

**FAMILY x SITE INTERACTION IN A PROGENY TEST
OF COASTAL DOUGLAS-FIR**

by

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ABSTRACT

Genotype x environment interaction in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) was evaluated for height at the 6th, 7th and 12th year and diameter at the 12th year. Data collected from 15 families of the Experimental Project 708 of the BCMF were used. In addition, family stability was quantified using 4 different methods.

Interaction was not statistically significant for any of the variables evaluated. These results support the findings of a previous study made by the BCMF in another set of families of the same program. Only 2 methods gave similar results when family stability was evaluated. In general, families kept a similar yield pattern for all the variables.

The lack of statistical significance of the interaction together with the results obtained in the study previously mentioned, suggest the possibility of working with only one breeding population for this program.

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CHAPTER 1: INTRODUCTION

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is one of the most economically important species in British Columbia (Orr-Ewing, 1969). In 1991, 3% of the 245 million seedlings planted on Crown land in British Columbia were coastal Douglas-fir (Miller, 1992). Reforestation with Douglas-fir in the coastal area of British Columbia has taken place since 1930. By the late 1950's, a tree improvement program for this species was underway (Orr-Ewing, 1969).

The necessity for a tree improvement program for coastal Douglas-fir in British Columbia was emphasized by an assessment of the Forest Service plantations in 1954 and a shortage of Douglas-fir seed in 1956. It began as a selection program for coastal Douglas-fir, by the Ministry of Forests of British Columbia (BCMF). Later on, various members of the forest industry joined the project following the leading role of the BCMF (Heaman, 1967). The purpose of the program was to provide coastal Douglas-fir seed for reforestation projects. The program is accumulating additional information concerning genetic variation of Douglas-fir (Heaman, 1977a).

Since 1972, the main emphasis of the program has been the evaluation of the genetic quality of the selected parent trees. Such evaluation has been made with 8 different progeny-test series planted between 1975 and 1985 in different sites along coastal British Columbia (Yeh and Heaman, 1987).

The program had many objectives one of which was to assess the size and importance of interactions of parents across a sample of environments representing future planting sites. If the variation among phenotypes in their response to different environmental conditions or interaction patterns are sufficiently important, these tests together with the provenance test information (Illingworth, 1976), already in the field, will provide a basis for subdividing the breeding population (Heaman, 1977a).

This study analyzed data obtained from a sample of 15 full-sibling families that were planted on 22 sites to evaluate genotype x environment interactions.

Objectives:

1. To quantify the genotype x environment interaction component and its significance for height and diameter among a subsample of families from the test which are planted in series II and III.
2. To identify and quantify the nature of stability in the families for the two series analyzed.

CHAPTER 2: LITERATURE REVIEW

The selection of trees with the most desirable traits for use as the breeding population has been a primary part of most present forest tree improvement programs. Selection is made based on the measure of the productive performance trees exhibit (Squillace, 1970).

The performance trees exhibit (phenotype) is partially dependent on the genetic potential that the trees inherit from their parents (genotype) and partially on the site where they grow (environment). In other words, there is always a genetic and an environmental component for each phenotype, since every phenotype is the result of both (Wright, 1976; Zobel and Talbert, 1984).

Ideally, genotype and environment contribute to the phenotype as independent effects (Gregorius and Namkoong, 1986; Wright, 1976; Zobel and Talbert, 1984). Gregorius and Namkoong (1986) stated that independence of effects simply means that the contribution of a particular genotype to the formation of the phenotype does not depend on environment. Conversely, a particular environment makes the same contribution when acting on different genotypes.

Nevertheless, it is quite common to find variation

between genotypes in their response to different environmental conditions (Burdon, 1977; Shelbourne, 1972; Squillace, 1970). Shelbourne (1972), defined the genotype x environment interaction as the "variation between genotypes in their response to different environmental conditions". Such interactions, according to Squillace (1970) could be assessed when at least two different genetic entities are tested in two different sites or environments .

The presence of genetic x environment interactions may reduce genetic gains achievable in breeding programs when the selected trees are adapted to a narrow range of site conditions and are used over a wider range (Carson, 1990; Johnson, 1992; Matheson and Cotterill, 1990). Freeman (1973) states that when interactions exist, the measures of genetic effects apply only to the range of environments studied and *vice versa*.

Practical consequences of these interactions are very important. Such interactions may determine the subdivision of the breeding population (Matheson and Cotterill, 1990; Matheson and Raymond, 1984; Namkoong, 1990; Shelbourne, 1972; Squillace, 1970). Furthermore, breeding regions could be defined not only on the basis of the environmental conditions but also according to the performance of the trees growing there (Carson, 1990; Matheson and Cotterill, 1990; Matheson and Raymond, 1986; Shelbourne and Campbell, 1976; Squillace, 1970) .

To have just one breeding population for any improvement program is always desirable, but it is not always the right alternative to achieve the goals of the breeding program (Burdon, 1977; Matheson and Raymond, 1984; Squillace, 1970). Subdivision of the breeding population results in higher costs of operation and more difficulties in managing the breeding program. Such factors should be compared against the yield gains expected to be achieved to evaluate the convenience of such process (Carson, 1990; Matheson and Raymond, 1984; Shelbourne, 1972; Squillace 1970). Furthermore, delineation of planting zones does not ordinarily eliminate interactions, it merely reduces them (Matheson and Raymond, 1984; Squillace 1970). For these cases, choosing material which will give the highest average yield in the whole zone is the most desirable (Finlay and Wilkinson, 1963; Hühn and Léon, 1969; Matheson and Raymond, 1986; Squillace 1970).

The existence of genotype x environment interactions has long been recognized as part of the phenotypic expression of any plant or animal (Namkoong, 1990; Wright, 1976; Zobel and Talbert, 1984). Freeman (1973) described that the earliest reference to interactions was reported in 1923, by Fisher and Mackenzie (1923, original not seen). They surmised about the existence of the interactions when they evaluated different potato varieties under several treatments. Since then, many researchers have developed various techniques to examine the statistical nature of these interactions. For example,

Sprague and Federer (1951) showed how variance components could be used to separate the individual effects of the genotypes, the environment and their interactions in the analysis of variance to their expectations. In terms of a mathematical model, the yield y_{ijk} of the k^{th} replicate of the i^{th} genotype in the j^{th} environment is made up of a general mean (μ), a genotype effect d_i , an environmental effect ϵ_j , an interaction effect g_{ij} , and a random error e_{ijk} , in a linear model:

$$y_{ijk} = \mu + d_i + \epsilon_j + g_{ij} + e_{ijk}$$

The statistical approach uses analysis of variance to separate variance into components assigned to genotypes, environments, interaction, and error. These variance components are then used to predict the consequences of the selection of genotypes (Gupta and Lewontin, 1982).

Lewontin (1974) reported that a second approach has been used to characterize the phenotype of a given genotype in a fixed series of environments and then to compare the genotypes with respect to their patterns of phenotypic response to different environments.

Originally introduced by Woltereck (1909, original not seen) the concept of norm of reaction of the genotype fits this approach (Gregorius and Namkoong, 1986). Schmalhausen, (1949, original not seen) defined norm of reaction as: "...the array of phenotypes that will be developed by the genotype over an array of environments" (Gupta and Lewontin, 1987).

Evaluation of the norms of reaction can be done graphically. Gupta and Lewontin (1984) plotted the environments or environmental variables against the mean yields for each genotype, to describe the norm of reaction for each genotype plotted. The lines the genotypes describe as norms of reaction indicate the existence of interactions when they cross each other (Lewontin, 1974).

Gupta and Lewontin (1984) pointed out that analysis of variance is not sufficient to affirm or deny the existence of the interactions. They argue that low mean square values for the interaction compared with the main effects, do not capture the essential feature of the norms of reaction. The essential feature is that they cross each other to denote the existence of interactions. The most important difference occurs when interactions are not statistically significant in the analysis of variance and the lines of the norms of reaction cross each other.

Lewontin (1974) suggested that the interpretation of the results of the analysis of variance and their use would critically depend on knowing the norms of reaction of the genotypes evaluated. As Gupta and Lewontin (1984) indicate, both the statistical and developmental approaches have limitations when they try to assert the interactions between environment and genome in creating the phenotype.

There have been several criteria used to classify interactions (Allard and Bradshaw, 1964). Lambeth (1979)

classified only two kinds of interactions: those due to change in genetic variance between sites and those due to rank changes in genotypes. He called the former "important interactions". Matheson and Cotterill (1990) classified the interaction according to their significance in a similar way Lambeth (1979) did. They created three categories:

- When interactions are not statistically significant.
- When interactions are statistically significant but of no practical significance, and;
- When interactions are of both statistical and practical significance.

For the second case, interactions are statistically significant but of no practical significance since the rankings for the genetic components remain the same in the different environments. Matheson and Cotterill (1990) pointed out that this is the case when mere statistical significance is not sufficient evidence that interactions are important for practical purposes.

The last case implies that the rankings of the genotypes change substantially from one environment to another. This is the case when one or several genotypes have higher yields in one or several environments and lower in others (Matheson and Cotterill, 1990; Shelbourne, 1972; Squillace, 1970).

In addition to interactions, there is the concept of stability. A stable genotype is the one that has a constant yield in a variety of environments to which it is exposed.

