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Intergenotypic Competition in Forest Trees

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Abstract

In contrast to the numerous investigations reported in crop plants, intergenotypic competition has been studied only to a minor extent in forest trees. The purpose of this paper is to emphasize the need for a better understanding of the role of competitive interactions in tree species through increased research. Intergenotypic competition needs to be considered, and may have important implications, in several aspects of population genetics and tree breeding, including: the maintenance of polymorphisms, development of selection theory, design of field plots, and the yield and phenotypic stability of genetically improved populations. Preliminary results from a greenhouse study of competition among hybrid poplar clones illustrate some of the above implications and show that competitive effect can be quite strong and varied. Five questions about competitive interactions that seem to be of particular interest, and which should be given priority in future investigations, are presented and discussed.

Introduction

The general influence of competition on the growth of trees in forest stands has been known for some time, and forms the basis of silvicultural practices such as thinning. However, only in recent years has it been recognized that there is a genetic component to competitive interactions among trees (Sakai *et al.* 1968, Libby *et al.* 1969, Adams *et al.* 1973). Sakai (1961) has pointed out that the growth of plants can be influenced by their neighbors in three ways: (1) The effect of density - High density results in reduced growth of all competing individuals, regardless of genetic constitution, and has the same effect as limiting the space and nutrition available to a plant. (2) Intragenotypic competition - Even with a population of identical genotypes, some plants may outgrow and subsequently suppress the growth of their neighbors because of advantages gained through chance environmental factors. (3) Intergenotypic competition - This is competition resulting from the differential growth of unlike genotypes due to the inherent differences between them. This is the type of competition of greatest interest to geneticists and will be the subject of this paper.

The performance (yield) of an individual genotype (or family, species, etc.) in competition with one or more other genotypes is known as competitive ability. Competitive ability is generally expressed as the difference in performance (i.e., in vegetative growth or reproductive output) when a genotype is grown in mixture and when it is grown in pure stands (i.e., when surrounded only by like genotypes). Since plant density, and thus the effect of spacing, is held constant in these experiments, any difference in yield of a genotype in mixture from its yield in pure stands must be in response to neighboring genotypes. This response can be either positive or negative. Therefore, we have a very simple competition model:

Performance of Genotype x_i in mixture = Pure-stand Performance of x_i + Competitive ability of x_i

If competition among only two genotypes is considered, four types of competitive effects may be recognized (Schutz and Brim 1967). Given that $K_{i/j}$ is the competitive ability of genotype x_i in competition with x(j), the four competitive effects are:

1. Neutrality ($K_{i/j} = K_{j/i} = 0$) - neither genotype is affected by competition, so that the yields of the genotypes in mixture are the same as their yields in pure stands.
2. Complementation ($K_{i/j} + K_{j/i} = 0$) - the gain in yield of one genotype in mixture is exactly counterbalanced by the loss in yield of the other genotype, such that the yield of the mixture is identical to the mean yield of the genotypes in pure stands.
3. Undercompensation ($K_{i/j} + K_{j/i} <> 0$) - the yield of the mixture is less than the mean yield of the genotypes in pure stands.
4. Overcompensation ($K_{i/j} + K_{j/i} > 0$) - the yield of the mixture is greater than the mean yield of the genotypes in pure stands.

Overcompensation is of particular interest in plant breeding because such interactions could be utilized as a means of improving yields.

