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TREEFALLS REVISITED: GAP DYNAMICS IN THE SOUTHERN APPALACHIANS[1]

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Abstract. In 1976–1977, 284 gaps (canopy-opening sizes 1–1490 m^2) were sampled (age, size, species composition) from old-growth mesic forests in Great Smoky Mountains National Park, Joyce Kilmer Wilderness Area and Walker Cove Research Natural Area. In 1983, the woody vegetation (stems ≥ 1 cm dbh) of 273 of these gaps was resampled, rates of gap closure by canopy tree branch growth and sapling height growth were estimated, and incidences of disturbances occurring since 1976–1977 were noted. The average yearly crown extension growth rate was 18 cm/yr, with much variation among species and individuals. Some individual crowns grew into the canopy opening as much as 4 m in the 7 yr. Saplings grew an average of 30 cm/yr in height, again with much variation. Overall, taller saplings grew somewhat faster than smaller ones and saplings in large gaps grew faster than those in small gaps. These two rates of gap closure together suggest that most saplings will require two or more gap episodes to reach the forest canopy.

For woody vegetation, basal area per unit gap area was originally highest in small gaps, though it increased between sampling dates most in large gaps. Stem density had been highest in small old gaps, but decreased the most in old gaps. *Tsuga canadensis, Fagus grandifolia, Acer saccharum,* and *Halesia carolina* were the most important species in the gaps studied. Most species did not change in relative density or dominance between the two sampling dates and showed no significant correlations between those parameters and gap size and age. Overall, *Tsuga* and *Fagus* decreased and *Acer saccharum* increased in importance. High rates of repeat disturbance favor species able to grow in intermediate light levels and to survive several periods of suppression before reaching the canopy.

Key words: Acer saccharum; *disturbance;* Fagus grandifolia; *forest dynamics; forest regeneration; gaps; Great Smoky Mountains National Park; Joyce Kilmer Wilderness Area; mixed mesophytic species; southern Appalachians;* Tsuga canadensis.

INTRODUCTION

Temperate forests vary greatly in their disturbance regimes (Runkle 1985*a*). In some forests, large-scale and often severe disturbances occur frequently enough to be the chief source of tree mortality. Regeneration of those forests occurs primarily in synchronized pulses following the major disturbance episodes. In other forests, regeneration proceeds much more asynchronously, stimulated by frequent small-scale, mild disturbances that often involve only one or a few canopy trees at a time. Such localized disturbances are often referred to as gaps (Watt 1947, Bray 1956). Because of the importance of gaps for sapling regeneration and thus the ability of a species to persist in an area, the study of gap-phase regeneration provides insight into species adaptations and overall patterns of forest species composition, growth, and physiognomy.

In 1976 and 1977, the senior author collected data on 407 gaps from several old-growth forests in the eastern United States (Runkle 1981, 1982). Canopy openings for those gaps ranged from 1 to 1490 m^2 (geometric mean = 65 m^2). Gaps formed at rates of $\approx 1\%$ of total land surface area per year. Gaps closed both by lateral branch growth of the surrounding canopy trees and by the height growth of saplings; which process prevailed depended on the size of the gap and the size of the advance regeneration. Species composition varied along gradients of gap size and age. Although those results were valuable, they were flawed in that a temporal sequence on one site was inferred from data on many sites of different ages. Therefore, in 1981 the senior author resampled the 36 gaps in Hueston Woods State Park, Ohio, that were first sampled in 1977, and clarified several aspects of gap-phase regeneration for that site (Runkle 1984). The present report is concerned with the 1983 resampling of 273 of the 284 gaps originally sampled in the southern Appalachians, including sites in Great Smoky Mountains National Park in Tennessee and North Carolina, Joyce Kilmer Wilderness Area in western North Carolina, and Walker Cove Research Natural Area near Ashville, North Carolina.

There were three specific objectives of this study. The first goal was to improve estimates of gap closure rates: sapling height growth rates were quantified and differences in the branch lengths of canopy trees surrounding gaps were computed. The second goal was to

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determine the frequency of new disturbances occurring next to the original gaps. The third goal was to determine what changes had occurred since 1976–1977 in the woody vegetation within gaps and whether those changes, for all stems together and for each species individually, were related to the age and size of the gap.