Stability values are related to the average performance of families in each environment, but an individual family stability value would be influenced by the nature of the other families involved in the tests (Finlay and Wilkinson, 1963; Hühn and Leon, 1984; Shelbourne, 1972; Squillace, 1970).

Several authors have proposed different methods to evaluate phenotypic stability (Hühn and Léon, 1969; Morgenstern and Teich, 1969). Finlay and Wilkinson (1963) proposed that a simple linear regression used to describe various types of variety adaptability to a range of environments also can be used as a quantitative measure of phenotypic stability. Their approach is based on plantation performance to compare the adaptability of several varieties grown at several sites for several seasons. For each variety, a linear regression of individual yield on the mean yield of all varieties for each site in each year was computed. The mean yield of all the varieties at each site (site mean) provides a numerical grading of sites. Site means are proposed as a useful evaluation of the productivity or quality of the site or environment.

The regression coefficient (b value) for each variety is proposed as a stability parameter. The population regression has a b value of 1.0, which is defined as the average stability of the population. Absolute phenotypic stability would be expressed as $b=0$. Values of b between 0 and 1 indicate that the individual family is more stable than the

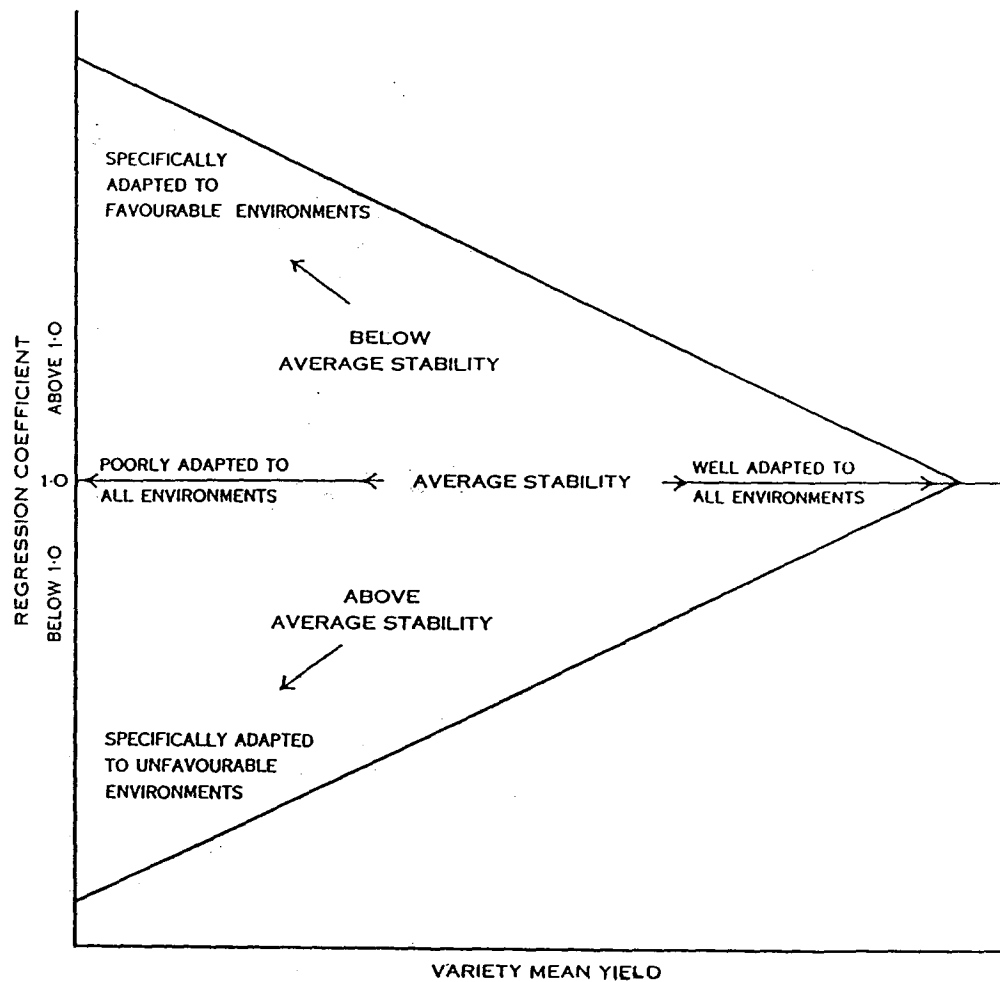


Figure 2.1 A generalized interpretation of the family population pattern obtained when the family regression coefficients are plotted against family mean yields (Finlay and Wilkinson, 1963).

average. A b greater than 1 indicates that the family has a stability below the average population stability (Figure 2.1).

Wricke (1962, original not seen) devised a method for the calculation of individual family contribution to the interactions (Morgenstern and Teich, 1969). He performed an analysis of variance using the mean values to get the usual sum of squares for families, sites, family x site interactions and total. The contribution of individual varieties (V_i) to the interaction is then calculated with the formula:

$$V_i = \sum_j [x_{ij} - (x_{i.} \div q) - (x_{.j} \div p) + (x_{..} \div pq)]^2$$

where x_{ij} is the yield of the i^{th} variety at the j^{th} site; $x_{i.}$ the sum of variety i over all locations; $x_{.j}$ the sum of all varieties at site j ; $x_{..}$ the grand total, that is, the yield of all varieties in all sites; q the number of sites and p the number of varieties. A variety contributing little to the interactions, is said to possess high stability.

Plaisted (1960, original not seen) calculated interaction mean squares omitting varieties one at a time (Morgenstern and Teich, 1969). This would give different values for the sums of squares of the FxS term. The higher the sums of squares of the FxS value results, the lower is the omitted family's contribution to the FxS. A family that possesses high stability should contribute little to the sums of squares of the FxS term.

Hühn and Léon (1984) used 5 different approaches to evaluate stability. They found none of the 5 methods used gave very similar results. They concluded that the mean rank-difference previously proposed by Hühn (1979, original not seen) showed some advantages over the others (Hühn and Léon, 1984).

Briefly, this method consists of transforming the yields of the families into ranks for each site separately. For each family, the mean of all possible, 2 by 2 absolute rank-differences between all possible pairs of different environments, is computed.

Morgenstern and Teich (1969) attribute more accuracy to the method proposed by Wricke (1962). The method has the advantage of breaking out the sums of squares by families or sites of the FxS interaction. In this way families could be evaluated according to the contribution they made to the interaction.

Shelbourne (1972) gave more importance to the method developed by Finlay and Wilkinson (1963), but Matheson and Raymond (1984) concluded that interacting families are not necessarily best identified by their regression on site means: the same family could be classified in several ways according to its regression coefficient (b value) and its mean yield.

CHAPTER 3: MATERIALS AND METHODS

Experimental Project 708 of the BCMF Research Branch forms the basis of the breeding program for coastal Douglas-fir in British Columbia. Initial tree improvement work emphasized phenotypic selection and seed orchard establishment. Phenotypically superior trees were selected until 1966 from a part of the natural distribution range of coastal Douglas-fir (Figure 3.1 and 3.2) that extends from northern California to central British Columbia (Heaman, 1977a). This population was propagated in a breeding arboretum and planted in seed orchards to meet the immediate seed requirements. Emphasis shifted to breeding of controlled pollinated progeny of the original plus trees selected, and in 1972 a decision was made to evaluate the genetic quality of the selected trees (Yeh and Heaman, 1987).

A total of 372 intensively selected trees from the original selected population were crossed and produced 1109 families through a controlled cross process from 1974 to 1985 (Table 3.1). Cross arrangement was according to a disconnected modified diallel design used for mating. With 5 crosses per parent this produces a balanced unit of 15 crosses (Heaman, 1982).

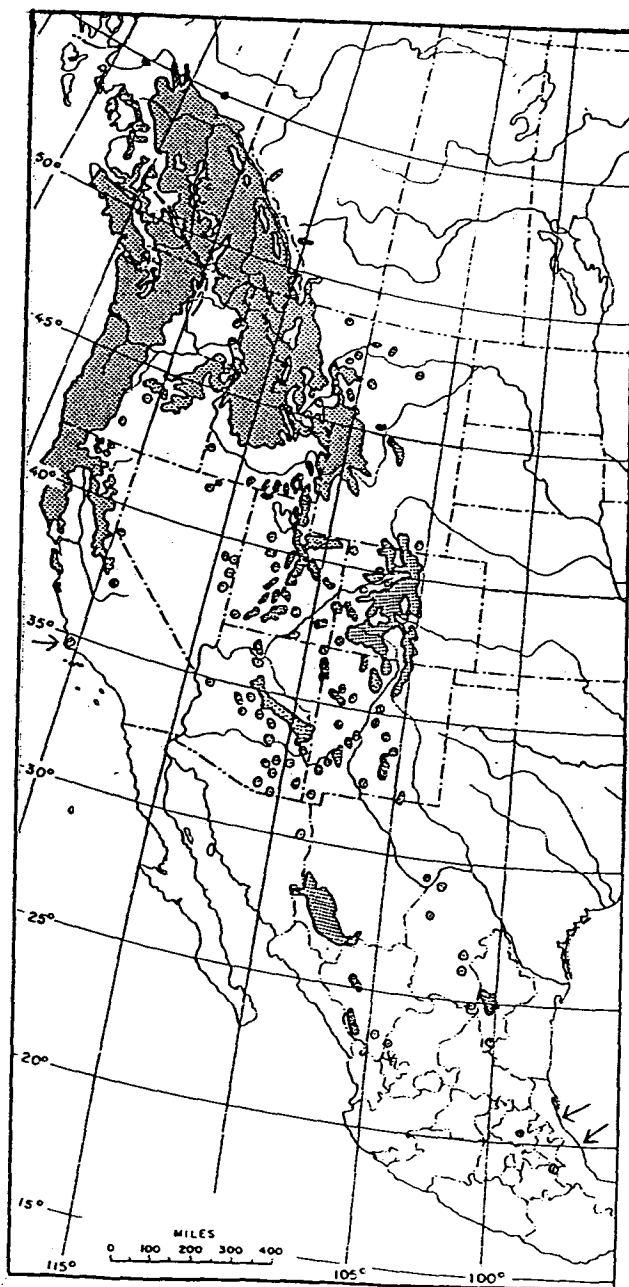


Figure 3.1 Map showing the approximate distribution of Douglas-fir (Fowells, 1965). Interior and coastal varieties are separated by a broken line.



