POPULATION DYNAMICS IN LOBLOLLY PINE STANDS: CHANGES IN SKEWNESS AND SIZE INEQUALITY¹

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Abstract. We determined the changes in size inequality and asymmetry that occurred over a 50-yr period in 16 even-aged, naturally seeded populations of *Pinus taeda*. Initial densities ranged from 618 to 28 861 stems/ha. We used these data to test four predicted trends in size structure. We found that (1) in young stands size inequality was greater at higher plant densities, (2) skewness of tree volumes was significantly greater at higher initial densities, whereas skewness of diameters was not, (3) size inequality increased significantly prior to the onset of self-thinning, then decreased during self-thinning, and (4) skewness did not increase before self-thinning or significantly decrease during self-thinning.

Numerous measures of size distribution have been employed to assess competition in plant populations, including various measures of inequality and skewness, as well as parameters of fitted distributions such as the Weibull distribution. We found the two-parameter Weibull distribution only moderately effective at capturing the forms of the distributions observed. Correlations showed very close linear relationships among the Gini coefficient, the coefficient of variation, and the shape parameter of the Weibull distribution—both within and across different measures of tree size. All three statistics were correlated with initial density. Skewness coefficients for distributions of diameter, height, and volume were not closely correlated with each other or with other population characteristics. We recommend measures of inequality as more suitable for summarizing biologically important properties of tree populations than measures of skewness or skewness-sensitive parameters of probability distributions.

Key words: density; Gini coefficient; intraspecific competition; *Pinus taeda*; plant competition; self-thinning; size distribution; size inequality; skewness; stand development; Weibull distribution.

INTRODUCTION

In their analysis of a now classic series of competition experiments, Koyama and Kira (1956) proposed using the distribution of sizes within a population as a statistical bridge between individual- and population-level results. Subsequently, numerous statistics have been used to summarize aspects of plant size distributions (Bailey 1980, Benjamin and Hardwick 1986). Probability distributions that have been fit to observed tree size distributions have taken a prominent place in forest modeling (e.g., Fries 1974), but have rarely been related to ideas about competition from plant population biology. Common to many studies of size structure is the idea that, other things being equal, information contained in a set of size measurements for a population of plants can be used to make inferences about past or present competitive environments within

that population (cf., Benjamin and Hardwick 1986, Weiner 1988, for other factors than competition). However, no consensus has emerged as to which statistics most reliably show effects of competition, or even what trends in the shape of size distributions appear consistently in even-aged, monospecific populations of plants.

We used data from naturally seeded tree populations to test four hypotheses about trends in size structure, derived largely from experiments with herbaceous species. We then examined the similarities and differences among alternative approaches to summarizing size distributions.

Hypotheses

In the literature on size structure in plant populations, trends in size inequality and size distribution asymmetry have each been associated with differences in degree of competition, and with changes during stand development. While it is possible that both features change predictably, Weiner and Solbrig (1984) have argued that inequality more directly reflects competi-

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TABLE 1. Characteristics of censuses from *Pinus taeda* permanent sample plots in the North Carolina piedmont, for censuses used in analysis of the dynamics of size structure.

Plot name	Area (ha)	First census*		Final census†		Number of censuses
		Age (yr)	No. stems	Age (yr)	No. stems	
Density series—control plots						
PSP12	.040	8	25	58	19	11
PSP14	.040	8	51	58	18	10
PSP15	.040	8	79	58	22	10
PSP17	.040	8	146	58	23	10
PSP19	.040	8	222	58	21	10
PSP21	.040	8	427	58	31	10
PSP23	.040	8	1168	51	38	9
Density series—treatment plots						
PSP13	.040	8	50	20	50	4
PSP16	.040	8	81	20	78	4
PSP18	.040	8	180	20	139	4
PSP20	.040	8	261	20	195	4
PSP22	.040	8	506	20	235	4
Other control plots						
PSP26	.101	19	212	70	34	10
PSP28	.081	15	446	46	80	8
PSP40	.081	15	433	64	36	8
PSP50	.101	25	118	73	26	9
Total censuses						125

* First complete census on the plot. This census was not used in the analysis of the density series plots; instead, analysis began with a census made at age 10 yr.

† The most recent census before artificial thinning, timber salvage, or the present work.

tive interactions. Consequently, we developed parallel pairs of hypotheses for size inequality and asymmetry.

Hypothesis 1a.—Given sufficient density for competition to occur, comparable periods of growth, and little mortality, inequality of plant size is greater at higher densities. This would be a consequence of preemption of resources by larger plants as predicted by Weiner's asymmetric model of plant competition (Weiner 1985, Weiner and Thomas 1986). The asymmetric model was supported by 14 of the 16 studies reviewed by Weiner and Thomas (1986), but it has not previously been tested in trees for natural populations of known age and history.

Hypothesis 1b.—After a fixed period of growth, skewness of plant size is greater at higher densities. This is Koyama and Kira's (1956) generalization about competitive interactions promoting the appearance of an L-shaped weight–frequency distribution, restated as an assertion about skewness.

Hypothesis 2a.—Biomass inequality increases due to differential growth until the onset of extensive self-thinning, and then decreases due to differential mortality (Weiner and Thomas 1986). This hypothesis has not previously been tested directly, using repeated measurements of the same individuals.

