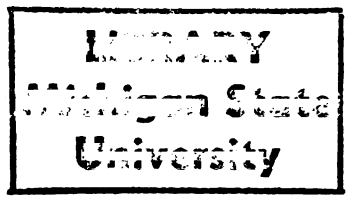


This is to certify that the

dissertation entitled

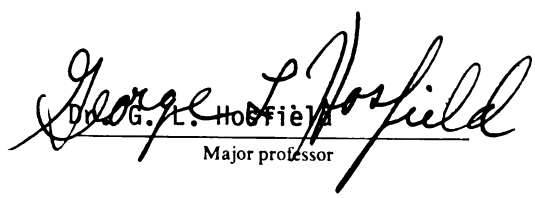
Genetic Analysis of Cooking time, Nutritional, and Culinary Quality in Dry Beans (Phaseolus vulgaris L.)

presented by

Nassratullah Naimatullah Wassimi

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in **Plant breeding**



Dr. G.L. Hosfield
Major professor

Date **April 3, 1985**

GENETIC ANALYSES OF COOKING TIME, NUTRITIONAL, AND CULINARY QUALITY IN DRY BEANS (*Phaseolus vulgaris* L.)

BY

NASSRATULLAH NAIMATULLAH WASSIMI

A DISSERTATION

SUBMITTED TO
MICHIGAN STATE UNIVERSITY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

DEPARTMENT OF CROP AND SOIL SCIENCES

1985

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ABSTRACT

GENETIC ANALYSES OF COOKING TIME, NUTRITIONAL, AND CULINARY QUALITY IN DRY BEANS (*Phaseolus vulgaris* L.)

BY

Nassratullah N. Wassimi

The importance of dry beans as a protein complement to cereal diets has long been recognized; however, the presence of antinutritional factors and prolonged soaking and cooking have caused people in lesser developed countries of the world to turn away from eating beans. In order to increase the consumption of beans it is necessary to develop high yielding cultivars that are resistant to pests and have good food quality. It will be difficult to incorporate selection for nutritional and culinary quality into bean breeding programs that historically selected for increased and stabilized yield. Modern technology has provided the means by which nutritional and culinary quality study may be conducted on small amounts of seed. The present study was undertaken to determine the inheritance of cooking time and uniformity, tannin and protein content, and the culinary quality of a diverse population of beans. Eight strains were crossed in diallel and the eight parents and F_2 and F_3 progenies grown at two locations for evaluation. Highly significant differences were observed among entries for cooking time, uniformity of cooking, tannin and protein

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content and for eight of nine culinary quality traits. Partitioning of variability into GCA, SCA, and reciprocal causes revealed highly significant GCA mean squares for the traits. In some cases SCA variance was also significant; however, when significant, SCA variance components were always smaller in magnitude than GCA components. Reciprocal differences were detected for a few traits but no consistent pattern over location or generation was noted.

Quick cooking characteristics of parental strains were transmitted to progenies. Crosses of low x low and high x high protein parents had progenies that were also low and high, in protein content, respectively. Highly significant correlation between GCA effects in the F_2 and F_3 and between parental values and the GCA effects of parents was observed. Selection aimed at improving the cooking time and cooking uniformity, soakability, and palatability of beans can be practiced in generations when plants are more heterozygous after the initial cross. Selection for low tannin and high protein among progeny from a cross should result in the stabilization of these traits in a single cultivar.

Note:

Note: This dissertation is presented as a series of three papers written in the style and format required by Crop Science and, the Journal of the American Society for Horticultural Science.

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To my father, and all other members of my family.

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As a major professor, Dr. George L. Hosfield provided many challenges and unlimited stimuli to my professional growth and understanding. Above all, he provided friendship that is sincerely appreciated. His strong professional guidance and criticism have equalled by support and encouragement in every aspect of research and academic advancement. It is with humbleness and sincere gratitude that I say thank you to Dr. G. L. Hosfield for the opportunity to have been his student.

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The friendship, encouragement and support of Catalina Samper, Joe Tohme, Khushal and Homyra Habibi, and all members of the "bean program" is sincerely appreciated.

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A study program such as this is not borne by the student alone. Family members offer support and tolerate uncomplainingly many inconveniences and disruptions to a 'normal' family life. Waranga, Wagma, and Atal are such a family and have greately contributed to the successful completion of this study program.

TABLE OF CONTENTS

CHAPTER 1

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CHAPTER 2

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LIST OF TABLES

CHAPTER

4. Ge
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CHAPTER 2 (Continued) Page

CHAPTER 2 (continued) Page

CHAPTER 3

CHAPTER 3 (continued) Page

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APPENDIX B (Continued) Page

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LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER

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INTRODUCTION

The high cost and general non-availability of animal protein in diets of people in poorer countries of the world necessitates seeking of alternative sources of protein to alleviate protein malnutrition. Edible legumes constitute one of the most important sources of plant protein the world and can go a long way in supplying this and other nutrients to consumers in lesser developed countries of the world.

Usually an increased and stabilized yield is the major objective of most legume breeding programs. However, since the primary use of edible legumes is a human food, nutritional, culinary and sensory qualities that are of direct concern to the consumer must be at an acceptable level (Hawtin, et al. 1977).

Dry beans (Phaseolus vulgaris L.) constitute 32% of the total world legume production (FAO 1982), and can provide significant amounts of protein, calories, minerals and vitamins to human diets. Despite the nutritional benefits, bean consumption on a world-wide basis is decreasing. The causes of the reduced consumption of beans, beside their low yields and high prices, are prolonged soaking and cooking times, tannins, and heat labile anti-nutritional factors.

Low sugar, fat, and high dietary fiber content of beans will not predispose consumers to diabetes and coronary heart disease (Walker, 1982). Leeds (1982) reported that

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diets containing large quantity of beans may have special advantages for diabetic patients, as carbohydrate from beans may be digested and absorbed more slowly from beans than from other foods. Simpson et al. (1981) reported that many indices of diabetic control were improved, but in particular blood glucose levels after meals were lower in patients treated with high-carbohydrate high-leguminous dietary fiber content. Bressani et al. (1963) reported that long (>30 min. at 16 lb pressure and at 49° C) cooking times decreased the nutritive value of bean protein but the addition of 0.2% methionine to the bean diet of rats significantly improved weight gain, protein efficiency and biological value. Bressani and Elias (1977) observed greater intraspecies and interspecies variability for heat labile anti-physiological factors responsible for low protein digestibility in beans.

Tannins are phenolic compounds that have the characteristic ability to precipitate protein (Gustavson, 1956). Their molecular weights usually range from 500 to 3,000MW. Tannins are generally classified as either hydrolyzable or condensed (non-hydrolyzable) tannins based on their structural type and their reactivity toward hydrolytic agents, particularly acids (Haslam, 1966).

The preparation of beans for consumption usually involves soaking in water to raise moisture content ranging between 53-57%, followed by cooking. The soaking and cooking characteristics of dry beans are important in any effort to

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improve nutrient delivery through increased utilization. uniform hydration and appropriate cooking of beans facilitates denaturation of protein and inactivation of toxic protein such as trypsin inhibitors and other proteases, and make them palatable. Bressani, et al. (1963) reported a reduction in protein efficiency ration from 1.08 to 0.63 of beans cooked for 30 and 180 minutes, respectively. One of the major limitations in the utilization of dry beans is the increase in cooking time that occurs when dry beans are stored at high temperatures and humidity (Morris, 1956 ; Muneta, 1964).

The culinary quality of dry edible beans is an aggregate of properties perceived by consumers and processors that have bearing on their preferences and requirements for dry and cooked grains (Hosfield, et al. 1984). There is more awareness on the part of the consumers in regard to characteristics relating to bean color and appearance, ease of preparation, wholesomeness , texture and digestibility.

The recognition of the nutritional importance of dry beans in the diets of a large proportion of consumers in the poorer countries of the world has led to breeding programs aimed at improving nutritional quality and ease of cooking. Realization of these goals could lead to an increased utilization ofbeans on a world basis.

This research investigation was part of an initiative to help improve nutrient availability and utilization of

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beans in human diets. A paucity of genetic information on nutritional and culinary traits in beans has hampered the development of efficient breeding strategies. The objectives of this research were to: (1) to study the inheritance of cooking time and the uniformity of cooking of individual grains, (2) ascertain the inheritance of tannin content in the seed coat and protein content of raw and cooked bean seed and (3) determine the genetic control of culinary quality traits.

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CHAPTER 1

GENETIC CONTROL OF COOKING TIME AND UNIFORMITY OF COOKING IN DRY EDIBLE BEANS (*Phaseolus vulgaris* L.)

Abstract

Prolonged cooking is one constraint that limits beans in diets of people in poor countries of the world. The presence of genetic variability for this trait would allow plant breeders to develop bean cultivars that are fast cookingandin which the individual grains cook to eating softness uniformly. The objective of this study was to investigate the genetic of cooking time to eating softness and uniformity in cooking of individual seeds. Eight parents were crossed in diallel fashion and genetic analyses of the F_2 and F_3 generations were made. Highly significant GCA and SCA were observed for cooking time but only GCA was significant for cooking uniformity. Examination of GCA effects of parents for cooking time revealed that fast cooking parents produced progenies that were also fast cooking. Highly favorable GCA effects for cooking time persisted in the F_3 generation indicated that selection could be practiced in the F_2. The V_r, W_r graphic analysis indicated that cooking time and uniformity in the parents were controlled by a system of genes that exhibited complete dominance.

Additional index words: diallel cross, general combining ability, specific combining ability, complete dominance, selection strategy.

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INTRODUCTION

Dry edible beans (Phaseolus vulgaris L.) are generally soaked and must be cooked before eating. Cooking tenderizes the cotyledons and increases palatability, renders protein and starch digestible, and inactivates endogenous toxic factors that can markedly limit final nutritional value.

Energy for cooking is becoming a limiting resource on a world wide basis. Some dry beans have a special problem in that they require a long cooking time with a high energy input to render them soft enough for eating. Prolonged cooking is one constraint that limits the utilization of beans in diets. The increased cost of energy required to cook beans, and the scarcity of fuels needed for preparation are forcing many consumers in poorer countries to turn away from eating beans.

Although beans with a relative short cooking time are needed in lesser developed countries, rapid and uniform cooking cultivars are also important characteristics for beans produced in the U.S.A. This is because a large proportion of U.S. grown beans, especially those that comprise colored seed coated market classes, are exported.

Although technological means are available to cook beans more quickly, these are energy intensive and require the addition of a large amount of sodium or phosphate salts to the cooking medium (Rockland, 1972). Increased salt consumption by swine, rats, and humans over a period of time

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has been associated with detrimental physiological effects (Gwotkin and Plummer, 1946; Hartroft, 1967; Altschul and Grommet, 1980).

The development of beans with a relatively short and uniform cooking time would be a useful plant breeding objective. It would save fuel, thus reducing costs and increase utilization through shorter preparation time. Since the application of heat to beans causes starch to gelatinize, protein to denature, pectic substances to precipitate, and cellular deformation, cooking time is probably a complex trait.

The present investigation was undertaken to ascertain through genetic analysis of an 8-parent diallel cross, the type of gene action involved in cooking time of beans. A further objective was to determine whether dry bean strains cooked uniformly and if this characteristic shows genetic variability.

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MATERIALS AND METHODS

Eight strains of dry beans adapted to the bean production areas of Michigan and differing in seed coat color, nutritional and culinary quality, growth habit and resistance to pests and environmental stresses were used as parents in the study. The strains Brasil-2 (B-2), FF 16-15-1-CM-M-M (FF), 15-R-148 (15-R), A-30, Black Turtle Soup (BTS), Sanilac (SAN), San Fernando (SF) , and Nep-2 (N-2) comprised a broad genetic base (Table 1) and were crossed in all possible combination in the winter of 1980-1981. The 8 parents and 56 F_1 hybrids were space planted in an unreplicated plot in a nursery the following summer. The seeds from the 8 parents and the F_1 plants from each cross were harvested in late September and bulked. A sample of seed from each parent and F_2 progeny was sent to the University of Puerto Rico, and planted in a winter nursery at the experimental farm at Isabela. In the summer of 1982, the F_3 and parental seed produced in Puerto Rico and remnant F_2 and parental seed produced in Michigan in the previous year were tested for time and uniformity of cooking at Pullman, Washington. The seeds of the 8 parents and 56 F_2 and parents and 56 F_3 progenies were divided into triplicate samples which served as laboratory replication and evaluated using the Washington State University modification (Hudson 1982) of the experimental bean cooker described by Mattson and Morris (1946). Since the experimental cooker operated on

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a force induced puncture principle brought about by gravity, the device will be referred to as the pin fall apparatus (PFA). The PFA contained 100 aluminum test cells arranged in a 10 x 10 grid. Each cell was filled with an individual bean. Prior to placing each bean in a cell, it was scarified by nicking a corner on the side opposite of the hilum, soaked for 12 hours in tap water at 27° C, and blotted dry. Each bean was placed in a cell of the PFA so it lay in a tangential plane. A small piece of seed coat on the upper and exposed bean surface was carefully peeled away to reveal a cotyledon. The 100 hollow stainless steel rods of the PFA each with a 1.47 mm flat tip and previously filled with 90.6±0.2 g of No. 8 bird shot were rested on the exposed cotyledon of each seed. The PFA with 100 seeds and 100 weighted rods (plungers) resting on each seed was lowered by a winch into a water bath at 93.3° C and cooked for 60 min. The time it took each bean to soften and the weighted plunger to penetrate was recorded. Ten seed of each strain were cooked simultaneously and ten strains were evaluated together in any replication. Any seed of an entry that did not soften during cooking (plunger did not penetrate) was considered as uncooked and hard seed. After 60 minutes, data were taken on each entry for average cooking time and percentage of hard (uncooked) seeds.

Statistical Analysis. All data were analyzed on an entry mean basis using the analysis appropriate to a randomized complete block design. Because the variation associated with

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entries was significant for the traits, analyses of combining ability were performed using the formulas of Griffing's (1956) model I, method I. These analyses were extended to include the partitioning of reciprocal variation into maternal and nonmaternal sources according to Cockerham (1963). In Griffing's (1956) model I all effects are fixed and the experimental material is the population about which inferences are made. Components of genetic effects for combining ability and reciprocal variations were computed using least square estimates according to Cockerham (1980). The effects model appropriate to this study were:

$$Y_{ijk} = \mu + b_i + g_j + g_k + s_{jk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$= \mu_G + b_i + A_j + A_k + \delta_{jj}D_{jj} + \delta_{jk}D_{jk} + \delta_{kk}D_{kk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$E(\hat{g}_j) = E\left[\, 1/2bp\ (Y_{.j.} + Y_{..j}) - \hat{\mu}\ \right]$$

$$= (A_j - \bar{A}_.) + \delta_{jj}(D_{jj} - \bar{D}_{jj.}) + \delta_{jk}(\bar{D}_{j.} - \bar{D}_{..})$$

$$E(\hat{s}_{jk}) = E\left[1/2b\ (\ Y_{.jk} + Y_{.kj}\ ) - \hat{\mu} - \hat{g}_j - \hat{g}_k\right]$$

$$= \delta_{jk}(D_{jk} - \bar{D}_{j.} - \bar{D}_{.k} + \bar{D}_{..})$$

Where:

μ is the population mean

b_i is the i^{th} block effect, $\Sigma b_i = 0$

g_j is the GCA effect associated with the j^{th} parent, $\sum_j^p g_j = 0$

s_{jk} is the SCA effect associated with the cross between the j^{th} female and the k^{th} male parents, $s_{jk} = s_{kj}$, $\sum_k^p s_{jk} = 0$

m_j is the maternal effect associated with the j^{th} parent when it is used as a female, $\sum_j^p m_j = 0$

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r_{jk} is the reciprocal effect associated with the cross between the j^{th} female and k^{th} male parent, $r_{jk}=-r_{kj}$, $\sum_{k\neq j}^{p-1} r_{jk}=0$

e_{ijk} is the error term associated with the j^{th} and k^{th} parent in the i^{th} block, $E_{ijk}\sim ND(0,\hat{\sigma})$

A_j is the sum of the additive effects for genes in a gamete from j^{th} parent.

$\bar{A}.$ is the mean additive effect.

$\bar{D}..$ is the mean dominance effect of the hybrid diallel population.

D_{jj} is the sum of the dominance effects associated with the jj^{th} parent.

$\bar{D}_{jj}.$ is the mean of the dominance effects associated with the j^{th} parent

$\bar{D}_{j}.$ is the mean of the dominance effects associated with progeny of the j^{th} parent

D_{jk} is the sum of the dominance effects for genes from mating of j^{th} parent with k^{th} parent

δ_{jj} is the expected proportion of loci homozygous for the allele derived from the j^{th} parent, $\delta_{jj}=1/2F$

δ_{jk} is the expected proportion of heterozygous loci, $\delta_{jk}=1-F$.

Analyses of covariance between the offspring of each parent (array) and the nonrecurrent parent minus the variance of their offspring in each parental array (W_r-V_r) were performed according to Hayman's (1954a, b) analyses of diallel experiments to ascertain whether gene expression was appropriate to an additive dominance model or whether

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appropriate to an additive dominance model or whether epistasis was a general feature of the system. A significant F test for the arrays indicate a failure of one or more of the seven assumptions underlying Hayman's diallel cross theory (1954a,b).

Genetic relationships among the parents were studied with the variance-covariance (V_r, W_r) graphical analysis technique developed by Jinks (1954) and Hayman (1954a, b). The V_r, W_r graph was drawn for the means of three replications. If the regression coefficient (b) of a graph was not significantly different from zero, a disturbance in the assumptions underlying the diallel analyses of Hayman (1954 a, b) was implied. To continue the analysis in the event of a disturbance, it was necessary to determine whether epistasis was a general feature of the genetic system, or whether it was due mainly to the influence of one or few parents. The procedure followed was suggested by Hayman (1954) and involved the removal of parental arrays until a subset of the diallel table is found that meets all the assumptions.

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RESULTS

The analyses of variance of cooking time and % hard seed indicated that significant differences existed in the F_2 and F_3 among parents and crosses for these traits (Table 2). This permitted the partitioning of among-entry variation into general and specific combining ability (GCA and SCA, respectively) and reciprocal effects. The analyses of variance of (W_r-V_r) exhibited no significant differences among the arrays (Table 3) indicating that the additive dominance model was adequate to describe the gene action involved in the expression of the traits. The F tests of GCA and SCA were highly significant for cooking time in both F_2 and F_3 generations, and the GCA mean square was highly significant for percent hard seed in both generations (Table 4). No differences were noted for SCA for the hard seed character. Significant reciprocal effects were present and were due to both maternal and nonmaternal causes (Table 4).

Estimates of variance components computed from the formulas outlined by Griffing (1956) revealed that variances of GCA effects predominated in the F_2 for percent hard seed while SCA effects predominated for cooking time (Table 4). In the F_3 generation these estimates were about equal for both traits (Table 4). General combining ability effects calculated for each parent indicated that B-2 and 15-R transmitted more genes for a longer and nonuniform cooking

time to their F_2 progenies than did the other parents (Table 5). San Fernando in addition to B-2 and 15-R, transmitted genes for prolonged cooking time and hardseededness to F_3 progeny (Table 5). A similar trend was observed when the mean of the parents was compared with the mean of crosses for cooking time in each generation (Table 6). Parents with longer cooking time generally produced progenies, that required a longer time to cook whereas the quicker cooking parents produced quicker cooking progenies (Table 6).

Examination of the V_r, W_r graphs for cooking time and percentage hard seed provide specific information on the type of gene action involved in trait expression for each parent and the relationship among parents for dominance or recessiveness of the trait (Fig.1,2,3 and 4). The regression coefficient of W_r on V_r for cooking time of the 8 parental arrays in the F_2 at East Lansing was significantly different from unity but not significantly different from zero. This indicated a failure in one or more of the diallel analysis assumptions (Hayman 1954 a, b) and prompted the elimination of A-30 (parent 4) from the analysis because it had an exceedingly large covariance. The subsequent analysis (A-30 eliminated) showed the regression coefficient to be significantly different from zero but not from unity (Fig. 1). Figure 1 showed that the regression line intersected the W_r axis slightly below the origin and was not significantly different from zero indicating that complete dominance governed the genes for cooking time. The position of the

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array point for B-2, SAN, and N-2 was distal to the origin on the V_r, W_r graph (Fig. 1) indicating that these strains carried a preponderance of recessive alleles for cooking time. The strains BTS and SF carried predominantly dominant genes for cooking time. The strains FF and 15-R exhibited genic interaction because these showed a high variance relative to covariance for cooking time (Fig. 1). The V_r,W_r graph for cooking time of F_3 seeds (produced in Puerto Rico) showed that the regression coefficient was significantly different from zero but not significantly different from a unit slope (Fig. 2). The intercept of the regression was above the origin and was not significantly different from zero indicating that complete dominance controlled the expression of this trait. Strains 15-R, A-30, SAN and N-2 clustered together close to the origin suggesting that these arrays carried an excess of dominant genes for cooking time. BTS and SF carried more dominant than recessive alleles while B-2, and FF exhibited a preponderance of recessive genes. The change in position of array points from the F_2 (seed produced in East Lansing) and F_3 (seed grown in Puerto Rico) indicated that generation and environmental effects both may have influenced the expression of cooking time.

The V_r,W_r graph for percent hard seed in the F_2 (Fig.3) showed that the regression coefficient was significantly different from zero but not significantly different from unity . The intercept of the regression line was above the origin and not significantly different from zero indicating that among the 8 parents overall, completely dominant genes

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controlled this trait. Within the set of parents, A-30, BTS and SF had mostly dominant genes for percent hard seed while B-2, SAN, FF and N-2 had both dominant and recessive genes for this trait. Strain 15-R had mostly recessive genes for percentage of hard seed.

Figure 4 showed that the percentage of hard seed in the F_3 generation was controlled by genes that exhibited complete dominance. The distribution of points representing the parental arrays showed that B-2 and BTS had a preponderance of recessive genes while the remaining 6 strains carried mostly dominant alleles for this trait (Fig. 4). The position of the points corresponding to the parental arrays near the limiting parabola (Fig. 4) indicated that these parents carried completely recessive alleles for percentage of hard seed. The proximity of points to each other suggested that these parents had a similar genetic make up for hard seeded trait and that differences among them were probably due to difference in background genes.

Table 1. (

Strain	
Brasil-2	
FF 16-15	
15-R-145	
A-30	
Black Tu	
Soup	
Sanilac	
San Fern	
Nep-2	

* = Incr
soaking
after 72
Y = Data

Table 1. Characteristics of 8 genotypes used in a diallel cross.

Strain	Source	Testa color	Wt.gain* after soaking (g)	Cooking time (min.)	Hard Texture[z] (Kg/100g)	seed (%)
Brasil-2	CIAT	Beige	11.5	30.1	469	3.6
FF 16-15-1	MSU	Red	11.1	27.9	992	5.9
15-R-148	UW	Red	9.5	40.3	870	24.6
A-30	CIAT	Yellow	5.1	35.1	1033	56.4
Black Turtle Soup	MSU	Black	11.6	30.7	665	0.0
Sanilac	MSU	White	11.4	26.3	605	0.0
San Fernando	MSU	Black	y	36.4	y	y
Nep-2	MSU	White	y	28.4	y	y

* = Increasein weight of 10 gram of seed after48hourof soakingin deionized water,z = Kg force per 100 gram of sample after 72 hour of soaking and 30 minutes of cooking at 93°C.
y = Data not taken.

Table 2.

Source of variation	
Entry	
Error	

** = Signif
z = The F_2
Puerto

Table 2. Mean squares of analyses of variances for cooking time and percent hard seed in F_2 and F_3 generation.

Source of variation	d.f.	Cooking time[z] (min)		Hard seed[z] (%)	
		F_2	F_3	F_2	F_3
Entry	63	51.54**	61.32**	63.72**	258.20**
Error	126	7.93	2.74	29.72	134.69

** = Significant at 1% probability level.
z = The F_2 data are from E. Lansing and the F_3 data are from Puerto Rico.

Table 3

Source of varia	
Array	
Error	

z = The
Puerto R

Table 3. Mean squares from analyses of variances of(W_r-V_r) for cooking time and percent hard seed to test the adequacy of additive-dominance model.

Source of variation	d.f.	Cooking time[z] (min.)		Hard seed[z] (%)	
		F_2	F_3	F_2	F_3
Array	7	35.0	34.8	173.1	833.2
Error	63	21.6	29.4	122.4	2399.4

z = The F_2 data are from E.Lansing and the F_3 data are from Puerto Rico,respectively.

Table 4.

Mean squa
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of varian

Mean squa	
Crosses	
GCA	
SCA	
Reciproca	
Materna	
Nonmate	
Recipro	
Error	
Component variance	
GCA	
SCA	
Reciproca	
MR	
NMR	

y,z = Gr
*,** sig

Table 4. Analyses of variance and estimates of variance components and their standard errors for general and specific combining ability and reciprocal effects for cooking time and percent hard seed measured on F_2 and F_3 progeny of an 8x8 diallel cross grown at two locations in 1981.

Mean squares and components of variance	d.f.	Cooking time (min.) F_2^y	Cooking time (min.) F_3^z	Hard seed (%) F_2^y	Hard seed (%) F_3^z
Mean squares					
Crosses	63	15.30**	20.39**	21.15**	87.20**
GCA	7	52.63**	107.03**	77.50**	278.78**
SCA	28	12.57**	9.65**	11.30	58.63
Reciprocal	28	8.71**	9.46**	16.90*	67.86
Maternal(MR)	7	5.55	15.67**	14.28	42.30
Nonmaternal Reciprocal(NMR)	21	9.76*	7.39	17.77*	76.38
Error	63	2.64	4.25	9.91	44.90
Components of variance					
GCA	7	3.12±1.55	6.42±3.15	4.22±2.29	14.62± 8.23
SCA	28	9.93±3.28	5.40±2.60	1.39±3.39	13.73±17.06
Reciprocal	28	3.03±1.19	2.61±1.32	3.49±2.42	11.48± 9.91
MR	7	0.18±0.17	0.71±0.46	0.27±0.44	0.0
NMR	21	3.56±2.91	1.57±2.30	3.93±2.76	15.73±11.93

y,z = Grown at East Lansing and Puerto Rico, respectively.
*,** significant at 5 and 1 % probability level, respectively.

Table 5.

Parents
B-2
FF
15-R
A-30
BIS
SAN
SF
N-2
$S\bar{Y}$
$S\bar{D}$

z=The F
Puerto
$S\bar{Y}$, $S\bar{D}$
between

Table 5. Estimates of general combining ability effects for cooking time and percent hard seed measured on F_2 and F_3 generation means of an 8-parent diallel cross grown at two locations in 1981.

	Cooking time[z]		Hard seed[z]	
Parents	F_2	F_3	F_2	F_3
B-2	1.74	2.08	1.09	5.32
FF	-1.68	-5.26	0.06	-5.10
15-R	3.53	2.04	4.85	3.44
A-30	-1.51	-1.81	-2.03	-2.38
BTS	-0.56	0.34	-1.62	1.77
SAN	-1.41	0.33	-1.20	-2.60
SF	0.16	2.66	-0.15	4.26
N-2	-0.27	-0.38	-0.99	-4.70
$S_{\bar{Y}}$	0.38	0.48	0.74	1.57
$S_{\bar{D}}$	0.58	0.73	1.11	2.37

z=The F_2 data are from E.Lansing and the F_3 data arefrom Puerto Rico.

$S_{\bar{Y}}$, $S_{\bar{D}}$ standard error and standard errore of the difference between two means, espectively.

Table 6. Mea
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Strain
3-2
??
15-R
A-30
BTS
SAN
SF
N-2

Y,Z = Grown

Table 6. Mean cooking time (min) of parents and crosses involving the parents in F_2 and F_3 generation grown at two locations in 1981.

Strain	F_2[y]		F_3[z]	
	Parents	Crosses	Parents	Crosses
B-2	30.1	36.8	50.0	42.2
FF	27.9	33.2	29.0	36.8
15-R	40.3	37.4	40.7	43.5
A-30	35.1	32.4	37.2	39.6
BTS	30.7	34.1	43.0	41.2
SAN	26.3	33.7	43.0	41.1
SF	36.4	34.1	47.3	43.8
N-2	28.7	34.7	44.2	40.2

y,z = Grown at East Lansing and Puerto Rico, respectively.

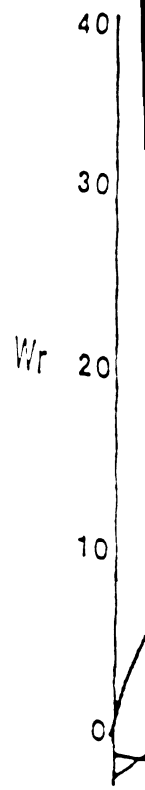

Figure 1.

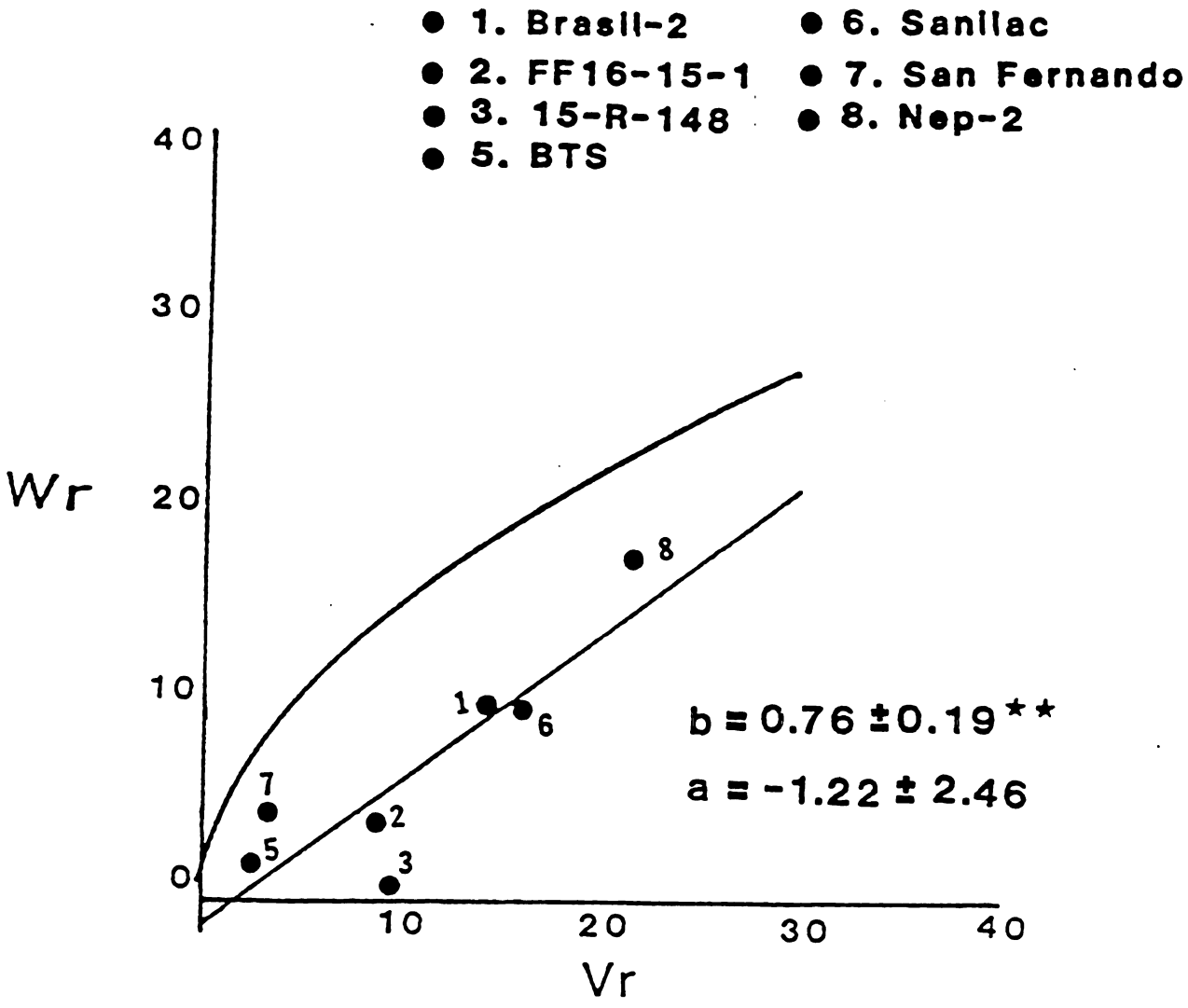

Figure 1. Variance (V_r)-covariance (W_r) graph for cooking time data of the F_2 generation grown at East Lansing and showing the position of points representing the 7 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

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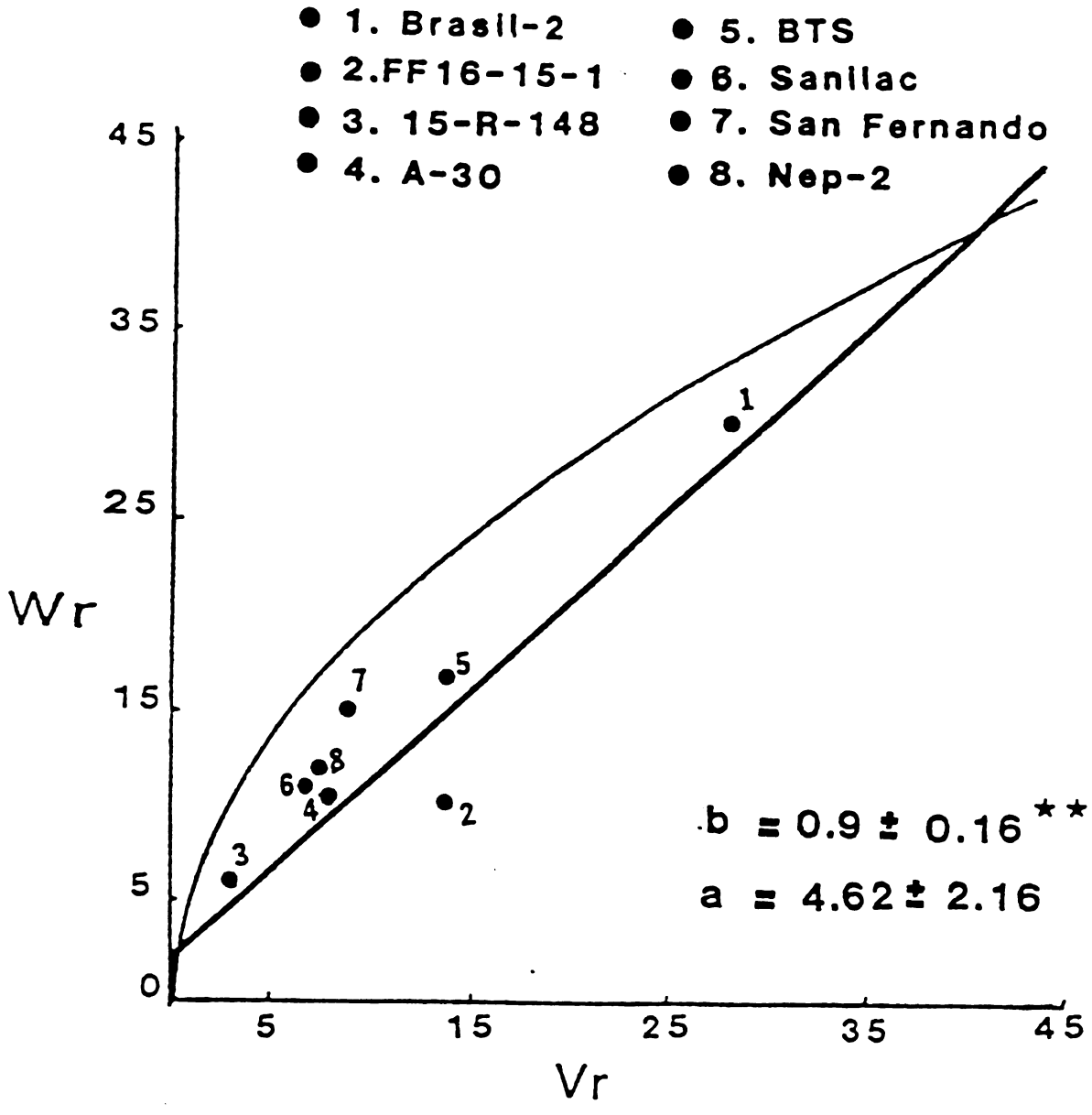

