

Heritability and Correlation of Biomass, Growth Rates, Harvest Index, and Phenology to the Yield of Common Beans

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Abstract. One-hundred-twelve common bean (*Phaseolus vulgaris* L.) lines of diverse origin were grown in three environments in 1986 and two environments in 1987. The purpose was to estimate broad-sense heritabilities of nine yield-related traits and the phenotypic, genetic, and environmental correlations among them. The traits and their heritabilities were seed yield (0.90), biomass (0.93), harvest index (0.92), days to maturity (0.96), days to flower (0.98), days of pod fill (0.94), biomass growth rate (biomass/days to maturity) (0.87), seed growth rate (seed yield/days of pod fill) (0.87), and economic growth rate (seed yield/days to maturity) (0.86). These high heritabilities were attributed to the broad genetic diversity and the comparatively small variances associated with the genotype × environment interactions. Genetic correlations of yield were: with biomass, 0.86; harvest index, 0.42; days to maturity, 0.40; days to flower, 0.33; days of pod fill, 0.24; biomass growth rate, 0.92; seed growth rate, 0.84; and the economic growth rate, 0.85. The concomitant phenotypic correlations were mostly equal to the genetic correlations for biomass and the three growth rates, but lower for the phenological traits (days to maturity, flower, and pod fill). Harvest index had the lowest correlations with yield. Correlations were also reported for the other 28 pairwise combinations among these nine traits. Indirect selection was explored with yield as the primary trait and the other eight as secondary traits. Estimates of relative selection efficiency (ρ) suggested that indirect selection was not a viable option for increasing common bean yields or identifying superior parents.

Yield improvement is a major breeding objective of most crop improvement programs (Hallauer, 1981; Wilson, 1981). In common beans, yield is improved by direct selection and by indirect selection for plant ideotype traits affecting yield. Adams (1982) has defined a common bean ideotype based mostly on morphological traits, while Wallace and Masaya (1988) have favored a combined phenological and physiological ideotype. In small grains, Rasmussen (1987) has incorporated both morphological and physiological traits into the ideotype concept. The traits recommended for the physiological ideotype include biomass, days to flower, days of pod fill, days to maturity, harvest index, seed growth rate, biomass growth rate, economic growth rate, and yield (Rasmussen, 1987; Wallace and Masaya, 1988). The collective term for these traits is “yield system” traits (Wallace and Masaya, 1988). Numerous studies have estimated the heritabilities and correlations of the morphological traits included in the bean ideotype, but few have focused on the phenological and physiological traits.

Broad-sense heritabilities of yield in common beans is reported to range from 1% to 82% (Coyne, 1968; Chung and Goulden, 1971; Chung and Stevenson, 1973; Davis and Evans, 1977; Zimmerman, 1983; Zimmerman et al., 1984). Coyne (1968) computed broad-sense heritabilities of 9% to 11% with five genetically diverse parents. Zimmerman (1983) reported broad-sense heritabilities of 23% and 21% for yield in monocrop and for beans intercropped with maize, respectively. She also esti-

ated the heritability of harvest index at 60% and 39% for monocropped and intercropped environments, respectively. Chung and Gorden (1971) reported the highest broad-sense heritability for yield at 46% to 82%. This was unusually high because the six parents were a genetically similar set of navy beans. Because Chung and Goulden (1971) used a single environment, the heritability estimates were biased upward due to genotype × environment interaction. Later, Chung and Stevenson (1973) removed the bias of a single environment and dominance gene action and estimated the narrow-sense heritability of yield at 1% to 5% for a similar set of navy beans. Chung and Stevenson (1973) also reported a 9% to 27% narrow-sense heritability for days to maturity. Davis and Evans (1977) estimated the broad-sense heritability of yield and days to maturity at 34% and 96%, respectively.

