

Heritability of Efficiency in Phosphorus Utilization in Beans (*Phaseolus vulgaris* L.) Grown under Phosphorus Stress¹

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Abstract. The heritability of efficiency in phosphorus utilization under deficiency stress was investigated using 6 bean families derived from crosses between selected efficient, moderately inefficient, and inefficient lines. Total plant dry weight (DW) was used as an index of efficiency. Epistasis, notably additive by additive and dominance by dominance gene effects, made major contributions to the efficiency in P utilization. Additive and dominance gene effects also made significant contributions. Estimates of broad sense heritability for total plant DW showed that efficiency in P utilization was a highly heritable trait. Narrow sense heritability estimates for total plant DW were high in all families studied.

The discovery of genetic variability in mineral nutrition within crop species has led to a search for genotypes of economic crops able to grow well in problem soils (2, 4, 6-10, 12, 14-18). Numerous soil and environmental factors can be responsible for the expression of quantitative differences among cultivars with respect to the absorption, translocation, and/or utilization of nutrients and tolerance to high mineral concentrations (5).

Quantitative differences in the efficiency of utilization of mineral elements, reflected among cultivars in wide variation in dry weight production, have been reported by many workers (4, 8, 9, 17, 18). Whiteaker et al. (17) isolated line of *P. vulgaris* showing quantitative differences in dry weight production when grown under P deficiency stress, and concluded that the genetic control of the differences was complex. The main objectives of our study were to estimate the components of genetic variance and determine the heritability of efficiency in P utilization in beans.

Materials and Methods

The 6 bean lines used in this study were isolated in a previous investigation on the inheritance and physiology of differential growth response under phosphorus stress. The bean lines, selected by Whiteaker et al. as representing the extremes in efficiency for P utilization, were classified as efficient (E), moderately inefficient (MI), and inefficient (I) (17).

All of the experiments reported here were conducted in a growth room at about 28°C and 151 klx (CW/SHO fluorescent tubes) for a 15-hr period in each 24-hr cycle. Each plant was cultured in a paper container lined with a polyethylene sheet and containing 1.6 liters of modified Hoagland's solution. The P stress level in all experiments was 3 mg P per plant. Details of the experimental procedure and of P analysis can be found in Whiteaker et al. (17).

Genetic studies were made on 6 families. A family was composed of 6 different progenies as follows: the 2 parents (P₁ and P₂), their F₁ hybrid, the backcrosses of the F₁ hybrids to each parent (BCP₁ and BCP₂, respectively), and an F₂ progeny derived by self-pollination of the F₁. The 4 parents (2E and 2I) provided 6 families including 1 represented by 2E parents, 1 represented by 2I parents, and 4 represented by the 4 possible combinations of E × I parents. Each parent population was homogeneous, having been derived originally from a single homozygous plant by self-pollination.

Seeds were germinated in perlite and, after 1 week of germination, seedlings were transferred to modified Hoagland's nutrient solution that provided the stress level of P. After 3 weeks in the nutrient solution, 10 plants of each backcross and 15 of the F₂ generation in each experiment were randomly selected, fresh weights were obtained, and the plants were then allowed to produce self-pollinated seed. The remaining plants were divided into tops and roots, and the fresh and dry weight determined. Self-pollinated progeny derived from the randomly selected plants, together with the parental lines, were grown in 6 additional experiments for the purpose of estimating heritability of P efficiency. Total plant dry weight production (DW) was used as an index of efficiency in all the experiments.

Statistical and genetic analyses were carried out on parental, reciprocal F₁, backcross, and F₂ populations of each family derived from the 6 lines. Each of the population means is expressed in terms of the F₂ mean (m); additive (a); dominance (d); additive × additive (aa); additive × dominance (ad); and dominance × dominance (dd) gene effects. These parameters were estimated by the relationships described by Gamble (5). These estimates indicate the type or types of interactions and the importance of each effect. The contribution to variation by the various gene effects in the families studied is indicated by the relative magnitude of the parameters a, d, aa, ad, and dd, respectively, compared to parameter m.

Broad sense heritability for total plant dry weight was estimated from phenotypic and genetic variances according to the methods described by Allard (1). Narrow sense heritability was estimated by regressing the mean total dry weight of progenies of selected plants on the mean total dry weight of their parents (3). Because only the fresh weights of the selected plants were available, the dry weight of parental plants had to be estimated by other means. The following formulation was used for this purpose.