Figure 2. Variance (V_r)-covariance (W_r) graph for cooking time data of the F_3 generation grown at Puerto Rico and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

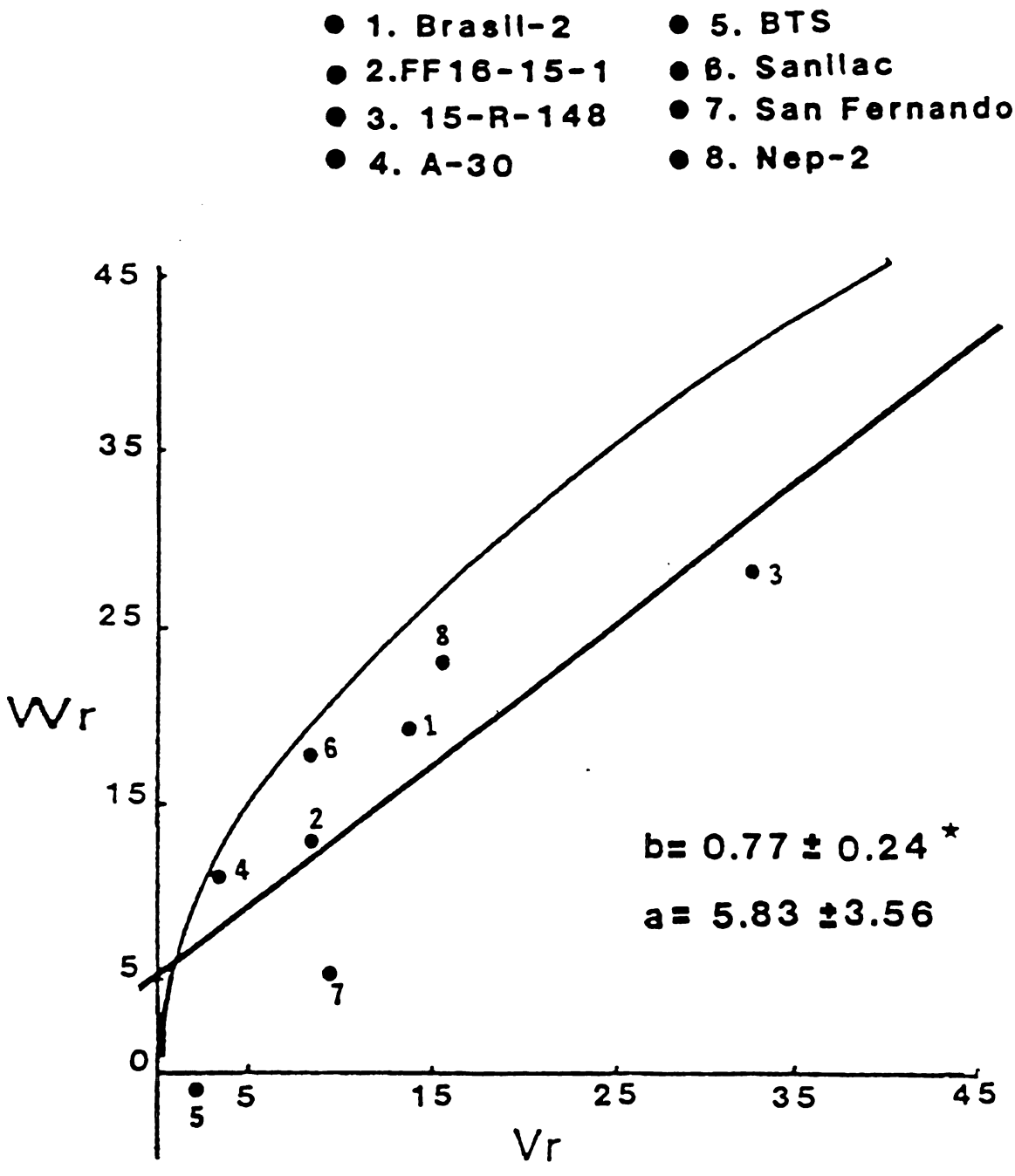

Figure 3. Variance (V_r)-covariance (W_r) graph for % hard seed data of the F_2 grown at E. Lanisng and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

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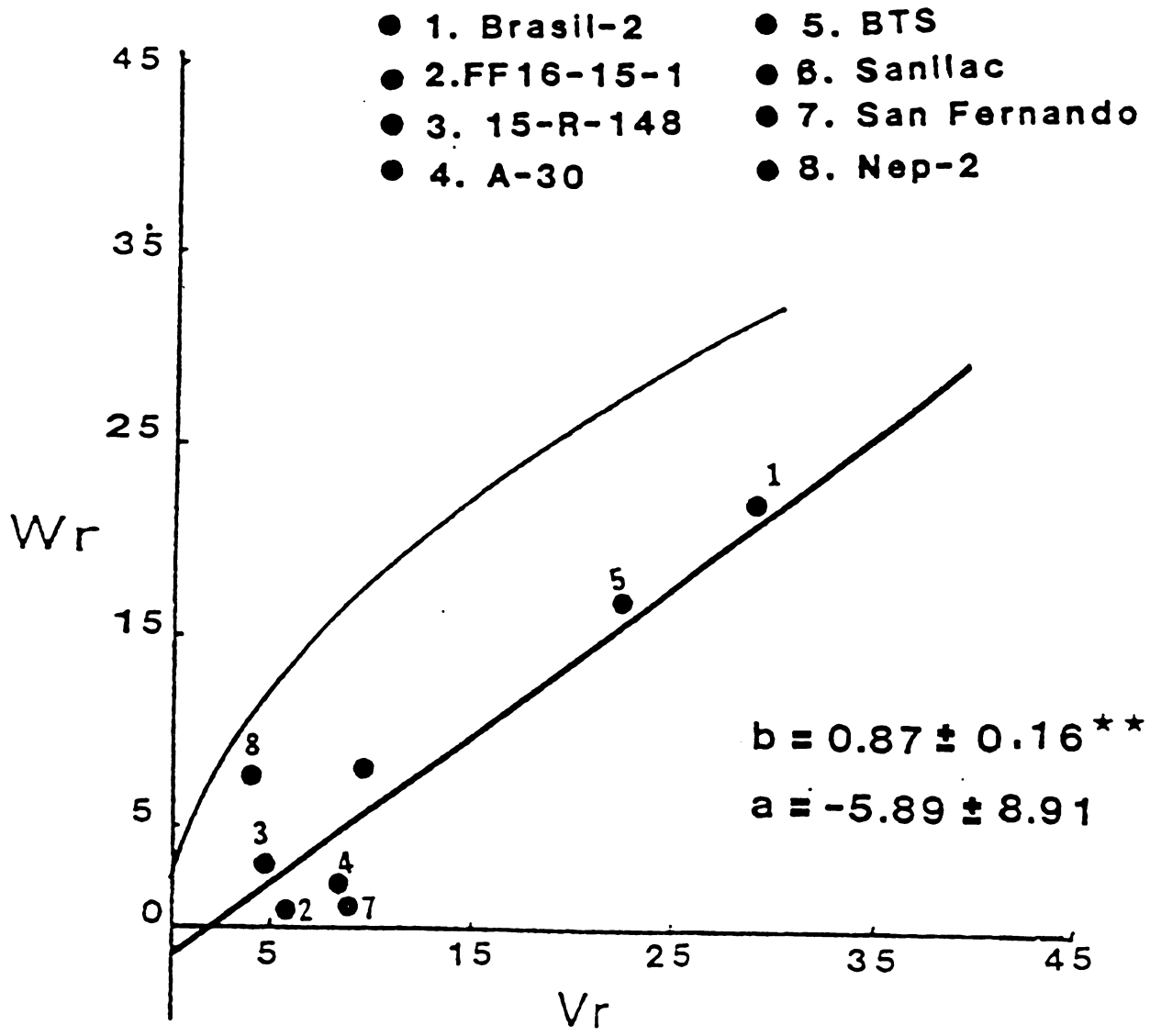

Figure 4. Variance (V_r)-covariance (W_r) graph for % hard seed data of the F_3 grown at Puerto Rico and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

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DISCUSSION

The distribution of array points representing the parents on the V_r, W_r graphs (Fig. 1,2,3 and 4) showed that both dominant and recessive genes controlled the expression of cooking time and percentage hard seed in this population. Parental arrays differed for dominance and recessiveness of trait expression depending on the generation. Differences between the F_2 and F_3 may have been due to location effects (East Lansing and Puerto Rico) or to the change in dominance relationship. This point needs further experimentation to resolve because the effects of location and generation were confounded in the present experiment. The combining ability mean squares indicated highly significant GCA for cooking time and percent hard seed in both F_2 and F_3 generations but the SCA mean square estimates were highly significant only for cooking time (Table 3). The magnitude of GCA was larger than SCA suggesting that the type of genetic variance in the reference population was mostly additive but that non-additive variance was also present and should not be overlooked. The significant GCA mean square for percent hard seed suggested that selection against hard seed defect will not be difficult. Superior performing progeny can be produced by crossing parents with high general combining ability. Parents with large SCA effects could also be crossed and recurrent selection practiced to maximize the use of fixable non-additive genetic variances. In the present study, parents with large negative effects for cooking time

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and percentage of hard seed after cooking would be the superior parents to use in crosses. For example, the use of FF in crosses should lead to an improvement in both traits. Although variance of reciprocal effects were sizable (Table 4) they were of mostly non-maternal origin. Non-maternal reciprocal effects are complex interactions that are difficult to interpret biologically. The use of such effects in plant breeding scheme would be largely unpredictable.

The reduction of cooking time in dry beans would be an important step to increasing the consumption of dry beans in human diets. This is especially true in lesser developed countries where beans are a staple in the diet but the shortage of fuel has forced people to turn away from eating beans. Uniformity in cooking, i.e., reduced percentage of hard seed after cooking, would improve the palatability of cooked beans. This characteristic is important for bean cultivars sold to bean processors in the U.S.A. and would be favored by both domestic and foreign consumers. The significance of this investigation to plant breeders is that it provided information about the genetics of the traits and their consistency in two different generations despite the fact that each generation was grown in a different environment.

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CHAPTER 2

GENETIC CONTROL OF TANNIN CONTENT AND PERCENTAGE PROTEIN OF DRY AND COOKED DRY BEANS (*Phaseolus vulgaris* L.)

ABSTRACT

The presence of tannins in the seed coat of colored beans has been associated with an impaired nutritional benefit from eating beans. Current thinking among breeders favors the strategy of breeding beans with a low tannin content and maintaining or increasing seed protein percentage. The present study investigated the inheritance of tannin and protein content in beans with varying seed coat colors. Eight parents were crossed in diallel fashion to produce an F_2 and F_3 generation on which to evaluate combining ability variance and effects. Tannin content was determined by the vanillin-HCl method and protein percentage was determined using an infrared reflectance analyzer. Parents and progeny differed among themselves for tannin and protein content. Both GCA and SCA mean squares were significant for tannin and protein percentage. Maternal effects for the traits were revealed. Strains that were high and low in tannin and protein content produced progenies that were also high and low in tannin and protein content. The correlations between parental values and their GCA effects for tannin and protein content in the F_2 were r

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= 0.88** and r = 0.94**, respectively. Graphical analyses revealed that both tannin and protein content were controlled by dominant genes.

Additional Index words: Diallel cross, combining ability, polyphenols, nutritional quality, gene action.

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INTRODUCTION

Grain legumes constitute one of the most important sources of food nutrients to the people in many countries of the world. They are good source of protein, carbohydrates, oil, minerals, and vitamins. In dry beans (Phaseolus vulgaris L.) crude protein percentage varies from 17 to 35 % (Meiners and Litzenberger 1975; Evans and Gridely 1979). Although bean protein is not complete, because of a deficiency in sulfur bearing amino acids, it has a high lysine content. High protein and high lysine in beans makes them an ideal complement to cereal based diets (Bressani, 1983).

The presence of variation in the protein content and amino acid profiles of beans indicates that it should be possible to improve this nutrient both qualitatively and quantitatively. Adams (1975) suggested the possibility of increasing seed protein percentage and sulfur amino acid content of dry beans by genetically manipulating regulator genes that control specific protein fractions. Osborne (1894) and Buchbinder (1980) recognized that bean seed protein could be separated into fractions based on solubility. The most abundant fraction had the properties of a globulin and was designated "phaseolin".

Enhanced seed protein percentage has been shown to be due to a increased amount of phaseolin and nonphaseolin protein (Sullivan and Bliss 1983). Breeding lines selected for either high or low seed protein percentage have been

reported to show corresponding increase or decrease in phaseolin content (Ma and Bliss 1979). A 60 % loss in protein content during cooking have been reported in dry beans (Watt, 1963). These losses might be associated with losses of soluble solids during cooking.

In addition to an imbalance in the amino acid complement of beans, antinutritional factors and poor digestibility limits bean nutritional quality. The poor protein digestibility of legumes, and certain cereal grains is in part thought to be caused by complexing of the protein with condensed tannins (Eliase, et al., 1979; Price and Butler 1980). Tannins are known constituents of many cereals and legumes. The type, amount and distribution of tannins within plants are characteristic for each species. Within a particular species, the variation depends on stage of growth, physiological condition of plant, time of year and the genotype (Johanson, 1940; Maxson, et.al. 1972). Tannin content has been shown to be under genetic control in several plant species including dry beans (Parada 1975; Ma 1978; Croft et al. 1980; Woodruff et al. 1982).

The objectives of this study were: 1) to look at the inheritance of tannin in the seed coat of diverse colors of dry bean seed using the diallel cross. 2) To study the inheritance of crude protein.

Protein. Sullivan and Bliss (1983) reported that seed protein percentage can be increased by raising the amount of accumulated protein in relation to a constant amount of non-protein dry matter or, conversely, by reducing the amount of accumulated non-protein dry matter while the total protein fractions remain unchanged. Hence, a change in protein percentage among several lines may be similar but the basis for the change may be different and may reflect differences in the genetic control of synthesis and accumulation of the constituent fractions. Mutschler et al. (1980) found that patterns of accumulation of phaseolin, nonphaseolin seed protein, and non-protein dry matter showed genetic variation, and that the accumulation patterns affected seed protein percentage. Leleji, et al. (1972) reported negative correlations (r=-0.45) between yield and percentage crude protein in F_2 and F_3 plant. Similar low and negative correlation (r=-0.30) between seed yield and percentage protein has been reported by Kelly and Bliss (1975). The same authors also showed that seed yield and percentage available methionine were uncorrelated, but a positive correlation (r=0.33) existed between percentage protein and percentage available methionine.

Definition of Tannins. Tannins are any naturally occurring water-soluble compounds of a high molecular weight (between 500 and 3,000 MW) and containing a sufficiently large number

of phenolic hydroxyl or other suitable groups to enable it to form effective cross-links between protein and other macromolecules (Jones, 1971). Tannins of biological significance are condensed molecules and are often called condensed tannins, condensed polyphenols, and procyanidins.

Localization of tannins. In pulses, the seed coat is tissue of maternal origin, and when the plant senescences, monomeric phenolic compounds are transformed into immobile polymers (condensed tannins and phlobaphenes; Freudenberg, 1962). Since condensed tannins are largely formed after physiological maturity, they might be expected to be found in high concentration in seed coats (Bakshy, et al. 1978). In sorghum (Sorghum bicolor L.) , cultivars with pigmented seed coat and dark pericarp are always higher in tannin content than the light colored cultivars (Freudenberg, 1962). The epicarp, hypocarp, and pericarp layers and testa in sorghum contain tannin and other pigments (Bate-smith, 1969). The presence of these layers is under genetic control (Quinby, 1954). Three major genes, B_1,B_2 and S, have been shown to control pericarp color, and the pigmented testa can significantly affect tannin content in sorghum seeds (Maxson, 1972). The presence or absence of pigments in the seed coat of lima bean (Phaseolus lunatus L.) is determined by a single locus (Allard, 1953). Only in the presence of recessive conditions, is pigment production restricted and a white seed coat results. In the presence of the dominant allele pigment is produced, but the particular pigment color

depends on genes at several other loci. In faba beans (Vicia faba L.) the palisade and hourglass cells are primarily responsible for seed coat thickness, and it is in the cell walls of the palisade cells and lumina of the hourglass cells that condensed tannins are deposited (Erith 1930).

Inheritance of Tannin. In faba bean the white flowers are determined by a single gene and produced a tannin-free seed coat (Croft, et al. 1980). The white flowers have a number of pleiotropic effects resulting in blockage of the production of certain phenolic compounds in stems, stipules, flowers, and testa. In faba beans, several sources of a gene for tannin-free seed coat have been found among cultivars with white flowers and white (or buff) seeds. There are at least two different complimentary genes that confer the tannin-free characteristic, suggesting that the synthesis of condensed tannins can be blocked in at least two different stages (Picard, 1976). Among the tannin-containing cultivars of faba beans there is a wide range of tannin concentration, but a considerable amount of the variability is due to environmental variation (Marquardt et al. 1978). On the other hand, the analysis of four F_2 populations of dry beans resulting from crosses between lines differing in tannin content revealed both a continuous and discontinuous pattern of inheritance (Ma, 1978). One F_2 population did not deviate significantly from an expected model of one incomplete dominant gene for tannin content. The other three F_2 populations showed a continuous pattern of inheritance (Ma 1978). Moreover, low tannin was dominant to high

tannin and broad sense heritabilities were 0.84 to 0.97. These results indicated that a few genes are probably responsible for genetic differences in tannin content. In sorghum tannin content has been shown to be controlled by few genes (Woodruff, et al. 1982) and low tannin was dominant to high tannin in one case Parada (1975) and high tannin to low in another case (Woodruff, et al. 1982). In birdsfoot trefoil (Lotus corniculatus L.) tannin content was controlled by a single gene and high tannin was dominant to low (Dalrymple, et al. 1984). In dry beans, the F_2 segregation for tannin content was not associated with a particular seed coat (Rannenkamp, 1977). This implies that tannin content and seed coat color are independently inherited.

Biological effects of tannins. Studies on tannins in different crops have indicated that tannin may affect the nutritional quality of and/or disease resistance (Lindgren 1975; Schaffert 1974; Staller 1970). Butler (1978) ascribed low nutritional value of high-tannin sorghum to the interaction of tannins with either dietary protein, lowering its digestibility, or with proteins from the digestive tract, diminishing the effectiveness of the digestive processes. A high tannin sorghum contains enough tannin to precipitate under optimal conditions more than twice as much protein as is in the grain. Feeding trials of rats (Butler, 1978,1982; Handler 1944; Joslyn 1969; Lease 1940) and poultry (Ringrose 1940; Rockland 1972) have shown that a small percentage of tannic acid in the diet resulted in lower

weight gains of experimental animals. When different sorghum cultivars were used to supply 50% of the diet of chicks, the cultivars with high tannin content produced a slow growth and similar to that produced when the same level of tannic acid was added to the diet (Chang 1964). The in vitro digestibility of faba bean seed coats by ruminant bacteria was three times greater when they contained no tannin (Bond 1976). It seemed likely that tannin inhibits enzyme systems responsible for fiber digestion either by inhibiting cellulases or other carbohydrases, or by inducing nitrogen deficiency in the in vitro systems due to protein binding, or both (Schaffert 1974). In a rat feeding trial using dry beans, a reduction in protein efficiency and weight loss was found with increased tannin content (Rannenkamp 1977). In poultry feeding trials with tannin-free and tannin-containing faba beans, nutrient retention increased with tannin-free cultivars (Marquardt 1979). In the same experiment, autoclaving of tannin-containing faba beans affected their use by presumably destroying condensed tannins which accounted for approximately one-half of the total growth depression.

However, not all workers agree that condensed tannin is an anti-nutritional factor. Feeding trials in rats, poultry, and pigs failed to show differences in feed intake and improved digestibility when faba beans with and without the testa and raw and autoclaved were compared (Muller 1953; Sjodin 1973; Wilson 1972).

It has been shown that condensed tannins retarded

preharvest seed germination in sorghum (Harris 1970), wheat (Triticum aestivum L.) Stoy (1976) and barley (Hordeum vulgare L.) Jacobson (1977). Tannins act as gibberellin antagonists in germinating wheat and barley seed, and the growth of cucumber (Cucumis sativus L.) and pea (Pisum sativum L.) seedlings (Corcoran 1972). High concentrations of phenolics and their derivatives have been found around points of infection in plants. In faba beans Levin (1971) reported an inhibitor of polyphenoloxidase. When this inhibitor was destroyed, the polyphenols were oxidized into compounds which inhibited the growth of pathogenic fungi. In certain herbaceous legumes, tannins complexing with proteins can be advantageous in preventing bloat in ruminants (Jones 1971). On the other hand, the disadvantage of tannin-containing plants is their astringency and low palatability that discouraged animal feeding (Abdalla 1976; Donnelly 1969).

MATERIAL AND METHODS

Genetic material. Twenty strains of dry beans were grown in a replicated nursery during the summer of 1980 at the Montcalm Research Farm near Stanton, Michigan. These strains comprised a broad genetic base and differed in seed-coat color, size, and shape. They varied in growth habit and plant morpholoIgy, reaction to heat and drought stress, seed filling characteristics, maturity, and yield.

After harvesting and threshing plants from one replication in the fall, seeds of each strain were evaluated for protein percentage, tannin content, and soaking characteristics including the percentage of hard seed after 48 hours soaking time (Wassimi, 1981). Based on the characteristics of dry and soaked seed, 8 strains (Table 1) were selected for genetic analysis of tannin content, and percentage crude protein. All possible F_1 hybrids were made in the greenhouse during the winter of 1980-81. The 56 F_1 crosses and 8 parents were grown in a nursery in East Lansing during the summer of 1981 to produce F_2 seed.

Field plot procedure. The F_2 seed from each cross was harvested in bulk in September of 1981, and a sample from each parent and each cross was grown in a winter nursery in Puerto Rico in the winter of 1981. Parental and F_3 generation seed was harvested in March of 1982 bulked and returned to East Lansing, Michigan. A random sample of 800 seeds from each cross of the Puerto Rico produced F_3 generation and parental strains and the remnant F_2 and 8

parents grown in Michigan the previous year were planted in an 11 x 12 rectangular lattice with three replications at the Saginaw Valley Bean and Sugar Beet Research farm near Saginaw and at East Lansing, Michigan in May and June of 1982. Seeds were precision drilled with a tractor mounted air planter (Taylor, 1975) into two row plots guarded on each side by the cultivar `Seafarer'. Rows were 4.9 meter long and 50.8 cm apart. Herbicide and fertilizer applications were made per seasonal recommendations.

Mature plants were harvested and threshed from a 6 meter row length of each plot in mid-to-late September. Clean seeds were used to determine percentage protein and tannin content.

Sample preparation

1. Crude protein. About 30 g of raw bean seed and 30 g from the dry cooked beans from another experiment of both F_2 and F_3 generations and grown at Saginaw and East Lansing were ground to a 40 micron particle size with a Udy- cyclone mill. The percent crude protein was determined on the dry and cooked bean flour with a Neotec GQA (model 31) near infrared reflectance (NIR) grain quality analyzer.

2. Tannin determination. For tannin determination only F_3 seed grown in two replications at each location were used. A random sample of 200 seed from each cross and parents was taken. The seeds from the crosses were separated according to testa color because of segregation for color in the progeny from variable testa colored parental material used

in the diallel cross. Based on the number of seeds for each color obtained from a cross, the proportion of each color that could comprise a 20 seed sample was determined and a composite of 20 plump seed prepared. Each individual seed was split in half and soaked in about 10-15 ml of n-Heptane for 12 hours. This facilitated removal of the seed coat by dissolving waxes. The heptane was decanted, and the seed coat was carefully removed using a fine pointed scalpel. The excised seed coat was dried for 12 hours at 60° C, and ground with a Wiley mill and passed through a no. 40. screen.

Methods of tannin determination. The vanillin hydrochloric acid method of Burns (1971) as modified by Telek (1983) was used to estimate tannin content. Since in the tannin procedure catechin equivalent is used as a standard, tannin content was estimated as % catechin equivalent. However, for purpose of this paper % catechin equivalent will herein after be referred to as % tannin. A detailed description of % crude protein extraction and determination of % tannin content are given in appendix A.

Statistical procedures. Separate analyses of variance were performed on F_2 data for tannin content and F_2 and F_3 for % protein at each location to test for variability among entries. Tests of homogeniety of error variance were also made. Error variances were found to be homogeneous by Bartlett's procedure described in Steel and Torrie (1980). Analyses of variance of combined data were computed. Data were subjected to combining ability analyses of model I

method I of the diallel cross of Griffing (1956). The fixed effects model of Cockerham (1980) was applied to the data and solved by unweighted least square procedure. The model was fitted to include general and specific combining ability effects and is as follows:

$$Y_{ijk} = \mu + b_i + g_j + g_k + s_{jk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$= \mu_G + b_i + A_j + A_k + \delta_{jj}D_{jj} + \delta_{jk}D_{jk} + \delta_{kk}D_{kk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$E(\hat{g}_j) = E\left[\ 1/2bp\ (Y_{.j.} + Y_{..j}) - \hat{\mu}\ \right]$$

$$= (A_j - \bar{A}_{.}) + \delta_{jj}(D_{jj} - \bar{D}_{jj.}) + \delta_{jk}(\bar{D}_{j.} - \bar{D}_{..})$$

$$E(\hat{s}_{jk}) = E\left[1/2b\ (\ Y_{.jk} + Y_{.kj}\ ) - \hat{\mu} - \hat{g}_j - \hat{g}_k\right]$$

$$= \delta_{jk}(D_{jk} - \bar{D}_{j.} - \bar{D}_{.k} + \bar{D}_{..})$$

Where:

μ is the population mean

b_i is the i^{th} block effect, $\Sigma b_i = 0$

g_j is the GCA effect associated with the j^{th} parent, $\sum_{j}^{p} g_j = 0$

s_{jk} is the SCA effect associated with the cross between the j^{th} female and the k^{th} male parents, $s_{jk} = s_{kj}$, $\sum_{k}^{p} s_{jk} = 0$

m_j is the maternal effect associated with the j^{th} parent when it is used as a female, $\sum_{j}^{p} m_j = 0$

r_{jk} is the reciprocal effect associated with the cross between the j^{th} female and k^{th} male parent, $r_{jk} = -r_{kj}$, $\sum_{k \neq j}^{p-1} r_{jk} = 0$

e_{ijk} is the error term associated with the j^{th} and k^{th} parent in the i^{th} block, $E_{ijk} \sim ND(0, \sigma^2)$

A_j is the sum of the additive effects for genes in a gamete from j^{th} parent.

$\bar{A}.$ is the mean additive effect.

$\bar{D}..$ is the mean dominance effect of the hybrid diallel population.

D_{jj} is the sum of the dominance effects associated with the jj^{th} parent

$\bar{D}_{jj}.$ is the mean of the dominance effects associated with the j^{th} parent

$\bar{D}_{j}.$ is the mean of the dominance effects associated with progeny of the j^{th} parent

D_{jk} is the sum of the dominance effects for genes from mating of j^{th} parent with k^{th} parent

δ_{jj} is the expected proportion of loci homozygous for the allele derived from the j^{th} parent, $\delta_{jj}=1/2F$

δ_{jk} is the expected proportion of heterozygous loci, $\delta_{jk}=1-F$.

Analyses of covariance between the offspring of each parent (array) and the nonrecurrent parent minus the variance of their offspring in each parental array (W_r-V_r) were performed according to Hayman's (1954a, b) analyses of diallel experiments to ascertain whether or not gene expression was appropriate to an additive dominance model or epistasis was a general feature of the system.

Genetic relationships among the parents were studied with the variance-covariance (V_r, W_r) graphical analysis technique developed by Jinks (1954) and Hayman (1954a, b). The V_r, W_r graph was drawn for the means of two replications.

RESULTS

Tannin content. The individual analyses of variance showed highly significant differences among entries for percent catechin equivalent (Table 2). Combining ability analyses of variance of separate location data for % tannin revealed highly significant GCA and maternal effects present in this population (Table 3). The SCA and nonmaternal reciprocal effect variances were significant only at Saginaw (Table 3). Estimation of the variance components for GCA, SCA, and reciprocal effects mean squares showed that GCA variance predominated in trait expression (Table 3). The GCA effects for % tannin calculated for each parent revealed that A-30, SAN and N-2 transmitted genes that reduced the tannin content of their progenies at both locations while the other five strains imparted a high % tannin content to their progenies (Table 4).

The combined analyses of variances revealed that interaction of combining ability and reciprocal variation with location was absent (Table 5). Reciprocal effects determined for each parent indicated that significant maternal variation was probably due to large maternal effects associated with FF (0.32), 15-R (-0.32), and SF (0.45) (data not given). The GCA effects in the combined analyses were consistent with those found in the separate analyses (Table 13). The tannin content of parental strains was reflected in their progenies (Tables 1 and 6). Parents with none or a low content of tannin produced progenies that also had a low

content of tannin in their seed coat. The analyses of variance of (W_r-V_r Table 7) showed that the F test for the arrays was not significant at either location indicating that an additive dominance model was adequate to describe gene action in the population. The regression of W_r on V_r for % tannin at East Lansing and Saginaw showed that the regression coefficients at East Lansing (b=0.92 $\pm$ 0.03**) and at Saginaw (b=0.98 $\pm$ 0.05**) were significantly different from zero but not significantly different from unity (Fig. 1 and 2). The intersect of the W_r axis at East Lansing (a= 0.13$\pm$0.01**) and at Saginaw (a=0.15$\pm$ 0.01**) are above the origin and are significantly different from zero . This indicates that a partially dominant gene system controlled tannin content (Fig. 1 and 2). The distribution of the parental array points under the limiting parabola along the regression line showed that the genes controlling tannin content for SAN and N-2 were predominantly recessive while the remaining parents had a relatively high proportion of dominant factors. The distribution of array points representing the parents under the limiting parabola along the regression line clustered consistently at each location for those entries with mostly recessive genes and those with mostly dominant genes (Fig. 1 and 2).

Variance of SCA calculated for each parent showed few non-additive effects for B-2, FF, 15-R, and A-30. However, it was indicated that the remaining parents (BTS, SAN, SF, and N-2) had high SCA variances. These results indicated

that progenies resulting from crosses of these parents would produce progeny with relatively more or less tannin than would be expected on the average (Table 16).

Crude protein. Analyses of the combined data indicated that significant differences existed among entries for percentage protein in raw and cooked beans (Table 13). This permitted the partitioning of the variation due to entries into GCA, SCA, and reciprocal effects. Variation from reciprocal differences among entries was further broken down into maternal and non-maternal causes. Mean squares for the various main effects and their interaction with locations are summarized in table 13. All F tests for GCA main effects for protein content were highly significant and the F tests for SCA main effects were significant or highly significant. The combined analyses reflected the significant GCA and SCA variation detected in the individual analyses except that the SCA mean square was nonsignificant at Saginaw for the F_3 generation (Table 10). Significant reciprocal effects were inconsistent in the various tests and were due to both maternal and non-maternal causes. Except for a significant non-maternal reciprocal effect in the F_2 for protein content of raw beans, reciprocal variation disappeared from the combined analyses (Table 13). A closer examination of reciprocal variation (Table 10) revealed that the significant non-maternal reciprocal variation for raw bean protein in the F_2 could have been caused by crosses of A-30 x 15-R, BTS x A-30, BTS x N-2, SAN x 15-R, and SAN x N-2. Interactions of the combining ability effect with

locations were essentially interaction of general combining ability effects with locations (Table 12). There were no significant interactions of SCA x locations. There was significant variation among generations for raw bean protein indicating that entries performed differently from the F_2 to F_3 generations. Variation among entries within a generation was also inconsistent from location to location; however, when the four tests (two locations and two generations) were combined together no entry x location interactions were noted (Table 13).

Estimates of variance components revealed that with the exception of the F_2 generation at Saginaw, GCA effects predominated for cooked beans (Table 14). The relative magnitude of these components indicated the relative importance of the sources of variation. In the combined analyses, the GCA to SCA ratio ranged from 3.7 : 1 for protein content of raw beans in the F_3 to 5.3 : 1 for raw bean protein in the F_2 (Table 14). These results indicated that additive effects of the parents were more important than non-additive effects in determining performance in crosses. Variance components for GCA and SCA x locations were always smaller than the main effect components (Table 14).

There was considerable variation in the general combining ability (GCA effects) contribution of each parent to protein content (Table 15). Specific rankings of the parent that increased or decreased the protein in raw and cooked beans were not exactly the same for each generation and

location. However, the same lines were generally in the same positive or negative grouping. In a few cases a line had a negative GCA effect at one location and positive GCA effect at the other. For example, BTS had a -0.10 value for protein content in raw beans at East Lansing and a 0.29 GCA effect value at Saginaw.

When means of the diallel progeny were examined individually, crosses of low x low and high x high parents tended to produce progenies that were low and high in protein content, respectively (Tables 18 and 19). Some parents had high SCA variances in one or both generations (Table 16) which indicated that progeny from these crosses could have a higher or lower protein content than what is expected on the average.

The analyses of variance of (W_r-V_r) were non-significant among arrays for protein content at both locations in the F_2 and F_3 generation, indicating that an additive dominance model was appropriate for describing gene action among crosses (Table 17). The regression of W_r on V_r (the covariance and variances of parental arrays) showed that the regression coefficients for percent protein in the F_2 ($b=1.02\pm0.16^{**}$ Fig. 3) and in the F_3 ($b= 1.08\pm0.32^{**}$) at E. Lansing was significantly different from zero but not significantly different from unity. Similarly, the regression coefficients for the F_2 ($b=1.09\pm 0.10^{**}$ Fig. 5) and for the F_3 ($b=1.25\pm0.30^{**}$ Fig. 6) at Saginaw were significantly different from zero but not significantly different from unity. The intercepts on the W_r axis were significantly

different from zero in the F_2 at E. Lansing (a=0.60±0.14**) and at Saginaw (a=0.79± 0.08**) indicating that genes controlling protein content were partially dominant. In the F_3 generation the intercepts on the W_r axis at E. Lansing (a=0.09±0.32) and at Saginaw (a=0.40±0.34) were not significantly different from zero, indicating that the genes controlling protein content were completely dominant. Distribution of array points representing the parental arrays along the regression line under the limiting parabola showed consistency for some parents from the F_2 to F_3 generation across locations but not for other parents (Fig. 3,4,5 and 6). This indicated that some entries were more stable than others.

Table 1. Seed coat color and tannin content and percentage of seed protein of 8 dry beans strains used as parents in a diallel cross.

