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Generation mean analysis of phosphorus-use efficiency in freely nodulating soybean crosses grown in low-phosphorus soil

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With 8 tables

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Abstract

Freely nodulating soybean genotypes vary in their phosphorus (P) uptake and P-use efficiency (PUE) in low-P soils. Understanding the genetic basis of these genotypes' performance is essential for effective breeding. To study the inheritance of PUE, we conducted crosses using two high-PUE genotypes, two moderate-PUE genotypes and two inefficient-PUE genotypes, and obtained F_1, F_2, BC_1 and BC_2 populations. The inheritance of PUE was evaluated using a randomized complete block design. A generation mean analysis of phenotypic data showed that PUE was heritable, with complex inheritance patterns and the presence of additive, dominance and epistatic gene effects. Seed P, shoot P, root P, P-incorporation efficiency and PUE were largely quantitatively inherited traits. There were dominance, additive × additive and dominance × dominance gene effects on PUE, grain yield, shoot dry weight, 100-seed weight, root dry weight and shoot dry matter per unit P for populations grown under low-P conditions. Dominance effects were generally greater than additive effects on PUE-related indices. These PUE indices can be used to select P-efficient soybean genotypes from segregating populations.

Key words: freely nodulating soybean — gene effects — generation mean analysis — phosphorus-use efficiency

Freely nodulating soybean genotypes are useful in the cereal- and legume-based cropping systems of the African savanna (Sanginga et al. 2002, Yusuf et al. 2008). Their production area has increased in the tropical moist savanna of West Africa. However, an increase in soybean yield in these regions is limited by phosphorus (P)-deficiency (Ogoke et al. 2004, 2006) resulting from low fertilizer inputs and fixation of P into insoluble forms (Thung 1991, Peretyazhko and Sposito 2005). In plants, P is required for many metabolic processes such as energy transfer, signal transduction, macromolecular biosynthesis, photosynthesis and respiration (Shenoy and Kalagudi 2005). Low-P availability results in poor seedling emergence, slow seedling growth, stunted mature plants, chlorosis (Giller and Wilson 1991, Singh et al. 2003) and impaired root growth (Fawole et al. 1982a,b Cumming et al. 1992, Jian et al. 2004). Consequently, strategies to improve and sustain soybean production in low-P soils with minimum P application have become a research priority.

The P-use efficiency (PUE) of a plant relates to its ability to recover P from fertilizer and soil, meaning that high-PUE plants will have high productivity per unit of P absorbed (Blair 1993, Ortiz-Monasterio et al. 2002). Differences in PUE can be attributed to three factors: (i) uptake efficiency, which is the ability of the root system to acquire P from the soil and accumulate it in the shoots; (ii) shoot growth rate; and (iii) the efficiency of P-use in the plant to produce the final yield. These three factors comprise PUE (Craswell and Godwin 1984).

Planting higher PUE strains would be a practical means to solve the P-deficiency problem that is endemic among smallholding farms in Africa. The need to clearly define PUE, which might refer to uptake, response, metabolism or dry matter (DM) production, is therefore important to soybean research. The physiological mechanisms of differential P absorption and translocation rates might be explained by genotypic differences in PUE. The genetic variation among soybean genotypes in their ability to thrive on P-deficient soil can be exploited to develop P-efficient genotypes (Lynch and Brown 1998). However, a lack of information on the genetic control of PUE and its associated traits in freely nodulating soybean genotypes hinders soybean breeding at present. Therefore, studying the genetic basis of PUE will be useful for developing strategies to select and develop genotypes with better PUE for increased seed yield with little or no fertilizer input.

Generation mean analysis is a tool for designing the most appropriate breeding approaches to develop crop varieties with desired traits and is commonly used in studies on the inheritance of quantitative traits. This type of analysis provides information on the relative importance of the average effects of the genes (additive effects, dominance deviations and effects due to non-allelic gene interactions) (Pooni and Treharne 1994, Iqbal and Nadeem 2003, Checa et al. 2006, Sharmila et al. 2007). Generation mean analysis produces a genotypic value for each individual such that mean genotypic values can be calculated for families and generations (Pooni and Treharne 1994). Gorny (1999) used generation mean analysis to investigate the inheritance of nitrogen (N)-use efficiency, PUE, and tolerance to low-P and low-N conditions in spring barley (*Hordeum vulgare*). O'Sullivan et al. (1974) studied the inheritance of N-use efficiency in tomato (*Lycopersicum esculentum*), and Makmur et al. (1978) studied the genetic basis of variations in potassium (K)-use efficiency in tomato. In bean (*Phaseolus vulgaris*), the inheritance of PUE was shown to vary among different genotypes (Whiteaker et al. 1976). Fawole (1979) reported that epistasis, notably additive and dominance × dominance gene effects, contributed to variations in PUE in bean, and Araújo et al. (2005)

confirmed an additive × additive type of epistasis for PUE in bean.

