

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.

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

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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.

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Zusammenfassung

Es wurden Vollgeschwisterfamilien von *Pinus taeda* L. unter Verwendung von 17 Elternbäumen nach einem diallelen Kreuzungsschema hergestellt. Die Analysen im Pflanzalter 5 lassen keine reziproken Effekte erkennen, aber eine signifikante allgemeine als auch spezifische Kombinationseignung, sowie Varianten für das Höhen- und Durchmesserwachstum und das Einzelvolumen. Das Verhältnis von Dominanz- zu additiv-genetischer Varianz ist gleich 2.5; 1.6 und 7.8 für Höhe, Durchmesser (d.b.h.) bzw. Volumen.

Die Effekte der allgemeinen und der spezifischen Kombinationseignung wurden zwischen den Eltern und Kreuzungen verglichen. Obwohl die Varianz der spezifischen Kombinationseignung signifikant war, kamen keine Unterschiede zwischen Eltern in der Varianz der Effekte der spezifischen Kombinationseignung vor. Deshalb übertrafen sich die Eltern weder durch größere noch geringere Eignung, gute spezifische und kontrolliert gekreuzte Familien zu produzieren. Die Konsequenz dieser Befunde für die Züchtung wird diskutiert.

Introduction

Diallel mating designs have become one of the most popular mating designs in forest genetics research and tree improvement. The design can be used to estimate a number of genetic and environmental parameters for a population (KEMPTHORNE 1956), and it is one of the most efficient designs for estimating these parameters (KEARSEY 1965; PEDERSON 1972). In addition, the design appears to be robust when there are missing values (BRAATEN 1965).

Despite its broad usage in forest genetics, few articles on studies utilizing the design have been published. This may be due to its relatively recent usage in forestry as compared to the North Carolina State Mating Design I and II (COCKERHAM 1961). Studies of populations of eastern white pine (*Pinus strobus* L.) (KRIEBEL *et al.* 1972), black spruce [*Picea mariana* (MILL.) B.S.P.] (MORGENSTERN 1974), longleaf pine (*Pinus palustris* MILL.) (SNYDER and NAMKOONG 1978), and loblolly pine (*Pinus taeda* L.) (BYRAM 1978) utilized diallel mating designs. These studies have generally shown additive genetic variance to be significant with varying degrees of dominance variance.

In this study, a diallel mating design was used for 17 parent trees of loblolly pine. Objectives of the study included:

1. estimation of additive and dominance genetic variances for the population, and
2. estimation of general combining abilities (gca) for the parents and specific combining abilities (sca) of the crosses for future selection and breeding.

Materials and Methods

The 17 loblolly pine trees used as parents in the crossing scheme were randomly chosen from Crown Zellerbach Corporation's tree improvement program. The selections originated from Washington (latitude 30°48' N., longitude 90°00' W.), Livingston (latitude 30°27' N., longitude 90°50' W.), and St. Helena (latitude 30°48' N., longitude 90°50' W.) Parishes in Louisiana and Lawrence Co., Mississippi (latitude 31°37' N., longitude 90°13' W.), (within 161 km of each other) and were grafted into the seed orchard, where the crosses were made.

Ninety-two of the 136 possible crosses in a 17-parent half diallel (without selfs) were completed. The number of

Table 1. — Field test layout and fifth-year data averages for loblolly pine families comprising a 17 parent partial diallel.

Test parameters and traits	Tests								
	1976		1978		1979			mean	
	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2	Set 3		
No. families(f)	16	14	10	10	15	17	10		
No. replications(r)	10	10	12	12	12	12	12		
No. individuals/f/r	7	7	8	8	8	8	8		
Spacing(m)	3.66x3.66		3.05x3.05						
Mean height(m)	3.08	3.99	4.06	4.32	3.89	4.48	4.22	4.01	
Mean d.b.h.(cm)	4.01	3.82	5.93	6.42	5.09	6.05	5.70	5.29	
Mean volume (dm ³)	1.95	1.67	4.59	5.59	3.25	5.38	4.52	3.85	
Survival(%)	62.4	65.7	89.0	85.5	57.5	56.4	70.5	69.6	

crosses per parent ranged from 5 to 15 with an average of 10.8.

This large number of families was divided into sets and planted over three years (1976, 1978, and 1979) with two or three sets of families planted each year (Table 1). All plantings were on a single site near Bogalusa, Louisiana (latitude 30°48' N., longitude 90°00' W.). The test design consisted of replications in sets of families (SCHUTZ and COCKERHAM 1966). A randomized complete block design was used for each set. Each set within a planting year included 10 to 20 families, either 10 or 12 replications, a row plot of 7 or 8 individuals per family per replication, a common check lot in each replication, with either a 3.05 × 3.05 m or a 3.66 × 3.66 m spacing (Table 1). In any one year, families were assigned to sets at random.