Figure 3.2 Map showing the approximate distribution of Coastal Douglas-fir in British Columbia (Heaman, 1967).

Table 3.1 **SERIES OF THE COASTAL DOUGLAS-FIR BREEDING PROGRAM
EXPERIMENTAL PROJECT 708**

Sowing Year	Series	Parents Involved	Families Planted	Test Sites
1975	I	60	177	11
1976	II	30	99	11
1977	III	54	165	11
1978	IV	54	170	11
1979	V	48	153	11
1980	VI	48	140	11
1981	VII	18	55	11
1985	VIII	60	150	11

The choice of trees as male or female parent was based on the availability of pollen and number of female strobili in the pollination year (Yeh and Heaman, 1987).

Crosses and seeds collections were made yearly. Seedlings were raised in the Cowichan Lake Nursery and planted as 1 year-old plugs. Progenies were established in field trials to assess their performance (Heaman, 1977a) along the coastal distribution area of Douglas-fir in southern British Columbia over eight different years (1975-1981 and 1985). Each different year represents a series. Each series has a different number of families planted (range from 55 to 177) in 11 sites per series. All families were planted at every site (Heaman 1977b and 1988).

Sites were chosen from available logging and rehabilitation sites. The most important criteria were within site "homogeneity", and localization of the sites inside the natural distribution area of coastal Douglas-fir

(Yeh and Heaman, 1987). Site location for series II and III are listed in Table 3.2 and shown in Figure 3.3.

The field design comprised of four replications of four-tree-row-plots of the families in each test site. The plantation was laid out as a randomized complete block design without sub-blocking by sets. A 3 x 3 meter spacing between seedlings was used. From the families planted each year, 15 (about 10%) were randomly selected from year to year and planted in 2 consecutive series (Yeh and Heaman, 1987; Heaman, 1977b). Height was measured in the 6th, 7th and 12th year (H6, H7, and H12, respectively) in centimetres and diameter at 130

Table 3.2 SITE LOCALIZATIONS FOR SERIES II AND III

Series	Site:	Latitude*	Longitude*	Elev.	Forest
#	# Name	o ' "	o ' "	(m).	District
II	12 Maquilla	50-04-20	126-21-10	545	Port McNeill
	13 Heber	49-49-55	125-57-02	303	Campbell River
	14 Sarita	48-51-23	124-52-54	364	Port Alberni
	15 Jordon	48-25-00	124-00-50	45	Duncan
	16 Muir	48-25-35	123-54-52	379	Duncan
	17 Bamberton	48-37-32	123-34-00	212	Duncan
	18 Sechelt	49-25-30	123-35-30	212	Sechelt
	19 Squamish	50-12-00	123-22-00	155	Squamish
	20 Chilliwack	49-05-25	121-40-35	303	Chilliwack
	21 Lost Creek	49-22-13	122-14-05	424	Maple Ridge
	22 Chelais	49-30-35	122-01-00	333	Maple Ridge
III	23 Adam	50-24-00	126-10-00	576	Campbell River
	24 Menzies	50-08-54	125-38-15	333	Campbell River
	25 Gold	49-51-30	126-04-55	561	Campbell River
	26 White	50-05-35	126-04-30	409	Campbell River
	27 Sproat Lake	49-17-25	125-03-05	318	Port Alberni
	28 Fleet	48-39-30	124-05-00	561	Duncan
	29 Tansky	48-27-45	124-01-45	545	Duncan
	30 Eldred	50-06-00	124-13-00	148	Powell River
	31 Squamish	50-12-05	123-22-30	135	Squamish
	32 Sechelt	49-25-20	123-35-27	212	Sechelt
	33 Lost Creek	49-22-15	123-14-10	424	Maple Ridge

* All latitudes North and all longitudes West.



Figure 3.3
Map showing the approximate
locality of sites in
series II (sites 12-22)
and series III (sites 23-33)
(Heaman, 1977b).

cm height in the 12th year in millimetres.

Twenty-two different parents were involved to produce 15 families (Table 3.3). Parent provenances extended from Vancouver Island (Gold River and Knight Inlet sites) to the Snoqualmie site in the interior of the State of Washington (latitude 47°10' to 51°05' N, longitude 121°30' to 126°07'). The seedling survival varied from site to site making the data unbalanced. The data were evaluated according to the following model:

$$Y_{ijklqr} = \mu + R_i + F_j + F_j \times R_i + S_{(i)l} + B_{(i)lq} + F_j \times S_{(i)l} + F_j \times B_{(i)lq} + E_{(ijklqr)}$$

where:

Y_{ijklqr} = observation of the $ijklqr$ th tree

μ = overall mean

R_i = Year effect ($i=2$)

F_j = Family effect ($j=15$)

$F_j \times R_i$ = Family x year interaction

$S_{(i)l}$ = Site effect nested in year ($l=11$)

$B_{(i)lq}$ = Block effect nested in site and year ($q=4$)

$F_j \times S_{(i)l}$ = Family x site interaction

$F_j \times B_{(i)lq}$ = Family x block interaction

$E_{(ijklqr)}$ = Residual or individual effect of r th tree ($r=4$)

All effects except the overall mean (μ) were considered random. Statistical analysis of the data was performed on the UBC mainframe computer using several procedures of the

Table 3.3 OVERLAPPING FAMILIES IN SERIES II AND III

Family ^a		Parents ^b							
Number		♀	Lat.	Long.	Elev.	♂	Lat.	Long.	Elev.
2	(158)	247	(47-10;	121-30;	1220)	* 418	(51-05;	125-35;	400)
12	(161)	418	(51-05;	125-35;	400)	* 101	(48-52;	124-06;	550)
15	(156)	440	(49-22;	123-13;	620)	* 101	(48-52;	124-06;	550)
18	(159)	495	(48-45;	124-10;	200)	* 573	(50-12;	124-36;	70)
21	(157)	107	(48-47;	123-56;	210)	* 287	(48-05;	124-00;	850)
39	(151)	67	(48-49;	124-07;	180)	* 452	(50-04;	123-20;	370)
44	(162)	28	(48-56;	124-07;	680)	* 452	(50-04;	123-20;	370)
67	(163)	73	(48-50;	124-10;	180)	* 56	(49-52;	126-07;	240)
68	(153)	73	(48-50;	124-10;	180)	* 581	(48-52;	123-49;	180)
69	(150)	73	(48-50;	124-10;	180)	* 48	(49-33;	125-03;	700)
73	(152)	49	(49-17;	124-33;	470)	* 48	(49-33;	125-03;	700)
74	(164)	102	(48-48;	124-00;	210)	* 56	(49-52;	126-07;	240)
88	(155)	83	(49-18;	122-34;	370)	* 32	(48-50;	124-05;	460)
89	(160)	32	(48-50;	124-05;	460)	* 423	(49-26;	123-32;	530)
94	(154)	152	(48-55;	124-05;	490)	* 70	(48-35;	123-58;	400)

Total: 15 families and 22 different parents.

a: Numbers in parenthesis correspond to series III in the original plan.
In this analysis, only the numbers for series II were used.

b: ♀=Seed or Female parent; ♂=Pollen or Male parent; Lat.=latitude West in grades and minutes; Long.= longitude North in grades and minutes; Elev.= elevation in meters above the sea level.

6.07 version of SAS (1990a, b, c).

Assumptions for the analysis of variance, namely homogeneous variances and normal distribution of observations (Walpole, 1982) were checked with the Discriminate Functions (Discrim Proc) and the Univariate Normal Procedures (Univariate Proc), respectively. The assumption of normality was met and the variances were within the acceptable range and therefore assumed homogeneous (Table 3.4). Sums of squares and the expected mean squares were calculated with the General Linear Model Procedure (GLM Proc) using type III sums of squares as well as the Duncan's multiple range test for the

Table 3.4 HOMOGENEOUS VARIANCES AND NORMAL DISTRIBUTION

Variable	Variances (χ^2)*	T Value**
H6	13.95 ^{NS}	0.71887
H7	14.18 ^{NS}	0.76850
H12	13.46 ^{NS}	0.74041
DIAM	13.87 ^{NS}	0.77153

NS = Not significant. χ^2 critical value = 29.141

* Bartlett's χ^2 test to compare variances. If value calculated \leq that value of tables at the probability level tested then there is not sufficient evidence to declare the variances heterogenous (Morrison, 1976).