In common beans, phenotypic (r_p) and genetic (r_g) correlations of -0.53 and -0.88 were reported for yield and days to maturity, respectively (Davis and Evans, 1977). Zimmerman (1983) estimated the phenotypic and genetic correlations between yield and harvest index as -0.11 and -0.20, respectively, for intercropped systems. Phenotypic correlations for yield and days to maturity ($r_p = 0.29$), yield and days to flower ($r_p = 0.42$), and days to maturity and flower ($r_p = 0.83$) were reported by Vaid et al. (1986). They reported similar genetic correlations among these traits as 0.33, 0.48, and 0.86, respectively.

The first objective of this investigation was to estimate the broad-sense heritability of yield, biomass, days to maturity, days to flower, days of pod fill, harvest index, seed growth rate, biomass growth rate, and economic growth rate in common beans. The second objective was to determine the phenotypic, genetic, and environmental correlations among these nine yield system traits, and estimate the efficiency of these traits as indirect criteria for yield improvement.

Materials and Methods

A broad genetic base was sampled to allow inference relative to the selection of parents for a breeding program focused on

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increasing yield. Inbred common bean lines (112 genotypes) of diverse origin and adaptation were grown on the research farms in East Ithaca, Freeville, and Mt. Pleasant, N.Y. in 1986, and East Ithaca and Freeville in 1987. Respectively, the soils found in these environments included: 1) Arkport fine sandy loam (coarse-loamy, mixed, mesic Psammentic Hapludalfs); 2) Howard gravelly loam (loamy skeletal, mixed mesic Glassoboric Hapludalfs); and 3) Mordin Channery silt loam (fine-loamy, mixed, mesic Typic Fragiochrepts). These locations were chosen at random from among nine possible research sites. The entries originated in either North (55), Meso (18), or South (20) America, with the remainder (19) from Africa and Europe and included .18 black, 16 brown/tan, six dark red kidney, 15 light red kidney, 12 pinto/cranberry, three red mexican, 13 small white, four snap bean, and 25 miscellaneous types. These entries were drawn randomly from a germplasm collection of 350 to 400 accessions. The field methods were standard for this crop (Scully, 1989).

The experiment was a completely randomized design (Federer, 1955) with three replications in each of the five environments. The plots were 1.7-m rows planted with 25 seeds, and spaced at ± 1.0 m to avoid inter-genotypic competition. Plots were arranged so that nearest neighbors were the same only by chance, removing any systematic error due to adjacent plots. The perimeter of each field included buffer rows. At maturity, biomass and seed were harvested and air-dried to $\approx 12\%$ moisture. Genotypes were assumed to be fully inbred and unrelated. Seed was produced in the greenhouse for two generations before each planting season, and monitored for off-types, outcrosses, and segregation of morphological traits. 'Only phenotypically uniform lines were used in this research.

Nine traits were measured on each plot. They included: 1) days to flower (DTF), determined as the days from 50% emergence to 50% anthesis; 2) days of pod fill (DPF), determined from 50% anthesis to 90% physiological pod maturity; 3) days to maturity (DTM) from 50% emergence to 90% pod maturity; 4) biomass measured as the defoliated aerial portion of the plant; and 5) seed yield. Additional traits estimated from these data included: 6) harvest index (HI), determined as (yield/biomass) $\times 100$; 7) seed growth rate (SGR), measured as yield/days of pod fill; 8) biomass growth rate (BGR), measured as biomass/days to maturity; and 9) an economic growth rate (EGR), determined as yield/days to maturity. Phenological data were taken at each site every 3d day.

Data were collected on a per-square-meter basis, and analyzed using the SAS ANOVA, GLM, and MANOVA procedures (SAS, 1985). Phenotypic variances (σ_p^2) and genetic variances (σ_g^2) were estimated from mean squares in the analysis of variance after being equated to their expected variance components (Wricke and Weber, 1986). A random effects model was assumed for environments and genotypes (Steel and Torrie, 1980). The standard errors of these estimated variances were computed in accordance with Hallauer and Miranda (1981).

The broad-sense heritability (H^2) was estimated as: $H^2 = \sigma_g^2 / \sigma_p^2$ (Doolittle, 1987). The standard error of this heritability (SE H^2) was approximated with the equation of Hallauer and Miranda (1981), as: $SE H^2 = \{SE(\sigma_g^2)\} / \sigma_p^2$.

