	6	0	0.97
Tsuga canadensis	423	67	91	0	2	4	2	<1	0.63
Betula alleghaniensis	97	48	92	0	2	5	1	0	0.61
Halesia carolina	375	44	93	<1	<1	3	2	1	0.49
Acer saccharum	327	63	95	0	0	3	1	1	0.33
Aesculus octandra	147	59	99	0	0	<1	<1	0	0.10
Liriodendron tulipifera	56	88	100	0	0	0	0	0	0.00
Sizes									
<25 cm dbh	84	⋯	95	0	0	1	4	0	0.35
25.0–50 cm dbh	806	⋯	95	<1	<1	3	1	1	0.39
50.0–75 cm dbh	670	⋯	92	<1	<1	4	3	1	0.59
75.0–100 cm dbh	304	⋯	88	0	1	5	4	1	0.87
≥100 cm dbh	144	⋯	82	0	2	9	6	1	1.41
All stems	2008	58	92	<1	<1	4	3	1	0.60

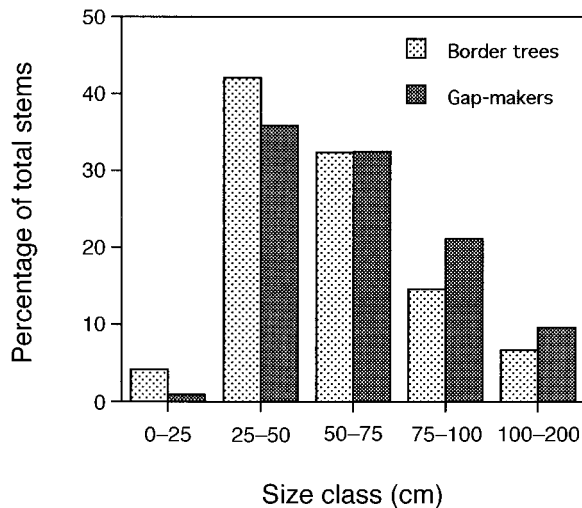†For injury-class definitions see Table 3; "<1" also implies ">0."

FIG. 1. Size (diameter at breast height) distribution of border trees and gap makers.

area per gap area did not vary significantly with gap size. Older gaps had significantly more stems in 1976/1977 than younger gaps and increased less in stem density through 1983. Basal area increased more in larger gaps.

These trends were consistent for smaller, more homogeneous study areas (Table 6). Although Roaring Fork, Albright Grove–Kalanu Prong, and Walker's Cove varied significantly in many parameters the overall pattern of change over time was consistent. In all three areas density increased from 1976/1977 to 1983 and then decreased while basal area steadily increased.

Basal area per gap area was significantly affected by the deaths of trees bordering gaps, but stem density was not (Table 7). Gaps were divided into four groups determined by recorded border-tree mortality in 1983 and 1990/1991, as described earlier. The four groups did not differ significantly in age in 1976/1977. Larger gaps were more likely to be affected by border-tree mortality in 1983 than were smaller gaps, probably because they had more border trees than did smaller gaps. Stem density did not vary significantly among the four groups in any year although gaps with border-

tree mortality had higher densities in 1990/1991 than gaps without border-tree mortality ($P = 0.18$). Basal area per gap area did not vary significantly in 1976/1977 between gap disturbance groups ($P = 0.41$) but varied in the two later samples ($P < 0.01$), with the highest values for gaps in which border-tree mortality was recorded in both resamples.

The size structure of gap sapling populations changed both over time for the same sampling period and between sampling periods (Fig. 2). Changes depended on whether the gap had been affected by the death of a border tree. The density of stems in gaps increased through age 7–12 (yr), by which time seedlings establishing after gap formation had grown ≥1 cm dbh. The 1983 sample had the highest values overall because more of its gaps were in those ages. After age 12 or so the number of stems decreased to low levels (equivalent to the levels in new gaps) in gaps without new disturbance. If a new disturbance did occur, however, stem numbers were maintained at about the same high values, with some tendency for a decline in the oldest gaps even with new disturbance. Basal area per gap area did not change as strongly with gap age (see also Table 5). The greatest values were found for gaps in the 1990/1991 sample that had some border-tree mortality (Fig. 2). Basal area in those gaps reached values of 10–15 m^2/ha, 2–3 times as high as in newly formed gaps.

Thirty-eight species were found in at least one gap and 16 species were found in >10% of the gaps sampled (Table 8). However, American beech, eastern hemlock, sugar maple, and mountain silverbell together totalled 70% of density and 80% of basal area in 1990/1991. The relative density or relative basal area of most species varied significantly with gap size or age for at least one sampling period, although the relationship changed from sample period to sample period.

