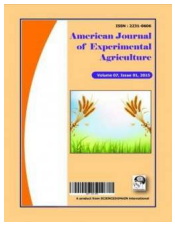

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Genetic Effects for Maize P Efficiency Traits in Acid and Non-acid Soils of Western Kenya

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Authors' contributions

This work was carried out in collaboration between both authors. Author OEO designed the study, conducted the experiment, managed the analyses of the study and wrote the first draft of the manuscript. Author GS wrote the protocol, reviewed the experimental design and all drafts of the manuscript. Both authors read and approved the final manuscript.

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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. The objectives of this study were to: (i) determine the genetic effects of certain traits associated with phosphorus efficiency in maize (ii) compare the genetic control of maize P efficiency traits in acid and non-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 and two low P non-acid soils in Kenya. Mean genetic effect (m), additive genetic effects (a), dominant genetic effects (d) and epistatic digenic effects (aa, ad, dd) were computed for 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 in both acid and non-acid soils. Means for all the traits studied were significantly higher at high P conditions (36 kgP/ha) in non-acid soils compared to acid soils for all the generations. Both RLD and PE exhibited higher means under non-acid soils compared to acid soils under both P conditions. Mean heritabilities were generally higher in non-acid soils compared to acid soils. There was higher reduction in PE in acid soils (25-50%)

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compared to non-acid soils (15 to 30%). The magnitude of both additive and non-additive gene effects were always greater in non-acid compared to acid soils pointing to the effects of soil acidity on gene action. The inheritance of major PE traits did not differ in acid and non-acid soils even though soil acidity affected the magnitude of the gene effects.

Keywords: Maize; acid soils; additive; dominant; epistatic effects; phosphorus efficiency.

1. INTRODUCTION

Soil acidity is a major constraint to maize (*Zea mays* L) productivity worldwide mainly because of Aluminium (Al) toxicity and phosphorus (P) deficiency [1]. 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 e.tc [2-4]. Soil acidity covers extensive areas in tropical, subtropical and temperate zones, and occurs in 30-40% of the world's arable soils [5]. 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 [6,3]. Different strategies have been suggested to improve the productivity of these soils including lime application, P replenishment through organic and inorganic sources and the development of tolerant cultivars [7,8,4]. The latter approach has been preferred as the most suitable, sustainable and cost effective. Enormous genetic variation for tolerance to soil acidity has been reported in several studies. [9] reported additive, dominance, and epistatic effects for P efficiency in maize with additive effects being more important while [10,11] reported the importance of both additive and dominance effects in controlling maize P efficiency traits. Other reports by [12,13] showed non-additive effects to be more important than additive effects for tolerance to low P soils. Further results from studies carried out by [14-16] 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. [17] reported that dominance followed by additive effects were more important for grain yield, plant height and days to anthesis in both acid and non-acid soils. According to [18], both additive and dominance effects were more important than epistatic effects in the inheritance of grain yield in acid soils. [18] further reported that for grain yield the additive-dominance model accounted for 91.1% of the variation in non-acid soils and 70.0% of the variation in acid soils, and that epistatic effects were more important in acid than in non- acid soils. These studies give hope that selection for P efficiency under acid and non-acid soils is possible.

So far, estimation of genetic effects on several important traits in maize evaluated under non-acid soils has been well documented [19-21]. 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, with increased use of inorganic P-based fertilizers to restore soil fertility in agricultural systems, it is expected that the world acid soil area will increase in the future [18]. This is because some of the available inorganic P sources contribute to further soil acidification. A clear selection criteria for P efficiency in acid and non-acid soils and a better understanding of their genetic control is crucial in selecting for target traits for yield improvement and QTLs mapping studies. This is expected to accelerate the development of P efficient maize cultivars. The objectives of this study were to (i) determine the genetic effects of traits associated with phosphorus efficiency in maize (ii) compare the genetic control of maize P efficiency traits in acid and non-acid soils.

2. MATERIALS AND METHODS

2.1 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 5046-2XMUL 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) and two non-acid soils sites (Migori and Koyonzo). The parents were selected based on tolerance to low P conditions and their combining abilities [8]. The crosses were developed in 2010. For each cross, the F1 was advanced by selfing to obtain F2 generation in 2011. 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 in 2012. At least 10 ears were saved and balance bulked to represent each generation.

2.1.1 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, Migori and Koyonzo sites (Table 1) during the long rains of 2013.

