

venile phase in blue spruce (SAFFORD, 1974). In a breeding program for colder areas, stands from the southernmost portions of the range should be avoided. Otherwise, the same selection program could be used.

Selection within the existing progeny test could be accomplished by means of a selection index. This would require the calculation of individual heritabilities and the assigning of weights for each trait. It should also be pointed out that the family heritabilities presented here are based on within stand deviations and therefore underestimate the family heritability over all families. Family heritability could be calculated over all families, but this would be an overestimate because the families are not part of one random mating population. The effectiveness of selection within the progeny tests could be improved by increasing the number of members per family.

The emphasis placed on selection within the existing progeny tests and on selection of new materials from the native range depends on many factors. In any case, the initiation of a tree improvement program with provenance-progeny tests will lead to more rapid genetic progress in the early stages of the program than if provenance tests alone are used.

Literature Cited

BECKER, W. A.: Manual of Quantitative Genetics, Fourth Edition. Academic Enterprises, Pullman, WA. 190 p., (1984). — BONGARTEN, B. C. and J. W. HANOVER: Provenance variation in blue spruce (*Picea pungens*) at eight locations in the northern United States and Canada. *Silvae Genetica* 35: 2-3, 67-74 (1986). — CHAMPBELL, R. K. and F. C. SORENSEN: Effect of test environment on expression of clones and on delimitation of seed zones in Douglas-fir. *Theor. Appl. Genet.* 51: 233-246, (1978). — CHRISTOPHE, C. and Y. BIROT: Ge-

netic variation within and between populations of Douglas-fir. *Silvae Genet.* 28: 197-206, (1979). — FALCONER, D. S.: Introduction to Quantitative Genetics. Longman, London. 340 p., (1980). — FRANKLIN, E. L.: Model relating levels of genetic variance to stand development of four North American conifers. *Silvae Genet.* 28: 207-212, (1979). — LIBBY, W. J.: Domestication strategies for forest trees. *Can. J. For. Res.* 3: 265-276, (1973). — MORRIS, W. G., R. R. SILEN and H. IRGENS-MOLLER: Consistency of bud bursting in Douglas-fir. *J. For.* 55: 208-210, (1957). — NAMKOONG, G.: Introduction to Quantitative Genetics in Forestry. USDA, For. Serv. Tech. Bull. No. 1588. 342 p., (1979). — NAMKOONG, G.: Inbreeding effects on estimation of genetic additive variance. *For. Sci.* 12: 8-13, (1966). — NAMKOONG, G. and M. T. CONKLE: Time trends in genetic control of height growth in ponderosa pine. *For. Sci.* 22: 2-12, (1976). — NAMKOONG, G., R. A. USANSIS and R. R. SILEN: Age-related variation in genetic control of height growth in Douglas-fir. *Theor. Appl. Genet.* 42: 151-159, (1972). — NIENSTAEDT, H. and A. TEICH: Genetics of white spruce. USDA For. Serv. Res. Pap. WO-15. 24 p., (1972). — REHFELDT, G. E.: Genetic variability within Douglas-fir populations: implications for tree improvement. *Silvae Genet.* 32: 9-14, (1983). — REICOSKY, D. A. and J. W. HANOVER: Seasonal changes in leaf surface waxes of *Picea pungens*. *Amer. J. Bot.* 63: 449-456, (1976). — SAFFORD, L. O.: *Picea A. Dietr.* In: Seeds of Woody Plants in the United States (ed. C. S. SCHOPMEYER) USDA, For. Serv. Ag. Handbook No. 450. pp. 587-597, (1974). — SHELBOURNE, C. J. A.: Genotype × environment interaction: its study and its implications in forest tree improvement. *Proc. IUFRO-SABRAO Joint Symp. Tokyo.* pp. B-1(1), 1-27, (1972). — SORENSEN, F. C.: Frequency of seedlings from natural self fertilization in coastal Douglas-fir. *Silvae Genet.* 22: 20-24, (1973). — USDA: Climate and Man. Yearbook of Agriculture. U.S. Govt. Printing Office, Washington, D.C., (1941). — WHITE, T. L., K. K. CHING and J. WALTERS: Effects of provenance, years and planting location on bud burst of Douglas-fir. *For. Sci.* 25: 161-167, (1979). — WRIGHT, J. W.: Introduction to Forest Genetics. Academic Press, New York. 463 p., (1976). — WRIGHT, J. W.: Genotype × environment interaction in the north central United States. *For. Sci.* 19: 113-123, (1973). — ZOBEL, B. and J. TALBERT: Applied Forest Tree Improvement. John Wiley and Sons, New York. 505 p., (1984).