A number of studies designed to measure intergenotypic competitive effects have been reported for various crop species (e.g., barley (Sakai 1955, Lee 1960, Wiebe *et al.* 1963, Allard and Adams 1969a, 1969b), flax and linseed (Kahn *et al.* 1975), oats (Jensen 1965, Frey and Maldonado 1967), rice (Sakai 1955, Jennings and Aquino 1968), soybeans (Shutz and Brim 1967, Lin and Torrie 1968, Brim and Shutz 1968), and wheat (Sakai 1961, Jensen and Federer 1965)). These studies show that intergenotypic competition can be a major force in molding plant population structure and lead to the following general conclusions: (A) Intergenotypic interactions can have strong and varied effects on the performance of plants at close spacing. (B) Competitive responses often differ for different characters measured. For example, while studies in crop plants generally have emphasized reproductive characters directly related to yield (e.g., seed number, seed weight, etc.), the influence of competition on vegetative response (e.g., plant height, weight, etc.) also is frequently reported. Both types of traits often are significantly affected by intergenotypic competition, but not always to the same magnitude or in the same direction (Sakai 1955, 1961, Shutz and Brim 1967, Kahn *et al.* 1975). (C) Competitive ability of a genotype varies with the genotype(s) of its neighbor(s). (D) Competitive ability of a genotype varies with its frequency. When mixtures of two genotypes are considered, the competitive ability of a genotype can often be closed approximated by a linear relationship with its frequency in the mixture (Sakai 1955, 1957, Shutz and Brim 1967, Kahn *et al.* 1975). (E) The best performing genotypes in pure stands are not generally those with the highest competitive ability. In fact, there are cases where yield in pure stands has been found to be negatively correlated with yield in mixture (Wiebe *et al.* 1963, Jennings and Aquino 1968). (F) In pairwise mixtures of crop varieties overcompensatory and complementary competitive effects are found to be relatively common, while undercompensation seems to occur relatively rarely.

In contrast to crop plants, intergenotypic competition in forest trees has been studied only to a minor degree. Apparently, there have been only two published reports of experiments designed specifically to test for intergenotypic interactions in forest trees. Both of these were greenhouse tests of short duration. One study involved measuring competition among full-sib families of loblolly pine (*Pinus taeda* L.) (Adams *et al.* 1973), and the second, competitive interactions among clones of black cottonwood (*Populus trichocarpa* Torr.) (Tauer 1975). Results of these investigations concur with the general conclusions reached in crop plants and indicate that intergenotypic competition can have quite significant effects on the growth of trees at the seedling stage.

A second approach has been to estimate, through various statistical procedures, the magnitude of intergenotypic competition in forest stands which were planted for other purposes (Sakai and Mukaide 1967, Sakai *et al.* 1968, Huhn 1969, 1970a, 1970c). While of heuristic value, the models used in these studies are probably of limited applicability because they rely on several simplifying assumptions about stand structure (e.g., trees must be uniformly spaced, even-aged, and be randomly distributed with regards to genetic composition (i.e., no family structure) , and competitive effects (e.g., some models assume that competition between any two trees is always complementary). Appraisal of the relative accuracy of these models or their improvement cannot be made until there is a much better understanding of the type and magnitude of intergenotypic interactions occuring in forest trees.

In this paper, I hope to convince the reader that research on intergenotypic competition in forest trees is in need of a much greater effort. I will first show why intergenotypic interactions are important to study. I will then present an example of a recent investigation in forest trees, and will conclude by listing questions I feel should be given priority in future studies.

Why Intergenotypic Competition is Important

There are five major areas where intergenotypic competiton can have a significant impact on the population genetics and/or breeding of forest trees. In order to evaluate the importance of intergenotypic competition in these five areas and to maximize breeding efforts, a better understanding of competitive interactions in forest trees is required.

1. Maintenance of Polymorphisms in Populations

Studies of population genetic structure, especially recent work utilizing allozymes (Hamrick *et al.* 1980), reveal that forest trees, in general, possess considerable amounts of genetic variation within populations. Since genetic diversity is probably of great value in buffering populations to the widely fluctuating environments experienced by forest trees, it is of great interest to determine the evolutionary mechanisms which are responsible for the maintenance of this variation. Recent theoretical investigations show that intergenotypic competitive interactions can lead to very stable frequency-dependent polymorphisms (Shutz *et al.* 1968, Allard and Adams 1969a, 1969b, Shutz and Usanis 1969, Huhn 1971). Simulating evolving populations on the computer with various kinds of interactions among competing individuals indicates that overcompensation can be especially powerful in maintaining stable equilibria; complementation can also lead to stable

equilibra, but under more restricted conditions. Undercompensation only leads to unstable equilibria and thus is probably of little or no importance in the long-term maintenance of genetic variation. Considering the high frequency with which overcompensatory and complementary interactions have been found to occur in plants, they may well be among the major forces maintaining genetic diversity in populations.

