INTER-FAMILY COMPETITION IN LOBLOLLY PINE
AND ITS EFFECTS IN GENETIC TESTS

by

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ABSTRACT

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Thirty-six unrelated full-sib families of loblolly pine were used to evaluate the effects of inter-family competition in genetic tests. Three-month-old seedlings were planted in a nursery with a uniform spacing of 8 cm x 8 cm in three plot layouts: a) 16-tree square plots; b) 2-tree row plots; and c) non-contiguous family plots. Five levels of inter-family competition were identified according to the number of unrelated competitors in the immediate vicinity of a subject tree. Eight of the families were deleted from the analyses of growth traits because of empty plots due to mortality at 20 months of age which was apparently unrelated to increases in inter-family competition levels. Family differences in competitive ability were significant, especially for stem volume and dry weight but less so for height growth. Low intraclass correlations for competitive ability in spite of the possible presence of non-additive genetic variance suggested that competitive ability is lowly heritable. Higher levels of inter-family competition increased intraclass correlations, indicating that interfamily competition leads to overestimation of family variances and of all parameters derived therefrom. Genetic phase changes during the stand development took place much earlier in more genotypically homogeneous stands. Individual families reacted differently to inter-family competition at different stages of growth. Since competitive ability did not correlate with growth traits at competition levels other than the one in which it was observed and showed low heritability, selections under intense inter-family competition in short-term genetic tests are not likely to increase genetic gain. A few families showed rank changes under inter-family competition but neither the magnitude or the direction of the change could be predicted on the basis of their performance in family blocks. Thinnings should become integral parts of loblolly pine genetic tests in order to reduce the bias in the estimation of genetic parameters and in ranking families for their genetic merit.

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INTRODUCTION

Forest geneticists have long been confronted with the problem of choosing a suitable experimental design. One approach was to use large square plots of up to 10 x 10 plants to simulate conditions found in operational plantings. However, this approach is not appealing because large genetic tests with higher costs of establishment and management are required when the number of genetic entries and replications is large.

Statistical efficiency is a crucial consideration for the choice of plot shape and size. This parameter was estimated by adapting Smith's (1938) method of relating plot size and variance by Wright & Freeland (1960) with red pine, Douglas-fir, and yellow poplar, and Conkle (1962) with loblolly and slash pines. In all cases, when evaluations were based on individual trees, the smallest plot (single-tree plot) was statistically the most efficient. However, at this extreme of plot sizes, conditions are conducive to intense intergenotypic competition and test results may become biased by the introduction of an additional source of variation due to competition among entries.

Based on studies of trends in genetic variance through the stages of development of a ponderosa pine stand, Namkoong & Conkle (1976) suggested a delay in selection until the stage of intense competition, which usually occurs at about half of the rotation age under normal operational plantations, or much earlier by inducing intense competition in closely spaced genetic tests (Franklin, 1979). Franklin (1979) studied the trends in additive genetic variance and in heritability through time in stands of Douglas-fir and ponderosa, slash, and loblolly pines, and suggested a model which divided the stand development into three genetic phases: the first, which he called juvenile genotypic phase, was characterized by the beginning of increase in additive genetic variance and heritability; the second stage, when heritability reached a maximum, was called mature genotypic phase; and the third stage, which he called codominance-suppression phase, was characterized by abrupt decreases in additive genetic variance and in heritability. Their idea is to maximize gains by selecting at the stage of stand development when genetic variances seem to be greatest.

The importance of intergenotypic competition in plant populations has been recognized for many decades. In its presence, the additional variance that is generated leads to an overestimation of genetic variance (Sakai, 1953; Sakai & Mukaide, 1967; Stern, 1969) and, consequently, of all parameters derived therefrom. Therefore, selections at the "mature genotypic phase" suggested by Franklin (1979) are not likely to result in additional genetic gain, unless the associated competitive ability is also heritable and positively correlated with growth traits.

The drastic drop in genetic variance and in the estimates of heritability observed by Franklin (1979) at the stage of density dependent mortality was no surprise since the less developed plants tend to be eliminated and the population as a whole tends to become more homogeneous across families. Similar trends were observed by Wearstler (1979) in a nursery study involving open pollinated loblolly pine progenies.

Given the apparent importance of the effect of competition on the estimation of genetic parameters in forest trees, further investigation is warranted to better understand inter-genotypic competition.

There is no single definition of competition among plants which is suitable for all situations. An ecologist may define it as the ability of a plant or group of plants, usually at the species level, to colonize more efficiently and ultimately become dominant in a given environment. This implies ability to reproduce more vigorously than the other groups in the same environment.

In forestry we are more interested in competition as the ability of trees to interact with the others and produce greater or less stem volume. It is of particular interest to quantify competitive interactions among individuals of the same species (intra-specific competition). At this level, Sakai (1961) enumerated the factors affecting the growth of plants in a population, namely: a) plant density; b) environmental effects; and c) inter-genotypic competition.

In species like loblolly pine (*Pinus taeda* L.), in which progeny tests are established mainly to rank families, it is more important to determine the influence of inter-family competition, rather than inter-genotypic competition; the latter term, although frequently used in a general sense, implies competition among individuals of different genotypes, which may include competition both between and within families.

Competition effects are usually evaluated by comparing performances of plants in pure versus mixed stands. Some examples in forestry are those reported by Adams (1980) and Williams *et al*. (1983). In a few cases different plot designs have been used to encompass several levels of competition (Adams *et al*., 1973; Stahl, 1977; Tauer, 1975; Rockwood, 1983).

Approaches used with loblolly pine families (Adams et al., 1973) and with poplar clones (Adams, 1980 and Tauer, 1975) involved interactions between pairs of genetic entries which permitted the characterization of competitive responses into the following categories described by Schutz & Brim (1967): 1) Neutral (each of the genotypes yields similarly in pure and in mixed stands); 2) Complementary (the loss in yield of a genotype is compensated by an equivalent gain of the other in the mixture, relative to their yields in pure stands); 3) Overcompensation (the combined yield of the genotypes in the mixture is greater than their yields in pure stands); 4) Undercompensation (the combined yield of the genotypes in the mixture is lower than their yield in pure stands).

All categories of competitive interactions were observed among pairs of loblolly pine families (Adams et al., 1973) and among pairs of poplar clones (Tauer, 1975). Only undercompensation was not observed by Adams (1980). However, the number of families included in his experiment was rather limited.

Information of this nature is useful where genetic entries are established in operational plantations in stands by family or clones. However, loblolly pine is usually planted in mixtures with seed from several families. A good competitor in this situation should express a net average overcompensation effect when competing with several families at random.

The approach used by Stahl (1977) was to compare performances of families in competition with increasing numbers of competitors assigned from other families at random. The positions of the subject trees in the square plots in a progeny test, which represented the various levels of competition with families allocated at random in adjacent plots, did not show the expected effect on height, stem diameter, or volume. The lack of competition effect was, from Stahl's judgment, due to the fact that the experiment had been established for purposes other than for a competition study. Moreover, the trees in the center of the square plots apparently received differential cultural treatments (more careful tending in the early years) than the border trees, thereby adding an extra source of variation which might have obscured the results.

Important assumptions needed in order to establish a working hypothesis are that competition between unlike genotypes benefits one of them at the expense of the other and that there is no competition among plants of similar genotypes. The term "competition" has often been used to designate the combined effects of inter-genotypic competition and stand density. As Sakai (1961) pointed out, plants of similar genotypes growing in a dense stand suffer the same restrictions as if they were planted individually in a limited space (e.g. small pots) and the effect on their growth is independent of inter-genotypic competition. That forest tree species of similar genotypes do not compete has been demonstrated by Sakai et al., (1965, 1968), Sakai & Mukaide (1967), and Adams et al., (1973). Therefore, competition among families constituted the focus of attention in this study, while intra-family competition was considered as part of the environmental effect.

The present work was proposed to study inter-family competition in conditions especially designed for this purpose and to determine how it influences the results of genetic tests.

Some of the questions not clearly answered previously were the objectives of this study and are as follows:

1. How does inter-family competition affect family performance and the estimates of genetic parameters?
2. Do families with good competitive ability tend to grow better than the poor competitors when planted in pure stands?
3. Are there family differences in competitive ability in loblolly pine?
4. Is competitive ability a heritable trait?
5. What are the implications of testing families in blocks and in non-contiguous family plots?

MATERIALS AND METHODS

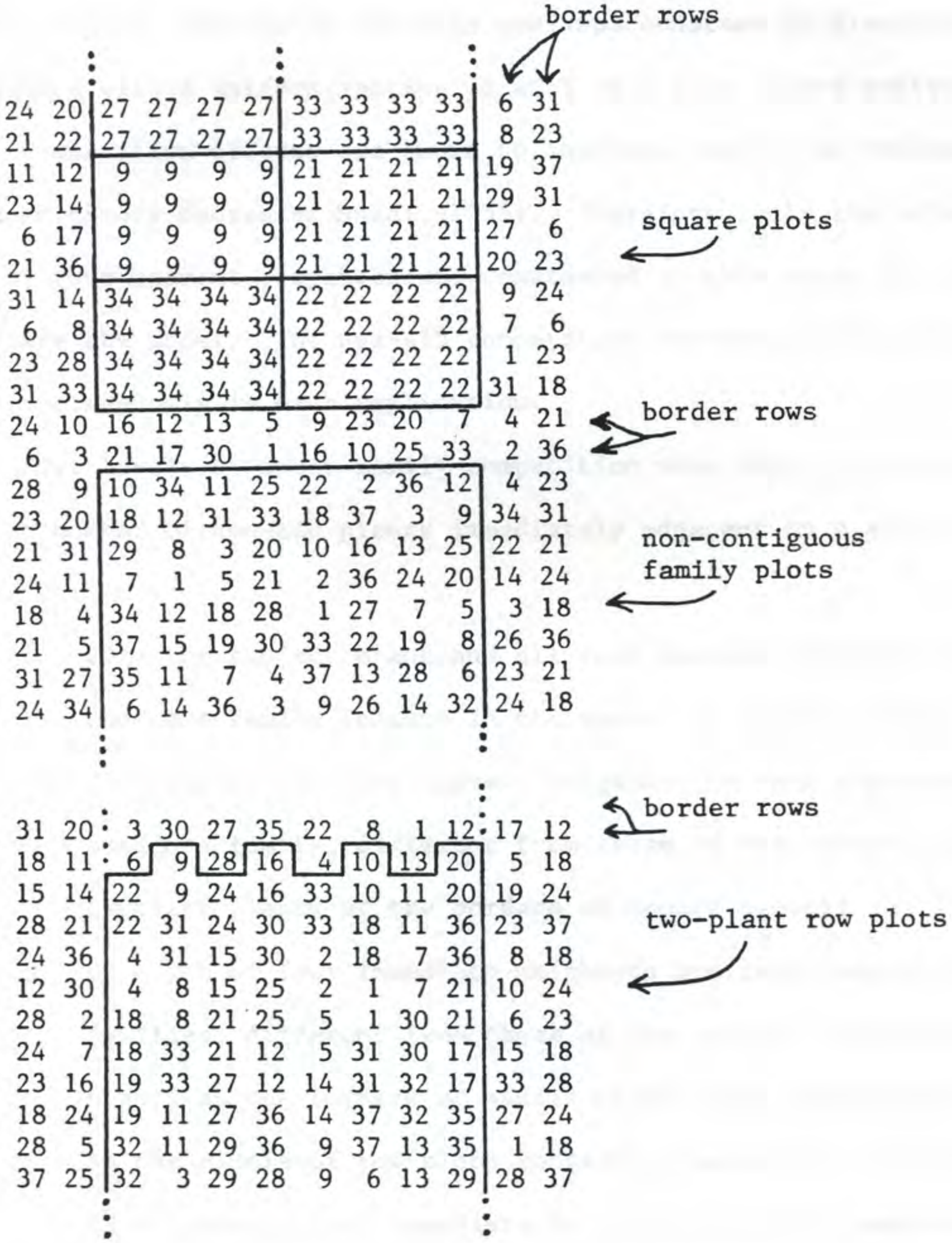
Thirty-six unrelated full-sib families of loblolly pine (Pinus taeda L.) (Appendix, Table A1) were used in this study. Most of them were crosses among parent trees from the Piedmont regions of Georgia, South Carolina, North Carolina, and Virginia. Two crosses involved South Carolina Coastal Plain sources and one involved a Georgia-Florida Coastal Plain source. The provenances of the parental trees are listed in Appendix, Table A2 and their breeding regions are illustrated in Appendix, Fig. A1.

