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RESEARCH ARTICLE

GENETIC VARIATION IN PHOSPHORUS EFFICIENCY TRAITS IN TROPICAL MAIZE IN LOW P SOILS

*Ouma E. Ochieng and Gudu Samuel

Rongo University College, P.O. Box 103-40404, Rongo, Kenya

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ABSTRACT

Low available phosphorus (P) still remains a major limitation to maize (*Zea mays* L.) productivity in low P soils. The objectives of this study were to (i) determine the extent of genetic variation in P efficiency among selected Kenyan maize under low P soils (ii) select P efficient maize experimental hybrids. A total of 32 experimental hybrids were evaluated for variation in tolerance to low P at high P (36kgP/ha) and low P (6kgP/ha) conditions across four locations using split plot arrangement in RCBD replicated three times. Mean grain yield was significantly lower (2.49 t/ha) across the low P treatment compared to the high P treatments (4.78 t/ha). Relative yield reduction was comparable across the four locations except at Sega where it was a little higher (59.4%). A 48.9% mean yield reduction was observed at the low P treatment compared with the high P treatment across the locations. Eighteen out of the 32 experimental hybrids exhibited Agronomic Efficiency (AE) above the locational mean > 44.8 kgkg⁻¹ P. Mean phosphorus efficiency ratio (PER) of 546.7 kgkg⁻¹ P was obtained across the four locations with Migori exhibiting the highest mean (556.5 kgkg⁻¹ P-1). Majority of the experimental hybrids (57%) had higher phosphorus acquisition efficiency (PAE) than the average of all the genotypes. A mean phosphorus efficiency (PE) of 71.6 % was recorded across the locations. In most cases, genotypes showing higher P efficiency traits (PE, PAE, PUE, AE, PER) had higher grain yield production under low P supply. The genetic variation observed among the maize genotypes demonstrates the potential for maize improvement which will facilitate efficient acquisition and utilization of the limited Pi fertilizers.

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INTRODUCTION

Phosphorus (P) is essential to plants and animal nutrition and is the secondmost limiting nutrient after nitrogen (N) for plant growth and crop production in many agricultural areas in the tropics (Parentoni *et al.*, 2010; Lynch, 2011). It is involved in several key plant functions including energy transfers, photosynthesis, transformation of sugar and starches, nutrient movement within the plants and transfer of genetic characteristics from one generation to the next (White and Hammond, 2008). Phosphorus exists in various mineral forms in the soil including phosphate rock (PR), which is partially made of apatite (an impure tri-calcium phosphate mineral); it is an important commercial source because of the high concentration of P minerals it contains (van Kauwenberg, 2006). Plant roots acquire P from the rhizosphere solution as phosphate (Pi), primarily in the form of orthophosphate ions (H₂PO₄⁻) (White and Hammond, 2008). The concentration of Pi in the soil solution is often low (2–10 μM) and, consequently, the supply of Pi to the root surface by diffusion is slow.

In general, it is estimated that P availability to plant roots is limited in nearly 67% of the cultivated soils, causing an important constraint to crop production (Batjes, 1997). The low available P in these soils is mainly due to the formation of poorly soluble P complexes with calcium in alkaline and aluminium and iron in acidic soils (Oztuk *et al.*, 2005). P deficiency is also due to inherent low soil P and insufficient fertilizer use to replace soil P removed through crop harvests (Obura, 2008).

The available P in western Kenyan acid soils ranges between 2 to 5 mg P/kg soil which is below the optimal range (10 to 15 mg P/kg soil) recommended for high crop productivity (Kisinyo *et al.*, 2013a). Moreover, these soils have high P sorption (107-258 mg P kg) because of the predominant high clay fractions mainly kaolinite, Al and Fe oxides which have large surface area exposed for P sorption (Tisdale *et al.*, 1990; Obura, 2008; Kisinyo *et al.*, 2013a). High P sorption in acid soils make crops to utilize only about 10-25% of the P fertilizer applied (Bahland Singh, 1986). This high rate of P fixation has resulted in very low soil available P hence low maize productivity (< 2 t/ha) in the western Kenya region (Ouma *et al.*, 2012; Ligeyo *et al.*, 2014). The use of Pi

*Corresponding author: Ouma E. Ochieng,
Rongo University College, P.O. Box 103-40404, Rongo, Kenya.

fertilizers to maintain yields, quality and crop production in the current world faces several challenges. For instance, most crops including maize do not recover the entire Pi fertilizer applied (Kisinyo *et al.*, 2013b) owing to P fixation, leaching and other factors (Malakouti *et al.*, 2008). Besides, the inorganic P fertilizer prices have been on the rise in recent years due to increasing demands for feed, food and fuel production (Cordell *et al.*, 2009, Leiser *et al.*, 2014b). Additionally, world experts have already raised alarm concerning the depletion of world's rock P reserves which may only last for the next 40-400 years (Van Kauwenbergh, 2010, Cooper *et al.*, 2011; Cordell and White, 2013; Obersteiner *et al.*, 2013).

These factors call for a quick diversification to more sustainable and ecologically sound crop production strategies. Selecting for P efficient cultivars is therefore very critical in achieving sustainability in agricultural production systems. Utilizing crops that acquire and/or use P more efficiently can greatly reduce the use of Pi fertilizers in agricultural systems. Differential capacity of plant genotypes to acquire and utilize P can be identified and used for germplasm improvement across the world. In other places, it has been shown that P efficient crops produced comparable yields/biomass with lower inputs of inorganic Pi fertilizers and had reduced physiological P requirements and tissue P concentrations, thus significantly reduced the amount of P removed by the crop (Hammond *et al.*, 2009; Oztuk *et al.*, 2005, Leiser *et al.*, 2014).

Efficiency concepts in plant mineral nutrition have been defined based on the processes in which plants acquire, transport, store and use the nutrient to better produce dry matter or grain at low or high nutrient supply (Horst *et al.*, 1993).

