

Intergenotypic Interactions Among Families of Loblolly Pine (*Pinus taeda* L.)

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Summary. The effects of competition on the growth of families of loblolly pine (*Pinus taeda*, L.) seedlings were investigated. The experimental design made it possible to evaluate the effects of crowding on growth and to determine the types and magnitudes of intergenotypic interactions among pairs of families. The results showed that intergenotypic interactions were both highly variable and pronounced in their effect on early growth. Evidence was also found for precompetition cooperating interactions occurring among seedlings surrounded by neighbors of the same family.

Much attention has been given to the study of intergenotypic competitive interactions in plants. Plant breeders in particular have been concerned with intergenotypic competition because of its effect on phenotypic performance and the evaluation of genotypes (Allard and Adams, 1968; Lin and Torrie, 1968) and also because mixing of crop varieties with favorable interactions can lead to increased yields above that expected from single variety plantings (Jensen, 1965; Frey and Maldonado, 1967; Brim and Schutz, 1968). In addition, findings by population geneticists indicate that certain types of intergenotypic interactions are important in the maintenance of polymorphisms since they result in frequency-dependent selection (Schutz *et al.*, 1968; Allard and Adams, 1969).

Most research on intergenotypic interactions to date have dealt with primarily self-pollinating species and little, if any, information is available on these effects in outcrossing species. The study described in this paper was undertaken to characterize such interactions in families of loblolly pine seedlings.

Materials and Methods

Seedlings from four control pollinated families of loblolly pine were grown under both competitive and competition-free conditions in a greenhouse for nine months. These families were derived by crossing trees selected from different natural populations for inclusion in seed orchards in the North Carolina State University Tree Improvement Program. The families involved had similar average seed weights.

One month old seedlings were transplanted into flats containing compartments filled with six inches of natural forest soil. Seedlings were arranged so that each compartment contained one of six treatments, five of which consisted of growing seedlings under conditions of high density conducive to the expression of competitive effects, if they existed, and one in which seedlings were grown in a competitive-free environment with space characteristic of low density conditions. In all compartments containing treatments other than the competitive-free one, a central seedling of a test family was surrounded by a hexagonal ring consisting of either zero, two, three,

four, or six seedlings of a competitor family. Positions in the hexagonal ring not occupied by seedlings of the competitor family were filled with seedlings from the test family. Each test seedling of a high density treatment was allocated 25.0 cm² of space which is equivalent to 37.2 seedlings per square foot. Seedlings receiving the competition-free treatment had 398.0cm² of growing space which is equivalent to a density of 2.3 seedlings per square foot. A diagram of the planting arrangement for each treatment is given in Fig. 1.

Each of the four families, designated as A, B, C, and D, was grown in association with each of the other three families both as a test family and as a competitor family, providing a total of six family combinations or twelve pairings when reciprocal combinations are included. These pairings were designated by two letters, e.g. AB or BA, where the first letter signified the test family and the second letter the competitor family.

The experiment was arranged in a split-plot design with nine replications. The seedlings for each family pair occurred as whole plots and seedlings assigned to the six treatments within a family pair served as the subplots.

Measurements were taken on the test seedlings only. Plant heights were measured monthly for the competition-free and pure stand (all competitors belong to the same family as the test seedling) treatments while seedling diameter, root surface area and dry weight were measured for all treatments at the conclusion of the experiment (37 weeks after transplanting) only. During the first eleven weeks after transplanting, before the seedlings set terminal buds, heights were taken to the tip of the termi-

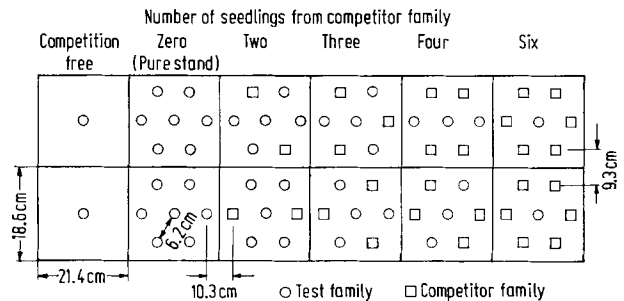


Fig. 1. Planting arrangement with spacing among seedlings for two adjacent whole plots. Note: In the actual experimental layout competition treatments were randomized within each whole plot

