International Journal of Agriculture and Crop Sciences.
Available online at www.ijagcs.com
IJACS/2015/8-2/203-213
ISSN 2227-670X ©2015 IJACS Journal

IJACS

Combining Ability And Heterotic Orientation Of Selected Zambian Maize Inbred Lines Under Low Soil Phosphorus Conditions

Chanda Richard[1,2]*, Lovemore Daka[3,4], David .S. Osiru[2], Mick .S. Mwala[4], Davies Lungu[4], Kalaluka Munyinda[4], Mweshi Mukanga[5]

1 Seed Control and Certification Institute, P.O. Box 350199, Chilanga, Zambia.
2. College of Agriculture and Environmental Science, Makerere University, P.O. Box , Kampala, Uganda.
3 . Present address: C/O Provincial Agricultural Coordinator, Ministry of Agriculture and Livestock, P. O. Box 110041, Solwezi. Zambia.
4. Department of Plant Science, University of Zambia, P.O. Box 32379, Lusaka, Zambia.
5 . Zambia Agriculture Research Institute, P/B 7, Chilanga. Zambia.

**** Corresponding author email:*** edchazm@gmail.com

ABSTRACT: Maize (Zea mays L.) production in sub-Saharan Africa (SSA) is limited by low availability of soil phosphorus, affecting 98% of maize fields grown by small scale farmers in Zambia. Therefore, developing and releasing P-efficient maize hybrids is the sustainable way of increasing maize yield in P deficient soils cultivated by small scale farmers. The present study was carried out to assess the mode of gene action and heterotic orientation of selected maize inbred lines to low P soils. Six maize inbred lines were crossed to three inbred testers and the 18 testcrosses were evaluated under low P soil conditions. General combining ability (GCA) effects were significant ($p<0.05$) for grain yield, phosphorus use efficiency (PUE) and phosphorus utilisation efficiency (PUtE) suggesting that genes with additive effects were controlling the traits. The phosphorus deficiency symptom, days to anthesis and phosphorus uptake were both under significant ($P<0.05$) GCA and specific combining ability (SCA) effects suggesting the importance of both additive and non-additive gene effects. However, the SCA variance was greater than the GCA variance for all the traits, suggesting the preponderance of non-additive over additive gene action. Stepwise multiple regression showed that PUtE was 9 times more important than PAE for grain yield. Therefore, inbred lines L152, J185 and Mo17 with positive GCA for GY, PAE and PUtE can be used in breeding. The lack of correlation between PAE and PUtE, indicates that simultaneous selection for these traits is possible.
Keywords: combining ability, phosphorus utilisation efficiency, phosphorus uptake efficiency, heterotic orientation, maize.

INTRODUCTION

Maize production in sub-Saharan Africa, especially under small holder conditions is constrained by several biotic and abiotic stresses. Low soil P is one of the constraints limiting maize production, as most of the soils are generally deficient in available P (Bekunda et al., 1997). Phosphorus is made unavailable under low soil pH (pH <5.5) as it is fixed by aluminum and iron oxides (Kochian, 1995). In the northern parts of Zambia, the soils are acidic with medium to high phosphorus fixing capacity (1-3ppm) (Malama, 2001). Low phosphorus and pH are estimated to occur in 98% of maize fields (Yerokun, 2008; Mason et al., 2011) such that the crops are not responsive to basal fertilizer application (Mason et al., 2011). Therefore, developing and releasing P efficient maize genotypes can increase crop production in p-deficient soils and reduce the cost of production associated with fertilizer application in intensive agriculture. The growing of P efficient genotypes is also environmentally friendly. Hence, breeding P efficient maize genotypes is one of the important goals of the Zambian maize breeding and programme.

Breeding for low P requires an understanding on the genetic components of P uptake (PU), P utilisation efficiency (PUtE), P use efficiency (PUE) and their correlations to grain yield under low soil P conditions. Increased PUtE adds to the gains that are made by improving PAE (Wang et al., 2010; Veneklaas et al., 2012), therefore breeders have to determine the relative importance of PAE and PUtE to plant P efficiency in breeding populations. However, the relative contribution of PAE and PUtE to plant P efficiency varies with species and level of P (Rose et al., 2013). PAE is high under low P and low under adequate P (Fageria et al., 1988). Comparatively, PAE is more important compared to PUtE under low P and vice versa under optimal P (Parentoni and Souza-Jr, 2008; Whang et al., 2010; DoVale and Fritsche-Neto, 2013). These results are in agreement with recent studies done on for ecosystem level nutrient use efficiency for phosphorus (Mathur, 2014).

Genetic studies have indicated that additive gene effects are more important for PAE and traits associated with PUE (DoVale and Fritsche-Neto, 2013). Others have reported that dominance effects are more important than additive effects for variations in PUE, PAE and PUtE (Mendes et al., 2014). However, when epistasis is present, the dominance and epistatic effects are more important than additive gene effects (Parentoni et al., 2010). In tropical maize, studies have shown that PAE is the main determinant of PUE (DoVale and Fritsche-Neto, 2013; Mendes et al., 2014), suggesting that maize genotypes with increased P efficiency can be obtained by increasing PAE and/or PUtE (Hirel et al., 2007). Furthermore, studies have shown that traits related to nutrient efficiency and those related to nutrient stress tolerance are controlled by different genes (Maia et al., 2011). Therefore, simultaneous selection for use efficiency and tolerance can be carried out as long as their mechanisms are not competitive (Maia et al., 2011). The confounding effects of genotype x environment interaction for low P tolerance breeding is of minor importance (DoVale and Fritsche-Neto, 2013). Therefore, it is recommended that selection for low P should be carried out at one site only, as soil type and management affects nutrient use efficiency and grain yield of maize (Ngome et al., 2013).

Currently, there is lack of knowledge on P uptake, P utilisation efficiency and heterotic orientation for low phosphorus tolerance among Zambian maize inbred lines. Thus, identifying the heterotic groups and heterotic patterns for low soil P of inbred lines will enhance the breeding of maize hybrids suited to low P soil conditions. Therefore, a study was carried out with the objectives of estimating (a) mode of gene action for P tolerance (b) the P uptake and utilisation efficiencies and (c) determine the heterotic relationships among 6 inbred lines for low soil P.

MATERIALS AND METHODS

MATERIALS

Generation of testcrosses

The testcrosses were generated by crossing six selected elite inbred lines of Zambia to three testers, two of temperate origin (Mo17 and B73) and one of tropical origin (J185) with Mo17 background. The North Carolina II mating Design was used for crossing at SCCI, in Zambia in 2012 and Muzarabani, Zimbabwe in 2011 during winter. The parents used and their successful crossings obtained are shown in Table 1.