Strain	Seed coat color	Tannin content[z] (%)	Protein content (%)
Brasil-2	Beige	9.6	22.5
FF 16-15-CM-M-M	Red	8.6	26.2
15-R-148	Red	8.1	27.9
A-30	Yellow	3.4	22.4
Black Turtle Soup	Black	4.7	23.9
Sanilac	White	0.0	23.0
San Fernando	Black	4.4	25.0
Nep-2	White	0.0	24.8

z = Tannin content is expressed as % catechin equivalent.

Table 2. Analysis of variance for tannin content of F_2 seed coats in dry bean parents and progeny of an 8x8 diallel cross.

Source of variation	d.f.	Mean squares	
		E.Lansing	Saginaw
Entries	63	9.3*	12.3*
Error	63	1.1	2.0

* = Significant at 1% probability level.

Table 3. Analysesof variance and estimates of variance components and their standard errors for general and specific combining ability and reciprocal effects for tannin content of seed coat of parents and of F_2 progeny indry dry beans parents and progeny of an 8x8 diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

Source	d.f.	Mean square	
		East Lansing	Saginaw
Entry	63	4.6**	10.5**
GCA	7	35.3**	26.5**
SCA	28	1.0	6.3**
Reciprocal	28	0.6	10.6**
Maternal (M)	7	1.4*	36.3**
Nonmaternal Reciprocal(NMR)	21	0.3	2.0*
Error	63	0.6	1.0
Component of variance			
GCA	7	2.17±1.04	1.60±0.78
SCA	21	0.39±0.26	5.32±1.63
Reciprocal	28	0.00	4.81±1.42
M	7	0.05±0.04	2.21±1.07
NMR	21	0.00	0.53±0.62

*,** = Significant at 5 and 1% probability level, respectively.

Table 4. General combining ability effects for tannin content of seed coats of each parent used in a diallel cross of dry edible beans and grown atE. Lansing and Saginaw, Michigan in 1982.

Parent	East Lansing	Saginaw
Brasil-2	1.58	0.99
FF 16-15-CM-M-M	1.29	0.64
15-R-148	0.54	0.94
A-30	-0.34	-0.21
Black Turtle Soup	0.28	1.39
Sanilac	-2.62	-2.21
San Fernando	1.10	0.02
Nep-2	-1.73	-1.58
$S_{\bar{Y}}$	0.18	0.23
$S_{\bar{D}}$	0.27	0.35

$S_{\bar{Y}}, S_{\bar{D}}$ = Standard error of a mean and standard error of a mean difference, respectively.

Table 5. Mean squares from analyses of variances and combining ability analyses for tannin content measured on parents and F_2 progeny from 8-parent diallel cross of dry edible beans grown in 1982.

Source of variation	d.f.	Tannin content[z]
Location(L)	1	29.8
Reps/L	2	4.9
Entry(E)	63	19.1 **
GCA	7	145.5 **
SCA	28	4.7 **
Maternal(M)	7	4.8 *
Nonmaternal reciprocal(NMR)	21	1.0
E x L	63	1.6
GCA x L	7	1.6
SCA x L	28	2.0
M x L	7	2.3
NMR x L	21	0.9
Error	126	1.6

z = Tannin content is expressed as % catechin equivalent.
*,** = Significant at 5% and 1% level of probability, respectively.

Table 6. Mean tannin content of seed coats of parents and F_2 progeny of an 8x8 diallel cross in dry beans grown at East Lansing and Saginaw, Michigan in 1982.

Parents and crosses	Percentage tannin content	
	East Lansing	Saginaw
Parents		
B-2 (1)	9.9	9.6
FF (2)	8.2	8.6
15-R(3)	6.2	8.1
A-30(4)	3.9	3.4
BTS (5)	5.6	4.7
SAN (6)	0.0	0.0
SF (7)	6.5	4.4
N-2 (8)	0.0	0.0
Crosses		
1 x 2	7.6	7.6
1 x 3	7.8	6.6
1 x 4	6.7	6.1
1 x 5	6.6	8.8
1 x 6	4.1	4.1
1 x 7	7.6	9.0
1 x 8	6.1	6.0
2 x 3	7.6	7.5
2 x 4	6.7	6.2
2 x 5	6.3	9.0
2 x 6	3.9	4.6
2 x 7	7.5	10.5
2 x 8	6.2	5.9
3 x 4	5.8	6.0
3 x 5	5.8	7.2
3 x 6	3.6	3.8
3 x 7	6.7	7.7
3 x 8	4.4	5.4
4 x 5	5.7	7.0
4 x 6	1.9	3.3
4 x 7	6.4	8.0
4 x 8	2.9	3.2
5 x 6	3.7	5.3
5 x 7	7.2	8.3
5 x 8	4.9	5.7
6 x 7	5.9	6.0
6 x 8	0.0	0.0
7 x 8	5.2	6.0
Mean (x)	5.5	6.2
$S_{\bar{D}}$	0.8	1.0

$S_{\bar{D}}$ = Standard error of the difference between two means.

Table 7. Analyses of variances of(W_r-V_r) for testing the adequacy of additive-dominance model for tannin content of F_2 progeny of an 8x8 diallel cross grown at E. Lansing and Saginaw, Michigan in 1982.

Source of Variation	d.f.	Mean squares	
		E. Lansing	Saginaw
Array	7	0.2	0.7
Error	15	0.1	1.1

Table 8. Analyses of variance for raw and cooked bean seed protein of parents and F_2 and F_3 progeny of an 8x8 diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

Source of variation	d.f.	Mean squares			
		East Lansing		Saginaw	
		F_2		F_3	
		Raw beans	Cooked beans	Raw beans	Cooked beans
F_2	63	2.8**	5.5**	3.53**	7.44**
F_3	63	2.7**	6.5**	7.49*	8.50**

*,** = Significant at 5% and 1% probability level,respectively.

Table 9. Correlation coefficient (r) indicating the relationship between F_2 and F_3 for protein content in raw (R) and cooked (C) beans grown at East Lansing (upper triangle) and Saginaw (lower triangle) and between locations (diagonal).

	Protein content (%)			
Generation	F_2R	F_2C	F_3R	F_3C
F_2 R	0.67*	0.77*	0.75*	0.71*
F_2 C	0.75*	0.69*	0.71*	0.70*
F_3 R	0.72*	0.88*	0.78*	0.85*
F_3 C	0.69*	0.86*	0.94*	0.85*

* = Significantat 1% probability level.

Table 10. Analyses of variances for general, specific combining ability and reciprocal effects for percent protein of parents and F_2 and F_3 progeny of an 8x8 diallel cross of dry beans and grown at East Lansing and Saginaw, Michigan in 1982.

Source of variation	d.f.	Mean squares			
		East Lansing		Saginaw	
		Protein (%)		Protein (%)	
		Raw	Cooked	Raw	Cooked
F_2					
Entry	63	1.45**	2.66**	1.44**	3.75**
GCA	7	9.44**	16.05**	7.63**	27.73**
SCA	28	0.47*	0.79	0.98**	1.08**
Reciprocal	28	0.44*	1.18*	0.36**	0.42
Maternal (M)	7	0.45	0.90	0.44**	0.41
Nonmaternal Reciprocal (NMR)	21	0.43*	1.35*	0.33**	0.43
Error	63	0.24	0.64	0.01	0.24
F_3					
Entry	63	1.39**	3.22**	1.78	4.24**
GCA	7	8.72**	21.35**	13.13**	32.36**
SCA	28	0.61*	1.19*	0.52	0.90**
Reciprocal	28	0.35	0.88**	0.20	0.54**
M	7	0.37	1.21*	0.19	0.66**
NMR	21	0.34	0.57	0.20	0.50**
Error	63	0.31	0.63	1.58	0.14

*,** Significant at 5 and 1 % probability level, respectively.

Table 11. Components of variance and their standard errors for general and specific combining ability and reciprocal effects for percent protein in raw and cooked bean seed of F_2 and F_3 generation means of an 8x8 diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

Location and source	Components			
	F_2		F_3	
	Raw beans	Cooked beans	Raw beans	Cooked beans
E. Lansing				
GCA	0.58±0.28	0.96±0.47	0.53±0.26	1.30±0.63
SCA	0.23±0.13	0.15±0.23	0.30±0.17	0.56±0.33
Reciprocal	0.10±0.06	0.27±0.17	0.02±0.05	0.13±0.13
Maternal (MR)	0.01±0.01	0.02±0.03	0.00	0.04±0.04
Nonmaternal reciprocal (NMR)	0.19±0.07	0.71±0.21	0.03±0.06	0.00
Saginaw				
GCA	0.48±0.25	1.72±0.82	0.72±0.39	2.01±0.95
SCA	0.97±0.25	0.84±0.28	0.00	0.76±0.23
Reciprocal	0.17±0.05	0.09±0.06	0.00	0.20±0.07
MR	0.03±0.01	0.01±0.01	0.00	0.03±0.02
NMR	0.32±0.05	0.19±0.07	0.00	0.36±0.07

Table 12. Estimates of general combining ability effectsof parents for protein content of raw (R) and cooked (C) bean seeds measured on F_2 and F_3 progeny of an 8x8 diallel cross and grown at East Lansing and Saginaw, Michigan in 1982.

	East Lansing				Saginaw			
	F_2		F_3		F_2		F_3	
	Protein(%)				Protein(%)			
Parents	R	C	R	C	R	C	R	C
B-2	-0.92	-0.99	-0.82	-0.76	-0.91	-1.11	-1.03	-1.35
FF	0.50	0.29	0.40	0.63	0.27	0.19	0.08	0.07
15-R	1.34	2.06	1.45	2.46	1.23	2.79	2.03	3.19
A-30	-0.95	-0.89	-0.85	-1.42	-0.90	-1.57	-0.69	-1.38
BTS	-0.10	-0.07	-0.04	-0.10	0.29	0.23	-0.03	-0.12
SAN	-0.39	-0.90	-0.21	-0.28	0.07	0.36	0.02	0.02
SF	0.12	0.29	-0.18	-0.44	0.03	-0.28	-0.29	-0.39
N-2	0.39	0.20	0.25	-0.09	-0.08	-0.62	-0.08	-0.22
$S_{\bar{Y}}$	0.06	0.15	0.07	0.15	0.002	0.06	0.37	0.03
$S_{\bar{D}}$	0.09	0.23	0.11	0.23	0.004	0.09	0.56	0.05

$S_{\bar{Y}}$, $S_{\bar{D}}$= Standard error of a mean and standard error of a difference between two means, respectively.

Table 13. Mean squares for locations, entries, generations, and general, and specific combining ability, reciprocal, maternal, and nonmateranl recirpocal effects and their interaction with locations for protein content of raw and cooked bean measured on combined data of parents and F_2 and F_3 progeny of an 8x8 diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

Source of variation	Degrees of freedom	Mean squares	
		Protein (%)	
		Raw beans	Cooked beans
Location(L)	1	617**	1147**
Reps/L	2	2.2	8.3
Entries(E)	127	5.7**	12.4**
Generations(G)	1	7.6**	5.0
G x L	1	0.4	0.5
Entry/G	126	5.7**	12.5**
Among F_2			
GCA	7	41.5**	81.0**
SCA	28	1.1*	2.6*
Maternal(M)	7	1.0	2.0
Nonmaternal reciprocal(NMR)	21	1.3*	1.9
Among F_3			
GCA	7	43.1**	107**
SCA	28	1.4**	2.8**
M	7	0.8	2.7
NMR	21	0.6	1.6
E x L	127	0.6	1.5
F_2x L			
GCA x L	7	2.3**	7.4**
SCA x L	28	0.6	1.2
M x L	7	0.7	0.6
NMR x L	21	0.3	1.5
F_3x L			
GCA x L	7	1.4*	2.9*
SCA x L	28	0.6	1.2
M x L	7	0.3	1.0
NMR x L	21	0.4	0.3
Error	254	0.5	1.2

*,** = Significant at 5% and 1% level of probability, respectively.

Table 14. Estimates of variance components of GCA, SCA, and reciprocal effects and their standard deviations for protein and tannin content measured on parents and progeny of an 8-parent diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

Component	Protein content		Tannin content[z]
	Raw beans	Cooked beans	
Among F_2			
GCA	0.64±0.31	1.24±0.59	2.25±1.07
SCA	0.12±0.08	0.29±0.18	0.76±0.31
Maternal(M)	0.01±0.01	0.01±0.02	0.05±0.04
Nonmaternal reciprocal(NMR)	0.16±0.10	0.10±0.15	0.0
Among F_3			
GCA	0.66±0.32	1.65±0.79	y
SCA	0.18±0.09	0.33±0.19	y
M	0.003±0.006	0.02±0.02	y
NMR	0.0	0.04±0.14	y
F_2 x L			
GCA x L	0.06±0.03	0.19±0.11	0.0
SCA x L	0.03±0.08	0.0	0.18±0.29
M x L	0.01±0.01	0.0	0.02±0.03
NMR x L	0.0	0.13±0.25	0.0
F_3 x L			
GCA x L	0.03±0.02	0.05±0.04	y
SCA x L	0.05±0.09	0.0	y
M x L	0.0	0.0	y
NMR x L	0.0	0.0	y

z = Tannin content expressed as catechin equivalent.
y = No data taken.

Table 15. General combining ability effects and their interaction with locations for protein and tannin content for each parent of an 8x8 diallel cross grown at East Lansing and Saginaw, Michigan in 1982.

	F_2			F_3	
	Protein content			Protein content	
Parents	Raw beans	Cooked beans	Tannin content (%)	Raw beans	Cooked beans
B-2	-0.965*	-1.034*	1.30*	-0.909*	-1.076*
FF	0.338*	0.287*	1.34*	0.225*	0.344*
15-R	1.6*	2.459*	0.49*	1.768*	2.87*
A-30	-1.939*	-1.226*	-0.58*	-0.805*	-1.405
BTS	0.035	0.06	0.58*	-0.097	-0.12
SAN	-0.204	-0.332*	-2.57*	-0.062	-0.048
SF	0.027	0.01	1.25*	-0.206*	-0.383*
N-2	0.108	-0.224	-1.82*	0.087	-0.181
S_Y	0.209	0.274	0.29	0.181	0.271
S_D	0.125	0.197	0.23	0.125	0.197
B-2 x L	0.025	0.045	0.19	0.124	0.278
FF x L	0.158	0.068	-0.04	0.136	0.267
15-R x L	-0.275*	-0.337*	0.06	-0.273*	-0.332
A-30 x L	0.085	0.328	0.13	-0.075	-0.031
BTS x L	-0.163	-0.186	-0.29	-0.008	-0.006
SAN x L	-0.189	-0.572*	-0.03	-0.104	-0.247
SF x L	-0.085	0.279	-0.13	0.058	0.012
N-2 x L	0.273*	0.373*	0.10	0.142	0.048
$S_{\bar{Y}}$	0.178	0.326	0.29	0.178	0.326
$S_{\bar{D}}$	0.128	0.197	0.23	0.128	0.197

* = Significant at 5% level of probability.

$S_{\bar{Y}}$, $S_{\bar{D}}$ = Standard error of a mean and standard error of difference between two means, respectively.

Table 16. Parental values for seed protein and tannin content of raw beans (Y_r) and variance of specific combining ability (S^2) of each parent from data measured on F_2 and F_3 progeny of an 8x8 diallel cross averaged over locations in 1982.

	Generation					
	F_2				F_3	
	Protein content (%)		Tannin content (%)		Protein content (%)	
Parents	Y_r	S^2	Y_r	S^2	Y_r	S^2
B-2	21.4	0.12*	9.6	0.14	22.6	0.07
FF	24.9	0.0	8.6	0.05	24.9	0.10
15-R	27.7	0.03	8.1	0.0	27.8	0.01
A-30	22.3	0.03	3.4	0.06	22.6	0.16**
BTS	23.8	0.02	4.7	0.47**	22.9	0.14*
SAN	22.6	0.18**	0.0	0.26*	23.4	0.13*
SF	24.0	0.0	4.4	1.34**	24.0	0.01
N-2	23.6	0.02*	0.0	0.83**	24.0	0.14*
$S_{\bar{Y}}$	0.25		1.28		0.25	
$S_{\bar{D}}$	0.36		1.28		0.36	

$S_{\bar{Y}}$, $S_{\bar{D}}$ = Standard error of a mean and standard error of a difference between two means, respectively.

Table 17. Analyses of variances of (Wr-Vr) for raw and cooked bean seed protein in the F_2 and F_3 generation of an 8x8 cross to test the adequacy of additive-dominance model.

Source of variation	d.f	Mean squares			
		East Lansing		Saginaw	
		Raw beans (%)	Cooked beans (%)	Raw beans (%)	Cooked beans (%)
F_2	7	0.09	0.18	0.02	0.17
F_3	7	0.09	0.17	1.07	0.40

Table 18. Mean protein content of raw and cooked bean seeds of parents and F_2 and F_3 progeny of an 8x8 diallel cross grown at East Lansing, Michigan in 1982.

Parent and cross	Protein content (%)			
	F_2		F_3	
	Raw beans	Cooked beans	Raw beans	Cooked beans
Parents				
B-2 (1)	22.5	21.4	24.6	22.8
FF (2)	26.2	24.6	26.3	25.9
15-R (3)	27.9	27.7	27.9	28.0
A-30 (4)	22.4	23.1	23.1	20.9
BTS (5)	23.9	22.4	24.0	22.9
SAN (6)	23.0	20.5	24.6	22.8
SF (7)	25.0	24.8	25.4	23.3
N-2 (8)	24.8	23.8	25.7	23.8
Crosses				
1 x 2	24.3	23.2	25.4	24.1
1 x 3	26.2	25.2	25.3	25.7
1 x 4	23.4	21.7	23.6	21.6
1 x 5	24.5	23.2	24.8	23.4
1 x 6	23.1	21.0	23.7	22.0
1 x 7	24.6	23.9	24.3	23.5
1 x 8	24.8	22.2	23.9	22.0
2 x 3	27.1	26.3	27.3	27.4
2 x 4	24.9	22.5	24.9	22.5
2 x 5	25.4	24.0	24.9	23.0
2 x 6	25.5	23.4	26.0	25.2
2 x 7	25.6	24.5	25.0	24.8
2 x 8	25.8	23.2	25.5	23.5
3 x 4	25.0	24.3	25.0	25.5
3 x 5	26.5	25.5	27.4	27.0
3 x 6	26.1	24.9	27.0	26.2
3 x 7	26.5	26.2	26.8	24.6
3 x 8	26.3	25.7	26.9	26.5
4 x 5	23.7	23.1	24.4	21.6
4 x 6	24.1	22.2	24.6	22.9
4 x 7	24.4	22.1	23.9	21.4
4 x 8	25.3	23.4	25.8	23.5
5 x 6	25.1	23.0	24.8	23.8
5 x 7	25.0	23.0	25.7	24.5
5 x 8	25.9	24.6	25.8	24.3
6 x 7	25.2	24.2	24.3	22.5
6 x 8	25.7	24.6	24.3	22.5
7 x 8	25.4	24.1	25.1	23.2
$S_{\bar{D}}$	0.59	0.98	0.68	0.98

$S_{\bar{D}}$=Standard error of a difference between two means.

Table 19. Mean protein content of raw and cooked bean seeds of parents and F_2 and F_3 progeny of an 8x8 diallel cross grown at Saginaw, Michigan in 1982.

Parents and cross	Protein content (%)			
	F_2		F_3	
	Raw beans	Cooked beans	Raw beans	Cooked beans
Parents				
B-2 (1)	20.4	17.0	20.6	18.2
FF (2)	23.7	21.9	23.7	21.6
15-R (3)	27.5	26.6	27.7	28.1
A-30 (4)	21.4	17.8	22.8	18.5
BTS (5)	23.8	21.2	23.8	20.4
SAN (6)	22.3	21.8	22.2	20.6
SF (7)	23.0	19.8	22.7	20.5
N-2 (8)	22.4	18.6	22.0	19.6
Crosses				
1 x 2	23.0	21.4	22.3	19.5
1 x 3	23.9	23.0	24.1	22.7
1 x 4	20.0	17.6	21.4	18.5
1 x 5	22.3	20.3	23.3	20.0
1 x 6	21.1	19.0	21.6	19.0
1 x 7	21.9	19.5	21.9	19.2
1 x 8	22.1	19.2	22.0	18.9
2 x 3	24.8	23.3	25.5	24.5
2 x 4	21.8	18.9	21.8	18.7
2 x 5	22.8	21.3	22.5	19.9
2 x 6	23.1	20.9	24.0	21.5
2 x 7	22.7	20.7	23.0	20.9
2 x 8	22.4	19.0	23.0	20.3
3 x 4	23.6	21.5	24.0	21.3
3 x 5	24.3	22.4	24.8	23.5
3 x 6	24.8	24.3	25.1	24.4
3 x 7	24.5	23.6	24.8	23.7
3 x 8	24.6	23.5	25.4	24.1
4 x 5	21.9	19.5	21.9	19.6
4 x 6	21.8	18.9	22.9	19.1
4 x 7	22.0	19.1	21.9	19.1
4 x 8	22.0	20.0	23.0	21.0
5 x 6	23.2	21.4	22.7	21.2
5 x 7	22.9	20.8	23.1	20.4
5 x 8	23.0	20.6	23.1	20.9
6 x 7	23.3	21.2	23.3	20.9
6 x 8	22.8	21.1	23.5	21.2
7 x 8	22.0	18.8	22.1	19.1
$S_{\bar{D}}$	0.13	0.60	1.54	0.46

$S_{\bar{D}}$= Standard error of a difference between two means.

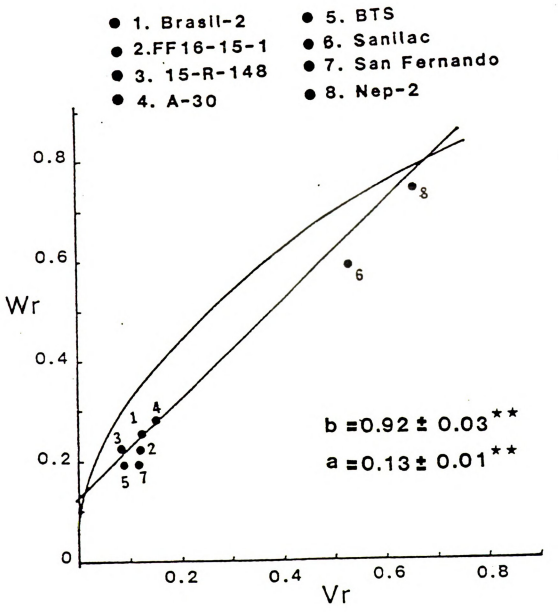

Figure 1. Variance (V_r)-covariance (W_r) graph for % tannin content data of the F_2 seed coat grown at East Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

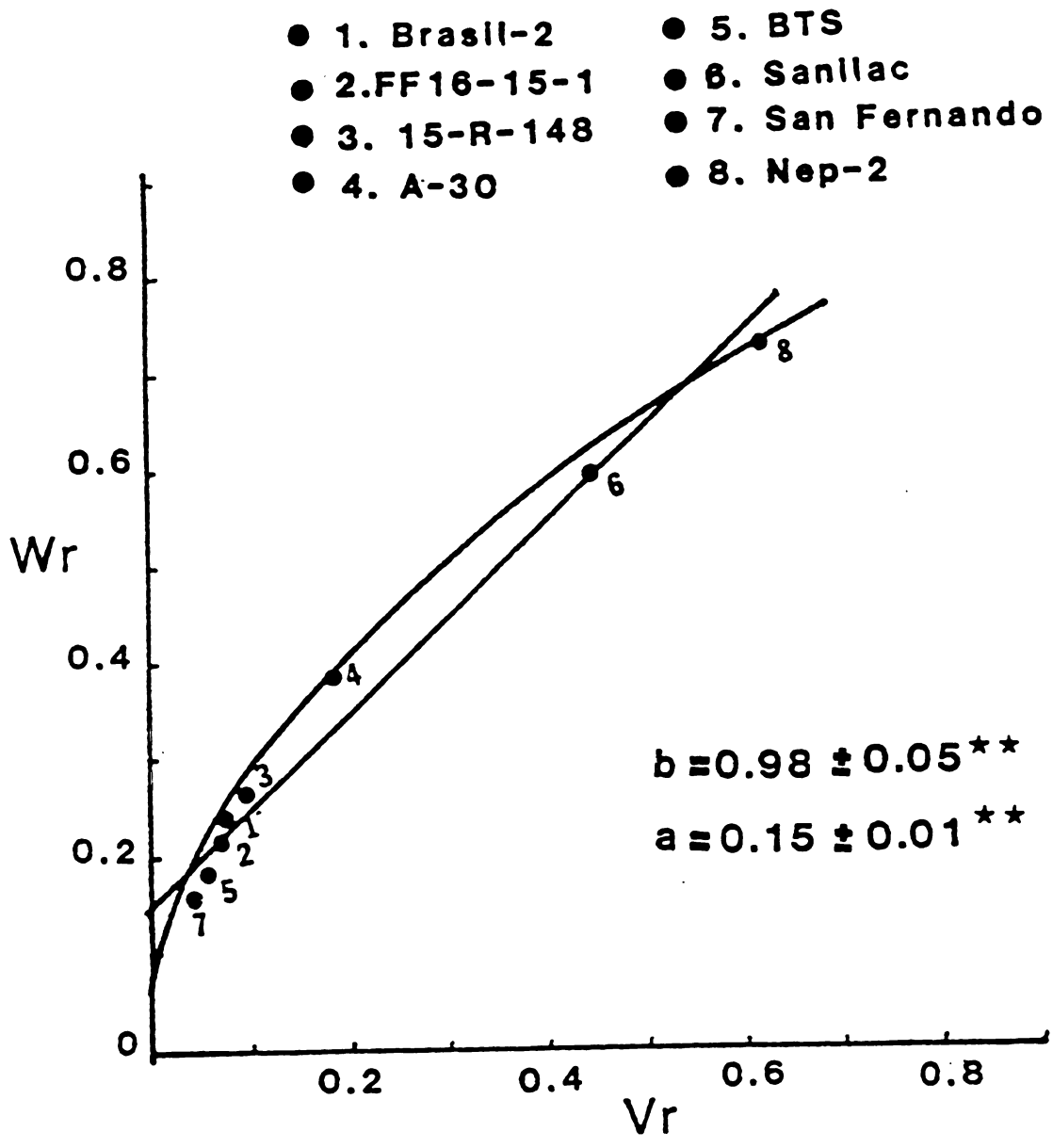

Figure 2. Variance (V_r)-covariance (W_r) graph for % tannin content data of the F_2 seed coat grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

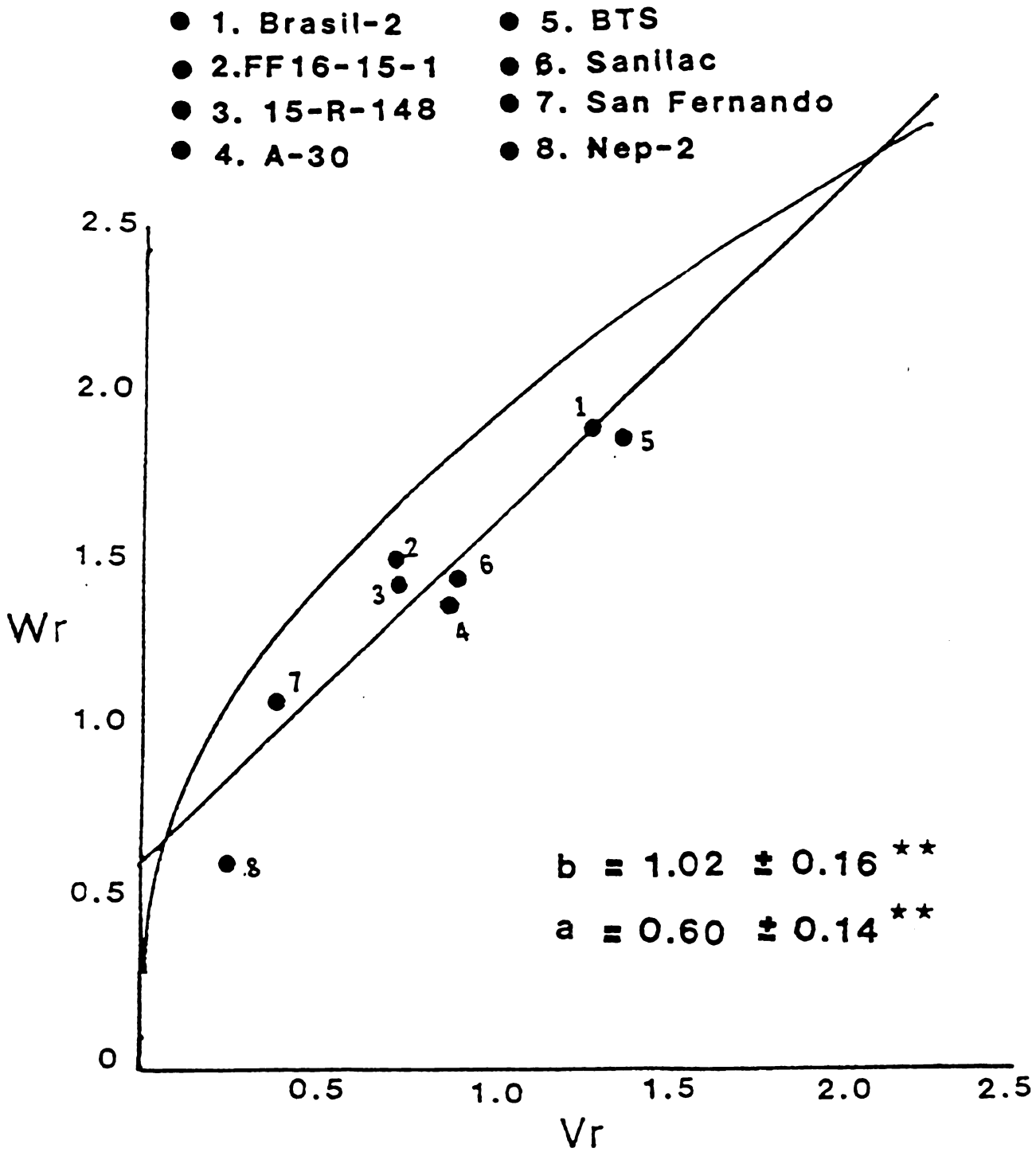

Figure 3. Variance (V_r)-covariance (W_r) graph for protein content data of the F_2 grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

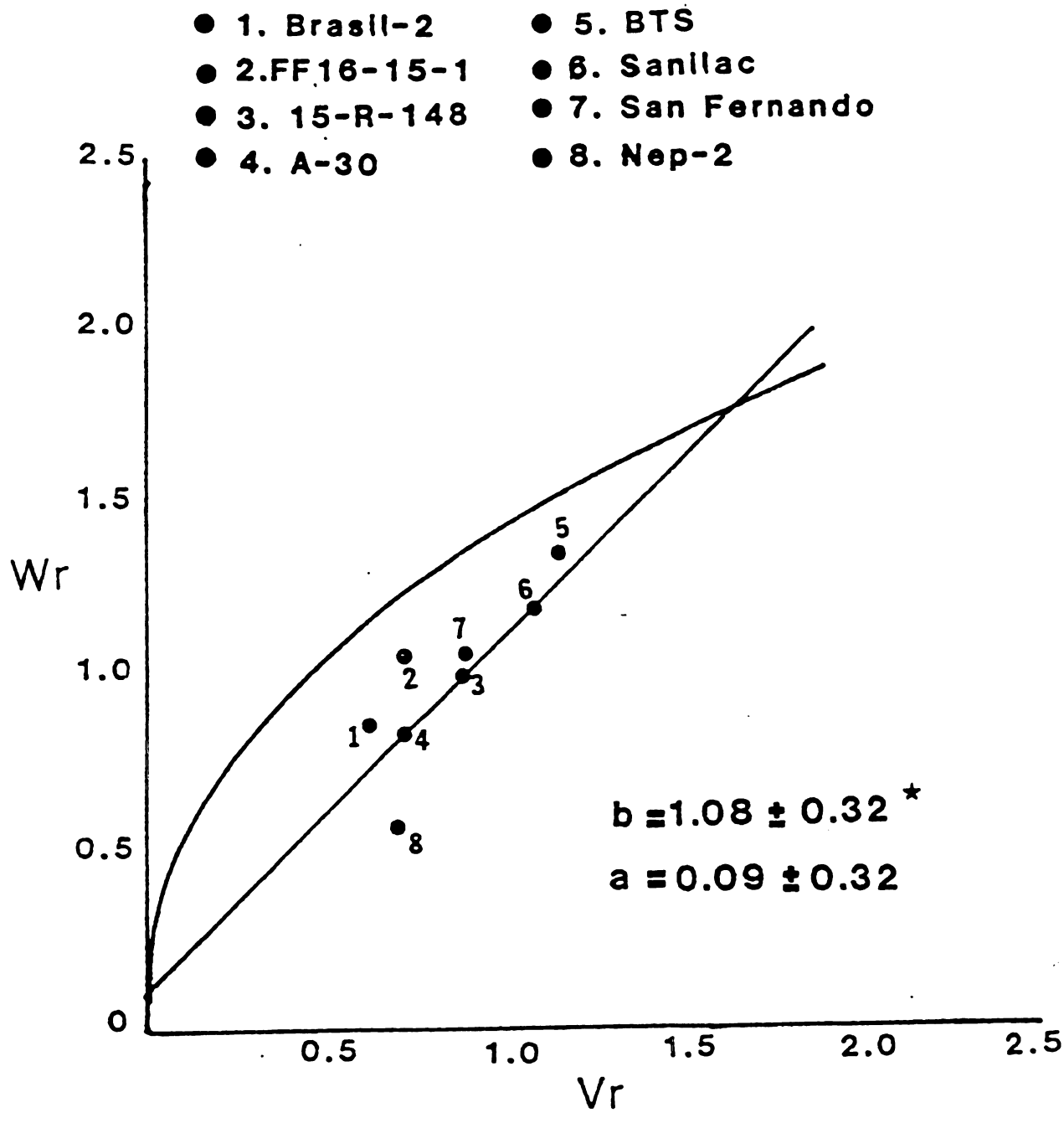

Figure 4. Variance (V_r)-covariance (W_r) graph for protein content data of the F_3 grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. * = Significant at the 5% level of probability.