The data analysis included three traits. Fifth-year height and d.b.h. were measured directly and individual-tree volume was derived using the following equation:

$$\text{volume} = (\text{height} \times \text{d.b.h.}^2) 0.02618^1$$

Data analysis consisted of two stages: 1) preparation of the data for diallel analysis and 2) diallel analysis.

The variance among the 92 full-sib families analyzed was confounded with reciprocal effects, year effects, and set-within-year effects. Reciprocals of six full-sib families were included in the tests. Paired t-tests showed no significant differences among reciprocals for the variables studied. Thus, reciprocal effects were assumed to be unimportant and ignored in further analyses.

Environmental effects were accounted for by deviating year-set-block means (plot means) from a common seedlot before analysis. The common seedlot was assumed to have average stability. Its growth performance increases linearly with increasing environmental quality. If the common seedlot had either more or less than average stability with environmental changes, bias would result when adjusting family means for environmental changes. A Livingston Parish, Louisiana seedlot was included in every year-set-block cell. Expressing full-sib family means as a deviation from the plot means for the common seedlot and the grand mean for each trait reduced the model to:

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$$y_{ijk} - \mu = g_i + g_j + s_{ij} + e_{ijk} \quad (1)$$

μ = population mean
 g_i = general combining ability effect (gca) of the i th parent, $i = 1, \dots, f$
 g_j = general combining ability effect of the j th parent
 s_{ij} = specific combining ability effect (sca) of the cross between i th and j th parents such that $s_{ij} = s_{ji}$
 e_{ijk} = pooled: remainder of the genetic variation and interactions of crosses, years, sets, and blocks for the k th ($k = 1, \dots, r$) plot of the ij th cross

The variance components associated with GCA (σ_{GCA}^2), SCA (σ_{SCA}^2), and environmental effects (σ^2) were estimated using DIALL (SCHAFER and USANIS 1969) and were equated to their genetic expectations (HALLAUER and MIRANDA 1981).

$$\sigma_{GCA}^2 = \text{cov HS} = 1/4V_A + 1/16V_{AA} + \dots \quad (2)$$

$$\sigma_{SCA}^2 = \text{cov FS} - 2 \text{cov HS} = 1/4V_D + 1/8V_{AA} + \dots \quad (3)$$

where,

- cov HS = covariance of half-sibs
- cov FS = covariance of full-sibs
- V_A = additive genetic variance
- V_{AA} = additive x additive epistatic genetic variance
- V_D = dominance genetic variance

Assuming no epistatic variance, then $4\sigma_{GCA}^2 = V_A$ and $4\sigma_{SCA}^2 = V_D$.

General combining ability effects (gca) and specific combining ability effects (sca) were estimated following GRIFFING (1956). The variance among sca values for a parent was calculated, and variances were compared among parents using Bartlett's Test of Homogeneity of Variance (SOKAL and ROHLF 1969).

Results

Survival and growth of the test families in the seven tests were within acceptable limits for comparable sites. Survival averaged 70 percent with a range among tests of 56 to 89 percent (Table 1). Average height after five years was 4.01 m with a range of 3.08 to 4.48 m. The average d.b.h. was 5.29 cm and average tree volume was 3.85 dm³.

An analysis of the Livingston Parish common seedlot provided an estimate of year and set-within-year effects. The pattern of environmental variation was similar for the three traits. Year effects were small and non-significant, while differences among sets-within-years were significant ($p \leq 0.05$).

The diallel analyses indicated that GCA and SCA were important sources of variation for the three traits. General combining ability (GCA) and SCA variance significantly influenced the variation in fifth-year height. General combining ability (GCA) variance exerted more of an influence on d.b.h., and SCA variance was more important for volume (Table 2). Specific combining ability (SCA) variance for volume apparently arose largely from SCA variance for height, not d.b.h.

Dominance variation exceeded additive variation for both height and volume. The ratios of dominance to additive variance was 2.5 : 1.0 for height and 7.8 : 1.0 for volume (Table 3).

¹) GCA and SCA refer to variances and gca and sca refer to effects (GRIFFING 1956).

General combining ability (gca) and sca effects were calculated for each parent and cross, respectively, from equation (1). Parent 5 had the largest gca values for all traits, whereas Parent 2 was the second highest for height but third for d.b.h. and fourth for volume. The worst parent for all traits was Parent 16 (Table 4).

