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# Response of the roots of oil palm O×G interspecific hybrids (*Elaeis oleifera* ×*Elaeis guineensis*) to aluminum ($Al^{3+}$) toxicity

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**Abstract**

Approximately 60% of the land in Colombia that is planted with oil palm is acidic with a high aluminum saturation of over 50% of the cation exchange capacity. To understand the physiological and biochemical response of oil palm rootlets to aluminum toxicity and to identify possible tolerance mechanisms and the materials best adapted to this stress, six oil palm interspecific O×G hybrids (U1273, U1737, U1757, U1859, U1914, and U1990) were planted in a hydroponic system with three levels of aluminum concentrations (0, 100 and 200 μM) in a randomized complete split-plot design with five replications. The root variables of growth, accumulation of aluminum, nutrient content, production of spermidine, and exudation of organic acids were recorded. High levels of aluminum inhibited root growth, altered the absorption of water and nutrients, especially nitrogen, calcium, iron, and manganese, and activated tolerance mechanisms, such as organic acid release, homeostasis of certain essential ions, and spermidine production. These responses were differential between the different hybrids, identifying the U1990 hybrid as the most tolerant to aluminum. Despite having the greatest accumulation of aluminum, the U1990 hybrid produced the longest and most abundant roots in response to the increased production of spermidine and oxalic, malic, and acetic acids and was better able to regulate nitrogen and manganese.

**Keywords:** Acidity; aluminum tolerance; exchangeable aluminum ($Al^{3+}$); growth; organic acids; polyamines.
**Abbreviations**: $Al^{3+}$_exchangeable aluminum in soil solution; $[Al^{+3}]$_ aluminum concentrations; $R^2$_ determination coefficient; FRT_fresh root tissue; VC_variation coefficient.

## Introduction

Soil acidity limits plant growth due to a combination of factors that affect soil pH that cause aluminum and manganese toxicity and low availability of essential nutrients, especially calcium, magnesium, phosphorus and other micronutrients (Kochian et al., 2004). However, the most important production-limiting factor in acidic soils is soluble aluminum in the form of $Al^{3+}$ (Liao et al., 2006; Horst et al., 2010; Hossain et al., 2006), which is the most abundant and most toxic to plant species (Poschenrieder et al., 2008). Approximately 30% of the agricultural area worldwide (3,950 million hectares) and 50% of potentially arable land surface is composed of acidic soils (Kochian et al., 2004; Liao et al., 2006), and 81% of tropical soils in the Americas are acidic with a high content of soluble aluminum. In Colombia, the percentage of acidic soils at pH values below 5.5 with low fertility and high concentrations of aluminum is approximately 85% of the national territory. An estimated 60% of the planted area has an aluminum saturation greater than 50% of the cation exchange capacity (Cristancho et al., 2011; Valencia and Ligarreto, 2012). In these soils, both *Elaeis guineensis* (native to Central and West Africa) and the interspecific hybrid, *Elaeis oleifera* x *Elaeis guineensis* (OxG), are cultivated. The interspecific hybrid is an alternative for improving the competitiveness and sustainability of the Latin American oil palm agro-industry because of its partial resistance to some lethal diseases and also because of the high quality of its oil (Rivera et al, (2013). Plants have developed adaptation mechanisms to grow in acidic soils with toxic levels of aluminum. Some of these mechanisms include the production of organic acids, which are substances that efficiently chelate metal cations to prevent their entrance or accumulation in the plant (Ma et al., 2001). The production of polyamines, such as spermidine, spermine, and putrescine (polybasic amines with a function in the DNA replication, transcription, cell division, modulation and activation of enzymes, and membrane stability), in tolerant species or varieties has also been noted (Gill and Tuteja, 2010; Kubis, 2005; Tang and Newton, 2005; Verma and Mishra, 2005). Oil palm tolerates large variations in soil moisture and acidity conditions. However, excess exchangeable $Al^{3+}$ plays a critical role in growth retardation, chlorosis, leaf burn, and decreased yield (Corley and Tinker, 2003). Note that the following: (i) aluminum toxicity limits plant growth (Liao et al., 2006; Macêdo et al., 2001; Tang et al., 2002) through its adverse effects on root growth and development (Chaffai et al., 2005), and plant growth may be used as an indicator of the plant's response to $Al^{3+}$ toxicity and even of the degree of tolerance (Silva, 2012); and (ii) there are very few studies on oil palm tolerance mechanisms and the degree of adaptation of commercial materials to this type of stress. Based on the standardized hydroponics technique described by Rivera et al. (2013), our research objective was to understand the physiological and biochemical response of the interspecific OxG oil palm hybrids grown in hydroponic medium to aluminum toxicity and to identify possible mechanisms of