METHODS

Gaps were relocated using the original field notes. Gaps had been recorded as occurring a given number of paces in a certain compass direction from a distinctive starting point. Point-centered quarter information (including dbh, diameter at breast height) also proved to be useful in retracing the transects established 6–7 yr previously. Gap identification was confirmed by the dbh of the trees that created the gaps (gapmakers), their orientation with respect to the transect, and by identification of other trees present. Using those techniques, 96% of the original gaps were resampled.

The original estimates of gap size (expanded gap: Runkle 1982) and age were used in this study. In several gaps, two ages had been recorded if two distinct episodes creating the gap seemed to have occurred. For analyses in this report, only the younger age was used, as it was assumed that the most striking gap effects should have been caused by the most recent disturbance episode.

Woody vegetation within gaps was resampled using the same techniques as in Runkle (1981, 1982). 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 hard to determine whether an individual near the gap margins had been previously counted. Whenever possible, questionable stems were checked against the earlier field notes on a one-by-one basis. Errors in the field notes or keypunching were detected by examining the distribution of differences (1983 values minus earlier values of species density and basal area) for each gap, examining extreme values closely.

During 1976, 384 canopy trees bordering gaps were selected and their dbh measured (Runkle 1982). A vertical projection of the distance from the bole to the furthest extension of the crown into the gap was measured for each tree. In 1983, 242 of these trees were reidentified by species and dbh. In most cases, these trees had been recorded in pairs, on opposite sides of the gap, with the distance measured along the line connecting the two trees. It therefore was possible in 1983 to measure the distance along the same line as earlier. The 1983 and 1976 dbh and lateral extension measurements were compared directly to estimate growth rates.

Height growth rates of saplings within gaps were measured as follows. The one to three saplings selected for each gap were chosen subjectively from the taller, faster growing stems most likely eventually to reach the canopy. Annual increment growth (distance between adjacent sets of bud-scale scars) was measured for as many years as possible. Saplings up to 12 m tall were pulled over and examined. Data from gaps ≤ 14 yr old in 1983 were collected, the most useful information being from gaps ≤ 11 yr old, due to increasingly unreliable measurements of height growth with increasing age. Sapling height growth values were not used if they were for a period too long before 1983 (5–14 yr, depending on the species). Older values were not used for two reasons. First, more growth increments usually could be observed for slow-growing stems than for fast-growing stems, thus, inclusion of older growth increments would bias the results toward slower-growing individuals. Second, the number of stems for which it was possible to observe old growth increments was small (usually 1–3 stems per species) and therefore not as clearly representative of average growth rates. One more sapling-use criterion was that good bud scars needed to be observed; in general this was possible for all important species in the areas studied except eastern hemlock (*Tsuga canadensis*).

To determine the frequency of new disturbance between 1976 or 1977 and 1983, canopy trees (number of individuals of each species) bordering gaps and gapmakers in 1983 were compared to those in the original field notes.

Statistical procedures used to evaluate changes in the vegetation within gaps come from the SAS statistical package (Ray 1982*a*, *b*). Relationships between variables are based on Pearson product-moment correlations or simple linear regressions, unless otherwise noted. Species names are taken from Little (1979).

RESULTS AND DISCUSSION

In this section we shall first examine the dynamics of the gaps themselves. Revised estimates of gap closure rates attributable to the branch growth of bordering canopy trees and to the height growth of saplings will be compared. The possible reliance of saplings on repeat disturbances will be explored and the actual frequency of repeat disturbances will be presented. These results will be related to earlier estimates of gap disturbance rates and to other literature studies implicating repeat disturbances as important for forest regeneration.

We shall examine changes in the woody vegetation. Values of total basal area (*TBA*) and number of all stems ≥ 1 cm dbh per unit gap area will be examined for the 1976–1977 data to determine if they are significantly correlated with gap size and age; if there are significant relationships, values will be given for selected gap size–age classes to elucidate patterns. Differences in *TBA* and stem density between 1976–1977 and 1983 will be analyzed to determine whether the changes are related to gap size and age, and to sum-

TABLE 1. Total changes in dbh and lateral extension distance of trees bordering gaps from 1976 to 1983. Terminology follows Little (1979).

