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Author(s): Craig G. Lorimer and Albert G. Krug
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Diameter Distributions in Even-aged Stands of Shade-tolerant and Midtolerant Tree Species

CRAIG G. LORIMER and ALBERT G. KRUG
Department of Forestry, University of Wisconsin, Madison 53706

Abstract: Characteristics of diameter distributions in 28 even-aged northern hardwood (*Acer-Betula-Tsuga*) and upland oak (*Quercus* spp.) stands were investigated to determine if even-aged stands of shade-tolerant and midtolerant (intermediate) species can be consistently identified without direct age determinations. The diameter distributions of midtolerant species consistently approximated a normal distribution. Those of tolerant species were highly variable, ranging from unimodal to steeply descending in form. Distributions of tolerant species that departed strongly from a unimodal form were those of stands having a large admixture of midtolerant species. Confusion with all-aged stands in such cases can be avoided if classification of age structure is based on the diameter distributions of midtolerant species. Even-aged and all-aged stands can generally be distinguished on the basis of diameter distributions, but even-aged stands cannot be consistently distinguished from multi-aged stands in which young trees are sparse or absent. In such cases, a number of direct age determinations would be necessary.

Introduction

Data on age structure of forest stands are often needed in ecological studies, especially for quantifying the role of natural and man-caused disturbances in forested landscapes. The only feasible nondestructive technique for direct interpretation of age structure requires the extraction of cores from trees in sample plots. This procedure is time-consuming and is not feasible when extensive areas must be inventoried. Accuracy in age determination of large trees is limited by the frequent occurrence of heart rot and by the fact that the number of rings above the butt swell does not indicate the total age of the tree. Indirect assessment of age structure has therefore been frequently attempted, of which the most promising method has been the interpretation of diameter frequency distributions.

To give a reasonable indication of age structure, diameter distributions must be plotted separately for individual species from small homogeneous stands (Hough, 1932). Even-aged stands of many species typically have unimodal diameter distributions that may show varying degrees of skewness at a young age but gradually approach a more symmetric normal distribution with time (Baker, 1923; Meyer, 1930; Hough, 1932; Schnur, 1934; Nelson, 1964; Mohler *et al.*, 1978). All-aged stands of shade-tolerant species with only light past disturbance, on the other hand, are well-known to have steeply descending, monotonic diameter distributions that can be approximated by the negative exponential and negative power functions (de Liocourt, 1898; Hough, 1932; Assmann, 1970; Leak, 1973, 1975; Hett and Loucks, 1976; Tubbs, 1977; Lorimer, 1980).

A third type of age structure may occur in stands having several age classes that may or may not be of equal prominence. Diameter distributions in such stands may vary from near normal to irregular negative exponential in form depending upon the dispersion of age classes and the degree of shade tolerance of the species (Hough, 1932; Henry and Swan, 1974; Leak, 1975; Oliver and Stephens, 1977; Harcombe and Marks, 1978; Lorimer, 1980, 1983a). Some stands of this latter type are technically uneven-aged or all-aged but nevertheless developed after heavy destruction of the overstory, and the wide range in age merely reflects the range of ages among smaller trees present prior to the disturbance (Henry and Swan, 1974; Lorimer, 1983a). In other cases, the restricted or unbalanced age distribution may be due to other external factors such as deer browsing, occurrence of surface fires, or climatic fluctuations (Hough and Forbes, 1943; Anderson and Loucks, 1979).

On the basis of previous studies, it therefore seems possible that at least two of these age-structure types (even-aged and all-aged) might be readily distinguished by the form of the diameter distribution. However, this principle needs additional testing because it rests largely upon a comparison of even-aged stands of species with fairly low shade tolerance (*e.g.*, *Pinus* spp., *Populus tremuloides, Pseudotsuga menziesii*) with all-aged stands of very tolerant species (*e.g., Acer saccharum, Tsuga canadensis, Fagus grandifolia*). Little detailed work has been done in diameter distributions in even-aged stands of shade-tolerant or midtolerant species, especially in the eastern deciduous forest region. In presettlement times, stands of tolerant species originating after catastrophic disturbances must have been common (Stearns, 1949; Henry and Swan, 1974; Canham, 1978), and in northern Wisconsin and Michigan there are currently extensive even-aged stands of sugar maple (*Acer saccharum*) that developed following commercial clear-cutting around the turn of the century (Buttrick, 1923; Westveld, 1933).

There are some considerations which suggest that the usual principles governing the form of diameter distributions for species intolerant of shade may not necessarily apply to tolerant species. The near symmetry of diameter distributions of intolerant species is presumably due to high mortality of trees that become suppressed during the self-thinning process, thereby preventing an accumulation of trees in small diameter classes. The ability of shade-tolerant trees to withstand suppression for long periods could conceivably result in so many living suppressed trees that a normal diameter distribution, if it ever existed at all, would soon be obscured. As time progressed, the development of suppressed trees of younger age classes beneath the main canopy might further enhance the difficulty of distinguishing even-aged from uneven-aged stands by the form of the diameter distribution. This study was undertaken to examine diameter distributions of tolerant and midtolerant species from stands known to have had heavy past disturbance in order to investigate underlying principles of curve form that could be useful in recognizing such stands without extensive age data.