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 two 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 four row plots were used. Two seeds were sown per hill and later thinned to one. Genstat software [22] 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 16 randomly selected plants 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 [23] and Manske [24] in order to determine RLD. The line-intercept method described by Tennant [25] was used to determine RLD. Shoot samples were oven dried at 80℃, ground and ashed at 550℃ 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 [26]. 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 [27,28]. The P efficiency ratio was calculated as the ratio of shoot dry matter production under low P to that under adequate P supply [29].

2.1.1.1 Data analysis

Generation means for each cross and P treatment were used to estimate the gene effects according to the [29] model following [30,31] 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 kth 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 [32] using the equation b =(X' D-1X)-1(X' D-1y), 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, α2, αβ, and β2), y is the column vector of the generation means and D-1 is a weighted diagonal matrix, where the

Table 1. Site biophysical characterization

Site	Latitude (°)	Longitude (°)	Altitude (masl)	pH	P (mg/kgP)	% Al sat.	Temp range (°C)	Annual rainfall (mm)	Soil type
Chepkoilel	0°37 'N	035°15'E	2143	4.8	4.4	45.6	13-2 6	1100	Chromic farralsols
Sega	0°15 'N	34°20'E	1200	4.5	2.2	44	17-30	1000	O rthic Acrisols
Migori	1°03 'S	34°24'E	1381	5.7	2.6	12	22-24	1200	Humic ferralsols
Koyonzo	0°25 'N	34°25'E	1310	5.4	3	15	20-22	1400	Luvisols

Note Al. sat- Aluminium saturation, P- Amount of soil available phosphorus (0-30 cm) (Kisinyo et al., 2013 [8]).

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 [33] 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 (H2) was estimated by variance components using linear mixed models (REML) as follows:

$H^2 = \sigma^2_g / \{(\sigma^2_g + (\sigma_{error}{}^2/r_j\}$, Where H^2 is broad sense heritability, σ^2_g is the generic variance, $\sigma_{error}{}^2$ is the error variance, r is the number of replicates per genotype [34].

3. RESULTS AND DISCUSSION

3.1 Trait Means and Heritabilities in Acid Soils of Western Kenya

In acid soils, 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 parentals, 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 (0.46 kg/plant) and low P (0.26 kg/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. 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 parentals 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

3.2 Trait Means and Heritabilities in Non-Acid Soils of Western Kenya

In non-acid soils, SDM yields were significantly higher under high P compared to low ones for all the generations. Mean SDM was increased at least two folds by the application of higher P in all the generations. The F1s attained the highest SDM under both high (0.52 kg/plant) and low P (0.229 kg/plant) supplies while the F2s yielded the lowest under high P (0.24 kg/plant) and low P (0.12 kg/plant). Mean broad sense heritability for SDM did not show any clear pattern. The BC1 exhibited the highest heritability under both high (0.76) and low P conditions (0.72) (Table 3). Under high P supply, the highest mean RLD was obtained in the BC1 (20 cm/cm3) and the lowest in the F2 generation (11.87 cm/cm3) while at low P, the backcrosses exhibited the highest RLD (14.1 cm/cm3) and the F2 generation the lowest (8.16 cm/cm3). The highest mean H2 was obtained in the F1s and BC1s under high and low P respectively while the lowest in the F2s. Low P supply resulted in a significant reduction (15.5 to 31%) in shoot P concentration (SPC) of genotypes in all the generations. Backcrosses exhibited the highest mean PUE (645.1 gSDM/gP) while parentals the least (485.88 gSDM/gP). The highest mean PE (59%) was measured in the F1s that also exhibited high mean SDM under low P conditions.

3.3 Mean Comparison and Heritabilities under Acid and Non-Acid Soils

Mean SDM was greater under nonacid soils compared to acid soils at high P supply (Table 4). However under low P, SDM values were generally higher in acid compared to non-acid soils for all the generations evaluated. Both RLD and PE exhibited higher means under nonacid soils compared to acid soils under both P conditions. Highest PE was exhibited by the F1s in both acid and non-acid soils although it was