Age was more often related to relative importance values (both relative density and relative basal area) in 1976/1977 than in later samples (Table 8). Species showing some tendency to be more important in young gaps (for at least one sampling period and at least one parameter) tended to be species that can reach larger sapling sizes under a closed canopy: hemlock, basswood, and buckeye. Species showing some tendency

Table 5. Changes in gap sapling density and basal area for stems ≥1 cm.

Parameters	Years			Changes	
	1976/1977	1983	1990/1991	1976/1977 to 1983	1983 to 1990/1991
No. of stems/gap	40.6 (+a, +s)	55.0 (+s)	43.3 (+s)	14.4 (−a, +s)*	−11.7 (−s)*
No. of stems/100 m^2	15.2 (+a, −s)	20.1 (−s)	16.7 (−s)	4.8 (−a)*	−3.4*
Basal area (cm^2)/gap	1452 (+s)	1965 (+s)	2360 (+s)	513 (+s)*	395 (+s)*
Basal area (cm^2)/100 m^2	534	689	809	155 (+s)	120*

Notes: The table also reports correlations with gap age and size: (+a) or (−a) indicates a significant ($P \leq 0.05$) positive or negative correlation with gap age; (+s) or (−s) indicates a significant ($P \leq 0.05$) positive or negative correlation with gap size. Values followed by an asterisk are significantly ($P \leq 0.05$) different from zero (*t* test).

TABLE 6. Differences in gap characteristics among three Great Smoky Mountain stands varying in species and elevation.

Year	Parameters	Albright–Kalanu	Roaring Fork	Walker Cove	Model P
1976/1977	Gap age (yr)	6.4	5.7	5.3	0.68
1976/1977	Expanded gap area (m^2)	296	253	284	0.56
1976/1977	No. of stems/100 m^2	13.5 (a)^A	18.8^B	18.6^B	0.01
1983	No. of stems/100 m^2	17.0^A	26.3^B	25.1^B	<0.01
1990/1991	No. of stems/100 m^2	16.4 (−s)	17.6 (−s)	19.6	0.38
1976/1977	Basal area (cm^2)/100 m^2	622^B	516^{AB}	371^A	0.03
1983	Basal area (cm^2)/100 m^2	835^B	584^A	477^A	<0.01
1990/1991	Basal area (cm^2)/100 m^2	1033^B	635^A	528^A	<0.01
	No. of gaps	71	37	33	

Notes: The table also reports correlations with gap age and size: (+a) or (−a) indicates a significant ($P \le 0.05$) positive or a negative correlation with gap age; (+s) or (−s) indicates a significant ($P \le 0.05$) positive or negative correlation with gap size. Values followed by the same superscript upper-case letter are not significantly ($P \le 0.05$) different from each other (analysis of variance with Tukey's test).

to become more important as the gaps aged included mostly species able to grow rapidly in the light: black cherry (*Prunus serotina*), yellow-poplar, silverbell, red maple (*Acer rubrum*), striped maple (*Acer pensylvanicum*), and beech.

Gap size was more consistently related to species relative values (both relative density and relative basal area) than was gap age for all three sampling periods (Table 8). All species that showed a significant relationship with gap size were more important in large gaps, including silverbell, striped maple, yellow birch, yellow buckeye, red maple, white ash (*Fraxinus americana*), black cherry, and yellow-poplar.

Most species changed significantly in relative density or basal area between one or both sampling periods (Table 9). For the most part those changes were not related to the size or age of the gap.

Several species showed significantly different changes in relative density from 1976/1977 to 1990/1991 between groups of gaps defined by border-tree mortality (Table 10). Hemlock increased in gaps with no border-tree mortality but decreased where mortality had been noted in 1983 or in both later samples. Black cherry increased only in the gaps where mortality was noted in both samples. Beech decreased except where mortality was recorded in 1983 but not later. Yellow-poplar, silverbell, yellow birch, and yellow buckeye all increased most where border-tree mortality was re-

corded in 1990/1991, although the differences were not statistically significant.

Species composition comparisons

All measures of species composition (based on relative density) except for the tornado area agree closely on the relative ranking of the major species (Table 11). The percentage similarity with the point-centered quarter-canopy data ranges only from 72% to 91% (excluding the tornado area). Sugar maple, hemlock, beech, and silverbell dominate all categories, with basswood, buckeye, and yellow birch being the primary associates.

The species composition of border trees was most similar (91%) to the point-centered quarter-canopy trees. Differences in species composition may be due to small differences in location and to slightly different size criteria: the point-centered quarter trees were set ≥25 cm dbh; some border trees were smaller. The main difference between the data sets was that border trees contained fewer beech.