STUDY AREAS

A number of stands were located in the northern hardwood region of Wisconsin and the upland oak region of Massachusetts and New York. In the northern hardwood stands, sugar maple (*Acer saccharum*) and hemlock (*Tsuga canadensis*) are rated as very tolerant, red maple (*A. rubrum*) as tolerant, and American elm (*Ulmus americana*) and yellow birch (*Betula alleghaniensis*) as intermediate (Baker, 1949). The oak stands are dominated by the midtolerant red oak (*Quercus rubra*) and chestnut oak (*Q. prinus*), mixed with red maple and occasionally sugar maple.

Four major criteria were used in selecting study areas:

(1) The stands must have originated after heavy or complete overstory removal, and thus have a narrow range of ages. The dates of clear-cutting of stands 1, 8, 9, 10 and 11 are known from experimental forest records (Table 1). Stands 2, 3, 4 and 5 also developed after commercial clear-cutting, and their even-aged character was verified by Carmean (1979) from stem cross sections. None of the latter four stands had overstory trees younger than 35 years or older than 85 years, and the average range of ages within a single stand was 29 years. Stands 6 and 7 are older stands with a broader range of ages, but both stands have one predominant age class and numerous releases from suppression corresponding to the decades 1870 and 1890, respectively, indicating that heavy disturbance of the overstory took place at those times (Lorimer, 1983a).

(2) Sites with permanent plots were used whenever possible so that trends over time could be studied. Stands 7, 8, 9, 10 and 11 have long-term permanent plots. All of the remaining stands have newly established permanent plots.

(3) Selected stands generally had not experienced any cutting or grazing in the previous 40 years. An exception is the permanent plots of stand 7, an old-growth stand

TABLE 1.—Study area characteristics

Stand no.	Location (Co., State)	Overstory species comp.[1]	Stand age (years)	Topography[2] (% slope, pos., aspect)	Soil drainage class[3]	Soil texture	Site index[4]	No. trees in sample	Source of age data
1	Forest, NE Wisc.	70% SM, 19% AE, 8% BAS	51	1% R, S	W	Silt loam	70 (SM)	396 (SM) 64 (AE)	Histor. records (Stoeckeler and Arbogast, 1947)
2	Sawyer, NW Wisc.	71% SM, 15% WA, 12% BAS	42	3% US, N	MW	Silt loam	70 (SM)	79 (SM)	18 stem XS (Carmean, 1979)
3	Vilas, NE Wisc.	39% AE, 26% SM, 16% BA	45	0% SWL	SP	San. loam	64 (SM)	166 (SM) 64 (AE)	18 stem XS (Carmean, 1979)
4	Sawyer, NE Wisc.	35% SM, 32% YB, 26% RM	80	0% R	MW	Loam	48 (SM)	63 (SM) 21 (RM)	19 stem XS (Carmean, 1979)
5	Vilas, NE Wisc.	80% SM, 13% BAS	45/85[5]	3% US, ENE	W	Silt loam	68 (SM)	301 (SM)	15 stem XS (Carmean, 1979)
6	Oneida, NE Wisc.	62% HEM, 18% SM, 16% YB	150[6]	3-15%, MS, NNW	W	Lo. sand	55 (HEM)	203 (HEM) 33 (YB)	17 inc. borings and stumps
7	Vernon, SW Wisc.	40% SM, 28% RO, 8% BAS	190[6]	5% R, NE	W	Silt loam	65 (RO)	334 (SM)	38 stem XS (Lorimer, 1983a)
8	Worcester, C Mass.	40% RO,30% PB, 12% RM	56	10% R, NW	E	San. loam	65 (RO)	238 (RO) 183 (RM)	Histor. records Harvard For. (Lutz and Cline, 1947)
9	Worcester, C Mass.	50% RO, 31% RM 11% YB	80	10% MS, SSW	MW, W, E	San. loam	65 (RO)	114 (RO) 205 (RM)	Histor. records Harvard For.
10	Orange, SE N.Y.	33% CO, 22% SM, 15% YB, 12% RO	85	15% LS, ENE	W	Clay loam	55 (RO)	33 (CO) 66 (SM)	Histor. records Black Rk. For., and 5 inc. cores
11	Orange, SE N.Y.	54% CO, 44% RO	65	15% MS, E	E	Clay loam	55 (RO)	131 (RO)	Histor. records Black Rk. For., and 5 inc. cores

[1]Abbreviations: AE = Amer. elm, BA = black ash, BAS = basswood, CO = chestnut oak, HEM = hemlock, PB = paper birch, RM = red maple, RO = red oak, SM = sugar maple, WA = white ash, YB = yellow birch

[2]Abbreviations: R = ridge top, US = upper slope, MS = midslope, LS = lower slope, SWL = swale

[3]Abbreviations: SP = somewhat poorly drained, MW = mod. well, W = well, E = excessively drained

[4]In feet at age 50 for species indicated

[5]Two-aged overstory

[6]Predominant age of overstory trees

that has received periodic selection cuts. Many of the stands (1-6 inclusive) have never been thinned and the others had only one thinning at an early age.

(4) Stands were located on gently rolling upland sites of average quality, typical of both regions. Steep slopes and extremely dry or wet sites were not sampled. Principal physical characteristics of the study areas are shown in Table 1.

