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PATTERNS OF DISTURBANCE IN SOME OLD-GROWTH MESIC FORESTS OF EASTERN NORTH AMERICA[1]

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Abstract. To characterize the disturbance regime of one type of vegetation, study areas in which relatively small-scale disturbance predominates were chosen in several old-growth mesic forests in the eastern United States. Canopy openings covered 9.5% of total land area. New gaps were formed at an average rate of 1% of total land area per year; old gap area closed at a similar rate primarily by sapling height growth.

With increased gap size, vegetation within gaps increased in woody species diversity, total basal area, and total number of stems. Stems also showed accelerated growth into larger size classes. As gaps aged, stems grew into larger size classes and basal area increased.

Species responses to canopy gaps varied. Some species survived and became established in fairly small gaps (50–100 m^2). Although in large gaps (up to 2009 m^2 in the present study) these species usually increased in total number of stems and basal area, they declined in importance relative to species which rarely survived in small gaps but grew rapidly in large gaps. The disturbance regimes in the forests studied favored tolerant species but allowed opportunists to persist at low densities.

Key words: climax; disturbance; forest regeneration; gaps; Hueston Woods; mixed mesophytic forest; patch dynamics; southern Appalachians; succession; Tionesta; windfalls.

INTRODUCTION

Communities change constantly as individuals die and are replaced. How deaths and replacements occur in time and space has an effect on many aspects of community structure and species composition. The relationship between community properties and the pattern of individual deaths (disturbance regime) has been examined recently (e.g., Jones 1945, Watt 1947, Loucks 1970, Wright 1974, Whitmore 1975, 1978, Connell 1978, Bormann and Likens 1979, White 1979). Detailed descriptions of natural disturbance regimes for various community types are necessary to evaluate recent theories, to understand community properties, and to provide information useful for landscape managers (Pickett and Thompson 1978). The natural disturbance regimes of several communities have been examined in some detail (e.g., Brunig 1973, Heinselman 1973, Henry and Swan 1974, Lorimer 1977, 1980, Zackrisson 1977, Hartshorn 1978, Reiners and Lang 1979, Sprugel and Bormann 1981). However, few studies compare several different communities or have been done in those temperate-zone areas where disturbances are usually small.

The goal of the present paper is to describe disturbance regimes characterized by small gaps created following the death of a single canopy tree, part of a canopy tree, or a very few individuals. A complete description of the disturbance regime involves two parts (Levin and Paine 1974): (1) the size and age distributions and birth and death rates of gaps, and (2) the response of species to the regeneration opportunities existing in gaps of different sizes and ages.

STUDY AREAS

In order to limit consideration to the formation and filling in of small gaps, criteria for choosing a suitable forest stand were that it be (a) without any obvious large-scale human or natural disturbances, as determined from historical records and the presence of very large individuals, and (b) without evidence of extensive chestnut (*Castanea dentata*) mortality (which would greatly affect estimates of more normal rates of gap formation and more normal gap sizes). To decrease variability within and among samples, stands were required to possess reasonably homogeneous canopy species composition for an area of at least several hectares and dominance by some combination of such mesic tree species as hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), yellow buckeye (*Aesculus octandra*), mountain silverbell (*Halesia carolina*), and white basswood (*Tilia heterophylla*).

Some stands within each of the following areas were sampled: Great Smoky Mountains National Park of North Carolina and Tennessee; Joyce Kilmer Wilderness Area of western North Carolina; Walker's Cove Research Natural Area near Asheville, North Carolina; Hueston Woods State Park near Oxford, Ohio; Tionesta Scenic and Natural Areas in northwestern Pennsylvania; Woodbourne Forest and Wildlife Sanctuary in northeastern Pennsylvania; and the Edmund Niles Huyck Preserve near Albany, New York. Species composing >10% of trees ≥ 25 cm dbh for

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each area are, for the Great Smoky Mountains: sugar maple, yellow buckeye, beech, silverbell, white basswood, and hemlock; for Joyce Kilmer: sugar maple, beech, silverbell, basswood, and hemlock; for Walker's Cove: sugar maple, buckeye, beech, and basswood; for Hueston Woods: sugar maple and beech; for Tionesta: beech and hemlock; for Woodbourne: sugar maple, white ash, and hemlock; and for Huyck: beech and hemlock (more details are given in Runkle 1979, 1981).

Although in general the stands studied seemed to fit the criteria concerning disturbance history and species composition listed above, large disturbances may have occurred in some stands and may have been important in determining some of the present species composition. In the Great Smoky Mountains National Park, some selective cutting may have occurred within some of the areas studied. Also, tornadoes that destroyed several hectares of forest have been noted and so may have affected the stands studied at some time in the past. In Joyce Kilmer, windstorms affecting several canopy trees occur periodically (Lorimer 1980) and probably are important in influencing canopy composition, though gaps created by single trees also are important. The present study of Joyce Kilmer included gaps created by single trees and by as many as nine canopy trees, and therefore should cover most of the range of gap sizes which normally occur. In northwestern Pennsylvania as a whole, large-scale disturbances have occurred frequently enough to have generated stands of white pine (*Pinus strobus*), such as those at Heart's Content and Cook's Forest (Morey 1936*b*). Bjorkbom and Larson (1977) state that although mature white pine has not been recorded at Tionesta, windstorms in 1808 and 1870 damaged two large areas within the Tionesta Scenic and Research Natural Areas, causing increases in relatively shade-intolerant hardwood species. In the areas sampled, however, no such disturbances are recorded in the literature. Another influence in Tionesta was heavy browsing by deer, which has seriously affected the regeneration of many hardwoods (Bjorkbom and Larson 1977). Hueston Woods has remained relatively undisturbed since its original purchase in 1797, serving primarily as a source of maple sugar. However, selective logging for desirable species probably occurred, and the undergrowth in some places has received heavy trampling. Some areas within Woodbourne were affected by a hurricane in 1950 (J. Stone, *personal communication*), and by a beech fungal disease (*Nectria coccinea* var. *faginata*); such areas were avoided in my samples. The Huyck Preserve also was affected by the beech fungal disease.

FIELD METHODS

Transects beginning at randomly chosen points were set up along compass lines parallel to the long axis of each suitable study area. At random distances along these transects the point-centered quarter method (Cottam and Curtis 1956) was used to characterize the canopy composition. The first point fell 0–25 paces from the beginning of the transect and subsequent points 25–75 paces ($\approx$17–50 m) apart. At each point, whether or not the point was in a gap, distances to and diameters of nearest trees $\geq$25 cm dbh in each quarter were measured; 25 cm dbh was generally the smallest size at which individuals were capable of creating overstory gaps.

Two types of gaps were defined. The canopy gap was the land surface area directly under the canopy opening. The expanded gap consisted of the canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap. The concept of expanded gap was useful for two reasons. First, it included areas directly and indirectly affected by the canopy opening; the effects of light often were offset from the gap center. Therefore simply measuring the canopy gap underestimated the true importance of the gap in the community. Second, at least some of the forestry literature (e.g., Tryon and Trimble 1969) defines "opening" in this way, although a precise definition of "opening" often is not given. For the purposes of this study, gaps were considered indistinguishable from the background vegetation when regeneration within the gap was $\approx$10–20 m tall.

