A review of the literature, clearly indicated the degree of dominance ranging from partial to over dominance with the highest degree of dominance being 3.64. Present grouping demonstrated that group 1 and 2 were in agreement with the previous findings, whereas group 3 and 4 were the consequence of some abnormality. GARDNER (1963) indicated that in early generations, the values tended to be overestimated because of the upward bias due to the repulsion phase of linkage. In later generations, the linkage was broken due to recombinations and a low degree of dominance was obtained. Keeping this factor and also the sampling errors in view, group 1 indicated partial dominance and group 2 over dominance. Groups 3 and 4 gave higher values. Now considering methodwise it can be clearly explained that HAYMAN (1954) was the only method which was lying in group 1 or 2. Hence the HAYMAN numerical approach was considered to be the best method.

Summary

The present investigation was planned to compare the relative efficiency of diallel and its modifications. Using six exotic and six indigenous varieties of barley the following experiments were conducted (a) Full diallel involving eight parents, (b) Partial diallel of twelve parents and (c) Triallel of six parents. The data were analysed following (a) GRIFFING, 1956 (b) KEMPTHORNE and CURNOW, 1961 (c) PONNUSWAMY, 1971 and (d) HAYMAN, 1954 approaches. For estimation of gca effects, it was found that half diallel and quarter diallel were as efficient as full diallel. The efficiency of partial diallel I (n = 12, s = 5), II (n = 12, s = 3), III (n = 8, s = 5) and IV (n = 8, s = 3) was far below those of full, half and quarter diallel. From among the partial diallels, however, PD III was the most efficient. In triallel analysis the ranking pattern of the parents on the basis of gca effects was not similar to that of full diallel. For estimation of sca effects also half and quarter diallels were similar to the full diallel. Considering average degree of dominance as a criterion of comparison, HAYMAN's approach was found the best followed by quarter diallel and partial diallel for grain yield. The situation was, however, different for different characters. The estimates of genetic parameters were discussed in view of their significance in barley breeding.

Key words: Half diallel, partial diallel, quarter diallel, triallel, degree of dominance, rank correlations.

Zusammenfassung

Zum Vergleich der relativen Effizienz des Diallels und seiner Modifikationen wurden ein Voll-Diallel mit 8 Sorten, partielle Diallele mit 12 Sorten und ein Triallel mit 6 Sorten erstellt, wobei die Modelle von Griffing, Kempthorne und Curnow, Ponnuswamy und Hayman verwendet wurden. Es hat sich dabei herausgestellt, daß ein Viertel- und ein Halb-Diallel genau so effizient sein können wie ein Voll-Diallel. Dagegen ergaben partielle Diallele weniger gute Schätzungen. Zur Schätzung des Dominanzgrades des Ertrages war das Modell von Hayman den anderen Überlegen.

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Genotype x Environment Interaction and Genotypic Stability in Loblolly pine*

III. Heterosis and heterosis X environment interaction

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Introduction

Because forest trees must withstand the vagaries of changing environments for many years, tree breeders have been deterred from exploiting chance heterotic combinations among genotypes which may otherwise have very restricted genetic bases. However, heterosis has been exploited or is of great potential utility at some phases of a tree improvement program. The most obvious is when inter-specific and inter-racial crosses prove far superior to intra-population selections. As examples, hybrids of European larch X Japanese larch (ROHMEDER, 1963) and of *Pinus taeda* X *P. rigida* (HYUN, 1969) are superior to either pair of parent species and are being commercially produced. The superiority of inter-racial crosses between Swedish and central European races of Norway Spruce (NILSSON and ANDERSON 1970, NILSSON 1974) is also well documented. Some heterosis upon inter-racial crossing in Douglas fir has been reported by ORR-EWING (1969) and, to a lesser degree, in loblolly pine (WOESSNER 1972).

Loblolly pine has a wide natural range and the results of Southwide seed source study (WELLS and WAKELY 1966) in-

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dicated the existence of divergent geographic races within the species. MOLL *et al.* (1965) have reported little heterosis resulting from wide crosses in maize. Furthermore, some workers on other plants and animals have reported that heterosis is sometimes expressed under certain environmental conditions but not under others (GRIFFING and ZSIROS 1971).

The investigations reported here revolved around the ideas above and were aimed at providing answers to the following questions:

1. Do inter-racial crosses of loblolly pine exhibit heterosis?
2. If heterosis is found, how stable is it over different environments?
3. Is there any relationship between the amount of heterosis and levels of genetic divergence?

