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DIALLEL ANALYSES AND CORRELATIONS AMONG YIELD, YIELD COMPONENTS AND ARCHITECTURAL TRAITS IN BUSH BEANS

Nienhuis, James and S.P. Singh

CIAT, Cali, Colombia

Economic seed yield in dry beans is the product of three components, pods/plant, seeds/pod and weight/seed. Among these yield components, pods/plant has been most commonly used as an indirect selection criteria for increased yield, primarily because if its relative ease of measure compared to the other yield components, and because of its high and consistent association with yield (1, 3, 9, 15). However, the effectiveness indirect selection for increased yield through yield components is problematic. The difficulties associated with indirect selection for yield have been attributed to the low heritabilities and large environmental effects associated with yield components, as well as due to the phenomena of yield component compensation (1, 3, 9, 15, 18).

The phenomena of yield component compensation in bean is due to developmental interdependencies among components of a complex trait, such as yield, which form sequentially (1). Thus, although yield components are

considered independent, as a result of component compensation, the correlations among components tend to be negative, especially in stress environments which promote within plant competition for metabolites (1, 3, 9, 18). Thus, indirect selection for increased pods/plant can result not only in a correlated response for increased yield, but also in fewer and smaller seed per pod. Correlated responses for reduced seed size would be of little concern if increased yield per se were our only objective; however, larger seeds generally tend to have greater consumer acceptance and command a better price in the marketplace compared to smaller sized beans. Therfore, a dilemma facing bean breeders is the identification or plant characters which constitute the most efficient and effective selection criteria for the development or high yielding large seeded bean cultivars.

In a search for alternatives to indirect selection for yield components, bean breeders have become increasingly interested in the explotation of architectural traits as a source or variation for increased yield (2, 4, 5, 6, 11). The existence or variation for architectural traits coupled with proposed physiological relationships between architectural traits and yield have lead to descriptions of bean plant ideotypes (2, 8, 9, 11, 13, 14, 15). Bean plant ideotypes are designed to maximize yield via enhanced morphological adaptation to specific cropping systems and/or environments. However, the question of what constitutes the optimum plant ideotype for a give environment, or conversely, over how wide a range of environments a given ideotype may be best adapted, is a vexing one for a breeding program whose target population of environments includes most of the world tropics. Moreover, knowledge of the strength and stability of the relationships between architectural components of ideotypes and yield,

and information regarding the inheritance of yield, yield components and architectural traits is needed to design of efficient and effective selection procedures for increasing yield in bush beans via improved plant architecture. Therefore, the objective of this study was to identify the principal types of gene action involved in the expression of yield, yield components and architectural traits in bush beans, and to determine the type and degree of association among those traits.

MATERIALS AND METHODS

A small (<.25 g), medium (.25 to 40 g) and large (>.40 g) seeded cultivar from each of three bush bean growth habits (Types I, II and III) were crossed in all possible combinations to give rise to a complete set of 72 F_1's (17). Parental, F_1 and reciprocal F_1 plants were grown at CIAT experimental farms at Palmira (1001 m.a.s.l., mean temperature 23.8°C) and Popayan (1850 m.a.s.l., mean temperature 17.5°C in 1982). The experimental design within each location was a split plot, with families as whole plots and entries as subplots. Each whole plot, replicated twice, included the two parents of a cross, their F_1 and reciprocal F_1. Each subplot experimental unit consisted of a single 3 m long row. To minimize potential biases due to variable inter-row competition, each experimental unit was bordered on either side by rows containing a mixture of the three parents corresponding to the same growth habit Type. Between row spacing was 60 cm in both locations. An effective plant density of 13.3 plants/m^2 was established by hill planting excess seed, an later thinning to one plant/hill. Regular applications of pesticides were used to control insects

and diseases, and supplimental irrigation was used as needed at the Palmira location.

At physiological maturity (90 percent of the pods yellow to yellow-green) data were collected on architectural traits by sampling three random plants within each experimental unit. The following architectural traits were measured:

a) Nodes/plant, defined as the number of nodes on the main stem plus the number of nodes on lateral branches;

b) Nodes on the main stem, defined as the number of nodes on the main stem beginning with the cotyledonary node and ending on the node site of the last fully expanded trifololiate leaf;

c) Lateral branches/plant, a lateral branch was defined as any appendange with at least one node;

d) Average number of nodes/lateral branch, calculated as the total number of nodes on lateral branches divided by the number of lateral branchesñ

e) Main stem length, measured as the distance from the cotyledonary node to the node site of the last fully expanded trifoliate leaf;

f) Average main internode length, calculated as the length divided by the number of nodes on the main stem.

