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FOREST COMPOSITION AS DETERMINED BY CANOPY GAP DYNAMICS:
A BEECH-MAPLE FOREST IN MICHIGAN

By

Gerard T. Donnelly

A DISSERTATION

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ABSTRACT

FOREST COMPOSITION AS DETERMINED BY CANOPY GAP DYNAMICS: A BEECH-MAPLE FOREST IN MICHIGAN

By

Gerard T. Donnelly

Forest regeneration was studied in Warren Woods, a mature beech-maple forest in southwestern lower Michigan to understand the role of treefall gaps in the maintenance of forest composition. Warren Woods is similar in composition to presettlement forests and to other old-growth remnant stands, and served as an excellent model of natural beech-maple forest.

Gap chronosequence analysis revealed that gaps closed in 34 yr by in-growth of surrounding trees, with tree density changing via shifts in recruitment and mortality. Gap vegetation was dominated by sugar maple, but all forest tree species were represented. Average height increase of beech and maple in gaps was similar, although maximum growth in maple was greater. Seedlings and saplings were not able to grow into the canopy as a result of a single gap exposure.

Suppression of small stems in closed gaps was followed by death or by re-release in subsequent gaps, as evidenced by the episodic radial growth associated with recurrent gaps of successful canopy trees. Beech was more shade tolerant than sugar maple, with greater survivorship during extended suppression between gaps; relative mortality was concomitantly greater in sub-canopy maple. Superior shade tolerance is the most important mechanism by which beech maintains dominance in natural forests.

Shade-intolerant yellow-poplar and black cherry were rare and non-randomly distributed in the forest, associated more with topographic, edaphic, and edge factors than with treefall gaps. Gap reconstructions around rare trees of the forest interior demonstrated that regeneration in single-treefall gaps was possible, although limited by seed dispersal and problems of germination and establishment. With a turnover time of 370-390 yr, Warren Woods incurs a lower rate of treefall disturbance than any other forest reported in the literature. This low rate of disturbance determines the dominance of shade-tolerant species and the rarity of shade-intolerant species.

To Michelle

ACKNOWLEDGEMENTS

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INTRODUCTION

The potential for maintenance or change in the composition of mature forests exists when dominant trees fall and leave a gap in the forest canopy. An understanding of the processes which determine the distribution and abundance of mature-forest species relies on a knowledge of the patterns and mechanisms of tree replacement in gaps.

Prevailing theory suggests that recurrent disturbance maintains species diversity by preventing monopolization by dominants (Dayton 1971) and by providing spatio-temporal heterogeneity or "phase differences" for sub-dominant or fugitive species (Levin and Paine 1974, Whittaker and Levin 1977). Variations in the frequency and intensity of disturbances, such as treefalls, provides for a variety of regeneration niches which can support a diverse mixture of species (Grubb 1977, Connell 1978, White 1979).

Studies of single-treefall disturbance in closed-canopy mesic forest have not always supported theory. While some have found that shade-intolerant species can replace fallen trees in gaps (Forcier 1975, Barden 1979, 1980), thus promoting species diversity, others have found replacements to be primarily by shade-tolerant dominant species (Brewer and Merritt 1978). In a compositionally-static system, the probability of a particular species acting as a replacement in a gap should be proportional to its density in the canopy. It is reasonable then to expect that the majority of replacement trees would be of a species which dominates the system, while shade-intolerant species, which are less important in mature forests, would infrequently also be successful in gaps.

Although considerable focus has been given to the effects of gap size on forest regeneration (see review in White 1979), the frequency of gap events may be of equal or greater importance. The intermediate disturbance hypothesis, regarding species diversity, equates size with frequency of disturbance (Levin and Paine 1974, Connell 1978, Miller 1982). While single-treefall gaps are on the small end of the disturbance size scale, variations in the frequency of gap disturbance could have considerable effects on forest composition and species diversity.

Strong (1977) has suggested that differences in species diversity between temperate and tropical forests may be, in part at least, attributed to the suspected greater rates of forest turnover in moist tropical forests (Leigh 1975, Hartshorn 1978). Although differences in the rate of forest turnover may not actually be much greater in tropical than in temperate forests (Leigh 1975, Abrell and Jackson 1977, Brewer and Merritt 1978, Hartshorn 1978, Runkle 1982, Uhl 1982, 1983), additional estimates of turnover rate are needed before objective comparisons can be made.

Approaches to the Study of Regeneration in Treefall Gaps

Forest regeneration trends have been studied through a variety of approaches. The abundance of a particular species in the forest understory has been interpreted as a predictor of its representation in the future forest (Esten 1932, Williams 1936, Potzger and Friesner 1940, Braun 1950, Connell 1978; see also review in Vankat et al. 1975). This probabilistic interpretation neglects certain biological differences between species, especially sapling survivorship (Braun 1916, Vankat et al. 1975, Connell 1978) and growth rates of trees from juvenile to canopy size classes (Jones 1945, Laufersweiler 1955).

Studies of replacement trends based on the density of individual species in gaps (Runkle 1981, 1982) or beneath canopies of trees that have yet to fall (Forcier 1975, Horn 1975, Fox 1977, Woods 1979, Woods and Whittaker 1981) are also subject to the criticism that ecological differences between species are ignored. Nonetheless, in certain of these studies using Markov analysis[1], models based on the density of saplings of different species (Horn 1975, Runkle 1981), or on average sapling composition (Runkle 1981), were able to predict current canopy composition in relatively undisturbed forests in the eastern United States. Runkle (1981) claimed that sapling composition in small gaps was sufficient to account for the diversity of tree species in the forest canopy. Where a single individual is selected as the tree most likely to succeed in windthrow gaps (Brewer and Merritt 1978, Barden 1979, 1980, 1981, 1983), observer bias reduces the credibility of otherwise interesting conclusions regarding replacement trends.

A more biologically realistic approach to the study of regeneration within gaps must involve a stronger autecological orientation regarding species that are of interest because they are forest dominants or because they appear to be gap-dependent (Dix and Swan 1971, Whitmore 1982). Factors which may be important in determining how different species respond to forest openings and how they are able to achieve canopy height include the following:

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[1] A matrix-based statistical procedure which predicts transitions from a particular state, such as forest patch composition in gaps, through successive generations. Ultimately a stationary state is achieved, assuming constant transition probabilities, that is used to predict steady-state forest composition.

magnitude and periodicity of seed production, diaspore dispersal, establishment requirements, size-dependent shade tolerance and survivorship, and growth rates.

Importantly, gap-related autecological factors are likely to change as a gap closes. Given that the longevity of gap openings is measured in decades (Runkle 1981), a chronosequence approach (Drury and Nisbet 1973, Brubaker 1981) to their study is in order.

Miles (1979) points out that the interpretation of sites in an age sequence, as though they represent changes in the development of vegetation over time, depends on certain important assumptions. Sites must have similar soils and climatic and microclimatic conditions, and have similar histories of environment and vegetation succession. Most of these requirements are met when the selected gaps of different age occur on homogeneous soils within a single forest stand, and when the range in gap ages is limited to only a few decades. Between-gap differences resulting from different histories of adjacent treefalls may be handled by replicated studies of gaps in different age categories, and by careful interpretation of chronosequence data.

Surprisingly, chronosequence methodology has not been used extensively to study gap regeneration. Its use has been limited primarily to analyses of the density of different species in gaps of various ages (Bray 1956, Runkle 1982). Nakashizuka (1983) studied height growth and mortality of beech (Fagus crenata Blume) seedlings in Japan, but did so in just two gaps of different age.

Regeneration and Forest Trends in Beech-Maple Forest

Interpretations of the successional status of beech-maple forests and the regeneration ecology of American beech (Fagus grandifolia Ehrh.[2]) and sugar maple (Acer saccharum Marsh.) have been confused (see Vankat et al. 1975), mostly because of the lack of conclusive information on replacement trends in gaps. Citing the absence of beech reproduction, the abundance of sugar maple in the understory, and the fast growth of sugar maple in openings, many investigators have suggested that sugar maple may be successionally replacing beech over time (Esten 1932, Cain 1935, Williams 1936, Keller 1945, Braun 1950, Ward 1956, Abrell and Jackson 1977), despite the fact that presettlement beech-maple forests were dominated by beech in the overstory, just as little-disturbed remnant stands are today. Detailed studies of growth and survivorship in beech and sugar maple, relative to the gap disturbance regime, are needed to resolve this issue.

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[2] Nomenclature follows Fernald 1950.

Research Objectives

The purpose of this research was to investigate the role of treefall gaps in the maintenance of forest composition and diversity by examining the patterns of regeneration in gaps of a mature beech-maple forest and by defining the manner in which trees grow to canopy size. Specific research objectives were as follows:

1. Determine the size, longevity, and pattern of closure of treefall gaps.
2. Measure the growth of trees in gaps to determine whether small seedlings and saplings of dominant species are able to grow to canopy size as a result of a single gap exposure, or, if not, to determine how trees grow into the forest canopy.
3. Contrast growth and survivorship of the two dominant species, beech and sugar maple, relative to gap disturbance, to determine the mechanism of beech dominance and the limitations to the success of sugar maple.
4. Consider the effects of gap frequency on growth and survivorship of trees, relative to species dominance and diversity, when gap size (single-treefalls) is held constant.

5. Determine abundance and pattern of distribution of two shade-intolerant sub-dominant trees, yellow-poplar (Liriodendron tulipifera L.) and black cherry (Prunus serotina Ehrh.).
6. Examine the influences of rarity, dispersion, and differences in seed dispersal (wind dispersal vs. bird dispersal) on the potential for yellow-poplar and black cherry to disseminate propagules into forest gaps.
7. Determine if yellow-poplar and black cherry trees are able to regenerate in single-treefall gaps and, therefore, to determine if gap disturbance contributes to or maintains species diversity.
8. Estimate the rate of forest turnover in mature beech-maple forest and relate it to disturbance estimates in other forest systems.

STUDY AREA DESCRIPTION

Warren Woods is possibly the best example of the mature beech-sugar maple forests of southern Michigan and other areas in the midwestern and eastern United States (Braun 1950), and certainly appears to be among the least-disturbed of forests of this type. The area of study is part of a 120 ha state nature study area and consists of approximately 15.5 ha in the NW. 1/4, Sec. 27 of Chikaming Township, R.20W., T.7S., in Berrien County, Michigan (Figures 1 and 2).

The forest is located on till plain between a series of two lake-border moraines which are associated with the southeastern shore of Lake Michigan (Burgh 1939). Soils in the study area are mostly Selfridge loamy sands, although some Blount loam and Pewamo silt loam soils are included (Larson 1980); the first two series are somewhat poorly drained, and the last is a poorly drained soil found in depressions. The stand is bordered on the south and east by the Galien River, with associated floodplain forest and steep sandy banks, and by an agricultural field on the west and a two-lane paved road on the north.

Warren Woods has a reputation as a virgin stand of beech-maple forest. Brewer (1980) has reviewed some of the

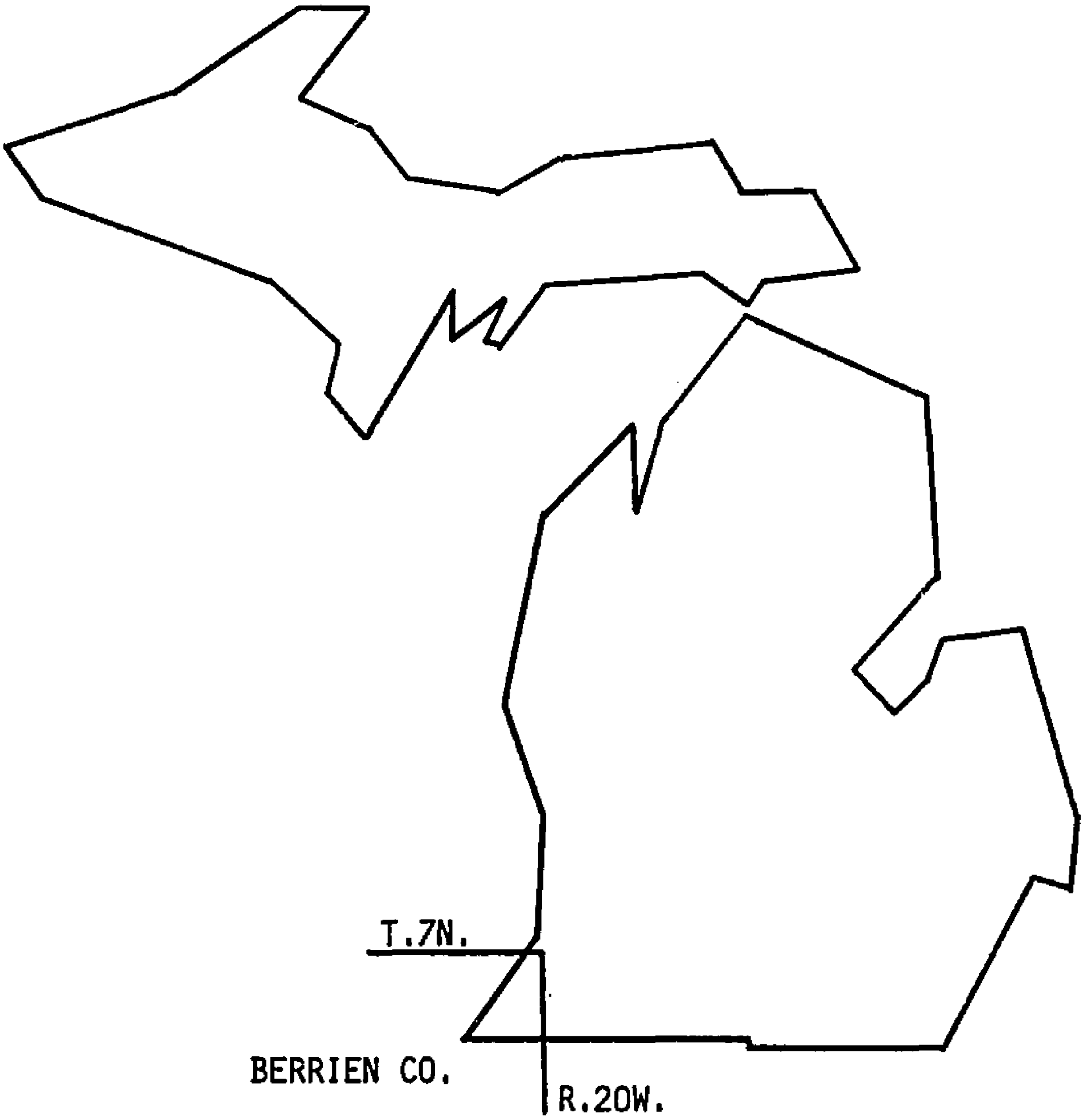
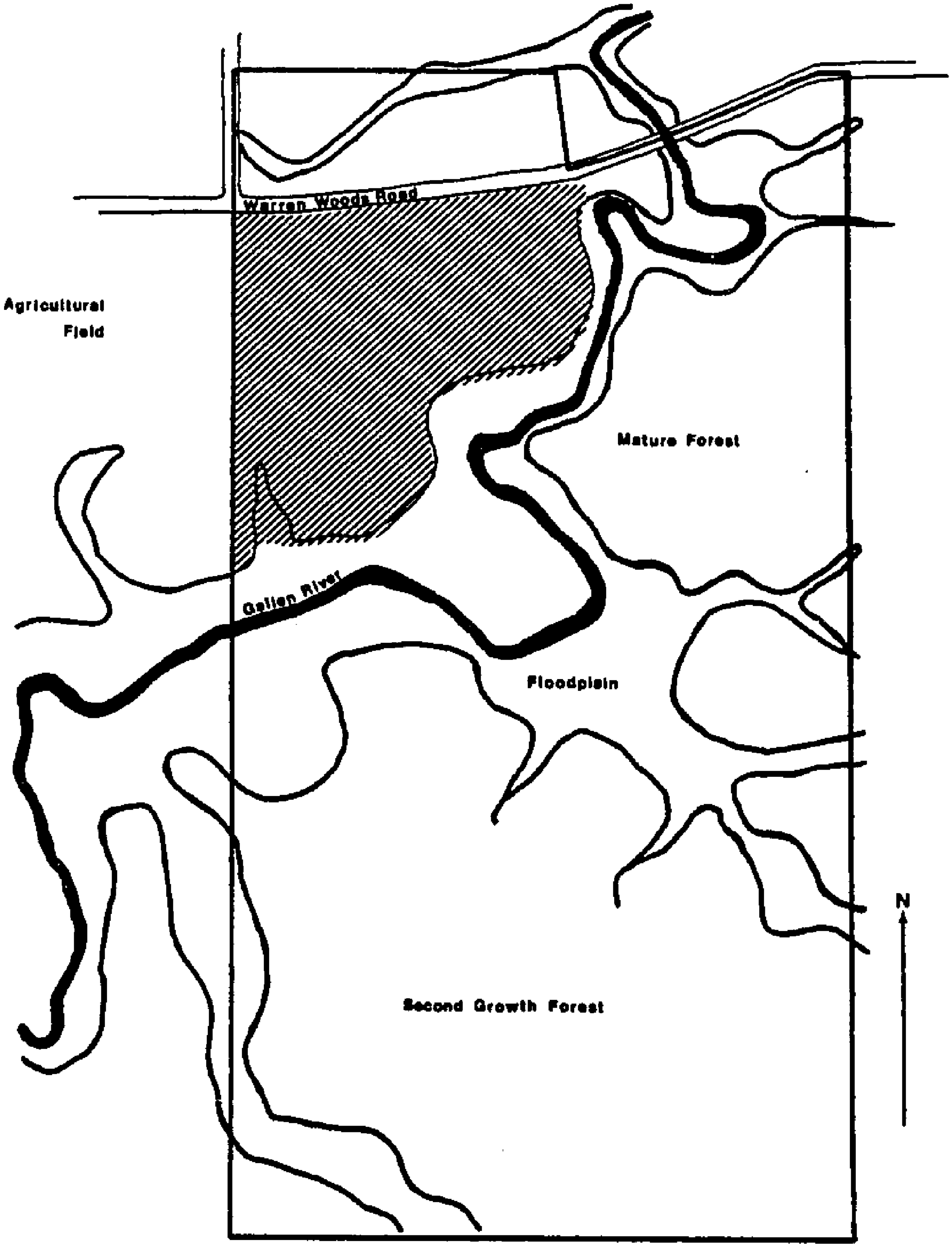


Figure 1. Location of Berrien County, Michigan. Town and range coordinates define the township within which Warren Woods is located.

Figure 2. Warren Woods Nature Study Area. General location of study site is indicated by hatched lines, and is bounded by the Galien River floodplain, an agricultural field, and Warren Woods Road. Adapted from Warren Woods Master Development Plan, Michigan Department of Natural Resources, Parks Division, 1970.


Warren Woods Road
Agricultural Field
Mature Forest
Galien River
Floodplain
Second Growth Forest
N

evidence available regarding the disturbance history of the woods and confirms that it has never been logged, burned over, or grazed. He refers to the limited selective cutting alluded to by Cain (1935) during the period 1885-1890, but does not clearly indicate the extent of the disturbance.