** T value obtained from the Kolomogorov D statistic to test normal distribution. If value calculated \leq to 0.775 the sample is considered normally distributed (Stephens, 1974)

means. The expected mean squares for the model are given in Table 3.5.

For sources of variation for which there was not a direct error term to test against, pseudo-*F* tests were constructed and the appropriate degrees of freedom calculated according to the Satterthwaite's (Hicks, 1982) approximation.

Evaluation of family stability across sites was done by 4 different methods: the Finlay and Wilkinson (1963) approach; the Wricke (1962) method; excluding one family at a time in the analysis of variance (Plaisted, 1960); and, with the mean rank-difference method (Hühn and Léon, 1969). The Regression Procedure (Reg Proc) was used for the first, the Analysis of Variance (Anova Proc) for the second and third, and a simple spread sheet for the last.

Scattergrams of family norms of reaction were constructed plotting family means against sites. Rank correlations for

Table 3.5 EXPECTED MEAN SQUARES FOR THE MODEL

Source	Expected Mean Squares						
Repetition (R)	V_E	$+c_1V_{F*B}$	$+c_2V_{F*S}$	$+c_3V_B$	$+c_4V_S$	$+c_5V_{F*R}$	$+c_7V_R$
Family (F)	V_E	$+c_1V_{F*B}$	$+c_2V_{F*S}$			$+c_5V_{F*R}$	$+c_6V_F$
FxR	V_E	$+c_1V_{F*B}$	$+c_2V_{F*S}$			$+c_5V_{F*R}$	
Site (S)	V_E	$+c_1V_{F*B}$	$+c_2V_{F*S}$	$+c_3V_B$	$+c_4V_S$		
Block (B)	V_E	$+c_1V_{F*B}$		$+c_3V_B$			
FxS	V_E	$+c_1V_{F*B}$	$+c_2V_{F*S}$				
FxB	V_E	$+c_1V_{F*B}$					
Error	V_E						

Range of the Coefficients (c_n):

		Variable			
		H6	H7	H12	DIAM
c_1	low	3.81	3.83	3.74	3.72
	high	3.87	3.89	3.83	3.82
c_2	low	15.25	15.35	15.01	14.92
	high	15.34	15.42	15.12	15.04
c_3	low	57.22	57.59	56.33	56.01
	high	57.29	57.64	56.44	56.12
c_4	low	228.91	230.38	225.39	224.11
	high	228.96	230.42	225.51	224.24
c_5	low	167.82	168.91	165.26	164.32
	high	168.03	169.08	165.46	164.53
c_6		335.85	337.99	330.72	328.85
c_7		2517.50	2533.70	2479.00	2464.90

families across sites were performed using the Kendal approximation (W) and Friedman's chi-square (χ_r^2) to evaluate ranking as suggested by Siegel (1967). Kendal approximation (W) and Friedman's chi-square (χ_r^2), or Spearman's regression coefficient (r_s) were also used to compare rankings of the results observed.

CHAPTER 4: RESULTS AND DISCUSSION

Analysis of variance for the variables is summarized in Table 4.1. Table 4.2 shows the components of variance for all the sources of variation. The largest variation for every variable was due to site (V_s). Sampling error (V_E) was the second largest source of variation for all variables. Variance components kept a similar proportion for H6, H7 and H12.

For all the variables the FxB interaction was significant ($P \leq 0.01$). The significance of this factor could be due to the poor homogeneity within sites, and/or the relatively small number of blocks (i.e. four).

The FxS interaction was not significant for any variable, but FxR was significant for H7 and H12 ($P \leq 0.05$), and highly significant for diameter ($P \leq 0.01$).

The FxS interaction on was not statistically significant. However, as was shown by the rank changes the interaction does exist. Norms of reaction of five families randomly selected were plotted. The occurrence of crossed lines indicates the existence of interactions (Figure 4.1). Rankings were evaluated with the χ_r^2 , r_s and/or W coefficients. The χ_r^2 determines whether the ranks totals

Table 4.1 LEAST-SQUARES ANALYSIS OF VARIANCE. F-VALUES.

<u>Source</u>	<u>D.F.</u>	<u>H6</u>	<u>H7</u>	<u>H12</u>	<u>Diam.</u>	<u>Test Term.</u>
F	14	4.38**	4.07**	4.81**	2.94*	$V_{F \cdot R}$
R	1	0.38 ^{NS}	0.10 ^{NS}	0.01 ^{NS}	0.17 ^{NS}	$V_{F \cdot R} + V_S - V_{F \cdot B}$
F*R	14	1.68 ^{NS}	2.12*	2.03*	2.25**	$V_{F \cdot S}$
S	20	58.70**	55.95**	57.40**	71.20**	$V_B + V_{F \cdot S} - V_{F \cdot B}$
B	66	2.28**	2.57**	2.28**	1.93**	$V_{F \cdot B}$
F*S	280	1.13 ^{NS}	1.15 ^{NS}	1.14 ^{NS}	1.08 ^{NS}	$V_{F \cdot B}$
F*B	924	1.87**	1.96**	2.10**	1.82**	V_E

**= Highly Significant ($P \leq 0.01$)

*= Significant ($P \leq 0.05$)

NS= Not Significant

differ significantly from one family to another. The r_s shows if the two rankings compared are significantly correlated. The W coefficient shows the association among several rankings. If the W value is high the rankings are statistically similar.

The W coefficients were low for every variable when computing the families rank correlation across sites. This means that family ranks were different from site to site. In addition, the χ_r^2 values were highly significant, denoting differences among families (Table 4.3). These results support the existence of the crosses of the lines of the norms of reaction.

Besides the families rank correlation across sites, two more rankings were calculated. One of them ranks families according the family overall mean for each variable and the other was the ranking mean or the sum of ranks of every family in every site divided by the number of sites. When

Table 4.2 COMPONENTS OF VARIANCE

Source	Variables:			
	H6	%	H7	%
V _R	0.00	0.00	0.00	0.00
V _F	73.85	1.43	146.89	1.63
V _{F*R}	19.40	0.37	49.14	0.55
V _S	2344.57	45.25	4323.90	48.08
V _B	86.45	1.67	180.47	2.01
V _{F*S}	32.99	0.64	61.63	0.69
V _{F*B}	470.97	9.09	849.10	9.44
V _E	2153.42	41.55	3382.92	37.60

Source	Variables:			
	H12	%	DIAM	%
V _R	0.00	0.00	0.00	0.00
V _F	723.42	2.07	11.19	1.06
V _{F*R}	184.88	0.53	6.18	0.59
V _S	16423.15	47.05	493.83	46.86
V _B	608.74	1.74	12.88	1.22
V _{F*S}	241.69	0.69	3.59	0.34
V _{F*B}	3792.64	10.87	95.33	9.05
V _E	12932.26	37.05	430.78	40.88

these two rankings of every variable were compared with r_s they were highly correlated.

When any pair of rankings of the height variables was compared, the r_s was very high ($r_s > 0.935$). When a ranking of any of the height variables was compared with the ranking of the diameter variable, the values were lower ($r_s > 0.76$). Nevertheless, every pair compared had significant values ($P > 0.01$) and all rankings were considered statistically similar. When all the rankings were compared using the W coefficient, it was significant, supporting the results obtained with the r_s coefficient. The χ_r^2 was significant too, denoting the differences in ranking among families (Table 4.4).

Overall site rankings were computed for every variable to see if the variables were good estimators of site quality as