The length of each transect was recorded as the total number of paces. In addition, the number of paces walked along the transect in each canopy gap and each expanded gap was recorded. When the transect intersected an expanded gap, the following additional measurements were taken. The area A for both expanded gaps and canopy gaps was estimated by fitting their length L (largest distance from gap edge to gap edge) and width W (largest distance perpendicular to the length) to the formula for an ellipse (most gaps were shaped at least roughly like an ellipse; $A = \pi LW/4$). Note that two distinctly different types of gap size measurements were taken: first, the fraction of transect in gaps, a quantity used to determine the fraction of total land surface area in gaps, and second, actual gap area, a quantity used to determine gap size distributions. The number and species of all woody stems $\geq$1 m high and the dbh, number, and species of all woody stems $\geq$2 m high were recorded. Where several stems were clearly from the same individual, the few largest were included. This report will refer to individuals $\geq$1 m high within gaps as saplings. The number, species, and type of injury sustained by trees creating the gaps ("gapmakers") also were noted.

Gap age (time since formation) was measured in several ways. Surrounding trees or smaller individuals within the gap were cored, and cores were sanded and examined under a microscope to look for release dates (noticeable and consistent increases in annual ring width). Sprouts that apparently originated when a tree was injured but not killed during gap formation were aged by taking cores, collecting cross sections of the sprout near its junction with the main stem for later laboratory analysis, or counting annual bud scars to determine sprout age. Changes in the rate of height or branch growth for saplings or shrubs within the gap were also noted by counting annual bud scars. Although for some gaps none of these methods provided clear results, in most cases the values probably were accurate to within a few years. For many gaps, several years after initial formation a canopy tree bordering the gap died or was broken off, adding to the gap area. In such cases gap age was dated from the initial disturbance. By convention the age of a gap was the maximum number of winters since formation; for example, for the 1976 data, a gap aged 1 occurred sometime after late summer 1975.

Details for individual gaps are given in Runkle (1979). Species nomenclature follows Radford et al. (1968).

RESULTS

Fraction of land area in gaps

Values for the fraction of land area in canopy gaps ranged from 3.2 to 24.2% for the different study areas (Table 1). Values for the fraction of land surface area in expanded gaps ranged from 6.7 to 47.0%. In general, relative gap area increased from the Pennsylvania and New York beech-hemlock stands to the Ohio beech-sugar maple stand to the southern Appalachians. Within the southern Appalachians trends were less clear.

Gap size distribution

Size distributions for both canopy gaps and expanded gaps were computed in three ways. First, areas for all gaps studied were averaged directly. Although this statistic was a useful description of the gaps analyzed, it did not accurately indicate the size distribution of gaps in the field, since a transect was more likely to intersect a large gap than a small one. Therefore, the second technique used was to divide each gap's area by the square root of its area, a term which should be proportional to its radius. The probability of a gap's being intersected is proportional to its radius. Although this technique accurately described the size distribution of gaps it is also meaningful to ask what was the average gap size associated with each pace or unit gap area. The third technique, therefore, was to weight each gap area by the number of paces (along the transect) which were in the gap. Data were fit to lognormal distributions (Table 2). This distribution is reasonable because it assumes that gap size is a result of many essentially random processes whose effects are multiplicative. Each distribution was checked for lognormality using the Kolmogorov-Smirnov test of goodness of fit (Ostle and Mensing 1975). In no case was the null hypothesis (that the distribution is lognormal) rejected at the .05 level.

TABLE 1. Percent of total land area in gaps, where EG = expanded gap, CG = canopy gap, and stands are as follows: GSM = Great Smoky Mountains National Park (stand numbers are as in Runkle 1979); JK = Joyce Kilmer Wilderness Area; WC = Walker's Cove Research Natural Area; HW = Hueston Woods State Park; TA = Tionesta Scenic and Research Natural Areas; WB = Woodbourne Forest and Wildlife Sanctuary; and HK = Huyck Preserve.

Stand	EG	CG	Total number of paces
GSM1	30.3	16.3	3182
GSM3	22.1	11.1	2568
GSM4	47.0	24.2	1283
GSM5	29.4	13.3	1972
GSM6	30.4	11.2	2036
GSM7	27.6	10.5	1822
GSM9	27.4	8.9	1346
GSM10	30.2	15.8	660
JK	29.7	17.3	1418
WC	20.6	8.2	3409
HW	14.1	7.0	5084
TA	12.0	5.0	10143
WB	6.7	3.2	1327
HK	13.8	4.8	457
All	21.0	9.5	36707

Gap sizes in the southern Appalachians and in Hueston Woods had similar mean values (t test; $P \leq .05$) but the variance in the southern Appalachians was significantly greater (F test; $P \leq .05$). On the other hand, gaps in the southern Appalachians were significantly larger ($P \leq .001$) and more variable in size ($P \leq .01$) than in Tionesta.

TABLE 2. Gap size: lognormal distributional parameters (mean ± SD, $\log_e$) for gap size in square metres (EG = area of expanded gap; CG = area of canopy gap) and sizes of largest gaps sampled. See text for discussion of different types of distributions. Stand symbols are explained in Table 1.

Stand	EG	CG
Size distribution of gaps with sampling bias		
GSM1–10,JK	5.47 ± 0.65	4.18 ± 1.13
WC	5.45 ± 0.69	4.28 ± 1.00
HW	5.43 ± 0.63	3.90 ± 1.09
TA	5.19 ± 0.55	3.85 ± 0.89
Unbiased size distribution of gaps (Gap area weighted by number of paces in gap)		
GSM1–10,JK	5.26 ± 0.63	3.44 ± 1.32
WC	5.20 ± 0.73	3.78 ± 1.00
HW	5.24 ± 0.60	3.33 ± 1.03
TA	5.02 ± 0.61	3.45 ± 0.89
Unbiased size distribution of gap area		
GSM1–10,JK	5.61 ± 0.70	4.73 ± 1.11
WC	5.64 ± 0.68	4.82 ± 0.99
HW	5.64 ± 0.65	4.63 ± 0.92
TA	5.30 ± 0.49	4.23 ± 0.81
Area (m^2) of largest gap sampled		
GSM1–10,JK	2009	1490
WC	804	707
HW	1039	507
TA	506	379

TABLE 3. Canopy gap age distribution by stand (total paces within gaps of each age as percentage of total paces). Gaps which were new in 1977 from study areas originally sampled in 1976 are not included. Stand symbols are explained in Table 1.