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Consider the 2 regression models:

- 1) $W_j = a + bX_j + \delta_j$, and
- 2) $Y_i = c + dX_i + \epsilon_i$

where W is the fresh weight of individuals from the parental stock, X is the dry weight of individuals from the parental stock, and Y is the dry weight of individual progeny. The subscript j indexes parental individuals from whom progeny were not obtained and subscript i indexes parental individuals from whom progeny were obtained as well as resulting progeny. The terms δ_j and ϵ_i represent random error. The first model relates fresh and dry weights of parental stock, whereas the second relates dry weight of progeny and dry weight of parent. Consider m joint observations on X_j, W_j and n joint observations on Y_i, W_i . The first set of data is used to determine the relationship between parental fresh and dry weight. Using this relationship, a parental dry weight, \hat{X}_i , can be estimated for each w_i in the second set of data. From the n joint values on Y_i, \hat{X}_i , an estimate for d , the heritability, can be obtained.

The estimator for b is the ordinary least squares estimator,

$$\hat{b} = \frac{\sum_{j=1}^m (X_j - \bar{X}_m) W_j}{\sum_{j=1}^m (X_j - \bar{X}_m)^2},$$

and for $i = 1, \dots, n$, the estimated \hat{X}_i is

$$\hat{X}_i = \bar{X}_m + (W_i - \bar{W}_m) / \hat{b}$$

where

$$\bar{W}_m = \sum_{j=1}^m W_j / m \text{ and } \bar{X}_m = \sum_{j=1}^m X_j / m.$$

Using the \hat{X}_i in equation (2), an estimator for d is given by

$$\hat{d}_o = \frac{\sum_{i=1}^n (\hat{X}_i - \bar{X}_n) Y_i}{\sum_{i=1}^n (\hat{X}_i - \bar{X}_n)^2}$$

where $\bar{X}_n = \sum_{i=1}^n \hat{X}_i / n$. Substitution for \hat{X}_i leads to

$$\hat{d}_o = \hat{b} \frac{\sum_{i=1}^n (W_i - \bar{W}_n) Y_i}{\sum_{i=1}^n (W_i - \bar{W}_n)^2}$$

where $\bar{W}_n = \sum_{i=1}^n W_i / n$.

This estimator for d is biased as the following calculations show. Rewrite \hat{d}_o ,

$$\begin{aligned} \hat{d}_o &= \hat{b} \frac{\sum_{i=1}^n (c + dX_i + \epsilon_i)(W_i - \bar{W}_n)}{\sum_{i=1}^n (W_i - \bar{W}_n)^2} \\ &= \hat{b} \left[\frac{d \sum_{i=1}^n X_i (W_i - \bar{W}_n) + \sum_{i=1}^n \epsilon_i (W_i - \bar{W}_n)}{\sum_{i=1}^n (W_i - \bar{W}_n)^2} \right] \\ &= \hat{b} \left[\frac{(d/b) \sum_{i=1}^n (W_i - a - \delta_i)(W_i - \bar{W}_n) + \sum_{i=1}^n \epsilon_i (W_i - \bar{W}_n)}{\sum_{i=1}^n (W_i - \bar{W}_n)^2} \right]. \end{aligned}$$

Then,

$$E(\hat{d}_o | \delta) = d(\hat{b}/b) \left[1 - \left(\frac{\sum_{i=1}^n \delta_i (W_i - \bar{W}_n)}{\sum_{i=1}^n (W_i - \bar{W}_n)^2} \right) \right].$$

Table 1. Variation in total plant mean dry weight and phosphorus deficiency symptoms between 6 bean lines when grown at low P (3 mg per plant) and adequate P (31 mg per plant).

Line	Low P			Adequate P	
	Dry wt (g)	Deficiency symptom rating	Ratio of dry wts shoot/root	Dry wt (g)	Ratio of dry wts shoot/root
3	1.27 a ^z	5 ^y	1.30	1.66 a	1.85
9	1.51 ab	3	2.31	3.75 b	4.22
6	1.59 b	3	2.03	4.19 b	4.54
12	1.60 bc	1	2.44	4.27 b	3.76
1	1.78 c	3	2.25	3.97 b	5.22
11	2.52 d	1	1.43	5.71 c	2.85

^zMean separation within columns by Duncan's multiple range test at 5% level.

^y0 = no deficiency; 5 = very stunted growth, severe necrosis.