tolerance to this stress based on the hypothesis that two different tolerance mechanisms, the reduction of oxidative stress and aluminum detoxification, exist.

**Results**

With the exception of the phosphorus, boron, sulfur, and magnesium contents, the physiological and biochemical responses of hybrid roots were significantly affected by aluminum concentrations after four months (120 days) of application. Additionally, the measured phosphorus, spermidine, and organic acid contents showed statistically significant differences due to the hybrid material origin and interaction ($p < 0.05$), whereas the nutrient content and growth of the root variables were not affected by the material origin or interaction (Table 1).

***Root growth: number of tips and length***

The root system growth decreased as the aluminum concentration increased. The number of tips showed statistically significant differences among the materials regardless of the dose of $Al^{3+}$. The U1990 hybrid had the most extensive root system, and the U1859 hybrid had the least extensive. The response of different hybrids to aluminum concentration in terms of root length was significant. The U1859 and U1273 hybrids were least affected by the toxicity; however, these hybrids showed lower growth in the absence of this ion, whereas the U1990 hybrid, under the three conditions of $Al^{3+}$, had the longest roots. The U1273, U1737, and U1914 hybrids had a considerable reduction of this variable when the aluminum concentrations were increased (Table 2).

***Accumulated aluminum in root: aluminum content and hematoxylin staining***

The amount of accumulated aluminum in root tissue was measured directly by an atomic absorption spectrophotometric method and semi-quantitatively with the hematoxylin staining method. The aluminum content increased as the aluminum concentration increased in the nutrient solution (Table 3). The aluminum accumulation was the same in all materials. The root tips and growth zones, which were approximately 5 mm from the root apex and were treated with aluminum solution (100 and 200 µM), showed the highest staining intensity with colors between soft blue and purple. The U1914 hybrid showed the lowest staining intensity, whereas the roots of the U1990 hybrid had the highest staining intensity in greater proportions. No root staining was detected in the absence of aluminum (Fig 1).

***Nutrient content in roots: macro- and micro-nutrients***

Phosphorus, potassium, magnesium, sulfur, boron, and zinc were unaffected by aluminum concentrations (Table 1). However, aluminum did cause a reduction in the root content of other macro- and micro-nutrients, such as nitrogen, calcium, iron, and manganese. The iron content varied among materials depending on the dose of $Al^{3+}$: in the absence of this ion, the U1273 hybrid showed a greater accumulation of iron, but this one was the most affected from aluminum toxicity, and the response was similar under treatment with the highest concentration of aluminum (Table 4). The contents of other nutrients (nitrogen, calcium and manganese) showed statistically significant differences among materials regardless of the dose of $Al^{3+}$ (Table 3): the U1990 hybrid had the greatest accumulation of nitrogen and


**Fig 1.** Hematoxylin staining of OxG hybrid primary roots subjected to different aluminum concentrations (0, 100 and 200 µM) for four months. A greater proportion and higher intensity of purple or blue colors represents a greater accumulation of aluminum in the root apex and root elongation zone; no root staining in the absence of aluminum was observed.

manganese, the U1273 and U1737 hybrids showed the greatest accumulation of calcium, and the U1914 and U1859 hybrids recorded the lowest nutrient content. The contents of nitrogen, manganese, and aluminum were quite sensitive to the concentration of aluminum and showed differential responses from 100 µM of $Al^{3+}$, whereas the calcium content recorded differences only under the highest dose of exchangeable aluminum.