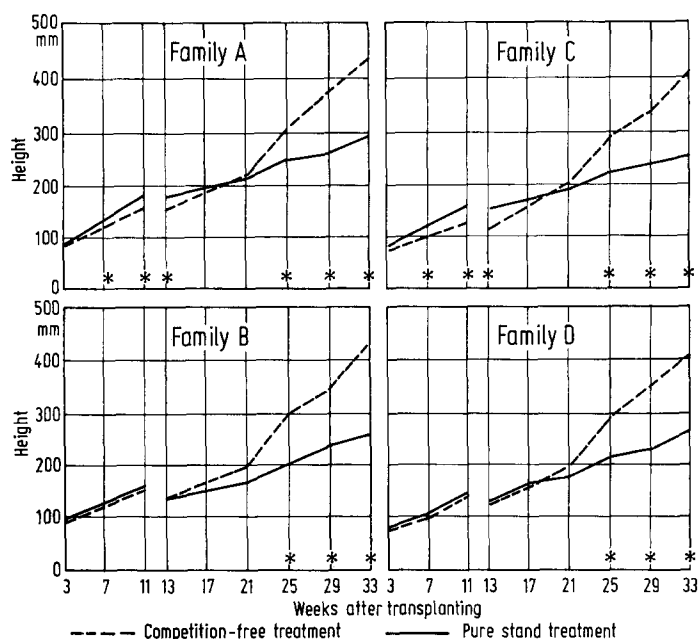


Fig. 2. Height growth means plotted for the competition-free and pure stand treatments over a 33 week period for each family. Means for each measurement date which differ significantly at the 0.05 probability level are denoted by asterisks

nal leader. Thereafter, heights were measured to the tip of the terminal bud. Relative root surface areas were determined by the titration method described by Wilde and Voight (1955).

The monthly height measurements were taken to determine the effect of surrounding neighbors of the same family on the rate of growth of test seedlings. Average height of test seedlings from pure stand and competition-free treatments were plotted over time for each family. A comparison of the growth curves for these two treatments was useful in describing the effect of crowding on growth. Also, since crowding eventually began to limit the growth of seedlings in pure stands while competition-free seedlings continued to grow unimpeded, the comparison of growth curves made it possible to determine the point in time in which competition first became a factor in the growth of pure stand test seedlings. This point in time was labeled the *limiting point*.

In the evaluation of interfamilial interactions only data from the plots containing the five high density treatments were used. Since interest was primarily in the analysis of the traits as they were affected by intergenotypic competitive effects only, height measurements for each test seedling, as recorded at the limiting point, were used to calculate height growth after the limiting point had been reached and as a covariate to adjust the values of the other traits to those that would have been obtained if the test seedlings in all treatments had a common height at the limiting point. Intergenotypic competition is defined as the deviation in yield of genotypes grown in mixture from that expected on the basis of pure stand performance. For this reason, adjustment for free growth prior to competition must be made on the basis of heights measured at the limiting point only. If, for example, each test seedling, regardless of its treatment, is adjusted using the height determined by its own growth curve, then the adjustment not only corrects for free growth but also may remove some of the intergenotypic competitive effect as well. This would occur if intergenotypic competition results in seedlings entering into competition earlier or later than seedlings of the same family found in pure stand.