The common measures of P efficiency include: grain yield under low P conditions, agronomic P use efficiency (AE) which is the increase in yield per unit of added P fertilizer (Kg kg^{-1}), P acquisition efficiency (PAE) which is the product of the increase in plant P content per unit of added P fertilizer ($\text{Kg P kg}^{-1} \text{g Pf}$), P utilization efficiency (PUE) which is the increase in yield per unit increase in plant P content (Kg kg^{-1}) and P efficiency (PE) (relative grain yield) (Moll, 1982; Baligar and Fageria, 1997; Oztuk *et al.*, 2005; White and Hammond, 2008; Hammond *et al.*, 2009; Serpher *et al.*, 2009). In this study selection based on P in acquisition and utilization efficiencies as well as grain yield under low P conditions were adopted for discriminating the genotypes. The objectives of this study were to (i) determine the extent of genetic variation in P efficiency among selected Kenyan maize under low P soils (ii) select P efficient experimental maize hybrids.

MATERIALS AND METHODS

Genetic Material

A total of 32 experimental maize hybrids comprising 9 three way cross hybrids, 5 double cross hybrids, 9 backcrosses, 5 single crosses and 4 checks (efficient and inefficient) were evaluated for tolerance to low P in a replicated trial at four locations (Sega, Chepkoilel, Migori and Koyonzo) during the long rain of 2013. The details of experimental locations are described in Table 1.

Table 1. Experimental Location characteristics

| Site | Latitude | Longitude | Altitude | mean | Annual | Soil type |
|-----------|----------|------------|----------|----------|--------------|--------------------|
| Name | (°) | (°) | masl | Temp(°C) | rainfall(mm) | |
| Chepkolel | 0° 37' N | 035° 15' E | 2143 | 22 | 1300 | Chromic ferralsols |
| Sega | 0° 15' N | 34° 20' E | 1200 | 25 | 1000 | Orthic Acrisols |
| Migori | 1° 03' S | 34° 24' E | 1381 | 24 | 1200 | humic ferralsols |
| Koyonzo | 0° 25' N | 34° 25' E | 1310 | 23 | 1400 | Luvvisols |

Soil Sampling, Preparation and Characterization

Soil sampling was done by taking six sub-samples with a soil auger at the 0-30 cm soil depth in a zig-zag pattern at the four locations. The sub-samples were thoroughly mixed and about 1.2 kg composite samples packed in a black polythene bag and transported to the lab where they were air-dried, ground and passed through a 2 mm sieve. They were then analysed for texture, pH (1:2.5 (soil: water), available P, exchangeable bases (Ca^{2+} , Mg^{2+} , K^{2+}) and Al^{3+} using the procedures of Okalebo *et al.* (2002) and Olsen *et al.*, 1954.

Experimental Design

The experiment was laid out in a split plot arrangement in RCBD replicated three times. Main plot contained 2 levels of P (6 KgP/ha and 36KgP/ha supplied as TSP) while the genotypes were randomized in the sub plot. Each genotype was planted in a two row plot measuring three meters long with inter and intra-row spacing of 0.75 m x 0.30 m respectively. Two seeds were sown per hill and later thinned to one per hill. Digger program in Genstat was used to generate randomization design and field layout. All the plots were side-dressed using calcium Ammonium Nitrate (CAN) at the rate of 75 Kg N/ha. All standard agronomic practices were followed.

Data collection

At maturity, data was collected on grain yield, (GYLD-t/ha), Stover yield (STV= leaves, stalks, ear husks and cobs- t/ha), grain P concentration (GPC %) and grain P content (GPcnt Kg/ha). At maturity, all the cobs in a row for each entry were harvested and adjusted to 13% moisture content while assuming an 80% shelling percentage. The moisture content was then determined from a sample of 10 randomly selected cobs. Stover samples were collected from 10 plants and a sample of 300g of grain obtained from each plot. These samples were oven dried at 80°C to a constant weight and grain and stover dry matter determined. Grain and stover samples were ground and analyzed for P concentration using the vanadomolybdate method (Westerman, 1990). Based on grain and stover dry matter yields, and on P concentration in these plant components, the phosphorus content in the grain and in the stover were determined. The P efficiency parameters were then obtained on a plot basis following the procedures of Moll *et al.* (1982, Hammond *et al.* (2009) and Parentoni *et al.* (2010) as follows:

- Agronomic P use efficiency (AE) = $(Y_{\text{high}} - Y_{\text{low}}) / D_{\text{Papp}}$ (kg/Kg Pf)

- b. P uptake efficiency (PAE) = $[(P_{high} \times Y_{high}) - (P_{low} \times Y_{low})] / D_{papp}$ (KgP/kgPf)
- c. P utilization efficiency (PUE) = $(Y_{high} - Y_{low}) / [(P_{high} \times Y_{high}) - (P_{low} \times Y_{low})]$ (kg/ kg)
- d. P efficiency ratio (PER) = $Y_{high} / (P_{high} \times Y_{high})$ or $Y_{low} / (P_{low} \times Y_{low})$ kg/kg
- e. Phosphorus Efficiency (PE) = $Y_{low} / Y_{high} \times 100\%$

Where: Y_{high} is the yield on a high P or fertilized soil; Y_{low} is the yield on a low P/unfertilized soil; P_{high} is the tissue P concentration on a high P or fertilized soil; P_{low} tissue P concentration on a low P or unfertilized soil; D_{papp} difference in amount of P applied as fertilizer between high and low P treatments; Pf- Pfertilizer.

Statistical Analysis

All means computation and variance analysis (ANOVA) were done using Genstat Version 18 (Payne *et al.*, 2014). The protected least significant difference (LSD) was used for mean separation. An individual Anova was done for all the traits in each of the 2 P levels per location. A combined ANOVA for the two P levels across the locations was done after verifying data homogeneity. ANOVA was done by fitting the split plot model for the data:

Where Y_{ijklm} is the observation on the $ijklm^{th}$ plot, μ – the general mean, S_i -the effect due to the i^{th} location, $B_{k(i)}$ the effect due to the k^{th} replication in i^{th} location, P_j -effect due to the j^{th} phosphorus level, SP_{ij} -effects due the interaction of the j^{th} phosphorus level with the i^{th} location, ϵ_{ijkl} -is the residual effect due to $ijkl^{th}$ whole plot, G_m is the effect due to the m^{th} genotype in the k^{th} replicate, SG_{im} is the effect due to the m^{th} genotype in the k^{th} replicate in the i^{th} location, SPG_{ijm} is the effect due to the m^{th} genotype in j^{th} level of phosphorus in the k^{th} replicate in the i^{th} location ϵ_{ijklm} is the residual effect due to *subplot* Relative Yield Reduction (RYR) was calculated according to Leiser *et al.*, 2012 where $RYR = 1 - (MeanYield_{-p} / MeanYield_{+p}) \times 100\%$.