After six weeks of cold stratification, the seeds were sown in individually labelled peat pellets in the greenhouse, in March, 1983. Healthy seedlings from each family were arranged in trays in the same positions relative to their neighbors as for the nursery experimental design. Family plots in blocks were filled with seedlings that had germinated on about the same day to confound germination date with blocks.

As the seedlings grew, many lateral roots went through neighboring peat pellets. The tap roots extended horizontally after reaching the bottom of the tray. These were pruned before transplanting into the nursery in June, 1983.

Fertilization and irrigation were supplied in the nursery during the first growing season to enhance growth.

Each of the eight replications contained representatives of all 36 families in each of the following plot shapes: a) square plots with 16 plants; b) two-plant (row) plots; and c) non-contiguous family plots (Fig. 1).



24	20	27	27	27	27	33	33	33	33	6	31
21	22	27	27	27	27	33	33	33	33	8	23
11	12	9	9	9	9	21	21	21	21	19	37
23	14	9	9	9	9	21	21	21	21	29	31
6	17	9	9	9	9	21	21	21	21	27	6
21	36	9	9	9	9	21	21	21	21	20	23
31	14	34	34	34	34	22	22	22	22	9	24
6	8	34	34	34	34	22	22	22	22	7	6
23	28	34	34	34	34	22	22	22	22	1	23
31	33	34	34	34	34	22	22	22	22	31	18
24	10	16	12	13	5	9	23	20	7	4	21
6	3	21	17	30	1	16	10	25	33	2	36
28	9	10	34	11	25	22	2	36	12	4	23
23	20	18	12	31	33	18	37	3	9	34	31
21	31	29	8	3	20	10	16	13	25	22	21
24	11	7	1	5	21	2	36	24	20	14	24
18	4	34	12	18	28	1	27	7	5	3	18
21	5	37	15	19	30	33	22	19	8	26	36
31	27	35	11	7	4	37	13	28	6	23	21
24	34	6	14	36	3	9	26	14	32	24	18

31	20	3	30	27	35	22	8	1	12	17	12
18	11	6	9	28	16	4	10	13	20	5	18
15	14	22	9	24	16	33	10	11	20	19	24
28	21	22	31	24	30	33	18	11	36	23	37
24	36	4	31	15	30	2	18	7	36	8	18
12	30	4	8	15	25	2	1	7	21	10	24
28	2	18	8	21	25	5	1	30	21	6	23
24	7	18	33	21	12	5	31	30	17	15	18
23	16	19	33	27	12	14	31	32	17	33	28
18	24	19	11	27	36	14	37	32	35	27	24
28	5	32	11	29	36	9	37	13	35	1	18
37	25	32	3	29	28	9	6	13	29	28	37

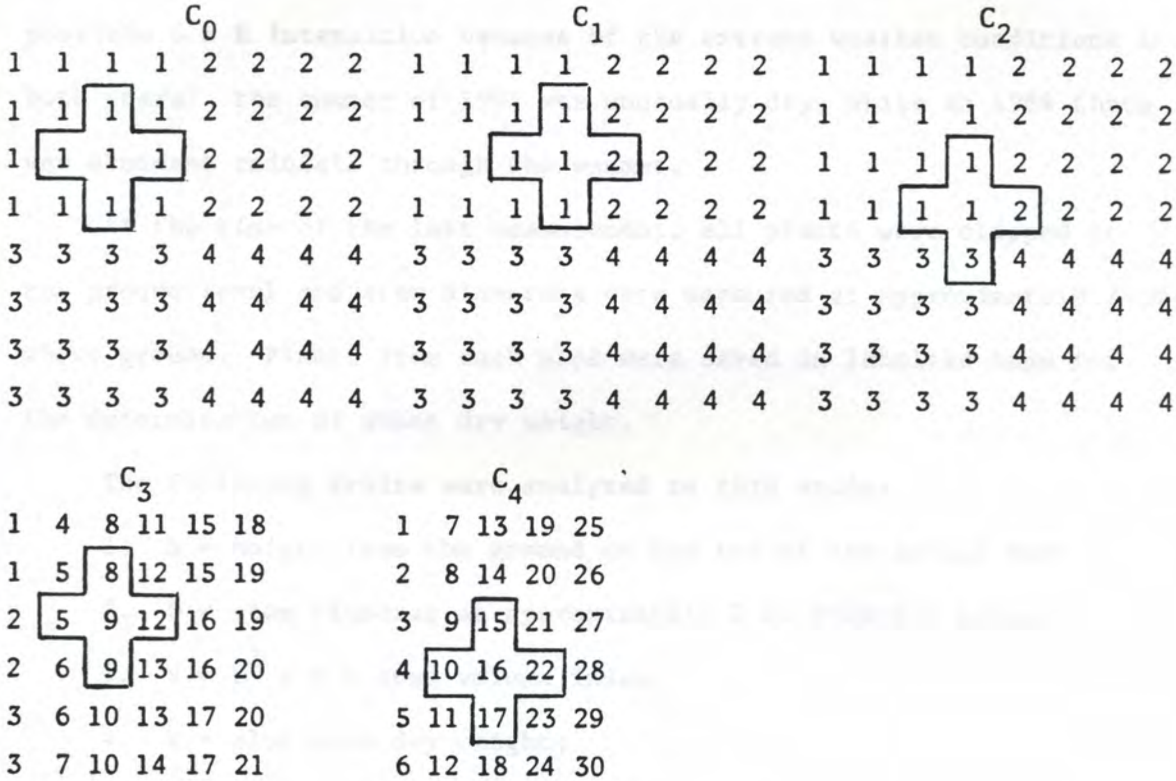
Fig. 1. Examples of plot layouts in the nursery used in the inter-family competition experiment. The numbers are the identifications of the families involved in the tests.

In order to distinguish the effect of competition from that of stand density, the latter variable was kept constant by planting all seedlings with a uniform spacing in an 8 cm x 8 cm square pattern.

Competition effects are known to increase rapidly as the spacing between plants decreases (Sakai, 1955). Therefore, only the effect of the four nearest neighbors was considered in this study in order to simplify the model. The non-sib competitors represented families assigned randomly in each replication.

Five levels of inter-family competition were identified according to the number of non-sib plants immediately adjacent to a subject plant (Fig. 2):

1. C0 = the subject plant and all four nearest neighbors are from the same family (plants in the center of square plots);
2. C1 = one of the four nearest neighbors is from a randomly assigned family, different from those of the subject plant (subject plants at the borders of square plots);
3. C2 = two of four immediate neighbors are from randomly assigned families, different from those of the subject plant (subject plants at the corners of square plots; also correspond to plants in the middle of row plots containing more than 2 plants);
4. C3 = three of four immediate neighbors are from randomly assigned families, different from those of the subject plant (subject plants in two-plant row plots; also correspond to plants at both ends of row plots);
5. C4 = all four immediate neighbors are from randomly assigned families, different from those of the subject plant (subject plants in non-contiguous family plots).



C_0

1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4

C_1

1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4

C_2

1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
1	1	1	1	2	2	2	2
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4
3	3	3	3	4	4	4	4

C_3

1	4	8	11	15	18
1	5	8	12	15	19
2	5	9	12	16	19
2	6	9	13	16	20
3	6	10	13	17	20
3	7	10	14	17	21

C_4

1	7	13	19	25
2	8	14	20	26
3	9	15	21	27
4	10	16	22	28
5	11	17	23	29
6	12	18	24	30

Fig. 2. Plot arrangements and levels of interfamily competition inflicted on the subject plants by the four closest neighbors; arrangements C0 to C4 refer to competition levels having from zero to four competitors, respectively.

Measurements of total height were taken soon after planting and were repeated in August and October, 1983, and in April, June, August, and November, 1984. There may have been some bias in this study due to possible G x E interaction because of the extreme weather conditions in both years: the summer of 1983 was unusually dry, while in 1984 there was abundant rainfall through the summer.

At the time of the last measurement, all plants were clipped at the ground level and stem diameters were measured at approximately 2 cm above ground. Plants from each plot were saved in labelled bags for the determination of shoot dry weight.

The following traits were analyzed in this study:

1. H = height from the ground to the top of the apical bud;
2. D = stem diameter at approximately 2 cm from the ground;
3. $V = D^2 \times H$ = stem volume index;
4. W = plot mean dry weight;
5. PW = W x S = total plot dry weight, where S = number of surviving plants per plot;
6. SV = (S/4) x 100 = percent survival per plot.

Statistical Analyses

To determine how competition influences the variances of family effects, analyses of variance were conducted for family performance under each competition level using the model in Table 1.

The response of each family to the fixed effects of competition was evaluated through analyses of individual families using the model in Table 2. The competitive ability of each family was estimated by the difference of their performance under competition with different

Table 1. Form of the analysis of variance for family effects by individual inter-family competition level.

Source	d.f.	E(MS)
Replication	r-1	
Family	f-1	$\sigma_e^2 + r\sigma_F^2$
Error	(r-1)(f-1)	σ_e^2

r = number of replications

f = number of families

σ_e^2 = experimental error

σ_F^2 = family variance

Table 2. Form of the analysis of variance for competition effect by family.

Source	d.f.	E(MS)
Replication	r-1	
Competition	c-1	$\sigma_e^2 + r\,\emptyset$
Error	(r-1)(c-1)	σ_e^2

r = number of replications

c = number of competition levels

σ_e^2 = experimental error variance

$\emptyset$ = component of the fixed effect of inter-family competition.

numbers of non-sib competitors and under pure stand conditions (no inter-family competition). Analyses of variance for family effects on competitive ability were conducted using the model in Table 1. The correspondence of family performances and competitive abilities under different competition levels was evaluated by the correlation coefficients (Steel & Torrie, 1980) among family means and competitive abilities in different competition levels averaged over replications.

Variance components were estimated from the analysis of variance table by equating the mean squares to their expectations and solving for the components. These were used for the estimation of intraclass correlations using the formula:

$$t = \frac{\sigma_F^2}{\sigma_F^2 + \sigma_E^2}$$

where:

t = intraclass correlations;

σ_F^2 = among family variance;

σ_E^2 = within family variance (Falconer, 1981).

RESULTS AND DISCUSSION

Overall Effects of Inter-family Competition

At 20 months of age eight of the families had empty plots due to mortality. Survival differences among inter-family competition levels were significant at 99% confidence level (Table 3). However, neither survival percentages or the distribution of empty plots seemed to follow a trend with increase in inter-family competition (Table 4).

The occurrence of empty plots leads to unbalance in the experimental design and this becomes rather difficult to handle for the estimation of variance components. Since mortality was apparently not related to the increased levels of inter-family competition, those families that had empty plots were deleted in order to simplify the analyses of growth traits and to permit a more precise estimation of variance components.

