academicJournals

Vol. 9(21), pp. 1651-1662, 22 May, 2014
DOI: 10.5897/AJAR2013. 7795
Article Number: 85DC12544802
ISSN 1991-637X

http://www.academicjournals.org/AJAR

African Journal of Agricultural Research

*Full Length Research Paper*

# Response of selected sorghum (*Sorghum bicolor* L. Moench) germplasm to aluminium stress

**Emily Jepkosgei Too[1]*, Beatrice Ang'iyo Were[1], Augustino Osoro Onkware[1], Justin Hanson Ringo[2], Peter Kisinyo[1], Anders S. Carlsson[3], Evans Ouma[1], Mulatu Geleta[3] and Samuel Gudu[4]**

[1]University of Eldoret, P. O. Box 1125-30100 Eldoret, Kenya.
[2]Mikocheni Agricultural Research Institute. P. O. Box 6226, Dar Es Salaam, Tanzania.
[3]Department of Plant Breeding Swedish University of Agricultural Sciences, Box 101, 230 53 Alnarp, Sweden.
[4]Rongo University College, P. O. Box 103-40404 Rongo, Kenya.

Received 8 August, 2013; Accepted 16 April, 2014

**Sorghum (*Sorghum bicolor* L. (Moench) is an important food security crop in sub-Saharan Africa. Its production on acid soils is constrained by aluminium (Al) stress, which primarily interferes with root growth. Sorghum cultivation is widespread in Kenya, but there is limited knowledge on response of the Kenyan sorghum cultivars to aluminium stress. The aim of the study was to identify and morphologically characterise aluminium tolerant sorghum accessions. The root growth of three hundred and eighty nine sorghum accessions from local or international sources was assessed under 148 µM Al in soaked paper towels, and 99 of these were selected and further tested in solution. Ten selected accessions were grown out in the field, on un-limed (0 t/ha) or limed (4 t/ha) acid (pH 4.3) soils with high (27%) Al saturation, and their growth and grain yield was assessed. Although the Al stress significantly (P ≤ 0.05) reduced root growth in most of the accessions, there were ten accessions; MCSRP5, MCSR 124, MCSR106, *ICSR110*, Real60, IS41764, MCSR15, IESV93042-SW, MCSRM45 and MCSRM79f, that retained relatively high root growth and were classified as tolerant. The stress significantly (P ≤ 0.05) reduced seedling root and shoot dry matter in the Al-sensitive accessions. Plant growth and yield on un-limed soil was very poor, and liming increased grain yield by an average 35%. Most of Kenya sorghums were sensitive to Al stress, but a few tolerant accessions were identified that could be used for further breeding for improved grain yield in high aluminium soils.**

**Key words:** Aluminium tolerance, grain yield, liming, root growth sorghum.

## INTRODUCTION

Sorghum (*Sorghum bicolor* L. Moench) is a staple cereal crop in many parts of Africa and Asia, especially in sub-humid and semi-arid agro-ecologies (Simpson and Conner-Ogorzaly, 2001). Despite its importance, sorghum grain yield in sub-Saharan Africa is low (2 t/ha) and has been declining over the years (Wortmann et al.,

*Corresponding author. E-mail: emiltoo2002@yahoo.com, Tel: +254 (0) 722 221828. Fax: +254 (0) 5343321.

2006) mainly because of poor agronomy, or abiotic and biotic stresses. Many of the soils used for sorghum cultivation in the tropics are acidic (pH<5.5). Soil acidity is common in the tropics and subtropics because of the nature of the parent rocks and the high degree of weathering and base leaching that has occurred (Johnson, 1988). The greater proportion of potentially arable land worldwide is acidic (Von Uexküll and Mutert, 1995), and in Kenya acid soils cover up to 13 % of the arable land (Kanyanjua et al., 2002).

Although Aluminium (Al) is one of the most abundant mineral elements in soil, it occurs in insoluble or non-toxic oxide and hydroxide compounds under neutral or basic pH. However, the compounds become more soluble under acidic (pH<5.5) conditions and release a variety of Al species, especially the trivalent aluminium ion ($Al^{3+}$) and soluble hydroxides. The $Al^{3+}$ is toxic to plants, and occurs both in solution and at the cation exchange sites, where it can be easily exchanged with other soluble cations. Acid soils in Kenya have between 8 and 61% Al saturation (Obura et al., 2010). Most plants are adversely affected if the soil contains more than 20% aluminium saturation.

The primary effect of Al stress is stunting of the roots (Rengel, 1996). The resulting restricted root system is inefficient in water and mineral absorption, making the plant more susceptible to water stress or mineral nutrient deficiency. The combined limitation on water and mineral nutrient absorption leads to poor plant development and low crop yield. However, aluminium tolerant plants maintain high root growth and plant vigour under Al through the exclusion of Al from the root symplasm or tolerance to high $Al^{3+}$ concentration in the symplasm (Kochian, 1995). The exclusion of Al from the root is achieved by releasing Al-chelating ligands such as organic acids. The organic acid exudates, secreted in significant amount by the tolerant genotypes, form Al-carboxylate complexes that are not taken up by plant roots. Al-tolerant sorghum genotypes have been shown to secrete relatively large quantities of citric, malic and transaconitic acids (Goncales et al., 2005; Magalhaes et al., 2007).

Although lime is conventionally applied to amend soil acidity and related stresses, the practice increases farming cost. Large quantities of lime (2 to 10 t/ha) are required to ameliorate the acidity and enhance growth of crops (Kisinyo et al., 2013). Moreover, sub-soil acidity is not effectively corrected by surface liming (Ernani et al., 2004) unless lime is applied in large quantities and mixed into the deeper soil layers. Therefore, the use of Al-tolerant crop cultivars in addition to lime application could greatly enhance yields in soils that have high percentage of exchangeable aluminium.

Sorghum has a significant genotypic variation in relation to tolerance to Al stress (Caniato et al., 2007) that can be exploited to develop varieties with superior tolerance. However, although significant sorghum cultivation in Kenya occurs on acid soils of western Kenya (Obura, 2008; Kisinyo, 2011), there has been limited selection and breeding for Al tolerant sorghum for this region. Moreover, the amount of yield loss occasioned by Al toxicity in Kenya is not known. The objectives of this study were to determine the level of tolerance in selected Kenyan sorghum lines and to identify Al tolerant accessions, under laboratory and field conditions with specific reference to seedling root growth and grain yield.

## MATERIALS AND METHODS

Three hundred and eighty nine sorghum accessions comprising of Kenyan landraces, commercial varieties, breeding lines, recombinant inbred lines (RILs) and Al tolerant and sensitive standard lines, hereinafter termed accessions, were pre-screened for tolerance to Al stress using moistened paper-towels. The sorghum seeds were surface sterilized in 1% sodium hypochlorite for 8 min, rinsed with sterile distilled water, germinated and grown at 26°C for 5 days between sterilized paper towels that were moistened with 10 ml treatment solution (pH 4.0) at two levels of Al stress; 0.82 mM Al or without Al (control). The cellulose fibres in the paper bind $Al^{3+}$ and thus reducing the effective concentration. Earlier studies had shown that 0.82 mM $Al^{3+}$ in filter paper tests is equivalent to 148 µM Al in free solution (Tamas et al., 2006). The root length was measured and root tolerance index (RTI) was calculated as follows:

$$\mathrm{RTI} = \frac{\text{Root length in aluminium}}{\text{Root length in control}} \qquad (1)$$

The RTI was used to group the accessions into tolerant or sensitive categories. After the pre-screening, a representative sample of 99 accessions (Table 1) that had been rated as tolerant, sensitive or intermediate were selected and subjected to Al stress in aerated nutrient solution (Magnavaca et al., 1987). Sterilized sorghum seeds were pre-germinated in the dark for 72 h at 25°C between sheets of sterilized paper towels that were moistened with sterile distilled water. Healthy seedlings with the similar root size and form were grown in the nutrient solution without Al for 24 h to equilibrate. The initial length of the main root (IRL) was measured and recorded. Thereafter the seedlings were transferred individually into the growth vials that were placed in holding plastic rafts and transferred to trays containing eight litres of nutrient solution without (control) Al or with 148 or 222 µM Al (Caniato et al., 2007). The seedlings were grown in a plant growth chamber with gentle, continuous aeration for 120 h at 28°C with 17/7 photoperiod and light intensity of 200 µmol $m^{-2}s^{-1}$. The set up was replicated five times. The length of the main root with branches in the control ($RLB_c$) and in the Al treatment ($RLB_{Al}$) was measured and recorded. The shoot and root dry weight (68°C for 48 h) of five representative sorghum accessions were determined and recorded.

