

Inheritance and Association of Flower, Ovule, Seed, Pod, and Maturity Characters in Dry Edible Beans (*Phaseolus vulgaris* L.)¹

Faisal A. Al-Mukhtar and Dermot P. Coyne^{2,3}

Department of Horticulture, University of Nebraska, Lincoln, NE 68583

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Abstract. The accessions, PI 255960 (P₁) (purple flowers, colored seed, curved pod tip, large seed) and G-19007 (P₂) (white flowers, straight pod tip, white seed) of *Phaseolus vulgaris* L., both late maturing with many ovules and seeds per pod, were crossed with each other and with 2 early maturing, white flowered, white seeded, straight pod tip, low ovule number/pod parents, 'Great Northern (GN) Emerson' (P₃) and 'GN UI#59' (P₄). P₁ and P₂ appeared to possess the same genes for high ovule number/pod. The continuous distributions of ovule number/pod, seed number/pod, and seed weight in the F₂ generations of the other crosses indicated quantitative inheritance. However, segregation data in their F₃ generations suggested that ovule number/pod may be determined by additive action of the alleles of a single major gene. Moderately high broad sense heritability estimates were obtained for these traits. Purple flower color and seed-coat color were controlled by 2 different complementary dominant genes. Striped pod color and curved pod tip shape (*Ct*) were each controlled by different single dominant genes. Days to flowering was controlled by a single completely dominant gene; pod maturity was controlled by a single incompletely dominant gene for lateness. Linkage occurred between genes for flower color and pod color pattern, flower color and pod tip shape, and flower color and maturity. High seed number/pod was associated with purple flowers, colored seeds, and late maturity in the F₂ of P₃ × P₁. Late maturity and high seed number/pod were also associated in the F₂ of P₄ × P₁, P₃ × P₂ and P₄ × P₂. Moderately large negative correlations were found between number of seeds/pod and seed weight in all crosses involving P₁ and P₂. High ovule number/pod was associated with indeterminate growth habit and moderately late flowering in the F₂ progeny from the indeterminate cultivar 'G.N. Nebr. #1', crossed with a determinate isolate. No association between seed weight & seed-coat color was observed in the F₂ of P₃ × P₁, and P₄ × P₁, but there was association between large seed and both late maturity and flower color.

Crop yield is the product of the interaction of a large number of genetically controlled physiological processes and morphological components that evolve in sequential developmental patterns. Ovule number/pod, seed number/pod, and seed weight in beans are important morphological yield components, and considerable variation for these traits exists in bean germplasm. Coyne (unpublished) found that *P. vulgaris* L., PI 255960 and G-19007 possessed 8-10 ovules/pod. Since ovule number/pod limits the number of seeds that can be produced per pod, information on the genetic control of this character is important in breeding for higher yield. There are no previous reports on the inheritance of ovule number/pod in beans (*P. vulgaris*) but reports in peas (14, 15) and alfalfa (6) indicated qualitative or quantitative inheritance. Negative associations have been observed between seed number/pod and seed weight in *P. vulgaris* (2, 4, 9, 11, 12, 16, 17, 18, 19, 21, 22).

This paper reports on the inheritance and association of ovule number/pod, seed number/pod, and seed weight, colors of flowers, testas and pods, pod tip shape and stages of maturity in dry

bean crosses, and the association of ovule number/pod with plant habit and time of flowering in crosses between near-isolines of 'G.N. Nebraska #1'. The implications of these results in breeding for higher yields are discussed.

Materials and Methods

Line PI 255960 is a late flowering, high ovule number (HO), dry bean with purple flowers, colored seeds, curved pod tip and large seed. Line G-19007 (P₂) (from PI station) is also a late flowering, HO, dry bean, but it has white flowers, white seeds, and straight pod tip. For early flowering, low ovule number (LO) parents we used 'G.N. Emerson' (P₃) and 'G.N. UI#59' (P₄). These lines have white flowers, white seeds, and straight pod tip. Seeds of the 4 parents were planted in the greenhouse at Lincoln, Nebraska, and the following crosses were made among the HO and LO parents in fall 1976: P₃ × P₁, P₄ × P₁, P₃ × P₂, and P₄ × P₂, and P₁ × P₂. F₁ plants from the 5 crosses were grown in the greenhouse in 1976-77 to produce F₂ seeds. All mature pods that developed on the F₁ plants were harvested, and seeds were bulked after threshing and cleaning. The F₁ plants were readily identified by means of marker genes.