Table 1. Location soil chemical and physical characteristics

| Experimental site | pH | P (mg/kg) | %N | %C | cmo/kg | | | | % Al | % Sand | % Clay | % Silt | Textural Class | |
|-------------------|------|-----------|------|------|--------|------|------|------|------|--------|--------|--------|----------------|-----------------|
| | | | | | K | Ca | Mg | Al | | | | | | ECEC |
| Koyonzo | 5.40 | 3.40 | 0.12 | 2.69 | 0.06 | 3.52 | 2.46 | 1.07 | 7.11 | 15 | 54 | 29 | 17 | sandy clay loam |
| Chepkoiel | 4.80 | 4.40 | 0.13 | 3.51 | 0.07 | 1.93 | 1.76 | 2.20 | 5.28 | 45 | 18 | 66 | 16 | clay |
| Sega | 4.65 | 2.30 | 0.13 | 2.69 | 0.04 | 2.81 | 1.72 | 2.10 | 6.54 | 30 | 28 | 56 | 16 | Clay |
| Migori | 5.80 | 2.66 | 0.10 | 1.60 | 0.80 | 3.47 | 1.73 | 1.02 | 6.40 | 12 | 32 | 33 | 15 | sandy clay loam |

Note: ECEC = effective cation exchange capacity, Al-aluminium.

RESULTS

Initial Soil Characteristics of the study Locations

The soils were found to be generally of low fertility. Sega and Chepkoiel soils were strongly acidic (pH 4.5 – 4.80), while Migori and Koyonzo soils were non-acidic (pH 5.4 – 5.8). However, soil available P was low at all the locations.

Total N, organic carbon, Ca and cation exchange capacity (CEC) were also low at all the locations (Table 2).

Table 3. Mean square for grain and stover yields for maize hybrids across 4 locations

| Source of variation | d.f. | GYLD | STV |
|-----------------------|------|------------|-------------|
| Replication | 2 | 0.07 | 0.8237 |
| Location (Loc) | 3 | 524.645*** | 3000.93*** |
| Phosphorus level (PL) | 1 | 347.01*** | 1209.30*** |
| Loc.PL | 3 | 19.63*** | 110.4318*** |
| Pooled Error (A) | 14 | 0.45 | 5.3892 |
| Genotype (Geno) | 31 | 10.44*** | 68.0895 |
| Loc.Geno | 93 | 2.34*** | 22.0055 |
| PL.Geno | 31 | 0.55*** | 3.5465 |
| Loc.PL.Geno | 93 | 0.67*** | 4.9123 |
| Pooled Error (B) | 493 | 0.13 | 0.8976 |
| Grand mean | | 4.11 | 8.5 |
| CV | | 8.7 | 11.1 |

Note. GYLD-grain yield, STV-Stover yield

Analysis of variance for agronomic traits and means

ANOVA Table shows highly significant variation ($P=0.01$) among Locations (L) for all the traits measured. Phosphorus levels (P) were also significantly different for all the traits (Table 3).

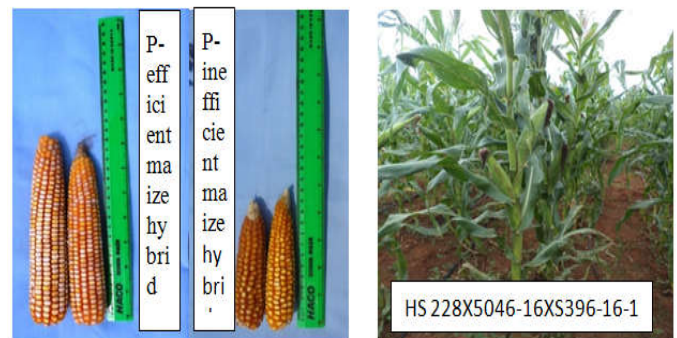


Figure 1. P-efficient (HS 228X5046-16XS396-16-1) and inefficient (S396-16-1) maize hybrids grown on low P soils of Migori location in 2013

The low P treatment generally exhibited reduced GYLD and STV relative to the corresponding high P treatment (Table 4).

Mean grain yield was significantly lower (2.49 t/ha) across the low P treatment compared to the high P treatment (4.78 t/ha) although there was a rather big range (35-95%) for relative yield reduction (RYR) among the hybrids. Figure 1 shows pictures of P-efficient and inefficient maize hybrids.

Table 4. Mean grain and stover yields and relative grain yield reduction of maize hybrids tested for P-efficiency across 4 locations in western Kenya

