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GENETIC VARIANCE, HERITABILITY AND EXPECTED RESPONSE
FROM SELECTION FOR DRY BEAN (Phaseolus vulgaris L.)
YIELD AND ITS COMPONENTS .

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Abstract

Genetic variance, heritability, and expected response from selection are useful in devising alternative methods and criteria of selection. The objectives of this study were to estimate these for seed yield and its components from 200 F_2 populations involving 80 cultivars and lines of mostly small-seeded dry bush bean (Phaseolus vulgaris L.) of growth habits I, II, and III. Most of the parental cultivars were either extensively grown in or bred for Argentina, Brazil, Central America, Colombia, Cuba, and Mexico and all were crossed in eight sets of ten parents each in a Design II mating system. The F_2 populations, without parents, were evaluated in the field in a replicates-in-sets design at two locations in Colombia in 1983.

Estimates of additive genetic variance were significant for yield, pods/plant, seeds/pod, and seed weight. Interaction with environments was also significant. Values for nonadditive genetic variance were not significant for either yield or yield components. The estimates of narrow sense heritability, based on the F_2 population mean, were 0.37 ± 0.24 for yield, 0.39 ± 0.25 for pod/plant, 0.59 ± 0.14 for seed/pod, and 0.88 ± 0.18 for seed weight.

The expected direct response from selection of the top 20% of F_2 populations for yield per se would result in a 5.8% increase in yield with a correlated response of 6.5% in seed weight. In contrast, the expected gain from direct selection for seed weight would result in a 12.8% increase in seed weight with a correlated gain of 6.8% for yield. Direct selection for pod/plant would decrease yield, seed/pod and seed weight, while direct selection for seed/pod would reduce pod/plant and seed weight.

Data on yield and seed weight from replicated trials in the early segregating generations could be utilized for identification and selection of promising crosses and families or lines within crosses for dry bean yield improvement.

Key words: Dry common bean - Phaseolus vulgaris - yield - yield components - genetic variance - heritability - gain from selection

HAMBLIN and EVANS (1976) reported that prediction of potential of a cross was possible, based on performance of parents or early generation progeny. In tropical and subtropical environments of Latin America, high yielding bean lines are often derived only from crosses involving high yielding parents, but it has been difficult to surpass the yield of the highest yielding parent. To increase yield we must develop, therefore, a more complete understanding of the range of available variation and its inheritance, the combining ability of parents, and the relative effectiveness of different criteria and methods of selection.

The growth habit, seed size, and days to maturity are intrinsic characteristics of each bean cultivar and are largely responsible for the gross differences in yield between cultivars even under the most optimum growing environments. Large variation for these traits is found among cultivars belonging to different gene pools (SINGH 1987) and, hence, in their yielding ability. Cultivar yields are also affected by cropping systems, agronomic management, inputs applied, and growing environments.

Selection for increased seed yield either directly or indirectly via yield components is difficult in dry bean, Phaseolus vulgaris L. (ADAMS 1967; CHUNG and STEVENSON 1973; COYNE 1968; DUARTE 1966; MCFERSON 1983; NIENHUIS and SINGH 1985; SARAFI 1978; SULLIVAN and BLISS 1983; TOLLA 1978). COYNE (1968) suggested that the failure to improve bean yield was due to low heritability and large environmental effects on the expression of yield and its components. Other causes for the lack of seed yield increase and ineffectiveness of selection include: 1) lack of desirable alleles in the base population (TOLLA 1978); 2) negative compensatory effect of yield promoting traits (ADAMS 1967; NIENHUIS and

SINGH 1985); and negative or zero general combining ability of high yielding small-seeded cultivars (NIENHUIS and SINGH 1987). Narrow sense heritability estimates are reported to be low for yield, intermediate for seeds/pod, and high for seed weight (CHUNG and STEVENSON 1973; CONTI 1985; COYNE 1968; MOTTI et al. 1978; MUTSCHLER and BLISS 1981; PANIAGUA and PINCHINAT 1976; SARAFI 1978; ZMMERMANN et al. 1984).