Hypothesis 2b.—Skewness increases to a maximum at the time self-thinning begins, then decreases during self-thinning. This is from the Mohler et al. (1978)

characterization of skewness of tree diameter and weight, and is also a consequence of Hara's (1984a) models of moment dynamics for plant size distributions. Previous tests have used plantations or replicate harvests, rather than repeated measurements of individuals in natural populations.

MATERIALS AND METHODS

Permanent sample plots

From long-term permanent sample plots (PSPs) located in the Duke Forest (Durham, North Carolina, USA), we selected those stands that were (1) naturally seeded, (2) even-aged, (3) nearly monospecific, (4) first sampled at a young enough age to allow us to determine the approximate age at which self-thinning began, and (5) not subject to confounding silvicultural treatments. These plots were part of a series of studies begun by the Duke Forestry School in the early 1930s.

The 16 plots studied were effectively monospecific populations of *Pinus taeda* (loblolly pine), though occasional stems of *Pinus echinata* were recorded but excluded from the present analysis. A few plots had substantial numbers of hardwood seedlings and saplings, but this hardwood ingrowth has only very recently begun to contribute an appreciable fraction of the biomass. Plot areas, initial and final stand ages, initial and final tree populations, and numbers of censuses are summarized in Table 1. Twelve plots referred to as the "density series" were established to study the effect of stand density on growth and development of individual trees, and upon branch retention and wood quality (C. K. Korstian, Duke Forest Archives). Five of these plots received silvicultural thinnings beginning in 1945—the five "treatment plots." Data collected after these thinnings began were excluded from this analysis. The "other control plots" were controls for other silvicultural experiments, similar in initial conditions to the middle range of the density series, but somewhat older at first measurement. Diameters at breast height (dbh) and heights were remeasured at intervals in the course of the studies. The interval between measurements averaged 5.4 yr, but measurements were made more frequently during the early years of the study.

The density series plots were placed across a gradient in sapling establishment density in an old-field pine stand, on sandy loam soils. Half of the 12 plots had some minor artificial thinning to establish the full range of initial densities and thus better match "treatment" and "control" plots. To assure that the size structure had at least 2 yr to adjust to the new densities in those plots and to retain a uniform starting age, the entire first set of measurements on all 12 plots was excluded from our analysis.

Volume estimation.—To estimate aboveground biomass, we used parabolic volume (Whittaker and Woodwell 1968) computed as:

$$V_p = \frac{1}{2}(\text{height})\pi(\text{dbh}/2)^2.$$

Parabolic volume is widely accepted as an excellent predictor for use in biomass regression models (e.g., Whittaker and Marks 1975). No adjustments were made for taper from base to breast height, or to account for different ratios of bole size to branch and foliage masses at different sizes, ages, and densities. Such adjustments would have required modeling some of the density and time effects that we sought to test.

Height interpolation.—Diameters of all trees were measured at each census. Complete sets of height measurements were obtained in the first two and final two censuses. In the middle years of the study, heights were measured on a sizable (but not random) sample of the trees.

Missing heights were interpolated using a method we devised specifically to preserve the variation in size needed for inference about size structures. For each plot, least squares regression and log transforms were used to fit the following model to the known heights:

$$\text{height} = a(\text{dbh})^b(\text{age})^c \exp[d(\text{age})]$$

where a , b , c , and d are fitted constants. This was the simplest model tried that consistently left no detectable trend in the regression residuals. The first three parameters of this four-parameter model were always positive, while the fourth was negative. The fourth parameter provided an exponential slowing term for height increase with age. Diameter accounted for most of the differences between trees: the combined R -squared value for prediction of known heights was >0.98 for most plots, and always >0.92 .

The model was not used to predict unknown heights directly. Instead, it provided appropriate curvature for ratio interpolation of unknown heights from known values for the same trees. Thus, known individual differences in allometry were incorporated in predictions of unknown heights. Between 29 and 54% of all height measurements in each plot were estimated in this fashion. In most plots $\approx 40\%$ of the heights were interpolated. Although variation around an age-dependent mean was preserved by using a known diameter and interpolating from known heights, differences between trends in height structure and diameter structure may have been underestimated.

Data quality control.—Procedures to assure data quality included careful manual examination of the recorded values, intermediate analyses to monitor results, and computerized data editing. Examination of residuals in the height interpolation model provided an additional means to detect anomalous values for investigation.

Size structure statistics

Inequality.—We calculated the Gini coefficient (G_i), a statistic that measures inequality as a function of the sum of the absolute differences between all pairs of

observations. The sum is scaled by mean and sample size to form a dimensionless coefficient ranging from zero to one (Sen 1973, Weiner and Solbrig 1984). The Gini coefficient was originally developed to measure inequality of income distributions (Sen 1973). Weiner and Solbrig (1984) suggested it as a direct measure of the inequality of plant sizes. We also computed the coefficient of variation, which is the sample standard deviation divided by the sample mean (expressed as a percent).

Asymmetry.—To measure asymmetry we used the familiar sample skewness coefficient, $\hat{g}_1$ (Fisher 1930). It has been recommended as the best numerical estimate of distribution asymmetry (Hutchings 1975). Unlike histograms, it allows changes in distribution asymmetry to be quantified. We also used a jackknife procedure to calculate skewness (Higgins et al. 1984) for some of the censuses with smaller sample sizes to check for differences between the usual coefficient and a potentially more robust measure.