Inter-family competition effects were statistically significant for all traits except for total plot dry weight (Table 5). A possible explanation for this exception is that individual families reacted differently to inter-family competition and, on the average, positive and negative reactions tended to cancel out.

In order to verify the types of competitive interaction as defined by Schutz & Brim (1967) that might have occurred in this experiment, only the means under C3 (row plots) and C4 (non-contiguous family plots) were compared with family blocks. Family performance under C1 and C2 (one and two unrelated competitors, respectively) were not included because many competing plants under these inter-family competition levels were not measured. The only significant differences were observed between C3 and C0 (family blocks) for stem diameter and

Table 3. Overall survival percentages at 20 months of age under each inter-family competition level.

Competition Levels [a]	Survival Percentages
C0	79.8
C1	76.4
C2	78.9
C3	74.7
C4	80.7

[a] C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

Table 4. Distribution of empty plots due to mortality among inter-family competition levels.

	Competition Levels [a]				
Families	C0	C1	C2	C3	C4
1				x	
3				x	x
6	x		x		
13		x			
15			x	x	
17	x				
31				x	
34				x	

[a] C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

Table 5. Overall means in traits at 20 months of age under each inter-family competition level.

	Traits [a]					
Competition Levels	H cm	D cm	V cm^3	W g	PW g	SV %
C0	81.81	0.8717	71.39	14.95	49.71	82.14
C1	81.24	0.8712	72.80	15.66	49.00	78.91
C2	82.96	0.9070	81.73	17.20	53.43	81.92
C3	83.43	0.9075	81.46	17.01	54.28	79.46
C4	80.10	0.8527	67.71	14.69	49.86	83.37
PR > F	0.021	0.001	0.002	0.044	0.369	0.011
C3 vs C0	ns	*	ns	ns	ns	*
C4 vs C0	ns	ns	ns	ns	ns	ns

[a] H = height
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

ns = statistically non-significant differences.
* = significant differences at 5% level.

survival percentages. Although for other traits the differences in performance under C0 and C3 or C4 were not statistically significant, there was a general tendency for all means in C3 to be slightly higher than under C0. Apparently a phenomenon analogous to overcompensation was in effect. However, this general overcompensation effect seemed to depend on the level of mortality because survival was 3% lower in row plots (C3) relative to that under family blocks (C0). For some unknown reason, the survival under non-contiguous family plots (C4) was slightly higher than within family blocks. Consequently, the stand under C4 was more crowded than the others and this was probably the cause of the reduction in growth traits in C4 relative to family blocks.

Family Effects on Growth Traits and Intraclass Correlations under Different Inter-family Competition Levels

Variances due to family effects in height growth were highly significant and increased relative to the error variances at higher inter-family competition levels at all ages from 3 months in June, 1983 through 20 months in November, 1984 (Appendix, Table A3). Similar patterns were observed for stem diameter, plot mean dry weight, total plot dry weight, stem volume index and survival percentage at 20 months of age (Appendix, Table A4). Thus, genetic variance and all genetic parameters derived therefrom are likely to be inflated with the additional variance generated by the inter-family competition.

The graphs in Figures 3 and 4 show that greater intraclass correlations in height growth at higher inter-family competition levels from 3 months (June 1983) to 15 months (June 1984) of age were mostly due to lower error variances. This was expected because of more

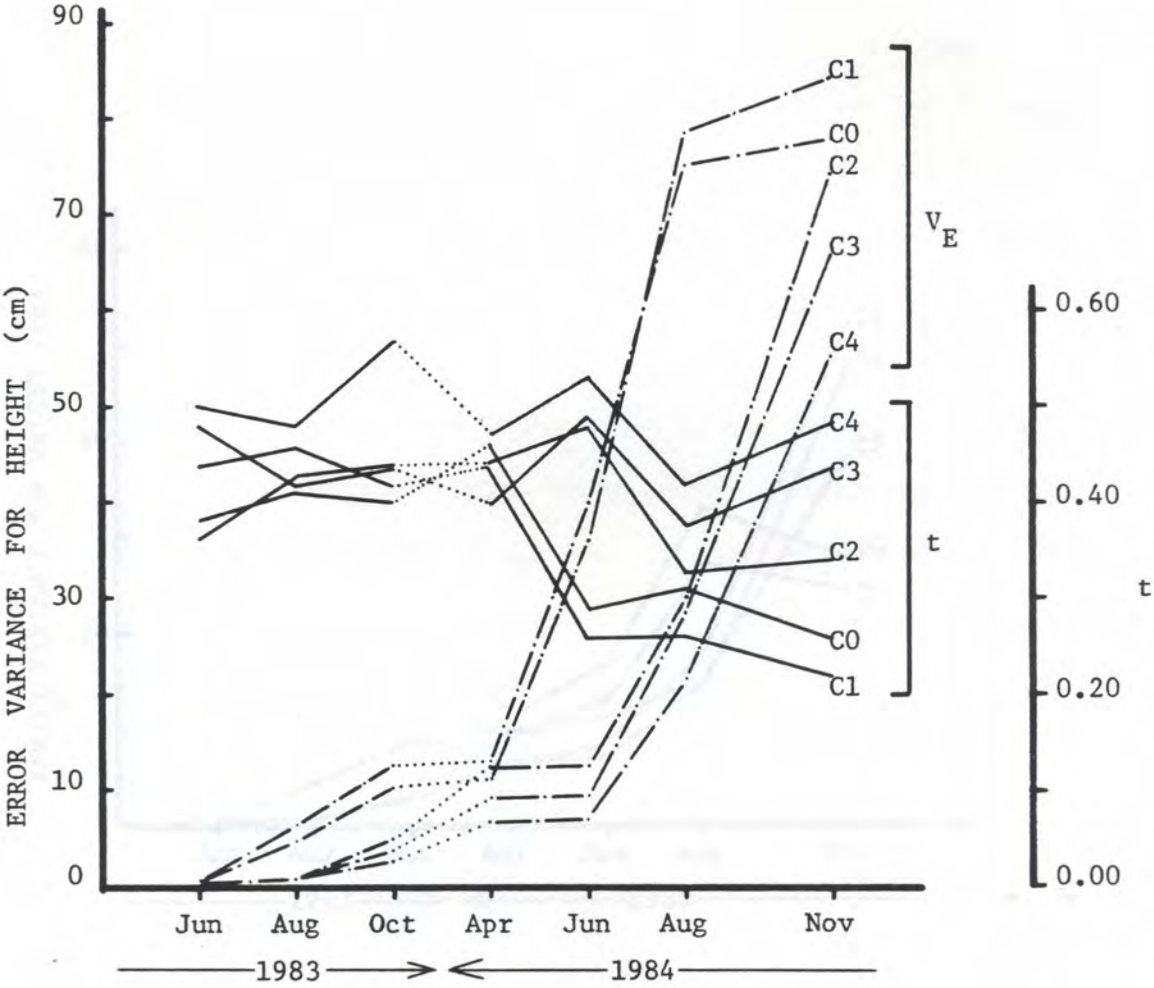


Fig. 3 . Trends in error variance (V_E) and in intraclass correlation (t) at each level of inter-family competition through the ages of 3 to 20 months (Jun.83 to Nov.84) from sowing. (... = no measurement in the Winter)

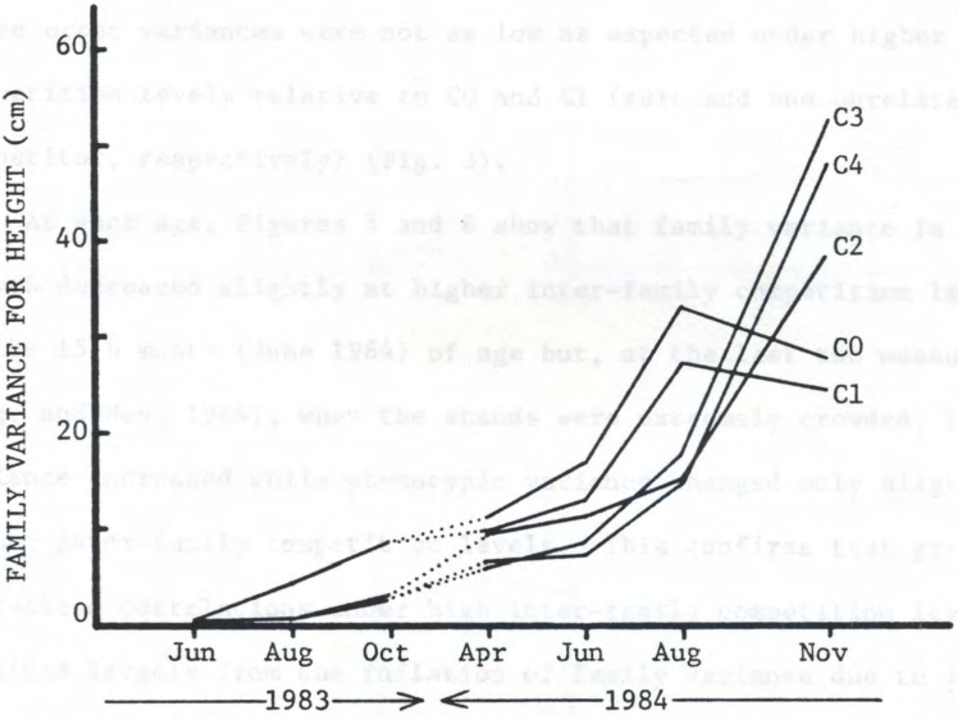


Fig. 4. Trends in family variance at each level of inter-family competition through the ages of 3 to 20 months (Jun.83 to Nov.84) from sowing. (... = no measurement in the Winter)

efficient plot designs at these competition levels and the possibility that inter-family competition was still not sufficiently strong to have a major effect. However, at 17 and 20 months of age (Aug. and Nov. 1984, respectively), greater intraclass correlations at higher inter-family competition levels were mostly due to greater family variances (Fig. 4) since error variances were not as low as expected under higher inter-family competition levels relative to C0 and C1 (zero and one unrelated competitor, respectively) (Fig. 3).

At each age, Figures 5 and 6 show that family variance in height growth decreased slightly at higher inter-family competition levels up to the 15th month (June 1984) of age but, at the last two measurements (Aug. and Nov. 1984), when the stands were extremely crowded, family variance increased while phenotypic variance changed only slightly at higher inter-family competition levels. This confirms that greater intraclass correlations under high inter-family competition levels resulted largely from the inflation of family variance due to inter-family competition. This finding is in accord with reports on other species by Sakai (1953), Sakai & Mukaide (1967), and Stern (1969). This indicates that inter-family competition enhanced differences among families by introducing an extra source of variation. Such increases in family variances with increases in intensity of competition led Namkoong & Conkle (1976) and Franklin (1979) to suggest delaying selection until intense competition begins as a means of increasing genetic gains.

The increases in family variances under higher inter-family competition levels show that plants of the same family reacted similarly to inter-family competition, thereby contributing to the increase of intraclass correlations.