Seeds of parents, F₁ and F₂ progenies from the first 4 crosses were planted on June 1, 1977 in 4 different experiments at the Mitchell farm, Panhandle Station, University of Nebraska, Scottsbluff. Each experimental design was a randomized complete block design, with 3 replications. Each replication consisted of 2 tiers, each containing 4 rows of the genetic populations and 2 guard rows of 'G.N. UI#59'. Two rows of each parent, one row of F₁, and 3 rows of F₂ seeds were planted in each replicate. Each row was 3.7 m long, the rows were spaced 56 cm apart with seed planted at 20-cm intervals within the row.

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²Graduate Student, Professor (Horticulture-Plant Breeding), respectively. The current address of the senior author is University of Baghdad, College of Agriculture, Abu-Ghraid, Baghdad, Iraq. The senior author wishes to acknowledge with appreciation the financial support provided by the Government of the Republic of Iraq.

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Ovule number was the average of 2 early-developing pods on each plant. Mean seed weight (g) was calculated from 6 pods, on a per plant basis for all replications. Data for flower color (purple vs. white), seed coat color (white vs. colored), pod color (green vs. red striped), maturity (date when lower pods turned yellow/brown) and pod tip shape (curved vs. straight) were determined for each plant in parental, F₁ and F₂ generations. In each cross, F₃ seeds were harvested from 26 to 31 F₂ plants selected at random.

Seeds of all parents, 27 F₃ families from P₄ × P₁, and 26 F₃ families from P₄ × P₂ were planted on June 5, 1978 at Scottsbluff, Nebraska. At the same time, seeds of all parents, 31 F₃ families from P₃ × P₁, and 28 F₃ families from P₃ × P₂ were planted on May 30, 1979 in Lincoln, Nebraska. The design of each experiment was a randomized complete block with 3 replications. Each replication consisted of 2 rows of each parent, 26–31 rows of F₃ families and guard rows of 'G.N. UI #59'. One row of each P₁, P₂, F₁ and 8 F₂ rows of P₁ × P₂ were planted also in a separate experiment. Row and seed spacings were the same as in 1977. Ovule number/pod and flower color were determined as described previously. The number of days to first flower was determined for all plants in all populations.

Parental and F₂ seeds from the cross 'GN Nebraska #1' (moderately early flowering, indeterminate) (P₅) × near-isogenic line (early flowering, determinate) (P₇) were planted on May 24, 1979, in the field at Lincoln. A randomized complete block design, with 3 replications, each containing 1 row of parents, 5 rows of F₂, and 2 guard rows of 'GN UI #59', was used. Seeds were spaced 30 cm apart in 6 m long rows, spaced 56 cm apart. Ovule number/pod, growth habit and days to first flower were determined for each plant.

Least square means were calculated where an unequal number of observations per treatment were involved. The F-test was used to test for significance between mean comparisons (20). Broad sense heritability (BSH) for each cross for ovule number/pod, seed number/pod, and mean seed weight, was estimated by dividing the mean of the phenotypic variances of the parents and F₁, by the phenotypic variance of the F₂ generation and subtracting this value from 1 (3). Wright's formula (8) was used to estimate the number of genes controlling ovule number/pod, seed number/pod, and mean seed weight. Simple correlation coefficients were estimated for seed weight and number of seeds/pod in the F₂ for each cross. Genetic interpretations were based on F₁ and F₂ generations for most traits but F₃ generations were grown also to study ovule number/pod, flower color and number of days to first flower. The genetic conclusions based on the latter data are stronger since the hypothesis developed with F₂ data can be tested in the F₃ generation.

Results

Inheritance of traits. A continuous distribution for number of ovules/pod was observed in the F₂ of P₃ × P₁, P₄ × P₁, P₃ × P₂, and P₄ × P₂, indicating quantitative inheritance (Table 1). The mean number of ovules/pod in the F₁ was similar to the midparent in the 4 crosses (Table 1). The recovery in each moderately-sized F₂ population of many plants with the same number of ovules/pod as each parent indicated that the parents differed only by 1 or 2 genes for this trait. Application of Wright's formula (8) also suggested that the parents differed by no more than 1 gene for this trait. The BSH estimates indicated that environmental factors contributed significantly to the observed phenotypic variations (Table 1), so

Table 1. Frequency distributions of percentage of ovule primordia, total number of plants, variances (σ^2), means, and broad sense heritability (BSH) in parents, F₁ and F₂ generations, derived from 5 dry bean crosses (1977).

