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AGE STRUCTURE AND DISTURBANCE HISTORY OF A SOUTHERN APPALACHIAN VIRGIN FOREST[1]

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Abstract. The frequency and intensity of natural disturbances in a montane old-growth forest of coniferous (*Tsuga*) and broad-leaved deciduous trees (*Liriodendron, Betula, Castanea, Fagus, Acer*) were investigated by means of diameter frequency distributions, diameter-age regressions, and analysis of radial growth patterns. The seven species investigated are represented by all-aged populations regardless of the degree of shade tolerance. The age distributions of most species, however, are irregular with several prominent peaks. Apparent coincidence of these peaks among some species suggests a common underlying influence. Radial growth patterns reveal higher than average numbers of abrupt and sustained increases in growth rate in most decades of peak recruitment which, along with other evidence, suggest that disturbance was the principal causal factor. There is evidence for eight partial disturbances in the past 250 yr, each of which generally removed <10% of the overstory trees. These fairly light disturbances appear to be sufficient to cause major deviations from the theoretical equilibrium diameter distribution of the forest.

Key words: age distribution; climax; disturbance; forest ecology; forest structure; southern Appalachian Mountains; windthrow.

INTRODUCTION

The frequency and magnitude of natural disturbances in temperate forests are important considerations in shaping management policies of both wilderness areas and commercial forest land. In the realm of forest management, uncertainty persists as to whether forests unaffected by man would be predominantly even aged or uneven aged. In some temperate regions the abundance of even-aged virgin stands and direct evidence on the frequency of large-scale natural disturbances have suggested that most forest stands would be in constant successional flux under natural conditions (Maissurow 1935, Graham 1941, Cline and Spurr 1942, Bloomberg 1950, Heinselman 1973, Spurr and Barnes 1973). Under such conditions all-aged forests would seldom develop even in the absence of man (Raup 1964, Sprugel 1976). In regions or physiographic sites with this type of disturbance regime, clearcutting of timber would more closely mimic the predominant process of tree mortality and replacement than would more conservative selection cutting.

The type of disturbance regime has significant bearing on wilderness area management as well since relatively few management options exist if an area is to retain its "primeval character and influence" and is to be "protected and managed so as to preserve its natural conditions" (Wilderness Act of 1964, United States Public Law 88-577). The mounting evidence that many conifer forests in western North America are adapted to frequent lightning fires has already led to a change in the traditional policy of total fire suppression is some wilderness areas (Kilgore and Briggs 1972, Chapman 1977). Difficult management problems arise when it is discovered, as in northern Minnesota, that the natural fire regime is probably one of frequent and extensive crown fires (Heinselman 1973). Thus it is clear that the natural disturbance regime of each region should be known in as much detail as possible.

The investigation of stand history in western conifer forests has concentrated primarily on determining fire frequency by cross-dating fire scars on old trees and by stand age determination (Fritz 1929, Wagener 1961, Arno 1976). Comparable evidence on the stand histories of eastern deciduous forests has been sparse because virgin stands in the region are rare and stand historical data are not easily obtained by nondestructive means. Most of the pertinent evidence in second-growth stands was removed by early logging or land clearing.

If climax forest types are defined as those capable of self-perpetuation in the absence of severe disturbance (such as beech-maple-hemlock), then it appears that climax types occupied a large proportion of eastern North America in presettlement times (e.g., Reed 1905, Lutz 1930, McIntosh 1962, Siccama 1971, Finley 1976). Such evidence, however, does not necessarily indicate that natural disturbances were rare or that these forests were predominantly uneven aged. Many types of disturbances such as windthrow, insect attack, drought, clearcutting, and repeated selection cutting cause mortality primarily among the overstory trees and leave many of the understory trees intact. In seral forest types, disturbance often hastens succession to the climax type by releasing the understory from suppression by the overstory (Lutz and Cline 1947, Brender and Nelson 1954, Spurr 1956, Trimble 1965, 1970, Henry and Swan 1974). Once the climax

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type is dominant, further disturbance will often perpetuate the existing climax type by releasing understory trees of the same species (Hough 1936, Leak and Wilson 1958, Ohmann and Ream 1971, Tubbs 1977). All-aged climax stands, however, can probably develop only if the recurrence interval between any type of major disturbance is longer than the life-span of the dominant tree species. Thus age structure is a more sensitive indicator of disturbance history than is species composition.

The recent study by Henry and Swan (1974) on the Pisgah Forest of New Hampshire appears to have been the first study specifically on stand history in a virgin forest of eastern North America. Detailed analysis of a 400-m^2 plot suggested that this particular stand, dominated by eastern white pine (*Pinus strobus*), experienced two severe disturbances over a 300-yr period, both of which killed nearly all the overstory trees in the plot. It is probable that many or most of such pine stands had a catastrophic origin, since those checked for age structure were usually even aged (Cary 1894, Spalding and Fernow 1899, Hough and Forbes 1943). An estimate of regional disturbance frequency from stand data, however, will require stand historical analysis for a variety of forest types and physiographic sites, with greater weight given to results from the predominant forest types. Although detailed stand historical analyses are lacking for the predominant cover types of the eastern deciduous forest region, the majority of remnant virgin stands in mesophytic types has been found, from examinations of cut stumps or increment cores, to be broadly uneven aged or all aged (Zon and Scholz 1929, Gates and Nichols 1930, Morey 1936, Maissurow 1941, Hough and Forbes 1943, Leak 1975, Hett and Loucks 1976, Tubbs 1977). Irregular age distributions in these stands, however, appear to have been common (Gates and Nichols 1930, Maissurow 1941, Hough and Forbes 1943), which raises the possibility that reasonably severe partial disturbance could still have a major influence on forest population dynamics. In the forest of Tionesta Creek, Pennsylvania, the age structure of hemlock (*Tsuga canadensis*) was nearly discontinuous so that well-defined age groups could easily be recognized, even though they were spatially intermixed (Hough and Forbes 1943). Since wind, fire, drought, climatic variation, and irregularities in seed production could all conceivably cause such peaks and gaps in the age structure, examination of additional evidence is necessary to establish the cause in such cases.

The purpose of this paper is to report evidence on the frequency and severity of natural disturbances in a virgin deciduous forest having a species composition typical of one of the principal cover types in the eastern deciduous forest region. The forest selected for study is one of the largest virgin forest remnants in the southern United States and in terms of species composition is fairly representative of the mixed mesophytic forest type of the southeastern and central United States (Braun 1950, Küchler 1964). This type generally contains a mixture of shade-tolerant and shade-intolerant species. An investigation of the relationship of size structure to age structure and natural disturbances should provide not only a case study of disturbance history in a specific forest, but also some general principles that can be used to interpret disturbance history for virgin tracts from which only tree diameter data are available.

THE STUDY AREAS

Two sites at low and middle to upper elevations were selected for detailed study in the Joyce Kilmer Memorial Forest, a wilderness preserve which encompasses the watershed of Little Santeetlah Creek in the mountains of southwestern North Carolina. This watershed has long been considered to have virgin timber because of its remoteness, the lack of road access for logging, and the large size of its trees (Anonymous 1910). Although most of the forest has never been cut, some logging did take place near the mouth of the creek around the turn of the century, and the early local residents started frequent surface fires in the area (Ayres and Ashe 1905). However, no evidence of fire, such as fire scars on trees or charcoal in the soil, was found on the two north-facing sites selected for study.

Braun (1950) lists the common dominants of the Mixed Mesophytic association as beech, tulip tree, white basswood, sugar maple, chestnut, yellow buckeye, red oak, white oak (*Quercus alba*), and hemlock, with local concentrations of sweet birch, yellow birch, and mountain silverbell (see Table 1 for scientific names). All of these species are important components of the study areas except for white oak. The two study areas comprise the principal tracts of mixed mesophytic forest within the preserve. Much of the remainder of the watershed was originally oak-chestnut forest.

The smaller study area is a 12-ha tract along the main branch of Little Santeetlah Creek and adjacent lower slopes (elevation range 715–790 m). The larger area is a 19-ha tract on the middle and upper slopes of Poplar Cove, 1.1 km from the Little Santeetlah tract and separated from it by two large spur ridges. The Poplar Cove tract has a greater variety of community types, ranging from hemlock forest of ravines or "coves" to oak forest of the ridge and upper slopes, in which chestnut was once a codominant species. The study area ranges from 757 to 930 m in elevation and spans 30–70% of the slope distance from valley bottom to ridgetop.

