Original Article

Tolerance, Heritability, and Heterosis for Aluminium Toxicity Tolerance for ALXMSV Maize Single Crosses

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ABSTRACT

Maize is an important cereal crop rated third to rice and wheat on the global scale of agricultural production. It is use spans a vast array of industrial as well as domestic uses, with its consumption as food and feed being the primary reason for its cultivation This globally produced and consumed commodity is however faced with an array of biotic and abiotic constraints with regard to its production, such as MSV, MLND, Smut, Lepidopteron pests, soil acidity, P deficiency, poor rains and drought. This study aimed at assessing tolerance, heterosis, and heritability of Al toxicity tolerance in the laboratory for MSV/AL single crosses in terms of Net root length. The research methodology followed the Magnavaca protocol for Al tolerance screening in nutrient solution. The genotypes in the study varied significantly in terms of response under Al toxicity, with 22.58% tolerant, 19.35% moderately tolerant, and 58.6% being susceptible. From the study, 22.6% of the single crosses were found to be tolerant to the stress under controlled condition and 12.9% were found to have positive heterosis for the trait. While all the female parents were tolerant except AO809, only one male (54B) was moderately tolerant, this could have led to the low heritability expressed by the single crosses for the trait. The identified single crosses should be further screened for tolerance and heterosis in the field. However, this study showed low heritability for Al tolerance (estimated at 16.9%) when crossing is done between susceptible and tolerant genotypes.

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INTRODUCTION

Maze has over time become one of the most important and most consumed cereals globally, providing raw materials for industries, as well as animal feed and human food (Dabija *et al.,* 2021; Gwirtz *et al.,*2014). Globally, 25% of harvested maize is utilised industrially while 67% is consumed as food or feed (Bekele & Rao, 2013). This unrivalled importance has resulted in decades of research that endowed the crop with generations of information in the development of high yielding varieties. These achievements have been achieved via breeding and selection for tolerance to specific productions constraints (Reif *et al.*, 2005). Among the most commonly faced challenges for maize production are soil infertility and soil acidity that leads to a deficiency of phosphorus (Ouma *et al*., 2013). This poor soil condition covers approximately 7.5 million ha of arable land in Kenya (Kisinyo *et al*., 2014). Being the most abundant light metal, aluminium comprises 7% of the earth's crust, and is the third most abundant element after oxygen and silicon (Abate *et al*., 2013; Mutale, 2013; Too *et al*., 2014). Its availability in the phytotoxic forms Al $(0H)^{2+}$, Al^{3+}, $Al(OH)^{2+}$ and $Al(0H)_2$ depends on soil pH and is prevalent in acid soils with a pH of 5.5 or lower (Kochian *et al*., 2004), and a concentration of >20mg/kg is considered as toxic to crops (Ligeyo, 2007; Ouma *et al*.,2013).

The presence of this phytotoxic element in acid soils results in the damage of plant roots with the root apex being the main center of activity for the toxin (Yin *et al*., 2009). This damage to the roots results in the impediment of water and mineral acquisition, resulting in poor overall development and necrosis due to shortage of phosphorus and nitrogen (Yang *et al*., 2012). However, different plant species have been screened and selected for an array of tolerance mechanisms, such as organic acid secretion (Abate *et al*., 2013; Blair *et al*., 2009; Garcia-Oliveira *et al*., 2016), root and shoot symplastic accumulation of aluminium (Wang *et al*., 2017), and the production aluminium tolerance enzymes in the plant cells (Panda *et al*.,2009). All these tolerance mechanisms are under genetic control by the ALMT (Aluminum Activated Malate Transporter) family, MATE (Multidrug and Toxic Compound Extrusion) family, ATP-binding cassette (ABC) transporter family of genes (Larsen *et al*., 2004; Larsen *et al*., 2006; Simões *et al*., 2012). According to Ouma *et al.* (2013) and Simões *et al.* (2012), this genetic control is via both quantitative and qualitative genes and can be transmitted from one generation to another, with hybrid vigour/heterosis expressed for the trait.