If yield components were more heritable than yield per se and a high genetic correlation existed among the components, yield might be more effectively increased by indirect selection for the component traits than by direct selection. Phenotypic and genotypic correlations between yield and pod/plant, and between yield and seed/pod are generally high and positive, while the correlation between yield and seed weight are often negative (HAMBLIN and EVANS 1976; NIENHUIS and SINGH 1985). Thus, it seems that pod/plant and/or seed/pod might serve as useful indirect selection criteria for yield. However, because the correlations of seed weight with yield, seed/pod, and pod/plant tend to be negative (NIENHUIS and SINGH 1985), selection for increased levels of expression of one yield component is seemingly compensated by a reduction in others (ADAMS 1967; COYNE 1968).

To improve the yielding ability of small-seeded cultivars suitable for sole cropping we intended to initiate alternative selection programs in 1982. However, due to lack of reliable information from tropical equatorial environments regarding sources of desirable germplasm, gene action, heritability, relative importance of general combining ability (GCA) and specific combining ability (SCA), and effectiveness of different criteria and methods of selection, a series of experiments was initiated at CIAT. From one such study of 9x9 diallel crosses,

NIENHUIS and SINGH (1986) reported that GCA was more important than SCA under optimum growing environments, for seed yield, its components, and most architectural traits in the F_1 analyses. In the F_2 , variance due to SCA was not significant for yield and its components. Only two parents were identified with positive GCA for seed yield in both F_1 and F_2 and the sources of germplasm for positive GCA could not be known with certainty. Therefore, two subsequent experiments, one involving 80 and another 64 parents, grouped according to seed size and evolutionary origin, were initiated. The latter study involving 64 medium- and large-seeded materials of South American, African, Mexican highlands, and other regions of origin is still in progress. The GCA of 80 parents of mostly small seeds has been reported (NIENHUIS and SINGH 1987). The objectives of this study were to estimate genetic variance, heritability, and expected gain from selection for yield and its components from 200 F_2 populations involving the same 80 cultivars and lines of dry bean.

Materials and Methods

Eighty dry bean parents were selected which ^{included} most of the commercial cultivars and donors of desirable genes for important production characteristics including early maturity, and tolerance or resistance to drought, low soil phosphorus, N_2 fixation, bean golden mosaic virus, rust (*Uromyces appendiculatus*), common bacterial blight (*Xanthomonas campestris* pv. *phaseoli*), anthracnose (*Colletotrichum lindemuthianum*), angular leaf spot (*Isariopsis griseola*), and leafhoppers (*Empoasca kraemeri*). A few improved lines of medium-sized seeds (26 to 40 g/100 seed) from Mexican and Andean highlands also were included to provide

additional genetic diversity. Extremely large-seeded (> 40 g/100 seed) lines were deliberately excluded due to their low yielding ability. Also, indeterminate, climbing beans of growth habit IV were not included due to difficulties in evaluation in sole crop without artificial support.

Eighty cultivars and experimental lines adapted to tropical environments of Latin America were randomly assigned to eight sets of 10 lines each and crossed in a Design II mating scheme (COMSTOCK and ROBINSON 1948). Within a set five parents were used as males and each was crossed to five other parents, used as females, to obtain the 25 F_1 crosses per set and 200 F_1 crosses from the eight sets. Seeds of each of the 200 F_1 hybrids were sown in January 1983, at the CIAT experimental farm at Palmira, Colombia. Each F_1 (an average of 45 plants/cross) was harvested to provide F_2 seed for replicated yield trials.

The 200 populations, excluding parents, were grown in two diverse environments during May-August planting season at Palmira (1,000 m above sea level, mean temperature 23.6 C) and during August-November season of 1983, at Santander de Quilichao (980 m above sea level, mean temperature 23.8 C), Colombia. The soil in Palmira is a fertile Mollisol with pH of approximately 7.5, whereas Santander de Quilichao has an Ultisol with a pH of 4.5. The latter soil is deficient in phosphorus and has toxic levels of magnesium and aluminum. Before sowing, recommended rates of fertilizer were applied at both sites and lime only at Santander de Quilichao to correct soil problems. The 25 F_2 populations from each set were planted in a replicates-in-sets design at each location, with two replications. The experimental unit was four 60 cm wide rows, 4 m long. Density of 22 plants/m² was established by planting excess seed and

thinning. Regular applications of insecticides and fungicides were used to control insects and diseases; and supplemental irrigation was used as needed at both locations. After the plants had matured in the field, pods were harvested from 2.25 m of bordered plants in the two center rows (net harvested area 2.7 m²). Pod number was determined for each plot, and seed counted, and weighed. Yield was expressed in terms of g/m² adjusted to a moisture content of 14% by weight. The mean number of seed/pod was calculated by dividing the number of seed/plot by the number of pod/plot. Seed weight was calculated by dividing yield by the number of seed/m².