The objectives of this study were to determine the nature and magnitude of the genetic effects for PUE and related characters (grain yield, shoot dry weight, 100-seed weight, root dry weight and shoot dry matter per unit P in the shoot) for a range of soybean crosses grown under low-P conditions. Ultimately, this information will be useful for selecting P-efficient soybean varieties for cultivation in low-P soils.

Materials and Methods

This study was conducted at the International Institute of Tropical Agriculture (IITA), Ibadan (07°30′N, 03°45′E), Nigeria. Ibadan lies within the derived savanna zone (transition forest ecosystem) of Nigeria and has a bimodal rainfall pattern with an average annual rainfall of 1300 mm. The soil in this area is dominated by Alfisols (oxicpaleustalf) (Moorman et al. 1975, Juo 1983). In the plot used for the inheritance study, the land was previously planted with cassava and then left fallow for 3 years before starting the study. Crosses were made in the greenhouse at IITA, Ibadan. No extra nutrients or soil amendments were added to the soil. Thirteen soybean (*Glycine max* L. Merrill) genotypes identified by Abdelgadir (1998) were screened for P-efficiency: TGm 1420, TGm 1511, TGx 1456-2E, TGm 1293, TGm 1360, TGm 1566, TGm 0944, TGm 1540, TGm 1196, TGx 1251, TGm 1419, TGm 1039 and TGm 1576. Briefly, the screening method to evaluate the PUE of these lines was as follows: the 13 genotypes were grown under different P conditions (0 kg P/ha, 30 kg P/ha of triple superphosphate; and 90 kg P/ha of rock phosphate), and then, the P contents in shoots and total grain were determined. The genotypes were then classified according to their growth responses: highly P-efficient lines used P in soil efficiently and showed substantially better growth under higher P supply; moderately P-efficient lines used P in soil moderately efficiently and showed moderate growth increases under higher P supply; P-inefficient lines did not use P in soil efficiently and did not show positive growth responses under higher P supply. The full screening method and the results of the P-efficiency screening are described in another paper (manuscript in preparation). From these 13 genotypes, six were selected based on their PUE phenotype (Table 1). The six genotypes were the highly P-efficient TGx 1456-2E and TGm 1419, the moderately P-efficient TGm 1196 and TGm 1576, and the P-inefficient TGm 1540 and TGx 1251.

Table 1: International Institute of Tropical Agriculture (IITA) soybean accessions used as parental stock and their phosphorus (P)-efficiency and relative maturity

IITA accession prefix	Origin	P-efficiency; relative maturity rating
TGm 0944	IITA, Nigeria	Moderately P-efficient; late maturing
TGm 1039	Taiwan	P-inefficient; late maturing
TGm 1196	Puerto Rico	Moderately P-efficient; late maturing
TGx 1251[1]	IITA, Nigeria	P-inefficient; late maturing
TGm 1293	USA	Moderately P-efficient; late maturing
TGm 1360	USA	Moderately P-efficient; late maturing
TGm 1419	USA	P-efficient; late maturing
TGm 1420	USA	P-inefficient; late maturing
TGm 1511	USA	Moderately P-efficient; late maturing
TGm 1540	USA	P-inefficient; late maturing
TGm 1566	USA	Moderately P-efficient; early maturing
TGm 1576	USA	Moderately P-efficient; late maturing
TGx 1456-2E[2]	IITA, Nigeria	P-efficient; late maturing

Source: Grain Legume Improvement Programme and Genetic Resources Unit, IITA, Ibadan.
[1]Pedigree: TGm 540 × TGx 709-06D (TGm 120 × TGm 80).
[2]Pedigree: TGx 539 (TGm 80 × TGm 618) × TGx 813 (TGm 1197 × TGm 618).

Inheritance study: Six genotypes, two of each of the three PUE phenotypes (efficient, E; moderately efficient, ME; and inefficient, IF), were selected in 2004 for the following crosses: cross 1: E × E, TGx 1456-2E × TGm 1419; cross 2: E × ME, TGx 1456-2E × TGm 1196; and cross 3: E × IF, TGx 1456-2E × TGm 1540). These crosses produced the F_1 generation. The F_1 generation was selfed to obtain the F_2 generation, and the BC_1 and BC_2 generations were produced by backcrossing the F_1 to each of the parental genotypes. Six genetic families (namely, P_1, P_2, F_1, F_2, BC_1 and BC_2) of each cross were evaluated in field trials at Ibadan under low-P conditions (Table 2). The families were grown in a randomized complete block design with three replications. A replication consisted of one row each of P_1 and P_2 (parental lines), one row of the F_1 generation, two rows each of BC_1 and BC_2, and seven rows of the F_2 progeny (i.e., 10 plants for the P_1, P_2, and F_1 families, 20 plants for the BC_1 and BC_2 families, and 70 plants for the F2 family). Four seeds were initially planted per hole and later thinned to one plant per stand. The rows were 1 m long, with 75-cm spacing between rows and 10-cm spacing within rows to obtain 10 plants per row.

