ISOZYME HETEROZYGOSITY, PHENOTYPIC FAMILY STABILITY, AND INTER-FAMILY COMPETITION AMONG SEEDLINGS OF LOBLOLLY PINE

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Abstract--Five open-pollinated families of loblolly pine were used to produce a seedling population, which was used to establish a competition diallel containing 20 family combinations. Each subject family was grown in combination with all other families at four subject family to competitor ratios (i.e., 16.67:83.33, 33.33:66.67, 83.33:16.67 and 100.0:0.00). The change in competitor genotype and competitor frequency significantly influenced subject tree growth. Twenty-four enzymes representing 41 isozyme locus were examined per mother-tree and 16 enzymes representing 19 isozyme loci were examined in the progeny of each mother-tree. Percent heterozygosity per mother-tree, mean percent heterozygosity per mother-tree family and percent heterozygosity per isozyme loci per mother-tree family were correlated to six-month-old seedling measurements obtained from the competition diallel to test the relationship between heterozygosity, fitness and variability. Twelve correlations with individual isozyme heterozygosity were significant at the 0.05 level (four more than expected by chance). Relationships between isozyme heterozygosity, phenotypic stability and competition are discussed.

Additional keywords: horizontal starch gel electrophoresis, genotype x environment interactions, balancing selection, Pinus taeda.

Competition is a biological interaction that occurs when the combined demands of all individuals within a given area exceeds the supply of necessary resources. This definition implies that competitors, within a given environment, act as biological agents limiting each neighboring individual's (i.e. the subject tree) growth. Competition can be viewed as a genotype by genotype interaction nested within the genotype by environment interaction from the equation:

$$\sigma^2_P = \sigma^2_G + \sigma^2_E + \sigma^2_{GE}.$$

Where, the genotype by environmental interactions is partitioned into genotype by climatic and edaphic factors and into genotype by biological factors. The biological factors include both interspecific and intraspecific interactions. The genotype by biological factors interaction, in particular,

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the intraspecific interactions, can be intentionally manipulated so that within a single physical environment numerous biological environments are created through combinations of various genotypes. This paper is concerned with the intentional manipulation of intraspecific, inter-family interactions.

Forest trees, unlike most domesticated crops, have to be adapted to a wide range of environments across space and time. Long generation intervals, wide geographic ranges, yearly climatic changes and successional changes all contribute to the environment of a single tree. Phenotypic stability in genetically improved material is a desirable trait. Phenotypic stability is defined as a consistency of performance, as measured by "yield", across a range of environmental conditions. Phenotypic (yield) stability has been important to corn and wheat breeders, leading to the development of double cross hybrids, bulk populations and pure line mixtures. Jones (1985) states that it is the consistency in yield across many locations and not the individual superiority at any one location that led to the acceptance of double cross hybrids over single cross hybrids. Phenotypic stability can be achieved through 1) phenotypic plasicity, 2) individual buffering relying on heterozygosity or 3) population buffering relying on genotypic mixtures. Creation of variable environments through competitive interactions, and subsequent testing of specific genotypes may allow for the selection of phenotypic stability in long-lived forest species.

Hamrick et al. (1981) has reported that trees contain significantly more isozyme variability and heterozygosity than most herbaceous plants. Strauss and Libby (1984) have suggested that balancing selection in a fluctuating environment may favor heterozygotes and thus may act to maintain genetic variability in forest populations. Ledig et al. (1983) described three relationships between heterozygosity and forest tree ontogeny. They were, with increased heterozygosity, 1) fitness should increase (as measured by growth), 2) phenotypic variability (as measured by the coefficient of variability) should decrease or phenotypic stability increase and 3) longevity should increase.

Working with knobcone pine (Pinus attenuata Lem.), Strauss and Libby (1984) reported a weak but significant relationship between heterozygosity and growth in crossbred progeny. This was particularly true in situations of fluctuating climatic conditions. Strauss and Libby (1984) also reported that a few polymorphic loci were responsible for the relationship between growth and heterozygosity, though no single locus could solely explain variation in growth. Likewise, Ledig et al. (1983) reported finding a few significant but inconsistent relationships between single locus heterozygosity and growth, and no significant relationships between heterozygosity and the coefficient of variability. Mitton et al. (1981) reported inconclusive results in the association of heterozygosity and growth in ponderosa pine (Pinus ponderosa Law.), lodgepole pine (Pinus contorts Dougl.) and aspen (Populus tremuloides Michx.). Heterozygosity was positively associated with growth in only one of the three species. Associations between heterozygosity and variability were inconsistent, being positive in two species and negative in one. Rajora (1986) found positive and negative correlations between heterozygosity and both rust resistance and growth variables in Populus hybrids.