| Hybrid Name | Grain yield (t/ha) | | RYR | Stover yield (t/ha) | |
|--|--------------------|-------------|-------|---------------------|-------------|
| | 36 kgP/ha | 6 kgP/ha | % | 36 kgP/ha | 6 kgP/ha |
| KML 036 XS396-16-1 | 5.43 | 3.05 | 43.81 | 10.87 | 8.93 |
| HS 228-5046-16XS396-16-1 | 5.56 | 2.89 | 47.99 | 11.11 | 7.91 |
| HS L3-5046-2XS396-16-1 | 5.14 | 2.61 | 49.14 | 10.21 | 7.65 |
| HS L3-5046-2XMUL 229 | 5.00 | 2.47 | 50.68 | 8.04 | 5.78 |
| KML 036 XMUL 229 | 5.17 | 2.69 | 47.92 | 8.81 | 6.25 |
| HS 228-5046-16XS396-16-1XHS 228-5046-16 | 4.32 | 2.00 | 53.74 | 8.36 | 7.23 |
| HS 228-5046-16XS396-16-1XS396-16-1 | 4.11 | 2.06 | 49.91 | 9.60 | 6.64 |
| KML 036 XS396-16-1XKML036 | 4.15 | 2.17 | 47.65 | 9.04 | 6.94 |
| KML 036 XMUL 229XKML036 | 4.62 | 2.20 | 52.37 | 7.80 | 5.70 |
| KML 036 XMUL 229XMUL 229 | 3.89 | 1.58 | 59.45 | 7.62 | 4.72 |
| HS L3-5046-2XMUL 229XHS L3-5046-2 | 4.53 | 2.29 | 49.41 | 8.66 | 6.11 |
| HS 228-5046-16XMUL 229XMUL229 | 4.06 | 2.10 | 48.26 | 7.61 | 5.98 |
| HS 228-5046-16XMUL 229XHS 228-5046-16 | 4.47 | 2.14 | 52.12 | 9.39 | 6.51 |
| HS L3-5046-2XS396-16-1XHS L3-5046-2 | 5.01 | 3.24 | 35.32 | 10.16 | 8.34 |
| KML 036 XAO89XMUAPII SR | 4.90 | 2.47 | 49.63 | 9.16 | 6.53 |
| MUL 229XHS 228-5046-16XHS L3-5046-2 | 4.56 | 2.93 | 35.67 | 8.72 | 7.43 |
| MUL 229XHS 228-5046-2XMUAP II SR | 4.56 | 2.27 | 50.20 | 8.98 | 6.90 |
| HS L3-5046-2XMUL 229XMUAP II SR | 5.30 | 2.75 | 48.17 | 10.80 | 7.98 |
| KML O36 XMUL 229XMUAP II SR | 5.36 | 3.05 | 43.04 | 9.43 | 7.52 |
| KML 036 XS396-16-1XPOOL 9A BASF | 4.59 | 2.31 | 49.73 | 11.11 | 8.36 |
| KML O36 XMUL 229XMUAP II SR | 5.23 | 2.75 | 47.37 | 10.68 | 7.58 |
| HS L3-5046-2XMUL 229XPOOL 9A BASF | 4.89 | 2.77 | 43.44 | 9.12 | 6.82 |
| S596-41-2-2-MUL 204XBRS1001XKRISTALOPVX82-93-3 | 5.42 | 3.27 | 39.64 | 11.44 | 9.31 |
| KML 036 XMUL 229XKML 036 XS396-16-1 | 4.34 | 2.54 | 41.48 | 12.06 | 7.54 |
| KML 036 XMUL 229XHS L3-5046-2XMUL 229 | 4.51 | 2.46 | 45.54 | 8.02 | 5.50 |
| S396-16-1XHS L3-5046-2XHS L3-5046-2XMUL 229 | 5.59 | 2.90 | 48.08 | 9.93 | 7.73 |
| MUL 229XHS 228-5046-16XHS L3-5046-2XMUL 229 | 5.03 | 2.64 | 47.54 | 8.94 | 6.44 |
| MUL 229XHS 228-5046-16XKML 036 XS396-16-1 | 4.98 | 2.44 | 50.91 | 11.56 | 8.38 |
| S396-16-1 | 2.20 | 0.12 | 94.78 | 8.88 | 4.43 |
| AO89 | 4.16 | 2.00 | 51.84 | 8.09 | 6.51 |
| H515 | 5.60 | 3.21 | 42.66 | 12.83 | 10.74 |
| MEDIUM ALTITUDE SYNTHETIC | 6.41 | 3.27 | 48.96 | 16.36 | 12.68 |
| G.MEAN | 4.78 | 2.49 | 48.95 | 9.79 | 7.28 |
| SE | 0.34 | 0.33 | | 0.54 | 0.44 |
| SED | 0.12 | 0.11 | | 0.26 | 0.25 |
| LSD (0.05) | 0.32 | 0.25 | | 0.90 | 0.53 |

Note. RYR-relative yield reduction

Table 5. Locational mean grain and stover yields of maize hybrids combined across 4 locations in 2014

| Location | P level | Grain yield t/ha | RYR % | Stover yield t/ha |
|------------|-----------|---------------------|----------|----------------------|
| Chepkoilel | 36 kgP/ha | 6.74 | 47.66 | 9.47 |
| | 6 kgP/ha | 3.60 | | 7.43 |
| Migori | 36 kgP/ha | 5.20 | 43.89 | 13.98 |
| | 6 kgP/ha | 2.97 | | 11.23 |
| Koyonzo | 36 kgP/ha | 5.14 | 42.49 | 9.12 |
| | 6 kgP/ha | 2.94 | | 6.88 |
| Sega | 36 kgP/ha | 2.12 | 59.35 | 4.99 |
| | 6 kgP/ha | 0.89 | | 3.46 |
| LSD (0.05) | 36 kgP/ha | 0.42 | | 1.16 |
| | 6 kgP/ha | 0.19 | | 0.64 |

Note. RYR-relative yield reduction

Mean grain yield was highest at Chepkoilel location for both P conditions (6.7 and 3.6 t/ha) and lowest at Segal location (2.1 and 0.9 t/ha)(Table 5). RYR was fairly comparable across the four locations (42.5-47.7%) except at Segal where it was higher (59.4%) (Table 5).

Other phosphorus efficiency traits

There was significant variations ($P=0.05$) for Agronomic P efficiency (AE), P-efficiency ratio (PER), P-acquisition efficiency (PAE), P-efficiency (PE) and P-utilization efficiency for the maize genotypes across 4 locations (Table 6). The P-efficiency traits measured were generally higher in the experimental hybrids compared to some of the checks. AE was in the range of 22.7-72.9 kgkg⁻¹ with a mean of 44.8 kgkg⁻¹. Eighteen out of the 32 genotypes exhibited AE above the mean > 44.8 kgkg⁻¹ while 13 of the hybrids had higher AE than the commercial hybrid check (H515) across the four locations (Table 6).

(85.2%) and the lowest in 31(48.4%). In most cases, genotypes showing higher PE also exhibited higher PER and PAE. Nine of the hybrids had higher PE than the commercial check while 13 genotypes exhibited higher PE than the average (Table 6). PUE ranged from 208.8 kgkg⁻¹ (hybrid 18) to 977.5 kgkg⁻¹ (hybrid 17). Majority of the genotypes (63%) gave lower values for PUE than the average (553.4kgkg⁻¹). In most cases genotypes with higher values of PUE also expressed higher values of PAE. A total of 12 hybrids were selected based on PUE above the average across the four locations. Majority of these were also the best performers under low P across the locations.

