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RESEARCH ARTICLE

Gene action conditioning phosphorus utilization in tropical maize

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Abstract

Maize (*Zea mays* L.) is an important economic crop on the African continent. However, its production is constrained by both abiotic and biotic factors. Among the abiotic stresses phosphorus (P) deficiency is one of the major constraints affecting maize productivity. The objective of this study was therefore to investigate the type of gene action conditioning phosphorus utilization in P-limited soils. Thirteen, previously screened inbred lines with varying performances relative to phosphorus utilization in P-limited soils, were mated according to North Carolina Design II (NCD II) (8 females × 5 males). Forty (40) progenies were evaluated in a screen house using a completely randomized design (CRD), with three replications, and two levels of P (0 kg P and 60 kg P). Shoot biomass, root biomass, plant biomass and plant height were measured after the plants were harvested and dried at 80 °C for 72 h. Specific combining ability (SCA) was found to be highly significant ($P < 0.001$) for all measured traits. General combining ability (GCA) was significant only for root biomass ($P = 0.05$). The Baker's ratio for plant height, shoot biomass, root biomass and plant biomass was 0.12, 0.15, 0.49 and 0.28, respectively, indicating that predominantly non- additive gene action conditioned all parameters, except root biomass, where both additive and non-additive gene action were found to be important.

Key words: Combining ability, North calorina design, P-limited soils, *Zea mays*

Introduction

Maize is the most important cereal crop and a staple food for most countries in sub-Saharan Africa (SSA) (Edmonds *et. al.,* 2009; Tembo *et. al.,* 2016a). The calories contribution from consumed maize is about 50% in Southern Africa when compared to other sources (Banziger and Diallo 2002). Per capital consumption of maize grain in Zambia was estimated at 140 kg per year (Smale and Jayne, 2003). Apart from home consumption, maize is a major ingredient in stock feed and in many industrialized food products (Sangare *et. al.,* 2019). It is grown in most areas, with the exception of wet, dry or infertile land where sorghum and millet are primarily grown (Reynolds *et. al.,* 2015). The demand for maize in Zambia and other developing countries is expected to surpass the demand for both wheat and rice by the year 2020 (Pingali and Pandey, 2001). However, average productivity of maize in several developing countries of the tropics in SSA is still considerably low as a result of both biotic and abiotic stresses (Shanta *et.al.,* 2019; Tembo *et.al.,* 2016b; Banziger and Diallo, 2002). Among the abiotic stresses, phosphorus (P) deficiency in the soil is the major factor for yield losses. Fertilizer application is one major method of replenishing P in depleted soils

(Rashid and Memon, 2001). However, P fertilizers are costly, nonrenewable, and potentially ineffective because of immobilization in the soil. Part of the applied mineral P fertilizer is transformed to organic form, a process known as microbial immobilization (Holford, 1997). Efficient phosphorus uptake and utilization are important to enhance the applied mineral P recovery and to improve P availability. Efficient P uptake is also useful in reducing environmental impact from fertilizer runoff and leaching (Guingo and Hebert, 1997). Phosphorus utilization efficiency is a term that generally describes the ability of crop species/ genotypes of a given plant species to give higher yield under P-limiting condition (Graham, 1984). Plant species as well as genotypes within the same species may differ in P utilization efficiency (Gunes *et. al.*, 2006). The ability of a genotype to give higher yield under P-limiting condition may be related to: the ability to take up more P from the soil under P-limiting condition (uptake efficiency) or the ability to produce higher dry matter per unit of P in the plant tissue (utilization efficiency) or a combination of both (Gahoonia and Nielsen, 1996). Thus, developing P-efficient maize cultivars which produce reasonably high biomass in low-P soils is not only feasible but also a cost-effective approach for small-scale farmers. However, use of an efficient breeding strategy for genotypes effective at utilizing phosphorous in P-limiting soils requires an understanding of the nature of inheritance of tolerance to P-deficiency in associated traits. Previous studies in maize suggested additive gene action as being important in influencing response of shoot and root traits in P-deficient soils (Da Silva *et. al.*, 1992). Genetic outcome can be influenced by the type of mating design utilized and the type of material under study (Nduwumuremyi *et. al.*, 2013; Simpasa *et. al.*, 2018). There is therefore need to further carry out genetic studies on a P-limited soil medium to mimic conditions in farmers' fields. The objective of the study was therefore to investigate the type of gene action in tropical maize associated to selected traits conditioning utilization of phosphorus in P-limiting soils.