The soil in the two study areas is a brown stony loam with a brown loam or clay-loam subsoil (Goldston and Gettys 1953). Based on soils data of Oosting and Bourdeau (1955) and the regression of tulip tree site index on depth of the A_1 soil horizon by Auten (1945), the predicted site index of the study areas for tulip tree (in metres at age 50 yr) is 25–30 at Little

Santeetlah Creek and 30 in the hemlock forest at Poplar Cove. Auten (1945) found that the average site index for 77 stands in which tulip tree occurred was 25. The site quality of the lower slopes would therefore probably be rated as good to excellent.

Based on an analysis of weather data from stations in the North Carolina-Tennessee mountains (Dickson 1959), the expected mean annual temperature for an elevation of 760 m is 13°C, with a January mean of 4°C and a July mean of 22°C. The mean annual precipitation at the nearest weather station (Andrews, North Carolina) is 156 cm, but the rainfall at the higher elevation Kilmer Forest is probably greater (Shanks 1954).

METHODS

Instead of a complete census of a small plot, sampling of tree diameters and ages was conducted on moderate-sized tracts. This makes it possible to identify disturbances that occurred over a fairly extensive area and eliminates the chance of confining the study area to a portion of the forest with an unrepresentative age structure. However, such data do not provide a detailed view of the spatial arrangement of age classes in a particular spot. This limitation was partly overcome by more intensive sampling in some areas.

The forest at Little Santeetlah Creek was sampled by 30 circular 405-m^2 plots, amounting to 10% of the study area. The first coordinate for each pair of plots was determined systematically at 85-m intervals along a sample line traversing the center of the tract. The second coordinate was determined by random distances on both sides of the line. All trees taller than 0.3 m were identified on each plot and diameters were measured at breast height (dbh or 1.4 m) for all trees > 2.5 cm dbh.

The Poplar Cove tract was mapped and sampled by the point-centered quarter method (Cottam and Curtis 1956) to provide a more detailed view of species and size distributions. The study area was divided into 92 rectangular blocks (64 × 32 m each) and the corners located on the ground by staff compass and pacing. A stratified random sample was obtained by locating two sample points by random coordinates in each block. At each sample point, distances to the nearest overstory tree (>15 cm dbh) and understory tree (>1 m tall and ≤15 cm dbh) and tree diameters were measured in each of four quadrants. The sampling intensity of overstory trees was 40 trees/ha, or ≈15% of the trees on the tract. A topographic map of the Poplar Cove study area (Fig. 1) was constructed from data on aspect and percent slope at each of the sample points. Slope distance was converted to horizontal distance and the elevation of each sample point computed trigonometrically, using the memorial plaque as a reference point.

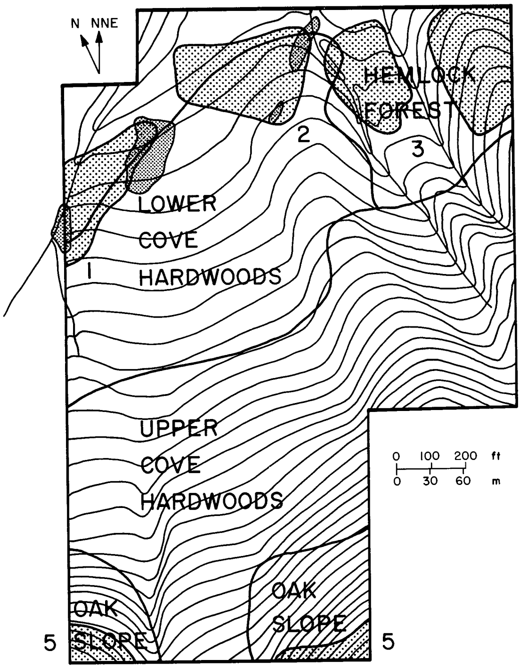


FIG. 1. Poplar Cove study area showing community types classified according to spatial distributions of dominant tree species. Lowest contour line (top) is 757 m (2485 ft). Contour interval is 4.6 m (15 ft). Numbered areas with light stippling indicate location of forest stands with higher than average number of age determinations. Areas 4 and 5 extend beyond study area boundaries (total of 2.5 and 4 ha, respectively) due to distribution of sectioned chestnut logs. Areas of dark stippling indicate location and size of windfalls that occurred in 1973–1975.

In Poplar Cove several community types were recognized to facilitate an analysis of spatial variation in the data. The distribution of canopy trees of the principal species was the main criterion for recognition of community types. Some species such as tulip tree and white basswood are well distributed over the tract, whereas others are common only in certain habitats or elevation ranges. The boundary of the hemlock type (Fig. 1) corresponds to the approximate upper limit of overstory hemlock, excluding scattered outliers. The boundary between the lower and upper cove hardwoods corresponds to the upper limit of overstory beech and the lower limit of red maple, sweet birch, and pignut hickory. The transition between the upper cove hardwoods and the oak type was determined by the points at which silverbell ceases to be the most common canopy tree and is superceded by chestnut oak. Maps for each species are available elsewhere (Lorimer 1976). At Little Santeetlah Creek two types of hemlock forest were recognized (with and without a dense woody understory of *Rhododendron maximum*) because of spatial segregation of yellow birch, silverbell, and beech in the two types.

Since chestnut was once a major component of the Poplar Cove forest, quantitative data were obtained on its density, diameter distribution, and age struc-

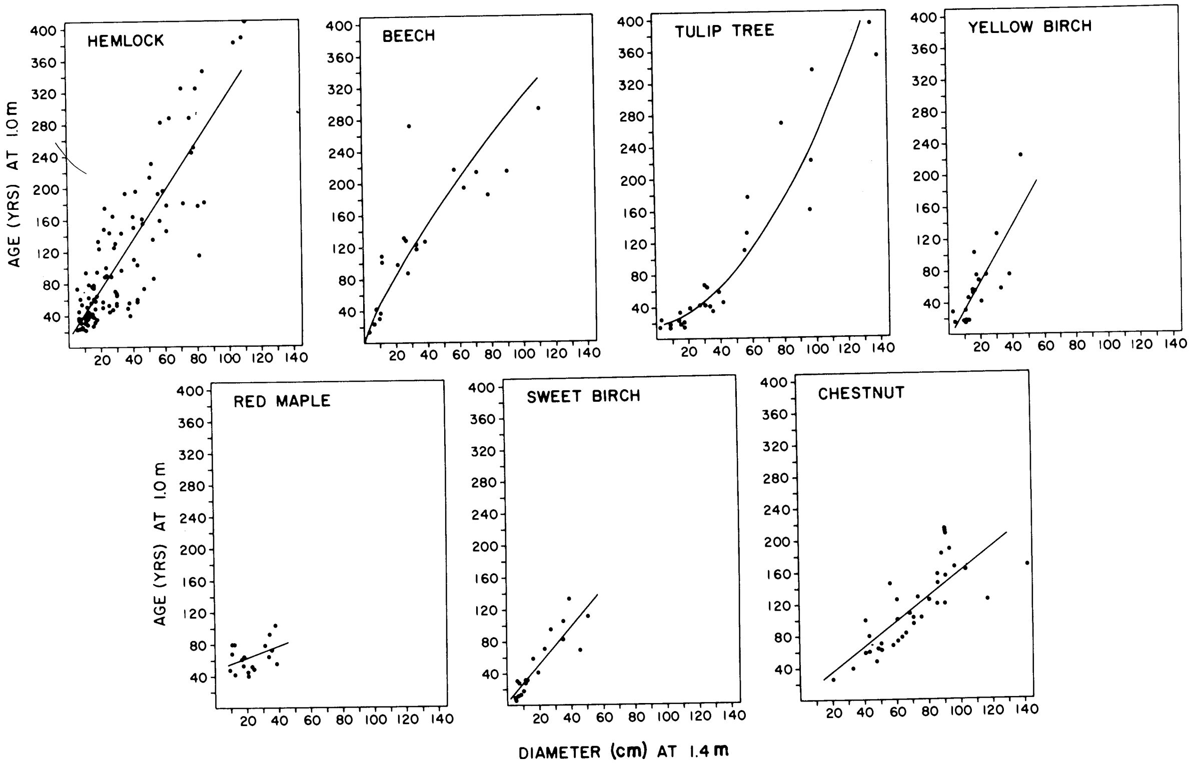


FIG. 2. Diameter-age relationships of the species selected for age structure analysis. Equations are: hemlock ($y = 9.1 + 3.09\ x$; $r^2 = .75$), beech ($y = 7.4x^{0.81}$; $r^2 = .81$), tulip tree ($y = 14.2 + 0.50x + 0.0188x^2$; $r^2 = .71$), yellow birch ($y = -4.1 + 3.53x$ $r^2 = .64$); red maple ($y = 47.8 + 0.74x$; $r^2 = .14$), sweet birch ($y = 3.7 + 2.36x$; $r^2 = .80$), chestnut ($y = 3.6 + 1.55x$; $r^2 = .61$).

ture. The chestnut logs are still well preserved due to their high tannin content, and can be readily distinguished in the field from those of associated species by their ring-porous wood and lack of visible rays (Panshin and de Zeeuw 1970). The diameter at breast height of a chestnut log and distance from sample point to root crown were recorded whenever the root crown was closer than the nearest standing tree in the quadrant.