Data collection: We measured the grain yield and related agronomic characters and the P content of the seeds, shoots and roots of individual plants. Plant height (cm) was measured using a metre rule from ground level to the terminal bud of the main shoot at flowering, mid-podding and harvest stages. The number of days to podding was recorded from sowing to the onset of podding. All pods borne on individual plants were detached and counted as the number of pods per plant. The 100-seed weight (g) was obtained by weighing 100 randomly selected seeds. The shoots of individual plants harvested at maturity were oven-dried to a constant weight to obtain shoot dry weight (g/plant). The roots were cut and oven-dried at 65°C for 48 h and then weighed. The total grain yield (g/plant) was determined at the harvest stage by threshing whole pods from individual plants and weighing the grains using a Mettler Easy Sampler 1210 balance (Mettler Toledo). Samples of seeds, shoots and roots were oven-dried and ground in a mill to a fine powder (screen size, 0.5 mm) before chemical analysis to determine the P content. For each organ, P content was determined as follows: samples were first digested in a hot sulphuric acid solution with an SeO_2 catalyst (Novozamsky et al. 1983). Then, the digested samples were analysed colorimetrically (Bremner and Mulvaney 1982) using a Technicon Autoanalyzer (Technicon Instrument Co, Tarrytown, NY, USA) according to the manufacturer's instructions. The efficiency indices were calculated from primary data and were defined as follows: P-incorporation efficiency = shoot DM per unit P in the shoot (g DM mg/P), where DM = dry matter; P-uptake = sum of total P in the grain plus total P in the vegetative part of the shoot plus total P in the root (Jones 1974, Blair and Cordero 1978); and PUE = grain yield/unit P-uptake (g/g) (Jones et al. 1989).

Generation mean analysis: The mode of inheritance of PUE was studied in the P_1, P_2, F_1, F_2, BC_1 and BC_2 populations using a generation mean analysis as described by Mather and Jinks (1982), and

Table 2: Physicochemical properties of experimental field soil

Soil characteristics	Ibadan
pH (1:1 H_2O)	5.4
Organic carbon (g/kg)	8.5
Total nitrogen (g/kg)	0.71
Available-Bray 1 phosphorus (mg/kg)	8.15
Soil Texture (g/kg)	
Sand	810.0
Silt	75.0
Clay	115.0
Textural Class	Loamy sand

Critical phosphorus value: 10–15 mg/kg; critical nitrogen value: 2.0–2.5 g/kg (Furlani et al. 1998).

Kearsey and Pooni (1996). The data were first analysed using a three-parameter model (Mather and Jinks 1971) to investigate the presence and magnitude of additive gene effects on the PUE and associated characters. The additive–dominance model was not adequate to explain the gene action contributing to PUE, even after the data were log-transformed. Therefore, the data were analysed using a six-parameter model to detect additive, dominance and gene interaction effects. We used the statistical analysis software SAS ver. 6.2 (SAS, Cary, NC, USA) to calculate generation mean, additive, dominance, and epistatic effects for PUE, grain yield and PUE-related characters (Kang 1994) in the soybean genotypes. A simple general linear model (GLM) was used to calculate the generation means, additive, dominance and epistatic effects; the model was fitted into the equations below.

$$(\mathrm{m}) = \frac{1}{2}\mathrm{P}_1 + \frac{1}{2}\mathrm{P}_2 + 4\mathrm{F}_2 + 2\mathrm{BC}_1 + \mathrm{BC}_2,$$

$$(\mathrm{a}) = \frac{1}{2}\mathrm{P}_1 - \mathrm{P}_2,$$

$$(\mathrm{d}) = 6\mathrm{BC}_1 + 6\mathrm{BC}_2 - 8\mathrm{F}_2 - \mathrm{F}_1 - \frac{3}{2}\mathrm{P}_1 - \frac{3}{2}\mathrm{P}_2,$$

$$(\mathrm{i}) = 2\mathrm{BC}_1 - 2\mathrm{BC}_2 - 4\mathrm{F}_2,$$

$$(\mathrm{j}) = 2\mathrm{BC}_1 - \mathrm{P}_1 - 2\mathrm{BC}_2 + \mathrm{P}_2, \text{and}$$

$$(\mathrm{l}) = \mathrm{P}_1 + \mathrm{P}_2 + 2\mathrm{F}_1 + 4\mathrm{F}_2 - 4\mathrm{BC}_1 - 4\mathrm{BC}_2$$

For the above equations, m is the mean of the inbred population derived from the cross between P_1 and P_2, and the gene effects are additive (a), dominance (d), additive × additive (i), additive × dominance (j) and dominance × dominance (l) (Hayman and Mather 1955, Jinks and Jones 1958, Gorz et al. 1987).