The range in sca effects for each parent appeared symmetrical with little or no indication that extreme values unduly influenced the gca estimate (Table 5). Variances of sca values (within a parent) were non-significant when compared among parents. The range in sca's appears to be quite similar for the parents.

Discussion

The diallel mating design was well implemented for the 17 parents, but the planting design was inefficient. Inclusion of 92 families would cause block sizes to be too large if planted in a single replication, but some type of incomplete block design (SCHUTZ and COCKERHAM 1966) would provide an efficient comparison among all the families. Three sets of 31 families would have been a better alternative than the actual layout (Table 1). Planting the complete study in a single year or replicating between years would also be preferable to confounding sets of families with different planting years.

The common checklot was planted in each replication of the seven tests. Theoretically, expressing each family plot mean as a deviation from the check plot mean eliminated the main environmental effects from the model. However, we have a concern involving this approach. Deviating family data from the checklot accounted for the main effects of years, the environmental component of sets-within-years, and blocks-within-sets but did not correct for interactions among these effects and between families and these effects. We were unable to estimate these interaction effects, therefore the error term in our model (Table 2) con-

Table 2. — Mean squares and F-tests for the loblolly pine diallel analyses.

Source	D. F.	Mean squares		
		Height	D. B. H.	Volume
GCA	16	2.72**	3.96*	9.42 ¹
SCA	75	0.97**	2.19 ¹	6.28**
Error	794	0.58	1.92	4.19

¹Significant at $p = 0.25$.

*Significant at $p = 0.05$.

**Significant at $p = 0.01$.

Table 3. — Genetic parameter estimates for the loblolly pine diallel analysis.

Parameter ^a	Estimate		
	Height	D. B. H.	Volume
σ_{GCA}^2	0.017	0.018	0.029
σ_{SCA}^2	0.042	0.029	0.225
σ^2	0.583	1.923	4.189
V_A	0.068	0.072	0.116
V_D	0.168	0.116	0.900
V_D/V_A	2.5	1.6	7.8

^aParameters explained in the text.

tains these interactions, causing conservative F-tests for GCA and SCA variance.

Results in this study indicated that dominance variance was generally greater than additive variance for the three traits. The ratio of dominance to additive variance for height equaled 2.5. This value compares to an average of 0.78 (range of 0 to 2.5) for other studies of height of loblolly pine (as cited in McKEAND *et al.* 1984). Diameter at breast height (d.b.h.) also had greater dominance variance although the ratio of dominance to additive variance (1.6) was less than for height. For fifth-year d.b.h. and tenth-year d.b.h., BYRAM (1978) and BRIDGWATER *et al.* (1983) found ratios of 0.0 and 2.8, respectively. The comparable ratio for volume in this study (7.8) exceeded considerably the same ratio established by MATZIRIS (1974) of 0.3, BRIDGWATER *et al.* (1983) of 1.5, and BUSBY (1982) of 1.9 for 8-, 10-, and 15-year volume, respectively. The ratio of dominance to additive genetic variance fell within the range of published results for height and d.b.h. but well outside the range for volume. This result for volume may simply be the consequence of sampling error for a ratio that has a high standard error.

The five controlled-cross families with the greatest mean heights (2 × 16, 2 × 3, 5 × 10, 1 × 5, and 5 × 11) were tallest primarily because at least one of the parents was a good general combiner. Both parents of family 2 × 5 have high gca and the family also has a moderately high sca. The other four crosses involve one high gca parent and either a moderate or low gca parent, but the sca was moderate (i.e., sca of family 1 × 5 equalled 0.27) to high (i.e., sca of family 2 × 16 equalled 0.94). In fact, the tallest full-sib family in the study was the result of a cross between the parent with the second highest gca (Parent 2) and the parent with the lowest gca (Parent 16).

Once desirable crosses are identified, several techniques exist to exploit them for increased gain. Large quantities of seed from full-sib families can be produced by supplemental mass pollination (BRIDGWATER and TREW 1981). Vegetative propagation provides the potential of: 1) expanding the number of plants produced from a small number of full-sib seed (ARMSON *et al.* 1980) or 2) selecting superior

Table 4. — Estimates of general combining ability (gca) effects for 17 parents in a loblolly pine diallel.

Parent	GCA effect		
	Height	D.B.H.	Volume
1	-0.014	-0.102	0.006
2	0.246	0.280	0.370
3	0.188	0.205	0.397
4	0.020	-0.057	0.034
5	0.346	0.500	0.596
6	-0.002	-0.001	0.031
7	0.067	0.064	0.098
8	-0.108	-0.058	-0.204
9	0.111	0.065	0.230
10	-0.130	-0.140	-0.325
11	-0.235	-0.355	-0.452
12	0.131	0.145	0.201
13	0.146	0.291	0.373
14	-0.149	-0.225	-0.233
15	-0.111	-0.163	-0.266
16	-0.354	-0.428	-0.622
17	-0.007	0.118	0.049

individuals, within full-sib families, for propagation (KLEIN-SCHMIT and SCHMIDT 1977).

