

AN ABSTRACT OF THE THESIS OF

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Computer simulations and experiments were used to determine the basis for skewness and inequality in size structures (frequency distributions of individual plant sizes) prior to self-thinning mortality. In simulated stands, density-dependent neighborhood heterogeneity caused variability in the growth rate of individuals with the same size, and such variability caused skewness to increase with time. In experimental stands of Pseudotsuga menziesii, skewness and inequality were caused by variance in growth rate of individuals with the same initial mass. Available space (measured by Thiessen polygons), but not maternal parent, was a source of such variation in these stands. In experimental stands of Fraxinus mandshurica in China, skewness and inequality increased with density and age. Vertical distributions of leaf area, light, and specific leaf area indicated that competition between large and small seedlings for light was asymmetric. However, such competition did not cause relative growth rates to be correlated with size.

A stochastic model of size structure dynamics was more appropriate for these stands than deterministic models that do not account for variation in the growth rates of plants with the same initial sizes.

Dynamics of Size Structures: Simulation and Experiments in
Seedling Stands of Pseudotsuga menziesii and Fraxinus mandshurica

by

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I dedicate this thesis to my wife, Margaret, and my five-year-old daughter, Allison. Just by observing Allison, I was constantly reminded that learning should be a joyful experience, a valuable reminder for someone in the throes of a Ph.D. program. Most of all, I am grateful for the unwavering love and encouragement from Margaret. She made it all possible.

PREFACE

Describing the historical background of the studies making up this dissertation should help them stand together as a more cohesive unit. My interest in competition and size structures arose during my tenure on the research and development staff of Champion International Corporation in western Montana. The objective of one of my studies there was to describe how competition from perennial grass altered the above-ground structure of young ponderosa pine stands. To accomplish this, frequency distributions of tree sizes were examined in stands with and without competitors.

I found that interspecific competition had several effects on stand structure (see Petersen 1988). Frequency distributions were more positively skewed with competition (i.e. the tail of the frequency distribution extended out to the right). More importantly, the increase in skewness could not simply be explained by the slower average growth rate of trees when they competed with grass. That is, when skewness of stands with and without competitors was compared at equal mean sizes (at different points in time), the differences in skewness persisted. I thought this was significant because it indicated that competition models based on mean growth rates are not able to describe aspects of stand structure that are of both practical and theoretical importance.

I then asked what the biological basis might be for the

effects of competition on stand structure. One potential explanation was based on the considerable genetic variation that exists in ponderosa pine populations. Perhaps it was possible that a few genotypes were less affected by competition than others. If relatively infrequent genotypes were able to maintain rapid growth rates in the face of competition, then the skewed size distributions that were observed would be as expected. This possibility was particularly interesting because of the implications for progeny testing programs. Progeny selected as having superior growth rates in competition-free environments, as was the standard practice in tree improvement programs, may not be the most productive in the more realistic conditions of operational plantations, where interspecific competition is never completely eliminated.

I returned to graduate school with the goal of testing this "genetic variation" explanation for the effects of competition on stand structure. As I became more familiar with the literature, my interests expanded to include alternative hypotheses that have been suggested for size structure dynamics in single-species stands. The one most often mentioned, particularly in stands of trees, is asymmetric competition (e.g. Ford 1975). I also became aware of the stochastic model of size structure dynamics developed by the Japanese (Hara 1984). This suggested to me an alternative to asymmetric competition for explaining skewed size structures. Rather than competition causing a disproportionate suppression of small

individuals, neighborhood heterogeneity may cause variation in growth of individuals of the same size, and this variation in growth may lead to skewness.

With financial support provided by Mike Newton, I was able to conduct several studies with Douglas-fir to evaluate the above explanations for skewed size structures. Towards the completion of these studies, the opportunity arose to spend a year working at Northeast Forestry University in Harbin, China. I was lucky enough to be able to work with Zhu Ning, a faculty member at Northeast Forestry University. Professor Zhu is a dedicated teacher of forest ecology who shares my interest in studying plant competition. He arranged for resources to be made available for a study with ash that further tested ideas that arose from my work with Douglas-fir. The four studies reported in this dissertation are the culmination of the above events.

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DYNAMICS OF SIZE STRUCTURES: SIMULATION AND EXPERIMENTS IN
SEEDLING STANDS OF PSEUDOTSUGA MENZIESII AND FRAXINUS MANDSHURICA

INTRODUCTION

Prior to the onset of self-thinning mortality, size structures (frequency distributions of plant sizes) often become positively skewed, with relatively few large individuals and many small ones. Koyama and Kira (1956) showed that variation in relative growth rates can lead to skewed size structures. In their work, skewness did not develop when all individuals had the same relative growth rate.

However, variation in relative growth rate does not always cause skewing. In the special case of constant absolute growth rate (i.e. relative growth rate decreases with size), skewness will not change with time. Thus, there must not only be variation in relative growth rate in the model of Koyama and Kira (1956), but also variation in absolute growth rate, for skewness to develop.

If variation in relative growth rate does exist in a population, it may arise from one or both of two sources: variation in the growth of plants with different sizes, or variation in the growth of plants with the same size. The first source of variation is described by the relationship between initial size and growth rate (Hara's (1984) $G(t,x)$ function). The second source of variation in relative growth rate is

described by the relationship between initial size and variance in growth rate (Hara's (1984) $D(t,x)$ function). Hara (1984), Westoby (1982), and others have described what forms of these relationships produce positive, negative, or no change in skewness. The functions will be discussed in more detail later in this thesis. They are the basis for the procedures I use to test various hypotheses.

There are many possible biological causes for skewness, in contrast to the above mathematical explanations for skewness. Any factor that accentuates the variation in growth rates, either of plants with the same initial size or those with different initial sizes, has the potential for contributing to skewed size structures.

The objective of this thesis is to first determine to what extent variation in relative growth rate is due to variation among seedlings with the same or different sizes. Once this is accomplished, it is possible to examine biological explanations for the mathematical functions that are responsible for skewing. It is not possible to determine the relative importance of biological factors until it is known which of the two types of variation in growth rates mathematically causes skewness. The following "biological" explanations for skewness are evaluated in this dissertation.

Asymmetric Competition. Competition is asymmetric when large individuals suppress smaller ones but not vice versa. Competition for light between individuals that have a vertical

separation of their leaf area can most easily be visualized as being asymmetric. In the models of Ford (1975), Schmitt et al. (1987), and others, asymmetric competition leads to skewness because mean relative growth rate is positively correlated with size. The existence of this positive correlation has been used as evidence that competition is asymmetric. Testing for the existence of asymmetric competition by examining the relationship between growth and size is a refinement of an earlier test proposed by Turner and Rabinowitz (1983). They suggested that if competition is asymmetric, maximum skewness should occur at the highest stand densities.

Neighborhood Heterogeneity. I propose that there are two limitations to the above procedures for determining the causes of skewed size structures: (1) factors other than asymmetric competition may be density-dependent and therefore confounded with any effects of such competition, and (2) skewness may develop because of variation in the growth of individuals with the same size even without a positive correlation between relative growth rate and initial size. Hara (1984, 1988) has mathematically described how variation in growth rates in general can lead to skewness in size structures. Therefore, examination of frequency distributions (as proposed by Turner and Rabinowitz (1983)) or the relationship between relative growth rate and size (as proposed by Schmitt et al. (1983)), without considering the potential effects of variation among individuals with the same size, may lead to erroneous

conclusions about the importance of asymmetric competition. Asymmetric competition may cause relative growth rates to be positively correlated with size, but because variation among individuals with the same size may also cause skewness, such competition may be unimportant as a cause of skewness.

One of many possible sources of variation in the growth of individuals with the same initial size is neighborhood heterogeneity due to the spatial arrangement of competitors. Particularly in young seedling stands, not all individuals of the same size will have the same number neighbors that are competitors. Therefore, such neighborhood heterogeneity may cause variation in growth rates of individuals with the same size, and thus lead to skewed size structures.

Maternal Heterogeneity. Individuals with different maternal parents may have different growth rates, either because of genotypic differences or because of environmental effects on the seed produced by different parents. Maternal effects, either genetic or environmental, could lead to skewness by two processes: (1) siblings within some families may have greater mean relative growth rates, leading to a positive correlation between growth and size (just as in the case of asymmetric competition models of Ford (1975) and Schmitt et al. (1987)), or (2) maternal heterogeneity may cause variation in the growth of individuals of the same size leading to skewness as described by Hara (1984).

The study described in Chapter One simulates plant growth

when the only sources of variation in rates are initial size and the number of competitors. Competition between individuals of different size is not asymmetric in this simulation. I expected that neighborhood heterogeneity would be density dependent. If density is so low that plants do not compete, neighborhood heterogeneity will not be a source of variable plant growth rates. I predicted that as density increases, so would the variance in growth rate of individuals with the same initial size. Therefore, skewness was expected to increase with density because of neighborhood heterogeneity, even though competition was not asymmetric. If this were the case, it would demonstrate the potential confounding between density-dependent factors that can cause skewness in size structures.

Chapter Two compares growth functions and size structures in Pseudotsuga menziesii seedling stands when spatial arrangement is either uniform or random. Size structures were expected to be more skewed when spatial arrangement was random because of the greater neighborhood heterogeneity. Chapter Two also includes an analysis of the Gini coefficient, a measure of size inequality. Simulations are conducted to determine whether the Gini coefficient responds to the growth variability in a manner similar to the skewness coefficient.

Chapter Three compares size structures at different densities in seedling stands of Fraxinus mandshurica. Growth rates of individual seedlings were measured so that the growth functions regulating the dynamics of size structures could be

quantified. Vertical distributions of leaf area and light are described to determine whether there exists a physical basis for asymmetric competition. The traditional model of asymmetric competition, in which relative growth rates become correlated with size, is evaluated as an explanation for the effects of density on skewness and inequality.

Chapter Four attempts to accomplish two objectives. First, the mathematical basis for skewness and inequality in Pseudotsuga menziesii stands is determined. The goal was to attribute increases in skewness and inequality during the second growing season to either a positive correlation between relative growth rate and initial size, or to variance in growth rate of individuals of the the same size. The second objective was to describe the underlying biological basis for the mathematical functions that cause skewness. The relative importance of maternal parent and available space are examined in stands in which the exact location and maternal parent of each individual is known.

EVALUATING THE DEVELOPMENT OF SIZE HIERARCHIES IN
DENSITY-DEPENDENT PLANT GROWTH BY ANALYZING
NEIGHBORHOOD HETEROGENEITY

SUMMARY

Although previous research has shown that one-sided competition can cause positively skewed size distribution (many small individuals and relatively few large ones) in density-dependent plant growth, neighborhood heterogeneity can also cause such skewness. In the model presented, competition is not one-sided and the only source of variation in the growth of plants with the same initial mass is the number of neighbors competing for resources. Neighborhood heterogeneity caused variation in the growth of these plants, changing distributions from normal to positively skewed as the plants grew. Positive skewness was highest at intermediate stand densities. Experiments that test for one-sided competition by comparing size distributions at different densities are inconclusive because of potential confounding between one-sided competition and density-dependent neighborhood heterogeneity.

INTRODUCTION

In many plant species, the size of a plant relative to other members of the stand determines its fecundity, probability of mortality, and biomass production (Harper 1977). Thus, frequency distributions of plant mass can be useful for studies in plant demography and the culture of crop plants. Before self-thinning mortality occurs, such frequency distributions in even-aged, monospecific stands are often positively skewed, with many small plants and relatively few large ones (Bazzaz & Harper, 1976; Ford, 1975; Gates et al., 1983; Naylor, 1976; Obeid et al., 1967; Waller, 1985). Since the initial work of Koyama and Kira (1956), there have been numerous studies that show competition can cause positive skewness. One-sided competition, in which large plants suppress small ones (but not vice versa) has often been considered to be a primary cause of positive skewness (Ford, 1975; Obeid et al., 1967; Schmitt et al., 1987; Firbank & Watkinson, 1985; Weiner, 1985).

Experimental methods for testing the one-sided competition model, however, have not always been clearly defined. Turner and Rabinowitz (1983) proposed that a critical test requires a comparison of frequency distributions of plant mass in even-aged monocultures grown at different densities. If one-sided competition is important, stands at high density should have greater skewness than low-density stands of the same mean mass. Weiner and Thomas (1986) reviewed 16 density experiments and

found that skewness increased with density in 14 of them. They cited these findings as evidence to support the one-sided competition model. Such density tests must assume, however, that one-sided competition is not confounded with other factors that are also density dependent and capable of causing skewness.

In this study, I examined an alternative to one-sided competition as an explanation for the relationship between plant density and skewness. If density is so low that ecological neighborhoods (Antonovics & Levin, 1980) do not overlap, variation in the number of neighbors will not cause plants with the same mass to grow at different rates. As density increases, and competition for limited resources occurs, not all plants with the same mass will have identical neighborhoods and there will be variance in growth caused by neighborhood heterogeneity. Previous models have demonstrated that variance in growth of individuals with the same mass can generate positive skewness if the variance in absolute growth rate is correlated with size (Aikman & Watkinson, 1980; Ford & Diggle, 1981; Hara, 1984; Koyama & Kira, 1956). Thus, differences in frequency distributions of stands with different densities may be caused by neighborhood heterogeneity, by one-sided competition, or both.

I believe it is not just the variance in growth rates of plants with the same sizes, but rather the distribution of such growth rates, that determines the degree of skewing. That is, two populations may have equal variance in relative growth rate,

but still have different size distributions at the end of the growth period, if the populations vary in the skewness of the relative growth rate distribution. It is possible to demonstrate with simple simulations (not reported in this thesis) that the skewness of the relative growth rate distribution can influence the skewness of the resulting size distributions. In particular, as relative growth rates became more positively skewed, so did the size distributions in the comparisons I made. Increasing skewness of size distributions with increasing skewness of relative growth rate distributions intuitively makes sense because an increasingly smaller percentage of plants of each size would have fast growth rates, and thus an increasingly smaller percentage of plants would be of large size at the end of the growth period. However, the generality of this prediction is not evaluated in this thesis.

Results from two studies of coniferous trees suggest that neighborhood heterogeneity may be involved in causing skewness of size distributions. First, in the absence of one-sided competition, variance in the growth of ponderosa pines (Pinus ponderosa Dougl.) with the same mass caused skewed frequency distributions to develop (Petersen, 1988). (A similar pattern was observed in herbaceous plants (Hara, 1984)). Second, stands of Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco), which were planted in different spatial arrangements, but had the same stand density, developed size distributions with different degrees of skewness (see Chapter 2 of this dissertation). Thus,

neighborhood heterogeneity can be sufficient to cause skewness, even if one-sided competition does not exist.

This study simulates plant growth over a wide range of stand densities with no mortality or one-sided competition. The only source of variation in growth of plants with the same mass is the number of neighbors with overlapping neighborhood areas. I thereby examine the potential for neighborhood heterogeneity that is density-dependent to cause skewed frequency distributions.

MODEL FORMULATION

Assumptions and Hypotheses

Suppose there are N plants of the same genotype and age growing in a uniform environment of unit area. Individuals are randomly located within this area, and the only source of variation in the growth of plants with the same mass is the number of neighbors that compete for resources. There is no mortality or recruitment of new individuals.

Assume the ecological neighborhood of a plant is circular and a function of mass:

$$r = k w, \quad (1)$$

where r is the radius of the neighborhood area, w is plant mass, and k is a constant of proportionality. Growth is not affected by other plants utilizing environmental resources from outside the area defined by r .

Previous simulations have modeled neighborhood area as being independent of plant size or, more commonly, as an exponential function of size. I did not examine how these various forms of Eqn. (1) affects the outcome of the simulations. In my model, with the number of neighbors being a constant proportion of plant size, larger plants will have more neighbors on the average than smaller ones. Other forms of Eqn. (1) could produce the same number of neighbors for plants of all sizes (e.g. when neighborhood area is constant), or even less

where g is relative growth rate, n is number of neighbors with overlapping neighborhood areas, g_m is relative growth rate when $n = 0$, and c is a decay constant. Because Equation (2) does not include the relative size of target plants and competitors, one-sided competition is not present in the model. Equation (2) fits the concave form of data on plant mass and indices of crowding often observed in plant populations (Silander and Pacala, 1985; Weiner, 1982). It is also analogous to models developed to describe mean yield-density relationships as suggested by the reciprocal yield law (Holliday, 1960; Kira et al., 1953; Willey & Heath, 1969).