After the plants had dried in the field, a 1.25 m section of the central row was hand harvested, the number of pods counted, and seed threshed. Yield was expressed in terms of g/m^2 and was adjusted to 14 percent moisture content.

Combined analyses of variance and covariance were performed for all traits. Genetic and environmental correlations were computed by equating variances and covariances to their expected mean squares and cross products (12).

For purposes of partitioning the crosses sums of squares into general and specific combining ability , the nine parents and their progeny were considered to represent a fixed set (10).

RESULTS AND DISCUSSION

Partitioning of the pooled entries in families sum of squares into three orthogonal contrasts revealed that differences between reciprocal F_1 hybrids were significant for only three of the ten yield and architectural traits measured, weight/seed, lateral branches/plant and main stem internode length (Tables 1 and 2). In those instances where differences between reciprocal F_1 hybrids were detected the magnitude of the mean squares was consistently less than those due to differences between parents. Differences between reciprocal F_1 hybrids were consistent over locations for all traits measured (Tables 1 and 2).

The orthogonal contrasts for pooled differences between parents in families were significant for all yield, yield components and architectural traits, except main stem internode length (Tables 1 and 2). Moreover, differences between parents in families were consistent over locations for all traits measured except weight/seed, lateral branches/plant, nodes in the main stem and main stem length (Tables 1 and 2).

The orthogonal contrast for heterosis, measured as the pooled difference between the mean of the two parents vs. the mean of the two reciprocal hybrids in a family, was significant for all yield, yield components and architectural traits measured (Tables 1 and 2). Heterosis by location interactions were significant for all yield and yield components except seeds/pod (Table 1). In contrast, heterosis by location interactions were significant for only two of six architectural traits measured, nodes in the main stem and main stem length (Table 2).

Significant heterosis for yield above the mid-parent was observed in 29 of 36 hybrids, and heterosis for yield above the high parent was observed in 17 of 36 hybrids (Table 3). When estimates of heterosis fall above the high parent it is tempting to conclude that this is due to overdominant type gene action, and that heterozygotes therefore represent the more ideal genotype. However, linkage between loci with partial to complete dominance can result in heterozygous effects which mimic those of overdominance for several generations after a cross (16). Regardless of the cause, the existence of heterosis above the high parent is encouraging to plant breeders, as it indicates that gene combinations do exist which can result in enhanced yield performance. If unfavorable linkages limit expression of gene combinations in homozigous lines then bean breeders should consider alternative selection methods, such as recurrent selection, which will increase the frequency of favorable genes and maximize the opportunity for recombination among linked loci.

General combining ability (GCA) means squares were significant for yield, yield components and all architectural traits measured (Tables 4 and 5). In addition, specific combining ability (SCA) mean squares, though consistently smaller in magnitude compared to GCA mean squares, were significant for all traits measured except seeds/pod and weight/seed (Tables 4 and 5). This result suggests that although both additive and non-additive gene action are involved in the expression of yield, yield components and architectural traits that additive gene action predominates. This result further suggest that selection should be effective in increasing yield and yield components, and in changing architectural display in bush beans.

The diallel analyses, and particularly the estimation of GCA effects, provides considerable information that can be useful in the selection of parents that have good general combining ability (12). Computation of GCA effects identified two parents, A 359 and A 231, which would be expected to contribute favorable additive effect for yield to their progeny (Table 6). However, the problem of increasing yield in dry beans is complicated by consumer preference for large seed size, and this combination has traditionally been the most difficult for bean breeders to achieve. All medium and large seeded cultivars within each growth habit had positive GCA effects for weight/seed, suggesting that medium and large seeded cultivars contribute favorable additive effects for increased seed size to their progeny (Table 6). However, only two parents, A 457 and a A 375, had positive GCA effects for both weight/seed and yield. Thus, the progeny of crosses involving A 457 and A 375

as parents would merit increased attention as populations from which high yielding large seeded lines may be extracted.

Computation of GCA effects identified at least one, and often several, superior parents for all architectural traits (Table 7). In general, indeterminate parents (growth habit Types II and III) tended to have larger positive GCA effects for all architectural traits than determinate (growth habit Type I) parents, except for lateral branches/plant. Thus, crosses involving indeterminate parents would likely result in overall larger more vigorous progeny than crosses involving only determinate parents.