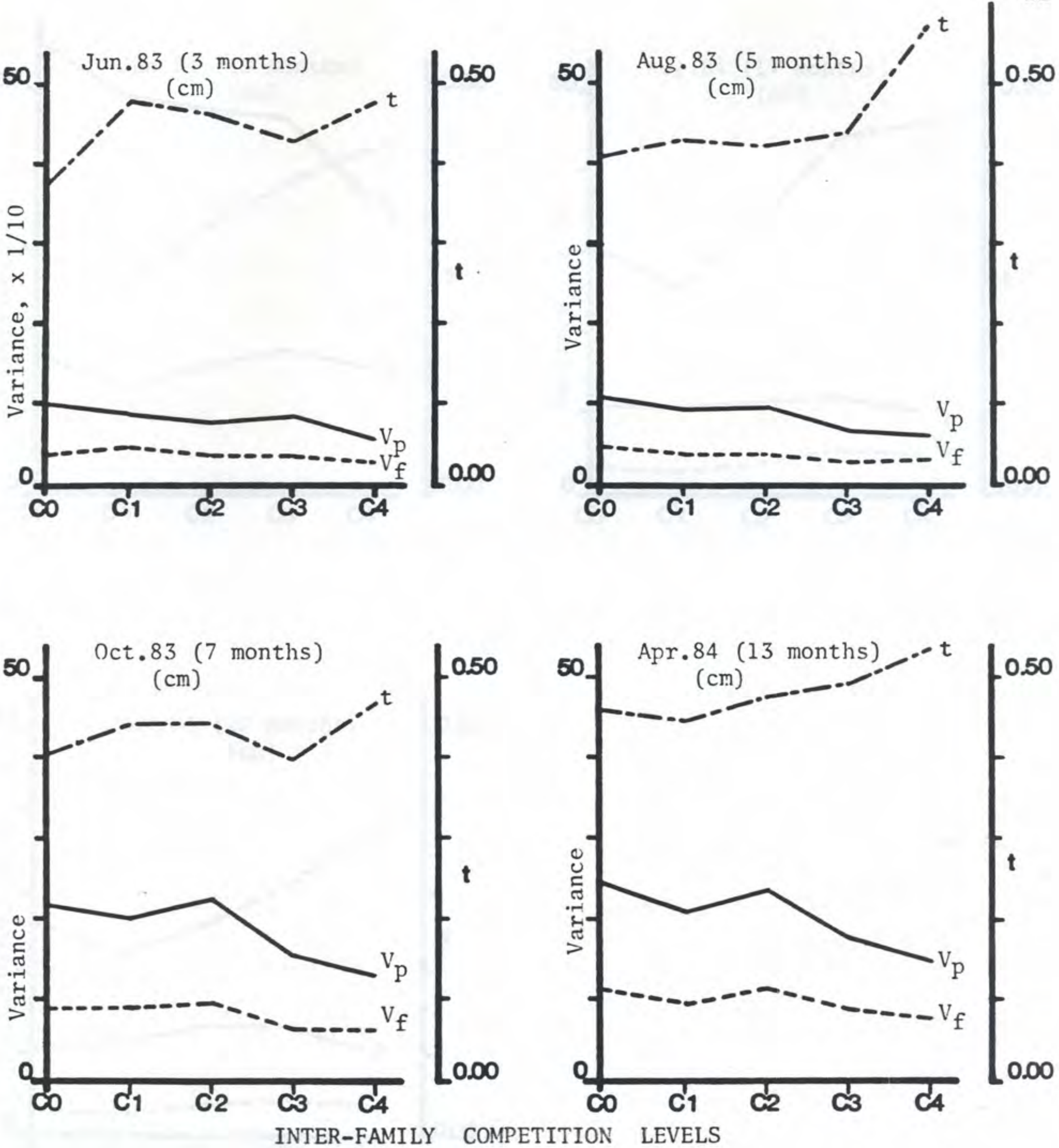


Fig. 5. Trends in family and phenotypic variances, and in intraclass correlations for height growth under different inter-family competition levels. V_f= family variance; V_p= phenotypic variance; $t = (V_f/V_p)$ = intraclass correlation.

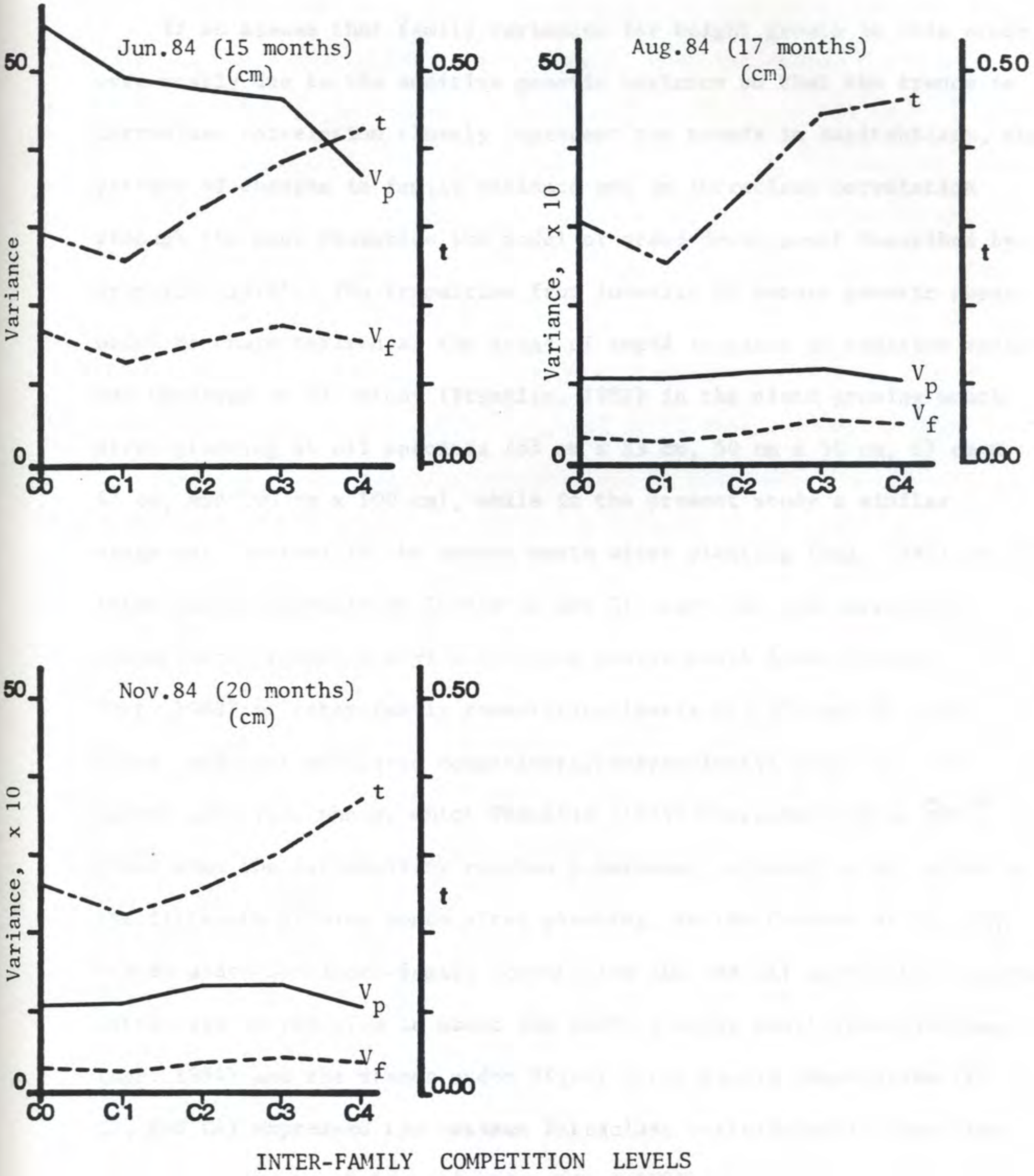


Fig. 6. Trends in family and phenotypic variances, and in intraclass correlations for height growth under different inter-family competition levels. V_f = family variance; V_p = phenotypic variance; t = (V_f/V_p) = intraclass correlation.

If we assume that family variances for height growth in this study were mostly due to the additive genetic variance so that the trends in intraclass correlation closely represent the trends in heritability, the pattern of changes in family variance and in intraclass correlation through the ages resembles the model of stand development described by Franklin (1979). The transition from juvenile to mature genetic phase which he characterized as the stage of rapid increase in additive variance was observed in his study (Franklin, 1983) in the ninth growing month after planting at all spacings (33 cm x 33 cm, 50 cm x 50 cm, 67 cm x 67 cm, and 100 cm x 100 cm), while in the present study a similar stage was observed in the second month after planting (Aug. 1983) at inter-family competition levels C0 and C1 (zero and one unrelated competitors, respectively) and in the fourth month from planting (Oct. 1983) at inter-family competition levels C2, C3, and C4 (two, three, and four unrelated competitors, respectively) (Fig. 4). The mature genotypic phase, which Franklin (1979) characterized as the phase when the heritability reaches a maximum, occurred in his study in the fifteenth growing month after planting; in the present study, the stands under low inter-family competition (C0 and C1) showed the highest intraclass correlation in about the sixth growing month from planting (Apr. 1984) and the stands under higher inter-family competition (C2, C3, and C4) expressed the maximum intraclass correlation in about the eighth growing month from planting (June 1984) (Fig. 3). A slightly higher peak in intraclass correlation was observed in the fourth growing month from planting (Oct. 1983) under inter-family competition level C4 (non-contiguous family plots) possibly by chance.

Consistent with Franklin's (1979) model, family variance decreased rapidly several months after the culmination of intraclass correlation but only at low inter-family competition levels (C0 and C1) (Fig. 3 and 4). For the high inter-family competition levels (C2, C3, and C4), family variances were still continuing to increase at steep rates up to the 17th month from planting (Nov. 1984). Therefore, the trends in variance that Franklin (1983) showed over a period of five years could be shown much earlier by planting at a spacing as close as 8 cm x 8 cm. Also, the progress through the phases of stand development seemed to depend on the intensity of inter-family competition, in the sense that in more genotypically heterogeneous populations such as in two-plant row plots (C3) and in non-contiguous family plots (C4), phase changes took place more slowly than in more genotypically homogeneous populations (family blocks).

Family variances in stem diameter and volume at 20 months of age fluctuated under inter-family competition levels C1 and C2 (one and two competitors, respectively), possibly due to sampling errors in diameter, which were carried along in the estimation of the stem volume index (Fig. 7). However, under two-plant row plots (C3) and non-contiguous family plots (C4), family variances increased substantially, resulting in high intraclass correlations in spite of large error variances observed under C3.

The steep increases in intraclass correlations for stem diameter, volume, and dry weight show that these traits were more strongly affected by inter-family competition than height growth.