Inherent Differences in Family Response to Inter-Family Competition in Loblolly Pine

By G. A. TUSKAN¹⁾ and J. P. VAN BUIJTENEN²⁾

(Received 1st October 1985)

Summary

The effects of inter-family competition on genetic parameter development and individual phenotypic response were examined. Two 20-year-old open-pollinated progeny tests of loblolly pine (*Pinus taeda* L.), and seedlings from five mother-tree families common to both tests were used to evaluate the above competitive effects. Genetic parameters from both the mature progeny tests and the seedling study changed over time. Response to competition was significantly different among families, and two indicators of competition suggested competition was occurring in all studies. However, genetic parameter changes expressed by these families were not in direct response to the onset of competition. The competition analysis revealed significant differences in the competitive abilities and competitive influences among the seedlings of the five tested families. Family S2PT10 was involved in the majority of the significant competitive effects. Transgressive overyielding and underyielding competitive effects were displayed among

the family combinations. No one family could be identified as consistently overyielding or underyielding.

Key words: Inter-family competition, competitive ability and competitive influence, genetic parameter.

Zusammenfassung

Es werden die Wirkungen von Konkurrenz auf die Entwicklung genetischer Parameter innerhalb der Familien, sowie die individuelle phänotypische Reaktion untersucht. Die Ergebnisse aus der Prüfung von zwei zwanzigjährigen frei abgeblühten Nachkommenschaften bei *Pinus taeda* L. und aus der Prüfung von Sämlingen von fünf Mutterbäumen, die in beiden Tests enthalten waren, wurden benutzt, um die oben erwähnte Konkurrenzwirkung zu bestimmen. Die genetischen Parameter von beiden, d.h. aus der Untersuchung der älteren Nachkommenschaften und der Sämlinge, wechselten über den Zeitraum. Die Reaktion auf die Konkurrenz war innerhalb der Familien signifikant unterschiedlich und zwei Konkurrenzindikatoren haben gezeigt, daß in allen Versuchen Konkurrenzeffekte auftreten sind. Die genetischen Parameterwechsel, die bei diesen Familien zum Ausdruck kamen, waren jedoch keine direkte Reaktion auf das Auftreten von Konkurrenz. Die Konkurrenzanalyse ergab signifikante Unterschiede in den

¹⁾ Assistant Professor, Department of Horticulture and Forestry, Fargo, ND 58105, USA

²⁾ Professor, Forest Science Department, Texas A & M University, College Station, TX 77840, USA

konkurrierenden Fähigkeiten und im konkurrierenden Einfluß unter den Sämlingen der untersuchten 5 Familien. Die Familie S2PT10 war zum größten Teil an den signifikanten Konkurrenzeffekten beteiligt. Überschreitende Konkurrenzeffekte in Richtung höherer bzw. geringerer Wachstumsleistung zeigten sich innerhalb der Familienkombinationen. Es konnte keine Familie ermittelt werden, die beständig mehr oder beständig weniger geleistet hatte.

Introduction

The success of any breeding program ultimately depends upon the ability to select individuals whose genotypes fulfill the breeding objectives. Two main factors influence an individual's phenotype; its genotype, which may or may not meet objectives, and the environment in which the individual occurs. A majority of the environmental variation can be controlled through proper randomization and replication within progeny tests. As a result, a more accurate evaluation of the parental genotype is possible. Still, environmental variation remains which affects the development and evaluation of appropriate genotypes. The amount and type of competition an individual receives during its development may account for some of this extraneous variation.

Information from a competition study, evaluating competitive effects on genetic parameter development and individual phenotypic response could benefit a tree breeding program during the selection of superior genotypes, during the production of seedlings in nurseries and during the growth and development of improved plantations. Based on the potential use of competition in a tree breeding program, and the paucity of comprehensive information from forest species, the following objectives were pursued:

1) To determine if seedlings from five half-sib families, grown under similar competitive regimes, respond differently to competitive stress.

2) To determine if genetic parameter changes estimated from seedlings experiencing inter-family competition can duplicate changes in genetic parameters of a 20-year-old progeny test.

3) To determine if the above changes in genetic parameters occur in a predictable manner.

Materials and Methods

Competition, in this study, was considered a biological interaction that occurs when the combined demands of all individuals within a given area exceed the supply of necessary resources (BIRCH 1957, DONALD, 1963). Neither physical interference nor allelopathy were evaluated. Further definitions include: *competitive ability*--the inherent ability of a subject family to obtain (and utilize) essential resources relative to its needs; *competitive influence*--the effect of inter-family competition, as measured by the subject family, on the availability (or quality) of essential resources; and *competitive effect*--the combined net-performance of two competing families; i.e., the sum result of the competitive abilities and competitive influences of all associated genotypes.

