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Phenotypic Plasticity of Sugarcane Genotypes under Aluminum Stress

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Authors' contributions

This work was carried out in collaboration between all authors. Author CM participated in the analyses and interpretation of data, in the writing of the manuscript and was responsible for editing of the research paper. Author PMAC participated in the designing of the study, in the conduction of the *experimental procedures and in the writing of the manuscript. Authors CFA, JAGMJ and GS collaborated in the conduction of the experimental procedures, in the sample analysis and in the editing of the manuscript. Authors LAP and LLB reviewed the manuscript and supported the statistical analysis. Author MHPB developed the genotypes, reviewed the manuscript and supervised the entire study. All authors read and approved the final manuscript.*

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ABSTRACT

The expand agricultural production to new crop areas in the tropical regions is an important strategy to supply the huge demand for food and renewable energy sources. However toxic aluminum (Al) present in tropical soils is a limiting factor for agricultural production. The objective of this study was to identify Al-tolerant and Al-sensitive sugarcane genotypes, based on phenotypic plasticity, and to

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determine the correlation between the traits associated with Al stress. Eleven sugarcane genotypes were evaluated under non-stress and Al-stress conditions. The experiment was conducted using randomized complete block design with three replications in a factorial scheme. The study was carried out at Department of Crop Science, Federal University of Viçosa, between January and May 2014. Genetic variability regarding Al tolerance was observed among the sugarcane genotypes by phenotypic plasticity. Al-stress caused a reduction in the primary root length and in the shoot dry weight, but an increase in the lateral root length. There was a difference between the genotypes related to Al accumulation in the roots and shoot, suggesting the existence of distinct tolerance mechanisms. Based on phenotypic plasticity, genotypes RB966928, RB867515, RB008041, and RB935744 were characterized as tolerant, and RB937570, RB92579, and RB928064 sensitive to Al. We characterized genotypes and elucidated the correlation between features associated with Alstress. The characterization of contrasting genotypes will be important for breeding programs involving sugarcane yield in regions subjected to stress.

Keywords: Abiotic stress; root system; Saccharum spp.; selection.

1. INTRODUCTION

Sugarcane (*Saccharum* spp.) crops occupy approximately 23 million hectares in more than 100 tropical and subtropical countries. Currently, sugarcane and its derivatives represent the second largest source of primary energy in the Brazilian energy matrix, and Brazil is responsible for the production of more than half of all globally commercialized sugar. Due to predicted population growth and increasing worldwide demand for renewable energy sources, there is a need to expand agricultural production to new crop areas in the tropical regions, including areas considered less appropriate for agriculture, i.e. with low fertility, low pH and aluminum (Al) toxicity [1].

Al-stress damages primarily the radicular system, with several secondary effects such as low water and nutrient absorption, and reduction of plant growth and development [2]. Growth impairment has been observed in the radicular system of sugarcane [3], corn [4], sorghum [5], rice [6], barley [7], and wheat [8].

The Al stress tolerance is associated with the ability to maintain cellular division and elongation, and the viability of meristematic tissues even under stress conditions [9]. Plants present two main mechanisms of resistance against toxic Al. With Al exclusion, they can prevent toxic Al from entering plant tissues through exudation of organic acids by the root tip and the consequent complexation of Al into nontoxic forms. In addition, plants possess tolerance mechanisms like Al detoxification inside the cells by means of complexation with organic compounds [10,11,12]. Genotypes that exhibit any of these mechanisms are Al-tolerant, if not exhibit are considered Al-sensitive. However, distinct crops show different tolerance levels. Higher tolerance is also observed in cereals crops, with rice being more tolerant to Al-stress, followed by corn, soybean, sorghum, and wheat [4]. In sugarcane, *Saccharum officinarum* is more tolerate to Al than *Saccharum spontaneum* [13].

Plants have developed several mechanisms to circumvent the lack of certain resources under stress conditions, among which is phenotypic plasticity, i.e., the ability to express an alternate phenotype under environmental stimuli to endure an adverse situation [14]. From the agronomic point of view, it could be reflected as the yield difference in contrasting environments. In plant breeding, such approach is crucial for the selection of genotypes since phenotypic plasticity has a strong correlation with stability, that is, low phenotypic plasticity implies high production stability [15,16].

Studies on Al-stress in sugarcane based on phenotypic plasticity are still scarce, especially on the selection of contrasting genotypes for use in breeding programs. Therefore, the present study was developed to identify Al-tolerant or Alsensitive sugarcane genotypes based on phenotypic plasticity, and to determine the association between the traits related to Alstress.