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	DSWT (kg per plant)		RTLV (cm/cm3)		PC (%)		PUTE	PE
	P36	P6	P36	P6	P36	P6	gSDM/gP	%
S1 (Parents)	0.248	0.185	5.657	3.244	0.163	0.126	570	48
K1	0.278	0.187	7.690	4.407	0.161	0.107	488	51
H2	0.253	0.172	7.455	3.349	0.170	0.130	382	56
H1	0.273	0.185	8.391	4.572	0.142	0.117	582	50
H3	0.176	0.130	5.422	3.611	0.157	0.121	566	48
M1	0.245	0.143	5.359	3.569	0.153	0.120	537	42
Mean	**0.25**	**0.17**	**6.66**	**3.79**	**0.16**	**0.120**	**520.98**	**49.22**
H2	0.581	0.395	0.227	0.607	0.645	0.404		
SE	0.020	0.020	1.162	0.854	0.010	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	0.460	0.233	8.591	5.011	0.155	0.117	588	45
H1XM1	0.385	0.237	10.974	5.435	0.156	0.110	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**	**6.30**	**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(Bcs)	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	0.460	0.278	8.989	4.944	0.156	0.130	641	58
K1XM1*K1	0.447	0.270	9.899	8.202	0.157	0.131	538	56
K1XM1*M1	0.388	0.186	11.226	8.339	0.162	0.120	602	45
H2XM1*H2	0.418	0.232	7.270	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	0.020	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)	0.260	0.135	4.626	3.862	0.141	0.117	689	42
H1XM1	0.310	0.175	7.394	4.905	0.160	0.100	492	50
H1XS1	0.243	0.133	8.250	4.440	0.145	0.128	391	50
K1XS1	0.270	0.113	7.341	5.010	0.145	0.098	689	40
H2XM1	0.230	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

higher in non-acid (59%) compared to acid soils (54 %). There was higher reduction in PE in acid soils (25-50%) compared to non-acid soils (15 to 30%). Measurement of PUE was greatly dependent on the generation for both soils. Mean PUE was higher for parentals and the F2 generations in acid (520.98 gSDM/gP and 539.38 gSDM/gP) compared to non-acid soils

(485.88 gSDM/gP and 515 gSDM/gP), while it was higher for F1s and BC1 in non-acid soils (538.29 gSDM/gP and 645.1 gSDM/gP) compared to acid soils (527.66 gSDM/gP and 559.28 gSDM/gP). However, there were no significant differences for PC between the two soils, although higher magnitudes of PC were detected for non-acid soils (Table 4). Mean heritabilities were generally higher in non-acid soils compared to acid soils although this depended on the generation, the trait and the level of P applied (Table 4).

Table 3. Mean Shoot Dry Matter (SDM), Root Length Density, (RLD) and P concentration (PC) of maize genotypes evaluated in 2 non-acid soil sites in western Kenya

Entry	DSWT (kg per plant)		RTLV (cm/cm3)		PC (%)		PUTE	PE
	P36	P6	P36	P6	P36	P6	gSDM/gP	%
S1 (Parents)	0.353	0.107	11.430	8.074	0.177	0.133	409	43
K1	0.258	0.120	12.906	10.650	0.174	0.163	693	53
H2	0.362	0.157	13.376	6.730	0.159	0.145	608	66
H1	0.338	0.217	13.091	10.958	0.165	0.133	307	65
H3	0.277	0.140	11.126	10.644	0.155	0.160	557	58
M1	0.262	0.140	12.704	7.489	0.134	0.110	341	54
Mean	**0.31**	**0.15**	**12.44**	**9.09**	**0.161**	**0.141**	**485.88**	**56.53**
H2	0.391	0.703	0.718	0.485	0.591	0.030		
SE	0.035	0.024	0.868	0.703	0.009	0.026		
L sd (0.05)	0.022	0.0107	0.85	0.64	0.0115	0.010	35.14	
K1XS1 (F1s)	0.492	0.203	20.000	12.575	0.144	0.142	630	59
H1XS1	0.561	0.263	18.998	12.976	0.127	0.130	608	62
H2XS1	0.574	0.227	21.998	11.214	0.141	0.142	760	52
H1XM1	0.518	0.277	10.606	10.407	0.164	0.132	361	73
H2XM1	0.497	0.177	13.215	12.622	0.189	0.123	457	47
K1XM1	0.483	0.230	25.291	17.333	0.158	0.136	413	64
MEAN	**0.521**	**0.229**	**18.351**	**12.855**	**0.154**	**0.134**	**538.298**	**59.432**
H2	0.504	0.618	0.781	0.621	0.598	0.159		
SE	0.025	0.017	1.281	0.865	0.011	0.024		
L sd (0.05)	0.025	0.015	1.42	0.85	0.0107	0.010	37.23	
H1XS1*H1(Bcs)	0.365	0.320	22.540	15.465	0.156	0.132	440	75
H1XS1*S1	0.378	0.240	17.778	9.570	0.141	0.113	659	70
K1XS1*K1	0.416	0.250	19.201	16.769	0.146	0.134	530	63
K1XM1*K1	0.462	0.237	27.044	18.140	0.150	0.116	694	58
K1XM1*M1	0.341	0.177	21.663	14.094	0.158	0.157	752	49
H2XM1*H2	0.418	0.187	19.928	14.680	0.166	0.140	716	49
H1XM1*M1	0.371	0.203	17.008	15.469	0.142	0.100	492	59
H1XM1*H1	0.362	0.167	16.801	13.777	0.162	0.102	874	47
H2XS1*H2	0.435	0.200	18.182	9.005	0.156	0.114	650	47
MEAN	**0.394**	**0.220**	**20.016**	**14.108**	**0.153**	**0.123**	**645.107**	**57.406**
H2	0.757	0.716	0.747	0.78	0.123	0.190		
SE	0.021	0.019	0.941	0.851	0.006	0.028		
L sd (0.05)	0.034	0.025	1.33	0.75	0.011	0.007	46.07	
K1XM1(F2 s)	0.236	0.143	11.796	7.893	0.170	0.126	393	64
H1XM1	0.300	0.113	12.568	9.808	0.167	0.101	653	42
H1XS1	0.231	0.123	11.897	9.063	0.172	0.105	329	53
K1XS1	0.205	0.150	13.229	8.317	0.153	0.124	482	67
H2XM1	0.236	0.103	10.350	8.608	0.167	0.128	591	46
H2XS1	0.244	0.097	11.401	5.291	0.187	0.114	648	41
MEAN	**0.242**	**0.122**	**11.873**	**8.163**	**0.169**	**0.117**	**515.892**	**52.290**
H2	0.524	0.45	0.454	0.509	0.316	0.17		
SE	0.023	0.016	2.156	1.808	0.010	0.014		
L sd (0.05)	0.0184	0.0093	0.91	0.63	0.013	0.0092	37.80	