Field evaluations

The 18 successive testcrosses (Table 1) were evaluated for agronomic performance at SCCI in Chilanga (26.26° East, 15.55° South and 1,227m above sea level), under optimal conditions and Mutanda (12° 11' East, 26° 24' South and 1,386m above sea level), under low phosphorus conditions. At SCCI (optimal site) the trials were basal dressed with compound D (10N:20P:10K) at 200kg/ha while at Mutanda (low phosphorus site), straight fertilizers were applied to supply the equivalent amount of potassium and nitrogen only. The trials were later top dressed 4 weeks after planting with Urea (46%N) at 200kg/ha. The experiments were kept weed free by hand weeding, using a hoe. The data on agronomic traits listed in Table 2 were collected. During the growing season, a dry spell occurred between late March and early April of 2013, lasting for four weeks. The plants were irrigated using a house pipe connected to a water bowser.

In addition to the traits listed in Table 2, the following parameters were collected (Akhtar et al., 2007):

(i) Phosphorus Acquisition Efficiency (PAE) = $\frac{\text{P content in shoot biomass}}{\text{P available in soil}}$

(ii) Phosphorus Utilisation efficiency (PUtE) = $\frac{\text{Grain weight } (\frac{\text{g}}{\text{plant}})}{\text{Shoot P in the plant } (\frac{\text{mg}}{\text{plant}})}$

(iii) Phosphorus Use Efficiency (PUE) = $\frac{\text{Grain weight } (\frac{\text{mg}}{\text{plant}})}{\text{P available in soil } (\frac{\text{mg}}{\text{g}})}$

Data Analysis

(a) Analysis of variance

The analysis of variance (ANOVA) for all the data was performed using PROC GLM procedures in SAS computer package, version 9.2 (SAS Institute, Cary, NC, USA) following a linear model:

$$Y_{ijkl} = \mu + rl + m_i + f_j + (mf)_{ij} + e_{ijkl}$$

Where: Y_{ijk} is the observed value of the progeny of the i^{th} male crossed with j^{th} female in the k^{th} replication; μ is the overall population mean; m_i is general combining ability of the i^{th} mother; f_j is the general combining ability of the j^{th} father; $(mf)_{ij}$ is the specific combining ability of the i^{th} x j^{th} cross; rl is the replication effect and e_{ijk} is the experimental error

The general and specific combining abilities for grain yield were estimated following the procedures described by Singh and Chaudhary (1982). The line x tester analysis method for 18 single-cross hybrids, after removing crosses for two lines due to missing crosses, were used in the study. The generic ANOVA for a line × tester analysis is similar to that of the NCD II mating design (Table 3).

The additive genetic variance ($\hat{\sigma}_A^2$) and dominance genetic variance ($\hat{\sigma}_D^2$) were determined by: $\sigma_m^2 = 1/4\,\hat{\sigma}_A^2$, $\sigma_f^2 = 1/4\,\hat{\sigma}_A^2$ and $\sigma_{fm}^2 = 1/4\,\hat{\sigma}_D^2$.

The GCA of lines (GCA_l) and testers (GCA_t), and SCA of crosses (SCA) and their standard errors were estimated (Dabholkar, 1992). The inbred lines were assigned to heterotic groups based on the heterotic specific-group combining ability (HSGCA) described by Fan et al., (2009). The HSGCA was computed as follows:

HSGCA = cross mean – testers mean = GCA + SCA.

The HSGCA is superior to SCA based grouping as it accounts for most of the variation in grain yield and increases the predictability of grain yield of testcrosses (Fan et al., 2009), also confirmed by recent studies (Akinwale et al., 2014). Fan et al., (2009) reported that using HSGCA increased the breeding efficiency by 16.7 – 23.6%.

The yield heterosis (YH_{ij}) of each cross was calculated as: $YH_{ij} = \frac{Y_{ij}-X}{X} \times 100$

Where YH_{ij} is heterosis yield of the cross, Y_{ij} is the grain yield of the cross and X is the mean of grain yield of the testcrosses (Xu et al., 2004).

Soil nutrient analysis

The soil analysis of the Mutanda Research Station trial site is shown in Table 6. The soil P level was below the optimal range of 10-15ppm for high crop productivity (Kisinyo et al., 2009) and thus the site was considered appropriate for low P evaluation (Figure 1). The pH based on $CaCl_2$ in the soil was 4.8, which is lower than pH 5.5 over which P is unavailable to the plants.

Stepwise multiple regression

Stepwise multiple regressions was carried on all the traits after eliminating highly correlated traits (Variance Inflation Factor >10.0). PUE and PAE were retained due to their agronomic importance. The SAS 9.0 software was used in the analysis, using 0.15 significance threshold.

RESULTS

Performance of testcrosses under low soil phosphorus

The testcrosses exhibited variation for performance under low phosphorus conditions (Table 5) with about 44% of the hybrids exhibiting positive heterotic responses ranging from 13.4% to 155.5%. This implies that most of the hybrids would be sources of inbred lines for low soil P breeding. The highest yielding hybrid, L151xJ185 had also the highest PUtE and scored low for P deficiency symptoms. The second highest yielding hybrid was L152xMo17 and the third being L151xMo17. On the other hand, negative heterosis ranged between -4.1% to -57.8%. Hybrid L911xMo17 invested a lot in partitioning the root biomass to the top soil layer (0-10cm). However, this did not correlate with phosphorus uptake efficiency (PAE), implying that much of the biomass produced was for structure build up and anchorage rather than yield related processes. On average, most of the hybrids had invested on average 56.8% of the total root dry matter on the topsoil (0-10cm). This indicates the foraging behaviour of maize genotypes to nutrient stress.

Grain yield and time to pollen-shedding (an indicator for maturity), divided the testcrosses into four quadrants (Figure 1). High yielding hybrids that mature early are desired than those that yield high but mature late. In this respect, hybrids in quadrant IV are preferred than those in quadrant I. Therefore, hybrid H5 can be recommended for release for low P soil conditions. The hybrids H12 and H16 should be preferred compared to H3 and H7 as all had comparative grain yield, except that they were H12 and H16 were early maturing. Hybrid H7 is undesirable as it is a late maturing but low yielding (below average). It means the variety spends much of its energy in non-reproductive processes. The earliest maturing variety was H10 with below average yield of 4.1%. The variety can be recommended for small scale production or late planting in high rainfall areas of Zambia.