2. MATERIALS AND METHODS

2.1 Plant Material and Experimental Design

Eleven sugarcane genotypes were evaluated: RB966928, RB867515, RB937570, RB957610, RB93509, RB92579, RB008041, SP801842,

SP813250, RB935744, and RB928064. These genotypes consisted of cultivars and clones occupying an extensive crop area in Brazil and/or are used as parental plants in the main breeding programs (Table 1). The experiment was carried out in a greenhouse located in Viçosa, Minas Gerais, Brazil (648 m altitude; 20°45' S latitude; and 42°52' W longitude).

The culms of the genotypes were cut in joints with one bud each and planted in trays filled with a mixture of vermiculite and the commercial

Table 1. Description of sugarcane cultivars and clones

Source: Program for Genetic Breeding of Sugarcane of the Federal University of Viçosa, Brazil

substrate Plantmax® in a 1:1 proportion. Sixteen days after germination, homogeneous plants were selected and transferred to PVC vases (10 cm diameter and 50 cm height) containing 7 dm³ substrate. The substrate consisting of a combination of sand and acid soil (1:1 proportion), for the Al-stress condition, and, sand and non-acid soil (1:1) for the Non-stress condition. We used a tropical soil with Al saturation and low pH. Thus, a non-acid soil was obtained, by the correction of the soil acid, and showed 0% Al saturation after correction. The acid soil was not corrected and showed 53% of Al saturation. Essential nutrients were added via fertilization as recommended for the culture [17], using a nutritive solution containing 0.3 M NH_4NO_3 , 0.43 M K₂SO₄, 0.74 M $NH_4H_2PO_4$, 3.88 mM FeSO₄.7H₂O, 6.59 mM MnCl₂.4H₂O, 2.40 mM H_3BO_3 , 3.19 mM ZnCl₂, 0.26 mM CuSO₄.5H₂O, and 0.15 mM (NH₄)₆MO₇O₂₄.4H₂O. The solution was applied at six time-points: 0, 15, 30, 45, 60, and 75 days after transplantation. Soil humidity was kept at 80 – 90% of the maximum retention capacity by daily irrigation with deionized water.

The experimental design consisted of randomized complete block design with three replications, in factorial scheme. Factor 1:11 genotypes and factor 2: Al conditions (Non-stress – with free of Al-stress, with 0% Al saturation, and the other one, Al-stress – subjected to Alstress with 53% Al saturation). This Al saturation was used according to Sobral and Guimarães [18]. The experimental unit consisted of a PVC vase containing one plant.

2.2 Phenotypical Evaluation

Plants were harvested 90 days after transplantation. The shoot was separated from the radicular system and dried in a forced-air incubator at 70°C for 72 h in order to determine the shoot dry weight (SDW, g). The roots were washed in tap water and preserved in 50% ethanol. The radicular system was evaluated by image analysis using the software WinRHIZO Pro 2009 a (Basic, Reg, Pro & *Arabidopsis* for Root Measurement) coupled to an Epson Perfection V700/V75 scanner equipped with an extra light and a resolution of 400 dpi. The length of the radicular system was divided into diameter classes (d) for the lateral roots (LRL, $d \le 0.5$ mm) and the primary roots (PRL, d>0.5 mm). The roots were dried in an incubator with forced ventilation at 70°C for 72 h, after which Al contents in the root (ALR, dag kg^{-1}) and in the

shoot (ALS, dag.kg $^{-1}$) were determined according to Fonseca Júnior et al. [6].

2.3 Statistical analyses

In the analysis of variance, the following model was considered, with all effects as fixed variables:

$$
Y_{ijk} = m + B_k + G_i + A_j + GA_{ij} + E_{ijk}
$$

where *Yijk* is the observation of the genotype *i*, at the Al concentration *j* and in the block *k*; *m* is the general average; B_k is the block effect k ; G_i is the genotype effect *i*; *Aj* is the effect of the Al concentration j ; GA_{ij} is the effect of the interaction between the genotype *i* and the Al concentration j ; and E_{ijk} is the residual effect of the observation *Yijk*.

The estimations of the coefficients of phenotypic correlation were achieved using the Pearson method, between traits evaluated and tested in regard to their significance using the t-test at significance levels of 0.01, 0.05, and 0.10. All analyses were performed using the GENES software [19].

3. RESULTS AND DISCUSSION

3.1 Experimental Analyses and Genotype Performance

Significant differences were observed between the genotype averages for all traits, suggesting the existence of genetic variability among the genotypes. Al concentration in the soil had a significant effect on all traits, except for primary root length and Al contents in the shoot, indicating that the experimental conditions were adequate for the evaluation of Al-stress in sugarcane. The GxA interaction was significant for all traits with the exception of shoot weight (data not shown), suggesting that the genotypes responded differently to the environmental variations, that is, to Al-stress.