Also known as hybrid vigour, heterosis refers to the superiority of the F_1 hybrid over its better parent (better parent heterosis) or the superiority of the F_1 hybrid over the mid parent (Mid-parent heterosis) (Acquaah, 2007; Soehendi & Srinives, 2005; Reif *et al*., 2005; Ryder *et al*., 2014). This superiority of the hybrids may be attributed to dominance of favourable genes (dominance) or superiority of the heterozygote over the homozygote (over-dominance) (Reif *et al*., 2005; Soehendi & Srinives, 2005). In addition to dominance and over dominance, epistasis is also hypothesised to have an effect in the expression of hybrid vigour (Gichuru, 2013; Merrick *et al*., 2011; Reif *et al*., 2005; Ryder *et al*., 2014). Despite heterosis being mainly used in reference to hybrid superiority, there exists the possibility in some instances that the hybrids may be inferior to the weaker parent, and this is also considered as heterosis. Whereas this negative heterosis is considered detrimental for a number of traits, it is considered advantageous for particular traits such

as earliness (Ryder *et al*., 2014; Venu *et al*., 2014). This study aimed at evaluating the level of heterosis, heritability, and tolerance expressed by aluminium tolerant X MSV (Maize Steak Virus) tolerant single crosses to aluminium toxicity under laboratory screening.

MATERIALS AND METHODS

Study Sites

The study had its objectives met at the Univerity of Eldoret, botany lab two. The University of Eldoret is located 2143m above sea level, experiences a rainfall range of 900-1000mmp.a, and temperature range 10-26ºC (Ouma *et al*.,2013). This location served as the site for the laboratory screening which was done as per the Magnavaca protocol of 1987 and edited as per Ringo et al. (2010) and Ouma *et al.* (2013). The crosses had been earlier developed in Rongo University farm in the 2015 short rain season.

Germplasm

The study used 31single crosses and 15 parental lines. The single crosses were obtained from a crossing endeavour at Rongo University in the short rain season of 2015, while the parental lines were sourced from Rongo University research and the University of Kwazulu Natal. In addition to these genotypes, a commercial line Olerai and susceptible SCH3 were used as checks.

Al Screening (LAB) In Nutrient Solution

The experiment was laid out in CRD (Completely Randomised Design) with three replications for each of the genotypes under control and aluminium treatment with 0 µM or 222 µM Al respectively (Ouma et al, 2013). The study involved 31 Al/MSV single crosses and their respective parental lines. Seeds from each genotype were sterilized using 1% hypochlorite, and then rinsed with distilled water to eradicate traces of hypochlorite. The seeds were then germinated in plastic containers lined with absorbent paper (serviettes) moistened with distilled water. The tins were sterilized and cleaned before use, and germination was carried out (in darkness) in a growth chamber at 26 ± 3 °C for a total of three days.

After three days, uniform, non-injured seedlings were transferred to the nutrient solution prepared according to Magnavaca et al. (1987) and Ringo et al. (2010), using modified cups and Styrofoam sheets. This initial solution was however an acclimatization solution devoid of Al, but was adjusted to a pH of 4.0. After 24 hours of acclimatization initial root length was measured following the transfer of the seedlings to fresh media and the addition of Al to the stipulated levels by use of $AlK(SO_4)_2.12H_2O$ into the media. The seedlings and the solution media were then transferred to a growth chamber with controlled temperatures and photoperiods.

Seventy-two hours after growth in the nutrient media, final root length was measured and net root length, to be used in the determination of tolerance, was calculated as the difference between final root length and initial root length. Tolerance was determined as relative net root length (Ouma et al., 2013).

Model: $Y_{ij} = \mu + G_i + \mathcal{E}_{ij}$

Where: Y_{ij} refers to jth observation for the ith treatment, μ refers to the general mean, G refers to the Genotype effect, $\mathcal{E}$ refers to the error term.

