

RESEARCH ARTICLE

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## Breeding Grain Sorghum for Tolerance to Aluminium Toxicity

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### Abstract

Aluminium (Al) toxicity is a common problem in acid soils where sorghum (*Sorghum bicolor* (L.) Moench) is grown. It contributes to grain yield reduction of between 30-40 % in sorghum and other cereals. Al interferes with plant development by inhibiting root growth, thus contributing to reduced uptake of water and mineral nutrients. The main aim of this study was to transfer Al tolerance to a local farmer preferred commercial variety. The specific objectives of the study were to (i) assess aluminium stress response of F2 sorghum segregating populations derived from a cross between Seredo and ICSR 110 together with the parental lines and the F1 hybrid in solution culture and (ii) to assess growth and production of the same panel of sorghum genotypes when grown in acidic soils with and without application of lime. A cross was made between Seredo (Al-sensitive commercial variety) and ICSR 110 (Al-resistant line). In the laboratory, seedlings of F1s and F2s and the parental lines were grown in nutrient solution culture without or with Al at 148  $\mu$ M and 222  $\mu$ M. The percent relative net root growth (% RNRG) and percent response were used to classify the populations into tolerant and sensitive to Al stress. In the field the parental lines, F1s and nine F2 segregating populations were grown in acid soil (pH 4.3) with high Al saturation (27%) without or with application of lime. The total number of leaves, plant height and seed yield per plant were evaluated. The F1s and some individual F2s performed better than the Al-tolerant parent both in solution culture and under field conditions. Al tolerance was therefore successfully transferred into the Al sensitive variety. The superior progenies developed need to be advanced to a stable generation and released to sorghum farmers.

**Keywords:** Aluminium Toxicity, Segregating Populations, Sorghum Seedlings, Relative Net Root Growth

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### INTRODUCTION

Sorghum (*Sorghum bicolor* L. Moench) a plant belonging to the family of Poaceae, is an important food security crop especially in low-income households in Kenya and other developing countries in Africa (Anglani, 1998). Sorghum is well adapted to the arid and semi-arid tropics and the majority of the soils in this region are acidic in nature (Sanchez & Salinas, 1981). In Kenya, sorghum growing areas have acid

soils with high levels of exchangeable aluminium (Kanyanjua *et al.*, 2002; Kisinyo, 2010). Mineral soils contain large amounts of Al, most of which occurs as insoluble aluminosilicates or Al oxides of the soil clays and does not pose toxicity hazard to plants (Kindraide, 1997). The aluminium minerals become soluble and potentially toxic to plants if the soil is acidic (pH < 5.5) (Kochian *et al.*, 2005; Vitorello *et al.*, 2005). In addition to high levels of

exchangeable Al, acid soils have low concentrations of the basic cations such as phosphorus, calcium and magnesium. These deficiencies are as a result of leaching of nutrients due to low soil cation exchange capacity (Kidd & Procto, 2001). High levels of Al primarily inhibit root elongation. Therefore, the ultimate consequence of high levels of exchangeable Al coupled with nutrient deficiencies, is a poorly developed root system that makes the crop vulnerable to drought and limited in nutrient uptake.

Many plants including sorghum have developed mechanisms to improve their growth and production on acid soils with high levels of exchangeable Al. These mechanisms are divided into those that exclude Al from the root apex and those that would enable plants to accommodate Al safely once it enters the symplasm (Horst *et al.*, 2010; Zakir Hossain *et al.*, 2006). Exclusion of toxic Al from the root is achieved by releasing Al-chelating ligands such as organic acids, which bind Al and limit its uptake into the cytosol. Detoxification of Al in the cytoplasm occurs via chelation to form harmless complexes or sequestration to less Al-sensitive cellular compartments. A lot of research on molecular aspects of resistance to Al toxicity has been done and genes that confer resistance in many crops have been identified (Hoekenga *et al.*, 2006; Foncheta *et al.*, 2007; Wright *et al.*, 2006; Caniato *et al.*, 2007). The identification of aluminium-resistance genes therefore provides opportunities for enhancing crop production on acid soils (Ryan *et al.*, 2011).

Sorghum has significant genotypic variation for resistance to aluminium (Mariano & Keltjens, 2003; Caniato *et al.*, 2007; Ringo *et al.*, 2010; Too, 2011). This variation can be exploited in plant breeding to generate genotypes adapted to aluminium-toxic soils. Limitation of crop production in acid soils could be overcome by addition of chemical amendments such as lime. However, this is not practical because of inaccessibility,

transportation costs and the difficulty in liming subsoil layers. Identification and development of sorghum superior lines that are resistant to Al stress will enhance yield per unit area of land therefore providing a practical and sustainable option.

This study was carried out to introgress Al-resistance into a farmer-preferred Kenyan sorghum commercial variety, with the aim of obtaining sorghum lines with improved grain yield per unit land area in acid soils of western Kenya.