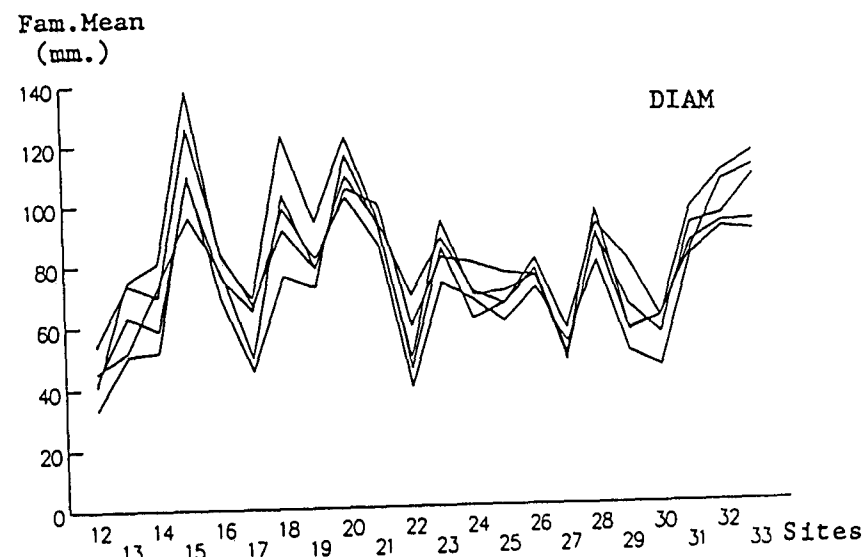
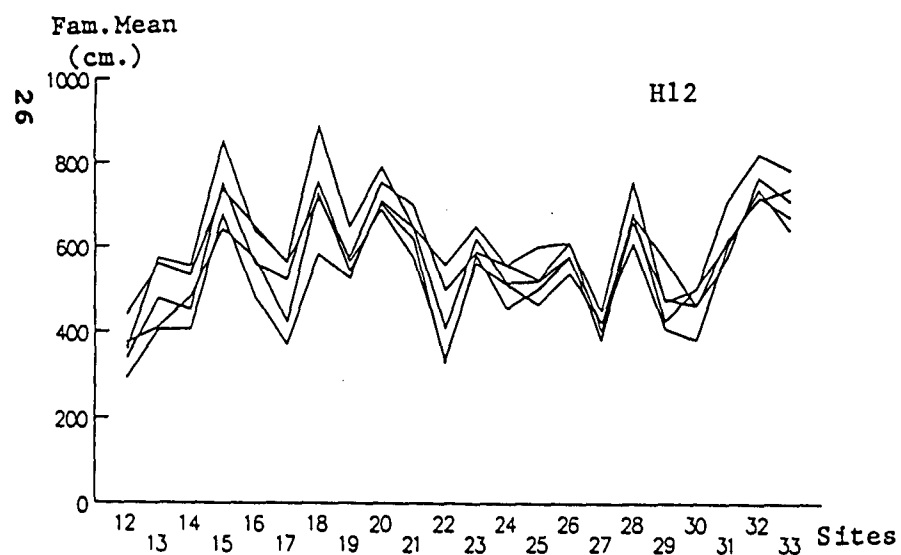
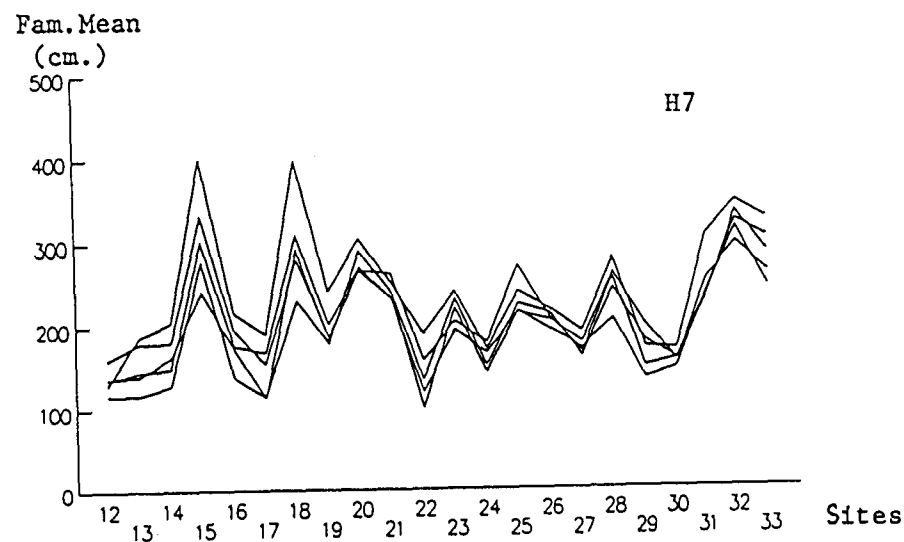
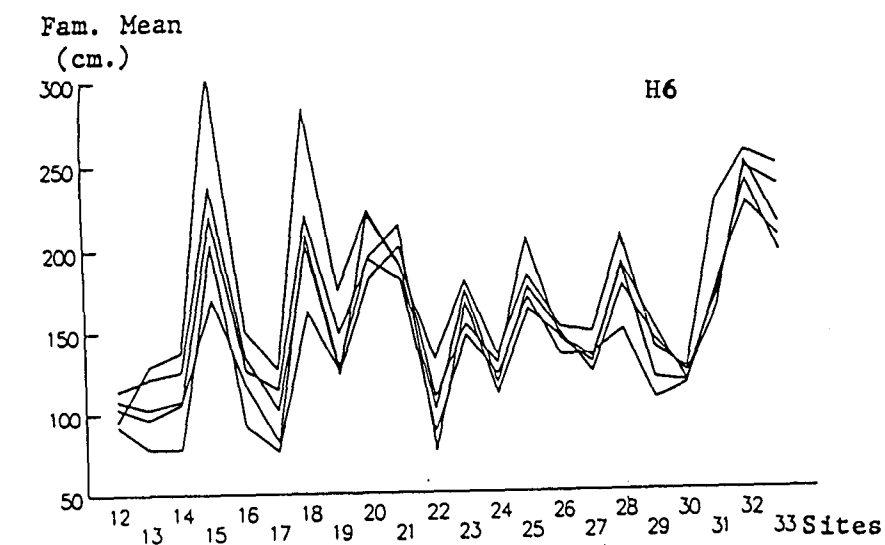


Figure 4.1 Norms of Reaction for all the variables representing 5 randomly selected families. Site numbers in the x axes and family means (in centimetres for H6, H7, H12 and in millimetres for Diam) in the y axes (See appendix).

Table 4.3 FAMILIES RANK CORRELATION ACROSS SITES

	H6	H7	H12	DIAM
χ_r^2	85.482**	96.536**	95.591**	72.582**
W	0.278	0.313	0.310	0.236

** = Highly significant ($P \leq 0.01$)

Table 4.4 OVERALL MEAN RANK AND RANKING MEAN OF FAMILIES

Family	Variables											
	H6	a*	b*	H7	a	b	H12	a	b	DIAM	a	b
2		15	14		15	14		15	14		14	14
12		6	5		6	5		7	7		1	1
15		12	12		12	12		12	12		3	3
18		5	4		4	4		4	4		7	6
21		11	9		9	9		8	8		11	11
39		13	13		13	13		13	13		13	12
44		9	10		10	10		10	9		8	8
67		3	3		3	2		2	2		5	5
68		8	7		8	7		6	5		10	9
69		10	11		11	11		11	11		12	13
73		7	8		7	8		9	10		9	10
74		14	15		14	15		14	15		15	15
88		1	1		1	1		1	1		2	2
89		2	2		2	3		5	3		4	4
94		4	6		5	6		3	6		6	7
r _s (a & b)		0.971			0.982		0.988			0.989		

** r_s H6-H7 0.996

** r_s H6-H12 0.936

** r_s H7-H12 0.948

** r_s H6-DIAM 0.754

** r_s H7-DIAM 0.754

** r_s H12-DIAM 0.682

**W 0.884

++W 0.975

** χ_r^2 49.53

++ χ_r^2 40.93

* a= Rank according to the overall mean of the family for the variable.

b= Rank according to the sum of rankings of every family divided by the number of sites, or ranking mean.

** = Values computed using the overall mean of the family rank.

++ = Values computed using the overall mean of the family rank for the height variables only.

suggested by Finlay and Wilkinson (1963): χ_r^2 was significant denoting the differences in ranking among sites. The W value was high denoting that the differences among variables in the overall site mean rankings were not statistically significant (Table 4.5).

The best families for variable H6 were 88, 89, 67, 94, 18, and 12 (Table 4.6); for variable H7 were 88, 89, 67, 18, 94 and 12 (Table 4.7); for H12 were 88, 67, 94, 18 and 89 (Table 4.8); for diameter were 12, 88, 15, 89, 67, 94, and 18 (Table 4.9).

The most stable families as determined by the Wricke (1962) method and omitting one family at a time for H6 were 15, 74, 73, 12 and 44 (Table 4.10); for H7 were 15, 74, 12, 44, 69 and 68 (Table 4.11); for H12 were 74, 12, 44, 15 and 69 (Table 4.12); for diameter were 68, 74, 12, 44, and 15 (Table 4.13).

The most stable families according to the method of Finlay and Wilkinson (1963) for H6 were 21, 74, 39 and 2 (Table 4.10); for H7 were 21, 39, 74, 2 and 18 (Table 4.11); for H12 were 21, 39, 89, 2, and 12 (Table 4.12); for diameter 21, 39, 74, 18 and 2 (Table 4.13).

Families closer to the average stability according to Finlay and Wilkinson (1963) for H6 were 44, 15, 12, 67, 18, and 89 (Figure 4.2); for H7 were 89, 12, 44, 15, and 18 (Figure 4.3); for H12 were 18, 67, 15, and 74 (Figure 4.4); for

Table 4.5 RANK CORRELATION OF SITES

	FOR HEIGHT VARIABLES ONLY	FOR ALL THE VARIABLES
χ_r^2	60.45**	79.85**
W	0.960	0.951

** = Highly significant ($P \leq 0.01$)

diameter were 89, 68, 67, 94, 2, and 12 (Figure 4.5).

Since the evaluation of site yields is not the goal of this study, sites are discussed as they relate to family yields. As mentioned before, Finlay and Wilkinson (1963) proposed site mean as an evaluation of the environment productivity. Therefore, comparing the means of the poor sites with the family means in these sites, would reveal the families with better yields in poor sites when their means in these sites were above the site mean. A similar comparison for the rich sites would delineate the families with better yields in rich sites. For H6, there were 12 sites with means below the overall mean or poor sites, and 10 sites with means above the overall mean or rich sites; for H7 were 12 poor sites and 10 rich sites; for H12 were 10 poor sites and 12 rich sites; for diameter there were 12 poor sites and 10 rich sites.