The significance of a particular parameter was tested by estimating the means of the ratio of each parameter and estimating the corresponding standard error; that is, the mean/SE ratio was used to test for significance of the three-parameter (epistatic) terms:

Mean = *X*
Variance = *V*
Mean variance or variance of the mean = *V*/n
Square root of *V*/n = SE (standard error of mean)

The ratio of *X*/SE was used to test for the level of significance of the epistatic parameters at the 1% or 5% probability levels depending on the magnitude. The various genetic effects were judged to be statistically significant at $P < 0.05$ (*0.05: significant; **0.01: highly significant; and ***0.0001: very highly significant).

Results

Shoot dry matter/unit P

Table 3 shows the generation mean, additive, and dominance, and epistatic gene effects for PUE and P-incorporation efficiency for the three crosses (E × E, E × ME and E × IF). The additive gene effect for PUE was positive and highly significant ($P < 0.01$) only for E × E, and the dominance effect was positive and highly significant ($P < 0.01$) for E × IF but not significant for the other two crosses. The dominance effect for PUE was 2–70 times larger than the additive effect for all the crosses. There were significant epistatic gene effects for PUE for E × E and E × IF but not for E × ME. The additive × additive effect was positive and highly significant ($P < 0.01$) only for E × IF, whereas the additive × dominance effect was negative and significant ($P < 0.05$) for E × E. The dominance × dominance effect was negative and highly significant ($P < 0.01$) for

Table 3: Mean, additive, dominance and epistatic gene effects in the six-parameter model for phosphorus-use efficiency (PUE) and shoot dry matter per unit P in the shoot in three soybean crosses

	PUE (PUE, g/g)				Shoot dry matter per unit of P in the shoot (incorporation efficiency, g DM mg/P)			
	Cross 1 (E × E)	Cross 2 (E × ME)	Cross 3 (E × IF)		Cross 1 (E × E)	Cross 2 (E × ME)	Cross 3 (E × IF)	
	TGx 1456-2E × TGm 1419	TGx 1456-2E × TGm 1196	TGx 1456-2E × TGm 1540		TGx 1456-2E × TGm 1419	TGx 1456-2E × TGm 1196	TGx 1456-2E × TGm 1540	
Mean (m)	0.02	0.02	0.01		4.99	5.39	4.87	
Additive (a)	0.01**	−0.001^{ns}	−0.004^{ns}		−1.09^{ns}	0.19^{ns}	0.63^{ns}	
Dominance (d)	−0.02^{ns}	−0.07^{ns}	0.01***		31.79***	40.10***	1.87^{ns}	
Additive × Additive (i)	0.003^{ns}	−0.03^{ns}	0.003**		9.36**	12.03***	2.56^{ns}	
Additive × Dominance (j)	−0.01*	0.01^{ns}	−0.001^{ns}		−2.13^{ns}	4.26**	−3.88*	
Dominance × Dominance (l)	0.01^{ns}	0.06^{ns}	−0.01***		−22.40***	−26.26***	−14.10*	

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at $P < 0.05$; **Significant at $P < 0.01$; and ***Significant at $P < 0.001$.

E × IF. For P-incorporation efficiency, the additive gene effect was not significant for any of the crosses. However, dominance gene effects were positive and very highly significant ($P < 0.001$) for E × E and E × ME but not significant for E × IF. The additive × additive gene effects were positive and highly significant for E × E and E × ME but not significant for E × IF. The additive × dominance gene effect was positive and highly significant for E × ME, negative and highly significant for E × IF, and not significant for E × E. Negative significant dominance × ominance gene effects for P-incorporation efficiency were observed for E × E and E × ME ($P < 0.001$) and E × IF ($P < 0.05$). The dominance and epistatic gene effects for PUE were significant for E × IF, whereas for P-incorporation efficiency, dominance and epistatic gene effects were significant for E × E and E × ME.