2. Influence on Selection Theory

Given the magnitude of intergenotypic competition that has been detected in plant populations, the adequacy of present selection theory which assumes that populations consist of non-interacting individuals must be questioned (Allard and Adams 1969b). For example, competitive interactions are likely to result in increased variation among genotypes in mixed populations, for at least some traits. This variation is due to genetic differences among individuals, but is not transmissible (i.e., at least through mass selection) to progeny. Thus, ignoring competitive effects will result in overestimates of genetic variation and subsequently, overestimates of heritability (h^2), and perhaps less efficient selection than might otherwise be possible (Sakai 1955, Huhn 1970a, 1971). Both Griffing (1967) and Huhn (1970a, 1970b, 1971) have investigated the impact of intergenotypic interactions on mass selection by developing quantitative genetic models which assume that the genetic value of an individual depends not only on its own genotype, but on the associate genotypes of its neighbors. These investigations revealed that when intergenotypic competitive effects are ignored, mass selection can be very inefficient, and actually lead to a negative response of the population mean under certain competitive conditions.

3. Design of Field Plots

The fact that a given genotype may perform differently depending on the genotypes of its neighbors also poses problems in the design of field plots. The most efficient designs in terms of size and shape of plots will depend not only on the types and magnitude of intergenotypic interactions, but also on the intended use of materials. For example, there is much interest in the southern United States in the operational planting of open-pollinated families of pine in pure blocks. [1] This could have several advantages from a silvicultural and management point of view. For instance, families with different growth properties or quality could be managed as separate units. Advantage might also be made of families with specific site adaptations, by matching particular families with particular sites. However, genetic testing of families in evaluation plantations is usually conducted in single row plots which are bordered on each side by different families. Since competitive ability is often poorly correlated with yield in pure stands, the results of such tests may not reveal those families with the best pure stand performance. Perhaps multiple-tree square plots would be more suitable for this purpose, where only trees in the centre of the plots would be measured. On the other hand, row plots or individual tree plots may be very adequate if families are intended for mixed plantings.

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[1]Talbert, J.T. 1980. Effect of interfamily competition on the growth of loblolly pine families - a work plan. N.C. State University-Industry Cooperative Tree Improvement Program. School of Forest Resources, North Carolina State University, Raleigh.

4. Utilization of Superior Mixtures

As mentioned previously, mixtures of crop varieties often are found to outperform the mean of the component varieties in pure stands (Simmonds 1962, Jensen 1965, Frey and Maldonado 1967, Brim and Shutz 1968, Allard and Adams 1969b, Trenbath 1974, Khan *et al.* 1975). In addition, they frequently exceed the highest component in the mixture and sometimes exceed the yield of the best performing variety in pure stands (Frey and Maldonado 1967, Brim and Shutz 1968, Trenbath 1974, Khan *et al.* 1975). These results are remarkable when one considers that typically the varieties tested in these studies were previously selected for high performance in pure stands, and the mixes formed without prior knowledge of the potential of the component varieties to interact favorably (Allard and Adams 1969b). Genotypes in forest tree populations have evolved under conditions of mutual selection and, therefore, might be expected to interact favorably in a high proportion of cases. Thus, the potential for improving yields in forest trees through judicious mixing of genotypes seems to be very favorable and needs to be explored fully.