Age determinations of 202 trees were made for seven of the principal species in order to plot diameter-age relationships. The 59 age determinations of hemlock were supplemented by an additional 42 determinations from the same site by Oosting and Bourdeau (1955 and original field notes). Because of restrictions on the number of cores, sampling among diameter classes was basically uniform to increase reliability over the range of tree size. Increment cores were taken at a height of 1.0 m. The center of the tree was reached in most coring attempts, but for some trees the center was not reached because of heartrot or because the tree radius was somewhat longer than the 46-cm bore length. Some of the incomplete cores (15) were retained if <10 cm of the radius (calculated as one-half the diameter) were missing. The remainder were rejected. The number of missing rings on incomplete cores was estimated from the diameter-age regression curves (Fig. 2). By this procedure, if the inner 2.5 cm of a core were lacking, the number of missing rings was estimated from the average age of a 5.0 cm diameter tree of that species. Since the standard error of the age of a small tree is relatively small, such a procedure should yield good estimates. Three incomplete cores from very large tulip trees, in which 20–28 cm were missing, were retained because of the low variability and rapidity of growth in young trees of this species.

Age determinations of chestnut logs were made from cross-sections of logs cut along trails. Correction factors to express age at the 1.0-m level were added or subtracted by assuming an average growth rate in height of 60 cm/yr (Zon 1904, Ayres and Ashe 1905). The average correction factor was 7 yr.

Yearly ring width measurements for 130 increment cores were made to the nearest 0.025 mm under a binocular microscope equipped with a movable stage and dial micrometer. It was necessary to sand or shave all increment cores of diffuse porous deciduous species in order to reveal the growth rings. In the laboratory, increment cores were moistened with water

TABLE 1. Relative density (%) of tree species in community types of the two study areas, Joyce Kilmer Memorial Forest (trees > 15 cm dbh).

Species	Little Santeetlah Creek		Poplar Cove			
	Hemlock/ rhodo-dendron	Hemlock/ herb	Hemlock/ herb	Lower cove hardwoods	Upper cove* hardwoods	Oak slope†
Hemlock (*Tsuga canadensis*)‡	32.2	47.4	55.0	7.4	6.8	0.9
Yellow birch (*Betula lutea*)	32.2	5.0	1.9	0.5	0.0	0.0
Sycamore (*Platanus occidentalis*)	0.8	0.0	0.0	0.0	0.0	0.0
Blackgum (*Nyssa sylvatica*)	0.8	0.0	0.0	0.0	0.0	0.0
Tulip tree (*Liriodendron tulipifera*)	8.1	8.8	6.3	9.3	5.8	8.6
White basswood (*Tilia heterophylla*)	7.2	9.6	8.1	7.9	8.2	6.0
Silverbell (*Halesia carolina*)	0.8	13.2	9.4	29.6	23.2	6.0
Beech (*Fagus grandifolia*)	0.8	7.9	6.9	17.1	1.7	1.7
Sugar maple (*Acer saccharum*)	0.8	2.6	8.1	12.5	10.6	0.0
Fraser magnolia (*Magnolia fraseri*)	2.4	0.0	0.0	0.9	0.3	0.0
Cucumber tree (*Magnolia acuminata*)	0.0	2.6	0.0	2.3	0.3	1.7
Buckeye (*Aesculus octandra*)	1.6	0.9	0.0	2.8	1.4	0.0
White ash (*Fraxinus americana*)	0.8	0.9	0.0	3.7	3.8	0.0
Sweet birch (*Betula lenta*)	8.1	0.0	0.6	2.3	13.7	14.6
Red maple (*Acer rubrum*)	1.6	0.0	2.5	0.9	12.0	18.1
Pignut hickory (*Carya glabra*)	0.0	0.0	0.0	2.3	6.5	8.6
Sourwood (*Oxydendrum arboreum*)	1.6	0.9	1.3	0.0	1.4	4.3
Black cherry (*Prunus serotina*)	0.0	0.0	0.0	0.0	0.3	0.0
Sassafras (*Sassafras albidum*)	0.0	0.0	0.0	0.0	0.0	0.9
Black locust (*Robinia pseudoacacia*)	0.0	0.0	0.0	0.0	0.0	1.7
Black oak (*Quercus velutina*)	0.0	0.0	0.0	0.0	0.3	0.9
Northern red oak (*Quercus rubra*)	0.0	0.0	0.0	0.5	2.7	7.8
Chestnut oak (*Quercus prinus*)	0.0	0.0	0.0	0.0	0.3	18.1
Number of sample trees	124	114	160	216	292	116
Number of trees per hectare	191.0	234.6	261.3	235.1	265.0	239.2

* Chestnut (*Castanea dentata*) comprised ≈20% of the trees >15 cm dbh in this community prior to the blight.
† Chestnut comprised ≈23% of the trees >15 cm dbh in this community prior to the blight.
‡ Nomenclature follows that of Fernald (1950).

after having been previously in an air-dry condition, thereby providing data on relative growth rates within a tree rather than absolute rates.

RESULTS AND DISCUSSION

Species composition and successional status

Species composition of each community is shown in Table 1. Based on species composition alone, the mesic communities would generally be considered climax because of the heavy dominance of shade-tolerant species. Climax status is also suggested by the fact that seedlings of all species are reasonably abundant, either beneath the forest canopy or in small gaps.

Species intermediate or intolerant of shade are well represented, however (cf. Baker 1949). The intermediate yellow birch is a codominant species in the hemlock forest along Little Santeetlah Creek. The intolerant tulip tree comprises 6–9% of the overstory density and 17–37% of the basal area in the various communities. Compared to 93 virgin mixed mesophytic stands sampled by Braun (1950), the Kilmer stands rank in the 74th percentile with respect to the relative density of overstory tulip tree. The oak-dominated forest has relatively few oak saplings >1 m tall (13 saplings/ha) but does have a dense understory of sugar maple, beech, basswood, hemlock, silverbell, and red maple (561 saplings/ha). Thus its successional status is uncertain. Since the observed type of species mixtures could be produced by a wide range of disturbance intensities, an analysis of age structure and growth rates is necessary to clarify the actual stand history and predominant mode of tree replacement.