## MATERIALS AND METHODS

The sorghum germplasm used in the study comprised parental lines *ICSR 110* (Al-resistant line) and *Seredo* (Al-sensitive commercial variety). F1 and F2 segregating populations that were derived from a cross between the two parents were also included in the study. The parental lines were selected from a large collection of sorghums that were sourced from International Crops Research Institute for the semi Arid Tropics (ICRISAT), Kenya Agricultural Research Institute (KARI) and farmers from several regions in Kenya because of their contrasting response to Al stress. *Seredo* is an aluminium sensitive Kenyan commercial variety, has medium height with medium field duration. Its kernels are cream and medium sized. *ICSR 110* is an inbred line developed by ICRISAT (Hyderabad, India). It is Al-resistant, has medium height with short field duration. The kernels are white and large in size. *Seredo* was the recipient parent and *ICSR 110* was the pollen donor.

Crossing was carried out using the polythene bag technique (House, 1985). Female heads were covered by special polythene in which the anthers would fail to dehisce because of high temperatures and humidity thus minimizing self-pollination. Emasculation was done on recipient *Seredo* at the onset of flowering by clipping off the upper and lower spikes leaving central uniform spikes, then covered with a polythene bag (Figure 1) for three days. Pollen from *ICSR 110* was collected and

dusted onto the stigmas of *Seredo* and covered with a paper bag to prevent any other pollen grains from accessing the recipient stigmas. The parental lines and F1s

were grown in the field and morphologically characterized. Nine (9) true F1 plants were selfed to generate 9 F2 segregating populations.



Figure 1: (a) Polythene bag emasculating of sorghum head and (b) Developing F1 seeds.

The sorghum materials were evaluated for Al resistance in solution-based culture in the laboratory and in the field.

Screening for Al resistance of the parental lines, F1s and F2s in solution culture was done according to the procedures described by Magalhaes *et al.* (2004) using the basal nutrient solution of Magnavaca *et al.* (1987). The threshold levels of Al concentrations used in the study (148  $\mu$ M and 222  $\mu$ M Al) were based on recommendations from previous studies (Magalhaes *et al.*, 2004; Caniato *et al.*, 2007). Classification of the sorghums into different groups based on their response to Al stress was done following criteria given by Caniato *et al.* (2007). The root growth indices (% response and % RNRL) were used to classify the *Seredo* x *ICSR 110* progenies into resistant or sensitive to Al stress in solution culture thus:

$$\% \text{ Response} = \frac{\text{FRL}_C - \text{FRL}_{Al}}{\text{FRL}_C} \times 100 \quad [1]$$

Where  $\text{FRL}_C$  = Final root length in control

$\text{FRL}_{Al}$  = final root length in aluminium

$$\text{RNRL} = \frac{\text{NRL}_{Al}}{\text{NRL}_C} \times 100 \quad [2]$$

Where RNRL = relative net root length

$\text{NRL}_{Al}$  = net root length in aluminium

$\text{NRL}_C$  = net root length in control

### Field Evaluation of Parental Lines, F1s and F2 Segregating Populations

Field evaluation of parental lines, F1s and F2 populations for resistance to aluminium stress was done at Bumala in Busia district. Bumala is located in western Kenya at N 00° 19' N 34° 12' E, with an altitude of 1294 m (coordinates were taken using My GPS Location Android App). The soils are acidic (pH 4.3), well drained firm nitisols with high Al saturation (27%) (Obura, 2008).

The parental lines (*Seredo* and *ICSR 110*), F1s and F2 segregating populations were grown in the field with or without lime. The field was divided into two blocks. Lime (21% Calcium oxide) was supplied in one block at a rate equivalent to 4 tonnes/ha. The seeds were hand sown at a spacing of 60 cm between rows and 20 cm within rows in plots measuring 2 m x 3 m. Both blocks received uniform application of 75 kg /ha of diammonium phosphate (DAP) at sowing. Total number of leaves per plant and plant height were assessed at flowering, while total seed yield per plant was assessed after harvest and recorded.

## RESULTS

### Response of Parental Lines and their Progenies to Aluminium Stress in Solution Culture

Two sorghum lines *Seredo* and *ICSR 110* that were contrasting in their response to Al stress at 148  $\mu\text{M}$  Al concentration were used as breeding parents. *ICSR 110* was resistant with only 15% reduction in root growth, while *Seredo* had 53% reduction in root growth. Both parental lines had severe but similar root growth inhibition at 222  $\mu\text{M}$  Al (Table 1). The F1 hybrids were relatively

more resistant to Al stress than the Al resistant parent with only 12% reduction in root growth at 148  $\mu\text{M}$  Al.