		Average annual increase*		Maximum annual increase*
Species	*N*	dbh (mm)	Extension (cm)	(Extension, cm)
Magnolia fraseri	2	10.7	31.4	32.9
Acer rubrum	9	3.0	28.7	58.6
Betula alleghaniensis	11	0.4	22.3	42.9
Liriodendron tulipifera	7	3.5	21.8	35.7
Acer saccharum	44	3.1	20.2	57.1
Halesia carolina	41	3.1	18.8	57.1
Magnolia acuminata	4	6.1	18.6	32.9
Fagus grandifolia	26	2.2	17.4	47.1
Aesculus octandra	20	2.9	17.4	37.1
Tilia heterophylla	14	2.7	17.3	31.4
Prunus serotina	1	5.7	17.1	17.1
Tsuga canadensis	60	2.2	13.1	40.0
Fraxinus americana	3	3.3	8.6	25.7
Overall	242	2.7	17.9	58.6

* Average and maximum annual increases were computed by dividing total increases in distance by 7.

marize major aspects of gap dynamics and demography. These analyses will be done for all species lumped together and then for important species individually.

Gap closure rates and repeat disturbances

Crowns of canopy trees bordering gaps grew into canopy openings an average of 18 cm/yr (Table 1). Species varied, but individuals within species varied even more, with the maximum increase being 4 m in 7 yr. Other individuals showed small or even negative growth rates, caused by terminal branch dieback. The average value was greater than the 4.1 cm/yr estimate in Runkle (1982), though close to values obtained by Trimble and Tryon (1966) in West Virginia and by Hibbs (1982) in Massachusetts. The estimates in Runkle (1982) and in the present study cannot be directly compared because the 18 cm/yr value is a more accurate estimate based on the growth rate of healthy canopy trees bordering the gap, whereas the 4.1 cm/yr figure was based on regressions of tree size and gap age and included trees that had lost branches due to normal causes following gap formation or due to injuries associated with gap formation. The earlier study also included trees that had begun bordering the gap sometime after the initial gap formed because of a second disturbance event.

On average, the taller regenerating saplings grew 30 cm/yr, again with much variation among species (Table 2). Overall, taller saplings grew somewhat faster than smaller ones and saplings in large gaps grew faster than those in small gaps (Table 2). Multivariate regression equations were used to relate sapling height growth to sapling height, gap size and age, and topographic position. Increasing height by 1 m or canopy-opening size by 100 m^2 increased sapling growth by $\approx$2 cm/yr. Other factors affecting sapling height growth rates in our study are examined elsewhere (Yetter 1984, Yetter and Runkle 1986). These rates are similar to those measured in Massachusetts (Hibbs 1985) and to those of primary species in Costa Rica (Brokaw 1985).

Given the rates calculated above for the two main mechanisms of gap closure, the average number of gaps required for seedlings to reach the canopy was estimated. Since gaps were approximately round, gap area was converted to a radius, which was then divided by the lateral extension growth rate (18 cm/yr) to calculate the number of years it would take for the gap to be closed solely by the branch growth of surrounding canopy trees. This time was multiplied by average sapling

TABLE 2. Sapling height growth. Significant ($P \leq .05$) changes (increases or decreases) in sapling annual height growth are based on coefficients of multivariate regressions. Dashes indicate no significant relationship. (This table is condensed from Yetter and Runkle 1986.)

				Significant changes (cm/yr)	
Species	No. stems	No. annual height increments	Mean (±SD) height growth (cm)	Per 1-m height increase	Per 100-m^2 increase in gap area
Halesia carolina	77	454	49 ± 30	2	...
Liriodendron tulipifera	27	149	43 ± 27	7	...
Magnolia fraseria	16	107	39 ± 28	−3	6
Tilia heterophylla	27	177	35 ± 23	4	3
Betula alleghaniensis	29	128	35 ± 21	3	3
Acer rubrum	10	66	33 ± 20	...	10
Magnolia acuminata	6	21	33 ± 28	...	−75
Aesculus octandra	15	94	29 ± 14	...	...
Acer saccharum	176	1339	26 ± 18	3	2
Prunus serotina	7	32	23 ± 12	...	...
Fraxinus americana	5	28	22 ± 14	...	...
Quercus rubra	4	23	19 ± 13	...	...
Fagus grandifolia	75	537	18 ± 11	...	2
Overall	474	3155	30 ± 23	2	2

