

Understory response to canopy gaps of varying size in a mature oak forest¹

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EHRENFELD, JOAN G. (Center for Coastal and Envir. Stud., Rutgers Univ., New Brunswick, New Jersey 08903). Understory response to canopy gaps of varying size in a mature oak forest. Bull. Torrey Bot. Club 107: 29-41. 1980.—I have studied canopy gaps in a mature oak forest to determine whether gap size is an important variable controlling the mode of response of the understory vegetation. A severe gypsy moth defoliation produced single-tree and multiple-tree openings, and I censused the vegetation in these openings and in matched control sites to see whether new plants became established, or whether existing plants reorganized their division of resources within the gap area. The data indicated that no "new establishment" of plants had occurred. Rather, the vegetation had reorganized itself, with understory species, principally *Cornus florida*, becoming the most important element in the lower stratum. The understory species evidently occurred in patches of high relative density, within which canopy-tree reproduction was apparently inhibited or excluded. Because most of the gypsy moth-caused gaps were smaller than these patches of understory growth, gap size did not appear to affect the mode of response of the vegetation. I suggest that gap dynamics can be understood, and perhaps predicted, by superposing the pattern of canopy openings on the patchwork of understory-species growth in the disturbed stand.

Key words: disturbance; forest ecology; gap dynamics; gypsy moths; shrubs.

This paper describes the response of the understory of a mature oak forest to tree mortality following a severe gypsy moth infestation in northern New Jersey. My purpose was to ascertain how the plant community changed with respect to its species composition and its physical structure, and how these changes could be understood in the context of the literature on the role of disturbance in forest ecology (Loucks 1970; Marks 1974; Mattson and Addy 1975; Connell and Slayter 1977; Grubb 1977; Oliver and Stephens 1977; Pickett and Thompson 1978).

Although gypsy moths (*Lymantria dispar* (L.)) are not a native source of disturbance to American forests, they are similar in their effects to many native pests; forest tent caterpillars, cankerworms and orange-striped oakworms can defoliate trees severely enough to cause mortality

(Fowells 1965), and 110 other oak defoliators are known to occur in eastern North America (Baker 1972). Indeed, Peter Kalm described extensive defoliation of oaks in southern New Jersey: "they (caterpillars) strip the trees so entirely of their leaves, that it has the fatal consequence that they cannot withstand the heat any longer, and dry up entirely. In this manner great forests are often ruined entirely. The Swedes . . . showed me . . . great tracts in the woods, where young trees were now growing instead of the old ones which some years ago had been destroyed by the caterpillars." (Entry of December 9, 1748, in Kalm 1770.) The damage caused by gypsy moths is especially useful in studying the role of disturbance in oak forests because the heavy infestations that produce mortality tend to occur in small to medium-sized spots or foci (Campbell and Sloan 1978; McGuire and Mulhern 1974). Such infestations tend to be synchronized across large areas (Campbell and Sloan 1978), and therefore many gaps of uniform age but variable size are produced in which replacement and growth responses can be monitored.

"Disturbance" is a broad term which

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includes diverse kinds of disruption of the forest matrix (cf. Bormann and Likens 1979; Grubb 1977; Pickett and Thompson 1978). Thus it is useful to circumscribe the term as it will be used below. The gypsy moth-caused disturbance is characterized by 1) the rapid death of mature trees from defoliation-induced stress or from secondary infection by fungus or borers (Dunbar and Stephens 1975), which produce 2) openings of the canopy that permit light to penetrate the forest, but 3) does not expose mineral soil through the formation of tip-up mounds. During the period of defoliation (1 to 2 years), the entire stand may be opened up to an increased penetration of light. However, during subsequent years, canopy gaps persist only around the dead trees; environmental conditions around these dead trees continue to contrast strongly with the surrounding recovered forest until the gaps are closed. Thus, it is reasonable to look for gap-related features in the vegetation beneath the dead trees that might contrast with the vegetation in the rest of the stand.

The variety of forest responses to disturbance have been subjected to some broad categorizations in the literature. Two major patterns of gap response have been succinctly described by Marks (1974). 1) The "reorganization" response involves the release of plants established prior to the disturbance, and the subsequent competition that results in a replacement individual. 2) the "new establishment" response involves the origin of new plants within the area of disturbance; these new individuals originate from buried seeds or from newly disseminated seeds. Connell and Slayter (1977) have described three models for the events which follow new establishment; the models differentiate communities in which the invading species facilitate, repress or simply compete with subsequent contingents of species. These various kinds of responses have each been observed in such a wide array of situations, however, that it is difficult to predict the conditions under which one or another of these patterns will prevail.

I have used the disturbance caused by the gypsy moth to ask the question: is gap size a critical factor in determining whether "reorganization" or "new establishment" occurs within a given gap? If not, are there other features of the vegeta-

tion or the disturbance which appear to control the mode of response of the plant community?

Several basic hypotheses concerning the events that occur in the "new establishment" process are explicit or implicit in most of the literature. They are:

1) Species diversity increases because pioneer (or fugitive) species invade areas of disturbance.

2) Total foliage cover of the ground decreases because of the loss of canopy trees; there is a concomitant change in microclimate at or near the forest floor.

3) Plant density within the area of disturbance increases significantly over that of the undisturbed forest, because of the influx of pioneer species and the initiation of tree seedlings.