Age structure

Scatter diagrams of age vs. diameter indicate that the forest is all aged for those species investigated, including the intolerant tulip tree and the mid-tolerant chestnut, yellow birch, and sweet birch (Fig. 2). There are sample trees in most 10-yr age classes up to ≈400 yr. These results support the principle that in old-growth forests, diameter distributions having a general form similar to the negative exponential distribution for individual species usually indicate all-aged structures (Hough 1932, Meyer and Stevenson 1943, Hett and Loucks 1976), even if the curves are highly irregular with prominent peaks. However, since each age class tends to have an approximately normal diameter distribution, and since the variance of diameter can be quite large in old age classes (Meyer 1930, Hough

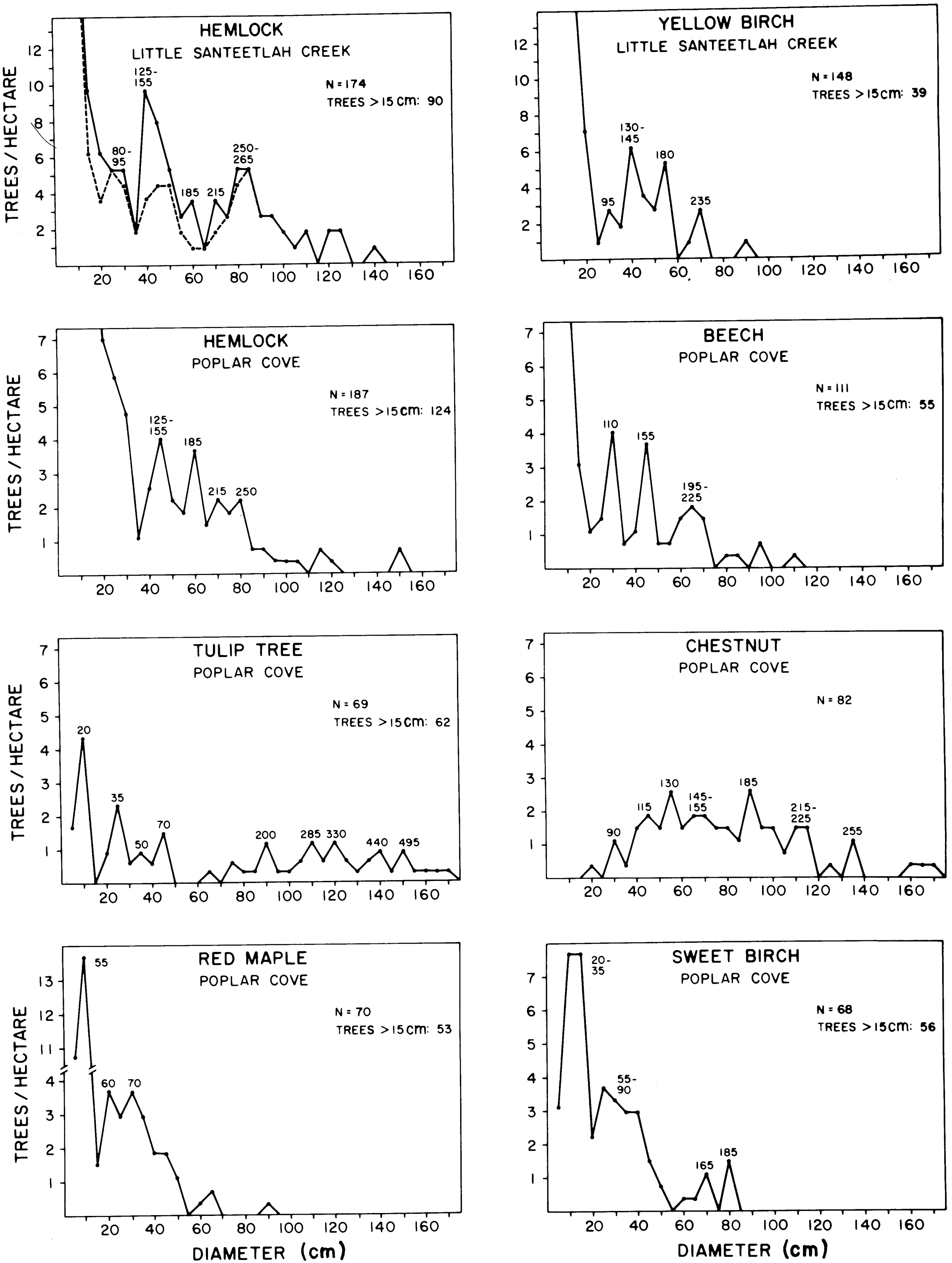


FIG. 3. Diameter frequency distributions for species having a sample size of >60 trees and for which age data are available. Numbers along abscissa are end points of 5-cm classes, and numbers above the peaks indicate predicted average age in years for class midpoints. Where more than one diameter class is incorporated into a peak, a range of age is indicated. For chestnut, 45 yr have been added to the predicted ages to account for the time elapsed since the chestnut blight. The dotted line for hemlock at Little Santeetlah Creek shows the distribution if four adjacent plots in the eastern part of the study area are omitted, revealing spatial clumping of trees in the 40- and 60-cm peaks.

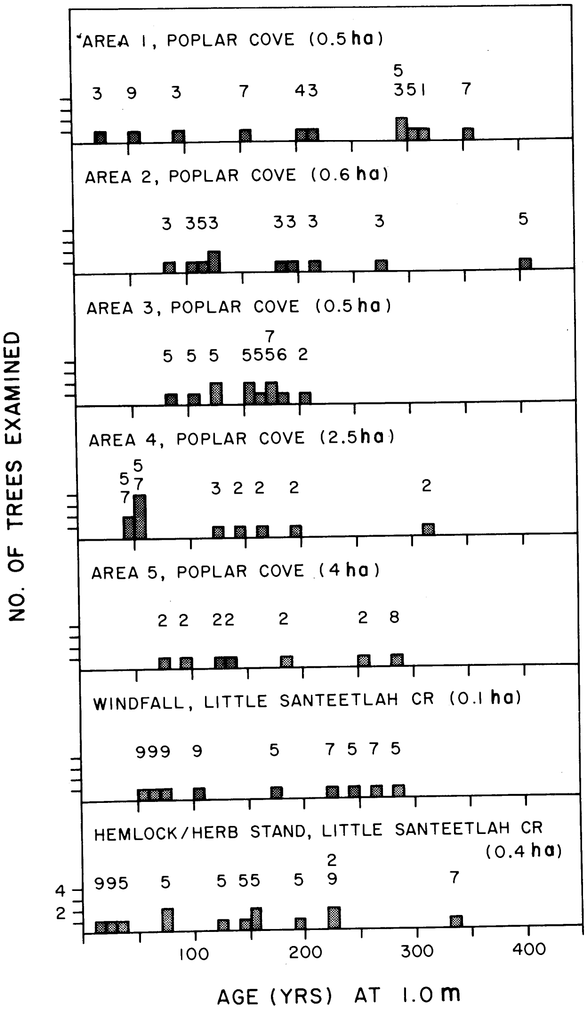


FIG. 4. Age distributions for stands having a higher than average number of age determinations (cf. Fig. 1). Numbers above the bars are species codes: 1 = white ash, 2 = chestnut, 3 = beech, 4 = sugar maple, 5 = hemlock, 6 = basswood, 7 = tulip tree, 8 = red oak, 9 = yellow birch.

1932), some exceptions can be anticipated. The most common case would be an old, even-aged overstory of a shade-tolerant species with a developing uneven-aged understory of the same species. Such a stand would have a curve similar to that of yellow birch in Fig. 3 and would be difficult to distinguish from a truly uneven-aged stand. It is also known that even-aged stands can have a negative exponential diameter distribution if many stands of dissimilar ages are grouped together or if several species in a stand are grouped (Hough 1932, Roach 1974, Oliver 1978).

Although both study areas are clearly all aged when considered as a whole, it is possible from the above considerations that each study area could be made up of several sizable even-aged stands of different ages. Therefore the data from five more intensively cored stands in Poplar Cove (Fig. 1) and two stands from Little Santeetlah Creek were analyzed separately. Each was found to have a wide range in tree age typical of uneven-aged stands, even for tracts as small as 0.1–0.5 ha (Fig. 4). Evidence of uneven-aged stand structure was found not only for mesic sites dominated by shade-tolerant species but also for a drier ridge site originally dominated by chestnut (Area 4, Fig. 1) and for the chestnut component of a high-elevation oak-chestnut site (Area 5, Fig. 1). The less intensively cored parts of the study areas also revealed trees of various ages scattered throughout. Thus if the study areas are comprised of even-aged groups, the average group size would have to be fairly small.

The diameter distributions of nearly all species have two or more well-defined peaks (Fig. 3). Since diameter is highly correlated with age (Fig. 2) it is probable that the peaks correspond to decades in which there was unusually high survival or recruitment of young trees. The estimated average age of trees in each peak was obtained from regression curves fitted by standard least squares techniques. This method provides unbiased parameters, which makes it preferable to the logarithmic transformations used in a previous analysis of the data (Lorimer 1976). For most species, linear equations were used. The data for tulip tree and beech showed strong indications of curvilinearity and were fit by the equations

$$y = a + bx + cx^2$$
$$\text{and } y = ax^b,$$

respectively, where y = tree age, x = diameter, and a, b, c are estimated parameters. The types of equations chosen seem biologically reasonable in view of the observed radial growth patterns.

