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Oxalato, the Ion that Hides: Intracellular Accumulation in an Aluminum Tolerant Rice Cultivar

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Abstract

Organic acid exudation is one of the main mechanisms of aluminum (Al) tolerance in plants. The contribution of intracellular accumulation of these compounds, nevertheless, remains much less explored, especially in rice. This study examined data from experiments carried out with two upland rice cultivars that differ in their response to Al: Comum branco (tolerant) and Caiapó (sensitive). The data come from the experiment described in Zonta *et al.* The new finding is that oxalate had a ratio of 2.6, while citrate and malate are mainly exuded. Principal component analysis (PCA) also shows that oxalate is functionally independent from the other organic acids. None of this was reported in the original study. The work used chromatographic profiles and multivariate statistics to investigate the distribution pattern of oxalate between root cellular content and exudate when plants were exposed to Al, and to contrast this pattern with those of citrate and malate. In the tolerant cultivar, oxalate concentration in the cellular content increased strongly under Al stress, with rises of 128% at 4 days and 113% at 15 days ($p < 0.01$). No change was detected in the exudate for oxalate, while for citrate and malate, the opposite happened as their concentrations in the exudate increased sharply under Al, with increases up to 10-fold larger in the tolerant cultivar than in the sensitive one. Chromatographic profiles taken 15 days confirmed these patterns. They showed large peaks of citrate and malate in the exudate of Comum branco, while oxalate was the dominant peak in the cellular content of the same cultivar. Principal component analysis revealed that oxalate is functionally independent from citrate and malate, as its vector stood perpendicular to the vectors of the two acids. The interaction between cultivar and detection site was significant only for oxalate. In the sensitive cultivar Caiapó, oxalate concentrations did not change in response to Al, regardless of the detection site. Together, these results demonstrate that the distribution profile of oxalate differs clearly from those of citrate and malate, and that this difference is expressed in distinct ways between the two cultivars. This progressive intracellular accumulation of oxalate, occurring alongside larger absolute amounts of citrate and malate, points to an energy-saving internal detoxification strategy in the tolerant cultivar.

Keywords

Oryza Sativa, Aluminum, Organic Acids, Oxalic Acid, Chromatographic Profile

1. Introduction

Aluminum ranks as the third most common element in the Earth's crust. Under acidic soil conditions, which cover about 30% of the world's arable land [1] and more than 50% of potentially arable land in tropical regions [2], Al dissolves into the toxic form Al^{3+}. This ion damages root growth and reduces the uptake of water and nutrients [3]. In Brazil, roughly 60% of cultivated soils are acidic [4]. The presence of Al in subsurface layers further restricts root development and makes plants more vulnerable to drought [5].

The first visible effect of Al toxicity is the fast cessation of root elongation. This leads to poor plant establishment and low productivity [6] [7]. To deal with this stress, plants have developed two broad types of defense. One type prevents Al from entering root cells, a strategy called external exclusion. The other type allows the plant to survive even after Al has entered the cell, a strategy known as internal detoxification [6] [7].

A well-known external exclusion mechanism involves the release of organic acids from root tips. Citrate, malate and oxalate can bind Al^{3+} in the soil solution around the root. The resulting complexes are stable and are not absorbed by the plant [8]. This process has been studied in detail in wheat, maize, and soybean, where the secretion of citrate and malate is linked to Al tolerance [9] [10].

Oxalate has received less attention in this context. In some species, such as buckwheat and taro, oxalate is secreted as a main tolerance mechanism [11] [12]. On the other hand, there is also evidence that oxalate can work inside the cell. It may chelate Al in the cytosol and help transport the metal into the vacuole [6] [7]. This internal strategy may be more efficient in terms of carbon use, because it avoids the constant loss of carbon that happens when organic acids are exuded into the soil [2] [6].

Rice (*Oryza sativa* L.) is a major food crop. It feeds more than half of the world's population [13]. In Brazil, most rice is grown in rainfed systems where Al toxicity is a primary constraint to yield [5]. Studies have shown that there is wide genetic variation for Al tolerance among traditional rainfed rice varieties [5]. Still, the mechanisms that explain this variation are not fully understood.