	Gap age (yr)															
Stand	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	>15
GSM1	4.0	0.8	0.7	0	0.1	1.9	4.6	0.2	0.6	0.2	1.3	0.3	0	0	0.2	1.2
GSM3	1.4	4.4	1.9	0.8	0	0	0.3	0	0.3	0	0.5	0	0.4	0	0	0.8
GSM4	6.5	0	3.0	1.2	0.3	0.9	1.4	0	1.7	3.7	1.4	0.8	0	0.9	1.2	1.4
GSM5	0.6	0	0.3	0.1	0.4	2.9	1.2	1.2	0	0.4	0.2	0.4	1.9	0	0	2.3
GSM6	2.0	0.2	0.9	0.6	0.7	0.2	0	0	0	1.5	0.2	1.0	0.6	0.8	2.1	0.4
GSM7	0	0.6	0	0.5	0.7	0	1.5	1.9	0.4	0.3	2.8	0	0.3	0	1.0	0.4
GSM9	0.4	1.3	3.0	0.2	1.5	0	0.8	0	0.9	0	0.3	0	0	0	0	0.6
GSM10	2.1	2.4	1.4	0	2.4	5.6	1.2	0	0	0	0.6	0	0	0	0	0
JK	0	7.4	2.5	1.8	0	0	1.0	2.0	0	0.9	0	0	0	0	1.7	0
WC	0.5	0	0.2	1.2	2.7	0.6	0.2	2.0	0	0	0	0	0	0	0	0.7
HW	0.2	1.3	1.2	0.8	0.4	1.0	0.2	0	0.1	0.9	0	0.3	0	0	0.1	0.4
TA	0.2	0.7	0.3	0.6	0.7	0.2	0.8	0.3	0.1	0.1	0.1	0.4	0.2	0	0	0.1
WB	0.5	1.4	0	1.4	0	0	0	0	0	0	0	0	0	0	0	0
HK	1.3	0	0	0	0.9	0	0	0	0	0	2.6	0	0	0	0	0
GSM,JK	2.0	1.8	1.4	0.6	0.5	1.0	1.6	0.4	0.6	0.8	0.8	0.3	0.2	0.2	0.9	0.8

Gap age distribution

To understand gap regeneration it is necessary to know the rates at which gaps are formed (gap birth rates), and the rates at which they close (gap death rates) (Paine and Levin 1981). Gaps die (become indistinguishable from the background vegetation) as a result of (1) lateral extension (branch) growth of canopy trees surrounding the gap, and (2) height growth of individuals either formerly suppressed or newly germinating from seeds. (In some cases stump sprouts of the former canopy individual also are present.) The relative importances of the sources of saplings vary. However, in the mesic forests studied, suppressed individuals were probably the most important, since almost all the major species are at least somewhat tolerant of understory conditions when small. Whether branch growth of large trees or height growth of saplings is more important in gap closure determines whether factors influencing sapling growth within the gap are apt to determine forest composition.

The observed age distribution of gap area, based on the fraction of land in gaps of each age, will be used to determine rates of gap birth and death; the concern here is with total land area in gaps of a certain age, not with amount of area per gap. For these analyses, only the canopy gap, the area directly under the canopy opening, was used. Table 3 gives the age distribution of land area in gaps for each study area individually. It is apparent that no area was in perfect equilibrium with respect to rates of disturbance (gap birth). Also, peak years of gap formation showed little regional synchrony; Great Smoky Mountains (GSM) 6 and GSM9, separated only by a large stream, had quite different distributions of gap age and area.

Lateral extension growth.—During the 1976 field season 384 trees bordering gaps were selected and their dbh measured. A vertical projection of the total lateral extent from the bole to the furthest extension of the crown into the gap was measured for each tree. The data were fit to the regression equation developed by Trimble and Tryon (1966):

TABLE 4. Average rates of lateral extension growth from the literature and from the regression equation: lateral extent (m) = $A + B^*$ Gap Age (yr) + C^* dbh (cm). Numbers missing from the table are not available from the references cited.

Species	A	B	C	r^2	P	Lateral extension growth (cm/yr)	Reference
All	2.42	.035	.017	6	.0001	4.1	Present study
Acer saccharum	0.84	.073	.041	25	.0002	8.3	Present study
Tsuga canadensis	1.06	.063	.021	25	.0001	7.0	Present study
Liriodendron tulipifera	0.90	.044	.066	22		9.4	Trimble and Tryon (1966)
Quercus rubra	0.14	.082	.109	48		16.5	Trimble and Tryon (1966)
Juglans nigra:							
Undisturbed						2.0	Phares and Williams (1971)
Partly released						5.5	Phares and Williams (1971)
Completely released						7.5	Phares and Williams (1971)
Betula lutea:							
16-yr-old stand						18–25	Erdmann et al. (1975)

$$\text{Lateral extent (m)} = A + B \times \text{gap age (yr)} + C \times \text{dbh (cm)}.$$

The annual increase in tree stem diameter was estimated using tree cores selected from canopy individuals sampled to calculate gap age. Overall values (mean ± SE) for stem diameter growth for years following release were 0.36 ± 0.026 cm/yr for a mix of species, 0.32 ± 0.024 cm/yr for hemlock, 0.24 ± 0.026 cm/yr for sugar maple, and 0.86 ± 0.058 cm/yr for tulip tree. Incorporating these results into the regression equations gave average rates of lateral extension growth per year (Table 4). Overall, a growth rate of 4 cm/yr was obtained, although hemlock and sugar maple grew about twice as rapidly. The values obtained were similar to other values in the literature (Table 4).

To determine the effect of lateral extension growth on each study area, gap dimensions were reduced by 4 cm on each side and paces in each gap were reduced by the fraction of gap area that had disappeared. For the 14 study areas, lateral extension growth filled in from 1.4 to 2.7% (average 1.9%) of total gap area each year.

Regeneration height growth and gap closure rates.—The rate at which gaps closed by the growth in height of new or formerly suppressed individuals was estimated in two ways. First, literature estimates of sapling height growth rates following cutting of the overstory were used to derive values for maximum expected time until disappearance of a gap. Second, the observed age distribution of gap area was used to approximate a survivorship function, from which an average rate of disappearance of gap area was computed.

For this study, a maximum value for gap longevity was the time required for new saplings to reach a height of 10–20 m. Many studies on natural growth rates for many species from different areas in the eastern deciduous forest show average growth rates of 0.5–1.0 m/yr following cutting or in naturally created openings (e.g., Kramer 1943, Downs 1946, Kozlowski and Ward 1957, Tryon and Trimble 1969, Marks 1975). Gaps should close even faster because they contain some advance regeneration when formed and because taller individuals grow faster than the rates given above (Laufersweiler 1955, Burton et al. 1969, Tubbs 1977*b*). In general, sprouting was rare or absent in most of the gaps observed. Using a minimum rate of growth in height of 0.5 to 1.0 m/yr and the regeneration height limit of 10–20 m mentioned earlier results in a range of maximum possible gap ages of 10–40 yr.

A more exact method of estimating the rate of gap closure used the observed age distributions of gap area (Table 3). For any group of gaps created during the same year, relatively little gap area will fill in the first few years because the regeneration for the most part will be small. However, on occasion large, formerly suppressed, individuals can eliminate some area even in young gaps. For the next few years, the regeneration in most gaps reaches a height at which gap area is converted rapidly into the background vegetation. Finally, although the annual survival rate of gap area may continue to decrease, the fraction of total land area converting from gaps to the background will decrease due to the relatively small fraction of land area that consists of old gaps.