Materials and methods

Germplasm used and location of experiment

The germplasm (Table 1) was obtained from the maize team at Golden Valley Research Trust (GART) in Chisamba District (latitude 14 º 40' S; longitude 25º 01'E, altitude 1140m). Previously screened inbred lines for P utilization efficiency in P-limited were used in the study (Table 1). The study was conducted at the University of Zambia screen house (latitude 15°23´42´´S, longitude 28°20´13´´E, altitude 1263 m), from December 2017 to May 2018.

Table1: Maize genotypes utilised in 8 (female) x 5 (males) NCD II mating design in the study

Designation	Genotype	Pedigree	R P
Male	L60	LacarxL 12-280-3-3-2-4-5-3-1-1	ME
Female	L61	LacarxL 12-280-3-3-2-4-5-3-1-2	LE
Female	L354	Ll2 Ml (220Gy)-150-3-2-l-l-4S6-S8-3-4-2- 4-2	ME
Female	L374	Ll2 Ml (220Gy)-150-3-2-l-l-4S6-S8-5-l-B-	ME
		2-3	
Female	L508	SW89300-IP5S2-5-##l-l-3-B X L9!7-2-8-1-	ME
		2-B-B-3	
Female	L542	x(discard)l X L917-l-5-2-3-6-2	ME
Female	L571	[Ent52:92SEW 1-2/{DMRESR-W]Early Sel	LE
		-#L-2-l-B/CML386)-B-22-l-B-4-#-B x L	
		1214-1-2-2-1-B-l-l	
Male	L584	[Ent52:92SEWl-2/{DMRESR-W]Early Sel	ME

		-#L-2-l-B/CMI.386) -B-22-1-B-4 -#-B x L	
		1214-2-4-1-2-4-1-6-2	
Male	L585	[Ent52:92SEWl-2/[DMRESR-W]EarlySel	LE
		-#L-2-l-B/CMI.386)-B-22-1-B-4-#-B x L	
		1214-2-4-1-2-4-1-6-3	
Female	L640	[EarlyMidl/KatumaniSR)-#-169-2-4-B X L	
		1214-4-4-4-2-2-B-B-2	
Male	L655	[EarlyMidl/KatumaniSR)-#-169-2-4-B X L	LE
		1214-4-5-2-2-3-B-B-l	
Male	L806	[MSR123Xll37TN-9-2-4-X-3/LZ946441)	LE
		-B-1-5-5-BB-3 X ZEWA-8-2-2-3-5-B-l	
Female	L807	CML388-9 X ZEWA-14-2-7-1-B-1	LE

RP-Response to limited Phosphorous soil; ME-Most efficient; LE-Less efficient

Conduct of experiments

Standard agronomic practices to raise the crop were followed. The crosses were made following the 8 (female) × 5 (males) NCD II, generating 40 crosses and were harvested at physiological maturity. The ears from crosses were hand-harvested, shelled and the F_1 (single-cross hybrid) seed was stored for evaluation. The evaluation of F_1 genotypes was carried on potted plants as two separate treatments (additions of 0kg/ ha P and 60 kg/ ha P) in the green house. The experiments were laid as a complete randomized design with 3replications. The soil used in pots (diameter 18 cm; height 20 cm) was collected from a P soil limiting area from Ngwerere (l5° 18’ 0” S, 28° 19’ 0” E) in Lusaka. The corrected soils were randomly sampled and analysed for soil attributes (Table 2).The plants were harvest at 28 days and air-dried for 72 hrs. The associated traits were considered as by Da Silva *et al.* (1992). These were shoot biomass, root biomass and plant biomass, with the inclusion of plant height.