Most research on Al tolerance in rice has focused on the exudation of citrate and malate [4] [15]. Compared with the external exclusion pathway, this internal mechanism remains poorly studied. The present work evaluated two upland rice cultivars with contrasting response to Al, namely Caiapó and Comum branco. The latter is a traditional, non-improved variety that has been grown by farmers for generations and is recognized as highly tolerant to Al. In contrast, Caiapó is a modern, improved cultivar developed by breeding programs for high yield and good adaptation to rainfed conditions, but it is not tolerant to Al [13].

The main objective was to investigate how oxalate is distributed between root cellular content and exudate under Al stress, an organic acid that has received little attention in previous studies. The distribution patterns of citrate and malate were also examined for comparison. An additional aim was to determine whether the oxalate distribution profile differs between the two cultivars. Unlike citrate and malate, which are rapidly exuded, oxalate may act as a delayed, energy saving internal chelator that accumulates progressively under prolonged Al stress. To investigate this, data from Zonta *et al.* [15] were examined with a focus on the distribution profile of oxalate and on the application of complementary multivariate approaches that were not explored in the original study.

2. Material and Methods

The experiment was carried out in a growth chamber located at the Soil Science Department of the Federal Rural University of Rio de Janeiro (Universidade Federal Rural do Rio de Janeiro, UFRRJ), located in Seropédica, Rio de Janeiro, Brazil. The chamber was set to a 12-hour photoperiod, irradiance of 300 μmol m^{-2} s^{-1}, and a temperature of 25 ± 2˚C. Two upland rice cultivars (*Oryza sativa* L.) with contrasting Al tolerance were used, namely the cultivars Comum branco (tolerant) and Caiapó (sensitive).

The experiment used a completely randomized design with two cultivars, two Al levels (0 and 160 μM), two harvest times (4 and 15 days) and two detection sites (root cellular content and exudate). This resulted in 16 treatment combinations, each with three replicates, totaling 48 experimental units. Oxalate, citrate and malate were measured from the same sample and treated as separate response variables, not as an additional factor in the design.

For each treatment combination, three independent replicates were used. Exudate and cellular content were collected from the same set of plants per replicate, and no sample pooling was performed across replicates.

Procedures for seedling growing in nutrient solution, sample collection, and calibration curves preparation followed Zonta [10]. The data analyzed here come from the experiment described by Zonta *et al.* [15]. The present analysis differs from the original study in its focus on oxalate distribution, its use of content to exudate ratios, and its application of principal component analysis (PCA) and correlation matrices.

For exudate collection, 200 mL of nutrient solution were taken at the beginning and at the end of each experimental period. Samples were concentrated in a rotary evaporator at 50˚C under vacuum, stored at 5˚C, and then macerated to extract the polar fraction [10].

Oxalate, citrate, and malate were quantified by high performance liquid chromatography (HPLC) using a Perkin Elmer system (Norwalk, CT, USA) equipped with a LC200 pump, an LC785A UV/VIS detector, and an ISS 200 autosampler. Separation was performed on an SUPELCOGEL C-610H ion exchange column (300 × 7.8 mm). The mobile phase was 0.1% phosphoric acid at 0.5 mL/min, and detection was carried out at 211 nm [10].

Concentrations are expressed as nmol per plant without biomass normalization. This choice was made because the study focuses on the relative distribution between compartments (content/exudate ratio).

Data were analyzed by factorial ANOVA using R version 4.5.0, with cultivar, Al, time and detection site as fixed factors. Each organic acid was analyzed separately. Descriptive statistics (means and standard deviations) were calculated for each treatment combination. Normality of residuals was checked with the Shapiro-Wilk test, and homogeneity of variances with Bartlett's test. When necessary, data were transformed to meet ANOVA assumptions. Means were compared using Tukey's test at $p < 0.05$. Multivariate analyses included Pearson's correlation matrix, principal component analysis (PCA: with variables centered and scaled), and multivariate analysis of variance (MANOVA) with Wilks' lambda. The content to exudate ratio was analyzed with a one-way ANOVA with cultivar and organic acid as factors. Cellular content and exudate were treated as independent observations because they came from different extraction procedures and were not paired at the plant level.