According to Finlay and Wilkinson (1963), families with better yields in all sites ($b \approx 1$ and $\text{mean} > \mu$) for H6 were 88, 89, 67, 94, 18 and 12; for H7 were 88, 89, 67, 18, 94, 12 and 73; for H12 were 88, 67, 94, 18, 89, 68, 12 and 21; for diameter were 12, 88, 15, 89, 67, 94, 18 and 44.

Families which tended to have better yield in poor sites

**Table 4.6 DUNCAN'S MULTIPLE RANGE TESTS AND FAMILIES MEANS
FOR H6**

Ranking	Family	Mean	P<0.01*	P<0.05*
1	88	178.02	A	A
2	89	176.10	A	A B
3	67	173.26	A	A B
4	94	170.25	A B	B
5	18	169.79	A B	B
6	12	168.89	A B	C B
7	73	161.74	B	C B
8	68	161.54	C B	C D
9	44	158.16	C D	D
10	69	157.34	C D	D
11	21	156.07	C D	E D
12	15	155.99	C D	E D
13	39	148.98	C D	E F
14	74	148.54	D	E F
15	12	148.07	D	F
Overall		162.27		

* Families with the same letter are not significantly different at the P level shown.

**Table 4.7 DUNCAN'S MULTIPLE RANGE TESTS AND FAMILIES MEANS
FOR H7**

Ranking	Family	Mean	P<0.01*	P<0.05*
1	88	247.03	A	A
2	89	238.88	A	A B
3	67	237.36	A B	A B
4	18	231.07	A B C	C B
5	94	229.88	A B C	C B
6	12	225.27	D B C	C D
7	73	220.29	D E C	E D
8	68	219.82	D E C	E D
9	44	215.52	D E	E F
10	21	215.08	D E	E F
11	69	213.57	D E F	E F
12	15	209.15	G E F	G F
13	39	202.49	G F	H G
14	74	199.74	G	H
15	2	199.37	G	H
Overall		220.07		

* Families with the same letter are not significantly different at the P level shown.

**Table 4.8 DUNCAN'S MULTIPLE RANGE TESTS AND FAMILIES MEANS
FOR H12**

Ranking	Family	Mean	P<0.01*	P<0.05*
1	88	247.03	A	A
2	67	623.98	A B	A B
3	94	617.85	A B C	A B C
4	18	616.85	A B C	A B C
5	89	615.93	A B C	A B C
6	68	605.87	D B C	D B C
7	12	598.44	D B C E	D C
8	21	596.38	D C E	D
9	73	586.95	D F E	D E
10	44	586.42	D F E	D E
11	69	573.91	F G E	E F
12	15	564.82	H F G	G F
13	39	552.97	H G I	G H
14	74	540.84	H I	H
15	2	538.44	I	H
Overall		590.40		

* Families with the same letter are not significantly different at the P level shown.

**Table 4.9 DUNCAN'S MULTIPLE RANGE TESTS AND FAMILIES MEANS
FOR DIAMETER**

Ranking	Family	Mean	P<0.01*	P<0.05*
1	12	86.45	A	A
2	88	84.85	A B	A B
3	15	84.59	A B	A B
4	89	84.25	A B	A B
5	67	83.29	A B C	A B C
6	94	82.67	A B C	B C D
7	18	81.71	A B C D	E B C D
8	44	81.44	B C D	E B C D
9	73	80.37	B C D	E F C D
10	68	80.23	B C D	E F C D
11	21	79.08	C D	E F D
12	69	78.65	C D	E F
13	39	77.53	E D	F
14	2	73.88	E F	G
15	74	71.44	F	G
Overall		80.70		

* Families with the same letter are not significantly different at the P level shown.

Table 4.10 FAMILY STABILITY RANKINGS FOR H6

Fam	A	B	C	D	E
2	15	15	4	8	12
12	4	4	8	3	14
15	1	1	7	2	3
18	10	10	5	5	11
21	7	7	1	15	15
39	9	9	3	12	7
44	5	5	6	1	10
67	12	12	9	4	6
68	8	8	11	7	13
69	6	6	15	13	8
73	3	3	14	11	4
74	2	2	2	14	1
88	11	11	13	10	2
89	13	13	10	6	5
94	14	14	12	9	9

$$\chi_r^2 = 13.05 \text{ NS} \quad W=0.233$$

NS= Not significant

A = As determined by Wricke (1962) method.

B = Omitting one family at a time.

C = As determined by Finlay and Wilkinson (1963) method $b = 0$.

D = As determined by Finlay and Wilkinson (1963) method $b = 1$.

E = As determined by Hühn (1979) method.

Rank position of the family according to that criterion:

1 the most stable, 15 the less stable.

Table 4.11 FAMILIES STABILITY RANKINGS FOR H7

Fam	A	B	C	D	E
2	13	13	4	9	12
12	3	3	6	2	6
15	1	1	9	4	3
18	12	12	5	5	13
21	8	8	1	15	15
39	11	11	2	13	11
44	4	4	8	3	7
67	10	10	10	6	4
68	6	6	11	7	5
69	5	5	15	14	9
73	7	7	14	11	10
74	2	2	3	12	1
88	9	9	13	10	2
89	14	14	7	1	8
94	15	15	12	8	14

$$\chi_r^2 = 17.00 \text{ NS} \quad W=0.243$$

NS= Not significant

A = As determined by Wricke (1962) method.

B = Omitting one family at a time.

C = As determined by Finlay and Wilkinson (1963) method $b = 0$.

D = As determined by Finlay and Wilkinson (1963) method $b = 1$.

E = As determined by Hühn (1979) method.

Rank position of the family according to that criterion:

1 the most stable, 15 the less stable.

Table 4.12 FAMILIES STABILITY RANKINGS FOR H12

Fam	A	B	C	D	E
2	15	15	4	9	9
12	2	2	5	6	7
15	4	4	7	3	6
18	9	9	8	1	12
21	8	8	1	15	14
39	12	12	2	12	5
44	3	3	12	8	4
67	10	10	9	2	10
68	6	6	11	7	8
69	5	5	15	14	3
73	13	13	14	13	15
74	1	1	6	4	1
88	7	7	10	5	2
89	11	11	3	11	13
94	14	14	13	10	11

$$\chi_r^2 = 20.87 \text{ NS} \quad W=0.298$$

NS= Not significant

A = As determined by Wricke (1962) method.

B = Omitting one family at a time.

C = As determined by Finlay and Wilkinson (1963) method $b = 0$.

D = As determined by Finlay and Wilkinson (1963) method $b = 1$.

E = As determined by Hühn (1979) method.

Rank position of the family according to that criterion:

1 the most stable, 15 the less stable.

Table 4.13 FAMILIES STABILITY RANKINGS FOR DIAMETER

Fam	A	B	C	D	E
2	15	15	5	5	7
12	3	3	10	6	3
15	5	5	14	11	4
18	9	9	4	8	12
21	11	11	1	15	15
39	14	14	2	13	14
44	4	4	11	7	6
67	13	13	8	3	10
68	1	1	6	2	2
69	7	7	15	14	11
73	10	10	12	9	9
74	2	2	3	12	1
88	6	6	13	10	5
89	8	8	7	1	8
94	12	12	9	4	13

$$\chi_r^2 = 11.73 \text{ NS} \quad W=0.168$$

NS= Not significant

A = As determined by Wricke (1962) method.

B = Omitting one family at a time.

C = As determined by Finlay and Wilkinson (1963) method $b = 0$.

D = As determined by Finlay and Wilkinson (1963) method $b = 1$.

E = As determined by Hühn (1979) method.

Rank position of the family according to that criterion:

1 the most stable, 15 the less stable (See appendix).

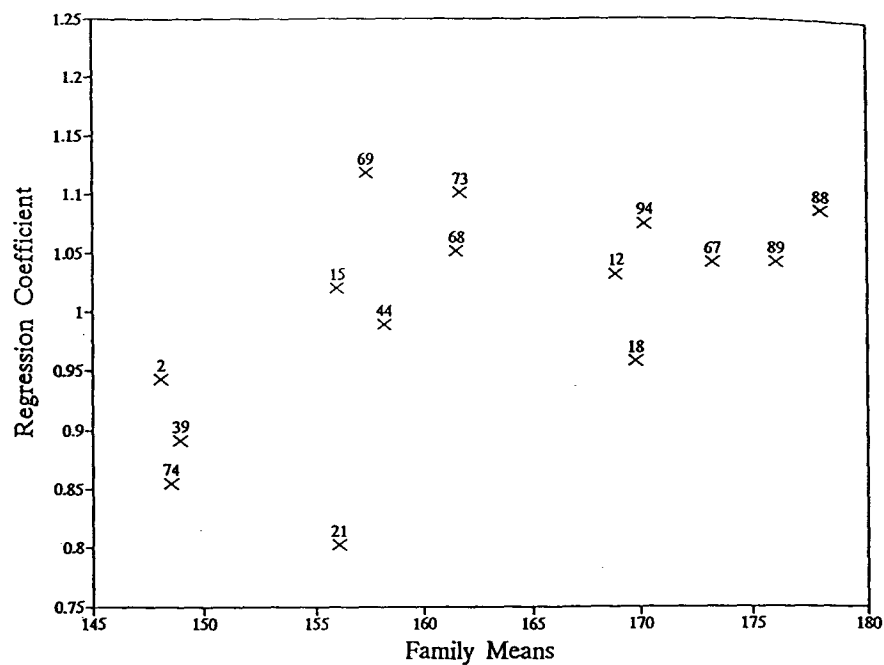


Figure 4.2 The relationship of family regression coefficients (b) and family mean yield of H6 variable.