The method described by Schutz and Brim (1967) was employed to determine the presence of interfamilial interactions. They defined three intergenotypic competitive effects on the basis of the size and sign of the linear regression coefficients for regression of a trait of the test genotype on the number of individuals of the competitor genotype. Complementation was defined as the effect that occurs when the regression coefficients for a family pair and its reciprocal are of equal magnitude and opposite sign. Overcompensation was described as the effect that occurs when the sum of the regression coefficients is greater than zero and undercompensation was said to result when the sum of the regression coefficients is less than zero. In this experiment, following Schutz and Brim (1967), the following methods were used to detect competitive effects. If the regression coefficients for a reciprocal pair of families were different in sign and significantly different from zero at the 5% level the effect was labeled complementation. If both of the regression coefficients for a reciprocal pair were found to be significantly greater than zero or one was found to be greater than zero whereas the other was not, the effect was classified as overcompensation. If both regression coefficients were negative and significantly different from zero or one was negative and different from zero but the other was not found to differ from zero, the effect was classified as undercompensation. If neither of the regression coeffi-

Table 1. Estimates of linear regression coefficients of height increment (mm), diameter (mm), relative root surface area (ml of titrant added) and dry weight (g) on the number of competitor plants. Regression coefficients significantly different from zero at the 0.05 probability level denoted by asterisks

| Test Family | Competitor Family | | | | | | | |
|-------------|-------------------|----------|-------------------|------------|------------------|----------|-------------------|------------|
| | A | | | | B | | | |
| | Height Increment | Diameter | Root Surface Area | Dry Weight | Height Increment | Diameter | Root Surface Area | Dry Weight |
| A | — | — | — | — | — 3.378 | —0.056 | —0.032 | —0.056 |
| B | 1.350 | —0.021 | —0.070 | 0.016 | — | — | — | — |
| C | — 4.544 | —0.056 | —0.001 | —0.120 | 7.638 | 0.010 | 0.213 | 0.037 |
| D | — 5.293 | —0.043 | —0.178 | —0.184* | —11.248* | —0.091* | —0.256 | —0.126 |
| | C | | | | D | | | |
| A | — 2.410 | 0.004 | —0.046 | —0.034 | 14.082* | 0.158* | 0.381 | 0.374* |
| B | — 2.526 | —0.008 | 0.445* | 0.056 | 2.506 | 0.068 | 0.464 | —0.040 |
| C | — | — | — | — | 11.032* | 0.088* | 0.252 | 0.177* |
| D | —17.206* | —0.091* | —0.141 | —0.171* | — | — | — | — |

cients were significantly greater than zero, the effects were considered to be neutral.

Results and Discussion

The height means for the competition-free and pure stand test seedlings within each family are plotted over

time in Fig. 2. Two patterns of growth developed among the four families. Families B and D had a pattern in which the growth of test seedlings for both treatments was almost the same until the limiting point was reached. At this time, the curves for the two treatments began to diverge as the pure stand test seedlings tapered off in growth due to density effects.

Families A and C have a somewhat different growth pattern from that of B and D, in that the pure stand test seedlings grew better during the period of earlier growth. Later, as crowding began to occur, the pattern changed with the pure stand test seedlings tapering off in growth as in families B and D. This early advantage in pure stand test seedlings is an example of cooperative interaction. Cooperative interaction has also been observed in *Drosophila* (Ayala, 1968). Whether such short lived affects are of any lasting significance is doubtful since any advantage due to cooperative interactions is overcome later by the effects of competition. It is conceivable, however, that these interactions may be important in early seedling survival.

Density effects were first evident in all families during the thirteenth week after transplanting. After the thirteenth week, growth of seedlings in the two treatments began to diverge in families B and D and converge in families A and C. Since this was the earliest date at which differences in growth patterns were detected, it was chosen to be the limiting point.

The computed regression coefficients for each family combination and its reciprocal are given in Table 1 and presented graphically in Fig. 3. Three family combinations for height increment, three for diameter, two for relative root surface area and two for dry weight showed intergenotypic interactions. In addition, all three of the possible types of genotypic interaction effects defined for pairwise competitive situations were found. Considering all traits, four family combinations exhibited overcompensation, two undercompensation, four complementation and the rest neutrality. These effects are summarized in Table 2 where the signs of the regression coefficients, if significantly different from zero, are listed for all traits and family combinations.

The types of competitive effects found for each family combination were not the same for all traits. This implies that intergenotypic interactions can only be properly discussed in terms of specific traits. Similar findings have been obtained in other plant species (Lin and Torrie, 1968; Sakai, 1961).