Significant positive phenotypic correlations were observed between yield and two yield components, pods/m^2 and seeds/pod (Table 8). In contrast, the phenotypic correlation between yield and weight/seed was negative. Among yield components, pods/m^2 and seeds/pod had negative phenotypic correlations with weight/seed.

The phenotypic correlations among traits were further partitioned into genetic and environmental components. Genetic correlations can be attributed to pleiotropism or linkage desequilibrium, whereas environmental correlations are due to environmental factors which influence expression of two traits simultaneously (12). Both genetic and environmental correlations have large associated errors; therefore, their primary utility in plant breeding is in the interpretation of observed phenotypic correlations, and in increasing our ability to predict

correlated responses to selection.

The genetic correlations between yield and yield components and among yield components were generally larger in magnitude and similar in sign to their corresponding phenotypic correlations (Table 8). This suggests that selection for increased pods/m^2 or seeds/pod will not only result in a correlated response for increased yield, but also for reduced weight/seed. Thus, although it is possible to identify parents which will increase the probability of recovering the desired yield and seed size characteristics, the phenomena of yield component compensation is generally observed in this popultion of hybrids. The large environmental correlation, and the reduced genetic compared to phenotypic correlation suggest that the observed association between yield and pods/m^2 is due in part to environments which promote enhanced expression of both traits simultaneously.

All architectural traits measured had significant positive phenotypic correlations with yield (Table 9). In addition, the corresponding genetic correlations between yield and architectural traits were similar in magnitude and sign to their phenotypic correlations, except for the negative genetic correlation between yield and lateral branches/plant. This result suggests that individual architectural traits, except lateral branches/plant, which result in a general increase in plant size are associated with increased yield. Moreover, the consistently smaller environmental compared to genetic correlations between yield and architectural traits indicate that genetic rather than environmental effects prevail in expression of the observed phenotypic associations.

The phenotypic correlations among architectural traits were either nonsignificant or significantly positive (Table 9). In addition, the majority of the corresponding genetic correlations among architectural traits were similar in sign and magnitude to their phenotypic correlations; however, genetic correlations involving lateral branches/plant and several genetic correlations involving main stem internode length were negative. Negative genetic correlations among architectural traits suggest that a relationship, similar to that observed among yield components, exists which results in architectural component compensation. Thus, selection for increased numbers of lateral branches/plant will result in a general reduction in expression of other architectural traits; and selection for increased main stem internode length will likely result in a reduction in nodes/plant. The magnitude of several of the environmental correlations among architectural traits further suggests that common environments can play an important role in the observed phenotypic associations among architectural traits.

In conclusion, the magnitude of the genetic correlations between architectural traits and yield, coupled with significant GCA mean squares for all architectural traits suggest that indirect selection criteria composed of one or more architectural traits could result in a correlated response for increased yield. However, caution should be exercised in be use of architectural traits as indirect selection criteria for increased yield, as the resulting composit of architectural expression, or ideotype, may have a specific environmental adaptation. Previous studies have shown that individual architectural traits which are positively associated

with yield in one environment may be negatively associated in another, and that the balance in expression among architectural traits may be important in adaptation to specific environments (7). Thus, shifts in the balance in expression among architectural traits may result in ideotypes unadapted to target environments. Clearly, knowledge of the components which contribute to the adaptation of ideotypes to specific environments would permit construction of weighted selection indices to simultaneously shift the levels of architectural traits to their optimum levels; however, the time and labor involved in the derivation and application of such an index would likely be prohibitive. A simplier alternative to the construction of architectural indices would be to select for yield per se in targe environments, within the restraints inposed upon architectural display by cropping systems. Since selection would be applied for only yield, unselected genetically correlated architectural traits would tend to move towards optimum values for maximum yield. Hence, selection would result in high yielding ideotypes best adapted to target environments and cropping systems.

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Table 1. Portion of the analyses of variance partitioning entries in families sums of squares into three orthogonal contrasts comparing reciprocal F_1's, parents vs. F_1's and parents within each family for yield and yield components in bush beans.