Note: H1-HSL3 X 5046-2, H2-HS 228, M1-MUL 229, S1-S396-16-11

3.4 Gene Effects in Acid and Non-Acid Soils

3.4.1 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. 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 0.0.27) (Table 5). In non-acid soils, majority of the crosses exhibited significant dominance gene action (83% and 67%) compared to additive (33 and 17%) gene action under high and low P respectively. Therefore mean dominance was higher compared to mean additive genetic effects (0.81 vs. 0.11 and 0.55 vs. 0.14) in high and low P conditions. Significant epistatic effects (dominance x dominance) were detected at both P levels. The magnitude of epistatic effects were greater than dominance under both P conditions, although they were more pronounced under low P (6.13) compared to high P(4.29) (Table 6). Therefore epistasis followed by dominance was more important in SDM inheritance compared to additive effects in non-acid soils.

3.4.2 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 7). No epistasis was detected for RLD in acid soils. The overall mean ratio for "a/m", "d/m", at low P was 0.39 and 2.88, respectively while they were 0.17 and 2.13 respectively at high 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.

The number of crosses with significant additive effects was smaller (33.3%) in high P compared to low P (50%) non-acid soils (Table 8). At both P conditions dominance effects were more important followed by epistatic effects and additive effects, although both dominance and additive effects had higher magnitude under low P conditions (d/m, a/m ratios of 3.55 and 0.36) than under high P conditions (d/m, a/m ratios of 2.0 and 0.33).

Epistatic effects (aa and dd) for RLD were detected at both P conditions in non-acid soil in four out of the six crosses although they were more pronounced at high P (epist/m ratio of 1.77)

Table 4. Mean broad sense heritabilities for SDM and other P efficiency traits in acid and non-acid soils

Acid soils (Chepkoilel and Sega)						
Trait	**SDM (Kg/plant)**		**RLD (cm/cm3)**		**PC (%)**	
Generation	**P36**	**P6**	**P36**	**P6**	**P36**	**P6**
Parents	0.581	0.395	0.227	0.607	0.645	0.404
F1s	0.603	0.576	0.638	0.583	0.100	0.441
Backcrosses	0.749	0.471	0.67	0.721	0.100	0.384
F2S	0.407	0.549	0.417	0.504	0.256	0.150
Acid soils (Chepkoilel and Sega)						
Trait	**SDM (Kg/plant)**		**RLD (cm/cm3)**		**PC (%)**	
Generation	**P36**	**P6**	**P36**	**P6**	**P36**	**P6**
Parents	0.391	0.703	0.718	0.485	0.591	0.300
F1s	0.504	0.618	0.781	0.621	0.598	0.159
Backcrosses	0.757	0.716	0.747	0.78	0.123	0.190
F2S	0.524	0.45	0.454	0.509	0.316	0.170

compared to low P (epist/m ratio of 1.08). These results agree with those of Wolf and Hallauer (1997) who concluded that epistasis in maize seems to be more important in either poorer or better environments. These findings also suggest that variation in P levels in non-acid soils did not affect the detection of epistatic effects for RLD.

