



Research Article

INHERITANCE OF MAIZE PHOSPHORUS EFFICIENCY IN ACID SOILS OF WESTERN KENYA

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ABSTRACT

Soil acidity is a major constraint to maize (*Zea mays* L.) productivity in tropical soils due to toxic levels of aluminium (Al) and phosphorus (P) deficiency. Selection for acid-soil tolerance is a sustainable way for increasing maize yields on these soils. The objectives of this study were to: (i) determine the genetic effects of maize traits associated with phosphorus efficiency (ii) compare the genetic effects of maize traits in low P and high P in acid soils. Six F1 single crosses derived from acid soil tolerant and susceptible lines were used in this study. The parental inbred lines, the F1's, F2's, BC1P1, BC1P2, from each of the six crosses were evaluated in two low P acid soils of western Kenya. Mean genetic effect (m), additive genetic effects (a), dominant genetic effects (d) and epistatic digenic effects (aa, ad, dd) were computed for Grain yield (GYLD), Shoot dry matter (SDM), Root Length density (RLD), P content (PC), P utilization efficiency (PUE) and P efficiency (PE). For most of the traits, greater variation was accounted for by dominance followed by epistatic and additive genetic effects under both P conditions. Means for all the traits studied were significantly higher at high P conditions compared to low P ones for all the generations. SDM, RLD, PC and PE exhibited higher means under high P for all the generations. Mean heritabilities were generally higher at high P although, dependent on the generation and the trait. Highest PE was exhibited by the F1s (59%) and lowest F2 (52%). The magnitude of both additive and non-additive gene effects were always greater in high P compared to Low P pointing to the possible effects of P variation on gene action. The results suggested that the genetic effects on major PE traits did not differ under different P regimes.

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INTRODUCTION

Soil acidity is a major constraint to maize (*Zea mays* L.) productivity worldwide mainly because of Aluminium (Al) toxicity and phosphorus (P) deficiency (Kochian *et al.*, 2015). Al toxicity limits plant growth through its effects on root growth and development while P starvation leads to stunted growth, thin and spindly stems with purpling of leaves, reduced grain yields etc (Parentoni *et al.*, 2010; Ouma *et al.*, 2012; Ligeyo *et al.*, 2014). Soil acidity covers extensive areas in tropical, subtropical and temperate zones, and occurs in 30-40% of the world's arable soils (Von Uexkull and Mutert, 1995). They are found mainly in South America (26.7%), North America (19.4%), Africa (19.1%) and Asia (15.1%) while the rest occur in Australia and New Zealand, Europe and Central America (Eswaran *et al.*, 1997, Ouma *et al.*, 2012). Genetic variation for tolerance to soil acidity that has been reported by various authors in several studies.

Duncan *et al.* (1994) reported additive, dominance, and epistatic effects for P efficiency in maize with additive effects being more important while Chaubey *et al.* (1994) and Furlani *et al.* (1998) reported the importance of both additive and dominance effects in controlling maize P efficiency traits. Other reports by Parentoni *et al.* (2006) and Chen *et al.* (2009) showed non-additive effects to be more important than additive effects for tolerance to low P soils. Further results from studies carried out by Magnavaca *et al.* (1987a); Pandey *et al.* (1994); Salazar *et al.* (1997) have shown that for grain yield, additive effects accounted for the major part of the total genetic variance, although non-additive effects were also significant. According to Pandey *et al.* (2007), both additive and dominance effects were more important than epistatic effects in the inheritance of grain yield in acid soils.

These studies imply that selection for P efficiency under acid soil is possible. However in most of these studies, the soil available P under acid soils were often higher than the Kenyan situation, (< 5mgP/kg vs > 10mgP/kg of soil, Olsen P) (Parentoni *et al.*, 2010) leading to (Kisinyo *et al.*, 2013) possibility in variation of results.