Source	d.f.	Means squares			
		Yield (g/m^2)	Pods/m^2	Seeds/pod	Weight/ seed
Entries in families	108				
difference between reciprocal hybrids	36	1569.6	1541.1	0.229	0.0009*
difference between parents	36	19710.4**	19710.4**	3.647**	0.0454**
heterosis[1]	36	61520.9**	23626.2**	0.722**	0.0035**
Locations x entries in families	108				
loc.x diff. between reciprocal hybrids	36	1923.4	1101.5	0.224	0.0005
loc.x diff. between parents	36	3649.3	1926.7	0.293	0.0011**
loc.x heterosis	36	7377.5**	3331.4**	0.282	0.0008**
(Error c)	216	2483.8	1559.9	0.197	0.0004

[1] F_1's compared to mid-parent.

**,* Significant at the .01 and .05 levels, respectively.

Table 2. Portion of the analyses of variance partitioning the entries in families sums of squares into three orthogonal contrasts comparing reciprocal F_1' s, parents vs. F_1' s and parents within each family for several architectural traits in bush beans.

Source	d.f.	Mean squares					
		Lateral branches /plant	Nodes/lateral branch	Nodes on main stem	Total nodes /plant	Main stem length	Main stem internode length
Entries in families	108						
diff.bet.reciprocal hybrids	36	0.89**	1.49	1.94	39.3	0.63	0.013*
diff.bet. parents	36	2.99*	14.67**	28.20**	270.0**	3.63**	0.021
heterosis[1]	36	1.60**	10.16**	14.29**	372.4**	2.41*	0.028*
Locations x entries in fam.	108						
loc.x diff.between reciprocal hybrids	36	0.39	1.13	2.11	28.4	0.56	0.006
loc.x diff.between parents	36	1.45**	2.01	2.75*	31.5	0.96*	0.018
loc. x heterosis	36	0.66	2.17	3.70**	47.3	1.09*	0.014
Error c	216	0.61	1.69	1.66	36.3	0.47	0.014

[1] F_1's compared to mid-parent.

**,* Significant at .01 and .05 levels, respectively.

Table 3. Mean yield of nine parents used in diallel crosses and F_1 heterosis above mid- and high-parent[1].

	A 132	A 476	BAT 1222	A 359	BAC 122	A 457	A 231	Toche 400	A 375
A 132	124.6			**	**	*	**	**	**
A 476		176.0		*	**	*	**	**	**
BAT 1222			162.4	**		**	**	**	**
A 359				334.9		**	**	*	*
BAC 122	**	*			178.6	**	**	**	**
A 457			*	*		275.4	**		**
A 231	**		**	**	**	**	279.1	**	
Toche 400	**	**	**		**			175.8	*
A 375	**	*			**	**			274.5

[1] Parental means on diagonal, heterosis above mid-parent above diagonal and heterosis above high-parent below diagonal.

**,* F_1 value significantly greater than mid- or high-parent at the .01 (L.S.D. = 90.9) and .05 (L.S.D. = 69.8) levels, respectively.

Table 4. Analyses of variance for yield and yield components in F_1 progeny from a nine parent diallel in beans, partitioning crosses sums of squares into general and specific combining ability.

Source	d.f.	Mean squares			
		Yield (g/m^2)	Pods/m	Seeds/pod	Weight/ seed
Crosses	35				
GCA	8	91026.9**	98507.3**	13.729**	0.1511**
SCA	27	19911.2**	13283.7**	0.402	0.0035
Crosses x location	35	10344.7*	5567.9	0.345	0.0022**
Pooled error	70	6387.7	3832.7	0.263	0.0007

**,* Significant at the .01 and .05 levels, respectively.

Table 5. Analyses of variance for several architectural traits in F_1 progeny from a nine parent diallel in bush beans, partitioning crosses sum of squares into general and specific combining ability.

Source	d.f.	Mean saquares					
		Lateral branches /plant	Nodes/lateral branch	Nodes on main stem	Total nodes /plant	Main stem length	Main stem internode length
Crosses	35						
GCA	8	4.37**	13.83**	85.69**	452.9**	2624.7**	0.079**
SCA	27	2.02*	9.32**	10.42**	259.9**	664.2*	0.024*
Crosses x locations	35	2.50**	3.69**	4.52**	129.2*	381.0	0.019
Error	79	0.72	1.53	2.32	38.2	299.1	0.011

**,* Significant at .01 and .05 levels, respectively.

Table 6. General combining ability effects for yield and yield components for nine parents used in diallel crosses.

