Inheritance of Physico-chemical Seed Characters Related to Culinary Quality in Dry Bean

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Abstract. Culinary quality in dry bean (*Phaseolus vulgaris* L.) depends on attributes of seeds prevailing at harvest and is determined by the genetic architecture of cultivars and by unpredictable environmental factors. Variation among genotypes for culinary quality has been shown to be heritable; however, the efficacy of selection depends on a knowledge of the genetic control of the measured traits. A diallel mating design was used to estimate the combining ability of parents and determine the inheritance of nine culinary quality traits important to processors and consumers. Genetic variability among eight parents, 56 F_2 , and 56 F_3 progenies was confirmed by significant mean squares from analyses of variance. Significant variability detected between F_2 and F_3 progenies for soaked bean weight (SBWT), soaked bean water content (SBWC), and clumps (CLMP) was due to inbreeding effects. General combining ability (GCA) components were highly significant and overshadowed specific combining ability (SCA) components in the F_2 and F_3 for SBWT, SBWC, split beans (SPLT), and the washed-drained weight coefficient (WDWTR), indicating that additive variance predominated. Ratios of GCA : SCA components were equal to or less than unity for CLMP, washed-drained weight (WDWT), and texture (TEXT), indicating that both additive and nonadditive effects contributed to trait expression. Significant SCA effect variances were noted for 'Sanilac', 'San Fernando', 'Nep-2', and 'A-30' for WDWT and TEXT, implying that progeny from crosses of these parents had higher or lower mean values for the traits than the average expected on the basis of GCA. Graphs of the regression of V_r on W_r showed that genes controlling WDWT and TEXT were completely dominant in most cases. Recurrent selection, which seeks to concentrate favorable alleles with additive effects in populations, may be an effective breeding procedure to improve the culinary quality of dry beans. It is not feasible to breed for TEXT and WDWT simultaneously because of a negative correlation between the traits.

Dry seeds of common bean are an important world food. Although the role of dry bean in human nutrition is well-established (Tobin and Carpenter, 1978; Hellendoorn, 1979), economic considerations determine consumer demand. Many middle- and low-income families in many poor countries of the world rely on beans to meet their needs for calories and protein.

Beans are generally soaked and must be cooked to render the seeds palatable, inactivate heat labile antinutrients, and permit the digestion and assimilation of protein and starch (Deshpande et al., 1983). The preparation conditions cause structural changes in cells that have a bearing on consumer and processor preferences and requirements for the soaked and cooked seeds. Consumers are most conscious of bean color and appearance, ease of preparation, wholesomeness, and texture (Adams and Bedford, 1973). Processors seek beans that expand rapidly and uniformly in the can during processing, leave no sludge at the bottom of the container, have acceptable drained weights and texture after cooking, and cook to tenderness rapidly and uniformly (Adams and Bedford, 1973; Deshpande et al., 1983).

Culinary quality is the aggregate of properties perceived as influencing consumer preferences and processor standards. Beans not meeting culinary quality expectations may be unacceptable for human consumption. Bean culinary quality depends on seed attributes at harvest and handling, storage conditions, and processing procedures. Seed characteristics at harvest are determined by the genetic architecture of cultivars and by unpredictable environmental factors.

Hosfield and Uebersax (1980) and Hosfield et al. (1984) developed various physical and chemical (physico-chemical) tests for beans that were related to culinary quality and that differentiated samples. The tests are routinely used by bean breeders to determine culinary quality at dry, soaked, and cooked stages of processing (Adams et al., 1986; Kelly et al., 1984a, 1984b).

Selection in segregating generations following hybridization is the current practice to make genetic advances for traits in beans. However; the efficacy of selection for culinary quality traits depends on a knowledge of the genetic control for the measured characters and the degree to which environmental influences affect their expression. Variation in dry beans for culinary quality traits is heritable (Hosfield and Uebersax, 1980; Hosfield et al., 1984; Wassimi et al., 1986). Studies also showed significant site and seasonal effects on trait expression (Hosfield et al., 1984; Ghaderi et al., 1984). Hence, a reasonable research objective would be to improve culinary quality in dry beans through selection in breeding populations and testing the selected lines. Mating designs that estimate the combining ability of parents are useful in ascertaining the genetic structure of breeding populations and determining the selection potential of

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progeny. The general combining ability (GCA) and specific combining ability (SCA) components are interpretable in terms of additive and nonadditive genetic effects, respectively (Cockerham, 1963).

Wassimi et al. (1986) found significant GCA effects for cooked bean texture and moisture content in a population of four dry bean accessions. However, there is limited knowledge of the inheritance of traits in beans that define culinary quality. The present study was undertaken to ascertain the nature of gene action for culinary quality in F_2 and F_3 bean populations derived from an eight-parent diallel cross. Specific objectives were to: 1) partition the genotypic sums of squares into components relating to GCA and SCA for nine characters measured on soaked and cooked seeds, and 2) consider the implications of the genetic effects estimated for each parent in improving culinary quality through breeding.