3.2 Shoot Weight

Under non-stress conditions, the average shoot weight was 96 g \pm 18.03 g. The cultivars RB937570 and RB92579 presented the highest (117 g), and RB966928 the lowest (69 g), value. Under Al-stress, the average was $53 g \pm 11.36 g$, with RB867515 being the genotype that produced the most shoot weight (73 g). In contrast, the genotype RB957610 produced only

38 g. These results reveal great genetic variability among the genotypes (Fig. 1).

Al-stress caused an average reduction of 44% (28–60%) in shoot weight, consequently will affecting the genotypes productive performance. Sugarcane cultivated in greenhouse trails under drought and soil acidity, showed a decrease of 71.8% and 58.9% in the growth of leaves and culms, respectively. However, in soil with sufficient water availability, increasing soil acidity resulted in a less drastic reduction of only 11% [20]. Ecco et al. [21] with the aim of to study the interaction between water deficit and soil acidity in sugarcane, two genotypes were evaluated in greenhouse with Al stress and the combinations of drought and Al stress. The author observed a 23% reduction in biomass production under Alstress and 69% under drought stress combined with Al toxicity.

The genotype RB966928 presented, under both cultivation conditions, an under-average shoot weight. Nevertheless, it showed less variation in biomass production between the different environments. On the other hand, the genotype RB928064 had an above-average performance under non-stress conditions and below average under Al-stress, showing the highest production amplitude between the different environments (Fig. 1). Plants have developed distinct strategies to deal with stress, among which is phenotypic plasticity, which is associated with productivity stability [15]. Genotypes with low phenotypic plasticity, that is, less productivity variation in different environments, present high stability and can be characterized as tolerant [14]. So, based on phenotypic plasticity and considering the plant shoot like the photosynthetic machinery, in the present study, the genotypes RB966928, RB867515, RB008041, and RB935744 can be regarded as tolerant. In contrast, the genotypes RB937570, RB92579, and RB928064 are considered sensitive to Al, and the remaining present intermediate tolerance. These results reveal that it is possible to identity tolerant genotypes based on phenotypic plasticity, enabling the use of natural variability in the breeding of the characteristic. This is the first work to study such strategy as a tool to evaluate the tolerance of sugarcane genotypes in Al stress.

3.3 Morphology of the Radicular System

For the variable primary root length (PRL), no significant differences were found between the Al-stress and the non-stress conditions, with averages of 3.40 ± 1.02 m and 3.70 ± 0.41 m, respectively (Fig. 2a). The wider dispersion around the average shows a great effect of stress on this variable and the different responses of each genotype to this condition. Under stress, the genotypes usually show distinct responses, resulting in larger variability of the affected characteristic since each genotype shows a distinct potential response to stress [22]. The genotype RB935744 showed the smallest phenotypic plasticity, that is, the greatest stability for the production of primary roots, while the greatest phenotypic plasticity was found for the genotype SP80-1842. Only the genotypes RB867515, RB957610, and RB928064 produced more primary roots when subjected to stress conditions than under non-stress conditions. This result suggests that these genotypes probably respond to stress using mechanisms different from those used by the other genotypes, producing more primary roots or increasing the root diameter in lieu of lateral root formation.

Regarding the variable LRL, there was an opposite effect. Al-stress caused an increase in the LRL from 15.2 ± 2.6 m to 19.3 ± 5.18 m (Fig. 2b). All genotypes produced more lateral roots under stress conditions, with the exception of RB008041 and SP80-1842. The genotype SP80- 1842 showed a drastic decrease in LRL under stress. RB957610 and RB008041 presented the greatest and the smallest phenotypic plasticity, respectively. When subjected to stress, the genotypes RB008041 and SP80-1842 produced approximately half the amount of lateral roots when compared to RB867515 and RB957610.

These results show that the sugarcane genotypes responded to Al-stress by modifying their radicular system, exhibiting phenotypic plasticity (i.e., the expression of alternative phenotypes under environmental stimuli). Under non-stress conditions, the radicular system consisted, on average, of 80% lateral roots and 20% primary roots. When subjected to Al-stress, there was an increase in the production of lateral roots (85%) in lieu of primary roots (15%). The genotype RB937570 produced less primary roots (25% under non-stress conditions and 12% under Al-stress) and more lateral roots (75% under non-stress conditions and 88% when subjected to Al-stress). RB928064 showed an opposite behavior, producing more primary roots (17% under non-stress conditions and 21% when subjected to stress) and less lateral roots (83% without stress and 79% under stress). The first symptom of Al toxicity is the rapid inhibition of root growth, especially under conditions of

relative surface of the radicular system [2].