The relatively greater impact of competition on diameter than on height growth agrees with the results reported by Sakai & Hatakeyama (1967)

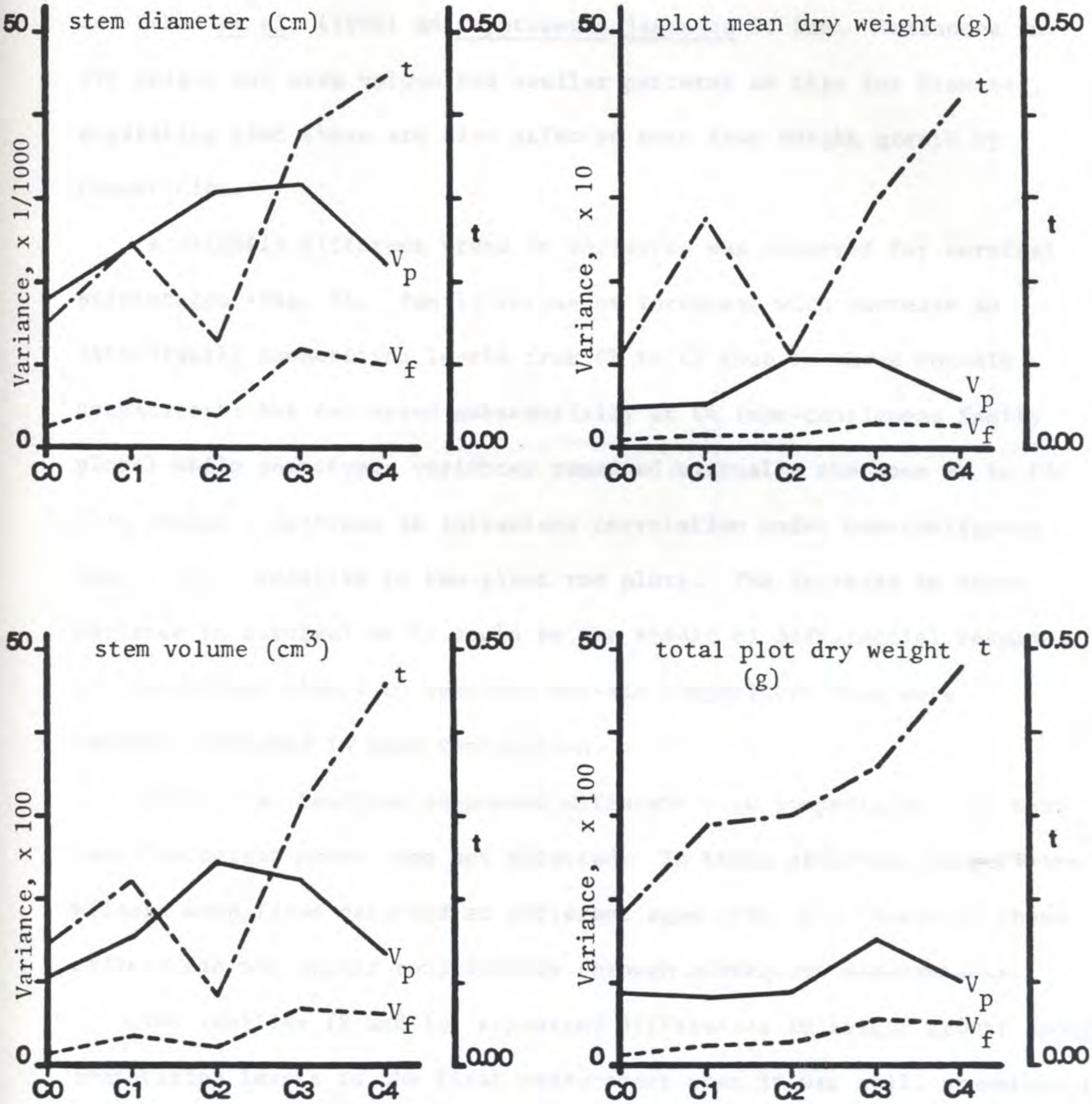


Fig. 7. Trends in family and phenotypic variances, and in intraclass correlations for stem diameter, plot mean dry weight, stem volume, and total plot dry weight at 20 months of age under different inter-family competition levels.
V_f = family variance; V_p = phenotypic variance;
$t = (V_f/V_p)$ = intraclass correlation.

and Sakai et al. (1968) in Cryptomeria japonica D. Don. Variances in dry weight and stem volume had similar patterns as that for diameter, suggesting that these are also affected more than height growth by competition.

A slightly different trend in variances was observed for survival percentages (Fig. 8). Family variances increased with increase in inter-family competition levels from C1 to C3 (one to three non-sib competitors) but decreased substantially at C4 (non-contiguous family plots) while phenotypic variances remained virtually the same as in C3. This caused a decrease in intraclass correlation under non-contiguous family plots relative to two-plant row plots. The increase in error variance in survival at C4 could be the result of differential responses of the subject plants to specific non-sib competitors that were randomly assigned in each replication.

Individual families responded differently to competition. In most families height growth was not affected. In those affected, competition effects were first detected at different ages (Fig. 9). However, these effects did not appear consistently through subsequent measurements.

Two families (8 and 10) expressed differences in height growth among competition levels in the first measurement when it was still premature to presume any competition among plants in the nursery. This could have occurred by chance or, possibly, inter-family competition was in effect since the greenhouse stage, as soon as lateral roots crossed and explored their neighbors' juxtaposed root spaces.

It is evident from observations in subsequent measurements that competitive responses depend on the seedlings' growth stage, similar to observations in rice plant weight by Jennings & Aquino (1968). For

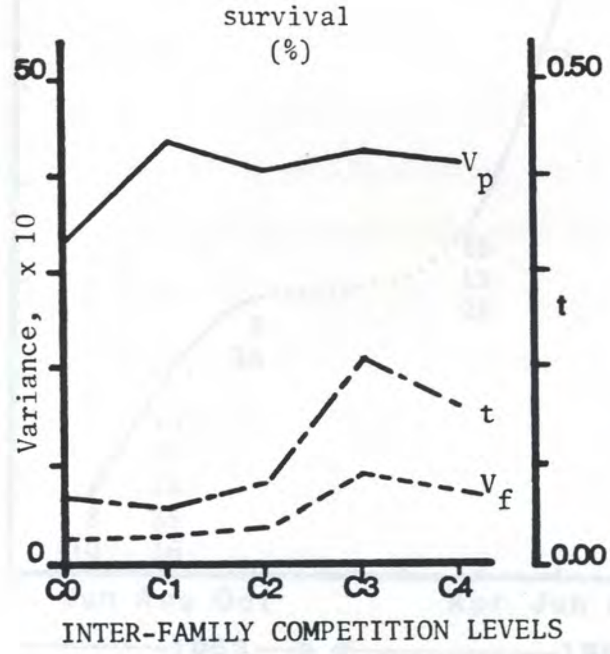


Fig. 8. Trends in family and phenotypic variances, and in intraclass correlations for survival percentages at 20 months of age under different inter-family competition levels.

V_f = family variance

V_p = phenotypic variance

$t = (V_f/V_p)$ = intraclass correlation.

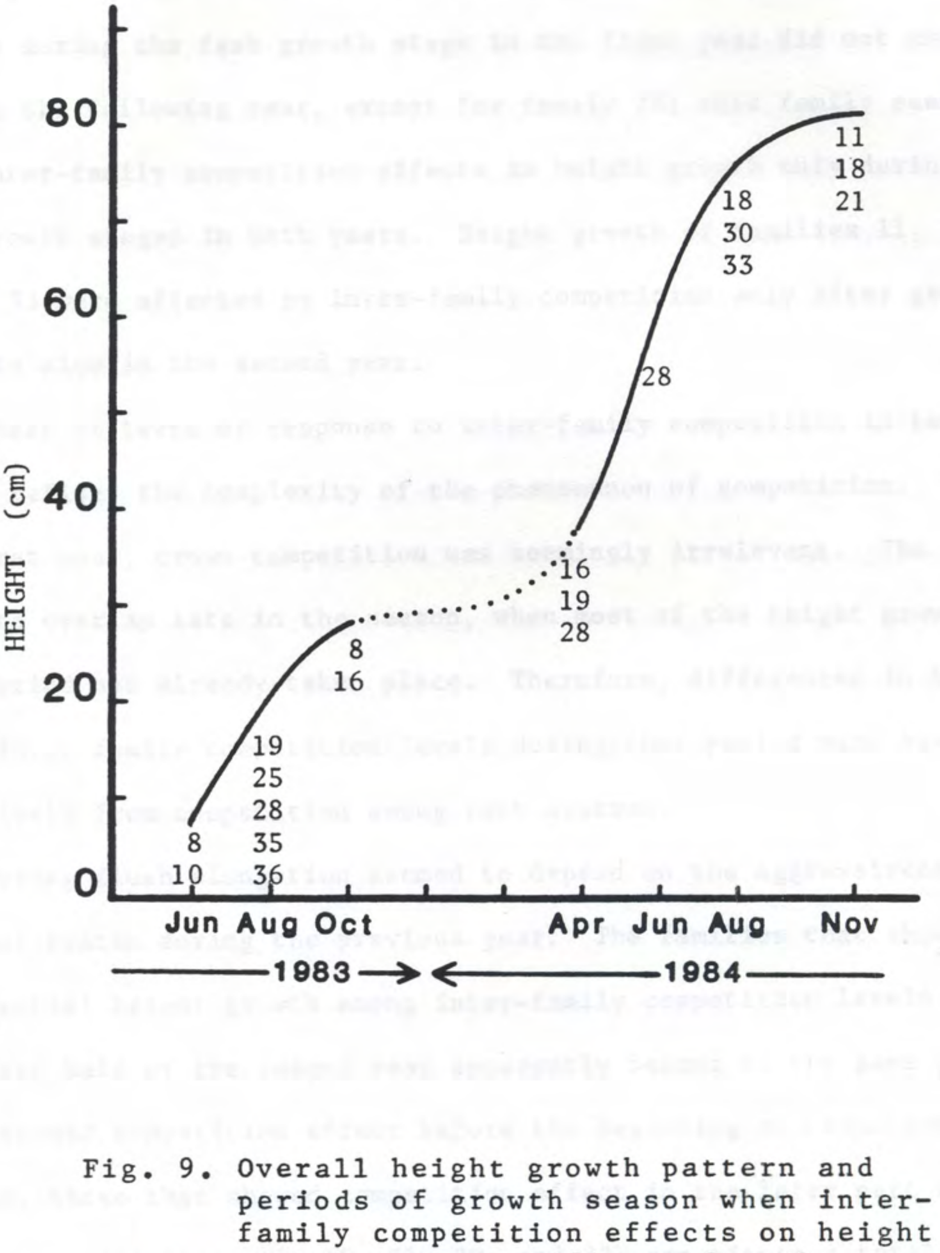


Fig. 9. Overall height growth pattern and periods of growth season when inter-family competition effects on height growth were significant for the families indicated.
..... = not measured.

example, families which showed significant inter-family competition effects during the fast growth stage in the first year did not show the same in the following year, except for family 28; this family seemed to show inter-family competition effects in height growth only during the fast growth stages in both years. Height growth of families 11, 18, 21, 30 and 33 were affected by inter-family competition only after growth began to slow in the second year.

These patterns of response to inter-family competition in height growth reflect the complexity of the phenomenon of competition. During the first year, crown competition was seemingly irrelevant. The crowns began to overlap late in the season, when most of the height growth for that period had already taken place. Therefore, differences in height among inter-family competition levels during that period must have arisen exclusively from competition among root systems.

Spring flush elongation seemed to depend on the aggressiveness of the root system during the previous year. The families that showed differential height growth among inter-family competition levels through the first half of the second year apparently belong to the same group which showed competition effect before the beginning of crown competition. However, those that showed competition effect in the later part of the second year (families 11, 18, 21, 30, and 33) constitute a totally different group.

Root competition in the second year was certainly more accentuated than in the previous year but it was no longer the only competitive factor affecting height growth. Crown competition intensified, especially in the second half of the growing season, after the full expansion of the spring and early summer flushes. Therefore, the second group of families represent those that are sensitive to inter-family competition only when root and crown competitions occur simultaneously.

Competition effects in stem diameter, plot mean dry weight, total plot dry weight, stem volume index, and survival percentage at 20 months of age were not detected in most families. Families and traits affected by inter-family competition at 20 months of age are listed in Table 6.

Only families 7 and 16 showed differences in survival among competition levels; also, in these families, competition effects were not detected in any other traits except total plot dry weight in family 16. This trait was expected to show the same trend as survival percentage inasmuch as it is partly a function of the number of surviving trees per plot.

Among all traits, total plot dry weight is perhaps most important in forestry as it is indicative of the plant's biomass productivity. Families 25 (Table 7) and 30 (Table 8) showed a decline in productivity when in competition with other families. If these results are indicative of performance at older ages, poor competitors such as these should be excluded from tree improvement programs where the objective is to develop higher yielding populations of mixed genetic entries but they should be favored for plantations in family blocks when their performances were superior.

Families 16 (Table 9) and 18 (Table 10) responded positively to competition with dramatic increase in total plot dry weight. Not only growth traits but also survival increased at higher competition levels in these families. Only occasionally was their performance under competition similar or inferior to their performance in family blocks, such as in height growth at competition level C2 (equivalent to positions in the middle of row plots), stem diameter in non-contiguous family plots (C4),

Table 6. Traits at 20 months of age in which inter-family competition effects were significant for the families indicated.