The data was used to calculate seedling growth indices: net root length (NRL), percentage of response (% response), relative net root length (RNRL) and percentage of reduction in root branching (% RRB) (Magalhaes et al., 2004), thus;

$$\mathrm{NRL} = \mathrm{FRL} - \mathrm{IRL} \qquad (2)$$

Where FRL is the final root length in both Al treated and control plants and IRL is the initial root length. The response (%) was measured as:

**Table 1.** Origin of selected sorghum germplasm used in the study.

| Sorghum Line | Source | Classification | Sorghum accession | Source | Classification |
|---|---|---|---|---|---|
| MCSR P5 | Oyugis | Landrace* | | | |
| MCSR124 | MUSRT | RIL | MCSRF-6 | Kilifi | landrace |
| MCSR106 | MUSRT | RIL | MCSR N140c | Isebania | Landrace |
| *ICSR110* | ICRISAT | Al standard | MCSRN79 | Kisii | Landrace |
| *Real60* | ICRISAT | Al standard | MCSRN102 | Karungu | Landrace |
| *IS41764* | ICRISAT | Al standard | MCSRN20 | Mosocho | Landrace |
| MCSR15 | MUSRT | RIL | MCSRI17 | Kilibasi | Landrace |
| *IESV93042-SW* | ICRISAT | Breeding line | MCSR N77 | Ndhiwa | Landrace |
| MCSRM45 | Koyonzo | Landrace | MCSRN140 | Isebania | Landrace |
| MCSRM79f | Nangeni | Landrace | MCSRM69e | Nangeni | Landrace |
| MCSRN24 | Mabera | Landrace | MCSRM42b | Nangeni | Landrace |
| MCSRM41 | Nangeni | Landrace | MCSR 60 | MUSRT | RIL |
| MCSR M65b | Nangeni | Landrace | MCSRJ3b | Makueni | Landrace |
| *Macia* | ICRISAT | Released Var. | MCSRM19 | Nangeni | Landrace |
| *ICSB609* | ICRISAT | Standard | MCSRT71 | ICRISAT | Landrace |
| MCSRN140b | Isebania | Landrace | MCSR140d | Isebania | Landrace |
| MCSRM42d | Nangeni | Landrace | MCSRF9b | Kilifi | Landrace |
| MCSRI6d | Kilibasi | Landrace | MCSRG1a2 | Ukunda | Landrace |
| MCSRN60 | Kanyamua | Landrace | MCSRM63c | Nangeni | Landrace |
| *PGRC/E216740* | ICRISAT | Breeding line | MCSRQ4 | Malaba | Landrace |
| MCSRM62 | Nangeni | Landrace | MCSR N74 | Ndhiwa | Landrace |
| MCSRN81 | Kisii | Landrace | MCSRM33a | Nangeni | Landrace |
| MCSRM5 | Nangeni | Landrace | *P20SP* | KARI | Breeding line |
| MCSRM23 | Nangeni | Landrace | MCSRN85 | Ndhiwa | Landrace |
| MCSRP3 | Oyugis | Landrace | MCSRN68 | Mabera | Landrace |
| *KAK7540* | KARI | Breeding line | *ICSB608* | ICRISAT | Standard |
| MCSRL3b | Busia | Landrace | MCSRN72 | Ndhiwa | Landrace |
| MCSRN21 | Mabera | Landrace | MCSRM33b | Nangeni | Landrace |
| MCSRQ3 | Malaba | Landrace | MCSRN88a | Ndhiwa | Landrace |
| MCSRN83 | Ndhiwa | Landrace | MCSRK5b | Eldoret | Landrace |
| MCSRI6 | Kilibasi | Landrace | *ICSB613* | ICRISAT | Standard |
| MCSRM68b | Nangeni | Landrace | MCSRN35 | Mabera | Landrace |
| MCSRH2a | Ukunda | Landrace | MCSRN2 | Mabera | Landrace |
| MCSRS66 | Sega | Landrace | MCSRN13 | Mabera | Landrace |
| MCSRL3 | Busia | Landrace | MCSRK5e | Eldoret | Landrace |
| MCSRM47g | Nangeni | Landrace | MCSRM21 | Nangeni | Landrace |
| MCSRF9d | Kilifi | Landrace | MCSRM73e | Nangeni | Landrace |
| MCSRL6 | Sega | Landrace | Serena x Esuti | KARI | Breeding line |
| MCSRS65 | Bumala B | Landrace | MCSR N157a | Karungu | Landrace |
| MCSRM69 | Nangeni | Landrace | MCSRM3 | Nangeni | Landrace |
| MCSRM33 | Nangeni | Landrace | MCSRN84 | Ndhiwa | Landrace |
| MCSRN103 | Karungu | Landrace | ICSV112 | ICRISAT | Breeding line |
| MCSRF-1 | Kilifi | Landrace | Pato | ICRISAT | Released var |
| Seredo | Kenya seed | Cultivar | MCSRG2 | Ukunda | Landrace |
| MCSR N51 | Migori | Landrace | MCSRM44 | Nangeni | Landrace |
| MCSRN57 | Mabera | Landrace | MCSRL5 | Sega | Landrace |
| MCSRN61 | Mosocho | Landrace | MCSRN120 | Karungu | Landrace |
| MCSRI19 | Kilibasi | Landrace | Hakika | ICRISAT | Released var |
| MCSRT94 | ICRISAT | Breeding line | MCSR N88 | Ndhiwa | Landrace |
| MCSRN88c | Ndhiwa | Landrace | MCSRM45b | Koyonzo | Landrace |

* The Landraces were purified through three cycles of selfing before they were tested. RIL – recombinant inbred line. The commercial varieties, standards and breeding lines are written in italics.

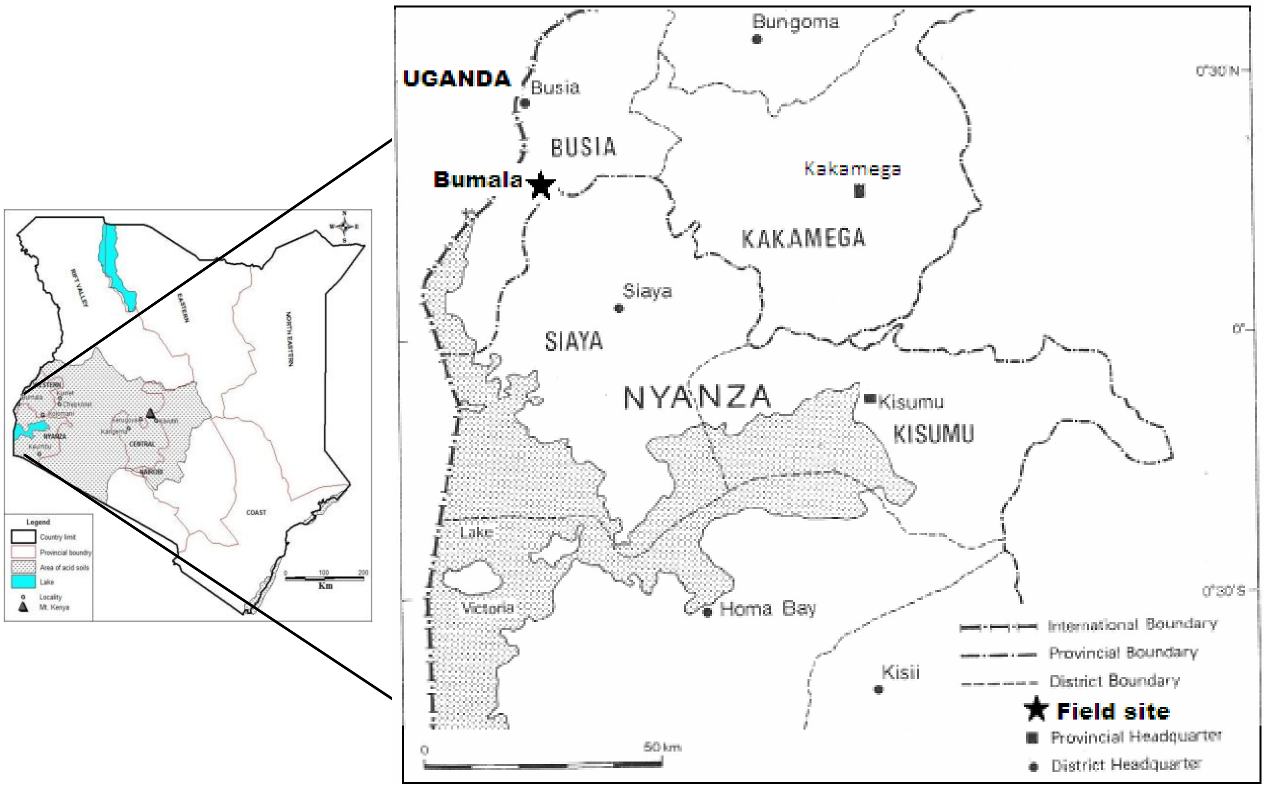



**Figure 1**. Map of Kenya showing field sites used in this study. Bumala site was used as a testing site and falls within regions with acidic soils, as characterized by Kanyanjua et al. (2002).