Data Collection

For the laboratory screening data on root initial (IRL), and final root length (FRL) was collected. This data was used to calculate Net Root length (NRL) as per Ligeyo (2009) using the formula;

NRL = final root length (FRL) – Initial Root length (IRL)

The values for NRL were then used in determining relative net root growth (RNRG) and %response using the formula;

$$Responce = \frac{FRL \text{ of control plants} - NRL \text{ of zero Al treatedplants}}{NRL \text{ of zero Al (control) plants}}$$

$$RNRG = \frac{NRL \text{ of Al treated plants}}{NRL \text{ of zero Al (control) plants}} \times 100$$

From the values obtained on determining net relative root growth (RNRG) or %response, heterosis for RNRG was obtained, with mid parent heterosis calculated as;

$$MP\% = \frac{F1 - MP}{MP} \times 100$$

And better parent heterosis calculated as;

$$BP\% = \frac{F1 - BP}{BP} \times 100$$

Where F1 = performance of hybrid, MP = average performance of both parents, and BP= performance of better parent (Gudu *et al.*, 2011). Broad sense heritability was estimated by variance component method according to (Acquaah, 2007; Wannows *et al.*, 2015);

$$H^2 = \frac{(MSSG - MSSE)/r}{\left[\frac{MSSG - MSSE}{r}\right] + MSSE}$$

Where; Variance between genotypes σ^2_g = (MSSG-MSSE)/r; Variance within the genotypes σ^2= MSSE; Phenotypic variance $\sigma^2_p = \sigma^2_g + \sigma^2$.

RESULTS AND DISCUSSION

There was a significant variation among the genotypes in the study (P<0.05) with regard to RNRG. The aluminium treatments also varied significantly with their effect in inhibiting root growth (P<0.05) (*Table 1*). Each of the genotypes whether inbred or single cross, expressed distinct root growth inhibition by the 222μM Al treatment. Most Al susceptible genotypes displayed the highest root inhibition values as well as highest values for NSRL under 0μM Al treatment. On the other hand, the most tolerant expressed NSRL lower than that of the sensitive at 0 μM Al treatment (*Table 1*). Majority of the single cross were categorised as susceptible (58.1%), while the rest were either tolerant (22.6%) or moderately tolerant (19.4%) (*Table 1*). The singe cross 54BXATPS4 had the highest relative net root growth (RNRG) of 1.2, followed by 44BXAO809 (1.1) and 1BX203B (1.0). All the above lines had an increase in final seminal root length (FSRL) above the control treatment indicating some root growth induction in the 222 μM Al treatment.

The F1 with the least RNRG was 1BXAO89, whose response was 20.7% under 222 μM Al treatment. With regard to the parental lines, all the Kenyan lines were either tolerant or moderately tolerant, with the exception of AO809 that was susceptible with a RNRG of 0.5. The most outstanding of the Kenyan inbred lines was 203B with a RNRG of 1.1 under 222 μM Al treatment. The South African parental inbred lines were all susceptible to Al toxicity with the best being 54B with a RNRG of 0.5 which was just at the moderate tolerance threshold. The most sensitive line among the South African materials was 44B with a RNRG of 0.10. 44B had the lowest RNRG, lower than even that of SCH3, one of the world's most susceptible checks (*Figure 1*).

Table 1: Means for Net Root Length, Relative Net Root Growth Rates, and Response values for selected maize single crosses tested for Al tolerance in solution culture for 3 days and Al tolerance classification.

GENOTYPE	Mean NRL 0 μM	Mean NRL 222 μM	RES PONSE	RNRG MEANS	STATUS
ATPS4 X 54B	5.4 n-r	5.2 a-f	114.6	1.2 a	HT
44B X AO809	7.5 h-q	5.2 a-f	109.3	1.1 a-d	HT
1B X 203B	5.4 n-r	3.6 c-l	103.9	1 a-e	HT
41B X CON5	7.0 i-r	4.3 a-j	90.9	0.9 a-f	T
54B X 203B	6.6 j-r	4.0 b-k	87.0	0.9 a-g	T
13B X 203B-9	7.9 g-q	3.3 d-m	84.0	0.8 a-h	T
44B X 203B-14	9.7 c-n	4.5 a-j	83.0	0.8 a-h	T
1B X 203B-1	10.3 c-l	5.6 a-d	63.3	0.6 a-j	MT
1B X CON5	8.7 e-p	4.8 a-i	56.6	0.6 a-j	MT