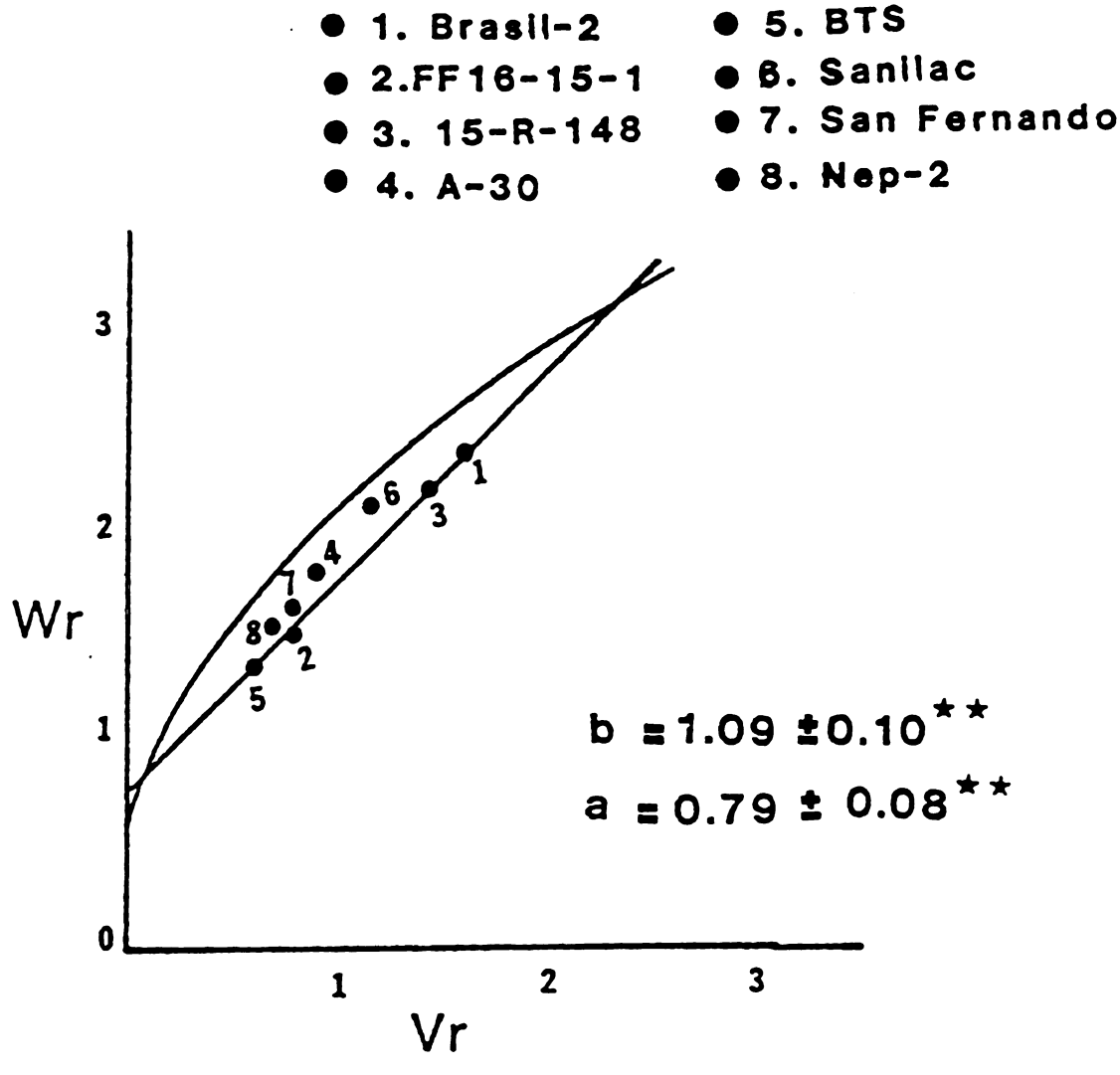

Figure 5. Variance (V_r)-covariance (W_r) graph for protein content data of the F_2 grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

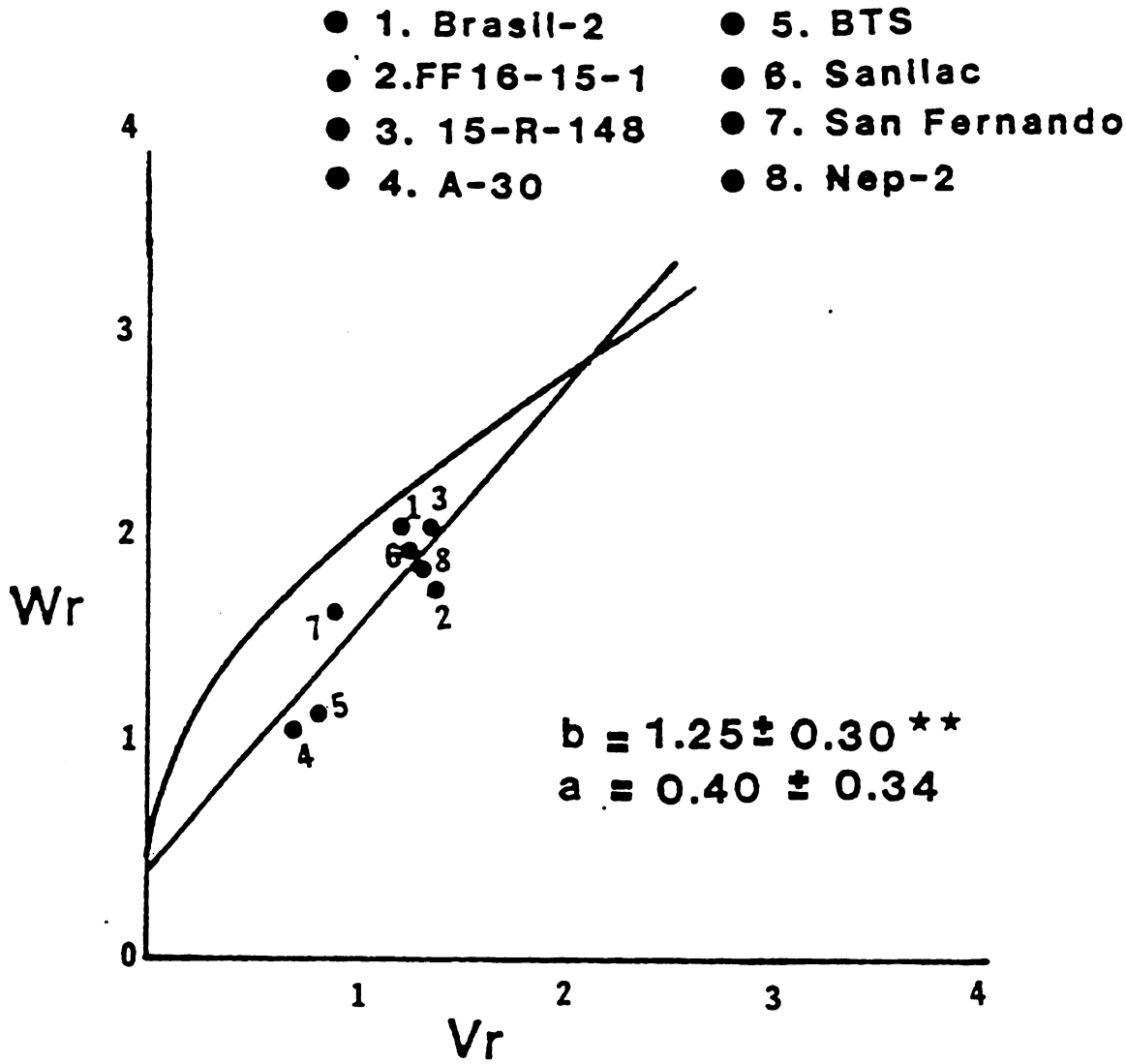

Figure 6. Variance (V_r)-covariance (W_r) graph for protein content data of the F_3 grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

DISCUSSION

The presence of genetic variation was demonstrated by the significant F test of entries for tannin content and % crude protein (Tables 2 and 8). The entry by location component was not significant. For percent protein the location effect was significant, leading to a significant GCA by location interaction (Table 12). The significant GCA mean square for tannin and crude protein % in the combined analyses using Griffing's model I method 1 (1956) indicated that the differences among progeny for these traits were due to genes with primarily additive effects. Although of lesser magnitude than GCA, significant SCA was involved in tannin and protein content in the F_2 generation at both locations. This suggests that non-additive genetic effects are also influencing traits expression in this generation. For the percent protein trait in the F_3, SCA variance diminished. This was possibly due to the reduction in heterozygosity accompanying selfing. The significance of maternal effects for % tannin could have arisen because seed coats are maternal tissue. Strength of this argument comes from the fact that parents with a high % tannin content contributed the most to the maternal effects mean square. These parents also had significant and positive GCA effects for this trait. For % protein the non-maternal reciprocal mean square was significant, primarily because of the contribution of A-30 x 15-R (0.58), BTS x A-30 (0.52), BTS x N-2 (0.62), SAN x 15-R (-0.67) and SAN x N-2 (-0.55). However

the number of crosses that contributed to non-maternal reciprocal effects decreased from 5 to 2 (FFxN-2=-0.53, BTSxFF=0.49) in the F_3 generation. The comparison of parental and progeny means revealed that genotypes with low tannin content produced progenies that were also low in tannin content. The GCA picture for tannin and protein content indicated that it should be possible to develop lines with low tannin and high protein content. This conclusion is supported by the high correlation between parental value and GCA effects for % tannin in the F_2 (r=0.88**) and % crude protein (r=0.97** and r=0.94**) in the F_2 and F_3 generation, respectively. Similarly significant correlations were obtained for GCA effects between F_2 and F_3 generation for raw (r=0.91**) and cooked bean protein (r=0.98**).

Graphical analysis of % tannin revealed that this trait is controlled by a gene system of complete dominance. Sanilac and Nep-2 with white seed coat and zero % catechin equivalent are the parents that carry a preponderance of recessive genes and the rest of the parents carry mostly dominant genes for this trait (Fig. 1 and 2). This finding is in agreement with the work of Croft et al. (1980) that the white or buff seed coat associated with white flower in Vicia fabaL. caused by a single recessive gene (Rowlands, 1962) had no tannin. White seed coat in Nep-2 has been reported to be caused by change of a single locus from the dominant to recessive (Moh, 1971). This indicated that the

color gene has a pleiotropic effect on substrate production leading to the sysnthesis of tannin .

Graphical analyses of % crude protein demonstrated that on the average a gene system with partial to full dominance controlled this trait. The position and distribution of array points representing the parents for % protein was relatively consistent for some of the genotypes within each generation and location, while consistency was lacking for other genotypes. This indicated the presence of genotype by environment interactions.

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CHAPTER 3

THE GENETIC CONTROL OF PHYSICO-CHEMICAL SEED CHARACTERISTICS RELATED TO CULINARY QUALITY IN DRY BEANS (*Phaseolus vulgaris* L.)

ABSTRACT

Dry edible beans (*Phaseolus vulgaris* L.) are important as a world food crop because they can provide significant amount of energy and nutrients to consuming populations. Middle and low income families in many poor countries of the world rely on beans for calories and protein. In order to encourage an increased production of dry beans in lesser developed countries, an economic incentive must be present. This could best be achieved by the development of high yielding cultivars that are resistant to diseases and insects and have acceptable culinary quality. Researchers have concentrated their efforts on the inheritance of yield components and factors causing yield reductions. Little information is available concerning the inheritance of culinary quality traits in dry beans. The type of gene action involved and the degree to which the expression of genes are influenced by environmental variation are determinant factors in the development of breeding strategies. Culinary quality is a complex trait and previous work has shown that several seed characteristics of a physico-chemical nature are related to culinary quality. The present study was undertaken to obtain information from an 8-parent diallel cross on the genetic control of culinary

quality traits in beans. The parents and 56 F_2 and F_3 progenies were grown at two locations and data were taken on nine traits.

Highly significant differences were observed among genotypes in both generations for the traits. Except for clumps, soaked bean weight and soaked bean moisture, there were no differences between generations. The variances due to GCA were highly significant in both generation for most characters. Significant SCA variances were noted for some traits but the SCA mean squares were always smaller than the GCA ones. Variance estimates of SCA effects for the washed drained weight and texture traits indicated that progeny resulting from crosses of 'A-30', 'SAN', 'SF', and 'N-2' will be better or poorer than the average expected on the basis of GCA. Genetic relationships among the parents were studied with the variance-covariance (V_r,W_r) graphical analysis technique and showed that most of the traits were controlled by dominant or partially dominant genes. Highly significant correlations were found between GCA effects in the F_2 and F_3 generations. The conclusion that genes with mostly additive effects controlled culinary quality traits in this population of genotypes was supported by the highly significant correlations between parental performance and their respective GCA effects.

Additional Index Words: Diallel analysis, Combining ability, Texture, Processing traits, texture.

INTRODUCTION

Legumes are an important source of protein, in human diets and especially in poorer countries of the world. In addition, legumes can make a significant contribution to the carbohydrate, mineral, and vitamin fraction of the diet (Hawtin et al. 1977). Because of the low sugar, low fat, high protein and high dietary fiber content of dry beans, their contribution to Western diets as a replacement for animal products in terms of dietary fiber and complex carbohydrates would bring diets in developed countries closer to recommended dietary goals (Walker 1982).

Legumes are most frequently considered in terms of their complementary nutritional value and particularly in relation to amino acids, to cereal diets for people living under marginal nutritional conditions. Legumes are low in the sulfur-containing amino acids but high in lysine (except for groundnut), Aykroyd et al. (1982). Consumers of food legumes have sensory and palatability requirements for the dry and cooked seeds. Seed characteristics not meeting consumer expectation may render a cultivar unacceptable regardless of how agronomically superior it is. Color, flavor, soakability, cookability, and degree of tenderness after cooking are important aspects of legume seeds that influence consumers preference and these seed characteristics are referred to as culinary quality. The genetic composition of legume seeds is a major determinant of culinary quality; however, other factors such as environmental

influences, handling and storage, and processing procedures play important roles (Ghaderi, et al. 1984).

Dry edible beans (Phaseolus vulgaris L.) are among the most important food legumes in the diets of humans in Latin America, parts of Africa, and India (Jaffe, 1972). Beans comprise 32 % of the world total of edible legumes. Eight percent of the world production of legumes is in the U.S.A. and domestic production of beans comprise 82 % of the total edible legumes grown (FAO, 1982).

Dry beans are generally soaked and must be cooked prior to eating to render seed palatable and the proteins nutritionally available. There are a number of tests that allow a food scientist to differentiate the quality of different samples. However, the utility of these techniques in bean breeding depends on the extent of genetic variation for the measured traits. Moreover, the type of gene action involved and the degree to which the expression of genes are influenced by environmental variations determine which breeding strategies would be most successful for trait improvement.

A diallel crossing system can be used to systematically evaluate a strain's performance. These techniques also provide an analytical tool to estimate the combining ability for traits under selection and to evaluated the selection potential of individual crosses. Superior performing parents may produce superior performing progeny in generations subsequent to hybridization.

There is relatively meager information concerning the inheritance of culinary quality traits in dry beans. The present investigation was undertaken to obtain genetic information in a population of dry beans and ascertain the effect of genotype x environmental interactions in trait expression. The implication of the work will be useful for bean breeding programs.

LITERATURE REVIEW

Good cooking quality in peas (Pisum sativum L.) was reported to be controlled by two recessive genes, although, there was some indication of genotype by environment interaction (Gfeller, 1967). Halstead (1964) studied the cooking quality of two cultivars of field peas and found improved culinary characteristics in one cultivar by adding P and K to the soil, the cooking quality of the other cultivar remained unchanged. The same author reported that cooking quality varied among cultivars with ash and phytin P content (Halstead 1964). Wassimi et al. (1978) reported that cooking quality of lentils (Lens culinaris Med.) grown in a pot experiment was significantly influenced by major and trace elements, particularly by high levels of Na and K. A significant genotype and genotype by season interaction and heritabilities of 37% and 63% were found for whole and dehulled pigeon peas (Cajanus cajan L.) seeds, respectively (Singh, et al. 1973). The addition of one percent sodium citrate solution, to the soak water greatly reduced the hardness of whole peas (Muller, 1967). Rizley and Sistrunk (1979) reported that black eyed peas soaked in 1% Pyrophosphate or 1% $NaHCO_3$ solution at pH 8.5 each produced softer texture peas. The bicarbonate treatments produced peas with less desirable color but with softer texture and better flavor as compared to the other treatments (Rizley and Sistrunk 1979). Fast cooking legumes were produced by Bjarkavist (1972) by soaking them in a solution of calcium

sequestering salts until they absorbed an amount of water equal to their dry weight and were dried to a 3 percent moisture content . A decrease in cooking time for beans (Phaseolus vulgaris L.) corresponded to an increased leaching of organic phosphate at cooking temperature of 90° C. Storage of cowpeas (Vigna unguiculata L.) at 85 percent relative humidity and 29° C for one year caused a decrease in cooking rate and formation of hard cooking seed. This was associated with an incomplete breakdown of the middle lamella (Sefa-Dedeh, et al. 1979). Bhatty et al. (1983) reported that location had greater influence on cooking quality of lentils than did the cultivar. The location and season effect was clearly demonstrated in the microstructure of cooked and undercooked lentils (Bhatty, et al., 1984). The microstructure of the lentils showing the degree of cellular breakdown closely correlated with the shear force values (texture) obtained with a Kramer shear press.

High temperatures, high moisture content, and long storage times contributed to impaired cookability in dry beans and lima beans (Phaseolus lunatus L.) (Burr, et al. 1968). A few-fold increase in cooking time was observed in beans held under conditions that may be often encountered in storage. For example, one year keeping time of 21° C and a moisture content below 18% (Burr, et al. 1968). Morris, et al. (1956) reported that beans held at 13 % moisture at 24° C deteriorated significantly in texture as well as flavor after six months while beans held at less than 10 % moisture

content maintained their cooking quality for two years almost as well as control samples stored at minus 10 F. Hosfield and Uebersax (1980) reported significant variability in important nutritional and processing traits among tropical and domestic dry beans. Large variability for five water-soluble vitamins and nine minerals was observed between different commercial classes of dry beans (Augustin, et al., 1981) with between class variability larger than within class. Increased firmness of dry beans has been observed with an increased calcium concentration in soak and brine liquid. A correlation of 0.97 to 0.99 between Kramer shear press values and calcium concentration was reported in a storage time study (Uebersax, 1980). Nordstrom and Sistrunk (1979) showed that bean type, blanch treatment, initial moisture and storage time all had a significant effect on shear press values and splitting of beans after cooking. Rockland and Metzler (1967) proposed a method for quick-cooking dry beans which consisted of loosening seed coats by vacuum infiltration of a salt solution, soaking the beans in the same salt solution and rinsing and drying. The resulting product cooked in 15 minutes (Rockland and Metzler 1967). Varriano-Marston (1979) reported that sodium salts affected the mineral content as well as the amount of pectic substances solubilizing from beans during soaking and cooking periods. X-ray microanalysis suggested that mechanisms of ion exchange and chelation were operative in the dissolution of the intercellular cement and the subsequent cell separation. Ghaderi, et al. (1984) observed

significant cultivar, and cultivar by location differences for culinary quality traits in navy and pinto classes of dry beans. Hosfield, et al. (1984) reported that the expression of soaked and cooked bean traits was strongly influenced by genotype x season interactions. The estimates of season and genotype x season variance components were larger than the genotype component. They also reported that strains differ in their genetic potential to respond to varying environments.

MATERIAL AND METHODS

Genetic material. Twenty strains of dry beans were grown in a replicated nursery during the summer of 1980 at the Montcalm Research Farm near Stanton, Michigan. These strains comprised a broad genetic base and differed in seed-coat color, size, and shape. They varied in growth habit and plant morphology, reaction to heat and drought stress, seed filling characteristics, maturity, and yield.

After harvesting and threshing plants from one replication in the fall,seeds of each strain were evaluated for protein percentage, tannin content, and soaking characteristics including the percentage of hard seed after 48 hours soaking time (Wassimi, 1981). Based on the characteristics of the dry and soaked seed, 8 strains were selected for genetic analysis of culinary quality characteristics. All possible F_1 hybrids were made in the green house during the winter of 1980-81. The 56 F_1 crosses and 8 parents were grown in a nursery in East Lansing during the summer of 1981 to produce F_2 seed.

Field plot procedure. The F_2 seed from each cross was harvested in bulk in September of 1981, and a sample from each parent and each cross was grown in a winter nursery in Puerto Rico in the winter of 1981. Parental and F_3 generation seed was harvested in March of 1982 bulked and returned to East Lansing, Michigan. A random sample of 800 seeds from each cross of the Puerto Rican produced F_3 generation and parental strains and the remnant F_2 and 8 parents grown in

Michigan the previous year were planted in an 11 x 12 rectangular lattice with three replications at the Saginaw Valley Bean and Sugar Beet Research farm near Saginaw and at East Lansing, Michigan in May and June of 1982. Seeds were precision drilled with a tractor mounted air planter (Taylor, 1975) into two row plots guarded on each side by the cultivar 'Seafarer'. Rows were 4.9 meter long and 50.8 cm apart. Herbicide and fertilizer applications were made per seasonal recommendations.

Mature plants were harvested and threshed from a 6 meter row length of each plot in mid-to-late September.

Quality evaluation. Single samples from each plot were evaluated for culinary quality traits of dry seeds and at soaked and cooked stages of processing. Prior to their being processed, bean moisture was determined and based on that moisture a 100 g equivalent weight of total solids was determined and weighed. The bean sample was placed in nylon mesh bags and soaked. The soaking treatment used in this study was a 2-stage procedure that has been shown to maximize differences between genotypes for water uptake, cotyledonary hydration, and the degree of cotyledonary softening during cooking. The initial soak was for 30 min in 21°C water to facilitate seed-coat softening and expansion. Immediately after the cold soak, beans were transferred to water maintained at 88° C in a stainless-steel kettle for an additional 30 min. All soaking was done in tap water containing about 50 ppm calcium. The soaking procedure just

described yields an end product that has minimum bean damage and is similar to beans soaked continuously in the high-temperature systems common throughout the U.S. canning industry. After soaking, beans were momentarily cooled under cold tap water and drained for 2 min. The weight gained through water imbibition during bean soaking was used to calculate:

a) Soaked bean weight which was measured in grams and b) the hydration coefficient which was calculated by dividing the weight of soaked beans by the fresh weight of the dry beans. The percentage water content of soaked beans was determined by the formula (Soaked bean weight (g)- Initial weight of beans (g)/ Soaked bean weight) x 100.

After weighing, beans were filled into 303 x 406 cans and covered with boiling brine prepared by adding 142.0 g of sucrose and 113.4 g of salt to 9.1 kg of tap water containing 50 ppm calcium. Cans were sealed and processed in a retort without agitation for 45 min at 116° C. After thermal processing, cans were uniformly cooled to 38° C under cold tap water and stored for 2 weeks at room temperature before evaluation. The storage period after processing permits canned beans to completely equilibrate with water in the canning medium.

After the cans were opened, the washed drained weight of processed beans was determined by decanting the can contents on a number 8 mesh sieve, rinsing them in 21° C tap water to remove adhering brine, draining for 2 min on the

sieve positioned at a 15° angle, and weighing (g). Texture was determined by using a Kramer Shear Press fitted with a standard multiblade shear compression cell (Food Technology Corp., Reston, VA.). A 100-g sample of washed processed beans was placed in the compression cell and force was applied until blades passed through the bean sample. The water content of the canned beans (final moisture percentage) was determined from the 100-g texture samples. These were oven dried at 81° C until the weight remained constant.

Subjective bean-quality evaluations were made on contents of all processed cans while beans were drained on the mesh screen. The degree of clumping (packing in can) and splitting were scored on a 1-5 scale (5-point range) to represent the minimum and maximum expression of the traits, respectively.

Statistical procedures. All data were subjected to an analysis of variance appropriate to a randomized complete block design. Separate analyses of variance were performed on F_2 and F_3 data at each location. Tests of homogeniety of error variance were made using Bartlett's procedure described in Steel and Torrie (1980). Analyses of variance of combined data were computed. In the mathematical model used for the combined analyses, replications and locations were considered to be a random sample of the population of replications and locations. Since the parental lines used were selected for their quality characteristics, the genetic effects of the strains were of primary interest.

Analyses of combining ability were performed using the program of the theory for combining ability formulas of Griffing (1956) model 1 method 1. Since the parental strains used in the diallel cross were selected, they does not represent a random sample of the population of dry beans genotypes. Therefore, the fixed effect model of Cockerham (1980) was applied to the data and solved by unweighted least square procedure. The model was fitted to include general and specific combining ability effects and is as follows:

$$Y_{ijk} = \mu + b_i + g_j + g_k + s_{jk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$= \mu_G + b_i + A_j + A_k + \delta_{jj}D_{jj} + \delta_{jk}D_{jk} + \delta_{kk}D_{kk} + m_j - m_k + r_{jk} + e_{ijk}$$

$$E(\hat{g}_j) = E\left[\ 1/2bp\ (Y_{.j.} + Y_{..j}) - \hat{\mu}\right]$$

$$= (A_j - \bar{A}_.) + \delta_{jj}(D_{jj} - \bar{D}_{jj.}) + \delta_{jk}(\bar{D}_{j.} - \bar{D}_{..})$$

$$E(\hat{s}_{jk}) = E\left[1/2b\ (\ Y_{.jk} + Y_{.kj}\ ) - \hat{\mu} - \hat{g}_j - \hat{g}_k\right]$$

$$= \delta_{jk}(D_{jk} - \bar{D}_{j.} - \bar{D}_{.k} + \bar{D}_{..})$$

Where:

μ is the population mean

b_i is the i^{th} block effect, $\Sigma b_i = 0$

g_j is the GCA effect associated with the j^{th} parent, $\sum_j^p g_j = 0$

s_{jk} is the SCA effect associated with the cross between the j^{th} female and the k^{th} male parents, $s_{jk} = s_{kj}$, $\sum_k^p s_{jk} = 0$

m_j is the maternal effect associated with the j^{th} parent when it is used as a female, $\sum_j^p m_j = 0$

r_{jk} is the reciprocal effect associated with the cross between the j^{th} female and k^{th} male parent, $r_{jk} = -r_{kj}$,

$\sum_{k \neq j}^{p-1} r_{jk} = 0$

e_{ijk} is the error term associated with the j^{th} and k^{th} parent in the i^{th} block, $E_{ijk} \sim ND(0, \sigma^2)$

A_j is the sum of the additive effects for genes in a gamete from j^{th} parent.

$\bar{A}.$ is the mean additive effect.

$\bar{D}..$ is the mean dominance effect of the hybrid diallel population.

D_{jj} is the sum of the dominance effects associated with the jj^{th} parent

$\bar{D}_{jj}.$ is the mean of the dominance effects associated with the j^{th} parent

$\bar{D}_{j}.$ is the mean of the dominance effects associated with progeny of the j^{th} parent

D_{jk} is the sum of the dominance effects for genes from mating of j^{th} parent with k^{th} parent

δ_{jj} is the expected proportion of loci homozygous for the allele derived from the j^{th} parent, $\delta_{jj} = 1/2F$

δ_{jk} is the expected proportion of heterozygous loci, $\delta_{jk} = 1-F$.

Analyses of covariance between the offspring of each parent (array) and the nonrecurrent parent minus the variance of their offspring in each parental array ($W_r - V_r$) were performed according to Hayman's (1954a, b) analyses of diallel experiments to ascertain whether or not gene expression was appropriate to an additive dominance model or epistasis was a general feature of the system.

Genetic relationships among the parents were studied with the variance-covariance (V_r, W_r) graphical analysis technique developed by Jinks (1954) and Hayman (1954a, b). The V_r, W_r graph was drawn for the means of three replications.

RESULTS

Analysis of variance of individual generation and location data revealed highly significant differences among entries. Combined data analyses of variance were computed after determining that error variance from the separate tests were homogeneous by Bartlett's procedure (Snedecor 1964). The test for hydration ratio, washed drained weight, and cooked bean moisture were not homogeneous. Except for hydration ratio, significant and highly significant differences were detected for all traits (Table 1). There were significant differences between generations for clumps, soaked bean weight and soaked bean moisture. The differences among entries within generation were highly significant for all the traits except hydration ratio (Table 1). The interaction of generation and entry by location were not significant for any of the traits investigated. The computation of general combining ability (GCA) mean squares in each generation over locations revealed (Table 1) that GCA mean square was highly significant for all the traits in the F_2 generation while specific combining ability (SCA) mean square was significant for clumps, washed drained weight, and texture (Table 1). Cooked bean moisture and hydration ratio were the trait for which the maternal and non-maternal reciprocal mean squares were significant, respectively. In the F_3 generation, the GCA mean squares were significant or highly significant for all traits except hydration ratio and the SCA mean squares were highly significant for clumps,

splits, washed drained weight, and texture (Table 1). Only washed drained weight showed significant maternal reciprocal effect mean squares and none of the traits showed any significance for the non-maternal reciprocals.

The traits splits, hydration ratio, and texture showed significant GCA x location and SCA x location mean squares in the F_2 generation (Table 1) but in the F_3 generation only the GCA x location interaction was significant for splits and texture. The interaction of location with maternal effects was significant for cooked bean moisture and the interaction of non-maternal reciprocal effects was significant for clumps, hydration ratio, cooked bean moisture and texture in the F_2 generation, but in the F_3 generation no significant reciprocal difference were detected (Table 1). The GCA effects and their interactions with environments were computed for the eight parents in each generation (Tables 2 and 3) which revealed a significant GCA variance for some parent for each traits. Some inconsistencies in the ranking of strains between generations were observed for GCA effects. Texture and washed drained weight were the traits that showed the most consistent GCA effects in both generations. For example, 15-R, A-30, BTS, SAN, and N-2 transmitted significantly large and negative effects to their F_2 and F_3 progeny for texture, but they transmitted significantly large positive effects to their progenies for washed drained weight (Tables 2 and 3). The interaction of GCA effects by location showed no consistency from genera-

tion to generation for most of the traits except texture. Parental strains B-2, FF, A-30, BTS, SAN in the F_2 and FF, A-30, BTS, SAN, SF in the F_3 generation had either significantly positive or negative GCA interaction effects with locations.

The estimates of variance components for GCA, SCA, maternal and non-maternal reciprocal effects showed (Table 4) that variance of GCA was significant for all the traits in the F_2 and all but hydration ratio in the F_3 generation. The SCA component of variance was significant for clumps, splits, hydration ratio, washed drained weight, and texture in the F_2 generation. Variance component for these traits in the F_3 generation were significant except for hydration ratio. The interactions between combining ability and maternal and non-maternal reciprocal effects variance components and locations generally followed similar trends as the main effects (Table 4).

The correlation of general combining ability effects between F_2 and F_3 generation for the measured traits were large and highly significant (Table 6). Strains A-30, BTS, SAN, SF, and N-2 had large and highly significant SCA effect variances in the F_2 for texture but in the F_3 strains B-2, A-30, SAN, and N-2 had large and significant SCA effect variances (Table 5).

Separate combining ability analyses for F_2 and F_3 generations at both locations showed that the GCA mean squares were highly significant for most of the traits (Tables 1 and 2, appendix B). Similarly, the SCA mean

square estimates were either significant or highly significant for all of the traits except clumps and hydration ratio at both locations and cooked bean moisture at East Lansing in the F_2 generation. In the F_3 generation the SCA mean square for splits, texture, and washed drained weight at East Lansing, and texture, hydration ratio, washed drained weight, and washed drained ratio at Saginaw were either significant or highly significant. Washed drained weight was the only trait that showed significant mean squares for maternal and non-maternal reciprocal effects across locations in both generations (Tables 1 and 2 appendix B). The magnitude of GCA mean squares was larger than SCA in most cases. The estimates of variance components of GCA and SCA in the F_2 and F_3 generation at each location are significant with SCA estimates being larger in magnitude than GCA (Tables 3 and 4 Appendix B). The estimates of variance components of maternal and non-maternal reciprocal effects were generally zero. In cases where these estimates were positive, they were not significant except for washed drained weight (Tables 3 and 4 Appendix B).

The adequacy of the additive dominance model was tested by the analysis of variance for covariance between the parents and their progenies in each array minus the variance of each array (W_r-V_r) for each trait according to Hayman (1954a,b). The mean squares for the traits measured on beans in the F_2 and F_3 generations grown at Saginaw were nonsignificant but the entries grown at East Lansing showed

significant mean squares for the traits soaked bean moisture in the F_3 and texture in the F_2 and F_3 generation (Table 5 Appendix B). The non-significant differences of mean squares of (W_r-V_r) for arrays is indicative of the adequacy of additive dominance model for describing the variation in these traits. However, the significant mean squares for some of the traits indicated that the additive-dominance model is not appropriate to describe the variation in the expression of these traits. This suggests that several assumptions underlying the diallel analysis are invalid (Hayman 1954a, b).

Correlation between pair of soaking traits in the F_2 at East Lansing were positive and significant (Table 7). However, when the soaking traits were correlated with washed drained ratio, they were significant but negative. No other trait showed any significant correlation except texture with soaked bean weight (r=-0.29*). A similar trend was observed in the F_3 generation at East Lansing except that clumps and washed drained weight were significantly correlated with soaked bean weight (r=0.28* and r=-0.28* , respectively). The clumping trait was significantly and negatively correlated with splits (r=-0.44** and r=-0.38**) and texture (r=-0.42** and r=-0.46) in the F_2 and F_3 generations, respectively. A negative correlation (r=-0.50**) between clumps and washed drained weight was observed in the F_3 generation at East Lansing (Table 7). The trend and the sign of the correlation coefficient was similar in both generations but the levels of significance of correlation varied from generation

to generation. Texture was negatively correlated with cooked bean moisture. Similar results were obtained in data from Saginaw with respect to water uptake traits in both soaked and cooked beans (Table 8). A negative correlation of texture with clumps, splits, washed drained weight, and cooked bean moisture was observed. Significant positive correlation coefficients were obtained for the measured traits between F_2 and F_3 generation.

Graphical analyses of traits identified parents with dominant and recessive factors influencing trait expression. The V_r, W_r graphs presented in this study are for clumps, splits, washed drained weight and texture, traits of primary importance to consumers and processors. Figure 1 showed that the regression coefficient (b=0.90$\pm$ 0.22**) for clumps in the F_2 generation after parent 3 which exhibited high variance was eliminated, was significantly different from zero but not significantly different from unity . The regression line intersected the W_r axis slightly below the origin (a=-0.001$\pm$0.045) but not significantly different from zero, indicating complete dominance of genes controlling the trait. Sanilac appeared to contain a preponderance of recessive genes for clumps in the F_2 generation at E. Lansing while the remaining parents carry mostly dominant genes for this trait. At Saginaw in the F_2 generation (Fig. 3) the regression coefficient (b= 1.24$\pm$0.37*) was significantly different from zero but not significantly different from unity. The intercept of the W_r axis was below the origin

(a=-0.16±0.11) but not significantly different from zero, suggesting that complete dominance of genes governs this trait. Here again Sanilac contained mostly recessive genes, while FF 16-15-1-CM-M-M and A-30 appeared to contain overdominant genes, and BTS had mostly dominant genes for this trait. The remaining parents were midway along the regression line indicating equal proportion of dominant and recessive genes. Figure 2 showed regression of W_r on V_r for clumps in the F_3 at E. Lansing. This indicated that the regression coefficient (b=0.53±0.18) was significantly different from zero but not significantly different from unity after elimination of parents 1 and 4 which showed relatively high covariances. The regression line intersected the W_r axis above the point of origin (a=0.03± 0.04) but it is not significantly different from zero indicating complete dominance. The distribution of array points representing the parents changed. Parents BTS and N-2 appeared to carry predominantly recessive genes while parents FF and 15-R seem to have dominant genes. Parents 6 and 7 were also near the origin. The graph of the F_3 generation at Saginaw for clumps (Fig. 4) after elimination of strain FF and SAN indicated that the regression coefficient is significantly different from zero but not significantly different form unity (b=0.99±0.19**). The intercept of W_r axis was above the origin (a=0.04±0.05) but not significantly different form zero suggesting full dominance. The distribution of points

representing parents showed that N-2 is carrying predominantly recessive genes. Strains B-2, 15-R, A-30, and BTS contained dominant gene, and strain N-2 had equal proportion of dominant and recessive genes. Figures 1, 2, 3, and 4 clearly revealed that the pattern of genetic influence for the clumping trait can not be easily be interpreted because of either genic interaction or errors in the way the trait was measured.