4) The species composition of the forest as a whole undergoes shifts as a result of gap formation, because less shade-tolerant species may gain prominence over those in the original forest, or over the more tolerant species expected to emerge as dominants.

The "reorganization" process, on the other hand, postulates two events.

1) Tree seedlings are released from light and root competition, and grow rapidly into the larger size-classes.

2) The species composition of the forest as a whole shifts as species that are more tolerant than the destroyed canopy trees assume dominant status.

I have analyzed data from 7 to 8-year-old gaps to see how well these various hypotheses fit the observations from gaps of various sizes.

Methods. My studies were conducted during 1976 and 1977 at the Morristown National Historical Park in northern New Jersey. A major gypsy moth outbreak began in 1967, and continued through 1970, at which time the population collapsed (Weig 1971); no chemical insecticides were applied during the outbreak. Subsequent surveys (Kegg 1971; Weig 1971) showed that approximately 10,000 oaks died during the last season of defoliation; this was, on average, 22 trees per hectare, or about 30% of the total population of oaks in the forest, and 7% of the total tree population. The defoliation-induced mortality was concentrated in patches of high mortality (70 to 100% of the oaks dead)

scattered among areas with little or no mortality.

The Park occupies two parallel ridges and the valley between them in the Highlands province of New Jersey. The soils are acid, stony loams derived from gneiss bedrock; the soils of the ridgetops are excessively drained, those of the slopes are deep and well-drained, and those of the valley bottoms tend to have restricted drainage because of fragipan development. The ridgetops support a community in which *Quercus prinus* L., *Betula lenta* L., and *Acer rubrum* L. have approximately equal relative densities in the canopy, and in which *Cornus florida* L. contributes over 60% of the understory stems. On the slopes, a mixture of *Quercus alba* L., *Q. rubra* L., and *Q. velutina* Lam. contribute 20 to 30% of the canopy stems, and the rest of the stand contains *Fagus grandifolia* Ehrh., *B. lenta*, *A. rubrum*, *A. saccharum* Marsh., *Liriodendron tulipifera* L., *Carya* spp., and other hardwoods; the understory contains a variety of small tree and shrub species. The stream bottoms contain relatively little oak (5%) and are dominated by *F. grandifolia*, *A. rubrum*, and *Betula lutea* Michx. f. Dominant and co-dominant trees range in age from 50 to 150 years, and average 80 years. Pit-and-mound microtopography, sprout clumps of most species, and historical analysis indicate that the forest was subject to moderate to light logging from the early 1800's until 1910, and has been free from disturbance since then (Ehrenfeld 1977).

I sampled the vegetation surrounding 29 dead oaks located throughout the Park, and 12 healthy oaks control sites located near the dead trees. The sampled trees included *Q. rubra*, *Q. alba*, and *Q. velutina*. Dead trees were selected that retained much of the bark on the lower trunk and that appeared to be at about the same stage of decay. "Small" gaps consisted of a single dead oak that had left an obvious hole in the canopy and that had living canopy trees surrounding the gap. "Large" gaps consisted of at least five dead dominant oaks that had had contiguous canopies; the sample plot was situated around the central tree. Control sites were centered on healthy dominant oaks located as close to the dead oak sites as possible. The control trees were carefully chosen so as to be in the same segment of the stand as a

gap site (for example, a lower north-facing slope), but sufficiently far away to exclude the effects of angled light entering from nearby gaps. Sampled trees in large gaps had an average diameter of 43.2 cm DBH (range 29.1 to 59.0 cm), those in small gaps a mean diameter of 46.1 cm DBH (25.9 to 80.0 cm), and those in control sites a mean diameter of 43.7 cm DBH (31.0 to 60.0 cm).

The large patches of mortality were found predominantly on the lower slopes and valley bottoms, whereas isolated dead trees were more frequent on the upper slopes and ridgetops. Thus, it proved impossible to include an equal representation of site types in both samples of gaps. However, the control trees were equally divided between upland and lowland areas. Statistical comparisons (two-way anovas) of upland vs. lowland sites were made for a variety of vegetational attributes (total number of stems per site; total cover, relative density of small size-class stems; species richness) and although upland and lowland sites differed significantly for various parameters, no site-gap size interactions were significant, and no evidence could be found to suggest that gap-phase phenomena differed among the habitat types encountered.

Each sample plot consisted of two 50 ft (15.15 m) line transects arranged perpendicular to each other and intersecting at the center tree. Each individual whose foliage covered the transect was recorded by species, size-class, and the length of the line transect that was covered. The size-classes were: 1 m tall to 2.5 cm DBH (small saplings), 2.5 to 10 cm DBH (large saplings), 10 to 25 cm DBH (lower canopy trees), over 25 cm DBH (dominant canopy trees). The line transect data were analyzed to yield total foliage cover, as a percent of the total length of the line transect, relative cover of a particular species or size-class, and relative density of stems contributing cover to the line transect.

Woody vegetation less than 1 m tall and herbaceous plants were sampled in four 1 m² quadrats uniformly located at 2.75 m along each transect line. Because of limited time available for the study, the quadrat data were taken in a subsample of the gaps. I chose those gap sites closest to the control sites; eight large gaps and 6 small gaps were thus studied.