GENOTYPE	Mean NRL 0 µM	Mean NRL 222 µM	RESPONSE	RNRG MEANS	STATUS
9B X SYNAL	12.5 a-f	6.5 a-b	55.8	0.6 a-j	MT
4B X SYNAL	9.9 c-m	5.2 a-f	54.6	0.6 a-j	MT
203B-9 X 4B	7.5 h-q	3.1 d-n	53.8	0.5 a-j	MT
1B X 203B-9	5.4 n-r	2.2 i-n	51.3	0.5 a-j	MT
9B X CON5	13.7 a-c	6.5 a-b	47.9	0.5 b-j	S
20B X CON5	9.2 d-o	4.1 a-k	47.3	0.5 b-j	S
41B X 203B-1	7.1 i-r	3.1 d-n	44.3	0.4 d-j	S
41B X AO809	8.6 f-p	1.3 l-n	26.0	0.3 f-j	S
1B X BRS	10.1 c-l	2.1 j-n	21.0	0.2 f-j	S
1B X AO809	10.8 c-k	2.3 h-n	20.7	0.2 f-j	S
MEAN	9.21	3.923	0.506	0.506	T 22.58%
CV	0.15922	0.2069	0.4196	0.4196	MT 19.35%
SE	17.2	13.5	0.4196	16.7	S 58.06%

Key: Means in the same column followed by the same letter are not significantly different at $P \leq 0.05$ according to DMRT; S - sensitive, MT – moderately tolerant; T-tolerant and HT – highly tolerant.

Additionally, other F1's (41BXCON5, 54BX203B, 13BX203B-9 and 44BX203B-14) exhibited a relative net root growth of above 75% under 222 µM Al concentration and hence were categorised as tolerant. Only six F1 expressed relative net root growth of between 50% and 75%, and were categorised as moderately tolerant. The remaining eighteen were susceptible to aluminium toxicity at 222 µM Al with a RNRG of below 50% (FIG 1).

The performance of the F1 single crosses were compared to the tolerant check 203B, susceptible check SCH3, and a commercial variety Olerai. The results showed that Majority of the F1s (70.83%) were more tolerant to Al toxicity than Olerai and that all the Kenyan inbred parents outperformed Olerai in terms Al tolerance. For the South African lines only 13B and 54B were more tolerant than Olerai (*Figure 1*).

Figure 1: Effects of Al treatment on net root growth of F1 and maize inbred lines grown for 3 days in solution culture with Al (222µM)
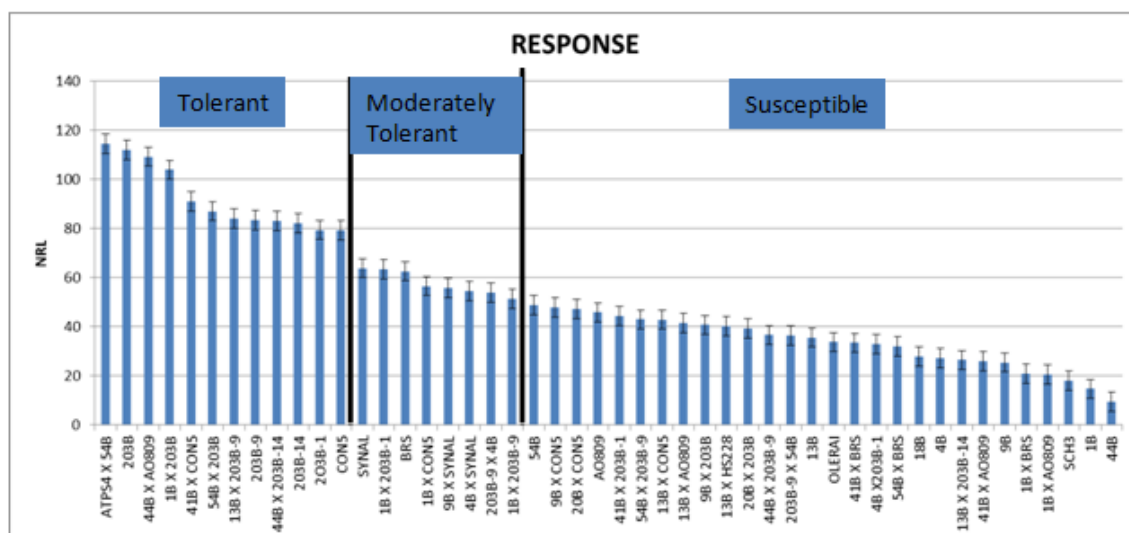