Parameters of fitted Weibull distributions.—To relate our results to the large body of silvicultural literature using the Weibull distribution, we fit Weibull distributions to data for diameter, height, and volume. The Weibull probability density function has the general form:

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

for $x \geq 0$, $b > 0$, $c > 0$; and $f(x) = 0$, elsewhere. The corresponding cumulative distribution function is:

$$F(x) = 1 - \exp[-(x/b)^c].$$

A three-parameter version of the Weibull is sometimes used where $(x - a)$ is substituted for the x on the right hand side. For most forestry applications $0 \leq a \leq x$. The conventional terms for parameters are: location (a), scale (b), and shape (c).

The Weibull distribution is attractive for model building due to its flexible form and mathematical tractability (Bailey and Dell 1973). The shape parameter can be interpreted in terms of asymmetry (Dell et al. 1984): the Weibull approximates a normal distribution for $3.25 \leq c \leq 3.61$, and exhibits progressively more positive skewness below this range and negative skewness above this range. If c is set equal to one, the Weibull reduces to a decreasing exponential distribution. The two-parameter Weibull has a fixed location ($a = 0$) and thus its shape does not readily reflect positive skewness for distributions with a minimum value far from the origin. Instead, the shape (c) of a two-parameter Weibull distribution can be related to the sample coefficient of variation (Newby 1980). The shape parameter increases as the coefficient of variation decreases. The scale (b) of the two-parameter Weibull (also called the "characteristic life") is related to the mean of the distribution.

Statistical testing

Two classes of statistical methods were employed. For explicitly formulated predictions, inferential tests were used. We controlled Type I error rates for pairs of related tests dealing with trends in two parts of the same time sequence, by halving the nominal alpha level in each test (see Miller 1966, on dependent tests). To compare different statistics and show interrelationships, correlations were used without formal inference.

Trend tests.—The second pair of hypotheses (2a and 2b) refers to the direction of change over time. Although estimates of inequality and asymmetry were sample statistics, movement from significance to non-significance (or vice versa) could not be used to assess trends; the sample sizes varied too much across plots and between early and later censuses. Also, unlike replicate sequential harvests, serial measurements on sample plots could not be treated as independent observations. Hence, though changes could be seen directly, conventional statistical tests were inappropriate.

The approach adopted was a simplified version of repeated-measures analysis of variance (Hand and Taylor 1987). For each plot and statistic, we computed a contrast variable as the average rate of change between censuses over the time interval of interest. A one-sided t test against a null hypothesis of no change ($H_0 = 0$) was then performed on this variable using all appropriate plots. The sample size for the t test was the number of sample plots with data for the appropriate phase. Because the intercensal intervals were not equal, contrast variables were based on the annual rate of change observed in intercensal intervals. To capture the average tendency rather than a net change between first and last observations, and to reduce the effects of measurement errors, annual rates were then averaged across the relevant intercensal intervals.

For example, to test the change in inequality before the onset of self-thinning, all plots with at least two censuses before the onset of extensive mortality (see below) were selected. Eleven of the 16 plots had appropriate data. Thus the sample size for that test was 11. Then, annual rates of change in the Gini coefficient were calculated for all the intercensal intervals before the start of self-thinning. Next, those rates were averaged across intervals for any plot that had data for more than one intercensal interval. This average rate of change formed the contrast variable. It has an expectation of zero under the null hypothesis of no change. Finally, as there was only a single group with a fixed null expectation instead of a comparison of two or more groups, we used a t test against ($H_0 = 0$) with $n = 11$ instead of ANOVA with an F test.

This is a conservative test procedure in that it makes no use of the often large number of observations going into each sample statistic for inequality or asymmetry, and makes no use of the number of intercensal differences averaged to form the contrast variable. It is a

simple, robust procedure which avoids the following problems: dependence between measurements of trees in the same plot, dependence between serial observations, inequality of sample sizes, and complexities of two-sample tests of inequality (Weiner 1985) or skewness (Higgins et al. 1984).

Self-thinning.—To avoid the ambiguity and theory dependence of defining self-thinning in terms of approach to an idealized thinning line on a biomass vs. density curve, an arbitrary mortality cutoff was adopted. Substantial crowding-dependent mortality was unlikely to have occurred before 20% of the original trees had died. So, following Westoby (1984) and Weiner and Thomas (1986), we arbitrarily classified intercensal intervals prior to 20% mortality as “before significant self-thinning.” The remaining intercensal intervals, from the occurrence of 20% mortality on, were termed “during self-thinning.” Tests of changes in size structure with these definitions cannot be considered biased or circular with respect to phases of stand development. However, these crude definitions could result in our overlooking patterns that might be seen with more natural phase boundaries (e.g., Peet and Christensen 1980).

RESULTS AND DISCUSSION

Density effects

Inequality versus density.—Inequality of size, as measured by parabolic volume, was greater at higher densities in young stands. Thus, hypothesis 1a was supported by our findings. Correlations between density and inequality across the density series plots (see Fig. 1, Table 2) were significantly positive at age 10 and age 13. The relationship was not perfect, but considering initial manipulation of the plots and natural variation in site quality, the finding was striking.