Because spatial arrangement is random, n is distributed as a Poisson variable with $\bar{n} = N\bar{w}^2$, where N is stand density. For a given N , $\bar{n}_i > \bar{n}_j$ if $w_i > w_j$, and the reduction in \bar{g} caused by competition will be greater for plants with more mass. Therefore, g does not become positively correlated with mass as N increases, as when one-sided competition causes positive skewness (Ford, 1975; Petersen & Newton, manuscript in review). In the absence of both mortality and a positive correlation between relative growth rate and mass, any positive skewness that develops must be caused by the stochastic effects of neighborhood heterogeneity on the growth of individuals with the same mass.

Simulation

The simulation involved generating 1000 random deviates, representing the mass of "target" plants at time t , from a normal distribution with $\mu = 5$ and $\sigma = 1$. Target plants were located at the center of a square of unit area. For each plant, I randomly assigned coordinates for N potential neighbors per unit area. The mass of each neighbor was generated from the same distribution as the target plants. Parameter values in Equations (1) and (2) were $k = 0.05$, $c = 1$, and $g_m = 0.5, 1.0, 1.5$, and 2 . N ranged from 5 to 230 at intervals of 25. The small value of k eliminated the potential edge effect of the square area. For each combination of parameters, the simulation was repeated ten times.

Neighborhood area for each target plant and the N potential neighbors using Equation (1) were calculated. The number of competitors, n , for each plant was then determined based on the intersection of neighborhood areas; g was calculated for each target plant as in Equation (2). W_t and g were used to calculate absolute growth rate and mass at the end of one growth interval, W_{t+1} . Asymmetry of frequency distributions of W_{t+1} was measured by the skewness coefficient, which was calculated as the scaled third product moment about the mean. Other statistics, such as the coefficient of variation and the Gini coefficient, have been used to characterize size distributions in plant populations (Weiner & Thomas, 1986). Under certain

conditions, these statistics may have more ecological significance than the skewness coefficient (Weiner & Solbrig, 1984). However, in this study the analysis is restricted to the skewness coefficient.

For $g_m = 2$, the mean, variance, and skewness of growth rates of individuals within class intervals of one unit mass were calculated.

DEPENDENCE OF FREQUENCY DISTRIBUTIONS AND
PLANT GROWTH RATE ON DENSITY

As expected, the mean mass-density relationships (Fig. 1.1A) were concave to the axis of density. The skewness of frequency distributions of plant mass at the end of the growth interval depended on density and the maximum growth rate without competition (Fig. 1.1B). At the lowest density, where $N = 5$, the skewness coefficient remained near 0, as in the original normal distribution. Positive skewness developed as density increased, and reached its maximum at an intermediate density. It then declined to 0 as density continued to increase. When maximum relative growth rate with no competition, g_m , was greater, the skewness coefficient increased and the peak occurred at a higher density. Maximum skewness roughly corresponded to the inflection points of the mean mass-density relationships.

Mean growth rate decreased with density as plants had more neighbors with overlapping neighborhood areas (Fig. 1.2A). The relationship between growth rate and initial mass was linear or slightly convex at all densities. Variance in growth rate of plants with the same initial mass was also dependent on stand density, with the maximum variance occurring at a relatively low density (Fig. 1.2B). While variance is often proportional to size, the simulation produced an interaction between the effects of density and mass on variance (Fig. 1.2B). The maximum

variance when $g_m = 2.0$ occurred at a lower density ($N = 30$) than that when skewness was greatest ($N = 105$).

Density also influenced the skewness of growth rates of plants with the same mass (Fig. 1.3). At the lowest stand density ($N = 5$), frequency distributions of growth rates within class intervals were negatively skewed because most plants of a given mass had relatively few competitors and thus maintained high growth rates. At higher densities, when most plants had many competitors, the situation was reversed and the frequency distributions of growth rates became positively skewed. As pointed out in the introduction, I believe such skewness in relative growth rates contributed to the skewness in size distributions, though I have not proven mathematically that this will always be the case.

DISCUSSION

The simulations indicate that density has four effects on size distributions when spatial pattern is random. These are as follows: (1) Variance in growth of plants with the same mass, as a result of neighborhood heterogeneity, declined after reaching a peak at a low density. As the variance decreases, the increase in skewness as plants grow is less, as shown by Hara (1984). Thus, the results suggest that neighborhood heterogeneity was a more important cause of skewness at lower densities than at higher ones. (2) In the absence of one-sided competition, the relationship between mass and growth rate was linear or convex to the axis of mass. Linear and convex functions increase the mean and variance with time, but do not generate positive skewness (Hara, 1984; Westoby, 1982). (3) The slope of the relationship between mass and growth rate decreased with increasing density. A smaller slope indicates less of a difference between small and large plants in their mean growth rates. Therefore, a decrease in slope would tend to cause less of an increase in skewness. (4) Growth rates of plants with the same mass become positively skewed as density increases. In contrast to the first three effects, this one would promote more positive skewness at higher densities.

These results indicate that the coefficient of variation is a key parameter in evaluating the mathematical basis for skewness. The effects of density on both the mean and variance in

growth rates of plants with the same size are reflected in the coefficient of variation. Because the coefficient of variation incorporates both a measure of the mean and variance, it may be the most useful statistic for evaluating the dynamics of size structures.

Density-dependent neighborhood heterogeneity had multiple effects on growth functions that regulate the development of size distributions. Some of these effects promote, and others inhibit, skewness. Given the conditions of my model (e.g., no one-sided competition or sources of variable plant growth other than neighborhood heterogeneity), the net effect is maximum skewness at intermediate densities.

The objective of this work was to answer a question with computer simulations that I found impossible to answer with a mathematical proof: "Does the variance in the number of neighbors of plants with the same size change with density such that skewed size distributions develop?". I wanted to answer this question in general, and not specifically for a given age, species, or environment. It is interesting, however, to note that maximum skewness at intermediate densities, as in the simulations, does not agree with experimental studies in which the maximum occurs at highest stand densities (Ford, 1975; Hawthorn and Cavers, 1982; Jack, 1971; Naylor, 1976; Obeid et al., 1967). There are several possible explanations for this result. First, the range of densities in experimental studies may not have been sufficiently high that skewness decreases

after reaching a maximum (i.e. beyond the inflection point of the mean mass-density relationship). This seems unlikely because many studies have included very dense stands. A more probable explanation is that other factors cause skewness at high densities where the effects of neighborhood heterogeneity become negligible. It is also possible that the high densities used in this study are not biologically realistic.

Comparison of my simulation with those density experiments cited in the previous paragraph therefore suggests that stand structure is a product of several processes. The relative importance of any one process likely depends on stand density. As the effect of neighborhood heterogeneity becomes increasingly less important at high densities, other processes such as one-sided competition, might become relatively more important. The net effect could then be a monotonic increase in skewness with density, as previously observed (Ford, 1985; Hawthorn and Cavers 1982; Jack, 1971; Naylor, 1976; Obeid et al., 1967). To evaluate this prediction, it would be useful to calibrate the simulation such that distances among neighbors, neighborhood areas, and the number of neighbors match known empirical data for a species of a given age.

The simulation only examined changes in skewness during one growth interval. Until mortality begins, the patterns observed would continue in future growth intervals, as long as the growth functions determined by Equation (2) are stable.

This simulation has several implications for experimental

studies designed to evaluate the relative importance of one-sided competition in determining stand structure. The simulations suggest that comparing skewness of stands at different densities is inconclusive because factors other than one-sided competition may also be density-dependent. If spatial arrangement is not uniform, neighborhood heterogeneity may cause skewness to increase with density by affecting the growth of plants with the same initial mass. If this is the case, positive skewness may be attributed to one-sided competition when variation in the spatial arrangement of neighbors is the primary cause.

Schmitt et al. (1987) pointed out that analyzing the relationship between growth rate and initial mass provides a less ambiguous test for the existence of one-sided competition than does analysis of skewness of size distributions. On the basis of the simulation results, I suggest that analysis of the variance in plant growth will also help clarify the relative importance of processes determining stand structure.

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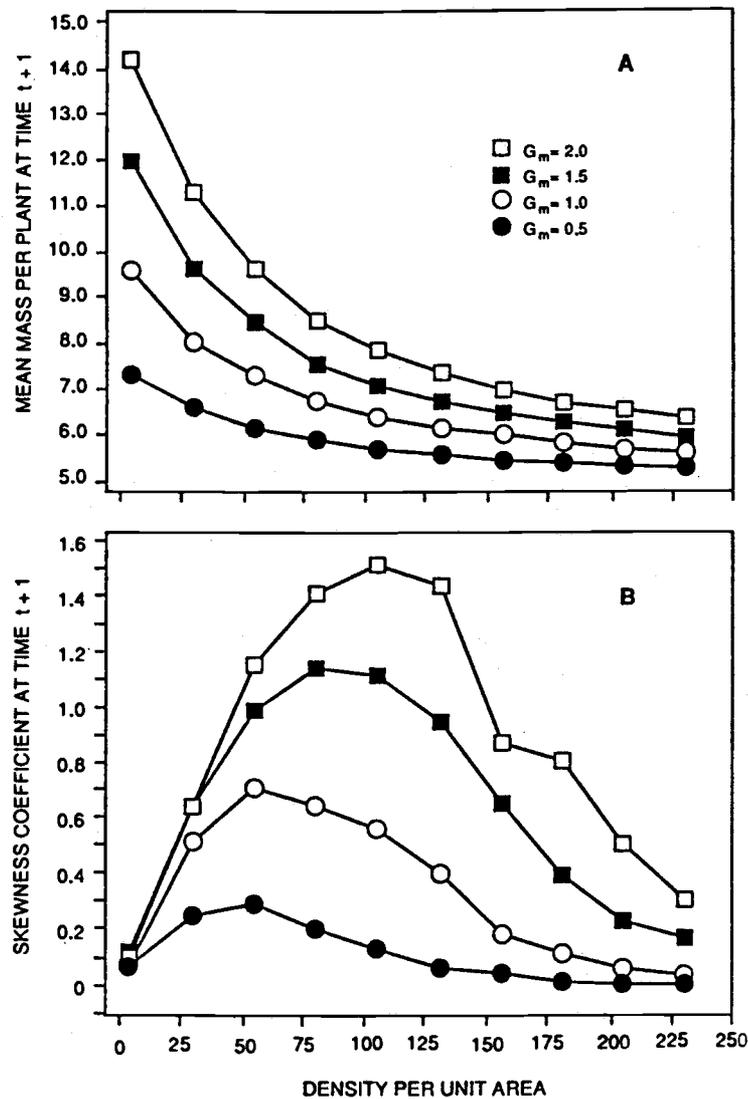


Figure 1.1. Mean (A) and skewness coefficient (B) for plant mass in computer-simulated stands at the end of one growth interval, time $t+1$, in relation to the density of plants per unit area. Data points are means of ten simulations, each with 1000 observations. Frequency distribution of mass at the beginning of the interval was normal with $\mu = 5$ and $\sigma = 1$. Data are for four values of maximum relative growth rate without competition, g_m , in the equation $g = g_m / (1 + n)$, where g is relative growth rate with competition and n is the number of neighbors with overlapping neighborhood areas.

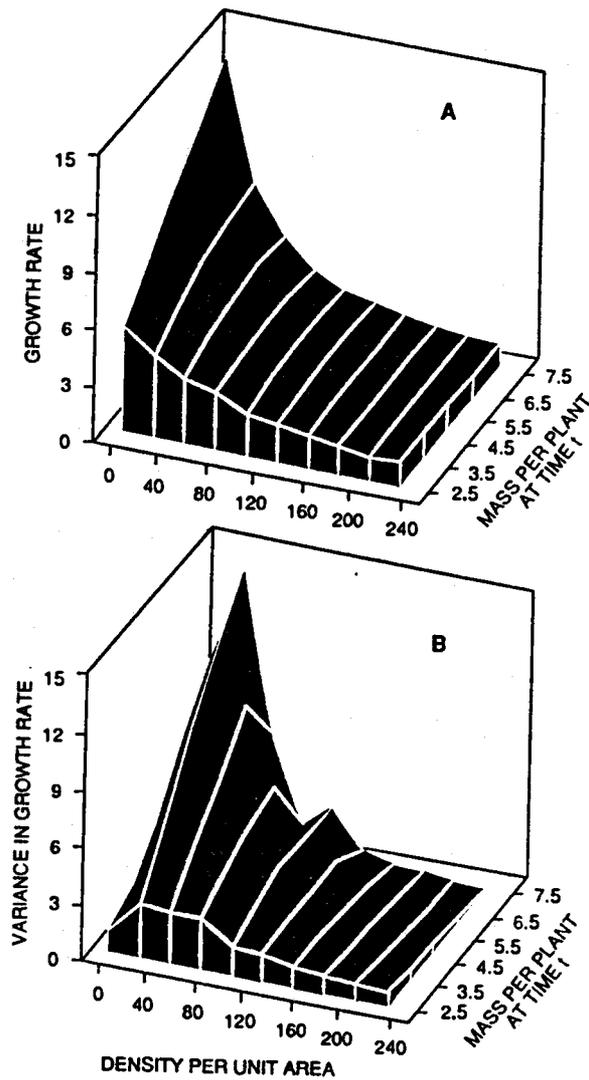


Figure 1.2. Mean absolute growth rate (A) and variance in absolute growth rate (B) in relation to initial mass at time t and the density of plants per unit area. Data points are means of ten simulations, each with 1000 observations. Data are for a maximum relative growth rate without competition, g_m , of 2 in the equation $g = g_m / (1 + n)$, where g is relative growth rate with competition and n is the number of neighbors with overlapping neighborhood areas.

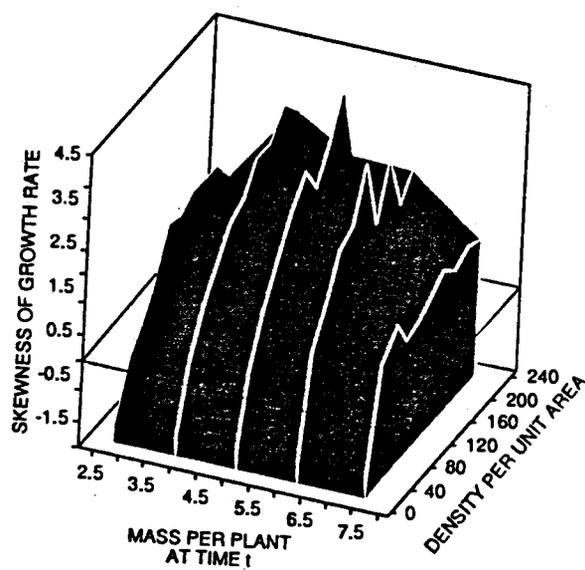


Figure 1.3. Skewness coefficient for growth rate in relation to initial mass at time t and the number of plants per unit area. Data points are means of ten simulations, each with 1000 observations. Data are for a maximum relative growth rate without competition, g_m , of 2 in the equation $g = g_m / (1 + n)$, where g is relative growth rate with competition and n is the number of neighbors with overlapping neighborhood areas.

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GENESIS OF SIZE HIERARCHIES IN
DOUGLAS-FIR (PSEUDOTSUGA MENZIESII) BY ONE-SIDED COMPETITION:
EFFECT OF SEEDLING SPACING

SUMMARY

Two explanations for the development of size hierarchies in stands of Pseudotsuga menziesii seedlings were evaluated: (1) one-sided competition causes absolute growth rates to be disproportionate to initial mass, and (2) variation in available space per seedling causes individuals with the same mass to have different growth rates. Seedlings were established in random or hexagonal arrangements at a total density of 400 m^{-2} . Mean growth from 46 wks to 58 wks after planting was directly proportional to initial mass at 46 wks in the random arrangement. In the hexagonal arrangement, the relationship between growth and mass was nonlinear and could be described by a second-order polynomial concave to the axis of initial mass. Skewness and inequality of frequency distributions of seedling mass in both arrangements were accentuated by variance in growth of seedlings with the same initial mass. Analysis of individual-plant growth provides a less ambiguous test of the one-sided competition model of size hierarchies than analysis based solely on frequency distributions of plant sizes.