Generations	No. of plants						Total no. of plants	σ^2	Mean ovule no./pod and SE	BSH ^z	Estimated gene number ^y	
	No. of ovule primordia per pod											
	4	5	6	7	8	9	10					
G.N. Emerson (P ₃)	10	94	43	1				149	0.37	5.3 ± 0.05		
PI 255960 (P ₁)				8	77	35	6	127	0.43	8.3 ± 0.06		
F ₁ (P ₃ × P ₁)			5	15	6			26	0.44	7.0 ± 0.13		
F ₂ (P ₃ × P ₁)	11	11	37	102	51	7	2	221	1.24	6.8 ± 0.08	0.67	1
G.N. UI #59 (P ₄)	8	52	53					113	0.39	5.4 ± 0.05		
PI 255960 (P ₁)				11	89	34	9	143	0.48	8.3 ± 0.06		
F ₁ (P ₄ × P ₁)			12	47	13			72	0.35	7.0 ± 0.07		
F ₂ (P ₄ × P ₁)	15	13	37	85	52	9	6	218	1.77	6.9 ± 0.09	0.78	1
G.N. Emerson (P ₃)	13	60	45					118	0.44	5.3 ± 0.06		
G-19007 (P ₂)				8	73	27	6	114	0.50	8.3 ± 0.07		
F ₁ (P ₃ × P ₂)			3	12	2			17	0.31	7.0 ± 0.13		
F ₂ (P ₃ × P ₂)	8	12	18	52	20	5	5	121	1.89	6.8 ± 0.12	0.78	1
G.N. UI#59 (P ₄)	8	37	57	3				105	0.49	5.6 ± 0.07		
G-19007 (P ₂)					59	27	4	90	0.40	8.3 ± 0.07		
F ₁ (P ₄ × P ₂)			4	10	5			19	0.50	7.1 ± 0.16		
F ₂ (P ₄ × P ₂)	4	8	20	40	23	4	1	101	1.45	6.8 ± 0.12	0.69	1
PI 255960 (P ₁)				1	9	7	1	18	0.50	8.4 ± 0.16		
G-19007 (P ₂)					12	7	2	21	0.46	8.5 ± 0.14		
F ₁ (P ₁ × P ₂)				2	7	7	1	17	0.49	8.4 ± 0.16		
F ₂ (P ₁ × P ₂)				6	69	72	9	156	0.80	8.5 ± 0.07		

^zBroad Sense Heritability

^yGene number (n) estimated using Wright's (8) formula:

$$n = \frac{R^2}{8(\sigma^2 F_2 - \sigma^2 F_1)}$$

R = difference in mean values of parents.

that it was not possible to isolate the effects of genotypes in the F₂ even though the inheritance was probably simple.

The standard unit method (13) was used to calculate narrow sense heritability estimates for ovule number/pod by the regression of F₃ family means on individual F₂ plants. The following moderately low estimates, .35±0.2, .39±0.9, .39±0.2 and .10±0.2- were obtained for the crosses P₃ × P₁, P₄ × P₁, P₃ × P₂, and P₄ × P₂, respectively.

In the F₂ generation of the cross P₁ × P₂ there was no evidence of transgressive segregation for ovule number/pod, indicating that the same genes controlled this trait in both parents. Also, there were no significant differences between the means of the parents, F₁ and F₂ generations of this cross (Table 1).

F₃ families showing the same range of variation for ovule number/pod as their respective parents were classified as non-segregating while those F₃ families overlapping both parental ranges were classified as segregating families. The number of non-segregating and segregating F₃ families were counted for each cross (Table 2). The occurrence of a high number of non-segregating F₃ families showing a range of ovule number/pod similar to either parents indicated that this trait was simply inherited (Table 2). The segregation data are suggestive that this trait may be determined primarily by additive action of the alleles of a single major gene since a good fit to a 3:1 ratio of number of combined families not segregating for low ovule number plus number segregating for ovule number to number of non-segregating families for high ovule number was observed in each cross and when combined over all crosses (Table 2). However, a poor fit to a 1:2:1 ratio of F₃ families non-segregating for low ovule number/pod, segregating for ovule number/pod and non-segregating for high ovule number/pod overall crosses was obtained (Table 2). Based on the expected segregation (1:2:1) there is a deficiency of families in the high ovule class and an excess number in the low ovule class. This may be due to a misclassification of some families.

A continuous distribution for number of seeds/pod was also observed in the F₂ generations in all crosses, also indicating a quantitative inheritance pattern (Table 3). The F₁ means for seed number/pod approached the midparent mean in each of the 4 crosses indicating a near-additive genetic effect (Table 3). P₁ and

P₂ had a higher percentage seed set than the G.N. cultivars, and dominance for high seed set was observed in crosses (Table 3).