Utilizing information from a seedling competition diallel study, this paper considers the relationship between isozyme heterozygosity and seedling height and shoot dry weight as expressed under various levels of inter-family competition.

MATERIALS AND METHODS

Competition Diallel

Seedlings from five open-pollinated families of loblolly pine (*Pinus taeda* L.) were used to establish a competition diallel containing 20 family combinations. The five families were S6PT6, S6PT3, S2PT10, S3PT7 and S4PT6. Each family was grown in combination with all other families as both a competitor and a subject family. Competitor frequency was varied in all combinations. The subject family to competitor family frequencies were 100.0:0.00, 83.33:16.67, 33.33:66.67 and 16.67:83.33. Competitor frequency levels per subject family/competitor combinations were replicated four times within a single greenhouse bench. Within each plot the competitor seedlings were four centimeters from the subject seedlings and the subject seedlings were 10 centimeters apart (Fig 1). A single border row surrounded the entire experiment. See Tuskan (1984) and Tuskan and van Buijtenen (1986a) for further details.

After 166 days the central subject seedlings were destructively sampled. Seedling height (mm) and shoot dry weight (mg) were recorded. Competitor genotypes had begun to influence subject seedling height at 72 days, and after 166 days mean subject family growth varied significantly ($a < 0.05$) by competitor families (Tuskan 1984, Tuskan and van Buijtenen 1986a). Subject families and competitor families were classified as to their competitive ability and competitive influence, respectively.

Competitive effects for each family combination at each competitor frequency level were also calculated for subject seedling height and shoot dry weight. Competitive effects for a binary family combination were calculated as the sum of the mixed plot yields divided by the sum of the pure plot yields. Within a population, the mean competitive effect is expected to equal one (van Buijtenen and Tuskan 1986).

Starch Gel Electrophoresis

Standard horizontal starch gel electrophoresis procedures (Conk le et al. 1982, Adams and Joly 1980, Jech and Wheeler 1984, and Cheliak and Pitel 1984) were followed using three buffer systems. Table 1 contains a list of enzymes, enzyme abbreviations and buffer systems used in this study. Megagametophytic tissue (1N) was used to characterize the maternal genotype and embryonic tissue (2N) was used to characterize the progeny. Twenty-four enzymes representing 41 isozyme loci were scored for each mother-tree (i.e. acid phosphatase (ACP), aconitase (ACO), adenylate kinase (AK), aldolase (ALD), catalase (CAT), diaphorase (DIA), fumerase (FUM), glucose-6-P-dehydrogenase (G6PD), glucose dehydrogenase (GLUDH), glutamate dehydrogenase (GDH), glutamic oxyalocecetic transaminase (GOT), glyceraldehyde dehydrogenase (GLYDH), hexokinase (HK), isocitric dehydrogenase (IDH),