A pooled analysis of variance was performed on the data by pooling sums of squares over sets and locations to obtain estimates of variance components (HALLAUER and MIRANDA 1981). Genetic components of variance and covariance were obtained by setting observed mean squares or cross products equal to expected values and solving for the desired component (HALLAUER and MIRANDA 1981; PANDEY and GRITTON 1975). Estimates of additive genetic variance (σ_a^2) were obtained by pooling the sums of squares associated with males and females. Gene frequencies were assumed to be 0.5 within and across each F₂ population, making σ_a^2 equivalent to the sum of σ_m^2 and σ_f^2 (STUBER 1970). Narrow sense heritability (h^2) estimates were obtained by dividing σ_a^2 by σ_p^2 and standard errors were estimated using methods of HALLAUER and MIRANDA (1981). Estimates of direct gain [$DG = k\sigma_{a_1}^2 / \sigma_{p_1}$] and correlated gain [$IDG = k \text{Cov}_{a_{12}} h_1 \sigma_{a_2}$] from selection for yield and yield components were calculated assuming a selection pressure of 20% ($k = 1.4$), where k = standardized selection differential, σ_{p_1} = square root of the phenotypic variance associated with the trait of interest, $\text{Cov}_{a_{12}}$ = the

additive genetic covariance between traits 1 and 2, h_1 = square root of the heritability of trait 1, and σ_{a2}^2 = the additive genetic variance associated with trait 2.

Results

Variance Components and Heritability

Table 1 presents the mean squares, estimates of variance components, and narrow sense heritability values for seed yield and its components. The mean squares for location (L), set (S), LxS, and replication/S/L were not significant for any character studied. Similarly, mean square values for male x female/S were nonsignificant for all traits.

Estimate of variance due to male/S (σ_m^2) was larger than that for female/S (σ_f^2) for seed yield and the converse was true for pod/m². However, the two values for seed/pod and seed weight were comparable as should be expected. The sum of values of σ_m^2 and σ_f^2 , which is equivalent to the additive genetic variance (σ_a^2), were larger than variance due to male x female/S (σ_{mf}^2). The latter is an estimate of the nonadditive genetic variance. The variance due to female/S x location (σ_{f1}^2) were larger than values for σ_f^2 for seed yields and pod/m². Likewise, the value for male/S x location (σ_{m1}^2) was significantly different from zero and it was slightly larger than the σ_m^2 estimate. In contrast, for seed/pod and 100-seed weight, first order variances (σ_m^2 and σ_f^2) were larger than the variance of their interactions (σ_{mf}^2) and their interactions with locations (σ_{m1}^2 , σ_{f1}^2 , σ_{mf1}^2).

Values for the additive genetic variance (σ_a^2) compared to phenotypic variance (σ_p^2) were relatively smaller for seed yield and pod/m² and larger for seed/pod and 100-seed weight. Consequently, the estimates of narrow sense heritability (σ_a^2/σ_p^2) were low for yield (0.37 ± 0.24) and pod/plant (0.39 ± 0.25), intermediate for seed/pod (0.59 ± 0.14), and high for seed weight (0.88 ± 0.18).

Correlations Among Traits

Both the phenotypic and genetic correlation coefficients were calculated between yield and its components (Table 2). Considering the relatively large number of observations that were utilized to obtain these values, all simple phenotypic correlations between seed yield and each of its three components were positive and highly significant. The correlation coefficient between yield and seed weight was the largest. The phenotypic correlations of pod/m² with seed/pod and seed weight and between seed/pod and seed weight were all positive and significant. Although it was not feasible to test the significance of the values for genotypic correlation coefficients, they tended to be larger than their corresponding phenotypic correlations for all combinations except yield and seeds/pod.

Expected Response From Selection

Values for expected direct and correlated response to selection for seed yield and its components are given in Table 3. From the data it appears that selection for seed weight and seed/pod would be about twice as effective as selection for pod/m² and seed yield for the improvement of each of these traits per se. For example, direct selection for yield

(g/m²) would result in an expected gain of 5.8%. Direct selection for seed weight would be expected to result in a 6.8% gain in yield and a 12.8% increase for seed weight per selection cycle.

