

Chapter II

Development of the Dominance/Suppression Theory of Intra-specific Competition

INTRODUCTION

Burkholder's (1952) adaptation of Haskel's (1949) classification scheme recognizes nine basic interactions between individuals in an ecological community: neutralism, competition (direct interference type), competition (resource use type), amensalism, parasitism, predation, commensalism, proto-cooperation, mutualism. Within a plant community, competition (resource use type) between individuals and species is of primary importance: "...the law of competition is here the dominant law of relationship" (Tansley 1920; p.124). The role of competition with regards to plant yields and survival has been studied extensively since the 1950's. Agronomists and foresters have a vested interest in how reaction to competition effects plant growth and survival.

Much discussion has centered around the definition of "competition" as applied within the context of interrelationships between individuals and species. With regards to the animal kingdom, the varied definitions have led Birch (1957) to conclude "... the word has largely lost its usefulness as a scientific term." The situation is less exacerbating in plant ecology following the work of Clements *et al.* (1929):

Competition arises from the reaction of one plant upon the physical factors about it and the effect of these modified factors upon its

competitors. In the exact sense, two plants, no matter how close, do not compete with each other as long as the water content, the nutrient material, the light and heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plant, competition begins.

This definition has been accepted by most plant ecologists with the notable exception of Harper (1961) who suggested the term “interference” so as to include possible allelopathic effects and the stimulus to produce secondary chemical compounds.

The definition of competition in terms of a reaction upon physical factors invalidates the view that plants possess “sphere of influence” (Clements *et al.* 1929). Nor can it be assumed that competition exists just because a factor is in short supply. If all plants in the population are short of the factor but the environment of each plant is independent of that of its neighbors, then there is no competition between the plants (Donald 1963). Throughout the literature, there are references to the “competition for space” between plants. With the possible exception of tuberous plants grown at extremely high densities, plants do not compete for space in the exact sense. However, the concept of space as an integrative resource (*e.g.*, the “biological space” of Ross and Harper (1972)) allows for the analysis of the proximity of neighbors without concern for the actual cause of the interaction (Radosevich and Osteroung 1987).

For a population over which resources are homogenous it is reasonable to consider space and its implied resources as the object of competition. Comparisons among individuals from different populations may not be reliable, however, due to differences in resource availability. Plants which are of similar size and distance apart, but located on different sites, may experience different levels of resource availability. Competition is a result of plant density and size relative to available resources (Zedaker 1982).

The process of competition is not measured directly. The presence and intensity of competition are inferred from stand- and tree-level attributes measured within populations grown under different density and site conditions and how these attributes change over

time. These density induced effects are assumed to be the outcome of competition between individual plants.

Plants respond to density induced stress (i.e., competition) via two negative feedback mechanisms: plasticity and mortality (Harper 1977). Plasticity refers to the ability of a plant to alter both the growth rates and actual numbers of their component parts as a reaction to changes in their immediate environment. Grime et al. (1986) consider plasticity as part of an active foraging mechanism by which plants attempt to locate functional leaves and roots in the resource rich zones of their surrounding environment. When the ability of a plant to compensate for competitive stress via plastic responses is exceeded, mortality occurs (Hutchings and Budd 1981).

Quantitative analysis of competition at the stand level initially focused on yield/density and size/density relationships. Generally, yield/density relationships have been expressed as total or mean yield per initial density. Mitscherlich (1919) presented one of the earliest models of the yield/density relationship. Kira's *et al.* (1953) well known Competition-Density effect model is a modification of Warne's (1951) equation. Another widely used model for the yield/density relationship is the reciprocal equation of Shinozaki and Kira (1956).

Rieneke's (1933) stand density index and Yoda's *et al.* (1963) -3/2's power rule are examples of size/density relationships. They incorporate plasticity and mortality by describing the size/density relationship of a "fully stocked" stand through time. These models imply that all stands which are undergoing self-thinning follow a specific relationship between mean size and density. The validity of such an assumption has been the subject of much spirited debate in the literature (see White and Harper 1970, Ford 1975, Mohler *et al.* 1978, Weller 1987, Zeide 1987).

Plants do not react to the overall density per se, but rather to the "immediate" environment around them. Consequently, studies of competition based on stand level parameters obscure plant-to-plant variation caused by competition. Approaches based on

measurements of individual plants have been used to quantify or compare the degree of competition in stands and to relate plant growth to differences in the level of competition experienced by the plant. Historically, efforts have focused on summary statistics derived from observed frequency distributions, though recently individual plant relative growth rates have been studied.