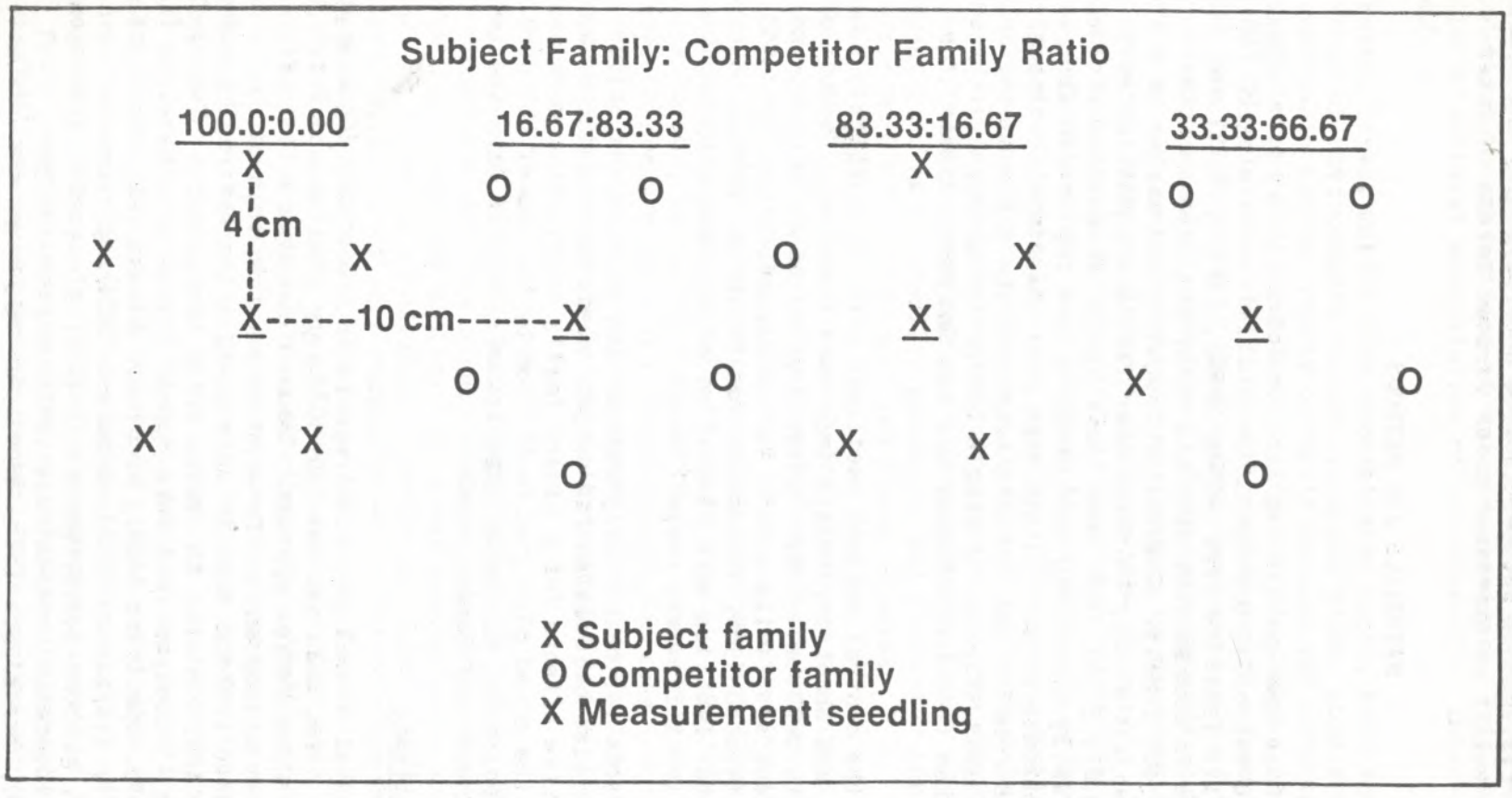

Figure 1. Representation of a single, randomized plot.

TABLE 1. ISOZYME DESCRIPTIONS INCLUDING ENZYME COMMISSION NUMBERS, BUFFER SYSTEM AND TISSUE TYPE.