Keywords: frequency distributions--stand structure--skewness--mass inequality.

INTRODUCTION

Before self-thinning begins, frequency distributions of plant mass often increase in asymmetry with time (Koyama and Kira 1956; Obeid et al. 1967; Ford 1975; Bazzaz and Harper 1976; Naylor 1976; Gates et al. 1983; Waller 1985). One factor often suggested as causing, or at least accentuating, asymmetry is competition described as asymmetric (Naylor 1976; Begon 1984; Huston and DeAngelis 1987), one-sided (Ford 1975; Ford and Diggle 1981; Cannell et al. 1984; Firbank and Watkinson 1985), dominance and suppression (Turner and Rabinowitz 1983; Weiner 1985; Schmitt et al. 1986), or resource pre-emption (Weiner and Thomas 1986). Larger individuals are thought to suppress small neighbors by preempting a disproportionate share of resources. Absolute growth rates become disproportionate to mass, and relative growth rates become positively correlated with mass. Asymmetric frequency distributions of plant mass result that reflect a hierarchy of dominance and suppression (White and Harper 1970).

Begon (1984) has suggested that size hierarchies result from a more general phenomenon: individuals that are fittest (as measured by size) before intraspecific competition are least affected by it, and the least fit plants are most affected. A plant has longer to accumulate mass before competing for resources if it emerges earlier or is more distant from its neighbors. The one-sided competition model predicts that

variation in spatial arrangement or time of emergence will accentuate differences in mass that are established early, producing a more hierarchical stand structure (Watkinson et al. 1983).

Theoretical and empirical evidence indicate that variation in growth of plants with the same initial mass can also accentuate asymmetry (Koyama and Kira 1956; Ford and Diggle 1981; Hara 1984). Hara (1984) developed a model of stand dynamics that included a mortality function and two "distribution-modifying" growth functions: (1) a deterministic function describing the relation between growth and initial mass, and (2) a stochastic function describing the relation between variance in growth and initial mass.

This study evaluates spatial arrangement as a determinant of intensity of one-sided competition and, consequently, the asymmetry and inequality of frequency distributions of plant mass. I first model one-sided competition using Hara's (1984) distribution-modifying functions. I then compare predictions from these simulations to results from experimental stands of seedlings of Pseudotsuga menziesii (Mirb.) Franco with constant total density but different spatial arrangements.

The hypothesis I test in this study has two parts: (1) frequency distributions of plant mass are more hierarchical when spatial pattern is random, and (2) greater asymmetric suppression of small plants by large ones is the reason for more skewness in random arrangements. The criterion for testing

these predictions are described in detail in the following sections.

Distribution-modifying functions and size hierarchies

Westoby (1982) and Hara (1984) have shown that asymmetry of size distributions changes with time and distributions remain unimodal when the relationship between initial mass (w_i) and absolute growth rate (dw/dt) is described by a second-order polynomial with respect to w_i :

$$dw/dt = \beta_1 + \beta_2 w_i + \beta_3 w_i^2 \quad (1)$$

or, in terms of relative growth rates, when

$$(1/w_i) \cdot (dw/dt) = \beta_1/w_i + \beta_2 + \beta_3 w_i. \quad (2)$$

These distribution-modifying functions are deterministic, since they do not account for variation in growth of plants with the same initial mass. If β_2 and β_3 are positive, Eq. (1) is concave to the axis of w_i , and positive skewness is generated as the relative frequency of small plants increases with time. If $\beta_3 = 0$, dw/dt is a linear function of w_i . When such a linear relationship exists, and if there is no variance in the growth of plants with the same mass, the mean and variance of the distribution increase but the degree of asymmetry remains constant (Westoby 1982).

The stochastic function that modifies distributions

describes the relationship between the variance in growth rate and initial mass. If the variance in absolute growth rate is proportional to w_i , such that

$$\sigma^2(dw/dt) = k w_i, \quad (3)$$

skewness will increase as plants grow, even if $\beta_3 = 0$ and dw/dt is a linear function of w_i (Hara 1984). Equation (3) can be restated in terms of relative growth rates as

$$\sigma^2(1/w_i \cdot dw/dt) = k (1/w_i), \quad (4)$$

since $\sigma^2(cx) = c^2\sigma^2(x)$, where c is a constant (Neter and Wasserman 1974). Differences among populations in the asymmetry of their frequency distributions can be attributed to the value of k if Eqs. (1) and (2) are the same for each population (assuming mortality functions are the same and distributions are identical at the beginning of the growth period).

Different combinations of the deterministic and stochastic functions may generate identical frequency distributions of plant mass. However, the functions probably represent quite different ecological processes. One-sided competition generates size hierarchies by making mean absolute growth rate disproportionate to mass and mean relative growth rate positively correlated with mass (Ford 1975). Relative growth rate of large plants may also be reduced by competition, but the traditional model of one-sided competition (Ford 1975) states that the reduction is less for large plants than for small ones.

One-sided competition is therefore expressed in the deterministic function (Eqs. (1) and (2)). In contrast, size hierarchies generated by variance in growth of plants with the same mass at the beginning of a growth period (Eqs (3) and (4)) result from environmental or genetic heterogeneity. Such size hierarchies cannot be considered evidence for one-sided suppression of small plants by large ones causing a positive correlation between relative growth rate and mass. It is impossible to infer which process has operated within a population from frequency distributions of plant mass. Conclusive demonstration that the intensity of one-sided competition causes differences in size hierarchies requires two conditions: (1) a difference in the deterministic function, reflecting greater suppression of small plants in populations with more asymmetric distributions and (2) constant stochastic effects of the second distribution-modifying function (as measured by the value of k in Eq. (3)). The importance of one-sided competition may be estimated incorrectly if evaluated on the basis of frequency distributions or a single distribution-modifying function.

METHODS

Experimental Design

Seedlings of *P. menziesii* were grown in an outdoor frame at the Forestry Sciences Laboratory of the U.S. Forest Service at Oregon State University, Corvallis. The frame (0.8 m x 1.6 m x 15 m) was filled with a local forest soil. Seedlings were grown from seed from four mature trees in a stand of Douglas-fir 50 km west of Corvallis. Progeny from each tree were at least half-siblings (only the maternal parent in common), but since the pollen source was unknown, some individuals from each family may have been full siblings. Eight hundred seed (200 from each family) were dried and individually weighed to the nearest 0.01 mg to determine the frequency distribution of seed mass.

Seeds were sown in two spatial arrangements on May 24 and 25, 1986: (1) random, in which planting spots corresponded to Cartesian coordinates selected with a random number generator, or (2) hexagonal, in which each individual had six equidistant first-order neighbors 5 cm away, 12 second-order neighbors 10 cm away, and so on. Planting spots (400 m^{-2}) were marked using a template with the proper coordinates. An equal proportion of the planting spots within each replication was assigned to each of the four families.

Each arrangement was randomly assigned to six 75- x 140-cm plots. Seeds were stratified before planting by soaking in

water for 24 hrs and cold storage at 20C for 4 wks. Three seeds were sown at each spot to increase the probability that at least one seedling would emerge. If more than one seedling emerged, those further from the marked spot were removed within three days of emergence. Most seedlings emerged within 2 weeks of planting, but some emerged up to 5 weeks later. At 1.3% of the planting spots, no seedling emerged within 6 weeks of planting. Seedlings planted adjacent to the experimental plots and from the same family as the missing ones were transplanted where seedlings failed to emerge. Transplanted seedlings and those in a 10-cm border of each plot were excluded from analysis. Plots were watered during dry periods throughout the experiment; seedlings were fertilized with a complete nutrient solution every 10 to 14 days during spring and summer.

Stem height and diameter of all seedlings were measured approximately 46 wks after planting. At this time, seedlings in one plot of each arrangement were harvested at ground level, dried at 65°C for 72 h, and individually weighed. Data from these seedlings were used to determine the allometric relationship between above-ground dry mass, seedling height, and basal stem diameter. The arrangements did not differ significantly ($P > 0.50$) in estimated coefficients of the allometric equations, so the data were pooled and seedling mass at 46 weeks (w_i) was predicted from height (h) and stem diameter (d) by the following equation ($r^2 = 0.88$):

$$\ln(w_i) = -5.79 + 1.14 \ln(h) + 0.88 \ln(d). \quad (5)$$

Approximately 58 weeks after planting, the seedlings in the remaining five plots of each arrangement were harvested, dried, and individually weighed. This was at the end of the period of active height growth, but earlier than originally planned. Some seedlings (<1%) were beginning to show symptoms of disease at 58 wks, and the decision was made to terminate the study early, rather than risk the potential for widespread disease. Absolute and relative growth rates of individual seedlings were calculated using predicted mass at 46 weeks from Eq. (5) and measured mass at 58 weeks. The final data set contained data from 1335 seedlings in the random arrangement and 1305 in the hexagonal.

To determine whether competition had reduced growth, I compared mean mass at 58 weeks to the mean mass of 120 seedlings (30 per family) that had been planted next to the plots at a 10-x 10-cm spacing. While not low enough to ensure total lack of competition, stand density was considerably lower than in the experimental plots.

Simulation

To simulate plant growth and evaluate the effects of the distribution-modifying functions on statistics describing frequency distributions of plant mass, random deviates (representing w_i) were generated from a normal distribution with

$\mu = 5$ and $\sigma^2 = 1$. Relative growth rates for each w_i were then generated from a normal distribution, with mean and variance as in Eqs. (2) and (4). Absence of one-sided competition was simulated by setting $\beta_1 = 0$, $\beta_2 = 2.0$, and $\beta_3 = 0$ (i.e., all individuals had a relative growth rate of 2.0). One-sided competition was simulated by making relative growth rate a positive linear function of initial mass (i.e., only $\beta_1 = 0$ in Eq. (2)). The slope of the relationship, β_3 , was calculated for each intercept value, β_2 such that relative growth rate for the largest individual was constant at 2.0. The simulation therefore represented extreme one-sided competition, in which the growth rates of the largest plants are unaffected by competition.

I modeled one-sided competition in this manner because my objective was to compare the relative importance of two causes of skewness: (1) one-sided competition that increases the slope of the RGR*size relationship, and (2) variation in growth of plants with the same size. By maintaining a constant RGR for the largest plants, the simulation maximized the effect of one-sided competition on skewing because the slope of the RGR*size relationship would be the maximum possible. In real stands, it is likely that the mean growth rates of large plants would also be reduced by competition and, therefore, the slope of the RGR*size relationship would be less than in the simulations. Thus, if increasing the intensity of one-sided competition in the simulations (i.e. increasing the slope of the RGR*size

relationship) has relatively little effect on the degree of skewing, the effect of such competition would be expected to be even less in real stands.

Values of β_2 ranged from 2.0 (absence of one-sided competition) to 0.75 (most intense one-sided competition). Values of k were 0, 0.3, and 0.6. When $k = 0$, growth rate is completely determined by the initial mass of an individual. As k increases, variance in growth of individuals with the same initial mass increases. For each combination of β_2 , β_3 , and k , the simulation was repeated ten times with distributions containing 1000 values.

Skewness and Gini coefficients were calculated for distributions generated by the functions at the end of one growth interval. The skewness coefficient, g_3 , was calculated as the scaled third product moment about the mean:

$$g_3 = n/(n-1)(n-2) \sum_{m=1}^n (w_m - \bar{w})^3 / s^3, \quad (6)$$

where n is the number of plants, w_m is mass of plant m at the end of the growth interval, \bar{w} is mean mass, and s is the standard deviation. Weiner and Solbrig (1984) criticized use of the skewness coefficient for ecological studies of frequency distributions because of its insensitivity to absolute plant mass. They suggested instead using the Gini coefficient, G , a measure of mass inequality. I calculated G as

$$G = \frac{1}{2 \bar{w} n (n-1)} \sum_{m=1}^n (2i - n - 1) w_m, \quad (7)$$

where the w_m are sorted from smallest to largest, and i is the ordered rank (Glasser 1962; Dixon et al. 1987). The theoretical range of G is 0 (complete equality of mass) to 1 (all mass concentrated in one individual).

Analysis

The Weibull distribution (Weibull 1951) was fitted to the seed and seedling data by the formula

$$f(w) = cb^{-c} w^{c-1} \exp(-(w/b)^c), \quad (8)$$

where $f(w)$ is the frequency of individuals with mass w , and b and c are parameters defining the shape and scale of the distribution. The Weibull approximates a normal distribution when $c = 3.6$ (Bailey and Dell 1973). Distributions are positively skewed when $c < 3.6$ and negatively skewed when $c > 3.6$. The Weibull function cannot describe the bimodal distributions that occur in some plant populations (Ford and Newbould 1970; Ford 1975; Mohler et al. 1978; West and Borough 1983). However, there was no indication of bimodality in my data (as judged by visual inspection of frequency distributions). The Kolmogorov-Smirnov one-sample test for goodness-of-fit was conducted using estimated Weibull parameters. Other distributions fit the data, but the Weibull distribution consistently provided the best fit.

The Gini and skewness coefficients for seed and seedling mass were calculated, and confidence intervals for each coefficient were determined by the bootstrap technique (Diaconis and Efron 1983). In this technique, each statistic is calculated for 1000 samples randomly taken from the original data with replacement, with sample size equal to the original number of seedlings in each arrangement. Confidence intervals are based on the distribution of the statistic calculated for each of the 1000 bootstrapped samples. Dixon et al. (1987) concluded that this method gives confidence levels for the Gini coefficient very close to stated values when sample sizes are large ($n > 100$).

The distribution-modifying functions describing the relation between growth and mass (Eqs. (1) and (2)) were fitted to the individual seedling growth data. Weighted least-squares regression was used to correct for heteroscedasticity (Neter and Wasserman 1974), as previously done with tree growth data by West (1980). The stochastic functions (Eqs. (3) and (4)) describing the relationship between mass and variance in growth at 46 weeks were estimated by calculating the variance in growth among seedlings within 0.5 g class intervals. Before estimating regression coefficients, I weighted the variance estimates by the frequency of seedlings within each class interval.

RESULTS

Simulation of Plant Growth

Plant growth did not change skewness when $\beta_3 = 0$ (relative growth rate independent of mass, absolute growth rate a linear function of initial mass) and $k = 0$ (no variance in the growth of individuals with the same initial mass) (Fig. 2.1a).

Skewness became more positive when k or β_3 increased; variance in growth could generate size hierarchies even if all plants had the same mean relative growth rate ($k > 0$ and $\beta_3 = 0$). The Gini coefficient (Fig. 2.1b) responded in a manner similar to skewness (Fig. 2.1a); as variance in growth increased, the effect of one-sided competition, as measured by β_3 , on skewness and inequality was reduced. Frequency distributions with equal values of inequality and skewness may be produced with different combinations of coefficients for the deterministic and stochastic distribution-modifying functions.

Comparison of Experimental and Predicted Values

The frequency distribution of seed mass was asymmetric, with relatively more large than small seeds (Fig 2.2a). However, seedling mass 46 weeks after planting was asymmetric in the other direction, with relatively more small seedlings than large (Figs. 2.2b and 2.2c). The Weibull function provided a good fit

to the frequency distributions of both seed and seedling mass (Kolmogorov-Smirnov test, $P > 0.99$). The skewness coefficient of seed mass was negative (Table 2.1). Seedling mass was positively skewed after 46 weeks and became more so after 58 weeks. Inequality of mass, as measured by the Gini coefficient, also increased with time in both arrangements. Inequality and skewness of seedling mass did not differ ($P > 0.05$) between the two arrangements at 46 weeks but did differ after 58 weeks, when both coefficients were greater in the hexagonal arrangement. Competition significantly reduced the mean biomass of seedlings in both high-density spatial patterns, as shown by the larger mean mass of seedlings planted at low density (Table 2.1).