METHODS

Permanent plots in the oak region are fairly large contiguous tracts of 0.10-0.58 ha in size, on which a full census of species and diameters at breast height was taken in each measurement period (stands 8, 9, 10, 11). Two of the stands in the northern hardwood region are newly established permanent plots of 0.40 and 0.61 ha (stands 1 and 6). These were supplemented by the data of Guldin (1982), a set of 21 circular 810 m^2 random plots in 21 northern hardwood stands identified as even-aged by Carmean (1979). Additional plots were measured in four representative stands in the latter group in order to increase the sample size and allow closer inspection of diameter distributions (stands 2, 3, 4, 5). The permanent plots from an old-growth maple stand in SW Wisconsin (stand 7) consist of 39 systematically spaced 810 m^2 circular plots. The number of sample trees in the diameter distribution of each major species is shown in Table 1. On all plots, crown class of each tree was recorded according to standard forestry definitions (Smith, 1962). Dominant, codominant and intermediate trees all receive some direct light from above and comprise the canopy layer. The lower threshold measurement of diameter in each stand is indicated in Figures 1 and 2.

Smooth curves were fit to the diameter distributions using the 2-parameter Weibull probability density function (Bailey and Dell, 1973):

$$f(x) = c/b\ (x/b)^{c-1} \exp\{-(x/b)^c\}.$$

The number of trees F(x) in diameter class x with class limits x − 1.0 cm and x + 1.0 cm is given by:

$$F(x) = N_{x-1}\int^{x+1} f(x),$$

where N = the total number of trees in all size classes. Parameter estimates b and c were obtained by the method of maximum likelihood and confidence limits for parameters derived from asymptotic variance estimates (Cohen, 1965). Estimates of parameters and variances for diameter distributions measured above a nonzero diameter threshold are direct analogues to those of diameter distributions starting at zero. The Weibull distribution is particularly appropriate for diameter distributions because it can assume a wide variety of shapes, which is regulated by the shape parameter c. At values of $c < 1$, the function is a steeply descending monotonic curve; at $c = 1$ it is the negative exponential distribution. The value of $c = 1$ is a kind of "boundary condition"; for all values of $c > 1.0$ the curve is unimodal, being positively skewed from $1.0 < c < 3.5$, approximately normal at $c = 3.5$, and negatively skewed at $c > 3.5$ (Bailey and Dell, 1973).

An additional descriptive curve type was recognized, which cannot be characterized by the Weibull or simple probability distributions, consisting of a steeply descending monotone in the understory diameter classes and a broad peak in the overstory classes. This "compound distribution" has characteristics of both descending monotonic and unimodal curves, and is typified by the diameter distributions of sugar maple in stands 4 and 7 (Fig. 1). When the first few understory diameter classes are omitted from compound distributions, the Weibull shape parameter is generally > 1.0 and these curves can be grouped with the unimodal type.

For comparative purposes, the Weibull distribution was also fit to a large number of single-species diameter distributions from even-aged and all-aged stands, reported in