Enzyme (Abbreviation)	E.C. Number	Buffer[1] System	Megagametophyte Locus Number	Megagametophyte Number of Alleles	Embryo Locus Number
Acid Phosphatase (ACP)	3.1.3.2	M	1	2	1
			2	2	
Aconitase (ACO)	4.2.1.3	M	1	3	1
Adenylate Kinase (AK)	2.7.4.1	H	1	1	
			2	2	
			3	1	
Aldolase (ALD)	4.1.2.13	H	1	1	
			2	1	2
Catalase (CAT)	1.11.1.6	L	1	1	
Diaphorase (DIA)	1.6.4.3	M	1	1	1
Fumerase (FUM)	4.2.1.2	H	1	1	
Glucose-6-P-Dehydrogenase (G6PD)	1.1.1.49	M	1	2	1
Glucose Dehydrogenase (GLUDH)	1.1.1.47	H	1	1	
Glutamate Dehydrogenase (GDH)	1.4.1.3	L	1	3	
Glutamic Oxyaloacetic Transaminase (GOT)	2.6.1.1	L	1	2	
			2	2	
			3	2	
Glyceraldehyde Dehydrogenase (GLYDH)	1.1.1.29	H	1	2	1
Hexokinase (HK)	2.7.1.1	H	1	2	1
Isocitric Dehydrogenase (IDH)	1.1.1.42	M	1	1	1
Leucine Aminopeptidase (LAP)	3.4.11.1	L	1	1	
			2	2	
			3	2	3
Malate Dehydrogenase (MDH)	1.1.1.37	M	1	2	
			2	2	2
			3	2	3
			4	1	
Malic Enzyme (ME)	1.1.1.40	M	1	2	1
Menadione Reductase (MNR)	1.6.99.2	H	1	1	
			2	2	
			3	1	
6-Phosphogluconate Dehydrogenase (6PGD)	1.1.1.44	M	1	2	1
			2	2	2
Phosphoglucomutase (PGM)	2.7.5.1	H	1	2	1
			2	1	
Phosphoglucose Isomerase (PGI)	5.3.1.9	L	1	2	1
			2	2	2
Phosphomannose Isomerase (PMI)	5.3.1.8	L	1	3	1
Shikimate Dehydrogenase (SKDH)	1.1.1.25	M	1	3	1
Uridine Diphosphoglucose Pyrophosphorylase (UGP)	2.7.7.9	M	1	1	
			2	1	

[1] M – Morpholine-citrate, pH = 6.1, Clayton and Tretiak (1972).
L – Lithium-borate, pH = 8.3, Ridgeway et al. (1970).
H – Histidine-citrate, pH = 7.0, Cheliak and Pitel (1984).

leucine aminopeptidase (LAP), malate dehydrogenase (MDH), malic enzyme (ME), menadione reductase (MNR), 6-phosphogluconate dehydrogenase (6PGD), phosphoglucomutase (PGM), phosphoglucose isomerase (PGI), phosphomannose isomerase (PMI), shikimate dehydrogenase (SKDH) and uridine diphosphosphoglucose pyrophosphoglase (UGP)), and 16 enzymes representing 19 isozymes loci were scored for 40 progeny of each mother-tree (i.e. ACP, ACO, ALD, DIA, G6PD, GLYDH, HK, IDH, LAP, MDH, ME, 6PGD, PGM, PGI, PMI and SKDH). Percent heterozygosity per mother-tree, mean percent heterozygosity per mother-tree family and percent heterozygosity per isozyme loci per mother-tree family were determined for each family in the competition diallel.

Data Analysis

Estimates of heterozygosity were correlated with indicators of fitness and variability using Pearson's correlation coefficient. It was assumed that variables reflecting growth were related to fitness, in that larger trees which suppress or eliminate competitors, or trees which co-exist and complement their competitors would survive and reproduce at a higher frequency. Height and shoot dry weight per mother-tree family were used as indicators of growth while mean competitive effect for height and shoot dry weight per mother-tree family were used as indicators of competitiveness. The coefficients of variability for all fitness variables were used in correlations as inverse indicators of phenotypic stability. Subject family means and coefficients of variability were estimated across competitor genotypes, competitor frequencies and replications, totaling 64 seedlings per estimate.

RESULTS AND DISCUSSION

Isozyme Variability

Sixty-two percent of the isozyme loci were polymorphic in the mother-tree population and 89 percent were polymorphic in the progeny; the average number of alleles per locus was 1.71 (Table 1). The difference between the percent polymorphic loci for the mother-trees and percent polymorphic loci for the progeny reflects sampling error. A greater number of monomorphic loci were scored for the mother-trees. The percent of polymorphic loci for the mother-tree population and the progeny are identical when considering the same loci. The estimates for percent polymorphic loci and number of alleles per locus are consistent with results reported by Hamrick et al. (1981) for other coniferous species. The 16 monomorphic loci in the mother-tree population and the two monomorphic in the progeny were not used in the remainder of the study.