Weiner (1985, Weiner and Thomas 1986) interprets results like these in the context of two families of mathematical models of plant competition. Under “resource depletion” models, competition is symmetric and proportionately reduces resources available to all individuals, leading to proportionately reduced growth rates and ultimately decreased size inequality at higher densities. Under “resource preemption” models, interactions between large and small individuals are asymmetric, and inequality becomes greater at higher densities. For a variety of different plausible models, asymmetric formulations produce increased inequality at higher densities, whereas symmetric versions produce decreased inequality at higher densities (Weiner and Thomas 1986). Thus, the predominant finding of greater inequality at higher densities is consistent with a predominantly asymmetric model of plant competition. Asymmetric competition in trees has previously been shown in an analysis of growth rates in planted *Picea sitchensis* and *Pinus contorta* (Cannell et al. 1984).

A plausible biological explanation for asymmetric

competition in trees is that interactions at high densities are mediated by competition for light. In a dense stand, larger trees preempt light and shade smaller neighbors. Belowground competition appears less likely to be strongly asymmetric (Weiner 1986). Nonetheless, soil nutrients or water could still have limited growth in our experiments, if asymmetry in light competition exaggerated differences in relative growth rates and rates of resource acquisition among neighbors.

Asymmetry vs. density.—Skewness coefficients for parabolic volume were initially correlated with stand densities, but not so strongly as were inequality measures (Table 3). The correlation of diameter distribution skewness with initial stand density was not statistically significant at the .05 level. Skewness in the height distributions was inversely correlated with density. Thus, while the simple hypothesis that skewness of plant volume (as a surrogate for biomass) is greater at higher density (hypothesis 1b) was accepted for these plots, we should not expect all measures of size to yield this relationship. In contrast, results for inequality were consistent across the three measures of plant size.

Some studies of planted trees have failed to find simple density-related increases in skewness of volume (Jack 1971) or girth (Ford 1975). Results regarding the impact of competition on skewness in herbaceous plants have also been inconsistent (compare with Kira et al. 1953, Koyama and Kira 1956, Hutchings and Barkham 1976, Turner and Rabinowitz 1983, Waller 1985).

Jackknifed skewness.—Due to uncertainty about the stability of the moment coefficient of skewness (e.g., Koyama and Kira 1956, Hutchings 1975), we applied the jackknifed skewness coefficient (Higgins et al. 1984) to a set of "worst case" measurements. The greatest average difference between the two coefficients ought to occur with the smallest sample size, so we applied both coefficients to data from censuses of trees surviving to 1984. Nine control plots had suitable data, with populations of from 18 to 36 individuals. Correlations between the two coefficients were between 0.975 (for V_p) and 0.982 (for height), across the nine plots. Spearman rank correlations between the two coefficients were >0.983 for all three size measures, convincing us that our results for distributional asymmetry would have

FIG. 1. Inequality (G_u) of parabolic volume (V_p) vs. population density for the density-series plots. Density is plotted on a $\log_{10}$ scale. Relationships for the first two censuses after initial measurement are shown. Modified from Knox (1987).

been essentially unchanged if we had used the more complicated jackknifed skewness coefficient.

Changes during stand development

Trends in inequality.—As predicted by hypothesis 2a, inequality of size (parabolic volume) increased before the onset of self-thinning and decreased during self-thinning. Statistical tests of the trend (see Table 4) were significant for both predictions. The annual rates of change detected were not large, as >30 yr would be required for an increase or decrease of 0.1 in the Gini coefficient. Initial differences in inequality, between high and low density plots, were 0.2–0.4. Differences in inequality that developed early in the study persisted throughout stand development.

Gini coefficients for successive censuses from 1935 to 1984 are shown in Fig. 2 for the seven control plots in the density series. The time sequence in the figure runs from right to left as a consequence of declining density. Plot PSP15 showed characteristic trends for a low-density stand. Inequality first increased, along with scattered mortality, then with substantial self-thinning, inequality leveled off. PSP21 showed a typical high-density pattern, with inequality first continuing the initial increase, but then rapidly falling with self-thinning.

TABLE 2. Correlation of inequality (G_u) of parabolic volume (V_p) of trees with the log of initial stand density, for the 12 density series plots.*

Stand age (yr)	Correlation	Number of plots	P
10	0.81	12	$<.01$
13	0.91	11†	$<.001$

* Density was log transformed to normalize the distribution of densities and permit use of Pearson product-moment correlations. Spearman rank correlation of untransformed data produced essentially the same results (see Table 3).

† Significant self-thinning ($>20\%$ mortality) occurred before age 13 yr in the most dense plot.

TABLE 3. Rank correlation of density with size inequality (G_u) and skewness for three size measures. Correlations were across 11 stands at age 13. V_p = parabolic volume. NS = nonsignificant.

Distribution attribute	Size measure	Correlation with density	P
Inequality	dbh	0.92	$<.001$
	height	0.91	$<.001$
	V_p	0.90	$<.001$
Skewness	dbh	0.57	NS
	height	-0.61	$<.05$
	V_p	0.81	$<.01$

FIG. 2. Inequality (G_u) of parabolic volume (V_p) vs. population density over 48 yr for control plots in the density series. Density is plotted on a $\log_{10}$ scale. Sequential measurements for each plot are connected by a line (running generally from right to left), and censuses from ages 10 to 58 yr are shown.

An unexpected finding was that inequality recovered somewhat in the last two or three intervals in the four high-density plots. This was despite continued self-thinning. The upturns all occurred at densities between 0.3 and 0.15 trees/ m^3 . This may represent a density range in which mortality is less dependent on relative size.

The line for PSP14 was anomalous in that despite a low starting density, inequality initially declined but then stabilized. This plot had the heaviest artificial thinning before the first census, and may have initially behaved more in accordance with its earlier density (estimated as 0.67 trees/ m^3).