Table 2: Soil characteristics of Ngwerere soils, utilised in the potted experiment at UNZA

Name	Threshold	Measured Quantity
Available Phosphorus	10mg/kg soil	5.60 mg/kg soil
pH		4.37

Statistical analysis

Mean performance of all measured parameters; root biomass, shoot biomass, plant length and plant biomass in P-limited soils (0 Kg P) and in P optimum soil (added 60 Kg P), were compared using a two-tailed paired T-test. Analysis of variance was performed using a fixed model and means of root biomass, shoot biomass, plant height and plant biomass were separated using the fisher protected Least Significant Difference (LSD) method, at a significant level of $\alpha= 0.05$.

The expected mean squares were estimated as by Singh and Choudhary (1985). Main effects due to females and males were independent estimates of general combining ability (GCA) variances while male × female interaction effects represented specific combining ability (SCA) variance. The genotypic GCA and SCA effects were estimated as done by Singh and Chaudhary (1985) and are as presented:

GCA= mean of parent – test mean or overall mean

SCA = observed mean of the cross - $[(GCA_m+GCA_f) + \text{test mean}]$

The variance components for GCA and SCA effects were calculated as described by Singh and Chaudhary (1985) and are as presented:

$\sigma^2_{sca=} MS_{mf} - MS_{mfc}/rc$, ii) $\sigma^2_{gca}m = MS_m - MS_{mf} - rf\sigma^2_{mc}/rcf$, and iii) $\sigma^2_{gca}f = MS_f - MS_{mf} - rm\sigma^2_{fc}/rcm$

The relative contributions of GCA and SCA were estimated using the Baker's ratio ($\sigma^2gca_f + \sigma^2gca_m)/(\sigma^2gca_f + \sigma^2gca_m + \sigma^2sca$), where σ^2gca_f and σ^2gca_m are the variance components of GCA due to female and GCA due to male respectively while σ^2sca is the variance component of SCA (Baker, 1978).

Narrow sense heritability estimates for each set were calculated using the formula:

$$h^2 = (\sigma^2gca_f + \sigma^2gca_m)/\ (\sigma^2gca_f + \sigma^2gca_m + \sigma^2sca + \sigma_e^2)$$

All the data analysis was carried out using GenStat statistical package (VSN International, 2014).

Results and discussion

Effect of phosphorous on productivity

The t-test showed that the mean performance for all measured parameters across genotypes was higher at an added rate 60 kg P/ ha than at no addition (0 Kg/ ha) (Table 3). Phosphorous is a key element in maize productivity (Rashid and Memon, 2001). This study confirmed that an increment in P availability to maize plants has a corresponding performance in its productivity (Table 3). The use of genotypes which produce relatively higher yield in P-limited soils enhance crop productivity (Da Silva *et. al.,* 1992). Further research was therefore undertaken to investigate the type of gene action conditioning utilization of phosphorous in P- limiting soils.

Table 3: Comparisons of mean performance across genotypes of measured parameters at added rates of 0 kg P and 60 kg P using a paired T- test

Parameter	Mean-0^x	Mean-60^Y	P- value
Plant height	2.00	16.90	< 0.001
Shoot biomass	1.07	13.21	< 0.001
Root biomass	0.92	3.72	<0.001
Plant height	37.80	79.89	<.001

^{X}-mean value of measured parameter at fertilizer application rate of 0 Kg P across genotypes,
^{Y}-mean value of measured parameter at fertilizer application rate of 60 Kg P across genotypes