5. Phenotypic Stability of Genetically Improved Populations

In addition to possible yield improvements, mixtures in crop plants have demonstrated another, perhaps more important, advantage in that they are generally more stable in yield than pure lines when tested over a variety of environments (Simmonds 1962, Jensen 1965, Frey and Maldonado 1967, Shutz and Brim 1971, Trenbath 1974). Furthermore, results from a study in soybeans (Shutz and Brim 1971) indicate that the degree of stability may be dependent on the types of competitive interactions involved in a mixture. Since populations of forest trees must endure extremely heterogeneous environments over both space and time, the possibility of utilizing competitive interactions to improve phenotypic stability should be tested.

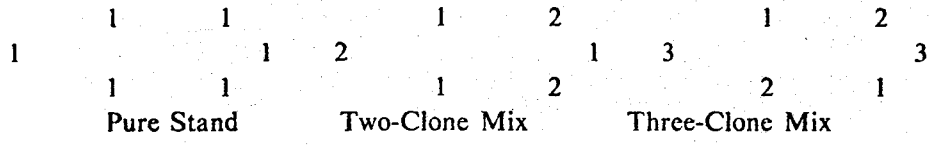
An Example of A Study of Intergenotypic Competition in Trees

In order to illustrate some of the concepts that have been mentioned, I will present some results from a recent investigation of intergenotypic competition among hybrid poplar clones. [2] This study was conducted by myself and Dr. Tim Demeritt of the Northeastern Forest Experiment Station at Durham, New Hampshire.

Two sets of six clones were investigated; one set, designated DN, consisted of *Populus deltoides* x *P. nigra* crosses and the other set, designated NE, consisted of a variety of American x European species hybrids originating from the Northeastern Forest Experiment Station. Within each set, pure stands of all six clones, all fifteen two-clone combinations, and all twenty three-clone combinations were tested in six-tree plots. Both sets were grown in the greenhouse during the summer of 1977. In addition a replicate of the DN set, with a difference of one clone, was planted in the field in 1978. In the greenhouse, unrooted cuttings were planted in pots in one of the following three hexagonal

[2]Adams, W.T. and Demeritt, M.E. Intergenotypic competition among hybrid poplar clones. Manuscript in preparation.

arrangements:



Cuttings were spaced 15 cm apart. The replicate DN cuttings were rooted in the greenhouse in the spring of 1978 and planted in the field in row plots. In all studies, competition treatments were replicated eight times in a randomized complete block design.

I will discuss some preliminary results from only the greenhouse DN experiment and will consider only one of the measured traits; height growth at the termination of the experiment, which was approximately four months after planting. It should be mentioned that two factors in the study led to quite a bit of uncontrolled variation in growth rate. Cuttings varied greatly within clones in both initial size and in date of bud break. For this reason, the total height of each cuttings was adjusted for initial cutting size and time of bud break by covariance analysis. However, even with the covariance adjustment, a great deal of error variation remained. We feel that the precision of the experiment could have been much improved if we had planted rooted cuttings and had made an effort to match up the size of cutting, by block, prior to planting.

The influence of intergenotypic competition on the growth of clones in pairwise mixtures is represented by a series of bar graphs in Figure 1, where the adjusted mean height of each clone in mixture is expressed as a percentage of its adjusted mean height when grown in a pure stand. Sets of histograms in Column I give the height growth of each of the six clones when in competition with each of the other clones (whose designations are indicated below the bars), and thus indicate competitive ability. Sets in Column II show the effect of each clone on the height growth of its neighbors (which can be referred to as the competitive influence of a clone). Bar graphs in Column III give the pure-stand growth of each clone relative to the poorest performer in a pure stand, clone 2, which had an adjusted mean height of 41.2 cm. Variation among clones in mean pure-stand heights was significant at the one percent probability level.