The F2 populations differed significantly in their response to aluminium at 148  $\mu\text{M}$  (Table 1; Figure 2). Populations O2 x C1-15, O2 x C1-13, O2 x C1-2 and O2 x C1-12 were significantly ( $P \leq 0.05$ ) more resistant than the other populations with 4, 8, 13 and 17% root growth inhibition, respectively. Interestingly, O2 x C1-15 and O2 x C1-13 progenies were more resistant to Al stress than the Al-resistant parent and the F1. Populations O2 x C1-3, O2 x C1-14, O2 x C1-9, O2 x C1-5 and O2 x C1-1 had similar response to Al stress and had between 22% and 33% root growth inhibition. The populations that were grouped together with the aluminium sensitive parent based on their mean response to aluminium were O2 x C1-6, O2 x C1-11 and O2 x C1-10, and all had > 45% root growth inhibition at 148  $\mu\text{M}$  Al. At 222  $\mu\text{M}$  Al, all the F2 populations and the parental lines had more than 40% root growth inhibition. Individual F2 seedlings that were tolerant or sensitive to Al stress were rescued and grown to maturity.

Table 1: Effect of aluminium stress on root growth of parental lines (*SEREDO* and *ICSR 110*), F1s and F2 progenies

Sorghum Line	NRL_0	NRL_148	NRL_222	% RESPONSE_148	% RESPONSE_222	%RNRL_148	%RNRL_222
<i>ICSR 110</i>	5.9 <sup>a</sup>	5.0 <sup>a</sup>	2.3 <sup>ab</sup>	14.9 <sup>bc</sup>	60.9 <sup>ab</sup>	85 <sup>abc</sup>	39 <sup>ab</sup>
<i>SEREDO</i>	4.2 <sup>ab</sup>	2.0 <sup>b</sup>	1.6 <sup>a-c</sup>	53.1 <sup>a</sup>	60.7 <sup>ab</sup>	47 <sup>c</sup>	39 <sup>ab</sup>
O2 x C1 F1	7.0 <sup>a</sup>	6.1 <sup>a</sup>	-	12.0 <sup>bc</sup>	-	88 <sup>abc</sup>	-
O2 x C1-15	3.9 <sup>b</sup>	3.8 <sup>ab</sup>	1.6 <sup>a-c</sup>	3.7 <sup>c</sup>	58.2 <sup>ab</sup>	96 <sup>a</sup>	42 <sup>ab</sup>
O2 x C1-13	4.7 <sup>ab</sup>	4.4 <sup>ab</sup>	1.4 <sup>bc</sup>	8.2 <sup>bc</sup>	67.2 <sup>ab</sup>	92 <sup>ab</sup>	33 <sup>ab</sup>
O2 x C1-2	4.2 <sup>ab</sup>	3.6 <sup>ab</sup>	2.1 <sup>a-c</sup>	12.6 <sup>bc</sup>	48.8 <sup>ab</sup>	87 <sup>abc</sup>	52 <sup>a</sup>
O2 x C1-12	4.9 <sup>ab</sup>	4.1 <sup>ab</sup>	2.8 <sup>a</sup>	16.7 <sup>bc</sup>	44.3 <sup>b</sup>	83 <sup>abc</sup>	56 <sup>a</sup>
O2 x C1-3	4.4 <sup>ab</sup>	3.4 <sup>ab</sup>	2.4 <sup>ab</sup>	22.0 <sup>abc</sup>	45.2 <sup>b</sup>	78 <sup>abc</sup>	55 <sup>a</sup>
O2 x C1-14	5.3 <sup>ab</sup>	4.1 <sup>ab</sup>	1.7 <sup>a-c</sup>	22.2 <sup>abc</sup>	67.0 <sup>ab</sup>	78 <sup>abc</sup>	33 <sup>ab</sup>
O2 x C1-9	4.5 <sup>ab</sup>	3.3 <sup>ab</sup>	2.4 <sup>ab</sup>	27.9 <sup>abc</sup>	47.1 <sup>b</sup>	72 <sup>abc</sup>	52 <sup>a</sup>
O2 x C1-5	4.2 <sup>ab</sup>	3.0 <sup>b</sup>	2.0 <sup>a-c</sup>	29.4 <sup>abc</sup>	53.1 <sup>ab</sup>	71 <sup>abc</sup>	47 <sup>ab</sup>
O2 x C1-1	4.2 <sup>ab</sup>	2.8 <sup>b</sup>	2.1 <sup>a-c</sup>	33.3 <sup>ab</sup>	51.5 <sup>b</sup>	67 <sup>abc</sup>	49 <sup>a</sup>
O2 x C1-6	4.4 <sup>ab</sup>	2.4 <sup>b</sup>	2.3 <sup>ab</sup>	45.0 <sup>a</sup>	48.1 <sup>b</sup>	55 <sup>c</sup>	52 <sup>a</sup>
O2 x C1-11	5.3 <sup>ab</sup>	2.9 <sup>b</sup>	1.9 <sup>a-c</sup>	46.2 <sup>a</sup>	64.4 <sup>ab</sup>	54 <sup>c</sup>	36 <sup>ab</sup>
O2 x C1-10	4.7 <sup>ab</sup>	2.5 <sup>b</sup>	2.3 <sup>a-c</sup>	47.0 <sup>a</sup>	51.2 <sup>b</sup>	53 <sup>c</sup>	49 <sup>a</sup>

Values with similar letters in each column are not significantly different at  $P \leq 0.05$ . N = 21.