Parent	Seed size	Growth habit	General combining ability effects ($\hat{g}_i$)[3]			
			Yield (g/m^2)	Pods/m^2	Seeds/pod	Weight/seed
A 132	S	I	-75.2	- 0.5	-0.42	-0.058
A 476	M	I	-97.6	-47.7	-0.63	0.010
BAT 1222	L	I	-65.8	-62.9	-1.36	0.153
A 359	S	II	82.8	75.4	1.35	-0.143
BAC 122	M	II	-47.2	5.4	-1.23	0.068
A 457	L	II	33.6	-87.9	1.15	0.069
A 231	S	III	133.1	181.6	0.87	-0.165
Toche 400	M	III	-42.2	-60.1	0.09	0.026
A 375	L	III	68.2	1.7	0.18	0.038
$S_{\bar{d}}$			7.1	5.5	0.46	0.002
Exp mean[4]			332.4	246.8	3.96	0.356

1 Small = <.25g, medium = .25 to .40g and large = >.40 g.

2 I = determinate, II = indeterminate erect, and III ideterminatee prostrate.

3 Hybrid mean (predicted) $\hat{X}_{ij}$ = mean + $\hat{g}_i$ + $\hat{g}_j$ + SCA effects.

4 Mean performance of nine parents.

Table 7. General combining ability effects for nine parents used in diallel.

Parent	Seed size[1]	Growth habit[2]	General combining ability effects (g_i)[3]					
			Lateral branches /plant	Nodes/lateral branches	Nodes on main stem	Total nodes /plant	Main stem length	Main stem internode length
A 132	S	I	0.61	-1.04	2.52	-0.17	- 0.19	-1.15
A 476	M	I	0.56	-0.66	-1.59	-0.91	-23.97	-1.58
BAT 1222	L	I	0.69	-1.53	-3.97	-8.24	-10.65	0.47
A 359	S	II	-0.56	0.32	5.96	1.01	1.08	0.25
BAC 122	M	II	-0.44	0.52	-2.28	-1.27	- 1.72	0.71
A 457	L	II	-0.84	-0.31	-0.05	-5.53	14.94	1.29
A 231	S	III	-0.16	1.29	4.07	9.58	8.74	-0.56
Toche 400	M	III	0.27	1.38	-0.71	8.05	- 7.37	-0.28
A 375	L	III	-0.12	0.02	1.32	-4.88	21.30	1.37
S $\bar{x}$			0.08	0.11	0.14	0.55	1.54	0.09
Exp. mean[4]			4.21	6.28	11.78	38.32	52.83	4.41

[1] Small = <.25g, medium = .25 to .40g, and large >.40g.

[2] I = determinate, II = indeterminate erect, and III = indeterminate prostrate.

[3] Hybrid mean (predicted) $\hat{X}_{ij}$ = mean + $\hat{g}_i$ + $\hat{g}_j$ + SCA effects.

[4] Mean performance of nine parents.

Table 8. Phenotypic, genetic and environmental correlations among yield and yield components in F_1 derived from a nine parent diallel bush beans.

	Yield	Pods/m^2	Seeds/pod	Weight/seed
Yield		.83**	.45**	-.36**
		.79	.54	-.64
Pods/m^2	.89		.17*	-.54
			.18	-.78
Seeds/pod	.15	-.12		-.56**
				-.63
Weight/seed	-.01	-.01	-.48	

rp
rg
re

Table 9. Phenotypic, genetic and environmental correlations between yield and architectural traits, and among architectural traits in F1's derived from nine parent diallel in bush beans[1].

	Yield	Lateral branches /plant	Nodes/lateral branch	Nodes on main stem	Nodes/plant	Main stem length	Main stem internode length
Yield		.34**	.50**	.33**	.61**	.60**	.59**
		-.56	.64	.66	.56	1.01	.50
Lateral branches/plant	.16		.03	-.05	.59**	.28**	.36
			-.68	-.78	-.31	-.91	-.04
Nodes/lateral branch	.41	-.15		.37**	.18**	.45**	.39**
				.65	.90	.68	.28
Nodes on main stem	.21	.21	.26		.43**	.60**	.21**
					.67	.61	-.20
Nodes/plant	.50	.36	.80	.48		.59**	.52**
						.44	-.59
Main stem length	.20	-.02	.28	.81	.44		.89**
							.68
Main stem internode length	.26	-.64	.24	.61	.38	.92	

1

re	rp rg