A continuous distribution for number of plants in different seed weight classes was observed in the F₂ generations of P₃ × P₁, and P₄ × P₁, indicating quantitative inheritance patterns (Table 4). Only F₁ of P₄ × P₁ was intermediate in seed weight, possibly indicating additive gene effects for seed weight. The recovery of a high number of plants in the F₂s with the same seed weight as each parent suggested that the parents differed only by 1 or 2 major genes acting additively. Estimates of gene numbers, using Wright's formula (8), indicated that the parents in the cross P₃ × P₁ differed by 1 gene while in the cross P₄ × P₁ they differed by 2 genes. The BSH estimates for seed weight were moderately high and indicated that environment, also contributed significantly to the variation for this trait (Table 4).

Moderately high negative correlations were determined between number of seeds/pod and mean seed weight in the F₂ generations of the four crosses. Significant correlation coefficients (r) between these traits were -0.51, -0.47, -0.50 and -0.42 for the crosses P₃ × P₁, P₄ × P₁, P₃ × P₂, and P₄ × P₂, respectively. This indicates that there is a tendency of mean weight to decrease as the number of seeds/pod increase.

Segregation in the F₂ generations of the crosses, P₃ × P₁ and P₄ × P₁, indicated that purple flower color was controlled by 2 complementary dominant genes (Table 5). Colored seed-coat also was controlled by 2 complementary dominant genes based on segregation in the F₂ of P₃ × P₁ (9:7, $\chi^2 = 3.44$, P .10-.05) and F₂ of P₄ × P₁ (9:7, $\chi^2 = .285$, P = 0.10-0.05). Since a wide range of seed-coat color variation occurred in the segregating populations, other genes for different color patterns were also involved. Pod color was controlled by 1 major gene, with striped pod color dominant to green pod color in each of the above 2 crosses, respectively (3:1, $\chi^2 = .94$, P = 0.50-0.25; 3:1, $\chi^2 = 0.49$, P = 0.50-0.25). One major gene determined pod tip shape, with curved tip shape being dominant over straight pod tip shape also in the above crosses, respectively (3:1, $\chi^2 = 3.33$, P = 0.10-.05; 3:1, $\chi^2 = 0.05$, P = 0.90-0.75). The symbol C₁ was assigned to the dominant gene controlling curved pod tip shape.

Table 2. Segregation for ovule number (O.N.)/pod in F₃ families derived from 4 dry bean crosses (1978).

Cross	No. of F ₃ families			No. of F ₃ families	
	NSLON ²	SON	NSHON	NSLON +	SON NSHON
G.N. Emerson (L.O.N.) × PI 255960 (H.O.N.)	10	17	4	27	4
	(1:2:1, χ^2 2.61, P= .50-.25)			(3:1, χ^2 2.42, P= .25-.10)	
G.N. Emerson (L.O.N.) × G-19007 (H.O.N.)	11	8	9	19	9
	(1:2:1, χ^2 5.42, P= .10-.05)			(3:1, χ^2 0.761, P= .50-.25)	
G.N. UI#59 (L.O.N.) × PI 255960 (H.O.N.)	11	13	3	24	3
	(1:2:1, χ^2 4.78, P= .10-.05)			(3:1, χ^2 2.777, P= .10-.05)	
G.N. UI#59 (L.O.N.) × G-19007 (H.O.N.)	10	7	9	17	9
	(1:2:1, χ^2 5.62, P= .10-.05)			(3:1, χ^2 1.283, P= .50-.25)	
Total	42	45	25	87	25
	(1:2:1, χ^2 9.48 P= .01-0.005)			(3:1, χ^2 .428 P= .75-.50)	
Heterogeneity	$(\chi^2 = 8.928, P = .05-.03)$			$(\chi^2 = 7.24-.428 = 6.81, P = .10-.05)$	

²NSLON = non-segregating for low ovule number (range for G.N. Emerson and G.N. UI#59 = 4-6).

SON = segregating for ovule number.

NSHON = non-segregating for high ovule number.

Table 3. Frequency distributions for number of seeds/pod, total number of plants, variances (σ^2), means and broad sense heritability (BSH) for number of seeds/pod in different genetic populations derived from four dry bean crosses (1977).