Despite the low statistical precision of the experiment, the heights of clones grown in mixtures were significantly different ($P = 0.05$) from their pure-stand heights in a number of cases. In addition, there was no consistent trend in competitive response, since the performance of clones was both enhanced and decreased by competition with genotypes other than their own. In general, the clones could be classified as good, poor, or neutral competitors or neighbors based on their average competitive ability or influence (Shutz *et al.* 1968,. Allard and Adams 1969a). For example, both clones 1 and 4 could be classified as good competitors and neutral neighbors, since their competitive abilities were either significantly positive or not detectably different from their pure stand performance, and they never caused a significant height change in their neighbors. Furthermore, clone 3 was a poor competitor and clones 2 and 5 were good and poor neighbors, respectively.

As often found in crop plants, the clones which performed the best in pure stands were generally poor competitors in mixture and vice versa. Thus, clones 1, 2 and 4, which had the poorest height growth in pure stands, could be classified as either good or neutral competitors, and clones 3 and 6, among the best performers in pure stands, could

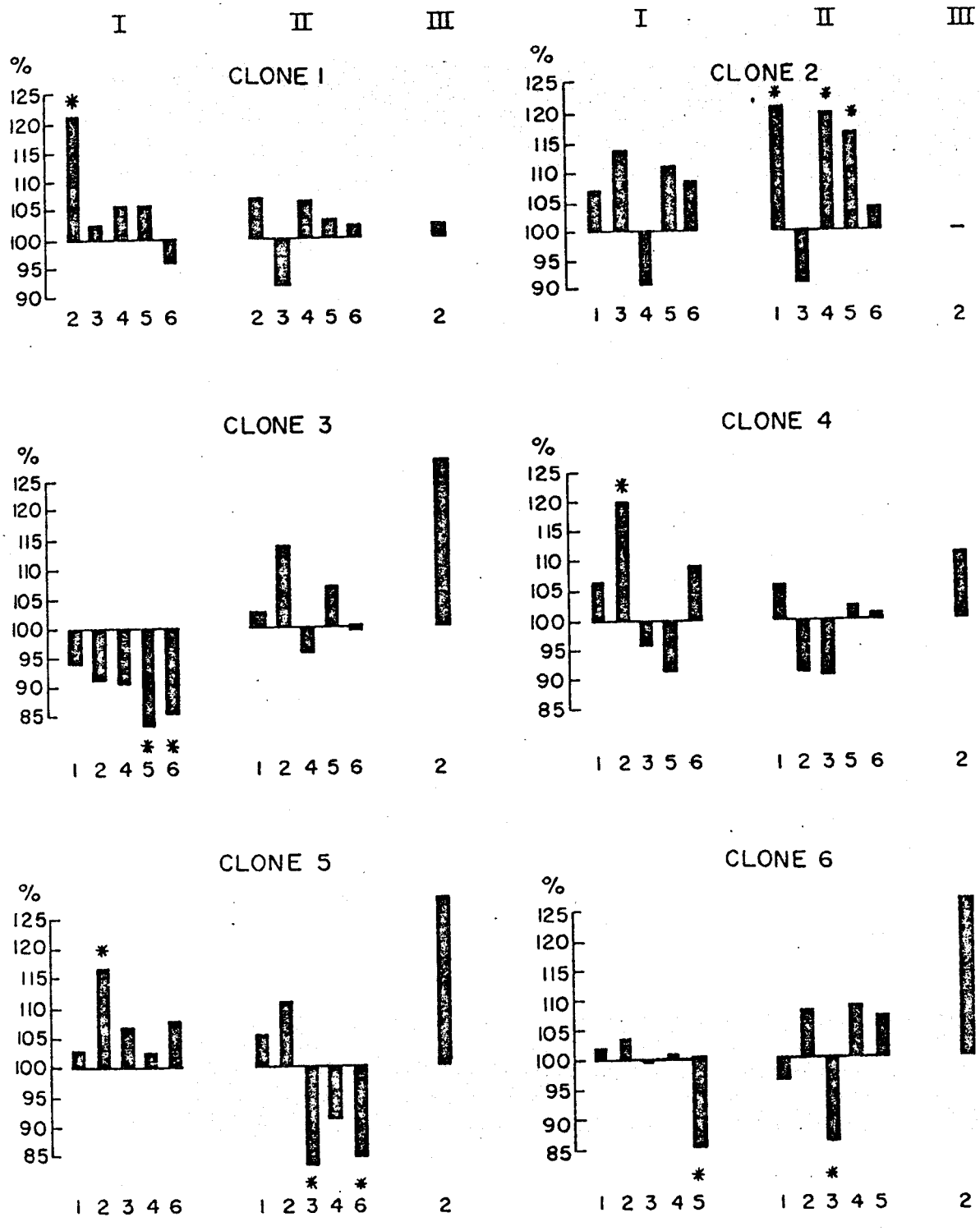


Figure 1. Graphical representation of the adjusted height growth of six hybrid poplar clones grown in pairwise mixtures, expressed as a percentage of the growth of each clone in competition with itself. Column I gives the effect of competition on each clone (competitive ability). Column II gives the effect of each clone on its neighbors (competitive influence). Column III gives the pure stand growth relative to clone 2. Adjusted heights significantly higher or lower than pure stand heights ($P = 0.05$) are marked with an asterisk.

be classified as poor competitors. This emphasizes the problems of selecting for pure-stand performance based on tests conducted in mixtures. Clone 5 seems to be an exception to the above pattern since it was the best pure-stand performer and could also be classified as a good competitor. However, this clone was also a poor neighbor. This is the kind of genotype that could cause real problems in a mass selection program. Because of their adverse effects on neighbors, selecting a high proportion of these genotypes might result in a reduced or even negative response in the population mean.

Analyzing the mean performance of the mixtures revealed that of the 15 two-clone combinations tested, two could be classified as overcompensatory, four as complementary, and the rest neutral in competitive effects. Overcompensatory mixtures were defined as those with mean heights greater than the mean height of the component clones in pure stands ($P = 0.05$). Mean heights of complementary mixtures were not significantly different from the mean of the components, but contained one clone with a significantly positive or negative competitive ability. Finding only