In the random arrangement, the quadratic term in Eq. (1) was not significant ($P = 0.86$) and growth and mass were related linearly (Fig 2.3a). Because absolute growth rate was proportional to mass, the deterministic function did not cause skewness or inequality to increase with time. In the hexagonal arrangement, in contrast, the quadratic term was significant ($P = 0.007$) and the function was concave to the axis of initial mass (Fig. 2.3a). The significant quadratic term indicates that mean growth was disproportionate to initial mass. Therefore, the relationship between growth and mass at 46 weeks contributed to the increase in skewness and inequality in the hexagonal arrangement.

Relative growth rate was inversely related to mass in the random arrangement (Fig. 2.3b). In the hexagonal arrangement,

there was relatively little variation in relative growth rate among seedlings with different mass. The primary difference between the arrangements was attributable to the higher relative growth rate in the random arrangement of seedlings with mass less than about 0.5 g.

In both arrangements, variance in absolute growth rate was directly proportional to initial mass (Fig. 2.4a), and variance in relative growth rate was inversely related to mass (Fig. 2.4b). Growth was more variable in seedlings of a given initial mass in the random arrangement than in the hexagonal. In both arrangements, the relationship between variance in growth and mass accentuated skewness and inequality.

DISCUSSION

Spatial Pattern and Stand Structure

I expected to find more intense one-sided competition and, since one-sided competition reduces the relative growth rate of small plants more than large ones, a more hierarchical stand structure when seedlings were arranged randomly. Neither prediction was supported by the experiment with *P. menziesii*. Three results suggest that one-sided competition was more intense and a more important cause of hierarchical stand structure when the spacing was uniform: (1) the relationship between absolute growth rate and initial mass was nonlinear in the hexagonal arrangement but linear in the random; (2) relative growth rates of small seedlings in the hexagonal arrangement were less than those of seedlings of the same initial mass in the random; (3) stand structure became more hierarchical in the hexagonal arrangement, as measured by the skewness and inequality of seedling mass.

The prediction that one-sided competition makes stand structure more hierarchical when spacing is random assumes that mass is determined by available space, as measured by indices such as Thiessen polygons (Mead 1966). Such predictors of plant performance do not consider factors such as seed mass, emergence time, and genotype that also cause variability in plant mass (Ross and Harper 1972; Gross 1984; Hendrix 1984; Stanton 1984; Winn 1985; Wulff 1986; Kromer and Gross 1987). One or more of

these factors may have caused some seedlings with large amounts of space to be small and vice versa. This would have two effects on the distribution-modifying functions and the stand structure that they generate: growth of plants with the same mass would be more variable than if space and mass were related exactly, and mean growth of small plants would be increased by the greater growth of small plants with large amounts of space. Both possibilities are consistent with the results (Figs. 2.3 and 2.4). In the random arrangement, there may have been one-sided competition between large seedlings with lots of space and small neighbors with little space. But because of size variability caused by factors other than space, stand-level responses, i.e. skewness and inequality, evidently were not affected by such competition, if it did exist.

The influence of spatial arrangement on development of size hierarchies has previously been evaluated by examining frequency distributions of plant mass. Skewness, kurtosis, and the coefficient of variation differed in stands of Lolium perenne sown at the same total density but in different spatial arrangements (Naylor 1976). Weiner (1985) established monocultures of Trifolium incarnatum and Lolium multiflorum in random and hexagonal arrangements under low- and high-nutrient conditions. He found no consistent difference in the Gini coefficient between the two arrangements and concluded that spatial pattern was not as important as other factors in determining inequality of plant mass. In my stands of P.

menziesii, distance to neighbors was important in determining the intensity of competition, as indicated by the differences in the distribution-modifying functions between the spatial patterns. But when variation in available space was combined with other factors causing size variability, the consequence for stand structure was opposite to what was expected.

Spatial Pattern and Distribution-Modifying Functions

Frequency distributions by themselves do not indicate to what extent the deterministic and stochastic functions are responsible for skewness and inequality. The effect of spatial pattern on one-sided competition needs to be evaluated in terms of the functions that cause size hierarchies to develop as plants grow. Relatively few studies have quantified both distribution-modifying functions associated with plant growth. I know of none done specifically to evaluate the relative importance of one-sided competition as a cause of hierarchical stand structure. Thus it is difficult to generalize about the growth functions observed in my stands of P. menziesii. The linear relationship between growth and initial mass in the random arrangement agrees with functions reported for young Pinus radiata (West and Borough 1983), Pinus ponderosa (Petersen 1988), and Pinus contorta (Cannell et al. 1984). Hara (1984) also found mean growth to be a linear function of mass in seedling populations of Helianthus annuus. In contrast, the

relationship I found in the hexagonal arrangement agree with work by Yoda et al. (1957), in which relative growth rate in a stand of Hibiscus moscheutos was positively correlated with a plant's initial size relative to neighbors. They attributed the correlation to competitive interactions among neighboring plants. A concave quadratic polynomial also represented the relationship between increment in basal stem diameter and initial diameter in 56-year-old stands of Eucalyptus spp. (West 1980). Relative growth rate was positively correlated with initial size in dense stands, but negatively correlated in artificially thinned stands of Impatiens capensis (Schmitt et al. 1987) and 20-yr-old P. menziesii (Perry 1985). The linear relationship between absolute growth rate and initial mass observed in young plants often becomes nonlinear as they age, presumably because of more intense competition (West and Borough 1983; Cannell et al. 1984; Hara 1984). These previous studies demonstrate that the form of the deterministic distribution-modifying function depends on stand density and age. My results indicate that spatial arrangement also will influence the relationship.

The stochastic distribution-modifying function has been quantified less often than the deterministic function. Hara (1984) found that variance in growth rates of individuals with the same initial mass in experimental populations of Helianthus annuus was a more important cause of skewness in the seedling stage than were size-dependent relative growth rates. Petersen

(1988) also attributed the development of skewed frequency distributions in stands of Pinus ponderosa to variation in growth rate of trees with the same initial size, rather than to a nonlinear relationship between absolute growth rate and initial size. Ford (1975) found that variation in relative growth rate was greater among large individuals of Picea sitchensis than among small ones, which may have contributed to the differences in skewness he observed among stands grown at different densities. Variance in absolute stem-diameter increment was correlated with initial diameter in stand of Eucalyptus spp. (West 1980), Pinus radiata (West and Borough 1983), and multi-species temperate rain forests (Kohyama 1987). In my experiment, the development of size hierarchies was accentuated by variance in growth of seedlings with the same mass.

The simulation of plant growth in monocultures by Aikman and Watkinson (1980) also demonstrated that more intense one-sided competition accentuates skewness of frequency distributions through time. Their model, however, included only a single level of variance in the growth rate of individuals with the same initial mass. My simulation results are also similar to those of Ford and Diggle (1981), except they used a deterministic growth function that results in bimodality (Westoby 1982). My results and theirs demonstrate that increasing variation in the growth of individuals with the same mass increases skewing. Ford and Diggle (1981) assumed that

variance in relative growth rate was constant among individuals of different mass, which is equivalent to a positive correlation between variance in absolute growth rate and initial mass. Therefore, variance in growth rate may provide an alternative explanation to one-sided competition for establishment and maintenance of size hierarchies in populations of many plant species.

An apparent anomaly exists among data presented in Table 2.1 and Fig. 2.4. Variation in mass relative to the mean mass (as measured by the Gini coefficient and the C.V.) was greater in the hexagonal arrangement by the end of the study (58 wks). But as shown in Fig. 2.4, growth rates of seedlings with the same size were more variable in the random arrangement. This greater variation, by itself, would cause the C.V. and the Gini coefficient to be greater in the random arrangement. The fact that this did not happen is further evidence that size structures are a product of both the deterministic (Fig. 2.3) and stochastic (Fig. 2.4) functions. Skewing due to variable growth rates (Fig. 2.4) was accentuated by the concave RGR*size relationship that existed in the hexagonal arrangement, but not in the random arrangement (Fig. 2.3). Apparently, the concavity of the RGR*size relationship more than compensated for less variation in growth of plants with the same size. The net effect was a greater C.V. and Gini coefficient in the hexagonal arrangement.

Tests of One-Sided Competition

Turner and Rabinowitz (1983) proposed that a critical test of the one-side competition hypothesis of size hierarchies requires a comparison of frequency distributions of plant mass in even-aged monocultures grown at different densities. If one-sided competition is important, stands at high density should have greater skewness (and inequality) than low-density stands of the same mean mass. Many tests of one-sided competition using this approach have appeared recently (Turner and Rabinowitz 1983; Waller 1985; Weiner 1985, 1986; Schmitt et al. 1986). Weiner and Thomas (1986) reviewed 16 experiments in which size inequality at different densities could be measured; fourteen showed increased inequality at higher densities, which they cited as evidence for one-sided competition. Similarly, studies in which inequality or skewness were consistently correlated with density have been cited to support other explanations (Turner and Rabinowitz 1983; Waller 1985).

While a change in skewness and inequality with density would be consistent with the one-sided competition model, I consider it to be inconclusive evidence. The same reasoning used in my study can be applied to the density test proposed by Turner and Rabinowitz (1983). Tests based on frequency distributions cannot reject alternative hypotheses the the structure of stands grown at different densities varies for reasons other than one-sided competition. If spacing is irregular, variance in growth

of plants with the same mass may change with stand density. If density is so low that zones of influence do not overlap, interference from neighbors will not add to variance in growth of plants with the same initial mass. As density increases, however, different plants with the same mass will have different numbers and arrangements of neighbors. Such increase neighborhood heterogeneity could increase variance in growth, just as I observed with random spacing. More hierarchical stand structure at higher densities could mistakenly be attributed to one-sided competition, when variation in neighborhood conditions is actually the primary cause.

Schmitt et al. (1987) pointed that analyzing the relationship between growth rate and initial mass provides a less ambiguous test for the existence of one-sided competition than does analysis of frequency distributions. Such analysis of the deterministic distribution-modifying function may be sufficient to test for the existence of one-sided competition, but determining its importance relative to other processes requires quantification of both distribution-modifying functions.

ACKNOWLEDGMENTS

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Table 2.1. Mass, skewness, and Gini coefficient for *P. menziesii* seed and seedlings. High-density seedlings were measured 46 and 58 weeks after planting in either a hexagonal or random arrangement; low-density seedlings were measured 58 weeks after planting. Bootstrapped 95% confidence intervals for the Gini and Skewness coefficients are in parentheses.

	Mass		Skewness (g ₃)	Gini (G)
	Mean	S.D.		
Seed (mg)	11.8	2.14	-.376(-.523- -.207)	.051(.048-.053)
Seedlings--46 wks (g)				
Random	1.41	.63	.469(.388-.545)	.126(.122-.130)
			NS	NS
Hexagonal	1.61	.74	.587(.463-.684)	.129(.125-.134)
Seedlings--58 wks (g)				
Random	3.45	1.72	.763(.656-.857)	.139(.135-.142)
			*	**
Hexagonal	3.53	1.94	.899(.774-.880)	.152(.147-.156)
Low density	5.68	5.10		

*, $P < 0.05$; **, $P < 0.01$; NS, nonsignificant difference between spatial arrangements.

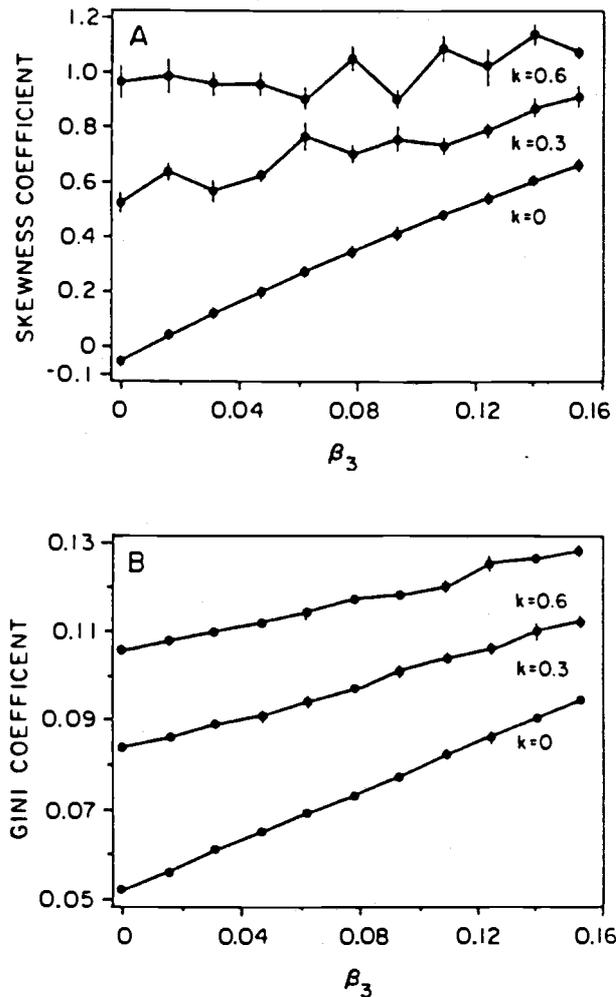


Figure 2.1. Skewness coefficient (A) and Gini coefficient (B) of frequency distributions produced when the two distribution-modifying functions are applied to an initially normal distribution. The x-axis is β_3 in the deterministic function (Eq. 2); k is the constant of proportionality in the stochastic function (Eq. 4). Each point is the mean of ten simulations, each with 1000 values. Vertical bars are standard errors.

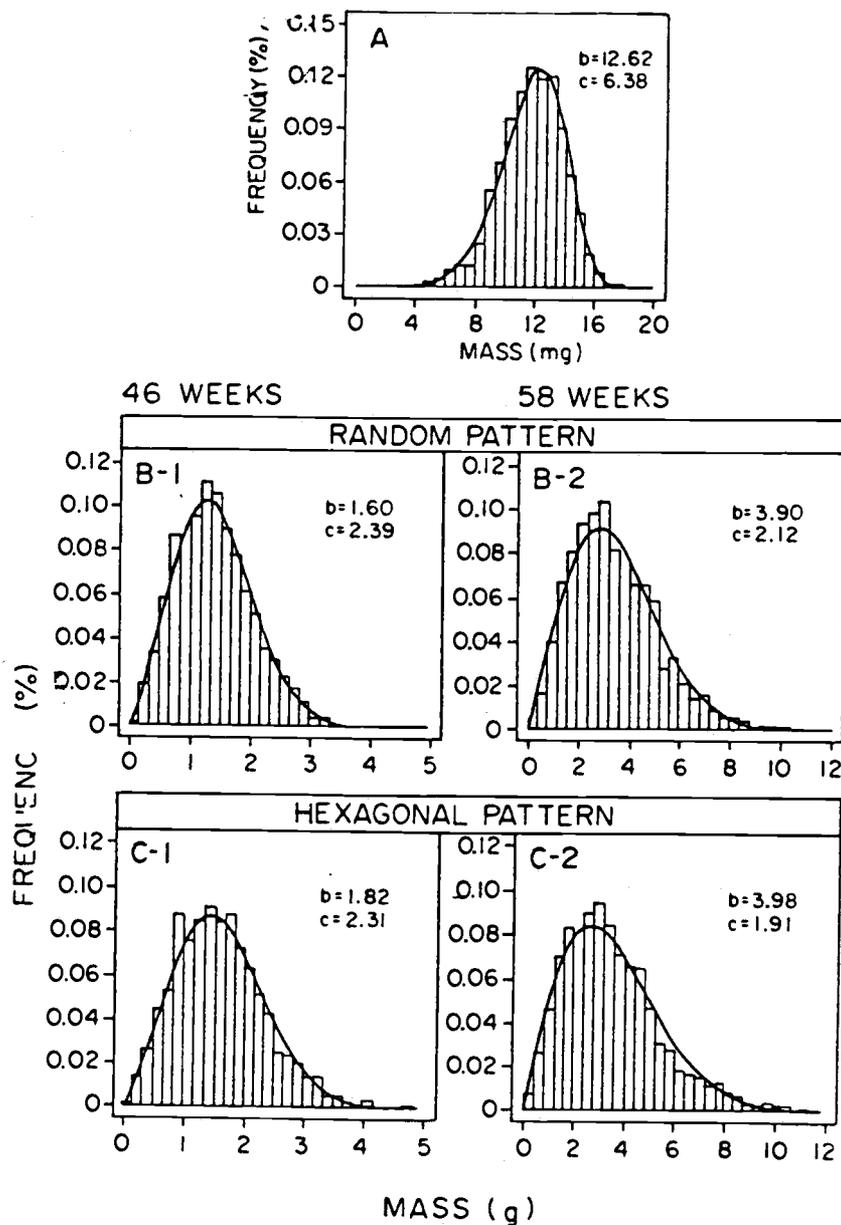


Figure 2.2. Frequency distribution of *P. menziesii* (A) seed mass, (B) mass of seedlings planted in a random design (B1) 46 and (B2) 58 weeks, and (C) mass of seedlings planted in a regular hexagonal design after (C1) 46 and (C2) 58 weeks. Predicted values (smooth curves) are from the Weibull function (Eq. 8) using estimated coefficients; b = scale parameter, c = shape parameter.