Combining ability Analysis for grain yield and other traits

The SCA effects were significant (p≤0.05) for purpling and Danth only. The GCA effects of the testers were significant for purpling while the GCA effects of the lines were significant for purpling, Danth, and PAE (Table 6). The GCA_f effects were significant (P≤0.05) for grain yield, PUE and PUtE. Significant GCA for grain yield has been reported before in maize under low N soil conditions (Miti, 2007). The significant GCA effects imply that additive gene effects were important for grain yield, PUE and PUtE. However, both the GCA and SCA effects were significant for purpling and Danth implying that both additive and non-additive effects, respectively, were important for controlling these traits. However, the GCA/SCA variance ratio was greater than 1, indicating the preponderance of additive gene action in most of the traits except for MSV, Pmgkg, PAE, RdmV20 and Topsoil.

The combining ability effects of the lines are shown in Table 7. All the lines had highly significant (P≤0.01) GCA effects for grain yield and phosphorus uptake. All the females, except L911 and L917 and only two males; B73 and Mo17 had showed highly significant (P≤0.01) GCA effects for PAE. Inbred line L151 and L152 are the best general combiners for grain yield and PUtE under low soil phosphorus. The inbred, L151, had negative GCA effects for days to anthesis and thus it would be useful for breeding high yielding but early maturing hybrids. To the contrary, L152 would be useful for developing late maturing hybrids. Both L151 and L1252 are generally good contributors to the progeny in terms of grain yield, PUE and PUtE. Among the males, Mo17 was the best general combiner for grain yield, P uptake and PAE. This was followed by J185 in terms of grain yield, but the best general combiner for PUtE. The specific combining ability effects revealed a wide range of variation for the traits (Table 8). The cross L917 x B73 had the highest effects for yield with increased PUtE and reduced time to maturity. In terms of PUtE, the cross L151 x J185 possessed the highest effects. In terms of time to maturity, the cross L911 x B73 possessed desirable traits.

Pearson correlation among traits and stepwise multiple regression

Grain yield (GY) was significantly and positively correlated to PUE and PUtE and the two traits were also positively correlated. PAE was negatively correlated to PUE and PUtE, while weakly correlated to GY (Table 9). Pmgkg and PAE where perfectly correlated (r = 1.00, p<0.0001). Highly significant and positive correlations of more than 0.88 were observed between GYkgha and PUtE, Pmgkg and PAE, RdmV0 and TotalRdm and RdmV0 and Topsoil. PAE was negatively correlated to PUE and PUtE, while weakly correlated to GY. RdmV0 was weakly correlated to GY but was strongly and positively correlated to PUE. Root volume at 0-20cm depth was positively correlated to PUE, while PUE was strongly correlated to GY. The P deficiency symptoms were negatively correlated to root biomass below 20-40cm depth.

Stepwise multiple regression showed that most of the traits had high VIF and therefore, only five traits were used in the final analysis (Table 10). Stepwise multiple regression indicated that PUtE explained 87.7% of yield variation and PAE explained only 10.1%, totalling 97.8% (Table 11). All the other traits could not be included as they were beyond the threshold of 0.15 significance for inclusion.

Heterotic orientation of lines

The heterotic group's specific and general combining ability (HSGCA) results are shown in Table 12 for grain yield, PAE and PUtE. These traits were selected as they were found to be highly correlated to grain yield, also supported by stepwise multiple regression (Table 11). Thus it was also necessary to see whether inbred line classification is trait dependent. There was consistency in the grouping of the six inbred lines, except for a few lines. According to Fan et al., (2009), a line that shows positive HSGCA with all the testers is treated as belonging to none of the heterotic groups of the testers. All the inbred lines were grouped into three heterotic groups for PAE. The other traits indicated the existence of a fourth group.

DISCUSSION

Correlation and regression analysis among selected traits

Understanding the interrelationship between nutrient acquisition and utilisation efficiency and how they affect grain yield is important for breeders to identify critical selection traits for enhancing phosphorus use efficiency in crops. The observed strong correlation between PUE and GY is in agreement with those reported by Mendes et al., (2014). The strong positive correlation between PUE and PUtE suggests that selection for increased PUE will result in increased PUtE leading to more increased GY, through PUtE than PUE. There was no correlation of PAE with PUtE and PUE, implying that selection simultaneous selection between PAE and PUtE can be carried out without affecting each other. These results are in agreement with those reported by Mathur (2014). The strong positive correlation between RdmV0 and PUE suggests that the topsoil root volume (0-20cm depth) is important for P uptake efficiency, which is in agreement with other research findings (Raza et al., 2014; Sattelmacher et al., 12994).

Enhancing P efficiency in plants can be achieved through improving PAE and /or PUtE. PAE refers to the ability of the plant to absorb P from the soil, while PUtE measures the ability of the plant to produce grain yield using the acquired P (Wang et al., 2010). Although different mechanisms are at play for PAE under low and optimal conditions, similar plant mechanisms occur for PUtE regardless of soil P level (Parentoni et al., 2010). In ecological studies, Mathur (2014) observed that PAE was 10-37times more important than PUtE. In this study, regression analysis showed that PUtE was 9 times more important than PAE. Our results are in agreement with those of Jiang et al., (2010) and Veneklass et al., (2012). All researchers concluded that PUtE is a reliable selection index for low soil P and potentially more powerful for breeding than PAE.

Heterotic orientation of maize inbred lines

The identification of inbred lines which are heterotic to each other under low soil phosphorus is very important for the release of high yielding and P efficient maize varieties. The identification of heterotic groups depends on the effectiveness of the testers used (Castellanos et al., 1998) and in this case the usage of proven testers with large genetic distance are effective (Melchinger, 1999). In most situations two testers are used for heterotic identification (Li and Chu-Wu, 2007), although it is advantageous to have multiple testers. The temperate testers used in the study had contrasting GCA effects for GY, PAE and PUtE, indicating that they were different. Therefore, they could be used for discriminating lines for low P tolerance. The inbred line, L152, had positive HSGCA for GY and PUtE implying it could be used in the production of 3way cross hybrids.

Combining ability and breeding for P tolerance

The selection criteria for parents for growing under low P soil conditions is based on SCA, GCA and hybrid mean (Aslam et al., 2012). Amongst all the hybrids that had above average grain yield, Hybrid H6 had negative SCA for grain yield and PUtE, while hybrids H9, H8 and H7 had positive and negative SCA for each trait. Aslam et al., (2012) stated that crosses with good mean yield, favourable SCA and at least one parent with high GCA tend to have increased favourable alleles. In our study, out of the 9 hybrids with above average yield, only H6 had unfavourable SCA for yield and PUtE, although all its parents had positive GCA for these traits. Hybrid H16 had favourable SCA (positive) but its parents had unfavourable (negative) GCA for yield and PUtE. Therefore, the only hybrids that met the conditions of accumulating favourable alleles, as suggested by Alam et al.,(2012) are hybrids H5, H3 and H12. We also observed crosses with both parents having favourable GCA for yield and PUtE but variable SCA effects for the two traits. These are hybrids H8 and H9, with H8 and H9 having positive SCA for PUtE and yield respectively. Hybrid H7 had only one parent with positive GCA for yield and PUtE but the SCA effect was positive for PUtE only.