Gapmaker composition was 80% similar to the canopy trees. Higher abundances for gapmakers than canopy trees, indicating recent high mortality, were found for beech and, to a lesser degree, for hemlock and basswood. Lower abundances of gap makers, indicating low mortality, were found for sugar maple, buckeye, and silverbell.

TABLE 7. Differences in gap characteristics between gaps affected or not by border-tree mortality.

		Samples in which border-tree mortality was noted				
Year	Parameters	Neither	Only in 1983	Both	Only in 1990s	Model P
1976/1977	Gap age (yr)	6.5	7.8	5.2	6.0	0.27
1976/1977	Expanded gap area (m^2)	263	357	354	269	0.03
1976/1977	No. of stems/100 m^2	15.1	14.4	14.8	16.4	0.79
1983	No. of stems/100 m^2	19.0	19.0	21.0	21.0	0.72
1990/1991	No. of stems/100 m^2	15.2	16.5	17.7	18.8	0.18
1976/1977	Basal area (cm^2)/100 m^2	508	446	554	604	0.41
1983	Basal area (cm^2)/100 m^2	619^A	525^A	852^B	718^{AB}	<0.01
1990/1991	Basal area (cm^2)/100 m^2	667^A	646^A	1065^B	882^{AB}	<0.01
	No. of gaps	113	22	62	53	

Notes: Values followed by the same superscript upper-case letter are not significantly ($P \le 0.05$) different from each other (Tukey's test). Sometimes, although the whole model had $P \le 0.05$, no two values differed significantly with $P \le 0.05$.
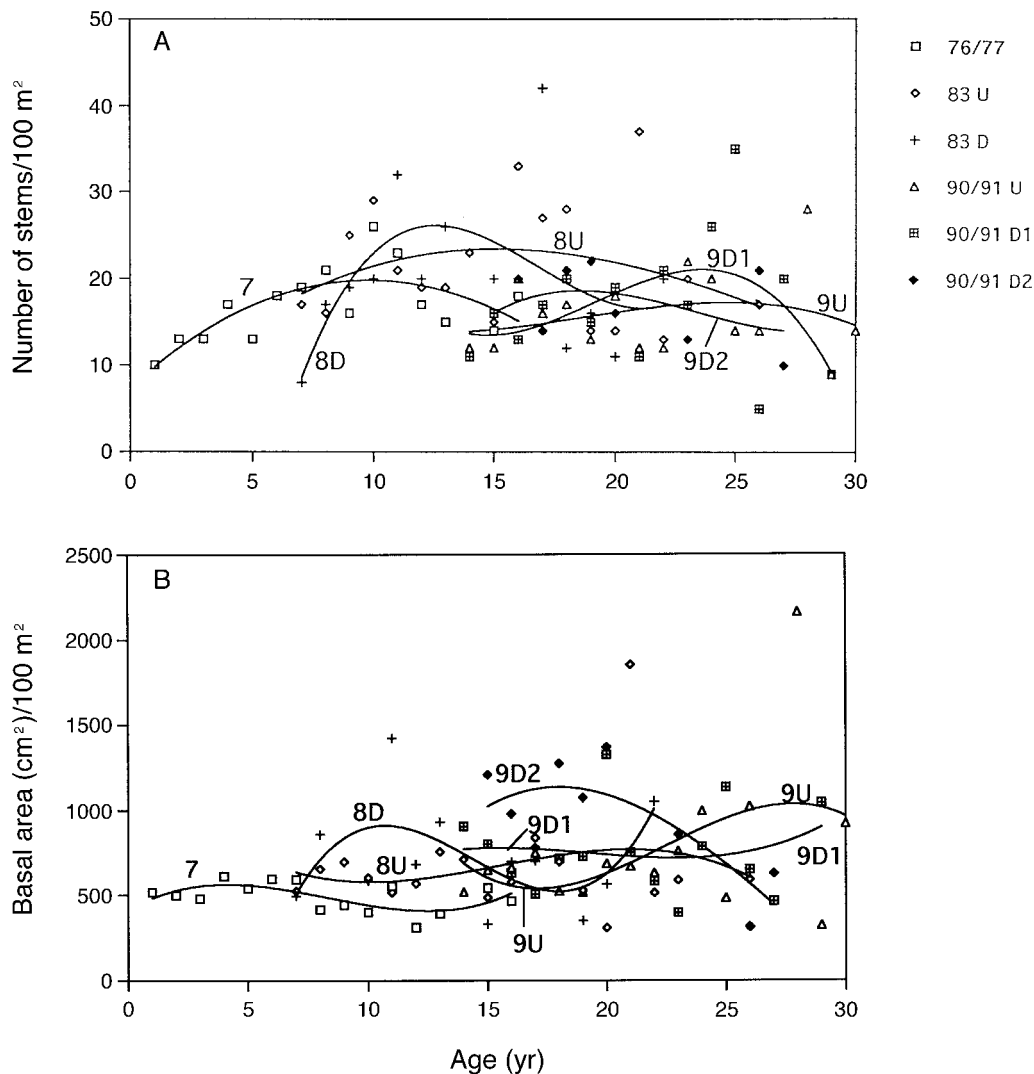
FIG. 2. Changes in gap vegetation over time, in gaps varying in sample dates and disturbance histories. Lines are fitted as third-order polynomials. Key code: 76/77 = original 1976/1977 values; 83 U = gaps with no border-tree mortality noted in 1983; 83 D = gaps with border-tree mortality noted in 1983; 90/91 U = gaps with no border-tree mortality noted in either 1990/1991 resample; 90/91 D1 = gaps with border-tree mortality noted in only one sample; 90/91 D2 = gaps with border-tree mortality noted in both samples. Years were reduced to a single digit representing the decade in the figure. (A) Number of stems per 100-m² gap area. Polynomial fits: (r^2) = 53% for 76/77, 8% for 83 U, 32% for 83 D, 6% for 90/91 U, 23% for 90/91 D1, 17% for 90/91 D2. (B) Basal area of stems per 100-m² gap area. Polynomial fits: r^2 = 40% for 76/77, 5% for 83 U, 35% for 83 D, 20% for 90/91 U, 3% for 90/91 D1, and 60% for 90/91 D2.