***Production of spermidine and organic acids***

The spermidine content was directly proportional to the aluminum concentrations (Table 4). In the absence of aluminum, the hybrid materials, except the U1914 hybrid, showed similar spermidine content; in treatments with aluminum, the U1990 hybrid showed the greatest production of this polyamine. The exudation of organic acids varied among materials depending on the concentration of $Al^{3+}$, although a general increase in the production of oxalic, malic, and acetic acids was found in response to the aluminum dose applied (Table 4). The U1859 hybrid showed a decrease in the levels of the three acids at 100 µM of $Al^{3+}$, and the U1757 hybrid showed a lower exudation of oxalic and acetic acids under the highest exposure to aluminum. The U1990 hybrid showed the highest concentrations of the three acids in response to aluminum treatments.Under aluminum treatments, the roots of the U1990 hybrid showed the highest levels of spermidine; malic, oxalic, and acetic acids; nitrogen; and manganese.

**Discussion**

The OxG hybrid materials were affected by the high aluminum concentration in the medium. The first symptom of

**Table 1**. Analysis of variance of the physiological and biochemical response of OxG hybrid roots subjected to different aluminum concentrations ([$Al^{+3}$]) for four months.

| Variable | | [$Al^{+3}$] | OxG Hybrid | [ $Al^{+3}$] × Hyb | $R^2$ | VC |
|---|---|---|---|---|---|---|
| Growth | Number of tips | ** | ** | n.s. | 78.6 | 20.4 |
| | Length | ** | ** | n.s. | 78.7 | 18.0 |
| Aluminum accumulation | Hematoxylin | ** | ** | n.s. | 92.8 | 23.6 |
| | $Al^{+3}$ | ** | n.s. | n.s. | 88.8 | 23.6 |
| Nutrition | Nitrogen | ** | ** | n.s. | 83.6 | 6.2 |
| | Phosphorus | n.s. | n.s. | n.s. | 74.2 | 14.2 |
| | Potassium | n.s. | ** | n.s. | 73.9 | 11.0 |
| | Calcium | ** | ** | n.s. | 82.8 | 9.8 |
| | Magnesium | n.s. | n.s. | n.s. | 62.7 | 13.0 |
| | Sulfur | n.s. | n.s. | n.s. | 57.5 | 8.6 |
| | Iron | ** | ** | ** | 82.5 | 35.0 |
| | Manganese | ** | ** | n.s. | 70.9 | 34.3 |
| | Zinc | n.s. | n.s. | n.s. | 69.2 | 28.0 |
| | Boron | n.s. | n.s. | n.s. | 75.7 | 9.7 |
| Polyamines | Spermidine | ** | ** | ** | 94.6 | 30.4 |
| Organic acids | Oxalic acid | ** | ** | ** | 93.2 | 13.6 |
| | Malic acid | ** | ** | ** | 93.8 | 16.1 |
| | Acetic acid | ** | ** | ** | 95.7 | 12.2 |

**Significant F test, $p \leq 0.05$ (Tukey's test). n.s. not significant. $R^2$: Determination coefficient VC: Variation coefficient.[$Al^{+3}$]×Hyb: Aluminum concentration x OxG hybrid interaction