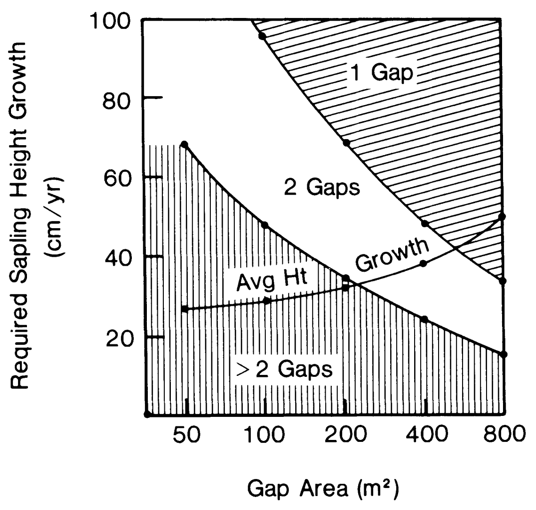

FIG. 1. Sapling height growth rates required for the sapling to enter the canopy during the life-spans of one, two, or more gaps, for different-sized gaps and for a lateral extension growth rate by surrounding canopy trees of 18 cm/yr. Average height growth is based on the quadratic regression of observed height growth on canopy gap area.

height growth rates, as adjusted for gap area, to determine the height of saplings at time of gap closure. By relating that height to the mature canopy height of ≈30 m (Whittaker 1966, J. R. Runkle, *personal observation*) we determined how many growth spurts would be experienced by a sapling to reach the canopy (Fig. 1). For these forests, 76% of the area in canopy openings was in canopy openings ≤200 m^2, although openings as large as 1000 m^2 occurred occasionally (Runkle 1982). Therefore, given the height growth rates in Table 1, it seems likely that very few trees in the forests studied reached the canopy following single disturbance episodes. It appears that ≥2 gap episodes usually occur before saplings reach the canopy, an estimate that agrees well with the results of Canham (1985). He found that sugar maples in unlogged stands in New York state all underwent 1–5 episodes of suppression, presumably caused by the closure of canopy gaps, before eventually growing into the canopy. These results suggest that repeat disturbances affecting the same location may be common. Of course, all the parameters involved in this simple model are variable, including rates of extension growth and rates of sapling height growth. Also, saplings might reach the canopy at heights <30 m. Therefore, the number of disturbances required by a sapling to reach the canopy cannot be estimated exactly.

For a new disturbance to help an already established sapling, it is not necessary for the first gap to have closed completely and for a new canopy-closing tree established there to die. The changes associated with gaps that help sapling growth, such as decreases in competition for light, soil, water, and nutrients (Geiger 1965, Minckler et al. 1973), are not restricted to locations directly under the canopy opening, but may also occur among neighboring trees (e.g., Tryon and Trimble 1969).

In the present study, we recorded injuries to these surrounding trees and other disturbances that had occurred since 1976–1977. In 42% of the gaps, at least one surrounding canopy tree had died or was obviously dying. In 23% of the gaps, the gapmaker (the tree whose death or injury had created the gap) had died completely if it had been previously injured or had fallen if it had been previously dead but standing. Both of those responses could prolong the time during which extra light and soil nutrients were available to a sapling. In 13% of the gaps, a new gap occurred near enough to influence the saplings within the gap studied. These new gaps were recorded only when they were particularly noticeable. No special efforts were made to locate them, so their true importance may be higher. In only 41% of the gaps were no new disturbances noted. In general, these results imply that the requirement of many saplings for repeat disturbance episodes is not unduly restrictive. Such episodes occurred frequently in the forests studied.

Are canopy trees bordering gaps more likely to die prematurely than canopy trees in general? Such self-augmenting effects are associated with certain other disturbance types, most strikingly with higher elevation fir forests (e.g., Sprugel and Bormann 1981). The relative frequency of disturbance, n, was predicted for the forests studied here, using the following equation: $bnt = d$, where b = the number of gap-border canopy trees that were alive at the beginning of interval t, n = the percentage of such trees dying each year, and d = the number of new dead or dying trees at the end of interval t. Substituting measured values for b, t, and d, we obtain

$$[475 \text{ trees} \times (n\%/\text{yr}) \times 6 \text{ yr}] + [1756 \text{ trees} \times (n\%/\text{yr}) \times 7 \text{ yr}] = 164 \text{ trees}.$$

Solving this equation for n gives an average relative frequency of disturbance of 1.08%/yr. This value compares very well with previous estimates of 1.2%/yr (Runkle 1982) for disturbance rates in these sites. Although the earlier estimate was based on the fraction of land area affected, rather than the fraction of indi-

TABLE 3. Average densities of stems ≥1 cm dbh for gap size–age classes. Values in table followed by the same letter are not significantly (P = .05) different from each other (Duncan's multiple range test).