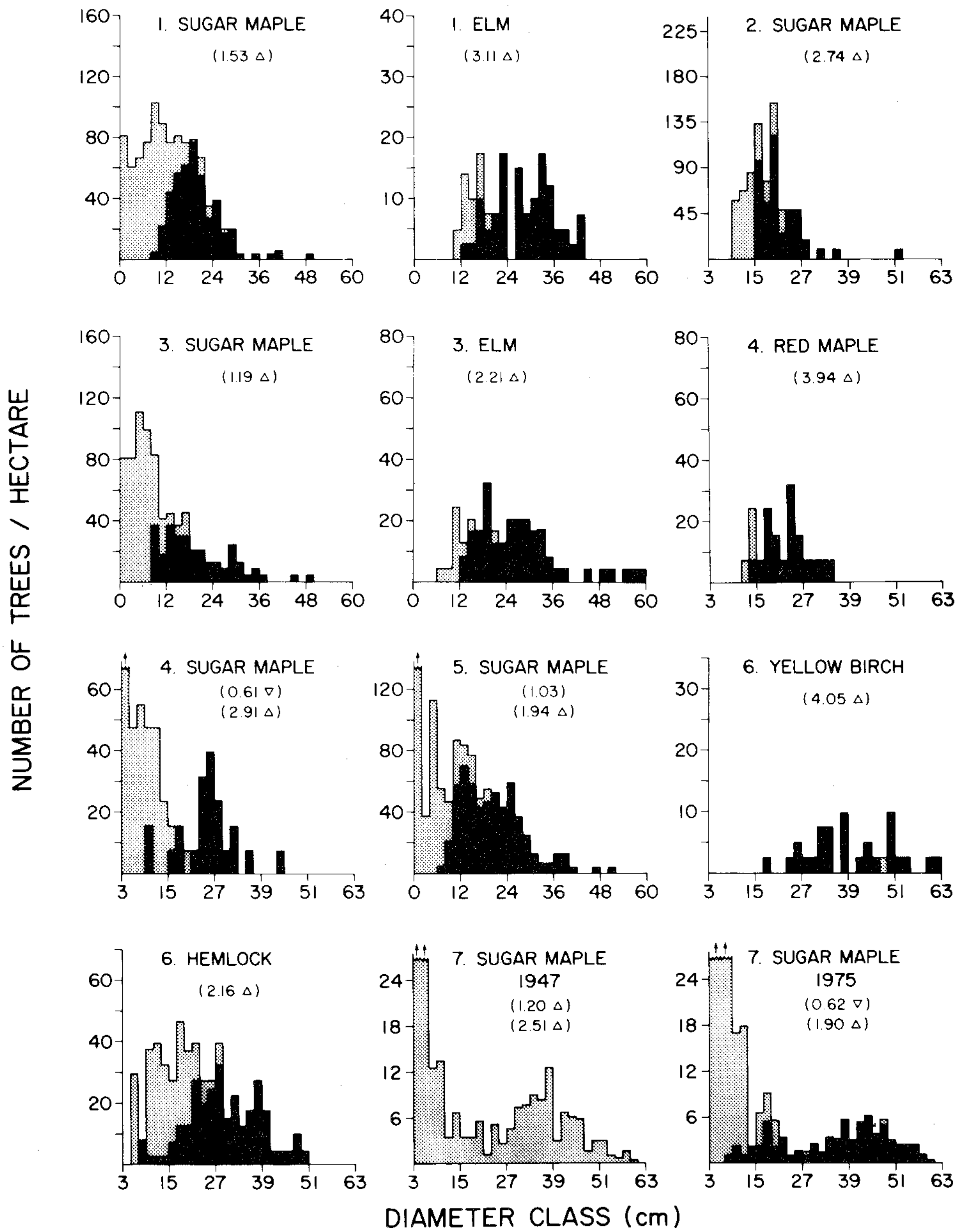

Fig. 1.—Diameter distributions for major species in seven northern hardwood stands in Wisconsin, plotted by 2-cm diam classes. Contribution by overstory trees (dominant, codominant, intermediate crown classes) is indicated by dark bars. Crown classifications not available for stand 7 in 1947. Stand numbers correspond to those shown in Table 1. Numbers in parentheses are values of the Weibull shape parameter c. Two numbers are shown for compound distributions, the lower number being the shape parameter when the first several understory diameter classes are omitted. Upward-pointing triangles indicate the parameters significantly > 1.0 at the .05 level; downward pointing triangles indicate parameters significantly < 1.0 at the .05 level