$Al^{3+}$-induced damage was the inhibition of root growth, which was primarily due to alterations in redox state, division, and cell elongation (Poschenrieder et al., 2008), as reported in *Cucurbita pepo* (Dipierro et al., 2005), *Glycine max* (Cakmak and Horst, 1991), *Cucumis sativus* (Pereira et al., 2010), *Vigna radiata* (Ali et al., 2008), *Zea mays* (Jones et al., 2006), *Pisum sativum* (Kobayashi et al., 2004), *Oryza sativa* (Meriga et al., 2004), *Elaeis guineensis* (Cristancho et al., 2010), and other crops (Kochian et al., 2004). Therefore, a change was observed in the absorption of water and nutrients, especially in nitrogen, calcium, iron, and manganese, which was accentuated by an increase in the aluminum concentration in the roots. Thus, the inhibition of the absorption of calcium ($Ca^{2+}$) and iron ($Fe^{2+}$) cations suggests that the absorption of aluminum may have occurred through these channels. This possibility is supported by several authors that have mentioned that even nanomolar concentrations (Giannakoula et al., 2008) of $Al^{3+}$ cause alterations in nutrient absorption and translocation, particularly of $Fe^{2+}$, $Ca^{2+}$, and $Mg^{2+}$ (Bose et al., 2011), which are affected by blockage of their entry channels in the plasma membrane (Rengel and Zhang, 2003), $NO_3^-$ (Rout et al., 2001), and $K^+$ (Kochian et al., 2004; Rout et al., 2001); this relationship is inversely proportional to root development (Silva, 2012) and crop yield (Akaya and Takenaka, 2001).

Hematoxylin staining showed that roots under aluminum stress develop a brownish color and short, crisp, and little branching roots. The apical and growth zones were the most affected with the highest accumulation of $Al^{3+}$. Similar results were found by Chaffai et al. (2005), Doncheva et al. (2005), and Zheng and Yang (2005), who reported that the first affected points in the roots are the apical regions, specifically the root cap, meristem, and elongation regions, which have the highest accumulation of aluminum and most sensitivity to physical damage compared with mature tissues.

The production of organic acids and polyamines was directly proportional to the concentration of aluminum in the medium. Mohapatra et al. (2010) reported that a high synthetic rate of polyamines is a response to the metal exposure, and the overexpression of spermidine synthase is a notable indicator of tolerance to $Al^{3+}$ (Chen et al., 2008; Wen et al., 2009; Zepeda et al., 2011). Similarly, the exudation of

**Table 2.** Means of the root growth of OxG hybrids subjected to different aluminum concentrations for four months. The interaction between aluminum concentration and OxG hybrid was not significant.

| Factor | | Number of Tips | Root length (cm) |
|---|---|---|---|
| OxG hybrids material | U1273 | 746.6 ab | 398,8 ab |
| | U1737 | 659.3 bc | 389,0 bc |
| | U1757 | 679.6 bc | 361,1 bc |
| | U1859 | 527.0 c | 286,2 c |
| | U1914 | 583.6 bc | 360,2 bc |
| | U1990 | 911.9 a | 481,1 a |
| $Al^{3+}$ (µM) | 0 | 851.0 a | 452,7 a |
| | 100 | 662.1 b | 367,3 b |
| | 200 | 540.9 c | 318,3 b |

Values shown with different letters are significantly different, p≤0.05 (Tukey's test).