Gap size (m^2)	Gap age (yr) 1–3		4–8		>9	
	Stems/m^2	No. gaps	Stems/m^2	No. gaps	Stems/m^2	No. gaps
≤200	0.15^{abcd}	34	0.19^{ab}	43	0.20^{a}	32
200–400	0.11^{cd}	48	0.15^{abcd}	32	0.16^{abc}	34
>400	0.10^{d}	25	0.14^{bcd}	16	0.14^{bcd}	9

TABLE 4. Species importance values and their correlations with gap size (expanded gap) and gap age (average of the two sampling times).*

Species	IV†	Presence‡ (% of gaps)	Relative frequency (%)	Relative dominance (%)	Relative density (%)	Changes from 1976–1977 to 1983§ Relative dominance (%)	Changes from 1976–1977 to 1983§ Relative density (%)
Tsuga canadensis	25	81	12	41	22	.10 (+a)	−2.34 (+a)
Fagus grandifolia	15	72	11	14	20	−1.80 (−a)	−2.56
Acer saccharum	12	77	12	9	16	1.41	4.76
Halesia carolina	12	70	11	12 (+a)	12	.79	−.003 (−a)
Acer pensylvanicum	5	46	7	3 (+a)	4	.42	.75
Betula alleghaniensis	5	46	7	3	4	−.26	−.44
Tilia heterophylla	5	43	7	4	4	.13	.47
Aesculus octandra	4	31	5	5	3	−.34 (−s)	−.62
Ostrya virginiana	3	18	3	3	3	.21	−.56
Acer rubrum	2	26	4	1	1	−.04	−.16
Rhododendron maximum	2	18	3	t	2 (+a)	−.01	.50
Magnolia fraseri	1	15	2	1	1	.11	.01
Fraxinus americana	1	18	3	t	1	.02 (+s)	−.16
Prunus serotina	1	15	2	t	1	−.06	−.06
Liriodendron tulipifera	1	11	2	t	t (+s)	−.02	−.13
Acer spicatum	1	6	1	t	1	.24	.20
Hamamelis virginiana	1	6	1	t	1	−.01	.13
Lindera benzoin	1	6	1	t	1	.11	.61 (+s)
Magnolia acuminata	t	7	1	t	t	.03	.08
Ilex montana	t	6	1	t	t	.06	.32
Carya cordiformis	t	5	1	t	t	.05	.10
Cornus alternifolia	t	6	1	t	t	−.03	−.06
Cornus florida	t	4	1	t (+s)	t (+s)	−.02 (−s)	−.07 (−s)
Amelanchier arborea	t	5	1	t	t	.01	−.04
Quercus rubra	t	4	1	t	t	−.02	−.07 (−a, +s)
Ilex opaca	t	4	1	t	t	−.08	−.03
Pyrularia pubera	t	2	t	t	t	.01	.16
Aralia spinosa	t	3	t	t (+a)	t	−.14 (−a)	−.09 (−a)
Sambucus pubens	t	2	t	t	t	.01	.04

* Relative density and dominance are averages of the two sampling times. (+a) or (−a) indicates a positive or a negative correlation ($P \leq .05$) with gap age. (+s) or (−s) indicates a positive or a negative correlation with gap size. t indicates a value of <1%.

† IV (importance value) = average of relative frequency, relative dominance (fraction of total basal area), and relative density.

‡ Presence = percent of total gaps (n = 271) in which the species occurred.

§ Underlined values are significantly ($P \leq .05$) different from zero (t test).

vidual trees, the two fractions probably are similar (Runkle 1985*b*). High rates of repeat disturbance occur because of canopy tree geometry. Small gaps have very large edge effects, with each one surrounded by 8.2 border trees on average; the probability is high that at least one of those trees will die before the gap has closed and the regenerating saplings have died. This type of disturbance regime therefore should favor tolerant species able to grow slowly but steadily through a series of small gaps, occasionally surviving for a few years under shaded conditions. Some of the larger gaps may be colonized by intolerant species, such as *Liriodendron tulipifera,* which can grow rapidly to reach the canopy under favorable conditions but which cannot survive for long if suppressed. Such a balance between common tolerant and occasional intolerant species occurs in these forests (Runkle 1985*a*).