SIZE VARIATION

In forestry, early efforts at quantifying temporal changes in size distributions were motivated by attempts to use mathematical distribution functions to generate stand tables. Knowledge of the relationship between stand-level parameters and attributes of the diameter distribution were used to drive distributions through time. Cajanus (1914) was one of the first (Meyer 1930) to use mathematical functions to describe a dbh distribution. Cajanus utilized the Gram-Charlier expansions which can approximate a wide variety of continuous distributions (Johnson and Kotz 1970). This family of curves is defined by four population parameters: mean, standard deviation, skewness, and kurtosis. Equations were developed to predict the mean and standard deviation from age and site class while skewness and kurtosis were assumed to be functions of site class only.

After Cajanus's seminal paper, research on diameter distributions progressed along similar lines. Depending on the shape of the observed distributions, a variety of mathematical distributions were advocated to develop stand tables (Baker 1923, Meyer 1930, Schnur 1934, Bliss and Reinker 1964, Nelson 1964, Clutter and Bennett 1965, Bailey and Dell 1973). These efforts did not attempt to formulate hypotheses on the causal mechanisms associated with observed changes in distributions over time. However, during the 1950's researchers in Japan initiated the first detailed studies into the nature of temporal changes in size distributions for even-aged monocultures.

Koyama and Kira (1956) used graphical analysis to examine changes in size distributions over time for a number of annual and perennial plants. From their

observations, they concluded that individual plant weight is approximately *normally* distributed during early development. However, over time the distribution becomes positively skewed as the mode of the distribution continues to shift toward the smaller size classes.

Skewness

Prior to 1975, studies of skewness in size distributions were based on visual interpretation of histograms (Koyama and Kira 1956, Obeid *et al.* 1967, Ford and Newbould 1970). Later, the skewness coefficient (γ_1) was introduced (Ford 1975) as a means of quantifying the degree of skewness. The γ_1 statistic provided a means of quantifying changes in skewness with density and stand development.

The population skewness is defined as

$$\gamma_1 = \frac{\mu_3}{\mu_2^{3/2}}$$

where μ_2 and μ_3 denote the second and third central moments. A sample based estimate (g_1) of γ_1 for a sample (x_1, x_2, \dots, x_n) is computed as

$$g_1 = \frac{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^3}{\left[\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2 \right]^{3/2}}$$

though g_1 is not necessarily unbiased for γ_1 .

The measure of individual plant size was largely determined for logistical reasons. For annual plants, g_1 was generally computed for total dry mass following the destructive harvest of selected individuals (Koyama and Kira 1956, Obeid *et al.* 1967, Ford 1975, Turner and Rabinowitz 1983). The expected time trend for g_1 was estimated from repeated destructive samples. With large perennial plants, some measure of stem diameter

was the usual measure of size and repeated measurements could be obtained from the same individuals.

Acknowledging the wide disparity in measurement protocols, Mohler *et al.* (1978) provided a general description of the dynamics of skewness in size distributions. Owing to the initial symmetric distribution of seed weight (Black 1957, Obeid *et al.* 1967), individual plant weights will be symmetrically distributed. As the stand develops, the weight distribution will trend toward positive skewness with the maximum skewness obtained just prior to the onset of self-thinning.

Based on the published allometric relationships for stem weight and diameter (Yoda *et al.* 1963, McMahon 1973) Mohler *et al.* 1978 concluded that the diameter distribution must be initially negatively skewed. By the onset of self-thinning, the diameter distribution is also positively skewed, albeit to a lesser degree than the weight distribution. During self-thinning, mortality is concentrated within the smallest size classes. Consequently, self-thinning will result in decreased skewness overtime. Eventually, the diameter distribution will approach symmetry while the weight distribution will remain somewhat positively skewed. Gates *et al.* (1983) published results from remeasured *Pinus radiata* which support the diameter skewness trends proposed by Mohler *et al.* (1978).

Size Inequality

Harper (1967) and Ford (1975) interpreted skewed size class distributions as implying the presence of a *hierarchy of exploitation* of resources. It was assumed that large plants grew larger at the expense of smaller plants which were assumed to be at a competitive disadvantage. Following their work, skewed size distributions became synonymous with the phrase *size hierarchies*.