malic, oxalic, and acetic acids exhibit highly detoxifying properties and form strong complexes with aluminum to protect the root (Kochian et al., 2004). At the encountered concentrations, this action is associated with tolerance to aluminum in many plant species, such as *Triticum sp*. (Macêdo et al., 2001), *Sorghum sp*. (Ma et al., 2001), *Avena sativa*, *Raphanus sp*., and *Secale cereale* (Tang et al., 2002). Cristancho et al. (2010) worked with oil palm seedlings that were subjected to $Al^{3+}$ concentrations of 0, 100, and 200 µM for 80 days and found an exponential increase in the release of oxalic acid as the aluminum concentration increased. However, these figures are lower than the figures obtained in this study. This difference is primarily due to genotype differences (*Elaeis guineensis* vs. *E. oleífera x E. guineensis*) and the time of exposure (80 vs. 120 days), which allows us to conclude that the release of organic acids in palm oil is rapidly activated once the plants are exposed to aluminum but is higher with exposure to higher concentrations of $Al^{3+}$; additionally, the exudation rate increases over time, as reported by *Cassia tora* (Ma et al., 1997), *Oryza sativa* (Li et al., 2000), *Populus sp.* (Naik et al., 2009), and *Triticale* (Ma and Hiradate, 2000). As reported by Auxtero and Shamshuddin (1991) and Cristancho et al. (2010), oil palm hybrids were able to tolerate aluminum concentrations (> 50 µM) that are lethal to other plant species. When $Al^{3+}$ concentrations were equal to or higher than 100 µM, the seedling growth rate decreased and tolerance mechanisms, including the release of organic acids, homeostasis of some essential ions, and production of spermidine, were activated. This response varied among materials and permitted the identification of the U1990 hybrid as tolerant. Despite the accumulation of the largest amount of aluminum in the root system under aluminum toxicity conditions, this hybrid had the longest and most abundant roots in response to greater production of spermidine and oxalic, malic, and acetic acids, as well as better regulation of nitrogen and manganese contents. This root system permits the U1990 material to penetrate a larger volume of soil and be more efficient in water and nutrient absorption in areas where the aluminum content may be a production-limiting factor, as in most areas of oil palm expansion in Colombia. This expression of physiological and biochemical traits by the U1990 hybrid could confer its adaptation to different stress conditions (biotic and/or abiotic), as reported by Rivera et al. (2013).

## Materials and Methods

### *Localization*

The study was conducted in a greenhouse in Barrancabermeja - Santander (Colombia). The altitude was 125 meters above sea level with an average temperature of 34 °C, a relative humidity of 70.5%, and an annual rainfall of 2,852 mm, creating tropical rainforest agro-ecological conditions (Holdridge life zones system).

### *Plant materials*

Six oil palm interspecific OxG hybrids, *E. oleifera* x *E. guineensis*, were evaluated: U1273, U1737, U1757, U1859, U1914, and U1990. Seeds with differentiated plumule and radicle were kept in sandbars until the appearance of the second open lanceolate leaf at phenological stage 102 (Hormaza et al., 2012). Later, the seeds were moved to a hydroponics system in a greenhouse, according to the method standardized by Rivera et al. (2013).

### *Treatments*

Seedlings were distributed in a randomized complete split-plot design, where the main plot was the aluminum concentration (0, 100 and 200 µM) and the sub plot was the hybrid material (U1273, U1737, U1757, U1859, U1914, U1990), with five replications and four seedlings per experimental unit. The Hoagland and Arnon nutrient solution was used at 0.5 of the original concentration (Jones, 2005), and the aluminum was added in the form of aluminum chloride ($AlCl_3 \cdot 6H_2O$). The solution was renewed weekly, and its pH was monitored every two days and held constant (4.0 ± 0.1) by adding 1% sodium hydroxide - NaOH or 0.05 M hydrochloric acid – HCl.

### *Traits measured*

The plants were kept in the system for 120 days until the phenological stage 109 with five open lanceolate leaves

**Table 3.** Means of aluminum and nutrient content in OxG hybrid roots subjected to different aluminum concentrations for four months. Variables in which the interaction between Aluminum concentration and the type of OxG hybrid was not significant are shown.