two overcompensatory interactions may seem a small percentage, but remember that the precision of the experiment was less than desired, and clones were chosen at random with regard to their potential to interact favorably. The two overcompensatory mixtures, combination of clones 1 and 2, and 2 and 5, were each a little over 14 percent greater than the mean of the components in pure stands. Furthermore, the combination of clones 2 and 5 had a mean adjusted height (53.7 cm) which was greater (although not significantly greater) than the best clone in pure stands (clone 5 with a mean height of 52.8 cm).

In testing three-clone mixtures, we were interested primarily in answering two questions: (1) Can competitive abilities of clones in more complex mixtures be predicted based on their mean competitive abilities in pairwise combination, or do higher order interactions play an important role in competitive response? (2) Can the proportion and degree of superiority of overcompensatory mixtures be increased when more complex combinations are employed? Question 1 has received only limited attention in crop plants (Brim and Shutz 1968), but it is generally assumed in theoretical investigations that intergenotypic competitive effects are additive in nature (Shutz *et al.* 1968, Allard and Adams 1969b). Question 2 also has been studied only to a limited degree. While one investigation in soybeans suggests that yields are increased in more complex mixtures (Brim and Shutz 1968), another study in oats revealed no association of yield with the number of components in mixtures (Frey and Maldonado 1967).

Consistent with observations in barley and oats (Allard and Adams 1969a), the mean competitive abilities (group means) of the six hybrid poplar clones in three-clone mixtures were relatively consistent with the mean competitive abilities of the same clones when tested in two-clone combinations (Table 1). For example, clone 3 was, on the average, a poor competitor whether competing with one or two other clones, and clone 5 was, on the averge, a good competitor. Mean adjusted heights of clones 2 and 4 were slightly superior to their pure-stand values when grown in two-clone mixtures and were slightly inferior when grown in three-clone mixtures, but in none of the cases were these differences significant at the five percent probability level. However, if specific three-clone combinations are considered, the heights of individual clones were not always as would be predicted based on the mean of their performance in pairwise combinations. Based on the competitive abilities of clone 1 in pairwise combinations with clone 2 (121.1) and clone 3 (102.6), the expected competitive ability of clone 1 in a three-clone mixture with these clones would be greater than 100 percent, as verified by the observed performance of

Table 1. Adjusted height growth of six hybrid poplar clones when competing with one or two other clones, expressed as a percentage of the adjusted height growth of each clone grown in competition with itself (pure stand).