Gap sapling composition was similar for all three sample periods. Sugar maple was the only major tree species for which 1990/1991 relative abundance of gap saplings was greater than the relative abundance of canopy trees. Lower sapling abundance, indicating possible future decreases in canopy abundance, was found for silverbell, basswood, and buckeye. Among the taller saplings (potential successors), hemlock showed the highest probability of increase (high ratio of sapling percentage to canopy percentage) and sugar maple the highest probability of decrease.

Sapling composition of the forest in general was sim-

ilar both to the canopy composition and to gap sapling composition—in these forests dominated by small gaps, few opportunities for light-demanding species exist. Larger saplings were heavily dominated by hemlock; otherwise the composition of stems 1–5 cm dbh was very similar to that of stems 1–24 cm dbh. Sugar maple was more common in gaps than in the forest as a whole. Beech and silverbell were less common in gaps. Hemlock was found at about the same level.

The tornado plots indicate that major disturbances produce forests quite different from those formed primarily by gaps. Tornado areas were characterized by

very high values for yellow-poplar and high values for silverbell and white ash. Sugar maple, hemlock, and beech were noticeably rare or absent.

DISCUSSION

Gap closure by lateral growth of border trees

The values obtained in this study for lateral growth into gaps of the crowns of bordering trees (12 cm/yr average) were lower than I had found earlier (Runkle and Yetter 1987; 18 cm/yr average). Part of the difference may be due to the slower growth of longer branches as given above. Branches still surviving after 14 yr also may preferentially be those that were growing more slowly than branches in general: Young and Hubbell (1991) found in tropical gaps that crown growth was preferentially into gaps; Young and Perkocha (1994) found that the resulting asymmetry increased the rates of tree and branch fall into gaps. Their results suggest that too rapid crown growth may lead to gap opening, not closure. This decreased growth rate in older gaps may allow more saplings in gaps to reach the canopy because the canopy gap should remain open longer than anticipated earlier (Runkle and Yetter 1987).

The rates computed from the 1990 survey are similar to others in the literature. Trimble and Tryon (1966) measured 7–9 cm/yr for West Virginia hardwoods. Hibbs (1982) measured 8–14 cm/yr for New York hardwoods and hemlock. Ogden et al. (1991) measured 8 cm/yr for montane forests in New Zealand. Valverde and Silvertown (1997) found canopy openings to decrease by a consistent 21%/yr, implying that the distance closed decreased each year.

The fates of gap makers and border trees

Only 20% of the 1976/1977 gap makers were uprooted (Table 3). Since some snags uproot over time (Table 3) the proportion of gap makers originally uprooted would have been smaller. This figure (<20%) is similar to that of other mesic primary forests, including coastal western hemlock (Lertzman et al. 1996: 24% uprooted), tropical rainforests in French Guiana (Van der Meer and Bongers 1996: 36% uprooted) and the Ivory Coast (Jans et al. 1993: 18% uprooted), a hemlock stand in New York and a sugar maple-beech stand in Ohio (Runkle 1991: 14% and 31% uprooted, respectively). Far lower rates of uprooting can occur under some situations: Clinton et al. (1993) reported only 4% uprooting of oaks in West Virginia following a severe drought. The fraction of trees uprooted varies with site and soil conditions (Jans et al. 1993). These results suggest that many trees may disturb adjacent saplings as they die standing then gradually deteriorate. The ''gradual'' gaps formed by gap maker disintegration are likely to have different effects than ''sudden'' gaps (Krasny and Whitmore 1992).