Tolerant genotypes had no observable difference in the root morphology of the seedlings when grown under 222µM and 0µM Al solution stress. However, sensitive genotypes expressed

inhibition of root elongation as well as lateral root hair development under 222µM (*Figure 2*). They also expressed a level of stunted growth,

stubbiness and appeared brittle under Al stress when compared to the control.

Figure 2: Lab screening for selected genotypes; 44B Susceptible, 13BX203B-9 moderately tolerant, ATPS4X54B Tolerant.
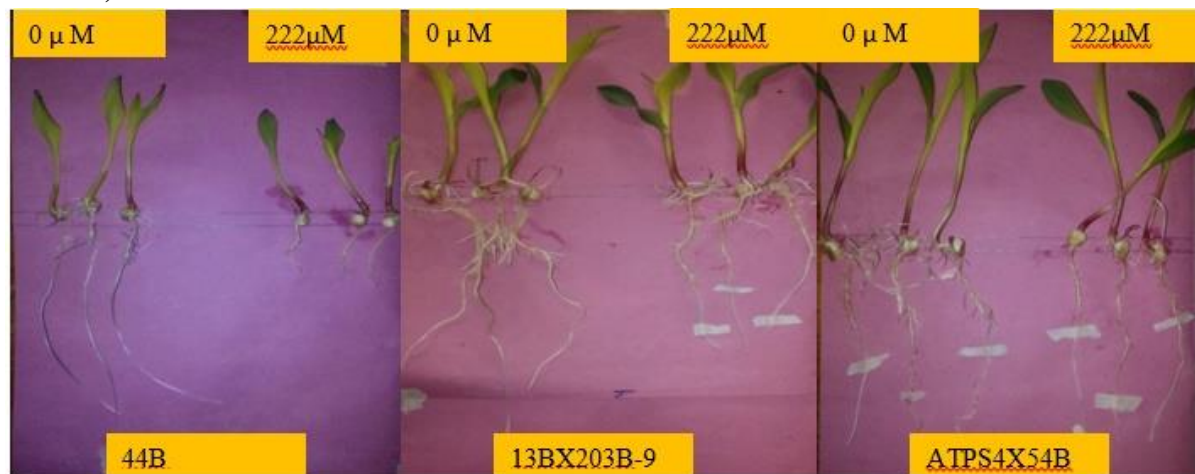
Heterosis and Heritability for RNRG among the Singe Crosses

Slightly above 12.9% of the single crosses expressed better parent heterosis while 48.4% expressed mid-parent heterosis for RNRG (*Table 2*). Most of those expressing heterosis were either tolerant or moderately tolerant while most of the sensitive F1 expressed negative heterosis for both mid and better parent (*Table 1*).

Heritability estimate for RNRG 16.9% (*Table 2*) was low, this means that only that 16.9% of the expressed tolerance can be attributed to inherited genetics. As such, phenotypic selection for the trait in the single crosses developed by crossing tolerant and susceptible genotypes may become more difficult.

Table 2: Mid parent heterosis, better Parent Heterosis, and Heritability values for RNRG for Selected Maize single crosses tested for Al tolerance in solution culture for 3 days.