3.4 Aluminum Contents

The average ALR and ALS were 1.33 dag.kg⁻¹ and 0.017 dag.kg⁻¹, respectively, varying between 0.78 and 2.39 dag.kg $^{-1}$ for ALR and 0.009 and 0.027 dag.kg $^{-1}$ for ALS (Fig. 3). Higher Al contents in the radicular system were expected since most of the absorbed element remains in the roots, and a small portion may be translocated to the leaves [2,3]. Some of the Al effects on the photosynthetic process are apparently a consequence of the toxic effects expressed initially in the roots [9]. A few studies show that Al affects the absorption and/or transport of mineral nutrients to the leaves [23], resulting in low rates of liquid $CO₂$ assimilation and reduced biomass accumulation [24].

mineral nutrients due to a decrease in the

The genotype RB92579 presented 97.3% of the Al in the radicular system and 2.7% in the shoot. In contrast, RB93509 had 99.4% and 0.6% of the Al in the roots and in the shoot, respectively (Fig. 3). RB957610, RB92579, and RB928064 showed the lowest Al contents in the plant (0.820, 0.808, and 0.792 dag.kg $^{-1}$, respectively), while RB008041 and SP80-1842 had the highest Al

contents $(2.402 \text{ and } 2.045 \text{ dag.kg}^{-1})$, respectively). These results suggest that different mechanisms of tolerance to Al exist in sugarcane.

Plants can express tolerance to toxic Al using two main mechanisms: (i) the exclusion of Al and (ii) tolerance of Al $[10,11,12]$. Exclusion of Al is associated with the exudation of organic acids by the radicular tip in the presence of activated Al, avoiding the toxic Al before its penetration in the plant. Exudation may occur through the overexpression of genes encoding enzymes involved in the synthesis of organic acids. The mechanisms of tolerance are associated with cellular detoxification of Al.

Exclusion can occur in different ways. The Alcarboxylate complex is not translocated into the roots or through the cellular membranes. The amount of activated carboxylated Al released depends on the Al activity in the rhizosphere, indicating that stress conditions are responsible for activating this mechanism [10]. In the presence of Al, wheat [25] and oat [26] exudate malate; corn [27], oat [26], rice [28], sorghum [29], and soybean [30] exudate citrate, while corn exudates also oxalate [31]. However, little is known about the organic acids exudated by sugarcane. Trejo-Tellez [32] reported that the overexpression of the enzyme pyruvate

Fig. 1. Averages of the shoot dry weight (SDW in grams), and phenotypic plasticity (PP, in grams) of 11 sugarcane genotypes evaluated under non-stress and Al-stress conditions. The horizontal lines indicate the general averages under non-stress (dotted) and Al-stress (dashed) conditions. Tukey's honestly significant difference (HSD) under Al-stress was 53.6 g (P = .01) and 44.2 g (P = .05), and under non-stress conditions was 106.5 g (P = .01) and 87.9 g (P = .05)

Fig. 2. Average primary root length (PRL, m), lateral root length (LRL, m), and phenotypic plasticity (PP, m) of 11 sugarcane genotypes evaluated in non-stress and Al-stress environments. The horizontal lines indicate the general averages under stress (dotted) or nonstress (dashed) conditions. (a) Tukey's HSD under stress conditions was 3.2 m (*P* **= .01) and 2.6 m (***P* **= .05), and under non-stress conditions was 2.8 m (***P* **= .01) and 2.3 m (***P* **= .05); (b) Tukey's HSD under stress was 17.2 m (***P* **= .01) and 14.2 m (***P* **= .05), and under non-stress conditions was 13.2 m (***P* **= .01) and 10.9 m (***P* **= .05)**

phosphate dikinase in tobacco roots causes an increase in the exudation of organic acid anions, with a strong reduction in Al accumulation in the plant. This observation suggests that the genotypes that least absorbed Al, such as RB957610, RB92579, and RB928064, probably use the mechanism of Al exclusion. However, further studies are needed in order to fully elucidate how this process takes place in sugarcane.