3. Results and Discussion

The analysis of variance showed that all main factors, including cultivar, Al concentration, time, detection site, and organic acid, as well as many of their interactions, were significant at $p < 0.05$. For oxalate, the factors cultivar ($p = 0.0007$), Al ($p = 0.0040$), time ($p = 0.0003$), and detection site ($p = 0.0006$) had significant effects. The interactions cultivar by detection site ($p = 0.0005$) and Al by detection site ($p = 0.0259$) were also significant. These results indicate that the concentrations of each organic acid varied with the experimental conditions and the response to Al was not the same for the two cultivars. The significant interaction between cultivar and detection site for oxalate ($p = 0.0005$) indicates that the distribution profile of this organic acid differs fundamentally between the two cultivars, a pattern not observed for citrate and malate.

The distribution of oxalate, citrate and malate between cellular content and root exudate after 15 days of exposure to 160 μM Al is shown in **Figure 1**. In the tolerant cultivar Comum branco, oxalate was much more concentrated inside the cells

(2105 nmol per plant) than in the exudate (810 nmol per plant). The ascending line in the graph clearly illustrates this preferential accumulation inside the root tissue. In the sensitive cultivar Caiapó, the distribution was more balanced, with 552 nmol per plant in the cellular content and 753 nmol per plant in the exudate. Thus, under Al stress, the tolerant cultivar had nearly four times more oxalate inside its root cells than the sensitive one. For citrate and malate, the pattern was reversed. In both cultivars, exudate concentrations exceeded cellular concentrations, and the difference was larger in Comum branco. Citrate in the exudate of Comum branco reached 10,791 nmol per plant, while its cellular content was only 5570 nmol per plant. For malate, the exudate concentration (4142 nmol per plant) was also higher than the cellular concentration (3106 nmol per plant). These findings agree with the well established role of citrate and malate as external chelators that bind Al^{3+} in the rhizosphere [1] [2]. The data are also consistent with the idea that oxalate participates in internal detoxification, while citrate and malate are mainly used for external exclusion [1] [3]. Recent work in rice has shown that oxalate accumulation inside root cells is associated with higher Al tolerance [4] [5].