The estimates of the correlation coefficients for any two traits i and j were defined as: $r_z = \sigma_{zij} / \{\sigma_{zi}^2 \times \sigma_{zj}^2\}^{1/2}$ with: z replaced by p for phenotypic correlation; g for genetic correlation; and e for environmental correlation (Searle, 1961; Turner and Young, 1969). The components of covariance (σ_{zij}) between any two traits i and j were partitioned from the expected mean cross products in the analysis of covariance.

The efficiency of indirect selection (p) of parents was computed in accordance with Searle (1965) as: $p = r_{ij} (H_i^2 / H_j^2)^{1/2}$ where: H_i^2 is the heritability of the primary trait (yield); H_j^2 is the heritability of the indirect or alternate trait; and r_{ij} is the genetic correlation between traits i and j .

Results and Discussion

Heritabilities. Broad-sense heritabilities (H^2) of the nine yield system traits ranged from 0.86 to 0.98, and all were significantly larger than 0 (Table 1). The estimated phenotypic and genetic variances averaged six to eight times larger than their standard errors, while the heritability estimates were five to eight times larger. The phenological traits (days to flower, maturity, and pod fill) had the highest heritabilities, with values > 0.93 . A similar heritability value ($H^2 = 0.96$) was reported for days to maturity by Davis and Evans (1977). The biomass traits (biomass, harvest index, and yield) had heritabilities of 0.90 to 0.93 (Table 1). The heritabilities of harvest index (0.92) and yield (0.90) were higher than those reported by Zimmerman et al. (1984) for harvest index ($H^2 = 0.60$), or the highest reported heritability for yield ($H^2 = 0.82$) (Chung and Goulden, 1971). The heritability estimates of the growth rates (biomass, economic, and seed) were lower, ranging from 0.86 to 0.87, and had higher standard errors (Table 1).

The extremely high heritabilities for these traits were attributed to the large genetic diversity among the 112 genotypes. Significance was detected for all sources of variation for all traits at a minimum of $P_\alpha \leq 0.001$ (Table 2). The F values for the mean square of genotypes and environments were at least 20.0, with some greater than 100.0, while F values for the mean squares of genotype \times environment (G \times E) interactions ranged from 2.0 to 6.0. These low G \times E interactions plus large genetic variation resulted in high heritability estimates for each trait. The lower mean squares for the G \times E interaction components suggested that genotypes responded similarly to the different environments, but also may have been influenced by the large number of degrees of freedom (444) associated with this source of variation.

Correlations. The phenotypic correlation (r_p) among traits is influenced by genotype and environment. Genetic correlation (r_g) is usually attributed to pleiotropy and linkage (Falconer, 1981; Turner and Young, 1969). Environmental correlation (r_e) reflects a similarity or dissimilarity in the response of two traits to a common environment. The environmental correlations do not carry forward to future generations, unless certain permanent environmental effects, such as soil type or photoperiod, affect the expression of these traits.

If the phenotypic correlation (r_p) and the genetic correlation (r_g) had the same sign, the environmental correlation (r_e) was expected to be negative, provided $r_p / r_g < (H_i^2 \times H_j^2)^{1/2}$ [or $r_p > r_g (H_i^2 * H_j^2)^{1/2}$], where H_i^2 and H_j^2 are the heritabilities of any two traits i and j (Searle, 1961; Turner and Young, 1969). In most cases, a negative r_e resulted in a higher genetic than phenotypic correlation among traits (Table 3). When $r_p < r_g$, and r_e was negative, it suggested that the same or linked genes that condition a trait responded differently to the environments. This result occurred when yield, biomass, or the biomass growth rate were correlated to the days to flower, maturity, or pod fill (phenological traits). For example, biomass and days to maturity had a genetic correlation of 0.76, but were phenotypically correlated at 0.73, because of an opposite response of these two traits to the environment (Table 3). Cool weather delayed ontogeny and enlarged the expression of these phenological traits, but con-

Table 1. Estimates of phenotypic variance (σ_p^2) genetic variance (σ_g^2) and broad-sense heritability (H^2) for nine traits measured on 112 inbred common bean genotypes grown in five environments.