Although populations in all these plots converged to ≈ 20 –30 individuals (per 405 m^2) by age 58, inequality did not converge as strongly. Lasting effects of early environment have also been shown in a greenhouse experiment, where survivor mass was better predicted by the area available to it as a seedling than by area available at time of harvest (Mithen et al. 1984). In short, Fig. 2 suggests that rates of change in inequality vary with density and time, and that the underlying pattern is consistent with, but more complex than, the

simple increase and decrease proposed in hypothesis 2a.

In an earlier study on *Pinus taeda*, Schnur (1934) plotted mean diameter against the coefficient of variation for 111 sets of measurements on permanent plots taken between 1906 and 1930. He required a 6.3 cm (2.5 inch) minimum diameter, and included no very young stands. If one equates average diameter with stand age his results showed a pattern roughly paralleling our results for inequality of bole volume. Relative variation in diameter decreased with size up to an intermediate size, and then remained roughly constant for larger mean sizes. The same general pattern appeared with data for six other North American conifer species analyzed by Meyer (1930). A less pronounced decline in inequality with mean size appeared in 87

TABLE 4. Average yearly changes in inequality (G_u) of parabolic volume (V_p), for two phases of stand development, with significance (P) from associated t tests (with $\alpha = 0.05/2$, for a total family error rate ≤ 0.05).

Phase	Change in G_u	Number of plots	P
Before self-thinning	0.0031	11	<.025
During self-thinning	-0.0030	14	<.025

TABLE 5. Average yearly changes in skewness of three size measures during two phases of stand development, with significance from associated t tests.* NS = nonsignificant.

Phase	Measure	Change in skewness	Number of plots	P
Before self-thinning	dbh	-0.0026	11	NS
	height	-0.0022	11	NS
	V_p	-0.0195	11	NS
During self-thinning	dbh	0.0089	14	NS
	height	0.0218	14	NS†
	V_p	-0.0063	14	NS

* None of these tests had a one-tailed $P < .05$. Acceptance of the family of one-sided null hypotheses is secure.

† t had a two-tailed $P = .034$, but for a change in the direction opposite that predicted.

TABLE 6. Descriptive statistics for size structure statistics over all included censuses on all plots. dbh = diameter at breast height; V_p = parabolic volume.

Size statistic	Size measure	Mean	Median	Range	
				Minimum	Maximum
Mean	dbh (m)	0.17	0.16	0.03	0.37
	height (m)	16.	16.	3.3	35.
	V_p (m ³)	0.34	0.18	0.001	2.0
Coefficient of variation (cv)	dbh	24.	23.	8.9	51.
	height	12.	11.	5.0	29.
	V_p	59.	55.	20.	143.
Gini coefficient (G_{ii})	dbh	0.14	0.13	0.05	0.29
	height	0.07	0.06	0.03	0.17
	V_p	0.31	0.30	0.12	0.56
Skewness ($\hat{g}_1$)	dbh	0.50	0.48	-0.45	1.5
	height	-0.13	-0.14	-1.3	0.98
	V_p	1.3	1.1	0.08	5.7
Weibull scale parameter (b)	dbh	0.18	0.18	0.03	0.40
	height	17.	16.	3.6	37.
	V_p	0.39	0.20	0.001	2.2
Weibull shape parameter (c)	dbh	4.9	4.6	2.1	13.
	height	11.	10.	4.0	22.
	V_p	2.1	2.0	0.84	5.4

even-aged mixed upland hardwood plots (Ginrich 1967). However, the same relationships with mean diameter would also be expected if stands with the smallest average diameter established at higher densities, and then tended to be underrepresented as older stands due to greater mortality rates or susceptibility to disturbance. Our results suggests that at least part of the decline in inequality with mean size seen in these studies was due to stand development and attributable to self-thinning.

Trends in asymmetry.—Under hypothesis 2b, we expected increases in skewness before self-thinning and decreases during self-thinning. These predicted trends in asymmetry were not found in this data set. Table 5 shows the average annual rates of change in intercensus intervals classified as before self-thinning and during self-thinning. Not only were none of the trends statistically significant in the predicted direction, but five of six were in the opposite direction.

The visual impression conveyed by graphs of skewness vs. stand age (10 through 58 yr) confirmed the lack of clear trends in these data (Fig. 3). Skewness coefficients may have been more similar near the middle of the study than at the beginning or end, but no overall trends were apparent. It does not appear that adjusting the definition of self-thinning would change this result.

The ranges for skewness coefficients were consistent with general allometric expectations for plants given by Mohler et al. (1978) and Hara (1984a): mass skewness is positive, diameter skewness is mostly positive, and height skewness is zero to negative. Height distributions showed both positive and negative skewness (Fig. 3, Table 6), but tended to be somewhat negative

on average ($P < .002$ for $H_0 = 0$). Diameter distributions tended to be positively skewed ($P < .0001$), but also included some negative values. All distributions of parabolic volume were positively skewed. Mean values for skewness, across the 125 censuses, were -0.128, 0.500, and 1.32 for height, diameter, and parabolic volume, respectively.