Materials and Methods

Genetic material. 'Brazil-2' ('B-2'), FF-16-15-CM-M-M (FF-16-15), 15-R-148, A-30, 'Black Turtle Soup' ('BTS'), 'Sanilac' ('SAN'), 'San Fernando' ('SF'), and 'Nep-2' were selected from a nursery grown on a McBride Sandy Loam (coarse-loamy, mixed, frigid Alfic Fragiothods) at the Montcalm Research Farm near Stanton, Mich. The parents represented a broad genetic base for the experiment and had good yield potential. The eight entries were a sample of promising experimental lines and named cultivars from various domestic and international breeding programs. The entries had been previously evaluated for adaptation to Michigan bean production areas and protein characteristics. B-2, 15-R-148, 'SAN', and 'SF' are genetic strains used frequently in bean experiments at Michigan State Univ. (MSU) because of unique quality characteristics (Agbo et al., 1987; Wassimi et al., 1986) and have been evaluated for cooked bean texture and moisture content.

All possible F_1 hybrids were made, and the 56 F_1 populations and eight parents were grown in a nursery on a Capac Loam (fine-loamy, mixed, mesic Aerlic Ochraqualfs) at East Lansing during Summer 1981 to produce F_2 seed. Seeds of the F_2 population from each cross were advanced to the F_3 during the winter of 1981-82 at Mayaguez, P.R., on a San Anton Clay Loam (fine-loamy, mixed, isohyperthermic Cumulic Haplustolls).

Field plot procedure. The 56 F_2 populations, 56 F_3 populations, and eight parents were planted in 11×12 rectangular lattices with three replications on a Charity Clay Loam [fine-illitic (calcareous); frigid typic Haplaquolls] at the Saginaw Valley Bean and Sugar Beet Research Farm near Saginaw and at East Lansing in 1982. The set of eight parents was included twice in each test. The remaining four plots ("fillers" in the lattice arrangement) were planted with 'Domino' and 'Black Magic' black beans, and 'Swan Valley' and 'Neptune' navy beans. Seeds were precision-drilled with a tractor-mounted air planter (Taylor, 1975) into two-row plots guarded on each side by a single row of 'Seafarer' navy bean. Rows were 5 m long and spaced 0.5 m apart. Within-row spacing was 0.12 m. Herbicide and fertilizer applications were made following recommendations for commercial bean production.

Mature plants of the 128 entries were harvested and threshed from 6 m of row in each plot. Seeds were cleaned and sized using 4×19 -mm slotted metal sieves and stored at room temperature ($\approx 22^\circ\text{C}$) until sample preparation and analysis.

Culinary quality evaluation. Duplicate samples from each plot were evaluated for physico-chemical seed traits at soaked and

cooked stages. Before processing, seed moisture percentage was determined on 250 g of beans using a Motomco (Model 919) moisture meter. Beans with a fresh-weight equivalent of 100 g total solids (Hosfield and Uebersax, 1980) were placed in nylon mesh bags and soaked for 60 min (Hosfield and Uebersax, 1980; Uebersax and Bedford, 1980). All soaking was done in tap water containing ≈ 50 ppm Ca. The soaking procedure produced a product with minimum damage similar to beans soaked continuously in the high-temperature systems common throughout the U.S. canning industry (Hosfield and Uebersax, 1980).

Soaked bean weight (SBWT) was the weight (in grams) gained by beans through water imbibition during soaking. The hydration coefficient (HC) and water content of soaked beans (SBWC) were calculated by standard procedures used in the MSU/USDA Food Quality Laboratory (Hosfield and Uebersax, 1980).

Number 303 tin cans (100×75 mm) were filled with soaked beans. During the can filling, boiling brine prepared by adding 142.0 g of sucrose and 113.4 g of table salt (NaCl) to 9.1 kg of tap water containing 50 ppm Ca ion was added. Cans were sealed and cooked in a retort without agitation for 45 min at 116°C and 10.4×10^4 Pa (15 psi). After cooking, cans were cooled under cold running tap water and stored for a minimum of 2 weeks at room temperature.

Cooked beans were evaluated for grams of washed-drained weight (WDWT) and cooked bean texture (TEXT). The procedures for calculating the two traits are published in detail (Hosfield and Uebersax, 1980). The washed-drained weight coefficient (WDWTR) was calculated by dividing the washed-drained weight (g) by soaked bean weight (g).

Subjective evaluations were made on contents of all processed cans. Clumping (CLMP) of the cooked grains was an indication of the degree to which beans remained compactly together in a can, while split (SPLT) beans indicated severe product breakdown during processing. CLMP and SPLT beans were scored on a 1 to 5 scale (5-point range) to represent the minimum and maximum expression of the traits, respectively. Water content of processed beans (PBWC) was determined from the 100-g TEXT samples that were oven-dried at 30°C until the weight remained constant. 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 the homogeneity of error variances were made using Bartlett's procedure described in Steel and Torrie (1980). Analyses of variance of combined data were computed.

Statistical procedures. Combining ability formulas were from Griffing's Method I, Model I (1956), with partitioning of reciprocal differences into maternal and nonmaternal sources according to Cockerham (1963). In Griffing's Model I all effects are fixed, and the experimental material is the population about which inferences are made. The fixed-effects model of Cockerham (1980) was applied to the data and solved by the unweighted least-squares procedure. The model was fitted to include GCA and SCA effects that were tested by t tests. The average SCA of a series of crosses involving one entry was compared to a series of crosses involving a different entry through computation of SCA variances for each parent (Griffing, 1956).