The V_r, W_r graph of splits in the F_2 generation at East Lansing is shown in figure 5. The regression coefficient ($b=1.00 \pm 0.12^{**}$) was highly significantly different from zero but not significantly different from unity. The intercept was ($a=0.06 \pm 0.06$) not significantly different from zero which indicated that complete dominance of genes controlled splits in these genotypes. The distribution of array points indicated that strain 15-R seemed to carry mostly recessive genes, strains BTS and SAN predominantly dominant, strains A-30 and N-2 had an intermediate balance of dominant and recessive genes for splits while parent SF shows overdominance for this trait. A similar picture appeared for splits in the F_3 generation at East Lansing (Fig. 6). The regression coefficient ($b=1.07 \pm 0.13^{**}$) was significantly different from zero but not significantly different from unity. The intersect on the W_r axis was through the origin indicating full dominance for splits in the F_3. The distribution of array points is similar to the F_2 except that strain SF showed interallelic interaction and strain BTS complete dominance. Strain FF was an outlier and A-30, SAN,

and N-2 had an intermediate balance of dominant and recessive genes. Strains B-2 and 15-R carried a preponderance of recessive genes. In the F_2 generation at Saginaw the V_r,W_r graph showed that the regression coefficient (b=0.94$\pm$ 0.13**) was significantly different from zero but not significantly different from unity (Fig. 7). The intercept of W_r axis was a=0.24$\pm$0.06* which was significantly above the origin. This response suggested that the gene system controlling this trait was partially dominant. Since the array points representing BTS and 15-R- are closest to the point of intersection between the regression line and limiting parabola, it indicated that BTS and 15-R carried a preponderance of dominant genes. B-2 and A-30 carried mostly recessive genes. Strains SAN and SF seemed to carry a balance of dominant and recessive genes while FF and N-2 seemed to carry dominant genes in excess of recessive genes. The over all picture of splits in the F_3 generation at Saginaw (Fig. 8) was the same. The regression coefficient was significantly different from zero but not significantly different from unity (b=0.94$\pm$0.12**) and the intercept of W_r axis was significantly above the origin (a=0.23$\pm$0.05*) indicating that genes with partial dominance effect controlled splits in the F_3. The distribution of array points indicated that recessive genes seemed to prevail in strains B-2 and SF while strain N-2 carried mostly dominant genes. The remaining parents had a balance of both dominant and recessive genes.

Figure 9 represented the V_r, W_r graph for washed drained weight in the F_2 generation at East Lansing. The regression coefficient (b=0.95 $\pm$ 0.15**) was significantly different from zero but not significantly different from unity. The intercept of the regression line was not significantly different from origin (a=-0.02$\pm$ 0.03) indicating that complete dominance of genes controlled this trait. Array point distribution showed that strains B-2 and SAN carried predominantly recessive genes, strain 15-R carried a preponderance of dominant genes, while N-2 showed a balance of dominant and recessive genes. Strains FF, A-30, BTS, and SF displayed interallelic interaction. The graph of washed drained weight in the F_3 generation at East Lansing was the same as that of the F_2 generation with respect to overall dominance (Fig. 10) but the distribution of array points representing the parents was different. The slope of the regression line was signiiicantly different from zero but not significantly different from unity (b=1.32$\pm$ 0.27**). The intersect of the regression was not significantly different from zero (a= -0.02$\pm$0.02) suggesting full dominance of genes for this trait. Parents FF and BTS carried mostly dominant genes but 15-R and SF carried mostly recessive genes. Parents A-30 and N-2 had a balance of dominant and recessive genes, while parents B-2 and SAN carried an excess of dominant genes for this trait. The graph of washed drained weight in F_2 in Saginaw was the same as the F_3 in E. Lansing (Fig. 11). In the F_3 generation at Saginaw the V_r, W_r graph for washed drained weight (Fig. 12)

showed that the slope of the regression line was significantly different from zero but not significantly different from unity (b=1.30±0.26*). The intersect of W_r axis was slightly below the origin but not significantly different from zero indicating that the gene system controlling this trait exhibited complete dominance. The distribution of array points representing the parents indicated that parents B-2, FF, 15-R, and BTS carried a preponderance of dominant genes, and parents A-30, SAN, and N-2 had mostly recessive genes. Parent SF had a balance of dominant and recessive genes for this trait.

The V_r, W_r graph of texture of the F_2 generation at East Lansing indicated that the regression coefficient (b=0.41 + 0.21*) was significantly different from one but not significantly different from zero (Fig. 13). This suggested that the assumption of no genic interaction was invalid in this case. This disturbance in the anticipated slope was caused by parents SF and N-2 which were interacting in this case in opposite direction. Elimination of these parents and recalculation of the regression of W_r on V_r (Fig. 14) showed that the slope of the regression line became significantly different from zero but not significantly different from from unity (b=1.08 ± 0.06**). The intercept of the W_r axis was significantly different from the origin (a=8.18±1.03**) indicating that partially dominant genes controlled this trait. This changed the distribution of array points along the regression line. Strain

15-R appeared to carry a preponderance of recessive genes, and FF and SAN seem to carried mostly dominant genes. B-2, A-30 and BTS exhibited a balance of dominant and recessive genes. Figure 15 showed the V_r,W_r graph for texture in the F_3 generation at East Lansing. The regression coefficient (b=0.85$\pm$0.19**) was significantly different from zero but not significantly different from unity. The intersect on the W_r axis was significantly above the origin (a=18.66$\pm$7.69**) suggesting that a partially dominance system of genes controlled this trait. Array points distribution indicated that strains FF, 15-R, BTS, and SF carried preponderance of dominant genes and strains SAN, and N-2 a preponderance of recessive genes. Parents B-2 and A-30 had an intermediate balance of dominant and recessive genes. The slope of the regression line for texture in the F_2 generation at Saginaw (Fig. 16) was significantly different from zero but not significantly different from unity (b=0.84$\pm$0.10**). The intercept of the W_r axis was significantly different from zero (a=15.05$\pm$3.0**). This suggested that a partially dominant system of genes controlled texture in the F_2. The distribution of array points representing the parents along the regression line indicated that SAN and N-2 carried a preponderance of recessive genes while BTS and SF carried mostly dominant genes for this trait. The remaining parents had a balance of both dominant and recessive genes for texture. Figure 17 showed tne V_r, W_r graph for texture in the F_3 generation at Saginaw, and revealed that the regression coefficient was significantly different from

zero but not significantly different from unity (b=1.0 ± 0.16**). The intersect of W_r axis was significantly above the origin indicating that a partial dominance of genes controlled this trait. The distribution of array points representing the parents indicated that A-30, SAN, and N-2 carried a preponderance of recessive gene and 15-R, BTS, and SF carried a preponderance of dominant genes while B-2 and FF had a balance of both dominant and recessive genes.

Table 1. Mean square from analyses of varaince and combining ability analyses and their interaction wiht location for 9 culinary quality traits measure on parents and F_2 and F_3 progeny of an 8x8 diallel cross in dry beans and grown at E. Lansing and Saginaw, Michigan in 1982.

Source of variation	d.f.	Clumps (scale)	Splits (scale)	Soaked beans weight (g)	Soaked beans moisture (%)	Hydration ratio
Toatal	768					
Location (L)	1	2.9	42.7	2094	79.7	1.28
Reps/L	4	19.6	3.8	4063	153	0.37
Entry	127	1.24**	3.1**	229**	9.2*	0.75
Generation (G)	1	1.09*	0.03	948*	30.0**	0.99
Entry/G	126	1.24**	3.07**	223**	9.0**	0.75
G x L	1	0.001	0.16	340	11.2	0.98
Among F_2						
GCA	7	4.91**	24.1**	951**	41.3**	2.31**
SCA	28	1.10**	0.93	185	7.3	1.11
Maternal (M)	7	0.50	0.42	62	2.2	0.87
Nonmaternal reciprocal (NMR)	21	0.45	0.54	76	3.2	1.92**
Among F_3						
GCA	7	6.07**	18.8**	1015**	38.6*	0.012
SCA	28	0.99**	1.17**	164	6.4	0.01
M	7	0.32	0.23	111	4.6	0.002
NMR	21	0.26	0.56	87	3.5	0.004
Entry x Loaction	127	0.50	0.60	140	5.8	0.71
F_2 x L						
GCA	7	0.48	1.29**	351	15.0	1.50*
SCA	28	0.58	0.99**	206	8.5	1.17*
M	7	0.34	0.25	62	2.2	0.80
NMR	21	0.67*	0.31	78	3.1	1.89*
F_3 x L						
GCA	7	0.77	1.17**	170	7.1	0.007
SCA	28	0.45	0.44	132	5.4	0.005
M	7	0.33	0.26	79	3.3	0.004
NMR	21	0.32	0.39	84	3.8	0.003
Error	508	0.41	0.42	119	4.8	0.72
Experiment mean		2.14	2.88	229	56.2	1.86
C.V. (%)		29.9	22.5	4.8	3.9	45.5

*,** = Significant at 5% and 1% probability level, respectiely.

Table 1. (cont'd.).

Source of variation	d.f.	Washed drained weight (g)	Washed drained ratio	Cooked beans moisture (%)	Texture (Kg/100 g)
Toatal	768				
Location (L)	1	80.7	0.11	0.5	2506
Reps/L	4	1720	0.07	8.1	196
Entry	127	331**	0.02*	2.7**	245**
Generation (G)	1	483	0.006	2.8	2.1
Entry/G	126	329**	0.02**	2.7**	247**
G x L	1	54	0.005	1.5	24
Among F_2					
GCA	7	1207**	0.10**	8.4**	1189**
SCA	28	245*	0.008	2.3	140**
Maternal (M)	7	16	0.003	5.0**	25
Nonmaternal reciprocal (NMR)	21	91	0.004	2.4	23
Among F_3					
GCA	7	1327**	0.10**	7.1**	1898**
SCA	28	332**	0.009	1.6	137**
M	7	325*	0.004	0.9	31
NMR	21	159	0.005	1.3	41
Entry x Loaction	127	137	0.01	1.7	39
F_2 x L					
GCA	7	186	0.01	1.1	147**
SCA	28	94	0.009	1.3	38*
M	7	73	0.004	3.6**	21
NMR	21	95	0.003	2.6*	31*
F_3 x L					
GCA	7	248	0.006	2.9	156**
SCA	28	107	0.005	1.0	22
M	7	271	0.002	0.6	28
NMR	21	205	0.004	1.7	11
Error	508	95	0.005	1.7	17
Experiment mean		311	1.36	64.5	44.8
C.V. (%)		3.1	5.2	2.0	9.2

*,** = Significant at 5% and 1% probability level, respectiely.

Table 2. General combining ability effects averaged over location and their interaction with location for culinary quality traits measured on F_2 progeny of an 8-parent diallel cross in dry edible beans in 1982.

Parent	Clump (scale)	Split (scale)	Soak bean weight (g)	Soak bean moisture (%)
Among F_2				
B-2	-0.109	-0.104	1.672*	0.351
FF	0.203*	-0.677*	2.649*	0.461*
15-R	0.286*	-0.823*	-1.066	-0.277
A-30	-0.276*	0.208*	-7.019	-1.470
BTS	0.161*	0.313*	1.094	0.263
SAN	0.161*	0.156*	1.738*	0.415
SF	-0.255*	0.375*	1.959*	0.415
N-2	-0.172*	0.552*	-1.027	-0.158
$S_{\bar{Y}}$	0.131	0.144	1.636	0.452
$S_{\bar{D}}$	0.102	0.112	1.707	0.348
F_2 x Location				
B-2 x L	-0.052	0.104	0.299	0.027
FF x L	0.073	0.177*	-1.755	-0.309
15-R x L	0.031	0.010	-2.774*	-0.594*
A-30 x L	0.010	0.104	-1.084	-0.261
BTS x L	-0.094	-0.104	2.321*	0.465*
SAN x L	-0.052	-0.114	0.084	0.018
SF x L	-0.031	-0.104	2.853*	0.594
N-2 x L	0.114	-0.073	0.056	0.060
$S_{\bar{Y}}$	0.116	0.116	2.037	0.409
$S_{\bar{D}}$	0.092	0.094	1.573	0.316

$S_{\bar{Y}}$ and $S_{\bar{D}}$ = standard error of means and standard error of a difference between two means, respectively.
* = Significant at 5% probability level.

Table 2. (cont'd.).

Parent	Hydration ratio	Wash drain weight (g)	Wash drain ratio	cooked bean moist. (%)	Texture Kg/100g
Among F_2					
B-2	-0.086	-2.236	-0.02*	-0.319*	2.172*
FF	-0.089	-0.458	-0.017*	-0.455*	4.199*
15-R	-0.103	0.132	0.009	-0.028	-0.783
A-30	-0.164*	5.628*	0.071*	0.011	-0.478
BTS	0.287*	-2.121	-0.017*	0.129	-1.846*
SAN	0.117	4.420*	0.006	0.383*	-6.077*
SF	0.115	-5.198*	-0.036*	-0.086	4.504*
N-2	-0.077	-0.166	0.004	0.365*	-1.690*
$S_{\bar{Y}}$	0.158	2.195	0.014	0.270	1.175
$S_{\bar{D}}$	0.121	1.689	0.014	0.185	0.904
F_2 x Location					
B-2 x L	0.079	0.802	0.002	-0.021	0.815*
FF x L	0.078	-0.219	0.008	-0.098	-1.651*
15-R x L	0.070	-2.658*	0.006	-0.081	0.567
A-30 x L	0.093	1.591	0.016*	0.071	-2.261*
BTS x L	-0.248*	-0.187	-0.015	0.091	0.794*
SAN x L	-0.087	-1.093	-0.005	-0.148	0.914*
SF x L	-0.076	1.390	-0.012	0.033	0.595
N-2 x L	0.091	0.374	-0.000005	0.153	0.227
$S_{\bar{Y}}$	0.158	1.824	0.013	0.243	0.772
$S_{\bar{D}}$	0.122	1.408	0.01	0.188	0.966

$S_{\bar{Y}}$ and $S_{\bar{D}}$ = standard error of mean and standard error of a difference between two mean, respectively.
* = Significant at 5% probability level.

Table 3. General combining ability effects averaged over location and their interaction with location for culinary quality traits measured on F_3 progeny of an 8-parent diallel cross in dry edible beans in 1982.

Parent	Clump (scale)	Split (scale)	Soak bean weight (g)	Soak bean moisture (%)
Among F_3				
B-2	-0.018	-0.044	0.669	0.156
FF	-0.080	-0.523	1.289	0.127
15-R	0.232*	-0.773	1.599	0.263
A-30	-0.258*	0.247*	-7.859*	-1.542*
BTS	0.242*	0.070	1.333	0.278
SAN	0.357*	0.122	1.095	0.283
SF	-0.331*	0.372*	2.126	0.413
N-2	-0.143	0.529*	-0.253	0.022
$S_{\bar{Y}}$	0.132	0.145	2.214	0.453
$S_{\bar{D}}$	0.102	0.112	1.707	0.348
F_3 x Location				
B-2 x L	0.070	0.039	1.072	0.189
FF x L	0.049	0.206*	-2.335*	-0.497*
15-R x L	0.049	0.018	-1.703	-0.338
A-30 x L	-0.065	0.059	1.294	0.222
BTS x L	-0.190*	-0.075	0.577	0.129
SAN x L	-0.013	-0.023	0.151	0.019
SF x L	0.070	-0.169*	0.926	0.235
N-2 x L	0.028	-0.055	0.018	0.041
$S_{\bar{Y}}$	0.119	0.121	2.044	0.409
$S_{\bar{D}}$	0.092	0.044	1.573	0.316

$S_{\bar{Y}}$ and $S_{\bar{D}}$ = standard error and standard error of difference respectively. * = Significant at 5% probability level.

Table 3. (cont'd.).

Parent	Hydration ratio	Wash drain weight (g)	Wash drain ratio	cooked bean moist. (%)	Texture Kg/100g
Among F_3					
B-2	-0.002	-2.930*	-0.017*	-0.302*	2.291*
FF	-0.016	-2.478*	-0.015*	-0.443*	5.417*
15-R	0.007	1.251	-0.003	0.012	-0.820
A-30	-0.077	5.164*	0.072*	-0.015	-0.537
BTS	0.027	-3.119*	-0.022*	0.137	-2.217*
SAN	0.034	2.775*	0.003	0.344*	-7.362*
SF	0.019	-4.584*	-0.033*	-0.039	6.005*
N-2	0.007	3.921*	0.016*	0.306*	-2.776*
$S_{\bar{Y}}$	0.136	2.196	0.014	0.242	1.177
$S_{\bar{D}}$	0.121	1.689	0.014	0.185	0.904
F_3 x Location					
B-2 x L	-0.0004	0.746	-0.003	0.206	-0.445
FF x L	-0.011	0.011	0.015*	0.054	-1.444*
15-R x L	-0.012	-2.673*	-0.0008	-0.206	0.412
A-30 x L	0.012	2.698*	0.005	0.069	-1.883*
BTS x L	-0.001	1.006	-0.00001	0.086	1.270*
SAN x L	0.005	0.197	-0.0001	-0.316*	1.114*
SF x L	0.007	-1.208	-0.012	-0.012	1.497*
N-2 x L	0.0009	-0.777	-0.004	0.119	-0.523
$S_{\bar{Y}}$	0.158	1.823	0.013	0.242	0.775
$S_{\bar{D}}$	0.122	1.408	0.01	0.188	0.966

$S_{\bar{Y}}$ and $S_{\bar{D}}$ = standard error and standard error of difference respectively. * =Significant at 5% probability level.

Table 4. Estimates of variance components and their interaction with locations for 9 culinary quality traits measured on parents, F_2 and F_3 progeny of an 8-parent diallel cross in dry edible beans grown at East Lansing and Saginaw, Michigan in 1982.

Components of variation	Clumps (scale)	Splits (scale)	Soaked bean weight (g)	Soaked bean moisture (%)	Hydration ratio	Washed Drained weight (g)	Washed Drained ratio	Cookbean moisture (%)	Texture (Kg force/ 100g)
Among F_2									
GCA	0.046±0.024	0.245±0.118	8.44± 4.68	0.37±0.20	0.017 ±0.011	11.1 ± 5.9	0.0009±0.0005	0.07±0.04	11.97±5.84
SCA	0.10 ±0.049	0.055±0.044	7.42± 8.96	0.24±0.36	0.067 ±0.052	17.9 ±11.3	---	0.11±0.11	16.81±6.14
Maternal (M)	---	---	---	---	0.002 ±0.004	---	---	0.03±0.002	---
Nonmaternal reciprocal (NMR)	---	---	---	---	0.202 ±0.097	---	---	0.12±0.13	---
Among F_3									
GCA	0.058±0.029	0.19 ±0.09	9.11± 4.99	0.34±0.19	---	12.4 ± 6.5	0.0009±0.0005	0.06±0.04	19.36±9.32
SCA	0.082±0.045	0.09 ±0.05	3.90± 8.16	0.09±0.32	---	32.4 ±14.8	---	---	16.33±6.03
M	---	---	---	---	---	1.95±1.61	---	---	---
NMR	---	---	---	---	---	3.55±8.78	---	---	0.27±2.33
Location x F_2									
GCA	0.002±0.005	0.02 ±0.01	4.84± 3.47	0.21±0.15	0.016 ±0.014	1.90 ±1.86	0.0001±0.00009	---	2.70±1.44
SCA	0.057±0.055	0.19 ±0.09	29.10±19.04	1.25±0.78	0.15 ±0.109	---	0.0013±0.0008	---	6.83±3.38
M	---	---	---		0.0017±0.008	---	---	0.04±0.04	0.08±0.21
NMR	0.087±0.07	---	---		0.39 ±0.19	0.02 ±10.88	---	0.31±0.27	4.46±3.16
Location x F_3									
GCA	0.008±0.008	0.02 ±0.01	1.07± 1.72	0.05±0.07	---	3.20 ±2.36	---	0.03±0.03	2.89±1.53
SCA	0.013±0.045	0.01 ±0.04	4.38±10.91	0.21±0.54	---	4.06 ±10.8	---	---	1.53±2.12
M	---	---	---	---	---	3.87 ±2.69	---	---	0.22±0.28
NMR	---	---	---	---	---	36.6 ±20.9	---	---	---

--- = negative or very small positive value.

Table 5. Parental values (y_r), for texture and washed drained weight and variances of specific combining ability effects(S^2_{si}) of 8 dry bean genotypes evaluated with their F_2 and F_3 progeny from an 8-parent diallel cross grown at East Lansing and Saginaw in 1982.

	Generation							
	F_2				F_3			
	Texture (kg Force/100g)		Washed drained weight (g)		Texture (Kg Force /100g)		Washed drained weight (g)	
Parent	Yr	S^2_{si}	Yr	S^2_{si}	Yr	S^2_{si}	Yr	S^2_{si}
B-2	49.1	0.0	297.6	14.7*	52.8	0.21	301.1	0.0
FF	54.1	0.0	306.5	0.0	56.0	0.0	307.7	9.25
15-R	45.5	1.27	311.9	0.0	44.6	4.87	304.2	17.35*
A-30	37.8	6.45**	333.1	21.9**	34.6	13.93**	323.6	2.39
BTS	38.3	5.47*	310.0	0.388	37.4	0.88	302.9	10.75
SAN	31.1	14.8**	321.9	16.7*	25.9	15.03**	312.9	0.28
SF	50.7	13.2**	302.3	2.78	55.5	14.71**	290.0	51.7**
N-2	34.1	28.3**	314.7	24.5**	31.9	16.86**	321.9	41.9**
$S_{\bar{y}}$	1.2		2.2		1.7		3.3	
$S_{\bar{D}}$	1.7		3.1		1.7		4.7	

$S_{\bar{y}}$ = Standard error of mean and general combining ability effect, respectively.

$S_{\bar{D}}$ = Standard error of difference between 2 means and general combining ability effects, respectively.

Table 6. Correlation coefficient (r) for general combining ability effects between F_2 and F_3 progeny of an 8x8 diallel cross and parental values vs. GCA effects in the two generations of dry edible beans grown at East Lansng and Saginaw, Michigan in 1982.

Traits	Correlation coefficient (r)[z]		
	GCA effects between F_2 and F_3	Parental value vs. GCA effects	
		F_2	F_3
Soaked beans			
Weight (g)	0.92**	0.88**	0.72*
Moisture (%)	0.92**	0.96**	0.93**
Hydration ratio	0.72*	0.62	0.59
Cooked beans			
Clumps(scale)	0.83**	0.77*	0.82**
Splits(scale)	0.98**	0.98**	0.87**
Moisture (%)	0.99**	0.76*	0.72*
Texture(kg force/100g)	0.99**	0.92**	0.94**
Washed drained weight (g)	0.86**	0.90**	0.91**
Washed drained ratio	0.98**	0.82**	0.76*

*,** = Significant at 5% and 1% probability level, respectively. z = Data averaged over 2 locations.

Table 7. Correlation coefficient (r) indicating the relationship between pairs of culinary quality traits of 56 F_2 (upper triangle) and F_3 (lower triangle) progeny of an 8x8 diallel cross grown at E. Lansing, Michigan in 1982.

Traits[z]	Correlation coefficient (r)*								
	Soaked beans weight (1)	Hydration ratio (2)	Soaked beans moist. (3)	Clumps (4)	Splits (5)	Texture (6)	Washed drained weight (7)	Washed drained ratio (8)	Cooked beans moisture (9)
1.	---	0.64	0.66	0.11	0.10	-0.29	-0.21	-0.77	-0.23
2.	0.62	---	0.83	-0.03	0.23	0.11	0.13	-0.85	0.11
3.	0.86	0.79	---	0.07	0.17	0.11	0.17	-0.85	0.01
4.	0.28	0.16	0.04	---	-0.38	-0.46	0.24	0.03	-0.12
5.	0.03	0.05	0.08	-0.44	---	-0.05	0.35	-0.04	0.11
6.	0.17	-0.09	0.10	-0.42	-0.07	---	-0.77	-0.37	-0.06
7.	-0.28	-0.17	-0.27	-0.50	0.46	-0.50	---	0.22	0.13
8.	-0.74	-0.71	-0.83	0.01	-0.04	-0.34	0.53	---	-0.02
9.	-0.13	0.14	0.12	-0.14	0.17	-0.30	0.35	0.42	---

z = Traits number in the column corresponds to those in the row.
* = Absolute value of coefficient equal to or greater than 0.26 and 0.34 are significant at the 5% and 1% probability level, respectively.

Table 8. Correlation coefficient (r) indicating the relationship between pairs of culinary quality traits of 56 F_2 (upper triangle) and F_3 (lower triangle) progeny of an 8x8 diallel cross grown at Saginaw, Michigan in 1982.

Traits[z]	Correlation coefficient (r)*								
	Soaked beans weight (1)	Hydration ratio (2)	Soaked beans moist. (3)	Clumps (4)	Splits (5)	Texture (6)	Washed drained weight (7)	Washed drained ratio (8)	Cooked beans moisture (9)
1.	---	0.69	0.40	-0.28	0.39	-0.14	0.34	-0.47	-0.10
2.	0.65	---	0.43	-0.10	-0.07	-0.09	0.02	-0.36	0.08
3.	0.72	0.82	---	-0.10	-0.19	-0.15	-0.32	-0.80	0.23
4.	0.28	0.36	0.26	---	-0.42	-0.10	-0.29	0.11	0.02
5.	-0.41	0.02	-0.28	-0.29	---	-0.30	0.39	0.08	0.35
6.	-0.19	-0.49	-0.21	-0.51	-0.13	---	-0.26	-0.15	-0.72
7.	0.22	-0.38	-0.26	0.02	0.21	-0.16	---	0.26	0.16
8.	-0.10	-0.58	-0.63	-0.25	0.21	-0.04	0.19	---	0.71
9.	0.10	0.47	0.15	0.31	0.19	-0.77	0.20	0.05	---

z = Traits number in the column corresponds to those in the row.
* = Absolute value of coefficient equal to or greater than 0.26 and 0.34 are significant at the 5% and 1% probability level, respectively.

Table 9. Means of texture and processing traits for two generations of an 8-parent diallel cross grown in East Lansing, MI (1982).

Parents and crosses	Generations					
	F_2			F_3		
	Traits			Traits		
	Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Clumps (scale)	Splits (scale)	Texture (Kf/100g)
Parents						
B-2 (1)	1.8	2.3	53.1	2.0	2.7	56.5
FF (2)	2.7	1.0	52.4	2.3	1.3	56.0
15-R (3)	2.3	1.0	49.7	2.7	1.7	46.9
A-30 (4)	1.0	4.0	38.6	1.7	3.7	34.7
BTS (5)	2.7	3.0	39.0	3.0	3.0	39.5
SAN (6)	3.3	2.3	37.6	3.0	3.7	30.4
SF (7)	1.7	3.3	50.8	1.7	3.7	60.1
N-2 (8)	2.0	3.7	33.3	1.7	4.0	33.8
Crosses						
1 x 2	2.5	2.8	50.8	2.0	2.8	49.3
1 x 3	2.0	1.8	53.4	2.5	1.8	50.3
1 x 4	1.7	3.5	45.4	2.0	3.8	45.7
1 x 5	2.0	3.5	49.3	2.0	3.5	47.8
1 x 6	2.0	3.2	43.8	3.0	2.8	40.4
1 x 7	1.3	3.8	42.9	1.7	3.8	53.8
1 x 8	1.8	4.0	48.3	2.2	3.2	44.8
2 x 3	2.5	1.2	50.1	2.5	1.6	49.8
2 x 4	2.0	3.0	48.5	1.3	3.5	48.5
2 x 5	2.2	3.0	48.1	1.8	3.0	51.3
2 x 6	2.3	2.8	44.8	2.5	3.2	44.7
2 x 7	2.0	3.3	52.7	2.0	2.8	58.2
2 x 8	2.3	3.8	45.0	2.2	4.0	47.9
3 x 4	2.0	2.7	42.8	1.8	2.0	46.6
3 x 5	2.3	3.0	43.1	2.7	2.8	44.8
3 x 6	2.3	3.0	40.3	2.3	2.7	42.1
3 x 7	3.0	2.3	44.8	2.3	3.3	43.3
3 x 8	2.3	3.5	46.3	2.3	3.3	43.3
4 x 5	2.0	3.8	40.5	2.0	3.7	42.8
4 x 6	2.0	3.7	43.0	1.7	3.2	38.3
4 x 7	1.7	4.0	49.3	1.7	3.3	52.2
4 x 8	2.2	3.3	46.7	2.0	3.7	48.3
5 x 6	2.0	3.7	42.1	2.3	2.8	40.9
5 x 7	2.0	3.2	49.8	2.2	2.8	51.7
5 x 8	1.7	3.5	51.8	1.3	3.2	47.6
6 x 7	1.2	3.7	54.7	1.8	3.5	57.5
6 x 8	2.3	3.5	29.3	2.8	3.3	30.3
7 x 8	1.2	3.5	59.6	1.5	3.7	53.6
$S_{\bar{D}}$	0.4	0.4	2.7	0.4	0.4	2.5

$S_{\bar{D}}$= Standard error of a difference between two means.

Table 10. Means for soaking and mass ratio traits for F_2 and F_3 progeny from an 8-parent diallel cross grown at East Lansing in 1982.

Parents and crosses	Generations					
	F_2			F_3		
	Soaked bean weight (g)	Soaked bean moisture (%)	Hydration ratio	Soaked bean weight (g)	Soaked bean moisture (%)	Hydration ratio
Parents						
B-2 (1)	231.8	46.8	1.9	235.3	44.5	1.9
FF (2)	230.4	43.8	1.8	232.2	44.1	1.8
15-R (3)	214.4	41.8	1.7	221.5	44.7	1.8
A-30 (4)	209.6	39.6	1.7	216.6	42.9	1.7
BTS (5)	232.6	47.3	1.9	228.4	46.7	1.9
SAN (6)	230.1	46.9	1.9	221.3	46.3	1.9
SF (7)	231.6	46.4	1.9	225.4	47.6	1.9
N-2 (8)	227.3	45.1	1.8	227.7	46.8	1.9
Crosses						
1 x 2	237.1	44.4	1.8	223.2	43.5	1.8
1 x 3	225.9	43.4	1.8	231.7	44.9	1.8
1 x 4	216.9	40.1	1.7	222.6	42.4	1.7
1 x 5	234.8	46.9	1.9	232.7	45.8	1.8
1 x 6	221.2	45.0	1.8	226.8	45.6	1.8
1 x 7	233.6	45.7	1.8	232.4	45.5	1.8
1 x 8	228.4	45.9	1.8	230.3	44.8	1.8
2 x 3	218.3	43.0	1.8	216.5	42.3	1.7
2 x 4	206.5	40.8	1.7	214.5	41.9	1.8
2 x 5	229.3	45.5	1.8	230.6	44.5	1.8
2 x 6	234.9	46.6	1.9	233.9	46.4	1.9
2 x 7	234.7	47.1	1.9	233.1	45.2	1.8
2 x 8	230.0	45.7	1.8	228.8	44.6	1.7
3 x 4	209.4	39.9	1.7	217.2	40.8	1.8
3 x 5	226.7	45.6	1.8	231.1	46.5	1.9
3 x 6	231.4	45.8	1.9	240.9	48.2	1.9
3 x 7	236.7	46.9	1.9	233.4	45.4	1.9
3 x 8	220.6	43.9	1.8	228.0	44.9	1.7
4 x 5	231.8	44.9	1.8	222.2	42.7	1.8
4 x 6	229.4	45.6	1.8	226.6	45.8	1.8
4 x 7	224.7	44.2	1.8	227.7	43.1	1.8
4 x 8	220.8	45.3	1.8	221.2	43.9	1.8
5 x 6	227.6	46.3	1.9	229.4	46.3	1.9
5 x 7	231.0	46.5	1.9	232.6	46.9	1.9
5 x 8	227.6	46.4	1.9	229.4	46.3	1.9
6 x 7	231.3	46.1	1.9	229.6	46.3	1.9
6 x 8	222.7	44.8	1.8	222.5	44.7	1.8
7 x 8	228.9	46.4	1.9	231.3	46.0	1.8
$S_{\bar{D}}$	5.9	1.2	0.05	6.4	1.3	0.13

$S_{\bar{D}}$= Standard error of a difference between two means.

Table 10. (cont'd.).

Parents and crosses	Generations					
	F_2			F_3		
	Wash drain weight (g)	Cooked bean moisture (%)	Wash drain ratio	Wash drain weight (g)	Cooked bean moisture (%)	Wash drain ratio
Parents						
B-2 (1)	373.3	63.4	1.3	376.1	63.2	1.3
FF (2)	379.3	64.2	1.2	376.1	64.1	1.3
15-R (3)	394.1	65.2	1.3	388.1	64.9	1.3
A-30 (4)	421.9	65.5	1.5	398.3	65.2	1.5
BTS (5)	386.8	64.1	1.3	376.1	64.0	1.3
SAN (6)	401.1	66.6	1.4	393.7	66.0	1.4
SF (7)	371.8	64.3	1.3	367.6	64.8	1.3
N-2 (8)	388.1	65.5	1.3	404.3	65.1	1.4
Crosses						
1 x 2	317.0	62.5	1.3	306.4	64.3	1.4
1 x 3	306.4	63.5	1.4	307.1	63.1	1.3
1 x 4	325.9	63.8	1.5	321.2	64.7	1.4
1 x 5	309.9	64.3	1.3	310.0	64.2	1.3
1 x 6	305.9	63.8	1.4	310.0	64.1	1.4
1 x 7	308.2	64.9	1.3	304.6	65.1	1.3
1 x 8	307.0	66.0	1.3	318.8	66.1	1.4
2 x 3	303.5	63.8	1.4	310.0	63.6	1.4
2 x 4	315.8	64.6	1.5	310.0	64.2	1.4
2 x 5	310.0	64.1	1.4	314.1	64.9	1.4
2 x 6	310.0	64.1	1.4	317.6	64.0	1.4
2 x 7	304.1	63.6	1.3	305.2	63.5	1.3
2 x 8	312.9	64.2	1.4	307.6	63.7	1.3
3 x 4	312.9	64.2	1.5	325.4	64.4	1.5
3 x 5	308.2	65.9	1.4	310.5	64.2	1.3
3 x 6	304.7	64.2	1.3	318.2	65.2	1.3
3 x 7	313.5	64.0	1.3	306.4	64.5	1.3
3 x 8	310.5	64.3	1.4	310.0	64.4	1.4
4 x 5	317.0	64.0	1.4	312.3	64.6	1.4
4 x 6	323.0	64.5	1.4	322.9	64.3	1.4
4 x 7	312.3	64.4	1.4	314.7	64.5	1.4
4 x 8	310.6	64.7	1.4	324.8	64.8	1.4
5 x 6	311.2	65.5	1.4	312.9	65.2	1.4
5 x 7	302.3	64.4	1.3	312.3	64.6	1.3
5 x 8	299.4	65.4	1.3	302.9	65.1	1.3
6 x 7	308.8	64.3	1.3	305.9	63.4	1.3
6 x 8	328.9	65.7	1.5	322.3	74.7	1.4
7 x 8	301.6	69.7	1.3	315.3	64.3	1.4
$S_{\bar{D}}$	4.3	1.2	0.04	5.3	0.7	0.04

$S_{\bar{D}}$= Standard error of differences.

Table 11. Means of texture and processing traits for two generations of an 8-parent diallel cross grow Saginaw, MI (1982).