A comparison of the predicted ages for peak diameter classes reveals apparent coincidence of peak age classes among a number of species (Fig. 3). For example, peaks in the 145–155 yr and 180–190 yr age classes are present in five out of seven cases in Fig. 3 (omitting red maple due to lack of old trees). Other peaks common to two or more curves are the 85–95, 110–115, 215–225, and 250–260 yr age classes. The major peak for hemlock (predicted age 125–155 yr) is included in the 145–155 yr age class because none of the trees sampled from this peak was between 125 and 145 yr old.

Independent random subsamples of various sizes (25, 50, and 75% of total sample) were used to test for variability in the form of the diameter distributions. Although there is some fluctuation in the height of the peaks among subsamples, the location of the peaks on the abscissa was consistent throughout.

It is evident that each age class peak generally covers a broad span of years. Even if the causal factor occurred within a narrow time interval (as with windthrow), it would not be possible to identify the exact year because a peak diameter class will inevitably include trees of other age classes due to differential

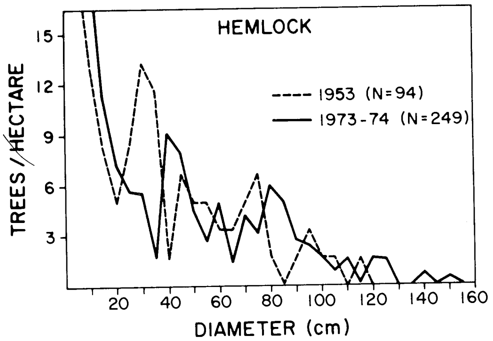


FIG. 5. Combined hemlock diameter distribution of both study areas compared to the distribution in 1953, plotted from original field notes of Oosting and Bourdeau (1955).

growth rates. Equally important is the fact that disturbances that kill primarily overstory trees (e.g., windthrow, insects, disease) typically "release" many understory saplings that not only pre-date the disturbance but may also have a wide range in age among individual saplings (Henry and Swan 1974). Even colonization of the disturbed site by new individuals will generally take place over a period of a decade or more. A diameter class peak can also be caused by the cumulative effect of several small disturbances over a period of one or more decades (Oliver and Stephens 1977).

The apparent coincidence of any particular peak age class among species is affected by this age span, and also by the standard error of the slope of each regression curve. The latter cannot be computed due to the marked inequality of variance (heteroscedasticity) in the diameter-age data. However, it is possible to test whether the overall pattern of coincidence among species could have occurred simply by chance as a result of random, unrelated events. If each age class has an equal chance of having peak numbers of trees of a species, then the number of age classes having 0, 1, 2 . . . n peaks should follow a Poisson distribution (Snedecor and Cochran 1967). A χ^2 test showed that the differences between the observed and expected (Poisson) distributions are significant at the .004 level ($\chi^2 = 13.21$, df = 3). There are more age classes with four or five peaks than expected by chance (observed = 4, expected = 1.2) and more age classes with zero peaks (observed = 8, expected = 4.1). The χ^2 test indicates that the probability of the 29 peaks ≥ 70 yr and ≤ 260 yr being distributed among 10-year age classes in such an aggregated manner by chance is <1%.

Development of the all-aged structure

The behavior of these peak diameter classes over time is suggested by a comparison of the combined 1973–1974 hemlock data from both study areas with a survey of the same sites by Oosting and Bourdeau in 1953. The three major peaks in 1953 are still recognizable in the 1973–1974 data, allowing for growth during the 20-yr period and reduction in height of the peaks due to mortality (Fig. 5). This evidence supports the interpretation of the peaks as well-defined size classes that retain their identity over a substantial period of time.

The apparent average mortality rate for trees in the three peaks during this time (20%) is close to what would be predicted from the slope of a smooth negative exponential curve (16%) or negative power function curve (16%) fitted by iterative nonlinear regression. The reduction in height of the peaks and extension of the smooth "tail" of the curve into the 20–30 cm classes have resulted in a better fit of the more recent data to theoretical distributions. For the negative exponential model ($y = 11.44e^{-0.0175x}$, $15 \leq x \leq 150$) the r^2 value has increased from .52 in 1953 to .66 in 1973–1974. For the negative power function model ($y = 102.29x^{-0.833}$, $15 \leq x \leq 150$) the r^2 has increased from .41 to .62. These changes suggest a trend toward a more balanced age structure over time in line with the classic all-aged model of stand structure (Meyer and Stevenson 1943). A poorer fit to the negative exponential distribution after 23 yr was found by Christensen (1977) in second-growth oak forest, and this was largely due to high mortality in the smaller size classes and low recruitment. It is probable that such species as oak and hickory are not sufficiently tolerant of shade to maintain the large numbers of suppressed trees needed for a good fit to the negative exponential distribution, and thus this distribution should probably be expected only for tolerant species.

Cause of age class peaks

Evidence on the cause(s) of the age class peaks can be obtained from the radial growth patterns of trees in the same decades. A period of favorable climate would be expected to produce a synchronous increase in growth rate among most overstory trees that would persist for the duration of the favorable period. Fritts (1962), for example, obtained multiple correlation coefficients of .83 to .90 for the relationship between radial growth and evapotranspiration data for beech and white oak. Disturbance would be expected to cause abrupt and sustained increases in growth of understory trees "released" by the death of nearby overstory trees, and also increased growth of some of the adjacent surviving trees in the upper crown classes. The number of trees responding to release would depend on the severity of the disturbance. A period of high seed production, on the other hand, would not cause an increase in radial growth unless it also was followed by a period of favorable climate.

Examination of the increment cores revealed no consistent trends in growth during the decades in question. The radial growth patterns are typically irregular, with major overlapping cycles of growth lasting from 5 to >60 yr, upon which are superimposed smaller yearly fluctuations. It is clear, however, that some trees display the types of growth patterns expected following disturbance. Several criteria were established for distinguishing trees showing a clear response to disturbance from other trees in which no pattern is evident or in which the pattern could have been caused by either climate or disturbance. The period of rapid growth had to occur abruptly and be sustained for at least 15 yr, and also had to be preceded by a period of relatively slow growth lasting at least 15 yr. The average rate for the 15-yr period following release had to be at least 100% greater than the previous average rate. For trees already showing moderate growth before release (>1.0 mm yearly radial increment, lab conditions), a 50% increase in average rate was required.

Examples of trees meeting these criteria are shown in Fig. 6. Periods of rapid growth following the year of abrupt increase, as well as the preceding periods of slow growth, are frequently sustained for 30 consecutive yr, and in some cases as many as 90 consecutive yr (Fig. 6, trees 2, 5, 6, 9, 10, 12). Due to the prolonged nature of these changes in growth rate, it is unlikely that climatic variation could be the principal causal factor. Climatic records for the nearest weather station in Andrews, North Carolina indicate short-term fluctuations with no evidence of longer cycles for the period of record (1909–1975). For example, the mean time interval between precipitation maxima and minima (years in which the deviation from the mean exceeds 50% of the maximum observed deviation) is 4.2 yr. Oscillations in temperature during the growing season have been less pronounced, and temperature alone or in combination with precipitation shows no consistent relationship to the frequency of abrupt increases in growth. Also, since sustained increases in growth can be found in nearly every decade (Figs. 6 and 7) it is unlikely that they are responses to favorable changes in climate. Even for trees showing abrupt increases in the same decade, the duration of rapid growth is highly variable. Disturbance is a reasonable explanation for the longer cycles because for many trees, growth rates prior to release are comparable to those of trees currently in the understory, while the rates following release are comparable to those of trees in the dominant or codominant crown class (Fig. 6, trees 1, 4, 5, 6, 7, 9, 11, 12, 13, 14). It is probable, however, that the smaller yearly fluctuations are climatically related.

Although releases, and hence overstory tree mortality, have occurred in nearly every decade, a summary compilation indicates higher than average frequency for the decades 1780, 1820, 1870, 1890–1900, 1920, and 1930 (Fig. 7). These correspond to age class midpoints 195, 155, 105, 75–85, 55, and 45, respectively. The percentages of trees showing release in these decades range from 73–250% higher than the average of the intervening decades. Four of these six decades are also represented by peak age classes. The two exceptions (1780 and 1930) may be related to age class peaks 185 and 35, since the span of years in these age classes (at least 10 yr) is such that the actual period of establishment would have overlapped with the time of releases.