Table 1. Components of species diversity in gaps and control sites. In this and all subsequent tables and figures, L = large gap, S = small gap, C = control site. Sample sizes given below apply to all subsequent tables and figures. Data are means $\pm$ standard errors. The '+' mark in this and subsequent tables indicates significant heteroscedasticity in the $F_{\max}$ test ($P < 0.05$), and indicates a Kruskal-Wallis test was used to compare values.

	L	S	C
Sample size	14	15	12
+ Mean total number of species per sample site	8.0 $\pm$ 0.80	6.7 $\pm$ 0.39	8.5 $\pm$ 0.74
Total number of species per site type	24	22	26
Similarity to control (Sorenson's Index)	80%	87%	—
+ Dominance (Simpson's Index)	0.336 $\pm$ 0.049	0.373 $\pm$ 0.040	0.205 $\pm$ 0.023 ¹

¹ $X^2 = 8.48$; $P < 0.02$.

All variables were tested for heteroscedasticity using the F-max test of Sokal and Rohlf (1969, p. 371). Variables not significantly heteroscedastic were analyzed by one-way anova; those (identified in the tables) with significant heteroscedasticity were analyzed by a Kruskal-Wallis test.

In the text which follows the population of woody stems between 1 m tall and 10 cm DBH will be referred to as the "lower stratum;" the term "understory" will be used solely for those species which are never part of the top canopy of the eastern deciduous forest.

Results. I will first consider how the observed vegetation in the gaps fits the "new establishment" and "reorganization" hypotheses.

The first question is whether the gap formation has been accompanied by an influx of species not characteristic of the pre-gypsy moth forest. Such species as *Betula populifolia* Marsh., *Rubus* spp., *Rosa* spp., *Prunus* spp., and sundry vines might be expected to invade areas of disturbance and remain for at least 7 yr (Gysel 1951; Siccama *et al.* 1976). Table 1 gives, for the woody species, the species richness and the species dominance (Simpson's index; Poole 1974) within the gap and control sites, and gives the similarity of the gap vegetation to the control site vegetation (Sorenson's index; Mueller-Dombois and Ellenberg 1974). The results indicate that there has been no significant increase in species richness in the gaps. The similarity of the gap vegetation to that of the control sites is high; vines were found at a few control sites as well as one gap site, and the other expected pioneers were absent altogether.

Simpson's index was computed using the relative density of each species at each site as the indicator of relative importance. This index of dominance reflects the degree to which relative importance is spread out over many species (low values) or concentrated in a small number of species (high values). The index was significantly greater in gaps than in control sites (Table 1). To analyze this difference further, the distribution of relative densities of all species at each type of site was plotted (Fig. 1). It is apparent that the gaps have a higher frequency of species with high relative density (over 50%) than do the control sites. Evidently, the higher concentration of relative abundance in a few species in the gaps is attributable to very high relative densities of individual species at some sites; in non-gap areas, such very high relative densities are not found. I then examined these data to determine which species accounted for the high relative densities. In all three types of site, *Cornus florida* was responsible for over four-fifths of these high densities. In only one site did canopy-member tree seedlings contribute a high relative density. The difference in Simpson's index between gaps and control sites, then, resulted from frequent very high densities of *Cornus* stems.

Thus, these data show that 1) the species richness component of diversity did not change in response to gap formation, but 2) the dominance component increased in gaps of both sizes because of an increase in relative density of an understory species. This result does not unequivocally support either the "new establishment" or the "reorganization" modes of gap response.

The second hypothesis of gap theory states that the foliage cover of the ground should change drastically, thereby altering the microclimate at the ground. The decrease in overstory cover should be paralleled by an increase in understory cover, through the ingrowth of new seedlings and saplings. Table 2 suggests that there are minimal differences between large and small gaps, and also between gaps and control sites. The total amount of vegetative cover in control sites just fails to be significantly larger than the cover in large gaps (Kruskal-Wallis test, $\chi^2 = 5.4$, $P = 0.06$). This trend probably reflects the addition of the cover from the live canopy tree in the control sites, but variation among sites is inherently large. Lateral expansion of tree crowns (Trimble and Tryon 1966) may be responsible for the fact that the total cover in small gaps is equivalent to that of control sites.

The data indicate that there is no tendency towards an increase in foliage cover in the lower stratum; if anything, the data point toward a more dense foliage cover in the lower stratum of the control sites. When the relative contribution of understory species is examined, however, it is apparent the understory species provide a significantly greater fraction of the leaf cover in gaps than in control sites (Table 2). (Although the comparison of large gaps and control sites just failed of significance, the trend appears to support the significant difference found between small gaps and control sites). This difference in source of foliage cover probably corresponds to the increase in relative density of *Cornus* discussed above.

The cover data thus do not conform to the expected result of a "new establishment" mode of gap response.