The observed differences in the GCA and SCA effects could be attributed to additive, additive x additive and higher order additive interactions while SCA may be due to the non-additive effects (Aslam et al., 2012). The cross with positive GCA involving parents that have positive GCA suggests an additive x additive type of gene action that can be fixed as long as no repulsion linkages are involved (Meseka and Ashaaq, 2012). On the other hand, the cross with positive SCA involving one parent having negative GCA and another having positive GCA indicates the involvement of additive x dominant gene interactions (Aslam et al., 2012). In such hybrids, the exploitation of heterosis in F1 generation for high yield and PUtE could not be fixed easily in the next generation (Aslam et al., 2012). These crosses can be released and used for commercial production.

The significant GCA effects implied that PUtE and PAE are controlled by additive gene effects. However, the GCA and SCA variances indicated that SCA were larger than GCA for PAE and vice versa for PUtE. This portrays the predominance of non-additive gene action for PAE and additive gene action for PUtE. This implies that recurrent selection for GCA of PUtE could be effective to enhance low P soil tolerance in base populations. The variance of GCA_m was larger than that of GCA_f for PUtE and vice versa for PAE. This indicates the possible role of maternal effects or cytoplasm effects in moderating PAE, hence requiring further study. Based on GCA effects for GY and PUtE, lines L151, L152, J185 and Mo17 are potential candidates for developing hybrids for high rainfall areas. Inbred lines L151 and Mo17 are suited for the development of early maturing varieties as they displayed desired negative effects for DAnth, The desirable GCA effects for GY and PUtE implies that simultaneous improvement for the traits is possible.

Amongst all the crosses with high grain mean yield, the cross involving L151xJ185, had the highest concentration of favourable alleles as all its parents had favourable GCA for yield and PUtE. According to Aslam et al., (2012), low GCA and SCA can be improved through inter and intra population selection. The low GCA for PUtE for inbreds J185 and Mo17 can be improved through inter population selection while the low SCA for yield and PUtE for L913xJ185, L911xMo17, L911xB73 and L1212xMo17 can be improved through intra- population selection. However, inter-population and inter-population crosses can be achieved when the inbreds are classified into heterotic grouping.

Hybrids or crosses with good SCA and *per se* performance can be selected to recover transgressive segregants. Similarly, hybrids with high SCA coming from parents with high x low or average x low GCA could be exploited for heterosis breeding. The high yield from such hybrids or crosses would be non-fixable (Aminu and Izge, 2013). This could be the case for hybrids involving lines L151 and L152 with Mo17 for PUtE and L151 with J185 for PAE. When grain yield is considered, all the hybrids involving lines L151 and L152 with all the testers would constitute high and low GCA crossing of parents.

Table 1. Maize inbred lines used in the study

#	Name	Type	Pedigree	Source
1	L913	Line	Yugoslav germplasm L9 version	ZARI
2	L911	Line	Yugoslav germplasm L9 version	ZARI
3	L917	Line	Yugoslav germplasm L9 version	ZARI
4	L1212	Line	Yugoslav germplasm L12 version	ZARI
5	L151	Line	V01/87923-x-7575-3-3-1-2-3-1	ZARI
6	L152	Line	V01/87923-x-7575-3-3-1-2-3-2	ZARI
7	J185	Tester	SYN Temperate A-SR-F2-4	CIMMYT - Zimbabwe
8	B73	Tester	Iowa Stiff Stalk Synthetic C5	USA
9	Mo17	Tester	C.I.187-2 x C103	USA

Table 2. Agronomic Traits collected

Trait	Description
Grain yield (GYkgha) in Kg/ha	Determined as the total weight of shelled grain harvested from a plot adjusted to 12% grain moisture in tons/ha.
Plant biomass (Biomass) in Kg	The weight of the above ground total dry matter including stalk and ears harvested from the plots.
Purpling score (purple)	Scored as: 1 = Green leaves, 2 = roughly purple leaves, 3 = mild purple leaves, 4 = purple leaves & 5 = very purple leaves. Scoring for purpling was done at grain filling stage (Figure 1).
Maize Streak Virus (MSV)	Maize streak virus score. Score as 1= tolerant/resistant and 5=susceptible
Anthesis silking interval (ASI)	Difference in days between time to silking and pollen shed
Plant tissue phosphorus (Pmg/kg)	Measured as the content of phosphorus in plant tissue using Bray-I method (Bray R.H. and L.T. Kurtz, 1945). Three plants were randomly selected per plot, milled and then sub-samples drawn for laboratory analysis of phosphorus content.
Root Dry matter per Volume (RdmVol) in kg/m^3	Determined by harvesting roots at physiological maturity using an auger (20 cm height and 4 cm radius) at 0-20 cm and 20-40 cm depths of soil. Roots were oven-dried to constant mass for 24 hours at the temperature of 75 ºC and then the average dry-mass taken. The root volume was finally calculated as the mass of dry roots per volume of soil held by the auger in kg/m^3.
Root Biomass Partitioning (Topsoil)	The ratio of root dry matter per volume between at 0-20cm and 20-40cm soil depths

Table 3. Analysis of Variance for combining ability

Source	df	Mean square	Expected mean square
Replication	r-1		
Male	m-1	MS_m	$\sigma^2_e + r\sigma^2_{fm} + rf\sigma^2_m$
Female	f-1	MS_f	$\sigma^2_e + r\sigma^2_{fm}{}^2 + rm\sigma^2_f$
Male × Female	(f-1)(r-1)	MS_{fm}	$\sigma^2_e + r\sigma^2_{fm}$
Error	fm(r-1)	MS_e	σ_e^2

Where: r= replications, m = number of males, f = number of females, σ^2_e = error variance, σ^2_m = variance due to testers, σ^2_f = variance due to lines and σ^2_{fm} = variance due to lines x testers.

Table 4. Soil analysis results (0 – 20cm soil depth)

SN	Element	Quantity
1	Phosphorus*	7.0ppm
2	Magnesium	10.0ppm
3	Potassium	8.0ppm
4	Aluminium	0.0 me%
5	Nitrogen	0.01%
6	pH ($CaCl_2$)	4.8

* Phosphorus level determined using the Bray-I method.