Selection for pod/m² would have negative effects on yield, seed/pod, and seed weight. Yield may increase only slightly by selection for seed/pod, but it would decrease pod/m² and seed weight. On the other hand, while selection for seed weight would have an adverse effect on seed/pod and increase the number of pods only slightly, it would be expected to result in a slightly larger increase in yield than selection for yield per se.

Discussion

Estimates of additive variance ($\sigma_a^2 = \sigma_m^2 + \sigma_f^2$) were larger than nonadditive genetic variance (σ_{mf}^2) for seed yield and all its components in this experiment. These results are in agreement with our previous study of combining ability in a nine-parent diallel cross where GCA was found to be more important than SCA for yield and yield components in the F₁ analysis and the SCA variance was nonsignificant for all traits in the F₂ (NIENHUIS and SINGH 1986) and for yield in F₃ (HARTANA 1986). HAMBLIN and MORTON (1977) also reported positive and significant additive effects for seed yield and seed weight. But for number of pod and seed/pod both negative and positive additive effects were found, depending upon the crosses. Significant dominance effects for all traits in all crosses were negative. Similarly, for yield under insect-protected conditions (KORNEGAY and TEMPLE 1986), for yield and number of pod/plant (SINGH and SAINI 1983), and for yield, pod/plant and seed weight (VAID et al. 1985), larger GCA than SCA variances were found.

On the contrary, FOOLAD and BASSIRI (1983) found larger SCA than GCA variances for yield and all its components except seed weight. CHUNG and STEVENSON (1973) reported dominance to overdominance for number of pods and seed yield but partial dominance for 100-seed weight. ZIMMERMANN et al. (1985) observed variable additive and dominance gene action depending upon the crosses and cropping systems.

Narrow sense heritability values found for yield and its components were comparable to those reported by PANIAGUA and PINCHINAT (1976) from tropical environments of Costa Rica. In a cross between a large-seeded cultivated and small-seeded wild bean, MOTTO et al. (1978) found that narrow sense heritability estimates for various seed size parameters, including weight, ranged between 0.72 and 0.87. In a cross of cultivated dry bean, CONTI (1985) reported narrow sense heritability values of 0.53 for seed/pod, 0.09 for seed length, 0.48 for seed thickness, and 0.65 for seed width. Although some of the heritability estimates for seed yield based on parent-offspring regression methods were similar to ours, values in some crosses, cropping system, and/or methods of estimation were higher (ZIMMERMANN et al. 1984). Nonetheless, CHUNG and STEVENSON (1973) reported lower values for yield, pod number, and seed weight and COYNE (1968) found negative and extremely low narrow sense heritability for seed yield and all its components. Part of the discrepancies in results obtained by different researchers could well be due to differences in methods of estimation, crosses utilized, and growing environments.

COYNE (1968) reported positive and significant simple and partial correlation coefficient values between yield and all yield components including seed weight, similar to our findings reported here. However,

these results were in contrast with our previous results (NIENHUIS and SINGH 1985) in which the phenotypic and genotypic correlations between yield and seed weight were found to be negative. The difference between results of the two studies could be due largely to the inclusion of mostly indeterminate and small and medium-seeded parents belonging to the Middle American center of domestication and use of a relatively large number (200) of F_2 populations in the present study. In our previous studies many parents were ~~also~~ large-seeded and low-yielding belonging to the Andean South American gene pools.

PANIAGUA and PIRCHINAT (1976) and ZIMMERMANN et al. (1984) reported expected and realized gains from selection for seed yield, respectively. These authors generally found much higher values than the expected gains reported in this article. COYNE (1968) did not realize any gains from selection in the F_2 for yield or its components. SARAFI (1978) reported higher expected gains from selection for pod/plant and seed/pod but much lower values for 100-seed weight than those reported here. Once again, the large discrepancies in results could be due to differences in source of germplasm, selection intensities, heritabilities, crosses, generations, growing environments, etc., utilized by different investigators.