$$\%\ \text{Response} = \frac{\text{FRL}_{\text{C}} - \text{FRL}_{\text{Al}}}{\text{FRL}_{\text{C}}} \times 100 \tag{3}$$

Where $FRL_C$ is final root length in control and $FRL_{Al}$ is the final root length in Al. RNRL was calculated as:

$$\text{RNRL} = \frac{\text{NRL}_{\text{Al}}}{\text{NRL}_{\text{C}}} \times 100 \tag{4}$$

Where $NRL_{Al}$ is net root length in Al, and $NRL_C$ is net root length in control

$$\%\ \text{RRB} = \frac{\text{RLBC} - \text{RLBAl}}{\text{RLBC}} \times 100 \tag{5}$$

Where % RRB is the percent reduction in root branching, $RLB_C$ is the length of root with branches in control, and $RLB_{Al}$ is length of root with branches in aluminium.

The percentage response to Al and RNRL were used to classify the sorghum lines as tolerant (≤30% response to Al; RNRL > 70%) or susceptible (>70% response; RNRL < 30%) as defined by Caniato et al. (2007).

A sample of five of the accessions: MCSRP5 (Al-tolerant popular landrace); ICSR110 (Al- tolerant standard check); MCSR15 (Al-tolerant RIL); Seredo (Al-sensitive commercial variety) and MCSRL5 (Al-sensitive popular landrace) were used to evaluate the effect of Al on root and shoot dry weight. To show root injury caused by Al stress the root tips of some lines were visualized and photographed using a microscope (Leica DMLB) fitted with a Leica DC 300 digital camera.

Ten accessions; *ICSR110*, Real60 and *IS41764* (Al-tolerant check), and MCSRM45 (Al-tolerant popular high yielding landrace); *Macia* (moderately tolerant released variety); *Seredo* (Al-sensitive commercial variety), MCSRM33, MCSRL5 and MCSRN61 (Al sensitive, high yielding popular landraces), and *ICSV112* (Al-sensitive breeding line) were evaluated in the field at Bumala in Busia, Western Kenya (Figure 1) for response to Al stress on basis of vegetative growth and grain yield. Bumala is located at N 00°19' E 034°12', at an altitude of 1294 m. The soil at the test site is well drained firm, acidic (pH 4.3), nitisol, with high (> 27%) Al saturation percentage (Obura, 2008; Kisinyo, 2011).

The accessions were grown out in plots in the field with or without lime in a split plot design. Lime (21% Calcium oxide) was applied and mixed with the top soil in one block 60 days before planting at a rate equivalent to 4 t/ha. The plots were ploughed to a fine tilt. The seeds were hand sowed at a spacing of 60 cm between rows and 20 cm within rows in plots measuring 2 × 3 m, which translated into 83,333 plants per hectare. Both blocks received uniform application of 75 kg/ha of diammonium phosphate (DAP) at sowing. The number of leaves and leaf area per plant were assessed at 50% flowering. The length and width of individual leaves per plant were measured using a meter ruler and then leaf area was calculated using the following formula (Stickler et al., 1961):

$$\text{Leaf area} = (\text{leaf length} \times \text{leaf width}) \times 0.75 \tag{6}$$

Grain yield and thousand-seed weight were assessed and recorded after harvest. All the data were subjected to analysis of variance

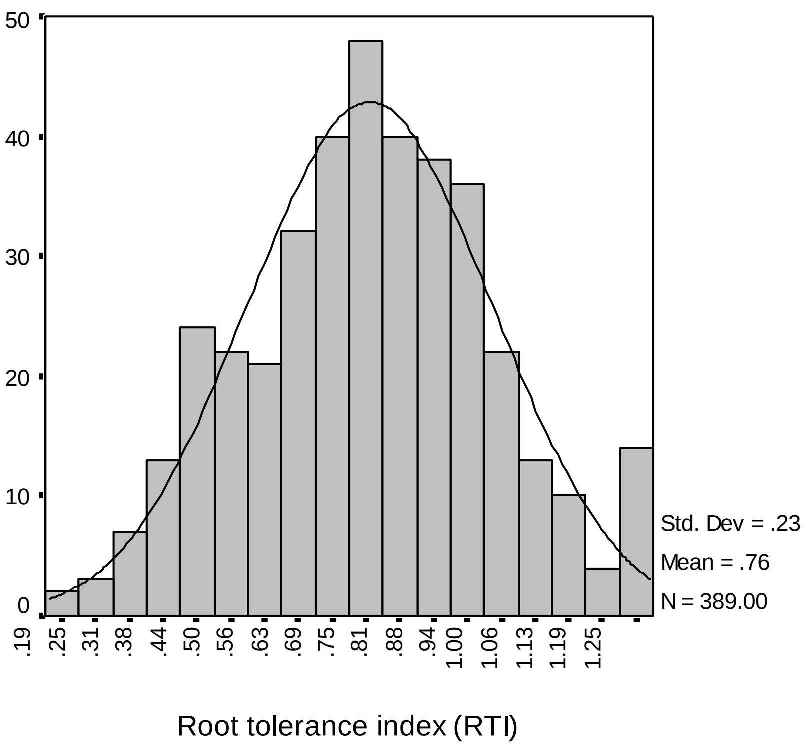



**Figure 2.** Frequency distribution of root tolerance indices of 389 Kenyan local sorghum accessions. Sterilized seeds were germinated and grown at 26oC for 5 days between paper towels moistened with nutrient solution containing 148 µM Al or without Al.

(ANOVA) using SPSS®. Differences were adopted as significant at P ≤ 0.05. Means were separated using Tukey's 'honestly significant difference' (HSD) test. The indices data were subjected to square root transformation before statistical analysis.

## RESULTS

It was possible to grade the 389 sorghum accessions for aluminium tolerance using the RTIs of filter-paper grown seedlings. Fifty percent of the accessions had RTI of more than 0.75, whereas the other half had RTI of less than 0.75 (Figure 2). Some of the resistant accessions had better root growth (RTI>1.0) when grown under the 148 µM than under control.

In the nutrient solution, the net root length of most sorghum accessions was significantly (P ≤ 0.05) reduced by the 148 µM Al stress (Table 2). Percent response to Al corresponds to Al-induced reduction in root growth. Only 10 accessions; MCSRP5, MCSR124, MCSR106, *ICSR110*, *Real60*, *IS41764*, MCSR15, *IESV93042-SW*, MCSRM45 and MCSRM79f, had less than 30% root growth reduction in response to Al (RNRL > 70%), and were therefore classified as tolerant to Al stress. Twenty-five accessions expressed root growth reduction ranging between 35 and 50% (RNRL- 50 to 65%), and were classified as moderately tolerant. Sixty-four accessions had between 51 to 82% root growth reduction (RNRL- 18 to 49%) and were classified as sensitive to Al stress. The accessions that expressed more the 70% reduction in root growth (RNRL ≤30%) were classified as highly sensitive; they included MCSRG2, MCSRM44, MCSRL5, MCSRN120, *Hakika,* MCSRN88 and MCSRM45b.

A relative effect of Al stress on root growth in representative sensitive and tolerant sorghum accessions is presented in Figure 3. The root growth in sensitive accessions was severely reduced by the stress, whereas that of tolerant accessions was only minimally affected. Figure 4 shows the appearance of root tips under bright field microscope examination. Although the root tip morphology of the Al-resistant accessions was fairly normal, those of Al-sensitive accessions developed surface lesions after 120 h of exposure to 148 µM Al.