Another frequently occurring result which has also been found in crop plants (Sakai, 1961; Schutz and Brim, 1967; Jennings and Aquino, 1968) was that the yield of families in pure stand was not correlated and in many cases was negatively correlated with their yield in mixture. Therefore, ranking the performance of genotypes based on their yield in mix-

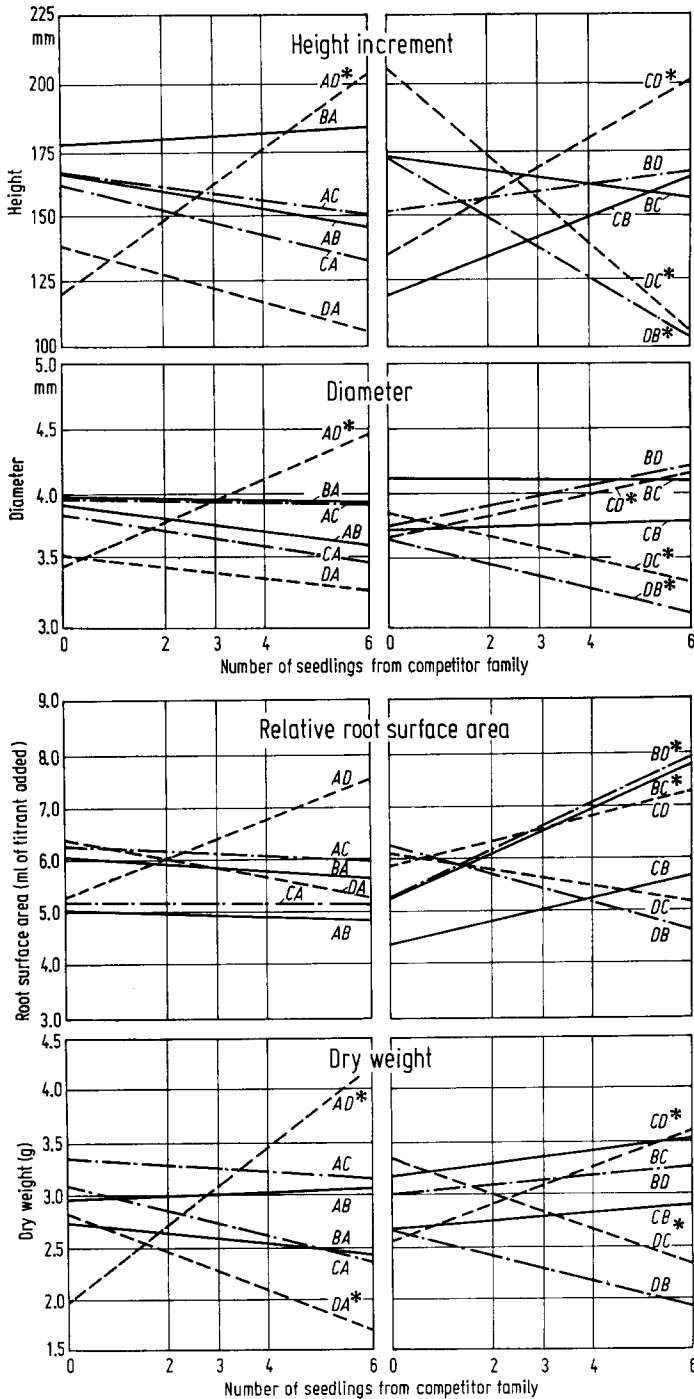


Fig. 3. Linear regression lines for yield of test families when grown in plots with varying numbers of trees of competitor families. Regression coefficients significantly different from zero at the 0.05 probability level are denoted by asterisks

ture (as is often done in progeny testing) will not always give a reliable ranking of performance to be expected from pure stand plantings.

Intergenotypic interactions were observed only for combinations involving family D and the combination of families B and C. These were the only combinations in which the test families and competitor families were unrelated. In all other combinations tested, seedlings of the families were half-sibs of the seedlings of the competitor families. Although these results do not establish conclusively that related families of loblolly pine seedlings are competitively neutral, it is likely that the failure to detect competitive effects among the related families in this experiment is due in part to their shared parentage.