Table 5. Performance of the testcrosses and the checks evaluated under low phosphorus*

Hybrid	Hybrid Code	YH%	GYkgha	DAnth	Purpling	MSV	TotRdm	Pmgkg
L1212xB73	H1	-57.8	1487.50	74.52	3.00	2.51	1.75	1244.18
L1212xJ185	H2	-16.0	2959.87	73.02	1.50	5.01	1.00	1830.68
L1212xMo17	H3	13.5	3998.92	72.38	1.57	3.13	2.36	1212.49
L151xB73	H4	-43.0	2009.66	70.29	3.06	3.10	1.84	1222.41
L151xJ185	H5	155.8	9015.21	68.74	0.95	3.91	1.90	1283.45
L151xMo17	H6	56.0	5495.99	69.92	0.99	2.97	1.96	1861.10
L152xB73	H7	16.7	4111.97	80.88	0.88	3.79	1.78	1567.64
L152xJ185	H8	35.5	4773.90	74.79	1.56	3.10	1.59	1233.91
L152xMo17	H9	90.4	6710.84	74.11	1.02	3.04	1.03	2194.26
L911xB73	H10	-4.1	3381.49	64.06	0.91	2.35	2.09	1677.79
L911xJ185	H11	-27.8	2545.02	71.20	2.54	3.57	2.55	1356.83
L911xMo17	H12	15.4	4068.19	69.83	0.97	4.44	1.44	1570.02
L913xB73	H13	-51.6	1704.83	73.33	4.97	1.94	0.94	1519.02
L913xJ185	H14	-41.8	2052.50	72.20	1.04	3.57	1.56	1814.33
L913xMo17	H15	-88.4	409.28	74.70	2.04	2.57	1.06	1456.33
L917xB73	H16	13.4	3995.71	68.11	4.02	4.04	0.78	1380.26
L917xJ185	H17	-45.6	1918.37	75.83	4.97	0.94	0.94	1919.52
L917xMo17	H18	-20.7	2793.41	66.61	3.02	4.04	1.03	1364.76
Mean			3524.0	71.9	2.2	3.2	1.5	1539.4
Maximum			9015.21	80.88	4.97	5.01	2.55	2194.26
Minimum			409.28	64.06	0.88	0.94	0.78	1212.49
$LSD_{0.05}$			3567.20	5.50	1.97	2.80	1.38	777.59

* YH% = Yield heterosis in percentage, Danth = Days to Anthesis, Purpling = Purpling of leaves, TotBiomass = Total biomass (t/ha), GYkgha = Grain yield (kg/ha), MSV = Maize streak virus, RdmV0 = Root dry matter per volume at 0-20cm soil depth (kg/cm^3), RdmV20 = Root dry matter per volume at 20-40cm soil depth (kg/cm^3), TotRdmV = Total root dry matter per volume at 0-40cm soil depth (kg/cm^3), Rpart = Root Dry matter partitioning between 0-20cm and 20-40cm soil depth, Pmgkg = plant tissue phosphorus content (mg/kg), PAE = phosphorus acquisition efficiency, PUE=phosphorus use efficiency, PUtE= phosphorus utilisation efficiency, Topsoil = proportion of total root dry matter partition to the top soil.

Table 5 (continued). Performance of the testcrosses and the checks evaluated under low phosphorus*

Hybrid	Hybrid Code	PAE	PUE	PUtE	RdmV0	RdmV20	Topsoil
L1212xB73	H1	177.75	0.82	1.23	1.00	0.75	54.88
L1212xJ185	H2	261.51	0.87	1.66	0.50	0.50	49.86
L1212xMo17	H3	173.23	1.72	3.43	1.53	0.82	63.66
L151xB73	H4	174.68	0.77	1.75	1.27	0.55	63.96
L151xJ185	H5	183.36	1.74	7.12	1.22	0.69	59.13
L151xMo17	H6	265.87	0.93	2.95	1.24	0.73	62.73
L152xB73	H7	223.90	0.84	3.11	1.19	0.62	64.56
L152xJ185	H8	176.26	1.07	3.72	1.02	0.55	61.48
L152xMo17	H9	313.47	0.76	3.29	0.51	0.52	49.56
L911xB73	H10	239.66	0.63	2.35	1.45	0.66	68.93
L911xJ185	H11	193.82	0.99	1.91	1.76	0.78	70.14
L911xMo17	H12	224.26	0.82	2.72	0.73	0.71	50.51
L913xB73	H13	216.99	0.40	1.07	0.48	0.46	50.47
L913xJ185	H14	259.25	0.72	1.12	0.52	1.03	36.77
L913xMo17	H15	208.04	0.52	0.34	0.97	0.54	64.89
L917xB73	H16	197.17	0.73	3.29	0.51	0.51	50.96
L917xJ185	H17	274.20	0.59	0.99	0.48	0.46	50.47
L917xMo17	H18	194.96	0.75	2.10	0.51	0.52	49.56
Mean		219.9	0.9	2.5	0.9	0.6	56.8
Maximum		313.47	1.74	7.12	1.76	1.03	70.14
Minimum		173.23	0.40	0.34	0.48	0.46	36.77
$LSD_{0.05}$		111.11	0.72	3.32	2.13	2.13	2.14

* YH% = Yield heterosis in percentage, Danth = Days to Anthesis, Purpling = Purpling of leaves, TotBiomass = Total biomass (t/ha), GYkgha = Grain yield (kg/ha), MSV = Maize streak virus, RdmV0 = Root dry matter per volume at 0-20cm soil depth (kg/cm^3), RdmV20 = Root dry matter per volume at 20-40cm soil depth (kg/cm^3), TotRdmV = Total root dry matter per volume at 0-40cm soil depth (kg/cm^3), Rpart = Root Dry matter partitioning between 0-20cm and 20-40cm soil depth, Pmgkg = plant tissue phosphorus content (mg/kg), PAE = phosphorus acquisition efficiency, PUE=phosphorus use efficiency, PUtE= phosphorus utilisation efficiency, Topsoil = proportion of total root dry matter partition to the top soil.