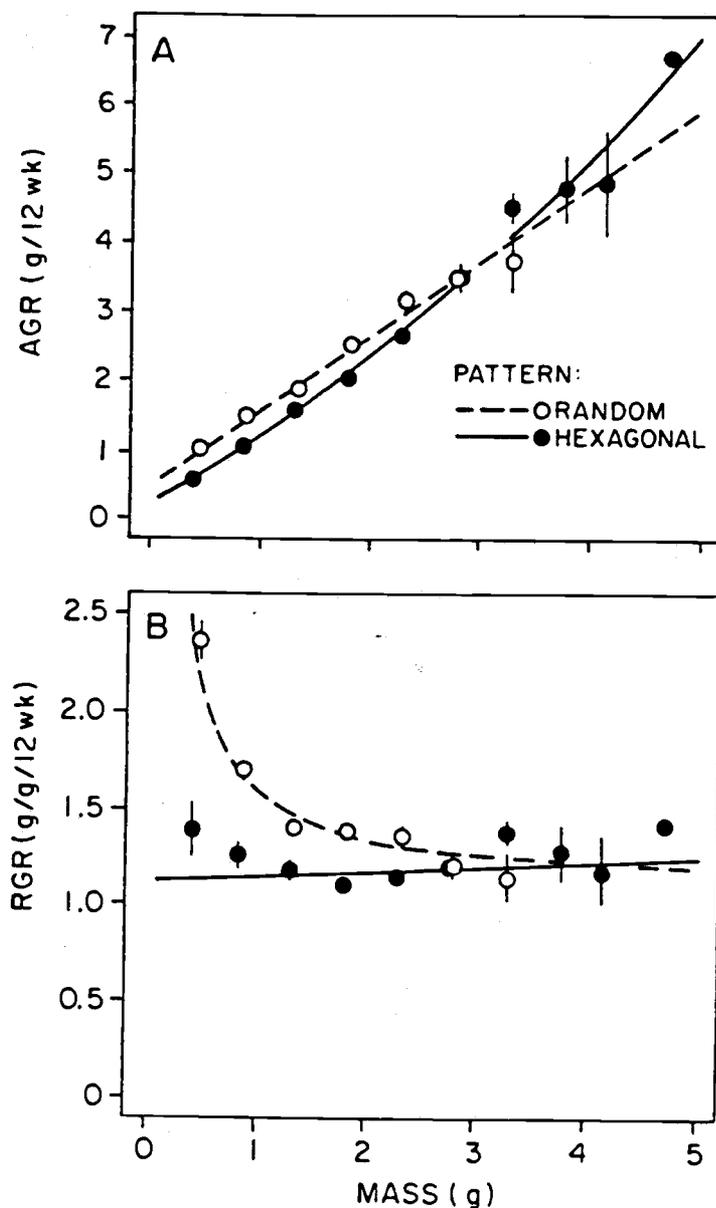


Figure 2.3. Relationship between seedling mass at 46 weeks and (A) absolute growth rate (AGR) and (B) relative growth rate (RGR) to 58 weeks, for *P. menziesii* seedlings arranged in a random or a regular hexagonal pattern. Curves showing predicted values are from regression equations using individual seedling data weighted by the variance in growth, as described in the text. Points are means within 0.5 g class intervals. Vertical bars are standard errors.

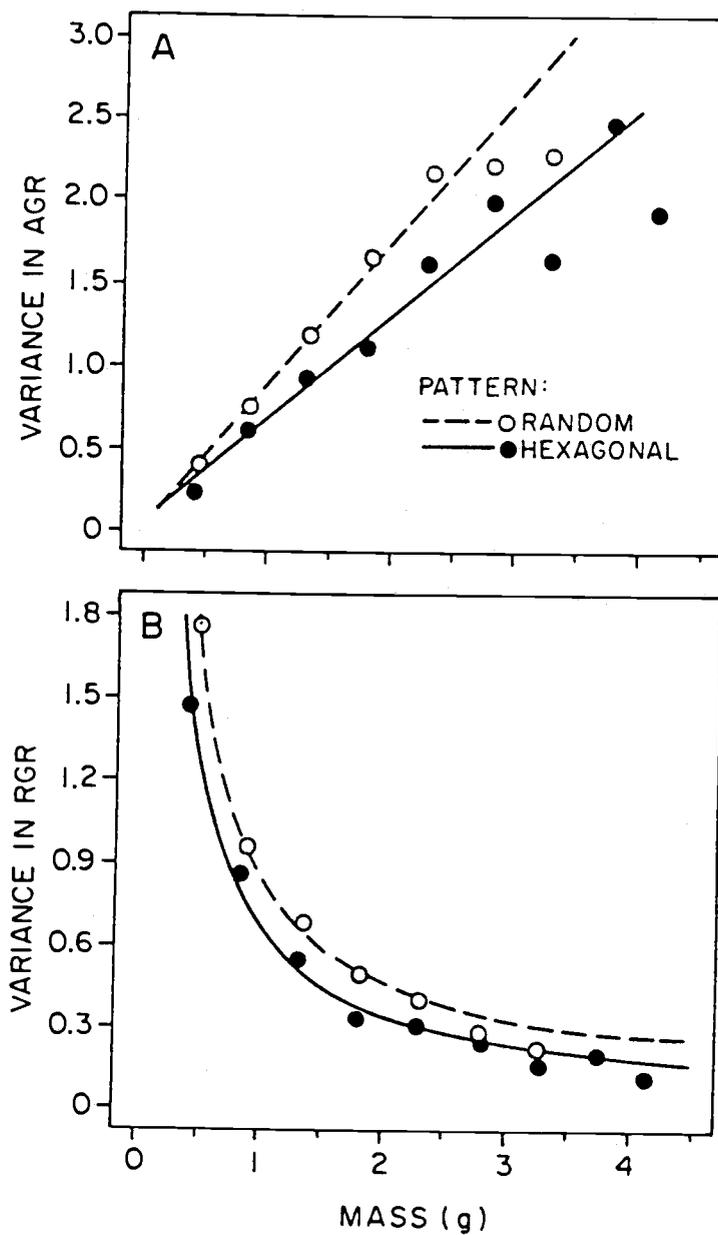


Figure 2.4. Relationship between seedling mass at 46 weeks and (A) variance in absolute growth rate (AGR) and (B) relative growth rate (RGR) to 58 weeks, for *P. menziesii* seedlings in a random or a regular hexagonal pattern. Variance estimates are based on seedlings within 0.5-g class intervals. Curves showing predicted values are from regression equations weighted by the frequency of seedlings within each interval.

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DYNAMICS OF SIZE STRUCTURES IN FRAXINUS MANDSHURICA
STANDS OF NORTHEAST CHINA

SUMMARY

Dynamics of size structures in seedling stands of Fraxinus mandshurica were examined by observing growth rates of individual seedlings. Experimental stands with varying densities were established from seed on an abandoned field in northeast China. In most stands, inequality and skewness in frequency distributions of mass increased with density and age. Vertical distributions of leaf area, light attenuation curves, and specific leaf areas indicated that competition between large and small seedlings was asymmetric, particularly at higher densities. Differences in size structures among density classes were attributed to variation in the growth of individuals with the same mass, rather than a positive correlation between relative growth rate and mass. A stochastic model describing asymmetric competition in heterogeneous neighborhoods are more appropriate for the size structure of these stands than are deterministic models that do not account for variance in growth rates of plants with the same size.

Keywords: asymmetric competition, density, mass inequality, Gini coefficient, skewness.

INTRODUCTION

The linear relationship between the reciprocal of mean plant weight and stand density is often considered to be one of the few "laws" of plant population ecology (Harper 1977, p. 156). Though less well studied than the mean, other characteristics of size structures (defined here as frequency distributions of plant mass) are also density-dependent. For example, inequality of plant mass increases with density of many species that have been studied (Weiner and Solbrig 1986). Because stands may have equal mean size, yet differ in traits such as inequality (Schmitt et al. 1986) and skewness (Petersen 1988), mean plant size is of limited value for describing size structures.

Hara (1984, 1988) has described how the dynamics of size structures can be modeled with three functions: (1) $G(t,x)$, the mean growth rate of individuals of mass x at time t , (2) $D(t,x)$, the variance in growth rate of plants with mass x at time t , and (3) $M(t,x)$, the mortality of plants with mass x at time t . These functions are used in this study to test alternative hypotheses for explaining differences in size structures among stands with varying densities. These alternative hypotheses are: (1) a positive correlation between relative growth rate and mass (the $G(t,x)$ function), suggesting that asymmetric competition is important (Ford 1975, Schmitt et al. 1987), and (2) if variation in growth of plants with the same mass (the

$D(t,x)$ function) is primarily responsible for skewing, then genetic, environmental, or neighborhood heterogeneity is suggested (Hara 1988). Because identical size structures may result from different combinations of the functions, analysis of the functions, rather than size structures themselves, provides more conclusive tests the alternative hypotheses.

This study describes how size structures in seedling stands of the tree, Fraxinus mandshurica, change with time and density prior to the onset of self-thinning mortality. Growth of individuals is analyzed to determine whether a positive correlation between relative growth rate and mass is responsible for these changes. Asymmetric competition for light is evaluated as an explanation for size structure dynamics by comparing growth functions, vertical distributions of leaf area, and light attenuation curves.

METHODS

Study Site and Experimental Design

The study was conducted at the Maoershan Experimental Forest (127° 34'E, 45°20'N) located about 90 km southeast of Harbin, China, in the Changbai Mountains. Forests of the region are mostly mixed conifer/broadleaf stands established after extensive cutting in the early part of this century. The experimental site was an abandoned field previously cleared of trees in order to produce food crops. The site had an extensive cover of herbaceous vegetation and a few young trees invading from adjacent stands. All plants were removed from the site before establishment of the study, and hand weeding was conducted as needed during the course of the study.

Four densities were each randomly assigned to two plots (50 cm x 50 cm) within each of four rows (a total of 32 plots). The rows were parallel to one another and separated by 75 cm. Seeds of F. mandshurica were sown in these plots at rates of 34, 79, 228, and 760 g m⁻². With a predicted germination rate of 60% (based on previous observations in a nearby tree seedling nursery) and a mean of 10.9 seeds g⁻¹ fresh weight, I expected the seed sown to produce seedling densities of 225, 500, 1500, and 5000 seedlings m⁻². Seeds for the lower three densities were sown over the entire plot. In order to conserve a limited supply of seed, the highest density was sown over a 35 cm x 35

cm area centered within each plot. Seeds were evenly distributed by hand in a random pattern on the soil surface and then covered with 2-3 mm of soil. 200 seeds (with wings removed) were dried and weighed so that frequency distributions of seed mass could be described.

Because of variation in actual germination rates and seed weight, the quantity of seeds sown in each plot did not result in exactly the nominal densities of seedlings. I did not thin or transplant seedlings to exact densities because of the difficulties of doing so without changing the relative frequencies of individuals with different sizes. Instead, I conducted the analyses within density classes after determining the actual density for each plot.

Measurements

Frequency distributions of mass were estimated at 57, 78, 85, and 97 days after sowing. Each row was randomly assigned to one of the sample dates. Because plots within each row were measured on only one of the four dates, the frequency distributions on different dates were independent of one another. One of the two plots of each density within each row were randomly selected for measurement of stem diameter at the base of the cotyledons. Abscission scars were visible on stems that had shed cotyledons. All seedlings more than 7.5 cm from the edge of the area sown with seed were measured. Actual stand

density was calculated based on the number of seedlings measured. I observed no mortality after emergence and the density at time of measurement was assumed to have existed throughout the study.

The second plot of each density within each row was used for quantifying the allometric relationship between stem diameter and above-ground dry mass. On the date the first plot was measured as described above, 20 seedlings from the second plot were measured for diameter, cut at ground level, dried at 105°C to constant weight, and weighed to the nearest .01 mg. Linear regression models were then fit to the logarithms of diameter and mass. The intercept of the models differed among the sample dates but there were no significant differences among densities within each date. I therefore pooled the data across densities and used a single equation for each sample date. These data are shown in Fig 3.1 and the allometric equations are given in Table 3.1.

Leaf area and light were measured in the stands sampled 85 days after sowing. Illuminance (flux) was measured with a hand-held light meter at 5-cm height intervals from the ground to the top of the canopies. At each height, the light probe was placed vertically in 5 positions spaced at 2-cm intervals along a transect running through the center of the stand. All densities were measured once and then the sampling sequence was repeated. All measurements were completed between 1200 and 1400 hrs. Mean light availability (% full sunlight at the top of the canopy)

was calculated for each height. The meter measured all wavelengths, not just photosynthetically active radiation.

After the light measurements were completed, the same stands were destructively harvested so that vertical distribution of leaf area could be described. Foliage within 5-cm height intervals was separated from woody tissue, dried to constant weight, and weighed. Specific leaf area (Evans 1972, p. 215) was calculated so that leaf area could be predicted from leaf mass. Within each 5-cm height interval, 5 leaves were collected and their dry weight and area determined. To avoid shrinkage of leaves prior to measurement, I drew outlines of the leaves on paper and the area of the outlines was determined several days later with a Licor area meter. Specific leaf area varied with height and density as shown in Fig. 3.2. Leaf area within each 5-cm height interval was estimated by multiplying the leaf mass times the specific leaf area for that interval. Leaf area index was calculated by dividing leaf area by ground area. Five seedlings within each 5-cm height interval were individually harvested so that the vertical distributions of leaf area for seedlings with different mass could be described. For each density, I compared the distributions of leaf area of large seedlings (mass > 90th percentile) to that of small ones (mass < 10th percentile).

Four weeks after sowing, 20 seedlings were marked with toothpicks in all stands except those in the row to be destructively sampled. Two transects were placed through the

stands and the nearest individual at 2-cm intervals along these transects was marked. Stem diameter of marked seedlings was measured at 57, 78, 85, and 97 days after sowing. For the three growth intervals defined by the four sample dates, relative and absolute growth rates in above-ground mass were predicted using the allometric equations of Table 3.1.

Analysis

The Gini coefficient, a measure of mass inequality, was calculated using the formula of Dixon et al. (1987) for the frequency distributions of seed and seedling mass. The Gini coefficient ranges from 0 (absolute equality in plant mass) to 1 (absolute inequality). As suggested by Weiner and Solbrig (1984), the Gini coefficient is now the most widely used statistic in studies of size structures. I also calculated the skewness coefficient (scaled third product moment) so that results could be directly compared to earlier work. Confidence intervals for both coefficients were determined using the bootstrap technique (Efron 1981, Diaconis and Efron 1983). Spearman's rank correlation coefficient was used to examine the relationship between relative growth rate and mass.