According to a local resident interviewed by Cain (1935), an estimated ten percent of the timber was taken, although no beech and little sugar maple was cut. Trees removed included basswood (Tilia americana L.), yellow-poplar, white oak (Quercus alba L.), and black cherry. Dice (1920) also noted that "...a number of trees have been cut out in former years, and although no trees are now being cut down, all the trees and branches which fall are being cut up for firewood." The removal of fallen wood for firewood ended when the tract was transferred to the Parks Division of the Michigan Department of Natural Resources in 1949.

With the exception of the loss of American elm (Ulmus americana L.), which, in 1933 represented 2.2% of all stems >1 in (2.5 cm) dbh (Cain 1935), and the very limited removal of other species from the stand, Warren Woods serves as an excellent representative of relatively undisturbed beech-maple forest. For this reason, the forest has been the subject of numerous ecological investigations and publications (Dice 1920, Cain 1935, Braun 1950, Lindsey and Escobar 1976, Fox 1977, Brewer and Merritt 1978, Woods 1979, Brewer 1980, Rogers 1981, Woods and Whittaker 1981, P. G. Murphy and G. C. Kroh, unpublished data).

Warren Woods as a Model of Natural Beech-Maple Forest

To investigate natural processes which determine and maintain forest composition, it was first necessary to determine that the present composition of Warren Woods was similar to that of natural, undisturbed beech-maple forest. Forest composition in Warren Woods and in presettlement beech-maple forests of Berrien County, Michigan was compared.

Methods

Warren Woods. Overall forest composition was studied in 25, 100 m^2 (10 x 10 m) plots. These plots were located throughout the study area by using random numbers corresponding to compass sight-line directions and distances along the lines. The minimum allowable distance between plots was 20 m. Plots with borders falling within 25 m of any forest edge were rejected. All stems $\geq$2.5 cm diameter at breast height (dbh) were identified and their dbh measured with a steel tape. From these data, values for density, dominance (in terms of basal area), and frequency were derived for each species and importance values were calculated from them (Curtis and McIntosh 1951). The importance value (IV) of a species is defined as the sum of relative density, relative dominance, and relative frequency. Importance values were converted into importance percentages by dividing each IV by three.

Presettlement Forests. Composition of the presettlement beech-maple forest of Berrien County was derived from data contained in the General Land Office survey of Michigan, conducted during the period 1825-1832. Data were kindly made available to me by L. G. Brewer, T. W. Hodler, and H. A. Raup, who had transcribed information contained in the surveyor's original field notes onto topographic maps. They used these data to construct a detailed map of the presettlement vegetation of southwestern Michigan (Brewer et al. 1984). The original field notes are on file in the Lands Division of the Michigan Department of Natural Resources in Lansing, Michigan.

Brewer, et al. (1984) delineated vegetation boundaries in ten counties, including Berrien, from witness and line trees and from slope contours on U. S. Geological Survey topographic maps. Methods used to distinguish adjacent categories of different vegetation are contained in Brewer et al. (1984). They indicated that their boundaries between beech-maple forest and northern coniferous-hardwood forest were accurate to ±1/2 mi (0.8 km); boundaries between beech-maple and oak (Quercus) forests were accurate to ±1/4 mi (0.4 km).

Relative values for density, dominance (basal area), and frequency were computed for all tree species included within areas of Berrien County designated as beech-maple forest by Brewer, et al. (1984). Their topographic maps, with tree data, and map overlays, which delineated different vegetation categories, were used in the analysis. Only the species of the witness and line trees, and their diameters, were recorded on the topographic maps; line-to-tree distances were not recorded. Accordingly, only relative values for tree species could be determined.

The total number of trees of each species was divided by the total number of all trees to determine values for relative density. Relative dominance was calculated from the basal area total for each species, which were expressed as percentages of the total for all species combined. Frequency values were derived from section corner trees only. A total of 47 section corners having four witness trees was contained within beech-maple forest areas of Berrien County. Frequency for a species was calculated as the number of corners, in percent, at which that species was present among the four trees. Relative frequency value for a species was computed as the percentage of the sum of the frequency values for all species that was attributed to that particular species. Importance values and importance percentages were calculated as before for the Warren Woods data.

Results

Warren Woods. Beech and sugar maple greatly exceeded all other species measured in density, in basal area dominance, and in frequency (Table 1). Together, these two species accounted for over 86% of the total importance for all species. All other species had importance percentages of 4.3 or less. The other species included, in order of importance, ironwood or blue-beech (*Carpinus caroliniana* Walt.), basswood, yellow-poplar, hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch), American elm, spicebush (*Lindera benzoin* (L.) Blume), and witch-hazel (*Hamamelis virginiana* L.).

Trees and shrubs present in low numbers in Warren Woods, but not found within the 2500 m^2 sampling area, included: red maple (*Acer rubrum* L.), pawpaw (*Asimina triloba* (L.) Dunal), bitternut hickory (*Carya cordiformis* (Wang.) K. Koch), shagbark hickory (*Carya ovata* (Mill.) K. Koch), white ash (*Fraxinus americana* L.) sycamore (*Platanus occidentalis* L.) black cherry, white oak, red oak (*Quercus rubra* L.) red-berried elder (*Sambucus pubens* Michx.), and mapleleaf viburnum (*Viburnum acerifolium* L.).

Table 1. Forest composition of Warren Woods*.

Species	Relative Density	Relative Dominance (Basal Area)	Relative Frequency	Importance Value**	Importance Percentage
Fagus grandifolia	43.8	68.2	38.6	150.6	50.1
Acer saccharum	47.6	20.0	40.4	108.0	36.0
Carpinus caroliniana	3.8	0.2	8.8	12.8	4.3
Tilia americana	0.5	6.3	1.8	8.6	2.9
Liriodendron tulipifera	0.5	5.3	1.8	7.6	2.5
Ostrya virginiana	1.4	0.0	3.5	4.9	1.6
Ulmus americana	1.4	0.0	1.8	3.2	1.1
Lindera benzoin	0.5	0.0	1.8	2.3	0.8
Hamamelis virginiana	0.5	0.0	1.8	2.3	0.8
TOTALS	100.0	100.0	100.3	300.0	100.1

*Trees and shrubs $\geq$2.5 cm dbh. Total area sampled, 2500 m^2.

**Importance value = relative density + relative dominance + relative frequency.

Beech (IV% = 50.1; Table 1) was more important in Warren Woods than sugar maple (IV% = 36.0), primarily because of the dominance by beech in the canopy layer. The ratio of beech dominance to that of sugar maple was 3.4. The ratio in density of trees $\geq$20 cm dbh of beech to sugar maple was 2.8. Among all stems $\geq$2.5 cm dbh, however, sugar maple relative density (47.6) and relative frequency (40.4) were higher than for beech (43.8 and 38.6, respectively). With beech more important in the canopy, the higher values of density and frequency for sugar maple indicated the abundance of sugar maple regeneration in the understory.

Presettlement Forests. The composition of beech-maple forests of Berrien County at the time of the original land survey is shown in Table 2. Beech clearly dominated over all other species in the original forests, with an importance percentage of 47.3. Beech had values for relative density, dominance, and frequency that were at least twice those of sugar maple, which was second in importance in all categories. Sugar maple appeared to be less important relative to beech in the original forests than in Warren Woods; the ratio in relative dominance of beech to sugar maple in presettlement times was 4.5. The ratio of beech to maple was 4.9 for all stems $\geq$8 cm dbh and 4.7 for trees $\geq$20 cm dbh.

A total of 18 tree species having an importance

Table 2. Composition of presettlement beech-maple forests of Berrien County, Michigan.

Species	Relative Density	Relative Dominance (Basal Area)	Relative Frequency	Importance Value*	Importance Percentage
Fagus grandifolia	53.5	45.2	43.3	142.0	47.3
Acer saccharum	11.1	10.1	18.4	39.6	13.2
Tilia americana	8.7	9.9	7.8	26.4	8.8
Fraxinus sp.	6.5	6.7	12.0	25.2	8.4
Ulmus americana	5.3	5.7	5.1	16.1	5.4
Quercus alba	2.3	4.9	5.1	12.3	4.1
Liriodendron tulipifera	2.4	5.8	0.9	9.1	3.0
Populus sp.	2.9	4.1	1.8	8.8	2.9
Ostrya virginiana	2.0	0.4	1.8	4.2	1.4
Quercus rubra	0.9	1.5	1.8	4.2	1.4
Prunus serotina	0.8	0.4	0.9	2.1	0.7
Carya sp.	1.1	0.8	0.0	1.9	0.6
Juglans nigra	0.4	0.5	0.9	1.8	0.6
Acer rubrum	0.6	0.5	0.0	1.1	0.4
Quercus velutina	0.3	0.4	0.0	0.7	0.2
Tsuga canadensis	0.3	0.3	0.0	0.6	0.2
Juglans cinerea	0.2	0.1	0.0	0.3	0.1
Quercus macrocarpa	0.1	0.1	0.0	0.2	0.1
TOTALS	100.2	100.1	99.8	300.0	98.8

*Importance value = relative density + relative dominance + relative frequency.

percentage $\geq$0.1 were recorded in the original forests, compared with the nine woody species measured in Warren Woods. The understory tree, ironwood, and the shrubs, spicebush and witch-hazel, were recorded in the Warren Woods survey, but were not included among the trees used or found by the surveyors.

Tree species of the presettlement forests that are not present in Warren Woods included: poplars (*Populus*), black walnut (*Juglans nigra* L.), black oak (*Quercus velutina* Lam.) hemlock (*Tsuga canadensis* (L.) Carr.) butternut (*Juglans cinerea* L.) and bur oak (*Quercus macrocarpa* Michx.).

Discussion

Warren Woods serves as an excellent model of natural beech-maple forest. The strong dominance of beech and sugar maple over all other species in this stand (Table 1) is typical for the forest type in the mature state (Braun 1950, Lindsey and Escobar 1976). Further, the much greater abundance of beech in the overstory and of sugar maple in small size classes has characterized other old-growth remnants of beech-maple forest throughout its range (Esten 1932, Morey 1936, Hough and Forbes 1943, Braun 1950, Petty and Lindsey 1961, Vankat et al. 1975, Abrell and Jackson 1977, Gilbert and Riemenschneider 1980, Rogers 1981). The ratio of the number of beech to sugar maple trees in the overstory in Warren Woods (2.8) is within the range of 1.5 to 3.1 reported for these other remnant stands. The relative rarity of the other associated species in Warren Woods, such as yellow-poplar and black cherry, is also similar to that observed in other mature beech-maple stands (Potzger and Friesner 1943, Hough and Forbes 1943, Braun 1950, Potzger 1950, Petty and Lindsey 1961, Beals and Cope 1964, Jackson and Allen 1968, Vankat et al. 1975, Abrell and Jackson 1977, Gilbert and Riemenschneider 1980).

These compositional characteristics for present-day Warren Woods are also similar to those of presettlement beech-maple forests. The original forests of Berrien County (Table 2) and of other areas in Indiana, Ohio, and Pennsylvania were also dominated by beech and sugar maple (Blewett and Potzger 1950, Potzger and Potzger 1950, Ross 1950, Shanks 1953, Goodlett 1954, Potzger et al. 1957, Lindsey et al. 1965, Whitney 1982). Beech was consistently more abundant than sugar maple in these presettlement forests, where the ratio in density of beech to sugar maple trees (~≥8 cm dbh) ranged from 2.5 to 5.9.

The apparently greater importance of beech over maple in presettlement forests relative to modern forests (Tables 1 and 2) has led some investigators to suggest that a successional shift in importance has taken place since the time of settlement (Ward 1956, Beals and Cope 1964). While changes in the importance of these two species may have actually occurred (and this will be discussed in the Discussion section on beech dominance), factors other than successional mechanisms may have contributed to the apparent difference.

Beech trees may be accorded greater importance than sugar maple in the surveyor's data because they did not record trees as small as those included in current ecological studies. Surveyors were sometimes instructed to measure only trees that were ≥5 in (~10 cm) diameter, although smaller trees were occasionally recorded (Bourdo 1956, and this study). Trees as small as 2.5 cm dbh, and sometimes 1.0 cm dbh, are commonly included in current sampling procedures. It is in these small size classes that the importance of sugar maple is elevated because of the density and frequency of occurrence of small sugar maple saplings in the understory.

Beech may also have been over-represented in the presettlement data because of surveyor's bias in favor of beech. Bourdo (1956) has reviewed the importance of bias in the survey data to the interpretation of presettlement forest composition. He suggested that beech may have been preferred by surveyors because its smooth bark did not need to be blazed to provide a surface for their iron marks. Beech may also have been selected because it was of little timber value at the time and because its smooth ashy-gray bark made it conspicuous for relocation (Gordon 1969).

Although bias was undoubtedly present, it probably is not of major consequence, since the range in species at any one sampling point was limited (Bourdo 1956).

Beyond the probable range of surveyor's bias, it is reasonable to assume that beech was more important than sugar maple in the forests of presettlement times, just as it is in present-day Warren Woods. It is also likely that the relative rarity of yellow-poplar and black cherry in Warren Woods (Table 1) and in other remnant stands reflects their natural rarity in presettlement times. Yellow-poplar and black cherry were rare in the presettlement beech-maple forests of Berrien County (Table 2) and of other areas for which survey data have been analyzed (Blewett and Potzger 1950, Potzger and Potzger 1950, Ross 1950, Shanks 1953, Goodlett 1954, Lindsey et al. 1965, Whitney 1982).

Overstory composition of present-day Warren Woods, therefore, is similar to other remnant beech-maple forests and to those that existed prior to settlement, at least in the relative proportion of the dominants and the rarity of the yellow-poplar and black cherry associates. This stand then represents a realistic model for beech-maple forest, and its composition likely reflects the result of natural forest processes which are the primary subjects of this research.

METHODS

Gap Chronosequence

All identifiable treefall gaps in the study area were surveyed and evaluated for inclusion in the chronosequence. Treefalls were identified by the presence of a fallen tree, a stump, or distinguishable pit and mound topography. Criteria required of gaps for inclusion in the chronosequence were that (1) the gap was created by the fall of a single tree; (2) the outline of the gap was discretely delineated on all sides by adjacent canopy trees; (3) the gap was not within 25 m of other gaps, or other areas of open canopy (e.g., wet areas, paths, forest edges); and (4) the age of the gap could be positively determined. Only single-treefall gaps were studied since this was the primary type of treefall disturbance.

Gap Age

Ages of gaps were determined from a variety of sources of corroborative evidence. Recent treefalls of known age were used as a check of the accuracy of age determination methods used. In young gaps, age was estimated as the time since release from suppression, as indicated by changes in the rate of height growth of seedlings and saplings within the gap. Growth was measured as the distance between successive years' terminal bud scale scars.

For all gaps, increment cores were taken from surrounding canopy trees that outlined the gap and from saplings and poles within the gap that were of sufficient size to be cored and that were probably present when the gap was created. Trees were cored at 1.5 m above the ground with an increment borer, and cores were dried, sanded, and mounted on wooden blocks. Radial increments were measured to the nearest 0.01 mm with an instrument designed for this purpose. Annual increment was plotted over time so that growth rate patterns indicative of responses to gap openings could be detected. A gap response was defined as at least a doubling of radial growth rate to increments $\geq$1.0 mm/yr that was sustained, on average, for $\geq$10 yr. In older gaps, where radial growth data were the only source of evidence, at least three trees yielding similar gap age estimates were required.

Other supporting evidence of gap age came from trees wounded by the fall of the gap-making tree, where one side of the bark of the wounded tree was scraped down through the vascular cambium. For four different gaps, increment cores from the wounded side of the tree and from an unwounded side, when matched, indicated the number of annual increments produced on the unwounded side since the gap-making tree fell. The degree of decay of the fallen trunk of the gap-maker was assessed by ranking the amount of bark loss, degree of firmness of trunk wood, and the intactness of the bole, and using this to support age estimates derived by other means.

Gap Character and Size

The location of each gap, its size, and the location of the gap-making tree were recorded. The identity of the fallen tree, its dbh and height, direction and type of fall (windthrow, snap, etc.), and degree of log decay were determined. Adjacent canopy trees that delineated the gap (outliners) were recorded as to their identity, location, dbh, and height. Canopy opening area and a standard measure of gap size (expanded gap) were also measured. The area of the canopy opening (gap as defined by Brokaw 1982) was estimated by measuring the longest gap diameter and its greatest perpendicular distance; gap geometry was assumed to be elliptical. The expanded gap is the area defined by the trunks of outlining canopy trees (Runkle 1982) and provides a standard, unchanging measure of gap size. This expanded gap presumably includes most of the area affected by the canopy opening. Expanded gap area was estimated by computing the average distance from the base of the fallen tree to each of the outliners, and by using this value as the radius to compute a circular area estimate. Gap area was plotted within age categories to determine the pattern and rate of gap closure.

Species Composition and Vegetation Structure

The composition and structure of vegetation contained within each expanded gap was determined. All saplings and poles $\geq$2.5 cm dbh were identified and their dbh, height, and location recorded. For each beech sapling (and poles if they were small enough), an attempt was made to determine whether it originated as a seedling or as a root sprout. This was achieved by excavating the soil from the area immediately surrounding the root collar to determine if the root system resembled that of known root sprouts. To some extent, this could be done without excavation, by examining the root collar and by attempting to shake or move the stem near its base in all directions (C. D. Canham, *personal communication*). Root sprouts will not move much in the direction toward or away from their connection with the parent tree.

For seedlings and saplings <2.5 cm dbh, plots of 0.25 m^2 or 1.0 m^2, depending upon stem density, were randomly located within the expanded gap. Ten or more plots were sampled, the number determined from a performance curve of cumulative average stem density versus sample size; sampling was considered adequate when density remained constant with increasing sample size. Species identity, diameter at base, and height were determined for each stem within the plots. Vegetation data were analyzed for changes in species diversity, seedling establishment, density, and for shifts in size structure through the chronosequence.

Growth of Dominant Species

Height Growth

Height growth of beech and sugar maple seedlings and saplings (0.5-3.0 m tall), determined using bud scale scars, was measured for 10 or more stems of each species in each gap. The number of stems measured was determined from a performance curve of cumulative mean height growth versus the cumulative number of measurements. Where the total number of stems of a species in a gap was less than 10, all stems of that species were measured. Average and maximum rates of height growth, and cumulative height increase, were plotted against gap age so that height growth responses to the opening and subsequent closure of treefall gaps could be detected.

Radial Growth

Increment cores from canopy trees that were used to age gaps were combined with cores from other mature trees to examine patterns of growth. Only those trees $\geq$20 cm dbh, with crowns exposed in the canopy, and for which a complete unrotted core could be obtained were included in the analysis. Annual increment was plotted against time. The number of gap responses, defined as before for the determination of gap age, was counted in each core. These responses were sometimes complex and highly variable. Intervening periods of slow growth could be more readily measured, however, because of the relatively stable and definite pattern of growth during suppression. Suppressed growth was defined as $\geq$10 consecutive years of growth at $\leq$1.0 mm/yr. The number of trees demonstrating suppression and the length of the suppressed period was determined for each species.