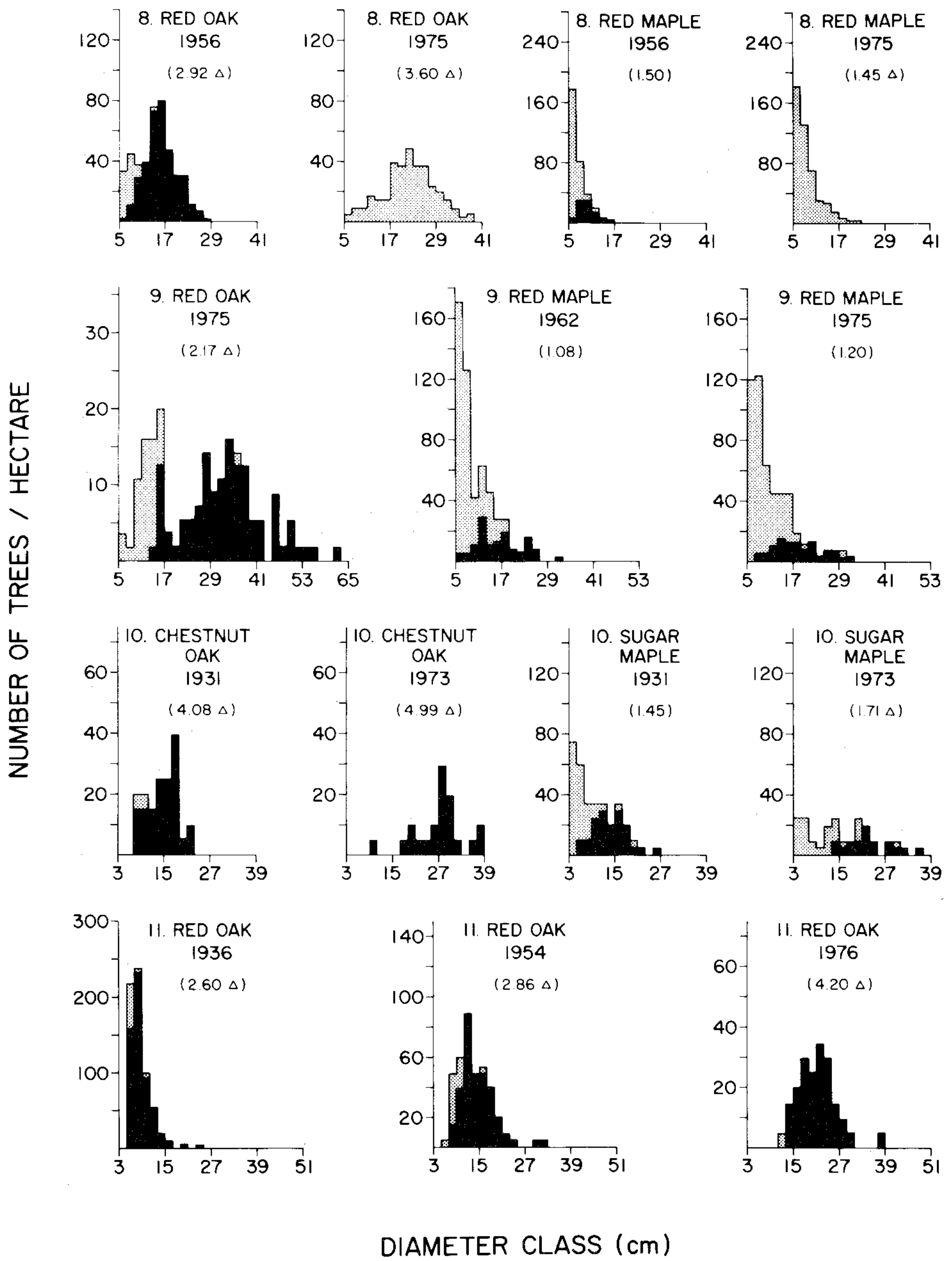

Fig. 2.—Diameter distributions for major species in four upland oak sites in Massachusetts and New York. Contribution by overstory trees is indicated by dark bars. Crown classifications not available for stand 8 in 1975. Stand numbers correspond to those shown in Table 1. Numbers in parentheses are values of the Weibull shape parameters explained in Figure 1

the literature, for which ages had been carefully documented from increment cores or stumps (Hough, 1932; Goff, 1967; Leak, 1975; Hett and Loucks, 1976; Oliver and Stephens, 1977; Lorimer, 1980).

Although the Weibull shape parameter reflects the degree of skewness in the distributions, it is not highly sensitive to the horizontal displacement of the mode from the median, which is a desirable analytical feature for some analyses. The coefficient of skewness (Snedecor and Cochran, 1967) has the same limitations. A more sensitive indicator of this property was devised (called the symmetry index) that is a ratio between the mode and the 95th percentile of the observed distribution:

$$I_S = (M - X_L)/(X_{.95} - X_L)$$

where I_S = symmetry index; M = mode of the distribution; X_L = lower threshold diameter; $X_{.95}$ = 95th percentile of the distribution.

This index measures the degree of symmetry in relation to the mode and consistently distinguishes between descending monotonic, skewed unimodal and symmetric unimodal curves. Negative exponential distributions have values close to 0, normal distributions have values close to 0.5, and positively skewed unimodal curves have values intermediate between the two. Negatively skewed distributions have values >0.5, with a theoretical maximum of 1.0.

RESULTS AND DISCUSSION

Curve types in even-aged stands. — Diameter distributions for the principal species (Figs. 1 and 2) indicate that a variety of curve types are present in both regions. For ease of discussion, these curves have been classified into several descriptive types in Table 2 based on the value of the Weibull shape parameter as described under Methods. Table 2 also includes Weibull parameters from species of lower importance value not included in Figures 1 and 2, as well as Weibull parameters for diameter distributions of other even-aged stands reported in the literature.

Shade-tolerant species have the greatest variety of curve forms and frequently deviate from a symmetric, unimodal form. The lack of symmetry among tolerant species is due to the large number of suppressed trees (Figs. 1 and 2). By contrast, the midtolerant species in nearly all cases have unimodal distributions with few suppressed trees. Although midtolerant species partly avoid suppression by rapid growth, considerable reduction in density by self-thinning occurs (Fig. 2, stands 8, 10, 11), and high mortality rates of suppressed trees contribute to the relatively low numbers of suppressed trees. High mortality rates of suppressed red oak, chestnut oak and white ash, averaging over 40% per 10-year period, have been demonstrated in stands 8, 9, 10 and 11 (Lorimer, 1981, 1983b). The nearly symmetric unimodal diameter distributions of canopy trees is a notable feature of all tolerant and midtolerant species.

The wide variety of curve types among tolerant species presents the greatest problem in distinguishing even-aged from all-aged stands. In some cases, tolerant species have distinct unimodal distributions with Weibull shape parameters significantly >1.0 at the .05 level (sugar maple in stands 1, 2, 6; basswood in stand 5; hemlock in stand 6; Fig. 1 and Table 2) and in other cases, the curves are compound distributions (sugar maple in stands 4, 5, 7). These two types of distributions show such a large deviation from the descending monotonic form that confusion with balanced, all-aged stands is not likely (*cf.* Table 3). But in several cases the curves of tolerant species are at least superficially similar in appearance to descending monotonic curves (sugar maple in stands 3 and 10; red maple in stands 8 and 9).