Weiner and Solbrig (1984) maintained that a size hierarchy, as envisioned by plant population biologists, encompassed more than mere positive skewness of size distributions. In addition to skewness, they argued that a size hierarchy also implied large

variation in individual sizes and that the largest individuals contained much of the total population biomass. The important attribute of a size hierarchy was not skewness, but rather the concentration of total biomass within few individuals. They referred to this degree of concentration as *size inequality*. To quantify this attribute, Weiner and Solbrig (1984) proposed a measure of inequality originally used to quantify the concentration of wealth in society.

a. Gini Coefficient

The origin of the Gini coefficient dates back to Lorenz's (1905) graphical approach for assessing inequality in income distributions. In this context, the income values were first ranked in increasing order. The cumulative percentage of total income was then plotted against the cumulative proportion of the population (Figure 2.1). The resultant curve is referred to as the Lorenz Curve. If there was perfect equality in the distribution of income, the Lorenz Curve would be a straight line with a 45 degree slope (Line of Equality). Lorenz suggested that the area between the Line of Equality and the Lorenz curve (Lorenz Area) be used as a qualitative measure of the inequality in income distributions.

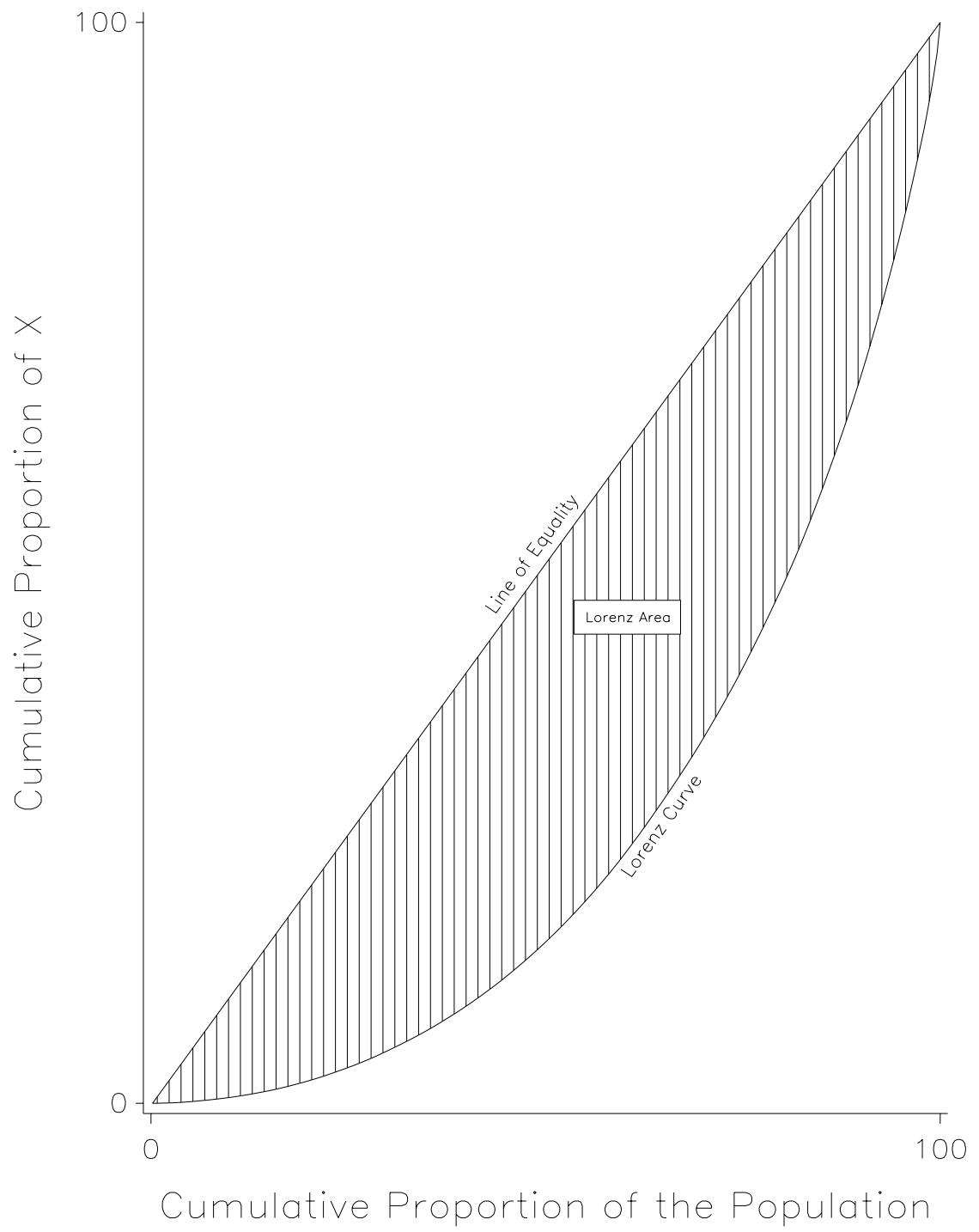


Figure 2.1. Relationship between Lorenz curve and Lorenz area for hypothetical populations. The Gini coefficient is the ratio of the Lorenz area to the area beneath the Line-of-Equality.