Some accessions, such as MCSR124, MCSR15, MCSR 17, MCSR60, MCSRJ3b, MCSRI19, *ICSV112*, *Pato* and MCSRM45b had significantly longer roots than the rest of the accessions when grown without Al stress. However, only two accessions from this group; MCSR124 and MCSR15, maintained high root growth under the Al stress. There was a significant (P ≤ 0.05) variation in root branching both among the different sorghum accessions grown without the Al stress, and among those subjected to the 148 µM of Al stress (Table 2). The root branching was significantly reduced by the stress, with most accessions having a percent relative root branching

**Table 2.** Effect of aluminium stress on seedling root growth in some selected sorghum plants.

| Sorghum accession | NRL-Al | %Resp | RNRL | %RRB | Sorghum accession | NRL-Al | %Resp | RNRL | %RRB |
|---|---|---|---|---|---|---|---|---|---|
| MCSRP5 | $3.68^{a-d\dagger}$ | $4.0^{p}$ | $96^{a}$ | $59^{a-d}$ | MCSRT71 | $2.90^{a-m}$ | $52.8^{a-k}$ | $47^{b-l}$ | $80^{a-c}$ |
| MCSR124 | $6.08^{a}$ | $7.0^{op}$ | $93^{a}$ | $48^{b-d}$ | MCSR140d | $2.04^{f-o}$ | $52.9^{a-k}$ | $47^{b-l}$ | $68^{a-c}$ |
| MCSR106 | $4.20^{ab}$ | $10.0^{op}$ | $90^{ab}$ | $56^{a-d}$ | MCSRF9b | $2.13^{e-o}$ | $53.7^{a-k}$ | $46^{b-l}$ | $80^{a-c}$ |
| ***ICSR110*** $^{S}$ | $4.23^{a}$ | $10.2^{op}$ | $90^{ab}$ | $51^{a-d}$ | MCSRG1a2 | $2.05^{f-o}$ | $53.7^{a-k}$ | $46^{b-l}$ | $94^{ab}$ |
| ***Real60*** $^{S}$ | $3.64^{a-e}$ | $14.55^{n-p}$ | $85^{abc}$ | $58^{a-d}$ | MCSRM63c | $2.88^{a-m}$ | $53.8^{a-k}$ | $46^{b-l}$ | $76^{a-c}$ |
| ***IS41764*** $^{S}$ | $3.66^{a-e}$ | $18.3^{m-p}$ | $82^{abc}$ | $67^{a-c}$ | MCSRQ4 | $2.45^{b-o}$ | $54.2^{a-k}$ | $46^{b-l}$ | $92^{ab}$ |
| MCSR15 | $5.28^{a}$ | $25.0^{l-p}$ | $75^{a-d}$ | $45^{b-d}$ | MCSRN74 | $2.18^{d-o}$ | $54.5^{a-k}$ | $46^{b-l}$ | $95^{ab}$ |
| *IESV93042 -SW* | $3.43^{a-f}$ | $25.5^{l-p}$ | $75^{a-d}$ | $50^{a-d}$ | MCSRM33a | $2.76^{a-n}$ | $54.6^{ak}$ | $45^{c-l}$ | $96^{ab}$ |
| **MCSRM45** $^{S}$ | $3.79^{abc}$ | $26.3^{k-p}$ | $74^{a-e}$ | $64^{a-d}$ | *P20SP* | $2.49^{b-o}$ | $54.7^{a-k}$ | $45^{c-l}$ | $68^{a-c}$ |
| MCSRM79f | $2.92^{a-l}$ | $28.6^{j-p}$ | $71^{a-f}$ | $96^{a-b}$ | MCSRN85 | $2.25^{c-o}$ | $54.7^{a-k}$ | $45^{c-l}$ | $75^{a-c}$ |
| MCSRN24 | $3.03^{a-l}$ | $35.0^{h-o}$ | $65^{a-g}$ | $62^{a-d}$ | MCSRN68 | $1.93^{f-o}$ | $54.8^{a-k}$ | $45^{c-l}$ | $88^{a-c}$ |
| MCSR M41 | $2.72^{a-n}$ | $35.2^{h-o}$ | $65^{a-g}$ | $87^{a-c}$ | *ICSB608* | $2.23^{c-o}$ | $55.2^{a-k}$ | $45^{c-l}$ | $100^{a}$ |
| MCSR M65b | $2.49^{b-o}$ | $37.1^{g-o}$ | $63^{a-h}$ | $78^{a-c}$ | MCSRN72 | $1.57^{i-o}$ | $55.5^{a-k}$ | $45^{c-l}$ | $70^{a-c}$ |
| ***Macia*** $^{S}$ | $3.26^{a-h}$ | $37.7^{g-o}$ | $62^{a-h}$ | $99^{ab}$ | MCSRM33b | $1.92^{f-o}$ | $55.9^{a-k}$ | $44^{d-l}$ | $99^{a}$ |
| *ICSB609* | $3.36^{a-g}$ | $38.7^{e-o}$ | $61^{a-h}$ | $70^{a-c}$ | MCSRN88a | $1.86^{f-o}$ | $56.7^{a-k}$ | $43^{d-l}$ | $94^{ab}$ |
| MCSRN140b | $3.15^{a-j}$ | $39.9^{d-o}$ | $60^{a-i}$ | $60^{a-d}$ | MCSRK5b | $2.32^{b-o}$ | $56.8^{a-k}$ | $43^{d-l}$ | $90^{ab}$ |
| MCSRM42d | $3.72^{a-d}$ | $40.2^{d-o}$ | $60^{a-i}$ | $84^{a-c}$ | *ICSB613* | $2.56^{b-o}$ | $57.0^{a-k}$ | $43^{d-l}$ | $95^{ab}$ |
| MCSRI6d | $2.28^{b-o}$ | $40.8^{d-o}$ | $59^{b-j}$ | $68^{a-c}$ | MCSRN35 | $2.49^{b-o}$ | $57.0^{a-k}$ | $43^{d-l}$ | $95^{ab}$ |
| MCSRN60 | $2.80^{a-n}$ | $41.7^{c-o}$ | $58^{b-j}$ | $70^{a-c}$ | MCSR N2 | $1.78^{h-o}$ | $57.1^{a-k}$ | $43^{d-l}$ | $95^{ab}$ |
| *PGRC/E216740* | $3.01^{a-l}$ | $42.5^{c-o}$ | $58^{b-j}$ | $86^{a-c}$ | MCSRN13 | $1.97^{f-o}$ | $57.6^{a-k}$ | $42^{d-l}$ | $93^{ab}$ |
| MCSRM62 | $2.80^{a-n}$ | $42.7^{c-o}$ | $57^{b-k}$ | $70^{a-c}$ | MCSRK5e | $2.27^{b-o}$ | $57.7^{a-k}$ | $42^{d-l}$ | $75^{a-c}$ |
| MCSRN81 | $3.34^{a-g}$ | $42.8^{c-o}$ | $57^{b-k}$ | $44^{b-d}$ | MCSRM21 | $2.18^{d-o}$ | $58.0^{a-k}$ | $42^{d-l}$ | $81^{a-c}$ |
| MCSRM5 | $2.49^{b-o}$ | $43.4^{b-o}$ | $57^{b-k}$ | $76^{a-c}$ | MCSRM73e | $1.73^{h-o}$ | $58.5^{a-j}$ | $41^{e-l}$ | $67^{a-c}$ |
| MCSRM23 | $2.49^{b-o}$ | $43.6^{b-0}$ | $56^{b-k}$ | $80^{a-c}$ | MCSRL6 | $2.05^{f-o}$ | $58.6^{a-j}$ | $41^{e-l}$ | $46^{cd}$ |
| MCSRP3 | $3.19^{a-i}$ | $44.7^{b-o}$ | $55^{b-k}$ | $77^{a-c}$ | MCSRS65 | $2.17^{d-o}$ | $59.4^{a-j}$ | $41^{e-l}$ | $62^{a-d}$ |
| *KAK7540* | $2.41^{b-o}$ | $45.6^{b-o}$ | $54^{b-k}$ | $52^{a-d}$ | MCSRM69 | $1.79^{g-o}$ | $59.5^{a-j}$ | $41^{e-l}$ | $58^{a-c}$ |
| MCSRL3b | $2.29^{b-o}$ | $46.1^{b-o}$ | $54^{b-k}$ | $71^{a-c}$ | **MCSRM33** $^{S}$ | $2.31^{b-o}$ | $59.6^{a-j}$ | $40^{e-l}$ | $82^{a-c}$ |
| MCSRN21 | $2.43^{b-o}$ | $46.5^{a-o}$ | $53^{b-k}$ | $93^{ab}$ | MCSRN103 | $1.93^{f-o}$ | $59.8^{a-j}$ | $40^{e-l}$ | $77^{a-c}$ |
| MCSRQ3 | $2.91^{a-m}$ | $47.1^{a-o}$ | $53^{b-k}$ | $92^{ab}$ | MCSRF-1 | $1.73^{h-o}$ | $61.0^{a-i}$ | $39^{g-l}$ | $100^{a}$ |
| MCSRN83 | $2.70^{a-n}$ | $47.6^{a-o}$ | $52^{b-k}$ | $89^{a-c}$ | ***Seredo*** $^{S}$ | $1.54^{k-o}$ | $61.2^{a-i}$ | $39^{g-l}$ | $57^{a-d}$ |
| MCSRI6 | $2.69^{a-n}$ | $47.9^{a-o}$ | $52^{b-k}$ | $70^{a-c}$ | MCSRN51 | $1.48^{l-o}$ | $61.3^{a-i}$ | $39^{g-l}$ | $59^{a-d}$ |
| MCSRM68b | $2.89^{a-m}$ | $48.3^{a-o}$ | $52^{b-k}$ | $88^{a-c}$ | MCSRN57 | $1.72^{h-o}$ | $61.9^{a-i}$ | $38^{g-l}$ | $90^{ab}$ |
| MCSRH2a | $2.89^{a-m}$ | $49.3^{a-o}$ | $51^{b-l}$ | $57^{a-d}$ | **MCSRN61** $^{S}$ | $1.97^{f-o}$ | $62.5^{a-i}$ | $38^{g-l}$ | $60^{a-d}$ |
| MCSRS66 | $1.84^{g-o}$ | $50.4^{a-o}$ | $50^{b-l}$ | $68^{a-c}$ | MCSRI19 | $2.63^{b-o}$ | $62.5^{a-i}$ | $38^{g-l}$ | $82^{a-c}$ |
| MCSRL3 | $2.14^{d-o}$ | $50.4^{a-n}$ | $50^{b-l}$ | $74^{a-c}$ | MCSRT94 | $1.92^{f-o}$ | $62.5^{a-i}$ | $37^{g-l}$ | $90^{ab}$ |
| MCSRM47g | $2.41^{b-o}$ | $51.0^{a-m}$ | $49^{b-l}$ | $95^{ab}$ | MCSR N88c | $1.86^{f-o}$ | $63.1^{a-h}$ | $37^{g-l}$ | $66^{a-c}$ |
| MCSRF9d | $2.88^{a-m}$ | $51.5^{a-m}$ | $49^{b-l}$ | $97^{a}$ | SerenaxEsuti | $1.94^{f-o}$ | $63.6^{a-g}$ | $36^{g-l}$ | $88^{a-c}$ |
| MCSRF-6 | $2.99^{a-l}$ | $51.5^{a-m}$ | $48^{b-l}$ | $100^{a}$ | MCSRN157a | $1.63^{i-o}$ | $64.4^{a-g}$ | $36^{g-l}$ | $68^{a-c}$ |
| MCSR N140c | $2.07^{f-o}$ | $51.6^{a-m}$ | $48^{b-l}$ | $76^{a-c}$ | MCSRM3 | $1.75^{h-o}$ | $64.6^{a-g}$ | $35^{g-l}$ | $81^{a-c}$ |
| MCSRN79 | $2.44^{b-o}$ | $51.6^{a-m}$ | $48^{b-l}$ | $75^{a-c}$ | MCSRN84 | $1.68^{h-o}$ | $64.8^{a-g}$ | $35^{g-l}$ | $75^{a-c}$ |
| MCSRN102 | $2.17^{d-o}$ | $51.7^{a-m}$ | $48^{b-l}$ | $70^{a-c}$ | ***ICSV112*** $^{S}$ | $2.52^{b-o}$ | $65.6^{a-f}$ | $34^{g-l}$ | $85^{a-c}$ |
| MCSRN20 | $2.62^{b-o}$ | $51.8^{a-m}$ | $48^{b-l}$ | $94^{ab}$ | *Pato* | $2.51^{b-o}$ | $67.1^{a-e}$ | $33^{h-l}$ | $84^{a-c}$ |
| MCSRI17 | $3.25^{a-h}$ | $52.1^{a-m}$ | $48^{b-l}$ | $65^{a-c}$ | MCSRG2 | $1.56^{j-o}$ | $70.1^{a-d}$ | $30^{i-l}$ | $42^{cd}$ |
| MCSRN77 | $2.71^{a-n}$ | $52.1^{a-m}$ | $48^{b-l}$ | $95^{ab}$ | MCSRM44 | $1.56^{j-o}$ | $70.4^{a-d}$ | $30^{i-l}$ | $89^{a-c}$ |
| MCSR N140 | $1.83^{g-o}$ | $52.2^{a-l}$ | $48^{b-l}$ | $83^{a-c}$ | **MCSRL5** $^{S}$ | $1.50^{j-o}$ | $73.0^{abc}$ | $27^{j-l}$ | $90^{ab}$ |
| MCSRM69e | $2.16^{d-o}$ | $52.2^{a-k}$ | $48^{b-l}$ | $88^{a-c}$ | MCSRN120 | $1.33^{mno}$ | $74.1^{abc}$ | $26^{j-l}$ | $71^{a-c}$ |
| MCSRM42b | $2.13^{e-o}$ | $52.2^{a-k}$ | $48^{b-l}$ | $77^{a-c}$ | *Hakika* | $1.07^{o}$ | $74.2^{abc}$ | $26^{j-l}$ | $89^{a-c}$ |
| MCSR60 | $3.83^{abc}$ | $52.0^{a-k}$ | $48^{b-l}$ | $70^{a-c}$ | MCSRN88 | $1.26^{no}$ | $77.2^{a}$ | $23^{kl}$ | $100^{a}$ |
| MCSRJ3b | $3.08^{a-k}$ | $52.6^{a-k}$ | $47^{b-l}$ | $82^{a-c}$ | MCSRM45b | $1.20^{no}$ | $82.0^{a}$ | $18^{l}$ | $95^{ab}$ |
| MCSRM19 | $2.78^{a-n}$ | $52.7^{a-k}$ | $47^{b-l}$ | $92^{ab}$ | | | | | |