To ensure that my definition of suppression could be applied equally to both beech and sugar maple, and to compare the rates of growth of these species while suppressed, increment cores were taken from five pairs of beech and maple saplings, in the size range of 6.0-15.0 cm dbh, growing together beneath a closed canopy. Members of sapling pairs were of similar diameter and height and occurred within 5 m of one another; such paired trees were considered to have had similar histories of canopy coverage.

Mortality of Sub-Canopy Trees

Mortality of standing saplings and pole-sized trees was assessed within 14, 5 m-wide transects that traversed the study area. Transects were laid out in parallel in an east-west orientation, at 25 m intervals. Transect length varied with the width of the study area. All stems 2.5-20.0 cm dbh were identified and recorded as being dead or alive. Mortality, expressed as the percentage of the total number of stems for each species that were dead, and relative mortality, the percentage of stems of each species represented in the dead group, were calculated.

Distribution of Canopy-Sized Yellow-Poplar and Black Cherry

All canopy-sized yellow-poplar and black cherry trees in the 15.5 ha study area were recorded. Location and dbh of each tree were determined and the general forest conditions (including evidence of gap disturbance, and the proximity to forest edges, slopes, and areas of pooled water) in which each was found was measured or described.

The dispersion of trees of these two species was analyzed to determine whether their distribution was random, or if it was aggregated (non-random). Various methods of analysis were used. In each case, data consisted of the number of trees in each of 62 continuous 0.25 ha square plots encompassing the study area (Figure 3). A chi-square statistic, based upon the variance to mean ratio, was computed as

$$\chi^2 = \frac{(n - 1)s^2}{\bar{x}},$$

where n is the number of plots, $\bar{x}$ is the mean number of trees per plot, and s^2 is the variance of the mean (Pielou 1977). This chi-square statistic (with n - 1 df) was compared to a table of percentage points of the chi-square distribution to determine the degree of significant departure from random.

A chi-square goodness of fit test was also performed, using the equation:

$$\chi^2 = \sum \frac{(O - E)^2}{E},$$

where O is the observed frequency of trees in each plot and E is the expected frequency of trees if uniformly distributed (Pielou 1977). This calculated value of chi-square was compared to a tabular value to determine the degree of departure from uniformity.

Finally, Morisita's Index of Dispersion (Morisita 1959) was calculated as

$$I_d = n \frac{\sum X^2 - N}{N(N - 1)},$$

where n is the number of plots, N is the total number of trees counted, and $\sum X^2$ is the sum of the squared number of individuals in each plot. An I_d=1.0 would result if the

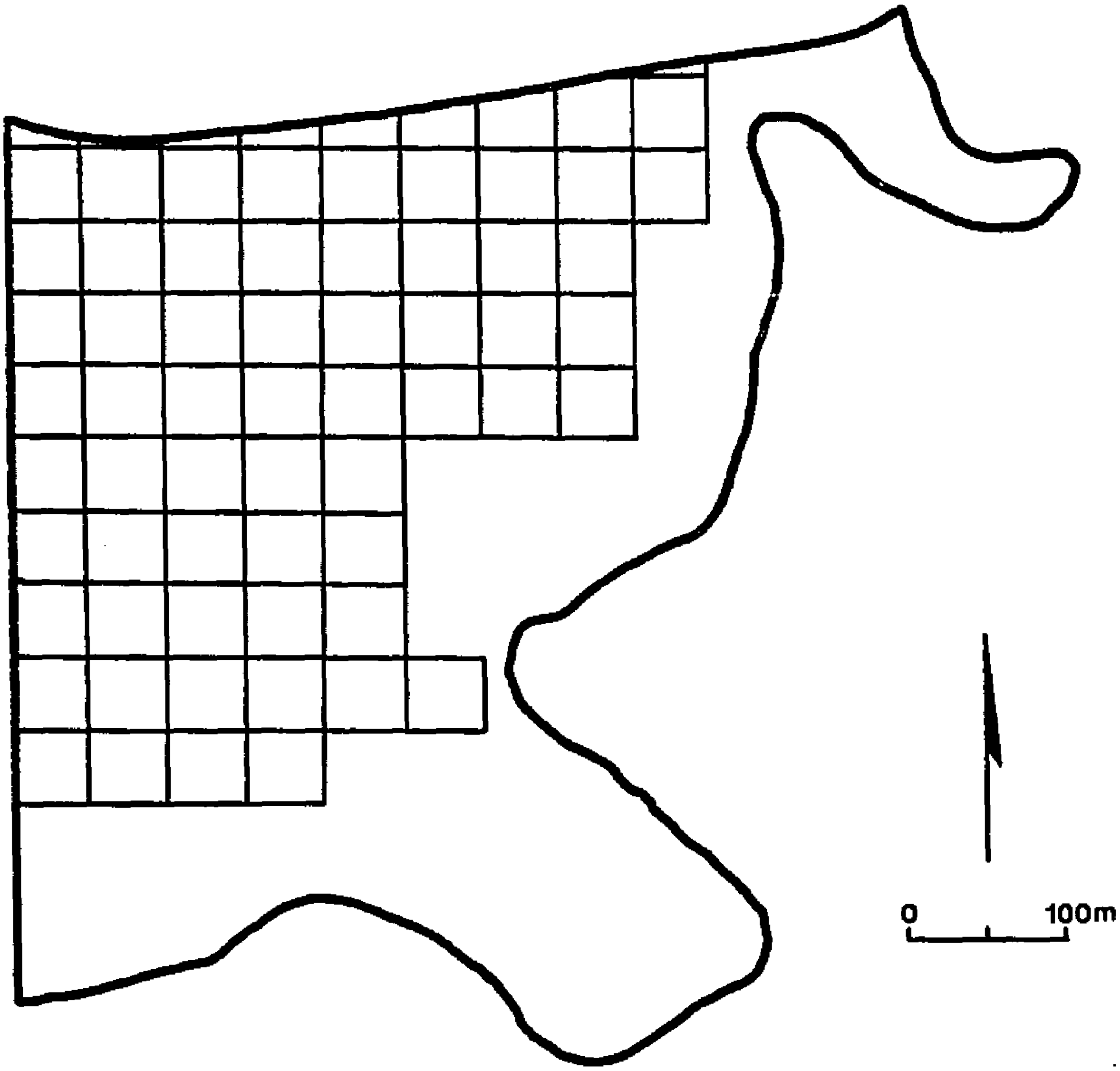


Figure 3. Study area used to examine distribution of canopy-sized yellow-poplar and black cherry trees. The 62, 0.25 ha plots encompass 15.5 ha.

dispersion of trees were random; I_d=0.0 if the dispersion were uniform; and I_d>1.0 if aggregated. A chi-square statistic was then computed as

$$\chi^2 = n\ X^2/N - N,$$

and was compared to a tabular value to assess the departure of the observed pattern of dispersion from random.

Diaspore Dispersal of Yellow-Poplar and Black Cherry

The dispersal of seed by yellow-poplar and black cherry was studied with seed traps placed at different distances around reproductively-mature canopy trees. Only those trees that were sufficiently isolated from other trees of the same species were chosen in an attempt to avoid contamination from other seed sources. Three traps were grouped together at distances of 5, 10, 20, 30, 40, 70, and 100 m in each of the four magnetic compass directions from five yellow-poplar trees, and at 5, 10, 20, 30, 40, and 60 m in each direction from five black cherry trees. Because of the limits of the study area and the proximity to other seed source trees, traps in certain directions and at certain distances could not be set (see Figure 4). Seed traps were similar to those described by Werner (1975), consisting of 150 x 15 mm disposable plastic Petri plate halves which were punctured to allow water

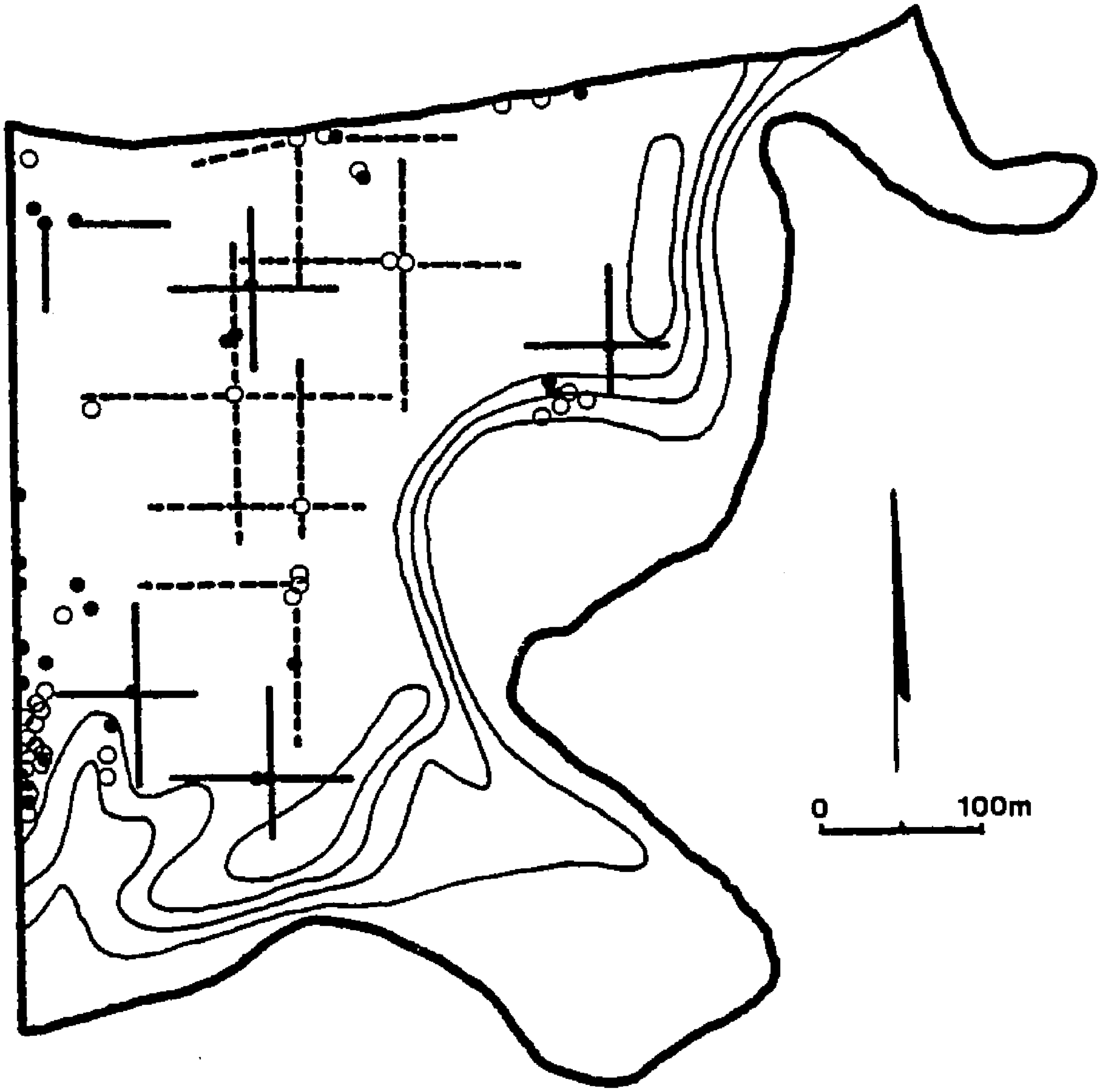


Figure 4. Sampling scheme for study of diaspore dispersal in yellow-poplar (○) and black cherry (●). Seed traps were placed to distances of 100 m from yellow-poplar trees and to 60 m from black cherry trees. Other canopy-sized trees of these two species are indicated, as are 10 ft slope contour intervals.

drainage. These plates were anchored to the forest floor with 10 cm spikes. Each plate was fitted with a 7 cm diameter filter paper disc coated with Tanglefoot, a compound which remains sticky after exposure to weather.

Black cherry traps were set during 28-29 July 1982 and yellow-poplar traps were set during 1-2 September 1982. Traps were checked for seeds between 28 December 1982 and 8 January 1983. The number of seeds of the appropriate species was counted and recorded for each trap. These data were used to estimate the maximum distance to which seeds of each of the tree species could be dispersed under the conditions that year. This distance was then used as the radius for plotting circular dispersal shadows around each mapped canopy yellow-poplar and black cherry tree. Total dispersal shadow area for each species was determined and expressed as a proportion of the total study area accessible to seed.

Reconstruction of Gaps Around Sub-Dominant Trees

An attempt was made to reconstruct the gaps involved in the recruitment of yellow-poplar and black cherry trees into the canopy. Only those gaps that were not within 25 m of any forest edge or any area of open canopy were considered for reconstruction. Also, only younger yellow-poplar and black cherry could be studied, since the analysis of expanded gap size required that there be older trees that delimited the original gap that surrounded them.

The sub-dominant tree and certain of the outlining trees were cored with an increment borer to determine the age of the yellow-poplar or black cherry and to determine the age of the gap. This was done to verify that the surrounding trees were large enough to have outlined the original gap.

Tree diameters were reduced by mean annual diameter increments, compounded over the number of years since the formation of the gap. Diameter increments were derived for beech and sugar maple trees by averaging diameter growth of the most recent 10 yr of 20 randomly-selected canopy trees (>20 cm dbh) of each species, and using these values to compute average annual diameter growth. Diameter increments for other species were obtained from the silvicultural literature. Certain trees were cored to determine their age and size at time of gap formation. If one of the suspected outlining trees was found not to have been ≥20 cm dbh at the time of gap formation, the gap outline was extended outwards to the next tree that was large enough.

Once the outlining trees were defined, distances from the sub-dominant tree to each of the outliners was measured and an average radius for the expanded gap was computed.

Circular gap areas were then derived and these were compared to known values for single treefall gaps.

Rate of Forest Turnover

Frequency of treefall disturbance has been measured in the literature in a variety of ways. The rate of gap formation, in number of gaps created per unit area per unit time, has been measured by Hartshorn (1978) and by Brokaw (1982a). The rate of treefall per unit area, or the percent of total trees falling per unit area per unit time, has been reported in several studies (Leigh 1975, Abrell and Jackson 1977, Brewer and Merritt 1978, Brokaw 1982a, Uhl 1982, 1983), but these measures cannot account for differences in gap size or in the number of trees that fall per gap. The rate of forest turnover is a measure of the gap area created per unit forest area per unit time (Brokaw 1982a), which corresponds to an estimate of the average time between successive gap events at the same location in the forest (Hartshorn 1980). Forest turnover rate has been reported by several investigators (Poore 1968, Hartshorn 1978, Hartshorn 1980, Runkle 1982, Brokaw 1982a, b, Uhl and Murphy 1981).

All treefalls were identified and measured in 15, 2500 m^2 square plots. Gap location within the plot, area of canopy opening, expanded gap area, and the number of trees fallen were measured and recorded. Fallen trunks and stumps were known to decay within 45 yr following gap formation, as evidenced by the age of old gaps where boles and stumps were nearly or completely decomposed. Accordingly, all gaps having an existing trunk or stump were considered to have been created within a period of 45 yr. Similarly, the rate of gap closure, derived from the analysis of the gap chronosequence, was used to make parallel calculations based on characteristics and numbers of open gaps. That is, all open gaps were considered to have been created within a period of time equivalent to the number of years required for gap closure.

The difference between the radius of new canopy gaps and their surrounding expanded gaps was calculated and this was used to estimate the original canopy gap sizes from the known expanded gap areas of all gaps in the 15 plots. Together, these data allowed the comparison of disturbance frequency in Warren Woods to that in other forests, regardless of how other measures were recorded.

RESULTS

Regeneration Within the Gap Chronosequence

Of the 58 single-treefall gaps considered, 19 were included in the chronosequence, with ages that ranged from 1-34 yr (Table 3). These gaps represented the full spectrum of stages in gap development, from new gap openings through closure of the canopy. Area of the expanded gap averaged 496.9 m^2 (SD = 160.5).

The species of tree that fell to create the gaps (gap-makers) generally reflected the abundance of species in the overstory. Of those gap-makers which could be identified with certainty, 14 were beech, while four were sugar maple. Gap-maker dbh averaged 69 cm (SD = 14), and ranged from 47-100 cm. The mean height (length) of the gap-makers in gaps $\leq$14 yr was 32 m (SD = 3); decomposition of trees in older gaps prohibited accurate estimates of original tree heights. Most of the gap-makers, 11 of 19, had been windthrown (uprooted), while eight had been snapped off at various heights along the bole.

Table 3. Characteristics of gaps included in the chronosequence.

Gap Age Class	No. in Class	Gap No.	Age	Canopy Gap Area (m2)	Canopy Gap Radius (m2)	Sub-Canopy Closed?	Expanded Gap Area (m2)	Expanded Gap Radius (m2)	Species of Gap-Maker	DBH of Gap-Maker (cm)	Height of Gap-Maker (m)	Type of Fall	Direction of Fall (o)
0-4	4	7	1	318.9	10.1	No	886.7	16.8	Fg	100	35	Snap (2m)	356
		6	2	190.1	7.8	No	353.0	10.6	Fg	100	36	Snap (18m)	50
		17	4	110.0	5.9	No	615.8	14.0	Fg	78	35	Windthrow	53
		19	4	112.3	6.0	No	422.7	11.6	Fg	62	35	Windthrow	105
5-9	4	27	5	132.7	6.5	No	357.4	10.7	As	51	31	Snap (6m)	324
		30	5	163.4	7.2	No	475.3	12.3	Fg	60	33	Snap (3m)	157
		25	7	155.5	7.0	No	555.7	13.3	As	60	26	Windthrow	107
		29	8	169.6	7.3	No	500.7	12.6	Fg	--	30	Windthrow	38
10-14	2	16	12	99.0	5.6	No	730.6	15.3	Fg	69	32	Windthrow	180
		31	13	27.5	3.0	No	537.8	13.1	Fg	70	29	Snap (7m)	293
15-19	3	36	15	51.1	4.0	No	504.1	12.7	Fg	47	25*	Windthrow	161
		37	17	56.7	4.2	No	439.9	11.8	Fg	80	28*	Windthrow	183
		34	19	47.1	3.9	Yes	471.4	12.3	Fg	67	25*	Windthrow	156
20-24	3	20	20	28.3	3.0	Yes	359.7	10.7	Fg	60	19*	Windthrow	150
		41	21	28.3	3.0	Yes	415.5	11.5	Fg	70	19*	Snap (0m)	73
		42	23	37.7	3.5	Yes	572.6	13.5	Fg?	74	29*	Snap (0m)	95
25-29	1	23	29	56.0	4.2	Yes	706.9	15.0	As	76	17*	Windthrow	167
30-34	2	21	30	18.8	2.4	Yes	326.9	10.2	As?	55	24*	Snap (0m)	169
		43	34	1.6	0.7	Yes	208.3	8.1	?	--	?*	Windthrow	71

*Crown and bole decay left only a portion of trunk remaining.