The descending monotonic curves in even-aged stands, however, can often be distinguished from those of all-aged stands by the Weibull shape parameter. The curves of tolerant species in stands 3, 8, 9 and 10 are all actually classified as positively

TABLE 2.—Weibull shape parameters for additional even-aged stands

Stand no.	Species	Shape parameter c	Age	Descriptive classification	Source of data	Location
Species not shown in Figures 1 and 2:						
5	Basswood	4.28*	45/85	Unimodal	Present study	Wisc.
6	Sugar maple	1.81*	150	Unimodal	Present study	Wisc.
8	Sweet birch (1956)	1.87*	37	Unimodal	Present study	Mass.
	Sweet birch (1975)	1.70*	56	Unimodal	Present study	Mass.
11	Chestnut oak (1936)	3.43*	25	Unimodal	Present study	N.Y.
	Chestnut oak (1976)	3.44*	65	Unimodal	Present study	N.Y.
Stands reported in literature:						
12-27	Sugar maple	mean 2.50 range 1.01-4.00[a]	48-93	Unimodal (16 stands)	Guldin (1982)	Wisc.
28	Sugar maple	0.79	57	Descending Monotonic (1 stand)	Guldin (1982)	Wisc.
29	Hemlock	2.52*[b]	350	Compound	Goff (1967)[d]	Wisc.
30	Hemlock	2.58*	—[c]	Unimodal	Goff (1967)	Wisc.
	Sugar maple	1.65[b]	—[c]	Compound	Goff (1967)	Wisc.
31	White pine	3.18*	135	Unimodal	Goff (1967)	Wisc.
	Hemlock	1.58*	135	Unimodal	Goff (1967)	Wisc.
	Sugar maple	1.68*	135	Unimodal	Goff (1967)	Wisc.
32	Red oak	2.12*	135	Unimodal	Goff (1967)	Wisc.
	Red maple	2.61*	135	Unimodal	Goff (1967)	Wisc.
33	Basswood	3.48*	135	Unimodal	Goff (1967)	Wisc.
	Sugar maple	0.92	135	Descending Monotonic	Goff (1967)	Wisc.
34	White pine	2.53*	25	Unimodal	Hough (1932)[e]	Penn.
35-38	White pine	3.03-4.00*[f]	65-70	Unimodal (4 stands)	Hough (1932)	Penn.
39-41	White pine	2.25-3.90*[f]	245	Unimodal (3 stands)	Hough (1932)	Penn.

* Significantly >1.0 at P<.05
[a] Significantly >1.0 at P<.05 for 14 curves
[b] First two understory diameter classes omitted for fits to compound distributions
[c] Stand age not known; heavy cutting for large trees 30 years before measurement
[d] Stands 4, 11, 10, 24, and 19, respectively, as numbered by Goff (1967)
[e] Stands 9, 13, A, 12, 16, Hearts Content, Cook Forest and "near Hearts Content," as designated by Hough (1932)
[f] Significantly >1.0 at P<.05 for all curves

skewed unimodal curves by the value of the shape parameter, although in some cases the parameter is not significantly > 1.0 at the .05 level (Figs. 1 and 2). The reason for this classification is that these curves do not display the sharp drop in the first few classes expected in negative exponential or descending monotonic curves (Table 3; *see also* Bailey and Dell, 1973). If a distinct peak in the curve is not evident, it may be only because the peak is currently to the left of the lower threshold diameter class or because the stand is not old enough for such a peak to be evident. A lower threshold diam of 5.0 cm for sugar maple in stand 3, for example, would mask the peak in that distribution, causing it to look more like a descending monotonic curve. For this reason it is recommended that all saplings taller than breast height be included as part of the smallest diameter class (*e.g.*, a 0-2 cm class), rather than a 2.5- or 5.0-cm threshold as is the usual practice.

Effect of stand age. — Three of the instances of tolerant species with steeply descending diameter distributions occur on permanent plots, and changes in curve form over time indicate a trend away from the descending monotonic form as the stands mature. The Weibull shape parameters for the maples in stands 9 and 10 showed a substantial increase between the two measurement periods (Fig. 2), and in stand 10, the steeply descending form of the sugar maple distribution had largely been lost by the time the stand was 85 years old in 1973 (Fig. 2). Red maple in stand 8 showed little change in the shape parameter between 1956 and 1975, but the curve nevertheless showed a more gradual drop in the first few classes, and in the latter period the classification of the curve as unimodal became statistically significant. Goff (1967) published the diameter distribution of a 135-year-old red oak stand in which red maple has a distinctly unimodal diameter distribution, with a Weibull shape parameter of 2.61 (stand 32, Table 2). A similar trend away from descending monotonic distributions as stands reach middle age has been noted by Christensen (1977) and Mohler *et al.* (1978). The probable reason for this trend is high mortality of small trees due to intense competition, and the resistance of stands of this age to new understory recruitment (Harcombe and Marks, 1978; Oliver, 1981). The only even-aged stand older than 85 years with a descending monotonic diameter distribution encountered in this study is that of sugar maple in a 135-year-old stand reported by Goff (1967) with a Weibull shape parameter of 0.92 (stand 33, Table 2).