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Overall, estimation of genetic effects on several important traits in maize evaluated under non-acid soils has been well documented (Hallauer *et al.*, 1988; Hallauer and Miranda Filho, 1988; Duncan *et al.*, 1994; Chaubey *et al.*, 1994; Furlani *et al.*, 1998). However information on the genetic control of maize P efficiency traits in acid soils is still inadequate given that the area under maize production in acid soils is quite substantial. Besides, information on the possible role of varying P fertilizer rate on gene action is scarce. A clear selection criteria for P efficiency in acid soils and a better understanding of their genetic control at varying P levels is crucial in selecting for target traits for yield improvement. The objectives of this study were to (i) determine the genetic effects of maize traits associated with phosphorus efficiency (ii) compare the genetic effects of maize traits in low P and high P in acid soils.

MATERIALS AND METHODS

Genetic Materials

A total of six single crosses (KML 036 X MUL 229, HSL3 X 5046-2 X S396-16-1, KML 036 X S396-16-1, HSL3 X 5046-2 X MUL 229, HS 228 X S 396-16-1 and HS 228 X MUL 229) were used to estimate the genetic effects in two acid soils sites (Sega and Chepkoilel). The parents were selected based on tolerance to low P conditions (Ouma *et al.*, 2013). For each cross, the F1 was advanced by selfing to obtain F2 generation. Backcross 1 to each parent (BC1P1 and BC1P2), were also obtained by crossing the F1 for each cross with each of its 2 parents, with the F1 as the female parent. At least 10 ears were saved and balance bulked to represent each generation.

Experimental Conditions

A total of 23 maize genotypes comprising 6 backcrosses (BC1), 6 F1 single crosses (SCH), 5 parental lines and 6 F2s were evaluated for tolerance to low P in a replicated trial at Sega, Chepkoilel, (Table 1) during the long rains of 2014.

Note Al. sat- Aluminium saturation, P- Amount of soil available phosphorus (0-30 cm) (Olsen, 1954) The experiment was laid out in an RCBD replicated three times. Treatment consisted of the 24 genotypes and 2 levels of P described as low P (6 KgP/ha) and high P (36 KgP/ha) supplied as TSP). Generations were allocated to different blocks and randomized independently. A four row plot measuring three metres long, with inter and intra-row spacing 0.75 m x 0.30 m was used for each generation except the F2 where six row plots were used. Two seeds were sown per hill and later thinned to one. Genstat software (Payne *et al.*, 2014) was used to generate the randomization and field layout. All the plots were side-dressed using calcium Ammonium Nitrate (CAN) at the rate of 75 Kg N/ha. Standard agronomic practices were followed to maintain the experimental plots.

Root length density (RLD), shoot dry matter (SDM), phosphorus utilization efficiency (PUE), Shoot P concentration (SPC) and P efficiency (PE) were measured at anthesis. Destructive sampling was done on 14 randomly selected plants according to Bell and Fischer, 1994 for all generations except F2 where 30 samples were used. Root sampling was done using the root box technique as described by Vepraskas and Hoyt (1988) and Manske (2002) in order to determine RLD.

The line-intercept method described by Tennant (1975) was used to determine RLD. Shoot samples were oven dried at 80°C, ground and ashed at 550 °C for determination of P concentration in the whole shoot. The ground samples were then dissolved in 3.3% HCl and analyzed for P using the method of Barton (1948). Based on shoot dry matter yield, and P concentration in these plant components, the P content in the shoot (PC) and PUE were determined using the method of Hammond *et al.* (2009) and Moll *et al.*, 1982. The P efficiency ratio was calculated as the ratio of shoot dry matter production under low P to that under adequate P supply (Oztuk *et al.*, 2005). At maturity, data was collected on grain yield, (GYLD-t/ha).