Generations	No. of plants with number of seeds/pod												Total no. of plants	σ^2	Mean seed no./pod and S.E.	BSH	Seed-set (%)
	2.5-3	3.1-3.6	3.7-4.2	4.3-4.8	4.9-5.4	5.5-6	6.1-6.6	6.7-7.2	7.3-7.8	7.9-8.4	8.5-9	9.1-9.6					
GN Emerson (P ₃)	7	30	64	34	13	1							149	0.31	4.0 ± 0.05		75.4
PI 255960 (P ₁)						3	19	48	21	27	7	2	127	0.53	7.4 ± 0.06		89.1
F ₁ (P ₃ × P ₁)					2	7	12	4	1				26	0.33	6.3 ± 0.11		90.0
F ₂ (P ₃ × P ₁)	7	6	8	19	24	65	49	28	10	4	1		221	1.27	5.8 ± 0.08	0.70	85.2
GN UI#59 (P ₄)	4	6	33	74	15	1							133	0.24	4.4 ± 0.04		81.4
PI 255960 (P ₁)						4	10	43	47	27	8	4	143	0.50	7.5 ± 0.05		90.3
F ₁ (P ₄ × P ₁)					6	10	43	4	9				72	0.37	6.4 ± 0.07		91.4
F ₂ (P ₄ × P ₁)	4	11	6	7	21	41	60	26	7	4	5		218	1.78	6.2 ± 0.09	0.80	89.8
GN Emerson (P ₃)	2	22	42	40	9	3							118	0.34	4.2 ± 0.05		79.2
G-19007 (P ₂)							11	35	35	20	8	5	114	0.54	7.5 ± 0.07		90.3
F ₁ (P ₃ × P ₂)					1	3	11		2				17	0.30	6.4 ± 0.13		91.4
F ₂ (P ₃ × P ₂)	3	6	10	1	10	16	42	9	14	4	5	1	121	1.30	6.1 ± 0.13	0.80	89.7
G.N. UI#59 (P ₄)	2	7	24	33	35	4							105	0.36	4.6 ± 0.05		82.1
G-19007 (P ₂)							4	26	31	14	11	4	90	0.52	7.6 ± 0.07		91.5
F ₁ (P ₄ × P ₂)					1	4	9	3	2				19	0.38	6.4 ± 0.14		90.1
F ₂ (P ₄ × P ₂)	5	8	2	11	13	36	10	11	3	2			101	1.48	6.1 ± 0.12	0.72	89.7

Table 4. Frequency distribution of number of plants in seed weight classes, mean seed weight (g), variances and broad sense heritability (BSH) estimates for mean seed weight for parents, F₁ and F₂ generations, derived from two dry bean crosses (1977).

Generations	Seed weight classes (g)										Total no. of plants	σ^2	Mean seed wt. ± SE	BSH	
	0.25-0.29	0.30-0.34	0.35-0.39	0.40-0.44	0.45-0.49	0.50-0.54	0.55-0.59	0.60-0.64	0.65-0.69	0.70-0.74					
GN Emerson (P ₃)				1	8	124	10	6				149	0.04	0.47 ± 0.02	
PI 255960 (P ₁)								20	89	15	3	127	0.05	0.63 ± 0.02	
F ₁ (P ₃ × P ₁)						2	3	17	4			26	0.04	0.58 ± 0.04	
F ₂ (P ₃ × P ₁)				12	26	27	83	39	24	7	3	221	0.09	0.53 ± 0.02	0.55
GN UI #59 (P ₄)	38	76	17	2								133	0.03	0.33 ± 0.01	
PI 255960 (P ₁)								29	84	28	2	143	0.04	0.63 ± 0.02	
F ₁ (P ₄ × P ₁)				2	10	42	12	6				72	0.04	0.48 ± 0.02	
F ₂ (P ₄ × P ₁)	3	8	12	14	30	91	32	22	3	3		218	0.08	0.50 ± 0.02	0.58

Table 5. Segregation for flower color and maturity in F₂ (1977) and F₃ (1978) generations derived from bean crosses.

Cross ²	No. plants F ₂ Segregation			χ^2	P	No. of F ₃ families			χ^2	P
	<i>Flower color</i>					<i>Flower color</i>				
	Purple	White	(9:7)			Purple	Seg.	White		
P ₃ × P ₁	128	93		0.29	.75-.50	4	17	10	3.28	.25-.10
P ₄ × P ₁	130	88		1.01	.50-.25	2	16	9	1.19	.75-.50
	<i>Pod maturity</i>					<i>Flowering</i>				
	Late	Mod late	Early			Late	Seg.	Early		
	(1:2:1)					(1:2:1)				
P ₃ × P ₁	45	113	63	3.04	.10-.05	6	17	8	.55	.90-.75
P ₄ × P ₁	50	104	64	2.55	.25-.10	4	17	6	2.11	.50-.25
P ₃ × P ₂	29	55	37	2.06	.50-.25	4	18	6	2.57	.50-.25
P ₄ × P ₂	19	55	27	2.07	.50-.25	7	15	4	1.31	.75-.50

²P₁ = PI 255960; P₂ = G19007; P₃ = 'GN Emerson'; P₄ = 'GN UI#59'.