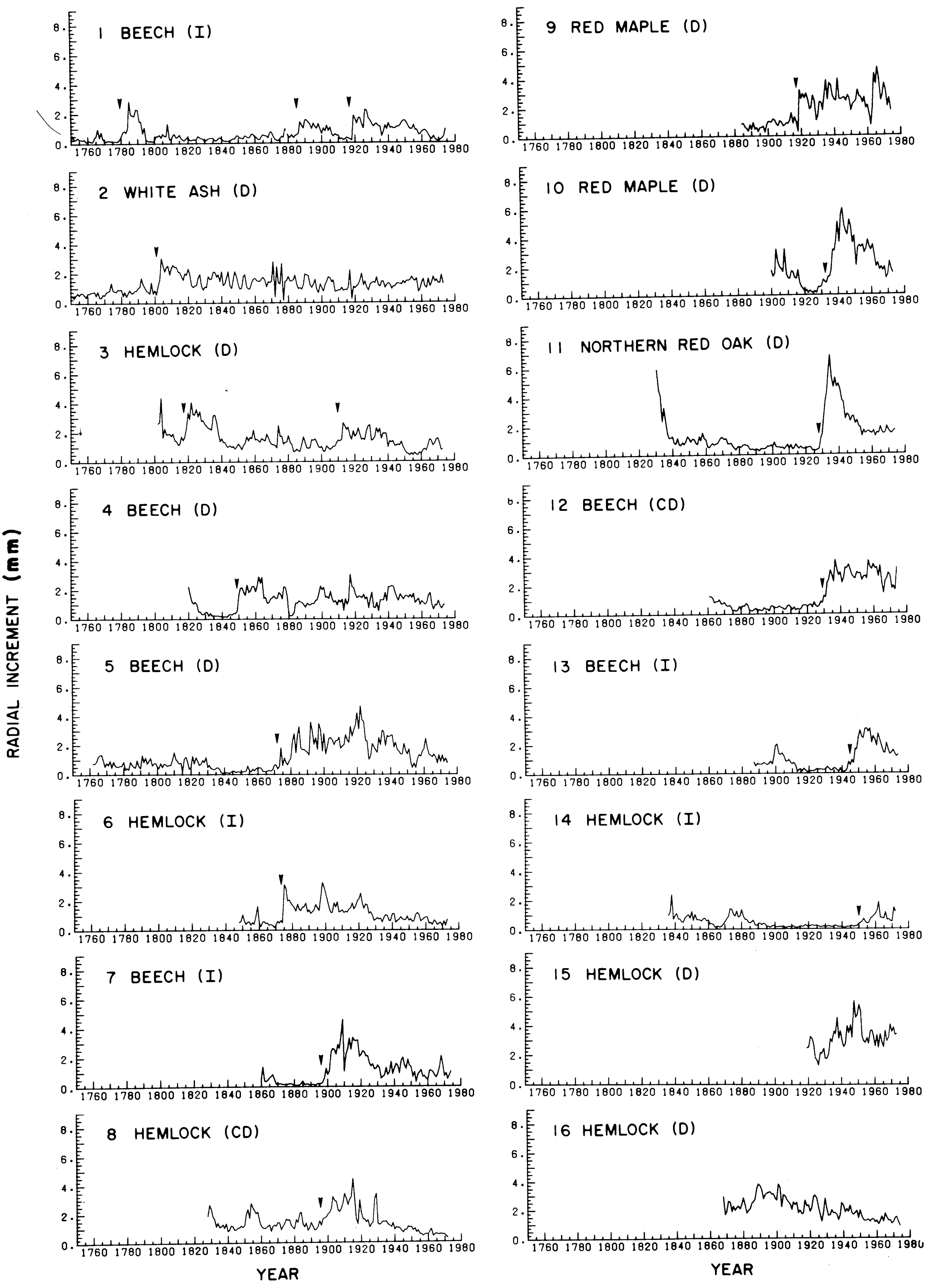
Further evidence on the growing conditions of trees during the decades of peak age classes pertains to the early growth of saplings. Since the standard core height was 1.0 m, the first 10 rings on each increment core reflect the growing conditions of each tree at the time that it was a small sapling. For trees in which the first 10 rings were formed in one of these six decades, 78.4% were growing at a moderate or rapid rate (>1 mm/yr radial increment). This is contrasted with 50.0% of the trees showing moderate or rapid initial growth in the intervening decades. Many of these trees were growing at rates comparable to those of canopy trees, suggesting that they were not growing under dense shade when in the sapling stage (e.g., Fig. 6, trees 4, 8, 11, 15, 16). This evidence is more direct in suggesting that many of the trees in peak age classes grew under postdisturbance conditions. Thus the possibility that the trees in peak age classes are simply a result of years of high seed production seems less plausible.

An illustration of the effects of a known disturbance is provided by the chestnut blight, an introduced disease which caused complete dieback of chestnut in the region from 1928–1938 (Braun 1942, Woods and Shanks 1959). The percentage of trees showing release in this decade is 153% higher than the average for nondisturbance decades. The percentage of releases in this decade is 717% higher if trees from the mesic communities that had little chestnut are eliminated from the sample (Fig. 7). The blight is probably responsible for major peaks in the age structure of sweet birch and tulip tree on the higher slopes (Fig. 3), although establishment of new seedlings appears to have lagged behind the immediate response of understory trees to the dieback of the crowns. Tulip trees of this age are largely restricted to the vicinity of chestnut logs in the upper cove hardwoods and oak slope communities of Poplar Cove.

It therefore seems that while radial growth patterns and population structure probably reflect the interaction of several factors, disturbance by itself is sufficient to account for abrupt and sustained increases in radial growth and peaks in the age structure. The other most likely factors (variation in climate and seed production) do not appear to be adequate causes in this case.

The principal disturbances and their extent

In addition to the disturbances for which both age class and radial growth evidence are available (1820,


1 BEECH (I)
2 WHITE ASH (D)
3 HEMLOCK (D)
4 BEECH (D)
5 BEECH (D)
6 HEMLOCK (I)
7 BEECH (I)
8 HEMLOCK (CD)
9 RED MAPLE (D)
10 RED MAPLE (D)
11 NORTHERN RED OAK (D)
12 BEECH (CD)
13 BEECH (I)
14 HEMLOCK (I)
15 HEMLOCK (D)
16 HEMLOCK (D)
RADIAL INCREMENT (mm)
0. 2. 4. 6. 8.
1760 1780 1800 1820 1840 1860 1880 1900 1920 1940 1960 1980
YEAR
YEAR

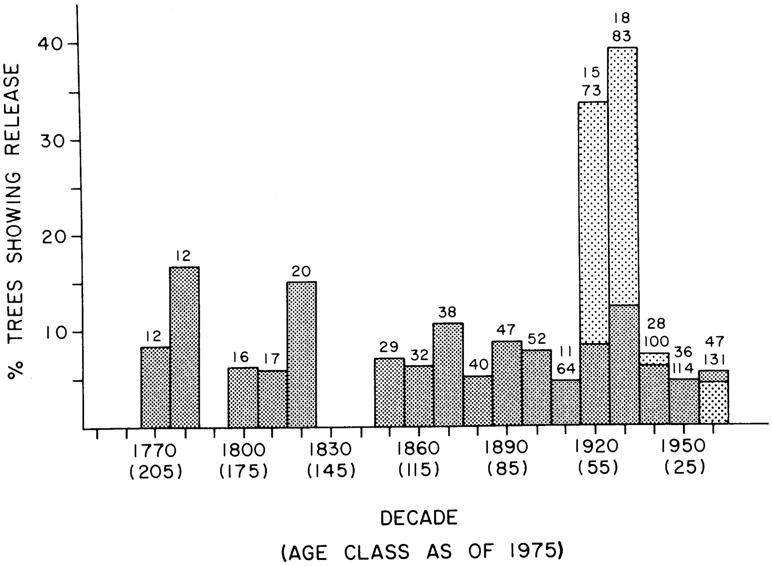


FIG. 7. Percentage of age-sampled trees showing release from suppression in each decade since 1750. Data from chestnut and tulip tree not included because these species rarely respond to release. Light stippled bars indicate percentage of trees showing release since 1905 in areas of >20% chestnut. No releases in chestnut areas were observed for 1910 and 1950; the percent release in 1960 in the chestnut areas is indicated by the lower horizontal bar. Sample size (number of trees) for each decade is shown above the bar; after 1905 the upper number indicates the sample size in the chestnut areas.