Gap Area

Average area of the canopy opening decreased through the sequence from 183 m^2 in the first four years to 10 m^2 in the 30-34 yr gap age class (Figure 5). Although the upper canopy remained open, by age 19 a subcanopy had been formed in the gap by the crowns of large saplings and poles already present on the site at the time of gap formation (Table 3); this subcanopy shaded the smaller stems below. Gaps in the upper canopy were 99% closed after 34 yr.

Composition and Structure of Regeneration

The density of seedlings and saplings <2.5 cm dbh within the expanded gaps increased following the opening of the canopy to a maximum averaging 30.0 stems/m^2 within the 5-9 yr gap age class (Figure 6). Density quickly declined to low levels in subsequent gap age classes, and ranged from 5.6 stems/m^2 in the 10-14 yr gap age class to 1.2 stems/m^2 in the 30-34 yr age class. Of the stems in gaps, 72.5% were sugar maple, 7.8% were beech, and 19.7% were stems of other species (Figure 7). Other species identified included all of those listed previously in the section on forest composition of the study area, except sycamore, as well as poison-ivy (Toxicodendron radicans (L.) Ktze.).

Recruitment of first-year seedlings was responsible, in part, for changes in stem density, and occurred

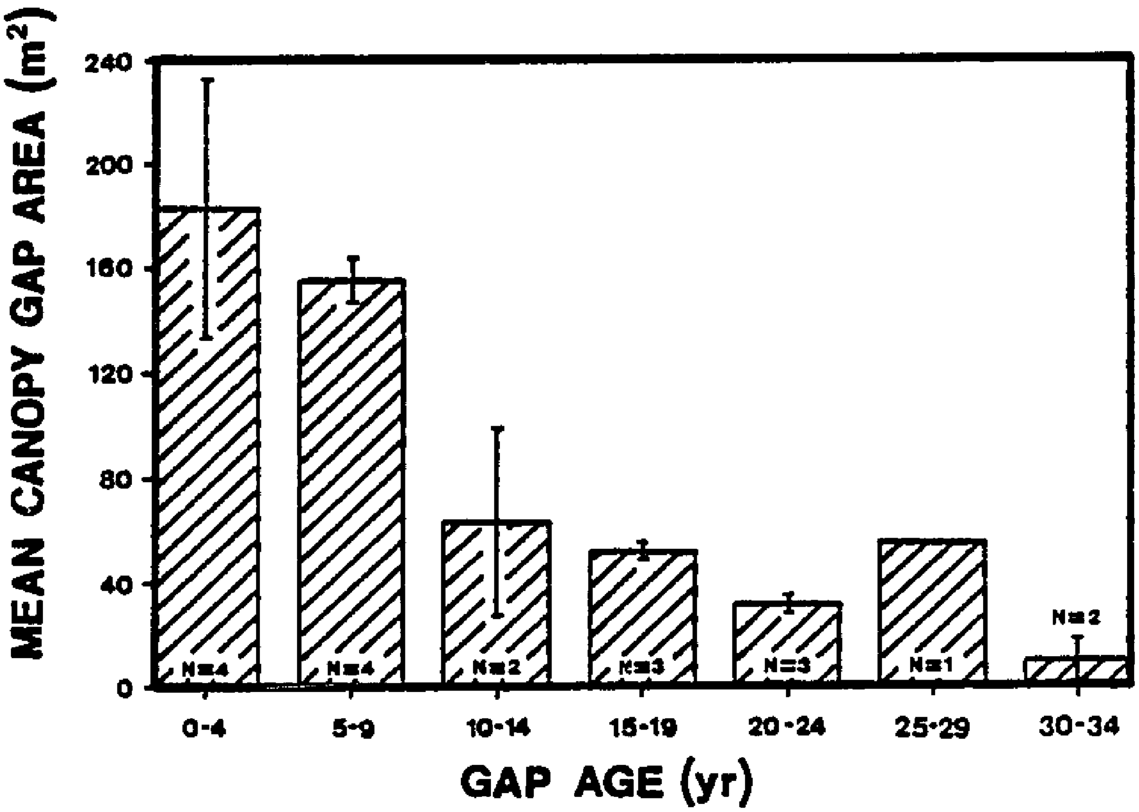


Figure 5. Change in gap size through the chronosequence. Vertical lines represent ± 1 SD of the mean gap area. The number of gaps (N) is shown for each age class.

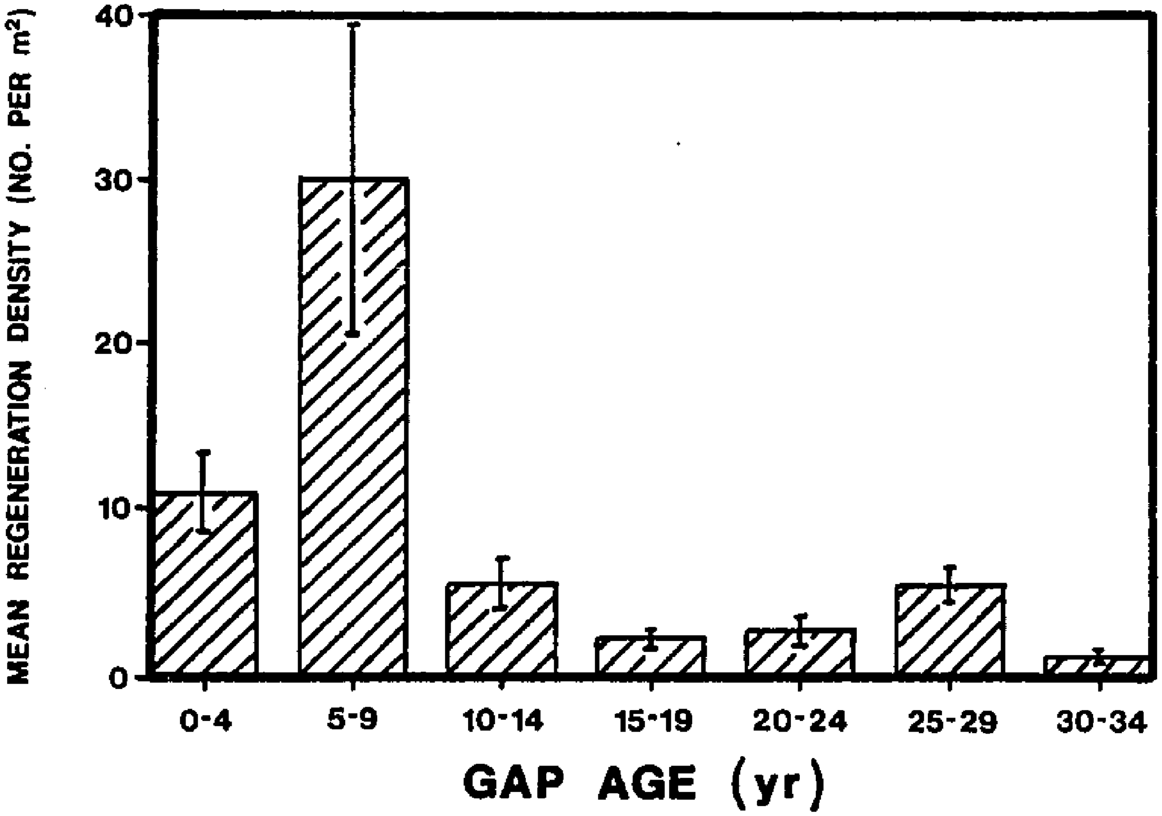


Figure 6. Mean density of seedlings and saplings <2.5 cm DBH within gaps of the chronosequence. Vertical lines represent ± 2 SE of the mean.

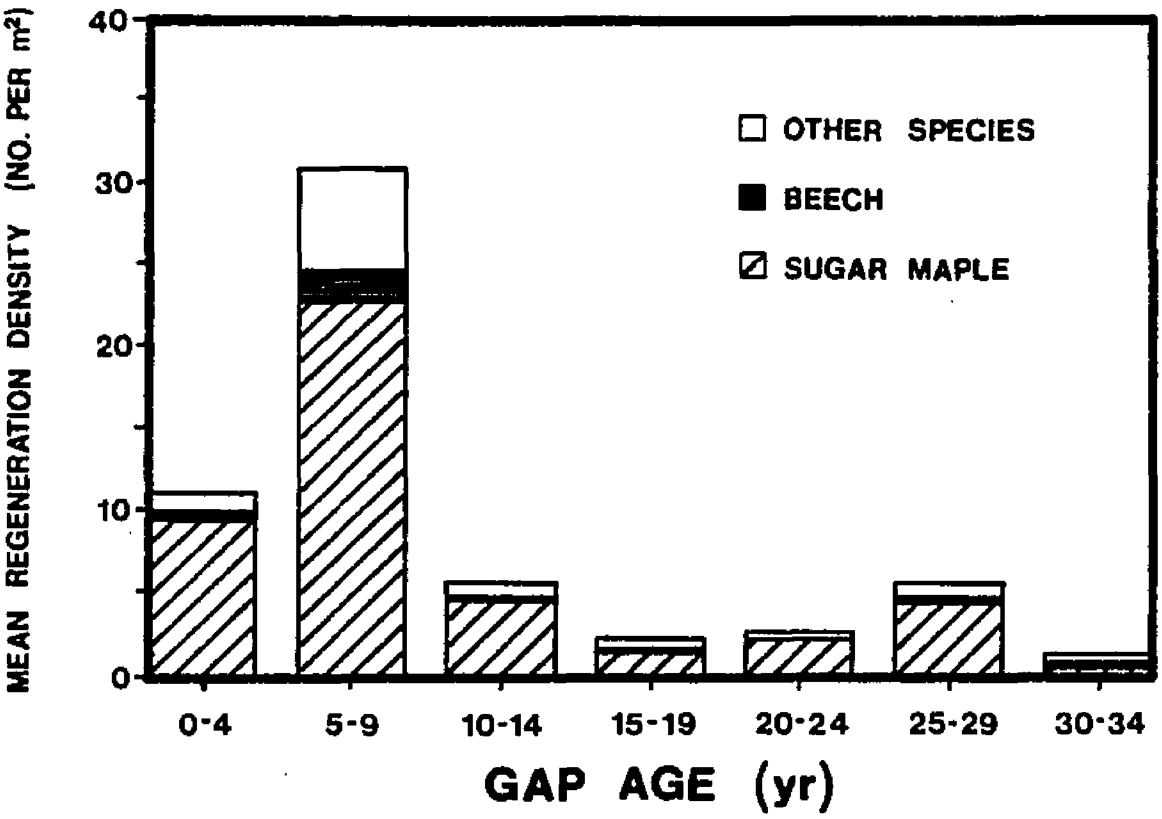


Figure 7. Mean density of seedlings and saplings <2.5 cm DBH within gaps of the chronosequence, stratified by species.

throughout the chronosequence (Figure 8). The number of first-year seedlings was greatest in new gaps at 2.1 seedlings/m^2, followed by a steady decline to a low of 0.2 seedlings/m^2 in the 15-19 yr gap age class. Subsequently, recruitment increased to 1.1 seedlings/m^2 in the 20-24 yr gap age class and then declined steadily to 0.6 seedlings/m^2 in the 30-34 yr age class.

The diversity of species (richness) of the woody vegetation in chronosequence gaps did not vary according to any recognizable trend (Figure 9). The mean number of species/gap varied from 4.7 to 7.8.

The height structure of woody vegetation <2.5 cm dbh was also analyzed over the gap chronosequence (Figure 10). In the initial (0-4) yr gap age class, stems to 3 m in height were recorded. An apparent build-up of the number of these smaller stems occurred by the 5-9 yr gap age class. There was no advance into larger size classes until gaps were 15-19 yr, where a maximum stem height of 5 m was recorded. The abundance of stems in intermediate and larger size classes (0.5-5.0 m) subsequently declined in older gap age classes, with no further increase in stem height. Throughout the chronosequence, there was a supply of seedlings in the 0-0.5 m height class; seedling densities in this size class were never below one seedling/m^2.

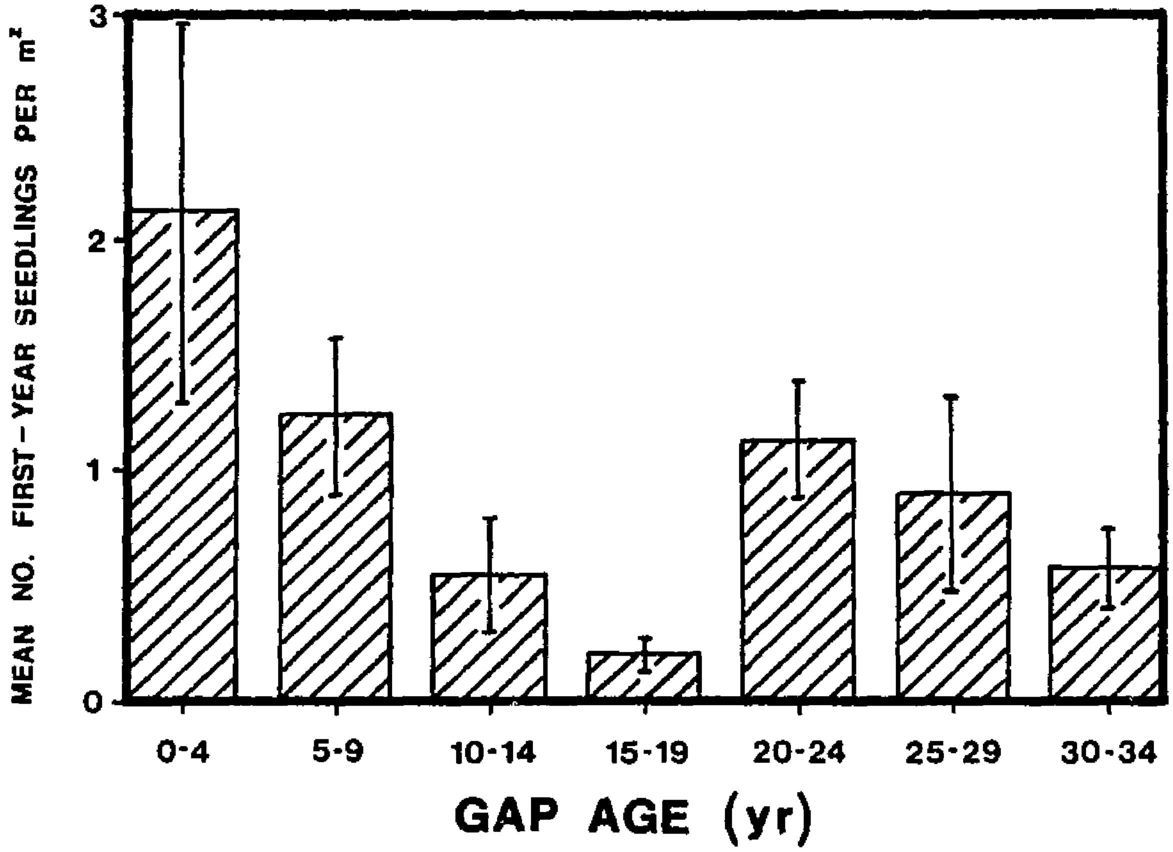


Figure 8. Recruitment of seedlings in gaps of the chronosequence. Vertical lines represent ±1 SE of the mean.

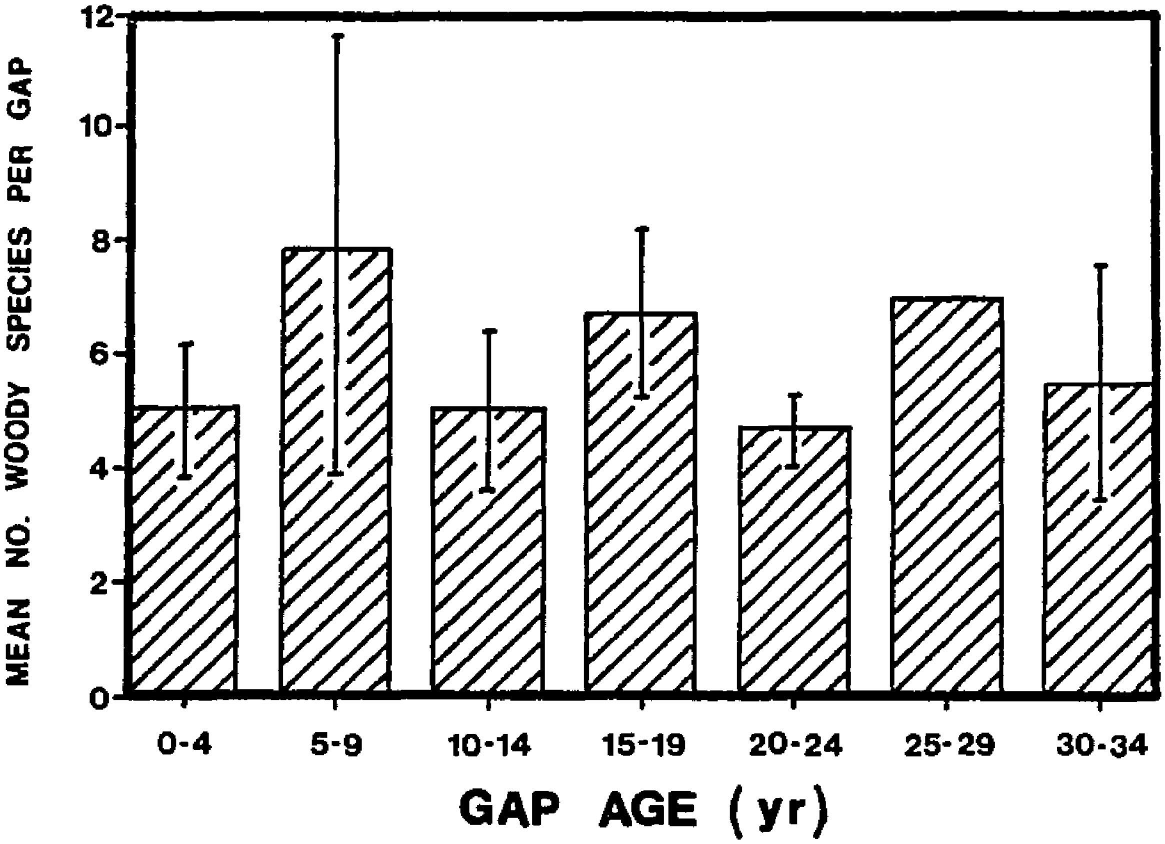
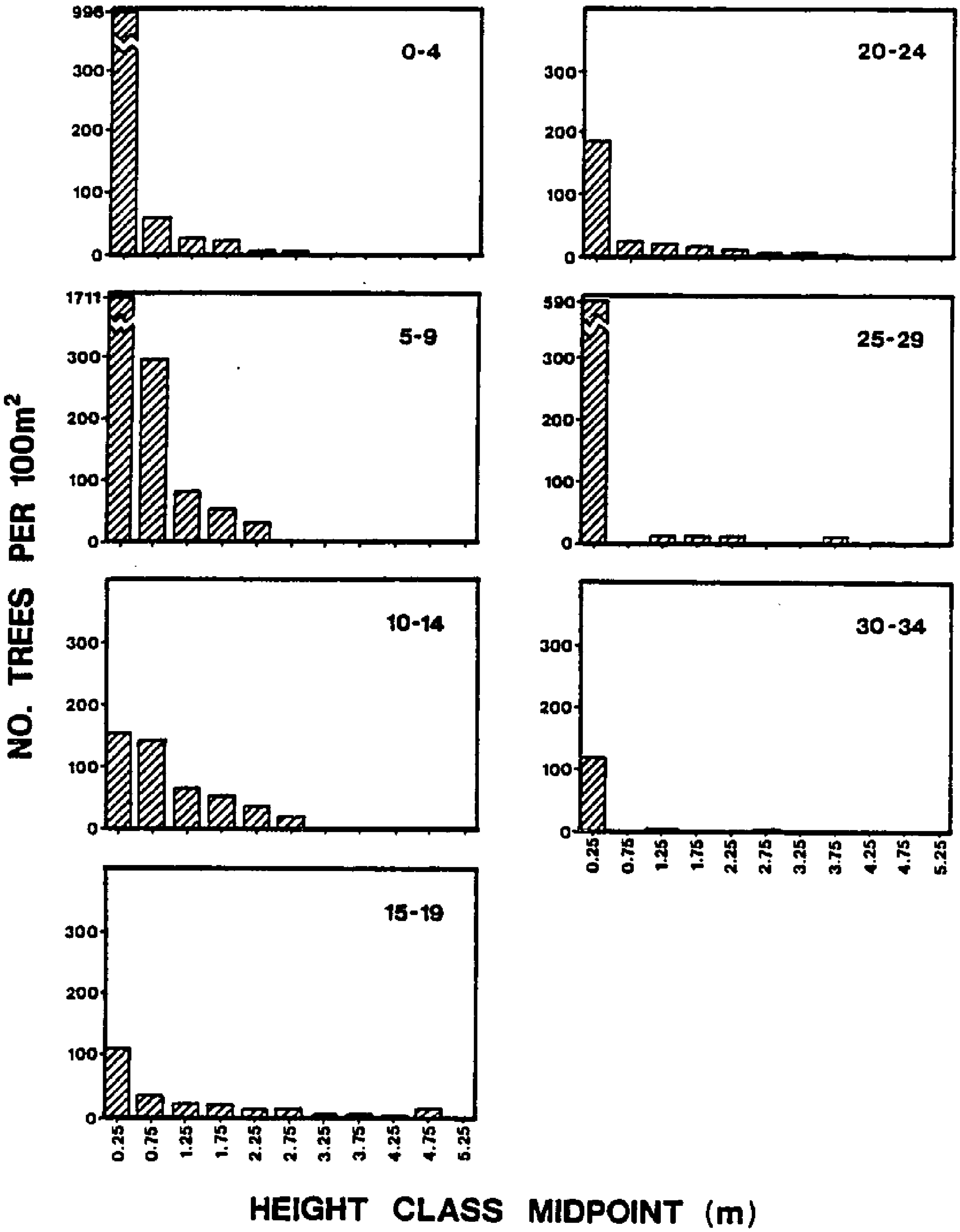