TABLE 5. Parameters for the logistic model of gap area, $N(t,a) = (49Ke^{r} - 50K)/(49e^{r} - 50 + e^{ra})$, where $N(t,a)$ is the percentage of land area in canopy gaps of age a at time t, and K and r are fitted constants. Stand symbols are explained in Table 1.

Stand	K	r	Inflection point (yr)	$N(t,1)$
GSM1	1.84	0.306	9.2	1.70
GSM3	2.97	1.487	3.4	2.89
GSM4	2.50	0.256	10.1	2.28
GSM5	1.20	0.121	13.8	0.84
GSM6	0.94	0.160	12.6	0.81
GSM7	0.87	0.172	12.2	0.76
GSM9	1.37	0.558	6.4	1.31
GSM10	2.43	0.465	7.2	2.30
JK	3.67	1.263	3.8	3.57
WC	1.01	0.358	8.4	0.94
HW	0.91	0.420	7.6	0.86
TA	0.60	0.325	8.9	0.56
WB	0.88	1.010	4.4	0.85
HK	0.47	0.213	11.1	0.42
GSM1–10,JK	1.49	0.291	9.4	1.37

Of several possible approaches to this process the logistic equation was examined in detail. Assume that the fraction of gap area surviving from age a to age $a + 1$ is independent of a:

$$\frac{dN(t,a)}{da} = -r_c N(t,a)$$

where $N(t,a)$ is the fraction of total land area in gaps of age a at time t, and r_c is a constant rate of gap closure. Next, let the rate of gap closure increase as the fraction of total land area in gaps decreases; when total gap area is small, gaps tend to be older and so should be closing more rapidly due to sapling height growth. A linear relationship will be used as a first-order approximation. Making r_c a linear function of $N(t,a)$ results in

$$\frac{dN(t,a)}{da} = -\left[r - \frac{r}{K}N(t,a)\right]N(t,a)$$

where r and K are constants. From a standard table of integrals, this equation has the following solution:

$$N(t,a) = \frac{K}{1 + e^{ra+b}}$$

where b is a constant. The assumption that at first, from age $a = 0$ to age $a = 1$, lateral extension growth is the only process of importance, in accordance with the pattern of change hypothesized above, gives

TABLE 6. Estimated birth rates (percent of total land area per year) for canopy gaps for each stand. Canopy gap dimensions were increased to compensate for lateral extension growth and then the total revised gap areas in each study area for the most recent 1-, 5-, and 10-yr periods were averaged together. Stand symbols are explained in Table 1.

Stand	Averages over		
	1 yr	5 yr	10 yr
GSM1	4.0	1.1	1.4
GSM3	1.4	1.7	0.9
GSM4	6.6	2.2	2.0
GSM5	0.7	0.3	0.9
GSM6	2.0	0.9	0.7
GSM7	0	0.4	0.6
GSM9	0.4	1.3	0.9
GSM10	2.1	1.8	1.7
JK	0	2.4	1.6
WC	0.5	1.0	0.8
HW	0.2	0.8	0.6
TA	0.2	0.5	0.4
WB	0.5	0.7	0.3
HK	1.3	1.2	1.1
GSM1–10,JK	2.0	1.2	1.1

$$.98 = \frac{N(t,1)}{N(t,0)}.$$

Solving for e^b and substituting back into the equation for $N(t,a)$ results in

$$N(t,a) = \frac{49Ke^r - 50K}{49e^r - 50 + e^{ra}}.$$

This equation was tested for goodness of fit to each study area using the least squares nonlinear procedure of the SAS statistical computer package (Barr et al. 1976), which also computed best fit estimates for r and K. F tests showed all the regressions but one (the Huyck Preserve, with its small sample size) to be highly significant ($P \leq .01$).

The inflection point or age at which gap area was being converted most rapidly into the background vegetation (defined here as 10–20 m tall) was found by solving for the second derivative of the preceding equation, resulting in

$$a = \frac{1}{r}\ln(49e^r - 50).$$

The value of a, the inflection point, was computed for each study area (Table 5); the average value of the 14 study areas was 8.5 yr, a reasonable result given the average rates of sapling height growth discussed previously.

A gap aged a is a fraction $N(t,a)/N(t,1)$ of its original size. An average annual survivorship rate may be computed by assuming the gap loses a constant fraction of its area each year. The fraction of gap area which survives each year (for $a - 1$ years) can be determined from the following equation:

$$\bar{S}_a = \left(\frac{N(t,a)}{N(t,1)}\right)^{1/(a-1)}.$$

This term was decomposed into a survivorship rate from lateral extension growth, $S_L = .98$ (which value should remain roughly constant), and a survivorship rate from sapling height growth, $\bar{S}_{H,a} = \bar{S}_a/S_L$. As an example of the relative importance of these two processes for gaps of different ages, the following results for the southern Appalachians (Great Smoky Mountains and Joyce Kilmer) were obtained:

a	$\bar{S}_a$	$\bar{S}_{H,a}$
2	.98	1.00
5	.96	.98
10	.93	.94
15	.88	.90
20	.85	.87
30	.82	.83

Therefore, after the first few years $\bar{S}_{H,a} < S_L$; i.e., sapling height growth is the more important means of gap closure, implying that sapling growth within even fairly small gaps may be important in determining forest composition.

In using the observed age distribution as a survivorship function it is assumed that the age distribution was approximately stable and stationary, having no major directional changes in gap birth rate. Several factors supported this assumption. First, predictions of the model agreed well with literature values concerning average rates of sapling height growth. Second, results from different study areas were similar, implying that a biological process more basic than random fluctuations was operating. Third, all areas but the one least sampled showed highly significant ($P \leq .01$) fits to the distribution, implying that it was related to a real biological phenomenon.

In addition, homeostatic mechanisms tend to keep the gap age distribution from fluctuating too greatly. The total fraction of land in gaps at time t, $M(t)$, should vary with rates of gap birth and death as follows:

$$dM(t)/dt = B'(t)[1 - M(t)] - D(t)M(t)$$

where $B'(t)$ is the fraction of area not in gaps which is converted into gaps at time t and $D(t)$ is the fraction of gap area which is converted into the background vegetation at time t. Thus, after several years of excessively high disturbance rates, $M(t)$ should be high, $B'(t)[1 - M(t)]$ should be relatively low, and $D(t)M(t)$ should be relatively high, resulting in a gradual decrease in $M(t)$ until more normal values are obtained. Also, as those trees most susceptible to disturbance are eliminated, the remaining individuals should be more resistant.

Birth rate.—The rate at which gaps were formed was estimated in several different ways. The most direct measure was the fraction of total land area covered by gaps ≤1 yr old. However, gap birth rates varied from year to year and so some sort of time averaging was necessary. A problem with time averaging was that original gap areas were not known exactly but had to be estimated from the rate of closure discussed previously.