Table 7 shows mean AE, PER, PAE, PE and PUE across 4 locations. AE was highest at Chepkoilel (104.5 kgkg⁻¹) and lowest at Segal (41 kgkg⁻¹). Koyonzo and Migori gave comparable AE. PER was highest at Migori (556.5 kgkg⁻¹) although this did not differ significantly with Segal (536.2) location while the lowest PER was realized at Koyonzo.

Table 6. Variation in Agronomic P efficiency (AE), P efficiency ratio (PER), P-acquisition efficiency (PAE), P efficiency (PE) and P use efficiency (PUE) of experimental maize hybrids tested for tolerance to low P soils across 4 locations in western Kenya

| Maize | AE | PER | PAE | PE | PUE |
|---|-------|---------|---------|-------|--------|
| Hybrid | Kg/Kg | Kg/Kg | KgP/kgf | % | Kg/Kg |
| KML 036 XS396-16-1 | 47.60 | 481.56 | 0.18 | 73.69 | 464.87 |
| HS 228-5046-16XS396-16-1 | 57.33 | 610.83 | 0.15 | 69.09 | 519.91 |
| HS L3-5046-2XS396-16-1 | 52.47 | 696.96 | 0.13 | 69.35 | 554.06 |
| HS L3-5046-2XMUL 229 | 52.80 | 597.01 | 0.14 | 68.32 | 670.27 |
| KML 036 XMUL 229 | 50.97 | 645.44 | 0.09 | 70.44 | 711.05 |
| HS 228-5046-16XS396-16-1XHS 228-5046-16 | 45.63 | 529.64 | 0.18 | 68.27 | 595.03 |
| HS 228-5046-16XS396-16-1XS396-16-1 | 36.73 | 442.94 | 0.06 | 73.19 | 747.88 |
| KML 036 XS396-16-1XKML036 | 34.27 | 452.35 | 0.13 | 75.23 | 349.59 |
| KML 036 XMUL 229XKML036 | 48.97 | 604.80 | 0.07 | 68.20 | 897.25 |
| KML 036 XMUL 229XMUL 229 | 45.37 | 445.50 | 0.15 | 64.99 | 487.66 |
| HS L3-5046-2XMUL 229XHS L3-5046-2 | 42.93 | 443.12 | 0.10 | 71.56 | 507.55 |
| HS 228-5046-16XMUL 229XMUL229 | 33.63 | 413.85 | 0.06 | 75.14 | 458.27 |
| HS 228-5046-16XMUL 229XHS 228-5046-16 | 46.07 | 506.17 | 0.13 | 69.11 | 586.88 |
| HS L3-5046-2XS396-16-1XHS L3-5046-2 | 27.27 | 555.23 | 0.07 | 83.66 | 398.61 |
| KML 036 XAO89XMUAPII SR | 49.37 | 510.15 | 0.08 | 69.76 | 977.49 |
| MUL 229XHS 228-5046-16XHS L3-5046-2 | 22.57 | 400.42 | 0.09 | 85.16 | 208.80 |
| MUL 229XHS 228-5046-2XMUAP II SR | 44.57 | 578.62 | 0.20 | 70.65 | 713.51 |
| HS L3-5046-2XMUL 229XMUAP II SR | 53.43 | 637.33 | 0.11 | 69.75 | 699.84 |
| KML 036 XMUL 229XMUAP II SR | 45.17 | 506.24 | 0.12 | 74.70 | 477.36 |
| KML 036 XS396-16-1XPOOL 9A BASF | 44.33 | 504.64 | 0.15 | 70.99 | 489.16 |
| KML 036 XMUL 229XMUAP II SR | 50.83 | 514.79 | 0.16 | 70.81 | 449.39 |
| HS L3-5046-2XMUL 229XPOOL 9A BASF | 39.13 | 535.85 | 0.20 | 75.99 | 428.93 |
| S596-41-2-2-MULXBRS1001XKRSTOPVX82 | 39.90 | 1248.73 | 0.20 | 77.90 | 538.64 |
| KML 036 XMUL 229XKML 036 XS396-16-1 | 28.40 | 583.88 | 0.07 | 80.39 | 498.24 |
| KML 036 XMUL 229XHS L3-5046-2XMUL 229 | 36.77 | 431.53 | 0.16 | 75.53 | 383.96 |
| S396-16-1XHS L3-5046-2XHS L3-5046-2XMUL 229 | 57.97 | 474.80 | 0.17 | 68.91 | 458.14 |
| MUL 229XHS 228-5046-16XHS L3-5046-2XMUL 229 | 48.03 | 413.57 | 0.19 | 71.35 | 411.11 |
| MUL 229XHS 228-5046-16XKML 036 XS396-16-1 | 52.77 | 495.79 | 0.16 | 68.18 | 498.55 |
| S396-16-1 | 37.87 | 232.06 | 0.14 | 48.39 | 435.15 |
| AO89 | 40.17 | 484.34 | 0.17 | 71.01 | 438.07 |
| H515 | 47.93 | 765.52 | 0.16 | 74.31 | 793.29 |
| MEDIUM ALTITUDE SYNTHETIC | 72.93 | 749.45 | 0.17 | 65.86 | 860.18 |
| G.MEAN | 44.82 | 546.66 | 0.14 | 71.56 | 553.40 |
| LSD (0.05) | 4.29 | 50.03 | 0.01 | 4.89 | 42.85 |

The genotypes attained a mean PER of 546.7 kgkg⁻¹ across the four locations. PAE ranged from 0.2–0.06 kgP/kgf. Hybrid 19, 24 and 25 exhibited the highest PAE while hybrid 8 and 14 the lowest. Majority of the genotypes (57%) had higher PAE than the average of all the genotypes. Eight of the hybrids (19, 24, 25,29,1,7,28 and 40) also showed higher PAE than the commercial check (H515) across the locations. Mean % PE was 71.6 % across locations with the highest in hybrid 18

PAE was highest at both Chepkoilel and Migori and lowest at Segal location while the highest PUE was realized at Segal followed by Koyonzo and was least at Chepkoilel (Table 7).