The mean percent heterozygosity did not vary greatly between the mother-trees and their respective progeny (Table 2). The greatest change in heterozygosity occurred with mother-tree S6PT3. The percent heterozygosity in the progeny of S6PT3, and progeny of all other mother-trees, was due to the number of heterozygous loci in the mother-tree and the sampling of gametes in the pollen cloud. The probability of the progeny being heterozygous at a locus which is heterozygous in the mother-tree, regardless of the allelic frequency in the pollen cloud, is 50 percent. If a mother-tree is homozygous at a locus then the probability that the progeny will be heterozygous at that

TABLE 2. PERCENT HETEROZYGOSITY FOR INDIVIDUAL MOTHER-TREES, MOTHER-TREE FAMILIES AND INDIVIDUAL ISOZYMES WITHIN MOTHER-TREE FAMILIES.

	Mother-Tree Family				
	S6PT6	S6PT3	S2PT10	S3PT7	S4PT6
% Heterozygosity per Mother-tree	17.1	43.1	26.8	17.1	19.5
Mean % Heterozygosity per Mother-tree family	19.0	17.9	24.5	22.9	19.5
% Heterozygosity per Mother-tree family for:					
Acp1	0.0	0.0	0.0	0.0	0.0
Aco	29.3	42.1	50.0	31.8	28.9
Ald2	24.4	11.9	10.0	22.7	26.3
Dia	11.1	21.4	43.3	8.3	5.3
Glydh	43.9	57.1	60.0	81.8	36.8
G6pd	14.6	2.4	20.0	59.1	42.1
Hk	0.0	21.7	26.7	16.7	40.0
Idh	0.0	2.4	0.0	0.0	0.0
Lap3	14.6	7.1	10.0	4.5	2.6
Mdh2	2.4	2.4	13.3	54.5	0.0
Mdh3	48.8	21.4	36.7	45.5	31.5
Me	24.4	52.4	36.7	40.9	42.1
6Pgd1	39.0	40.5	36.7	50.0	71.1
6Pgd2	2.4	14.3	23.3	13.6	2.6
Pgi1	0.0	0.0	0.0	0.0	0.0
Pgi2	19.5	0.0	33.3	4.5	34.8
Pgm1	39.0	4.8	10.0	0.0	0.0
Pmi	0.0	0.0	0.0	16.7	13.0
Skdh	7.3	52.6	25.0	9.1	0.0

locus depends upon the frequency of the alternative alleles. Thus, a mother-tree which is homozygous for rare alleles at several loci will have a greater chance of producing a higher percentage of heterozygous progeny than a mother-tree which is heterozygous at the same loci. Examples of mother-trees which are heterozygous for rare alleles are S6PT6 at Pgm1, S6PT3 at Skdh and S3PT7 at Mdh2 (Table 2). In all of these cases the mother-trees produced heterozygous progeny approximately 50 percent of the time.

Indicators of Fitness and Variability

At the end of six months mother-tree families had significantly ($a < 0.05$) different mean heights. Mean heights ranged from 162 mm for S6PT3 to 186 mm for S2PT10 (Table 3). The coefficients of variability for height also varied from 4.75 for S3PT7 to 14.81 for S6PT6. The mean competitive effects for height ranged from .968 for S4PT6 to 1.013 for S6PT6. Mean competitive effects below 1.00 indicate that mixtures containing that particular mother-tree family performed poorer on the average than the sum of the pure plots. Conversely values greater than 1.00 indicate that mixtures containing that particular family did better than the sum of the pure plots.

Values for mean shoot dry weight ranged from 318 mg for S6PT6 to 394 mg for S4PT6 (Table 3). Mean competitive effects for shoot dry weight ranged from 0.878 for S6PT3 to 1.007 for S3PT7. S6PT6 had the highest coefficient of variability for shoot dry weight and for the competitive effect for shoot dry weight, while S3PT7 had the lowest coefficient of variability for both variables.

Subject family performance was significantly influenced by competitor genotype (Tuskan 1984, Tuskan and van Buijtenen 1986a, 1986b). Competitor frequency also influenced subject family performance (Table 4). S2PT10 ranged from having one of the poorest heights in the study, (137 mm with S4PT6 at a 16.67 : 83.33 competitor to subject family ratio) to having the best height in the study (230 mm with S6PT6 at a 16.67:83.33 competitor to subject family ratio).