RESULTS

Size Structures

Frequency distributions of seedling mass at the first sampling date (57 days) were slightly skewed and the variability in mass was low in all densities (Table 3.2). Distributions tended to become more positively skewed and have higher inequality with increasing age and density. For example, all stands sampled at the end of the study (97 days) had significantly greater inequality than stands sampled at the beginning (57 days), based on the bootstrapped confidence intervals. For stands sampled at 78, 85, and 97 days, the skewness of the highest density stand was significantly greater than the lowest density stand. The trend of greater skewness and inequality with age and density, however, was not entirely consistent. For example, the Gini coefficient was not significantly different among densities in the stands sampled 85 days after sowing. Taken as a data set, however, I conclude that there is a trend of increasing skewness and inequality with density and time.

For a given mean mass, skewness and inequality were greater in stands with higher density (Fig. 3.3). Competition caused seedlings to not only grow slower on the average, it also changed the relative frequency of seedlings with different mass. Higher density stands took longer to obtain the same mean mass, but when they did, they

still had different size structures.

Growth Functions

Spearman's rank correlation between relative growth rate and mass was significantly different from zero ($p < .05$) only during the last growth interval (Table 3.3). Increasing density did not cause relative growth rate to become positively correlated with mass. There was no evidence that a positive correlation in the $G(t,x)$ function is responsible for the greater inequality and skewness observed at higher densities.

Variance in absolute growth rate increased with mass (Fig. 3.4). Thus, the type of $D(t,x)$ function that causes skewness to increase with time (Hara 1984) existed in all stands. Negative growth rates were predicted for some seedlings, perhaps due to either error in allometric predictions or abscission of leaves without compensating new growth.

Light Availability

The highest density had the largest leaf area index (Fig. 3.5). Vertical distribution of leaf area in this stand, however, was restricted to a smaller space than in lower density stands. As a result, light attenuation occurred over a shorter vertical distance (Fig 3.5). As leaf area index increased with density, light became less available for most leaves.

Large seedlings (mass > 90th percentile) in the lowest density had most of their leaf area distributed above 15 cm, where light was at least 50% of full light at the top of the canopy (Fig. 3.5). The smallest seedlings (mass < 10th percentile) in this density also had much of their leaf area in relatively high light. In contrast, leaves of small seedlings in the highest density were exposed to much lower light (< 5% of full light). Because most of the leaf area of large seedlings was above that of small seedlings, shading by large seedlings made light less available for small ones, but not vice versa.

DISCUSSION

Size structures of F. mandshurica are consistent with those studies that have reported greater inequality or skewness at higher densities or in older stands (Koyama and Kira 1956; Obeid et al. 1967; Bazzaz and Harper 1976; Ford 1975; Naylor 1976; Waller 1985). One factor often suggested as causing, or at least accentuating, such patterns is asymmetric competition between plants with different sizes (Naylor 1976, Huston and DeAngelis 1987, Ford 1975, Firbank and Watkinson 1985, Schmitt et al 1986, Weiner and Thomas 1986). Larger individuals are thought to suppress small neighbors by pre-empting a disproportionate share of resources. As competition intensifies at higher densities, small plants are suppressed and relative growth rates become positively correlated with mass (i.e. the $G(t,x)$ function is density-dependent).

Size structures and growth functions of F. mandshurica are not entirely consistent with such a model. As predicted, inequality and skewness did tend to be greater at higher densities and in older stands. But relative growth rate was independent of mass during most growth intervals. Size structures in the high density stands demonstrate that a positive correlation between relative growth rate and mass was not necessary for inequality and skewness to develop. This result refutes previous studies that have stated that a positive correlation is necessary for skewness to develop. Also, stands

in which the correlation was positive (primarily the two lowest densities) did not develop the greatest inequality and skewness. Both results highlight the fact that the $G(t,x)$ function is not the sole cause of inequality and skewness in frequency distributions of seedling mass.

It is possible that relative growth rates were not positively correlated with mass at higher densities because competition was not asymmetric or that light was not a limiting resource. I believe both possibilities are unlikely. The vertical distributions of leaf area, light attenuation curves, and gradients in specific leaf area suggest large seedlings preempted light sufficiently to suppress smaller neighbors. In contrast, large seedlings, with most of their leaf area above smaller neighbors, competed only with other large seedlings for light. Photosynthetic studies have not been conducted with F. mandshurica that would allow light availability to be interpreted in terms of expected rates of carbon fixation. However, the light response curves for photosynthesis of many tree species (Kramer and Kozlowski 1979, pp. 189-196) are such that the small seedlings of F. mandshurica were in a light environment (<5% full light) that was likely to have been considerably less favorable for photosynthesis and growth. Thus, conditions necessary for asymmetric competition appeared to have existed within these stands, particularly at higher densities.

The consequence of such competition, however, was not a

positive correlation between relative growth rate and mass at higher densities. Given this result, and because there was no mortality, I attribute the differences in size structures to the variance in growth of seedlings with the same mass (the $D(t,x)$ function). Variable growth of plants with the same mass is sufficient to cause skewness to increase with time, if the variance in absolute growth rate is positively correlated with mass (Hara 1984). Simulations I have conducted indicate that the Gini coefficient responds similarly (unpublished data). Such variance can cause skewness and inequality, even if mean relative growth rate is independent of mass (or equivalently, absolute growth rate is linearly related to mass as in Hara's (1984) model or Westoby's (1983) distribution modifying function).

The first two chapters of this thesis demonstrated that spatial arrangement can influence the degree of skewing. In the present study, spatial pattern was random and the locations of seedlings was variable among replications of the same density. Neighborhood heterogeneity could have therefore accentuated the differences in skewing among replications of the same density, and among stands of different densities.

Estimating parameters for the $D(t,x)$ function would require many more observations of plants with the same mass than available in my study. However, it is clear that variance in absolute growth rate increased with mass (Fig. 3.5). A positive correlation between variance in absolute growth rate

and initial size has been observed in many tree species (West 1980, West and Borough 1983, Kohyama 1987) and is probably a fundamental property of tree growth. Because of this pattern and the absence of positive correlations in the $G(t,x)$ function, I conclude that the $D(t,x)$ function is primarily responsible for the observed differences in inequality and skewness.

These results suggest that an alternative model of competition would be appropriate for seedling stands with random spatial arrangements. In this model, asymmetric competition influences size structures through the $D(t,x)$ function, rather than the $G(t,x)$ function. With non-uniform spatial arrangements, some large germinants will initially encounter large neighbors, while in other localized neighborhoods, large germinants may have only small neighbors. If competition were asymmetric, large seedlings with small neighbors would grow free of competition until their neighborhoods expand sufficiently to encounter other large individuals. As a result, early growth of seedlings with the same mass would be more variable and the $D(t,x)$ function would have a greater influence on size structure dynamics. Asymmetric competition may thereby contribute to the development of skewness and inequality, without causing the mean relative growth rate of small seedlings to be less than large ones. Such a model would be consistent with the patterns observed with *F. mandshurica*.

ACKNOWLEDGMENTS

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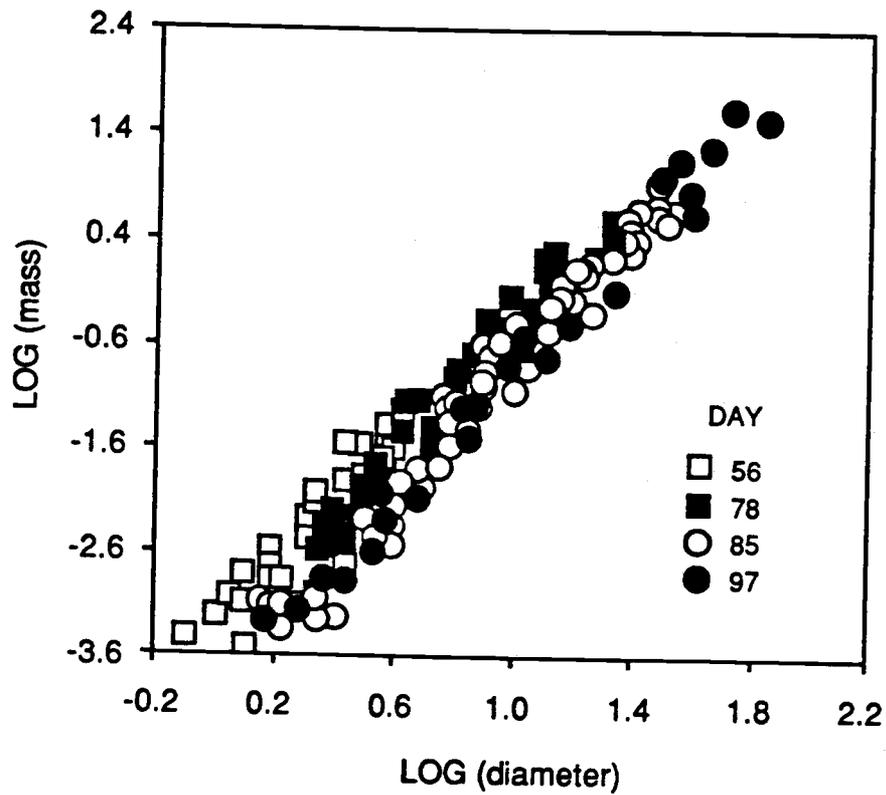


Figure. 3.1. Allometric relationship between stem diameter at the base of the cotyledons and the above-ground dry mass of *Fraxinus mandshurica* seedlings at 57, 78, 85, and 97 days after sowing.

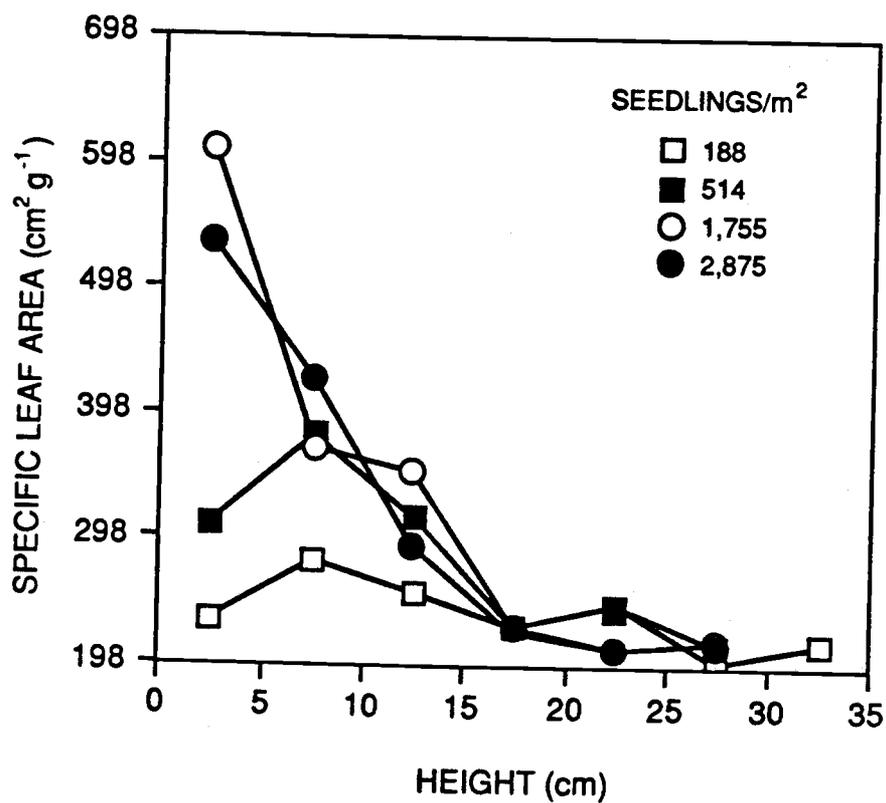


Figure. 3.2. Specific leaf area of *F. mandshurica* 85 days after sowing in relation to canopy height for stands of four densities (seedlings m⁻²).

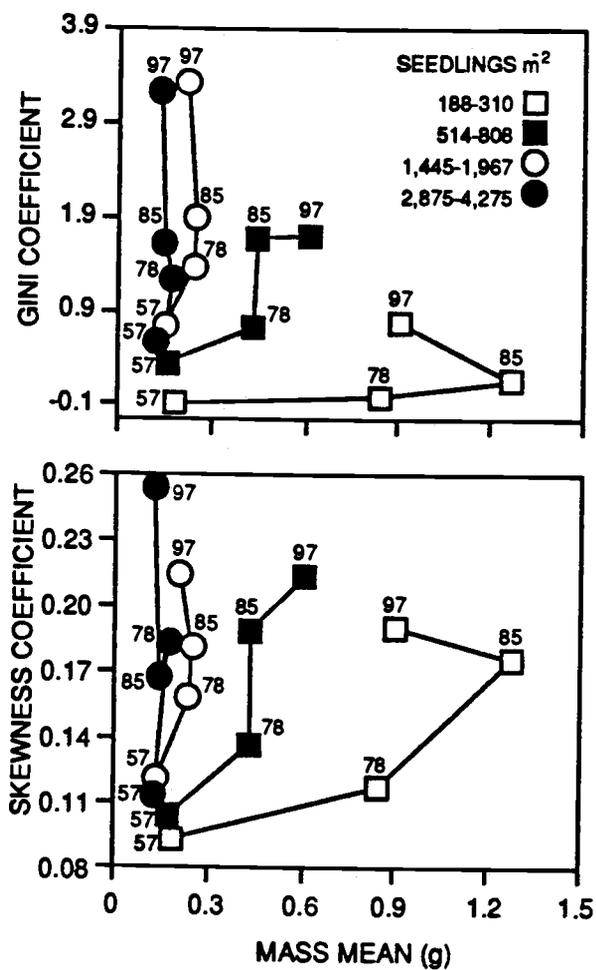


Figure. 3.3. Coefficient of skewness (left) and Gini coefficient (right) for the mass of *Fraxinus mandshurica* seedlings in relation to mean mass in four density classes: (I) 188-310, (II) 514-808, (III) 1445-1967, and (IV) 2875-4275 seedlings m⁻². Data are for (1) 57, (2) 78, (3) 85, and (4) 97 days after sowing.

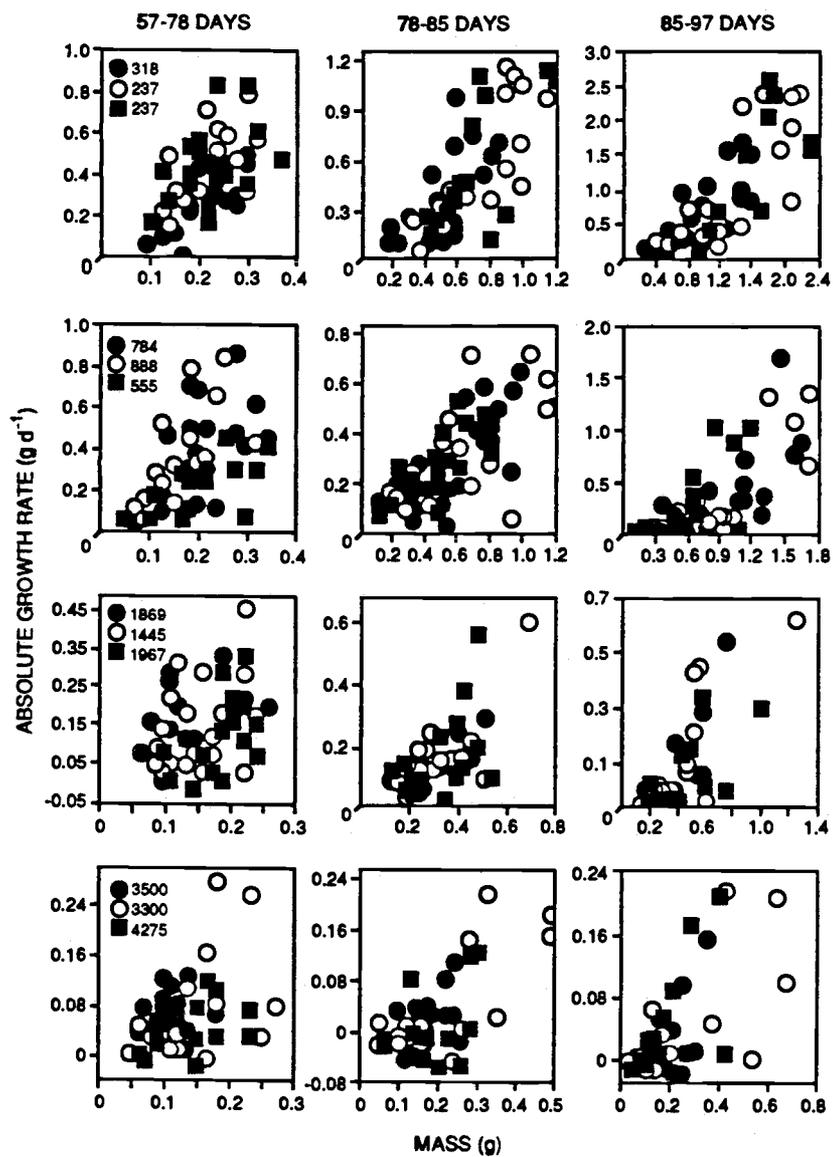


Figure. 3.4. Absolute growth rate in relation to initial mass for three growth intervals: (left) 57-78 days, (middle) 78-85 days, and (right) 85-97 days. Data points are from three stands in each of four density classes.