Parents and crosses	Generations					
	F_2			F_3		
	Traits			Traits		
	Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Clumps (scale)	Splits (scale)	Texture (Kf/100
Parents						
B-2 (1)	1.3	2.0	45.1	2.3	2.0	49.2
FF (2)	1.7	1.0	55.8	1.3	1.0	56.0
15-R (3)	2.3	1.0	41.3	2.3	1.0	42.2
A-30 (4)	1.7	3.0	37.0	2.3	3.3	34.5
BTS (5)	2.3	3.7	37.6	3.3	3.3	35.4
SAN (6)	3.7	3.7	24.5	3.3	3.3	21.3
SF (7)	1.3	3.7	51.3	1.3	3.7	50.8
N-2 (8)	1.0	3.3	34.9	1.0	3.7	29.7
Crosses						
1 x 2	2.7	1.0	54.0	2.3	1.8	55.7
1 x 3	2.2	1.5	45.6	2.3	1.5	45.7
1 x 4	1.7	2.3	47.8	2.0	3.0	43.9
1 x 5	2.8	3.0	39.4	2.2	2.8	40.1
1 x 6	2.5	2.7	39.2	2.7	2.7	37.1
1 x 7	1.8	3.5	45.5	1.2	3.8	48.2
1 x 8	1.8	3.3	40.4	2.2	3.0	44.3
2 x 3	2.2	1.5	45.5	1.8	1.3	45.1
2 x 4	2.0	1.7	52.2	1.3	2.0	55.2
2 x 5	2.5	2.3	45.7	2.7	2.2	43.4
2 x 6	2.0	2.2	40.7	2.5	1.8	41.4
2 x 7	2.5	2.2	51.0	2.3	2.2	50.5
2 x 8	2.8	2.3	48.2	2.5	3.2	50.0
3 x 4	2.5	1.5	43.4	2.5	1.8	45.1
3 x 5	2.8	2.8	39.4	2.8	2.2	39.0
3 x 6	2.8	1.8	34.2	2.8	2.5	34.2
3 x 7	2.2	1.8	45.2	2.5	2.0	40.6
3 x 8	2.3	2.5	40.6	2.2	2.7	40.5
4 x 5	2.2	3.2	40.8	2.5	2.8	41.3
4 x 6	1.3	3.3	41.4	1.8	3.0	40.8
4 x 7	2.0	3.5	49.9	1.7	3.7	52.0
4 x 8	1.7	3.3	47.7	2.2	3.2	45.6
5 x 6	2.5	2.8	36.7	2.8	2.7	33.8
5 x 7	2.2	3.2	42.0	2.3	3.5	42.4
5 x 8	2.0	3.5	43.3	2.7	3.0	39.0
6 x 7	2.2	3.0	45.1	2.2	3.0	45.0
6 x 8	2.0	3.7	28.1	2.7	3.5	26.2
7 x 8	1.3	4.0	47.4	1.2	3.8	48.9
$S_{\bar{D}}$	0.4	0.3	2.0	0.4	0.4	2.1

$S_{\bar{D}}$= Standard error of a differences between two means.

Table 12. Means for soaking and mass ratio traits for F_2 and F_3 progeny of an 8-parent diallel cross grown at Saginaw in 1982.

Parents and crosses	Generations					
	F_2			F_3		
	Soaked bean weight (g)	Soaked bean moisture (%)	Hydration ratio	Soaked bean weight (g)	Soaked bean moisture (%)	Hydration ratio
Parents						
B-2 (1)	231.7	45.0	1.8	231.6	45.6	1.8
FF (2)	255.9	47.8	1.9	246.6	48.7	1.8
15-R (3)	242.8	46.3	1.9	241.5	48.2	1.9
A-30 (4)	223.4	41.5	1.7	220.8	41.5	1.7
BTS (5)	233.2	46.4	1.9	226.9	46.2	1.9
SAN (6)	234.1	47.3	1.9	232.6	46.3	1.9
SF (7)	229.2	47.7	1.9	234.0	47.3	1.9
N-2 (8)	233.4	45.9	1.8	236.5	46.7	1.9
Crosses						
1 x 2	235.4	44.9	1.8	234.8	44.8	1.8
1 x 3	234.8	45.0	1.8	226.9	43.6	1.8
1 x 4	229.1	42.0	1.7	220.8	43.0	1.7
1 x 5	228.4	45.1	1.8	238.3	47.2	1.9
1 x 6	225.6	45.7	1.8	231.6	45.8	1.8
1 x 7	233.7	46.0	1.8	230.2	45.5	1.8
1 x 8	230.2	45.5	1.8	235.0	45.8	1.8
2 x 3	241.0	45.0	1.8	239.6	45.6	1.8
2 x 4	227.6	42.5	1.7	221.0	40.5	1.7
2 x 5	226.9	44.5	1.8	237.8	45.5	1.8
2 x 6	232.0	45.5	1.8	238.5	46.4	1.9
2 x 7	218.2	42.0	1.7	238.4	45.0	1.8
2 x 8	228.7	44.1	1.8	230.8	44.4	1.8
3 x 4	222.4	42.1	1.7	234.4	44.1	1.8
3 x 5	224.9	44.9	1.8	228.7	45.6	1.8
3 x 6	231.8	45.6	1.8	237.7	47.4	1.9
3 x 7	232.8	44.6	1.8	245.9	47.2	1.9
3 x 8	221.2	43.1	1.8	229.7	44.7	1.8
4 x 5	220.7	41.2	1.7	223.7	43.2	1.8
4 x 6	229.2	43.2	1.8	226.8	44.8	1.8
4 x 7	215.1	41.0	1.7	211.9	40.0	1.7
4 x 8	215.0	40.2	1.7	225.9	43.1	1.8
5 x 6	228.9	45.5	1.8	237.1	47.0	1.9
5 x 7	230.8	46.7	1.9	233.5	47.3	1.9
5 x 8	226.4	45.7	1.8	238.4	47.2	1.9
6 x 7	229.2	45.8	1.8	235.2	45.9	1.8
6 x 8	232.5	45.3	1.8	226.6	46.2	1.9
7 x 8	233.9	46.5	1.9	233.4	46.2	1.9
$S_{\bar{D}}$	5.3	1.1	0.03	6.7	1.3	0.13

$S_{\bar{D}}$= Standard error of differences.

Table 12. (cont'd.).

Parents and crosses	Generations					
	F_2			F_3		
	Wash drain weight (g)	Cooked bean moisture (%)	Wash drain ratio	Wash drain weight (g)	Cooked bean moisture (%)	Wash drain ratio
Parents						
B-2 (1)	373.3	63.4	1.3	376.1	63.2	1.3
FF (2)	379.3	64.2	1.2	376.1	64.1	1.3
15-R (3)	394.1	65.2	1.3	388.1	64.9	1.3
A-30 (4)	421.9	65.5	1.5	398.3	65.2	1.4
BTS (5)	386.7	64.1	1.3	376.1	64.0	1.3
SAN (6)	401.1	66.6	1.4	383.7	66.0	1.4
SF (7)	371.8	64.3	1.3	367.6	64.8	1.3
N-2 (8)	388.1	65.5	1.3	404.3	65.1	1.4
Crosses						
1 x 2	305.3	63.9	1.3	302.4	63.2	1.3
1 x 3	302.3	63.2	1.4	308.3	63.6	1.4
1 x 4	311.8	64.1	1.4	312.4	64.3	1.3
1 x 5	308.8	64.1	1.4	307.6	64.5	1.3
1 x 6	307.6	64.7	1.4	309.8	64.8	1.4
1 x 7	307.6	64.3	1.3	304.1	64.6	1.3
1 x 8	305.1	64.6	1.3	307.1	64.3	1.3
2 x 3	318.8	64.4	1.3	317.7	64.5	1.3
2 x 4	309.4	63.8	1.4	307.1	64.0	1.4
2 x 5	308.8	64.1	1.4	312.4	64.2	1.3
2 x 6	315.3	64.2	1.4	313.6	64.5	1.3
2 x 7	304.7	64.8	1.4	303.5	64.0	1.3
2 x 8	308.8	63.9	1.3	307.6	64.3	1.3
3 x 4	312.9	64.3	1.4	324.1	64.6	1.4
3 x 5	307.6	64.7	1.4	312.4	65.2	1.4
3 x 6	317.7	64.8	1.4	319.5	65.7	1.3
3 x 7	307.1	64.1	1.3	315.9	64.9	1.3
3 x 8	311.2	64.4	1.4	314.1	64.6	1.4
4 x 5	311.2	64.5	1.4	311.7	64.5	1.4
4 x 6	317.1	64.2	1.4	317.1	65.0	1.4
4 x 7	299.4	64.1	1.4	305.3	64.0	1.4
4 x 8	309.4	64.1	1.4	316.8	64.5	1.4
5 x 6	311.8	64.8	1.4	309.4	65.2	1.3
5 x 7	300.0	64.8	1.3	301.7	64.9	1.3
5 x 8	303.5	64.3	1.3	304.7	64.7	1.3
6 x 7	306.5	64.3	1.3	302.9	64.8	1.3
6 x 8	323.6	65.7	1.4	320.0	66.0	1.4
7 x 8	301.1	64.3	1.3	337.2	64.7	1.4
$S_{\bar{D}}$	4.3	0.4	0.03	7.7	0.4	0.05

$S_{\bar{D}}$= Standard error of differences.

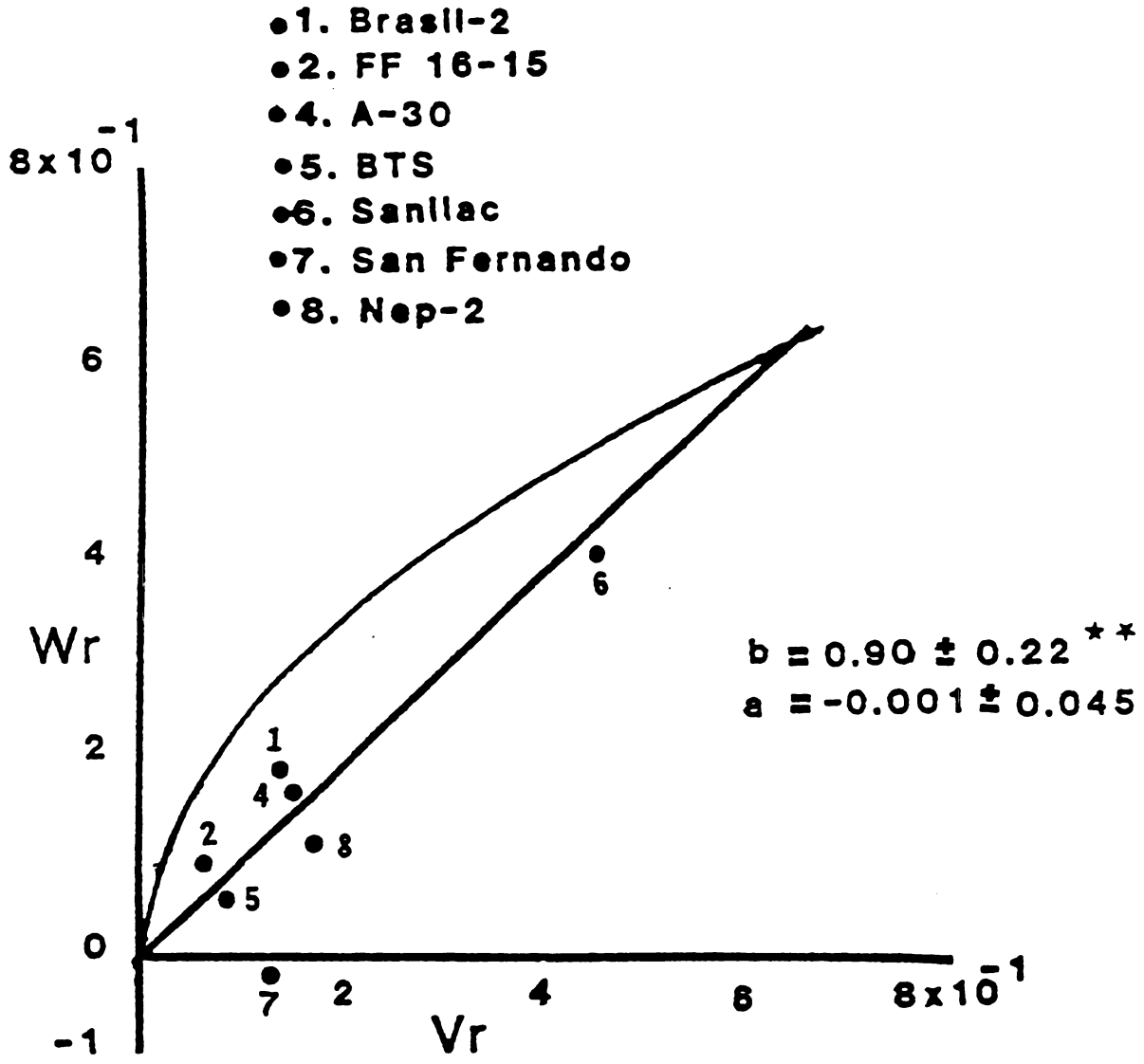

Figure 1. Variance (V_r)-covariance (W_r) graph for clump data of the F_2 generation grown at E. Lansing and showing the position of points representing the 7 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

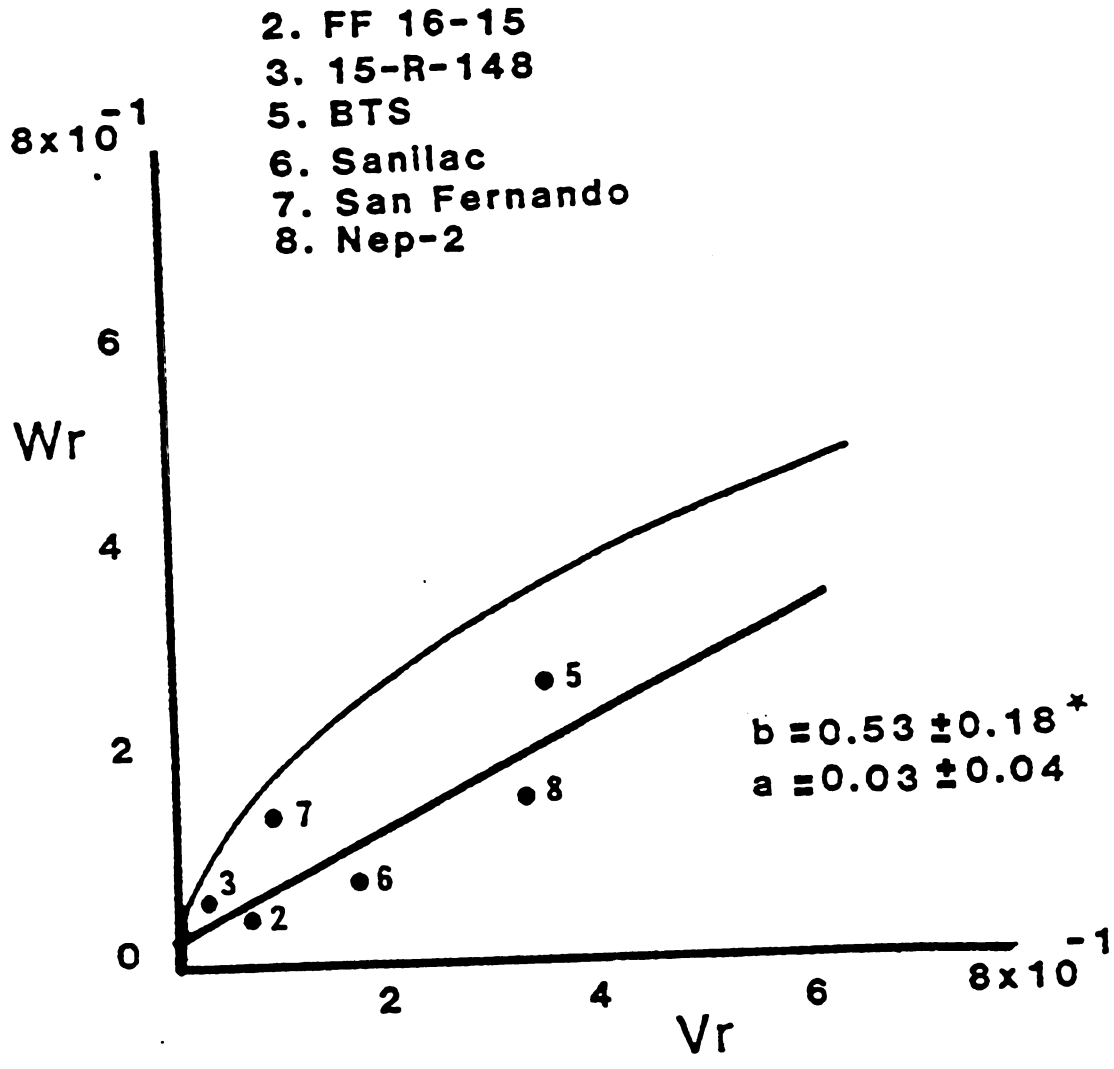

Figure 2. Variance (V_r)-covariance (W_r) graph for clump data of the F_3 generation grown at E. Lansing and showing the position of points representing the 6 parental arrays and their regression line relative to a limiting parabola under which all points must lie. * = Significant at the 5% level of probability.

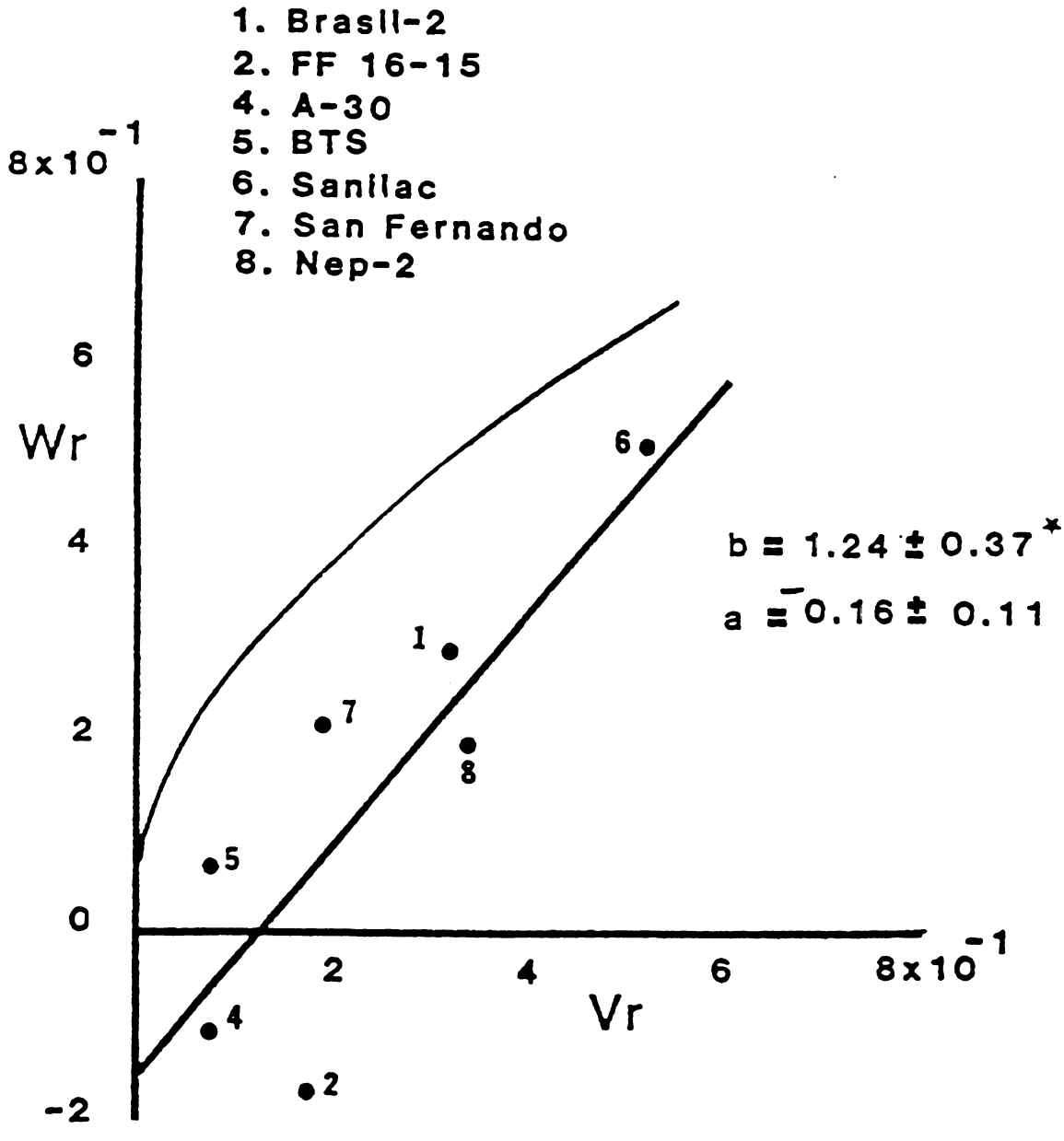

Figure 3. Variance (V_r)-covariance (W_r) graph for clump data of the F_2 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. * = Significant at the 5% level of probability.

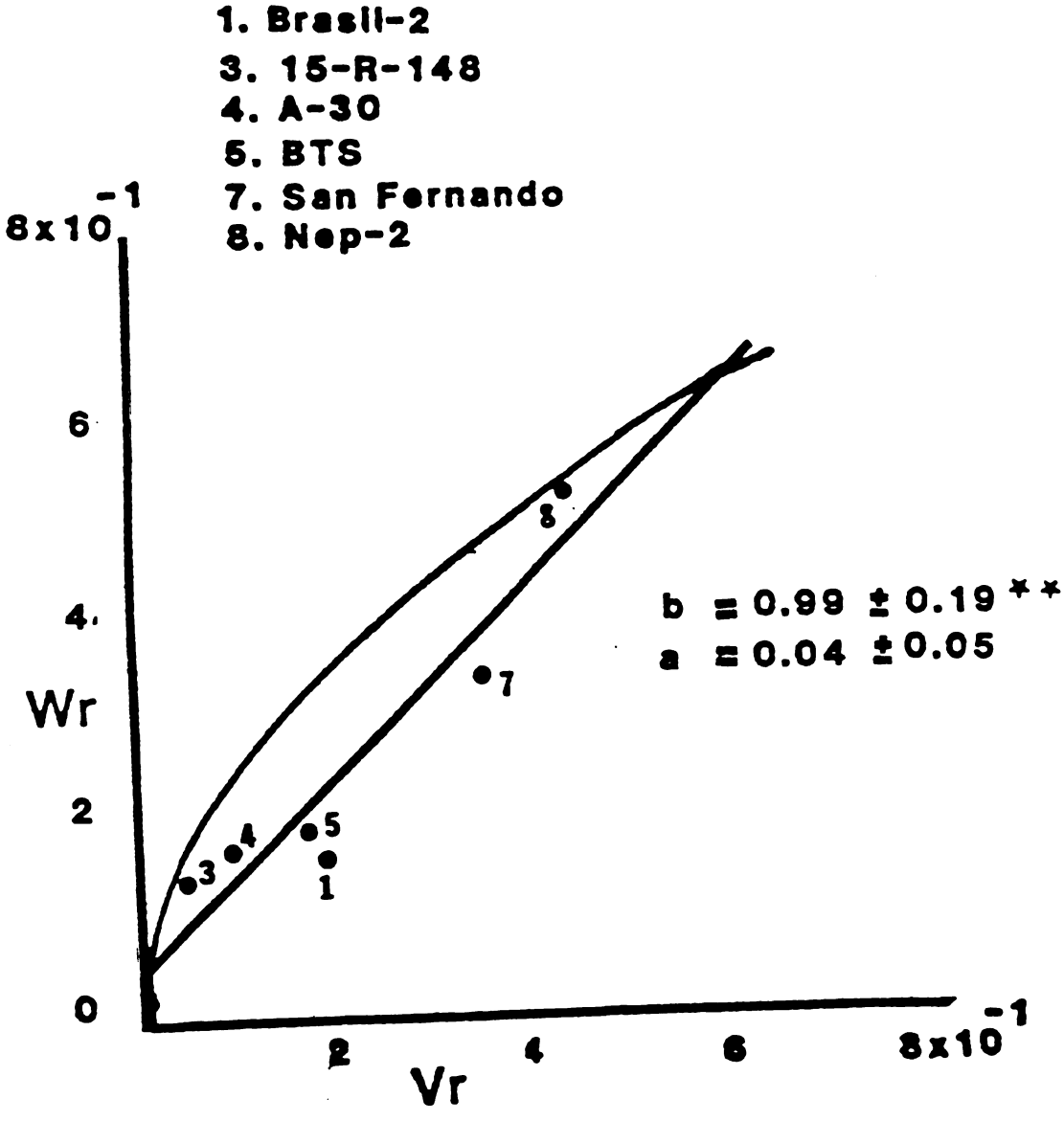

Figure 4. Variance (V_r)-covariance (W_r) graph for clump data of the F_3 generation grown at Saginaw and showing the position of points representing the 6 parental arrays and their regressionline relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

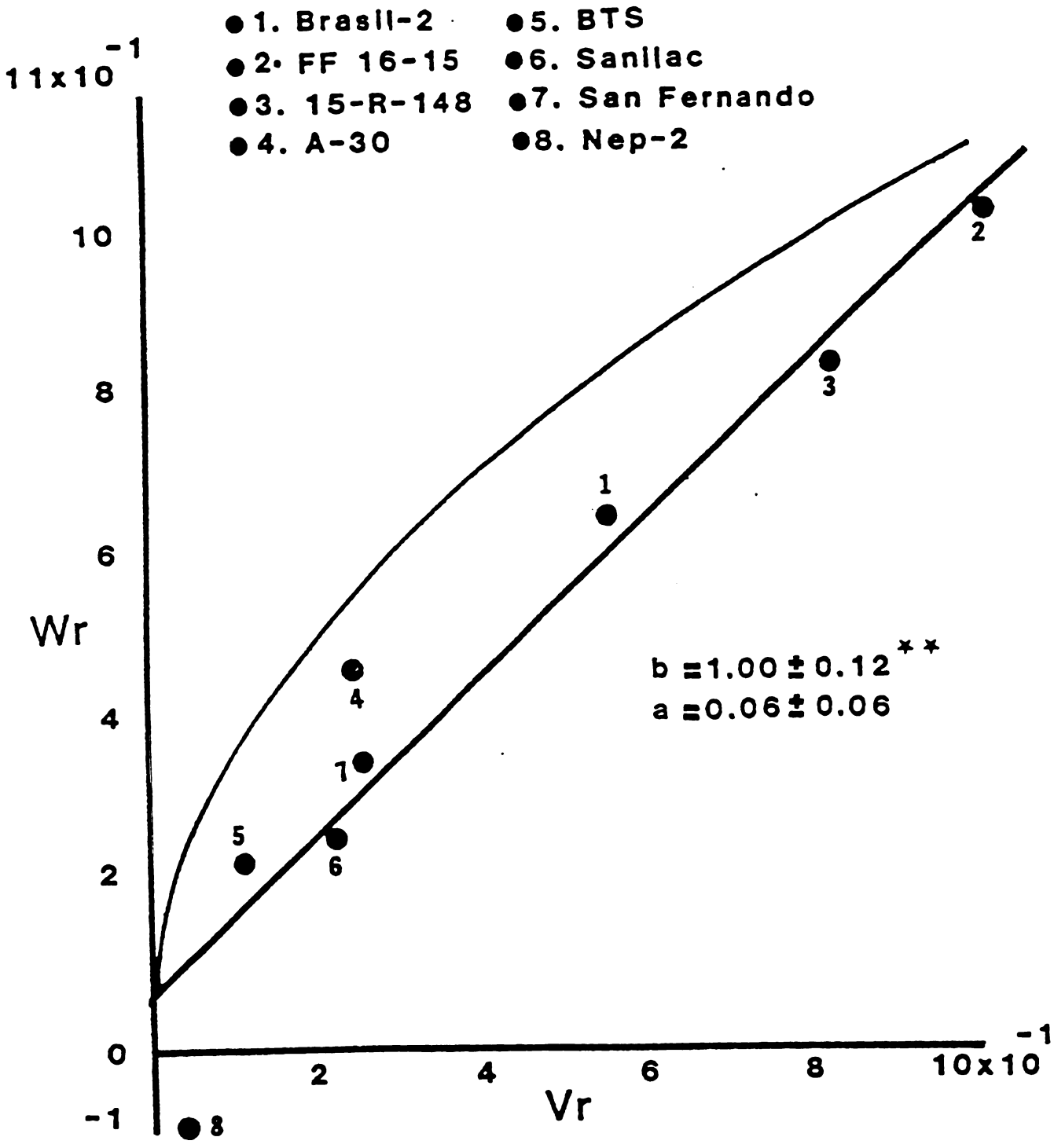

Figure 5. Variance (V_r)-covariance (W_r) graph for slpits data of the F_2 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

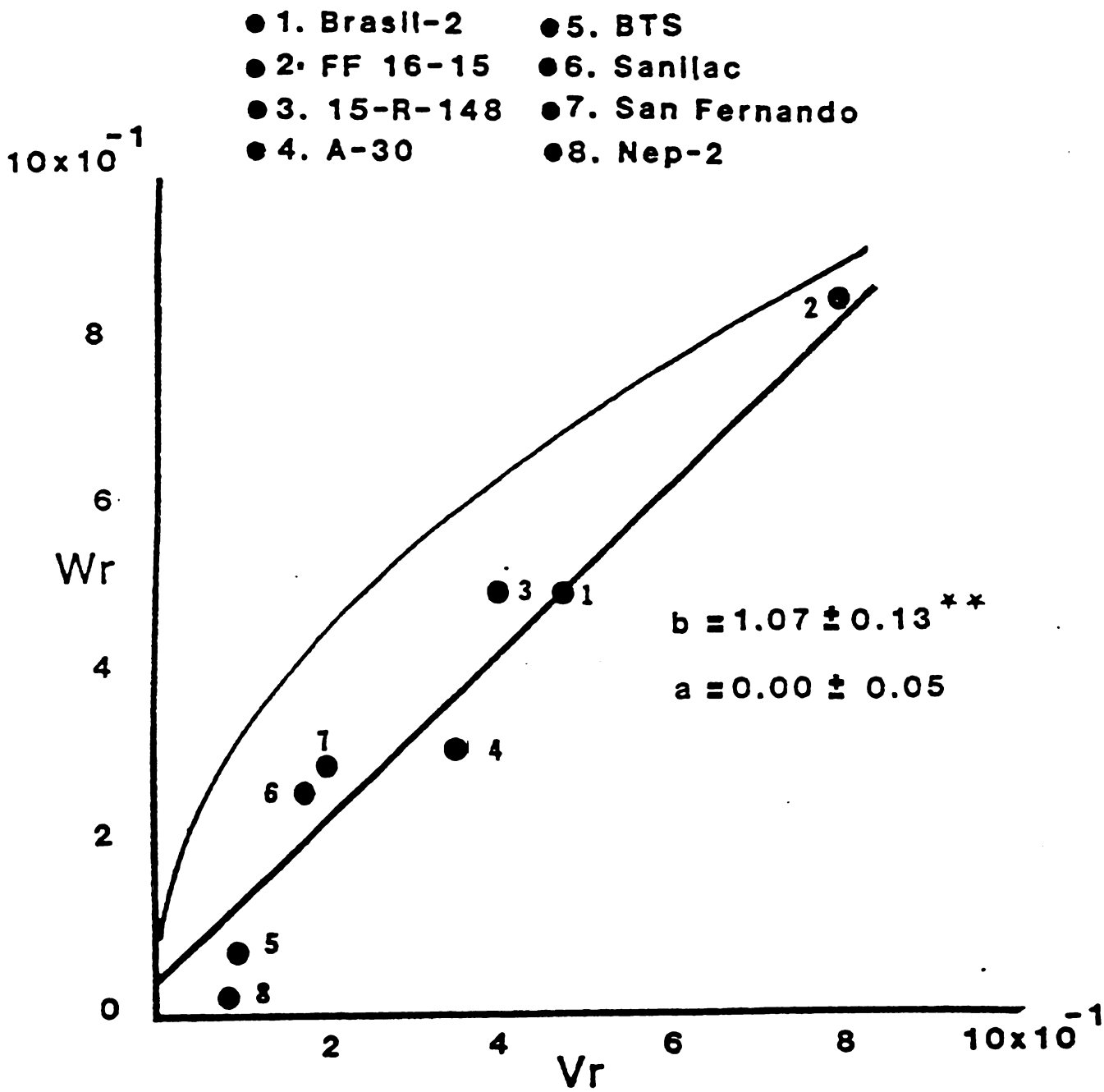

Figure 6. Variance (V_r)-covariance (W_r) graph for splits data of the F_3 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

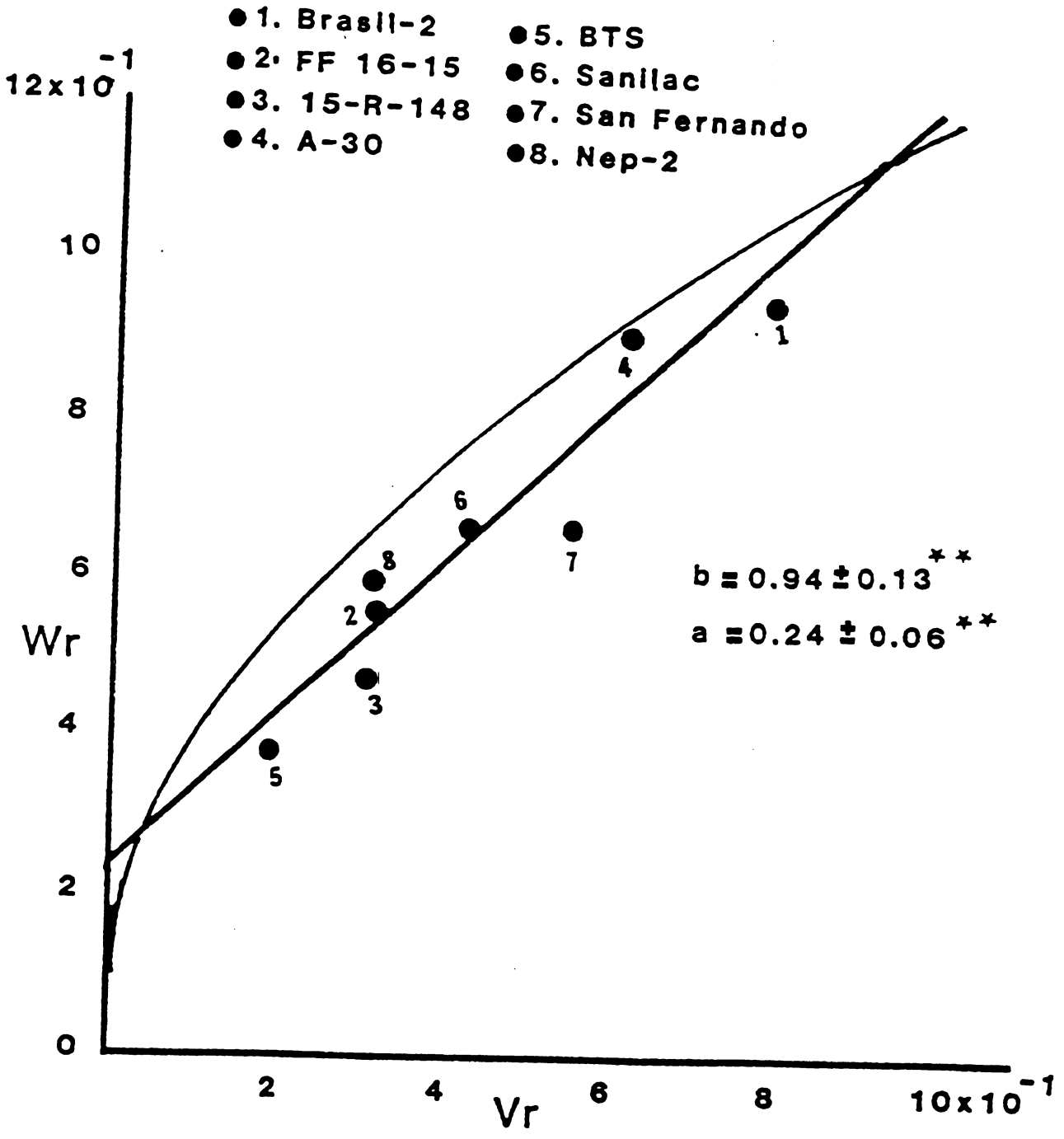

Figure 7. Variance (V_r)-covariance (W_r) graph for splits data of the F_2 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