The objective of the CIAT bean improvement program is the development of germplasm which combines the high and stable yield desired by the growers with the different seed types preferred by the consumers. However, the effectiveness of selection for seed yield largely depends upon the magnitude of useful genetic variance present in the population for seed yield and its components, heritability, method

and intensity of selection employed, and degree of the interdependence or compensation among component traits.

Significant additive genetic variance for seed yield and its components (Table 1) supports the proposed use of parental performance for predicting high yielding cross combinations for hybridization (HAMBLIN and EVANS 1976). But it should be clear from the following discussions that parental performance alone would not be sufficient. Though intermating among bean types with extreme differences in growth habit and seed size is achieved easily, generating large genetic variation in segregating populations, most of the recombinants are of inferior performance to the parents themselves (EVANS 1970; SINGH and GUTIERREZ 1984). Growth habit, maturity, and seed size are traits controlled either by major genes (COYNE and MATTSON 1964; KRETCHMER et al. 1979; MASAYA et al. 1986; PADDA and MUNGER 1969; RAM and PRASAD 1985) or are of high heritability (MOTTO et al. 1978). Also, these are intrinsic characteristics and primary determinants of yielding ability of each bean cultivar. Consequently, the masking or epistatic effects of genes controlling these traits probably does not allow adequate random genetic recombination and expression of other yield-governing genes in crosses among parents with these contrasting characters. Thus, making almost impossible the selection of genotypes with determinate growth habit, large seed size, and/or early maturity which have the yielding ability of the indeterminate, small-seeded, late maturing parents in equatorial tropical environments. It is common to find a large proportion of the recombinant plants which either do not flower or have excessive abortion of flowers, developing ovules, and pods, and which remain green for a longer period (SINGH and GUTIERREZ 1984). Why

this occurs is not understood. The small-seeded bean from Middle America and large-seeded forms from South America probably differ in key developmental pathways which are disrupted upon intermating two such very different parents. Incompatibility has also been found in some crosses between small- and large-seeded types (GEPTS and BLISS 1985; GUTIERREZ and SINGH 1982; SINGH and GUTIERREZ 1984). The incompatibility was controlled by two complementary dominant genes, one affecting root and the other affecting shoot growth (SHII et al. 1981).

From Table 3 it is logical to think that selection for seed size should be more efficient in increasing both yield and seed weight than selection for yield per se. This increased effectiveness is because of the high heritability of seed weight (0.88) compared with yield (0.37) and the high positive association ($r=0.77$) between seed weight and yield (Table 2). These results differ from our previous reports of negative association of seed weight with yield (NIENHUIS and SINGH 1985). However, selection beyond the upper limits of a given seed size class (e.g., small $26 < \text{g}/100$; medium 26 to 40 $\text{g}/100$; and large $> 40 \text{ g}/100$ seeds) should be avoided because yield might decline with increasing seed size from small to medium and medium to large, especially in bush bean (SINGH 1987). The use of seed weight as an indirect selection criterion in early segregating generations should result in greater efficiency because it is easier to measure seed weight than it is to measure yield with precision when the number of progenies is large and seed is a limiting factor.

Because of positive phenotypic and genetic correlations of mainstem length and mainstem-internode length with seed size and yield (NIENHUIS and SINGH 1985), intensive selection for seed weight may result in

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changes in the plant growth habit toward a tall, viny plant type, which would be poorly adapted to sole cropping without artificial support.

Selection for morphological traits positively associated with yield and pod/plant did not increase yield in dry bush bean of growth habits I, II and III (NIENHUIS and SINGH 1985). Therefore, breeders should use yield and seed weight as selection criteria for yield improvement of small-seeded dry bean for sole crops. All F_2 , F_3 and F_4 populations should be yield tested in replicated trials at commercial cropping densities within target environments. High yielding populations could then be identified for each maturity and growth habit group. Our preliminary data demonstrates the effectiveness of both the early generation yield tests (EGT) of bulk populations and mass selection combined with EGT for yield improvement in dry bean crosses (SINGH 1988). Within acceptable commercial limits of each seed size class, mass selection based on mean performance of crosses for seed weight should be practiced cautiously in early generations, because of its high heritability and expected high positive correlated gain for yield, followed by single plant selection for both yield and seed weight from F_5 on.