Data Analysis

Generation means for each cross and P treatment were used to estimate the gene effects according to the Mather and Jinks (1982) model following Gamble's (1962) notation to define the genetic parameters in the model. This model was as follows:

$Y_k = m + \alpha a + \beta d + \alpha^2 aa + \alpha\beta ad + \beta^2 dd$, where α and β are the coefficients for additive and dominance effects, Y_k = the observed mean across locations of the k^{th} generation
 m = mean of all possible homozygous locus, considering all locus controlling the trait;
 a = pooled additive effects
 d = pooled dominance effects
 aa = additive x additive gene interaction effects
 ad = additive x dominance gene interaction effects
 dd = dominance x dominance gene interaction effects

Estimates of additive, dominance and epistatic effects were computed for each cross by weighted least square regression analysis (Rowe and Alexander, 1980; Mather and Jinks, 1982) using the equation $b = (X' D^{-1} X)^{-1} (X' D^{-1} y)$, where b is the vector of genetic effects (m , a , d , aa , ad , and dd), X is the incidence matrix of the genetic effects coefficients (α , β , α^2 , $\alpha\beta$, and β^2), y is the column vector of the generation means and D^{-1} is a weighted diagonal matrix, where the diagonal elements were the reciprocals of the variances of each generation mean computed for each generation (P's, F1's, F2's, and BC's). Statistical Analysis System (SAS, 2000) was used to estimate the genetic effects from the generation means of each cross at each P level and combined over locations. F test of the sum of squares for the genetic effects was used to reduce the model appropriately. In the selected model, genetic parameters having significant effects were included and all the non-significant parameters excluded from the model. For each cross in each trait, the ratios a/m , d/m and $epistasis/m$ were calculated using absolute values.

Only data where the parameter estimates (a , d and $epistasis$) were significant were used in these calculations. For each trait and at the two P levels across the locations, a general mean of the ratios a/m and d/m was calculated using data from all crosses with significant effects. Broad sense heritability (H^2) was estimated by variance components using linear mixed models (REML) as follows:

$H^2 = \sigma_g^2 / \{(\sigma_g^2 + (\sigma_{\text{error}}^2/r_i))\}$, Where H^2 is broad sense heritability, σ_g^2 is the generic variance, σ_{error}^2 is the error

variance, r is the number of replicates per genotype (Ribaut *et al.*, 1996 and Oakley *et al.*, 2006).

RESULTS

Trait means and heritabilities in acid soils of western Kenya

Shoot dry matter yields (SDM) were significantly higher at high P compared to low P ones for all the generations tested. Higher P supply increased mean SDM from 0.17 to 0.25 kg per plant in the parents, 0.26 to 0.46 kg/plant, in the F1s, 0.25 to 0.45 kg/plant for the backcrosses and 0.13 to 0.26 kg/plant for the F2s (Table 2).

The F1s attained the highest SDM under both high (0.46kg/plant) and low P (0.26kg/plant) supplies while the parental lines yielded the least (0.25 kg/plant) under high P and the F2s gave the least under low P (0.13 kg/plant). Mean H^2 for SDM was generally higher under high P compared to low P conditions for all the generations except for the F2s where the reverse was true. The F1s exhibited the highest heritability at high (0.603) and low P conditions (0.57) (Table 2). The highest mean root length density (RLD) was obtained in the F1 at high P (10.23 cm/cm^3) and lowest in the parents (6.66 cm/cm^3) while the backcrosses exhibited the highest RLD (6.37 cm/cm^3) under low P. The highest heritability for RLD was obtained in the backcrosses while lowest in the F2s.

Table 1. Site biophysical characterization

Site	Latitude	Longitude	Altitude	pH	P	Al.sat	Temp	Annual	Soil type
	($^{\circ}$)	($^{\circ}$)	masl		mgkg-1	(%)	range (oC)	rainfal (mm)	
Chepkolel	0 $^{\circ}$ 37'N	035 $^{\circ}$ 15'E	2143	4.8	4.4	45.6	13-26	1100	Chromic ferralsols
Sega	0 $^{\circ}$ 15'N	34 $^{\circ}$ 20'E	1200	4.5	2.2	44	17-30	1000	Orthic Acrisols

Table 2. Mean shoot dry matter (SDM), root length Density, (RLD) and P concentration (PC) of maize genotypes evaluated in 2 acid soil sites in western Kenya