The third hypothesis predicts an increase in stem density in gaps. An average

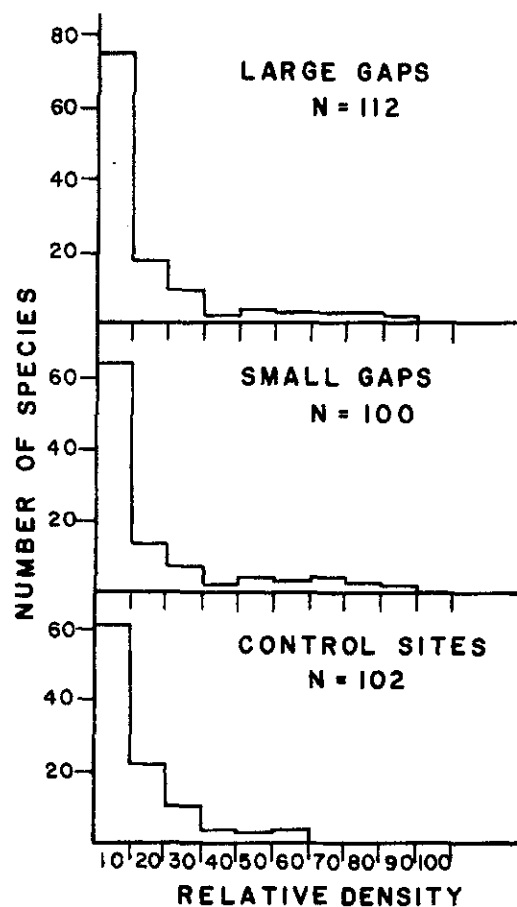


Fig. 1. Distribution of the relative densities of species in three kinds of sites. All species measured in all sites of each type are pooled (N). The abscissa indicates relative density, and the ordinate indicates the number of species having a given relative density.

of 29.3 (± 2.51) stems contributed cover to the line transects in control sites, 31.9 stems (± 2.97) were found on average in large gaps, and 26.6 (± 1.45) stems were found in small gaps; there were no sig-

Table 2. Foliage cover (%) of 30.3 m line transect.

	L	S	C
+Mean total cover of all woody plants per site	262.5 $\pm$ 16.07	283.5 $\pm$ 9.48	299.3 $\pm$ 12.32
Mean relative cover of small saplings	13.34 $\pm$ 1.82	7.73 $\pm$ 2.94	12.89 $\pm$ 2.69
Mean relative cover of large saplings	26.08 $\pm$ 4.02	20.84 $\pm$ 3.44	25.99 $\pm$ 2.57
+Mean relative cover from understory species (all size-classes)	43.48 $\pm$ 8.29	44.94 $\pm$ 5.39	28.32 $\pm$ 4.65 ¹

¹ Small gaps significantly greater than control sites at $P < 0.05$, 1 tailed t-test, $t = 1.939$, $df = 24$.

Table 3. Relative densities (percent of total stems) of major canopy and understory species; mean $\pm$ s.e.

	L	S	C
<i>Acer rubrum</i>	9.98 $\pm$ 3.17	4.61 $\pm$ 1.65	9.33 $\pm$ 3.31
<i>Betula lenta</i>	9.47 $\pm$ 3.03	6.69 $\pm$ 1.99	12.05 $\pm$ 2.54
<i>Fagus grandifolia</i>	9.45 $\pm$ 3.29	8.41 $\pm$ 3.36	6.03 $\pm$ 2.69
<i>Quercus</i> spp. ¹	4.89 $\pm$ 1.43	9.54 $\pm$ 1.83	12.02 $\pm$ 2.92
All canopy species	44.51 $\pm$ 7.69	41.53 $\pm$ 5.45	50.16 $\pm$ 6.30
<i>Cornus florida</i>	36.25 $\pm$ 8.44	39.83 $\pm$ 7.02	27.87 $\pm$ 5.31

¹ Includes individuals of *Quercus alba*, *Q. rubra*, *Q. velutina*, *Q. coccinea*, *Q. prinus*.

nificant differences among the sites. Table 3 gives the mean relative densities of the major species in each type of site. Again, there were no significant differences. If anything, there is a suggestion that the density of woody plants in large gaps is more similar to that of control sites than to that of small gaps (again reflecting habitat differences that are independent of gap type differences).

It is possible that an increased reproduction of forest species, or an influx of pioneer species would be more apparent among the small stems that were recorded in the quadrat samples. These data are shown in Table 4. The increase in canopy-tree seedlings in gaps (Table 4) is not statistically significant; wide variation among the sites was again apparent. However, some of the seedlings data do suggest a "new establishment" kind of response. The difference in total tree seedling density is attributable to a higher density of ash seedlings in large gaps than in small gaps or control sites, and this difference is attributable to both a higher frequency of seedlings and the occurrence of high densities in a few quadrats (Table 5). An increase in establishment by the light-seeded, wind-dispersed ashes is an expected (Bormann and Likens 1979) and previously observed (Watt 1925) feature of

gap dynamics, and thus these data suggest that a "new establishment" response occurred in some of the gap sites. However, the remainder of the data in Table 4 reinforces the impression that the "new establishment" response was localized in occurrence; neither understory woody plants nor herbs showed significant differences in density among the sites. No difference was apparent in the herbaceous species present in gap and control sites; cinnamon fern (*Osmunda cinnamomea*), sensitive fern (*Onoclea sensibilis*), Canada may-flower (*Maianthemum canadensis*), *Viola* spp., and other typical woodland herbs were abundant at all sites. These results parallel the data on foliage cover presented above. Together, they strongly suggest that changes in the microclimate of the forest floor following gap formation were insufficient to trigger the germination of buried or newly dispersed seeds. This result conforms closely to that reported by Jerusalemov (1972).