The V_r W_r graphical analysis technique (Jinks and Hayman, 1953; Hayman, 1954a, 1954b, and 1958) was used to make an overall genetic evaluation of the variation among parental and progeny means in a fixed set of genetic material and ascertain the distribution of genes in the parents. The V_r and W_r statistics conform to the additive-dominance model of Mather (1949).

The model is $W_r - V_r = 1/4 (D - H_1)$, where V_r = the variance of the r^{th} array of a diallel cross, W_r = the covariance of the r^{th} array with all the parents, D = the additive genetic variance, and H_1 = the dominance genetic variance. The model is based on the assumptions (Mather and Jinks, 1971) of 1) diploid inheritance, 2) differences between reciprocal crosses due only to environmental effects, 3) independent action of non-allelic genes, 4) no multiple alleles in the parents, 5) homozygous parents, and 6) genes independently distributed among parents.

In the absence of nonallelic interaction and with distribution of genes among parents, W_r is related to V_r by a straight regression line of unit slope (Mather and Jinks, 1971). Conformity of the model to the assumptions provides a measure of the average level of dominance by the departure from the origin of the point where the regression line intersects the W_r axis. The distance of this point from the origin is $1/4 (D - H_1)$; therefore, $D > H_1$ when the intercept is positive, $D = H_1$ when the line passes through the origin, and $D < H_1$ when the intercept is negative (Mather and Jinks, 1971). The relative order of points along the regression line indicated whether parents carried mostly dominant or recessive genes for the measured traits.

In some cases, the line drawn for the regression of W_r on V_r was not of unit slope and indicated that the genetic system for a trait was complicated by genic interaction. In cases where the assumption of no epistasis underlying the diallel theory was not valid, parental arrays were removed until a subset of the diallel table was found that was consistent with the assumption (Hayman, 1954a, 1954b).

Results and Discussion

Comparisons of error variances from individual analyses for HC, WDWT, and PBWC were not homogeneous; nevertheless, data for these traits were combined to ascertain trends. Caution was exercised in the interpretation of the F tests.

Mean squares for entries were significant for all traits except HC (Table 1). The among-cross variation was partitioned into GCA, SCA, and reciprocal effects for the respective traits. The generation mean square was significant for SBWT, SBWC, and CLMP (Table 1), indicating significant inbreeding effects for these traits in the population. Although the location (L) mean squares for the traits were large in magnitude compared to other sources of variability, they were nonsignificant and led to no genotype (G) $\times$ L interactions (Table 1). The absence of interactions indicated that rankings of the genotypes were fairly consistent over locations. Other experiments with dry beans showed that the expression of processing traits interacted with the production site (location). Ghaderi et al. (1984) found significant G $\times$ L interactions for the HC, CLMP, SPLT, and PBWC traits in navy and pinto bean cultivars. Perhaps the lack of significant G $\times$ L interactions for soaking and processing traits in the current study is attributable to our evaluation of segregating populations (F_2 and F_3), while Ghaderi et al. (1984) evaluated more narrowly adapted pure-line cultivars.

In general, reciprocal effects were of minor importance in the present study (Table 1). However, a significant maternal effect in the F_2 was noted for the PBWC trait. No significant reciprocal variation was detected for traits in the F_3 . The magnitude of the maternal effect mean-square component (Table 2) relative to the larger GCA component for PBWC was an indication of the minor importance of reciprocal variation in terms of this trait's expression.

Combining ability analyses. GCA main effect mean squares

were significant for all traits in the F_2 and all traits except HC in the F_3 (Table 1). SCA main-effect mean squares were significant for CLMP, WDWT, and TEXT traits in the F_2 and all the processed bean traits in the F_3 except WDWTR and PBWC. Inspection of data (Table 2) showed that the SCA mean-square components for CLMP, WDWT, and TEXT measured on F_2 and F_3 progeny were about equal to or larger than the GCA mean-square component. This finding indicated that both additive and nonadditive effects significantly influenced the expression of CLMP, WDWT, and TEXT. Significant GCA $\times$ L interactions were detected for HC, SPLT, and TEXT in the F_2 and SPLT and TEXT in the F_3 (Table 1). However, GCA main-effect mean-square components overshadowed the corresponding GCA $\times$ L components for all traits, indicating that GCA effects of this genetic material can be estimated accurately from a single location (Table 2). The SCA $\times$ L mean-square components for SBWT and SBWC were larger than the SCA main-effect components in both the F_2 and F_3 , while the interaction components for several other traits (HC, SPLT, WDWTR) were larger than the SCA main-effect components in the F_2 only (Table 2). Genetic variances estimated from experiments that do not adequately sample the environmental conditions to which the predictions will apply are often inflated by G $\times$ year (Y) or G $\times$ L interactions. Insufficient seed of F_2 and F_3 populations precluded our replicating the experiment over time (years); thus, we acknowledge that bias in the variance estimates may exist because of G $\times$ Y interactions.

GCA effects associated with individual parents for the F_2 and F_3 generations were significant for the traits under study (Table 3). A strain's GCA effects provided information on the average deviation from the population mean for a trait that can be expected in the progeny from a particular parent when that parent is in hybrid combinations with all the other parents included in the reference population.