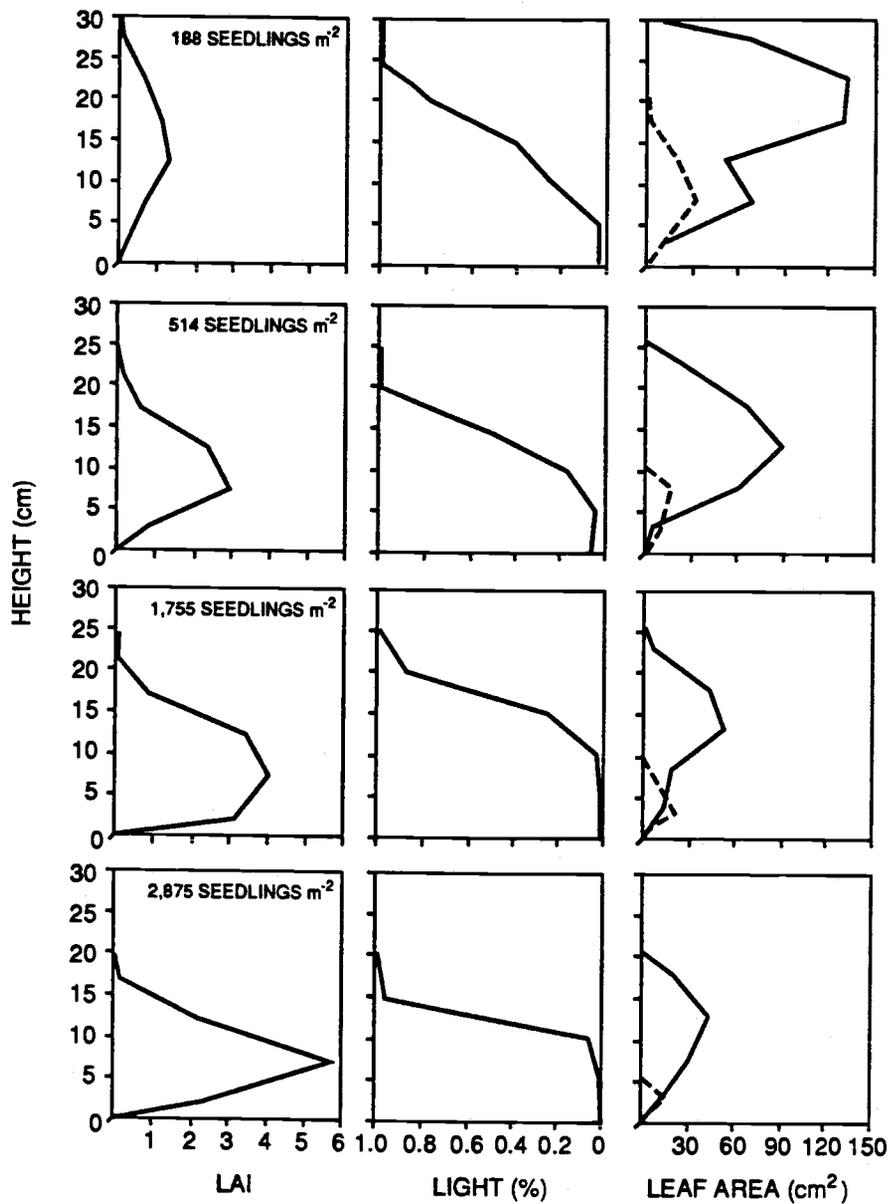


Figure. 3.5. Vertical distribution of (left) leaf area index, (middle) percent full light, and (right) leaf area of large seedlings (mass > 90th percentile) (solid line) and small seedlings (mass < 10th percentile) (dashed line). Graphs are for stands with (a) 188, (b) 514, (c) 1755, and (d) 2875 seedlings m⁻² sampled 85 days after sowing.

Table 3.1. Allometric equations used to predict dry mass (g) from stem diameter (mm).

Days since Sowing	Equation	r^2
57	$\ln(\text{mass}) = -3.328 + 3.035 \ln(\text{diameter})$.85
78	$\ln(\text{mass}) = -3.493 + 3.104 \ln(\text{diameter})$.95
85	$\ln(\text{mass}) = -3.879 + 3.178 \ln(\text{diameter})$.95
97	$\ln(\text{mass}) = -3.810 + 3.078 \ln(\text{diameter})$.97

Table 3.2. Mean, standard deviation, skewness, and the Gini coefficient for the dry mass of *Fraxinus mandshurica* seed and seedlings in stands of different ages and densities. Bootstrapped 95% confidence intervals for the Gini and skewness coefficients are in parentheses.

Age (dy)	Density (m ²)	Mass			
		Mean (g)	S.D. (g)	Skewness Coefficient	Gini Coefficient
57	237	0.176	0.055	-0.097 (-.828-.551)	0.089 (.061-.108)
	808	0.158	0.056	0.348 (-.206-.807)	0.100 (.084-.112)
	1445	0.130	0.053	0.652 (.278-1.006)	0.114 (.102-.124)
	3500	0.130	0.051	0.611 (.367-.837)	0.110 (.097-.121)
78	237	0.848	0.326	0.019 (-.489-.573)	0.112 (.084-.139)
	555	0.437	0.207	0.713 (.201-1.119)	0.131 (.109-.153)
	1967	0.238	0.138	1.342 (.856-1.727)	0.155 (.141-.167)
	3300	0.171	0.114	1.243 (.752-1.705)	0.180 (.159-.198)
85	188	1.275	0.752	0.185 (-.423-.839)	0.173 (.124-.213)
	514	0.444	0.322	1.683 (.729-2.397)	0.187 (.153-.211)
	1755	0.252	0.176	1.883 (.957-2.534)	0.179 (.163-.194)
	2875	0.147	0.093	1.616 (.925-2.015)	0.164 (.141-.182)
97	310	0.898	0.605	0.826 (.317-1.385)	0.188 (.152-.220)
	784	0.609	0.501	1.699 (.944-2.242)	0.212 (.185-.236)
	1869	0.215	0.200	3.320 (1.448-4.394)	0.214 (.192-.235)
	4275	0.130	0.157	3.215 (2.029-3.979)	0.256 (.226-.281)

Table 3.3. Rank correlation coefficients for the relationship between relative growth rate during three time intervals and mass at the beginning of the interval for stands in four density classes. Probabilities that the coefficients are zero are given in parentheses (*, $P < .10$; **, $P < .05$)

Density		Days Since Sowing		
		57 - 78	78 - 85	85 - 97
Class I	310	.185 (.419)	.105 (.646)	.473 (.039)**
	237	.043 (.868)	.443 (.077)*	.428 (.087)*
	237	-.340 (.160)	.282 (.244)	.735 (.002)**
Class II	784	.153 (.505)	.123 (.592)	.551 (.016)**
	808	.260 (.284)	.096 (.692)	.506 (.037)**
	555	-.138 (.559)	.318 (.166)	.546 (.017)**
Class III	1869	-.174 (.515)	.455 (.088)*	.304 (.255)
	1445	-.074 (.755)	.433 (.066)*	.511 (.030)**
	1967	.290 (.219)	.352 (.136)	.128 (.586)
Class IV	4275	-.303 (.186)	.141 (.549)	-.082 (.728)
	3500	.445 (.059)*	.459 (.066)*	-.005 (.984)
	3300	.049 (.836)	.204 (.387)	.259 (.272)

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SIZE STRUCTURES OF PSEUDOTSUGA MENZIESII STANDS
WITH NEIGHBORHOOD AND MATERNAL HETEROGENEITY

SUMMARY

Growing space (measured by Thiessen polygons) and maternal parent were evaluated as sources of variable growth rates in experimental stands of Pseudotsuga menziesii seedlings. Skewness and inequality of size structures increased during the second growing season after germination. Variance in the growth rate of individuals with the same mass was the cause of skewness and inequality, not a positive correlation between relative growth rate and initial size. Seedlings with the same mass grew faster when they had more space. In contrast, maternal parent was not a significant source of variation in growth of seedlings with the same mass. These results suggest that spatial arrangement of neighbors, but not maternal parent, influences the development of skewed size structures.

INTRODUCTION

Prior to the onset of self-thinning mortality, size structures (defined here as frequency distributions of plant sizes) often become increasingly skewed. In the absence of mortality or recruitment of new individuals, skewness is the consequence of individual plants having different growth rates. Hara (1984, 1988) has described how the effects of variation in growth on size structures can be modeled with two functions: (1) $G(t,x)$, mean growth rate of individuals of mass x at time t , and (2) $D(t,x)$, variance in growth rate of plants with mass x at time t . Positive skewness develops when: (1) variance in absolute growth is positively correlated with size, provided all variation is random and normal, and/or (2) the relationship between absolute growth and size is concave to the size axis (equivalent to positive and linear correlation between relative growth rate and size).

Before the biological basis for skewness can be explained, it is necessary to determine the relative importance of Hara's (1984) two functions as causes of skewness. If skewness increases with time because of the $D(t,x)$ function, biological factors that cause variation in the growth of individuals with the same size need to be identified. In contrast, if the $G(t,x)$ function is responsible, then variation in growth of individuals with different sizes needs to be explained.

This study describes size structures in seedling stands of

Douglas-fir (Pseudotsuqa menziesii) in which the maternal parent and spatial location of each individual is known. With this information, it is possible to determine to what extent maternal and neighborhood heterogeneity are sources of variable growth described by the $G(t,x)$ and $D(t,x)$ functions. Their importance in causing skewed size structures can then be described.

METHODS

Experimental Design

Seedlings of *P. menziesii* were grown in an outdoor frame at the Forestry Sciences Laboratory of the U.S. Forest Service at Oregon State University, Corvallis. The frame (.8 m x 1.6 m x 15 m) was filled with a local forest soil. Seedlings were grown from seed from four mature trees in a stand of Douglas-fir 50 km west of Corvallis. Progeny from each tree were at least half-siblings, but since the pollen source was unknown, some individuals from each family may have been full-siblings. Eight hundred seeds (200 from each family) were dried and individually weighed to the nearest 0.01 mg to determine the frequency distribution of seed mass.

Seeds were sown on May 24 and 25, 1986 in a random spatial arrangement in which planting spots corresponded to Cartesian coordinates selected with a random number generator. Six stands were established with dimensions of 75- x 140-cm. Planting spots (400 m^{-2}) were marked using a template with the proper coordinates. An equal proportion of the planting spots within each stand was assigned to each of the four families.

Seeds were stratified before planting by soaking in water for 24 h and cold storage at 2°C for 4 wks. Three seeds were sown at each spot to increase the probability that at least one seedling would emerge. If more than one seedling emerged, those

farther from the marked spot were removed within three days of emergence. Most seedlings emerged within 2 wks of planting, but some emerged up to 5 wks later. At 1.3% of the planting spots, no seedling emerged within 6 wks of planting. Seedlings planted adjacent to the experimental stands and from the same family as the missing ones were transplanted where seedlings failed to emerge. Transplanted seedlings and those in a 10-cm border of each plot were excluded from analysis. The stands were watered during dry periods throughout the experiment; seedlings were fertilized with a complete nutrient solution every 10 to 14 days during the spring and summer.

Measurements

Stem height and diameter of all seedlings were measured approximately 46 wks after planting (the beginning of the second season of active growth). At this time, seedlings in one stand were harvested at ground level, dried at 65°C for 72 h, and individually weighed. Data from these seedlings were used to determine the allometric relationship between above-ground dry mass, seedling height, and basal stem diameter. The families did not differ significantly ($p > 0.50$) in estimated coefficients of the allometric equations, so the data were pooled and seedling mass at 46 wks (w_i) was predicted from height (h) and stem diameter (d) by the following equation ($r^2 = 0.88$): $\ln w_i = -5.79 + 1.14 \ln h + 0.88 \ln d$. Approximately 58

wks after planting (the end of active shoot elongation), the seedlings in the remaining five stands were harvested, dried, and individually weighed. Absolute and relative growth rates of individual seedlings were calculated using predicted mass at 46 wks and measured mass at 58 wks. To determine whether competition had reduced growth, I compared mean mass at 58 wks to the mean mass of 120 seedlings (30 per family) that had been planted next to the stands at a 10- x 10-cm spacing. While not low enough to ensure total lack of competition, stand density was considerably lower than in the experimental stands.

Analysis

Neighborhood area was calculated for each seedlings using Thiessen polygons (Mead 1966). Spearman's rank correlation was used to examine the relationship between neighborhood area and seedling mass. Kruskal Wallis one-way analysis of ranks was used to test for significant differences among families in their mean mass at 46 and 58 wks.

The Gini coefficient, a measure of mass inequality, was calculated using the formula of Dixon et al. (1987) for the frequency distributions of seedling mass. The Gini coefficient ranges from 0 (absolute equality in plant mass) to 1 (absolute inequality). As recommended by Weiner and Solbrig (1984), the Gini coefficient is now widely used in studies of size structures. The skewness coefficient was calculated as the

scaled third product moment so that the results could be directly compared to earlier studies. Confidence intervals for both coefficients were determined using the bootstrap technique (Efron 1981, Diaconis and Efron 1983).

Spearman's rank correlations coefficient was used to examine the relationship between relative growth rate and mass at 46 wks. The significance of these correlations provided the criterion for testing whether the $G(t,x)$ function contributed to temporal changes in skewness and inequality. The variation in growth rates of seedlings with the same mass due to neighborhood area or maternal parent was analyzed using the rank regression procedures described by Iman and Conover (1970). A regression model with relative growth rate as the dependent variable and mass at 46 wks, family, and neighborhood area as the independent variables was fit to the ranked data. F values were then calculated using standard procedures. Because variation in relative growth rate due to initial mass was accounted for in the model, a significant family or neighborhood effect indicates that they contributed to variation in growth of individuals with the same mass (the $G(t,x)$ function).

RESULTS

Size Structures

Frequency distributions of seedling mass were positively skewed at 46 wks (Table 4.1). Skewness increased at 58 wks for most families and stands. Inequality as measured by the Gini coefficient also increased from 46 to 58 wks. There were significant differences among families in their mean mass at both 46 and 58 wks (Kruskal Wallis rank test, $P < .05$). The ranking of mean mass was fairly consistent among stands, with family 2 the smallest and family 3 the largest. Mass at 46 wks was not significantly correlated with neighborhood area, as measured by the Thiessen polygon (Table 4.2). Thus, differences among seedlings in their mass at the beginning of the growth interval (46 wks) are partly attributable to maternal parent, but not neighborhood area.

G(t,x) function

The correlation between between relative growth rate and mass at 46 wks was either not significant (one stand) or negative (three stands) (Table 4.2). Mean relative growth rates in relation to mean mass at 46 wks are shown in Fig. 4.1. Because of the absence of a positive correlation between relative growth rate and initial mass, the G(t,x) function did

accentuate the development of positive skewness and inequality.