F1s were not evaluated at 222  $\mu\text{M}$  Al



Figure 2: Seedlings of F2 (*Seredo* x *ICSR 110*) progenies depicting segregation for aluminium resistance after growth in nutrient solution treated with 148  $\mu\text{M}$  aluminium for 120 hours.

#### Morphological Characteristics of Parental Lines *Seredo* and *ICSR 110* and F1 Progeny

Vegetative and yield attributes for parental lines and the F1s are given in Table 2. *Seredo* had significantly higher ( $P \leq 0.05$ ) number of leaves per plant, height at panicle emergence and total seed weight per plant than *ICSR 110*. However, both had similar number of tillers, leaf length and width, total plant height at maturity, days to 50% flowering and 1000 seed weight. The F1

hybrids had similar number of leaves and tillers, leaf length and width, days to 50% flowering and 1000 seed weight as *Seredo* parent. However, the F1s were significantly taller and had higher yields than either parent. The two parental lines and the F1s had similar number of tillers and leaf length.

Table 2: Vegetative and yield attributes of parental lines (*Seredo* and *ICSR 110*) and their F1 progenies

Attributes	Sorghum Genotype		
	<i>Seredo</i>	F1s	<i>ICSR 110</i>
Number of leaves per plant	11.8 <sup>a</sup>	12.0 <sup>a</sup>	9.5 <sup>b</sup>
Number of tillers	2.3 <sup>a</sup>	2.5 <sup>a</sup>	1.0 <sup>a</sup>
Leaf Length (cm)	63.8 <sup>a</sup>	67.3 <sup>a</sup>	60.9 <sup>a</sup>
Leaf width (cm)	7.2 <sup>ab</sup>	7.8 <sup>a</sup>	6.3 <sup>b</sup>
Height at Panicle Emergence (cm)	121.5 <sup>b</sup>	163.0 <sup>a</sup>	98.0 <sup>c</sup>
Height at Maturity (cm)	130.3 <sup>b</sup>	184.5 <sup>a</sup>	133.0 <sup>b</sup>
Days to 50% flowering	64 <sup>ab</sup>	68 <sup>a</sup>	62 <sup>b</sup>
Total seed weight per plant (g)	49.0 <sup>b</sup>	73.0 <sup>a</sup>	36.7 <sup>c</sup>
1000 seed weight	26.1 <sup>ab</sup>	28.5 <sup>a</sup>	22.0 <sup>b</sup>

Values with similar letters within the rows are not significantly different at  $P \leq 0.05$ . Means were separated using Tukey's HSD test.

### Effect of Lime Application on Number of Leaves per Plant

The morphological attributes for the parental lines, F1 and F2 progenies in both limed and non-limed soil are presented in Table 3. Parental line *Seredo* had fewer leaves than *ICSR 110* in both the limed and non-limed soil. The F1 progeny had more leaves per plant than either of the parents in both limed and non-limed soils. For the F2 segregating populations the box plots showing the spread of number of leaves per

plant of individual progenies derived from the same F1 are presented in Figure 3 and Figure 4. Individual F2 progenies had different number of leaves per plant some having lower or higher number of leaves than either of the parents. In unlimed soils, the number of leaves per plant in individual F2 progenies ranged between 4 and 11. Twenty seven percent (27%) of the F2 progenies had fewer leaves per plant than either of the parents.

Table 3: Mean number of leaves, total plant height and total seed weight in parental lines, F1 and F2 segregating populations grown on non-limed and limed (4t/ha) acid soils