† Means sharing letters within the columns are not significantly different at $P \leq 0.05$. Means were separated using Tukey's HSD test. NRL-Al = net root length in aluminium, % resp = percentage response to 148 µM Al, RNRL = relative net root length, RLB148 = length of branched root in 148 µM Al, and % RRB = percentage reduction in root branching. Accessions written in bold with superscript letter 'S' were selected for field experiments.


**Figure 3.** Effect of aluminium stress on root growth and morphology of selected sorghum accessions; (A) Al-sensitive (MCSRM44) and (B) Al-tolerant (MCSRP5) after screening in solution culture. (C) Al-sensitive accession (MCSRN88) depicting stunted roots with brown colouration after screening using the paper towel method. The seedlings to the left are the controls.

reduction of >50% (Table 2). However, some accessions, such as MCSR124, MCSR15, *IESV93042-SW*, MCSRN81, MCSRL6 and MCSRG2 had ≤50% relative reduction in root branching, whereas in some, root branches were initiated but failed to elongate. The roots of MCSRF-6, *ICSB608*, MCSRF-1 and MCSRN88, did not branch at all under the Al stress.

Aluminium stress at 148 µM significantly ($P \leq 0.05$) reduced root and shoot dry weight in MCSRL5, *Seredo* and MCSRP5, but not in *ICSR110* and MCSR15 (Figure 5a and b). MCSR15 and MCSRP5 had the highest root and shoot dry weight, respectively, at 148 µM, whereas MCSRL5 and *Seredo* had the lowest root and shoot dry weight, respectively. At 222 µM Al, all the accessions had a significant reduction in root and shoot dry weight ($P \leq 0.05$).