Effects associated with various parents were significant for the traits under study (Table 3). In bean processing trials, FF-16-15 and A-30 have generally shown a high and low SBWT, respectively (data not shown). On average, FF-16-15 increased the SBWT of its F_2 progeny by 2.6 g, while A-30 reduced the mean of its progeny for this trait in the F_2 by 7.0 g (Table 3). The SBWT is important to processors because soaking is the first step in canning beans. Cans are filled with soaked beans for thermal processing on the basis of weight (fill weight). Fill weight requirements for beans are fairly rigid in the canning industry and bean cultivars are preferred that meet canner expectations for SBWT (M. El-Kassakany, personal communication).

The 'B-2', FF-16-15, and 'SF' strains significantly increased the firmness (TEXT) of cooked beans in their F_2 and F_3 progenies (Table 3). When the GCA effects for TEXT of 'B-2', FF-16-15, and 'SF' were averaged across the F_2 and F_3 , the progenies of 'B-2', FF-16-15, and 'SF' were firmer than the population mean by a force of about 2.2, 4.8, and 5.3 kg/100 g, respectively (Table 3). However, 'SAN' reduced the TEXT trait of its progeny, on average, by $\approx$ 6.5 kg/100 g (Table 3).

In general, parents that imparted cooked bean firmness to their progeny (e.g., 'SF') tended to have a low WDWT, while parents that imparted a soft TEXT (e.g., 'SAN') value had higher WDWT values than other parents (Table 3). 'SAN' significantly increased the WDWT of its F_2 and F_3 progeny over the population mean by an average of $\approx$ 3.3 g.

The TEXT and WDWT traits are important for beans because they are major criteria that consumers and processors use to

Table 1. Mean squares from analyses of variance and combining ability analyses and their interaction with locations for nine dry bean culinary quality traits measured on parents and F₂ and F₃ progeny of an eight-parent diallel cross.

Source of variation	Degrees of freedom	Soaked beans			Processed beans					
		Weight (g)	Water content (%)	Hydration coefficient (ratio)	Clumps (scale)	Splits (scale)	Washed-drained		Water content (%)	Texture ^a (kg/100 g)
							Weight (g)	Coefficient (ratio)		
Location (L)	1	2094	80	1.28	2.9	42.7	81	0.11	0.5	2506
Reps/L	4	4063	153	0.37	19.6	3.8	1720	0.07	8.1	196
Entry	127	229**	9.2*	0.75	1.2**	3.1**	331**	0.02*	2.7**	245**
Generation (G)	1	948*	30.0**	0.99	1.1*	0.03	483	0.006	2.8	2.1
Entry/G	126	223**	9.0**	0.75	1.2**	3.1**	329**	0.02**	2.7**	247**
Among F ₂	63									
GCA	7	951**	41.3*	2.3**	4.9**	24.1**	1207**	0.10**	8.4**	1189**
SCA	28	185	7.3	1.11	1.1**	0.93	245*	0.008	2.3	140**
Maternal (M)	7	62	2.2	0.87	0.50	0.42	15.6	0.003	4.9**	25
Nonmaternal reciprocal (NMR)	21	76	3.2	1.92**	0.45	0.54	91	0.004	2.4	23
Among F ₃	63									
GCA	7	1015**	38.6*	0.012	6.1**	18.8**	1327**	0.10**	7.1**	1898**
SCA	28	164	6.4	0.01	0.99**	1.2**	332**	0.009	1.6	137**
M	7	111	4.6	0.002	0.32	0.23	325*	0.004	0.9	31
NMR	21	87	3.5	0.004	0.26	0.56	159	0.005	1.3	41
Entry × Location	127	140	5.8	0.71	0.50	0.60	137	0.01	1.7	39
G × L	1	340	11.2	0.98	0.001	0.16	54	0.005	1.5	24
F ₂ × L	63									
GCA	7	351	15.0	1.50*	0.48	1.3**	186	0.01	1.1	147**
SCA	28	206	8.6	1.17*	0.58	0.99**	94	0.009	1.3	38*
M	7	62	2.2	0.80	0.34	0.25	73	0.004	3.6**	21
NMR	21	78	3.1	1.89*	0.67*	0.31	95	0.003	2.6*	31*
F ₃ × L	63									
GCA	7	170	7.1	0.007	0.77	1.2**	248	0.006	2.9	156**
SCA	28	132	5.4	0.005	0.45	0.44	107	0.005	1.0	22
M	7	79	3.3	0.004	0.33	0.26	271	0.002	0.6	28
NMR	21	84	3.8	0.003	0.32	0.39	205	0.004	1.7	11
Error	508	119	4.8	0.72	0.41	0.42	95	0.005	1.7	17
Experiment mean		229	56.2	1.86	2.1	2.9	311	1.36	64.5	44.8
cv (%)		4.8	3.9	45.5	29.9	22.5	3.1	5.2	2.0	9.2

^aTexture is a measure of the kilograms of force required to bring cooked beans to the point of extrusion.

*Significant at *P* = 0.05 and 0.01, respectively.