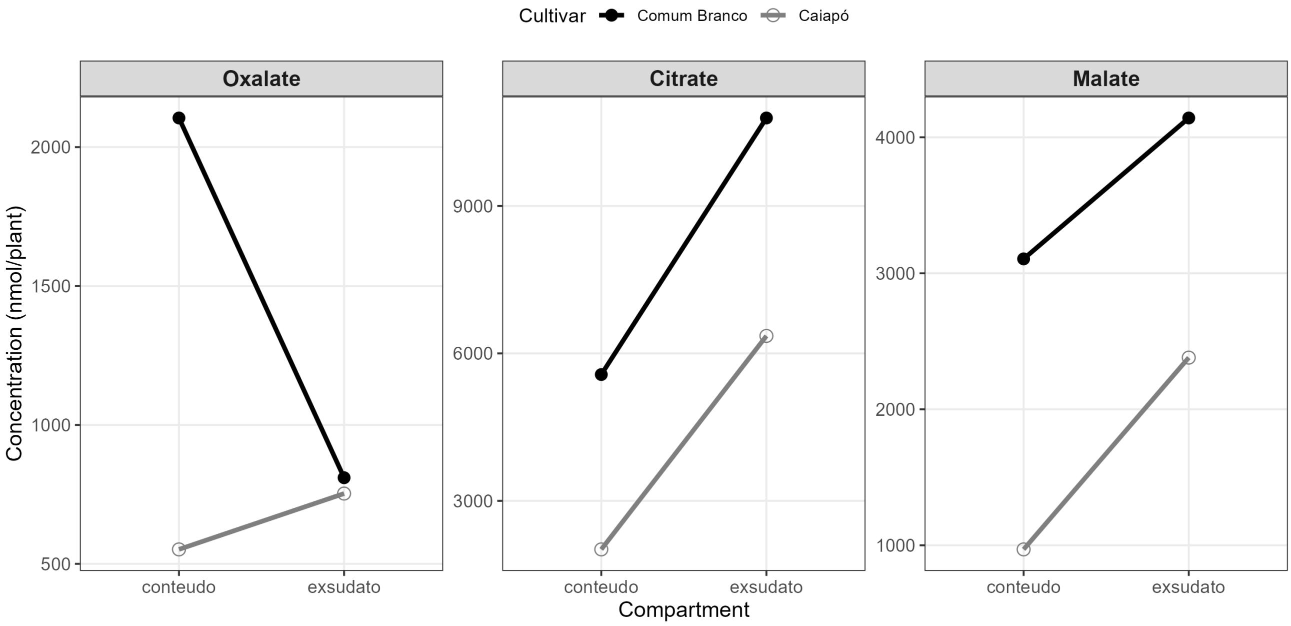


Figure 1. Concentrations of oxalate, citrate and malate (nmol per plant) in the cellular content and root exudate of the cultivars Comum branco (black circles) and Caiapó (open circles) after 15 days of exposure to 160 μM Al. Lines connect the two compartments for each cultivar.

The same information is summarized in **Figure 2** by the ratio between the concentration in the cellular content and that in the exudate. Only oxalate in Comum branco gave a ratio greater than 1, reaching 2.6. This value was significantly different from all other combinations ($p < 0.05$, Tukey test), all of which had ratios below 1. The ratio for oxalate in Caiapó was 0.73, for citrate in Comum branco 0.52, for malate in Comum branco 0.75, and for the two acids in Caiapó even lower. This result demonstrates that intracellular oxalate accumulation is specific response of the tolerant cultivar and is not observed in the sensitive one.

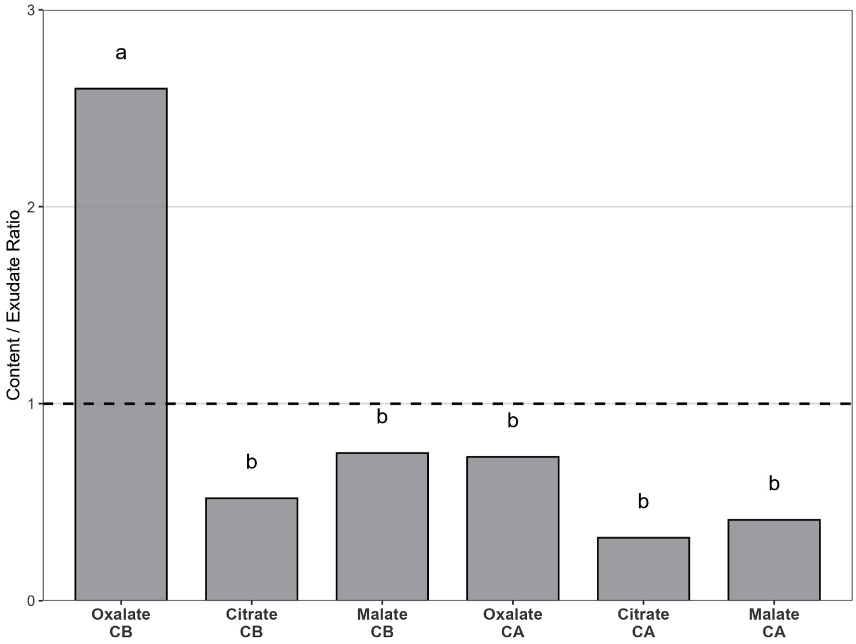


Figure 2. Ratio between concentrations of oxalate, citrate and malate in the root cellular content and exudate (content/exudate) of the cultivars Comum branco and Caiapó after 15 days of exposure to 160 µM Al. The dashed horizontal line indicates ratio = 1. Values above the line indicate preferential accumulation in cellular content. Values below the line indicate predominance in exudate. Different letters indicate significant differences by the Tukey test ($p < 0.05$).

The content to exudate ratio provides a direct measure of the preferential distribution of each organic acid. Values above 1 indicate intracellular accumulation, while values below 1 indicate predominance in the exudate. This metric allows direct comparison between acids with different absolute concentrations and synthesizes the information from Figure 1 and Figure 3 into a single value per treatment. Only oxalate in the tolerant cultivar Comum branco had a ratio above 1 (2.6), demonstrating that its intracellular accumulation is a specific response associated with Al tolerance. In contrast, the ratios below 1 for citrate and malate in both cultivars confirm that these acids are preferentially exuded, consistent with their role in external Al chelation.

