

Exudation of organic acid anions by different maize cultivars as affected by phosphorus deficiency and aluminium toxicity

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Abstract

We investigated the release of citrate and malate from 8 maize cultivars pre-cultured in nutrient solution supplied with and without 40 μM phosphorus (P) for 7 days then exposed to 0 and 50 μM aluminium (Al). Only cv ICA V-109 responded to P deficiency (-P,+Al) by increasing mainly citrate exudation, which was highly reduced by Al. Aluminium stimulated citrate and malate exudation by other cultivars in the order C525M >> PM > Sikuanani = ATP-Y > HD 9148 > HS 11x723 > Lixis, which reflected their Al resistance. Kinetics of the organic anions exudation of -P+Al plants at a constant pH of 4.3 showed a decrease of the exudation rate with time. Root tips (10 mm) exhibited higher Al-induced exudation rates as well as higher contents of organic acid anions.

Introduction

In highly acid soils, it is difficult to differentiate between the effect of Al and P-deficiency stress. Exudation of organic acid anions, especially citrate and malate, by plant roots probably provide an efficient mechanism by which some species or cultivars enhance their abilities to acquire P (Kamh, *et al.*, 1999) and to detoxify Al (Delhaize *et al.*, 1993; Miyasaka *et al.*, 1991). The present work aimed to study the Al and P deficiency-induced exudation of citrate and malate from 8 maize cultivars grown in hydroponic culture.

Materials and methods

Different maize (*Zea mays* L.) cultivars were pre-cultured in nutrient solution supplied with and without 40 μM P for 7 days. Seedlings from both P treatments were then exposed to 0 and 50 μM Al at an initial pH of 5.5 and 4.3, respectively. Organic acid anions exuded by the intact roots for 4 h into a 0.5 mM CaCl_2 solution with and without Al supply were run first through a cation and then through an anion-exchange resin. In a second experiment, organic anions were collected every 4 h for a 24 h period using the same technique. For the quantification of organic acid-anion exudation from root apices, a small cup (3 ml) containing an anion-exchange resin was used to capture the root exudates from the 10-mm root tips of 4 days-old intact seedlings. The concentrations of organic acid anions recovered from the anion exchange resin were analysed by HPLC.

Results

The exudation rates of citrate and malate differed widely between 8 maize cultivars and were highly dependent on Al supply rather than on the P nutritional status of the plants (Fig. 1). Phosphorus deficiency enhanced citrate exudation only in cv ICA V109. This

exudation was strongly reduced in the presence of Al. Exposing the plants to Al (P/Al, 0/50) stimulated citrate and malate exudation by the other cultivars. The sum of citrate and malate exudation rate of the cultivars in the -P, +Al treatment decreased in the order cv C525M >> cv PM > cv Sikuanani = cv ATP-Y > cv HD 9148 > cv ICA V109 > cv HS 11x723 > cv Lixis. Exudation rates of plants pre-cultured at high P supply were reduced by Al supply in all cultivars.

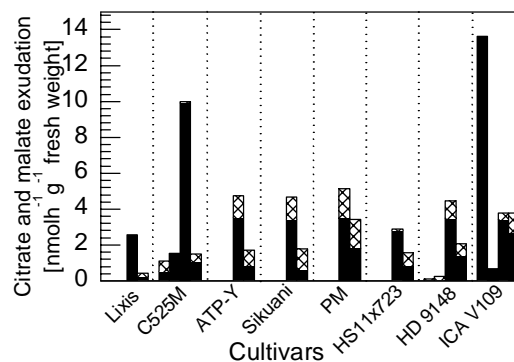


Figure 1. Citrate and malate exudation rates from roots of 8 maize cultivars grown in nutrient solution for 8 days at low and high P supply and treated with Al for 20 h. Columns from left to right present P/Al ratios (μM), 0/0, 40/0, 0/50, and 40/50.