One approach was to increase gap dimensions (length and width) by 8 cm (Table 4) for each year the gap existed. Thus a gap aged 10 yr was assumed to have been 80 cm longer and wider when formed and the original gap area was calculated using these new dimensions. The number of paces in each gap was increased in proportion to this increase in size. All these paces within one study area were summed to result in a new gap age distribution, based on estimated original gap sizes. These estimates of original gap area were averaged for the most recent 5- and 10-yr periods (Table 6). Averages for 5 yr are probably the best available estimates of gap birth rate. Averages for 10 yr are less accurate due to an increase in gap closure by sapling height growth.

A second approach was to use the model described previously (Table 5), letting $a = 1$. In general all methods gave similar estimates, both in actual value and in the relative magnitude of disturbance rates in the different areas. Gap birth rate values from study areas in the southern Appalachians ranged from 0.3 to 3.6%, using different methods, with an average of about 1.2 to 1.7%. Hueston Woods averaged about 0.7 to 0.8% per year of new gaps; Tionesta, 0.5 to 0.7%.

As a check on these values, 54% of the 1976 transect distance was repaced in 1977, resulting in 10 new gaps, for which the canopy gaps made up 1.2% of the ground surface area.

Species responses to gaps

How did different species respond to the variations in gap size and age described above? To help answer this question, Gaussian curves for species were fit using either gap size or age as the abscissa. For gap size, expanded gap area was used in order to include more completely the direct and indirect effects of the gap on forest regeneration. Four measures of species importance were used: total basal area (sum of basal areas of all individuals of the given species within the gap), total number of stems (total number of stems of the given species ≥1 m high within the gap), relative basal area (total basal area of the given species divided by the sum of total basal areas of all species), and relative number of stems. The data were further divided into gaps from three major geographic regions: Tionesta, Hueston Woods, and the southern Appalachians (Great Smoky Mountains, Joyce Kilmer, and Walker's Cove). Gaussian curves also were fit for several gap community properties. In all cases Gaussian curves were fit using Cornell Ecology Program 12 (Gauch and Chase 1974). This program computed the percentage of variance accounted for by each fitted curve and for all curves together as a measure of goodness of fit. F values were computed as follows:

$$F_{2,n-3} = \left(\frac{PV}{1 - PV}\right)\left(\frac{n-3}{2}\right),$$

where n was the number of points (gaps) in the sample and PV was the fraction of total variance (corrected for the mean) accounted for by the Gaussian model. This term underestimated the significance of the results because the error mean square probably was inflated by unaccounted for but real factors such as differences in elevation, soils, topography, or geography.

Curves of several community properties vs. gap size and age were fitted for the southern Appalachians, in

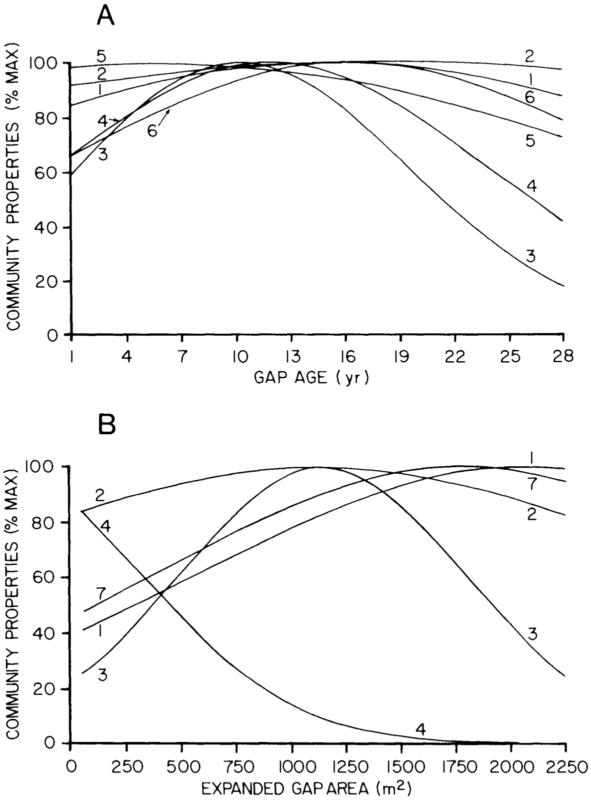
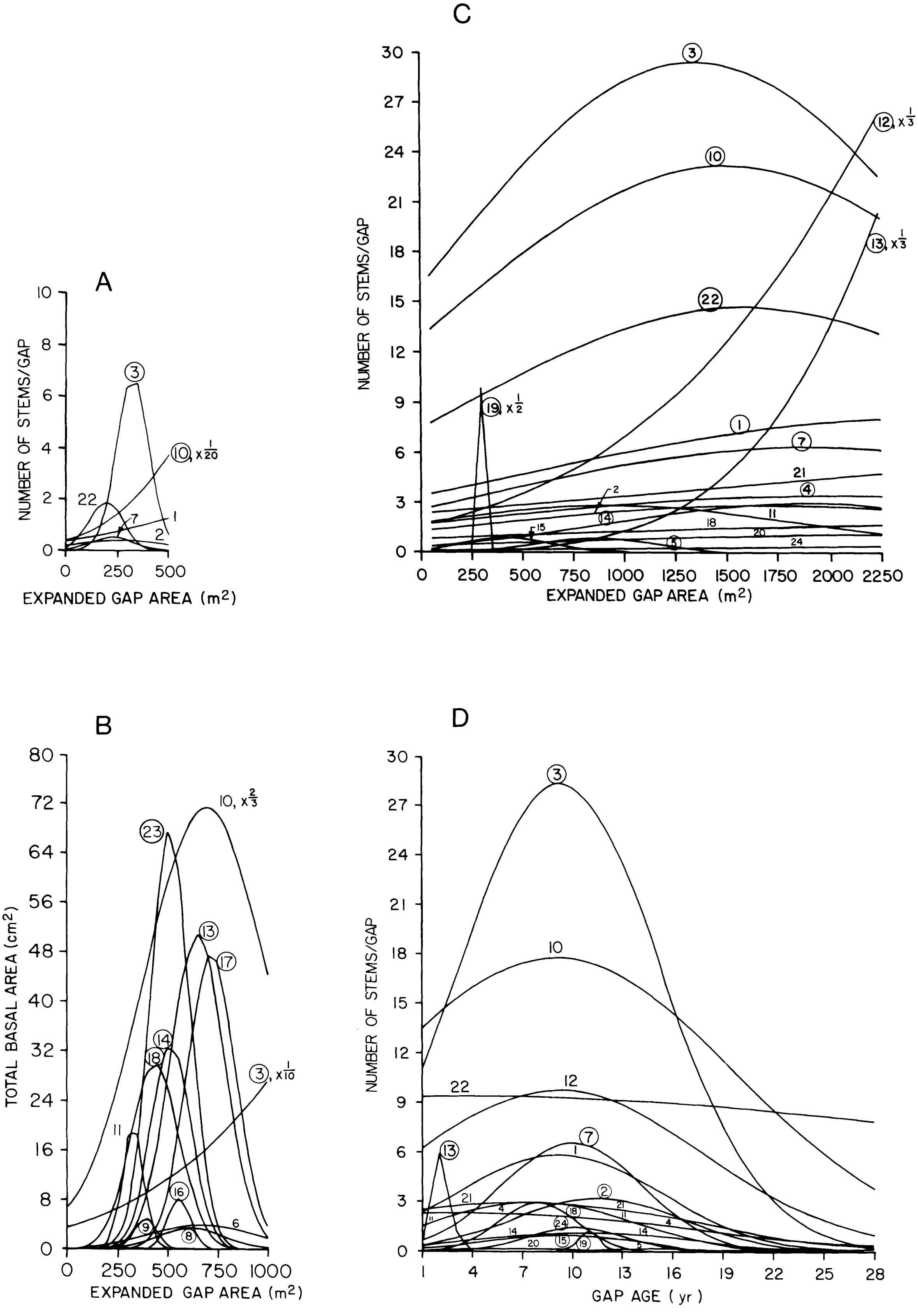