Table 6. Mean square probability for Line x Tester Analysis*

Source	DF	Purpling	Danth	GYkgha	MSV	TotRdm	Pmgkg
Rep	1	0.724	0.081	0.547	0.005	0.902	0.674
GCA_f	5	0.001	0.001	0.007	0.862	0.056	0.894
GCA_m	2	0.015	0.425	0.118	0.778	0.865	0.412
SCA	10	0.036	0.015	0.103	0.208	0.521	0.176
GCA/SCA ratio	-	0.62	0.34	0.25	0.38	0.62	0.17

Source	DF	PAE	PUE	PUtE	RdmV0	RdmV20	Topsoil Partition
rep	1	0.675	0.866	0.913	0.741	0.549	0.329
GCA_f	5	0.895	0.041	0.054	0.091	0.773	0.365
GCA_m	2	0.412	0.067	0.566	0.845	0.914	0.746
SCA	10	0.176	0.166	0.176	0.498	0.737	0.604
GCA/SCA ratio	-	0.17	0.28	0.27	0.32	0.03	0.14

* Danth = Days to Anthesis, Purpling = Purpling of leaves, TotBiomass = Total biomass (t/ha), GYkgha = Grain yield (kg/ha), MSV = Maize streak virus, RdmV0 = Root dry matter per volume at 0-20cm soil depth (kg/cm^3), RdmV20 = Root dry matter per volume at 20-40cm soil depth (kg/cm^3), TotRdmV = Total root dry matter per volume at 0-40cm soil depth (kg/cm^3), Rpart = Root Dry matter partitioning between 0-20cm and 20-40cm soil depth, Pmgkg = plant tissue phosphorus content (mg/kg), PAE = phosphorus acquisition efficiency, PUE=phosphorus use efficiency, PUtE= phosphorus utilisation efficiency, Topsoil = proportion of total root dry matter partition to the top soil.

Table 7. GCA effects for grain yield and other traits

Lines	GYkgha	Purpling	RdmV0	DAnth	PAE	PUE	PUtE
L1212	-708.61**	-0.14	0.07	1.39**	-15.75**	0.26	-0.35
L151	1982.92**	-0.50	0.31	-2.27**	-11.94**	0.28	1.49**
L152	1674.87**	-1.01**	-0.03	4.67**	17.97**	0.02	0.92*
L911	-192.47**	-0.69*	0.38	-3.55**	-0.66	-0.06	-0.12
L913	-2135.17**	0.51	-0.28	1.49**	8.18**	-0.32	-1.61**
L917	-621.54**	1.84	-0.44*	-1.73**	2.20	-0.18	-0.32
Males							
B73	-742.18**	0.64	0.05	-0.05	-14.88**	-0.17	-0.32
J185	353.44**	-0.07	-0.02	0.71	4.82	0.13	0.30
Mo17	388.73**	-0.57	-0.02	-0.66	10.06**	0.05	0.02

*= significant at p=0.05 and **= significant at p=0.01

Table 8. SCA effects for grain yield and other selected traits

Hybrid	GYkgha	DAnth	PAE	PUE	Purpling	PUtE	RdmV0
L1212 x B73	-585.75**	1.27	-11.53*	-0.15	0.34	-0.56	-0.0566
L1212 x J185	-209.01**	-1.00	52.52**	-0.39	-0.45	-0.75	-0.4871
L1212 x Mo17	794.76**	-0.27	-40.99**	0.53	0.11	1.31	0.5437
L151 x B73	-2755.11**	0.69	-18.41**	-0.21	0.75	-1.87*	-0.0194
L151 x J185	3154.81**	-1.62	-29.43**	0.47	-0.64	2.88**	-0.0004
L151 x Mo17	-399.70**	0.93	47.84**	-0.26	-0.11	-1.01	0.0199
L152 x B73	-344.76**	4.34**	0.91	0.12	-0.91	0.05	0.2379
L152 x J185	-778.44**	-2.52	-66.44**	0.05	0.48	0.05	0.1359
L152 x Mo17	1123.20**	-1.83	65.53**	-0.18	0.43	-0.10	-0.3738
L911 x B73	792.10**	-4.25**	35.30**	-0.01	-1.20	0.34	0.0932
L911 x J185	-1139.99**	2.12	-30.24**	0.05	1.14	-0.72	0.4647
L911 x Mo17	347.89**	2.13	-5.05**	-0.04	0.06	0.37	-0.5579
L913 x B73	1058.13**	-0.02	3.78	0.03	1.65*	0.55	-0.2171
L913 x J185	310.19**	-1.92	26.33**	0.04	-1.57*	-0.03	-0.1181
L913 x Mo17	-1368.32**	1.95	-30.11**	-0.07	-0.08	-0.52	0.3352
L917 x B73	1835.39**	-2.02	-10.05**	0.21	-0.62	1.48	-0.0379
L917 x J185	-1337.57**	4.94**	47.27**	-0.22	1.04	-1.44	0.0051
L917 x Mo17	-497.82**	-2.92	-37.21**	0.01	-0.42	-0.04	0.0329

*= significant at p=0.05 and **= significant at p=0.01

Table 9. Pearson Correlations of Grain Yield with other secondary traits for 18 maize hybrids[1]

	Purpling	GYkgha	MSV	TotRdm	Pmgkg	PAE	PUE	PUtE	RdmV0	RdmV20	Topsoil
DAnth	0.05*	-0.18	-0.21	-0.14	0.14	0.14	-0.09	-0.22	-0.12	-0.10	-0.04
	0.83	0.48	0.41	0.59	0.57	0.57	0.72	0.39	0.64	0.68	0.89
Purpling		-0.52	-0.49	-0.46	-0.18	-0.18	-0.43	-0.44	-0.36	-0.50	-0.20
		0.03	0.04	0.06	0.48	0.48	0.08	0.07	0.14	0.04	0.41
GYkgha			0.33	0.19	0.12	0.12	0.65	0.94	0.14	0.06	0.07
			0.18	0.44	0.63	0.63	0.00	<0.0001	0.57	0.82	0.78
MSV				0.04	-0.13	-0.13	0.33	0.37	-0.04	0.18	-0.15
				0.89	0.59	0.59	0.18	0.13	0.89	0.47	0.56
TotRdm					-0.36	-0.36	0.57	0.29	0.93	0.66	0.66
					0.14	0.14	0.01	0.24	<0.0001	0.00	0.00
Pmgkg						1.00	-0.40	-0.20	-0.46	-0.09	-0.41
						<0.0001	0.10	0.42	0.06	0.71	0.09
PAE							-0.40	-0.20	-0.46	-0.09	-0.41
							0.10	0.42	0.06	0.71	0.09
PUE								0.77	0.51	0.39	0.28
								0.00	0.03	0.11	0.26
PUtE									0.28	0.09	0.19
									0.27	0.72	0.45
RdmV0										0.41	0.88
										0.09	<0.0001
RdmV20											-0.03
											0.90

* = probability in italics

[1] Danth = Days to Anthesis, Purpling = Purpling of leaves, TotBiomass = Total biomass (t/ha), GYkgha = Grain yield (kg/ha), MSV = Maize streak virus, RdmV0 = Root dry matter per volume at 0-20cm soil depth (kg/cm^3), RdmV20 = Root dry matter per volume at 20-40cm soil depth (kg/cm^3), TotRdmV = Total root dry matter per volume at 0-40cm soil depth (kg/cm^3), Rpart = Root Dry matter partitioning between 0-20cm and 20-40cm soil depth, Pmgkg = plant tissue phosphorus content (mg/kg), PAE = phosphorus acquisition efficiency, PUE=phosphorus use efficiency, PUtE= phosphorus utilisation efficiency, Topsoil = proportion of total root dry matter partition to the top soil.