Selection for seed size was found to be superior to single-seed-descent and to selection for yield per se for developing high yielding lines of chickpea, Cicer arietinum (BISEN et al. 1985). Mass selection combined with early generation yield test as proposed by SINGH (1988) also should facilitate stabilization and selection of other desirable agronomic traits including seed color, shape, and brilliance.

The data presented here would indicate that selection for number of pod and seed/pod should be avoided because of their negative effect on

yield and/or seed size (Table 3). However, data from actual field experiments utilizing different criteria and methods of selection would be required to test the validity of the quantitative genetic information reported here.

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Table 1. Mean square, estimates of variance components, and narrow sense heritability (h^2) for yield and its components in dry bush bean from a design II mating system, sown at two locations in Colombia in 1983.

Source	d.f.	Yield	Pod/m ²	Seed/pod	Seed weight
		-- g/m ² --	----- No. -----		-- g/100 --
Location (L)	1	77464.1	87378.6	6.56	36.43
Set (S)	7	76349.2	33865.1	8.54	194.83
L x S	7	42157.7	25593.5	1.15	68.69
Replication/S/L	16	8474.9	5733.7	0.58	11.75
Male/S	32	3521.8**	2441.1**	2.11**	54.56**
Female/S	32	2515.9	2802.5	1.82**	69.02**
Male x Female/S	128	1104.7	1033.3	0.37	5.80
Male/S x L	32	1543.2*	1123.5	0.50**	7.88*
Female/S x L	32	2105.7**	1974.3**	0.38	8.35**
Male x Female/S x L	128	888.9	781.8	0.26*	4.54**
Pooled error	384	866.6	727.4	0.20	3.01

Table 1 (continued):

	Yield	Pod/m ²	Seed/pod	Seed weight
	Variance components			
σ_m^2	88.1 ± 47.5	28.8 ± 33.6	.07 ± 0.03	2.27 ± 0.67
σ_f^2	9.7 ± 40.7	53.3 ± 42.3	.08 ± 0.02	2.97 ± 0.84
σ_{mf}^2	54.0 ± 43.9	62.9 ± 72.3	.06 ± 0.01	0.32 ± 0.22
σ_{m1}^2	65.4 ± 39.0	34.2 ± 28.9	.02 ± 0.01	0.33 ± 0.19
σ_{f1}^2	121.7 ± 52.5	119.3 ± 48.9	.01 ± 0.01	0.38 ± 0.21
σ_{mf1}^2	11.2 ± 63.3	27.2 ± 55.1	.03 ± 0.02	0.76 ± 0.30
	Narrow sense heritability			
σ_a^2	97.8	82.2	0.14	5.25
σ_p^2	260.2	213.2	0.24	5.92
h^2	0.37 ± 0.24	0.39 ± 0.25	0.59 ± 0.14	0.88 ± 0.18

$\sigma_m^2 = \sigma_f^2 = 1/2 \sigma_a^2$, h^2 was calculated on the basis of entry means. *, ** significant at $P = 0.05$ and $P = 0.01$, respectively.

Table 2. Phenotypic (above diagonal) and genotypic (below diagonal) correlations among yield and its components in dry bean.

	Yield	Pod/m ²	Seed/pod	Seed weight
Yield (g/m ²)		0.33**	0.22**	0.47**
Pod/m ²	0.46		0.41**	0.18*
Seed/pod	0.20	0.81		0.28**
Seed weight (g/100)	0.77	0.22	0.32	

*, ** Phenotypic correlations significant at $P = 0.05$ and $P = 0.01$, respectively.

Table 3. Expected direct (on diagonal) and correlated (off diagonal) response¹ to selection for yield and its components in dry bean based on mean performance of F₂ population over two locations.

Selection criteria	Response to Selection			
	Yield	Pod/m ²	Seed/pod	Seed weight
Yield (g/m ²)	5.77	-2.28	1.57	6.46
Pod/m ²	-2.67	5.06	-6.54	-1.85
Seed/pod	1.41	-5.04	10.01	-3.31
Seed weight (g/100)	6.84	1.67	-3.89	12.83
Trait Mean	147.10	155.70	4.05	23.50

¹ Percent of the mean of F₂ populations at 20% selection intensity.

$$\text{Direct response} = k \sigma_{a_1}^2 / \sigma_{p_1}, \quad \text{correlated response} = k \text{Cov}_{a_{12}} h_1 \sigma_{a_2}, \quad k = 1.4$$