Grain and stover P concentration

Grain and Stover P concentrations were generally higher with high P regimes than low ones for all the genotypes.

Table 7. Locational mean agronomic efficiency, P-efficiency ratio, P-acquisition efficiency, P-efficiency and P-utilization efficiency of maize experimental hybrids tested at 4 locations in 2014

| Site | AE | PER | PAE | PE | PUE |
|------------|--------|--------|---------|-------|---------|
| | Kg/Kg | Kg/Kg | KgP/kgf | % | Kg/Kg |
| Chepkoilel | 104.5a | 494.4a | 0.21a | 52.3b | 723.5a |
| Migori | 74.4b | 556.5b | 0.20a | 56.1a | 778.5ab |
| Koyonzo | 73.2b | 486.2a | 0.15b | 57.5a | 969.6c |
| Sega | 41.0c | 536.2b | 0.09c | 40.6c | 971.6c |

Means in the same column followed by the same letter are not significantly different: AE-agronomic efficiency, PER-phosphorus efficiency ratio, PAE-P acquisition efficiency, PE-phosphorus efficiency, PUE- phosphorus utilization efficiency

With the application of high P, the average grain P concentration increased significantly from 0.15% to 0.19% while that of stover P from 0.03 to 0.06%. Under high P supply, grain P was highest in hybrids 25, 18 40, 23 and 1 (0.21%) while lowest with hybrid 27 (0.18%), while stover P concentration was highest and lowest (0.09, 0.05 %) in, genotypes 31 and 39, respectively. Under low P supply, grain P concentration (GPC) ranged from 0.14 to 0.17 % while stover P concentration (STVPC) from 0.01 -0.05 % (Table 9).

Grain and Stover P content

For grain and stover P contents, application of high P level resulted in 2 folds increment in these parameters (Table 8). Moreover, genetic differences were evident among the genotypes. Grain P content was generally higher than stover P content at both P levels for the 32 maize genotypes across the four locations. Low P supply resulted into significant reduction (up to 52%) in grain P content and up to 85% in stover P content across the four locations (Table 8). For grain P content the reduction due to low P supply ranged from 1.6 kg/ha at Sega to 4.7 kg/ha at Chepkoilel. Similarly, stover P content reduced from 0.5 kg/ha in Sega to 3 kg/ha in Chepkoilel location. Chepkoilel location exhibited the highest grain P content while Sega the lowest (Fig 2).

DISCUSSION

Estimates of overall efficiency of applied P fertilizer are often very low (less than 10%). Plants that are efficient in absorption and utilization of nutrients greatly enhance the efficiency of applied fertilizers hence reducing costs to farmers, and preventing losses of nutrients to ecosystems (Fageria and Baligar, 1999).

Table 8. Effects of high and low phosphorus on grain and Stover P concentration and grain and Stover P content of experimental maize hybrids tested for P-efficiency across 4 locations in Kenya

| Maize | Grain P conc. (%) | | Stover P conc. (%) | | GPCNT (Kg/ha) | | SPCNT (Kg/ha) | |
|------------|-------------------|---------|--------------------|---------|---------------|---------|---------------|---------|
| | 36 kgP/ha | 6kgP/ha | 36kgP/ha | 6kgP/ha | 36kgP/ha | 6kgP/ha | 36kgP/ha | 6kgP/ha |
| Hybrid | | | | | | | | |
| 1 | 0.21 | 0.14 | 0.07 | 0.03 | 11.3 | 6.5 | 6.4 | 2.6 |
| 2 | 0.20 | 0.15 | 0.06 | 0.03 | 9.1 | 4.1 | 4.1 | 1.6 |
| 3 | 0.19 | 0.15 | 0.06 | 0.04 | 7.4 | 2.8 | 4.0 | 1.4 |
| 5 | 0.18 | 0.15 | 0.07 | 0.04 | 8.4 | 4.3 | 5.5 | 2.3 |
| 6 | 0.20 | 0.15 | 0.06 | 0.03 | 8.0 | 4.2 | 3.7 | 1.7 |
| 7 | 0.19 | 0.15 | 0.06 | 0.01 | 8.1 | 4.1 | 5.6 | 1.0 |
| 8 | 0.19 | 0.15 | 0.06 | 0.04 | 9.3 | 6.1 | 5.1 | 3.2 |
| 9 | 0.19 | 0.14 | 0.06 | 0.04 | 9.2 | 4.5 | 4.3 | 1.8 |
| 10 | 0.19 | 0.16 | 0.06 | 0.03 | 7.6 | 4.3 | 4.3 | 2.3 |
| 11 | 0.19 | 0.15 | 0.06 | 0.02 | 8.7 | 4.2 | 4.5 | 1.5 |
| 13 | 0.19 | 0.17 | 0.06 | 0.04 | 10.2 | 6.0 | 4.9 | 3.0 |
| 14 | 0.18 | 0.15 | 0.04 | 0.03 | 9.8 | 5.9 | 3.5 | 2.4 |
| 15 | 0.19 | 0.15 | 0.06 | 0.03 | 8.8 | 4.8 | 5.6 | 2.7 |
| 16 | 0.17 | 0.15 | 0.05 | 0.04 | 9.0 | 5.3 | 4.3 | 2.9 |
| 17 | 0.19 | 0.17 | 0.05 | 0.03 | 9.6 | 6.4 | 3.8 | 1.5 |
| 18 | 0.21 | 0.15 | 0.05 | 0.05 | 11.4 | 6.4 | 5.0 | 4.1 |
| 19 | 0.19 | 0.15 | 0.08 | 0.02 | 7.9 | 4.3 | 7.3 | 1.7 |
| 20 | 0.19 | 0.15 | 0.06 | 0.03 | 8.3 | 4.3 | 4.1 | 1.5 |
| 21 | 0.20 | 0.15 | 0.05 | 0.04 | 10.6 | 6.0 | 4.6 | 2.6 |
| 22 | 0.18 | 0.14 | 0.05 | 0.02 | 9.1 | 4.7 | 4.5 | 1.4 |
| 23 | 0.21 | 0.16 | 0.07 | 0.05 | 10.1 | 5.1 | 5.9 | 3.1 |
| 24 | 0.19 | 0.15 | 0.06 | 0.02 | 9.1 | 4.7 | 6.9 | 2.3 |
| 25 | 0.21 | 0.15 | 0.08 | 0.06 | 4.3 | 0.4 | 7.7 | 2.4 |
| 26 | 0.18 | 0.16 | 0.05 | 0.04 | 7.4 | 4.0 | 4.1 | 2.3 |
| 27 | 0.18 | 0.15 | 0.07 | 0.03 | 10.4 | 5.9 | 7.7 | 4.3 |
| 28 | 0.19 | 0.15 | 0.05 | 0.04 | 11.8 | 6.3 | 5.0 | 2.3 |
| 29 | 0.20 | 0.16 | 0.08 | 0.04 | 12.2 | 7.0 | 10.2 | 6.7 |
| 30 | 0.20 | 0.17 | 0.05 | 0.02 | 10.0 | 5.2 | 4.2 | 1.2 |
| 31 | 0.19 | 0.15 | 0.05 | 0.03 | 9.5 | 5.2 | 4.4 | 1.4 |
| 33 | 0.20 | 0.16 | 0.06 | 0.02 | 8.6 | 4.1 | 5.3 | 1.6 |
| 39 | 0.19 | 0.17 | 0.09 | 0.03 | 7.3 | 3.8 | 6.4 | 2.0 |
| 40 | 0.21 | 0.16 | 0.08 | 0.05 | 8.6 | 4.3 | 6.5 | 2.5 |
| G.MEAN | 0.19 | 0.15 | 0.06 | 0.03 | 9.10 | 4.85 | 5.29 | 2.36 |
| SE | 0.02 | 0.02 | 0.01 | 0.01 | 1.08 | 0.93 | 0.74 | 0.63 |
| SED | 0.01 | 0.01 | 0.01 | 0.01 | 0.27 | 0.20 | 0.18 | 0.14 |
| lsd (0.05) | 0.011 | 0.009 | 0.004 | 0.001 | 0.71 | 0.33 | 0.30 | 0.23 |