Table 2. Components of mean squares for GCA, SCA, and reciprocal variation and their standard deviations for nine dry bean culinary quality traits from combined analyses of an eight-parent diallel cross.

Source of variation	Soaked beans ^a					Processed beans ^a				
	Weight (g)	Water content (%)	Hydration coefficient (ratio)	Clumps (scale)	Splits (scale)	Washed-drained		Water content (%)	Texture ^a (kg/100 g)	
						Weight (g)	Coefficient (ratio)			
Among F ₂										
GCA	8.4 ± 4.7	0.4 ± 0.2	0.017 ± 0.011	0.046 ± 0.024	0.25 ± 0.12	11.1 ± 5.9	0.0009 ± 0.0005	0.07 ± 0.04	12.0 ± 5.8	
SCA	7.4 ± 9.0	0.2 ± 0.4	0.067 ± 0.052	0.10 ± 0.049	0.06 ± 0.04	17.9 ± 11.3	0.0	0.11 ± 0.11	16.8 ± 6.1	
Maternal (M)	0.0	0.0	0.002 ± 0.004	0.0	0.0	0.0	0.0	0.03 ± 0.002	0.0	
Nonmaternal reciprocal (NMR)	0.0	0.0	0.202 ± 0.097	0.0	0.0	0.0	0.0	0.12 ± 0.13	0.0	
Among F ₃										
GCA	9.1 ± 5.0	0.3 ± 0.2	0.0	0.058 ± 0.029	0.19 ± 0.09	12.4 ± 6.5	0.0009 ± 0.0005	0.06 ± 0.04	19.4 ± 9.3	
SCA	3.9 ± 8.2	0.1 ± 0.3	0.0	0.082 ± 0.045	0.09 ± 0.05	32.4 ± 14.8	0.0	0.0	16.3 ± 6.0	
M	0.0	0.0	0.0	0.0	0.0	2.0 ± 1.6	0.0	0.0	0.0	
NMR	0.0	0.0	0.0	0.0	0.0	3.6 ± 8.8	0.0	0.0	0.3 ± 2.3	
Location × F ₂										
GCA	4.8 ± 3.5	0.2 ± 0.2	0.016 ± 0.014	0.002 ± 0.005	0.02 ± 0.01	1.9 ± 1.9	0.0001 ± 0.00009	0.0	2.7 ± 1.4	
SCA	29.1 ± 19.0	1.3 ± 0.8	0.15 ± 0.109	0.057 ± 0.055	0.19 ± 0.09	0.0	0.0013 ± 0.0008	0.0	6.8 ± 3.4	
M	0.0	0.0	0.0017 ± 0.008	0.0	0.0	0.0	0.0	0.04 ± 0.04	0.08 ± 0.2	
NMR	0.0	0.0	0.39 ± 0.19	0.087 ± 0.07	0.0	0.02 ± 10.9	0.0	0.31 ± 0.27	4.5 ± 3.2	
Location × F ₃										
GCA	1.1 ± 1.7	0.1 ± 0.1	0.0	0.008 ± 0.008	0.02 ± 0.01	3.2 ± 2.4	0.0	0.03 ± 0.03	2.9 ± 1.5	
SCA	4.4 ± 10.9	0.2 ± 0.5	0.0	0.013 ± 0.045	0.01 ± 0.04	4.1 ± 10.8	0.0	0.0	1.5 ± 2.1	
M	0.0	0.0	0.0	0.0	0.0	3.9 ± 2.7	0.0	0.0	0.2 ± 0.3	
NMR	0.0	0.0	0.0	0.0	0.0	36.6 ± 20.9	0.0	0.0	0.0	

^aZeros denote negative or small positive values.

^bTexture is a measure of the kilograms of force required to bring cooked beans to the point of extrusion.

Table 3. General combining ability effects of individual strains averaged over locations for nine dry bean culinary quality traits measured on F₂ and F₃ progeny of an eight-parent diallel cross.