According to the review by Nygard and Sanstrom (1989), Gini (1914) later proposed that the ratio between the observed Lorenz Area and the largest possible Lorenz Area be used as a measure of inequality. This ratio is called the Gini coefficient and can be calculated for a sample of size n as:

$$G = \frac{1}{2\bar{x}n^2} \sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|$$

where n = the number of observations in the sample,
 \bar{x} = the mean of the sample,
 x_i, x_j = denote the i'th and j'th elements of the sample.

Note that the Gini coefficient is bounded by 0 and $1 - \frac{1}{n}$.

As a more direct measure of the concentration of biomass, Weiner and Solbrig (1984) argue that the Gini coefficient captures the essence of an ecologist's definition of inequality. However, a choice between various quantitative measures must also include consideration of specific mathematical properties. For non-negative, right-skewed distributions, the skewness and Gini coefficients are generally highly correlated (Bendel and Carlin 1988, Bendel *et al.* 1989) though there are important differences between the two.

Skewness is a measure of distribution shape and does not depend directly on the mean or variance of the distribution. Consequently, the skewness coefficient is invariant to changes in both scale and location. The Gini coefficient is the ratio between a measure of dispersion and the mean and therefore changes as the ratio changes. Though it is invariant to changes in scale, the Gini coefficient is not invariant to changes in location. As the distribution is shifted to the right, the value of the Gini coefficient decreases.

In general, the transfer of material from a larger individual to a smaller individual should always decrease the amount of inequality in the population. This is often referred to as the *Pigou-Dalton condition* or the *principle of transfers* (Sen 1973). Unlike the Gini coefficient, the skewness coefficient does not in general satisfy this condition. Of the statistics that satisfy the principle of transfers, there are differences in sensitivity to transfers between different locations on the scale (Atkinson 1970). The Gini coefficient is robust to transfers within the upper and lower tails. It is most sensitive to transfers that affect the middle of the distribution.

b. Other Measures

Within the sociological and economic literature, there is considerable discussion on measures of inequality. Often "*... the choice of an inequality measure is properly regarded as a choice among alternative definitions of inequality rather than a choice among alternative ways of measuring a single theoretical construct.*" (Allison 1978). While the Gini coefficient is widely used, other statistics have been advocated (Atkinson 1970, Sen 1973, Allison 1978). Two of these have also been reported in the ecological literature.

Though the coefficient of variation has long been used to assess variation in plant populations, it has more recently been used as a measure of inequality (Knox *et al.* 1989). As a measure of inequality the coefficient of variation is similar to the Gini coefficient in many respects. It is invariant to changes in scale but is not invariant to changes in location. Though the coefficient of variation exhibits the principle of transfers it differs from the Gini coefficient in that it is sensitive to transfers at any point in the distribution (Allison 1978). In computer simulations, Bendel *et al.* (1989) found it to be most sensitive to changes within the right-hand tail of the distribution. They recommend the coefficient of variation may be the best choice to assess inequality in seed production.

Theil's Inequality Index (Theil 1967) has not been widely used to date in studies of structure in plant populations. Like the Gini coefficient, Theil's index was first used to quantify income inequality. Van Andel *et al.* (1984) used Theil's index to derive an index of population variation for dry matter partitioning. As a measure of inequality, Theil's index is invariant to scale but not location. It adheres to the principle of transfers and is most sensitive to transfers within the left-hand tail.

c. Size Inequality Trend

Studies of the temporal trend of size inequality and the relationship between inequality and initial density have focused on annual species. Weiner (1985) used green house plantings of annuals *Lolium multiflorum* and *Trifolium incarnatum* grown in monocultures and mixtures. A wide range in initial densities were crossed with two levels of soil fertility. Mortality was negligible in all densities. Inequality increased with increasing initial density. In populations where competition was evident, inequality increased with increased soil fertility. Weiner and Thomas (1986) report similar conclusions in a review of 16 published studies.