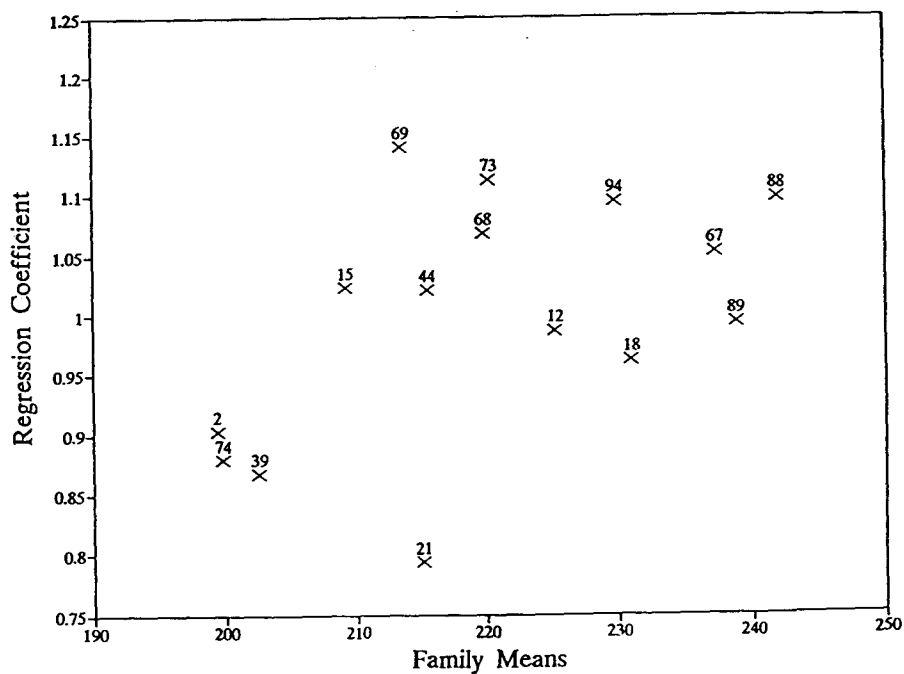


Figure 4.3 The relationship of family regression coefficients (b) and family mean yield of H7 variable.

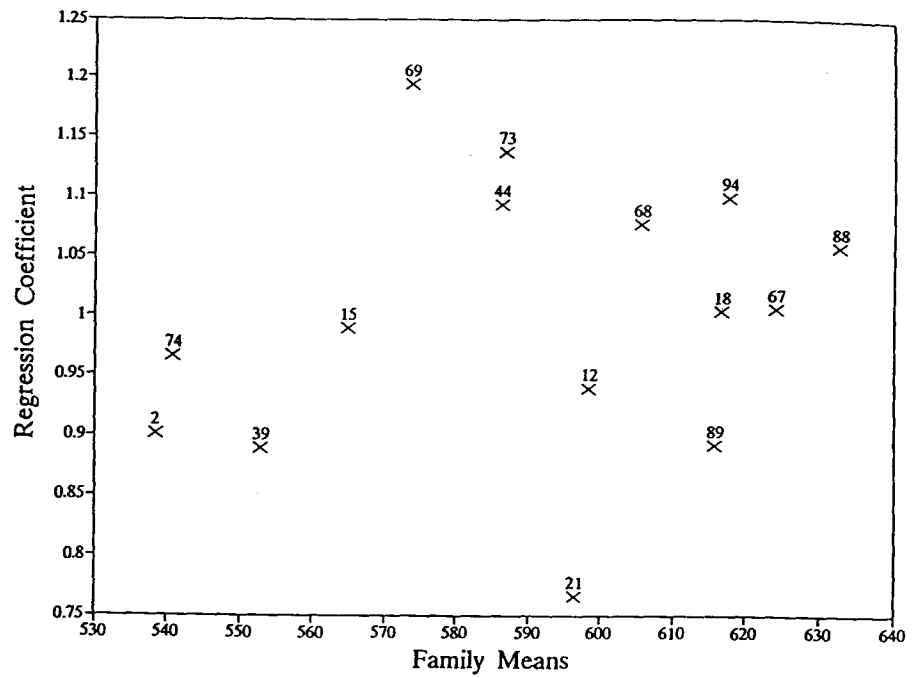


Figure 4.4 The relationship of family regression coefficients (b) and family mean yield of H12 variable.

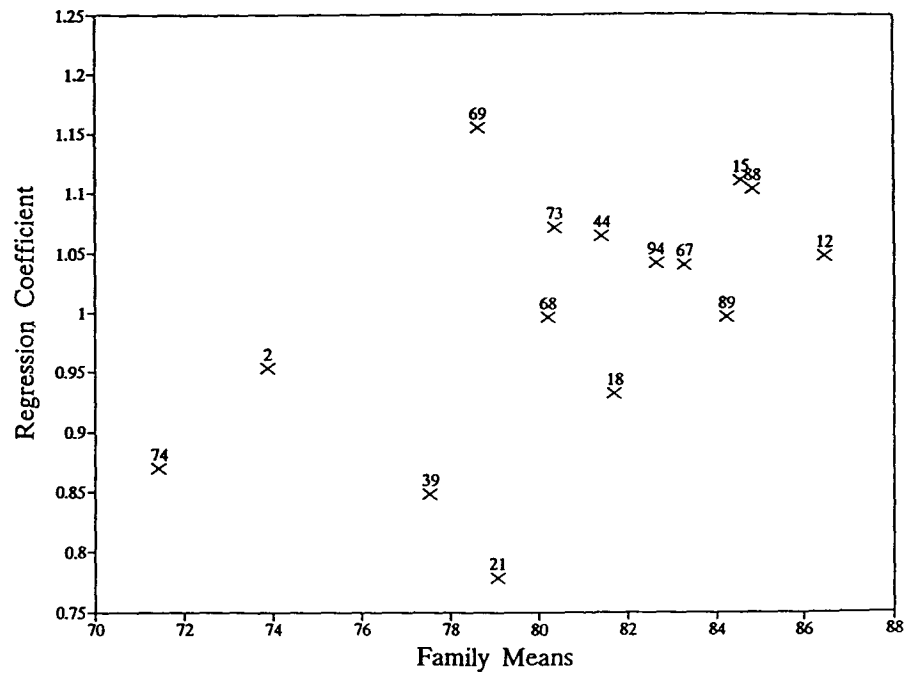


Figure 4.5 The relationship of family regression coefficients (b) and family mean yield of Diameter variable.

($b < 1$ and $\text{mean} < \mu$) for H6 were 21, 39, 74 and 2; for H7 were 21, 39, 74 and 2; for H12 were 39 and 2; for diameter were 21, 39 and 74. Nevertheless, the analysis of the results did not support this criterion in the majority of the cases. The attribute of better yield in poor sites was quite notable for family 21 in variables H6, H7 and diameter, but the other sets of families did not show this quality, especially family 2 which had means below the site means in almost every case for H6, H7 and H12. Finlay and Wilkinson (1963) explained their low mean yields as a consequence of high phenotypic stability: they are so stable that they are unable to exploit high yield environments.

The Finlay and Wilkinson (1963) approach suggests that families with better yields on rich sites ($b > 1$ and $\text{mean} < \mu$) for H6 were 88, 94, 73, 68 and 69; for H7 were 68 and 69; for H12 were 73, 44 and 69; for diameter were 73 and 69. Again, as in the case of the families with better yields in poor sites, the analysis of results did not support this criterion for H6 and H7. However, this attribute was appropriate for the set of families mentioned for the H12 variable, especially family 44, and in the diameter variable for family 73.

The most stable families according to the mean rank-difference for H6 were 74, 88, 15, 89, and 73 (Table 4.10); for H7 were 74, 88, 15, 67 and 68 (Table 4.11); H12 were 74, 88, 69, 39 and 44 (Table 4.12); for diameter were 68, 74, 12, 44 and 15 (Table 4.13).

Family rankings for stability gave low W values for all the variables denoting the significant differences existing among rankings. χ_r^2 values were not significant for any variable either: the lack of significance may be associated to the considerable differences among rankings that made it impossible to detect any significant difference among families.

CHAPTER 5: CONCLUSIONS

Family rankings for H6 and H7 were very similar: only 2 pairs of families interchanged positions. This similarity is obviously due to the proximity in time in which the data were taken. Comparing the rankings of H6 and H7 with H12, more notable differences appeared. However, the Spearman's correlation coefficients (r_s) were very high for any pair of rankings compared, showing the similarity of rankings for all the variables.