Results on the effect of soil liming on plant growth in the field are presented in Table 3 and Figure 6. There were differences in vigour between sorghum plants grown in the limed and un-limed field plots at the early vegetative stages with the crop in the limed plots showing higher vigour than those in the un-limed plots (Figure 6). Lime application did not cause a significant change in leaf area per plant in any of the sorghum accessions (Table 3). ICSV112 and MCSRM33 had the highest and the lowest total leaf area per plant, respectively, in un-limed

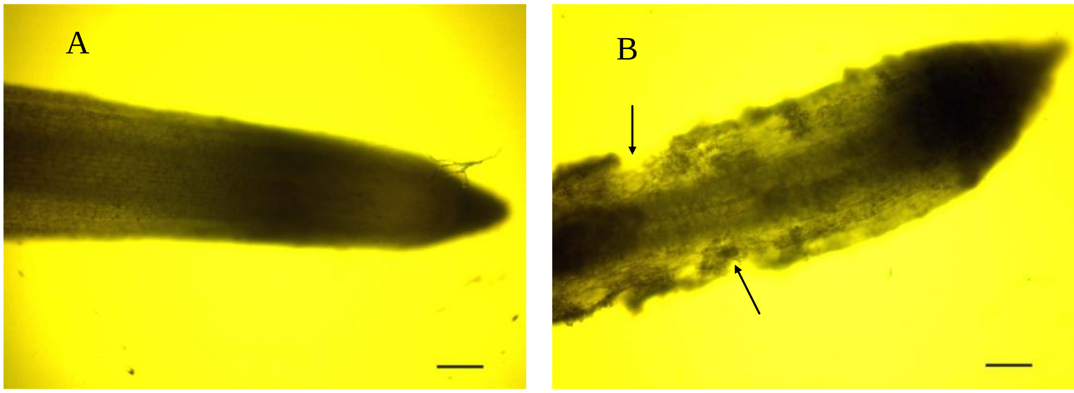
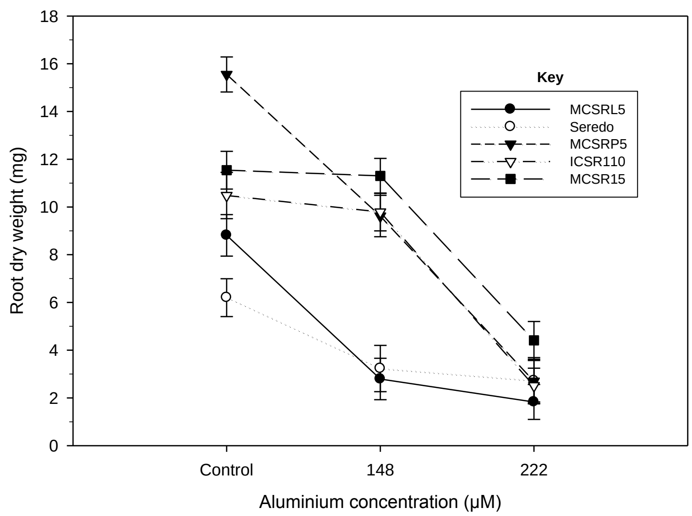



**Figure 4.** Bright field micrographs showing root tips of (A) Al-tolerant (ICSR110) and (B) Al-sensitive (MCSRL5) sorghum accessions subjected to 148 μM Al for 120 hours. The arrows point at lesions caused by aluminium stress. Scale bars = 200 μm.



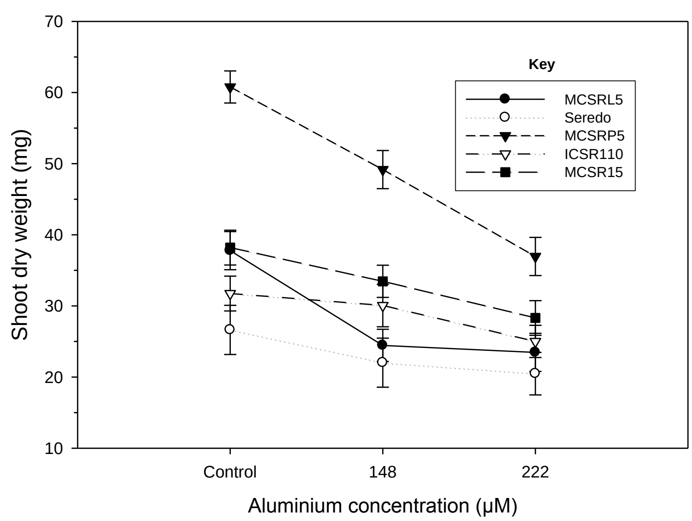




**Figure 5.** Effect of aluminium stress on (a) root and (b) shoot dry weight (mg) of selected sorghum accessions. Data were subjected to one-way ANOVA and means were separated using Tukey's HSD test. The vertical bars represent standard error.

**Table 3.** Effect of liming (4 t/ha) on total leaf area and number of leaves per plant of selected sorghum accessions.

| Sorghum line | Leaf area per plant ($cm^2$) | | Number of leaves per plant | | C |
|---|---|---|---|---|---|
| | -Lime | +Lime | -Lime | +Lime | |
| *Macia* | $1935^{b-d†}$ | $2073^{a-d}$ | $7.8^{d-g}$ | $9.5^{a}$ | MT |
| Real60 | $1972^{b-d}$ | $1996^{b-d}$ | $8.0^{c-g}$ | $9.5^{a}$ | T |
| MCSRM45 | $2075^{a-d}$ | $2845^{ab}$ | $7.1^{fg}$ | $7.6^{e-g}$ | T |
| MCSRL5 | $2109^{a-d}$ | $2561^{abc}$ | $6.8^{g}$ | $8.6^{a-e}$ | HS |
| *Seredo* | $1858^{cd}$ | $2150^{a-d}$ | $7.6^{e-g}$ | $8.4^{b-f}$ | S |
| ICSR110 | $2032^{b-d}$ | $2279^{abc}$ | $8.1^{b-g}$ | $8.8^{a-e}$ | T |
| IS41764 | $2294^{abc}$ | $2989^{a}$ | $8.3^{b-g}$ | $9.0^{ab}$ | T |
| MCSRM33 | $1267^{d}$ | $1996^{b-d}$ | $6.8^{g}$ | $7.5^{e-g}$ | S |
| ICSV112 | $2642^{abc}$ | $2766^{ab}$ | $8.2^{b-g}$ | $8.4^{b-f}$ | S |
| MCSRN61 | $1952^{b-d}$ | $2679^{ab}$ | $7.8^{d-g}$ | $8.4^{b-f}$ | S |
| Mean | 2013 | 2433 | 7.7 | 8.6 | |

† Values with similar letters within the column and row of the same attribute are not significantly different at P ≤ 0.05. The means were separated using Tukey's HSD test. S.E. 273 and 0.46 for total leaf area and number of leaves respectively. C= Classification based on solution culture assay for response to Al stress; HS = highly sensitive, MT = moderately tolerant, S = sensitive, T – tolerant.


**Figure 6.** Twenty six days old sorghum growing on limed (A) and non-limed (B) plots at Bumala site.

soil. *IS41764* had the highest, whereas MCSRM33 and Real60 had the lowest total leaf area per plant in the limed soil. The number of leaves per plant was significantly higher in limed soil than in non-limed soil in *Macia, Real60* and MCSRL5 (P ≤ 0.05), whereas lime application had no significant effect on number of leaves in the rest of the accessions. In non-limed soil, MCSRL5 and MCSRM33 had the least number of leaves per plant whereas *IS41764* had the highest number of leaves per plant.

In non-limed soils, MCSRM33 had the lowest grain yield per plant (21.2 g – equivalent to 1767 kg/ha), while *Real60* had the highest grain yield per plant (47.9 g – equivalent to 3916 kg/ha) (Table 4). In limed soils, *ICSR110* had the lowest grain yield (33.9 g – equivalent to 2825 kg/ha), while *ICSV112* had the highest grain yield

**Table 4.** Effect of liming (4 t/ha) on 1000 seed weight (g) and grain yield per plant in some selected sorghum accessions.

| Sorghum line | 1000 seed weight (g) | | Total grain yield (g) per plant | | I | C |
|---|---|---|---|---|---|---|
| | -Lime | +Lime | -Lime | +Lime | | |
| *Macia* | 22.8$^{de\dagger}$ | 29.4$^{bc}$ | 24.1$^{ij}$ (2008) | 39.9$^{c-j}$ (3325) | 40 | MT |
| Real60 | 20.1$^{fg}$ | 28.8$^{bc}$ | 47.9$^{b-l}$ (3916) | 64.3$^{a-d}$ (5358) | 26 | T |
| MCSRM45 | 20.1$^{fg}$ | 23.9$^{d}$ | 42.1$^{b-j}$ (3508) | 65.9$^{abc}$ (5492) | 36 | T |
| MCSRL5 | 23.3$^{d}$ | 28.1$^{bc}$ | 45.9$^{b-j}$ (3825) | 61.9$^{a-e}$ (5158) | 26 | HS |
| *Seredo* | 23.4$^{d}$ | 34.3$^{a}$ | 38.6$^{d-j}$ (3217) | 56.3$^{a-f}$ (4692) | 31 | S |
| ICSR110 | 17.2$^{h}$ | 18.8$^{gh}$ | 25.7$^{h-j}$(2142) | 33.9$^{f-j}$ (2825) | 24 | T |
| IS41764 | 20.3$^{efg}$ | 24.9$^{d}$ | 42.3$^{b-j}$(3525) | 61.0$^{a-e}$(5083) | 31 | T |
| MCSRM33 | 12.8$^{i}$ | 20.4$^{efg}$ | 21.2$^{j}$ (1767) | 36.9$^{e-j}$(3075) | 43 | S |
| ICSV112 | 19.6$^{fgh}$ | 34.5$^{a}$ | 44.0$^{b-j}$ (3667) | 81.4$^{a}$ (6783) | 46 | S |
| MCSRN61 | 21.5$^{ef}$ | 28.6$^{bc}$ | 37.8$^{e-j}$ (3150) | 66.2$^{ab}$ (5517) | 43 | S |
| Mean | 20.1 | 27.2 | 37.0 (3083) | 56.8 (4733) | 35 | |

† Values with similar letters within the column and row of the same attribute are not significantly different at P ≤ 0.05. The means were separated using Tukey's HSD test. S.E 0.8 and 7.6 for 1000 seed weight and total grain yield respectively. The values given in brackets are equivalent to grain yield in kg/ha. I = percent increase in grain yield. C= Classification based on solution culture assay for response to Al stress; HS = highly sensitive, MT = moderately tolerant, S = sensitive, T – tolerant.