Arguing by analogy to Seber (11),

$$E d_o \approx d \left[1 - n \sigma_\delta^2 / (b^2 \sum_{i=1}^n (X_i - \bar{X}_n)^2 + n \sigma_\delta^2) \right]$$

where $\sigma_\delta^2 = \text{VAR} \delta_j$, X_i is the true (but unobservable) parental dry weight, and $\bar{X}_n = \sum X_i / n$. The given expression is valid for large n . Again by analogy to Seber, a reasonable estimator for d which corrects for the bias is

$$\hat{d}_1 = \hat{d}_o \left[1 + n \hat{\sigma}_\delta^2 / \sum_{i=1}^n (W_i - \bar{W}_n)^2 \right]$$

where $\hat{\sigma}_\delta^2$ is the standard regression estimator of σ_δ^2 obtained from the m observations on X_j, W_j .

As this bias correction technique relies on asymptotic results, it was necessary to determine the appropriateness of the technique for the sample sizes considered here. A brief simulation study (not further reported here) demonstrated that the procedure was acceptable.

Results

The relative differences between lines at stress and adequate P are rather similar with line 11 the most efficient at both levels (Table 1). The 6 components of genetic effects that can be estimated from the progeny of 6 matings based on total plant DW are listed in Table 2. The additive gene effect was significant in only 4 families. Dominance, additive \times additive, and dominance \times dominance effects were highly significant in many of the families. All gene effects, except dominance, were important in the E \times E family. Only additive and dominance \times dominance effects contributed to variation in the E \times I family.

Total genetic variance, estimated as the difference between the phenotypic variance and the environmental variance, is greater than the environmental variance (Table 3). Except for one family, broad sense heritability for DW is greater than 70%. The estimates of additive and dominance genetic variance for F_2 populations are variable and are either positive or negative. These estimates were made on the assumption of no epistasis in the families studied. In all cases, narrow sense heritability was extremely high (Table 4).

Discussion

Based on an examination of the frequency distributions, the mean dry weight and the P-efficiency ratios (PER) of tops of 15

Table 2. Mean estimates of the 6 gene effects (upper figures) and their SE (lower figures) based on total plant dry weight for the 6 families.

Family ^z	m ^y	a	d	aa	ad	dd
11(E) & 1(MI)	1.825** ^y 0.061	0.115 0.082	1.305** 0.015	1.166** 0.022	-0.031 0.064	-0.324 0.234
11(E) & 3(I)	1.897** 0.040	0.374** 0.068	-0.048 0.125	-0.030 0.151	-0.040 0.053	0.958** 0.180
11(E) & 6(MI)	1.750** 0.066	0.200* 0.080	-1.243* 0.188	-1.000** 0.226	-0.004 0.067	2.870** 0.240
11(E) & 9(MI)	1.956** 0.110	0.005 0.091	1.208* 0.150	1.158** 0.181	-0.285* 0.071	-1.017** 0.228
11(E) & 12 (E)	2.003** 0.050	0.279** 0.062	0.089 0.143	0.306* 0.172	0.113* 0.049	0.533* 0.187
9(MI) & 6(MI)	1.996** 0.042	-0.108* 0.086	0.288* 0.140	0.284 0.170	-0.078 0.066	-0.018 0.213

^zE = efficient, MI = moderately inefficient, I = inefficient.

^yGene effects: m = mean; a = additive; d = dominance; aa, ad, and dd are additive x additive, additive x dominance, and dominance x dominance epistasis, respectively.

^xSignificant at 5% (*) and 1% (**) probability levels by use of t-test.

families derived from the same bean lines used in the present study, Whiteaker et al. (17) concluded that the inheritance of efficiency in P utilization was genetically complex. Using total plant dry weight as an index of efficiency in P utilization, the data in our investigations indicated that epistatic gene effects make major contributions to efficiency in P utilization. Additive and dominance effects also were significant. Other investigators also have reported that epistasis is important in nutrient utilization in tomatoes (8, 9).

Broad sense heritability was greater than 70 for total plant DW. Both uncorrected (\hat{d}_0) and corrected (\hat{d}_1) estimates of narrow sense heritability were relatively high in all families. As indicated

previously in this paper, the DW of plants selected for heritability studies was estimated from the fresh weight of the selected plants using the regression coefficient (b) of the fresh weight of unselected plants on their dry weight. Although the correlation between fresh and dry weight was high, the error variance associated with the regression is likely to be sizable because of the magnitude of the difference between total plant fresh weight and total plant dry weight. For a given value of this variance, the uncorrected coefficients must be adjusted to account for the error variance. The error variance is minimized if the correlation between fresh weight and dry weight is as high as possible. Consistently high correlations might be difficult to obtain in the type of investigation reported

Table 3. Estimated total plant DW variances of segregating populations together with estimates of additive and dominance genetic variance for F₂ populations.