The time course of the response is shown in Figure 3. Oxalate in the cellular content of Comum branco increased steadily from 1343 nmol per plant at 4 days to 2105 nmol per plant at 15 days. In Caiapó, the values remained almost unchanged, with 549 and 552 nmol per plant. This gradual rise in the tolerant cultivar indicates that oxalate accumulation is not an immediate response but builds up progressively under prolonged stress. In contrast, citrate and malate in the exudate of Comum branco increased sharply between 4 and 15 days, reaching 10,791 and 4142 nmol per plant, respectively. This fast and large exudation of citrate and malate is typical of an external exclusion mechanism that acts quickly after the onset of stress.

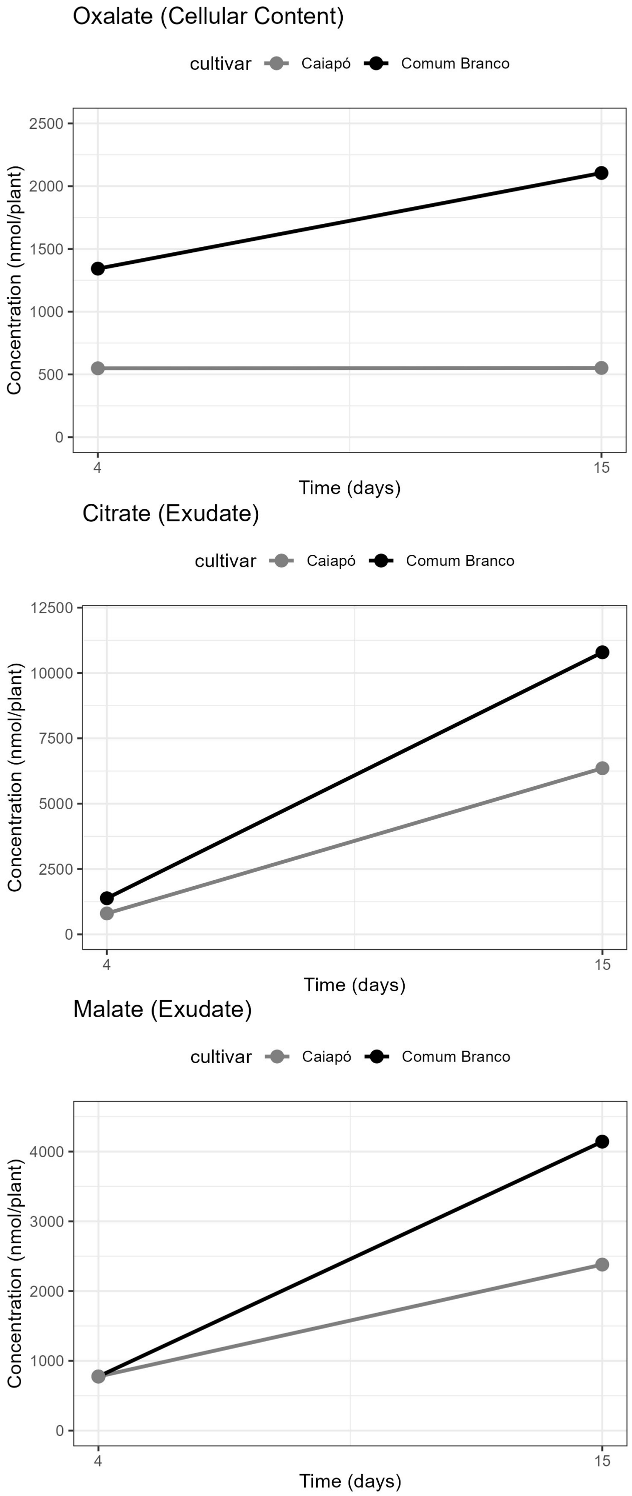


Figure 3. Concentrations of oxalate (cellular content), citrate (exudate) and malate (exudate) in cultivars Comum branco (black) and Caiapó (gray) after 4 and 15 days of exposure to 160 µM Al. Points and lines represent means of three replicates.