Fig. 3. Average Al contents in the root (ALR, in dag.kg-1) and in the shoot (ALS, in dag.kg-1) and the ratio between them (expressed in percentage of the average) of 11 sugarcane genotypes evaluated under Al-stress. Tukey's HSD was 1.16 dag.kg⁻¹ ($P = .01$ **) and 0.96 dag.kg⁻¹ (** $P = .05$ **) for ALR, and 0.018 dag.kg-1 (***P* **= .01) and 0.015 dag.kg-1 (***P* **= .05) for ALS**

In the tolerance mechanism, Al enters the cytoplasm, and, once inside the cell, a detoxification process takes place with Al complexation with organic compounds [12]. Several compounds can form stable complexes with Al within the cell, including organic acids such as citrate, oxalate, malate, and proteins [11]. Free $Al⁺³$ or AI complexed with chelating agents can be translocated into the cellular vacuole, where they are stored without causing toxicity [2]. Tolerance to acid soils with high toxic Al concentration involves a complex interaction that is controlled by many genes and transcription factors [10]. This mechanism is associated with plant growth even in the presence of Al, that is, Al in its inactive form. Thus, the genotypes RB867515, SP81-3250, and RB935744, which presented elevated Al contents in the plant $(1.4, 1.1,$ and 1.2 dag.k⁻¹ Al, respectively), were able to produce a fair amount of shoot (73, 67, and 67 g SDW, respectively).

3.5 Correlation Analysis

Most of the correlations between SDW and Al contents (ALR and ALS) and root length (LRL and PRR) were negative, meaning that high values for those components are associated with low SDW, or vice-versa (Table 2). Al contents in the roots were also negatively correlated with the other variables in both environments. These results indicated that, upon sufficient nutrient availability and absence of exchangeable Al, plants tend to maintain satisfactory shoot biomass production since there is low or null assimilation of the phytotoxic element by the radicular system (reflecting the negative correlation between ALR and SDW).

ALR and ALS values do not necessarily result in uniform effects on biomass production, as each genotype shows a different level of tolerance to Al-stress. For instance, genotypes RB92579 and RB928064 had low levels of Al in the plant and were nevertheless the most sensitive to stress. On the other hand, even with high Al levels in the plant, RB92579 and RB928064 presented low phenotypic plasticity, that is, a smaller difference between shoot biomass production in the two environments. It is important to observe the responses of the individual genotypes to stress, in order to select the parental lines to be used in breeding programs for Al tolerance.

The characterization of genotypes, and knowledge of the relationship between the traits involved in tolerance to Al-stress, constitute the initial step in the breeding for tolerance against

Table 2. Phenotypic correlations between the traits associated with Al-stress in sugarcane genotypes evaluated in environments under Al-stress (lower diagonal) or in non-stress (upper diagonal) conditions

** and + significant at P = .05 and P = .10 probability, respectively, according to the t-test. SDW: shoot dry weight; LRL: lateral root length; PRL: primary root length; ALR: Al contents in the root; ALS: Al contents in the shoot*

abiotic stresses. From that point, breeders have the challenge to plan breeding strategies in order to increase production under stress conditions. Parentoni et al. [33] suggested that, for corn, a satisfactory selection criterion to increase the efficiency of P utilization should include grain production under P stress and the evaluation of P contents in the grain under conditions of high P. Mundim et al. [34] concluded that, for popcorn, the selection performed in environments with contrasting P conditions should be performed in each of these environments, via direct or indirect selection. An attempt to select genotypes subjected to low fertilization hinders the optimal expression of many desired traits, especially those associated with productivity and quality [35]. The identification of sugarcane genotypes tolerant to Al must consider traits of the roots and the shoots, as well as a possible correlation with productivity at advanced stages of plant development.

4. CONCLUSION

The present study revealed genetic variability between sugarcane genotypes' tolerance to Al by the phenotypic plasticity approach. Al-stress caused a reduction in the SDW and PRL, as well as an increase in the LRL.

The genotypes RB867515, SP81-3250, and RB935744, even presenting high contents of Al in the plant, still produced a fair amount of shoot. Based on the phenotypic plasticity, that is, the ability of a genotype to produce an alternative phenotype under environmental stimuli in order to circumvent adverse conditions, RB966928, RB867515, RB008041, and RB935744 were classified as tolerant. On the other hand, the genotypes RB937570, RB92579, and RB928064 were considered as sensitive to Al.

The path analysis indicated that traits associated with the radicular system are of great importance in plant biomass production under conditions of Al-stress. In order to meet the challenge of increasing production under such conditions, knowing the correlation between the traits required for Al tolerance is crucial and constitutes the initial step in breeding programs. In the present study, the genotypes were characterized and the relationships between some of the features involved in Al tolerance were elucidated. The identification of sugarcane genotypes tolerant to Al should consider root properties as well as the phenotypic plasticity.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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