The collection of the exuded organic acid anions every 4 h during a 24 h period is shown in Fig. 2. The highest exudation rates were obtained after the first 4 h collection period and then tended to decrease. Exudation rates of particularly citrate were consistently higher in Al-resistant (eg. ATP-Y) than in Al-sensitive cultivars (eg. Lixis). Also Al-resistant cultivars were capable of maintaining a higher

exudation rate when the period of Al treatment was extended. Root tips of the Al-resistant cultivars (ATP-Y, C 525M) proved to be the most active root zone in organic acid-anion exudation (Fig. 3). The rates of Al-induced exudation of citrate and malate were 2 (cv C525M) to 4 (cv ATP-Y) times higher than those estimated on the basis of the total root system (compare Figs. 1 and 3).

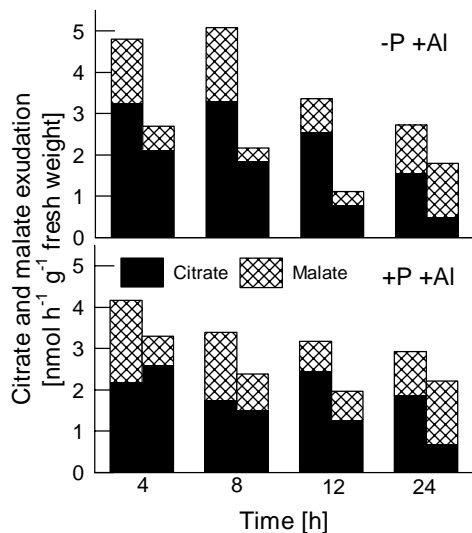


Figure 2. Citrate and malate exudation rates with time for cv ATP-Y (left column) and cv Lixis (right column) grown in nutrient solution for 8 days at 0 and $40 \mu\text{M}$ P supply and then exposed to $50 \mu\text{M}$ Al.

Discussion

Several plant species respond to P deficiency and to toxic levels of Al by releasing organic acid anions (Jones, 1998). Low P supply enhanced citrate exudation by ICA while other cultivars did not express this trait (Fig. 1). In these cultivars, stimulation of citrate and malate exudation could only be observed as a response to Al stress. Aluminium-resistant cultivars excreted organic acid anions at a greater rate than Al-sensitive cultivars (Joge *et al.*, 1997; Gaume, 2000; Fig. 1). However, the exudation rates by both, resistant and sensitive cultivars decreased with time (Fig. 2). Differences found in the amount of organic acid-anion exudation may reflect cultivar differences related to Al resistance. Increased pH in the P/Al 40/50 μM treatment (not shown) is probably indicative of precipitation of Al phosphate (Miyasaka, 1991) and strongly reduced monomeric Al concentration in the solution (not shown), resulting in a reduction of citrate exudation in the high P treatment (Fig. 1).

The release of organic acid anions in response to Al appears to be highly localised to the root-tip zone (Kochain, 1995; compare Fig. 3 with Fig. 1), which is the primary site of Al toxicity. Root tips exhibited also much higher contents of organic acids compared to the zone 1-6

cm behind the root tip (not shown). However, the root contents of organic acids were not different between Al-resistant and Al-sensitive cultivars. An external release of organic acids might explain the lack of correlation between Al resistance and changes in internal organic acid content (Foy *et al.*, 1990). Foy *et al.* (1972) suggested that part of the mechanism of Al resistance in 'Dade' was due to its ability to maintain P uptake through release of citrate into the rhizosphere. Our results show that the highest rate of citrate exudation was obtained under P and Al stress, suggesting that both, mobilisation of P and complexation of Al, could occur simultaneously in the rhizosphere of Al-resistant cultivars.

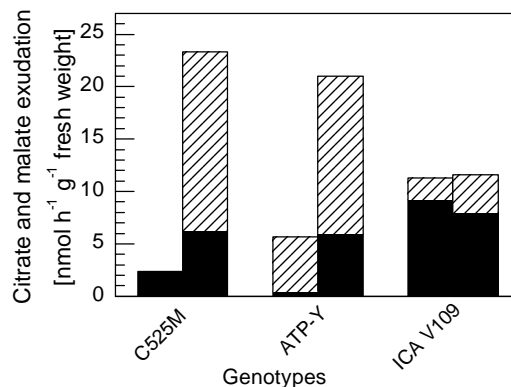


Figure 3. Effect of Al supply on citrate and malate exudation by 10 mm root tips of 3 maize cultivars grown in P-free nutrient solution for 4 days. Left column 0, right column $50 \mu\text{M}$ Al supply.

Acknowledgement

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