Figure 9.- Diversity (richness) of species identified in gaps of the chronosequence. Vertical lines represent ±1 SD of the mean.

Figure 10. Height class distribution of seedlings and saplings < 2.5 cm DBH through the gap chronosequence. Horizontal axis scaled in midpoints of 0.5 m height classes.


0-4
996
300
200
100
0
5-9
1711
300
200
100
0
10-14
300
200
100
0
15-19
300
200
100
0
20-24
300
200
100
0
25-29
590
300
200
100
0
30-34
300
200
100
0
0.25
0.75
1.25
1.75
2.25
2.75
3.25
3.75
4.25
4.75
5.25
NO. TREES PER 100m²
HEIGHT CLASS MIDPOINT (m)

Eighteen percent of the beech stems measured in gaps of the chronosequence were determined to have been sprouts. There was no apparent trend in the relative abundance of beech sprouts through the gap age sequence.

Growth and Survivorship of Beech and Sugar Maple

Height Growth

Preliminary measurements of height growth of beech and sugar maple seedlings and saplings 0.5-5.0 m tall were made in open gaps and beneath closed canopy (Table 4). Beech grew an average of 9.7 cm/yr beneath closed canopy, significantly greater ($P<.001$; t test) than the average rate of growth for sugar maple in the shade at 5.4 cm/yr. Saplings of both species grew at significantly greater rates ($P<.001$; weighted t test for unequal variances, Steel and Torrie 1960) in gaps than in the shaded understory, but there was no significant difference between the two species. However, sugar maple appeared to have been capable of greater maximum growth rates than beech in gaps.

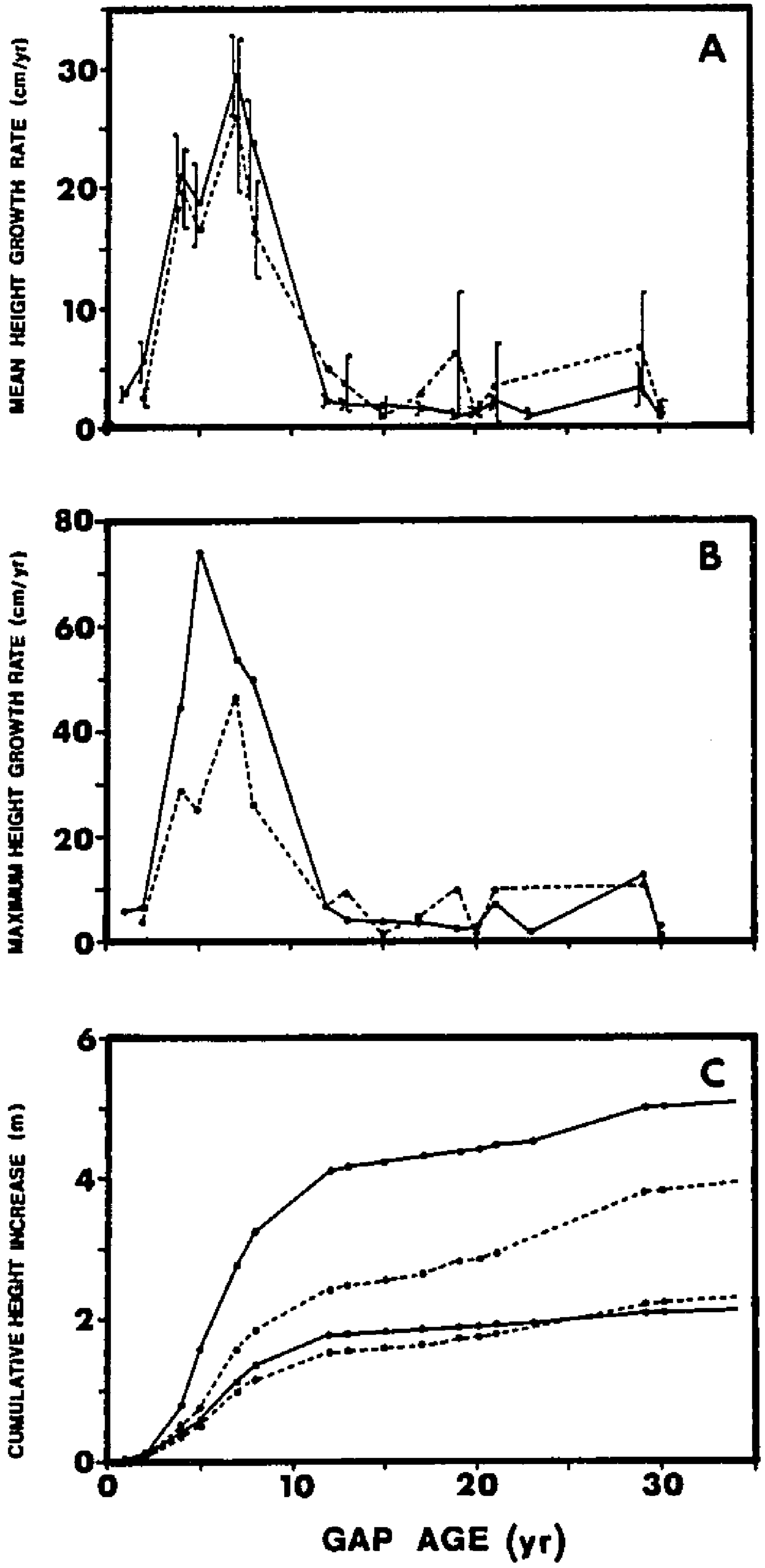
Height growth was also measured in beech and sugar maple seedlings and saplings 0.5-5.0 m tall in gaps of the chronosequence to examine changes through time (Figure 11). These small trees exhibited a pulse of rapid growth during the first 10 yr while gaps were fully open, but growth rates sharply declined during gap closure (Figure 11A).

Table 4. Terminal leader extension growth of beech and sugar maple saplings 0.5-5.0 m tall beneath a closed canopy and in open gaps.

	Canopy		Gap	
	Beech	Sugar Maple	Beech	Sugar Maple
Mean leader growth (cm/yr)	9.7	5.4	26.3	26.1
SE	0.8	0.5	1.4	2.0
Range	1.0 - 37.0	1.0 - 25.5	2.0 - 63.0	0.5 - 93.0
N	100	100	100	100

All comparisons significantly different ($P < .001$; *t* tests weighted for unequal variances), except between species in gaps.

Figure 11. Height growth of beech (dashed lines) and sugar maple (solid lines) saplings (0.5-3 m tall) through the gap chronosequence. A) Mean height growth rate ± 2 SE. B) Maximum rate of growth measured in each gap age. C) Cumulative mean and maximum increases in height derived from growth rate data in A and B; height increases for intervening years were interpolated.


A
MEAN HEIGHT GROWTH RATE (cm/yr)
0
10
20
30
B
MAXIMUM HEIGHT GROWTH RATE (cm/yr)
0
20
40
60
80
C
CUMULATIVE HEIGHT INCREASE (m)
0
2
4
6
0
10
20
30
GAP AGE (yr)

Mean height growth rate peaked at 29.7 cm/yr in sugar maple and at 26.1 cm/yr in beech. Average growth rates of beech and sugar maple were not significantly different ($P > .01$; $\underline{t}$ tests) in any of the gap ages of the chronosequence.

The maximum rate of height growth that was measured within gaps in each age category also pulsed within the first 10 years of the chronosequence (Figure 11B). Throughout this initial period, maximum sugar maple height growth rate exceeded that of beech, in one case by as much as 300%. The greatest rate of growth measured for sugar maple was 74.5 cm/yr, whereas for beech the maximum was 47.0 cm/yr.

Mean and maximum growth rates through the chronosequence were used to estimate the overall cumulative increase in height that would result from a single gap exposure (Figure 11C). Growth rates were interpolated for years intervening between those for which measurements were taken. Height increases for beech and sugar maple derived from average height growth rates were nearly equal at just over 2 m after 34 yr. The maximum increase in height possible by sugar maple was limited to 5.1 m as a result of a single gap exposure; beech could potentially increase by 3.9 m.

Patterns of Radial Growth

Radial growth rates exhibited a pulsing or episodic pattern similar to that seen for height growth (Figure 12). Of the 67 mature trees studied, 88% were determined to have responded in growth to two or more gap events ($\overline{x}$ = 2.7 gap responses/tree; SD = 0.7). The mean number of gap responses per tree in beech and in sugar maple were equal. The other 12% of the trees examined all had grown at high rates of growth throughout their histories. While it is assumed that repeated or sustained canopy openings were responsible for the fast growth of these trees, it was not possible to define distinct gap responses associated with such openings.

Although there was no difference in the number of definable gap events influencing mature beech and sugar maple trees, it appeared that more beech had been suppressed than maple, and that suppressed periods lasted longer in beech (Figure 12). In fact, 77% of the canopy-sized beech sampled exhibited suppressed growth, whereas only 53% of mature sugar maple had been suppressed (Table 5). The mean length of the suppressed period in beech (64.5 yr) was over twice as long ($P < .005$; weighted t test; Steel and Torrie 1960) as in sugar maple (26.6 yr). In addition, the maximum length of suppression in beech (174 yr) was nearly three times that in sugar maple (61 yr).

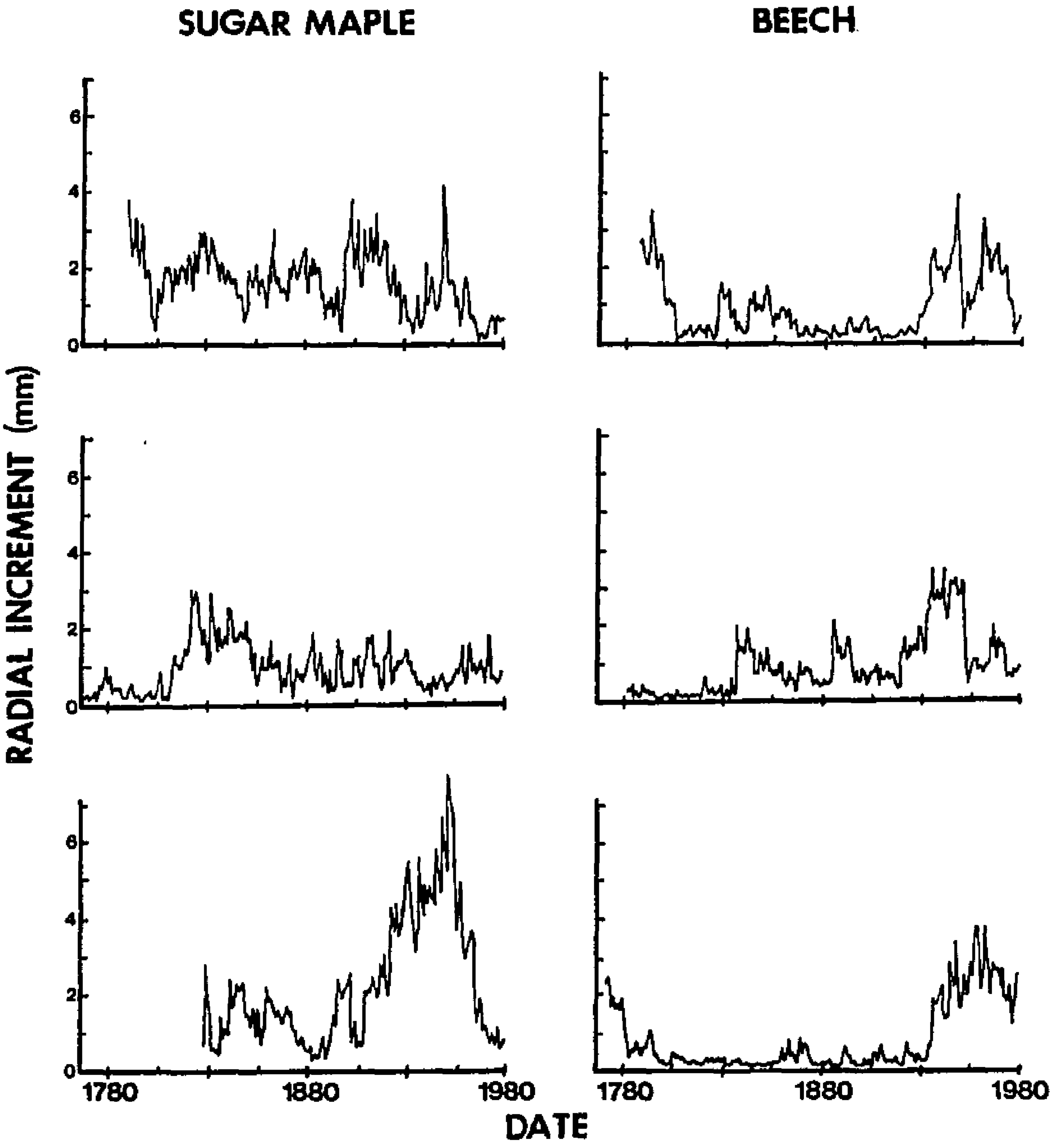


Figure 12. Radial growth rate patterns of canopy-sized sugar maple and beech trees selected to show differences in patterns of episodic growth. Pulses of fast growth are related to periodic openings of the canopy (gaps), while periods of slow growth are the result of intervening times of suppression beneath a closed canopy.

Table 5. Proportion of trees showing suppression* and duration of suppression in canopy-sized ($\geq$20 cm dbh) beech and sugar maple.

Species	N	No. of Trees Suppressed	%	Length of Suppressed Period (yr)		
				$\bar{x}$ (SE)	N**	Range
Beech	34	26	77	64.5 (10.4)	18	10-174
				P .005***		
Sugar Maple	34	18	53	26.6 (3.1)	18	10-61

*Suppression defined as $\geq$10 consecutive years of growth at $\leq$1.0 mm/yr.

**Sample size for suppressed trees determined by number of suppressed sugar maple trees. Number of suppressed beech trees analyzed was reduced by random selection to this value.

***Weighted <u>t</u> test for unequal variances.

Radial Growth of Suppressed Trees

Radial growth rates of suppressed beech and sugar maple saplings (6.0-15.0 cm dbh) that were growing together showed similar patterns, reflecting a shared history of canopy coverage. Figure 13 depicts the patterns from the five pairs of trees. Actual yearly increment data were filtered using five-year moving averages, where the average rate of growth for a given year was calculated from the growth rates of that year and of the two preceding and two subsequent years. Average actual growth rates of the suppressed pairs of trees were compared using a *t*-test for paired observations, where the difference in the radial increment between trees of the pair was computed for each year. In four of the five pairs, there was no significant difference between the mean growth rates, while in the fifth pair, the mean growth rate of beech (1.04 mm/yr) was significantly greater ($P < .01$) than that of sugar maple (0.84 mm/yr).

Mortality of Sub-Canopy Trees

Sixty-five percent of the dead sub-canopy trees (2.5-20.0 cm dbh) were sugar maple, although this roughly corresponded to the relative abundance of sugar maple (59.3%) in this size class (Table 6). Eight percent of all sub-canopy sugar maple were standing dead. If mortality

Figure 13. Radial growth of five pairs of suppressed beech and sugar maple saplings growing within 5 m of one another. Increment data were filtered using five-year averages as described in the text.