The tolerant cultivar Comum branco thus appears to employ two complementary strategies against Al. On one hand, it exudes large amounts of citrate and malate into the rhizosphere, which helps keep Al away from the root surface. On the other hand, it accumulates oxalate inside its root cells. Exudation of organic acids is energetically costly. Estimates suggest that under Al stress, plants can lose up to 15% of their photosynthetically fixed carbon through this pathway [2]. By storing oxalate inside the cell, the plant retains the carbon that it has invested. This carbon can then be used to form stable complexes inside the cell, likely in the vacuole [1] [3]. Such an internal strategy may be metabolically more economical, especially under longer periods of stress, as seen by the steady increase of oxalate in Comum branco over 15 days. The gradual rise in oxalate concentration in Comum branco, from 1343 nmol per plant at 4 days to 2105 nmol per plant at 15 days, contrasts with the rapid exudation of citrate and malate, which increased sharply between 4 and 15 days. This temporal difference suggests that oxalate accumulation is not an immediate response but rather a sustained, energy conserving mechanism that becomes increasingly important under prolonged stress. However, direct measurements of carbon costs or metabolic flux would be required to confirm this hypothesis.

Studies in other species, such as buckwheat and taro, have shown that oxalate can act both as an exuded chelator and as an internal sequestering agent [11] [12]. In rice, the fact that the tolerant cultivar accumulates oxalate inside its cells while the sensitive one does not suggest that this trait may contribute to the higher tolerance of Comum branco.

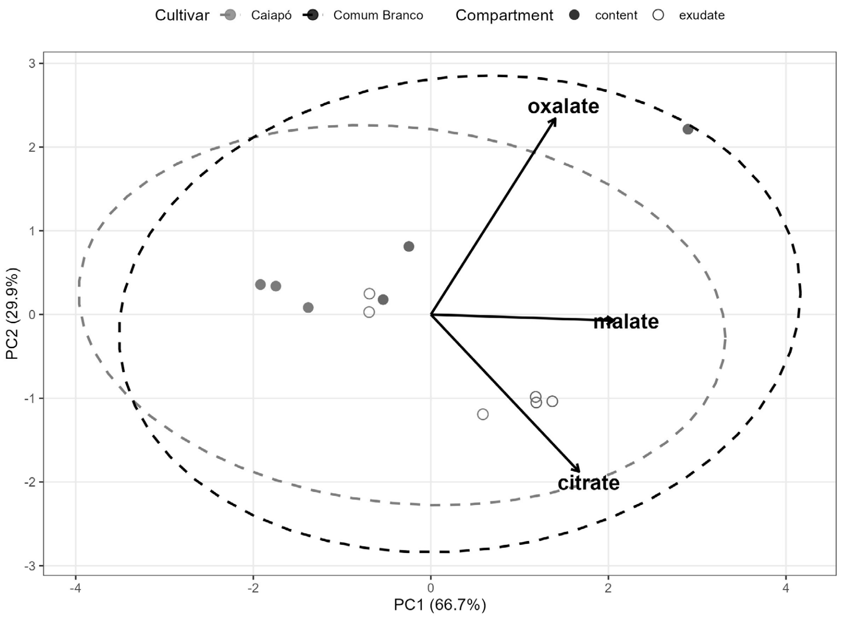
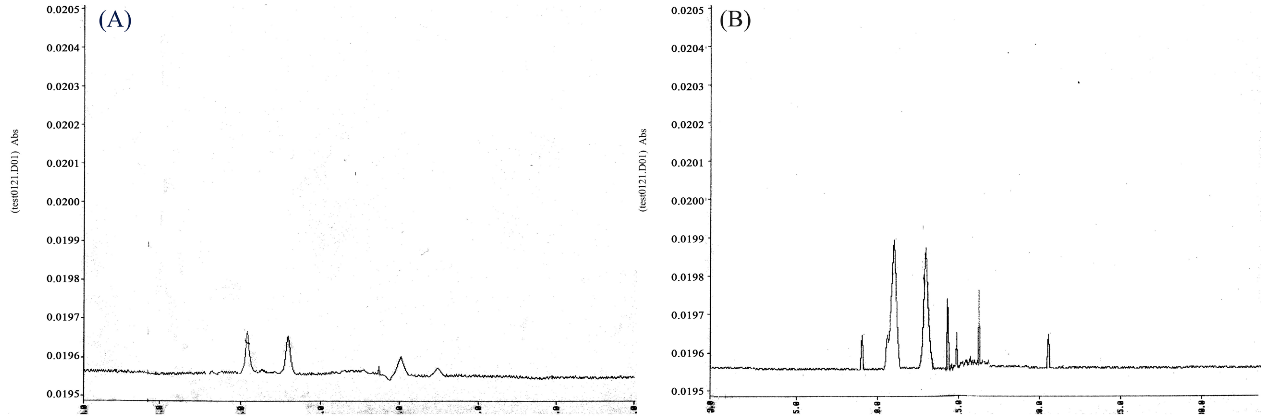