Seedlings representing five families common to two 20-year-old open-pollinated progeny tests of loblolly pine, originally selected for productivity, were arranged into a competition diallel. These families were S6PT6, S6PT3, S2PT10, S3PT7 and S4PT6. The progeny tests were PLT006 and PLT007. Each subject family was used in association with the remaining four families to create twenty family combinations. Within each family combination, a single, central subject seedling was surrounded by five seedling

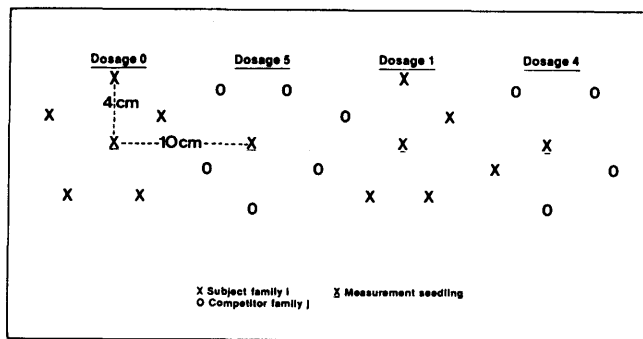


Figure 1. — Representation of a single, randomized plot grown in a greenhouse bench.

positions (Fig. 1). The competitor seedlings were four centimeters from the subject seedling; the distance between subject seedlings was 10 centimeters. In each replication, a subject family/competitor family combination contained three subject seedlings in mixed-stands and one subject seedling in a pure-stand condition. Differences among dosage levels in mixed-stands were shown to be non-significant; therefore, dosage effects were pooled to represent a single mixed-stand plot with a 44:56 subject seedling to competitor ratio. Replications were run lengthwise within a single greenhouse bench to block out variation due to the edge effect. Likewise, no replications began or ended less than 60 cm from the end of the bench. A single border row surrounded all four replications. In addition to the subject seedling there were two seedlings per subject family per replication which were "open-grown". These seedlings were used to indicate the point at which competition began to affect growth.

Biweekly height measurements were recorded for all subject seedlings and all open-grown seedlings four weeks after germination. Crown cross-sectional area was recorded for the open-grown seedlings, and was calculated as crown radius squared times pi. All subject seedlings were destructively sampled after 172 days of growth. Measurements included root and shoot dry weight, root and shoot volume, diameter at the cotyledons and hypocotyl length. Data was analyzed based on the following linear additive model:

$$Y_{ijk1} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma_{(B)kj} + \alpha\gamma_{(B)kj} + \epsilon_{1(ijk)}$$

where, μ = overall mean

α_i = replications, $i=1,2,3,4$

β_j = subject families, $j=1,2,3,4,5$

$\gamma_{(B)kj}$ = competitor families within subject families, $k=1,2,3,4$ for all j 's

$\epsilon_{1(ijk)}$ = experimental error, $i=1,2,3,4$ for all ijk 's.

The analysis began by calculating the point in time when competition began affecting growth. The divergence of open-grown and stand-grown seedlings height growth curves was used as one indicator (ADAMS *et al.* 1973). A second indicator, crown competition factor (KRAJICEK *et al.* 1961) was also examined. Crown competition factor was based on the relationship between crown cross-sectional area and height of the open-grown seedlings applied to the seedlings grown under competition.

$$CA_{1j} = b_0 + b_1(HT_{1j})$$

$$CA_1 \cdot (HT_1^2 / HT_{172}^2) = \text{Total Crown Area}$$

$$\text{Crown Competition Factor} = \text{Total Crown Area} / \text{Area Available}$$

where, CA_{1j} = crown cross-sectional area for tree j at age i

HT_{1j} = height for tree j at age i .

Average height at age i squared divided by the average final height squared was used as a weight for crown cross-

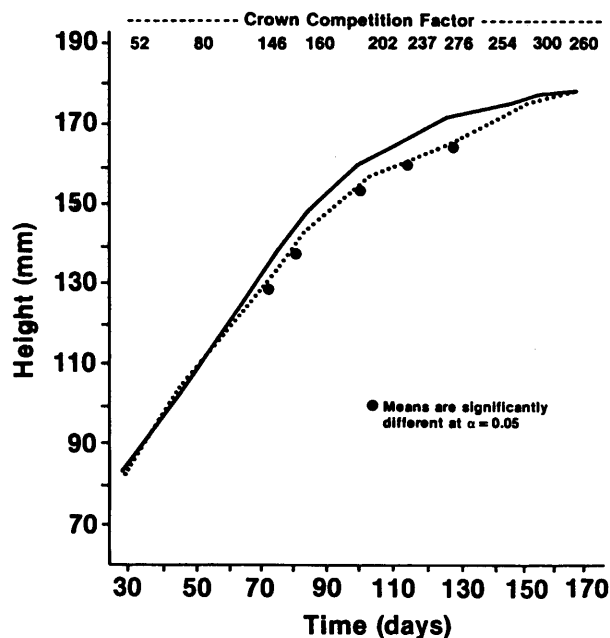


Figure 2. — Indicators of competition: Average height growth over time for all open-grown seedlings (—) and all seedlings grown under competition (.....) and crown competition factor.

sectional area to compensate for the lack of crown density at the early ages. Competition has been shown to occur after the crown competition factor reaches 100 (STRUB *et al.* 1975).

The phenotypic, genetic and environmental variances, plus intraclass correlations were calculated for each height measurement. These genetic parameters were plotted over time and compared to the patterns revealed in the mature progeny tests. The approximate time when competition began to influence growth was used in the interpretation of the effect competition had on the genetic parameter development.