Note: GPCNT-grain P content, STVPCNT-Stover P content

The present study shows the existence of substantial variation for phosphorus efficiencies which are known to be under genetic and physiological control and is modified by plant interactions with environmental variables (Baligar *et al.*, 2001, Baligar and Fageria, 1997). From the results, all the soils were P deficient ($2.3 - 4.4 \text{ mg P kg}^{-1}$) (Table 2). According to Okalebo *et al.* (2002), bicarbonate extractable P levels below 10 mg P kg^{-1} of soil are considered inadequate for good and healthy plant growth. Besides, all the locations had low C ($5.28-7.11 \text{ cmol kg}^{-1}$) and exchangeable Ca ($2-4 \text{ cmol kg}^{-1}$) except Koyonzo ($\text{Ca}=4 \text{ cmol kg}^{-1}$). According to Landon (1984), a $\text{CEC} < 15 \text{ cmol kg}^{-1}$ and exchangeable $\text{Ca}^{2+} < 4.0 \text{ cmol kg}^{-1}$ are considered low for crop production. These results compare well with those of Kisinyo *et al.* (2013a) who also reported low available P ($2.13-6.08 \text{ mg P kg}^{-1}$), low CEC ($6.01-7.08 \text{ cmol kg}^{-1}$) and high % Al saturation in similar region. From the soil chemical and physical properties observed (with low base cations, available P, C, and N), it was evident that the western Kenya soils are depleted and unsuitable for healthy maize growth. The low available P is attributed to P fixation to clay minerals (Al and Fe oxide) (Van straten, 2007). The low P and N could also have been due to continuous cultivation without proper soil replenishment as have been suggested by Okalebo *et al.*, 2006.

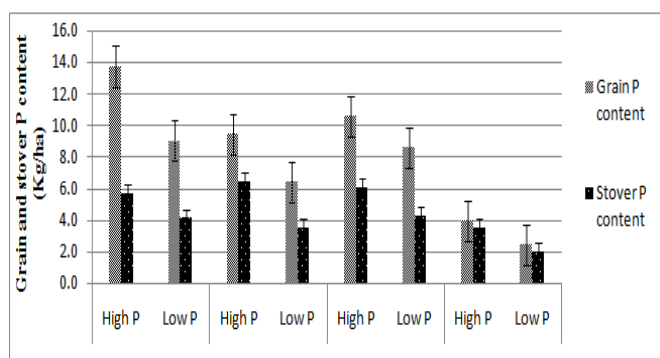


Figure 2. Mean grain phosphorus (P) content and Stover P content of maize hybrids tested across 4 locations in 2014

Significant variation ($P=0.01$) among Locations (L) and between the P levels implied that Locations were different and that P fertilizer application had an effect on the performance of maize hybrids. The interaction LXP was also significant ($P=0.05$) for all the traits implying differential location response to P application.

This was expected because of the variation in P levels recorded across the locations. Genotypic (G) differences were highly significant ($P=0.01$) for all the traits measured. This can be attributed to genetic variation in P efficiency amongst the genotypes. G X L and G X P level was significantly different for all the traits measured. Such substantial genetic variation in response to P deficiency and P supply has been shown previously in maize hybrids (Parentoni *et al.*, 2010, Ligeyo *et al.*, 2014), sorghum (Leiser *et al.*, 2014), wheat (Osborne and Rengel, 2002), Oztuk *et al.*, 2005 and in rice, Wissuwa *et al.* (2002). The large yield reductions between the two P levels demonstrated that the two conditions did differ, for P stress and therefore suitable for selection. Clear discriminative differences based on grain yield suggested that selection based on grain

yield at varying P levels is an appropriate criteria. The application of P fertilizer increased grain yield because of the increased soil available P, which is necessary for healthy plant growth, (Tisdale *et al.*, 1990). Such yield increments have been reported by Kisinyo *et al.* (2013b) and Ligeyo *et al.* (2014). A 48.9% mean yield reduction across soil P levels was observed, which compares well with those of Fox (1978) and Parentoni *et al.* (2010), who reported mean grain yield reductions of 35% and 47%, respectively in maize hybrids due to low P levels. Results by other authors (Manske *et al.*, 2000; Chen *et al.*, 2009; Cichy *et al.*, 2009; Ouma *et al.*, 2013 and Ligeyo *et al.*, 2014) also support this finding.