Recruitment of understory stems accelerates as stands reach the old-growth stage, however, and it is probable that a diameter distribution of the compound type eventually undergoes a transition to the descending monotonic type as understory stems increase in size and the age distribution broadens. Correct diagnosis of age structure or disturbance history therefore requires information on the rate of this process. The available data suggest that this transition is very slow. The "gap" and "bulge" characteristic of the unimodal and compound distributions are still obvious in stands 6 and 7 (Fig. 1) which are 150 and 190 years old, respectively. The unimodal and compound forms are also evident in the 240-year-old stands of the midtolerant white pine reported by Hough (1932) and in nearly all of the 135- and 350-year-old stands of tolerant and midtolerant species reported by Goff (1967) (Table 2). Data on the rate of gap closure in the compound distribution are also available from a comparison of the sugar maple diameter distribution in stand 7 between 1947 and 1975. The gap was ca. nine classes wide in 1947 and six classes wide in 1975. The observed rate of gap closure is probably higher than normal because of selective cutting of 27% of the trees ≥ 25 cm dbh, which has reduced the height of the "bulge" and increased the growth rate of formerly suppressed trees. Nevertheless, the gap is still wide enough that the result of heavy past disturbance is readily apparent at stand age 190. Calculation of diameter transition probabilities for individual trees in this stand (Table 4) shows that of the 11-23 cm trees in the gap, 33% moved two or more 4-cm classes during the 28-year period, compared to 48% of the 27-39 cm trees in the lower half of the peak. This suggests that higher growth rates of overstory trees help maintain the presence of a gap in the curve.

TABLE 3.—Weibull shape parameters for all-aged and multi-aged stands

Stand no.	Species	Shape parameter c	Descriptive classification	Source of data	Location
Species with all-aged populations:					
42	Hemlock	0.63*	Descending monotonic	Hett and Loucks (1976)	Ont.
43	Hemlock	0.60*	Descending monotonic	Hett and Loucks (1976)	Ont.
44	Hemlock	1.10	Compound	Hett and Loucks (1976)	Wisc.
45	Hemlock	1.28	Compound	Hett and Loucks (1976)	Wisc.
46	Red spruce	0.23*	Descending monotonic	Leak (1975)	N.H.
	Balsam fir	0.87*	Descending monotonic	Leak (1975)	N.H.
47	Sugar maple	0.20*	Descending monotonic	Leak (1975)	N.H.
	Beech	0.38*	Descending monotonic	Leak (1975)	N.H.
48	Hemlock	0.72*	Descending monotonic	Lorimer (1980)	N.C.
49	Hemlock	0.68*	Descending monotonic	Lorimer (1980)	N.C.
	Beech	0.34*	Descending monotonic	Lorimer (1980)	N.C.
50	Sugar maple	0.74*	Descending monotonic	Lorimer (unpubl.	Mich.
	Hemlock	0.98	Descending monotonic	Lorimer (unpubl.)	Mich.
51	Sugar maple	0.61*	Descending monotonic	Lorimer (unpubl.)	Mich.
52	Sugar maple	0.82*	Descending monotonic	Lorimer (unpubl.)	Mich.
Species with multi-aged populations:					
41	Hemlock	1.85[a]	Unimodal[b]	Hough (1932)	Penn.
47	Yellow birch	2.27[a]	Compound	Leak (1975)	N.H.
48	Yellow birch	0.64*	Descending monotonic	Lorimer (1980)	N.C.
49	Red maple	1.05	Unimodal	Lorimer (1980)	N.C.
	Sweet birch	1.29	Unimodal	Lorimer (1980)	N.C.
	Chestnut	3.29[a]	Unimodal	Lorimer (1980)	N.C.
53	Red oak	1.76[a]	Unimodal	Oliver & Stephens (1977)	Mass.
	Red maple	1.79[a]	Unimodal	Oliver & Stephens (1977)	Mass.
	Hemlock	1.10	Unimodal	Oliver & Stephens (1977)	Mass.

* Significantly <1.0 at $P<.05$
[a] Significantly >1.0 at $P<.05$
[b] Many age classes present but heavy disturbance in stand 245 years before measurement (forest near Hearts Content)

TABLE 4.—28-year diameter transition probabilities for sugar maple in stand 7, southwest Wisconsin

Diameter class midpoint (cm)	Initial no. 1947	Died	Cut	No Change	1 Class	2 Classes	3 Classes	4 Classes	5 Classes	Final no. 1975
5	49	.20	.00	.14	.41	.16	.06	.02	.00	52
9	23	.22	.13	.09	.22	.26	.09	.00	.00	43
13	9	.11	.00	.00	.44	.22	.22	.00	.00	18
17	6	.33	.00	.00	.33	.17	.17	.00	.00	14
21	6	.50	.00	.17	.17	.17	.00	.00	.00	8
25	16	.25	.19	.06	.12	.12	.06	.19	.00	8
29	38	.24	.05	.00	.21	.32	.08	.10	.00	12
33	52	.12	.14	.06	.23	.15	.21	.08	.02	15
37	66	.09	.23	.04	.15	.21	.20	.04	.03	28
41	30	.17	.27	.03	.10	.20	.23	.03	.00	26
45	37	.13	.47	.00	.04	.07	.11	.00	.00	32
49	14	.14	.64	.00	.00	.14	.07	.00	.00	25
53	12	.25	.50	.17	.00	.00	.08	.00	.00	14
59	7	.29	.43	.00	.00	.29	.00	.00	.00	10
61	1	.00	1.00	.00	.00	.00	.00	.00	.00	1