GENOTYPE	MP	BP
44B X AO809	1040.6	138.3
1B X 203B	64.0	-7.2
41B X CON5		14.6
54B X 203B	8.2	-22.3
13B X 203B-9	41.1	0.7
44B X 203B-14	78.6	-0.4
1B X 203B-1	29.0	-24.1
1B X CON5	20.3	-28.6
9B X SYNAL	24.9	-12.7
4B X SYNAL	19.8	-14.5
203B-9 X 4B	-2.7	-35.5
1B X 203B-9	4.5	-38.5
9B X CON5	-8.7	-39.6
41B X 203B-1		-44.2
54B X 203B-9	1.0	-12.2
13B X CON5	-25.3	-45.8
13B X AO809	1.9	-9.4
9B X 203B	-40.7	-63.6
44B X 203B-9	-21.1	-56.0
203B-9 X 54B	-44.8	-56.2

GENOTYPE	MP	BP
4BX203B-1	-38.2	-58.5
54B X BRS	-42.7	-49.0
13B X 203B-14	-55.4	-68.1
1B X BRS	-45.8	-66.5
1B X AO809	32.9	-54.9
HERITABILITY	16.9%	
BP	12.9%	
MP	48.4%	

Notes: MP-Mid-parent heterosis; BP-best parent heterosis

DISCUSSION

The genotype 203B is a Kenyan landrace collected in the highly aluminium saturated (60%) area of Muranga in Central Kenya. It's maintenance and cultivation by farmers in the acid soils of Central Kenya could be due to its possession of alleles for tolerance to Al toxicity. However, certain derivatives (F_1) of the landrace were susceptible probably due to negative transgressive inheritance. The other Al tolerant standard CON5 that was also used as a parental line in this is study exhibited a root growth of 79.3%. These findings compare well with those of Matonyei (2010) and Gudu *et al.* (2011), with Gudu *et al.* (2011) classified the genotype as tolerant with a root growth of 105%. Previous studies show that 55% of Al toxicity tolerance by this genotype CON5 is due to the activity of ZmMate1 gene and root tip exclusion of Al (Matonyei, 2010). The results presented in this study are consistent with these previous studies.

The clear expression of phenotypic differences among the single crosses and parental lines for the root trait measured can be attributed to the genetic variations to tolerance to Al toxicity in maize genotypes. In this study only 12.9% of the F1 expressed better parent heterosis for RNRG, while 48.4% expressed mid parent heterosis for this trait. The expressed heterosis can be attributed to dominance, over dominance, or epistasis (Merrick et al., 2011; Reif et al., 2005; Ryder et al., 2014) that ensued in the single crosses expressing a RNRG better than mid or better parent. The remaining 51.6% of the F1 were not heterotic for the trait. This observation could be due to negative transgressive inheritance with the offspring that underperformed both parents (Holzman & Hulsey, 2017). These findings coincide with Ouma et al. (2013), who also reports both negative and positive heterosis.

Majority of the single crosses, (70.83%) outperformed Olerai, indicating potential for further use in germplasm improvement in Al toxic zones in Kenya. The low heritability (16.94%) displayed by some of the single crosses alludes to the unfavourable variable genetic combinations inherited by these F1s for tolerance to Al toxicity stress.

CONCLUSION

Hybrids do outperform the parents but not always and hybrids obtained from high yielding lines do not always express high yield per se (Assunção *et al.,*2010; Matin *et al.,*2016). However, they have a tendency towards earliness, high grain yield values, and high heterosis for grain yield. Some single cross hybrids between the Kenyan and South African materials notably 44B X AO809, 1B X 203B, 41B X CON5, and 44B X 203B-14 showed high heterosis for Al tolerance. However, heritability was generally low for Al toxicity tolerance. This showed that developing Al tolerant single crosses by crossing Al sensitive and Al tolerant materials may not result in expression of the trait in a majority of the single corsses due to low heritability. Also, this low heritability value and the variability of RNRG between the genotypes presents a case for additive genes acting to control this trait, alluded to by Matonyei (2010). 203B, ATPS4X54B, and 44BXAO89 were identified as the three best materials with regard to Al toxicity tolerance in solution culture. These materials can therefore be utilised in further improvement studies for maize

with regard to tolerance to Al, as well as adopted for crop production under such environments.

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