	Traits [a/]					
Families	H	D	W	PW	V	SV
7						x
10			x			
11	x					
16				x		x
18	x	x	x	x	x	
21	x					
25			x	x		
30			x	x		
32		x	x		x	
33		x	x		x	

[a/] H = height
D = stem diameter
W = plot mean dry weight
PW = total plot dry weight
V = stem volume index
SV = survival percentage

x = significant inter-family competition effect

Table 7. Performance of family 25 at 20 months of age under different inter-family competition levels (means of 8 replications).

Competition Levels [b]	Traits [a] H cm	 D cm	 V cm^3	 W g	 PW g	 SV %
C0	77.23	0.7960	55.64	11.88	39.38	81.25
C1	72.09	0.7615	45.82	9.88	25.88	62.50
C2	78.71	0.8641	71.56	15.88	38.50	56.25
C3	72.30	0.7074	38.76	8.00	19.50	59.38
C4	68.38	0.7026	36.83	7.00	18.00	62.50

[a] H = height
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] C0...C4 = inter-family competition levels represented by zero to four non-sib competitors.

Table 8. Performance of family 30 at 20 months of age under different inter-family competition levels (means of 8 replications).

	Traits [a]					
Competition Levels [b]	H cm	D cm	V cm^3	W g	PW g	SV %
C0	78.48	0.8103	64.50	13.75	33.75	78.13
C1	74.57	0.7658	51.97	10.25	24.63	68.75
C2	74.46	0.7498	48.68	11.13	35.25	81.25
C3	65.98	0.6756	31.56	6.88	10.88	46.88
C4	74.47	0.7597	45.83	10.13	25.13	68.75

[a]
H = height
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] C0...C4 = inter-family competition levels represented by zero to four non-sib competitors.

Table 9. Performance of family 16 at 20 months of age under different inter-family competition levels (means of 8 replications).

Competition Levels [b]	Traits [a]					
	H cm	D cm	V cm^3	W g	PW g	SV %
C0	74.33	0.7988	50.84	10.13	28.75	71.88
C1	76.66	0.8128	59.76	12.50	30.25	59.38
C2	74.17	0.8349	62.01	12.38	40.75	84.38
C3	80.80	0.8976	71.33	14.75	48.88	87.50
C4	74.90	0.7930	52.10	11.50	37.88	87.50

[a] H = height
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] C0...C4 = inter-family competition levels represented by zero to four non-sib competitors.

Table 10. Performance of family 18 at 20 months of age under different inter-family competition levels (means of 8 replications).

Competition Levels [b]	H cm	D cm	V cm^3	W g	PW g	SV %
C0	84.99	0.9840	93.91	16.88	58.25	87.50
C1	90.22	1.1491	138.70	23.00	87.63	90.63
C2	84.99	0.0526	105.74	17.25	59.63	93.75
C3	97.43	1.2652	177.84	32.63	118.88	90.63
C4	93.68	1.2228	169.01	33.25	109.25	96.88

Traits [a]

[a] H = height
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] C0...C4 = inter-family competition levels represented by zero to four non-sib competitors.

and in survival percentage at competition level C1 (border trees in family blocks). The causes of these results are not clearly understood.

Good competitors such as families 16 and 18 may have depressed the growth of some immediate neighbors but they were apparently responsible for the tendency toward a general overcompensation effect observed under inter-family competition level C3 (two-plant row plots).

The majority of families did not show a competition effect in the traits measured. These could represent families with overall neutral reaction to competitive interactions.

Families with both neutral and overcompensation effects are desirable in tree improvement programs for their ability to perform as well or better with mixed families as in pure family blocks. A further advantage of families in these categories is that, if selected for increased growth, they contribute also to the genetic polymorphism in the improved population (Mather, 1969; Adams, 1980). Genetic polymorphism is important in buffering the populations against changes in biotic and non-biotic factors of the environment. However, it must be emphasized that "poor" and "good" competitors alluded to in this study refer to the specific environment of the experimental plots and cannot be safely extrapolated to a general situation before testing their competitive abilities in several environments and under more normal conditions.

Family Effects on Competitive Ability and Intraclass Correlations

Competitive ability as measured by the difference between the performance of families with different numbers of non-sib competitors and in pure stands was extremely variable.

The values of F-statistics from the analyses of variance of family effects on competitive ability are presented in Table 11. Family effects were not significant at competition levels C1 (plants at the border of family blocks), and C2 (plants at the corners of family blocks) in any of the traits, possibly due to large error variances or to the weak effect of inter-family competition when only one or two of the nearest neighbors were non-sibs.

Lack of statistical significance of family effects can result from large error variances *i.e.*, plot to plot variances within families. This was most likely the case in the present study because plots within families in each competition level differed as to which competitor families were represented as non-sib neighbors. Therefore, variances of plot means may have been inflated by the variety of competitive interaction responses of the subject plant to specific individuals that were randomly assigned as non-sib competitors in each replication. Drastic differences in competitive responses to non-sib neighbors in pairwise interactions were reported by Adams *et al.*, (1973) in loblolly pine seedlings, Tauer (1975) in poplar clones, and Sakai (1953) in wheat varieties.

At competition level C3 (row plots) family effects were great enough to be detected at the 99% confidence level in all traits. This indicates that, when inter-family competition becomes intense, family variances in two-plant row plots may become highly inflated by the effect of inter-family competition.

The decline in family variance relative to the error variance for height and diameter at C4 (non-contiguous family plots) was not expected. However, maximum family differences in competitive ability in volume and dry weight were observed in non-contiguous family plots as expected.

Table 11. Family effects on competitive ability (F-tests) for several traits at 20 months of age under different inter-family competition levels.

Traits [a]	Competitive Abilities [b] (C1-C0)	(C2-C0)	(C3-C0)	(C4-C0)
H	0.94	1.08	1.80**	1.09
D	1.00	0.94	1.82**	1.45
V	1.16	0.97	1.81**	1.87**
W	1.15	1.03	1.90**	1.96**
PW	0.86	0.89	2.17**	2.41**
SV	0.83	1.07	1.97**	0.94

[a] H = height growth
D = stem diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b] competitive ability = (performance in mixed stand with 1...4 unrelated competitors) - (performance in pure stand)

C1...C4 = interfamily competition levels represented by one to four unrelated competitors

** significant at 1% level.

If selections were based on family performances under intense inter-family competition, some individuals may be chosen mainly because of their outstanding competitive ability in spite of their mediocre genetic merit under other conditions, while others may be rejected because of poor competitive ability in spite of their true genetic superiority under other conditions. It would be reasonable to select families under intense inter-family competition only if competitive ability were inherited, not negatively correlated with growth traits and if the trees were grown under intense inter-family competition.

Estimates of heritability per se were not possible in this study because it involved only unrelated full-sib families and non-additive variance may have been substantial. The presence of dominance effects in loblolly pine has been demonstrated indirectly by the existence of strong inbreeding depression (Franklin, 1968; Sniezko, 1984). Inbreeding depression would not have been observed if there were no dominance. Therefore, only rough estimates of heritability can be made in the form of intraclass correlations, which is a measure of differences among classes (families), estimated by the ratio of among family variance over the phenotypic variance. Also, under inter-family competition, the genetic value of an individual (or family) depends in part on the genetic value of its competitors.

From the estimates of intraclass correlations for competitive ability among families (Table 12), it seems evident that this trait is lowly heritable and depends very much on the environment since intraclass correlation is an upper limit for heritability. Very low heritabilities of competitive ability were also reported by Sakai (1961) for rice plant

Table 12. Intraclass correlations among full-sib families for competitive abilities under different levels of competition at 20 months of age.

Competition Levels [b/]	Traits [a/]					
	H	D	V	W	PW	SV
C1	0^-	0	0.020	0.018	0^-	0^-
C2	0.010	0^-	0^-	0.004	0^-	0^-
C3	0.091	0.093	0.092	0.101	0.127	0.114
C4	0.011	0.053	0.098	0.108	0.150	0^-

[a/] H = height
D = diameter
V = stem volume index
W = plot mean dry weight
PW = total plot dry weight
SV = survival percentage

[b/] C1...C4 = one to four non-sib competitors

0^- = estimates less than zero

weight and Sakai & Mukaide (1967) for stem diameter and height in *Cryptomeria japonica* D. Don.

The strategy to use early selection to obtain genetic gains for growth traits at mature ages is usually ineffective because of low age-age correlations, especially when age differences are large. However, even with modest age-age correlations, which occur for growth traits after the first year, genetic gains per unit time can be increased because early selections permit faster generation turnovers (Lambeth, 1980). This strategy, however, depends on the magnitude of the heritabilities at the juvenile and mature ages. The efficiency of early selection will be greater if the heritability at the juvenile age is higher relative to mature age. While short-term genetic tests planted at close spacings as suggested by Franklin (1979) may still produce increased genetic gains per unit time, its efficiency may not be as great as expected because of the upward bias in the heritability at juvenile age due to non-heritable variation in family competitive ability.

Phenotypic Correlations among Competition Levels and Competitive Abilities

Correlations of family means across competition levels were reasonably high, except for survival percentage (Table 13 for height and diameter; Table 14 for plot mean and total plot dry weight; Table 15 for stem volume and survival percentage).

In general, there was a consistency of families ranking among the top 20% at different inter-family competition levels (Appendix, Table A5-A10). However, there were some rank changes related to competition. For example: family 18 had the highest increase in all traits by increasing competition levels but in C0 (family blocks) it was not among the top 20% in height,

Table 13. Correlation coefficients of family means across different inter-family competition levels and competitive abilities at 20 months of age (n=28).
Height = above diagonal; Diameter = below diagonal

	Competition Levels a/					Competitive Abilities b/			
	C0	C1	C2	C3	C4	C10	C20	C30	C40
C0	1	0.85**	0.84**	0.68**	0.80**	-0.34	-0.09	-0.22	-0.21
C1	0.78**	1	0.87**	0.74**	0.84**	0.21	0.21	0.03	0.10
C2	0.80**	0.87**	1	0.72**	0.75**	-0.01	0.46*	0.01	-0.06
C3	0.69**	0.86**	0.81**	1	0.77**	0.06	0.21	0.57**	0.23
C4	0.76**	0.91**	0.80**	0.83**	1	0.03	0.07	0.13	0.43**
C10	-0.03	0.60**	0.37*	0.50**	0.49**	1	0.53**	0.46*	0.56**
C20	-0.03	0.39*	0.58**	0.42*	0.31	0.66**	1	0.38*	0.24
C30	0.13	0.55**	0.46*	0.81**	0.52**	0.71**	0.59**	1	0.54**
C40	0.13	0.59**	0.40*	0.56**	0.74**	0.77**	0.50**	0.66**	1

a/ C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

b/ C10 = (family mean in C1) - (family mean in C0) = competitive ability at C1 level, etc.

* = significant at 5% level (Ho: rho=0)
** = significant at 1% level (Ho: rho=0)

Table 14. Correlation coefficients of family means across different inter-family competition levels and competitive abilities at 20 months of age (n=28).

Plot mean dry weight = above diagonal; Total plot dry weight = below diagonal.