Gourley *et al.* (1993) defined condition to categorize a pair of genotypes as "P efficient" and "P inefficient. Such genotypes should achieve comparable yields with optimum P availability and should show significant differences under low P supply. Therefore considering the grain yields presented in Table 4, hybrids 1, 39, 25, 16 among others are P-efficient while 31, 7 and 11 are P-inefficient. Hybrids 28 and 40 can be categorised as P efficient as well as good responders to P application while genotypes 23, 2, 30, and 20 are only good responders probably due to superior cell metabolism. The high grain yield at Chepkoilel is attributable to the longer growth period experienced resulting in higher accumulation of the photosynthates hence higher yield and biomass production.

Measurements of lower P-efficiency traits in low P sensitive maize lines and vice versa is consistent with those of Jiang *et al.* (2010) who reported lower grain P utilization in low P tolerant maize compared to their tolerant counterparts regardless of whether they were planted in low or high P conditions. The reported range for AE in this study compare well with previous studies such as those of Baligar *et al.* (2001) and Baligar and Fageria (1997) although they reported higher AE (79 kg kg^{-1}) than observed in this study (72.9 kg kg^{-1}). This is probably because of some of the major soil chemical constraints reported in the western Kenya soils where this study was conducted such as high levels of Al toxicities, elemental deficiencies (very low N and P levels), and very low organic matter content (Table 2). These constraints can greatly reduce AE (Baligar and Bennet, 1986, Baligar and Fageia, 1997). According to these authors, these factors affect mineralization and immobilization, fixation by adsorption, precipitation mechanisms, and leaching e.t.c. The findings further compares well with those of Kisinyo *et al.* (2013b) who reported on average a slightly higher range of values for AE ($55-70 \text{ kg kg}^{-1}$), compared to this study ($22.9-72$) probably because of the inclusion of lime amendments since liming corrects soil chemical constraints by improving the availability of Ca, Mg, Mo, P, soil structure, and CEC (Adams, 1984).

The average PER for the 32 genotypes was 546.7 kg/kg which is well within the range reported by other studies, ($525-625 \text{ kg/kg}$) for P-efficient maize (Fageria and Baligar, 1999). From the results presented in Table 7, majority of the genotypes expressing higher PE also showed higher PAE, PUE and PER implying a good correlation between these traits. Overall, efficient entries (higher PE values) were far superior in utilizing the absorbed nutrients compared to the inefficient ones.

The finding that both PUE and PAE exhibited larger range than PER and PE implies that PUE and PAE contributed more to the observed genetic variations in P-efficiency than the latter parameters. The mean PE and PUE was 553.4 kg/kg and 71.6, respectively which compare well with the values of Sepehr *et al.* (2009) who reported a mean PE and PUE of 550 kg/kg and 71%, respectively in genotypes of wheat, rye and triticale. They also compare well with those of Parentoni *et al.* (2010) who reported PUE of 400 kg/kg in tropical maize and those of Fageria *et al.* (2006) who reported PUE of 388 kgkg⁻¹ in maize cultivated in red oxisols. The disparity with the findings of Fageria *et al.* (2006) could be attributed to differences in soil available P used in the two studies. In the present study soil available P was extremely low (2.3-4.7 mgP/kg of soil) across the locations while in Fageria *et al.* (2006) study soil available P was in the range of 4.4 -7.37 mgP/kg of soil. The natural genetic variation observed among genotypes of maize demonstrates the potential for breeding cultivars with improved nutrient use efficiencies (NUE), which will ultimately acquire and utilize applied inorganic Pi fertilizers more efficiently.

The increase in grain and stover P concentration due to high P levels compare well with those of Hammond *et al.* (2009) who reported 4.9 fold increases in STVPC in *Brassica Oleraceae*. They are also in agreement with the results reported by Liao *et al.* (2005); Sepehr *et al.* (2009) and Ozturk *et al.* (2005) who reported significant increase in stover P as a result of high P regimes. Majority of the genotypes with low GPC in their tissues had higher PUE showing that they were able to utilize P better. From these findings, it can be suggested that selection for reduced GPC in maize lines may increase phosphorus utilization. Moreover, Parentoni *et al.* (2010) suggested that reduction in GPC would have a positive impact on animal nutrition, since grain P is stored as the anti-nutritional factor (phytate). A lower GPC will also reduce environmental pollution from high P manure produced by large animal feeding facilities. However, the strategy of reducing GPC should have a limit, since grain P is needed in the grain filling process and is also important in seed germination.

Large genetic differences for grain and stover P content reported in this study compares well with those of Batten (1984) and Osborne and Rangel (2002) who also reported large genotypic differences in P content in cereals. The differences were attributed to root size, root morphology and changes in the rhizosphere which were not investigated in this study. The highest % reduction in grain P content at Segal site was probably attributable to the total available P which was lowest at Segal and highest at Chepkoilel. However, for stover P content, Migori was the leading followed by Koyonzo while Segal still produced the least implying that the genotypes had better P acquisition efficiency at Migori and Koyonzo probably because of low levels of Al concentration in these soils.

Conclusions

This study has selected at least 20 experimental hybrids very suitable for growing in low P soils of western Kenya. Fairly similar hybrids were selected on the basis of Grain yield under low P alongside P efficiency parameters studied (PAE, PUE, PER, AE and PE) implying these parameters are a suitable

criteria and useful for consideration under indirect selection for tolerance to low P in maize. A large genetic variation in P efficiency existed amongst the hybrids both at low P supply and in response to P application. The finding that both PUE and PAE exhibited larger range than PER and PE implies that in this study, PUE and PAE contributed more to the observed genetic variations in P-efficiency traits than the latter parameters. A 48.2% mean relative grain yield reduction was observed at low P compared to high P supply. The natural genetic variation observed between the maize genotypes demonstrates the potential for breeding cultivars with improved phosphorus efficiency, which will ultimately acquire and utilize applied inorganic Pi fertilizers more efficiently.

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