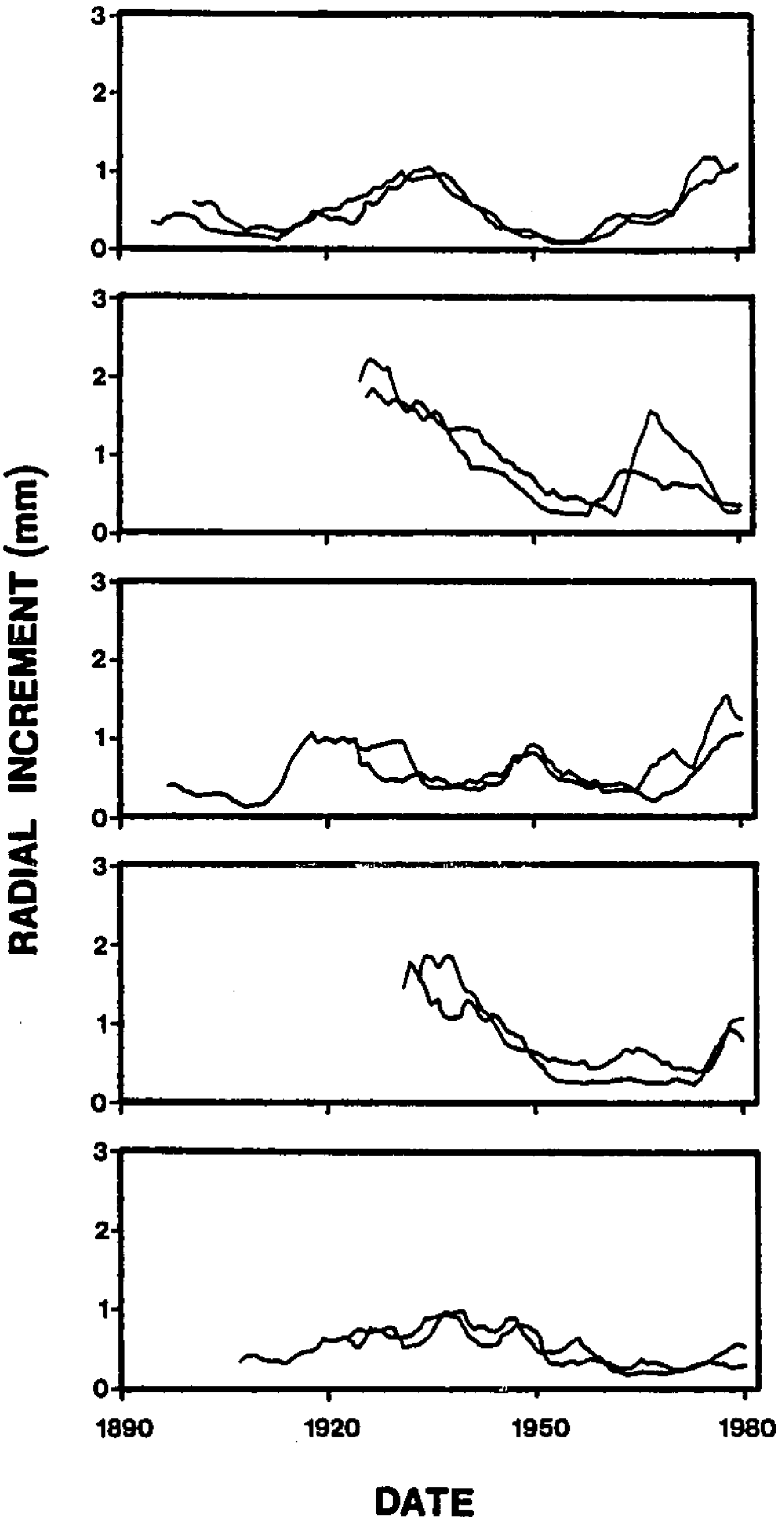

RADIAL INCREMENT (mm)
0
1
2
3
1890
1920
1950
1980
DATE

Table 6. Composition and mortality of sub-canopy beech and sugar maple trees 2.5-20.0 cm dbh.

Species	No. Trees Sampled	Percent Composition	No. Dead	Percent of Total Dead	Percent Mortality by Species
Beech	386	30.6	7	7.5	1.8
Sugar maple	748	59.3	60	64.5	8.0
Other species	127	10.1	26	28.0	20.5
Totals	1261	100.0	93	(7.4)	100.0

were similar in all species, then the proportion of dead stems of a particular species should have been equal to its representation in the stand. However, whereas beech represented 30.6% of all sub-canopy trees, only 7.5% of dead standing trees were beech. Percent mortality in beech was correspondingly low at 1.8%. In contrast, all species other than beech and sugar maple combined made up 10.1% of sub-canopy trees, but accounted for 28.0% of dead standing trees. This greater representation of other species among dead trees resulted in a higher (20.5%) mortality value.

Regeneration of Yellow-Poplar and Black Cherry

Distribution of Mature Trees

A total of 34 canopy-sized yellow-poplar trees and 29 mature black cherry trees were located in the 15.5 ha area sampled (Figure 14). Diameters of these trees averaged 57.5 cm dbh (SD = 15.8; range = 28.1-96.7) for yellow-poplar and 39.5 cm dbh (SD = 15.7; range = 18.5-76.8 cm dbh) for black cherry. The total of 63 canopy trees of these two species corresponds to an average of 4 trees/ha, or about 2.6% of the total number of canopy trees ($\geq$20 cm dbh) in the stand.

Dispersion of yellow-poplar and black cherry was analyzed for randomness (Table 7). Results were similar for each species considered separately and when both were

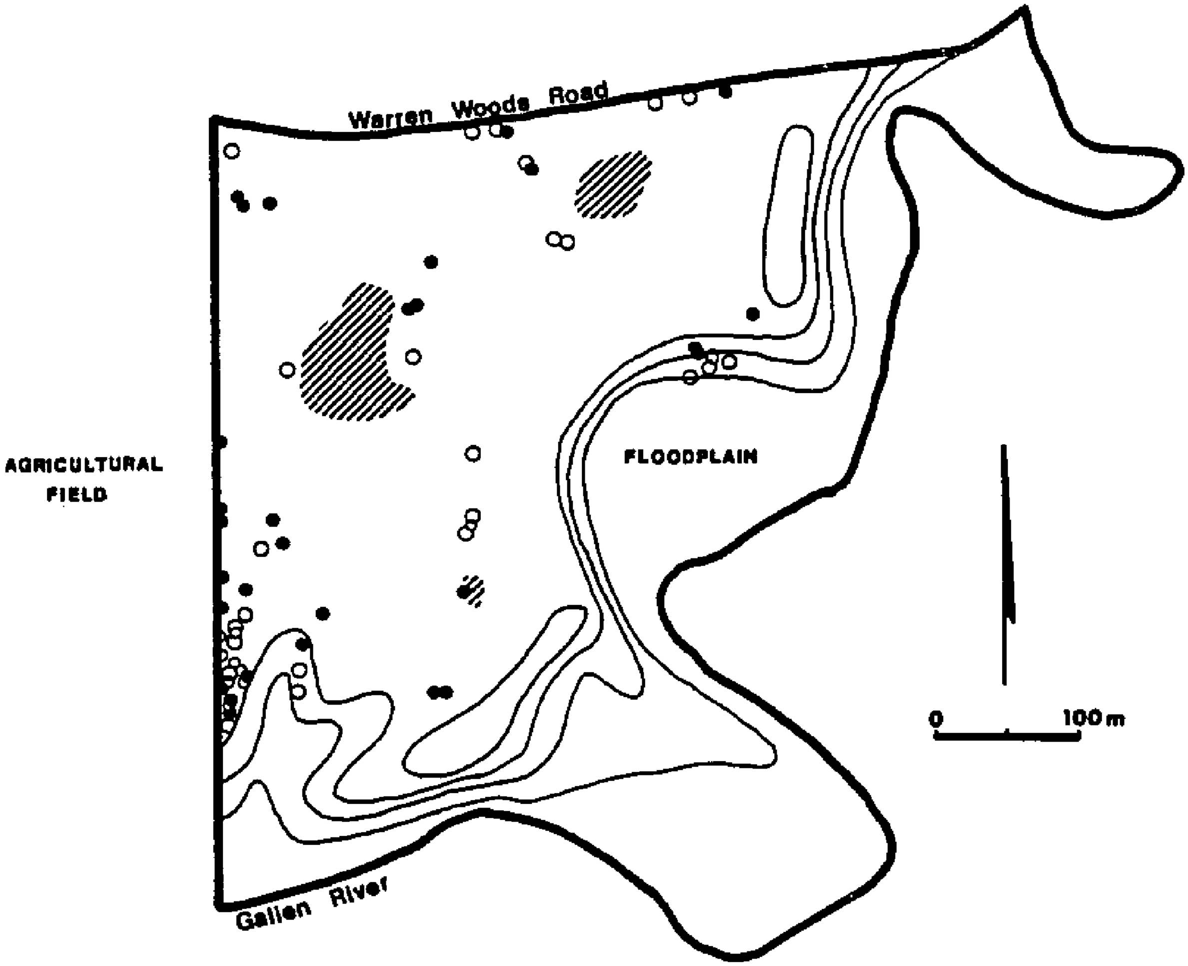


Figure 14. Distribution of canopy-sized yellow-poplar (○) and black cherry (•) trees in the 15.5 ha sampling area. Isolines represent 10 ft slope contour intervals associated with the banks of the Galien River floodplain. Hatched areas indicate the extent of pockets of poorly-drained soils which are commonly covered with water.

Table 7. Analysis of dispersion of canopy-sized yellow-poplar and black cherry trees in 15.5 ha study area, based upon the frequency of individuals occurring in 62 continuous 0.25 ha plots.

	Total No. Trees in Study Area	Mean No. Trees Per Plot	Variance* to Mean Ratio	$\chi^2 = \frac{(n - 1)s^2}{\bar{x}}$ (df)	$\chi^2 = \Sigma \frac{(O - E)^2}{E}$ (df)	Morisita's Index of Dispersion	
						$I_d = n\frac{\Sigma X^2 - N}{N(N - 1)}$**	$\chi^2 = n\ \Sigma X^2/N - N$ (df)
Yellow-poplar	34	0.5	3.2	195.2 (61) $P<.005$	24.4 (2) $P<.005$	5.4	195.8 (61) $P<.005$
Black cherry	29	0.5	2.1	125.9 (61) $P<.005$	31.9 (2) $P<.005$	3.4	127.1 (61) $P<.005$
Both species	63	1.0	3.9	240.4 (61) $P<.005$	32.7 (3) $P<.005$	3.9	241.1 (61) $P<.005$

* If >1.0, then non-random.

** If >1.0, then aggregated.

combined. All tests indicated patterns of dispersion which were significantly different from random. Specifically, variance to mean ratios were all greater than 1.0 (see also first chi-square statistic, Table 7). The chi-square goodness of fit test (second chi-square statistic, Table 7) indicated patterns of dispersion that were significantly ($P<.005$) non-uniform throughout the stand. Similarly, Morisita's Index of Dispersion values were all greater than 1.0, which implied aggregated patterns of dispersion (see third chi-square statistic, Table 7).

In the field, it became apparent that the majority of yellow-poplar and black cherry trees were associated with a variety of forest edges (Figure 14). These edges included forest boundaries on the perimeter of the stand (an agricultural field on the west, and Warren Woods Road on the north), relatively steep slopes associated with the Galien River floodplain on the east and south ends of the stand, and areas of pooled water over pockets of poorly-drained silt-loam soils in the forest interior. These wet areas were covered with water for most of the growing season. Trees tended not to establish in these inundated areas, leaving a relatively open canopy. Over 76% of canopy-sized yellow-poplar trees and over 72% of mature black cherry trees were within 15 m of stand boundaries, the innermost slope contour line, or wet soils. The 15 m distance was arbitrarily chosen because it approximated the mean diameter of a tree crown.

Diaspore Dispersal

A total of 29 yellow-poplar samaras were caught in the 330 traps set around the five reproductively-mature yellow-poplar trees, while only nine black cherry drupes were found in the 297 traps set around black cherry trees. The maximum distance to which fruits were dispersed from source trees was 40 m for yellow-poplar and 5 m for black cherry (Figure 15). These maximum dispersal distances were used to plot arbitrary circular dispersal shadows around all 63 canopy-sized trees of these two species in the study area (Figure 16). Just over half (53.4%) of the study area was accessible to yellow-poplar samaras, while only 12.6% of the stand was accessible to black cherry drupes.

Reconstructed Gaps

Seven gaps were reconstructed around canopy-sized subdominant trees; two around yellow-poplar trees, four around black cherry trees, and one gap which involved one tree of each species (Table 8). Expanded gap areas of the reconstructed gaps ranged from 314.2-931.8 m^2. These gap sizes were compared to gap areas of known single-treefall gaps. The mean expanded gap area of 38 single-treefall gaps was found to be 494.6 m^2 (SD = 200.7). Six of the seven reconstructed gaps had expanded gap areas that were

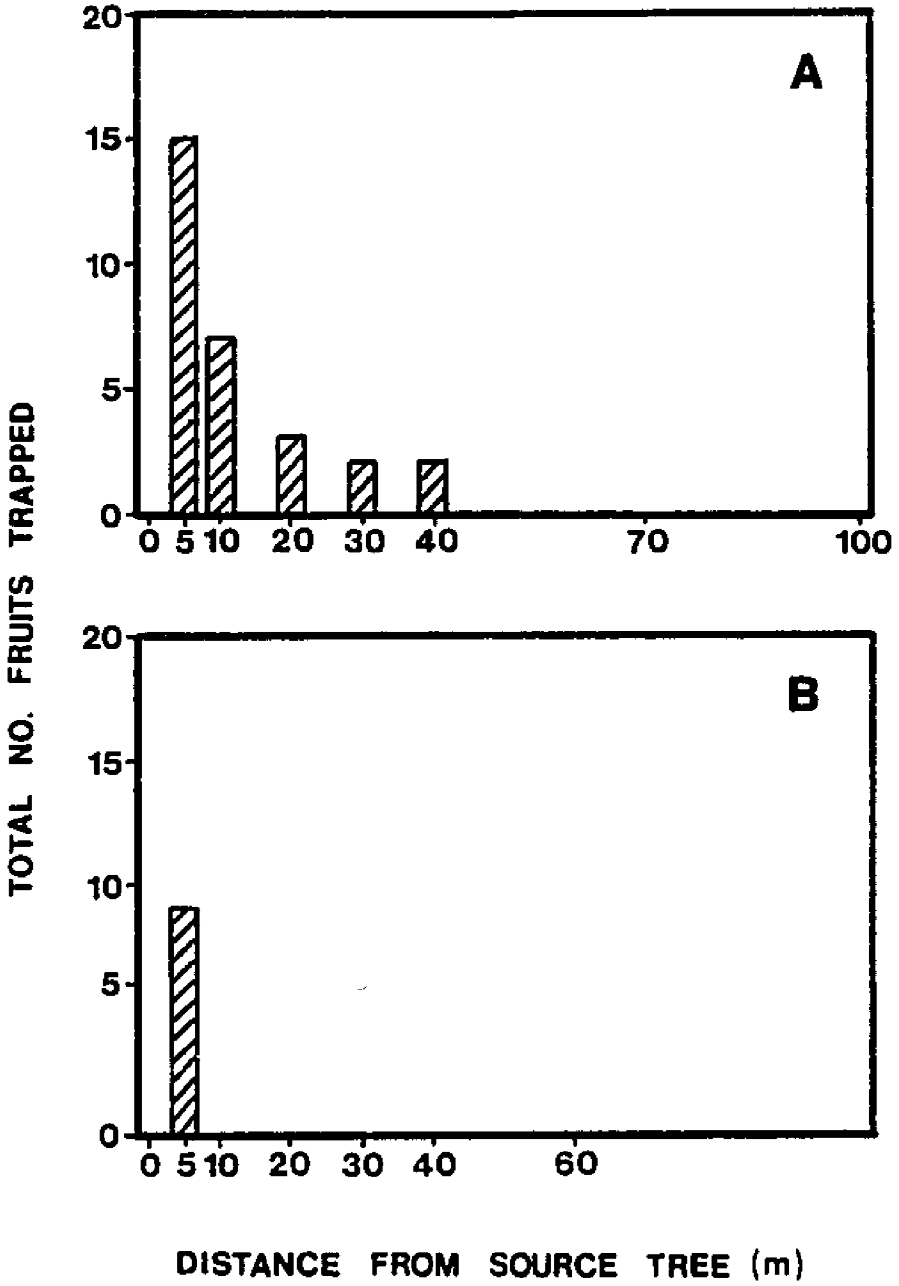


Figure 15. Dispersal distances of yellow-poplar samaras (A) and black cherry drupes (B) from source trees.

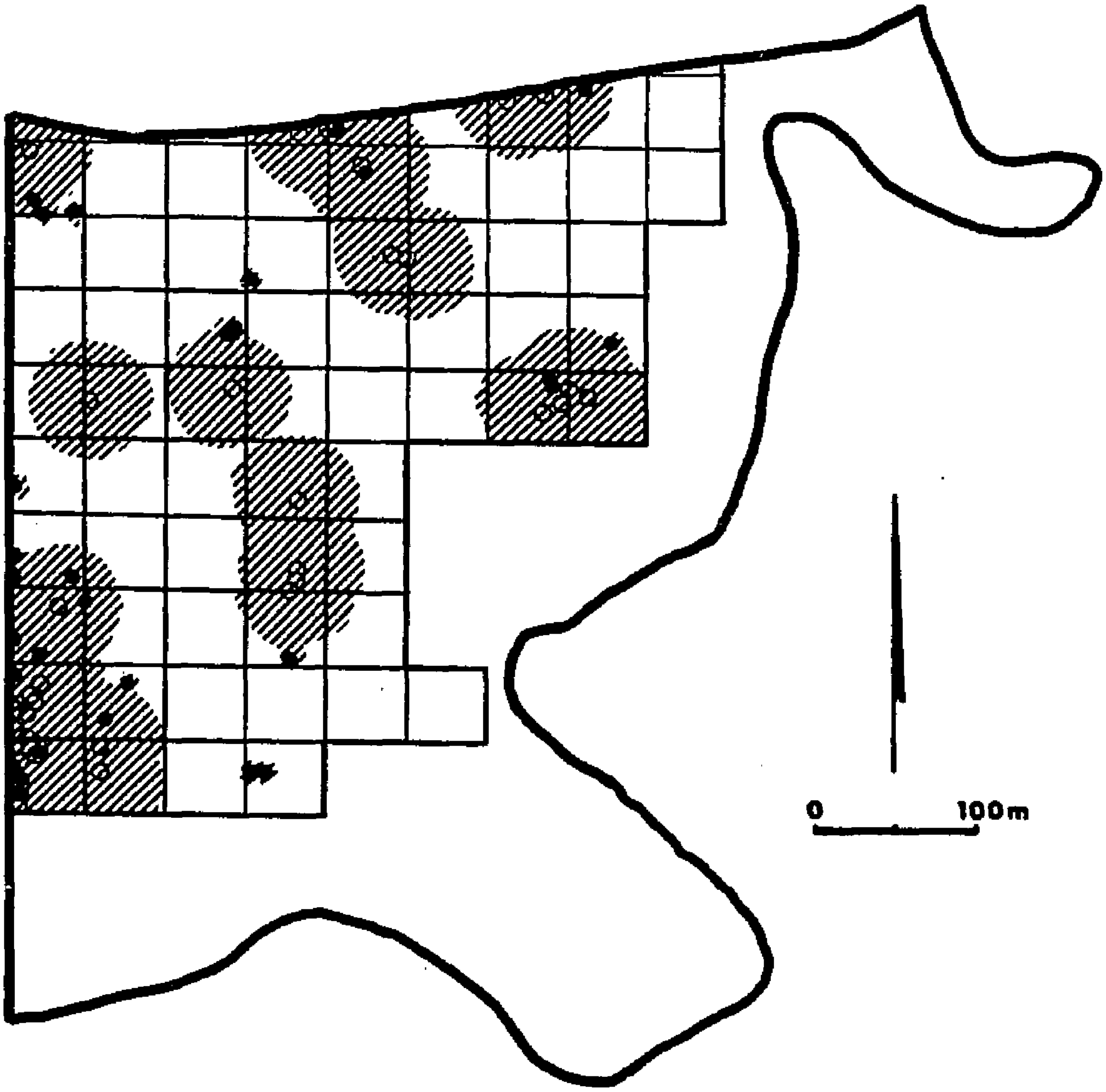


Figure 16. Proportion of sampling area accessible to fruits dispersed from yellow-poplar (O) and black cherry (•) trees.