Parents ^a	Soaked beans			Processed beans					
	Weight (g)	Water content (%)	Hydration coefficient (ratio)	Clumps (scale)	Splits (scale)	Washed-drained		Water content (%)	Texture ^y (kg/100 g)
Among F ₂									
B-2	1.7*	0.35	-0.09	-0.11	-0.10	-2.2*	-0.020*	-0.32*	2.2*
FF-16-15	2.6*	0.46*	-0.09	0.20*	-0.68*	-0.5	-0.017*	-0.46*	4.2*
15-R-148	-1.1	-0.28	-0.10	0.29*	-0.82*	0.1	0.009	-0.03	-0.8
A-30	-7.0*	-1.47	-0.16*	-0.28*	0.21*	5.6*	0.071*	0.01	-0.5
BTS	1.1	0.26	0.29*	0.16*	0.31*	-2.1	-0.017*	0.13	-1.8*
SAN	1.7*	0.42	0.12	0.16*	0.16*	4.4*	0.006	0.38*	-6.1*
SF	2.0*	0.42	0.12	-0.26*	0.38*	-5.2*	-0.036*	-0.09	4.5*
N-2	-1.0	-0.16	-0.08	-0.17*	0.55*	-0.2	0.004	0.37*	-1.7*
S _y	1.6	0.45	0.16	0.13	0.14	2.2	0.014	0.27	1.2
S _o	1.7	0.35	0.12	0.10	0.11	1.7	0.014	0.19	0.9
Among F ₃									
B-2	0.7	0.16	-0.002	-0.02	-0.04	-2.9*	-0.017*	-0.30*	2.3*
FF-16-15	1.3	0.13	-0.016	-0.08	-0.52*	-2.5	-0.015*	-0.44*	5.4*
15-R-148	1.6	0.26	0.007	0.23*	-0.77	1.3	-0.003	0.01	-0.8
A-30	-7.9*	-1.54*	-0.077	-0.26*	-0.25*	5.2*	0.072*	-0.02	-0.5
BTS	1.3	0.28	0.027	0.24*	0.07	-3.1*	-0.022*	0.14	-2.2*
SAN	1.1	0.28	0.034	0.36*	0.12	2.3*	0.003	0.34*	-7.4*
SF	2.1	0.41	0.019	-0.33*	0.37*	-4.6*	-0.033*	-0.04	6.0*
N-2	-0.3	0.02	0.007	-0.14*	0.53*	3.9*	0.016*	0.31*	-2.8*
S _y	2.2	0.45	0.136	0.13	0.15	2.2	0.014	0.24	1.2
S _o	1.7	0.35	0.121	0.10	0.11	1.7	0.014	0.19	0.9

^aS_y, S_o = SE and SE of the difference between two GCA effects, respectively.

^yTexture is a measure of the kilograms of force required to bring cooked beans to the point of extrusion.

*Significant at *P* = 0.05.

judge product acceptability. The TEXT is a measure of the force required to bring cooked beans to point of rupture and catastrophic breakdown of individual grains, and serves as an estimate of bean textural properties. In turn, texture affects the perceived stimulus for chewing and, hence, acceptance of a food product. Although TEXT measurements were not correlated with sensory evaluations of bean texture, the force required to bring a food to catastrophic failure (extrusion) as determined with a Kramer shear press is associated with the sensory perception of texture (Kramer, 1964).

The WDWT is a measure of the rinsed weight of canned beans after draining (i.e., net weight of processed beans) and is important to canners because it indicates the degree of hydration during soaking, blanching, and processing. WDWT also aids the industry in complying with federal labeling regulations.

As beans cook, they absorb and adsorb water. The water-holding capacity is associated with physical entrainment and the **hydrophilic properties of macromolecules**. Beans may lose solids during cooking, and solids loss is accompanied by structural changes that reduce physical entrainment. In some cases, the weight loss due to the loss of solids may be greater than the weight gain due to the water absorbed (Quast and da Silva, 1977). A bean sample with an excessive loss of solids may have an atypically low WDWT because water entrainment is low and the solids lost are heavier than the water absorbed.

An atypically high WDWT may occur when beans have a large swelling capacity and physical entrainment is high. Beans with an atypically high WDWT occupy a greater volume than beans with typical or atypically low WDWT. Since beans are eaten on a volume basis, a sample characterized by an extremely

high WDWT could be nutrient-deficient because much of the volume consumed is comprised of water.

Values for WDWT have different interpretations depending on the point of view under consideration. Beans with a typical WDWT favor consumers because more solids are available for consumption on a volume basis than in beans with atypically low or high WDWT. In contrast, processors benefit from beans with relatively high WDWT because of a greater unit output (cans/mg). Of course, there are limits to the range of WDWT that are permissible. The improvement of TEXT and WDWT through breeding is a worthwhile research objective.

Variances of specific combining ability effects were computed for the TEXT and WDWT traits (Table 4). Large and

Table 4. Specific combining ability variances associated with each parent for texture and washed-drained weight of processed beans from an eight-parent diallel cross.

Parent	Texture ^a		Washed-drained weight	
	F ₂	F ₃	F ₂	F ₃
B-2	0.0	0.2	14.7*	0.0
FF-16-15	0.0	0.0	0.0	9.3
15-R-148	1.3	4.9	0.0	17.4*
A-30	6.5**	13.9**	21.9**	2.4
BTS	5.5*	0.9	0.4	10.8
SAN	14.8**	15.0**	16.7*	0.3
SF	13.2**	14.7**	2.8	51.7**
N-2	28.3**	16.9**	24.5**	41.9**

^aTexture is a measure of the kilograms of force required to bring cooked beans to the point of extrusion.

**Significant at *P* = 0.05 and 0.01, respectively.

significant SCA effect variances for TEXT were found for 'A-30', 'SAN', 'SF', and 'N-2' in the F_2 and F_3 and for 'BTS' in the F_2 . The significant SCA effect variances indicated that, although a particular parent contributed the same sample of genes to each of its progeny for the traits in question, the genes had a greater or lesser effect when in a particular hybrid combination. There were specific combinations involving these parents with considerably firmer or softer textures than expected on the basis of GCA effects. Lack-of significant SCA TEXT effects for 'B-2', FF-16-15, and 15-R-148 indicated that these parents uniformly transmitted their respective textural characteristics (e.g., firm TEXT for 15-R-148) to their hybrids. Significant SCA effect variances exhibited by the eight parents for WDWT were fewer and not as consistent from the F_2 to F_3 as for TEXT (Table 4).