Three pod maturity classes; early, moderately late, and late, occurred in the F₂ segregating generations of the crosses P₃ × P₁, P₄ × P₁, P₃ × P₂, and P₄ × P₂ (Table 5). Pod maturity was controlled by 1 major gene, with incomplete dominance for late maturity. Segregation for days to first flower (late vs. early) supported the hypothesis that a single major gene with complete dominance for late flowering primarily determined this trait (Table 5).

Association of traits. In the F₂ of P₃ × P₁ the mean number of seeds/pod was greater in the purple flowered plants than in the white flowered plants (Table 6). Colored-seeded F₂ plants had a higher mean number of seeds/pod than white-seeded F₂ plants. F₂ plants with striped pods had a higher mean number of seeds/pod than plants with green pods. The difference between the mean number of seeds/pod of F₂ plants with curved pod tip and plants with straight pod tip was non-significant. Significant differences were detected among the mean number of seeds/pod for F₂ maturity classes in this cross as well as in the crosses P₄ × P₁, P₃ × P₂, and P₄ × P₂. In the F₂ of the cross P₄ × P₁, the differences in the mean seed number/pod for the other different trait alternatives were non-significant (Table 5). In the F₂ of P₃ × P₁, the mean seed weight (g) for the purple-flowered plants was greater than that of the white-flowered plants (Table 6). Mean seed weight of the late maturing plants was greater than that of the early maturing F₂ plants in this cross as well as in the cross P₄ × P₁.

Linkage was detected between genes controlling flower color and pod color pattern, flower color and pod tip shape, and flower color and maturity in the F₂ of the crosses 'G.N. Emerson' (P₃) × PI 255-960 (P.) and 'G.N. UI #59' (P₄) × PI 255-960 (P₁) (Table 7). No linkage between genes controlling flower color and seed-coat color or seed-coat color and pod color pattern was detected in these 2 crosses (Table 7).

In the cross P₅ × P₇, a continuous distribution for number of ovules/pod was observed in the F₂ generation, indicating quantitative inheritance (Table 8). The mean number of ovules/pod for the F₂ indeterminate plants was greater than that of the F₂ determinate plants. Competition between the indeterminate and determinate plants was not a factor because of wide spacing. Thus lower ovule number/pod of the determinate plants can be attributed to genetic linkage. The ovule number/pod was also greater for the F₂ late flowering plants than in the F₂ early flowering plants (Table 8). These results indicated an association between the traits high

ovule number/pod with indeterminate plant habit and later flowering in this cross. However, some determinate and early flowering plants with high ovule number/pod were observed, indicating that recombination occurred.

Discussion

The information on the inheritance of ovule number/pod, seed number/pod, and seed weight should be useful to breeders for developing breeding strategies for higher yield in dry beans. The continuous distributions of these traits in the F₂ generations of the different crosses suggested quantitative patterns of inheritance. However, the high proportion of F₃ families with ovule numbers per pod similar to the high and low ovule parents suggested that the parents differed by a few genes. Chi-square analysis of the F₃ families suggested that ovule numbers/pod may be determined by additive action of the alleles of a single major gene.

Seed number/pod and seed weight in the crosses reported here appeared to be more simply inherited than previously reported (9, 16, 17, 19, 22). Additive gene action was indicated which agrees with the findings of Coyne, et al (12), Al-Mukhtar (4), Motto, et al (16), and Chung, et al (9), but disagree with Sarafi (17) and Sirks (19) who found partial dominance and complete dominance for seed weight, respectively. Sarafi (17) also found partial dominance for seed number/pod.

Pod maturity was found to be incompletely dominant while late flowering was completely dominant in the crosses between the PI lines and 'Great Northern' cultivars. More research is necessary to elucidate the basis of this observation. It is speculated that in moderately late maturing heterozygous plants the opening of subsequent flowers was more rapid, pod development more rapid, the duration of flowering was shorter, or a combination of these factors was involved compared to the late maturing homozygous dominant plants. The shorter flowering period would occur if the F₁ plants had fewer nodes than the later PI lines. The authors observed in the field over a number of years that the late PI lines had more nodes than the early flowering parents but no comparisons were made with the F₁ plants. The late flowering of the PI lines was found by Al-Mukhtar to be due to long photoperiod and high temperature (5).

This is the first report on the inheritance of pod tip shape; a trait that could serve as a useful genetic marker. Linkage was detected between pod tip shape and flower color but not with the other

Table 6. Least square means for number of seeds/pod, and seed weight (g) for different trait variations in F₂ populations derived from 4 dry bean crosses (1977).