| Factor | Variable | N (%) | $Ca^{2+}$ (%) | Mn (ppm) | Root area stained with hematoxylin (%) | $Al^{+3}$ (ppm) |
|---|---|---|---|---|---|---|
| OxG hybrids material | U1273 | 1.19 abc | 0.37 a | 42.53 ab | 38.3 b | 2193.3 a |
| | U1737 | 1.23 ab | 0.37 ab | 32.86 ab | 35.2 b | 1770.0 a |
| | U1757 | 1.11 cd | 0.32 bc | 38.89 ab | 38.8 b | 1764.4 a |
| | U1859 | 1.14 bc | 0.30 c | 32.39 ab | 37.2 b | 1914.4 a |
| | U1914 | 1.06 d | 0.32 bc | 24.92 b | 29.1 c | 1571.1 a |
| | U1990 | 1.28 a | 0.34 abc | 49.67 a | 44.0 a | 2076.7 a |
| $Al^{3+}$ (µM) | 0 | 1.26 a | 0.38 a | 50.87 a | - | 656.1 c |
| | 100 | 1.19 b | 0.35 a | 34.44 b | 34.6 b | 2322.2 b |
| | 200 | 1.05 c | 0.28 b | 25.32 c | 39.6 a | 2666.7 a |

Values shown with different letters are significantly different, $p \leq 0.05$ (Tukey's test).

**Table 4.** Means ± standard deviations of iron, spermidine and organic acid content in OxG hybrid roots subjected to different aluminum concentrations for four months. The interaction between aluminum concentration and OxG hybrid was significant.

| | Aluminum concentration (µM) | | |
|---|---|---|---|
| OxG hybrids material | | | |
| | 0 | 100 | 200 |
| Fe (ppm) | | | |
| U1273 | 1266.8 ± 311.4 a | 372.9 ± 81.8 ab | 293.6 ± 49.4 a |
| U1737 | 678.1 ± 271.4 d | 563.4 ± 115.6 a | 166.7 ± 7.1 a |
| U1757 | 831.7 ± 250.3 c | 541.2 ± 156.0 a | 271.1 ± 40.5 a |
| U1859 | 694.7 ± 148.3 d | 416.4 ± 109.9 ab | 346.0 ± 76.6 a |
| U1914 | 559.3 ± 25.2 d | 312.2 ± 81.6 b | 231.2 ± 37.5 a |
| U1990 | 1036.3 ± 181.1 b | 476.8 ± 121.5 ab | 281.6 ± 44.6 a |
| Spermidine (nmoles / g FRT) | | | |
| U1273 | 101.97 ± 17.17 a | 465.88 ± 36.36 b | 1601.09 ± 298.34 b |
| U1737 | 45.77 ± 11.35 bc | 471.34 ± 40.99 b | 1406.51 ± 347.42 bc |
| U1757 | 70.97 ± 20.29 b | 524.54 ± 108.11 ab | 1133.70 ± 188.62 c |
| U1859 | 78.71 ± 26.47 b | 511.30 ± 52.4 b | 1641.05 ± 435.15 b |
| U1914 | 28.42 ± 8.47 c | 466.12 ± 35.76 b | 1843.96 ± 481.87 ab |
| U1990 | 82.96 ± 29.98 a | 624.23 ± 85.33 a | 2323.86 ± 324.38 a |
| Oxalic acid (µmoles / g FRT) | | | |
| U1273 | 131.68 ± 24.91 b | 222.33 ± 20.56 a | 255.87 ± 3.25 a |
| U1737 | 122.66 ± 5.72 b | 188.15 ± 6.06 ab | 224.38 ± 44.53 a |
| U1757 | 131.60 ± 20.97 b | 224.10 ± 46.83 a | 116.88 ± 8.35 b |
| U1859 | 117.50 ± 11.20 b | 78.71 ± 12.08 c | 257.77 ± 5.38 a |
| U1914 | 151.13 ± 4.97 a | 198.54 ± 0.93 ab | 232.08 ± 12.7 a |
| U1990 | 67.35 ± 7.80 c | 154.36 ± 10.77 b | 247.76 ± 36.46 a |
| Malic acid (µmoles / g FRT) | | | |
| U1273 | 149.47 ± 17.97 ab | 281.69 ± 38.24 a | 288.04 ± 30.29 b |
| U1737 | 129.82 ± 20.40 b | 224.01 ± 28.98 b | 265.49 ± 59.28 b |
| U1757 | 132.52 ± 15.24 ab | 109.70 ± 45.11 d | 310.34 ± 39.75 ab |
| U1859 | 100.59 ± 29.90 b | 77.36 ± 14.13 d | 191.10 ± 14.49 c |
| U1914 | 156.02 ± 15.76 a | 227.11 ± 8.16 b | 270.77 ± 18.22 b |
| U1990 | 72.67 ± 5.22 c | 170.64 ± 26.31 c | 326.19 ± 27.20 a |
| Acetic acid (µmoles / g FRT) | | | |
| U1273 | 144.75 ± 7.99 b | 241.11 ± 33.43 a | 268.45 ± 21.76 a |
| U1737 | 127.83 ± 28.18 b | 220.71 ± 22.10 a | 284.98 ± 13.34 a |
| U1757 | 146.62 ± 15.6 b | 236.53 ± 42.10 a | 123.97 ± 2.48 b |
| U1859 | 171.02 ± 7.68 a | 84.23 ± 15.65 c | 268.4 ± 23.23 a |
| U1914 | 123.95 ± 13.71 b | 205.54 ± 49.41 a | 274.47 ± 3.91 a |
| U1990 | 76.49 ± 2.86 c | 133.33 ± 18.00 b | 305.74 ± 59.07 a |