FIG. 1. Fitted Gaussian curves for properties of woody stems within each gap as a function of gap age (A) and expanded gap area (B) for the southern Appalachians as a whole. Community properties included are (1) number of woody species with individuals at least 1 m high; (2) complemented Simpson index, $DS = 1 - \sum_i P_i^2$, where P_i is the average of relative number of stems and relative basal area for sapling species i; (3) total number of stems ≥1 m high; (4) density, i.e., number of stems ≥1 m high divided by expanded gap area; (5) fraction of stems ≥1 m high but <1.0 cm dbh (this property is plotted only for part A); (6) fraction of stems 1.0–2.5 cm dbh (this property is plotted only for part A); and (7) total basal area of all stems (this property is plotted only for part B).


A
NUMBER OF STEMS/GAP
EXPANDED GAP AREA (m2)
3
10, x1/20
22
7
1
2
B
TOTAL BASAL AREA (cm2)
EXPANDED GAP AREA (m2)
10, x2/3
23
13
17
14
18
3, x1/10
11
16
9
8
6
C
NUMBER OF STEMS/GAP
EXPANDED GAP AREA (m2)
3
12, x1/3
10
13, x1/3
22
19, x1/2
1
7
21
4
2
14
15
18
11
20
24
5
D
NUMBER OF STEMS/GAP
GAP AGE (yr)
3
10
22
12
7
1
13
2
21
11
4
18
24
14
20
15
19
5

which the sample size was sufficient to detect significant relationships accounting for only 2–30% of the total variance (Fig. 1). Gap size and age varied more or less independently; correlations between them were very low. As gap size increased, the number of species increased and the concentration of dominance decreased. Total basal area and number of stems increased for most of the range of gap sizes encountered. The decrease in these terms for very large gaps may have been an artifact since few large gaps were sampled. Sapling density (number per square metre) decreased as gap size increased, however, probably because an increasing fraction of the ground surface was covered by fallen boles, branches, and other debris.

Gaps of different ages were interpreted generally to form a single chronological sequence. However, different gaps filled in at different rates, and gaps that were detectable but relatively old (>15 yr, say) were in some sense peculiar or else they would already have disappeared. Therefore the response of community properties and species for very old gaps was interpreted with caution. New species and new individuals were added to the gap for 10–15 yr after gap formation (Fig. 1). Although only individuals ≥1 m high were measured, these results imply that gaps were open to invasion by new individuals for several years. Whether such new individuals could outcompete those already established is questionable, however. Finally, the fraction of stems ≥1.0 m high but <1.0 cm dbh increased for 5 yr, after which it declined and the fraction 1.0–2.5 cm dbh increased.

The responses of individual species to differences in gap size and age also were examined, choosing those relationships shown to be most significant in Table 7 (Fig. 2). In Tionesta the number of stems of beech, the dominant species, increased with increased gap size for the range of values recorded. Most other species peaked in number of stems at intermediate values of gap size, perhaps because the higher overall number of stems in larger gaps attracted more deer, favoring the relatively unpalatable beech (Bjorkbom and Larson 1977). Hueston Woods also showed a general direct relationship between number of stems and gap size for most species. The final increase in sugar maple and decrease in most other species may have occurred because the two largest gaps both were created at most 3 yr before my sampling, and relatively few species (other than sugar maple) were abundant. In the southern Appalachians, also, larger gaps contained more individuals of most species; however, few very large gaps were sampled. Densities (number of stems per square metre) for most species were greater in small gaps than in large gaps. Although large gaps probably had more favorable growth conditions and so might be expected to have had higher sapling densities than small gaps, large gaps also had relatively greater area unavailable to sapling growth due to fallen boles, branches, and leaves. In the southern Appalachians most species reached their maximum densities at gap ages of 7–12 yr, in good agreement with the rates of gap closure estimated earlier.

TABLE 7. Variance accounted for (%) by fitting Gaussian curves to sets of species importance values. EG = Expanded gap area. Significance values are symbolized by * for .01 < $P \leq .05$, ** for $P \leq .01$.

Measure of species importance	Percent variance accounted for					
	Hueston Woods		Tionesta		Southern Appalachians	
	Age	EG	Age	EG	Age	EG
Relative density	2	5	1	3	1	1
Relative basal area	4	5	2	2	1	1
Total number of stems	4	20*	0	49**	3*	7**
Total basal area	8	37**	2	17**	1	6**

To what degree did species respond individualistically to differences in gap age and size? No two species had identical curves (Fig. 2). However, the variance in the curves was large and much overlap among species existed. Also, in no case was the overall pattern of variation in relative number of stems or relative basal areas significant (Table 7). The dominant species were found in gaps of all ages and sizes.

To examine different species patterns further, weighted average ordinations were run using Cornell Ecology Program 25B (Gauch 1977). Only species occurring in at least 10% (41) of the total number of gaps sampled were used. Their importance (measured as the average of relative number of stems and relative

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FIG. 2. Fitted Gaussian curves for species importance values: (A) Tionesta, total number of stems vs. expanded gap area; (B) Hueston Woods, total basal area (cm^2) of stems vs. expanded gap area; (C) southern Appalachians as a whole, total number of stems vs. expanded gap area; and (D) southern Appalachians as a whole, total number of stems vs. gap age. Species are, by number, (1) *Acer pensylvanicum*, (2) *A. rubrum*, (3) *A. saccharum*, (4) *Aesculus octandra*, (5) *Aralia spinosa*, (6) *Asimina triloba*, (7) *Betula* spp., (8) *Carya cordiformis*, (9) *Celtis occidentalis*, (10) *Fagus grandifolia*, (11) *Fraxinus americana*, (12) *Halesia carolina*, (13) *Lindera benzoin*, (14) *Liriodendron tulipifera*, (15) *Magnolia acuminata*, (16) *Morus rubra*, (17) *Ostrya virginiana*, (18) *Prunus* spp., (19) *Pyrularia pubera*, (20) *Sambucus pubens*, (21) *Tilia heterophylla*, (22) *Tsuga canadensis*, (23) *Ulmus rubra*, and (24) *Viburnum alnifolium*. Curves which are significant ($P \leq .05$) have the species number circles. Fractions ($\times ^1/_{20}$, $\times ^2/_3$, etc.) indicate extent to which the amplitude of a curve has been reduced from its original value to fit on the same scale as the other curves.