(81.4 g – equivalent to 6783 kg/ha).

Lime application caused a significant increase in total grain yield per plant in *ICSV112* and MCSRN61 (P ≤ 0.05). The increase in grain yield ranged from 24 to 46%, where *ICSR110* and *ICSV112* had the lowest and highest increase in grain yield, respectively. An average of 35% increase in overall grain yield was registered as a result of lime application. Similarly, the application of lime significantly increased the 1000 seed weight in all the sorghum accessions, except *ICSR 110* (P ≤ 0.05; Table 4).

## DISCUSSION

Differential response to Al stress was observed at 148 µM Al concentration, where only 10% of the 389 accessions were tolerant. At 222 µM Al root growth was severely restricted in all the sorghum accessions, which showed that this concentration was too high to be used to differentiate sorghum response to Al stress. Therefore, screening for Al resistance in sorghum should be carried out at 148 µM Al concentration. Aluminium concentrations at 148 µM and 222 µM correspond to 27 µM and 39 µM free Al ions ($Al^{3+}$) (Magalhaes et al., 2004). These concentrations have previously been reported to reduce root growth in sorghum (Caniato et al., 2007). In this study, some of the accessions had inherently long roots in nutrient solution without Al. A few of these accessions were tolerant to Al stress, whereas most of them were sensitive. These accessions can be crossed with the sorghums that had short roots but tolerant to Al stress. A combination of long roots and Al tolerance are good attributes for enhanced acquisition of nutrients and moisture in acid soils with high levels of Al consequently improving growth, drought tolerance and grain production in such soils.

The most Al sensitive accessions used in this study which included MCSRG2, MCSRM44, MCSRL5, MCSRN120, *Hakika,* MCSRN88 and MCSRM45b had stubby roots with brown colouration at the 148 µM Al concentration. The root tips had surface lesions due to injury caused by Al stress. Similar observations on root injury due to Al stress have been previously reported (Mossor-Pietraszewska et al., 1997). Root stunting is a consequence of Al-induced inhibition of root elongation, which is the most evident symptom of Al toxicity (Matsumoto, 2000). Aluminium stress has been reported to reduce cell wall extensibility in wheat roots and that this Al-induced change in the cell wall contributes to the inhibition of root growth (Ma et al., 2004). In addition, Al-induced inhibition of K+ uptake by blocking the responsible channels would interfere with turgor driven cell elongation (Liu and Luan, 2001).

Aluminium stress significantly reduced root branching in most sorghum accessions; where ninety five percent of the accessions had ≤50% reduction in root branching. The most sensitive accessions did not develop any lateral roots, while in some, the root branches were initiated but failed to elongate, which is in line with previous reports (Roy et al., 1988). Differential elongation of root branches in response to aluminium stress was also reported in maize (Bushamuka and Zobel, 1998) and apparently is a common reaction of plant root systems to the stress.

Aluminium stress significantly reduced root and shoot dry matter especially in the Al-sensitive sorghum accessions. The Al tolerant accessions had higher average root and shoot dry matter than the susceptible accessions. Similar results have been reported in barley (Foy, 1996). Aluminium has been reported to interfere with uptake, transport and utilization of nutrients, especially Ca, Mg, P, N and K and reduce accumulation of dry matter (Nichol and Oliveira, 1995). Larger root systems are known to have a greater capacity for absorbing water and minerals, as they are able to explore a larger rhizosphere (Osmont et al., 2007).

The sorghum accessions grown on acid non-limed soil had lower above ground growth and yield compared to that grown in limed soil. Some sorghum accessions that were Al-sensitive in solution culture were also severely affected by the stress in the field. Application of lime significantly increased total leaf area and number of leaves per plant. High leaf area is important in interception of photosynthetic active radiation, which translates to enhanced rates of photosynthesis and consequently high biomass accumulation. It has been reported that high levels of Al inhibited leaf growth in soybean (Zhang et al., 2007). The significant increase in growth and production in the limed soil can be attributed to increased root growth and establishment which translates to improved access to water and nutrients. Liming the acid soil raised soil pH, as reported by Kisinyo (2011), and because the solubility of Al is highly pH dependent, this could result in concentrations of exchangeable Al being lowered to negligible levels that did not limit sorghum growth.

Soil chemical factors that limit root growth in acid soils, such as aluminium diminish crop production through a rapid inhibition of root growth that translates to a reduction in vigour and crop yields (Kochian et al., 2005). Plants grown in soils with high levels of aluminium have reduced root systems and exhibit a variety of nutrient-deficiency symptoms, with a consequent decrease in yield. Decreased above ground plant growth in soil with high percentage of Al saturation has been reported (Miller et al., 2009). This was accompanied by reduced uptake of P and N in the acidic soil. An Al-tolerant maize line had increased levels of mineral nutrients in roots and shoots compared with a sensitive inbred line when grown in an Al-treated-nutrient solution (Giannakoula et al., 2008). Genotypic variation in nutrient uptake in the presence of toxic levels of aluminium has also been reported in sorghum (Baligar et al., 1993), where the Al-tolerant genotypes had higher nutrient uptake efficiency than the Al-sensitive genotypes.

An overall 35% reduction in sorghum grain yield was realized in non-limed soil, with the Al-sensitive accessions having higher reductions than the Al-tolerant accessions. In this regard, some researchers (Gallardo et al., 1999) reported 50 and 30% reduction of grain yield in Al sensitive and resistant cultivars of barley respectively, when they were grown in soil that contained high levels of exchangeable Al.

The Al tolerant standard check *ICSR110* registered low grain yields in non-limed soil but had the lowest response to lime application. Similar results have been reported in maize (*Zea maize*), where 'Cateto', one of the most Al-tolerant Brazilian lines has been shown to be a low yielder and has been used as a source of genes for Al tolerance in maize breeding programmes (Ouma et al., 2013). The Al sensitive lines MCSR L5 and *ICSV112* had relatively higher yields but had low and moderate response to lime respectively. The yield of these accessions could be improved in acid Al-toxic soils by crossing with *ICSR 110* which had better root growth under Al stress conditions. *Real60* and MCSRM45 registered high yields and were also tolerant to Al stress in solution culture and therefore in addition to *ICSR110* are potential sources for Al tolerance genes in sorghum breeding programmes.

## Conclusions

Al toxicity significantly reduced development and elongation of main roots and root branches in aluminium sensitive sorghum accessions. Only 10% of the sorghum accessions used in the study were tolerant Al stress reduced root and shoot dry weight as well as the plant growth and grain production under field conditions. Therefore, there is a need to disseminate the Al-tolerant lines to the sorghum farmers for cultivation in areas where soil acidity and aluminium stress are known to occur. Future sorghum breeding programmes should include the identified superior sorghum accessions as donors of aluminium tolerance genes to the locally adapted sorghums cultivated in acid soils with high levels of Al.

## ACKNOWLEDGEMENTS

This work was financially supported by the Swedish International Development Agency (SIDA/SAREC) through the BIO-EARN programme and the Swedish University of Agricultural Sciences (SLU) through funding from the Swedish Ministry of Foreign Affairs as part of its special allocation on global food security (UD40). The authors are grateful to ICRISAT, KARI and the Kenyan farmers for providing the sorghum germplasm and to Moi University and SLU for experimental facilities. Professor Rodomiro Ortiz is greatly acknowledged for critically reviewing the manuscript.

## Conflict of Interests

The author(s) have not declared any conflict of interests.