Early selection techniques were explored using simple correlations between seedling measurements and average 20-year-old progeny test performance. Correlations were calculated between biweekly height measurements for each family averaged across all competitors and 1) average family volume superiority and 2) mean general combining ability from mature progeny tests.

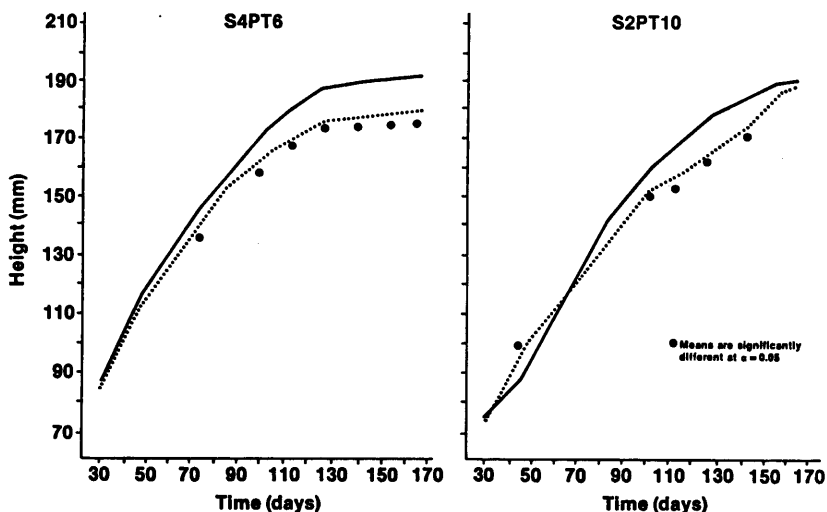


Figure 3. — Average height growth over time for open-grown seedlings (—) and seedlings grown under competition (.....).

The competitive effect of each family combination was evaluated using a technique for detecting competitive interactions among binary combinations of species (BRESE and HILL 1973). Values for pure-stand and mixed-stand subject seedling were individually pooled, averaged and re-partitioned by replications to represent a complete competition diallel. Pure-stand plots for each family signified the main diagonal, and the mixed-stand combinations represented the off-diagonals. The competition diallel was analyzed in an analysis of variance based on the following linear additive model:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk}$$

where, μ = overall mean

α_i = replications, $i=1,2,3,4$

β_j = subject families, $j=1,2,3,4,5$

γ_k = competitor effects, $k=1,2,3,4,5$

When a significant family by competitor interaction was present ($\alpha = .05$), the column means—an index of each family grown with an average common competitor, were used to predict the linear response of each family in relation to a changing competitive environment. The differences in slope for each family regression were tested by partitioning the family by competitor interaction into the heterogeneity of the regression equations and a lack of fit (NETER and WASSERMAN 1974). A significant heterogeneity component indicated that at least one of the family combinations represented a unique type of *competitive effect*. The partitioning of the interactions respectively represent additive and non-additive responses. Additivity corresponded to DE WIT's (1960) basic model of competition and the non-additive responses indicated transgressive yields were occurring.

Results and Discussion

Changes in Genetic Parameters

Analyses of variance results demonstrated that seedlings within plots were highly variable and family differences among traits were present until competitor effects became significant at 72 days. The two indicators of competition suggested that competition was influencing growth after 58 days. The point of separation for the height growth curves for the open-grown and stand-grown seedlings was at 58 days, yet the curves did not significantly ($\alpha = .05$) diverge until 72 days (Fig. 2). After 72 days crown

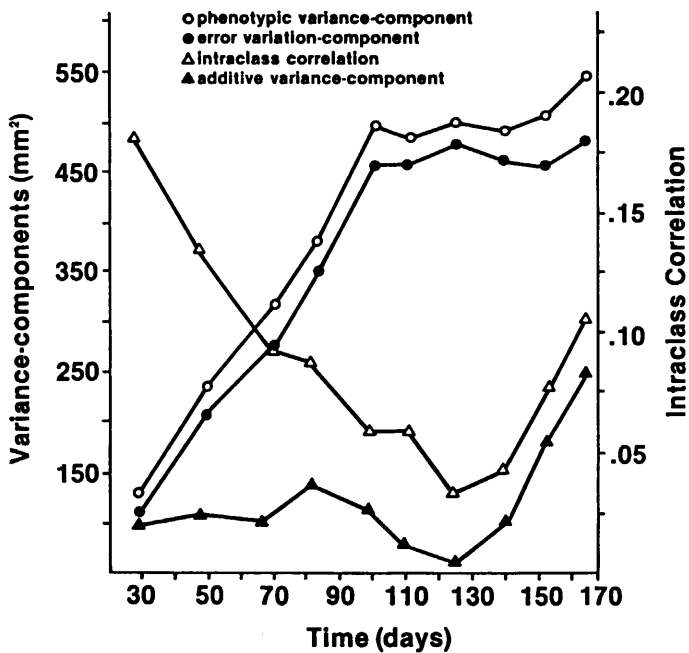


Figure 4. — Changes in genetic parameters over time for height in the competition study.

competition factor also indicated that competition influenced growth; crown competition factor equaled 100 at approximately 52 days. During this period, when competition was influencing growth, family S2PT10 had the steepest rate of height growth (Fig. 3). Seedlings from most families began setting buds after 100 days, causing overall average height to level-off. Yet, seedlings from S2PT10 rarely set buds, and after 127 days their ability to maintain growth while under competition increased the variability among families.