Other researchers have also failed to find expected trends in distributional asymmetry for sizes of trees (Schnur 1934). Meyer (1930) found that diameter distributions for older stands were generally less asymmetric, but species differed in rates of change and final levels of asymmetry. Both Schnur's and Meyer's analyses make deductions about trends in young stands questionable because they confounded the possible effects of age and initial density on asymmetry in a single measure (mean size), and because measurements excluded trees below a threshold diameter. More recently, Pielou et al. (1985) found decreases in skewness of diameter with age in even-aged stands of *Populus tremuloides* in two of three regions of Canada, but no change in skewness with age or mean size in a third region. Work on herbaceous species has usually emphasized increases in skewness with time since germination (Benjamin and Hardwick 1986), rather than the decreases with mean size sometimes seen in trees. Our findings seem to contrast with results for some agriculturally important herbaceous species, which showed parallel trends (uniformly increasing over time) in skewness and relative variation of dry mass (Naylor 1976).

Gates et al. (1983) documented development of negative skewness in stem diameter distributions, followed by a later increase in skewness, in plantations

FIG. 3. Size distribution skewness vs. stand age for control plots in the density series. Skewness coefficients are plotted for distributions of: (a) diameter at breast height, dbh; (b) total height above ground, height; (c) parabolic volume, V_p .

of *Pinus radiata*. (Gates [1982] modeled this development of negative skewness during initial competition, with a zone-of-influence competition model.) The degree of spatial aggregation of a population may influence the form of the size distribution it develops (Hegyi 1974, Wyszomirski 1983), so results from plantations are not strictly comparable to spontaneous stands. Since our trees were at least 10 yr old in the first measurements used for testing, and were not regularly spaced, we did not expect to see this initial decline. However, Mohler et al. (1978) and Hara (1984b)

did find initial declines in skewness of diameter or height in some data sets.

Weibull distributions

Three-parameter Weibull.—We encountered difficulties fitting the three-parameter Weibull distribution to some of our data. The most common approach, a maximum likelihood algorithm (see Zutter et al. 1982a, b, Zarnoch and Dell 1985), did not converge for a number of the distributions. Other estimators of Weibull parameters have various difficulties. Some meth-

FIG. 3. Continued.

ods depend on the smallest observed size for selecting the location parameter and are thus extremely sensitive to sampling effects. Other methods may predict negative values for the location parameter which must be artificially set to zero (Burk and Newberry 1984), or depend strongly on the specified initial values because of problems with local minima (Krug et al. 1984). Even with simulated data and maximum likelihood estimators, parameters of the three-parameter form may not be recovered accurately: because the parameters are correlated, various combinations of parameters can lead to very similar distributions (Zarnoch and Dell 1985).

Two-parameter Weibull.—For consistency across plots and years, and to avoid instability of parameters in the three-parameter form, we chose to report a two-parameter Weibull for frequency distributions of diameter, height, and volume, for all plot censuses. Values for the scale parameter (b) approximately followed the distribution means, as expected. Values for the shape parameter (c) spanned a wide range (see Table 6). Shape values were lowest for volume and much greater for height. Diameter distribution shapes ranged from values typical of volumes to those typical of height distribution. The average of 4.5 was slightly lower than published values for plantations of *Pinus taeda* and higher than values for *Pinus strobus* (Schreuder and Swank 1974). The range was comparable to the 1.3–8.8 interval seen for 175 tree diameter data sets for *Pinus elliottii* (Schreuder et al. 1979). None of our diameter distributions had shape parameters (c) of <2.0 , confirming expectations for even-aged stands of shade-intolerant species (Lorimer and Krug 1983).

Distribution forms.—Among the 375 size distributions were studied, we selected 20 diameter distributions and 4 distributions each of height and volume, to illustrate the forms of distributions found. Fig. 4 shows diameter distributions for five of the control plots from the density series. Histograms of relative frequencies were generated for 1 cm diameter classes, to permit display of early measurements and yet retain consistent class lengths. Solid curves connect values for corresponding intervals of fitted Weibull distributions. These permanent sample plots (PSPs) represented a wide range of initial densities (note sample sizes). Distributions separated by ≈ 10 -yr intervals were chosen for presentation.

Several features are visually apparent in these graphs. In addition to low density plots having higher average diameters, they also produce curves with less spread at the same age. Distributions at all densities were fairly symmetric at age 10, but at the beginning of self-thinning the curves became left truncated. The left-truncation appeared earlier at higher density. (Height and diameter distributions increased in skewness in the first time interval classified as during self-thinning.) The diameter distributions for two higher density plots were less markedly truncated after age 20. This may reflect a relaxation in the size-specificity of mortality, late in self-thinning, as suggested by the rebound in Gini coefficient values in Fig. 2, and by studies of mortality risk-factors in these populations (N. L. Christensen, *personal observation*).

The height and volume distributions (Fig. 5) both changed in parallel with the diameter distributions, but remained rather different from each other. As expected

FIG. 4. Diameter class histograms and corresponding class sums for fitted Weibull distributions for five control plots in the density series, shown for roughly 10-yr intervals from age 10 to age 41. Axes are uniform and histograms cover constant 1-cm intervals of diameter at breast height (dbh) for all densities and ages. Surviving population sizes (n) are shown on each graph. Initial densities increase from (a) to (e). Data are from: (a) PSP12, (b) PSP15, (c) PSP17, (d) PSP19, and (e) PSP21.

from the skewness results, distributions of parabolic volume had long right tails, whereas tree heights tended to converge on a canopy level characteristic of the stand age, making height distributions appear right truncated.