TABLE 4. SEEDLING HEIGHT FOR SUBJECT FAMILY S2PT10 GROWN WITH ALL COMPETITOR GENOTYPES AND FREQUENCIES.

Competitor Frequency	Competitor Genotype			
	S6PT6	S6PT3	S3PT7	S4PT6
	mm			
0.00	190	190	190	190
16.67	230	180	185	137
66.67	195	171	197	174
83.33	214	169	189	192

Correlations between heterozygosity and indicators of fitness.

Assuming heterozygosity increases fitness and phenotypic stability, then correlations between heterozygosity and indicators of fitness should be

TABLE 3. MEAN HEIGHT, SHOOT DRY WEIGHT AND COMPETITIVE EFFECTS FOR HEIGHT AND SHOOT DRY WEIGHT OBTAINED FROM 6-MONTH-OLD LOBLOLLY PINE SEEDLINGS GROWN IN A COMPETITION DIALLEL.

Mother-tree Family	Height at 166 days(mm)		Shoot Dry Weight (mg)		Competitive Effect[1/] for Height		Competitive Effect[1/] for Shoot Dry Weight	
	Mean[2/]	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
S6PT6	173 A	14.81	318 A	32.56	1.013	9.60	0.991	20.39
S6PT3	162 B	13.13	322 A	19.00	0.979	6.93	0.878	17.06
S2PT10	186 A	12.61	338 A	25.84	1.000	9.32	0.995	17.99
S3PT7	171 A	4.75	343 A	18.56	0.993	3.94	1.007	8.71
S4PT6	176 A	5.70	394 A	19.96	0.968	5.57	0.893	12.79

1/ Competitive Effect = mixture yields divided by pure-stand yields; i.e., $(Y_{ij} + Y_{ji})/(Y_{ii} + Y_{jj})$.

2/ Means connected by similar letters are not significantly different at a < 0.05 as determined by SNK's multiple range test.

positive, while correlations between heterozygosity and indicators of variability should be negative. Though none of the correlations using percent heterozygosity per mother-tree or mean percent heterozygosity per mother-tree family were significant ($a < 0.05$), the correlations between mean percent heterozygosity per mother-tree family and all indicators of fitness and stability reflected the hypothesized relationships (Table 5). The correlations involving height, shoot dry weight and the competitive effects for height and shoot dry weight were positive, while correlations involving the coefficients of variability were all negative.

Correlations involving estimates of heterozygosity for individual isozymes revealed 12 significant ($a < 0.05$) relationships; three with indicators of fitness and nine with indicators of variability (Table 5). The individual isozymes involved were G6pd, Lap3, Mdh3, Me, 6Pgd1, Pgm and Pmi. Eight of the significant correlations occurred with three of the 16 isozymes; **i.e.,** G6pd, Lap3 and Pmi. Nine of the significant correlations displayed the predicted relationships, particularly those involving G6pd and Pmi. The three significant correlations involving indicators of fitness were all positive, as predicted, and six of the nine significant correlations involving indicators of variability were negative.

Competitor genotypes and frequencies were used in this study to rank mother-tree family performance in various competitor environments. The extreme responses are: 1) a U-shaped curve, indicating superior performance in a few environments and inferior performance in others; and 2) a bell-shaped curve, indicating average performance across environments (Allard 1961). Based on the relationship between heterozygosity and phenotypic stability we expected U-shaped curves for more homozygous progeny and bell-shaped for more heterozygous progeny. Mother-tree family S3PT7 displayed a bell-shaped curve with average performance across competitive environments and was the family with the highest levels of heterozygosity for G6pd and Pmi (Fig 2). Conversely, S6PT6 had a U-shaped curve with superior performance in some competitive environments and inferior performance in others. S6PT6 had one of the lowest percent heterozygosities for G6pd and Pmi. The remaining mother-tree families were intermediate in curve shape and percent heterozygosity. Similar curves and results can be obtained for shoot dry weight, and competitive effects for height and shoot dry weight.