Competition among trees has been reported as one factor which may influence changes in genetic parameters (NAMKOONG *et al.* 1971, NAMKOONG and CONKLE 1976). FRANKLIN (1979) has suggested that these changes occur in a predictable manner, such that additive variances remain static and heritabilities decrease until intertree competition influences tree growth. Applying the knowledge of when competition began to affect seedling growth, and the expressed pattern of genetic parameter development, it was

possible to test proposed models of age trends in mature genetic parameter development on seedling parameter development.

In the seedling study, the phenotypic variance-components were proportional to the error variance-components; increasing for the first 100 days, then remaining relatively level to the end of the study (Fig. 4). The proportionality of these variance-components reflects the large contribution within plot variability made to the total phenotypic variance. Family variance-components remained relatively constant for the first 127 days, and intraclass correlations, a surrogate for heritability, declined for the first 127 days. At 127 days, 69 days after competition had affected seedling growth, both parameters increased. Again, S2PT10's performance while under competition may solely account for the increase in family variance-components and intraclass correlations.

The changes in genetic parameters from the seedling study failed to duplicate changes in the genetic parameters of the mature progeny tests. Specifically, the intraclass correlation changes were different. For both mature tests the intraclass correlations increased for the first 15 years then declined through year 20 (Fig. 5). The crown competition factors for both progeny tests indicated competition was occurring after year 5, a full 10 years before these parameters began to change. The changes in the mature phenotypic and error variance-components were similar to the changes that occurred in the seedling study; i.e., the variance-components increased proportionately (Fig. 4 and 5). Increasing phenotypic and error variances are compatible with age trend models of parameter development, yet this is only a descriptive feature of the models and not a predictive one.

As evidenced by the two mature progeny tests and the seedling study it appears that inter-family competition can influence genetic parameter estimates, yet parameter changes were not in direct response to competition and parameter response was unique to each test. The changes in parameter estimates from either the seedling study or mature progeny tests could not have been predicted based on an age trend model of competition.

LAMBETH *et al.* (1983) reported that early selection of superior families can be effective despite changes which occur in the genetic parameters of a progeny test. Therefore, average family performance for certain variables

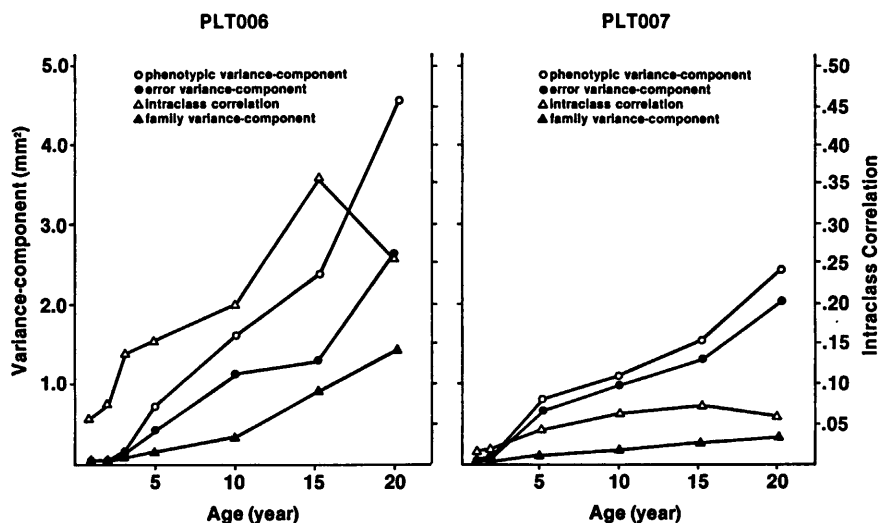


Figure 5. — Changes in genetic parameters over time for heights in plantations 006 and 007.

Table 1. — Simple correlations of average volume superiority and mean general combining ability to family means of variables obtained in the competition study.

Seedling Variables	General Combining Ability	Average Volume Superiority
Height at 82 days	.59	.80
Height at 113 days	.54	.75
Height at 141 days	.51	.54
Height at 141 days minus Height at 47 days	.15	.21
Hypocotyl Length	-.24	.13
Diameter at Cotyledons	.34	.72
Total Volume	.88*	.89*
Shoot Dry Weight	.83*	.84*
Root Dry Weight	.94**	.76
Shoot:Root Ratio	-.61	-.31

1/ ** and * indicate significance at $\alpha = 0.01$ and 0.05 , respectively.

recorded during the competition study were correlated to indicators of mature field performance. Average volume superiority and mean general combining ability were selected as the mature variables. The seedling variables are presented in Table 1. Height at 82 days, height at 113 days and height at 141 days were selected to represent the ages when competition was influencing height. The differences between heights at 141 days and heights at 42 days represents the cumulative effect of competition. Additional seedling variables included hypocotyl length, diameter at cotyledons, total volume, shoot dry weight, root dry weight and shoot : root ratios. These correlations were based on 4 d.f. and can be viewed only as an indication of the potential use of competition in early selection.