Combining abilities and type of gene action

In P- limiting soil, significant differences ($P \leq 0.001$) were obtained among the crosses for all the measured parameters (Table 4). SCA was highly significant across all the measured parameters ($P \leq 0.001$). However, GCA was only significant for the root biomass ($P \leq 0.05$). Table 5 presents the specific combining ability effects of the F_1 crosses for parameters that were considered in the study. Crosses (L60 × L807), (L585 × L354), (806 × L374) and (L655 × L508) exhibited positive significant SCA effects from zero on all the measured parameters. Two crosses, L655 × L374 and L806 × L61 exhibited negative significant SCA effects across all the four measured parameters. Significant GCA for root biomass revealed that the GCA effects for female parental lines L354 and L640, and a male parental line L 60 were positively significant from zero with values of 0.48, 0.14 and 0.28, respectively (Table 6). Parental lines L61, L508, L807 and L585 exhibited negative significant effect from zero of -0.18, -0.23, -0.14 and -0.12 respectively. In this regard positive combining ability effects are desirable because they indicate contribution of favorable alleles associated with enhanced phosphorus utilization in P limiting soil, while it is the reverse with negative significant combining ability effects (Ndeke and Tembo, 2019). However an inbred line with a high negative GCA can be crossed with the other line with high positive GCA to create a mapping population for utilization in identifying QTL's associated with phosphorous utilization in P- limited soils (Tembo *et. al.*, 2014)

The Baker's ratio for plant height, shoot biomass, plant biomass and root biomass were found to be 0.12, 0.15, 0.28 and 0.49, respectively. Narrow sense heritability estimates were found to be 0.08, 0.11, 0.21 and 0.30 for plant height, shoot biomass, plant biomass and root biomass respectively. Thus, all the evaluated traits were found to be conditioned by non- additive gene action, except root biomass which was conditioned by both additive and non-additive gene action in influencing P-uptake. The findings of non-additive gene action imply that for a breeding scheme, hybridization can be the best option to employ especially with regards to selection for plant height, shoot biomass and plant biomass. The presence of non-additive gene action implies that the effects of dominance and/ or epistatic gene action is at play (Adeniji and Kehinde, 2003). Therefore, significant gains in breeding for phosphorus utilization efficient genotypes can be achieved through hybridization to capitalize on the dominance/ epistatic gene effect. For the root biomass which showed both additive and non-additive, the implication is that population improvement through a reciprocal recurrent section approach can be employed (Acquaah, 2012). The low narrow sense heritability (30%) for root biomass obtained indicate that transmissibility of desirable traits between generations is low, and thus several cycles should be undertaken to achieve the desired population (Adefris and Becker, 2005).

Table 4: Analysis of variance for mean squares of measured parameters in phosphorous limiting soil

SOV	df	PH	SB	RB	PB
Replication	2	0.50	0.01	0.04	0.07
Crosses	39	150.00***	0.98***	0.39***	2.39***
GCA_{males}	4	191.31	1.51	0.80*	4.26
$GCA_{females}$	7	169.82	0.89	0.67*	2.89
SCA	28	136.84***	0.87***	0.25***	1.85***
Error	78	24.07	0.11	0.08	0.25

SOV-Source of variation, GCA- General combining ability, SCA specific combining ability, df- Degrees of freedom**,** Plant height- PH, shoot biomass -SB, root biomass -RB, plant biomass -PB. *, *** significantly different at 0,05 and 0,001 respectively.