The few studies with perennial plants report similar conclusions. Knox *et al.* (1989) studied inequality in natural stands of loblolly pine for a wide range of initial densities. Compared to skewness coefficients, correlations of inequality with density were much stronger and insensitive to the measure of tree size (dbh, height, volume) used. Prior to self-thinning, inequality increased through time. After the onset of self-thinning, size inequality decreased over time. However, for the highest densities size inequality increased for the last few measurement intervals. Knox *et al.* (1989) suggested this increasing inequality corresponded to a time when mortality is more random across size classes and not confined mostly to the smaller trees.

Liu and Burkhart (1993) investigated the dynamics of size inequality in young loblolly pine stands. Inequality in groundline diameter decreased through ages 1 to 5 years. Similarly, inequality in dbh decreased through ages 5 to 8 years. They attribute the decline in size inequality at these early ages to the rapid increase in mean tree size which offset the competition effects on variability. At a given age, size inequality increased with increasing planting density.

SIZE RELATED GROWTH DIFFERENCES

Analysis of growth rates for individual plants provides insights into the nature of size variation in even-aged monocultures. Since absolute growth is clearly a function of the initial size of the plant, growth rates are usually expressed in relative terms.

Historically, relative growth rates were commonly used. Recently, the efficacy of relative growth rates applied to perennial plants has been questioned (South 1991). Alternative measures of growth have been proposed (Brand *et al.* 1987) to account for the large proportion of structural material in trees.

Relative Growth Rate

The use of relative growth rate as an overall growth index for individual plants originated with Blackman's (1919) assertion that plant growth be regarded as *compound interest*. Blackman considered this index to be a physiological constant which represented the efficiency of the plant as a producer of new material. West *et al.* (1920) showed that the index was not constant but varied over the course of plant development. They proposed the term *relative growth rate* to avoid the notion of constancy associated with Blackman's efficiency index.

In plants the internal changes in structure and function of individual components is termed ontogenetic drift (Evans 1972). In natural populations, it is not possible to partition effects on relative growth rate into internal and external influences. However,

experiments in controlled environments have shown that any departure from an adequate supply of light, nutrients, or water produces a clearly adverse effect on relative growth rates (Hunt 1978).

Historically, relative growth rate referred to growth in total dry weight. The concept however is applicable to any plant component or dimension and the computations are directly analogous to those for relative growth rate for total dry weight (Hunt 1978). Defined as the rate of increase in plant material per unit of material per unit of time, the instantaneous relative growth rate (r) (Fisher 1921) is given by

$$r = \frac{1}{w} \cdot \frac{\partial w}{\partial t} \quad (9)$$

or

$$r = \frac{\partial \ln(w)}{\partial t} \quad (10)$$

where w denotes weight and t denotes time. The logarithmic¹ progression of weight on time may be used as the basis for computing relative growth rates. At any point in time, the relative growth rate is equal to the slope of the curve at that point.

Whatever the distribution of r , the mean relative growth rate (\bar{r}) over any interval of time is obtained by integrating equation [12] over that interval:

$$\bar{r} = \frac{\ln(w_2) - \ln(w_1)}{t_2 - t_1}$$

Successive intervals can then be used to estimate the trend of relative growth rates. However, the accuracy of the estimate decreases with increasing interval width.

Studies of the relationship between relative growth rate and initial size have reported varying patterns. Harper's (1975) analysis of one 5-year basal area increment

¹ Natural logarithms are used throughout this thesis.

with 30-year-old *Picea sitchensis* showed mean relative growth rate was positively correlated with initial basal area across a range of initial planting densities. Harper (1975) reported similar results in an analysis with various annual plants. Over successive measurements, the slope of the relationship between relative growth rate and initial plant weight decreased but remained positive.

Cannel *et al.* (1984) examined the relationship between mean relative growth rate in height over 1-year intervals for closely spaced seedlings stands of *Picea sitchensis* and *Pinus contorta*. In contrast to Harper's (1975) findings with annual plants, relative growth rate was negatively correlated with initial size in the early measurements. The slope of the relationship increased with each successive interval until relative growth rate became positively correlated with size at age 7-years. Working with red pine (*Pinus resinosa*), Larocque and Marshall (1993) reported similar results for mean relative growth rate in dbh. They concluded the relationship between relative growth rate and size became positive only after the onset of intra-specific competition.