The density of snags and tall stumps in these forests is set by the balance between formation rates of newly dead stems and the deterioration of the taller dead stems to lower sizes. Rates of deterioration and decay can be rapid (Onega and Eickmeier 1991), implying that formation must be a more-or-less continual process. Old-growth mesic forests in the central parts of eastern North America tend to have ≥10 snags/ha that are ≥10 cm in diameter at breast height (Parker 1989, Runkle 1991, Martin 1992). Northeastern forests may have substantially more (e.g., 40–100 standing dead stems/ha for hemlock and northern hardwood stands, including second-growth stands; Tritton and Siccama 1990). Mortality rates needed to generate that steady state (10 snags/ha) can be calculated as follows. From the data presented here, after 14 yr it is necessary to replace 65% of snags and tall stumps. Such dead stems make up 34% of gap makers. So the total number of gap makers required to generate replacement snags (here, including tall stumps) is expressed as

$$[(0.65 \text{ disappearance}) \times (10 \text{ snags/ha})]$$
$$\div [(0.34 \text{ snags/gap maker}) \times (14 \text{ yr})]$$
$$= 1.4 \text{ new gap makers} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}.$$

Given ~250 trees/ha (Runkle 1979, Parker 1989, Martin 1992) this rate can be obtained by a canopy-tree mortality rate of ~1.4/250 = 0.56%/yr. That value agrees closely with the amount actually measured (Runkle 1982). Therefore, the richness in structural complexity of dead stems associated with old-growth forests (Davis 1996) appears to result from a balanced dynamic equilibrium.

The death of canopy trees bordering gaps is more common and probably has greater impact on gap saplings than does gap-maker deterioration. Despite the large number of gaps (46%) affected by border-tree mortality, the mortality rate of such trees seems no higher than canopy-tree mortality in general. The overall mortality rate of 0.60%/yr for border trees is slightly lower than overall mortality rates for those stands (Runkle 1982, Runkle and Yetter 1987). This rate may be somewhat lower than reality—I may have missed some border trees from 1976/1977 that died before I resurveyed gaps in 1990/1991. The high rate of repeat gap disturbance still is due more to the large number of canopy trees that border gaps (8.1 trees/gap here) than to high disturbance rates. This conclusion is somewhat surprising, given the tendencies of border trees to extend their crowns into gaps and to preferentially fall into gaps (Young and Hubbell 1991, Young and Perkocha 1994). These tendencies may be counteracted, however, by the tendency of border trees to be smaller than gap makers (Fig. 1). Border trees may be smaller than either gap makers or canopy trees in general because of the tendency for trees to become increasingly regularly dispersed as they get larger (Runkle 1990b): competition presumably drives large stems to be further apart than random, with the interstices of

TABLE 8. Relative density and basal area of species found in ≥10% of gaps for the three sampling years.

Species	Frequency in gaps (%)	Relative density		
		1976/1977	1983	1990/1991
Acer saccharum	87	16	22	22
Tsuga canadensis	84	18 (−a)	16	21
Fagus grandifolia	78	24 (+a)	21	17
Halesia carolina	75	12 (+s)	11 (+s)	10 (+s)
Acer pensylvanicum	58	5 (+a, +s)	5 (+s)	6 (+s)
Betula alleghaniensis	55	4	4 (+s)	4 (+s)
Tilia heterophylla	55	3	4	4 (−a)
Aesculus octandra	38	2 (+s)	2 (−a, +s)	2 (−a, +s)
Acer rubrum	36	1 (+a, +s)	1	1 (+s)
Fraxinus americana	28	1 (+s)	<1 (+s)	<1 (−a, +s)
Rhododendron maximum	27	1	2 (+a)	2
Magnolia fraseri	22	<1	1	1
Prunus serotina	22	<1 (+a, +s)	<1 (+s)	<1
Ostrya virginiana	21	4	3	2
Liriodendron tulipifera	19	<1 (+a, +s)	<1 (+s)	<1 (+s)
Magnolia acuminata	12	<1	<1	<1

Notes: The table also reports correlations with gap age and size: (+a) or (−a) indicates a positive or a negative correlation ($P \leq 0.05$) with gap age; (+s) or (−s) indicates a positive or negative correlation with gap size.

the forest filled by smaller stems. Smaller trees have lower mortality rates than larger ones (Table 4).