Trait	Phenotypic variance ($\sigma_p^2 \pm SE$)		Genetic variance ($\sigma_g^2 \pm SE$)		Broad sense heritability ($H^2 \pm SE$)
Yield	7,386.84 ±	982.73	6,659.99 ±	983.94	0.90 ± 0.16
Biomass	24,873.00 ±	3,309.05	23,232.47 ±	3,310.88	0.93 ± 0.14
Harvest index	50.36 ±	6.70	46.49 ±	6.70	0.92 ± 0.14
Days to maturity	183.35 ±	24.39	176.76 ±	24.40	0.96 ± 0.14
Days to flower	46.19 ±	6.14	45.34 ±	6.15	0.98 ± 0.14
Days of pod fill	78.72 ±	10.47	73.61 ±	10.48	0.94 ± 0.14
Seed growth rate	1.83 ±	0.24	1.59 ±	0.24	0.87 ± 0.15
Biomass growth rate	1.19 ±	0.16	1.03 ±	0.16	0.87 ± 0.16
Economic growth rate	0.57 ±	0.08	0.48 ±	0.08	0.86 ± 0.17

Table 2. Analysis of variance for nine traits measured on 112 inbred common bean genotypes grown in five environments.

Source	df	Mean squares ^z								
		Yield ($\times 10^4$)	Biomass ($\times 10^4$)	Harvest index	Days to maturity	Days to flower	Days of pod fill	Seed growth rate	Biomass growth rate	Economic growth rate
Genotypes (G)	111	11.08	37.31	755.45	2750.19	692.86	1180.81	27.50	17.86	8.56
Environments (E)	4	37.35	25.29	7075.60	6427.06	397.52	5256.33	233.34	350.72	68.86
G × E	444	10.91	24.61	58.07	98.81	12.79	76.62	3.53	2.40	1.24
Error	1120	0.458	1.216	14.18	17.57	2.42	17.96	1.17	1.09	0.44

^zExpected mean squares: Error = σ_e^2 ; (G) × (E) = $\sigma_e^2 + r\sigma_{g \times E}^2$; environments = $\sigma_e^2 + r\sigma_{g \times E}^2 + rg\sigma_{E}^2$; genotypes = $\sigma_e^2 + r\sigma_{g \times E}^2 + rE\sigma_g^2$; where: r = reps = 3; g = genotypes = 112; and E = environments = 5. All mean squares were significant at a minimum of $P_\alpha \leq 0.01$.

currently slowed the rate at which biomass accumulated and grew. Warm weather had the reverse effect. These opposite responses to environment resulted in negative r_E values.

In cases where $r_p \neq r_g$, a positive r_E was expected because $r_p/r_g > (H^2 \times H_p^2)^{1/2}$, unless the heritability of both traits (H_p^2 and H_g^2) approached 1.0, then r_E approaches 0. Positive environmental correlations suggested that the same or linked genes conditioning two traits responded similarly to the environment. As an example, the phenotypic correlations of biomass to the growth rates were greater than or equal to their respective genetic correlations, and all had positive environmental correlations (Table 3). Many of the other traits followed this expectation. Under circumstances of low heritability and poor correlation, r_p and r_g could have opposite signs, but this did not occur.

Seed yield is the trait of primary interest and had the highest genetic, phenotypic, and environmental correlations with biomass and the three growth rates (Table 3). All these correlations were positive, >0.75, and the phenotypic and genetic correlations were nearly all equal. These correlations suggested that the genes conditioning yield, biomass, and the growth rates or were closely linked in coupling phase. These traits responded similarly to the environments.

The phenotypic and genetic correlations between the phenological traits and yield were lower than those between the growth rates (Table 3). The genotypic correlations ranged from 0.30 to 0.42, with lower phenotypic correlations. As a result, the environmental correlations were negative, as expected. The explanation of this result is similar to that developed previously for biomass and the phenological traits. Harvest index had the lowest correlation with yield at the phenotypic and genetic level.