	Competition Levels [a/]					Competitive Abilities [b/]			
	C0	C1	C2	C3	C4	C10	C20	C30	C40
C0	1	0.72**	0.55**	0.56**	0.60**	-0.07	-0.18	-0.02	-0.05
C1	0.79**	1	0.71**	0.84**	0.80**	0.63**	0.24	0.54**	0.42*
C2	0.79**	0.86**	1	0.66**	0.52**	0.42*	0.72**	0.44*	0.21
C3	0.61**	0.86**	0.79**	1	0.84**	0.59**	0.32	0.84**	0.60**
C4	0.63**	0.85**	0.70**	0.83**	1	0.48**	0.11	0.61**	0.77**
C10	-0.17	0.47**	0.24	0.51**	0.46**	1	0.55**	0.76**	0.66**
C20	-0.08	0.32	0.55**	0.44*	0.29	0.63**	1	0.50**	0.28
C30	-0.01	0.49**	0.39*	0.80**	0.57**	0.77**	0.62**	1	0.75**
C40	-0.06	0.41*	0.22	0.54**	0.74**	0.74**	0.02	0.72**	1

[a/] C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

[b/] C10 = (family mean in C1) - (family mean in C0) = competitive ability at C1 level, etc.

* = significant at 5% level (Ho: rho=0)
** = significant at 1% level (Ho: rho=0)

Table 15. Correlation coefficients of family means across different inter-family competition levels and competitive abilities at 20 months of age (n=28).

Stem volume = above diagonal; Percent survival = below diagonal.

	Competition Levels a/					Competitive Abilities b/			
	C0	C1	C2	C3	C4	C10	C20	C30	C40
C0	1	0.73**	0.54**	0.60**	0.68**	-0.02	-0.25	0.06	0.07
C1	0.51**	1	0.69**	0.85**	0.86**	0.67**	0.16	0.56**	0.54**
C2	0.52**	0.51**	1	0.66**	0.58**	0.42*	0.68**	0.45*	0.33
C3	0.36	0.52**	0.42*	1	0.85**	0.59**	0.23	0.83**	0.64**
C4	0.52**	0.52**	0.59**	0.61**	1	0.52**	0.08	0.60**	0.78**
C10	-0.41*	0.58**	0.05	0.21	0.06	1	0.50**	0.76**	0.72**
C20	-0.39*	0.07	0.58**	0.11	0.14	0.45*	1	0.47**	0.33
C30	-0.33	0.17	0.07	0.76**	0.26	0.49**	0.38*	1	0.76**
C40	-0.26	0.16	0.23	0.39*	0.69**	0.42*	0.49**	0.57**	1

a/ C0...C4 = inter-family competition levels represented by zero to four unrelated competitors.

b/ C10 = (family mean in C1) - (family mean in C0) = competitive ability at C1 level, etc.

* = significant at 5% level (Ho: rho=0)
** = significant at 1% level (Ho: rho=0)

plot mean and total plot dry weight; family 20 was among the top 20% in almost all traits at C0 but was surpassed by others under competition levels C2, C3, and C4 (two, three, and four non-sib competitors, respectively). This calls attention to the fact that not all fast growers are good competitors and not all good competitors do well in pure stand conditions.

"Crop" and "competition" ideotypes described by Donald & Hamblin (1976) seem to exist in loblolly pine, although it was not an objective of this study to characterize morphological traits that enable particular plant forms to excel in pure or mixed stands.

The occurrence of highest correlations between competitive ability at a given competition level with family performance at the same levels of competition (*e.g.* C10 *vs* C1, C20 *vs* C2 etc., Tables 13-15) suggests that competitive ability is very specific to the composition of a competing neighborhood in which it is observed. In other words, neither the performance in pure family blocks or in row plots seems to be a good predictor of a family's competitive ability in mixed stands. In general, correlations among competitive abilities under different levels of competition were inconsistent.

It is risky to assume that selections based on the performance in either row or non-contiguous family plots in experiments under intense inter-family competition will perform well in pure family plantations. In this study, correlations of family performances at competition levels C0 (family blocks) and C3 (row-plots) or C4 (non-contiguous family plots) were generally low (except for height).

Families selected as good competitors under test environments may not necessarily perform equally well under operational plantations due to the diversity of environments found in the field. Reports from previous work with different species by Sakai (1961), Lin & Torrie (1968), and Tauer (1975) indicate that responses to competition depend largely on the environment in which the material is tested.

Further comments based on the findings from this experiment are warranted with regard to the genetic testing procedures presently in use:

a) Family differences in competitive ability among unrelated full-sib families of loblolly pine were detected in the nursery at 20 months of age only under conditions in which the subject trees had 3 or 4 unrelated competitors in their immediate neighborhood (Table 11). If we assume that the phenomenon of inter-family competition in field plantations is similar to that observed in the nursery, it may be of little importance as a source of bias in the evaluation of families under standard procedures of genetic testing because of the wide spacing and the plot shape. For example, genetic tests using six-tree row-plots at a 9' x 9' spacing as recommended by the North Carolina State University-Industry Cooperative Tree Improvement Program will be virtually unaffected by inter-family competition on an average site, provided that some precautionary measures be adopted in the near future. In six-plant row plots (or longer) the intensity of inter-family competition becomes similar to the level C2 (two unrelated competitors) of this study, which did not show family differences in competitive ability. However, if trees were allowed to compete, a complicating factor may arise under normal testing procedures because all trees in a plot will have two unrelated competitor families in common. This will generate an additional source of variation which is due to the competitive interactions with two specific families. Therefore, thinning in genetic tests may be more important than previously thought. From the statistical point of view, row plants laid out in parallel to a fertility gradient are preferable to square plots in order to reduce the effects of soil heterogeneity (Christidis, 1931) when such gradient is apparent; if the site were extremely variable with no apparent fertility gradient, then non-contiguous family plots should be considered. In all cases the stand should be thinned in order to reduce the effects of inter-family competition. The family performance in square plots, where only the central trees are measured, will have a minimum of inter-family competition to interfere with the estimate of family variance. Therefore, heritability estimates under this condition will be closer to their true value than when inter-family competition exists. With few exceptions, families ranking among the top 20% in growth traits in this study were generally consistent through different inter-family competition levels. Thus, any plot design would reveal most of the families which, in general, would perform well. However, while families selected in pure stands represent those that perform well in family block plantations, those selected under different intensities of inter-family competition may not represent families that perform well under competition in mixed stands because of the possible specificity of the environment for the expression of inter-family competitive ability.

b) In short-term genetic tests with close spacing (Franklin, 1979, 1983) inter-family competition starts much earlier than in usual tests. Its effect in inflating the genetic variance may be substantial, relative to the low genetic variance observed during the first few years (Franklin, 1983). Therefore, family performance in short-term genetic tests with close spacings becomes strongly influenced by inter-family competition. Since competitive ability does not seem to be heritable nor to correlate with growth traits, selection based on such genetic tests may not be an effective way to increase genetic gain.

CONCLUSIONS

One- and two-year-old loblolly pine full-sib families differ in average competitive ability, especially for stem volume and dry weight, but less so in height growth. This is as one would expect because, among all traits analyzed in this study, height growth is the least affected by competition.

Although estimates of heritability per se were not possible with the mating design used, low intraclass correlations for competitive ability in spite of the possible presence of non-additive genetic variance suggest that competitive ability has a very low heritability.

Intraclass correlations for traits other than height increased substantially at high competition levels at 20 months of age. This suggests that heritability figures based on measurements in populations under intense competition tend to be grossly overestimated because of the involvement of a non-genetic effect, common to all individuals within families in a specific environment.

Phase changes characterized by the patterns of additive genetic variance and heritability during the stand development can be induced at very early ages by planting at a spacing as close as 8 cm x 8 cm. Changes from juvenile to mature genotypic phase and from mature to codominant-suppression phase as described by Franklin (1979) occur much faster under low levels of inter-family competition and take longer as the levels of inter-family competition increase. This suggests that genotypically heterogeneous populations are more buffered against changes in the environment (increasing crowding effect due to the increase in plant size at the same spacing), probably because of the diversity of niches that each family is capable of exploring for its subsistence under harsh conditions. When the individuals are more genotypically similar, a larger proportion of the population will compete with similar aggressiveness for similar niches. Thus, under restricted space, the individuals in genotypically homogeneous families can either stagnate or continue to grow all at approximately the same pace, depending on the importance of the factor that is in short supply for their growth. This results in higher variances among families very early in the development of the stand.

Individual families reacted differently to competition in height growth and they seemed to be differentially vulnerable to the effects of inter-family competition at different stages of growth.

Selections in populations under intense inter-family competition in short-term genetic tests are not likely to increase genetic gain, since a substantial portion of the variance among families is due to competition and competitive ability does not seem to be heritable or to correlate with growth traits under inter-family competition levels other than the one in which it is observed.

Family performance under mixed stand condition gives an indication of its competitive ability but it seems to be specific for the level of inter-family competition in which it is observed, and possibly to the specific environment of the test site. In order to confirm the specificity of the environment for the expression of family competitive ability, a series of experiments, similar to this but using only the families that showed inter-family competition effects should be established in several different sites.

Although tests under different inter-family competition levels did not substantially change the ranks in growth of most families, rank changes for some families were quite substantial. Therefore, we must be aware that not all good competitors are fast growers or perform as well when planted in family blocks, and not all fast growers in family blocks are good competitors in mixed stands. This indicates that growth rate can be positively or negatively affected by inter-family competition but the sign and magnitude of the change cannot be predicted on the basis of the family performance in pure stand conditions.

Inter-family competition does not seem to constitute a problem under standard genetic testing procedures in loblolly pine if tests were properly thinned.

Row plots running parallel to a fertility gradient should be used in preference to square plots in order to reduce the effects of soil heterogeneity in sites which present such characteristics. If the site is extremely variable with no apparent gradient in fertility, then non-contiguous family plots should be used in spite of the difficulty in the establishment and monumentation of individual trees.

In all cases thinnings will be necessary to reduce inter-family competition. In order to allow for repeated thinnings, row-plots should be established with a larger number of trees (longer row-plots) but, in the case of non-contiguous family plots, a more elaborate design such as the random non-contiguous plots in interlocking field layouts (Libby & Cockerham, 1980) should be used.