Seed, shoot and root P

Table 4 shows the mean, additive, dominance, and epistatic gene effects for the seed, shoot and root P in the selected soybean crosses. Additive gene effects were positive and significant only for shoot P in E × E and E × IF, and were not significant for seed P or root P in any of the crosses. The dominance gene effect was negative and significant ($P < 0.001$) for seed P in E × IF; negative and significant ($P < 0.01$) for shoot P in E × E; positive and significant ($P < 0.01$) for shoot P in E × IF; and negative and significant ($P < 0.01$) for root P in E × IF. Significant additive × additive gene effects were recorded for seed P in all three of the crosses, for shoot P in E × E and E × IF, and for root P in E × IF. The additive × dominance effects were not significant for seed P in any of the three crosses, but were significant for shoot P in E × ME and E × IF, and for root P in E × ME. Dominance × dominance gene effects were significant for seed P in E × IF, shoot P in E × E and E × IF, and root P in E × IF.

Duplicate epistasis was observed for seed P in E × IF, shoot P in E × E and E × IF, and root P in E × IF, because they either had a positive significant additive × additive gene effect as well as a negative significant dominance × dominance gene effect or the reverse (a negative significant additive × additive gene effect as well as a positive significant dominance × dominance gene effect).

Six-parameter model for grain yield

Table 5 shows the mean, additive, dominance and epistatic gene effects in the six-parameter model for grain yield in six soybean crosses. The additive, dominance and epistatic gene effects on grain yield differed among the crosses. Among the main effects, dominance was greater than additive gene effects. The additive gene effects were positive and highly significant ($P < 0.001$) in E × IF and ME × IF, positive and significant ($P < 0.05$) in IF × IF, and negative and highly significant ($P < 0.01$) in E × E. Additive gene effects were not significant in E × ME and ME × ME. Except for E × IF, dominance gene effects were positive and highly significant ($P < 0.01$ to 0.001). Dominance gene effects contributed more than additive gene effects to variations in grain yield. Additive × additive gene effects were positive and highly significant in E × E, E × ME and ME × IF, but not significant in E × IF, ME × ME and IF × IF. The additive × dominance gene effects were negative and highly significant only in E × ME, and the dominance × dominance gene effects were negative and highly

Table 4: Mean, additive, dominance, and epistatic gene effects for seed, shoot and root phosphorus content (mg P/g DW) in soybean crosses

Gene effects	Seed P			Shoot P			Root P		
	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540
Mean (m)	7.08	6.83	7.45	1.14	0.96	0.88	0.67	0.59	0.62
Additive (a)	-0.11^{ns}	0.46^{ns}	0.22^{ns}	0.33*	0.17^{ns}	0.23*	-0.02^{ns}	-0.59^{ns}	-0.04^{ns}
Dominance (d)	-3.00^{ns}	6.62^{ns}	-5.72^{***}	-3.74^{**}	-0.04^{ns}	2.95**	-0.46^{ns}	0.26^{ns}	-1.77^{**}
Additive × Additive (i)	−1.50*	3.50**	−1.50**	−1.37**	0.02ns	1.11**	−0.25ns	0.16ns	−0.69**
Additive × Dominance (j)	0.62^{ns}	0.81^{ns}	0.31^{ns}	0.09^{ns}	0.34*	0.51**	0.02^{ns}	−0.14*	0.11^{ns}
Dominance × Dominance (l)	2.15^{ns}	-4.27^{ns}	3.91**	2.23**	0.03^{ns}	−2.24**	0.11^{ns}	-0.10^{ns}	0.99**

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at $P < 0.05$; **significant at $P < 0.01$; and ***Significant at $P < 0.001$.

significant ($P < 0.01$ to 0.001) in all of the crosses except for E × IF. The dominance × dominance gene effects were generally larger than the combined additive × additive and additive × dominance effects. The positive and significant dominance gene effects for grain yield that were recorded in all, but the E × IF cross reflect the directional dominance for increasing alleles, in contrast to negative and significant dominance gene effects that indicate directional dominance for decreasing alleles. Duplicate epistatic gene effects were observed in E × E, E × ME and ME × IF, as evident from their positive significant additive × additive gene effects and negative significant dominance × dominance gene effects.

One hundred-seed weight

Table 6 summarizes the mean, additive, dominance and epistatic gene effects in the six-parameter model for 100-seed weight in selected soybean crosses. Additive gene effects were positive and highly significant ($P < 0.01$) in E × E, E × IF, and ME × IF, but negative and significant ($P < 0.05$) in IF × IF, and not significant in ME × ME. Dominance gene effects were also positive and highly significant ($P < 0.01$ to 0.001) in E × ME, E × IF, ME × ME and IF × IF. There were significant epistatic gene effects on the 100-seed weight in all of the crosses. The additive × additive effects were positive and significant ($P < 0.05$ to 0.001) in E × E, E × ME, E × IF, and IF × IF, and the additive × dominance effects were negative and highly significant in E × ME and ME × IF, but not significant in the other four crosses (Table 6). There were significant ($P < 0.05$ to 0.001) dominance × dominance effects for 100-seed weight in all of the crosses, except for ME × IF. The significant gene effects were negative for E × ME, E × IF, ME × ME and IF × IF, but positive for E × E.