The correlation between yield and harvest index also failed to follow theoretical expectations (Table 3). Because $r_p (= 0.27) > r_g (= 0.24)$, a positive r_E was expected; or with $r_E = 0$, r_p should have been less than or equal to r_g . This did not occur. The correlation between harvest index and the biomass growth rate also deviated from expectations in that r_E should have been positive. For all the 36 paired correlations, the relationship of yield to biomass and to the growth rates were among the highest.

The efficiency of indirectly selecting parents was evaluated for yield, the primary trait of interest, with each of the eight other traits of secondary interest. Evaluation was based on the theoretical criterion that relative selection efficiency (p) must be ≥ 1.0 (Searle, 1965). For these data, p ranged from a low of 0.24 for the indirect selection of yield via harvest index to a high of 0.90 for yield via the biomass growth rate. Indirect selection of parents for high yield was not considered appropriate in these environments. The results of Coyne (1968), Chung and Goulden (1971), Davis and Evans (1977), and Zimmerman (1983) were also subjected to the theoretical criterion of Searle (1965); p > 1.0 occurred in only one case. The result of Davis and Evans (1977) indicated that the yield of common beans in southern England could be increased indirectly by the selection for days to maturity.

Based on the large heritabilities estimated for all nine traits in this investigation, direct empirical selection for yield should result in reasonable genetic gain from crosses among superior parents in a breeding program. However, if superior individuals are intercrossed, the heritability estimates would be lower in the resulting progeny because of decreased genetic diversity. Direct selection use could then be less effective, and indirect selection

Table 3. Phenotypic (r_{Pij}), genetic (r_{Eij}), and environmental (r_{Eij}) correlations for nine traits measured on 112 inbred common bean genotypes.

Trait i with trait j	r_{Pij}	r_{Eij}	r_{Eij}
Yield (i)			
Biomass	0.86	0.86	0.75
Days to maturity	0.39	0.42	-0.64
Days to flower	0.38	0.40	-0.18
Days of pod fill	0.30	0.33	-0.66
Harvest index	0.27	0.24	0
Seed growth rate	0.84	0.84	0.94
Biomass growth rate	0.92	0.92	0.82
Economic growth rate	0.86	0.85	0.98
Biomass (i)			
Days to maturity	0.73	0.76	-0.39
Days to flower	0.64	0.66	-0.63
Days of pod fill	0.62	0.66	-0.26
Harvest index	-0.24	-0.28	-0.66
Seed growth rate	0.52	0.51	0.64
Biomass growth rate	0.78	0.78	0.98
Economic growth rate	0.53	0.51	0.75
Days to maturity (i)			
Days to flower	0.82	0.83	0.47
Days of pod fill	0.90	0.90	0.97
Harvest index	-0.66	-0.68	-0.09
Seed growth rate	-0.09	-0.07	-0.80
Biomass growth rate	0.30	0.33	-0.56
Economic growth rate	-0.12	-0.11	-0.77
Days to flower (i)			
Days of pod fill	0.48	0.50	0.27
Harvest index	-0.53	-0.55	-0.79
Seed growth rate	0.14	0.16	-0.26
Biomass growth rate	0.31	0.34	-0.65
Economic growth rate	-0.01	0	-0.32
Days of pod fill (i)			
Harvest index	-0.61	-0.67	-0.32
Seed growth rate	-0.24	-0.23	-0.82
Biomass growth rate	0.20	0.25	-0.47
Economic growth rate	-0.18	-0.17	-0.76
Harvest index (i)			
Seed growth rate	0.59	0.59	0.08
Biomass growth rate	0.14	0.11	-0.55
Economic growth rate	0.63	0.63	-0.04
Seed growth rate (i)			
Biomass growth rate	0.82	0.81	0.76
Economic growth rate	0.97	0.97	0.98
Biomass growth rate (i)			
Economic growth rate	0.85	0.84	0.85

acceptable. Because yield has a positive genetic correlation with all the other traits, selection for yield should result in a positive correlated response. However, these correlations are also expected to change in a new population developed from superior parents. This investigation suggests that indirect selection would be less efficient than direct selection to increase yield and suggested consideration of a selection index.

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