Statistical models and data analysis

Because of seed shortage, open-pollinated progeny were planted only in Halifax County, N.C. and at a few other locations. Heterosis, when calculated as the deviation of the F, from the mean of the corresponding open-pollinated progeny, was studied only with the planting in this county. The model used was:

$$H_{ij} = F_{1ij} - \frac{1}{2}(O.P._{\cdot i} + O.P._{\cdot j}) \text{ where}$$

H_{ij} is the heterosis exhibited by the cross between the i^{th} population and the j^{th} population. $\bar{F}_{1ij}$ is the mean of all crosses between the i^{th} and j^{th} populations. $O.P._{\cdot i}$ and $O.P._{\cdot j}$ are means of the open-pollinated progeny from the i^{th} and j^{th} populations respectively.

For the study of heterosis X environment interaction, another definition of heterosis was adopted as follows:

$$\hat{h}_j = \bar{X}_{wj} - \bar{X}_{lj}$$

where $\hat{h}_j$ is the expression of heterosis in the j^{th} location. $\bar{X}_{wj}$ and $\bar{X}_{lj}$ are the means, in the j^{th} location of wide crosses and local (within orchard) crosses respectively. If we further define the environmental index as $\bar{X}_{lj} - \frac{1}{2}\hat{h}_j$, then heterosis X environment interaction, gh, can be expressed as:

$$gh = \bar{X}_{wj} - \hat{h}_j - \hat{h}_j/p - (X_{lj} - \hat{h}_j)$$

where p is the number of locations. The linearity of heterosis with the environmental index can therefore be measured by $b_h = [(X_{lj} - h_j).h_j]/(X_{lj} - h_j)^2$ while that of heterosis X environment interaction can be measured by

$$b_{gh} = \Sigma[\{(\bar{X}_{lj} - \tfrac{1}{2}\hat{h}_j)\}.\{\bar{X}_{wj} - \tfrac{1}{2}\hat{h}_j - \hat{h}_j/p - (\bar{X}_{lj} - \tfrac{1}{2}\hat{h}_j)\}]/\Sigma(\bar{X}_{lj} - \tfrac{1}{2}\hat{h}_j)^2$$

Results and Discussion

Calculated percent heterosis figures are shown in ***table*** 1. There were *a* few cases of negative heterosis. There was some indication that the greater the genetic divergence, the greater the heterosis. For example, height growth of local crosses grown in halifax County, N.C. showed average heterosis of 1.71% while these of intermediate and wide crosses averaged 3.16% and 8.35% heterosis respectively.

For studying consistency of heterosis across environments, it was necessary to adopt a different method of calculating heterosis since open-pollinated progeny were not planted at some locations. Heterosis, in this case, was calculated as percent of within orchard cross mean at each location. Four family sets were chosen for this study and regressions of heterosis on environmental quality were carried out as shown graphically in ***figure*** 1 and by the regression coefficients on ***table 2.*** It can be clearly seen from ***figure 1*** and ***table*** 2 that there is no relatioship between heterosis and environmental quality.

Studies in corn (MOLL, personal communication) and *Arabidopsis* (GRIFFING and ZSIROS 1971) have indicated that heterosis can be linearly related to environmental quality. Depending on whether the observed regression coefficient is above or below 1.0 the breeder may choose to exploit heterosis in the good or poor environments respectively. Results from the present investigations show that such linear trends do not exist for loblolly pine although it is important to note that measurement of heterosis in this study was not very sensitive.

Heterosis observed from inter-racial (wide) crosses can be explained by one or a combination of genetic mechanisms. CRESS (1966) has developed the relationship between heterotic response and genetic diversity in terms of gene frequency differences in the parental populations. There

Table 2. — Mean height growth (ft), heterosis (percent of within orchard cross means) and regression coefficients of heterosis b_h) based on performance at nine locations.

Cross	Mean Mean height	Heterosis	b_h
Albemarle x Louisiana	10.56	—5.37	.052
Albemarle × Texas	10.81	—3.27	—.062
Albemarle x Westvaco	10.82	—3.18	.024
Weyerhaeuser × Bowaters	10.90	3.16	.009

Table 1. -- Heterosis (percent of mid open-pollinated progeny values) in height growth of local, intermediate and wide crosses based on field performance in Halifax County, N.C.