Clone 1		Clone 2		Clone 3		Clone 4		Clone 5		Clone 6	
Competitor(s)	Height, %	Competitor(s)	Height, %	Competitor(s)	Height, %	Competitor(s)	Height, %	Competitor(s)	Height, %	Competitor(s)	Height, %
2	121.1*	1	107.0	1	93.9	1	106.2	1	103.3	1	102.0
3	102.6	3	113.8	2	91.0	2	120.0*	2	116.7*	2	103.6
4	105.6	4	90.9	4	90.5	3	95.5	3	106.7	3	99.6
5	105.7	5	111.1	5	83.4*	5	91.0	4	102.3	4	100.7
6	96.0	6	108.2	6	85.3*	6	108.9	6	107.5	5	84.3*
Group Mean	106.2		106.2		88.8*		104.3		107.3		98.0
2+3	120.4*	1+3	101.7	1+2	92.2	1+2	91.1	1+2	112.3	1+2	84.6
2+4	111.3	1+4	97.1	1+4	89.5	1+3	115.1	1+3	112.5	1+3	110.6
2+5	84.8	1+5	88.4	1+5	80.0*	1+5	94.9	1+4	116.5*	1+4	93.7
2+6	126.6*	1+6	99.3	1+6	84.3	1+6	86.0	1+6	98.3	1+5	86.1
3+4	123.1*	3+4	108.2	2+4	77.8*	2+3	99.9	2+3	111.3	2+3	88.8
3+5	91.8	3+5	88.8	2+5	89.8	2+5	95.5	2+4	109.1	2+4	118.6*
3+6	105.8	3+6	87.5	2+6	94.6	2+6	112.2	2+6	111.2	2+5	97.8
4+5	111.0	4+5	89.7	4+5	88.9	3+5	91.2	3+4	118.5*	3+4	105.1
4+6	117.9	4+6	114.8	4+6	85.9	3+6	116.1	3+6	109.3	3+5	93.9
5+6	97.4	5+6	91.3	5+6	90.0	5+6	84.5	4+6	112.8	4+5	103.3
Group Mean	109.0		96.7		87.3*		98.6		111.2*		98.3

*Significantly greater (or less) than pure stand adjusted height (P = 0.05).

120.4. Similar reasoning would also lead to an expected performance of greater than 100 percent for clone 1 when competing with clones 2 and 5. But in this case, the observed competitive ability was much less than 100 percent (84.8). Thus, even though a statistical analysis of the significance of such interactions has yet to be carried out, there is at least an indication in these data that higher order interactions could have an important impact on competitive response.

Using criteria similar to those described for the two-clone mixtures, 12 of the 20 three-clone combinations could be classified as neutral in competitive effects, seven as complementary and one as overcompensatory. The one overcompensatory mixture, a combination of clones 2, 4 and 6, was 15.3 percent superior in mean height than the mean of the component clones in pure stands, and was nearly identical in performance to the best two-clone mixture. There is no evidence from these results that either the proportion or magnitude of overcompensatory mixtures is generally increased when more complex combinations of genotypes are utilized.

Questions for Future Research

Clearly, our understanding of intergenotypic competition in forest trees is extremely limited and a wide variety of studies is needed in this area. However, five questions seem to be of particular interest and should be given priority in future investigations.