Trait	Alternative character	Cross ²	Mean no. seeds/pod	F value	Mean seed wt (g)	F value
Flower Color	Purple:white	P ₃ × P ₁	5.9:5.4	7.47*	.56:.51	5.14*
		P ₄ × P ₁	6.0:5.8	1.00 ns	.49:.48	.01 ns
Seed color	Color:white	P ₃ × P ₁	5.8:5.5	4.59*	.54:.53	1.42 ns
		P ₄ × P ₁	6.1:5.8	3.21 ns	.49:.47	.01 ns
Pod color	Green:striped	P ₃ × P ₁	5.4:5.9	14.66*	.53:.54	0.51 ns
		P ₄ × P ₁	5.9:6.0	0.22 ns	.48:.49	0.51 ns
Maturity	Early:late:mod. late	P ₃ × P ₁	5.0:6.3:5.6	18.34*	.52:.58:.52	4.23*
		P ₄ × P ₁	4.7:6.7:6.4	39.60*	.36:.54:.55	33.28*
		P ₃ × P ₂	4.8:7.4:6.1	57.24*	---	---
		P ₄ × P ₂	4.7:7.3:6.2	46.87*	---	---
Pod tip shape	Curved:straight	P ₃ × P ₁	5.8:5.5	3.45 ns	.54:.54	0.51 ns
		P ₄ × P ₁	6.1:5.8	3.24 ns	.47:.48	0.19 ns

²P₁ = PI 255960; P₂ = G-19007; P₃ = 'GN Emerson'; P₄ = 'GN UI #59'.

NS,*] Nonsignificant (NS) or significant at 5% level. (*)

Table 7. Segregation of different combinations of traits in the F₂ from dry bean crosses 'G.N. Emerson' (P₃) × PI 255960 (P₁) and 'GN UI #59' (P₄) × PI 255960 (P₁) (1977).

Cross	Trait combinations and observed no. of plants in classes						Expected phenotypic frequency	χ ²	P value		
P ₃ × P ₁	Purple flower colored seed		Purple flower white seed		White flower colored seed		White flower white seed		81:63:63:49	6.60	0.05-0.10
P ₄ × P ₁	86		42		52		41				
P ₃ × P ₁	Purple flower striped pod		Purple flower green pod		White flower striped pod		White flower green pod		27:9:21:7	9.95 ^z	0.01-0.025
P ₄ × P ₁	109		19		63		30				
P ₃ × P ₁	Colored seed striped pod		Colored seed green pod		White seed striped pod		White seed green pod		27:9:21:7	6.79	0.05-0.10
P ₄ × P ₁	112		26		60		23				
P ₃ × P ₁	Purple flower curved pod tip		Purple flower straight pod tip		White flower curved pod tip		White flower straight pod tip		27:9:21:7	30.58 ^x	<0.005
P ₄ × P ₁	106		22		48		45				
P ₃ × P ₁	Purple flower early		Purple flower mod. late		White flower early		White flower mod. late		1:18:9:	58.40 ^y	<0.005
P ₄ × P ₁	13		77		50		36				
P ₃ × P ₁	Purple flower late		Purple flower early		White flower mod. late		White flower late		7:14:7	19.62 ^w	<0.005
P ₄ × P ₁	22		68		42		36				

^z Linkage χ² = 9.95 - 0.294 - 0.942 = 8.714 P(χ² ≥ 8.71) = <0.005

^y Linkage χ² = 11.38 - 1.013 - 0.494 = 9.873 P(χ² ≥ 9.87) = <0.005

^x Linkage χ² = 30.58 - 0.294 - 3.330 = 26.956 P(χ² ≥ 26.96) = <0.005

^w Linkage χ² = 19.62 - 1.013 - 0.054 = 18.553 P(χ² ≥ 18.55) = <0.005

^v Linkage χ² = 58.40 - 0.924 - 3.044 = 55.062 P(χ² ≥ 55.06) = <0.005

^u Linkage χ² = 30.75 - 1.013 - 2.068 = 27.669 P(χ² ≥ 27.67) = <0.005

Table 8. Frequency distributions of mean number of ovules/pod for parents and two types of growth habit (determinate vs. indeterminate) and number of days to first bloom (early vs. late) in the F₂ generation derived from the cross of the near-isogenic lines 'G.N. Nebraska #1' (P₅) (indeterminate) × 'G.N. Nebraska #1 (determinate)' (P₇) (Lincoln, 1979).