Table 5. Estimates of genetic effects for shoot dry matter (Kg/plant) evaluated in two acid soil locations in western Kenya

Shoot dry matter (Kg/plant) at High P acid soils of Chepkoilel and Sega									
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 (Kg/plant) at Low P acid soils of Chepkoilel and Sega									
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; Significance at 5% (*) and 1% (**) probability level

Table 6. Estimates of genetic effects for shoot dry matter evaluated in two low P non-acid soil locations in western Kenya

Shoot dry matter (Kg/plant) at High P non-acid soils of migori and Koyonzo									
Cross	**m**	**a**	**d**	**aa**	**ad**	**dd**	**a/m**	**d/m**	**Epist/m**
K1XS1	0.20**	-0.04	0.98**	-	-	-1.37*	-	4.78	6.85
H1XS1	0.23**	-0.01	0.64*	-	-	-	-	2.75	-
H2XS1	0.24**	-0.09*	1.01**	-	-	-1.26*	0.35	4.16	5.25
H1XM1	0.30**	-0.01	0.34	-	-	-	-	-	-
H2XM1	0.24**	0.04	0.70*	-	-	-0.91*	-	2.95	0.67
K1XM1	0.24**	0.12*	0.74**	-	-	-1.06*	0.51	3.14	4.41
Mean	0.242	0.11	0.81	-	-	-1.23	0.43	3.56	4.29
Shoot dry matter (Kg/plant) at Low P non-acid soils of migori and Koyonzo									
Cross	**m**	**a**	**d**	**aa**	**ad**	**dd**	**a/m**	**d/m**	**Epist/m**
K1XS1	0.14**	0.05	0.15	-	-	-	-	-	-
H1XS1	0.12**	0.01	0.59*	-	-	-0.72*	-	4.92	6.00
H2XS1	0.11**	-0.02	0.71*	-	-	-0.86*	-	6.46	7.80
H1XM1	0.13**	-0.06	0.46*	-	-	-	0.46	3.44	-
H2XM1	0.13**	0.05	0.21	-	-	-	-	-	-
K1XM1	0.15**	0.14*	0.46*	-	-	-0.69*	0.93	3.18	4.60
Mean	0.13	0.14	0.55	-	-	-0.75	0.67	4.5	6.13

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; Significance at 5% (*) and 1% (**) probability level

Table 7. Estimates of genetic effects for root length density evaluated in two acid soil locations in western Kenya

Root length density (cm/cm3) at High P acid soils of Chepkoilel and Sega									
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	15.76	-	-	-	0.39	2.88	-
Root length density (cm/cm3) at Low P acid soils of Chepkoilel and Sega									
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; Significance at 5% (*) and 1% (**) probability level

Table 8. Estimates of genetic effects for root length density evaluated in two non-acid soil locations in western Kenya

Root length density (cm/cm3) at High P non-acid soils of Migori and Koyonzo									
Cross	**m**	**a**	**d**	**aa**	**ad**	**dd**	**a/m**	**d/m**	**Epist/m**
K1XS1	13.2**	4.77*	32.10**	24.27*	-	-	0.36	2.43	1.83
H1XS1	11.9**	5.89*	20.6**	-	-	-	0.50	1.76	-
H2XS1	11.40**	3.00	18.44*	-	-	-30*	-	1.62	2.6
H1XM1	12.6**	2.31	8.97	-	-	-	-	-	-
H2XM1	10.34**	3.68	17.10*	16.93*	-	-	-	1.65	1.64
K1XM1	11.8**	4.05*	45.4**	32.89*	-	-21.17*	0.24	3.85	0.99
Mean	11.87	4.9	26.7	-	-	-	0.37	2.26	1.77
Root length density (cm/cm3) at Low P non-cid soils of Migori and Koyonzo									
Cross	**m**	**a**	**d**	**aa**	**ad**	**dd**	**a/m**	**d/m**	**Epist/m**
K1XS1	8.32**	1.77	36.48**	30.27*	-	-43.93*	-	4.39	1.63
H1XS1	9.06**	5.89*	20.28**	-	-	-	0.65	2.24	-
H2XS1	5.29**	1.00	19.66**	-	-	-	-	3.72	-
H1XM1	9.81**	-1.69	23.44**	19.26	-	-32.49*	-	2.39	1.32
H2XM1	8.61**	3.68	25.44**	16.93	-	-22.82*	-	2.96	0.68
K1XM1	7.89**	4.05*	44.16**	32.89*	-	-38.56*	0.51	5.59	0.72
Mean	8.16	4.97	28.24	-	-	-	0.58	3.55	1.08