The alternate model of gap response, the "reorganization" pattern, assumes that tree seedlings which were established prior to the disturbance are released from suppression after the opening of the canopy, and grow rapidly to fill the gap. Evidence for such a response was sought by looking at the size-class distributions of the major

TABLE 4. Average density (numbers/m²) of herbaceous and woody plants less than 1m tall. Each variate is the average of 4 m² quadrats per sample; variates are averaged within site types. Mean $\pm$ standard error.

	L	S	C
Number of Samples	8	6	12
Life-form			
Canopy tree seedlings	1.66 $\pm$ 0.59	1.38 $\pm$ 0.40	0.90 $\pm$ 0.30
Understory trees, vines and shrubs	11.28 $\pm$ 3.29	13.38 $\pm$ 1.98	15.67 $\pm$ 3.81
Herbs	17.06 $\pm$ 5.56	8.29 $\pm$ 3.46	17.31 $\pm$ 5.83
Total plants	30.00 $\pm$ 6.49	23.05 $\pm$ 4.01	33.88 $\pm$ 6.97

Table 5. Occurrence of ash seedlings in the forest floor quadrat samples.

	L	S	C
N (total number of quadrats)	32	24	48
Mean density number/m ² ± s.e.	0.69 ± 0.51	0.08 ± 0.06	0.06 ± 0.05
Frequency (number of quadrats with seedlings/N); %	12.5	8.3	4.2
Maximum observed number of seedlings/m ²	16	1	2

species. (Correlations between age and diameter obtained for these species (Ehrenfeld 1977) and in general for forest trees (Buchholz and Pickering 1978) support the use of size-class distributions to indicate age.) Figure 2 shows the size-class distributions of *Cornus* and five canopy-member species. It is apparent that *Cornus* stems over 10 cm DBH are common in gaps and virtually absent from control sites. This result suggests that *Cornus* has responded to gap formation through an increase in radial growth. According to Fowells (1965), *Cornus* is capable of add-

ing up to 5 cm per year radial increments when the plants are young, which would explain the observed change in size-class distribution. Figure 2 shows some evidence for similar release among the canopy species. Beech shows the most pronounced shift; seedlings are much more common in control sites than in either kind of gap, where larger size-classes predominate.

The final hypotheses that contrast the "reorganization" and "new establishment" patterns of gap response concern the kinds of successional change in forest composition that follows the disturbance. A "new

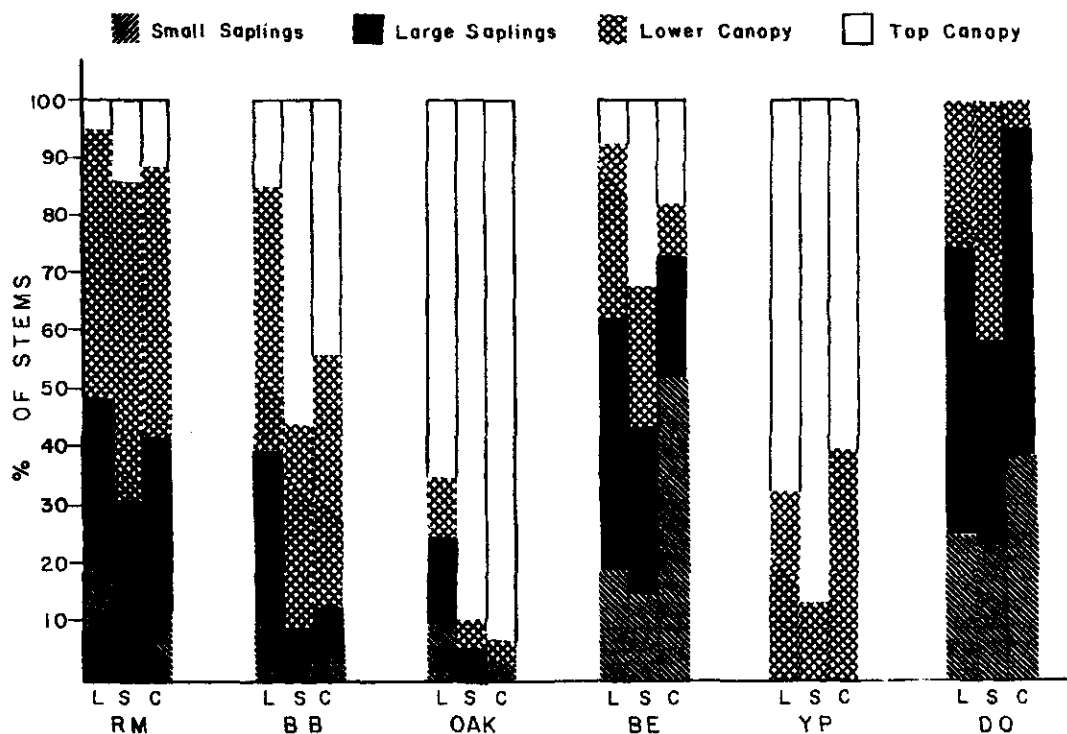


Fig. 2. Proportion (%) of the stems of each of the major species found in each size-class. See text for size-class limits. L = large gaps, S = small gaps, C = control sites. RM = *Acer rubrum*, BB = *Betula lenta*, OAK = *Quercus* spp., BE = *Fagus grandifolia*, YP = *Liriodendron tulipifera*, DO = *Cornus florida*.