Following the death of border trees the gap saplings increase in both density (although with $P = 0.18$) and basal area ($P < 0.01$) per area (Table 7, Fig. 2). Some species also change in relative importance depending on whether or not border trees have died (Table 10). These results support the theoretical argument by Moloney and Levin (1996) that an important part of a disturbance regime is the spatial and temporal autocorrelation of disturbances, i.e., their proximity to each other in time and space.

Changes in gap vegetation

Gap age and size affected long-term gap dynamics differently. Gap age was significantly related to the number of stems and to species importance (both relative density and relative basal area) in the 1976/1977 samples but had few significant relationships with vegetation characteristics from later samples (Tables 5 and 8). Presumably, over time other events, including death of border trees and deterioration of gap makers, become more important in determining the vegetation of gaps, as has been found for gaps in a beech–sugar maple woods in Ohio sampled 5 times (Kupfer and Runkle 1996). Gap size more permanently influenced the vegetation, with significant relationships in all three sampling periods.

The same species were dominant in all three sampling periods, although some small significant changes in relative importance occurred (Tables 8 and 9). In this sense the gaps were more similar to those of coastal British Columbia, where a limited set of shade-tolerant species dominate all gaps (Lertzman 1992), than those of oak–pine stands in Arkansas, where tolerant species increased and intolerant ones decreased over time (Cain and Shelton 1995).

Species patterns

Acer saccharum.—Sugar maple was found at relatively small sizes both in the understory and in gaps (Table 11). It also increased in density both in gaps and the understory from the 1970s to the 1990s (Table 11). Its relative density in gaps was greater than in the understory (Table 11). Its increase in relative density in gaps was mostly between 1976/1977 and 1983, with no significant relationships to gap size or age (Tables 8 and 9). Its increase did not differ significantly with border-tree mortality (Table 10). As a canopy tree it had a relatively low mortality rate (small gap maker percentage [Table 11] and low border-tree mortality [Table 4]). The low canopy mortality plus increases in gaps indicate that it may be increasing in the stands studied.

These findings match other descriptions of sugar maple. It is very shade tolerant but can increase in importance relative to beech and hemlock following disturbances (Burns and Honkala 1990b, Lorimer and Frelich 1994) such as gaps (Barden 1983, Canham 1988, 1990, Pacala et al. 1996, Poulson and Platt 1996), drought (Parshall 1995), and glaze storms (DeSteven et al. 1991). On the other hand, sugar maple does not survive as long in the shade as beech and hemlock (Kobe et al. 1995). The higher mortality rates of sugar maple may explain its decrease in the larger sapling classes (Table 11). Sugar maple mortality rates vary with site conditions (Kobe 1996). Barden (1983) found large saplings of sugar maple in the southern Appalachians to have the longest period of pre-gap suppression of any species measured, while Kobe et al. (1995) found hemlock and beech to survive longer in the understory in New England.

Tsuga canadensis.—Eastern hemlock was distinctive in both its size-class structure and its response to dis-

TABLE 8. Extended.

Relative basal area		
1976/1977	1983	1990/1991
7 (+s)	7	7
50	50	49
12 (+a)	11 (+s)	11
12 (+a, +s)	13 (+a, +s)	13 (+a, +s)
2 (+a, +s)	2 (+s)	2 (+s)
3	3 (+s)	3 (+s)
4	2	3 (+s)
4 (+s)	4 (−a, +s)	4 (−a, +s)
1 (+a, +s)	1 (+s)	1 (+s)
<1 (+s)	<1 (+s)	<1 (−a, +s)
<1	<1 (+a)	<1
<1	<1	<1
<1 (+a, +s)	<1 (+s)	<1
2	2	<1
<1 (+a, +s)	<1 (+s)	1 (+s)
<1	<1	<1

turbance. It had a higher percentage of large saplings than any other species, both in the understory and in gaps (Table 11). It was the only species that decreased in relative density in disturbed sites while increasing in undisturbed sites (Table 11). During the three samples the relative density of hemlock first decreased significantly as overall stem density increased. The decrease was largest for younger gaps, in which overall stem density increased the most (Table 5). Later, as overall stem density decreased, the relative density of hemlock increased (Table 11). Hemlock seemed to respond to openings more by growth of its large, previously suppressed stems than by an increase in density. Hemlock's mortality rates were average (Table 4), leading to approximately equal representation in the canopy, in border trees, and among gapmakers (Table 11).