In all cases, it was possible to distinguish 3 sets of families:

- The top class: 18, 67, 88, 89 and 94.
- The middle class: 12, 21, 44, 68, 69 and 73.
- The lower class: 2, 15, 39 and 74.

Of the top 5 families, family 88 was highest for the 3 variables. According to the Duncan's multiple range test, there were not statistically significant differences among them ($P < 0.01$).

The families of the middle group showed more changes in their rankings. There were different rankings for each variable, but most of the changes were only 1 or 2 places in the ranking.

The lower 4 families (15, 39, 74 and 2) kept the same ranking for the 3 variables. According to the Wricke method (Morgenstern and Teich, 1969), family 2 was among the lesser of the stable families. In contrast, the Finlay and Wilkinson (1963) method classified this family as one of the most stable families for all variables. Given the poor concordance between what Finlay and Wilkinson (1963) suggested and the results obtained, it seems that the Finlay and Wilkinson (1963) method is not the most suitable to evaluate stability, as Matheson and Raymond (1984) suggest.

For diameter, the families in general kept the same pattern as the ones showed for height variables. The exceptions were families 12 and 15 that were among the middle and low families for height increments and were ranked as 1 and 3, respectively, for diameter. Height and diameter were good estimators of site quality as suggested by Finlay and Wilkinson (1963), given the similarity of the ranking for sites for the 4 variables.

The significance of the FxR interaction for the H7, H12 and diameter variables could be due to the environmental differences from one year to the next. Sites were located within the same general climatic area, but different weather conditions in different years could produce such significant interaction. Squillace (1970) suggested that given the long life span of most trees, this kind of interaction becomes nonsignificant over a period of 30 years. In this study, a

peak value of the FxR interaction for height was attained at the 7th year, but for the whole study the maximum was for diameter which was measured at the 12th year.

The lack of significance of the FxS interaction in this sample of families supports Yeh and Heaman (1987), and the prospect of working with only one breeding population seems appropriate.

The high correlation between the ranking of the family means and the ranking mean of the families reinforce the observed lack of significance of the FxS term. In spite of the results of the rank correlation of families across sites that showed the significance in the change of the family rankings from site to site, other results suggest that even with the significance of changes in rankings site, such changes are not statistically significant with other methods.

Four different methods were used to calculate family stability. They gave very different family stability ranks. The W values were very low showing no relation or similarity among the ranks. The χ_r^2 were not significant in any case, and did not show any significant differences among the families.

Only the method suggested by Wricke (1962) and the one omitting one family at a time for the calculation of the FxS interaction, gave similar rankings' results. Comparing rankings of both methods the correlations were 1 for every variable because rankings were identical.

The methods suggested by Finlay and Wilkinson (1963) and

by Hühn (1979) gave very different results. The mean rank-difference expresses only the rank changes of the families from site to site, but it does not take account of any site value and the possible links with the stability of the families. In this study, the Finlay and Wilkinson approach always classified as the most stable families the less productive ones. Considering the regression coefficient of 1 (average stability) to rank families, the differences in rankings with the other methods to evaluate stability, still persisted. Considering the family means and the regression coefficient together, to classify family stability, was also not very consistent. Families with mean values greater than the overall mean and stability values (*b*) close to 1 were on average the most productive families for all variables. Families that were classified as with better yields in poor or rich sites did not exhibit any consistency for such traits.

This study did not show genotype x environment interaction for the families and sites evaluated. This result together with the results obtained by Yeh and Heaman (1987) suggest the possibility of working with only one breeding population for the program, and of selecting the families and/or parents with higher yields to be used for the planting programs in the area.

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APPENDIX

An example of the data used to calculate the stability rankings:

FAMILY STABILITY VALUES FOR DIAMETER

Fam	A		B		C	(*)	(&)	D	
2	1913.13	15	15614.32	15	0.953	5	5	318.95	7
12	615.74	3	17004.39	3	1.047	10	6	193.45	3
15	883.64	5	16717.36	5	1.110	14	11	224.00	4
18	1353.94	9	16213.45	9	0.932	4	8	405.05	12
21	1383.84	11	16181.42	11	0.778	1	15	472.77	15
39	1853.94	14	15677.75	14	0.848	2	13	439.27	14
44	782.46	4	16825.75	4	1.063	11	7	296.77	6
67	1574.31	13	15977.35	13	1.039	8	3	360.36	10
68	453.76	1	17177.94	1	0.996	6	2	186.77	2
69	1105.36	7	16479.79	7	1.154	15	14	373.45	11
73	1383.50	10	16181.79	10	1.071	12	9	351.45	9
74	519.14	2	17107.88	2	0.870	3	12	114.00	1
88	1103.70	6	16481.58	6	1.102	13	10	230.95	5
89	1260.14	8	16313.96	8	0.996	7	1	323.86	8
94	1477.44	12	16081.14	12	1.041	9	4	416.77	13
1.000(**)									

A = Contribution to the FxS SS according to Wricke (1962) method.

B = FxS SS omitting one family at a time.

C = Regression Coefficient (*b*) according to Finlay and Wilkinson (1963) method.

Families were ranking according closeness to the *b* value of 0(*) and 1(&).

D = Mean-rank deviation according to Hühn (1979) method.

Rank position of the family according to that criteria: 1 the most stable, 15 the less stable.

(**) 1.00 is the average regression coefficient for the whole sample.

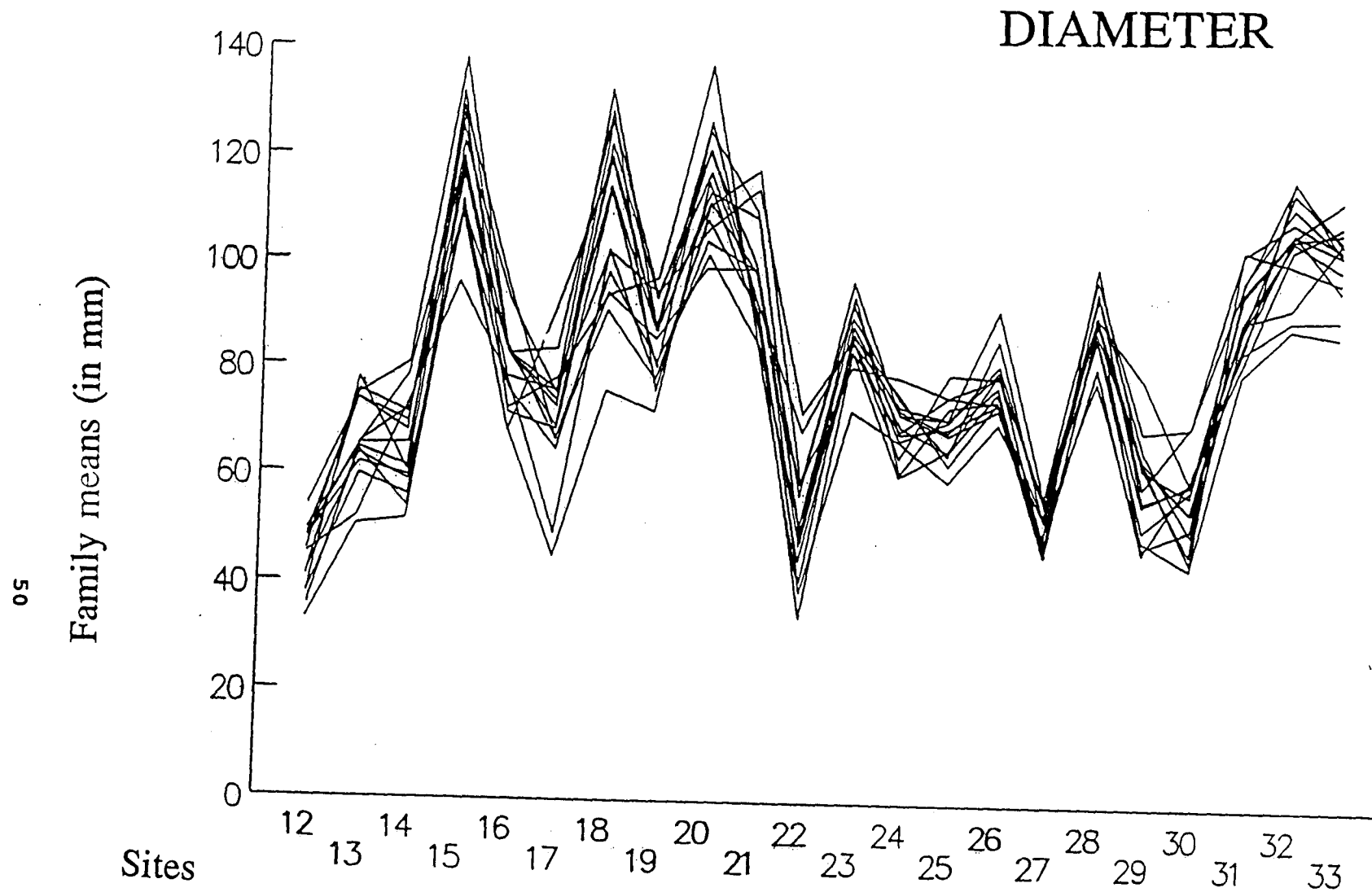


Figure to show the norms of reaction of the 15 families for the variable diameter (Sites numbers in the x axe, and family means in the y axe in millimetres).