Values shown with different letters are significantly different, $p \leq 0.05$ (Tukey's test). FRT: Fresh root tissue.

(Hormaza et al., 2012). At that time, the following variables were recorded in the roots: growth (number of tips and root length), nutrient content (macro- and micronutrients), accumulation of aluminum (staining with hematoxylin and an atomic absorption spectrophotometric method), spermidine production, and organic acid exudation (oxalic, malic, and

acetic acids). The longest primary root and its secondary and tertiary roots were placed on acrylic trays with water and scanned with an Epson Expression 10000 XL scanner. Later, the WinRHIZO software version *Pro 3.5* (Regents Instruments Inc., Canada) was used to measure the total number of tips and the total length of the primary, secondary and tertiary roots. The root nutrient content was determined using colorimetric (P by 'Wet acid digestion extraction'), colorimetric-Azomethine H (B by 'Dry digestion extraction'), atomic absorption (K, Ca, Mg, Na, Fe, Mn, Zn and Al by 'Wet acid digestion extraction'), and turbidimetric (S by 'Dry digestion extraction') detection methods. Furthermore, the roots were stained with hematoxylin (Tang et al., 2002), and the stained area was determined to be the ratio between the root stained area (purple or blue areas) and the total projected root area using the Winrhizo system (Regents Instruments Inc., Canada), multiplied by 100 (%). The root samples were cut into small pieces, macerated in liquid nitrogen, and stored at - 80 °C. The spermidine content was determined using the methodology proposed by Moreno-Chacón et al., 2013, and the organic acids were determined according to Hernández et al., 2007. The HPLC (Chromatograph LaChrom Merck Hitachi Autosampler L-7200) was used to take biochemical measurements of the macerated substance.

***Statistical analysis***

The generated data were subjected to an analysis of variance, and the mean comparison was calculated by Tukey's test ($p \leq 0.05$) using SAS® statistical software, version 9.1 (SAS Institute, the USA).

**Conclusions**

Aluminum toxicity is a major problem in a large portion of arable land. Although the ideal conditions would keep exchangeable aluminum contents low, this is not always possible due to technical and/or economic limitations. Therefore, genetic selection is the most promising and appropriate solution. In this study we not only determined the physiological and biochemical response of oil palm genotypes to aluminum toxicity but also identified the tolerance mechanisms that could be used in breeding programs for the selection of $Al^{+3}$ toxicity-resistant genotypes. Using hydroponics and nursery plants, tolerant materials were identified using relatively simple methods; this could speed up the identification of sources of tolerance and also the selection and incorporation of new tolerant strains into commercial industry, which is a necessary task for a rapidly growing productive sector facing challenging biotic and abiotic stress risks.

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