In an analysis of 2-year basal area growth response to thinning in 20-year-old *Pseudotsuga menziesii* across a range of relative densities, Perry (1985) found mean relative growth rate was negatively correlated with initial size at low densities. At high densities, relative growth was positively correlated with initial size. In high density stands, thinning to low relative densities resulted in a switch back to the negative correlation between growth and size. The return to a negative correlation between growth and size suggests that the heaviest thinnings had significantly reduced competition.

Working with closely spaced seedling stands of *Fraxinus mandshurica*, Peterson *et al.* (1990) found little relationship between mean relative growth rate and initial plant mass measured at 57-, 78-, 85-, and 97-days. They conclude increasing density did not cause relative growth rate to become positively correlated with initial size.

Relative Production Rate

Expressing growth relative to the amount of material present has been called into question with respect to large woody stem perennials. As trees grow, much of the stem contains non-productive tissues which do not contribute to growth. As the proportion of productive to non-productive tissue falls, relative growth rates for trees become very small and seemingly less sensitive to environmental conditions.

Brand *et al.* (1987) argue that the primary attribute of interest with respect to perennial plants is the current increment of growth and how it compares with previous increments. They propose that analysis of growth be based on the relative growth of annual increment rather than of total size. The relative production rate (P_i) is defined as:

$$P_i = \frac{d(\ln(y_i))}{dt}$$

where y_i is the current annual increment of some measure of tree growth. As with the relative growth rate, the mean relative production rate over any interval is defined as:

$$\bar{P} = \frac{\ln(Y_i) - \ln(Y_{i-1})}{t_2 - t_1}$$

Brand and Magnussen (1988) used data from several unreplicated spacing trials with *Pinus resinosa* to investigate the relationship between their relative production rate and size of individual trees. Based on functional growth analysis (Hunt 1982), they created hypothetical stands of equal mean size for the selected plots. Their results are similar to those reported by Cannell *et al.* (1984) and Perry (1985) with respect to the relationship between growth rates and initial size across a range of density levels.

THE ROLE OF COMPETITION

Inequality in plant size and variation in growth rates is likely a result of the interaction among several factors: genetic variation, environmental heterogeneity, intra-

specific competition. Two conceptual models of the role of competition in the dynamics of size structures have been proposed (Weiner 1985, Weiner and Thomas 1986). The first assumes that competition acts on all individuals equally or in direct proportion to their size. Competition is assumed to be *two-sided* and described as *resource depletion*. In the second model, competition is thought to be disproportionate to plant size. Large plants usurp resources at the expense of smaller plants. This type of competition is termed *one-sided* and is categorized as *resource pre-emption*. In the most extreme form of one-sided competition, smaller individuals would exhibit no competitive influence on larger neighbors.

Resource Depletion

The first model originates from a narrow interpretation of the first investigations into the development of increased skewness in even-aged populations. Koyama and Kira (1956) concluded that interaction between individual plants was not necessary to explain the development of skewed size distributions. They argued that intrinsic variation in relative growth rates transforms the distribution from essentially *normal* to one which becomes increasingly positively skewed over time. To test their hypothesis, they used mathematical simulation of individual plant growth. Their model was based on the assumption that growth over any short time interval could be approximated by an exponential growth model. Initial weights and relative growth rates were generated from specified *normal* distributions. Subsequent changes in characteristics of the weight distribution were analyzed in terms of changes in the distribution of relative growth rates.

Within the context of their simplified growth model, weight distributions became positively skewed over time. Both the rate of increase and magnitude of skewness were positively correlated with the degree of variation in relative growth rates. Furthermore, the trend toward positive skewness occurred whether or not the initial weights and relative growth rates were correlated. Hozumi *et al.* (1955) and Koyama and Kira (1956)

concluded competition is not necessary for size distributions to become increasingly skewed over time, since a positive correlation between initial size and relative growth rates indicates the existence of a competitive interaction. The development of skewed size distributions was simply the expected outcome of variation in growth rates acting upon an intrinsically exponential growth process.

Under the resource depletion hypothesis, competition for resources is assumed to reduce the relative growth rates of all competing plants by the same proportion (Weiner 1985). A constant proportional reduction in relative growth rates necessarily reduces the variation in growth rates. Citing Koyama and Kira's contention that the degree of skewness is controlled by the variation in growth rates, this hypothesis predicts that competition will reduce skewness. It is further postulated that the effects of competition will tend to decrease size inequality.