Significant correlations were obtained between seedling dry weight and both average volume superiority and mean general combining ability (Table 1). Total seedling volume was also highly correlated with the same mature variables. Significant correlations between seedling dry weights and mature field performance substantiates reports by WAXLER and VAN BUIJTENEN (1981) and DAVISON (1984). This was anticipated because induced stress or reduced resource availability are substitutes for competition (BREESE and HILL 1973). None of the remaining seedling variables displayed significant relationships with mean general combining ability or average volume superiority. Height was the only variable measured during the length of the study, and changes in mean family heights were not correlated to mature performance. Yet, all seedling variables are in part the result of inter-family competition, and the correlations obtained for dry weight and volume indicate that early selection of superior families from within a large juvenile competition study merits further investigation.

In summary, 1) competition influenced seedling growth after 58 days, 2) family response to competition was varied, 3) genetic parameters from families under competition did vary, but not in direct response to changes in competition, and 4) parameter changes in the juvenile study did

not duplicate changes which had occurred in the mature progeny tests.

Competition Diallel Analysis

The analyses of variance indicated that family differences were only present at the beginning of the experiment (Table 2). The variation that was present as a competitor within families prior to the re-partitioning was now expressed as significant ($\alpha = .05$) family by competitor interactions. In separating the family by competitor interaction into the linear response of each family to average competitor values and the non-linear lack of fit, only the lack of fit remained significant (Table 2). This implied that family performance across competitors was not additive and that pairwise performance was specific to each family/competition combination. The lack of fit became highly significant between 82 days and 141 days, the period when competition was prevalent.

The diallel analysis results on variables recorded at the end of the competition study produced no overall trends; the competitive effect for each family combination varied by each trait measured (Table 2). For example, hypocotyl length and diameter at cotyledons contained significant family differences. Differences among competitors were expressed in root volume and root dry weight. Family by competitor differences were only present in shoot dry weight (Table 2). In analyzing this interaction, only the lack of fit remained significant.

To interpret family performance individual family combinations had to be examined. Pairwise family combina-

Table 2. — Analyses of variance results for seedling measurements obtained in the competition experiment.

Variables	F-test Results ^{1/}			
	Families	Competitors	Family x Competitor Heterogeneity	Residual
Height at 30 days	**	NS	NS	**
Height at 47 days	*	NS	— ^{2/}	—
Height at 72 days	NS	NS	NS	*
Height at 82 days	NS	NS	NS	**
Height at 100 days	NS	NS	NS	**
Height at 113 days	NS	NS	NS	**
Height at 127 days	NS	NS	NS	**
Height at 141 days	NS	NS	NS	**
Height at 155 days	NS	NS	NS	*
Height at 166 days	NS	NS	NS	*
Hypocotyl Length	**	NS	—	—
Diameter at Cotyledons	*	NS	—	—
Shoot Volume	NS	NS	—	—
Root Volume	NS	*	—	—
Shoot Dry Weight	NS	NS	NS	*
Root Dry Weight	NS	*	—	—

1/** and * indicate significance at $\alpha = 0.01$ and 0.05 , respectively.

2/ The interaction had to be significant before the heterogeneity among regressions was examined.

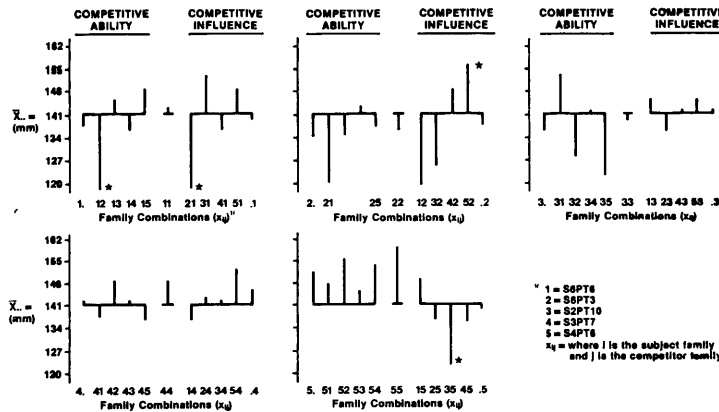


Figure 6. — Competitive abilities and competitive influences among family combinations for height at 82 days. (* indicates means are significantly different from the pure-stand mean; \bar{X}_{ij} , at $\alpha = 0.05$).