1976–1977 total basal area and density

In 1976–1977, the average value ($\bar{X} \pm$ SD) of total basal area (*TBA*) per gap area for the 273 gaps resampled in 1983 was 5.42 ± 4.44 cm^2/m^2. This parameter was not correlated with gap age, but it was correlated with gap size (expanded gap area, *EG*):

$$TBA/EG = 6.1 - (0.0025)(EG);\ n = 273,\ P = .04.$$

A multiple regression equation relating *TBA*/*EG* to age and *EG* was not significant ($P > .05$), although the coefficient for *EG* was significant ($P = .04$).

The average stem density (*TDEN*, $\bar{X} \pm$ SD) was

TABLE 5. Relative dominance (percent of total basal area) and density (percent of all stems) values for selected species in gap size and age (1976–1977 values) classes. Values are amounts in 1976–1977 plus or minus differences (in parentheses) between that period and 1983.

	Relative dominance					
	Gap age class (yr)			Gap size class (m^2)		
Species	1–3	4–8	9+	≤200	200–400	>400
Tsuga canadensis	46 (−2)	38 (−<1)	37 (+4)	39 (+<1)	43 (−<1)	42 (−<1)
Fagus grandifolia	13 (−<1)	17 (−<1)	14 (−5)	17 (−3)	13 (−<1)	14 (−2)
Acer saccharum	8 (+1)	9 (+<1)	9 (+3)	7 (+2)	10 (+<1)	7 (+<1)
Halesia carolina	10 (+1)	11 (−<1)	16 (+1)	13 (−<1)	10 (+1)	14 (+2)
Acer pensylvanicum	1.4 (+0.8)	2.7 (+1)	5 (−0.9)	2.6 (+0.6)	2.8 (+0.2)	3.1 (+0.5)
Aesculus octandra	6.7 (−1)	6.2 (+0.1)	2.7 (−<0.1)	5.5 (+0.7)	5.3 (−0.9)	5.7 (−1.4)
Liriodendron tulipifera	0.19 (<0.01)	0.49 (−0.04)	0.61 (−0.03)	−0.28 (+0.04)	0.53 (−0.13)	0.38 (+0.08)

0.15 ± 0.095 stems/m^2. *TDEN* was positively correlated with gap age (*AGE*) and negatively correlated with gap size (*EG*):

$$TDEN = 0.13 + (0.0032)(AGE),\ P < .01.$$
$$TDEN = 0.18 - (0.000091)(EG),\ P < .01.$$

A multiple regression equation (*TDEN* relative to both *EG* and *AGE*) also showed both of the latter parameters to be highly correlated with density. To examine these relationships in more detail, gaps were segregated into nine size–age classes, whose limits were set so as to produce approximately equal sample sizes (Table 3). Stem density increased with gap age for all gap size classes. Stem density also decreased with increases in gap size in all gap age classes, perhaps because of the increased area associated with fallen stems and branches in large gaps (J. R. Runkle, *personal observation*).

Basal area and density changes: 1976–1977 to 1983

From 1976–1977 to 1983, basal area per unit gap area increased by 1.81 ± 2.45 cm^2/m^2 ($\bar{X}$ ± SD), an average increase of 33%, which was highly significant ($P \leq .01$). Increases in basal area were not significantly ($P \geq .05$) correlated with gap age or gap size. More complicated multivariate parametric tests incorporating both size and age were not significant. Segregating gaps into the nine size–age classes used in Table 3 revealed no significant pattern.

From 1976–1977 to 1983, total stem density increased by 0.050 ± 0.093 stems/m^2 ($\bar{X}$ ± SD), an average increase of 26%, which was highly significant ($P \leq .01$). Density changes were not related to gap size according to any of the univariate or multivariate tests used. Density changes were negatively correlated with gap age:

$$TDEN\,(1983) - TDEN\,(1976,\ 1977) = 0.077 - (0.0029)(AGE);\ P \leq .01,$$

which indicates that younger gaps increased in density faster than older gaps, where competition from preexisting larger saplings apparently hindered the establishment of new stems. Similarly, Brokaw (1985) found that as gaps age, fewer new stems are added each year and eventually, for many gaps, total density begins to decline. Also, saplings present in a gap during its 1st yr grow faster than saplings established later.