Family ^z		Estimated variances					Broad sense heritability (%)
		Phenotypic	Environmental	Genetic	Additive	Dominance	
11(E) & 1(MI)	BCP ₁	0.089	0.029	0.060			86.0
	BCP ₂	0.184	0.029	0.115			
	F ₂	0.206	0.029	0.177	0.139	0.038	
11(E) & 3(I)	BCP ₁	0.084	0.025	0.059			71.3
	BCP ₂	0.104	0.025	0.079			
	F ₂	0.087	0.025	0.062	-0.014	0.076	
11(E) & 6(MI)	BCP ₁	0.139	0.058	0.081			75.8
	BCP ₂	0.114	0.058	0.056			
	F ₂	0.240	0.058	0.182	0.227	-0.045	
11(E) & 9(MI)	BCP ₁	0.094	0.035	0.059			68.2
	BCP ₂	0.240	0.035	0.205			
	F ₂	0.110	0.035	0.075	-0.114	0.189	
11(E) & 12(E)	BCP ₁	0.159	0.019	0.140			80.4
	BCP ₂	0.136	0.019	0.117			
	F ₂	0.097	0.019	0.078	-0.101	0.179	
9(MI) & 6(MI)	BCP ₁	0.060	0.026	0.034			81.2
	BCP ₂	0.093	0.026	0.067			
	F ₂	0.138	0.026	0.112	0.123	-0.011	

^zE = efficient, MI = moderately inefficient, I = inefficient.

Table 4. Regression coefficients and heritability estimates for families used in the inheritance studies.

Family		Predicted mean dry weight of designated parents (g)	Mean dry weight of selfed progeny of designated parents (g)	Narrow sense heritability	
				uncorrected (d0)	corrected (d1)
11(E) & 1(MI) ^z	BCP ₁	2.42	2.17	0.536	0.786
	BCP ₂	2.24	2.19	0.683	0.723
	F ₂	2.42	2.30	0.545	0.736
11(E) & 3(I)	BCP ₁	2.09	1.96	0.762	0.832
	BCP ₂	1.95	1.81	0.459	0.880
	F ₂	1.90	1.70	0.447	0.538
11(E) & 6(MI)	BCP ₁	2.13	1.98	0.567	0.771
	BCP ₂	2.05	2.08	0.502	0.682
	F ₂	2.26	2.04	0.580	0.883
11(E) & 9(MI)	BCP ₁	2.24	2.16	0.688	0.951
	BCP ₂	2.36	2.30	0.610	0.915
	F ₂	2.37	2.27	0.642	0.806
11(E) & 12(E)	BCP ₁	2.37	2.24	0.703	1.051
	BPC ₂	2.23	2.07	0.661	0.754
	F ₂	2.12	2.00	0.746	0.949
9(MI) & 6(MI)	BCP ₁	1.91	1.85	0.750	0.855
	BCP ₂	2.33	2.16	0.624	0.889
	F ₂	2.09	2.04	0.716	1.126

^zE = efficient, MI = moderately inefficient, I = inefficient.

here, because some plants are likely to respond to nutrient stress in a way that weakens the relation between fresh weight and dry weight, for example, by desiccation of the lower leaves. In spite of this problem, the observed correlations between fresh weight and dry weight are still quite high. The precision with which the narrow sense heritability (d) is calculated can be increased by increasing the number of F₂ or backcross plants selected and hence the number of progeny which are regressed on their parents. The simulation study that was carried out to check the validity of the procedure for computing the regression coefficients was also used to assess the effect of the variance of δ_i on the distribution of the corrected regression coefficients. This variance, σ_{δ}^2 , was a major component of the total variance of the corrected coefficients.

Both broad sense and narrow sense heritability were high in all bean families studied. High heritabilities have been reported for N, K, Mg, and Ca utilization by others (8, 9, 13). Because dominance and epistasis made large contributions to the inheritance of P efficiency, rapid advance in a breeding program to incorporate this characteristic into commercial bean cultivars would best be made using a procedure which emphasized these gene effects, for example, the pedigree and the backcross methods. Since improved inbred lines are the desired product, selection should not be too severe in the early stages to allow for desirable gene recombinations.

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