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APPENDIX

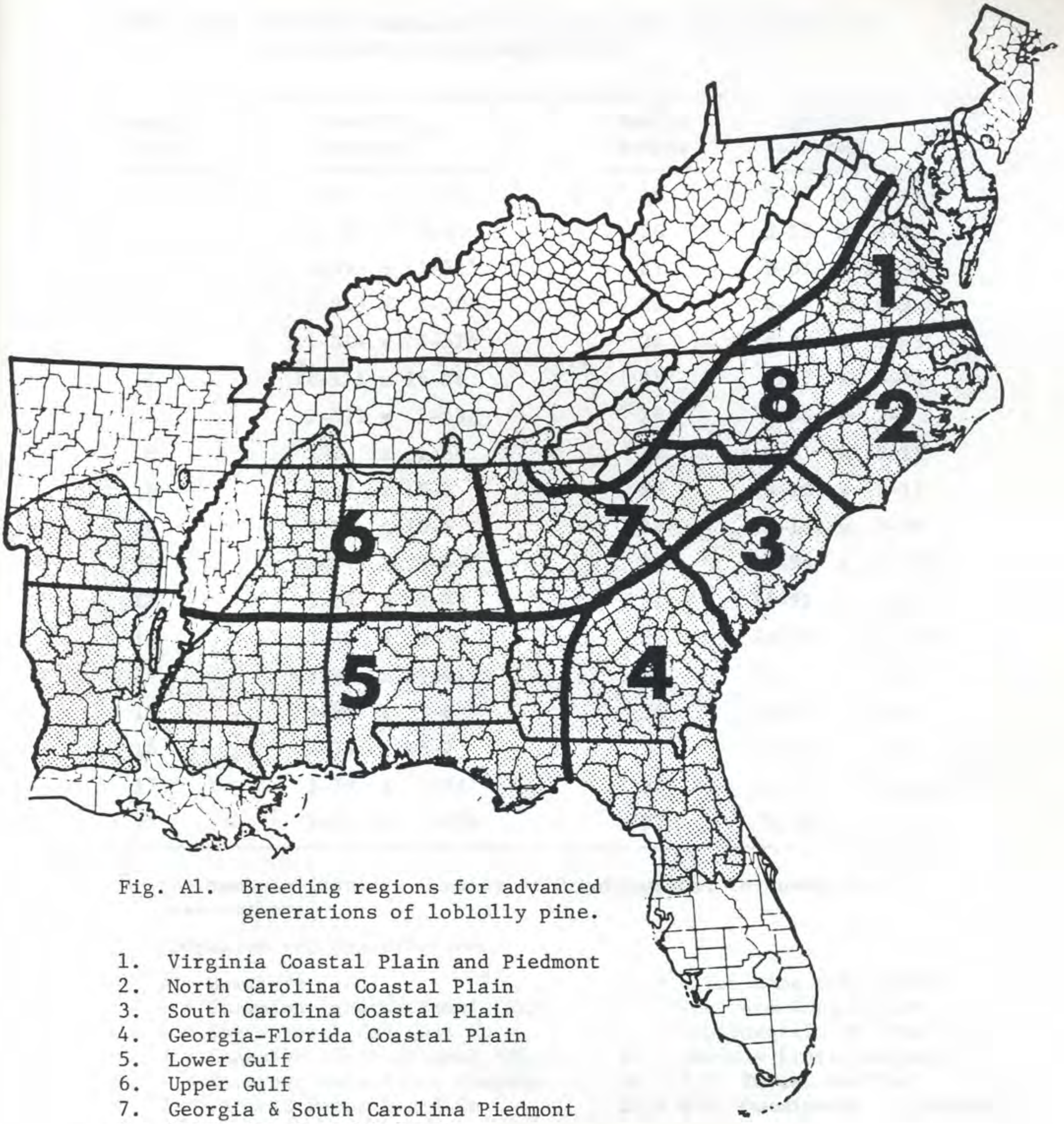

Fig. A1. Breeding regions for advanced generations of loblolly pine.

1. Virginia Coastal Plain and Piedmont
2. North Carolina Coastal Plain
3. South Carolina Coastal Plain
4. Georgia-Florida Coastal Plain
5. Lower Gulf
6. Upper Gulf
7. Georgia & South Carolina Piedmont
8. North Carolina Piedmont

(from: North Carolina State University-Industry Cooperative Tree Improvement Program).

Table A1. Full-sib families of loblolly pine included in the inter-family competition study.

Family Number	Specific Crosses [a]	Family Number	Specific Crosses
1	1-14 x 5-33	19	3-55 x 11-76
2	1-501 x 5-40	20	5-15 x 1-11
3	1-512 x 1-523	21	5-51 x 15-35
4	1-513 x 1-509	22	6-9 x 6-2
5	1-514 x 1-516	24	6-33 x 9-43
6	16-111 x 16-58	25	7-77 x 5-41
7	1-521 x 1-532	26	7-56 x 7-2
8	3-7 x 1-64	27	9-9 x 9-15
9	3-13 x 18-1	28	9-10 x 9-12
10	3-17 x 10-5	29	16-164 x 9-26
11	3-24 x 3-4	30	14-89 x 14-509
12	3-26 x 3-35	31	14-92 x 14-31
13	3-30 x 3-20	32	14-508 x 14-510
14	3-34 x 18-41	33	15-9 x 1-10
15	3-36 x 3-6	34	15-33 x 10-27
16	3-38 x 18-2	35	15-37 x 5-21
17	3-39 x 3-33	36	16-22 x 16-114
18	3-43 x 1-524	37	1-515 x 1-527

[a] The numbers indicate Company or Organization, followed by the tree number.

Companies and Organizations:

1 = Bowaters
3 = Champion International (SC)
5 = Continental Can (Ga)
6 = Champion International (NC)
7 = International Paper Company
9 = Federal Paper Board Co.
10 = Union Camp Corporation
11 = Westvaco Corporation
14 = Continental Can (Va)
15 = Georgia Kraft Company
16 = N.C. Forest Service
18 = S.C. Commission of Forestry

Table A2. Provenances of the parent trees involved in the crosses.

Tree	County, State	R[a]	BR[b]	Tree	County, State	R	BR
1-10	Meriwether, GA	P	7	3-20	Newberry, SC	P	7
1-11	Meriwether, GA	P	7	3-24	Newberry, SC	P	7
1-14	Barrow, GA	P	7	3-26	Newberry, SC	P	7
1-64	Cherokee, GA	P	7	3-30	Laurens, SC	P	7
1-501	Laurens, SC	P	7	3-33	Laurens, SC	P	7
1-509	Newberry, SC	P	7	3-34	Laurens, SC	P	7
1-512	Newberry, SC	P	7	3-35	Laurens, SC	P	7
1-513	Richmond, NC	P	8	3-36	Newberry, SC	P	7
1-514	Kershaw, SC	P	7	3-38	Edgefield, SC	P	7
1-515	Kershaw, SC	P	7	3-39	Saluda, SC	P	7
1-516	Kershaw, SC	P	7	3-43	Fairfield, SC	P	7
1-521	Newberry, SC	P	7	3-55	Newberry, SC	P	7
1-523	Fairfield, SC	P	7	5-15	Saluda, SC	P	7
1-524	Fairfield, SC	P	7	5-21	Lincoln, GA	P	7
1-527	Union, SC	P	7	5-33	Richmond, GA	C	4
1-532	Chesterfield, SC	P	7	5-40	Newberry, SC	P	7
3-4	Newberry, SC	P	7	5-41	Laurens, SC	P	7
3-6	Newberry, SC	P	7	5-51	Jones, GA	P	7
3-7	Newberry, SC	P	7	6-2	Warren, NC	P	8
3-13	Newberry, SC	P	7	6-9	Warren, NC	P	8
3-17	Laurens, SC	P	7	6-33	Durham, NC	P	8

Table A2. Provenances of the parent trees involved in the crosses. (Page two)

Tree	County, State	R [a]	BR [b]	Tree	County, State	R	BR
7-2	Georgetown, SC	C	3	14-508	Amelia, VA	P	1
7-56	Williamsburg, SC	C	3	14-509	Amelia, VA	P	1
7-77	Newberry, SC	P	7	14-510	Nottoway, VA	P	1
9-9	Anson, NC	P	8	15-9	Heard, GA	P	7
9-10	Anson, NC	P	8	15-33	Jasper, GA	P	7
9-12	Anson, NC	P	8	15-35	Jones, GA	P	7
9-15	Anson, NC	P	8	15-37	Monroe, GA	P	7
9-26	Montgomery, NC	P	8	16-22	Vance, NC	P	8
9-43	Richmond, NC	P	8	16-58	Wake, NC	P	8
10-5	Jasper, SC	C	3	16-111	Durham, NC	P	8
10-27	Hancock, GA	P	7	16-114	Franklin, NC	P	8
11-76	Saluda, SC	P	7	16-164	Anson, NC	P	8
14-31	Chesterfield, VA	P	1	18-1	Edgefield, SC	P	7
14-89	Franklin, NC	P	8	18-2	Greenwood, SC	P	7
14-92	Franklin, NC	P	8	18-41	Fairfield, SC	P	7

[a] R = Physiographic regions (P = Piedmont; C = Coastal)

[b] BR = Breeding regions adopted by N.C. State Univ.-Industry Cooperative Tree Improvement Program.

Table A3. Ratios of mean squares of family effects over the experimental errors (F-tests) for height growth under different levels of inter-family competition from 3 months (June 1983) to 20 months (Nov. 1984) of age.*

Competition Levels [a]	Measurement Dates						
	June 1983	Aug. 1983	Oct. 1983	Apr. 1984	June 1984	Aug. 1984	Nov. 1984
C0	5.88	6.50	6.44	7.45	4.30	4.52	3.83
C1	8.31	6.91	7.33	7.39	3.81	3.78	3.30
C2	7.85	6.76	7.27	8.30	4.88	5.19	3.77
C3	6.89	7.27	6.31	8.33	5.92	7.35	4.48
C4	8.28	11.61	8.00	9.72	6.85	8.00	5.67

* All values are significant at the 1% level.

[a] C0...C4 = inter-family competition levels having from zero to four unrelated competitors.

Table A4. Ratios of mean squares of family effects over experimental errors for traits at 20 months of age.*

Competition Levels [b]	Traits [a]				
	D	W	PW	V	SV
C0	2.56	2.44	3.14	2.92	1.70
C1	3.37	3.74	2.94	3.34	1.63
C2	2.50	2.76	3.71	2.81	2.28
C3	6.11	6.58	8.58	6.21	3.87
C4	6.22	5.98	6.70	6.08	2.80

* All values are significant at the 1% level.

[a] D = stem diameter
W = plot mean dry weight
PW = total plot dry weight
V = stem volume index
SV = survival percentage.

[b] C0...C4 = inter-family competition levels having from zero to four unrelated competitors.

Table A5. Families in the upper and lower 20% in rank in height growth at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Height Growth											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	5	20	26	2	7	9	19	36	16	29	24	32
C1	5	2	18	20	26	21	16	29	8	30	25	24
C2	5	2	21	8	27	26	36	12	32	30	16	24
C3	18	2	5	22	26	27	36	10	21	25	24	30
C4	18	5	2	26	37	9	16	30	19	24	32	25

Table A6. Families in the upper and lower 20% in rank in stem diameter at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Diameter											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	5	18	20	9	2	7	8	16	25	24	32	29
C1	18	2	5	27	20	28	16	29	30	25	24	8
C2	2	5	18	27	35	21	37	19	16	12	24	30
C3	18	2	28	27	5	33	8	24	10	32	25	30
C4	18	2	5	9	7	4	29	10	30	24	25	32

Table A7. Families in the upper and lower 20% in rank in plot mean dry weight at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Plot Mean Dry Weight											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	5	2	7	20	9	27	25	24	32	29	36	16
C1	2	18	5	20	26	21	29	16	19	30	25	24
C2	2	5	21	35	27	8	32	14	16	12	30	24
C3	2	18	5	27	26	22	36	10	32	24	25	30
C4	18	2	5	9	7	37	14	19	30	24	32	25

Table A8. Families in the upper and lower 20% in rank in total plot dry weight at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Total Plot Dry Weight											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	2	5	7	9	27	20	32	24	30	29	36	16
C1	2	18	5	7	20	26	11	24	29	30	16	25
C2	2	5	21	18	27	7	36	30	32	14	25	24
C3	2	18	5	26	27	28	29	36	32	24	25	30
C4	18	2	5	9	7	4	19	14	32	30	24	25

Table A9. Families in the upper and lower 20% in rank in stem volume at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Stem Volume											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	5	20	9	18	2	26	25	36	24	16	32	29
C1	18	2	20	5	27	26	37	29	30	8	25	24
C2	2	5	35	27	18	21	37	14	16	12	30	24
C3	18	2	27	28	22	5	36	32	10	24	25	30
C4	18	2	5	9	7	4	29	19	30	24	25	32

Table A10. Families in the upper and lower 20% in rank in percent survival at 20 months of age under each inter-family competition level.

Competition Levels	Ranks in Percent Survival											
	1	2	3	4	5	6	23	24	25	26	27	28
C0	10	7	2	27	5	26	11	29	14	35	16	36
C1	4	18	7	26	2	28	11	20	30	25	29	16
C2	7	5	18	4	37	2	36	27	34	29	14	25
C3	2	4	5	18	28	16	19	29	22	25	34	30
C4	4	9	18	2	7	5	33	35	30	8	25	24