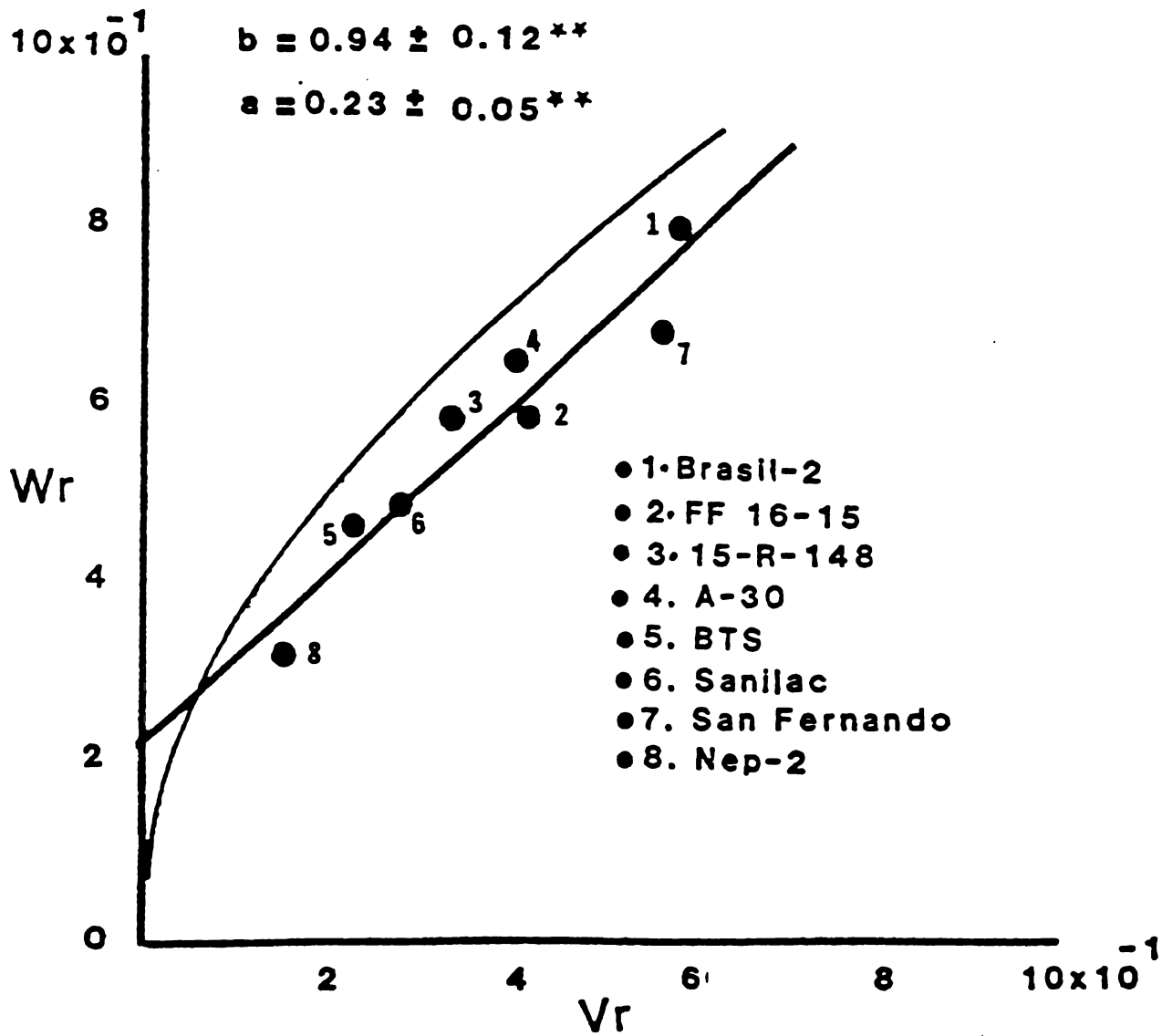

Figure 8. Variance (V_r)-covariance (W_r) graph for splits data of the F_3 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

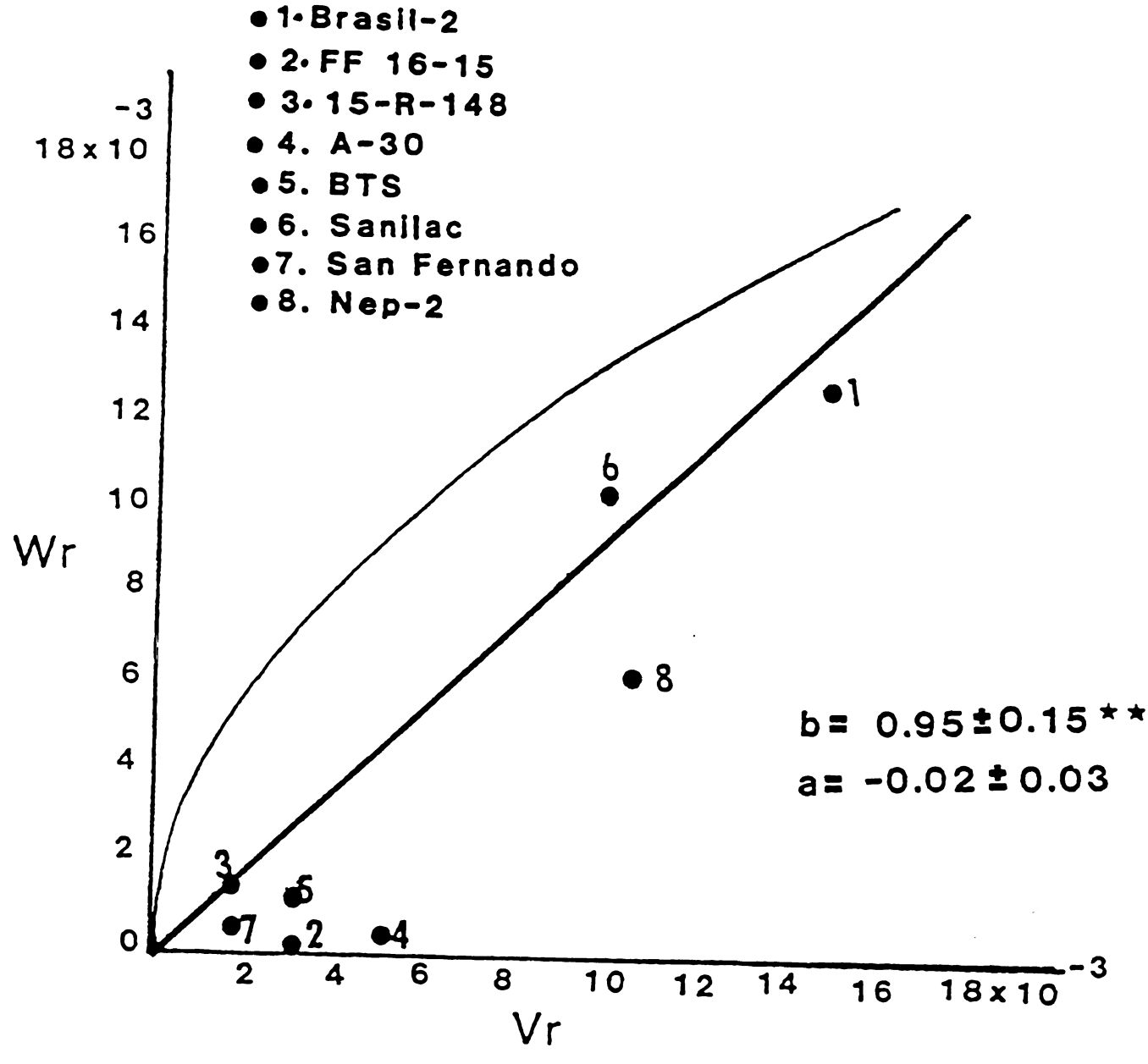

Figure 9. Variance (V_r)-covariance (W_r) graph for washed drained weight data of the F_2 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

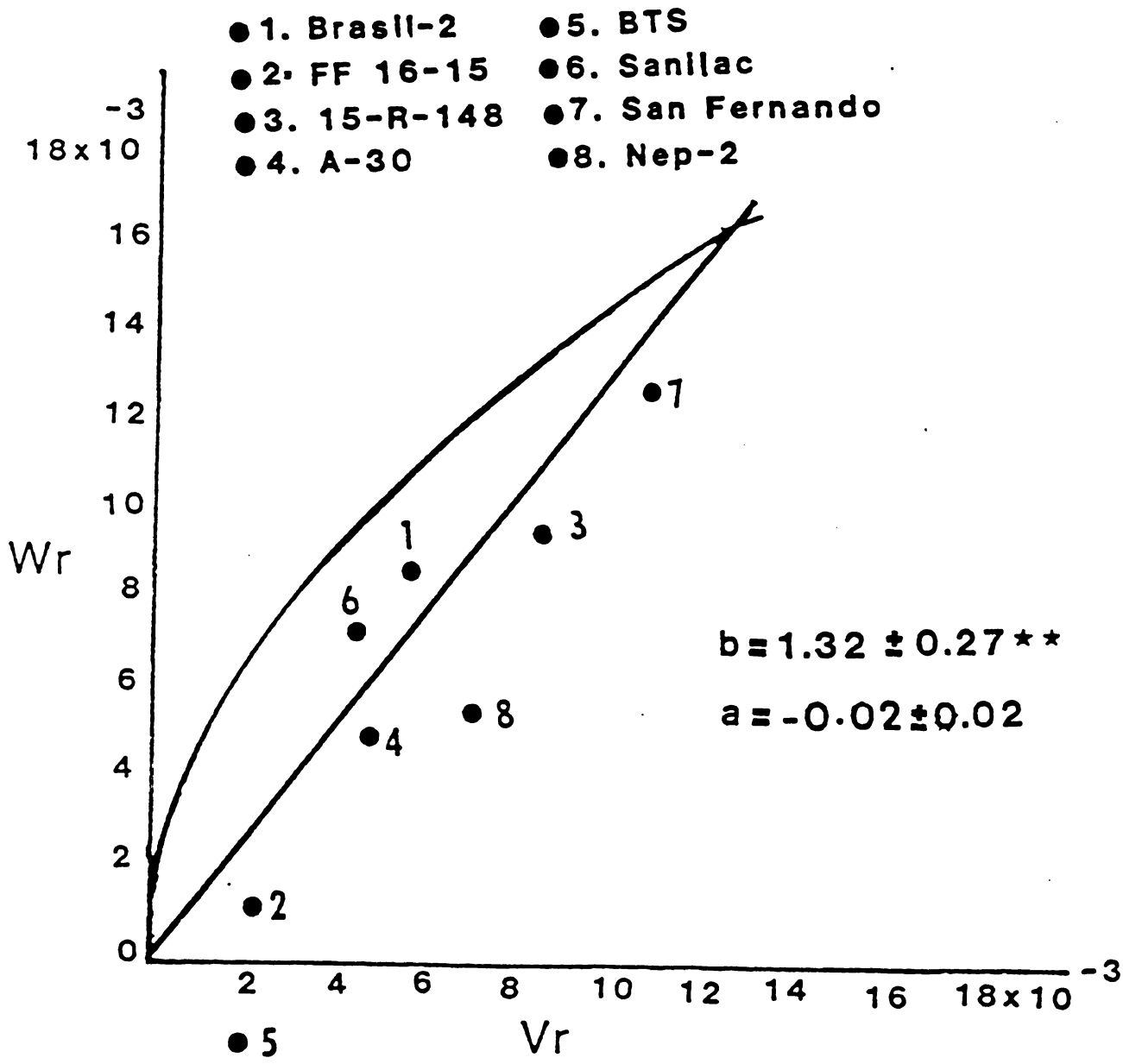

Figure 10. Variance (V_r)-covariance (W_r) graph for washed drained weight data of the F_3 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie.** = Significant at the 1% level of probability.

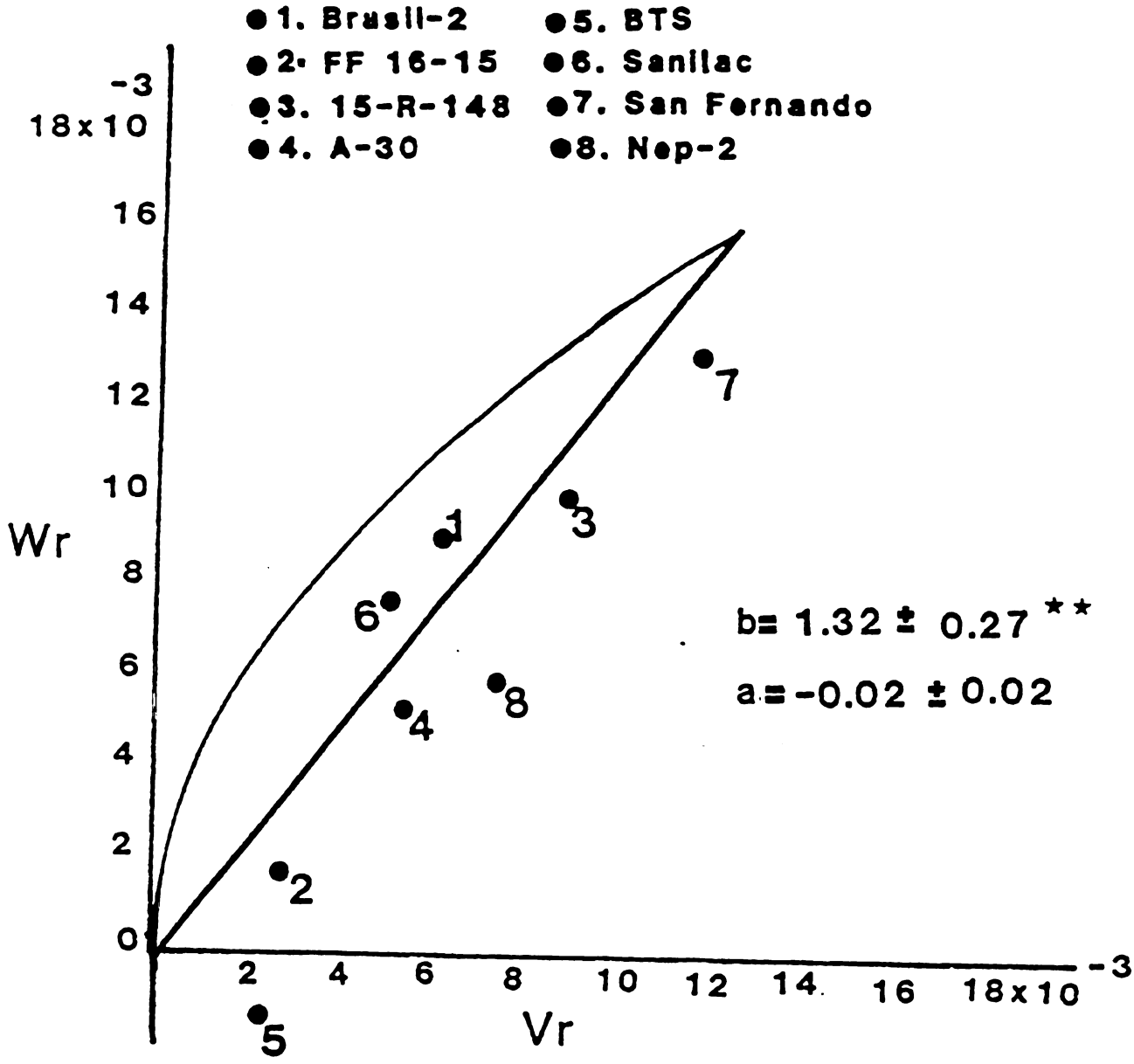

Figure 11. Variance (V_r)-covariance (W_r) graph for washed drained weight data of the F_2 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at 1% level of probability.

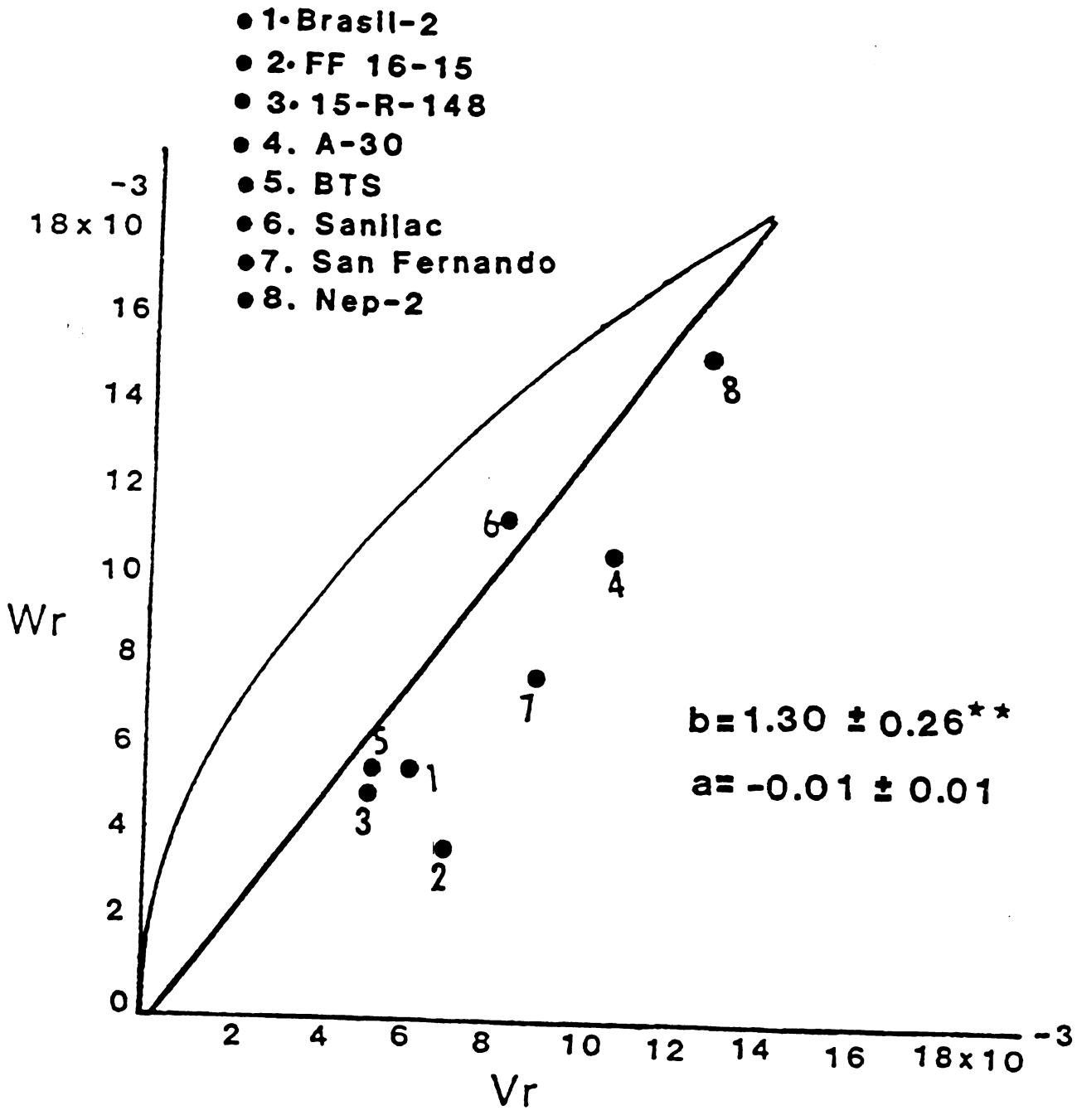

Figure 12. Variance (V_r)-covariance (W_r) graph for washed drained weight data of the F_3 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

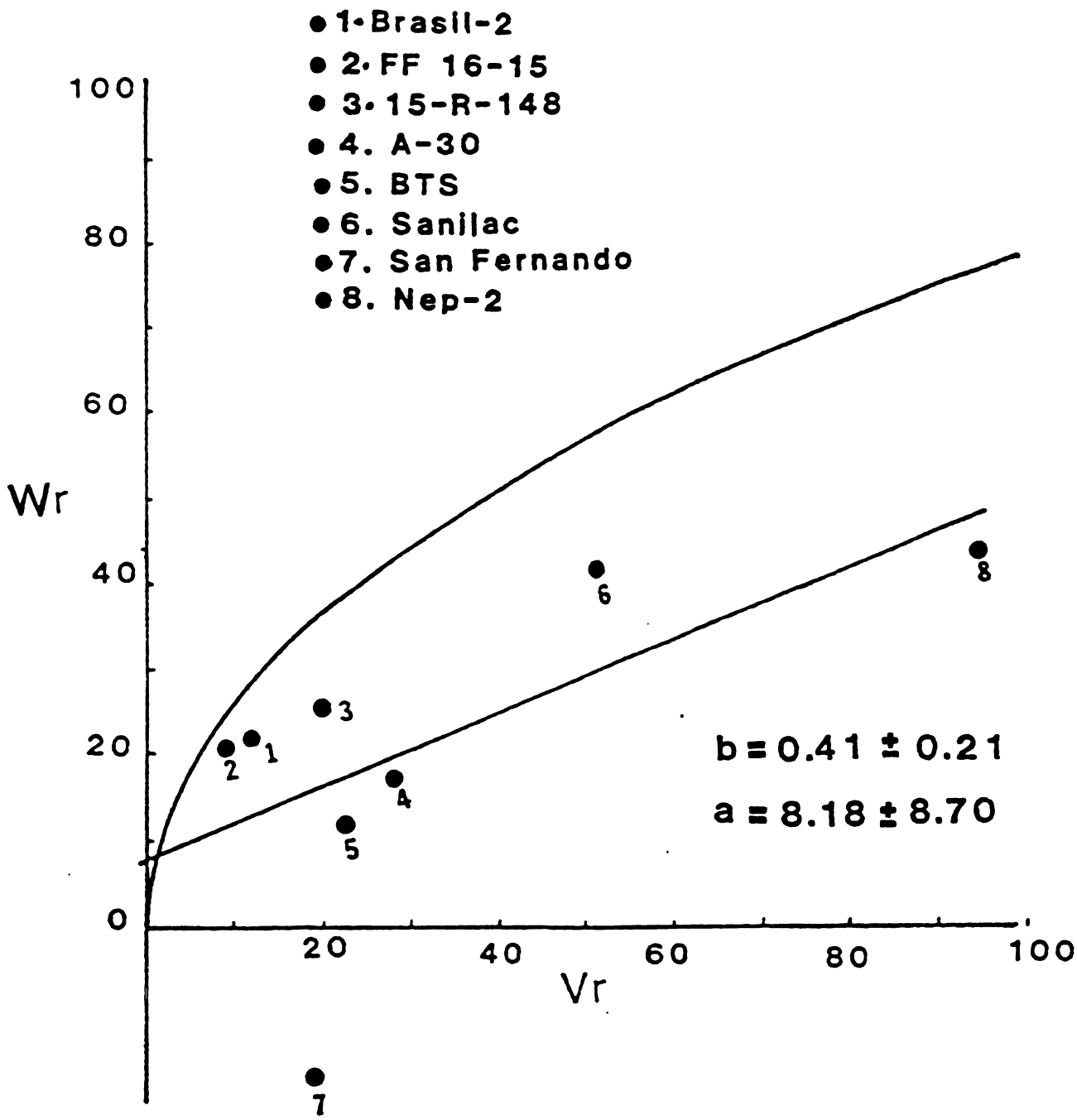

Figure 13. Variance (V_r)-covariance (W_r) graph for texture data of the F_2 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie.

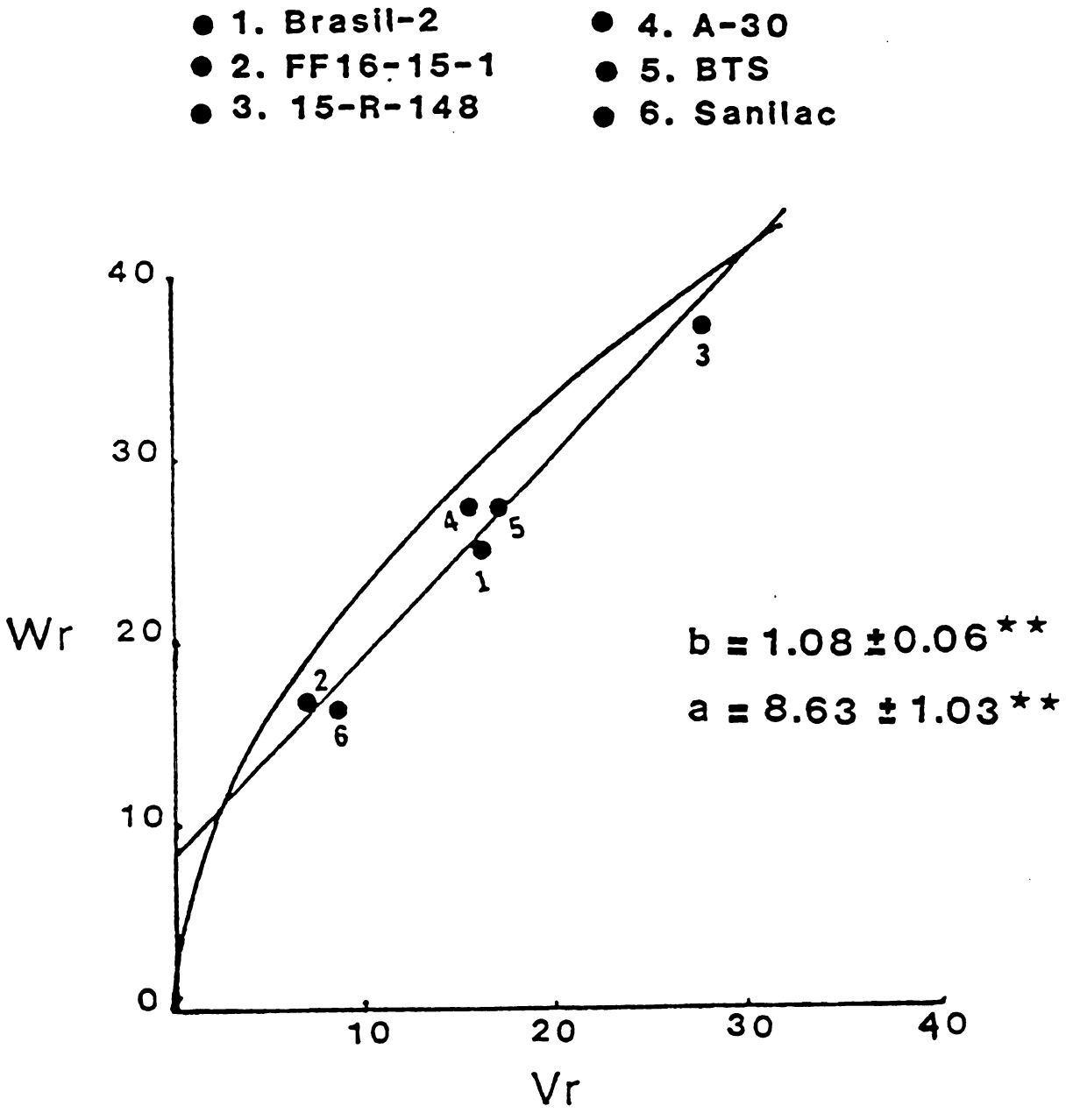

Figure 14. Variance (V_r)-covariance (W_r) graph for texture data of the F_2 generation grown at E. Lansing and showing the position of points representing the 6 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

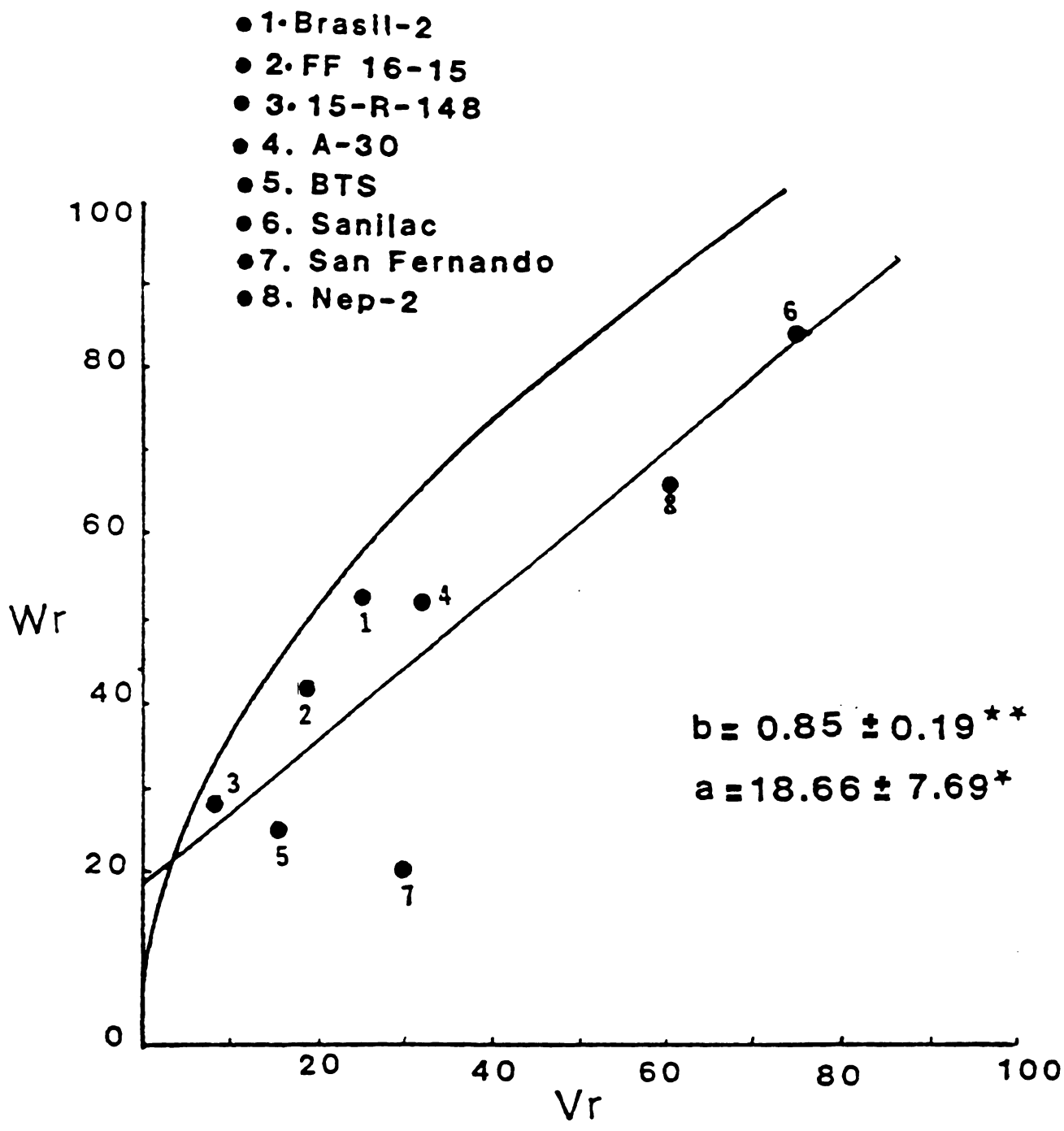

Figure 15. Variance (V_r)-covariance (W_r) graph for texture data of the F_3 generation grown at E. Lansing and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. *,** = Significant at the 5% and 1% level of probability, respectively.

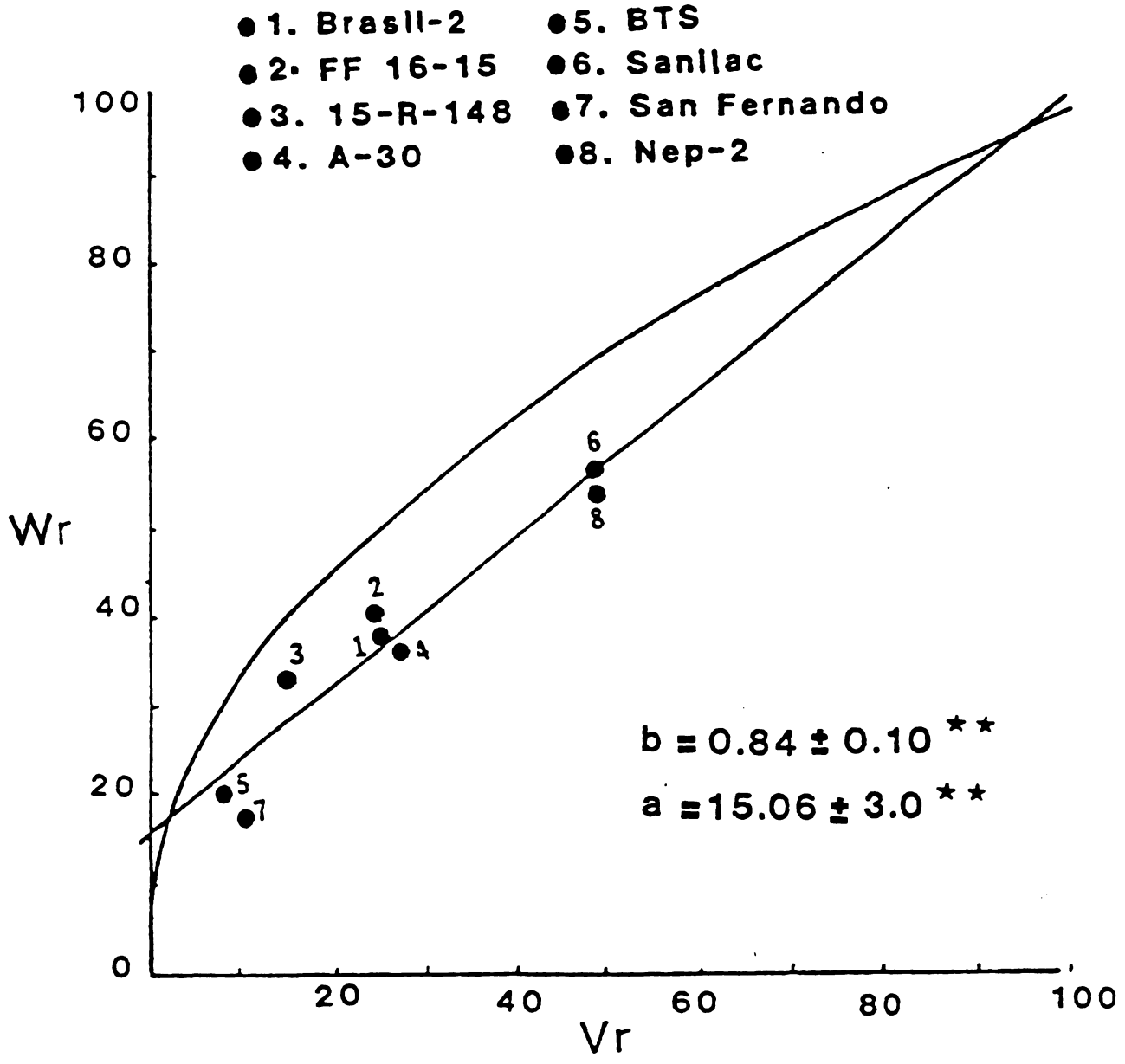

Figure 16. Variance (V_r)-covariance (W_r) graph for texture data of the F_2 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie. ** = Significant at the 1% level of probability.