Sorghum ID	Number of leaves		Plant height (cm)		Seed yield (g)	
	-Lime	+ Lime	-Lime	+Lime	-Lime	+Lime
<i>SEREDO</i>	7.6 ± 0.7	8.4 ± 0.7	155.8 ± 6.8	183.0 ± 6.8	38.6 ± 3.9	56.3 ± 3.9
<i>ICSR 110</i>	8.0 ± 0.7	8.8 ± 0.7	122.4 ± 6.8	139.00 ± 6.8	25.7 ± 3.0	33.9 ± 3.9
F1	8.2 ± 0.7	9.0 ± 0.9	206.3 ± 8.8	217.8 ± 6.8	82.9 ± 3.8	85.2 ± 5.0
O2 x C1-1	6.8 ± 0.3 (4-10)	7.4 ± 0.2 (4-10)	163.4 ± 7.0 (110-210)	188.2 ± 5.0 (130-230)	49.71 ± 4.9 (24.9-79.9)	49.8 ± 3.4 (39.0-71.2)
O2 x C1-2	7.1 ± 0.3 (4-10)	7.8 ± 0.3 (5-9)	171.3 ± 6.0 (110-225)	180.2 ± 6.3 (112-230)	41.8 ± 4.2 (12.0-84.2)	45.0 ± 6.0 (16.9-87.2)
O2 x C1-3	7.5 ± 0.3 (4-10)	7.8 ± 0.3 (5-11)	168.6 ± 6.3 (90-197)	185.8 ± 5.8 (120-220)	29.5 ± 5.0 (14.9-59.6)	39.5 ± 4.3 (15.0-71.0)
O2 x C1-5	6.9 ± 0.3 (5-10)	7.5 ± 0.3 (4-9)	179.2 ± 6.0 (113-230)	183.4 ± 5.2 (115-220)	47.1 ± 6.7 (20.7-85.3)	49.0 ± 3.93 (46.0- 75.0)
O2 x C1-6	7.3 ± 0.3 (5-10)	8.2 ± 0.2 (5-10)	181.8 ± 7.0 (130-210)	181.0 ± 4.7 (120-240)	59.1 ± 5.0 (20.0-103.6)	59.5 ± 3.7 (46.0-77.9)
O2 x C1-9	7.4 ± 0.3 (5-11)	7.7 ± 0.3 (5-10)	181.3 ± 5.9 (108-230)	198.8 ± 5.2 (130-240)	40.3 ± 4.1 (16.5-85.0)	41.9 ± 3.7 (11.8-85.6)
O2 x C1-10	6.8 ± 0.3 (4-10)	7.1 ± 0.3 (4-10)	163.6 ± 6.3 (103-220)	192.6 ± 5.7 (110-230)	38.4 ± 4.2 (11.9-84.8)	39.8 ± 4.7 (13.1-73.9)
O2 x C1-11	6.9 ± 0.3 (5-10)	7.3 ± 0.2 (4-9)	166.1 ± 6.0 (120-230)	187.3 ± 5.0 (120-238)	40.5 ± 4.0 (11.2-108)	44.6 ± 3.4 (15.6-89.1)
O2 x C1-12	7.7 ± 0.3 (5-11)	7.9 ± 0.3 (5-12)	178.2 ± 7.2 (137-230)	188.4 ± 5.3 (116-230)	49.8 ± 4.7 (7.5-94.0)	51.0 ± 3.7 (33.3-125.2)
O2 x C1-13	7.4 ± 0.4 (4-10)	7.4 ± 0.3 (5-13)	171.6 ± 8.9 (110-245)	184.3 ± 5.8 (136-225)	52.3 ± 7.1 (18.4-93.8)	52.9 ± 6.3 (23.8-95.8)
O2 x C1-14	7.1 ± 0.4 (4-10)	7.5 ± 0.2 (6-10)	169.8 ± 7.9 (130-206)	191.7 ± 4.4 (102-235)	39.6 ± 6.0 (14.0-75.2)	41.1 ± 3.5 (24.0-63.1)
O2 x C1-15	7.3 ± 0.4 (6-9)	7.8 ± 0.2 (6-10)	163.6 ± 8.9 (100-181)	192.4 ± 4.9 (100-230)	40.3 ± 6.3 (8.3-75.2)	44.6 ± 3.5 (19.9-91.0)

The ranges of data for the F2 segregating populations from the highest to the lowest for each attribute is indicated in brackets. The value after ± = standard error.

Similarly, 27% of the F2s had more leaves than both parents and 46% had number of leaves similar to or in between both parents. Variation existed between populations where O2 x C1-3 and O2 x C1-12 had higher mean number of leaves than the rest of the populations because most of their individual F2s had higher number of leaves than both parents (Figure 3).