1870, 1890, 1920, 1930, and possibly 1785), there is evidence for several disturbances which either occurred so long ago that few radial growth data are available, or so recently that peaks have not yet developed in the diameter distributions. A disturbance or series of disturbances about 1755 is suggested by 215–235 yr peaks for hemlock in both study areas, yellow birch at Little Santeetlah Creek, and beech and chestnut at Poplar Cove. An earlier one about 1720 is suggested by 255-yr peaks for hemlock in both study areas and chestnut in Poplar Cove. Even earlier disturbances as far back as 1550 are almost certainly indicated by substantial numbers of the intolerant tulip tree in corresponding age classes.

There have been several cases of obvious disturbance in recent decades. Four plots in the hemlock-rhododendron forest of Little Santeetlah Creek were situated in windfalls which, based on the ages of yellow birch that had germinated on the fallen logs, all occurred about 1953. These windfalls were the final result of the death of several large trees and ranged from 200 to 400 m^2 in ground surface area for a total of 1330 m^2. From 1973–1975, while field work for this study was in progress, three sizable windfalls occurred in the lower portion of the Poplar Cove study area, amounting to 2200 m^2 or 1.2% of the tract (Fig. 1).

Disturbances of higher than average intensity have therefore occurred at ≈30-yr intervals in the past 250 yr for the study areas as a whole, and ≈40-yr intervals for a given community. The areal extent of each disturbance is indicated primarily by the location of communities in which corresponding age class peaks are found. The curves in Fig. 3 suggest that the disturbances of 1720, 1750, 1785, and 1820 were well distributed in both study areas whereas those of 1870, 1890, and 1920 were possibly more localized.

Severity of disturbances

The severity of disturbances is an important topic in relation to the management issues raised in the introduction. Estimates of severity are possible from two lines of evidence. Data on the percentage of trees showing release in each decade (Fig. 7) can be converted to estimates of overstory mortality in each decade if a ratio of the proportion of trees killed to the proportion released can be calculated. The number of

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FIG. 6. Yearly radial increments for a subsample of trees showing abrupt and sustained increases in growth rate (trees 1–14). Arrowheads identify periods that qualify as releases from suppression by the criteria outlined in text. Trees 15 and 16 are examples of trees with no history of suppression. Letters in parentheses indicate crown class in 1975. Dominant (D) and codominant (CD) trees are in the canopy layer. Intermediate trees (I) are taller than 12 m and partly overtopped by other trees.

trees sampled in each age class forms a roughly constant proportion of the trees in all older classes capable of responding to release. This permits a direct comparison of the intensity of different disturbances.

In principle, if overstory and understory trees are more or less uniformly distributed on an area, then mortality of overstory trees on 10% of the total area should remove 10% of the overstory trees and release 10% of the understory trees, giving a ratio of the percent mortality to percent release of 1:1. In reality, however, several complications occur. It is not likely that all understory trees released by disturbance would meet the necessary criteria for release in this study, yet lesser criteria would make it difficult to separate climatic effects. Large trees bordering a patch disturbance sometimes respond with increased growth. Also, a substantial proportion of understory trees is usually killed by the falling canopy trees, although this may be somewhat offset by a higher chance of subsequent survival for those not killed. These factors make it desirable to derive empirical estimates of the mortality:release ratio.

Long-range estimates of overstory mortality are probably best provided by the slopes of the relatively stable diameter distributions of shade-tolerant species. The slopes of the fitted negative exponential curves in conjunction with growth rate data from the diameter-age relationships yield a predicted average 10-yr mortality rate of 5.6% for hemlock and 6.5% for beech (among overstory trees >30 cm dbh). Since the mesic communities are heavily dominated by shade-tolerant species, an overall average of 6% for the forest is probably a reasonable estimate. From Fig. 7, the average 10-yr rate of release in the last 200 yr has been 6.9%. This suggests an approximate 0.9:1 ratio of mortality to release.

The chestnut blight, a disturbance of known severity, provides a second estimate of the mortality:release ratio. There is currently an average of 51.9 chestnut root crowns/ha in the two upper communities in Poplar Cove, the only areas in which chestnut was common. Assuming an average total stand density of 250 trees/ha (Table 1), chestnut would have comprised 20% of the stand in this area. The proportion of releases during the decade of the blight (1928–1938) was 33%. If we assume that 6% release was due to normal mortality unrelated to the blight, as calculated above, the incidence of release caused by the blight alone would have been 27%. This yields a mortality:release ratio of 0.7:1.

From the average 0.8:1 ratio we can estimate from Fig. 7 that in the disturbance decades of 1780, 1820, 1870, 1890, 1920, and 1930, the amount of overstory mortality was ≈14%, 12%, 8%, 6%, 6%, and 10%, respectively. Since the average or normal 10-yr mortality rate for the 200-yr period is 5.5% (6.9% × 0.8) and even nondisturbance decades have an expected mortality of 3.8%, we can conclude that the premature mortality of trees that could be accounted for by exogenous disturbance alone was in the range of 2–10%, and perhaps closer to a range of 1–9%. The latter estimate is probably more accurate since disturbance in a particular decade would generally remove old trees that would have died anyway during that time, and because premature removal of trees in disturbance decades would cause the mortality in subsequent decades to be below average. Thus the long-range average mortality rate of 6% probably most closely approximates expected mortality under steady state conditions. The indicated disturbance intensity of <1% in 1890 and 1920 might seem rather low, but the disturbances of 1973–1975 in Poplar Cove that blew down several large patches of trees were of this same magnitude (Fig. 1).

The relative numbers of the intolerant tulip tree in each decade provide independent evidence on the severity of disturbances. Fewer tulip trees appear to have been established between 1785 and 1920 than during the chestnut blight, which removed 10% of the overstory on the Poplar Cove tract and has resulted in ≈4 tulip trees/ha surviving in age classes 35–50. In the upper communities, where chestnut comprised 20% of the overstory, 11 tulip trees/ha are present in these age classes, and in the lower cove hardwoods, where chestnut comprised 6% of the overstory, 3 tulip trees/ha are present. By comparison, 2.5 tulip trees/ha are present in age classes 75–200 yr. If tulip tree mortality rates are similar to those of even-aged oaks and tulip trees on comparable sites (30% mortality from age 40–60, 25% from age 60–80, 15% from age 80–100; McCarthy 1933, Schnur 1937), then 2.5 trees/ha projected backward from age 180 to age 40 would give a predicted maximum density of 10.7 trees/ha. The disturbance level necessary for this level of density would therefore be ≈20% (exogenous) overstory mortality, distributed over a period of 115 yr. Three principal disturbances occurred during this period, which suggests that each would have removed <10% of the overstory. The relatively high numbers of tulip trees in age classes 250 and older may indicate that disturbances between 1550 and 1725 removed >10% of the stand. The presence of large 30–50 yr peaks for sweet birch and red maple in areas affected by the chestnut blight (Fig. 3) supports the viewpoint that relatively light disturbance (i.e., 20% mortality) can cause major deviations from the negative exponential form.

Spatial variations in disturbance intensity

Although the trees killed in most of the disturbances seem to have been distributed over a large area, there is evidence that at least some of the disturbances were spatially variable in their intensity. The location of trees in peak diameter classes on maps revealed a few cases of pronounced clumping. Twelve of the 24 trees in the peak 40–50 cm class of hemlock at Little San-

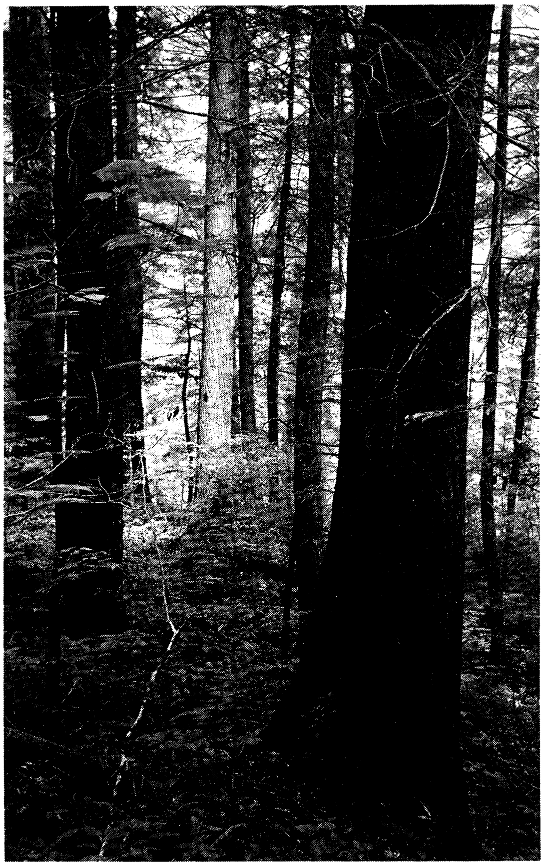

FIG. 8. Hemlock-dominated forest, Area 3 of Poplar Cove (cf. Figs. 1 and 4), heavily influenced by disturbances in 1785 and 1820. Most canopy trees range from 32 to 96 cm in diameter and 125–185 yr in age.