Mean shoot dry weight

Table 7 shows the gene effects on shoot dry weight for the six studied crosses. The additive gene effect was positive and highly significant ($P < 0.01$) for E × E and IF × IF; the dominance effect was also positive and highly significant ($P < 0.01$) for all of the crosses except for E × ME and ME × ME. The additive × additive gene effects were significant in all of the crosses except for E × ME. The significant additive × additive effects were positive for all of the crosses except for ME × ME. There were negative and significant ($P < 0.05$ to 0.01) additive × dominance gene effects for all of the crosses except for E × ME and ME × IF. The dominance × dominance effects were negative and highly significant ($P < 0.01$ to 0.001) for all of the crosses except for E × ME and ME × ME.

Mean root dry weight

Table 8 shows the mean, additive, dominance and epistatic gene effects for root dry weight in the soybean crosses. The additive gene effect was positive and highly significant ($P < 0.01$) for E × E and IF × IF, but negative and highly significant for E × IF and ME × IF. The dominance gene effect was positive and highly significant ($P < 0.01$) for all of the crosses, except for E × ME. The dominance gene effect ranged from 10 to more than 1000 times the additive effect in all of the crosses, except for E × ME. The additive × additive effect was positive and highly significant ($P < 0.01$) for E × E, ME × ME and ME × IF, but not significant for the remaining three crosses, whereas the additive × dominance effect was negative and highly significant for E × E, E × IF and ME × ME, but not significant for the remaining three crosses. The

Table 5: Mean, additive, dominance and epistatic gene effects for grain yield (g/plant) in soybean crosses

Gene effects	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 4 (ME × ME) TGm 1196 × TGm 1576	Cross 5 (ME × IF) TGm 1196 × TGm 1540	Cross 6 (IF × IF) TGm 1540 × TGx 1251
Mean (m)	91.1	85.7	77.8	100.7	86.1	57.0
Additive (a)	−7.7**	-1.4^{ns}	24.5***	-5.9^{ns}	27.0***	6.2*
Dominance (d)	228.1***	204.1**	28.9^{ns}	152.2**	286.3***	133.4**
Additive × Additive (i)	86.2***	62.6**	-34.0^{ns}	32.4^{ns}	75.3**	18.6^{ns}
Additive × Dominance (j)	-11.3^{ns}	−33.8**	-9.6^{ns}	-6.5^{ns}	1.1^{ns}	3.5^{ns}
Dominance × Dominance (l)	−132.5***	−135.8**	-33.5^{ns}	−108.3**	−158.4**	−98.8**

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at $P < 0.05$; **Significant at $P < 0.01$; and ***significant at $P < 0.001$.

Table 6: Mean, additive, dominance and epistatic gene effects for 100-seed weight (g) in soybean crosses

Gene effects	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 4 (ME × ME) TGm 1196 × TGm 1576	Cross 5 (ME × IF) TGm 1196 × TGm 1540	Cross 6 (IF × IF) TGm 1540 × TGx 1251
Mean (m)	8.38	11.8	7.84	13.73	10.72	8.01
Additive (a)	0.55**	-0.47^{ns}	1.56***	-0.23^{ns}	2.99***	−2.72*
Dominance (d)	-2.37^{ns}	41.78**	20.87***	21.41**	-0.55^{ns}	9.44***
Additive × Additive (i)	1.84*	10.65**	6.89***	4.82^{ns}	2.12^{ns}	7.40***
Additive × Dominance (j)	-0.40^{ns}	−7.42***	-0.98^{ns}	-2.16^{ns}	−4.50**	1.09^{ns}
Dominance × Dominance (l)	4.03*	−29.01**	−13.62***	−13.75**	7.19^{ns}	−7.27*

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at $P < 0.05$; **Significant at $P < 0.01$; and ***Significant at $P < 0.001$.