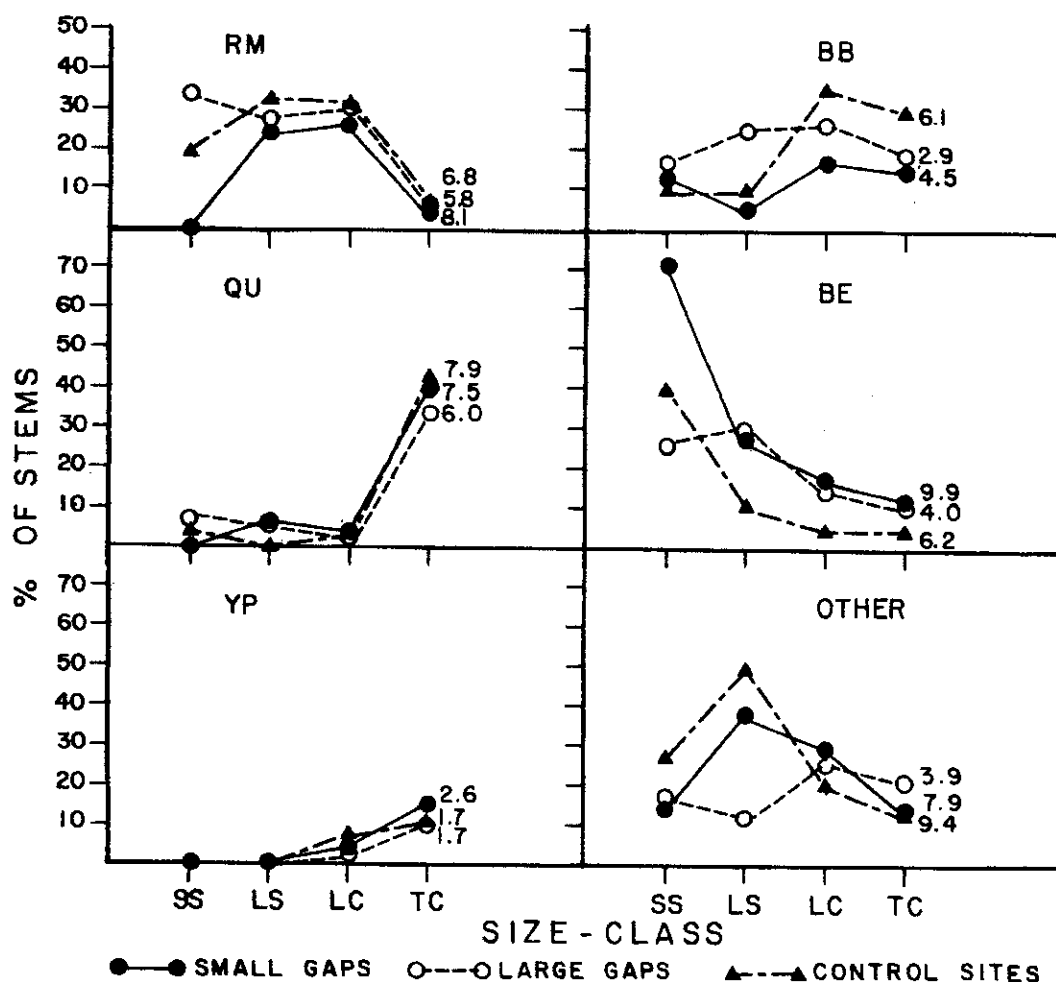


Fig. 3. Compositional change in gap sites and control sites. The percentage of a given canopy species in the total population of tree stems in each size-class (ordinate) is plotted against the 4 size-classes (Abcissa). Numbers at the end of each line are the average percent change between size-classes. SS = small saplings, LS = large saplings, LC = lower canopy, TC = top canopy.

establishment" response is expected to promote a shift toward species less tolerant or equally tolerant to the affected canopy, whereas the "reorganization" response is expected to promote a shift towards species more tolerant than the existing canopy. Compositional change in the three kinds of sites was analyzed following the methodology of Goff (1968). For each of the four size-classes, the total number of canopy-species stems was tabulated, and the percentage contribution to the size-class of each of the major species was computed. These percentages were then plotted as a function of the four size-classes (Fig. 3).

In theory, a self-perpetuating species should be equally important in all size-classes (equal percentage representation forming a horizontal line on the graph), whereas a species disappearing from the stand should lose importance in the small size-classes, and one newly entering the stand should be unimportant in the large size-classes. For each species, I also computed the mean difference in percentage representation between adjacent size-classes; this mean serves as an indicator of the degree to which the role of the species is changing in the community.