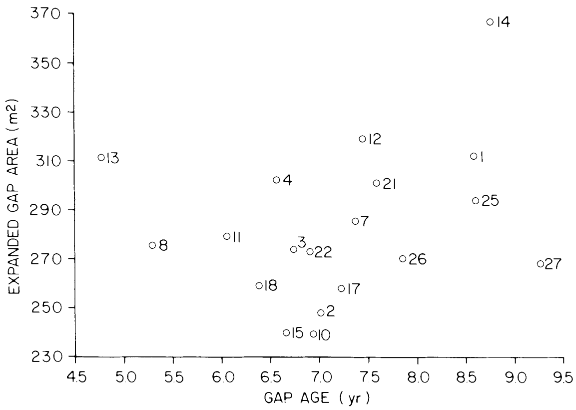

Fig. 3. Distribution of species present in ≥10% of all gaps in relation to gap age and expanded gap area, based on averages of species importance values weighted by gap size and age. Species are numbered as in Fig. 2, with additional species (25) *Amelanchier arborea*, (26) *Magnolia fraseri*, and (27) *Rhododendron maximum*.

basal area) in each gap was weighted by the age of the gap for the first ordination axis and by the expanded gap area for the second ordination axis. Results (Fig. 3) show the scattering of species along one primary gradient, from species reaching maximum importance in small young gaps (understory tolerants, e.g., beech) to those doing best in large old gaps (opportunists, e.g., tulip tree). The correlation coefficient for the two axes is $r = .262$, resulting in $F(1,17) = 4.45$, significant at $P \leq .05$. Two shrubs had somewhat anomalous response patterns. *Lindera benzoin* grew rapidly in large gaps but was overtopped by tree saplings and so did relatively better in young gaps. *Rhododendron maximum*, a shade-tolerant species able to expand vegetatively, did well in fairly small gaps but reached maximum importance in relatively old gaps. It may have grown fairly rapidly even in small gaps; an alternate explanation, however, is that its presence inhibited the growth of other species, so that gaps which were relatively old but still recognizable tended to be those in which site conditions were favorable for rhododendron.

In addition to having somewhat different responses to gap size and age, species also showed differences in the types of injuries they received when they created gaps (Table 8). Only 19% of the gapmakers were uprooted. More commonly trees broke off at some height above ground, about evenly divided between breaks >2.5 m high (28%) and ≤2.5 m high (30%). Finally, about equal numbers died standing (10%) or contributed to a gap by losing large branches though remaining alive (13%). Several species showed significant ($P \leq .05$) propensities for certain types of injuries. Beech was partly uprooted 26% of the time vs. 19% for all species, perhaps due to its shallow spreading root system (Fowells 1965). Living red (*A. rubrum*) and sugar maples and white ash contributed to gaps relatively more than did living trees of other species. Hemlock was less likely to be totally uprooted (7 vs. 14% for all species) but more likely to break at ≤2.5 m (37 vs. 30% for all species). The existence of many snags has important implications for wildlife, a topic of much current interest (Hardin and Evans 1977, Scott et al. 1977, Evans and Conner 1979).

Discussion

The observed gap birth rates of ≈1%/yr (ranging from ≈0.5 to ≈2%/yr for large samples) were similar to disturbance rates for northern conifer forests (Heinselman 1973, Zackrisson 1977), an old-growth beech-maple forest in Indiana (Abrell and Jackson 1977), and tropical rainforests (Leigh 1975, Hartshorn 1978). Inverting the figure for gap birth rate resulted in a natural rotation time, that is, a measure of the average number of years required in nature to regenerate an area equal to the total area under consideration (cf. Heinselman 1973). Both the present study and those studies cited above gave a natural rotation of ≈100 yr, varying from ≈50 to ≈200 yr.

Two questions emerged from these results. First,

Table 8. Gapmakers: frequencies (%) for species-injury classes for species represented by more than four trees. Significance levels are marked † for $.05 < P \leq .10$, * for $.01 < P \leq .05$, and ** for $P \leq .01$.

Species	*N*	Alive but injured	Standing dead	Snag >2.5 m high	Snag ≤2.5 m	Partly uprooted	Uprooted
Acer rubrum	9	44*	11	0	22	0	22
A. saccharum	64	20†	12	27	27	3	11
Aesculus octandra	17	18	6	41	12	6	18
Betula lutea	19	16	21	26	26	5	5
Castanea dentata	7	0	13	12	25	0	50*
Fagus grandifolia	237	11	10	25	29	7	19**
Fraxinus americana	8	62**	12	0	12	0	12
Halesia carolina	71	13	7	34	24	6	17
Magnolia fraseri	13	8	0	38	46	8	0
Tilia heterophylla	47	4	2†	40†	40	6	6
Tsuga canadensis	163	10	12	28	37*	6	7*
All	674	13	10	28	30	6	14

Table 9. Longevities at key sizes for canopy trees. Minimum, average, and maximum sizes of gapmakers are taken from the present study. Relationships between tree size and age are taken from the literature cited below. Stand symbols are explained in Table 1.

Source of size-age relationships	Stands to which relationship applies	Species	Average age (yr) at 25 cm dbh	Years from 25 cm dbh to average dbh of gapmakers	Age of largest gapmaker (yr)
R. H. Whittaker (personal communication)	GSM	All	91	127	441
		Acer saccharum	79	64	197
		Aesculus octandra	95	141	431
		Fagus grandifolia	101	54	220
		Halesia carolina	78	51	201
		Liriodendron tulipifera	55	153	226
		Tilia heterophylla	54	49	198
		Tsuga canadensis	106	211	525
Morey (1936*a*)	TA	*Tsuga canadensis* (two sites)	185, 119	181, 84	607, 315
		Fagus grandifolia (two sites)	179, 122	93, 85	412, 334
		Betula lutea	100	110	251
Tubbs (1977*a*)	HW	*Acer saccharum* (virgin stand)	177	78	372
		Acer saccharum (managed stand)	93	67	260
Gates and Nichols (1930)	HW	*Acer saccharum*	129	40	229
	TA	*Tsuga canadensis*	165	107	415

how could one reconcile a 100-yr rotation with the fact that dominant forest trees are known to live for much longer periods? Second, were the observed similarities in yearly disturbance rates among the several different communities solely a matter of coincidence or was some underlying mechanism responsible?