Resource Pre-emption

The resource pre-emptive model of competitive influences on size distributions can be traced back to Harper's (1967) interpretation of size differences among plants implying "... a hierarchy of exploitation." Larger plants are able to secure more than their proportional share of resources as based on their relative size (Weiner and Thomas 1986). As a consequence, we would expect smaller plants will have a smaller relative growth rate (Ford 1975). Under this model, competition would tend to increase size inequality.

Discussion

Most analyses support the existence of a dominance/suppression relationship in even-aged plant monocultures. That is, competition acts through resource pre-emption. In fact, the references to Koyama and Kira's (1956) work as a basis for the resource depletion model are weak. Though they concluded competition is not necessary for the

development of skewed size distributions, Koyama and Kira (1956) state that such interactions clearly hasten the development of skewed size distributions.

Koyama and Kira's (1956) conclusion was based on observations of increased skewness with increased initial density for a wide range of annual and perennial plants. From a limited analysis of these data, they concluded that while increased density lowers the mean relative growth rate for the population, the variation in relative growth rates is increased with higher initial densities. They conjectured that increased variability in relative growth rates is a direct outcome of competitive interactions between neighboring plants.

More than three decades after Koyama and Kira published their findings, some debate continues as to what role, if any, competition plays in the dynamics of size structures. In most reports, size inequality (diameter, height, volume) is found to increase with increasing density and time. This is the expected outcome under the resource pre-emptive or dominance/suppression view of competitive interaction. There are, however, voices of dissent on the role of dominance/suppression in the development of size distributions.

Turner and Rabinowitz (1983) concluded that the development of skewed size distributions in populations of *Festuca paradoxa* were not caused by dominance/suppression relationships. Since skewness was highest on plants grown in individual containers, they concluded skewness in mass distributions was caused by intrinsic variation in relative growth rates acting upon an exponential growth process. It is further postulated that dominance/suppression may be important in competition for light but not for below ground resources. In their study " . . . the erect 'vertical' form of grass seedlings may render light competition less crucial than below ground resource depletion."

Further evidence that competitive relationships differ for various resources is provided by the work of Schmitt *et al.* (1986). Shade cloth was used to grow cultivated

radish (*Raphanus sativus*) at different densities and light levels. At the highest light levels, analysis of size inequality indicated dominance and suppression was not prevalent. However, in populations grown under shade cloth inequality increased with density indicating the existence of dominance/suppression.

Perhaps the most direct test available for dominance/suppression is an analysis of the relationship between relative growth rates and size (Ford 1975, Cannell *et al.* 1984, Schmitt *et al.* 1987). There is general agreement that prior to the onset of competition, relative growth rates are negatively correlated with size. Smaller plants have higher relative growth rates and are considered to be more efficient in obtaining resources. As plants begin to compete for resources relative growth rates are constant across size classes. Once self-thinning begins, there is a positive correlation between relative growth rates and size. Brand and Magnussen (1988) found similar trends in an analysis of relative production rates with spacing data from red pine plantations. These trends are consistent with the resource pre-emption model of competition.

There are however, some reports where competitive interactions did not result in a positive correlation between relative growth rate and size. Petersen *et al.* (1990) analyzed the distribution of relative growth rates in *Fraxinus mandshurica* seedlings grown over a range of densities. Though size inequality increased with density and time, they concluded that these trends were attributed to variation in growth rates of individuals with the same mass. In their work, relative growth rates did not suggest a dominance/suppression relationship even though analysis of light-attenuation curves suggested light was a limiting factor.

In general, the dominance/suppression view of competition is well supported in published analysis with annual plants. This interpretation is supported by analysis of size inequality trends and in changes in the distribution of relative growth rates within a cohort. There has been less analysis with perennial species, though there is evidence that similar relationships exist in even-aged forest plantations.

APPLICATION TO PLANTATION GROWTH AND YIELD MODELING

If dominance/suppression relationships are a major determinate of stand dynamics in even-aged loblolly plantations, growth models should reflect these patterns. Magnussen and Brand (1989) developed a distance independent individual-tree growth model, for red pine plantations, based on the concept of dominance/suppression as presented in the ecological literature. The relative growth rates of an initial diameter distribution are modeled as a function of absolute tree size, size relative to the median size, and overall stand density. Other models also estimate growth as a function of some measure of relative size (Pienaar and Harrison 1988, Zhang *et al.* 1993). However, with the complexity of these models it is not readily apparent that these describe a dominance/suppression relationship.