Several trends are apparent in Figure

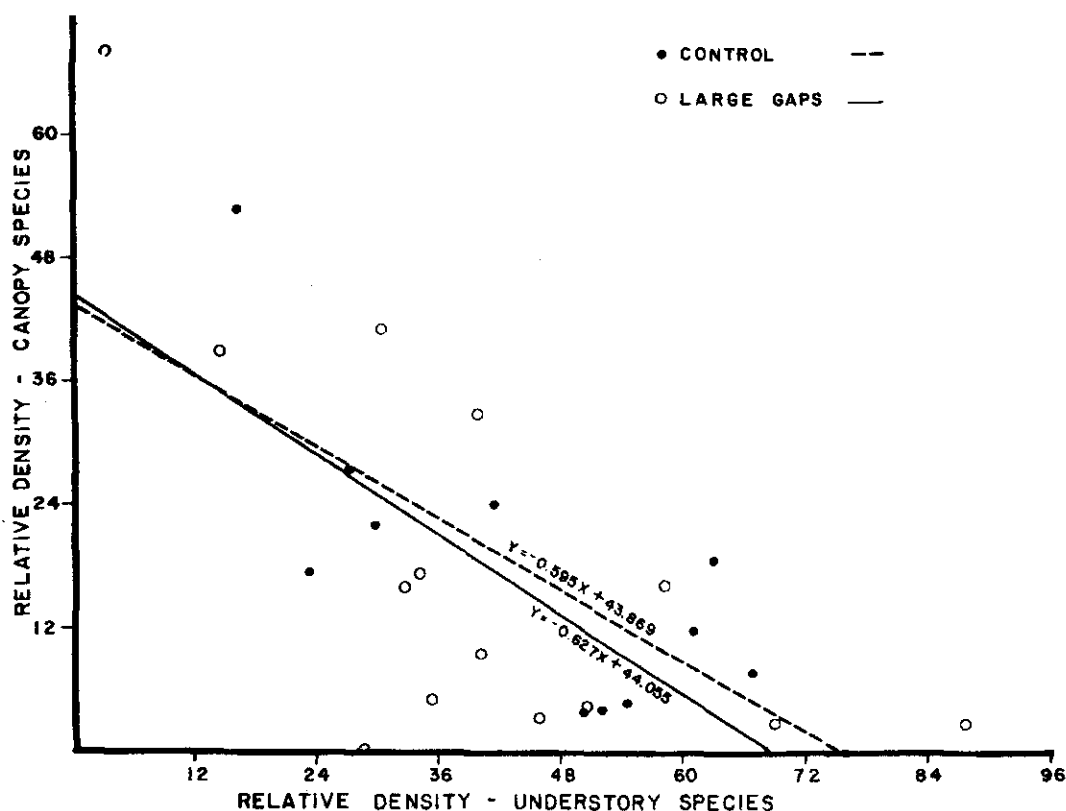


Fig. 4. Regression of the relative density of canopy-species stems against the relative density of understory-species stems. Relative densities for both kinds of species are for stems between 1 m tall and 10 cm DBH. For the large gap regression, $F=10.12$, $df=13$, $P<0.001$; for the control site regression, $F=14.065$, $df=11$, $P<0.005$.

3. The absence of small stems of the oaks and yellow-poplar strongly suggests that these species are disappearing from the stand. The opening of the canopy in the gaps evidently did not promote recruitment of these species. The seedling population shows the greatest differences in species composition. The most important species of seedling in large gaps is *A. rubrum* but is *F. grandifolia* in the small gaps. Control sites have a mixture of species in this size-class, and beech and red maple are both abundant. Red maple and beech are classified as tolerant and very tolerant, respectively (Forbes 1956; Fowells 1965), whereas oaks and yellow-poplar are classified as intermediate in tolerance. Thus, Figure 3 indicates that a trend toward species of increased tolerance (in the forster's sense of shade-tolerant) characterizes the stand regardless of the presence or absence of canopy gaps. This result

strongly supports the "reorganization" model of gap response.

To summarize, neither of the hypotheses of gap theory has been unequivocally demonstrated by the data for these defoliation-induced gaps. Rather, there is some evidence pointing towards the "reorganization" mode of gap response: there has been a change in the size-class distributions of key species, and the successional trend in gaps, as in control sites, is towards more tolerant species than those presently dominating the canopy. However, the data also suggest that understory species, principally *Cornus*, are enjoying much of the benefit of the reorganization, thus delaying the restoration of an overstory and perhaps altering its eventual composition.

The density of young individuals of canopy species is likely to be inversely related to the density of the understory species; as understory species occupy a greater

Table 6. Proportion of stems (%) of selected species among all lower stratum stems (1 m tall to 10 cm DBH) at some representative sites.

Site	<i>Cornus florida</i>	<i>Lindera benzoin</i>	<i>Carpinus caroliniana</i>	Canopy-tree Reproduction	Other Understory Species
Gap number					
L14	5.0	—	—	95.0	—
S3	9.5	—	71.0	19.1	—
S7	100.0	—	—	—	—
S17	—	100.0	—	—	—
L19	75.0	15.0	—	2.5	7.5
Control site number					
LC2	25.7	—	45.7	22.9	5.7
LC5	6.9	69.0	—	10.3	13.8
CU4	93.3	—	—	6.7	—
LC4	15.3	—	—	76.9	7.7

proportion of the "growing space" of the lower stratum, there is less room available for canopy tree stems. Such a relation has previously been described in southern forests by Harcombe and Marks (1978). In order to test whether such a relation existed in this forest, I calculated a regression of the relative densities of all saplings of understory species against the relative densities of canopy-member stems in those size-classes. (Fig. 4.) For large gaps and control sites, there is a clear inverse relationship between the relative density of understory-species stems and the relative density of canopy-species stems. There was no significant regression relationship for the data from the small gaps, which probably resulted from a complete absence of canopy-member species in the lower stratum at half of the small gap sites. The biological reason for the lack of canopy-tree reproduction is not clear, but is possibly related to site factors independent of the presence of gaps.