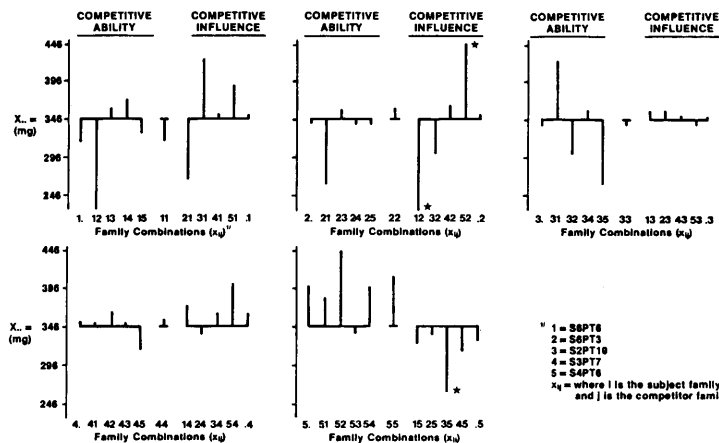


Figure 7. — Competitive abilities and competitive influences along family combinations for shoot dry weight. (* indicates means are significantly different from the pure-stand mean; \bar{X}_{ij} , at $\alpha = 0.05$).

tions were examined if the lack of fit for a particular trait was significant. Height at 82 days was used to represent all significant height measurements. Family combinations for shoot dry weight were also examined.

For height at 82 days, mean *competitive ability* ($\bar{X}_{i.}$) varied among families (Fig. 6). S4PT6 had a large *competitive ability* while all other families had average or below average *competitive abilities*. S4PT6 also exhibited a slight negative relationship between *competitive ability* and *competitive influence*. The correlation between *competitive ability* and pure-stand performance (X_{ii}) was significant and positive ($r = .99^{**}$). These results agree with reported cereal crop performance of vegetative yields. That is, the families which expressed high *competitive abilities* in mixed-stands were the families with the taller, larger seedlings in pure-stand conditions.

Both transgressive (i.e. $(X_{ij} + X_{ji})/2 > X_{ii}$ or $< X_{jj}$, where X_{ii} = larger family and X_{jj} = smaller family) and non-transgressive (i.e. $X_{ii} > (X_{ij} + X_{ji})/2 > X_{jj}$) *competitive effects* were present throughout the study. At 82 days S6PT6 with S6PT3 and S2PT10 with S4PT6 both transgressively underyielded (Fig. 6). The remaining combinations displayed non-transgressive overyielding or non-transgressive underyielding (Fig. 6). Very few combinations were strictly compensating (i.e. $(X_{ij} + X_{ji}) = (X_{ii} + X_{jj})$). At 141 days all significant transgressive *competitive effects* involved S2PT10; e.g., S2PT10 with S6PT6 transgressively

overyielded. At the conclusion of the study, S2PT10 with S3PT7 was also transgressively overyielding, while S4PT6 with S6PT3 proved to be one of the few compensating family combinations.

For shoot dry weight mean *competitive ability* ($\bar{X}_{i.}$) and mean *competitive influence* ($\bar{X}_{.i}$) closely resembled the results obtained for height at 82 days (Fig. 7). Pure-stand yields (X_{ii}) and mixed-stand *competitive abilities* ($X_{i.}$) were positively correlated ($r = .89^*$). These positive correlations found for both height and shoot dry weight suggest that selections of superior families from within mixed-stand progeny tests may produce progeny that will perform well in pure-stand plantings.

The *competitive ability* of S4PT6 for shoot dry weight was again negatively correlated to *competitive influence*. Apparently S4PT6 exerts influence on the competitor family by gaining an unequal share of the resources. S4PT6 could be classified as a "competitor" ideotype (TUSKAN and MCKINLEY 1984). ADAMS (1980) stated that if such ideotypes are placed in a breeding program reductions in future plantation yields might occur.

In summary: 1) competition affected phenotypic family performance, 2) families responded differently to competition, 3) *competitive effects* varied by traits within family combinations and 4) family response was competitor dependent. All types of *competitive effects* were displayed among pairwise family combinations. And one family,

S2PT10, was involved in the majority of all significant *competitive effects*.

Conclusions

TRENBATH (1974) has suggested five causes of transgressive yields which could be applied to forest species: 1) stratified growth, 2) pathogen escape, 3) nutritional compensation, 4) allelopathy and 5) asynchronous growth. Of these, stratified growth, nutritional compensation and asynchronous growth may have influenced seedling growth in this study.

Stratified root or shoot architecture would allow adjacent families to utilize different aspects of the same microsite. A stratified canopy in a young stand, containing shorter seedlings with broad crowns and taller seedlings with erect crowns could result in transgressive overyields (CANNEL 1982). The lack of stratified architecture would result in transgressive underyields. Nutritional compensation would also allow mixtures to transgressively overyield. For example, one family may require large amounts of phosphorus while the adjacent family does not. The opportunities for nutritional compensation increase as seedlings within each competing family become genetically more uniform. That is, competing clones of different genetic makeup are more likely to have different nutritional requirements than are competing individuals from open-pollinated families. Finally, asynchronous growth may also produce transgressive yields. Two adjacent families would place maximum demands on the resources and at the same time avoid direct competition through asynchronous growth. The transgressive overyielding of S2PT10 is interpreted as the result of asynchronous growth in combination with S6PT6 and S3PT7. It then becomes apparent that transgressive underyielding is the result of competition whereas transgressive overyielding is the avoidance of competition.