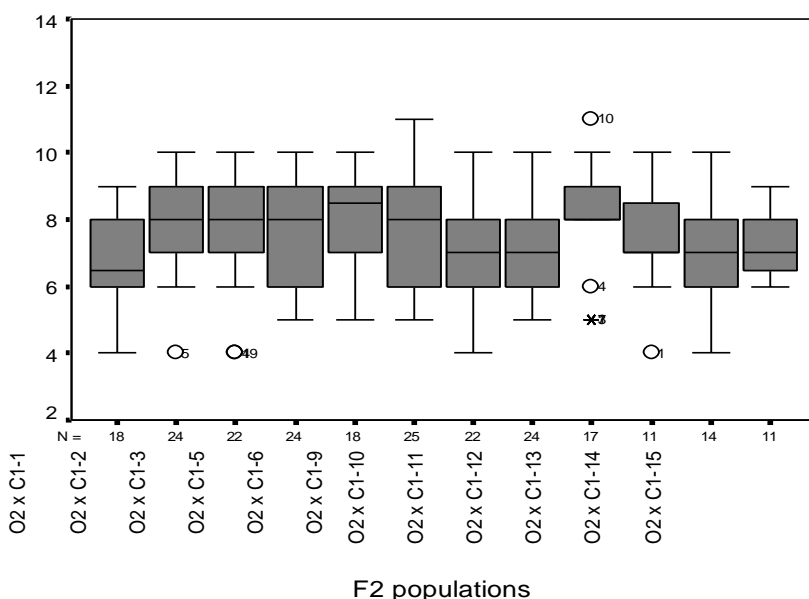
The number of leaves per plant among the F2 populations when grown in limed soil ranged between 4 and 13 (Figure 4). Fifty percent (50%) of the F2 individuals had fewer leaves per plant than the parental lines and seven percent (7%) had more leaves than both parents. The rest of the progenies (43%) had number of leaves similar to or in between both parents. Population O2C1-6

had the highest while O2 x C1-10 had the lowest mean number of leaves.

**Effect of Lime Application on Plant Height**

Both parental lines and F1s were taller in limed than non-limed soil (Table 3). The F1s were taller than both parents in both limed and non-limed soils indicating heterosis. The spread of plant height of F2 individuals in non-limed soil that ranged between 90 cm and 245 cm, is shown in Figure 5. Seventy two percent (72%) of the

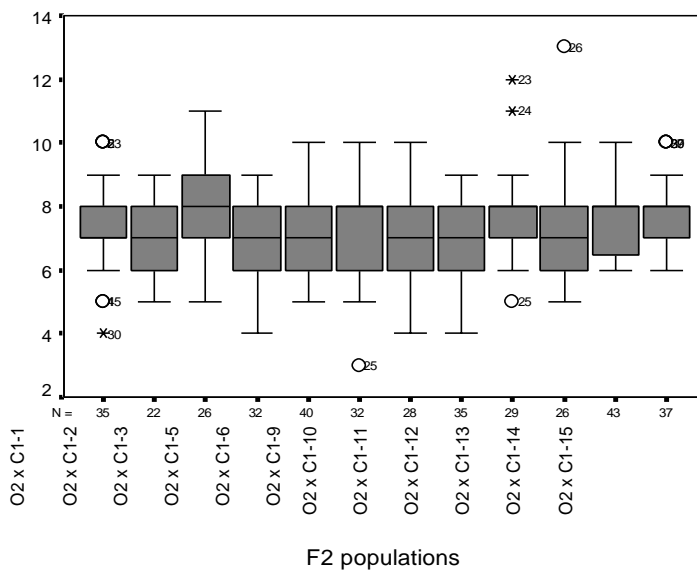
F2 individuals were taller than the taller parent (*Seredo*), 6% were shorter than *ICSR 110*, 18% had similar height as *ICSR 110* and 14% had similar height as *Seredo*. In limed soil, plant height for the individual F2 progenies ranged between 100 cm and 240 cm (Figure 5). Sixty four percent (64 %) of the F2 progenies were taller than the taller parent *Seredo*, eight percent (8%) were shorter than *ICSR 110*, eighteen percent (18%) and ten percent (10%) were as tall as *Seredo* and *ICSR 110*, respectively.



O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

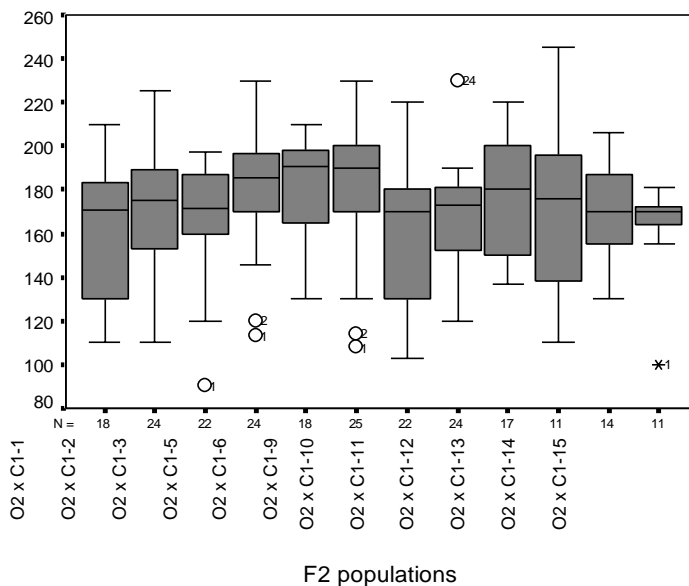
Figure 3: Box plot of the number of leaves per plant in O2 x C1 F2 populations grown on non-limed soil (The vertical bars show the lowest and highest values within a population).