Bimodality has been repeatedly suggested as an important, if problematic, feature of size distributions in

populations showing dominance and suppression, or "one-sided" competition (see Huston and DeAngelis 1987 and references therein). Some of the distributions in Fig. 4 may have a secondary mode. The graph for age 30 in Fig. 4c is the most suggestive. However, bimodality was not a prominent feature of most of these distributions. The multiple peaks visible are

FIG. 5. Histograms with corresponding size class sums and shape (c) parameters of fitted Weibull distributions for three size measures: (a) diameter at breast height, dbh; (b) total height above ground, height; (c) parabolic volume, V_p . Frequencies are grouped to form approximately the same number of classes for each graph and horizontal axis lengths are rescaled for each maximum value. Data are from an intermediate-density control plot, PSP17.

probably fluctuations due to finite sample sizes (Westoby and Howell 1986).

The unimodal Weibull curves had difficulty fitting some simpler characteristics of the distributions. Some of the frequency distributions were noticeably more peaked, or kurtotic, than the corresponding fitted curves. Also there were obvious gaps between fitted distributions and observed data with strongly positively skewed distributions. The limited range of skewness and kurtosis values that can be represented with Weibull distributions (Hafley and Schreuder 1977) restricts the utility of this distribution for describing size structure.

Goodness of fit.—Kolmogorov–Smirnov statistics for testing an observed vs. a predicted distribution with fitted parameters (Sokal and Rohlf 1981) suggested moderately poor fits for the Weibull distributions. Most distributions from populations of >25 individuals were “significantly” different ($P < .01$) from fitted Weibull curves. However, extremely poor fits were not common, and simple probability distribution functions fitted to diameter distributions often have a high rate of rejection (e.g., Burkhardt and Strub 1974). Measurements on neighboring trees cannot be considered independent, so the test statistics should be interpreted merely as indices of agreement between observed and fitted distributions, rather than as strict tests of fit (Ek and Monserud 1979).

Some of these size distributions would have been better approximated by three-parameter Weibull functions, but then the behavior of the distribution parameters (a , b , and c) would not have been as predictable. With the shape parameter of the three-parameter distribution being more sensitive to skewness than relative variation in size, it would be subject to the same unpredictability we found in distributional asymmetry. This phenomenon has been seen in forest modeling applications of the three-parameter Weibull distribution (Feduccia et al. 1979, Rennolls et al. 1985). Variability in the pattern of mortality among the smaller trees limited the accuracy of parameter predictions. Distributions other than the Weibull, such as Johnson’s S_H distribution, might have better accommodated the range of skewness and kurtosis values seen in our data (Hafley and Schreuder 1977). But, again, simple models of the competitive dynamics of the stand probably could not have accurately predicted the broader range of forms represented. In fitting statistical distributions to sets of measurements of tree size, there appears to be an inherent conflict between detailed recovery of distribution form and predictability of parameter behavior.

Interrelationships

We used the density-series plots to examine interrelationships between size structure statistics. Because

these plots were established in stands of the same age and near one another, and early densities were well known, variation due to differences in age and initial density should be most apparent in them.

Pair-wise correlations revealed intercorrelation between all the statistics except skewness of height. Values of the coefficient of variation (*cv*) were closely related to Gini coefficient values. Spearman rank correlations between the two statistics were 0.997, 0.997, and 0.994, for diameter, height, and volume, respectively. The dependence between sequential measurements tends to inflate these correlations, but looking only across plots, rank correlations were still high. At the beginning of the study they ranged from 1.00 (*dbh* and V_p) to 0.993 (height), for 12 plots. In 1977, for seven unmanipulated control plots, rank-orderings were identical for the two statistics. These findings agree with a high correlation (0.99) reported for other data sets (Weiner and Thomas 1986).

The only notable difference in these two coefficients was in their distribution across plots and censuses. Although the coefficients were similarly distributed for diameter and height, the distribution of *cv* for parabolic volume was markedly more skewed than the corresponding Gini coefficient. This probably reflects a greater sensitivity to outliers in a squared deviation measure (*cv*) as compared with an absolute deviation measure (G_u).

As expected from the close relationship of the Weibull shape parameter (*c*) to the coefficient of variation (Newby 1980), shape had large negative rank correlations (−0.962 to −0.997) with *cv* and G_u for the same size measures.

Factor analysis of G_u , *cv*, skewness, Weibull shape (*c*), and Weibull scale (*b*), for all three size measures, and age at census, initial density, density at census, mean *dbh*, mean height, mean V_p , and basal area revealed two highly intercorrelated clusters of variables (Knox 1987). Inequality statistics were correlated across size measures, and were more strongly related to initial density than current density. Much of the information summarized by the Gini coefficient or Weibull shape parameter was also found in the more familiar coefficient of variation, and could be predicted from a single size measure. A second cluster included mean sizes (for three size measures), Weibull scale parameters, and plot age. The skewness statistics did not fall into either of these clusters. Of the skewness statistics, skewness of parabolic volume had the highest correlation with the various inequality measures and initial density. Skewness of diameter was somewhat more independent. Skewness of height was not significantly correlated with other size structure statistics or other stand attributes.

CONCLUSIONS

Either inequality or skewness of volume responds to early competitive interactions, as summarized by stand

density. Correlations of inequality with density were stronger and insensitive to the measure of tree size used.

Inequality provided a robust indicator of density effects on growth and traced the effects of size-selective mortality. We recommend the Gini coefficient, or the more familiar coefficient of variation, for monitoring those effects.