Species relationships to gap size and age

Altogether, 29 species were found in > 1% of the 271 gaps studied (Table 4). Two gaps were deleted from this analysis because changes in their species composition seemed due primarily to uncertainties in relocating exact gap boundaries. Four species in particular dominated the gaps studied, together constituting 70% of the stems ≥1 cm dbh and 76% of the basal area: hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and silverbell (*Halesia carolina*). Of these four, hemlock was usually found as large saplings (high ratio of relative basal area to relative density), while beech and sugar maple were more prevalent as smaller saplings.

The overall relationship of the vegetation to gap size and age was described earlier. This section will stress relative species importance values. A nonsignificant relationship means that the species responded in the same manner as did the average species overall. A significant relationship means that a given species responded uniquely.

Most species followed the general changes in basal area and density discussed above (Table 4). Only a few showed significant ($P \leq .05$) correlations between relative importance values (average of the two sampling

TABLE 5. Continued.

Relative density					
Gap age class (yr)			Gap size class (m²)		
1–3	4–8	9+	≤200	200–400	>400
29	20	19	22	24	23
(−5)	(−2)	(+2)	(−1)	(−3)	(−4)
17	24	23	23	20	19
(−1)	(−3)	(−4)	(−2)	(−2)	(−3)
11	14	18	14	13	16
(+5)	(+5)	(+4)	(+4)	(+5)	(+6)
12	11	11	11	11	14
(+2)	(−2)	(−2)	(−<1)	(+<1)	(−<1)
3.2	3.8	5.4	3.4	4.1	5
(+0.3)	(+1.7)	(+0.2)	(+1.3)	(+0.2)	(+0.8)
4.4	2.4	2.2	2.5	4	2.6
(−1.5)	(−<0.1)	(−0.1)	(−0.4)	(−0.9)	(−0.4)
0.41	0.24	0.80	0.12	0.64	0.80
(−0.04)	(+0.04)	(−0.47)	(+0.06)	(−0.32)	(−0.15)

times) and gap size or age (average of the two sampling times). Older gaps had somewhat greater relative dominance values than younger gaps for *Halesia carolina, Acer pensylvanicum,* and *Aralia spinosa,* and greater relative density values for *Rhododendron maximum.* Larger gaps had somewhat greater relative dominance and relative density values than smaller gaps for *Cornus florida* and greater relative density values for *Liriodendron tulipifera.* More complicated regression analyses (all combinations of age, age squared, size, size squared) confirmed these same relationships and added three others. *Lindera benzoin* showed two significant quadratic relationships to gap size: its relative dominance decreased then increased, with a minimum for gaps of 623 m^2; and its relative density reached a minimum at a gap size of 483 m^2. The third additional relationship was that the relative density of *Fraxinus americana* reached a minimum at a gap size of 444 m^2.

The relative importance of several species also changed significantly between the two sampling times, although for most species no significant changes occurred (Table 4). Only two species showed significant changes in relative dominance: *Acer saccharum* increased and *Fagus grandifolia* decreased. For relative density, *Acer saccharum, Acer pensylvanicum, Rhododendron maximum, Lindera benzoin, Ilex montana,* and *Carya cordiformis* increased while *Tsuga canadensis, Fagus grandifolia, Aesculus octandra,* and *Ostrya virginiana* decreased.

Changes in the importance of several species also were significantly correlated with gap size and age. *Tsuga canadensis* increased the most in old gaps (relative density and dominance); *Fagus grandifolia* (dominance), *Halesia carolina,* and *Quercus rubra* (density), and *Aralia spinosa* (density and dominance) increased the most in young gaps. Also, *Aesculus octandra* (dominance) and *Cornus florida* (density and dominance) increased most in small gaps while *Fraxinus americana* (dominance), *Lindera benzoin,* and *Quercus rubra* (density) increased most in large gaps.

Again, more complicated regression models merely repeated these relationships, with two exceptions. *Aesculus octandra* had a significant quadratic relationship with size; it increased in relative dominance in small ($<$205 m^2) gaps, decreased in larger gaps, and increased again in very large ($>$1960 m^2) gaps. *Liriodendron tulipifera* had a significant quadratic increase in relative dominance with increased gap size; it changed very little in importance for small gaps but showed greater and greater increases in relative dominance for very large ($\geq$708 m^2) gaps.