Conclusions

Despite the fact that this study involved families of an outcrossing species in which considerable amount of internal genetic variation is to be expected, a high frequency of intergenotypic competitive effects for combinations involving unrelated families were detected. This suggests that such effects must at least be moderately prevalent in natural seedling populations of loblolly pine. However, little can be concluded from the results of this experiment with respect to the frequencies with which the various types of intergenotypic interaction effects occur in such populations. Since the results of this study are comparable to those found in predominantly self-pollinating species it seems likely that future study will reveal that these interactions are as important in the population dynamics of outcrossing species as they appear to be in the more selfed plants.

Acknowledgement

Thanks are due to Hoeruer Waldorf Paper Company and Federal Papers, Inc. for the contribution of control pollinated seed used in this study. A traineeship from

Table 2. Summary of the competitive relationships among the family combinations and their reciprocals

| Traits | Family Combination × Reciprocal Pair | | | | | |
|------------------|--------------------------------------|-------|-------|-------|-------|-------|
| | AB,BA | AC,CA | AD,DA | BC,CB | BD,DB | CD,DC |
| Height Increment | 0,0 | 0,0 | + ,0 | 0,0 | 0,- | +,- |
| Diameter | 0,0 | 0,0 | + ,0 | 0,0 | 0,- | +,- |
| Relative Root | | | | | | |
| Surface Area | 0,0 | 0,0 | 0,0 | + ,0 | + ,0 | 0,0 |
| Dry Weight | 0,0 | 0,0 | +,- | 0,0 | 0,0 | +,- |

Responses are categorized as overcompensatory (+, 0 or 0, + or +, +), undercompensatory (-, 0 or 0, - or -, -), complementary (+, - or -, +) or neutral (0, 0), where 0 signifies a nonsignificant linear regression coefficient at the 5 percent level and + and - signify significant regression coefficients of opposite sign.

the National Science Foundation provided financial support and is gratefully acknowledged.

Literature

- Allard, R. W., Adams, J.: The role of inter-genotypic interactions in plant breeding. 12 Int. Congr. Genet. Proc. 3, 349-370 (1968).
- Allard, R. W., Adams, J.: Population studies in predominantly self-pollinating species XIII. Intergenotypic competition and population structure in barley and wheat. Amer. Nat. 103 621-645 (1969).
- Ayala, F. J.: Genotype, environment, and population numbers. Science 162, 1453-1459 (1968).
- Brim, C. A., Schutz, W. H.: Inter-genotypic competition in soybeans II. Predicted and observed performance of multiline mixtures. Crop Sci. 8, 735-739 (1968).
- Frey, K. J., Maldonado, V.: Relative productivity of homogeneous and heterogeneous oat cultivars in optimum and suboptimum environments. Crop Sci. 17, 532-535 (1967).
- Jennings, P. R., Aquino, R. C.: Studies on competition in rice III. The mechanism of competition among phenotypes. Evolution 22, 529-542 (1968).
- Jensen, N. F.: Multiline superiority in cereals. Crop Sci. 5, 566-568 (1965).
- Lin, C. S., Torrie, J. H.: Effects of plant spacing within a row on the competitive ability of soybean genotypes. Crop Sci. 8, 585-588 (1968).
- Sakai, K. I.: Competitive ability in plants: its inheritance and some related problems. Symp. Soc. exp. Biol. 15, 245-263 (1961).
- Schutz, W. M., Brim, C. A.: Inter-genotypic competition in soybeans I. Evaluation of effects and proposed field plot design. Crop Sci. 7, 371-376 (1967).
- Schutz, W. M., Brim, C. A., Usanis, S. A.: Inter-genotypic competition in plant populations I. Feedback systems with stable equilibria in populations of autogamous homozygous lines. Crop Sci. 8, 61-66 (1968).
- Wilde, S. A., Voight, G. K.: Analysis of soils and plants for foresters and horticulturists. Ann Arbor, Mich.: J. W. Edwards Publisher, Inc. (1955).

Received September 26, 1972

Communicated by R. W. Allard

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