Inferences from this study are limited because of the small number of families used, yet detailed information was compiled for these families and several conclusions can be drawn. Genetic parameters from seedlings did vary with time; family variance-components and intraclass correlations changed in magnitude, but not in direct response to competition. The changes in the seedling parameters did not duplicate mature parameter fluctuations. Family performance across all competitors was not additive; each

family combination had to be evaluated individually. Family S2PT10 was involved in the majority of the *competitive effects*. Family S4PT6 had high *competitive ability* and a strong negative *competitive influence*. Family performance for these five families suggests that mixed-stand *competitive ability* can be used as an indicator of pure stand performance.

Acknowledgement

This research was funded by the Texas Forest Service and the Forest Science Department, Texas A & M. Their support is gratefully acknowledged.

Literature Cited

- ADAMS, W. T.: Intergenotypic competition in forest trees. Proc. 6th North Amer For Biol Workshop, Aug. 11–13. p. 1–14, (1980). — ADAMS, W. T., J. H. ROBERDS and B. J. ZOBEL: Intergenotypic interactions among families of loblolly pine (*Pinus taeda* L.). Theor. App. Gen. 43: 319–322, (1975). — BIRCH, L. C.: The meaning of competition. Amer. Nat. 91: 5–18, (1957). — BRESE, E. L. and J. HILL: Regression analysis of interactions between competing species. Hered. 31 (2): 181–200, (1973). — CANNEL, M. G. R.: "Crop" and "Isolation" ideotypes: Evidence for progeny differences in nursery-grown *Picea sitchensis*. Silvae Genet. 31 (2/3): 60–66, (1982). — DAVISON, M.: Early testing of loblolly pine based on seedlings response to daylength variation within growth chamber environments. Master's Thesis. Texas A & M University. 73 pp., (1984). — DE WIT, C. T.: On competition. Versl. Landbouwk Onderz. 66: 1–82, (1960). — DONALD, C. M.: Competition among crop and pasture plants. Adv. Agron. 15: 1–118, (1963). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genet. 28 (5/6): 207–212, (1979). — KRAJICEK, J. E., K. A. BRINKMAN and S. F. GINGRICH: Crown competition—a measure of density. Forest Sci 7: 35–42, (1961). — LAMBETH, C. C., J. P. VAN BUIJTENEN, S. D. DUKE and R. B. McCULLOUGH: Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genet. 32 (5/6): 210–215, (1983). — NAMKOONG, G. and M. T. CONKLE: Time trends in genetic control of height growth in ponderosa pine. Forest Sci 22: 2–12, (1976). — NAMKOONG, G., R. A. USAMS and R. R. SILEN: Age-related variation in genetic control of height growth in Douglas-fir. Theor. App. Gen. 42: 151–159 (1972). — SCHUTZ, W. M. and C. A. BRIM: Intergenotypic competition in soybeans. I. Evaluation of effects and proposed field plot design. Crop Sci 7: 371–376, (1967). — STRUB, M. R., R. B. VASEY and H. E. BURKHART: Comparison of diameter growth and crown competition factors in loblolly pine plantations. Forest Sci 21 (4): 427–431, (1975). — TRENBATH, B. R.: Biomass productivity in mixtures. Adv. Agron. 26: 177–210, (1974). — TUSKAN, G. A. and C. R. MCKINLEY: The use of competition indices in advanced-generation selection. Silvae Genet. 33 (6): 209–215, (1984). — WAXLER, M. S. and J. P. VAN BUIJTENEN: Early genetic selection of loblolly pine. Can. J. Res. 11: 351–355, (1981).

Genetic Analysis of Fifth-Year Data from a Seventeen Parent Partial Diallel of Loblolly Pine

By G. S. FOSTER¹⁾ and F. E. BRIDGWATER²⁾

(Received 4th November 1985)

Abstract

Full-sib families of loblolly pine (*Pinus taeda* L.) were created using 17 parents and a diallel mating design. Analyses of fifth-year data revealed no reciprocal effects, yet significant GCA as well as SCA variance for height, d.b.h., and individual-tree volume was obtained. The ratio of do-

minance to additive genetic variance equaled 2.5, 1.6, and 7.8 for height, d.b.h., and volume, respectively.

Gca and sca effects were compared between parents and crosses, respectively. Although SCA variance was significant, no differences occurred among parents in the variance of sca effects. Therefore no parents excelled in either higher or lower ability to produce good specific controlled-cross families. The consequences of this finding for tree improvement are discussed.

Key words: general combining ability, specific combining ability, additive genetic variance, dominance genetic variance.

¹⁾ Manager Forestry Research and Tree Improvement, Crown Zellerbach Corp., Box 400, Bogalusa, LA 70427, U.S.A.

²⁾ Research Geneticist, Southeastern Forest Experiment Station, USDA Forest Service, School of Forest Resources, N.C. State University, P.O. Box 8002, Raleigh, NC, 27695, U.S.A.