Isozyme heterozygosity may be related to fitness and phenotypic stability by three means. First, isozyme heterozygosity may be an indicator of inbreeding depression. Ledig et al. (1983) suggests that deleterious genes are expressed as a result of ancestral mating, and therefore outcrossing as indicated by heterozygosity is advantageous. It is unlikely though that inbreeding occurred during the creation of the progeny used in this study since all mother-trees are first generation selections contained in a clone bank. Second, individual allelic differences in the enzymes themselves may convey an advantage to heterozygous individuals (Fincham 1972). Electrophoretic techniques stain for enzymes involved in major metabolic pathways, and it is improbable that fitness is directly and solely related to such genes. Finally, heterozygosity may be related to fitness through linkage of isozyme variants and genes directly related to survival and reproduction. Stuber et al. (1982) reported, that because of linkage , isozyme patterns in

TABLE 5. PEARSON'S CORRELATION COEFFICIENTS AMONG INDICATORS OF HETEROZYGOSITY, GROWTH AND VARIABILITY.

	Height at 166 days		Shoot Dry Weight		Competitive Effect for Height		Competitive Effect for Shoot Dry Weight	
	Mean	C.V.	Mean	C.V.	Mean	C.V.	Mean	C.V.
	r							
% Heterozygosity per mother-tree	-.42	.43	-.35	-.34	-.34	.13	-.61	.31
Mean % Heterozygosity per mother-tree family	.74	-.25	.06	-.01	.31	-.01	.71	-.28
% Heterozygosity per mother-tree family for:								
Aco	.34	.44	-.35	-.04	.09	.42	.03	.35
Ald	-.13	-.51	.47	.08	-.07	-.38	.06	-.37
Dia	.53	.52	-.36	.20	.28	.59	.20	.47
Glydh	-.12	-.30	-.34	-.40	.20	-.44	.50	-.53
G6pd	.18	-.93*	.59	-.42	-.20	-.76	.34	-.89*
Hk	.27	-.53	.81	-.64	-.84	-.39	-.55	-.41
Idh	-.72	.35	-.39	-.39	-.77	.03	-.67	.20
Lap3	.17	.86	-.75	.92*	.87*	.88*	.45	.85
Mdh2	-.02	-.58	-.06	-.37	.17	-.61	.60	-.74
Mdh3	.32	-.07	-.18	.58	.76	.12	.88*	-.05
Me	-.47	-.31	.21	-.89*	-.80	-.56	-.69	-.41
6Pgd1	.01	-.78	.94*	-.49	-.74	-.64	-.44	-.61
6Pgd2	.32	.14	-.32	-.22	.13	.12	.27	-.01
Pgi2	.85	-.03	.57	.36	-.02	.37	.08	.21
Pgm	.07	.72	-.57	.95*	.79	.76	.38	.76
Pmi	-.06	-.98*	.66	-.60	-.43	-.90*	.06	-.95*
Skdh	-.42	.51	-.55	-.25	-.12	.19	-.41	.33

* - indicates a significant correlation at $\alpha \leq 0.05$.