ENTRY	SDM (kg/plant)		RLD (cm/cm 3)		PC (%)		PUTE gSDM/gP	PE %
	P36	P6	P36	P6	P36	P6		
S1 (Parents)	0.248	0.185	5.657	3.244	0.163	0.126	570	48
K1	0.278	0.187	7.69	4.407	0.161	0.107	488	51
H2	0.253	0.172	7.455	3.349	0.17	0.13	382	56
H1	0.273	0.185	8.391	4.572	0.142	0.117	582	50
H3	0.176	0.13	5.422	3.611	0.157	0.121	566	48
M1	0.245	0.143	5.359	3.569	0.153	0.12	537	42
MEAN	0.25	0.17	6.66	3.79	0.16	0.12	520.98	49.22
H2	0.581	0.395	0.227	0.607	0.645	0.404		
SE	0.02	0.02	1.162	0.854	0.01	0.006		
LSD (0.05)	0.016	0.011	0.77	0.47	0.01	0.008	35.2	
K1XS1 (F1s)	0.485	0.253	8.457	6.455	0.149	0.125	583	48
H1XS1	0.452	0.287	9.372	6.147	0.144	0.116	463	59
H2XS1	0.46	0.233	8.591	5.011	0.155	0.117	588	45
H1XM1	0.385	0.237	10.974	5.435	0.156	0.11	491	65
H2XM1	0.477	0.252	9.331	5.844	0.133	0.127	567	48
K1XM1	0.518	0.297	14.681	8.898	0.139	0.103	474	60
MEAN	0.46	0.26	10.23	6.3	0.15	0.116	527.66	54.03
H2	0.603	0.576	0.638	0.583	0.1	0.441		
SE	0.025	0.019	1.009	0.821	0.006	0.005		
LSD (0.05)	0.038	0.021	0.79	0.48	0.01	0.008	37.4	
H1XS1*H1(E)	0.458	0.242	13.255	6.759	0.158	0.127	589	52
H1XS1*S1	0.493	0.222	8.844	6.016	0.167	0.112	773	40
K1XS1*K1	0.46	0.278	8.989	4.944	0.156	0.13	641	58
K1XM1*K1	0.447	0.27	9.899	8.202	0.157	0.131	538	56
K1XM1*M1	0.388	0.186	11.226	8.339	0.162	0.12	602	45
H2XM1*H2	0.418	0.232	7.27	5.627	0.179	0.114	406	51
H1XM1*M1	0.487	0.247	9.516	5.828	0.156	0.133	553	52
H1XM1*H1	0.412	0.262	7.135	5.734	0.266	0.117	384	57
H2XS1*H2	0.467	0.277	11.198	5.856	0.167	0.116	548	56
MEAN	0.45a	0.25a	9.70b	6.37a	0.17	0.12	559.28	51.84
H2	0.749	0.471	0.67	0.721	0.1	0.384		
SE	0.02	0.016	0.546	0.156	0.019	0.006		
LSD (0.05)	0.029	0.017	0.7	0.63	0.009	0.0075	36.8	
K1XM1(F2 s)	0.26	0.135	4.626	3.862	0.141	0.117	689	42
H1XM1	0.31	0.175	7.394	4.905	0.16	0.1	492	50
H1XS1	0.243	0.133	8.25	4.44	0.145	0.128	391	50
K1XS1	0.27	0.113	7.341	5.01	0.145	0.098	689	40
H2XM1	0.23	0.147	10.714	5.184	0.143	0.115	294	62
H2XS1	0.231	0.087	6.197	4.271	0.149	0.112	682	49
MEAN	0.26	0.13	7.42	4.61	0.15	0.11	539.38	49.02
H2	0.407	0.549	0.417	0.504	0.256	0.15		
SE	0.019	0.015	1.212	0.598	0.006	0.006		
LSD (0.05)	0.017	0.008	0.9	0.51	0.008	0.006	40.4	

Note: H1-HSL3 X 5046-2, H2-HS 228, M1-MUL 229, S1-S396-16-1

Table 3. Estimates genetic effects for Grain yield (GYLD) evaluated in two low P acid soil locations in western Kenya