Factors influencing curve variability. — Why do sugar maple and other tolerant species have unimodal distributions in some even-aged stands and descending monotonic or compound distributions in other stands of similar ages on similar sites? Comparison of stand attributes suggests that species composition may be an important factor. Stands 1 and 2, with unimodal sugar maple distributions, both have maple as the principal overstory species, comprising 70 and 71% of the overstory trees, respectively. The tolerant species with diameter distributions that deviate strongly from the unimodal form (stands 3, 4, 8, 9, 10) occur in mixture with midtolerant species such as American elm, American basswood (*Tilia americana*), yellow birch, red oak and chestnut oak. Maples in these stands comprise only 12-35% of the overstory stems. Further analysis was conducted by calculating the symmetry index for the five northern Wisconsin sugar maple diameter distributions in Figure 1 as well as for the 17 other sugar maple stands measured by Guldin (1982). Nearly all of the stands with <55% overstory sugar maple (generally <170 sugar maple overstory trees/ha at this age) have highly skewed or descending monotonic curves, with an average symmetry index of 0.17. Stands with >55% overstory sugar maple (generally >200 sugar maple overstory trees/ha at this age) have near-normal distributions with an average symmetry index of 0.42. A t-test indicated that these means are significantly different at the .02 level. The 135-year-old even-aged maple stand with the descending monotonic curve measured by Goff (1967) is also a stand with a large component of overstory basswood (stand 33, Table 2).

The effect of midtolerant species on the diameter distributions of tolerant species may be related to differences in growth rate. Oliver (1978) has shown that red maple in even-aged oak stands becomes overtopped by the faster-growing oaks at an early stage and remains in mature forests as part of the subcanopy layer. Tolerant species in the northern hardwood region likewise appear to be at a competitive disadvantage with midtolerant species on some sites (Guldin, 1982), which may cause a greater proportion of the maples to become suppressed. Species of lower shade tolerance also appear to have less dense canopies (Graham, 1954; Horn, 1971; Spurr and Barnes, 1973), which may permit more of the suppressed maples to survive in stands with a high proportion of midtolerant overstory trees. Both factors would contribute to the asymmetry of the diameter distributions.

Symmetry of the sugar maple diameter distributions is not significantly correlated with current total overstory density or site index. However, Guldin (1982) found that the relative growth performance of tolerant and midtolerant species is influenced by soil drainage and fertility and thus is probably habitat-dependent. Other factors that could not be measured, such as initial density of regeneration and the degree of segregation or intermingling of species after clear-cutting, are possible factors in influencing curve variability.

Comparisons with all-aged and multi-aged stands. — Fits of the Weibull distribution to all-aged stands reported in the literature confirmed that the shape parameter c is <1.0 in most cases (Table 3) and therefore distinct from the shape parameters of even-aged stands. Two of the stands had compound distributions; a history of significant partial disturbance may be a causal factor in these exceptional cases.

Species with multi-aged populations have variable diameter distributions with a wide range of Weibull shape parameter values, depending on the shade tolerance of the species, the number of age classes present, and whether young ages are represented. Midtolerant species seldom have shape parameters <1.0, probably because recruitment of young trees is episodic and small trees have high mortality rates except in disturbance-created gaps. If younger age classes are well-represented, however, the diameter distributions of midtolerant species in multi-aged stands deviate strongly from the symmetric, unimodal form of even-aged stands (Table 3). Unimodal distributions appear to be prevalent among tolerant species in multi-aged stands (Table 3), but compound distributions would be expected in stands with a developing understory (*e.g.*, stand 7).

CONCLUSIONS

Even-aged stands of tolerant or midtolerant species and other stands with heavy past disturbance can probably be distinguished in most cases from all-aged stands with only light past disturbance if certain principles of interpretation are followed. When the overstory of an even-aged stand is heavily dominated by shade-tolerant species, diameter distributions for individual species are generally unimodal in young stands and compound in old-growth stands. Both curve types are easily distinguished from the steeply descending curves of all-aged stands. When the overstory contains a large proportion of midtolerant species, however, the diameter distributions of tolerant species may be similar in form to those of all-aged stands, especially in young stands. In such cases classification of age structure should be based largely on the diameter distributions of the midtolerant species that dominate the overstory. Midtolerant species have near-normal diameter distributions in all even-aged stands investigated for this study. In all-aged stands, midtolerant species have distributions that deviate strongly from the symmetric, unimodal form.

While it therefore seems possible to distinguish even-aged and all-aged stands of tolerant and midtolerant species on the basis of diameter distributions, even-aged stands may be difficult or impossible to distinguish from multi-aged stands in which younger trees are sparse or absent. Unimodal and compound distributions may represent either even-aged or multi-aged forests and cannot always be correctly interpreted without actual age data (Tables 2, 3). In ambiguous cases, collection of a few increment cores would be all that is necessary to reveal whether the range of ages is broad or narrow. Interpretation of diameter distributions can therefore reduce but not eliminate the need for increment boring in classification of age structure. In cases where it is important to determine the disturbance history of multi-aged stands in detail, there is probably no alternative to intensive analysis of tree ages and radial increment patterns.

A striking feature of the stands investigated for this study is the near-normal diameter distributions of all species when only overstory trees are included, even when the total distribution is highly skewed or descending monotonic in form. In all-aged stands the frequent occurrence of gaps should result in many small nonsuppressed trees as in stand 7. Further investigations of the vertical canopy structure of all-aged stands may be worthwhile to see if diameter distributions of overstory trees only are better diagnostic features of age structure than total distributions.

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