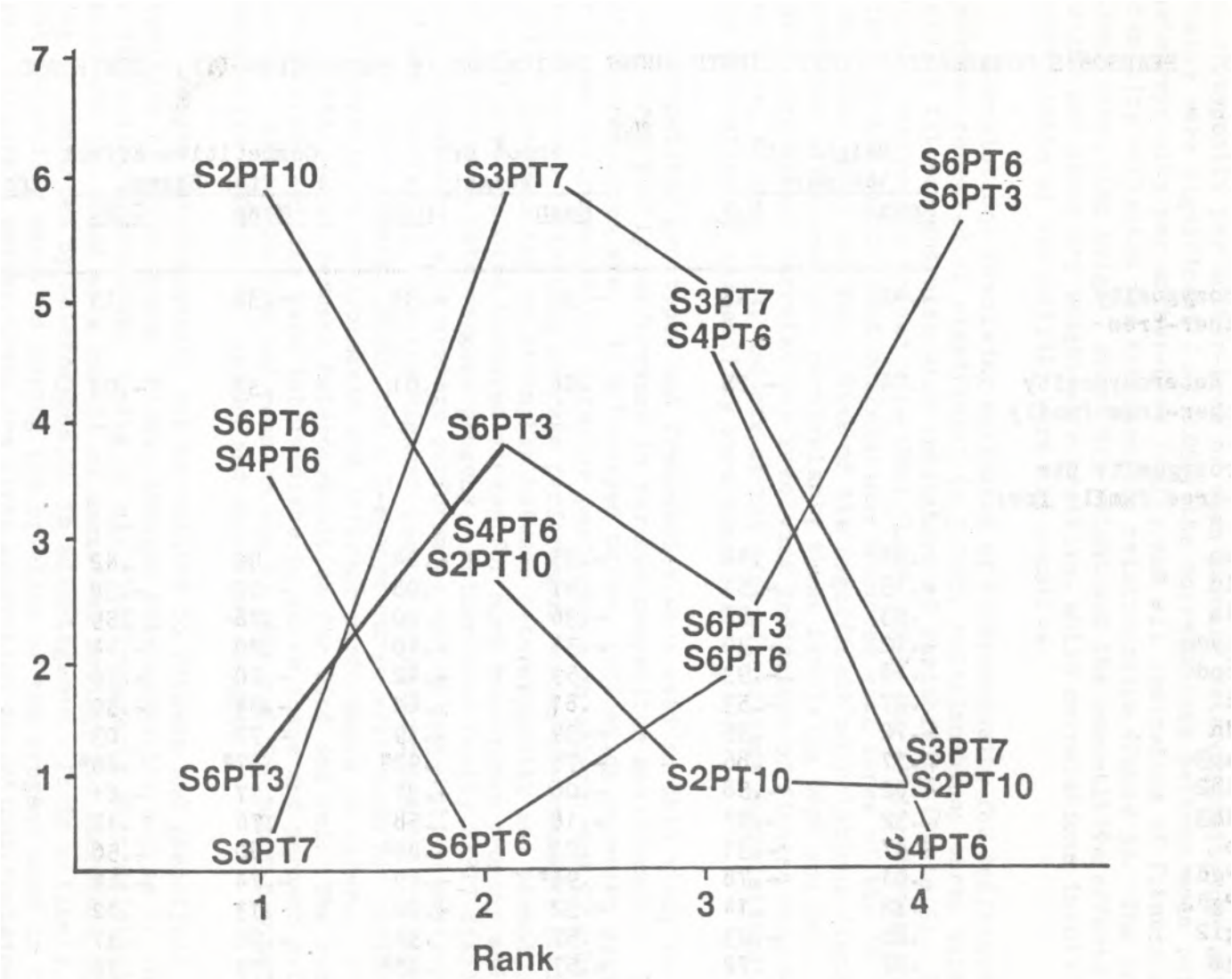

Figure 2. Frequency with which mother-tree families ranked first through fourth for seedling height in 15 competitor genotype-competitor frequency environments.

selected populations of corn could be used to improve unselected populations by breeding solely for the isozyme pattern displayed in the improved population.

It is likely that heterozygosity in genes for growth habit would be important in situations where competition is occurring, particularly when competitive effects are greater than one. For seedling mixtures to perform better than the mean of the pure plots limited resources would have to be utilized more efficiently within the mixed plots. Several plant growth habits--stratified seedling architecture, nutritional compensation and asychronous growth, have been used to explain superior performance of mixtures (Trenbath 1974), and could possibly be the result of heterozygosity in a mother-tree family growing in competition with a genetically dissimilar family.

SUMMARY

The long life expectancy of most forest trees creates a situation where genotypes within a population are exposed to continuously fluctuating environmental conditions. Climatic variability and changing competitive circumstances may act to maintain genetic variability through balanced selection over the life of a forest stand. Several authors have reported that trees contain significantly more isozyme variability than other plant species and that heterozygosity may convey some adaptive advantage in fluctuating environments. A competition diallel was used to create several different competitive environments in which the relationship between heterozygosity, fitness and phenotypic stability could be tested for five mother-tree families of loblolly pine. Significant relationships occurred 12 times, mainly involving isozyme heterozygosity in G6pd and Pmi and the coefficients of variability for height, shoot dry weight and the competitive effects for height and shoot dry weight. Correlations indicated that as heterozygosity for G6pd and Pmi increased phenotypic stability increased. A weak, positive relationship was also expressed between heterozygosity and fitness as measured by shoot dry weight and the competitive effects for height and shoot dry weight.

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