Grain yield (t/ha) at High P (acid soils of Chepkoilel and Segla)									
Cross	m	A	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	2.6**	0.63	5.67*	-	-	-	-	2.18	-
H1XS1	3.6**	0.47	3.22	-	-1.10*	-	-	-	0.31
H2XS1	3.0**	0.73*	4.20*	-	-	-1	0.24	1.40	-
H1XM1	2.9**	0.70*	7.60**	4.29*	-1.12*	-	0.24	2.59	1.0
H2XM1	4.0**	0.29	4.72*	-	-1.72*	-	-	1.17	0.43
K1XM1	2.9**	-0.31	7.38**	5.21*	-1.58*	-7.96*	-	2.57	1.49
Mean	3.2	0.71	5.91	-	-	-	0.24	1.98	0.80
Grain yield (t/ha) at low P (acid soils of Chepkoilel and Segla)									
Cross	m	A	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	2.4**	-0.25	2.93*	-	-1.75*	-	-	-	0.73
H1XS1	2.6**	-0.13	1.48	-	-1.29*	-	-	-	0.50
H2XS1	2.6**	-0.34	2.48*	-	-1.44*	-	-	-	0.55
H1XM1	1.1**	-0.60	5.02**	-	-2.23**	-	-	7.49	2.0
H2XM1	1.3*	1.07*	7.00**	7.94*	-	-12.12*	0.81	7.80	9.3
K1XM1	1.0*	-0.08	5.00**	6.27*	-1.17*	-8.03*	-	7.90	8
Mean	1.8	1.07	4.4	-	-	-	0.81	2.4	3.5

Gene effects: m: mean; a: additive; d: dominance; aa, ad and dd are additive x additive, additive x dominance and dominance x dominance epistasis, respectively; Only significant estimates of the parameters were used to obtain the means. . Means were obtained using absolute values; **, * Significant at 5% (*) and 1% (**) probability levels.

Table 4. Estimates of genetic effects for shoot dry matter (Kg/plant) evaluated in two acid soil locations in western Kenya

Shoot dry matter at High P (acid soils of Chepkoilel and Segla)									
Cross	M	A	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	0.27**	0.05	0.80**	-	-	-	-	2.96	-
H1XS1	0.24**	-0.04	1.04**	0.93*	-	-1.25*	-	4.28	1.33
H2XS1	0.23**	0.05	0.98**	0.85*	-	-1.04*	-	4.23	0.82
H1XM1	0.31**	-0.08*	0.60	-	-	-0.91*	0.24	-	2.93
H2XM1	0.23**	0.07*	0.76*	-	-	-	0.30	3.32	-
K1XM1	0.26**	0.06	0.81*	-	-	-	-	3.11	-
Mean	0.26	0.075	0.88	-	-	-	0.27	3.58	1.69
Shoot dry matter at low P (acid soils of Chepkoilel and Segla)									
Cross	M	A	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	0.11*	0.10*	0.54*	0.47*	-	-	0.85	4.80	4.3
H1XS1	0.13*	0.02	0.50	-	-	-	-	-	-
H2XS1	0.09*	0.09*	0.64*	-	-	-0.69*	1.00	7.35	6.9
H1XM1	0.18*	0.02	0.37	-	-	-	-	-	-
H2XM1	0.15*	0.08*	0.27	-	-	-	0.52	-	-
K1XM1	0.14*	0.08*	0.48	-	-	-	0.62	-	-
Mean	0.13	0.085	0.59	-	-	-	0.74	6.1	5.6

Gene effects: m: mean; a: additive; d: dominance; aa, ad and dd are additive x additive, additive x dominance and dominance x dominance epistasis, respectively; Only significant estimates of the parameters were used to obtain the means. . Means were obtained using absolute values; **, * Significant at 5% (*) and 1% (**) probability levels.