Table 8. Characteristics of reconstructed sub-dominant gaps.

Gap No.	Sub-Dominant Tree(s)			Gap Age and Time of Release (yr)	Outlining Trees			Mean Expanded Gap Radius (m)	Expanded Gap Area (m^2)	Within ±1 SD of Mean Expanded Gap Area?[c]
	Species	DBH (cm)	Age (yr)		Species	DBH (cm)	DBH at Time of Formation[b] (cm)			
ND2	Lc[a]	36.5	48+	49	Fg	48.5	28.4	13.4	566.5	Yes
	Ps	24.5	50		Fg	70.5	50.4			
					Fg	79.5	59.4			
					Fg	66.5	46.4			
					Fg	65.5	45.4			
					Fg	46.5	26.4			
					Fg	50.5	30.4			
ND3	Lc	43.5	71	66	Fg	55.6	28.5	12.4	486.0	Yes
					Fg	56.0	28.9			
					Fg	81.9	54.8			
					Fg	83.5	56.4			
					Fg	87.0	59.9			
					Fg	72.5	45.4			
					Fg	61.0	33.9			
					Fg	73.5	46.4			
					Lc	90.5	68.1			
ND4	Ps	60.7	75	71	Fg	50.8	21.7	17.2	931.8	No
					Fg	63.1	34.0			
					Fg	82.9	53.8			
					Fg	70.0	40.9			
					Fg	66.2	37.1			
					Fg	66.5	37.4			
					Fg	73.2	44.1			
					Fg	50.3	21.2			
ND5	Ps	21.9	58	58[d]	Fg	58.6	34.8	10.0	314.2	Yes
					Fg	57.5	33.7			
					Fg	41.7	17.9			
					Fg	51.5	27.7			
					Ar	51.7	NA			
					Fg	70.0	46.2			
ND7	Lc	42.3	59	60	Fg	53.0	28.4	12.7	507.8	Yes
					Fg	63.7	39.1			
					Fg	67.5	42.9			
					Fg	66.3	41.7			
					Fg	76.2	51.6			
					Fg	67.5	42.9			
					Fg	57.6	33.0			
ND8	Ps[a]	38.1	73	71	As	64.5	35.4	14.6	673.6	Yes
	Ps	30.8	73		As	58.4	29.3			
					As	55.6	26.5			
					Fg	89.6	60.5			
					As	65.7	36.6			
					Fg	64.5	35.4			
					Fg	54.2	25.1			
ND10	Ps	28.0	39	39[d]	As	84.0	68.0	12.7	506.7	Yes
					Fg	46.7	30.7			
					As	69.0	53.0			
					Qr	94.1	74.6			
					As	75.2	59.2			

[a] Gaps containing two sub-dominant trees.

[b] Approximated by reducing current DBH by product of (species specific mean annual diameter growth of mature trees) X (gap age); mean diameter growth rates were: Fg, 0.41 cm/yr (from this study); As, 0.41 cm/yr (this study); Lc, 0.34 cm/yr (McCarthy 1933); Qr, 0.50 cm/yr (Fowells 1965).

[c] $\bar{x} \pm 1$ SD = 293.92 - 695.24.

within ± 1 SD of this mean single-treefall expanded gap size. The remaining gap was too large at 931.8 m^2, but even this value was within the range of single-treefall expanded gap areas measured.

Rate of Forest Turnover

A total of 30 open gaps were found in the 3.75 ha sample surveyed, while the total number of gaps identified, including those which had been closed, was 38. From analysis of the gap chronosequence, gaps were known to close in 34 yr, while stumps and logs, which were used to identify closed gaps, were observed to decay within 45 yr. The total area in open gaps was 5,344.2 m^2, which corresponded to 14.3% of the study area.

Fifty six trees had fallen in the 30 open gaps studied, and these were assumed to have fallen within a period of 34 yr. The rate of treefall, based on these open gaps, was, therefore, computed to be 0.4 trees $ha^{-1} \cdot yr^{-1}$. Based on all gaps, where the 67 fallen trees were assumed to have fallen in a 45 yr period, a treefall rate of 0.4 trees $ha^{-1} \cdot yr^{-1}$ was derived. Expressed as proportions of the total number of trees ≥20 cm dbh in the stand (144 trees/ha, from forest composition data in this study), 0.3% of canopy trees fell per hectare per year, based on estimates of open gaps and of all gaps combined.

Rate of gap formation based on open gaps and on open and closed gaps combined, was computed as 0.2 gaps $ha^{-1}.yr^{-1}$. To calculate the rate of forest turnover, the average area of the original canopy opening of these gaps had to be estimated. The difference between the radii of new expanded gaps and their respective canopy openings averaged 6.8 m (N =17; SD = 1.99). The mean radius of all expanded gaps in the turnover rate plots was 12.8 m (SD = 4.0). Therefore, the estimated mean radius of the original canopy openings of gaps in the survey area was 6.0 m, and average canopy gap area was 114.2 m^2. Total area of original canopy gaps, based on the number of open gaps, was 3426.9 m^2, while total area of canopy openings based on all gaps was 4340.8 m^2. The rate of forest turnover, computed as the plot area divided by the total area of the canopy opened by gaps, and multiplied by the number of years within which these openings were created, was estimated as 372 yr for open gaps and as 389 yr for all gaps.

DISCUSSION

Canopy Dominance as a Function of Gap Dynamics

Gap Closure

The rate of gap closure measured in this study lies within the range of closure rates estimated for other temperate forests. Gaps were essentially closed in 34 yr (Figure 5). Rates of lateral extension growth into openings reported in studies of a variety of forest types range from 6-26 cm/yr (Trimble and Tryon 1966, Erdmann et al. 1975, Hibbs 1982, Runkle 1982). Single treefall gaps of the size found in Warren Woods ($\bar{x}$ gap radius = 7.6 m) would be predicted to remain open for 29-127 yr, based upon closure by lateral extension of surrounding trees only. However, gaps may also be closed from within by growth in height and crown diameter of large sapling/poles which were suppressed prior to gap opening. Runkle (1982) placed considerable importance on height growth of saplings in the closure of gaps in mesic forests, and predicted gap longevities of 10-40 yr.

The rate of gap closure did not appear to be constant in this study (Figure 5). There was no significant decrease in gap size from the 0-4 yr age category to the 5-9 yr category, but there was a relatively quick decline in gap area between the 5-9 and 10-14 yr age categories. The rate of gap closure decreased in subsequent years. This pattern corresponds remarkably well with that suggested by Runkle (1982), who calculated the age at which gap area may be expected to decrease most rapidly to be 8.5 yr. A subcanopy formed by saplings released within gaps, similar to that observed in Warren Woods, was reported by Nakashizuka (1983) in gaps of mature Fagus crenata forest in Japan. Whereas he found that saplings formed a "well closed canopy" in about 10 yr following treefall, the subcanopy in this study closed in 19 yr.

Structure and Composition of Regeneration

The density of seedlings and saplings <2.5 cm dbh changes as gaps close. Initially, when gaps are open, there is a rapid increase in stem density (Figure 6) which is driven by the high rate of seedling establishment during this period (Figure 8). With gap closure, however, density declines (Figure 6). This is caused in part by the slow reduction in seedling establishment (Figure 8) and, presumably, by mortality of the densely-crowded stems as the gaps close.

The majority of seedlings and saplings in gaps are sugar maple (Figure 7). Beech makes up relatively few of these stems in gaps, but it is present throughout the chronosequence. Species other than beech and sugar maple are also present as seedlings and saplings in gaps, and, surprisingly, woody species richness shows no obvious trend through the chronosequence (Figure 9).

Height Growth Response to Canopy Opening

Beech and sugar maple respond to canopy opening with a pulse of growth (Figures 11A, B), the relative length of which corresponds to the short period of time in which gaps are fully open. Height growth rates of small beech and sugar maple trees closely tracked the changing size of the gap opening, with fast growth limited to the first 10 yr following treefall. Subsequently, growth rates declined as gaps closed. Hibbs (1982) also reported a decline in growth rates in the later years of gap closure, and suggested that trees were being overtopped by the surrounding canopy.

As a result of the pulse response to gaps, the maximum possible increase in height of small-size sugar maple was just over 5 m, while the maximum increase possible by beech was under 4 m (Figure 11C). Analysis of height class distribution of all stems <2.5 cm dbh through the chronosequence suggests that stems did not advance into height classes greater than 5 m (Figure 10). Small stems of these shade tolerant species, present as advance regeneration at the time of gap formation, are not capable of growth to canopy size as a result of a single gap exposure.

These results contrast with the finding implicit in many studies of temperate forest dynamics that trees are able to grow to canopy height from small size classes within the duration of a single gap event. Oliver and Stephens (1977), studying tree growth in a mixed-species forest in Massachusetts, stated that the canopy layer of the forest was "composed of two types of trees: those which grew immediately to the overstory after a disturbance; and those which stratified beneath other...trees and later accelerated again upon removal of the overstory." Similarly, Hibbs (1982), working in the same Massachusetts forest, suggested that fast-growing species "may be able to regenerate successfully" in moderate-sized openings, while shade-tolerant hemlock grew too slowly to reach the canopy before gaps closed.

Hibbs, et al. (1980) suggested that sugar maple requires an opening "large enough to remain open overhead until it reaches the canopy." Poulson and Platt (1981) specifically stated that, following the fall of a single tree in a beech-maple forest (Warren Woods), "maple seedlings, released from shade-suppression, increase rapidly in height. One enters the canopy after only 20-30 years..." This study demonstrates that beech and sugar maple do not grow at their potential maximum rates of growth throughout the time course of the gap opening; they are incapable of growing into the overstory fast enough within this 34 yr period.

Growth of Trees into the Canopy

Three possibilities exist for saplings which are re-suppressed following gap closure: 1) they may continue to grow slowly and, after a very long period of time, slowly penetrate the canopy; 2) they may continue to grow slowly until another gap is formed, which will again initiate greater rates of growth; or 3) they may die if another gap is a very long time in coming.

The first possibility, of slow growth into the canopy under suppression, is arguable because of the low rates of growth of beech and sugar maple under suppression (Table 4; also see Canham 1981, 1982). Trees that have been advanced to 4-5 m heights as a result of a single gap event (Figure 11C) are still far short of the canopy in Warren Woods. Under suppression, 161-276 yr would be required for these trees to reach the bottom of the canopy at 20 m. While it may be possible for trees to survive such prolonged periods of suppression, high rates of mortality may be expected, even in these shade-tolerant species.

Furthermore, this scenario is unrealistic as other gaps would likely be created above or near these trees in the course of such long time periods. Runkle (1984) studied a mature beech-maple forest in Ohio and found that, within a four-year time period, 17 of the 36 gaps he studied had been affected by some new treefall disturbance in or near the same location as the original gap. Such recurrent disturbance would tend to release suppressed trees before they could reach the canopy by growing slowly.

The strongest evidence against slow growth of suppressed trees to canopy position are the growth records of trees that have successfully entered the canopy (Figure 12). None of the mature trees cored in this study demonstrated a pattern of complete, continuous suppression. In fact, trees either exhibited an episodic pattern of diameter growth, representing two or more gaps, or grew at rates which suggested more frequent or prolonged canopy exposures. Given the preceding arguments, it therefore is unlikely that trees slowly grow into the canopy under suppression.

The second and third possibilities depend on the frequency of subsequent gaps (i.e., the time period of suppression intervening between gap episodes). It has been shown that mature beech were more likely to have undergone periods of suppression than sugar maple, and that these suppressed periods lasted significantly longer in beech

(Table 5). It is assumed that gaps are created at random relative to individual understory trees. That is, there is no reason to expect that beech saplings would be more likely to be suppressed than sugar maple saplings, nor should suppression last any longer for beech than for maple. If anything, because of the greater abundance of sugar maple in the understory, the probability of any one sugar maple individual being suppressed is likely to be greater than the probability of suppression in beech.

Given the randomness of gaps, there are two hypotheses that could explain the observed patterns of suppression in beech and maple. The first hypothesis is that sugar maple saplings grow in diameter at much greater rates than beech saplings when both are suppressed. In this case, a greater tendency for suppressed growth increments in mature beech than in mature sugar maple would be expected. However, the paired tree experiment showed this not to be the case (Figure 13). Patterns of radial growth were remarkably similar in the two species, and overall average growth rates were either not significantly different, or were actually greater in beech. Therefore, the hypothesis of faster growth in diameter of suppressed sugar maple is not supported.

The alternative hypothesis is that suppression is not observed in mature sugar maple to the extent exhibited by beech because sugar maple does not survive long periods of suppression as well as beech. Sugar maple trees that make it to the canopy are those exposed to gaps frequently enough to allow a more continuous advance to the canopy (second possibility). Maple saplings that do not encounter frequent gaps do not survive the long intervening periods of shade suppression that beech is able to withstand (third possibility). That is, beech is more shade tolerant than sugar maple.

Shade Tolerance

Differences in shade tolerance between beech and sugar maple have not been resolved by traditional forestry methods of assessment (Baker 1949). These methods are based on differences in the density or occurrence of small trees in the understory, response to release, tree architecture, and growth rates, among other factors (Spurr and Barnes 1980). Both beech and sugar maple have been ranked as very shade tolerant.

Physiological studies have provided incomplete and conflicting assessments of the photosynthetic efficiency of beech and sugar maple. Loach (1967) suggested that differences in rates of respiration may be the most important determinants of success or failure in the shade. He found that tolerant species exhibited a lower light compensation point and a lower rate of respiration in the shade. He detected a much lower rate of respiration for beech than for sugar maple, but did not compare the light compensation point of these two species. Grime (1965) reported a trend of decreasing dark respiration rate with increasing shade tolerance, but found that sugar maple exhibited a lower rate of dark respiration than beech. The light compensation point of sugar maple has been reported to be lower than that of beech (Burns 1923), but the validity of this type of analysis as a measure of tolerance has been subject to question (Fowells 1965). Physiological evaluations of shade tolerance in beech and sugar maple, therefore, are inconclusive.

The greater shade tolerance of beech relative to sugar maple detected in this study is an ecological assessment of the tolerance of these species to extended periods of shade suppression. Shade tolerance is referred to here as the ability to survive shading. While it most certainly has a physiological basis, other factors, such as susceptibility to insects, disease, and other problems associated with reduced vigor, may also be involved. In addition, root-zone competition and differences in the nature of the root system, root growth, and turnover are certainly also important in determining differences between species in their ability to survive shading. Differences in relative shade tolerance may be verified only by long-term studies of survivorship of permanently-marked trees under natural forest conditions. However, the significance of differences in the shade tolerance of these important forest species is worthy of consideration.

Beech Dominance

The greater relative shade tolerance and concomitant greater survivorship of beech as compared to maple provides a logical mechanism for the dominance of beech over maple in presettlement and old-growth remnant stands. Beech would be competitively advantaged under the natural conditions of infrequent gap disturbance, where intervals of suppression between gap events are long.

In other attempts to explain the importance of beech in the canopy, many investigators have referred to the ability of beech to produce root sprouts (Illick and Frontz 1928, Hough 1936, Williams 1936, Hough and Forbes 1943, Laufersweiler 1955, Ward 1956, Curtis 1959, Ward 1961, Beals and Cope 1964, Forcier 1975, Vankat et al. 1975, Abrell and Jackson 1977). It has been suggested that root sprouts compensate for the low abundance of beech in the understory and that sprouts may be able to grow and survive better than independent beech saplings of seed origin. Canham (1982), however, found no difference between the rates of growth in beech of seed and sprout origin.

Ward (1961) reported that the importance of root sprouts varied widely with geographic location of the stand. He found that in certain stands, even those dominated by beech in the canopy, beech did not produce root sprouts. Only 18% of all beech stems found within gaps at Warren Woods were of sprout origin. There are no data available on the potential for root sprouts to achieve canopy size, as has been suggested by Curtis (1959) and others. These arguments suggest that the ability of beech to produce root sprouts is not an adequate explanation for the dominance of beech in the forest canopy.

There has been some suggestion that beech is capable of greater rates of vertical growth than sugar maple, and that this advantage may contribute to its importance in the forest. Laufersweiler (1955), in a widely-cited paper, found that beech stems were consistently taller than maple stems at a given tree age (to 63 yr), but he did not consider whether these trees were growing in gaps or beneath a closed canopy. There is no difference between the average rates of height growth in beech and sugar maple in gaps in Warren Woods (Table 4), although it appears that sugar maple is capable of greater maximum rates of growth in gaps (Figure 11). Under suppression, however, beech grows faster in height than sugar maple (Table 4). Given the episodic influence of treefall gaps on the growth of trees, the relative proportion of periods of release and suppression will determine the difference in relative height growth of beech and sugar maple.

If root sprouts and differences in the rates of growth provide inadequate or incomplete explanations for beech dominance, then its superior shade tolerance over that of sugar maple is even more significant. A difference in relative shade tolerance may explain the apparently greater rates of mortality of intermediate-sized sugar maple relative to beech. While sugar maple is more abundant in smaller size classes, the rate of reduction in number of stems with increasing size is greater for sugar maple than for beech, as indicated in analyses of size class distributions for beech and sugar maple in Warren Woods (P. G. Murphy and G. C. Kroh, unpublished data) and of those in the literature (Esten 1932, Cain 1935, Williams 1936, Laufersweiler 1955, Pell and Mack 1977).

Although rate of mortality was not measured in Warren Woods, a greater proportion of sub-canopy trees was standing dead in sugar maple, with a percent mortality more than four times that of beech (Table 6). This difference suggests only that beech survivorship is very high, not that sugar maple survivorship is low. For comparison, other less shade-tolerant species collectively exhibited 2.5 times greater mortality than sugar maple. Presumably, higher survivorship of beech can be attributed to its ability to tolerate extended periods of shade suppression.

These results refute the speculation that sugar maple, because it is typically more abundant in the understory (see review in Vankat et al. 1975, also Rogers 1981), and because of its fast growth in gaps, may increase in relative importance over time (Esten 1932, Cain 1935, Williams 1936, Keller 1945, Braun 1950, Ward 1956, Abrell and Jackson 1977). In fact, beech in Warren Woods has increased in relative dominance (basal area) to a greater extent than sugar maple during the period 1933-1974 (P. G. Murphy and G. C. Kroh, unpublished data).