Table 7: Mean, additive, dominance and epistatic gene effects for shoot dry weight (g/plant) in soybean crosses

Gene effects	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 4 (ME × ME) TGm 1196 × TGm 1576	Cross 5 (ME × IF) TGm 1196 × TGm 1540	Cross 6 (IF × IF) TGm 1540 × TGx 1251
Mean (m)	27.2	26.96	29.14	24.25	30.63	30.68
Additive (a)	5.28**	0.38^{ns}	−3.78^{ns}	0.26^{ns}	−1.53^{ns}	8.40***
Dominance (d)	120.92***	17.27^{ns}	107.69**	−9.68^{ns}	185.35***	195.72***
Additive × Additive (i)	37.59***	1.20^{ns}	27.67*	−12.45*	54.69***	59.65***
Additive × Dominance (j)	−13.47**	3.75^{ns}	−11.62*	−9.54**	−1.99^{ns}	−8.92*
Dominance × Dominance (l)	−76.06***	−15.41^{ns}	−74.99**	0.69^{ns}	−124.29***	−121.44***

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at P < 0.05; **Significant at P < 0.01; and ***Significant at P < 0.001.

Table 8: Mean, additive, dominance and epistatic gene effects for root dry weight (g/plant) in soybean crosses

Gene effects	Cross 1 (E × E) TGx 1456-2E × TGm 1419	Cross 2 (E × ME) TGx 1456-2E × TGm 1196	Cross 3 (E × IF) TGx 1456-2E × TGm 1540	Cross 4 (ME × ME) TGm 1196 × TGm 1576	Cross 5 (ME × IF) TGm 1196 × TGm 1540	Cross 6 (IF × IF) TGm 1540 × TGx 1251
Mean (m)	1.94	2.28	3.01	2.04	2.69	2.73
Additive (a)	0.35***	−0.31^{ns}	−0.59***	0.003^{ns}	−0.34**	0.38**
Dominance (d)	6.34***	0.19^{ns}	6.66**	5.64***	12.56***	6.93**
Additive × Additive (i)	1.82***	0.32^{ns}	1.19^{ns}	1.38**	3.37***	0.88^{ns}
Additive × Dominance (j)	−0.73***	−0.25^{ns}	−0.94**	−0.82***	−0.29^{ns}	−0.01^{ns}
Dominance × Dominance (l)	−3.47***	−1.44^{ns}	−4.26**	−4.18***	−8.76***	−5.77**

ns, not significant; E, Efficient genotype; ME, moderately efficient genotype; IF, inefficient genotype.
*Significant at P < 0.05; **Significant at P < 0.01; and ***Significant at P < 0.001.

dominance × dominance effect was negative and highly significant in all of the crosses, except for E × ME. There was a duplicate epistatic gene effect for root dry weight in E × E, ME × ME and ME × IF.

Discussion

Strategies to improve and sustain soybean production in P-deficient soils with minimum or no P application have become a research priority. Our results show that additive and dominance gene effects and their corresponding epistatic effects were significant for the measured traits in the majority of the crosses. Dominance and dominance × dominance gene effects were greater than those of the additive and additive × additive effects on variations in the measured P-efficiency indices. The fact that dominance effects were generally greater than additive effects indicates that qualitative genes are likely to affect the performance of agronomic traits under P-stress in soybean. Good performance under low-P conditions and PUE are complex traits that are affected by many factors. In fact, a recent large-scale study on genes that are differentially expressed under P-deficiency revealed that at least 42 genes and three pathways are involved in the response to low-P in soybean (Wang et al. 2016). Several recent studies have identified particular genes or gene clusters that appear being important for PUE in soybean. For example, recent genetic mapping analyses suggested that genes encoding acid phosphatase, a phosphate transporter, protein kinase and photosynthetic components are important under P-limited conditions and for PUE in soybean (Li et al., 2016; Song et al. 2014, Zhang et al. 2014, 2016a,b) .

Both PUE and P-incorporation efficiency provide information on plants' ability to grow in low-P soils. For PUE, a significant additive gene effect was only observed for E × E; therefore, the additive gene effect accounted for most of the variation in PUE in this cross. Previous findings have indicated that both additive and non-additive gene effects are significant in the accumulation and uptake efficiency of N, P, and K in sorghum and wheat (Gorz et al. 1987, Gamzikova 1992, Ahsan et al. 1996). Gorny (1999) found that additive and non-additive gene effects were important for N-use efficiency and PUE in barley, as well as for K-use efficiency in wheat (Woodend and Glass 1993). Kolmakova et al. (1983) found that additive genetic effects mainly controlled PUE in wheat, and Fawole et al. (1982a,b) reported that epistatic gene effects were important for PUE in beans. Furlani et al. (1998) found that the PUE of juvenile maize plants grown in low-P conditions were mainly controlled by additive gene effects. Barriga and Marambio (1995) observed a relatively larger proportion of dominant genes for PUE and P content in bread wheat. Barriga and Proschle (1995) reported that non-additive gene effects accounted for a large proportion of the variation in the PUE in wheat at maturity.