Table 5: Estimates of genetic effects for Root Length density evaluated in two acid soil locations in western Kenya

Root Length density (cm/cm ³) at High P (acid soils of Chepkoilel and Segla)									
Cross	M	a	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	7.34**	2.99*	2.40	-	-	-	0.41	-	-
H1XS1	8.25**	4.41*	13.55*	-	-	-	0.53	1.64	-
H2XS1	6.20**	4.20*	13.64*	-	-	-	0.68	2.20	-
H1XM1	7.39**	2.38*	6.82	-	-	-	0.32	-	-
H2XM1	10.71**	1.27*	-13.39*	-	-	-	0.12	1.25	-
K1XM1	4.63**	-1.33*	29.90**	-	-	-	0.29	6.46	-
Mean	7.42	2.76	15.46	-	-	-	0.39	2.88	-
Root Length density (cm/cm ³) at Low P acid soils of Chepkoilel and Segla)									
Cross	m	a	d	aa	ad	dd	a/m	d/m	Epist/m
K1XS1	5.01**	0.62*	0.27	-	-	-	0.12	-	-
H1XS1	4.44**	0.74*	8.78*	-	-	-	0.17	1.98	-
H2XS1	4.27**	0.89*	5.84*	-	-	-	0.21	1.37	-
H1XM1	4.91**	-0.29	4.12*	-	-	-	-	0.84	-
H2XM1	5.18**	-0.25	4.46*	-	-	-	-	0.86	-
K1XM1	3.86**	-0.34	21.8*	-	-	-	-	-	-
Mean	4.61	0.75	9.00	-	-	-	0.17	2.13	-

Gene effects: m: mean; a: additive; d: dominance; aa, ad and dd are additive x additive, additive x dominance and dominance x dominance epistasis, respectively; Only significant estimates of the parameters were used to obtain the means. . Means were obtained using absolute values; **, * Significant at 5% (*) and 1% (**) probability levels.

Low P supply resulted in a significant reduction by (23 to 50%) in shoot P concentration of genotypes in all the generation. Backcrosses exhibited the highest mean PUE (559.28 gSDM/gP) while parents the least (520.9 gSDM/gP) although the difference was not large. The highest mean PE (54%) was measured in the F1s that also exhibited very high mean SDM under low P conditions.

Gene effects

Grain Yield

In high P acid soils, significant epistatic effects were detected for grain yield, additive x additive (aa) in two crosses, additive x dominance epistasis (ad) in four crosses and dominance x dominance (dd) in two crosses. For grain yield the mean value of the ratios a/m, d/m, and epist/m were 0.24, 1.98 and 0.8, respectively indicating that dominance effects, followed by epistatic effects were more important than additive effects. In low P, similar results were reported with ratios a/m, d/m, and epist/m being increased at least 3.6 folds (0.81, 7.73 and 3.5, respectively) (Table 3). These findings compare well with those of Parentoni *et al.* (2010) and Richard *et al.* (2015) who reported the importance of dominance effects, followed by epistatic effects than additive effects for maize grain yield in acid soils.

Shoot dry matter

In high P acid soils, majority of the crosses (83%) exhibited significant dominance gene action compared to additivity (33%) although additivity was more pronounced under low P supply (67%). Consequently the magnitude of mean dominance was higher under both P conditions compared to mean additive genetic effects (0.88 and 0.55 vs. 0.075 and 0.085) for dominance and additive under high and low P respectively. Epistatic effects were only detected for a few crosses under both P conditions.

The mean of ratio "a/m", "d/m", and "epistasis/m" at high P was 0.27, 3.58 and 1.69 respectively while they were 0.74, 6.1 and 5.6 at low P, respectively (Table 4). This indicates that dominance and epistatic effects were more important in the expression of SDM than additive effects under both P conditions in acid soils. However, both dominance and additive effects had higher magnitude under low P conditions (d/m, a/m ratios 6.1 and 0.74) compared to high P conditions (d/m, a/m ratios of 3.5 and 0.27) (Table 4). Table 4: Estimates of genetic effects for shoot dry matter (Kg/plant) evaluated in two acid soil locations in western Kenya.

