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Aluminium-induced callose formation in root apices: inheritance and selection trait for adaptation of tropical maize to acid soils

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Abstract

Aluminium (Al) toxicity limits maize production on acid soils of the tropics. However, wide genetic variation exists in maize for Al resistance. The objective of this study was to assess the Al resistance of open pollinated tropical maize cultivars, from widely differing origin, and their diallel crosses based on callose formation as a physiological marker, and study the inheritance and combining ability for Al resistance. Fifteen maize cultivars from 4 maize breeding programmes and their 105 crosses were grown under controlled environmental conditions in a growth chamber and treated without or with 25 μM Al at pH 4.3. After 12 h of Al treatment, callose contents of 1 cm root apices were determined. There was a significant genotypic variation in callose formation under Al stress. Furthermore, diallel analysis indicated a significant general combining ability (GCA) but not specific combining ability (SCA), indicating that Al resistance is mainly controlled by additive genes. In general, Al-resistant cultivars showed favourable GCA effects while the sensitive cultivars had unfavourable GCA effects clearly indicating the dominant role of Al-resistant cultivars in the development or improvement of Al-resistant maize varieties. Moreover, a relatively high heritability ($h^2 = 0.7$) was obtained for Al resistance in nutrient solution. Aluminium resistance as revealed by callose content in Al-treated root apices was positively correlated to the relative grain yield of the same crosses evaluated across five tropical environments. In addition, strong genetic correlation was observed as GCA of callose formation in nutrient solution closely correlated with GCA of yield on acid soils. These findings suggest that Al-induced callose formation is a powerful tool to enhance the breeding of maize cultivars with superior adaptation to acid and Al-toxic soils.

Keywords: Aluminium toxicity; Callose; Diallel cross; General combining ability (GCA); Maize (*Zea mays* L.); Soil acidity

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1. Introduction

Maize (*Zea mays* L.) is the third most important cereal crop covering worldwide 140 million ha (Aquino et al., 2001) out of which 26 million ha are located in acid soil environments (Von Uexküll and Mutert, 1995). The crop yield on acid soils is mainly limited by aluminium toxicity. In addition, other acidity-related stresses, such as proton toxicity, Mn toxicity, and nutrient deficiencies particularly of P, Mg, Ca, and Mo are also important constraints (Marschner, 1995).

Though abundant in the earth's crust, Al occurs as insoluble and non-toxic forms in neutral soils. However, as the soil pH (H_2O) drops below 5.5, Al enters into the soil solution and affects plant growth. The first visible Al injury is the inhibition of root elongation. This has been widely used as a trait for the screening of cultivars for Al resistance (Foy, 1976; Foy et al., 1993). Al-induced callose formation particularly in root apices has been reported to be an even more sensitive physiological marker of Al injury (Wissemeier et al., 1987; Wissemeier and Horst, 1995) and an indicator of genotypic differences in Al sensitivity in maize (Horst et al., 1997; Collet et al., 2002), wheat (Zhang et al., 1994), and soybean (Wissemeier et al., 1992).

To overcome the problem of Al toxicity, breeding of resistant cultivars was suggested as the best option (Bellon, 2001). This is particularly true since liming, the most common practice to alleviate the problem of soil acidity, is too expensive for small farmers, and also not effective to correct soil acidity in deep soil layers. Developing Al-resistant and acid-soil tolerant cultivars could offer a less expensive, ecologically friendly and permanent solution (Granados et al., 1993) if combined with measures to avoid further soil acidification.

Considerable genetic variations in maize for Al resistance and adaptation to acid and Al-toxic soils have been reported with both qualitative inheritance (Rhue et al., 1978; Miranda et al., 1984) and quantitative inheritance (Lima et al., 1992; Duque-Vargas et al., 1994; Pandey et al., 1994; Borrero et al., 1995; Salazar et al., 1997). Thus, the potential of improving adaptation to acid and Al-toxic soils in maize is promising. We used diallel crosses among 15 maize cultivars selected for their adaptation to varying tropical environments to study their performance, breeding value, as well as gene effects across five tropical acid soil environments. In the present study, the same set of cultivars was tested for Al resistance under controlled climatic conditions, using callose formation as a physiological marker. The objectives were to assess the Al resistance of tropical maize cultivars and study the inheritance of Al resistance based on callose formation in Al-enriched nutrient solution, and relate Al-induced callose formation to grain yields on acid soils.

2. Materials and methods

The plant materials consisted of seeds of 15 open-pollinated maize cultivars (Table 1) and 105 F1 crosses obtained among them in a diallel mating design. Two contrasting checks, Al-resistant cv ATP-Y and Al-sensitive cv Lixis were also included. The F1 was developed by using bulk pollen of 100 plants of each cultivar to pollinate at least 25 female plants of each of the 14 other parents. Seeds from the 25 ears obtained per cross (both direct and reciprocal crosses) were bulked, shelled, and random samples of the bulk seed for each cross were used in this study. Crosses were made by IRAD, Cameroon, and testing materials were transferred to INRA-Guadeloupe for distribution to the other partners.

The seeds were surface sterilized for 1 min in diluted sodium hypochlorite with 3–7% active chloride and germinated between wet filter papers soaked in 1 mM $CaSO_4$ solution. After 4–5 days, seedlings were transplanted to 22 l pots containing nutrient solution of the following composition [μM]: KNO_3 400, NH_4NO_3 200, KH_2PO_4 10, $MgSO_4$ 100, H_3BO_3 8, $CuSO_4$ 0.2, $ZnSO_4$ 0.2. $MnSO_4$ 1, $(NH_4)_6Mo_7O_{24}$ 0.1, Fe-EDTA 20, $CaSO_4$ 250.

During 2 days of preculturing, the pH of the nutrient solution was lowered gradually to 4.3 and kept constant during the experiment using an auto-titration device with 0.1 M HCl/KOH. Half of the pots were treated with 25 μM Al (as $AlCl_3$) and the remaining half were kept without Al. The number of replications per cultivar was four. After 12 h Al treatment, 1 cm root tips were cut from the primary or the longest seminal root of each plant and immediately transferred to 96% ethanol or shock frozen in liquid