However, under conditions of greater canopy disturbance than that found under natural conditions (e.g., greater frequency of treefall caused by stand isolation, or more prolonged canopy opening through stand thinning), sugar maple would be predicted to gain in importance, relative to beech. This would decrease the frequency and duration of periods of suppression between gap events and would decrease the competitive advantage of the more shade-tolerant beech, relative to the more abundant and potentially faster-growing sugar maple. Such a shift toward the increased importance of sugar maple relative to beech has been widely reported for many isolated, or disturbed, remnant stands in the midwestern USA (Elliott 1953, Shanks 1953, Ward 1956, Beals and Cope 1964, Abrell and Jackson 1977).

An episodic pattern of growth to canopy height, similar to that demonstrated in this study, has also been reported for hemlock, another shade-tolerant species that has the potential to dominate the forests in which it is found. Hemlock has been shown not to be able to reach the canopy in small gaps (Hibbs 1982), and exhibits a step-like or episodic pattern of growth indicative of alternating periods of suppression and release (Oliver and Stephens 1977).

The significance of episodic treefall disturbance (i.e., repeated gap events, alternating with periods of suppression) to the regeneration of shade-tolerant tree species adds considerable complexity to the analysis of tree replacement in mesic forests. Predictions of forest trends based solely on the density or importance of individual species in the understory or in gaps cannot account for later differences in survivorship in shade-dominated stands. A knowledge of the frequency of gap events, or the rate of forest turnover, relative to species characteristics, is a necessary component of the analysis of forest regeneration.

Maintenance of Sub-Dominant Species

Distribution and Abundance

Yellow-poplar and black cherry are considered archetypal gap-phase species (Watt 1947), dependent upon treefall gaps for growth to canopy height (yellow-poplar: McCarthy 1933, Minckler and Jensen 1959, Smith 1963, Buckner and McCracken 1978, Barden 1980, Wallace and Dunn

1980, Beck and Della-Bianca 1981; black cherry: Curtis 1959, Hough 1960, Auclair and Cottam 1971, Auclair 1975, Barden 1980). These species are characterized as being fast-growing, shade-intolerant trees which are relatively rare in mature forests (yellow-poplar: McCarthy 1933, Baker 1949, Den Uhl 1962, Grime 1965, Olson 1969, Loach 1970, Buckner and McCracken 1978, Wallace and Dunn 1980, Beck and Della-Bianca 1981; black cherry: Baker 1949, Husch 1954, Curtis 1959, Hough 1960, Den Uhl 1962, Grime 1965, Auclair and Cottam 1971, Auclair 1975, Barden 1981). Both species produce prolific quantities of seed, are thought to possess efficient diaspore dispersal mechanisms, and exhibit the potential for delayed seed germination in the soil seed pool (yellow-poplar: McCarthy 1933, Smith 1963, Clark and Boyce 1978, Beck and Della-Bianca 1981; black cherry: Husch 1954, Auclair and Cottam 1971, Wendel 1972, Auclair 1975).

In Warren Woods, however, the importance and distribution of canopy-sized yellow-poplar and black cherry appeared more strongly associated with topographic, edaphic, and edge factors than with recognizable treefall gaps. Gaps occur throughout the forest, and yet the relatively rare yellow-poplar and black cherry trees exhibited a non-random pattern of dispersion (Table 7), and appear facultatively linked to these other factors (Figure 14).

Slopes, wet areas, and forest edges may all be areas of enhanced light availability, which would tend to favor fast-growing, shade-intolerant tree species. Gysel (1951) found a greater abundance of yellow-poplar and black cherry trees near openings and borders in second-growth mesic forest woodlots in Michigan. Yellow-poplar and black cherry were reported by Braun (1916) to increase in importance on ravine slopes in Ohio beech forests. Williams (1936) observed a greater abundance of yellow-poplar in ravines than in other forest areas, and mapped black cherry only near forest edges and ravines. Auten (1937) and Schomaker (1958) reported vigorous yellow-poplar growing on slopes, and both made the suggestion that more favorable soil moisture conditions on ravine slopes may also be an important site factor for the growth of yellow-poplar. It is possible then that treefall gaps may not actually be required for regeneration of these shade-intolerant tree species in these areas.

It is recognized that gaps are also likely to occur, perhaps with even greater frequency, near these different forest "edges". In such gaps, the effects of these edges may be to allow in even more light (e.g., in a gap on a south-facing ravine slope), or to prolong the time period required for gap closure. The combination of gap and "edge" would further favor yellow-poplar and black cherry.

Limitations in Seed Dispersal

Besides the high demand for light, the relative rarity and non-random distribution of yellow-poplar and black cherry may represent further limitations to their successful colonization of, and regeneration in, treefall gaps. Although the findings on seed dispersal in this study are tentative (Figures 15 and 16), dispersal of propagules of these species into all gaps of the forest interior is improbable.

While maximum dispersal distances of up to 200 m have been reported for wind-dispersed yellow-poplar samaras (McCarthy 1933, Engle 1960), inadequate seeding is expected beyond 50-120 m from source trees (Engle 1960), or when seed trees are more than 80-100 m apart (Beck and Della-Bianca (1981).

The bulk of black cherry seed falls to the ground in the vicinity of the seed source tree (Hough 1960, Smith 1975). Fruits may be harvested by any of 47 different species of birds, which most often regurgitate the seed while still perched in the source tree (Martin et al. 1951, Smith 1975, Hoppes 1983). Birds may also occasionally distribute the seed in droppings away from the seed source (Martin et al. 1951). Hoppes (1983) found black cherry drupes to be dispersed to an average distance of only ~2 m, with a maximum distance of 15 m. Smith (1975) reported a maximum distance to which seeds were deposited of 25 m.

Accordingly, Husch (1954) reported that the most dense cherry regeneration was found beneath seed-bearing trees. He did indicate that seedlings could be found far from seed source trees, presumably through longer-distance dispersal by birds. Similarly, in this study, black cherry seedlings were found in gaps outside of cherry seed shadows, despite the report by Smith (1975) that fruit-bearing birds avoid open spaces, such as gaps, in depositing seed.

Green (1983) discussed the efficacy of dispersal relative to the density of safe sites suitable for establishment, such as gaps. He suggested that plant species that are able to disperse propagules over relatively long distances are more effective when the number of safe sites is limited. Concentrated, short-range dispersal patterns are more effective when safe sites are abundant. Yellow-poplar and black cherry conform to this model well.

Yellow-poplar requirements for seed germination and subsequent establishment of seedlings are very exacting (McCarthy 1933, Auten 1937, Boyce and Parry 1958, Tryon and Carvell 1960, Clark 1962, Smith 1963, Olson 1969, Trimble and Tryon 1969, Beck and Della-Bianca 1981). Yellow-poplar occurs almost exclusively on moderately moist, well-drained soils of loose texture. Germination and establishment requirements include bare soil (A horizon more than B horizon) or thin litter, constant moisture, an abundant supply of light, and an absence of excessive competition. These requirements define safe sites which are rare in mature mesic forests; they are met only in certain parts of certain treefall gaps and in other open areas. In Warren Woods, yellow-poplar seedlings were found most often on or near the rim of pits created by uprooted trees. The long-distance dispersal capability of yellow-poplar makes for more effective dispersal under these narrowly-defined conditions of germination and establishment, as modeled by Green (1983).

Black cherry, conversely, is known for its very flexible seedbed requirements, and can establish under even shaded conditions (Husch 1954, Hough 1960, Auclair and Cottam 1971, Auclair 1975, Smith 1975). The relatively short dispersal distances reported for the bulk of cherry seed conforms well to Green's (1983) prediction for species with abundant safe sites.

Despite the expected effectiveness of dispersal of these species, certain limitations exist which are either imposed or made more significant by their rarity and pattern of dispersion. Although yellow-poplar can disperse samaras to relatively long distances from seed trees, it is characterized as having exceedingly low viability, averaging 3-15% (McCarthy 1933, Engle 1960, Tryon and Carvell 1960, Beck and Della-Bianca 1981). Such low viability, when coupled with exacting requirements for germination and establishment, are severe limitations for the success of yellow-poplar in closed-canopy mesic forests.

While black cherry is flexible in germination and establishment requirements, it still exhibits a low rate of germination (Smith 1975) and is subjected to great density-dependent seed predation by rodents (Hough 1960, Smith 1975). Further, seedlings experience high rates of mortality beneath a closed canopy and can survive and continue to grow only under conditions of high light intensity (Hough 1960, Auclair and Cottam 1971). Abundant seedlings dispersed only short distances from source trees then do not have great potential, unless the seed tree is near an area where light intensity is high, such as forest edges or in gaps.

Seed dispersal from rare, clumped seed trees, in conjunction with problems of viability, germination and establishment requirements, predation, and high light demands, represent significant limitations to the success of yellow-poplar and black cherry in gaps.

Regeneration in Gaps

Although limitations to the establishment of yellow-poplar and black cherry in gaps relegate them primarily to forest edges and slopes, these species can also apparently succeed in single-treefall gaps (Table 8). It is likely that at least six of the seven sub-dominant trees (86%) studied in the forest interior regenerated in gaps comparable in size to those of known single-treefall gaps.

Barden (1980), in a study of tree replacement in cove forests of the southern Appalachians, concluded that yellow-poplar was able to persist in single-tree gaps with infrequent success, while most all of the silvicultural literature clearly indicates that much larger openings are required (McCarthy 1933, Minckler and Jensen 1959, Smith 1963, Little 1967, Sander and Clark 1971, Minckler et al. 1973, Wallace and Dunn 1980, Beck and Della-Bianca 1981). Gap size required for the regeneration of black cherry is less well-studied; Barden (1980) suggested that the perpetuation of this species requires gaps larger than those caused by the fall of a single tree.

Yellow-poplar and black cherry are among the fastest growing trees in mesic deciduous forests of the eastern United States (McCarthy 1933, Hough 1936, Meyer and Plusnin 1945, Husch 1954, Hansen and McComb 1955, Hough 1960, Fowells 1965, Olson 1969, Auclair and Cottam 1971, Buckner and McCracken 1978, Beck and Della-Bianca 1981). It is possible that, with the >1 m/yr height growth rates reported possible for these species, trees could grow into the canopy within the duration of a single gap event (Figure 5). However, it is more likely that in small, single-tree gaps these growth rates would not be maintained as gaps close (see data for beech and sugar maple, Figure 11). Larger, multiple-tree gaps or, as this study shows for sugar maple, a high frequency of successive single-tree gaps, are most probably required for the regeneration of yellow-poplar and black cherry.

Yellow-poplar and black cherry, being very shade-intolerant after establishment, are not able to survive long in the understory (McCarthy 1933, Hough 1960, Auclair and Cottam 1971, Wallace and Dunn 1980, Beck and Della-Bianca 1981). If trees fall behind into intermediate and suppressed positions, they decline in growth rate and eventually die (Hough 1960, Beck and Della-Bianca 1981). This would account for the relatively large proportion of sub-canopy trees of these species which are standing dead in Warren Woods (Table 6). In addition, black cherry is considered not to be able to respond to release following prolonged suppression (Hough 1960, Auclair and Cottam 1971). Therefore, for these shade-intolerant trees to regenerate in small gaps, very frequent treefalls above or adjacent to the small gap are likely required. Frequent treefalls would maintain an open canopy with no, or at least short, periods of intermittent suppression similar to the open conditions in larger openings, or near forest edges.

While such frequent gap disturbance in any one location in the forest is indeed possible, the probability of occurrence is quite low under natural forest conditions. Together with the problems of dispersal and establishment in these shade-intolerant species, the regeneration of yellow-poplar and black cherry in single-treefall gaps is only infrequently possible. Treefall gaps play only a minor role in the maintenance of species diversity, at least with regard to these two species, in beech-maple forests. Topographic and edge factors combine to contribute most to what little species diversity there is in these light-limited forests.

Species Composition and Diversity Relative to Forest Turnover

Warren Woods exhibits lower rates of treefall disturbance and forest turnover than any other forest for which these data are available (Table 9). Such a low rate of disturbance has been shown in this study to be an important determinant of the success or failure of different tree species. Dominance of beech over sugar maple and the rarity of shade-intolerant yellow-poplar and black cherry are more pronounced in Warren Woods than in other remant stands that experience higher rates of disturbance.

Effects of treefall gap frequency on species diversity cannot account for the much greater species diversity in

Table 9. Comparison of the rates of treefall, gap formation, and forest turnover in Warren Woods, other temperate forests, and tropical forests.

	Rate of Treefall (trees·ha^{-1}·yr^{-1})	Rate of Treefall as Percent of Total No. Canopy Trees (% trees·ha^{-1}·yr^{-1})	Rate of Gap Formation (no. gaps·ha^{-1}·yr^{-1})	Forest Turnover (yr)
Warren Woods, Michigan Beech-Maple Forest -This study.	0.4[a] 0.4[b]	0.3[a] 0.3[b]	0.2[a] 0.2[b]	372[a] 389[b]
Warren Woods -Brewer and Merritt 1978	0.2			
Hoot Woods, Indiana Beech-Maple Forest -Abrell and Jackson 1977	0.8	1.2		
Eastern USA Mesic Forests		0.5-2.0		50-200
Southern Appalachians Mixed Mesophytic				67
Hueston Woods, Ohio Beech-Maple Forest				133
Tionesta, Pennsylvania Beech-Hemlock -Runkle 1982				167
Malaysia -Poore 1968				250
Various Tropical Forests				
Malaysia		1.3		
Ivory Coast		1.4		
El Verde, Puerto Rico		1.2		
Barro Colorado Island (BCI), Panama -Leigh 1975		4.5		
BCI, Panama				
-Brokaw 1982a				113-126
-Brokaw 1982b	0.6		1.1	114
La Selva, Costa Rica				
-Hartshorn 1980	1			
-Hartshorn 1978			1.2	80
			0.7	119
			1.3	138
			0.9	135
San Carlos, Venezuela -Uhl and Murphy 1981				100
-Uhl 1982	2			
-Uhl 1983	2.5			

[a] Based on number of open gaps and rate of gap closure

[b] Based on all identifiable gaps and rate of log and stump decomposition

tropical forests as compared to those in temperate areas, as has been proposed by Strong (1977). There is no clear latitudinal trend in the rate of forest turnover that could parallel differences observed in species diversity, although additional estimates of turnover are needed. Current research on species diversity in tropical forests has emphasized more the importance of within- and between-gap heterogeneity (Denslow 1980, Putz et al. 1983) and how this heterogeneity may differ between tropical and temperate forests (Orians 1982).

SUMMARY AND CONCLUSIONS

Patterns and mechanisms of forest regeneration were studied in an undisturbed beech-maple forest in Michigan. The primary goal of this research was to understand the role of treefall gaps in the maintenance of forest composition. The study was conducted in Warren Woods, a State Nature Study Area in Berrien County, Michigan. Warren Woods was found to be similar to other old-growth remnant stands of beech-maple forest and to presettlement beech-maple forests of Berrien County with respect to the dominance of beech in the overstory, the co-dominance of sugar maple, and the relative rarity of shade-intolerant species such as yellow-poplar and black cherry. In this respect, the study site served as an excellent model of beech-maple forest and the natural forest processes which work to determine the composition of these forests.

A chronological sequence of gaps of different age was used to examine regeneration and tree growth in gaps as if through time. Gaps were found to close within 34 yr by the growth of trees surrounding the gap. The density of stems growing within gaps changed as gap closure proceeded as a result of shifts in the levels of seedling recruitment and tree mortality. Sugar maple comprised most of the regeneration, although most all other important forest species were also found growing in gaps. Surprisingly, there was no clear trend in species richness through the chronosequence.

The distribution of trees in different height classes changed during gap closure. Predictably, the number of stems in small size classes increased soon after the gap was created, with gradual growth into larger size classes with time. Ultimately, abundance in all size classes was reduced as gaps closed, leaving very few trees remaining in the tallest height class. Trees were not found in height classes greater than 5 m, which suggested a possible limitation to the growth of young trees in gaps.

Analysis of the rates of growth of beech and sugar maple in gaps confirmed that trees were not able to grow to canopy height as a result of a single gap exposure. Rates of height growth declined from initially high values as gaps closed and indicated a maximum potential increase in height of just over 5 m.

Once trees were re-suppressed in closed gaps, their continued growth and survivorship were influenced by the frequency of subsequent gap events and the intervening periods of suppression. Patterns of radial growth in mature trees were examined using increment cores to determine the history of treefalls with which they were associated. There were no trees that had grown slowly into the canopy under suppression without benefit of gap exposure. Radial growth records of both dominant species exhibited an episodic pattern of growth asssociated with recurrent canopy opening.

Radial growth records also indicated that more beech trees had survived suppression between gap episodes than sugar maple, and that the length of suppressed periods was significantly greater in beech. This difference is a result of the greater relative shade tolerance of beech with respect to sugar maple; that is, sugar maple cannot tolerate periods of extended shade suppression as well as beech. There was a greater relative amount of sub-canopy mortality (standing dead as percent of total) in sugar maple than in beech, which corresponds to this apparent difference in shade tolerance. Greater relative shade tolerance in beech may be the most important mechanism by which it maintains dominance over sugar maple in presettlement and little-disturbed beech-maple forests.

With regard to the maintenance of shade-intolerant species, the distribution of yellow-poplar and black cherry canopy-sized trees in Warren Woods was more strongly associated with topographic, edaphic, and edge factors than with gap disturbance. These species are rare in the forest and together comprise only 2.6% of the total number of trees in the canopy. Although gaps occur throughout the forest, yellow-poplar and black cherry trees were non-randomly distributed in association with ravine slopes, poorly-drained soils covered with pooled water, and stand edges. These edges are similar in that light availability is greater there than in other areas of the forest interior and is a likely factor which favors these shade-intolerant species.

The rarity and clumped pattern of dispersion of these trees may create difficulties for the effective dispersal of seeds into all favorable sites for regeneration. However, trees growing in areas not associated with various edges appeared to have regenerated in treefall gaps. Past gaps were reconstructed around young canopy trees and were found to be similar in size to current single-tree gaps. While these trees are very fast growing, it is probable that recurrent treefalls, occurring in close proximity in time and space to one another, are involved in the growth of these shade-intolerant trees in small gaps.

Warren Woods was found to incur a low rate of treefall disturbance relative to other closed-canopy forests. A period of 370-390 yr is required for complete forest turnover at the current rate and scope of treefall, and this figure is the highest reported for any other forest studied in this way.

This study demonstrates the importance of disturbance frequency on forest regeneration and composition when the size of disturbance is held relatively constant (single-treefall gaps). Different rates of recurrent treefall disturbance determine a range in length of periods of shade suppression. Species abundance and distribution are sorted along a gradient of disturbance frequency on the basis of relative shade tolerance. Accordingly, the overwhelming dominance of beech, the most shade-tolerant species in the forest, and the relative rarity of the very shade-intolerant yellow-poplar and black cherry, which are relegated mostly to forest margins, reflects the very low rate of treefall disturbance in this forest.

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