Root Length Density

The number of crosses under high P acid soils with significant additive effects was larger (100%) than those with significant additive effects in low P (50%) (Table 5). No epistasis was detected for RLD in acid soils. The overall mean ratio for "a/m", "d/m", at high P was 0.39 and 2.88, respectively while they were 0.17 and 2.13 respectively at low P. This shows that dominance was more important than additive effects in the inheritance of RLD in both P conditions. Both dominance and additive effects were more pronounced at high P conditions compared to low P conditions.

DISCUSSION

Maize genotypes differed significantly both in shoot and root growth at low P supply and in response to increased P application. This observation agrees with those of other authors who worked on maize hybrids (Parentoni *et al.*, 2010; Yan *et al.*, 2014, Ligeयो *et al.*, 2014), sorghum (Hufnagel *et al.*, 2014; Leiser *et al.*, 2014), and *Brassicaoleracea* (Hammond *et al.*, 2009). The application of high P fertilizer increased SDM, RLD, PE and PUE in acid soils was due to the increased soil available P which is often fixed in acid soils (Kisinyo *et al.*, 2013). Similar results have been reported in maize for increased root length density, grain yield, PE and PUE due to increased P application. (Hajabbasi and Schumacher 1994; Deng *et al.*, 2010) and in wheat (Monasterio *et al.*, 2002; Oztuk *et al.*, 2005). The increments in P efficiency traits measured were also due to other additional roles involving P in plants such as energy transfers, photosynthesis, transformation of sugar and starches, nutrient movement within the plants e.t.c (White and Hammond, 2008), hence the increase in growth, biomass and production.

Lower heritabilities in low P conditions were probably due to high experimental error and low genetic variations depicted under such conditions (Table 2). These findings compare well with those of Ceccarelli (1994) who obtained lower heritabilities estimates under stress environments. However, in part of this study, higher heritabilities were reported in low P compared to high P for certain traits (PC, RLD). These findings also compare well with those of Ceccarelli (1996), who reported greater genetic variation under stress environments and suggested that heritability in such environments can sometimes be comparable to non-stress environments or even higher if the experimental error is of the same magnitude. According to Gambles, (1962), the relative importance of additive (a), dominance (d), and epistatic (epist) effects, compared with the mean effect (m) can be obtained for each cross where the parameters are significant. An overall mean of these ratios from the different crosses can then be used to verify the relative importance of these gene effects in trait expression. In both P conditions, dominance and epistasis were more important than additive portion although epistatic effects were more pronounced in low P compared to high P for GYLD and SDM. The higher magnitude for additivity, dominance and epistasis under low P compared to high P conditions for GYLD and SDM imply the suitability of selecting for these traits in low P conditions under acid soils.

These findings compare well with those of Oztuk *et al.* (2005); Cichy *et al.* (2009) and Hammond *et al.* (2009) who reported the suitability of using SDM under low P as a suitable selection criteria for P efficiency for both beans, brassica and wheat genotypes. For RLD, there was higher magnitude of additivity in high P acid soils compared to the low magnitude of additivity at low P acid soils (Table 5). These findings imply that selection for RLD in acid soils is more suitable under high P conditions because of high additive effect. Such selection strategy may lead to identifying good responders rather than efficient genotypes. However, it would still be suitable in acid soils considering that a large proportion of soil P is held very tightly to the surface of soil particles as organic phosphorus compounds and hence unavailable even at high P supplementation.

Conclusion

Both additive and non-additive effects were detected under high and low P in acid soils. Dominance effects played a more important role than epistatic effects and the latter were more important than additive effects in the inheritance of maize P efficiency traits studied in acid soils. The magnitude of both additive and non-additive gene effects was always of greater importance in high P supplementation compared to low P pointing to the possible effects of P variation on gene action in acid soil. The inheritance of GYLD, RLD and SDM did not differ under different phosphorus variation in acid soils.

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Authors' Contributions

This work was carried out in collaboration between the authors who all read and approved the final manuscript

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