Regression of array covariance (W_r) on variance (V_r). Graphs of the V_r -on- W_r regression analysis were drawn for WDWT and TEXT (Figs. 1 and 2). The V_r - W_r graph for TEXT of F_2 data for East Lansing indicated that the regression coefficient differed from unit slope but not from zero (data not shown), which led us to conclude that the assumption of no epistasis underlying the diallel theory for TEXT was invalid. The manifestation of significant nonadditive effects in the F_2 and F_3 for A-30, 'SAN', 'SF', and 'N-2' led us to suspect complex (epistatic) inheritance, and when these arrays were removed from the F_2 analysis at East Lansing, a subset of the diallel table was found that showed no epistasis. The redrawing of V_r on W_r excluding 'SF' and 'N-2' (arrays 7 and 8) indicated that epistasis was not a

Fig. 1. Variance (V_r)-covariance (W_r) graph for texture (TEXT) of dry beans showing the position of the parental arrays and their regression line relative to a line of unit slope (-----) and a theoretical parabola within which all points must lie. (A) and (B) F_2 generation grown at East Lansing (EL) and Saginaw (S), Mich., respectively; (C) and (D) F_3 generation grown at EL and S, respectively. Parental arrays nos. 7 and 8 omitted from analysis (A).

Fig. 2. Variance (V_r)-covariance (W_r) graph for washed-drained weight of dry beans showing the position of the parental arrays and their regression line relative to a line of unit slope (-----) and a theoretical parabola within which all points must lie. (A) and (B) F_2 generation grown at East Lansing (EL) and Saginaw (S), Mich., respectively; (C) and (D) F_3 generation grown at EL and S, respectively.

general feature of the genetic system controlling texture, but was due mainly to the influence of 'SF' and 'N-2' (Fig. 1A). The graph drawn for the reduced diallel table (Fig. 1A) indicated that genes in the partially dominant range controlled TEXT. The V_r - W_r graph for TEXT in the F_3 at East Lansing (Fig. 1C) indicated that complex genic interaction was absent, and the hypothesis of a simple additive-dominance model for specifying the genetic component of the generation means was valid. The intersect of the regression line with the W_r axis was significantly above the origin, indicating that a partial dominance gene system influenced TEXT. The slope (b) and intercept (a) statistics obtained for the regression of W_r on V_r for TEXT in the F_2 (Fig. 1B) and F_3 (Fig. 1D) at Saginaw favored the interpretation of a simple additive-dominance model as a general feature of the underlying genetic system, and TEXT was governed by genes with partial dominance.

The V_r - W_r graphs of WDWT for the F_2 and F_3 at East Lansing and Saginaw indicated that a simple additive-dominance model was a general feature of the genetic system (Fig. 2). The intersect of the regression line on the W_r axis with the origin indicated that WDWT was governed by genes with complete dominance (Fig. 2).

Graphical analyses of W_r on V_r also showed the distribution of dominant and recessive genes in the parents for TEXT and WDWT. Arrays clustering close to the origin had mostly dominant alleles for a trait, while the presence of arrays distant from the origin were parents with mostly recessive alleles. The relative order of the points representing the common parents on the regression line of the arrays was fairly consistent in each of the two generations and locations for some parents but not others. In the case of TEXT, 'BTS' (array 5) and 'SF' (array 7) generally carried dominant alleles at a higher proportion of the loci than did the other parents, while 'SAN' (array 6) and 'N-2' (array 8) carried a preponderance of recessive alleles (Fig. 1). The 'B-2' (array 1) and A-30 (array 3) parents had a balance

of both dominant and recessive genes (Fig. 1). Line 15-R-148 was inconsistent in its dominance-recessive gene relationship for TEXT (Fig. 1).

FF-16-15 (array 2) and 'BTS' (array 5) carried a preponderance of dominant genes for WDWT in most cases, while 'SAN' appeared to carry a balance of dominant and recessive genes in some instances and recessivity in others (Fig. 2).

Breeding implications. Significant variation in culinary quality among the strains in the present study indicated that the measured traits can be changed by selection. Since gene action in the experiment was predominantly additive (Table 2), recurrent selection should be effective for trait improvement. This could be accomplished by intermating parents with favorable mean values in each selection cycle to increase the frequency of favorable genes with additive effects. The lack of consistent reciprocal effects indicated that it makes little difference whether a plant is used as a seed or pollen parent (Tables 1 and 2).

Large and significant correlations between parental values and GCA effects (Table 5) suggested that a strain's performance per se is a useful predictor of the mean performance of backcross or inbred populations derived from a parent. Based on the correlations between GCA effects in the F_2 and F_3 (Table 5), one should be able to identify individuals with superior selection potential even though the progeny are relatively heterozygous (e.g., F_2 generation). Shebeski (1967) reported that superior wheat (*Triticum aestivum* L.) lines could be identified in the F_2 .