Table 10. Parameter estimates, Tolerance and VIF of the agronomic traits*

	All traits		Selected Traits	
Variable	Tolerance	VIF	Tolerance	VIF
DAnth	0.73206	1.36601	0.90963	1.09935
Purpling	0.09463	10.56784	0.61280	1.63186
MSV	0.25596	3.90684		
TotRdm	0.0077	129.789		
Pmgkg	1.12E-07	8910176		
PAE	1.12E-07	8917148	0.15767	6.34230
PUE	0.0577	17.33108	0.09646	10.36715
PUtE	0.20983	4.76579	0.31908	3.13403
RdmV0	0.0013	770.9532		
RdmV20	0.03314	30.17731		
TopsoilPartition	0.00289	345.8021		

* SE = Standard error, VIF = Variance inflation factor

Table 11. Relative contribution in predicting grain yield and regression model

Parameter	Estimate	Standard error	Probability	Partial R squared
Intercept	-3395.72	483.96	<0.0001	-
PAE	16.35	1.97	<0.0001	0.101
PUtE	1355.61	52.99	<0.0001	0.877
CV	9.29%			
R-Square	0.978			
R-adjusted	0.975			
Cp	-2.71			

Prediction equation: GY = 16.35PAE + 1355.61PUtE – 3395.72

Table 12. Heterotic grouping of the lines based on HSGCA for 3 traits

(a) Grain yield (kg/ha)

	B73	J185	Mo17	HG
L1212	-2036.53	-564.17	474.89	B73
L151	-1514.37	5491.17	1971.95	B73
L152	587.93	1249.87	3186.80	Cautious
L911	-142.55	-979.02	544.15	J185
L913	-1819.21	-1471.53	-3114.75	Mo17
L917	471.67	-1605.66	-730.63	J185

(b) Phosphorus Acquisition Efficiency (PAE)

	B73	J185	Mo17	HG
L1212	-42.16	41.60	-46.68	Mo17
L151	-45.23	-36.55	45.96	B73
L152	3.99	-43.65	93.56	J185
L911	19.75	-26.09	4.35	J185
L913	-2.92	39.34	-11.87	Mo17
L917	-22.74	54.29	-24.95	Mo17

(c) Phosphorus Utilisation Efficiency (PUtE)

	B73	J185	Mo17	HG
L1212	-1.22	-0.80	0.98	B73
L151	-0.70	4.67	0.50	B73
L152	0.65	1.27	0.84	Cautious
L911	-0.10	-0.54	0.26	J185
L913	-1.38	-1.34	-2.12	Mo17
L917	0.84	-1.47	-0.35	J185

(d) summary of groupings

	Grain yield	PAE	PUtE	Final
L1212	B73	Mo17	B73	B73
L151	B73	B73	B73	B73
L152	Cautious	J185	Cautious	New
L911	J185	J185	J185	J185
L913	Mo17	Mo17	Mo17	Mo17
L917	J185	Mo17	J185	J185

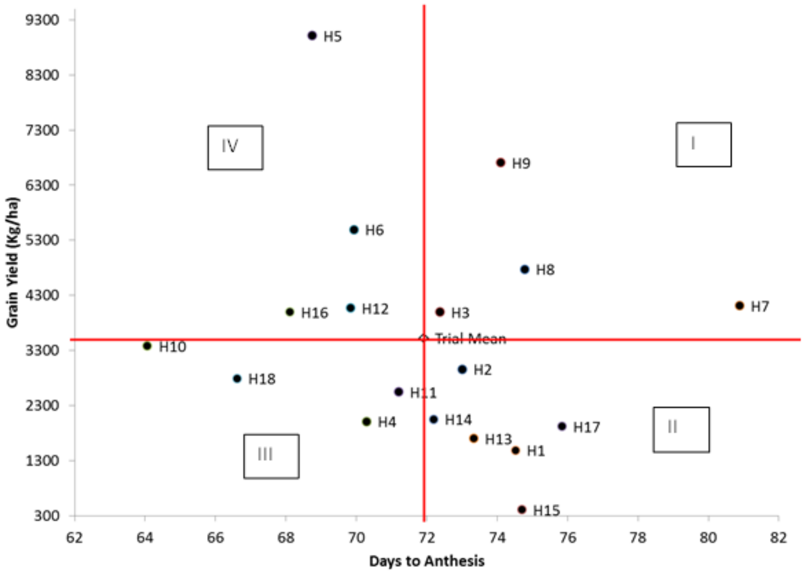

Figure 1. Classification of testcrosses

CONCLUSION

The data presented showed that additive gene action is important for inheritance of grain yield, PUE and PUtE under low P soil conditions. Although, both additive and non-additive gene action seemed important for symptoms of P deficiency (purpling) and phosphorus uptake, there was a preponderance of additive gene action over non-additive gene action for PUE, PUtE, purpling and grain yield. PutE was more important than PAE and therefore, breeders should first select for high grain yield under low P conditions, as suggested by Becker et al., (2013) and DoVale and Fritsche-Neto (2013), followed by PUtE. The inbred lines L151 and L152 had significant GCA effects for grain yield, PUE and PUtE and these can be used for developing low soil P tolerant maize hybrids. The testers, Mo17 and B73 have shown their potential for screening southern African inbred lines. The hybrids, L151xJ185 and L152xJ185 can be released as commercial hybrids as they had high grain yield and PUtE. The hybrids, L917xB73, L151xMo17, L911xMo17, L152xMo17 and L1212xMo17, can be used for extracting inbred lines as they exhibited above average grain yield.

ACKNOWLEDGEMENT

The financial assistance of CIMMYT and AGRA is acknowledged. We thank Mr. George Muchineripi for making the crosses at Muzarabani, Zimbabwe. The contribution made by anonymous reviewers to the earlier draft is appreciated.

REFERENCES

Akhtar MS, Oki Y, Adachi T, Khan MHR. 2007. Analyses of genetic parameters (variability, heritability, genetic advance, relationship of yield and yield contributing characters) for some plant traits among *brassica* cultivars under phosphorus starved environment. Journal of the Faculty of Environmental Science and technology, Okayama University, 12(1): 91 - 98.

Akinwale RO, Badu-Apraku B, Fakorede MAB, Vroh- Bi I. 2014. Heterotic grouping of tropical early-maturing maize inbred lines based on combining ability in striga-infested and striga-free environments and the use of ssr markers for genotyping. Field Crops Research, 156: 48-62.