teetlah Creek occurred in four adjacent plots in the eastern part of the study area. Coring of trees in this area revealed that trees of this size were 150–160 yr old with a history of moderate to rapid growth and no suppression, and therefore probably date from the disturbance of 1820. Hemlock trees in the 60–70 cm peak were entirely restricted to this area. Five of the 12 yellow birch trees in the 35–45 cm peak were located in one plot in the northwest part of the study area. Trees in other peaks were fairly well distributed.

Direct age analysis also revealed some spatial clumping of age classes. Area 3 of Poplar Cove has a relatively restricted age distribution, with most overstory trees between 125 and 185 yr old (Figs. 4 and 8). Area 4 in Poplar Cove was heavily influenced by the disturbance of 1920, and subsequently by the chestnut blight. Most of the overstory hemlocks in this area were 55 yr old in 1975, showing rapid growth dating from 1920 and a further increase about 1930 (e.g., Fig. 6, tree 15). In some cases, areas heavily influenced by disturbance may have had complete mortality in patches as was the case for the disturbances of 1953 and 1973–1975. In other cases it was apparently partial mortality within a group. The eastern portion of the Little Santeetlah tract, for example, still has survivors from age classes much older than 1820 (Fig. 4, graph 7).

Causes of disturbance

Relatively little direct evidence is available on the causes of these disturbances. All of the patch disturbances of 1973–1975 were clearly windfalls. Instances of scattered standing dead trees, alone or in groups of two, were also common at this time. Such mortality can be due to a number of causes, including physiological senescence, insects, disease, lightning strikes (Taylor 1973), ice storms (Downs 1938), and drought (Hough 1936, McIntyre and Schnur 1936). Epidemics of insects and disease are rare among species of mixed mesophytic forests (Fowells 1965, Hepting 1971), but minor fluctuations in mortality from these causes may partly account for the past disturbances.

Hurricanes have been known to move inland over North Carolina (Tannehill 1956) but such storms ordinarily lose much of their force due to friction with the land surface and loss of sustaining energy from the warm ocean surface (Battan 1961, Critchfield 1974). Records from the nearest weather station with windspeed data (Asheville, North Carolina) indicate that the two highest windspeeds recorded for the period 1911–1972 were 84 and 97 km/h, generally below the windspeeds of hurricanes and tornadoes. Two periods in which windfalls were known to occur (1951–1953 and 1973–1974) each had maximum observed windspeeds of 64 km/h. This might indicate that patch windfalls can be caused by moderate windspeeds, although localized occurrence of brief, intense winds could easily escape documentation.

Fire is a possible but less likely cause for the disturbances after 1800, because the fires would have had to be intense enough to cause significant overstory mortality, but not intense enough to kill the fire-sensitive saplings of hemlock and beech, many of which clearly survived the disturbances. There is insufficient evidence for disturbances prior to 1800 to assess the possibility of fire in those centuries.

GENERAL DISCUSSION

Irregular diameter or age distributions of the negative exponential type, such as those from the Kilmer Forest, appear to have been common in mixed-species virgin forests of eastern North America. Curves for single species reported in the literature (Hough and Forbes 1943, Leak 1975, Willis and Coffman 1975, Hett and Loucks 1976) and curves for single species plotted from stand table data (Cary 1896, Hosmer 1902, Chittenden 1905, Gates and Nichols 1930, Oosting and Billings 1939-original field notes, Maissurow 1941, Whittaker 1948, Eyre and Zillgitt 1953) reveal that of 48 stands, 56% were of the irregular negative exponential type, 25% were of the smooth negative exponential type, and 19% approached a normal distribution. An additional seven virgin deciduous forest stands in northern Wisconsin were reported to be all aged by Zon and Scholz (1929), making a total of 32 remnant virgin stands known to be uneven aged or all aged by direct analysis. Thus the evidence available to date suggests that the uneven-aged condition was probably common in mesic forest types, especially those dominated by shade-tolerant species. Even at the northern limits of the eastern deciduous forest, where natural catastrophes are fairly common, the recurrence interval for such disturbances appears longer than the time interval needed to develop an uneven-aged structure (Lorimer 1977, Canham 1978). The even-aged condition has been more frequently observed in pine stands than in forests of shade-tolerant species (Cary 1894, Spalding and Fernow 1899, Hough 1932, Hough and Forbes 1943, Henry and Swan 1974), but it is probable that a significant proportion of mesophytic stands did develop following tornadoes or other violent windstorms.

Age structures in oak-chestnut and oak-pine forests are not well known. This study and that of Morey (1936) provide preliminary evidence that indicates the existence of uneven-aged structures in stands in which oak and chestnut were intermixed with more mesic species. Clearly, more work needs to be done in the more xeric types, but due to the geographical distribution of virgin stands, such analyses will be largely limited to montane oak stands in the Great Smoky Mountains National Park and the Kilmer Forest. The oak-chestnut forests, however, had a high frequency of fire disturbance of human origin during the early settler period. Ayres and Ashe (1905), for example, found evidence of frequent light fires on 80% of a 2.3×10^6 ha area examined.

It appears from the results of this study that relatively light disturbances are capable of causing peaks commonly found in irregular diameter distributions. Allowing for the normal 10-yr mortality rate of ≈6% due to such factors as competition and old age, an additional 6–8% premature mortality in a particular decade caused by disturbance appears capable of generating a major peak in the distribution. Such peaks appear to form when many gaps occur in the overstory over a short period of time, leading to higher than normal survival of the understory trees (Hough and Forbes 1943, Eyre and Zillgitt 1953) and new recruitment of seedlings (Trimble 1965). After the gaps close, new recruitment of seedlings would probably drop off for several decades as usually occurs in young even-aged stands. Although exogenous disturbance (including drought) is probably the major cause of irregular patterns of mortality, it is probable that even random fluctuations in mortality unrelated to disturbance could also cause irregular diameter distributions due to their effect on temporal patterns of seedling establishment. Because of the apparent sensitivity of diameter distributions to light disturbance, irregular distributions with major peaks may not necessarily indicate two- or three-aged stands that developed in response to moderately severe disturbances.

Light disturbances do not always appear to produce peaks in the size structure, especially in stands of young trees that have the capacity to fill gaps by crown expansion (Oliver and Stephens 1977). And since diameter distributions of even-aged stands may show some irregularities with several peaks (Hough 1932), it is possible that a partial disturbance can also cause more than one peak. For these reasons, the analysis of radial growth pattern for release from suppression in conjunction with diameter distributions is preferable to analysis of size or age distributions alone.

With respect to wilderness preservation, much concern over possible aesthetic deterioration of the Kilmer Forest and similar areas has been expressed in relation to the possible loss of the famed tulip trees or yellow-poplars, which attain diameters up to 2 m and for which Poplar Cove was originally named. Under the assumption that these stands were even aged and that tulip trees would be succeeded by more tolerant species, silvicultural manipulation was recommended or discussed by some individuals and groups (North Carolina Forestry Council 1971, Miller 1972, Simmons 1972). The fairly stable age distribution and the frequency of disturbance, however, indicate that major change in tulip tree abundance would be unlikely in the next two centuries. The recent windfalls in Fig. 1 have been colonized by many vigorous seedlings of this species. There also has not been much apparent change in the population in recent decades. The percentage of tulip tree in the dominant/codominant crown class was 16% in 1940 as sampled by Braun (1950), compared to 14% in 1973–1974. A moderate decline can be anticipated as a result of the small number of trees in the 90–190 yr age classes, but the young trees from recent disturbances will help counteract this trend.

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