Figure 4. Principal component analysis of oxalate, citrate and malate concentrations. Points represent observations, colored by cultivar (Comum branco-black and Caiapó-gray) and with distinct shapes for cellular content (filled circle) and exudate (open circle). Ellipses indicate 95% confidence intervals for each cultivar. Vectors indicate the contribution of each organic acid.

The independence of oxalate from citrate and malate was further examined by principal component analysis, shown in **Figure 4**. The first two components together explained 97.9% of the total variance. The first component, PC1 with 79.4%, was dominated by citrate and malate, while the second component, PC2 with 18.5%, was dominated by oxalate. The oxalate vector was nearly perpendicular to the vectors of the other two acids. The two cultivars separated clearly along PC1, indicating that they differ fundamentally in how they integrate their response to Al. The perpendicular orientation of the oxalate vector suggests that changes in oxalate concentration are not closely linked to changes in citrate and malate. This reflects different biosynthetic routes. Citrate and malate are intermediates of the Krebs cycle, whereas oxalate can be formed through alternative pathways, such as ascorbate breakdown or the glyoxylate cycle [6] [7]. In addition, citrate and malate concentrations were strongly correlated, with a correlation coefficient of 0.854 ($p < 0.001$). Oxalate was weakly correlated with citrate ($r = 0.481$, $p < 0.001$) and moderately correlated with malate ($r = 0.604$, $p < 0.001$). These results confirm that the distribution profile of oxalate is distinct from those of citrate and malate.

The chromatographic profiles in **Figure 5** fully supported these findings. In the cell content of Comum branco, the oxalate peak increased markedly from 4 days (**Figure 5(B)**) to 15 days (**Figure 5(D)**), indicating progressive intracellular accumulation over time. Notably, the oxalate peak at 15 days was well resolved and symmetrical, suggesting not only increased accumulation but also metabolic stability of this organic acid under prolonged Al stress. In contrast, the oxalate peak at 4 days was smaller and broader, indicating a delayed activation of oxalate metabolism compared to citrate and malate. Although the absolute peaks of citrate and malate remained larger, the relative increase of oxalate from a small peak at 4 days to a substantially larger one at 15 days, highlights its role as an energetically economical internal detoxification strategy under prolonged Al stress. In Caiapó, there was no sizable accumulation of oxalate inside the cells at either time point (**Figure 5(A)** and **Figure 5(C)**), and the oxalate peak remained consistently small. These visual profiles provide direct qualitative confirmation of the quantitative results described above.