Aminu D, Izge AU. 2013. Gene action and heterosis for yield and yield traits in maize (*zea mays* l.), under drought conditions in northern guinea and sudan savannas of borno state, nigeria. Peak Journal of Agricultural Sciences, 1 (1): 17-23.

Aslam M, Khan IA, Basra SMA. 2012. Combining ability estimates and some mode of inheritance for drought related traits in genetically distant maize accessions (*zea mays*). Journal of Animal and Plant Sciences, 22(3): 679-682.

Bekunda MA, Bationo A, Ssali H. 1997. Soil fertility management in africa: A review of selected research trials. In: Replenishing soil fertility in africa, R. J. BureshP. A. Sanchez and F. Calhoun, (Eds.). Soil Sci. Soc. of America, Madison Wisconsin, USA: pp: 63-80.

Castellanos JS, Hallauer AR, Córdova HS. 1998. Relative importance of testers to identify elite lines of corn (*zea mays* l.). Maydica, 43: 217-226.

DoVale JC, Fritsche-Neto R. 2013. Genetic control of traits associated with phosphorus use efficiency in maize by reml/blup. Revista Ciencia Agronomica, 44(3): 554-563.

Fageria NK, Baligar VC, Wright RJ. 1988 Aluminum toxicity in crop plants. Journal of Plant Nutrition 11: 303-319.

Fan XM, Zhang YM, Yao WH, Chen HM, Tan J, Xu CX, Han XL, Luo LM, Kang MS.2009. Classifying maize inbred lines into heterotic groups using a factorial mating design. Agronomy Journal, 101(1): 106-112.

Hirel B, Le-Gouis J, Ney B, Gallais A. 2007. The challenge of improving nitrogen use efficiency in crop plants: Towards a more central role for genetic variability and quantitative genetics within integrated approaches. Journal Experimental Botany, 58: 2369-2387.

Kisinyo P, Gudu S, Okalebo CJ, Ochuodho J, Agalo J, Ng'etich W, Opala P, Maghanga J, Osiyo R, Ligeyo D. 2009. Residual effects of lime and phosphorus application on soil and maize (zea mays l.) performance in a kenyan highlands acid soil. Journal of Agriculture, Pure and Applied Science Technology, 3: 1-10.

Kochian LV.1995. Cellular mechanism of aluminum toxicity and resistance in plants. Ann. Rev. J. Plant Physiol., 46: 237-260.

Li L, Chu-Wu L. 2007. Genetic diversity and molecular markers of five snapper species. Chinese Journal of Agricultural Biotechnology, 4: 39-46.

Maia C, DoVale JC, Fritsche-Neto R, Cavatte PC, Miranda GV. 2011. The difference between breeding for nutrient use efficiency and for nutrient stress tolerance. Crop Breeding and Applied Biotechnology, 11: 270-275.

Malama CN. 2001. Evaluating the agronomic potential of tithonia diversifolia prunings in the acid soils on northern zambia. In: CIMMYT, (Ed.) Anonymous, pp: 372 - 376.

Mason NM, Burke WJ, Shipekesa A, Jayne TS.2011. The 2011 surplus in smallholder maize production in zambia: Drivers, beneficiaries, and implications for agricultural and poverty reduction policies. Food Security Research Project: pp: 35.

Mathur M. 2014. Species level phosphorus acquisition efficiency and their relation with bottom-up and top-down factors. Applied Ecology and Environmental Research, 12(1): 123-142.

Melchinger AE. 1999. Genetic diversity and heterosis. In: J. G. Coors and S. Pandey, (Eds.) ASA, CSSA and SSSA, pp: 99-118.

Mendes FF, Guimarães LJM, Souza JC, Guimarães PEO, Magalhaes JV, Garcia AAF, Parentoni SN, Guimaraes CT. 2014. Genetic architecture of phosphorus use efficiency in tropical maize cultivated in a low-p soil. Crop Sci, 54: 1-9.

Meseka S, Ashaaq J. 2012. Combining ability analysis among sudanese and iita maize germplasm at gezira research station. Journal of Applied Biosciences, 57: 4198-4207.

Miti F. 2007. Breeding investigations of maize (zea mays l.) genotypes for tolerance to low nitrogen and drought in zambia. In: School of Biochemistry, Genetics, Microbiology and Plant Pathology. University of KwaZulu-Natal, Petermarizberg: pp: 215.

Ngome AF, Becker M, Mtei MK, Mussgnug F. 2013. Maize productivity and nutrient use efficiency in western kenya as affected by soil type and crop management. International Journal of Plant Production 7 (3): 517-536.

Parentoni SN, Jr CLd, Alves VMC, Gama EEG, Coelho AM, deOliveira AC, Guimarães PEO, Guimarães CT, Vasconcelos MJV, Pacheco CAP, Meirelles WF, deMagalhães JV, Guimarães LJM, daSilva AR, Mendes FF, Schaffert RE. 2010. Inheritance and breeding strategies for phosphorus efficiency in tropical maize (zea mays l.). Maydica, 55: 1-15.

Parentoni SN, Souza-Jr CL. 2008. Phosphorus acquisition and internal utilization efficiency in tropical maize genotypes. Pesq Agropec Bras, 43: 893-901.

Raza A, Imtiaz M, Mohammad W. 2014. Root research for sustainable use of natural resources: A review. January Journal of Scientific Research and Reviews 3(1): 001 - 007.

Rose TJ, Liu L, Wissuwa M. 2013. Improving phosphorus efficiency in cereal crops: Is breeding for reduced grain phosphorus concentration part of the solution? Frontiers in Plant Science, 4(444): 1-6.

Sattelmacher B, Horst WJ, Becker HC.1994. Factors that contribute to genetic variation for nutrient effeciency of crop plants. Z. Pflanzenerriahr Boderic, 157: 215-224.

Veneklaas EJ, Lambers H, Bragg J, Finnegan PM, Lovelock CE, Plaxton WC, Price CA, Scheible W, Shane MW, White PJ, Raven JA. 2012. Opportunities for improving phosphorus use efficiency in crop plants. New Phytologist, 195: 306-320. DOI 10.1111/j.1469-8137.2012.04190.x.

Wang X, Shen J, Liaoa H. 2010. Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops? Plant Science, 179: 302-306.

Whang X, Shen J, Liao H. 2010. Acquisition or utilization, which is more critical for enhancing phosphorus efficiency in modern crops? Plant Science, 179(4): 302-306.

Xu S, Liu J, Liu G. 2004. The use of ssrs for predicting the hybrid yield and yield heterosis in 15 key inbred lines of chinese maize. Hereditas 141: 207-215.

Yerokun OA. 2008. Chemical characteristics of phosphorus in some representative benchmark soils of zambia. Geoderma, 147: 63-68.