My observations also suggested that the understory species were often found in discrete, conspicuous "patches" of high density. Table 6 shows the structure of the lower stratum at some representative individual study sites. The existence of such patches is clearly shown in both gap and control sites (e.g., M7 and CU4, Table 6). However, some sites (e.g., H19 and CL2, Table 6), were not located within such patches, and the understory was more diversified. Indeed, in a few of the gaps that were not within a patch of understory species growth, I found pioneer species (such

as *Rubus* spp. and *Rosa* spp.) that are typically associated with the "new establishment" mode of gap response.

Discussion. The results of the study suggest a general scheme of gap response for this forest. The lower stratum of the forest consists of a mixture of small individuals of canopy member species and individuals of understory species. The latter tend to occur in patches of high density, within which the establishment of canopy tree reproduction is inhibited or prevented. A disturbance (such as defoliation-induced tree mortality) creates openings of various sizes in the canopy above this patchwork lower stratum. When the canopy gap is smaller than a patch of an understory species, that species increases its relative importance in the vegetation by increase in the size of individuals and in their relative density within the patch. When the gap is superposed over a lower stratum of mixed species, or when the patch of understory species is smaller than the gap, then the response would depend on a number of other factors. For example, a sparse lower stratum and proximity to a source of seeds from pioneer herbaceous and woody species might promote a "new establishment" response, whereas a more dense lower stratum might result in release of canopy-tree saplings (a classic "reorganization" response).

The relative sizes of the patches of understory species and the gaps would also affect the way in which the gap response might vary with gap size. In the forest at Morristown National Historical Park, most

of the gaps were evidently included within the pattern of patches formed by *Cornus* and other understory species. Gaps produced in this forest on a larger scale of sizes would probably show a greater sensitivity to size variation. Windthrow (Brewer and Merritt 1978), insect predators in addition to gypsy moths (McCambridge and Knight 1972) and other kinds of disturbance that open the canopy (Pickett and Thompson 1978) produce openings in a wide range of sizes. Although much less is known of the population structures of understory species, it is highly likely that most species will show clumped distributions (Whitford 1949; Kershaw 1973).

The pattern of gap response characterized by an increase in the relative importance of long-lived understory species has been observed elsewhere, but has never commanded adequate attention. Woods and Shanks (1959) described the formation of dense thickets of *Kalmia* in chestnut-blight-produced gaps in the Smokies, and Keever (1953) mentioned similar thickets of *Gaylussacia* in chestnut-blight-produced gaps in the Blue Ridge Mountains. Good and Good (1972) observed increased shrub density with increasing light penetration at the expense of the growth of seedlings and saplings of canopy trees. Minckler *et al.* (1961), Trimble (1973), and Crawford (1976), among others, have reported that shrub biomass increased in the canopy openings caused by the partial cutting of timber.

This growth of understory species has probably not been considered important because it is often implicitly assumed that shrubs and understory trees have no role in the development of the canopy. However, these species have been shown to form associations which are stable (i.e., resistant to change) over several decades, and perhaps longer (Egler and Foote 1975; Niering and Goodwin 1974). It is likely that the processes observed by these workers on rights-of-way are mimicked on a small scale within forests (Niering, pers. comm.). Harcombe and Marks (1978) demonstrated, for example, that understory species were outcompeting the tree reproduction in a Texas forest. Even if these understory patches persisted for only 10 to 20 years, they probably would have a profound effect on tree recruitment and thus on the eventual canopy composition in their vicin-

ity. In view of the lack of information on the ecology of most understory species, further speculation is futile; however, this appears to be a fertile field for future research.

The original question posed in this paper asked whether the size of a canopy opening determined the kind of response observed in the vegetation in the gap. The answer, for the gypsy moth-caused gaps in the Morristown National Park, is negative; no differences were found between large and small gaps. The second question posed—whether other features of the vegetation appear significant in directing the course of the gap's dynamics—is answered by identifying two such factors. One is that the spatial distribution and the relative densities of the plants that comprise the lower stratum appear to be critical factors in determining the pattern of forest response to canopy gaps. Secondly, the variations observed in the mode of forest response to disturbance can be understood, and perhaps predicted, by viewing a disturbance as the result of an interaction between patches of destroyed canopy superposed over patches of varied composition in the lower stratum.

The results of this study have important implications for the analysis of defoliation-related damage to deciduous forests. The effects of the gypsy moth are frequently termed "catastrophic" (e.g., Kegg 1971). My study has attempted to document the nature of the catastrophe in terms of the evidence present 7 years after the fact. The results of the study show that "catastrophe" is an inappropriate word; the structure of the forest itself provides the resilience necessary to minimize any irreparable change. The long-term effects of defoliation are less drastic than might be imagined from first sight of the defoliated trees. Mine is not the first study to suggest this: Stephens and Hill (1971) have stressed the minimal impact of gypsy moth defoliation on Connecticut oak woods, Campbell and Sloan (1976) compare gypsy moth defoliation to a "thinning from below" and Ghent (1958), Mattson and Addy (1975) and others have described other non-catastrophic effects of defoliators. The term "catastrophe" thus is both inappropriate and misleading when applied to the ecology of gypsy moth-oak forest interactions, and should be avoided in favor of a

more community-oriented approach to the problem.

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