In an improvement program to exploit dominance variance, the most desirable parents would be ones that had both high gca effects and combined with other parents to consistently produce families with high sca. The high gca would insure a high expected full-sib family mean when the parents were crossed, and the high sca potential would provide the possibility of producing better-than-expected specific crosses. GRIFFING (1956) gave an example of this type of parent in corn (*Zea mays* L.). Otherwise if all parents have equal potential for generating crosses with high sca, then many crosses must be made in search of a randomly-

Table 5. — Estimates of specific combining ability (sca) effects for fifth-year height of control-cross families in a 17 parent diallel of loblolly pine.

Parent number	Parent number																σ _g ² *
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
1	-.29	-.40	-.07	.27	.24		.28	.30	-.30			.33	.03		-.57	.41	0.11
2		.31	.06		.04	.09	-.50				.11	-.15	-.05	.05	.94	-.50	0.15
3							.18	.18	-.18	-.09				.12	-.36	.35	0.08
4					.33		.06	.54	-.42	.38		.10			.10		0.09
5					-.53	.27		-.27	.44	.47	-.01	-.29	-.03	.19	.10	-.05	0.09
6							-.02	.04	.31	.46	-.56	.33	.10		-.06	.48	0.12
7							-.16		.23							.11	0.04
8								-.15	.01		.27	.00		.33	.21		0.06
9									-.29	.19		-.04	.56	-.06	-.09	.77	0.11
10										.21	.40	-.14	.07	-.17	-.28	.27	0.08
11												-.35	-.58	-.74	-1.39	0.38	
12												-.37		.17	-.02	0.10	
13													-.33	.18		0.05	
14														.26		0.08	
15															-.56	0.10	
16																-.15	0.18
17																	0.34

occurring, high sca cross. In this study, all 17 tested parents displayed equal sca variance (Table 5). If this holds for other populations of loblolly pine, it would not be possible to increase the probability of producing good specific combinations by favoring one parent over another.

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Atypical Seedlings of *Populus L.*: Their Genetic Significance and Value in Breeding

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Summary

The incidence of abnormal, albino and chlorophyll-deficient seedlings, pleiocotyly and polyembryony is reported in *Populus L.* With the exception of chlorophyll-deficient seedlings, this may be the first record of these occurrences in this genus. The possible use and significance of these atypical phenomena in *Populus* breeding are briefly discussed.

Key words: *Populus L.*, controlled crosses, progenies, genetics, breeding, unusual seedlings.

Zusammenfassung

Es wird über das Vorkommen von abnormalen, albino und chlorophyll-defizienten Sämlingen, Pleiokotylye und Polyembryonie bei *Populus L.* berichtet. Mit Ausnahme der chlorophyll-defizienten Sämlinge, könnte dies der erste Bericht über solche Vorkommen in dieser Gattung sein. Der mögliche Gebrauch dieser atypischen Formen in der Pappezüchtung wird kurz diskutiert.

Introduction

Seedling morphology has been widely used in applied genetics and plant breeding to permit early screening and selection from large populations within a limited space (HASKELL 1961). The genetic significance and value of unusual seedlings for early screening in *Eucalyptus* breeding

was discussed by VENKATESH and SHARMA (1974). The unusual *Populus L.* seedlings which are described in this report were observed when hybrid seed was germinated. Their possible genetic significance and value in breeding are also discussed.

Hybrid seed resulted from a series of intra- and inter-specific crosses of *Populus deltoides* MARSH., *Populus nigra* L. and *Populus maximowiczii* HENRY made in 1982 and repeated in 1983. The seeds were germinated in Petri dishes on sterilized silica sand in the laboratory in both years. Seedlings were then transplanted into polystyrene Leach tubes (super cell containers of 164 cm³, Ray Leach Container Nursery, Canby, Oregon, U.S.A.) filled with Pro-mix (a mixture of 60% peat moss, 20% perlite and 20% vermiculite). The seedlings were grown in a greenhouse for about three months in both years. The surviving seedlings were then moved into a shade house for over wintering.

The different atypical seedlings recovered from the progenies of various crosses were broadly classified into four types, namely (1) abnormal seedlings, (2) albinos and chlorophyll-deficient seedlings, (3) pleiocotylyous seedlings, and (4) twins.

Observations

Abnormal Seedlings

These were characterized by malformation or total atrophy of root or hypocotyl. The frequency range of ab-