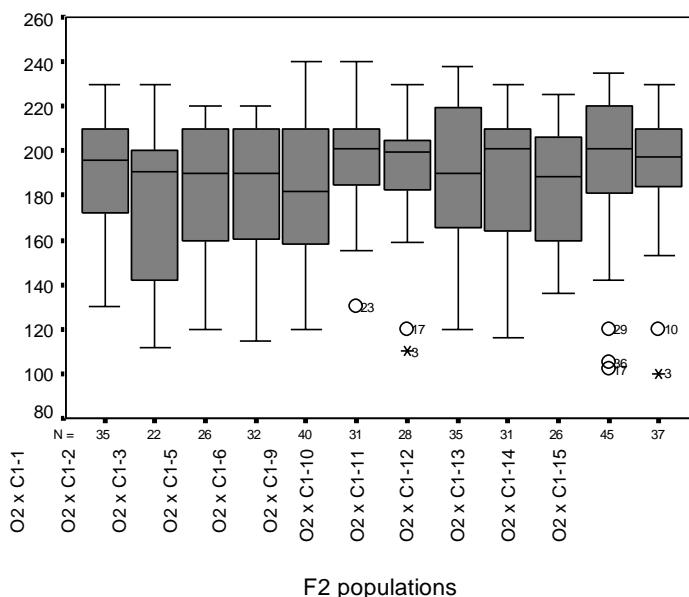
O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

Figure 4: Box plot of the number of leaves per plant in O2 x C1 F2 populations grown on limed soil (The vertical bars show the lowest and highest values within a population).



O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

Figure 5: Box plot of the plant height of O2 x C1 F2 populations grown on non-limed soil (The vertical bars show the lowest and highest values within a population).



O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

Figure 6: Box plot of the plant height of O2 x C1 F2 populations grown on limed soil (The vertical bars show the lowest and highest values within a population)

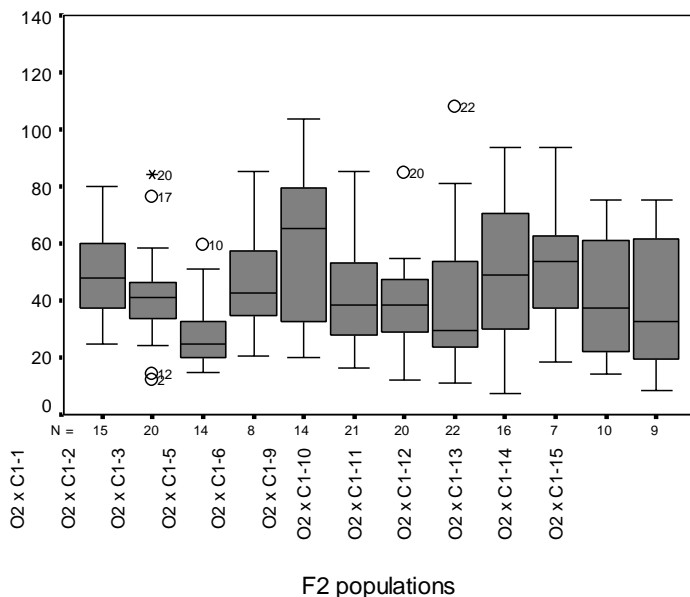
**Effect of Liming on Seed Yield per Plant**

In both limed and non-limed soils, *Seredo* had higher yield per plant than *ICSR 110*. However, the F1s significantly ( $P \leq 0.05$ ) outperformed both parents with more than double seed yield per plant (Table 3). Lime application increased seed yield by 32% and 46% in *ICSR 110* and *Seredo* respectively, but had no significant effect ( $P \leq 0.05$ ) on seed yield in the F1 hybrids.

The seed yield for individual F2s in non-limed soil ranged between 7.5 g and 108 g (Table 3; Figure 7). Forty nine percent (49%) of the F2 progenies had higher seed yield than either parent, twenty three percent (23%) had lower seed yield than low yielding parent and ten percent (10%) and eighteen percent 18% had seed yield similar to *Seredo* and *ICSR 110*, respectively. Population O2C1-3 had the