### REFERENCES

Baligar VC, Schaffert RE, Dossantos HL, Pitta GVE, Bahia AFD (1993). Soil aluminum effects on uptake, influx, and transport of nutrients in sorghum genotypes. Plant Soil 150:271-277. http://dx.doi.org/10.1007/BF00013024

Bushamuka VN, Zobel RW (1998). Maize and soybean tap, basal, and lateral root responses to a stratified acid, aluminum-toxic soil. Crop Sci. 38:416-421. http://dx.doi.org/10.2135/cropsci1998.0011183X003800020024x

Caniato F, Guimarães C, Schaffert R, Alves V, Kochian L, Borém A, Klein P, Magalhaes J (2007). Genetic diversity for aluminum tolerance in sorghum. Theoret. Appl. Genet. 114:863-876. http://dx.doi.org/10.1007/s00122-006-0485-x

Ernani PR, Ribeiro MFS, Bayer C (2004). Chemical modifications caused by liming below the limed layer in a predominantly variable charge acid soil. Communications in Soil Science and Plant Analysis 35:889-901. http://dx.doi.org/10.1081/CSS-120030365

Foy CD (1996). Tolerance of barley cultivars to an acid, aluminum-toxic subsoil related to mineral element concentrations in their shoots. J. Plant Nutr. 19:1361-1380. http://dx.doi.org/10.1080/01904169609365205

Gallardo F, Borie F, Alvear M, Von Baer E (1999). Evaluation of aluminum tolerance of three barley cultivars by two short-term screening methods and field experiments. Soil Sci. Plant Nutr. 45:713-719. http://dx.doi.org/10.1080/00380768.1999.10415834

Giannakoula A, Moustakas M, Mylona P, Papadakis I,Yupsanis T (2008). Aluminum tolerance in maize is correlated with increased levels of mineral nutrients, carbohydrates and proline, and decreased levels of lipid peroxidation and Al accumulation. J. Plant Physiol. 165:385-396. http://dx.doi.org/10.1016/j.jplph.2007.01.014

Goncalves JFD, Cambraia J, Mosquim PR, Araujo EF (2005). Aluminum effect on organic acid production and accumulation in sorghum. J. Plant Nutr. 28:507-520. http://dx.doi.org/10.1081/PLN-200049202

Johnson GV (1988). Causes and effects of soil acidity. Oklahoma State Univ. Ext. Facts, Oklahoma Coop. Ext. Serv. No. 2239.

Kanyanjua SM, Ireri I, Wambua S, Nandwa SM (2002). Acidic Soils in Kenya: Constraints and Remedial Options. KARI, Nairobi. P. 28.

Kisinyo PO (2011). Constraints of soil acidity and nutrient depletion on maize (*Zea mays,* L.) Production in Kenya. Department of Soil Science, D. Phil.Thesis, Moi University, Kenya.

Kisinyo PO, Othieno CO, Gudu SO, Okalebo JR, Opala PA, Ng'etich WK, Nyambati RO, Ouma EO, Agalo J, Kebeney SJ, Too EJ, Kisinyo JA, Opile WR (2013). Immediate and residual effects of lime and phosphorus fertilizer on soil acidity and maize production in western kenya. Expl. Agric. Cambridge University press.doi:10.1017/S001447913000318.

Kochian LV (1995). Cellular mechanisms of aluminum toxicity and resistance in plants. Ann. Rev. Plant Physiol. Plant Mole. Biol. 46:237-260. http://dx.doi.org/10.1146/annurev.pp.46.060195.001321

Kochian LV, Pineros MA, Hoekenga OA (2005). The physiology, genetics and molecular biology of plant aluminum resistance and toxicity. Plant Soil 274:175-195. http://dx.doi.org/10.1007/s11104-004-1158-7

Liu K, Luan S (2001). Internal aluminum block of plant inward K+ channels. Plant Cell 13:1453-1465. http://dx.doi.org/10.1105/tpc.13.6.1453

Ma JF, Shen RF, Nagao S, Tanimoto E (2004). Aluminum targets elongating cells by reducing cell wall extensibility in wheat roots. Plant Cell Physiol. 45:583-589. http://dx.doi.org/10.1093/pcp/pch060

Magalhaes JV, Garvin DF, WangY, Sorrells ME, Klein PE, Schaffert RE, Li L, Kochian LV (2004). Comparative mapping of a major aluminum tolerance gene in sorghum and other species in the poaceae. Genetics 167:1905-1914. http://dx.doi.org/10.1534/genetics.103.023580

Magalhaes JV, Liu J, Guimaraes CT, Lana UG, Alves VM, Wang YH, Schaffert RE, Hoekenga OA, Pineros MA, Shaff JE, Klein PE, Carneiro NP, Coelho CM, Trick HN, Kochian LV (2007). A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. Nat. Genet. 39:1156-1161. http://dx.doi.org/10.1038/ng2074

Magnavaca R, Gardner C, Clark R (1987). Comparison of maize populations for aluminium resistance in nutrient solution. In Gabelman H, Loughman BC (eds) Genet. Aspects Plant Min. Nutr. pp 189-199. Martinus Nijhoff, Dordrecht, Netherlands. http://dx.doi.org/10.1007/978-94-009-3581-5_17

Matsumoto H (2000). Cell biology of aluminum toxicity and tolerance in higher plants. In Jeon KW (ed) International Review of Cytology - a Survey of Cell Biology, 200:1-46.

Miller G, Mamo M, Drijber R, Wortmann C, Renken R (2009). Sorghum growth, root responses, and soil-solution aluminum and manganese on pH-stratified sandy soil. J. Plant Nutr. Soil Sci. 172:108-117. http://dx.doi.org/10.1002/jpln.200700227

Mossor-Pietraszewska T, Kwit M, Legiewicz M (1997). The influence of aluminium ions on activity changes of some dehydrogenases and aminotransferases in yellow lupine. Biol. Bull. 34:47-48.

Nichol BE, Oliveira LA (1995). Effects of aluminum on the growth and distribution of calcium in roots of an aluminum-sensitive cultivar of barley (Hordeum vulgare). Can. J. Bot. 73:1849-1858. http://dx.doi.org/10.1139/b95-197

Obura PA (2008): Effects of soil properties on bioavailabilty of aluminium and phosphorus in selected Kenyan and Brazilian soils. Ph.D Thesis, Purdue University, USA.

Obura PA. Schulze DG, Okalebo JR, Othieno CO, Johnston CT (2010). Characterization of Selected Kenyan acid soils. 19$^{th}$ world congress of soil Science, Soil Solutions for a Changing World. 1-6$^{th}$ August 2010, Brisbane, Australia.

Osmont KS, Sibout R, Hardtke CS (2007). Hidden branches: Developments in root system architecture. In Ann. Rev. Plant Biol. pp. 93-113.

Ouma E, Ligeyo D, Matonyei T, Agalo J, Were B, Too E, Onkware A, Gudu S, Kisinyo P, Nyangweso P (2013). Enhancing maize grain yield in acid soils of western Kenya using aluminium tolerant germplasm. J. Agricult. Sci. Technol. A. 3:33-46.

Rengel Z (1996). Tansley review no 89 - Uptake of aluminium by plant cells. New Phytol. 134:389-406. http://dx.doi.org/10.1111/j.1469-8137.1996.tb04356.x

Roy AK, Sharma A, Talukder G (1988). Some aspects of aluminum toxicity in plants. Bot. Rev. 54:145-178. http://dx.doi.org/10.1007/BF02858527

Simpson BB, Conner-Ogorzaly M (2001). Economic Botany: Plants in Our World. McGraw-Hill.

Stickler FC, Wearden S, Pauli AW (1961). Leaf area determination in grain sorghum. Agron. J. 53:187-188. http://dx.doi.org/10.2134/agronj1961.00021962005300030018x

Tamas L, Budikova S, Simonovicova M, Huttova J, Siroka B, Mistrik I (2006). Rapid and simple method for Al-toxicity analysis in emerging barley roots during germination. Biol. Plantarum 50:87-93. http://dx.doi.org/10.1007/s10535-005-0079-5

Von Uexküll HR, Mutert E (1995). Global extent, development and economic impact of acid soils. Plant Soil 171:1-15. http://dx.doi.org/10.1007/BF00009558

Wortmann CS, Mamo M, Abebe G, Mburu C, Kayuki KC, Letayo E, Xerinda S (2006). Atlas of Sorghum (*Sorghum bicolor* (L.) Moench) Production in Five Countries of Eastern Africa. The Board of Regents of the University of Nebraska., Lincoln, Nebraska. P. 20.

Zhang XB, Liu P, Yang Y, Xu GD (2007). Effect of Al in soil on photosynthesis and related morphological and physiological characteristics of two soybean genotypes. Bot. Studies 48:435-444.