Traits	No. of plants					Mean no. of ovules/pod	Mean comparisons
	Ovule no. classes						
	3	4	5	6	7		
G.N. Nebraska #1 (indet.) (P ₅)			9	27	13	6.1	31.73 ^z
G.N. Nebraska #1 (det.) (P ₇)	8	25	13			4.1	
Growth habit (F ₂)							
Determinate	7	17	13	8	4	4.7	6.34 ^y
Indeterminate	9	21	23	85	37	5.7	
Days to first bloom (F ₂)							
Early	15	28	11	7	2	4.5	10.77 ^y
Late	1	10	25	86	39	5.9	

^zIndicates value derived from *t* test.

^yIndicates value derived from F test.

*Indicates significant differences at the 5% level.

traits studied. The findings reported here on the inheritance of flower, seed-coat and pod color agree with previous reports (6) except that the genes controlling flower color and seed color were inherited independently. Although a genetic association occurred between high ovule number/pod, moderately late flowering, and indeterminate type of growth habit in the F₂ generation of the cross P₅ × P₇ (Table 7), and unfavorable genetic associations were detected between late maturity and high seed number/pod, and also with high seed weight, desired recombinants were obtained. Recombinants were also readily detected between other traits so should not pose problems to breeders. An association between seed-coat color and high seed weight was reported by earlier workers (12, 18) but no association was found in crosses reported here.

Negative correlations have been reported (2, 4, 11, 21) among the different yield components which result in yield component compensations and yield stability. Such correlations tend to retard progress in breeding for higher total yield when only 1 or 2 yield components are emphasized in selection. Hopefully the obstacle to breeding for higher yield can be overcome by recombining favorable genes controlling many different morphological and physiological yield components. Some physiological components such as higher net assimilation rate and increased partitioning of the products of photosynthesis to the sinks should be emphasized. These are complex traits of low heritability and can be subdivided into a number of further physiological components (21). A recurrent selection program, used in conjunction with the single seed descent breeding method developed by Brim (7) and

extended by Compton (10), might aid in attempts to recombine the different physiological and morphological components of yield. It remains to be seen if higher yielding recombinants can be obtained through physiological and morphological complementation.

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Effects of Between-row Spacing, Cultivation, and Genotype on Growth and Yield of Black Beans¹

Brian A. Kahn,² Peter J. Stoffella,³ Roger F. Sandsted,² and W. Larry Hymes²

Department of Vegetable Crops, Cornell University, Ithaca, NY 14853

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Abstract. Two lines of black bean (*Phaseolus vulgaris* L.), '70001' and 'Strain 39', were grown at between-row spacings of 76, 61, and 46 cm. Cultivation treatments included an uncultivated check and a single cultivation at 1 of 3 plant growth stages: first trifoliolate leaf fully expanded; anthesis; or pod elongation. Root weight, shoot weight, and shoot:root ratio of individual plants decreased linearly as between-row spacing decreased. Biological yield increased linearly as between-row spacing decreased, but seed yield and harvest index did not show significant responses to spacing. None of the measured parameters gave a significant response when the uncultivated control was compared with the average of the 3 time-of-cultivation treatments. Root weight of individual plants and biological yield gave quadratic responses within the 3 time-of-cultivation treatments, both decreasing most markedly with cultivation at the pod elongation stage. Plants of '70001' were larger and lodged less compared to those of 'Strain 39'. Seed yields of both lines were similar. Results suggest that a single shallow cultivation may be used for black beans grown in narrow rows through anthesis. Although cultivation at the pod elongation stage was generally not detrimental to seed yield, it is not recommended.

Recent developments in herbicide technology have reduced the need for mechanical weed control in dry beans and created interest in increasing the plant population per area in an effort to raise

yields. Rows still need to be wide enough to permit cultivation if the chemical used fails to control all species of weeds which are present in significant numbers (16). However, crops grown with relatively narrow rows often require no more than a single cultivation in addition to an herbicide treatment for satisfactory weed control (9). This effect has been attributed to the increased competition experienced by the weeds (16). Further, shallow cultivation sometimes increases crop yields even when few or no weeds are present, particularly on soils prone to crusting, by improving moisture infiltration and soil aeration (9, 10).

Several studies with soybeans [*Glycine max* (L.) Merr.] (2, 9, 16, 17) and snap and dry beans (*Phaseolus vulgaris*) (3, 7, 8, 18) have demonstrated the potential for increased yields with narrow between-row spacings. Cultivars have been found to differ in

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²Graduate Research Assistant, Professor, and Research Support Specialist, respectively.

³Former Graduate Student. Present address: Assistant Professor, IFAS Agricultural Research Center, University of Florida, P.O. Box 248, Fort Pierce, FL 33454.