The first question was answered partially as follows. The rotation time was not equivalent to the total longevity of a canopy tree but to the average time a tree was canopy size and capable of creating a gap. Therefore, rotation time was approximately equal to the difference in tree age between the time the average tree entered the canopy and the time it died. Setting 25 cm dbh as the approximate lower limit for canopy trees worked fairly well. Of 2921 trees recorded using the point-centered quarter method (nearest four trees either alive and ≥25 cm dbh, or dead and contributing to a gap), only seven individuals were ≥25 cm dbh and dead without creating a gap, and only two individuals <25 cm dbh created gaps. The data from this study on 666 gapmaking individuals ≥25 cm dbh provided an estimate of the size at which trees reaching the canopy die. These sizes were converted to ages using relationships given in the literature and then into the time it took an individual to grow from 25 cm dbh to the average diameter at death for the given species and region (Table 9). The values obtained agree well with the previously estimated natural rotation period of 50–200 yr.

Two factors produce maximum ages greater than these values. First, most of the important species can persist for many years under a closed canopy, growing very slowly (Table 9). Scattered pole-sized survivors were found in many of the gaps studied and undoubtedly were important in gap closure. Second, gaps can occur on one site several times before they occur on a second site. Therefore, individuals on some locations can live longer than the average (Table 9).

Reasons for similarities among different forest types were investigated using a simple model. If an area were subjected to an average rate of disturbance x (fraction of land area per year), a fraction y of the total area would not be affected by disturbances of age $\leq a$. These parameters were related as follows:

$$(1 - x)^a = y$$

This model assumed that the probability of any point undergoing disturbance was independent of the time since last disturbance, with some points likely to undergo a disturbance many times while others remained undisturbed. Table 10 gives the minimum age (a) of five fractions of the stand, y = 50% through 0.01%, for several rates of disturbance (x). For instance a birth rate of 1%/yr would result in 50% of the stand being over 70 yr old, 10% over 229 yr old, and 1% over 458 yr old. The age at which only 0.01–1% of the stand had not undergone disturbance would approximate the normal maximum life span of the forest dominants. Much literature, for both temperate (Jones 1945, Fowells 1965) and tropical regions (Budowski 1965, Ashton 1969), has suggested that forest dominants usually have life spans of 100–1000 yr. These values correspond to disturbance rates of about 0.5–2.5%/yr, similar to those values given above.

It is unclear whether internal (physiological or structural) constraints or external forces were more important as causes of mortality, although both probably were involved (Bormann and Likens 1979, White 1979). For a forest to maintain itself, disturbance rates need to be low enough so that trees can reach maturity

TABLE 10. Hypothetical gap birth rates (percent of total land area) with expected age distribution for land area.

Birth rate (%)	% of stand at least given age (yr)				
	50%	10%	1%	.1%	.01%
	Age (yr)				
0.1	693	2301	4603	6904	9206
0.3	231	766	1533	2299	3066
0.5	138	459	919	1378	1837
1.0	70	229	438	687	916
1.5	46	152	305	457	609
2.0	34	114	228	342	456
2.5	27	91	182	273	364
5.0	14	45	90	135	180
10.0	7	22	44	66	87
20.0	3	10	21	31	41

TABLE 12. Observed size distribution for all gaps taken together.

Size class maximum value (m^2)	Canopy gaps		Expanded gaps	
	Number	% land area	Number	% land area
25	84	0.89	0	0
50	72	1.04	2	0.04
75	57	1.11	13	0.49
100	67	1.92	30	1.12
150	52	1.40	59	2.47
200	28	0.82	70	3.19
400	32	1.28	171	8.98
700	11	0.70	44	3.08
1000	2	0.13	12	0.97
1500	1	0.20	4	0.38
2500	0	0	1	0.26
Sum	406	9.50	406	20.98

and reproduce. On the other extreme, as trees increase in size (age), they decrease in the efficiency of transporting water, nutrients, and photosynthate (Spurr and Barnes 1973, Oldeman 1978), in the favorability of the root/shoot ratio (Borchert 1976), and in the ratio of photosynthetic to nonphotosynthetic tissue (Harper 1977). The net result is a decreased ability to withstand climatic extremes and an increased susceptibility to attack by insects and fungi. Therefore, even in the absence of any severe disturbance, canopy trees in general have only a restricted range of possible longevities, and forests in approximate equilibrium have only a narrow range of possible disturbance rates, falling near 1%/yr.

The preceding analysis implies that a forest's response to disturbance depends not so much on the average rates of disturbance as on the distribution of disturbance in time and space.

To compare openings of different sizes, the most meaningful measure of gap size is the ratio of the diameter D of the gap to the mean height H of the surrounding stand. Several studies have shown that both light and soil moisture in the center of the gap increase as this ratio increases, leveling off when D/H reaches ≈ 2 (Geiger 1965, Minckler and Woerheide 1965, Minckler et al. 1973). For the present study, average stand heights were estimated to be 32 m in the southern Appalachians, 27 m in Hueston Woods, and 25 m for the other northern sites. These estimates are based on occasional direct measurements using an optical rangefinder, lengths of fallen trees, and some literature values (Whittaker 1966). The average of gap width and length was used for the gap diameter. For most gaps $D/H \leq 0.5$, although 18% of the gaps had higher values, one with $D/H = 1.6$ (Table 11).

TABLE 11. Frequency distribution for canopy gap diameter (D)/canopy height (H). Canopy gap segments distinct enough to warrant individual dimensions were treated as separate gaps.

D/H class maximum value	Number of gaps
0.2	89
0.4	189
0.6	99
0.8	30
1.0	8
1.1	2
1.6	1

A great many forestry studies and general reviews state that the selective cutting of individual trees will favor shade-tolerant species such as beech, hemlock, and sugar maple, at the expense of light-demanding species such as black cherry, white ash, tulip tree, and yellow birch (e.g., United States Department of Agriculture 1973, McCauley and Trimble 1975, Leak and Filip 1977, Tubbs 1977*b*). However, openings as small as 400 m^2 have been found sufficient for tulip tree and yellow birch to maintain themselves in a forest (Merz and Boyce 1958, Tubbs 1969, Trimble 1970, Schlesinger 1976).

If "opening," as defined by foresters, is equivalent to "canopy gap," then 1.03% of the land area was in gaps greater than the 400-m^2 limit given above (Table 12). If "opening" is equivalent to "expanded gap," then 4.69% of the total land area was in gaps of the appropriate size. In either case the observed size distribution seemed sufficient to allow some light-demanding species to persist in these forests.

CONCLUSIONS

In areas of deciduous forest protected from large-scale disturbances of wind or fire, disturbances on the scale of a single dead tree made up a significant fraction of the total land area. Gaps in the forest canopy closed primarily due to the height growth of sapling or subcanopy individuals, not to the lateral spread of other canopy trees. Therefore, even small disturbances provided regeneration possibilities for forest species.

Species responses to the regeneration opportunities varied. Tolerant species were present as suppressed saplings before the gap was formed and dominated small, young gaps. Although these species also were abundant in larger, older gaps, their relative importance was lower because of the increased success of opportunists (species unable to survive under a closed canopy or in small gaps but able to grow rapidly in larger gaps), which became more important with time. The observed disturbance regime strongly favored tolerant species but allowed opportunists to persist in low densities.

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