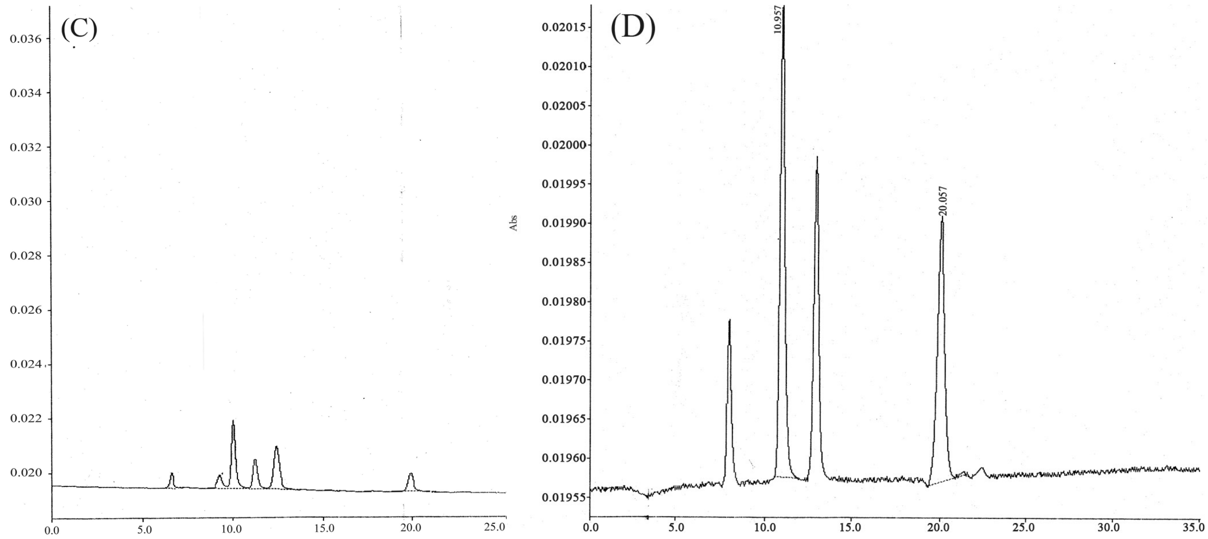


Figure 5. Representative chromatographic profiles of exudate and cellular content of the cultivars Comum branco and Caiapó subjected to 160 µM Al at 4 and 15 days of exposure. Peaks are identified by their respective retention times. Oxalate appears at about 8.5 minutes, citrate at about 10.5 minutes and malate at about 12.0 minutes. (A) Caiapó, 4 days; (B) Comum branco, 4 days; (C) Caiapó, 15 days; (D) Comum branco, 15 days.

The sensitive cultivar Caiapó did not show any increase in oxalate concentration under Al stress. Its breeding history may explain this absence. Caiapó was developed for high productivity and good adaptation to rainfed conditions, but it was not selected for Al tolerance [13]. During the selection process for yield and agronomic performance under favorable conditions, it may have lost alleles that are needed for oxalate accumulation. In contrast, Comum branco is a traditional landrace that has been maintained by farmers for generations. Its higher tolerance to Al may be linked to its ability to accumulate oxalate inside roots cells, a trait that was never deliberately selected against. Similar cases have been reported in the other crops, where breeding for yield under optimal conditions led to the loss of alleles that confer tolerance to abiotic stress [9] [14]. In rice, the ability to accumulate oxalate has been linked to the expression of genes involved in oxalic acid metabolism [4]. It is possible that this trait was unintentionally neglected in favor of performance under favorable conditions.

Although gene expression was not investigated here, transporters involved in internal Al detoxification have been described in rice. For example, OsALS1 moves Al into root vacuoles, and OsNIP1; 2 has been linked to Al distribution. What remains unknown is whether oxalate interacts with these transporters or whether its accumulation is related to their expression. Answering these questions will be important to confirm that oxalate plays a role in internal detoxification.

4. Conclusions

Oxalate showed a distribution profile that differed from those of citrate and malate. It accumulated inside the cells of the tolerant cultivar Comum branco, giving a content to exudate ratio of 2.6. In the sensitive cultivar Caiapó, no such accumulation occurred. Citrate and malate increased in the exudate of both cultivars, with larger increases in the tolerant one.

Principal component analysis placed oxalate on an independent axis (PC2), perpendicular to the vectors of citrate and malate. This finding supports the idea that oxalate is metabolically distinct, and it is backed up by chromatographic profiles.

The distribution profile of oxalate is not the same as that of citrate and malate. Intracellular oxalate accumulation is restricted to the tolerant cultivar. The absence of this response in the improved cultivar Caiapó suggests that trait may not have been fixed during genetic breeding. Furthermore, the progressive accumulation of oxalate over time, despite its lower absolute concentrations compared to citrate and malate, supports the interpretation that this internal detoxification pathway is energetically more economical and may be particularly advantageous under prolonged Al stress.

The interpretation remains a hypothesis. Direct functional validation, including metabolic flux analyses and molecular studies of transporters and biosynthetic enzymes, is needed to confirm it.

5. Future Perspectives

The present study revealed that oxalate accumulation in root cellular content is a specific response of the tolerant cultivar Comum branco. Gene expression analyses of enzymes involved in oxalic acid metabolism (e.g., oxalate oxidase, glyoxylate oxidase) are needed to understand the biosynthetic pathways underlying oxalate accumulation. Additionally, experiments under soil conditions are required to validate whether the patterns observed in hydroponic solutions are maintained in more realistic environments. Time course metabolic studies could help elucidate why oxalate accumulation is delayed compared to citrate and malate, and whether this delay reflects differences in gene expression, enzyme activity, or substrate availability.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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