Males	Females		Mean of cross	Cross type mean
	Albemarle	Weyerhaeuser	cross type	
Albemarle	—	3.34	3.34 Local	
Westvaco	—2.23	—	—2.23 Local	
Union Canmp	4.03	—	4.03 Local	
				1.71
Continental Can	—.1.12	4.98	1.93 Intermediate	
Kimberly-Clark	2.20	—	2.20 Intermediate	
Bowaters	14.49	4.68	9.56 Intermediate	
Champion	—	—1.05	—1.05 Intermediate	
				3.16
Louisiana	14.15	5.33	9.74 Wide	
Texas	8.77	5.16	6.96 Wide	
				8.35

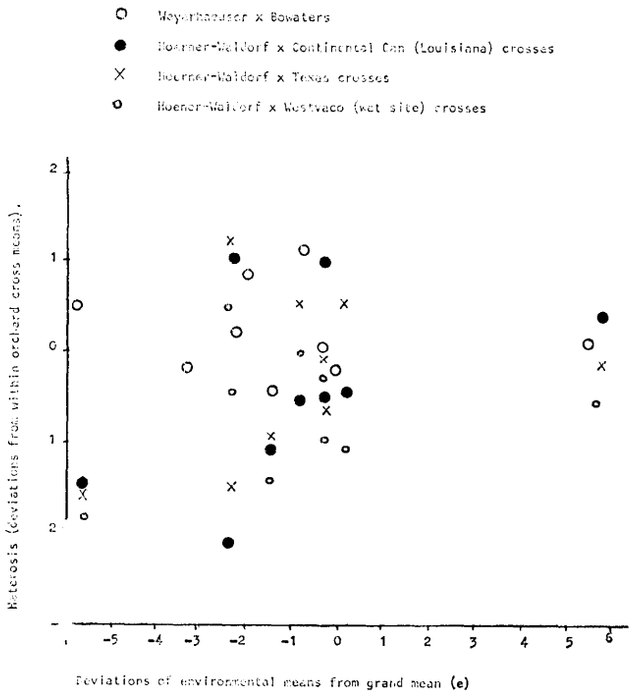

Figure 1. — Graphical presentation of the relationship between heterosis and the environmental index.

are reports for other crops in which heterosis was observed to increase as the level of genetic diversity increased. Two well known examples are the wide cross study in corn (MOLLET *et al.* 1962, 1965) and the inter-genomic crosses study in tobacco (MATZINGER and WERNSMAN 1967).

In the present study with loblolly pine, wide crosses exhibited average heterosis of 8.35%. This is slightly less than the 10% heterosis observed for inter-genomic crosses in tobacco and much less than the 25% heterosis observed in the corn wide cross studies mentioned above. It must, however, be realized that forest trees are more heterozygous than corn or tobacco and have not been subjected to any selective pressures other than the slow process of natural selection. For these reasons, less genetic divergence can be expected in trees than in the two crops.

Theoretical arguments for expected heterosis of interracial crosses without invoking genetic differentiation were presented by CROW (1952) who predicted maximum heterosis of 5% when complete dominance is present and lesser values for partial dominance or additive gene action. The small amount of heterosis observed for loblolly pine wide crosses could therefore be due to non additive gene effects rather than differences in gene frequencies.

Since loblolly pine generally outcrosses, the classical hypotheses of dominance and overdominance requires additional assumption of isodirectional gene fixation in the different populations. Probably the most realistic explanation of the observed heterosis is physiological mosaic dominance (CROW 1952) whereby alleles differ or are complementary in action. In tree breeding, this has been referred to as 'combinational heterosis' and many examples are known. For example, Norway spruce inter-racial hybrid (NILSSON 1974) combines the cold hardiness genes of the northern race and fast growth genes of the southern race. In the present investigation, crosses of drought hardy loblolly from Texas with fast growing loblolly from the east coast could exhibit sizeable heterosis if tested in dry sites. Limitations in the field design, however, precluded such analysis in the present investigation.

Summary

Average heterosis of 8.35% was observed for height growth in the wide cross progenies. A slight trend was observed between heterosis and the degree of genetic (geographic) divergence. No linear relationship was found between heterosis and environmental quality; suggesting that selecting in good environments may be just as reliable as selecting in less favourable environments.

Key words: Pinus taeda, wide crosses, heterosis, height growth.

Zusammenfassung

Nach Kreuzung von geographisch weit auseinander liegenden Provenienzen bzw. Rassen von *Pinus taeda* konnte bei den Nachkommenschaften eine Zunahme des Höhenwachstums um durchschnittlich 8,35% festgestellt werden. Hierbei war mit zunehmender Entfernung der Herkunftsorte ein gewisser Trend zu höherer Wachstumsleistung zu erkennen.

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