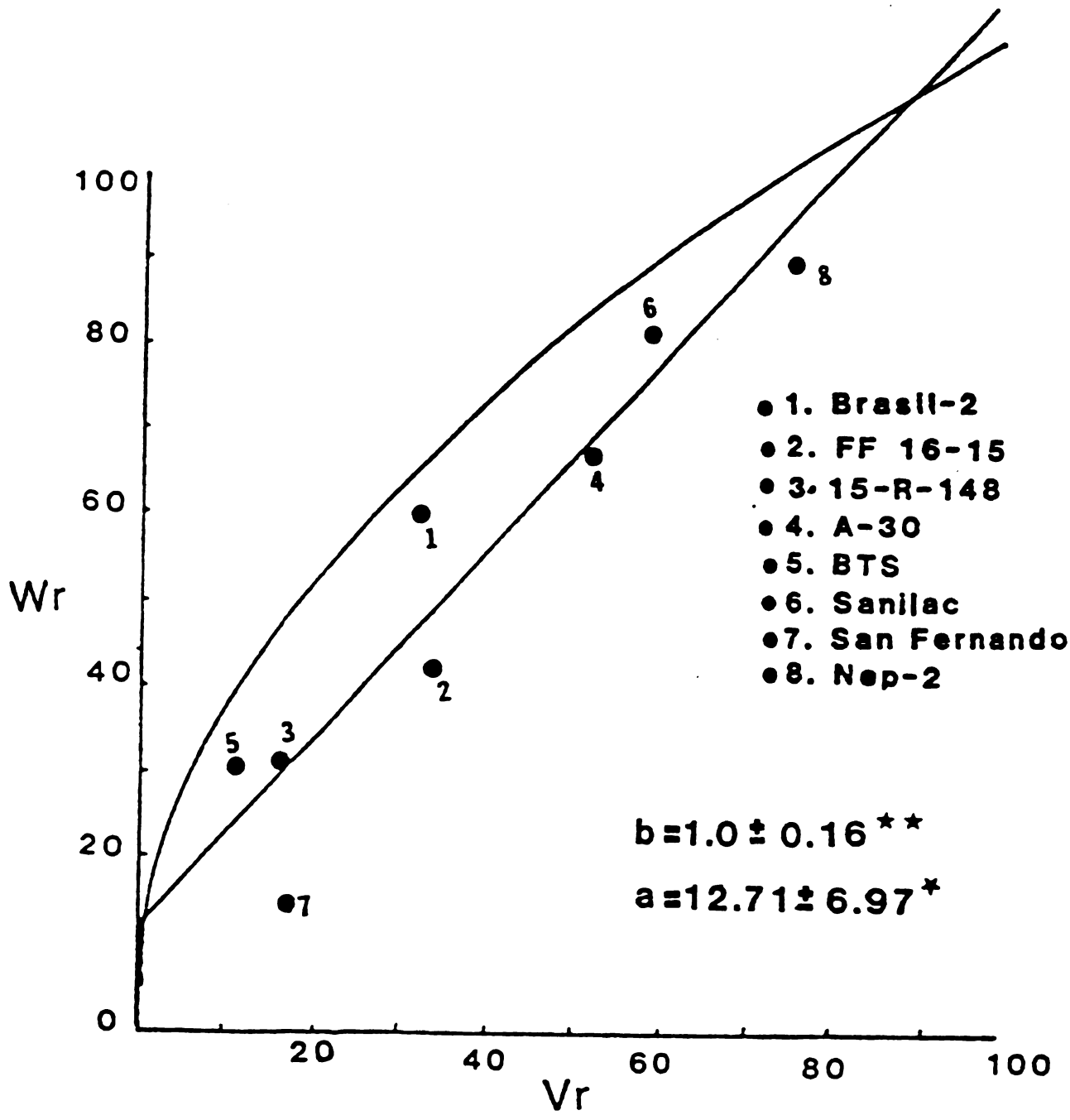

Figure 17. Variance (V_r)-covariance (W_r) graph for texture data of the F_3 generation grown at Saginaw and showing the position of points representing the 8 parental arrays and their regression line relative to a limiting parabola under which all points must lie.*,** = Significant at the 5% and 1% level of probability, respectively.

DISCUSSION

Significant F tests of culinary quality traits indicated that genetic variability existed among the parents and progeny for these traits (Table 1). Significant genetic variability indicated that these traits would lend themselves to improvement through selection. Clumps, splits, washed drained weight, and texture, are traits important to consumers and processors and were significantly different within the F_2 and F_3 generations at both locations. The generation mean square was not significant except for clumps, soaked bean weight, and soaked bean moisture. The nonsignificant generations mean square indicated that the expression of culinary quality traits was similar from one generation to the next. Location effects for the traits were nonsignificant. This was surprising because location and seasonal effects are generally significant for culinary quality traits in dry beans. These results could be due to the larger F value required to declare significance because of a few number of degrees of freedom for testing locations or the fact that we evaluated segregating populations that were more broadly adapted. The interaction of generations x locations and entries x locations was not significant. This suggested that the performance among crosses was similar at each location.

The combining ability effects can be measured on populations at any level of inbreeding but its estimates depends on the generation tested and on the other hand additive

variance remain constant for a given population through a generation of inbreeding provided no selection occurs but the dominance variance decreases with inbreeding. The GCA effect of a parent comprises its additive effect and the average dominance interaction associated with that parent in hybrid combination with all other parents and with itself. With inbreeding, GCA includes a genetic component associated with the set of dominance interactions within the homozygous loci of the parent itself. The contribution of this component increases and the contribution of average dominance decreases in proportion to the level of inbreeding.

Significant GCA mean squares were observed for all traits in the F_2 and 8 out of 9 traits in the F_3 generation, suggesting that genes with primarily additive effects controlled trait expression. Significant SCA mean squares for splits, clumps, washed drained weight and texture (Table 1) showed that nonadditive genetic variance was also important in trait expression. In most cases the GCA mean square was larger than SCA mean square. The type of genetic variance in a reference population indicates the type of breeding scheme that maximizes trait improvement. In this case the preponderance of additive variation for traits and the presence of significant SCA suggested that reciprocal recurrent selection would be useful strategy for utilizing both additive and the fixable component of non-additive genetic variance in trait improvement. Parents with large SCA effects could be crossed and reciprocal recurrent

selection practiced to maximize the use of both types of genetic variance in advanced generations.

The lack of consistent reciprocal and maternal effects indicated that it makes little difference as to the choice one makes for use of a plant as either a pollen of seed parent. Reciprocal and maternal effects are generally absent in plant species. However, they have been shown in some crops, for example, onions (Alium cepa L.) in which cytoplasmic male sterility was used to control pollen. These effects arose probably because of relic heterozygosity present in an essentially homozygous seed (nonrecurrent) parent after its development by back crossing. This situation does not occur in bean breeding because a useful male-sterile is not available thus limiting the production of hybrids in favor of pure lines. The interaction of GCA and SCA with locations for several traits (Table 1) suggested that effects changed from location to location.

GCA effects and their interaction with locations indicated the contribution that a parent made to its progeny and the uniformity of this performance from site to site (Tables 2 and 3). The GCA changed in direction and magnitude for some of the traits depending on the location. Texture and washed drained weight were two traits in which parents showed a consistent GCA in both the F_2 and F_3 generations. Strains A-30, 15-R, BTS, SAN, and N-2 (Tables 2 and 3) transmitted significantly large and negative GCA effects for texture and significantly large and positive GCA effects for washed drained weight to their progeny. Up to a point,

negative GCA effects for texture are desirable because beans with firm texture (positive effects) may be discriminated against by consumers. Because texture affects the perceived stimulus for chewing, it influences to a large degree a consumer's acceptance of a food product. Textural properties of processed beans must fall within prescribed acceptability limits (Adams and Bedford, 1973). Beans may be unacceptable if they are too firm "tough beans", or too soft, "mushy beans" , after cooking.

High values for the washed drained weight trait in beans are desirable to consumers because the washed drained weight indicates the amount of total solids available for consumption. It has been shown that washed drained weight and texture are negatively correlated in beans (Hosfield and Uebersax, 1980, 1984; Nordstrom and Sistrunk 1977).

Variances of specific combining ability of parents for washed drained weight and texture (Table 5) showed that some highly significant non-additive effects were present in some parents while other parents had no significant SCA variance.

The highly significant correlations of general combining ability effects between F_2 and F_3 generation (Table 6) indicated that the mode of gene action did not change from generation to generation. This suggested that recurrent selection could be useful in fixing additive genetic variance in early generations following hybridization. Moreover, it should be possible to identify progeny with desirable gene combination even though they are hetero-

zygous. This point of view is held by Shebeski (1967) and supported by our data (Table 6) showing a highly significant correlation between parental value for texture (r=0.92** and 0.94**) and the washed drained weight (r=0.90** and 0.91**) in the F_2 and F_3 generation, respectively. The correlations between pairs of the 9 culinary quality traits in the F_2 and F_3 generations at each location indicated that the soaking characters were significantly and positively correlated among themselves and negatively correlated with the washed drained ratio. The washed drained ratio and washed drained weight were significantly and positively correlated (Tables 7 and 8). Texture was negatively correlated with the washed drained weight . The pattern of correlation between the soaking traits and texture was negative in both F_2 and F_3 at Saginaw but inconsistent in direction and magnitude at East Lansing. Since correlation between pairs of traits varied from generation to generation and locations, they would be unreliable in a plant breeding program.

Graphical analyses developed by Jink (1954) and Hayman (1954) of the covariance between the offspring of each parental array and the nonrecurrent parent (W_r) and the variance of their offspring in each parental array (V_r) for clumps, splits, washed drained weight and texture in both generation at each location revealed that the regression coefficient was significantly different from zero but not significantly different from unity (Figures 1...17). The intersects of the W_r axis passed through the origin for most of the traits except texture, where it intersected the axis

above the origin. These data indicated that genes controlling the expression of clumps, splits, and the washed drained weight were completely dominant, but that genes with partially dominant effects controlled the expression of texture.

Comparison of array point distribution and GCA effects for texture in the F_2 and F_3 generation at East Lansing and Saginaw revealed that the SAN, and N-2 had a preponderance of recessive alleles for texture and also a significantly large and positive GCA effects. It is tempting to speculate that soft texture is a recessive trait while firmness is under the control of dominant alleles. With respect to the washed drained weight trait, it was observed that strains with a reduced washed drained weight had significant and negative GCA effect values and those with a high washed drained weight value, had significant and positive GCA effect values. The distribution of array points for this trait showed similar results for SAN and N-2. This suggested that for these two genotypes, washed drained weight is controlled by recessive alleles but controlled by dominant alleles in the other strains.

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INTERPRETIVE SUMMARY

The studies presented in this thesis have dealt with the genetic of cooking time and uniformity of cooking of individual seed, tannin and protein content, and culinary quality traits of dry beans (Phaseolus vulgaris L.). Both GCA and SCA effects were significant for determining cooking time and uniformity of cooking in parents and progeny of an 8x8 diallel cross. The magnitude of GCA was larger than SCA for both traits. This suggested that the genetic variance in this population was primarily additive in nature but non-additive effects also influenced trait expression. It was noted that quick cooking parents produced progenies that were also easy to cook. Thus it should be possible to select superior cooking progenies from crosses involving quick and uniform cooking parents because of the preponderance of additive genetic variance. Graphical analyses for cooking time and % hard seed revealed that these traits were governed in the parents by both dominant and recessive alleles. It was observed that B-2, SAN, and N-2 carried a preponderance of recessive genes for cooking time while BTS and SF had predominantly dominant genes. The GCA effects of each parent revealed that FF, A-30 and N-2 contributed genes for quick cooking and a reduced percentage of hard seed while B-2 and 15-R contributed genes for longer cooking time and a higher percentage of hard seed.

The partitioning of the among entry source of variance for the % tannin trait into GCA, SCA and reciprocal effects

indicated highly significant GCA and SCA mean squares. Estimates of variance components revealed that GCA variance predominated in tannin content expression. The GCA effect of each parent indicated that A-30, SAN and N-2 reduced the % tannin content in their progenies at both locations under test while the other strains contributed to a higher tannin content in their progenies. Reciprocal effects determined for each parent indicated that the significant maternal effect present for % tannin content was probably due to the large maternal effects of FF (0.32), 15-R (-0.32) and SF (0.45). It was also observed that parents with non or low tannin content produced progenies that also had low tannin content in their seed coats.

Graphical analyses revealed that tannin content was controlled by partially dominant systems of genes. It also indicated that SAN and N-2 had a preponderance of recessive genes and the remaining parents had a relatively high proportion of dominant factors. The data indicated that in this population the difference among progenies for tannin content was due to genes with primarily additive effects but nonadditive effect had also influenced trait expression.

Significant differences among entries were present for percentage protein in raw and cooked beans. All F tests for GCA main effect were highly significant and the F tests for SCA were either significant or highly significant for both raw and cooked bean protein content. No consistency in the

reciprocal variation was observed. Estimates of variance components revealed that GCA effects were more important than SCA in both cases suggesting that additive effects of parents were more important than non-additive effects in determining protein content in crosses. Comparison of parental and progeny means indicated that crosses of low x low and high x high parents tended to produce progenies that were low and high in their protein content, respectively. The crude protein content of uncooked parents and progenies was reflected in similar fashion in the cooked bean samples. Graphical analyses of raw bean seed protein content revealed that this trait was controlled by a partial to complete dominance system of genes. The presence of genetic variability suggested that selection in this population for low tannin and high protein content would be possible.

The genetic analysis of culinary quality of dry beans revealed significant and highly significant differences among entries for all traits except the hydration ratio. It was found that GCA mean squares were highly significant for all traits in the F_2 while SCA mean squares were significant for clumps, washed drained weight and texture. In the F_3 generation the GCA mean square was significant for all the traits except the hydration ratio and the SCA mean square was significant for clumps, splits, washed drained weight and texture. The GCA effect for each parent in each generation was significant for texture and washed drained weight. Estimates of variance components showed that GCA variance was significant for all the traits in the F_2 and

all but hydration ratio in the F_3 generation. The SCA components of variance was significant for clumps, splits, hydration ratio, washed drained weight, and texture in the F_2 generation. SCA variance component for these traits in the F_3 was significant except for hydration ratio. The interactions between combining ability effects and locations generally followed a similar trend as the main effects. Variances of SCA for A-30, BTS, SAN, SF and N-2 were significant in the F_2 for texture but in the F_3 parents B-2, A-30, SAN and SF had significant SCA variances. This might have led to the significant SCA variability for texture. The results also indicated that certain crosses among parents would produce progenies that would be either firmer or softer than expected on the average. Highly significant correlation between parental value and GCA effects, and GCA effects between F_2 and F_3 generation indicated that the mode of gene action did not change from generation to generation.

The following conclusions are drawn on the basis of this research:

1) Significant GCA and SCA mean squares for cooking time and % hard seed suggested that both additive and nonadditive variance influenced trait expression. However, additive effects were of greater influence. Reciprocal recurrent selection would be appropriate to improve traits in this population by utilizing both additive and fixable non-additive variance.

2) High tannin content was dominant to low tannin content.

3) Strains with white or beige seed coats had no or low tannin content and should produce progenies that also have low tannin. Similarly, it would be possible to select progenies that would have low tannin content and high protein content.

4) This research indicated that protein losses during cooking are not as severe as one might expect.

5) Both dominant and recessive genes influenced culinary quality traits. Strains B-2, SAN, and N-2 had mostly recessive genes for texture and the washed drained weight and crosses among these parents should produce progenies that have softer texture and a higher washed drained weight.

6) The high correlation coefficients between parental value and GCA effects and between the GCA effects of the F_2 and F_3 suggested that the mode of gene action did not change from generation to generation.

The genetic control of cooking time and cooking uniformity of individual grains, tannin and protein content, and culinary quality traits in dry beans provided information to develop efficient breeding strategies to improve bean cultivars.

Appendix A

Appendix A

The methods of protein and % catechin equivalentare described step by step as it follows:

A. Crude protein determination.

Prior to the analysis of raw and processed bean flour for protein content, a sample of 20 strains of dry beans representing a wide range in color, growth habit, and protein content was analyzed for percentage protein by the Kjeldahl method of nitrogen determination. The nitrogen content of each sample was multiplied by 6.25 to obtain the total percent crude protein. These samples were tested for percent crude protein by the NIR method and the results compared. A correlation coefficient of (0.98) was obtained. The samples from crosses and parental material was then tested by the NIR method for protein content and the results were checked every 20 samples with an internal standard.

B. Sample extraction for tannin content.

The sample preparation for extraction and phenolics determination was done according to Telek (1983). The procedure described step by step as follows:

1. A 0.15-0.20 gram sample of ground testa is carefully weighed and transferred into a 100 ml medicine bottle.
2. An acidic methanol solution is made by thoroughly mixing 80 ml absolute methanol:19.5 ml distilled H_2O: 0.5 ml concentrated hydrochloric acid, (V/V/V).

3. Take 35 ml of the acidic 80% methanol solution and add to the bottle containing the ground testa.
4. Extract in a shaker bath at 70°C for 30 minutes.
5. Decant the extract over a porcelain filter crucible lined with glass microfiber filter (GF/D whatman, 2.5 cm) into a 100 ml volumetric flask.
6. Take the residue from the filter and repeat step # 5 two additional times. Combine all extracts, and make up the volume with 80% acidic methanol solution.
7. Carefully pipette 5 ml of the extract into a 25 ml volumetric flask and bring up to volume with a 30% sulfuric acid solution.
8. From this 25 ml volume, carefully pipette a 3 ml sample into each of three 10 ml volumetric flasks.
9. Add 3 ml of a 0.5% vanillin solution to two of the 10 ml sulfuric acid solution.
10. Add only the sulfuric acid solution to the third 10 ml flask.
11. Let all 3 flasks stand for 20 minutes. Read the absorbance of each flask at 500 nm.
12. While the flasks are standing, prepare 2 the vanillin blanks, by pipetting 3 ml of 0.5% vanillin solution intoa 10 ml volumetric flask and bring up to volume with a 30 % sulfuric acid solution.

C. Preparation of the catechin standard

1. A 0.05 gram sample of catechin is carefully weighed and transferred into a 50 ml volumetric flask. It is dissolved in 1-2 ml absolute methanol and brought to

volume with distilled water.

2. A 5 ml sample of the catechin solution is pipetted into a 200 mlvolumetric flask and brought to volume witha 30 % sulfuric acid solution.
3. A 3 ml sample is pipetted from this 200 ml into a 10 ml volumetricflask in duplicate,a 3 ml of a 0.5% vanillin solution is added to each of the flasks and broughtto volume with a 30% sulfuric acid solution.
4. Prepare the 0.5% vanillin and catechin solutions fresh eachday and just prior to pipetting the seed coat extract into the 10 ml volumetric flasks.

D. Reading the absorbance

1. Set the spectrophotometer to zero witha vanillin blank by putting the blank in both sample and reference cuvette.
2. The vanillin blank is left in the reference cell and the catechin standard is read at 500 nm against a vanillin blank.
3. The sample blank is placed in both the reference and sample cell and read, then the sample cuvette is rinsed and the actual sample is poured into the cuvette and read against the sample blank.

Determining the catechin equivalent

A. Day factor

Day factor=(wt. of catechin/ O.D of catechin) x (dilution factor of sample / dilution factor of catechin) x 100

B. % catechin equivalent =(O.D. of sample/wt. of sample)
x Day factor

Appendix B

Table 1. Mean squares from combining ability analyses of variance of 9 culinary quality traits of dry edible beans measured on F_2 and F_3 generation means of an 8-parent diallel cross in dry edible beans grown at E. Lansing, Michigan, 1982.

Generation and source of variation	d.f.	Traits								
		Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture (%)	Cooked bean moisture (%)	Hydration ratio	WD† ratio	Soaked bean weight (g)	WD† weight (g)
F_2										
Entry	63	0.293**	0.594**	43.462**	2.790**	1.398	0.004**	0.005**	61.418**	69.890**
GCA	7	0.858**	3.072**	180.250**	12.954**	1.868	0.024*	0.026**	197.689**	94.264**
SCA	28	0.249	0.418**	39.864**	2.591*	0.825	0.003	0.003**	47.398	77.047**
Reciprocal	28	0.196	0.140	12.864*	0.448	1.853	0.001	0.001	41.370	56.639**
Maternal	7	0.228	0.151	11.147	0.683	2.781	0.001	0.001	34.141	43.917**
Nonmaternal	21	0.185	0.137	13.436*	0.369	1.544	0.001	0.001	43.779	60.880**
Error	63	0.153	0.158	7.530	1.502	1.341	0.002	0.0013	34.49	18.840
F_3										
Entry	63	0.237*	0.477**	51.068*	2.241	0.735	0.004**	0.004**	51.305	70.893**
GCA	7	0.891**	2.383**	279.629**	6.141*	0.994	0.018**	0.021**	108.341*	192.554**
SCA	28	0.200	0.451**	31.570**	1.823	0.669	0.002	0.002	33.127	56.215*
Reciprocal	28	0.111	0.136	13.426**	1.684	0.737	0.002	0.002	55.223	55.156*
Maternal	7	0.078	0.104	12.350	1.718	0.406	0.002	0.001	74.360	9.767
Nonmaternal	21	0.122	0.147	13.785*	1.672	0.847	0.002	0.002	48.844	70.286**
Error	63	0.146	0.148	6.520	1.800	0.569	0.002	0.002	40.670	28.270

*, ** = Significant at 5% and 1% probability level, respectively.

† = WD = Washed drained

Table 2. Mean squares from combining ability analyses of variance of 9 culinary quality traits of dry edible beans measured on F_2 and F_3 generation means of an 8-parent diallel cross in dry edible beans grown at Saginaw, Michigan, 1982.

Generation and source of variation	d.f.	Traits								
		Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture (%)	Cooked bean moisture (%)	Hydration ratio	WD† ratio	Soaked bean weight (g)	WD† weight (g)
F_2										
Entry	63	0.311**	0.749**	39.927**	2.508**	0.354**	0.010**	0.003**	63.196**	62.085**
GCA	7	0.938**	5.358**	264.879**	5.811**	1.298**	0.017**	0.012**	161.296**	193.733**
SCA	28	0.313	0.215**	19.419**	2.684*	0.362**	0.008	0.002**	65.971**	46.767**
Reciprocal	28	0.153	0.131	4.198*	1.506	0.111	0.010**	0.001	35.896	44.491**
Maternal	7	0.053	0.083	4.072	0.786	0.064	0.004**	0.001	25.677	52.259**
Nonmaternal	21	0.186	0.147	4.240*	1.746	0.126	0.012**	0.001	39.302	41.901**
Error	63	0.124	0.110	4.020	1.176	0.138	0.001	0.001	28.320	18.860
F_3										
Entry	63	0.321**	0.629**	57.420*	2.330	0.396**	0.004**	0.004**	68.956	177.348**
GCA	7	1.397**	4.298**	382.411**	8.322**	2.289**	0.023**	0.016**	257.986*	326.440**
SCA	28	0.286	0.197	25.767**	2.263	0.194	0.003**	0.011**	53.726	133.918**
Reciprocal	28	0.090	0.142	7.825	0.899	0.126	0.001	0.001	36.927	183.501**
Maternal	7	0.140	0.059	11.820*	0.734	0.054	0.001	0.0013	43.269	226.559**
Nonmaternal	21	0.073	0.169	6.490	0.954	0.149	0.001	0.0013	34.813	169.149**
Error	63	0.126	0.160	4.598	1.558	0.189	0.0013	0.0013	44.880	59.960

*, ** = Significant at 5% and 1% probability level, respectively.

† WD = Washed drained

Table 3. Estimates of variance components and standard error of GCA, SCA, reciprocal and maternal effects measured on 9 culinary quality traits of F_2 and F_3 generation mean of an 8-parent diallel cross in dry edible beans grown at E. Lansing, Michigan, 1982.

Generation and component	Traits								
	Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture(%)	Cooked bean moisture(%)	Hydration ratio	WD† ratio	Soaked bean weight	WD† weight (g)
F_2									
GCA	0.04±0.03	0.18±0.09	10.8± 5.3	0.72±0.38	0.03±0.06	0.001±0.001	0.001±0.001	10.2± 5.8	4.7± 2.8
SCA	0.09±0.07	0.27±0.11	32.3±10.4	1.09±0.72	----	0.001±0.001	0.002±0.001	12.8±13.7	58.2±20.2
Reciprocal	0.02±0.03	----	2.7± 1.9	----	0.26±0.27	----	----	3.4± 6.3	18.9± 7.7
Nonmaternal	0.01±0.06	----	2.9± 4.2	----	0.10±0.51	----	----	4.6± 7.1	21.0± 9.1
Maternal	0.01±0.01	----	0.23±0.34	----	0.90±0.08	----	----	----	1.6± 1.3
F_3									
GCA	0.05±0.03	0.14±0.07	17.1± 3.2	0.27±0.18	0.03±0.03	0.001±0.001	0.001±0.001	4.2± 3.2	10.3± 5.7
SCA	0.05±0.06	0.19±0.09	25.1± 8.2	0.02±0.57	0.10±0.20	----	----	7.3± 8.2	13.4± 7.8
Reciprocal	----	----	3.5± 1.9	----	0.08±0.11	----	----	----	27.9±15.3
Nonmaternal	----	----	3.6± 4.2	----	0.14±0.27	----	----	4.1± 8.0	21.0±10.7
Maternal	----	----	0.36±0.37	----	----	----	----	2.1± 2.2	----

---- = Indicates negative or very small positive number.

† WD = Washed drained

Table 4. Estimates of variance components and standard error of GCA, SCA, reciprocal non-maternal and maternal effects measured on 9 culinary quality traits of F_2 and F_3 generation mean of an 8-parent diallel cross in dry edible beans grown at E. Lansing, Michigan, 1982.

Generation and component	Traits								
	Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture(%)	Cooked bean moisture (%)	Hydration ratio	WD† ratio	Soaked bean weight	WD† weight (g)
F_2									
GCA	0.05±0.03	0.33±0.16	16.3± 7.8	0.29±0.17	0.07±0.04	0.001±0.005	0.001±0.003	8.3± 4.8	10.9± 5.7
SCA	0.19±0.08	0.11±0.06	15.4± 5.1	1.51±0.72	0.22±0.09	0.007±0.002	0.001±0.005	37.7±17.7	29.9± 5.7
Reciprocal	0.02±0.02	0.01±0.07	0.2± 0.2	----	----	0.004±0.001	----	3.8± 5.4	12.8± 6.2
Nonmaternal	0.03±0.06	0.02±0.05	0.1± 1.4	0.28±0.55	----	0.06±0.004	----	5.5± 6.3	11.5± 6.4
Maternal	----	----	0.03±0.13	----	----	----	----	----	2.1± 1.6
F_3									
GCA	0.08±0.04	0.26±0.13	23.6±11.3	0.42±0.25	0.13±0.07	0.001±0.001	0.001±0.001	13.3± 7.6	16.7± 9.6
SCA	0.16±0.08	0.04±0.06	21.2± 6.7	0.71±0.65	0.01±0.06	0.002±0.001	0.01±0.003	8.8±15.9	73.9±36.1
Reciprocal	----	----	1.6± 1.1	----	----	----	----	----	25.1±61.8
Nonmaternal	----	----	0.9± 2.1	----	----	----	----	----	54.6±25.5
Maternal	----	----	0.45±0.35	----	----	----	----	----	10.4± 6.7

---- = Indicates negative or very small positive number.

†WD = Washed drained

Table 5. Estimates of general combining ability effects for 9 culinary quality traits measured on F_2 and F_3 generation mean of an 8-parent cross in dry edible beans grown at E. Lansing, Michigan, 1982.

Parent	Generation	Traits								
		Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture (%)	Cooked bean moisture (%)	Hydration ratio	WD† ratio	Soaked bean weight (g)	WD† weight (g)
Brasil 2	F_2	-0.16	-0.02	3.0	0.38	-0.34	-0.008	-0.019	2.9	-0.6
	F_3^2	0.05	-0.01	2.1	0.34	-0.10	-0.002	-0.020	3.3	-1.6
FP-16-15-1-	F_2	0.28	-0.50	2.6	0.15	-0.55	-0.012	-0.008	-1.5	-1.3
CM-M-M	F_3^2	-0.03	-0.32	4.2	-0.37	-0.39	-0.029	-0.001	-0.6	-0.6
15-R-148	F_2	0.32	-0.81	-0.2	-0.87	-0.11	-0.033	0.015	-4.5	-0.3
	F_3^2	0.28	-0.76	-0.2	-0.07	-0.19	-0.005	-0.005	-1.8	-1.7
A-30	F_2	-0.27	-0.30	-2.7	-1.73	-0.08	-0.071	0.087	-5.3	4.4
	F_3^2	-0.32	0.31	-2.2	-1.32	0.05	-0.065	0.077	-4.4	6.0
Black Turtle	F_2	0.07	0.21	-1.1	0.73	0.22	0.040	-0.034	2.8	-3.0
Soup	F_3^2	0.05	-0.01	-1.6	0.41	0.23	0.027	-0.022	3.2	-0.5
Sanilac	F_2	0.11	0.05	-5.2	0.43	0.24	0.030	0.001	1.5	2.8
	F_3^2	0.35	0.10	-6.1	0.30	0.03	0.039	0.004	0.4	2.6
San Fernando	F_2	-0.29	0.28	5.1	1.01	-0.05	0.039	-0.047	4.3	-1.8
	F_3^2	-0.26	0.20	6.9	0.65	-0.05	0.026	-0.045	1.3	-5.7
Nep-2	F_2	-0.06	0.49	-1.5	-0.10	0.52	0.013	0.005	-0.2	-0.1
	F_3^2	-0.12	0.47	-3.1	0.06	0.42	0.009	0.012	-1.4	1.6
$S_{\bar{y}}$	F_2	0.09	0.09	0.6	0.29	0.27	0.010	0.008	1.4	1.0
	F_3^2	0.09	0.09	0.6	0.31	0.18	0.011	0.011	1.5	1.2
$S_{\bar{D}}$	F_2	0.14	0.14	1.0	0.43	0.41	0.016	0.013	2.1	1.5
	F_3^2	0.14	0.14	0.9	0.47	0.28	0.016	0.016	2.3	1.9

$S_{\bar{y}}$, $S_{\bar{D}}$ = Standard error and standard error of the difference, respectively.

†WD = Washed drained

Table 6. Estimates of general combining ability effects for 9 culinary quality traits measured on F_2 and F_3 generation mean of an 8-parent cross in dry edible beans grown at Saginaw, Michigan, 1982.

Parent	Generation	Traits								
		Clumps (scale)	Splits (scale)	Texture (Kg/100g)	Soaked bean moisture (%)	Cooked bean moisture (%)	Hydration ratio	WD† ratio	Soaked bean weight (g)	WD† weight (g)
Brasil 2	F_2	-0.06	-0.21	1.4	0.33	-0.30	-0.024	-0.023	1.4	-3.0
	F_3^2	-0.09	-0.08	2.7	-0.06	-0.46	0.001	-0.014	-0.7	-6.3
FF-16-15-1-	F_2	0.13	-0.85	5.9	0.77	-0.36	0.021	-0.026	4.7	-0.5
CM-M-M	F_3^2	0.13	-0.73	6.9	0.59	-0.51	-0.003	-0.030	4.1	-4.4
15-R-148	F_2	0.26	-0.83	-1.4	0.32	0.05	0.014	0.002	1.9	2.7
	F_3^2	0.18	-0.79	-1.2	0.57	0.27	0.017	-0.002	3.5	4.6
A-30	F_2	-0.29	0.10	1.8	-1.21	-0.06	-0.069	0.056	-6.0	4.2
	F_3^2	-0.29	0.19	1.4	-1.67	-0.10	-0.088	0.066	-8.9	3.5
Black Turtle	F_2	0.26	0.42	-2.6	-0.20	0.04	-0.026	-0.001	-1.0	-2.5
Soup	F_3^2	0.43	0.14	-3.5	0.12	0.04	0.027	-0.023	-0.4	-3.1
Sanilac	F_2	0.21	0.27	-7.0	0.40	0.53	0.015	0.012	1.8	4.2
	F_3^2	0.37	0.14	-8.5	0.36	0.64	0.029	0.003	2.2	2.9
San Fernando	F_2	-0.23	0.48	3.9	-0.18	-0.12	0.003	-0.024	-1.3	-5.2
	F_3^2	-0.40	0.54	4.5	0.15	-0.04	0.012	-0.022	0.3	-2.4
Nep-2	F_2	-0.29	0.63	-1.9	-0.22	0.21	0.019	0.004	-1.4	0.1
	F_3^2	-0.17	0.58	-2.3	-0.05	0.17	0.007	0.021	-0.2	5.3
$S_{\bar{y}}$	F_2	0.08	0.08	0.5	0.25	0.09	0.007	0.007	1.3	1.0
	F_3^2	0.08	0.09	0.5	0.29	0.10	0.008	0.008	1.6	1.8
$S_{\bar{D}}$	F_2	0.04	0.12	0.7	0.38	0.13	0.011	0.011	1.9	1.5
	F_3^2	0.13	0.14	0.8	0.44	0.15	0.13	0.013	2.4	2.7

$S_{\bar{y}}$, $S_{\bar{D}}$ = Standard error and standard error of the difference, respectively.

† WD = Washed drained

Table 7. Analyses of variance of (W_r-V_r) for culinary quality traits to test the adequacy of additive-dominance model.

Traits	East Lansing		Saginaw	
	F_2	F_3	F_2	F_3
Soaked beans				
Weight	3765.8	4505.2	1647.11	5330.3
Hydration ratio	6.34	8.54*	3.61	7.13
Moisture (%)	0.0	0.0	0.0	0.0
Cooked beans				
Clumps(scale)	0.04	0.024	0.05	0.0227
Splits(scale)	0.03	0.013	0.03	0.0093
Washed drained wt.	1004.3	1796.2	631.40	35364.9
Washed drained ratio	0.0	0.0	0.0	0.0
Texture kg/100g	1546.1*	421.4*	125.1	219.5
Moisture (%)	3.93	1.08	0.033	0.107

*,** = Significant at 5% and 1% probability level,respectively.

Table 8. Correlation coefficients indicating relationships between F_2 and F_3 generation means for culinary quality tarits measured on 56 crosses of an 8-parent diallel grown in two locations in 1982.

Traits	Correlation coefficient (r)* East Lansing	Saginaw
Soaked bean		
1. Weight (g)	0.56**	0.44**
2. Moisture (%)	0.56**	0.44**
3. Hydration ratio	0.70**	0.23
Cooked bean		
4. Clumps (scale)	0.42**	0.49**
5. Splits (scale)	0.67**	0.77**
6. Texture (Kg/100g)	0.76**	0.87**
7. Wash drain Wt.(g)	0.39**	0.64**
8. Wash drain ratio	0.71**	0.36**
9. Moisture (%)	0.10	0.57**

** = Significant at 1 % probability level .

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