*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; *, and **, Significance at 5% (*) and 1% (**) probability level*

4. DISCUSSION

Maize genotypes differed significantly both in shoot and root growth at low P supply and in response to P fertilization. Such substantial genetic variation in response to P deficiency and P supply was also observed in past studies for maize hybrids [2,35,4] sorghum [36,37], *Brassica oleracea* [27] and wheat [29]. The application of high P fertilizer increased SDM, RLD, PE and PUE in both acid and non-acid soils because of the increased soil available P, which is

necessary for healthy plant growth and high grain production. Besides, Soil P availability is critical for the early growth and development of maize as it affects root morphological and physiological characteristics that are important for eventual P uptake since P is immobile and often unavailable in most soils [38,39]. Similar results have been reported in maize for increased root length density, grain yield, PE and PUE due to increased P application. [38,40] and in wheat [41,29]. The increments in P efficiency traits measured were also due to the fact that P is involved in several key plant functions including energy transfers, photosynthesis, transformation of sugar and starches, nutrient movement within the plants etc [42] hence the increase in SDM and root growth and development. The finding for RLD is however contrary to those of [43] who recorded a decrease in root growth as a result of increased P supply in bean recombinant inbred lines. The contrasting results could be explained by the difference in plant types, adaptation and growth habits between maize and beans.

There was a general reduction in SDM and other P efficiency traits in acid soils compared to non-acid soils. This was in addition to the higher reduction in PE in acid soils (25-50%) compared to non-acid soils (15 to 30%). These results compare well with those of [17] who observed significant decrease in maize grain yields and plant height for parentals, F1, F2 and Backcross generations. [24] also reported decrease in RLD as a result of soil acidity in bread wheat genotypes. These observations can be attributed to the detrimental effects of soil acidity on maize performance, grain yield and other agronomic traits [44,19,2,7,8,4]. Apart from the low available P, the crops in the acid soils also suffered from Al toxicity which decreased their cell division hence reduced SDM, RLD and PE.

Lower heritabilities in acid soils were probably due to high experimental error and low generic variations depicted under such conditions. These findings compare well with those of [45] who obtained lower heritabilities estimates under stress environments. However, in part of this study, higher heritabilities were reported in acid soils compared to non-acid soils. These findings compare well with those of [46] 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.

In both acid and non-acid soils, dominance and epistasis were more important than additive portion although epistatic effects were more pronounced in non-acid soils while dominance more pronounced in acid soils for SDM. The magnitude of additive, dominance and epistasis was always higher in low P compared to high P in both acid and non-acid soils. This implies that selecting for SDM is more suitable under low P soils in both acid and non-acid soils. These findings compare well with those of [29,43,27] who found SDM as suitable selection criteria for P efficiency under low P conditions for 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 (Tables 7 and 8). 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. In contrast, selection for RLD in non-acid soils is more suitable at low P levels because of high additivity and dominance gene effects.

5. CONCLUSION

Both additive and non-additive effects were detected in both acid and non-acids soils although this was more dependent on the trait studied and the level of available P. Dominance effects played a more important role than epistatic effects and the latter were more important than additive effects in the inheritance of majority of P efficiency traits studied in maize in both acid and non-acid soils. In most cases, epistasis was specifically more important in non-acid soils while dominance in acid soils. Additive gene effects were fairly of similar magnitude across the acid and non-acid soils. The magnitude of both additive and non-additive gene effects were always greater in non-acid soils compared to acid soils pointing to the detrimental effects of soil acidity in the detection of gene actions in maize. Our results suggest that the inheritance of Root Length Density and Shoot Dry matter did not differ in acid and non-acid soils. The overall results of this study showed that soil acidity significantly reduced P efficiency traits in maize and affected the detection of the genetic effects for these traits.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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