In the absence of a mechanistic model of stand development, use of skewness or related parameters of fitted distributions to monitor or test for changes in competitive interactions in trees is probably not justified. Tree allometry also appears to vary sufficiently with density that trends in skewness of biomass cannot be simply extrapolated to trends in skewness of diameter and height distributions. Although we found that changes in size distribution skewness did not follow the broad trends described in previous publications, we did note a tendency for self-thinning to begin by truncating the lower end of diameter distributions and increasing the skewness of height distributions. Measures of spread of size distributions reflected past crowding and had predictable changes during stand development, whereas measures of asymmetry changed more erratically and individually. The difficulties in prediction experienced with the skewness coefficient were not found with a measure of size inequality.

Our results do not dictate a particular theory of competition between even-aged trees, but they do suggest some general features. Initial density effects produce increased inequality at greater density, implying asymmetric interactions. Inequality also follows the broad time-trends of increase before self-thinning and decrease during self-thinning described by Weiner and Thomas (1986). However, decreases do not necessarily continue in the later stages of self-thinning. Future theory may be able to accurately predict the course of change in size distributions over the life of forest stands such as these, but we doubt it will do so with the kind of appealingly simple, linear or two-phase trends frequently proposed in the past.

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CONTRASTING WINDSTORM CONSEQUENCES IN TWO FORESTS, ITASCA STATE PARK, MINNESOTA¹

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Abstract. Thunderstorm winds ($\approx 25\text{--}35$ m/s) often damage scattered trees in northern Minnesota forests. Following one moderate windstorm on 3 July 1983, I surveyed damaged trees within two Itasca Park study areas (1) to identify mortality patterns and their correlates, (2) to evaluate windstorm consequences for shade-intolerant species, and (3) to investigate formation of light-gaps.

Risk of direct wind damage was predicted best by tree size (in both stands) and either tree species (in a *Pinus/Acer* stand) or species wood strength (in a *Pinus/Abies* stand). However, the overall risk of mortality, combining direct wind damage and damage from falling trees, was more complex. Tree mortality in the *Pinus/Acer* study area was related to tree size, species, species wood strength, and incidence of species-specific fungal pathogens. Mortality in the *Pinus/Abies* study area, where many understory trees were killed, was not predictable on the basis of tree size, but mortality risk was affected by tree species and species wood strength (data on fungal pathogens were unavailable for this stand). Within most populations, the size distribution of windstruck trees differed from the population size distribution. However, mortality risk, including that from falling trees, increased with tree size only for *Populus tremuloides*. In one study area, smaller trees were most vulnerable within the *Picea* and *Pinus strobus* populations. The difficulty of generalizing about windstorm consequences is illustrated by large intraspecific variation in amount of damage between different populations of *Betula papyrifera*, *Pinus resinosa*, and *Pinus strobus*.

For shade-intolerant species expected to benefit from disturbance, windstorm consequences differed in the two stands, despite shared postfire origins and several tree species in common. In the *Pinus/Acer* forest, heavy mortality to shade-intolerant *Populus tremuloides*, *Pinus resinosa*, and *Pinus strobus* combined with a well-developed, windfirm understory and infrequent light-gap formation to benefit existing shade-tolerant, windfirm *Acer saccharum* and tall shrubs. In the nearby *Pinus/Abies* forest, the windstorm produced more regeneration opportunities for shade-intolerant species (*Betula papyrifera*, *Populus tremuloides*, *Fraxinus pennsylvanica*), because the shade-tolerant understory species of this stand (*Abies balsamea*, *Picea glauca*) were more heavily damaged, and because more light-gaps formed, although such light-gaps were small relative to published gap size thresholds for tree establishment. Differences between the two communities in their responses to the same storm event appear to result from differences in forest structure and differences in the windfirmness of shade-tolerant understory taxa.

Key words: disturbance; forests; gaps; Minnesota vegetation; succession; tree mortality; windstorms.

INTRODUCTION

The gusty winds of up to 35 m/s (75 miles per hour) that precede frequent midcontinental thunderstorms (Battan 1961, Trewartha 1968) often damage scattered trees in northern forests. The ecological consequences of such winds are not well understood, although more severe storms with higher windspeeds (> 35 m/s) that form large blowdown areas (> 1 ha) have received more attention from ecologists (Sauer 1962, Henry and Swan 1974, Lorimer 1977, Oliver and Stephens 1977, Savill 1983, Canham and Loucks 1984). I examined patterns of mortality, damage, and light-gap formation following a moderate windstorm in two compositionally and structurally distinct Minnesota forests, located just 8 km apart. I asked the following questions:

1) Is tree species an important predictor of damage and mortality? Trees of some species may be more prone to wind damage because of weak wood (Putz et al. 1983), tree geometry (King 1986), and species-specific wood-rotting fungi. Alternatively, damage and mortality may be determined by factors unrelated to tree species such as tree size or chance.

2) When mortality is uneven among species, what are the consequences for community composition? Interspecific differences in mortality might remove superior competitors for light, benefiting less shade-tolerant species. Alternatively, mortality might be heaviest for shade-intolerant species, many of which have rapid growth rates and weak wood. If so, windstorms might increase the importance of shade-tolerant species.

3) How commonly does tree damage in moderate windstorms produce light-gaps where shade-intolerant trees can become established? Windstorms can influ-

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