Eastern hemlock has been called the most shade-tolerant tree species in eastern North America but is still able to respond to release with increased diameter and height growth (Burns and Honkala 1990*a*, Lorimer and Frelich 1994). It grows faster in stem radial growth in full sun than either beech or sugar maple, though not as fast as yellow birch (Pacala et al. 1995). However, at the low light levels of small gaps it grows the slowest of those species: below 5% sunlight sugar maple grows faster than hemlock (Pacala et al. 1996). It survived at those low light levels better than sugar maple but worse than beech. In models of mixed communities hemlock did well because of its high survivorship in low light coupled with fast growth in high light. It shows more regional variation in growth rates, indicating perhaps a greater sensitivity to soil conditions, than do its associated hardwoods (Kobe 1996). Barden (1983) found hemlock to grow slower than any species examined except yellow buckeye before release and both beech and yellow buckeye after release. He also found hemlock to have long suppression times before release in gaps.

Fagus grandifolia.—Beech was found mostly as small stems but unlike sugar maple it showed relatively high levels of border-tree mortality, it decreased in relative density for both gaps and the understory, and its relative density was lower in gaps than in the understory (Table 11). Its likely decrease in the forests studied is indicated by the decrease in relative density from gap makers (canopy trees of the past) to present canopy to border trees (canopy of the future) (Table 11).

American beech is one of the most shade-tolerant species of eastern forests (Burns and Honkala 1990*b*). Its seedlings grow best under partial shade. It decreases in importance following clear-cutting (Burns and Honkala 1990*b*). Barden (1981) found beech to show the greatest decrease in importance (relative density of re-

TABLE 9. Differences in relative density and basal area of species found in ≥10% of gaps for the two sampling intervals.

Species	Differences in relative density		Differences in relative basal area	
	1976/1977–1983	1983–1990/1991	1976/1977–1983	1983–1990/1991
Acer saccharum	4.71*	0.17*	1.41	0.93
Tsuga canadensis	−2.32 (+a)*	4.41*	−0.33 (+a)	1.76
Fagus grandifolia	−2.80*	−2.09*	−1.42*	−0.81
Halesia carolina	0.20	−1.13*	1.14	−0.72
Acer pensylvanicum	0.73*	0.80*	0.49	0.18
Betula alleghaniensis	−0.42	−0.33	−0.24 (+s)	−0.14
Tilia heterophylla	0.46	0.01	−0.36 (−a)	0.85 (−a)*
Aesculus octandra	−0.63*	−0.27	−0.28	0.21
Acer rubrum	−0.19 (−s)	−0.30*	−0.04	−0.11 (−a)
Fraxinus americana	−0.18	−0.42*	0.01 (+s)	0.01
Rhododendron maximum	0.48*	−0.02	0.00	0.12 (−a)
Magnolia fraseri	0.06 (+s)	0.11 (−s)	0.19	−0.07
Prunus serotina	−0.07	−0.29 (−s)*	−0.07	0.07
Ostrya virginiana	−0.59*	−0.66*	0.25	−0.47
Liriodendron tulipifera	−0.14 (−a)	−0.01*	−0.02 (+s)	−0.09
Magnolia acuminata	0.09	0.04	0.03	0.26

Notes: The table also reports correlations with gap age and size: (+a) or (−a) indicates a significant ($P \leq 0.05$) positive or a negative correlation with gap age; (+s) or (−s) indicates a significant ($P \leq 0.05$) positive or negative correlation with gap size. Values followed by an asterisk are significantly ($P \leq 0.05$) different from zero (*t* test).

TABLE 10. Differences in species relative density between gaps affected or not by border-tree mortality. Values are relative species density in 1976/1977 subtracted from values in 1990/1991.

	Samples in which border-tree mortality was noted				
Species	Neither	Only in 1983	Both	Only in 1990s	Model P
Acer saccharum	4.0	8.1	5.1	5.1	0.60
Tsuga canadensis	6.2[B]	−5.7[A]	−2.5[A]	2.1[AB]	<0.01
Fagus grandifolia	−5.9	0.68	−6.9	−2.8	0.03
Halesia carolina	−2.1	−1.9	0.11	0.79	0.12
Acer pensylvanicum	1.5	1.5	2.0	1.5	0.99
Betula alleghaniensis	−1.6	−1.7	0.89	−0.47	0.09
Tilia heterophylla	−0.025	0.29	0.28	1.6	0.42
Aesculus octandra	−0.43	−1.3	0.68	0.16	0.13
Acer rubrum	−0.59	−0.72	−0.23	−0.48	0.86
Fraxinus americana	−0.69	0.04	−0.21	−1.10	0.66
Rhododendron maximum	−0.11	−0.10	−0.07	−0.07	0.99
Magnolia fraseri	−0.05	1.79	0.12	0.01	0.17
Prunus serotina	−0.53[AB]	−1.59[A]	0.10[B]	0.00[B]	<0.01
Ostrya virginiana	−0.41[B]	−0.45[AB]	−0.79[B]	−3.88[A]	<0.01
Liriodendron tulipifera	−0.55	0.10	0.34	0.00	0.11
Magnolia acuminata	0.06	0.41	0.35	−0.11	0.06