1. What it the magnitude and frequency of intergenotypic competition in different species?

   In order to evaluate the generality of competitive interactions in forest trees a number of species needs to be investigated. It would be interesting to learn whether the magnitude of competitive responses is associated with taxonomic or ecological classification of species. For example, would competitive interactions be more prevalent in hardwoods than conifers, or in early successional species than late successional species? It might be hypothesized that the magnitude of intraspecific intergenotypic competition would be greater in early successional species, because individuals of these species are often subjected to strong competition with other individuals of the same species. On the other hand, individuals of late successional species must be adapted primarily to compete with individuals of other species.

2. What morphological and physiological mechanisms result in competitive interactions, especially in overcompensation?

   Particularly in forestry where testing can be very long-term, the random mixing of genotypes in search of favorable combinations would be very inefficient and costly. We need to understand the underlying mechanisms which result in superior combinations. Tests could then be based on combinations likely to yield favorable responses. The best initial approach would be to first find a variety of genotypes that interact favorably and then study their morphological and physiological characteristics. To ensure the necessary precision in replication, these studies would need to be done in species that can be clonally propagated with ease. Since favorably interacting genotypes are those which somehow are able to share limited resources more efficiently, characteristics which allow them to utilize non-overlappin parts of the environment should be explored (Trenbath 1974). For

example, does the physical structure of genotypes in overcompensatory mixtures differ in crown characteristics, branch or leaf angle, or in the form or compactness of their roots? Are their growth patterns different in timing or duration? Is one genotype more photosynthetically efficient at lower light intensities than the other?

3. To what extent do competitive interactions change with stand development?

Well designed long-term field experiments need to be established so that the role of intergenotypic interactions in stand development and on the performance of rotation-age trees can be assessed. The genetic materials used in these experiments should be from readily available sources (e.g., easily propagated clones or full-sib families) so that short-term tests with young trees of the same stocks could be carried out either in conjunction with the field experiments or in the future. In this way, the degree to which juvenile testing is able to predict competitive effects in older trees can be determined.

In addition to the hybrid poplar study that has been described, I know of three other field experiments that have been established in recent years. Two of these are investigations of intergenotypic competition in southern pine species. One study in slash pine (*Pinus elliottii* Engelm.) is being carried out by Dr. Donald Rockwood at the School of Forest Resources and Conservation, University of Florida. The second, a study of competitive interactions among wind-pollinated families of loblolly pine, is being conducted by John Talbert of North Carolina State University - Industry Pine Tree Improvement Cooperative. A third experiment, one to investigate intergenotypic competition among black cottonwood clones at close spacing, has recently been terminated after several years of growth in the field, and is presently being analyzed. This study is under the direction of Dr. Carl Mohn at the College of Forestry, University of Minnesota.

4. To what extent do competitive responses depend on particular environments or cultural conditions?

Studies in crop plants show that both the magnitude and direction of competitive responses can vary when competition experiments are carried out under different environmental conditions (Sakai 1961, Frey and Maldonado 1967, Shutz and Brim 1967, Lin and Torrie 1968, Khan *et al.* 1975). For example, Sakai (1961) found that competitive ability, both in oats and rice, varied dramatically with level of soil fertility. Plant density also has been found to have an important influence on competitive response; while the magnitude of competitive effects usually increases as the spacing between plants decreases (Sakai 1961, Shutz and Brim 1967), exceptions to this pattern have been reported (Lin and Torrie 1968). Certainly, if competitive interactions (particularly overcompensation) are to be exploited in tree improvement programs, the range of environmental conditions under which stability in performance can be expected needs to be determined. The general stability of mixtures observed in crop plants suggests that this range could be quite broad. It is also important to find out whether particular types or combinations of interactions lead to greater stability than others.

5. What is the magnitude of higher order interactions in competitive effects?

If the performance of multiple component mixtures could be predicted fairly accurately by summing the pairwise interactions of the components, both the testing and utilization of mixtures for tree improvement programs, as well as the construction of competitive models, would be greatly simplified. Whatever the findings, studies on the magnitude of higher order competitive interactions need to be carried out, so that precise models and efficient testing schemes can be developed.

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