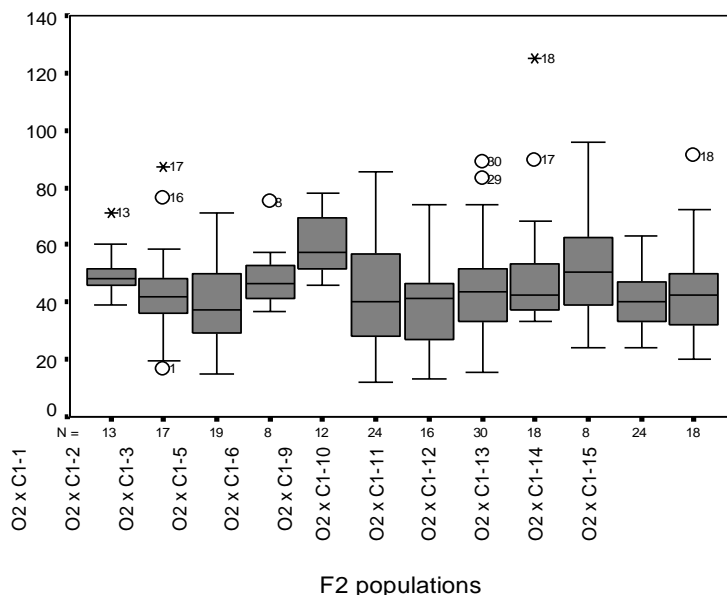
lowest seed yield per plant and O2C1-6 had the highest seed yield per plant. Some of the individual F2s that had high yields are indicated as outliers (Figure 7).

In limed soil, the seed yield for individual F2 progenies ranged between 12 g and 125 g (Table 3; Figure 8). Fifty five percent (55%) of the F2 individuals had seed yield in between those of the parental lines. However twenty percent (20%) of the F2 individuals had higher seed yield than *Seredo* and twenty five percent (25%) had lower seed yield than both parents. Population O2C1-3 had the least mean seed yield per plant because most of the individual F2s had low yields, while O2C1-6 had the highest mean seed yield because most of the individual F2 progenies had high yields (Figure 8).



O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

Figure 7: Box plot of seed yield per plant in O2 x C1 F2 populations grown on non-limed soil.



O, \* = Outliers, scores that are different from the rest of the samples, either much higher or much lower

Figure 8: Box plot of seed yield per plant in O2 x C1 F2 populations grown on limed soil.

## DISCUSSIONS

Soil chemical factors that limit root growth in acid soils, such as aluminium reduce crop production (Mossor-Pietraszewska, 2001). The main symptom of aluminium toxicity is inhibition of root growth, but this translates to a reduction in crop yields (Kochian *et al.*, 2005). However, genetic differences in nutrient uptake, nutrient use efficiency and transport have been reported for sorghum cultivars and genotypes subjected to aluminium stress (Baligar *et al.*, 1989). Identification of genotypes having high yield both in the absence and presence of Al, will be useful in sorghum breeding programmes in producing cultivars with high adaptability to acid soils. In this study, it has been demonstrated that the Kenyan sorghum germplasm contain useful genetic variation for resistance to Al toxicity which can be used to develop cultivars adapted to acid aluminium-toxic soils. The transfer of Al tolerance quantitative trait loci (QTLs) or genes was possible in this study. Some *Seredo* x *ICSR 110* progenies were more resistant to Al stress than both parents, probably taking advantage of additive gene effects. Similar results were reported by Caniato *et al.*, (2007). Therefore, careful selection among the *Seredo* x *ICSR 110* segregating populations could lead to generation of lines that are highly resistant to Al stress. Furthermore, varied genetic gains of aluminium resistance has also been reported for three different sorghum segregating populations (Anas *et al.*, 2019). These results imply that several genes could be involved in contributing to aluminium resistance trait in sorghum. In fact, Caniato *et al.* (2011) reported that multiple alleles at the  $Alt_{SB}$  locus, where a major gene conferring Al resistance in sorghum resides explains the wide range of Al resistance in sorghum.

In the current study, lime application increased sorghum grain yield in both parental lines and some of the F2 segregating populations. This is in agreement with findings of Getahum *et al.* (2018) though these authors did not have

segregating populations in their experiments. Most of the F2 segregating populations had higher mean grain yields when grown without lime compared with those in plots with lime supplementation. The varied performance of the F2 segregating populations in terms of grain yield could be attributed to unique genetic composition of the segregating F2 populations.

The F1 hybrids outperformed both parents in either limed or non-limed soil at Bumala. This may be attributed to heterosis or hybrid vigour. The F2s showed segregation in all the parameters assessed. However, some of the individual F2s far outperformed both parents in non-limed soil suggestive of positive transgressive segregation. These promising progeny lines need to be advanced and tested for use in future breeding programmes and also for use in acid soils with high levels of aluminium. Although the Al-resistant *ICSR 110* parental line had lower yields than the Al-sensitive *Seredo* parental line, recombinant inbred lines that are high yielding and are Al-resistant can be selected from the progenies and advanced to stable generations.

The superiority of some F2 progeny lines in terms of grain yield in acidic non-limed soils may require further investigation. It is not immediately known whether the superior progenies have better root growth therefore enhancing nutrient uptake which translates to improved yields. It may also be important to investigate the mechanism (s) of aluminium resistance in these progenies after advancement to genetically stable generations.

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