Consequently, breeding programmes that aim to improve crop PUE should concentrate on crosses between varieties with high PUE to produce P-efficient progeny. For P-incorporation efficiency (shoot dry matter per unit P), however, dominance gene effects accounted for most of the variation in E × E and E × ME. Because additive gene effects did not contribute to P-incorporation efficiency in these crosses, progress in selecting for high P-incorporation efficiency is expected to be very slow.

The negative significant additive × dominance gene effect that was observed for root P in E × ME indicated that there was duplicate epistasis between additive- and dominance-increasing alleles (Sharmila et al. 2007). Epistatic gene effects may be considered either complementary or duplicate depending on whether the additive × additive and dominance × dominance interactions are all significant and positive/negative or all significant

with one negative and the other positive. Two epistatic gene effects with the same sign are complementary, whereas different signs indicate duplicate epistasis (Kearsey and Pooni 1996). In this study, duplicate epistasis for PUE was observed for the E × IF cross. For P-incorporation efficiency, duplicate epistasis was observed for E × E and E × ME. In every case, the additive × additive gene effect was positive and highly significant, whereas the dominance × dominance gene effect was negative and highly significant. These additive and dominance gene effects and their interactions, which controlled PUE in some of the studied crosses, suggest that PUE is a heritable trait. The significant negative additive × dominance gene effect for PUE in the E × E cross indicates duplicate epistasis between additive- and dominance-increasing alleles. Similarly, a significant negative additive × dominance gene effect for P-incorporation efficiency was observed in the E × IF cross, indicating duplicate epistasis between additive- and dominance-increasing alleles (Sharmila et al. 2007). At least two of the five gene effects were as significant for both PUE and P-incorporation efficiency for the other crosses, except for E × ME, in which none of the gene effects were significant for PUE. These results illustrate that the six-parameter model was adequate for detecting epistasis in most of the crosses examined in this study.

Significant additive gene effects for 100-seed weight were detected in E × E, E × IF and ME × IF, indicating that significant progress could be made in selecting for high 100-seed weight in soybean populations derived from crosses between parents with varying PUE. There were significant additive × additive gene effects for 100-seed weight in E × E and E × IF. Consequently, E × E and E × IF would be preferable crosses to ME × IF to breed for higher 100-seed weight (Wehrmann et al. 1987).

Both additive and dominance gene effects were significant for shoot dry weight. However, the contribution of the dominance was generally larger than that of additive gene effects in most of the crosses. The crosses E × E, E × IF, ME × IF and IF × IF showed duplicate epistatic gene effects because their additive × additive effects were positive and significant, while their dominance × dominance effects were negative and significant. The positive dominance and negative dominance × dominance gene effects observed for E × IF and ME × IF indicate duplicate epistasis between dominance-increasing alleles.

Dominance gene effects were significant for root dry weight, except in the E × ME cross. The significant positive dominance and negative dominance × dominance gene effects that were detected for all of the crosses, except for E × ME, indicated duplicate epistasis between dominance-increasing alleles for root dry weight. A large root system is an important adaptation for growth in low-P soil and is therefore an important contributor to P-uptake. Our results indicate that higher root dry weight is a heritable trait in soybean, as has been shown in the Common Bean (Fawole et al. 1982a,b).

One limitation of this study was the relatively small sample sizes for the studied populations. Soybean has a high degree of inbreeding, and individuals in the P_1, P_2 and F_1 generations are assumed to have a high degree of genetic uniformity. Smaller seed samples are acceptable for breeding trials of soybean because it is highly homozygous. Thus, we believe that the number of plants (10) analysed for P_1, P_2 and F_1 is sufficiently representative, given the low level of heterozygosity after each mating generation.

In this study, crossing P-efficient and P-inefficient soybean genotypes increased the genetic base of the populations for selection. The different types of gene effects detected in the populations are useful for analysing the genetic architecture of PUE in soybean. Estimates of the genetic parameters will be helpful for identifying progeny with high PUE. Careful estimates of gene effects in the crosses between efficient × inefficient crosses for the studied traits indicate that dominance and epistatic gene effects, especially dominance × dominance and additive × additive effects, were significant for P-uptake and use in soybean. Our results indicate that seed P, shoot P, root P, P-incorporation efficiency and PUE are largely quantitatively inherited traits. Recurrent selection procedures could, therefore, increase the frequency of favourable alleles in breeding populations to enable the selection/development of genotypes with superior PUE. Such genotypes/varieties could be cultivated in areas with low-P soils to improve the yields of resource-poor farmers who cannot afford P fertilizer.

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