Several bean strains showed promise to improve cooked bean characteristics through breeding. A-30 and 'SF' manifested a low incidence of clumping (data not shown), which they transmitted to their progeny (Table 3). 'SAN' would be a good parent to introduce genes for relatively soft-texturedness (TEXT) into a breeding population and also increase the WDWT at the same time. 'SAN' significantly reduced TEXT (-6.5 kg force/100 g) while increasing the WDWT (3.4 g) of its F_2 and F_3 progeny (Table 3). 'BTS' was also a relatively soft-textured bean and transmitted soft texture to its progeny (Table 3). However, 'BTS' tended to decrease the WDWT of its crosses (Table 3), which suggested that 'BTS' progeny may have lost more solids or absorbed less water during processing than did 'SAN' progeny.

Table 5. Correlation coefficients for GCA effects on dry bean culinary quality traits from an eight-parent diallel cross.

Trait	Correlation coefficient		
	GCA effect between F_2 and F_3 for all parents	Parental value vs. corresponding GCA effect averaged over all parents	
		F_2	F_3
Soaked beans			
Weight	0.92**	0.88**	0.72*
Water content	0.92**	0.96**	0.93**
Hydration coefficient	0.72*	0.62	0.59
Processed beans			
Clumps	0.83**	0.77*	0.82**
Splits	0.98**	0.98**	0.87**
Washed-drained weight	0.86**	0.90**	0.91**
Washed-drained coefficient	0.98**	0.82**	0.76*
Water content	0.99**	0.76*	0.72*
Texture	0.99**	0.92*	0.94**

***Significantly different from zero at $P = 0.05$ and 0.01 , respectively.

It will be difficult to improve TEXT and WDWT simultaneously through selective breeding because of a negative correlation between the traits (Nordstrom and Sistrunk, 1977; Hosfield et al., 1984). Another problem facing the breeder is where to set the limits for TEXT and WDWT improvement, because these traits must 'fall within acceptability limits prescribed by consumers and processors (Adams and Bedford, 1973). Beans may be unacceptable if they are too soft ("mushy"), or too firm ("tough").

Generally, cooked bean TEXT for commercially processed beans in brine or tomato sauce ranges from 35 to 65, 45 to 75, and 50 to 85 kg/100 g for navy, BTS, and kidney beans, respectively (G.L.H., unpublished data). The breeder may wish to increase cooked bean TEXT up to an ideal value in a population under selection by introducing relatively firm textured strains as parents. However, a population with a relatively firm TEXT initially might best be improved by selecting for decreased TEXT values through the introduction of TEXT genes from soft-textured parents. Improvement in the WDWT trait could proceed in similar fashion to TEXT by setting an ideal value and selecting for high and low WDWT values in populations using appropriate parents. Since a negatively correlated response between TEXT and WDWT indicates that a change in one trait leads to a simultaneous change in the other, but in the opposite direction, a method of tandem selection (Lerner, 1958) in which selection alternates for two characters in succeeding generations may prove successful to improve the traits. The development of a selection index is another method for improving two or more traits in a breeding program.

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Gene Transfer of Multiple Flowers and Pubescent Leaf from *Capsicum chinense* into *Capsicum annuum* Backgrounds

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Abstract. The inheritance of multiple flowers and leaf pubescence resulting from the crosses between accessions from pepper species *Capsicum annuum* L. and *C. chinense* Jacq. was examined. Hand cross- and self-pollinations were made in a glass greenhouse. Only eight normal F₁ plants were obtained from crosses between the two species when *C. annuum* L. was the female parent. F₂ and backcross generations obtained from the F₁ and the two parents were grown in the field. Two field studies indicated that multiple flowers and leaf pubescence were controlled by dominant genes. A three-gene model leading to an F₂ segregation ratio of 45:9:10 and a two-gene model leading to an F₂ segregation ratio of 13:3 were suggested for the inheritance of multiple flowers and leaf pubescence, respectively. Epistasis was evoked in the interpretation of the data. No linkage was found between the two characters. The inconsistencies between F₂ and backcross data might be due to selective elimination of genes from one or the other parent in an interspecific hybridization. Segregation ratios from intraspecific crosses for leaf pubescence supported a two-gene model and gave an F₂ ratio of 13 pubescent leaf : 3 glabrous leaf progeny.

Although pepper plants have often been studied for their agricultural value, the inheritance of certain morphological traits has not been well established (Lippert et al., 1966). Because of the interest in transferring useful genes from wild-type peppers into widely grown cultivars, it is desirable to have genetic information on important morphological traits.

C. annuum L., the most widely grown pepper species on a world basis, sets a single flower at each node, whereas *C. chi-*

nense Jacq., a popular pepper species grown in Latin America, sets two or three flowers at each node. The character of two or three flowers set at each node was defined as the multiple-flower trait. Multiple flowers may be potentially useful to increase yield and enhance uniform maturity, which may make mechanical harvesting feasible.

Subramanya (1983) reported a possible gene introgression for the multiple-flower trait from *C. chinense* (PI 159236) into *C. annuum* ('Delray Bell'). He suggested that three major dominant genes may control double flowers at each node, and that additional genes may be involved in the expression of more than two flowers at each node. Tanksley and Iglesias-olivas (1984) employed co-segregation of isozyme genes as markers and concluded that at least five independently segregating chromosomal segments are involved in the multiple-flower inheritance of PI 159234 in crosses with the *C. annuum* cultivar NM 6-4. Greenleaf (1986) cited an unpublished conclusion by J.E. Watson and

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