To show some of the actual variation in importance values, the following procedure was used. Gaps were divided into the nine size–age (in 1976–1977) categories already described (Table 3). Averages of relative density and dominance in 1976–1977 and of changes in each through 1983 were computed for each category, and significant differences among classes were calculated using Duncan's procedure (Table 5). Most species showed no strong variation, in accordance with the results just discussed. A few species did show notable patterns. *Tsuga canadensis* varied relatively little with gap size, but seemed most important (density and dominance) in young gaps, as befits its great shade tolerance and tendency to be found as relatively large saplings able to survive well in periods of suppression between gaps. *Fagus grandifolia* and *Acer saccharum* both increased in relative density from young to old gaps in 1976–1977, but *Acer* increased and *Fagus* decreased in importance from 1976–1977 to 1983. *Halesia carolina* varied little among size–age classes except for relatively high importance in large, old gaps. *Acer pensylvanicum* increased in importance in older gaps. *Aes-*

culus octandra was most important in young gaps. Like *Tsuga* it had a high ratio of relative dominance to relative density and seemed able to withstand relatively long periods of suppression. *Liriodendron tulipifera* had its maximum relative density in large old gaps.

CONCLUSIONS

Although for any one given time and place, the existence of a gap is unpredictable, for the forest as a whole, certain patterns recur often enough to be of evolutionary significance. Constraints set by sapling height growth rates and by rates of canopy tree branch growth interact with the geometry of disturbance to determine the frequency and necessity (for successful regeneration) of repeat disturbances. Dominant species in the forests studied were able, on average, to persist as gaps began to close until new gaps appeared. As a result, the species composition of individual gaps remained fairly constant over time. Hence, the vegetational composition of a gap at any given time should be a good predictor of its composition in the future.

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LITERATURE CITED

Bray, J. R. 1956. Gap phase replacement in a maple–basswood forest. Ecology **37**:598–600.

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

Canham, C. D. 1985. Suppression and release during canopy recruitment in *Acer saccharum.* Bulletin of the Torrey Botanical Club **112**:134–145.

Geiger, R. 1965. The climate near the ground. Translation from the fourth German edition of Das Kilma der bodennahen Luftschicht. Harvard University Press, Cambridge, Massachusetts, USA.

Hibbs, D. E. 1982. Gap dynamics in a hemlock–hardwood forest. Canadian Journal of Forest Research **12**:522–527.

Little, E. L. 1979. Checklist of United States trees (native and naturalized). United States Agriculture Handbook **541**.

Minckler, L. S., J. D. Woerheide, and R. C. Schlesinger. 1973. Light, soil moisture, and tree reproduction in hardwood forest openings. United States Department of Agriculture Forest Service Research Paper **NC-89**.

Ray, A. A., editor. 1982*a*. SAS user's guide: basics. SAS Institute, Cary, North Carolina, USA.

———, editor. 1982*b*. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology **62**:1041–1051.

———. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63**:1533–1546.

———. 1984. Development of woody vegetation in treefall gaps in a beech–sugar maple forest. Holarctic Ecology **7**: 157–164.

———. 1985*a*. Disturbance regimes in temperate forests. Pages 17–33 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

———. 1985*b*. Comparison of methods for determining fraction of land area in treefall gaps. Forest Science **31**:15–19.

Sprugel, D. G., and F. H. Bormann. 1981. Natural disturbance and the steady state in high-altitude balsam fir forests. Science **211**:390–393.

Trimble, G. R., and E. H. Tryon. 1966. Crown encroachment into openings cut in Appalachian hardwood stands. Journal of Forestry **64**:104–108.

Tryon, E. H., and G. R. Trimble. 1969. Effect of distance from stand border on height of hardwood reproduction in openings. Proceedings of the West Virginia Academy of Science **41**:125–133.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology **35**:1–22.

Whittaker, R. H. 1966. Forest dimensions and production in the Great Smoky Mountains. Ecology **47**:103–121.

Yetter, T. C. 1984. Height growth rates of canopy tree species in natural windfall gaps, Great Smoky Mountains National Park. Thesis. Wright State University, Dayton, Ohio, USA.

Yetter, T. C., and J. R. Runkle. 1986. Height growth rates of canopy tree species in southern Appalachian gaps. Castanea **51**:157–167.