Notes: Values followed by the same superscript uppercase letter are not significantly ($P \leq 0.05$) different from each other (Tukey's test). Sometimes, although the whole model had $P \leq 0.05$, no two values differed significantly with $P \leq 0.05$.

placement saplings) from single tree gaps to multiple tree gaps. Although beech can respond with increased growth to gaps (Canham 1990, Poage and Peart 1993), it grows slower in gaps (height growth of saplings) than does sugar maple (Runkle and Yetter 1987, Canham 1988, Runkle 1990a, DeSteven et al. 1991, Poulson and Platt 1996). Pacala et al. (1996) found beech to grow slowly in full sun (less than any other species sampled) or in the shade (slower than sugar maple or yellow birch although faster than hemlock). Barden (1983) found it to grow slower both before and after

release in gaps than any species other than yellow buckeye. Its success in forests comes from having the best survivorship in the shade (Kobe et al. 1995, Pacala et al. 1996).

Halesia carolina.—Silverbell was important in the understory, with nearly the same relative densities for large and small stems (Table 11). It increased in relative density in disturbed gaps and decreased in undisturbed gaps (Table 10). It showed the most consistent increase in relative density with increased gap size for the major species and was the only one of the

TABLE 11. Variation in species relative densities among data sets. Numbers in brackets (i.e., [7], [8], and [9]) refer to decade of sampling (1976/1977, 1983, and 1990/1991, respectively).

Species	Cano-py† [7]	Border‡ [9]	Gap maker [7]	Gap saplings			Tall gap saplings§ [9]	Understory‖		Tornado¶ 1–24 [8]
				[7]	[8]	[9]		1–24 [8, 9]	1–5 [8, 9]	
Acer saccharum	17	17	10	16	22	22	12	11	15	2
Tsuga canadensis	23	21	26	18	16	21	32	27	12	0
Fagus grandifolia	18	13	26	24	21	17	17	24	32	0
Halesia carolina	17	19	14	12	11	10	16	23	24	24
Acer pensylvanicum	0	0	0	5	5	6	<1	0	0	0
Betula alleghaniensis	3	5	3	4	4	4	4	4	5	7
Tilia heterophylla	7	7	9	3	4	4	5	4	5	3
Aesculus octandra	8	8	3	2	2	2	6	2	2	2
Acer rubrum	1	2	<1	1	1	1	2	0	0	0
Fraxinus americana	2	2	2	1	<1	<1	<1	0	1	10
Rhododendron maximum	0	0	0	1	2	2	<1	0	0	3
Magnolia fraseri	<1	1	2	<1	1	1	1	1	1	0
Prunus serotina	<1	<1	0	<1	<1	<1	<1	0	0	0
Ostrya virginiana	<1	<1	<1	4	3	2	2	0	0	0
Liriodendron tulipifera	1	3	<1	<1	<1	<1	<1	0	0	40
Magnolia acuminata	1	1	<1	<1	<1	<1	<1	0	0	4
Percentage similarity to canopy trees	100	91	80	74	72	75	83	78	83	31

†Sampled by point-centered quarter technique.
‡Canopy trees surrounding gap.
§Potential successors.
‖Sampled along transects, mostly not in gaps; ''1–24'' and ''1–5'' refer to no. of centimeters in diameter at breast height (dbh).
¶Saplings in area regenerating following a tornado; ''1–24'' cm dbh.

major species to be abundant in the tornado area (Tables 8 and 11).

Silverbell has been little studied because as a major canopy tree its range is restricted to coves and north-slope sites within the Great Smoky Mountains (Burns and Honkala 1990*b*). Its height growth in gaps was the fastest of the species measured in Runkle and Yetter (1987). Its diameter growth is average, less than sugar maple but more than beech and hemlock, both before and after release in gaps (Barden 1983). Barden (1981) found it to have higher densities in multiple treefall gaps than in single treefalls. Its canopy residence time is short (Runkle 1982).

Gaps in these forests perpetuate species that dominate the canopy. All four dominant species were abundant in the understory. They all are known to be able to persist in the understory for long periods. They also are known to respond well to small increases in light created by canopy gaps. Species more demanding in their light needs (*Betula alleghaniensis, Liriodendron tulipifera*) are less important in these forests where large openings are rare. In general, then, light gaps in these forests serve to boost species already present in the understory, not to create opportunities for a new set of species.

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