Table 5: Genotypic specific combining ability effects of crosses on measured parameters

Genotypes	PH	SB	RB	PB
L60 xL6l	4.0	0.09	0.16	0.24
L60 x L354	-5.37	-0.45*	-0.10	-0.54
L60 x L374	- 1.67	-0.10	0.20	0.10
L60 xL508	-4.50	-0.48*	-0.38	-0.86*
L60 x L542	4.26	0.03	-0.01	0.01
L60 x L571	3.63	0.30	0.01	0.32
L60 xL640	-8.90*	-0.55*	-0.25	-0.79*
L60 x L807	8.43*	1.16***	0.36*	1.52***
L584 x L61	2.93	0.08	-0.02	0.05
L584 x L354	-1.70	-0.01	-0.07	-0.08
L584 x L374	5.10	0.12	0.14	0.24
L584 x L508	0.06	-0.15	-0.06	-0.23
L584 x L542	3.06	0.22	0.03	0.24
L584 x L57l	-4.34	-0.20	-0.12	-0.33
L584 x L640	3.63	0.48*	0.22	0.69*
L584 x L807	-8.64*	-0.49*	-0.12	-0.62*

L585 x L61	-3.90	-0.15	-0.36*	-0.50
L585 x L354	6.66*	1.05***	0.46'''	1.53***
L585 x L374	-9.23**	-0.47*	-0.24	-0.72*
L585 x L508	-3.44	-0.19	0.00	-0.20
L585 x L542	7.58	0.16	0.02	0.17
L585 x L571	3.96	0.34	0.23	0.58*
L585 x L640	0.36	-0.40*	-0.11	-0.51
L585 x L807	-1.54	-0.35	0.02	-0.34
L655 x L6l	4.76	0.42*	0.52*	0.94*
L655 x L354	-1.24	-0.35	0.07	-0.27
L655 x L374	-6.77*	-0.45*	-0.38'''	-0.83*
L655 x L508	11.53**"	1.04***	0.52**	1.56***
L655 x L542	-4.37	-0.21	-0.05	-0.26
L655 x L571	-0.27	-0.06	-0.33'''	-0.37
L655 x L640	-1.34	-0.24	-0.20	-0.43
L655 x L807	-2.17	-0.16	-0.15	-0.31
L806 x L6l	-7.82'''	-0.43*	-0.33'''	-0.73*
L806 x L354	1.46	-0.25	-0.40'''	-0.60*
L806 x L374	12.30***	0.91***	0.34*	.18***
L806 x L508	-3.80	-0.20	-0.11	-0.27
L806 x L542	-10.27**	-0.18	-0.03	-0.17
L806 x L57l	-2.87	-0.40*	0.16	-0.19
L806 x L640	6.50*	0.69**	0.30	1.04**
L806 x L807	3.96	-0.17	-0.12	-0.24
S.E	2.83	0.19	0.16	0.29

Standard errors (S.E) of the effects, plant biomass -PB, shoot biomass -SB, root biomass -RB, Plant height –PH,

*, **,*** - Significant different from zero at 0.05, 0.01 and 0.001 respectively

Table 6: Genotypic general combining ability effects for root biomass on parental lines

Genotypes	**RB**
Females	
L61	-0.18*
L354	0.48*
L374	0.06
L508	-0.23*
L542	-0.01
L571	-0.12
L640	0.14*
L807	-0.14
S.Em	0.07
Male	
L60	0.28*
L584	-0.05
L585	-0.12*
L655	0.00
L806	-0.10
S.Em	0.06

S.E$_f$ and S.E$_m$**,** standard error of the effects for GCA female and GCA male respectively, *- Significant different from zero at P< 0.05, RB-root biomass

Conclusion

The Baker's ratio for plant height, shoot biomass and plant biomass associated traits were found to be 0.12, 0.15 and 0.28 respectively. This implied that non additive gene action conditioned the response of plant height, shoot biomass and plant biomass to P-limiting soils. In this regard hybridization can be used in a breeding scheme when interest of selection is based on plant height, shoot biomass and plant biomass. On the other hand, association of root biomass to P-utilization in P limited soils was conditioned by both additive and non-additive gene action. Implying that when selection is based on root biomass, population improvement through a reciprocal recurrent selection approach can be employed. However, the low narrow sense heritability (30%) computed indicate that transmissibility of desirable traits between generations is low, and thus several cycles should be undertaken to achieve the desired population.

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