D(t,x) function

Neighborhood area was positively correlated with the growth of seedlings with the same mass in three of the four stands (Table 4.3). There was a negative relationship between RGR and mass in all stands. Seedlings with different maternal parents had different initial mass on the average, but maternal parent had no effect on the D(t,x) function (variation in growth of seedlings with the same initial mass).

The increase in skewness and inequality from 46 to 58 wks is attributed to the D(t,x) function -- variance in growth of seedlings with the same mass at 46 wks. Based on the F tests of Table 4.3, neighborhood area, but not maternal parent, was a significant source of such variation.

DISCUSSION

The size structures of seedling stands of P. menziesii demonstrate that inequality and skewness can develop when RGR is negatively correlated with initial mass. Hara (1984) has demonstrated with theoretical models that variation in growth of plants with the same mass is sufficient to cause the skewness coefficient to increase with time, even if individuals with different mass have the same mean relative growth rate (or equivalently, a linear relationship exists between absolute growth rate and mass). Simulations described in the second chapter of this dissertation indicate that the Gini coefficient responds to changes in parameters of the $G(t,x)$ and $D(t,x)$ functions in the same way as the skewness coefficient. Because relative growth rate was negatively correlated with mass, I attribute the positive skewness and inequality to the variation in the growth of plants with the same mass.

Given this conclusion, maternal and neighborhood heterogeneity contribute to skewness only to the extent that they are a source of variation in the growth of seedlings with the same mass. There was no evidence that seedlings from different parents, but with the the same size at 46 wks, varied in their subsequent growth rates. Therefore, maternal parent was not a source of variance in plant growth that contributed to skewness, even though it was a source of size variability. In

contrast, some of the variation in growth of seedlings with the same mass was caused by differences in neighborhood area. Thus, neighborhood area did contribute to the development of skewed size structures.

Indices of available growing space, such as the Thiessen polygons used in this study, often explain relatively little variation in tree size in older stands. This suggests that the patterns observed in seedling stands of Douglas-fir may not persist during later stages of growth. If seedlings with more space continued to have greater growth rates, a positive correlation between size and space would eventually develop. The fact that such correlations are often low suggests that the relative importance of factors such as neighborhood space and maternal parent changes as stands develop. This is suggested by Hara's (1984) observation that the relative importance of the $D(t,x)$ and $G(t,x)$ functions depends on stand age. Biological factors underlying these mathematical functions may also be age-dependent.

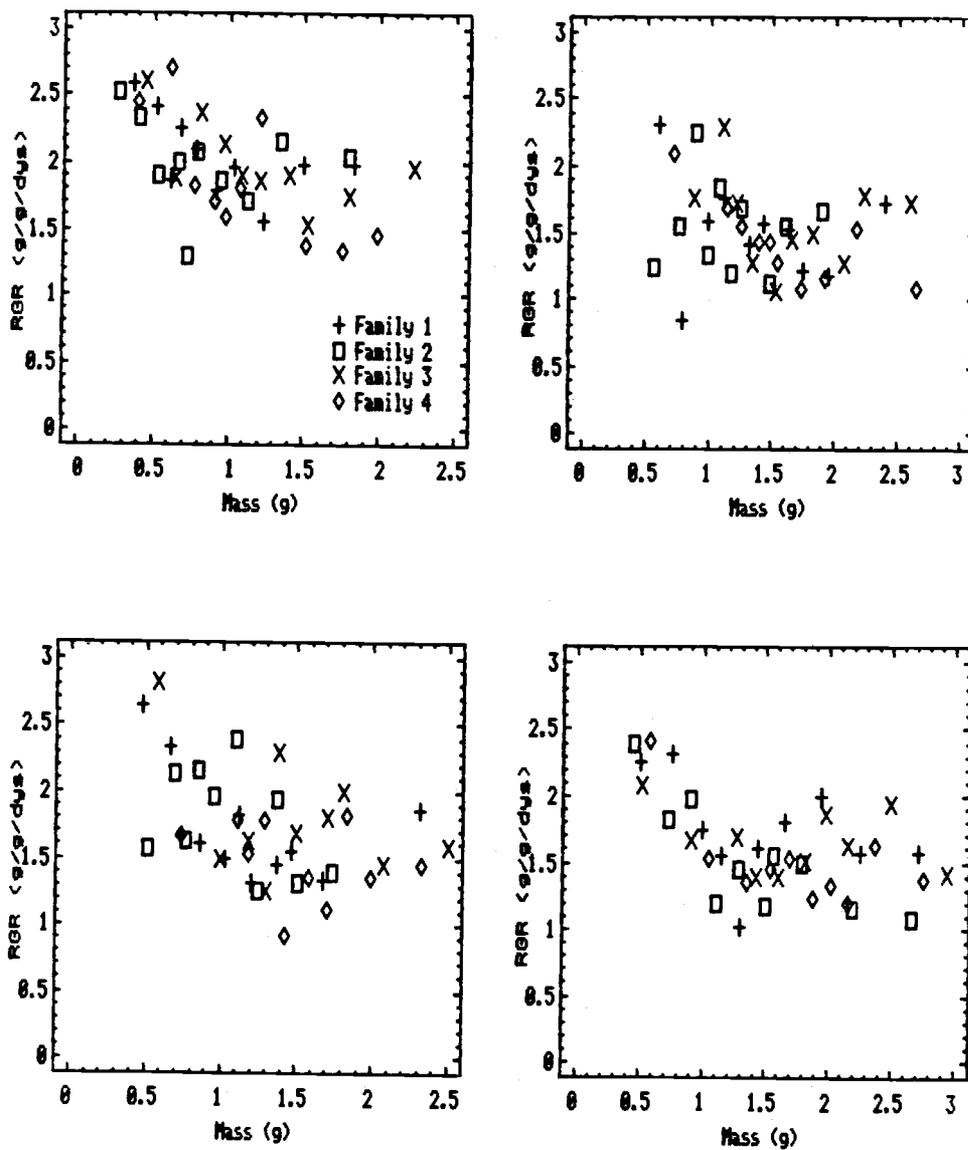


Figure 4.1. Mean relative growth rate (from 46 to 58 wks) in relation to mean mass at 46 wks for Douglas-fir seedlings from four half-sibling families in each of four stands.

Table 4.1. Mean, skewness coefficient, and Gini coefficient for seedling mass 50 and 70 days after sowing and mean relative growth rate during the interval for four maternal families in four stands. Standard errors are in parentheses for the means; bootstrapped 95% confidence intervals are shown for the skewness and Gini coefficient.

Stand	Family	n	Mass (g)		Skewness Coefficient		Gini Coefficient		RGR
			Day 50	Day 70	Day 50	Day 70	Day 50	Day 70	
1	1	81	0.94 (.05)	2.80 (.16)	0.77 (.34-1.20)	1.12 (.64-1.55)	0.134 (.116-.148)	0.139 (.116-.158)	2.05 (.09)
	2	72	0.85 (.05)	2.51 (.18)	0.86 (.41-1.28)	1.40 (.70-1.96)	0.146 (.124-.165)	0.163 (.137-.184)	2.00 (.10)
	3	76	1.20 (.06)	3.51 (.18)	0.46 (.08-.83)	0.71 (.31-1.04)	0.123 (.104-.138)	0.126 (.105-.142)	1.99 (.11)
	4	83	1.11 (.05)	3.03 (.15)	0.41 (.06-.79)	0.82 (.26-1.26)	0.125 (.106-.141)	0.126 (.105-.145)	1.86 (.11)
	all	312	1.03 (.03)	2.97 (.09)	0.61 (.41-.80)	0.94 (.71-1.16)	0.135 (.126-.143)	0.141 (.130-.150)	1.97 (.05)
2	1	73	1.39 (.06)	3.46 (.18)	0.38 (-.08-.77)	0.79 (.23-1.19)	0.109 (.092-.125)	0.125 (.104-.142)	1.53 (.08)
	2	65	1.16 (.05)	2.99 (.18)	0.51 (-.08-1.03)	1.67 (.20-2.44)	0.095 (.079-.111)	0.129 (.102-.154)	1.56 (.10)
	3	75	1.63 (.06)	4.19 (.20)	0.29 (-.18-.76)	1.04 (.48-1.44)	0.092 (.079-.101)	0.112 (.091-.127)	1.59 (.06)
	4	74	1.59 (.06)	3.74 (.16)	0.44 (.00-.86)	0.68 (.15-1.08)	0.094 (.076-.108)	0.105 (.089-.119)	1.43 (.09)
	all	287	1.45 (.03)	3.62 (.09)	0.46 (.24-.66)	0.94 (.66-1.28)	0.103 (.095-.112)	0.121 (.111-.130)	1.52 (.04)
3	1	77	1.20 (.06)	3.18 (.17)	0.87 (.13-1.34)	1.37 (.49-1.78)	0.118 (.096-.138)	0.124 (.101-.143)	1.75 (.05)
	2	75	1.07 (.04)	2.89 (.14)	0.26 (.12-.61)	0.21 (-.13-.53)	0.101 (.087-.113)	0.125 (.108-.140)	1.76 (.11)
	3	73	1.49 (.06)	4.06 (.20)	0.19 (-.27-.66)	0.42 (-.05-.81)	0.101 (.081-.119)	0.117 (.095-.131)	1.81 (.10)
	4	85	1.51 (.05)	3.68 (.17)	-0.03 (-.42-.41)	1.04 (.12-1.57)	0.086 (.072-.099)	0.116 (.094-.134)	1.47 (.09)
	all	310	1.32 (.03)	3.45 (.09)	0.40 (.16-.65)	0.86 (.55-1.14)	0.108 (.099-.117)	0.125 (.115-.134)	1.69 (.05)
4	1	75	1.46 (.08)	3.90 (.23)	0.51 (.07-.95)	0.75 (.18-1.21)	0.129 (.110-.146)	0.142 (.121-.159)	1.74 (.09)
	2	67	1.40 (.08)	3.35 (.18)	0.51 (.01-.97)	0.54 (.04-.99)	0.132 (.108-.153)	0.128 (.107-.146)	1.54 (.09)
	3	71	1.69 (.08)	4.43 (.26)	0.05 (-.33-.39)	0.61 (.18-.96)	0.121 (.098-.142)	0.136 (.114-.158)	1.66 (.09)
	4	84	1.72 (.07)	4.16 (.18)	-0.23 (-.62-.11)	0.18 (-.30-.56)	0.103 (.085-.121)	0.114 (.096-.132)	1.51 (.08)
	all	297	1.57 (.04)	3.98 (.11)	0.18 (-.01-.37)	0.64 (.40-.90)	0.122 (.113-.132)	0.132 (.122-.142)	1.61 (.04)

Table 4.2. Rank correlation coefficients for neighborhood area (a), mass at day 50 (m_1) and 100 (m_2), and relative growth rate (rgr). Probability that the coefficient is significantly different from zero are given in parentheses (*, $P \leq .05$; **, $P \leq .01$).

	family	a vs. m_1	a vs. m_2	rgr vs. m_1	rgr vs. a
Stand 1	1	.115 (.304)	.182 (.103)	-.159 (.154)	.104 (.353)
	2	-.130 (.273)	-.100 (.397)	-.072 (.541)	.083 (.487)
	3	.022 (.848)	.127 (.271)	-.273 (.018)*	.249 (.031)*
	4	-.023 (.836)	-.068 (.539)	-.320 (.004)**	-.012 (.910)
	all	-.004 (.950)	.030 (.591)	-.205 (.001)**	.094 (.096)
Stand 2	1	-.112 (.343)	-.037 (.752)	-.092 (.438)	.043 (.715)
	2	.181 (.148)	.164 (.190)	-.030 (.811)	.063 (.612)
	3	.146 (.210)	.287 (.014)*	-.105 (.365)	.190 (.103)
	4	-.127 (.279)	.067 (.566)	-.292 (.013)*	.277 (.018)*
	all	.003 (.956)	.115 (.052)	-.111 (.060)	.277 (.018)*
Stand 3	1	-.058 (.616)	.059 (.606)	-.294 (.010)**	.109 (.343)
	2	.356 (.002)**	.293 (.012)*	-.118 (.311)	-.041 (.726)
	3	-.174 (.140)	-.060 (.608)	-.106 (.369)	.154 (.190)
	4	.132 (.228)	.311 (.004)**	-.119 (.276)	.258 (.018)*
	all	.032 (.572)	.133 (.020)*	-.173 (.002)**	.121 (.033)*
Stand 4	1	.055 (.635)	.017 (.886)	-.162 (.164)	-.046 (.694)
	2	.096 (.436)	.184 (.135)	-.380 (.002)**	.114 (.354)
	3	.000 (.998)	.104 (.386)	-.034 (.775)	.191 (.111)
	4	-.012 (.914)	.104 (.345)	-.081 (.459)	.177 (.106)
	all	.046 (.428)	.102 (.079)	-.184 (.002)**	.114 (.050)*

Table 4.3. F values for testing the null hypothesis that relative growth rates of seedlings with the same mass is independent of family and neighborhood area. Probabilities of obtaining a larger F value given that the null hypothesis is true are given in parentheses (*, $P \leq .05$; **, $P \leq .01$).

stand	family	neighborhood area
1	1.18 (.316)	3.18 (.075)
2	0.78 (.507)	6.89 (.009) **
3	1.17 (.321)	6.73 (.010) **
4	2.25 (.083)	4.09 (.044) *

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CONCLUSION

The simulations and experiments in this thesis suggest the following process for the genesis of skewed size structures in seedling stands. A range in sizes of germinants is initially established because of density-independent factors such as time of emergence, seed size, or local environmental conditions. Size distributions of recent germinants are normal or only slightly skewed (positive or negative). Positive skewness quickly develops, however, as seedlings grow. The following conclusions summarize the main points about this period of stand growth in which skewness develops.

(1) Variance in the growth of seedlings with the same size was the primary cause of skewness (and inequality), not variation in the growth of seedlings with different sizes. Both the form and the amount of variation determines the degree of skewing. Skewness was not the exclusive result of a positive correlation between relative growth rate and size. Previous studies that have failed to examine the contribution of variable growth rates of plants with the same size (e.g. Ford 1975, Schmitt et al. 1987), may have overestimated the importance of a size-dependent growth rates as a cause of skewness. In order to understand the biological basis for skewed size structures, it is necessary to determine the causes of variation in the growth of individuals with the same size.

(2) Deterministic models were limited in their ability to model the dynamics of size structures. Deterministic models

(e.g. Westoby 1980) predict positive skewness will develop only when relative growth rate is correlated with size. Even though there was no such positive correlations in the Douglas-fir and ash stands, their size structures developed considerable positive skewness. If skewness and inequality of size structures are of interest, then stochastic models that account for variation in growth of plants with the same mass will be needed.

As stands approach the beginning of mortality, the correlation between relative growth rate and size will shift from zero or negative to positive. The patterns observed in stands of this thesis are those during very early periods of stand establishment. The relative importance of mathematical and biological causes of skewing will likely depend on stand age.

(3) Asymmetric competition contributed to the development of skewness by accentuating the variance in growth of individuals with the same size. I found no evidence to support the model of asymmetric competition that states that skewness develops because of disproportionate suppression of small seedlings. Increasing stand density did not cause relative growth rates to be correlated with size. The leaf area and light data in the third study of this dissertation suggests competition was asymmetric in stands of Fraxinus mandshurica. However, such competition contributed to skewness and inequality by accentuating the variance in growth of individuals with the same

mass, not by causing mean relative growth rate of small individuals to be less than large ones.

(4) Size structures were the consequence of interacting factors. As shown in the second study of this dissertation, variation in the spatial arrangement of competitors caused greater variation in growth rates. Asymmetric competition accentuates such variation because the growth of large plants with small neighbors is unaffected by competition, while the growth of large plants that have large neighbors is reduced. The result is growth rates that are more variable. In this way, factors such as neighborhood heterogeneity and asymmetric competition interact to produce size structures with greater skewness.

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