Distributing stand-level growth over size classes

Growth models have recently been developed in which stand-level estimates of growth are distributed over initial diameter distributions (Harrison and Daniels 1988, Pienaar and Harrison 1988, Zhang *et al.* 1993). Since estimates of future size distributions are conditioned on stand-level estimates, these models tend to provide reliable estimates of long-term growth while providing individual-tree resolution and utilizing initial tree lists when available. Harrison and Daniels' (1988) model bases the distribution of stand-level basal area growth on the linear relationship between increment and initial size proposed by Zeide (1986) and Hilt (1983).

Zeide (1986) contended that a linear relationship between diameter increment and initial diameter exists in pure even-aged stands and that the coefficients of this relationship are related to specific periods of stand development. Prior to the onset of competition for light, Zeide argues that diameter increment is proportional to initial diameter. The proportionality constant changes with age but is constant for any given cohort. In terms of relative growth rates, this implies that for any given cohort growth is constant across

initial diameter. This contention is not in agreement with the observed trends reported in the literature cited above.

Following crown closure, Zeide (1986) proposed the relationship between increment and size can be expressed as:

$$i = q + pd$$

where i denotes diameter increment and d is the initial diameter. The value of q is dependent upon the process of self-thinning. Initially the intercept is assumed to be negative but as mortality continues q becomes positive. This implies that relative growth rates are positively correlated to initial size at the onset of self-thinning but become negatively correlated as mortality progresses. If dominance/suppression relationships drive stand dynamics, relative growth rates should remain positively correlated with size throughout the self-thinning phase of stand development.

Hilt (1983) developed an individual-tree growth model for managed, even-aged, upland oak stands. The model is based on the assumption that basal area growth is proportional to the initial diameter squared. Such a relationship implies relative growth rate is constant over all size classes. This assumption is said to hold in "... stands where size differentiation has already occurred." Yet, review of the literature on dominance/suppression clearly indicates that relative growth rates would not be constant in this case.

Quantifying the onset of dominance/suppression

Growth and yield models may consist of a stand-level component and a distance dependent individual-tree component. In one example (Burkhart *et al.* 1987), the stand-level portion is assumed to apply prior to the onset of competition, arbitrarily taken to be at age 8-years. As competition begins to drive stand dynamics, the individual-tree component of the model is used. The relationship between stand-level attributes and the

beginning of competitive relationships has not been quantified. There is some agreement that crown closure represents the beginning of competitive interactions (Strub *et al.* 1975) but we lack methods to easily identify this point (Zeide 1986). McMurtrie (1981) suggests that a critical stage is reached in stand development where the dominance/suppression phenomenon comes into effect. An analysis of the relationship between relative growth rates and individual-tree size over stages of stand development may enable us to quantify that critical point.

Modeling the response to silvicultural treatments

Westoby (1982) introduced the concept of a distribution-modifying function (DMF). DMFs show the relationship between growth and initial size for a given cohort. Over time, the development of a stand is described by a series of DMFs. Graphs of relative growth rates over size are one type of DMF. Westoby shows that the shape of the DMF determines changes in the shape of the frequency distribution and conjectures that the general shape of the DMF remains similar for long periods of stand development. He argues that our understanding of the changes in stand structure would be enhanced by analysis of DMFs. For example, several authors have reported the development of bimodal size distributions in pure even-aged stands (Ford 1975, Cannell *et al.* 1984). Westoby shows that this would occur from sigmoid-shaped DMFs.

Silvicultural treatments can affect stand dynamics by altering the growth rates of individual trees. Perry (1985) presented evidence that the relationship between relative growth rates and initial size are reversed following heavy thinning in dense stands of Douglas-fir. In dense stands, the thinning would tend to reduce the degree of intra-specific competition allowing the smaller trees to respond proportionately greater than the dominant trees. Rogers' (1978) study on the impact of mid-rotation fertilization in loblolly pine plantations suggests that the linear slope between relative growth rate and initial size becomes steeper following treatment. Under a dominance/suppression

relationship, the dominant trees are in a more favorable position to capture the additional nutrients.

In stand-level growth models, responses to silvicultural treatments are often modeled by changing stand-level attributes (*e.g.*, site index) or varying the parameters of specific stand-level attributes. With models that provide individual-tree or size-class resolution, it is assumed that these changes will correctly translate to the response in terms of individual tree growth. Analysis of the distribution of relative growth rates may provide insights into the response of individual trees to silvicultural treatments.