ARTICLE ADDENDUM

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# Interactive regulation of nitrogen and aluminum in rice

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**Despite many studies on the high aluminum (Al) tolerance of rice (*Oryza sativa*), its exact mechanisms remain largely unknown. It is also unclear why Al improves growth of some plants. Our research on interactions between nitrogen (N) and Al may help to understand these phenomena. Previously, we found that ammonium-supplemented rice was more Al tolerant than nitrate-supplemented rice. Furthermore, Al-tolerant rice varieties preferred ammonium, while Al-sensitive ones preferred nitrate; in fact, Al tolerance was significantly correlated with the ammonium/nitrate preference among rice varieties. Al even enhanced growth of ammonium-supplemented rice, while it inhibited growth of nitrate-supplemented rice. Based on our own and other reports on N-Al interactions, we propose that intermediate products of N metabolism may play a role in rice Al tolerance. Al-enhanced ammonium utilization may explain why Al promotes growth of some plants, since Al often coexists with higher levels of ammonium than nitrate in acid soils.**

Aluminum (Al) toxicity is the primary factor limiting crop growth in acid soils. Rice (*Oryza sativa*) is considered as the most Al-tolerant crop among small grain cereals.[1] Most plants tolerate Al toxicity by secreting organic acids that immobilize Al ions in the rhizosphere,[2] whereas this mechanism cannot explain the high Al tolerance in rice.[1,3,4] Other Al-tolerance mechanisms (e.g., phosphate exudation from roots, and an increase in rhizospheric pH) are also not responsible for Al tolerance in rice.[5] The Al tolerance of rice has been altered by mutations of several genes, including those encoding a Cys2His2-type zinc-finger transcription factor, a bacterial-type ATP-binding cassette, and transporters of citrate, Al, or magnesium.[6] Cell wall polysaccharides play a role in excluding Al from the root apex and thus might play a role in rice Al tolerance.[4] However, these mechanisms are not sufficient to explain the high Al tolerance of rice, especially the genotypic differences in Al tolerance among cultivars. Our recent research on the interaction between Al and N yielded new information to increase our understanding of genotypic differences in Al tolerance.[7-9]

Previously, we demonstrated that ammonium alleviates Al toxicity to rice and *Lespedeza bicolor*, compared with nitrate.[7,8] A similar phenomenon was also reported for other plant species.[10-14] Recently, we found a significant correlation between Al tolerance and the ammonium/nitrate preference of rice varieties: Al-tolerant rice varieties showed a preference for ammonium while Al-sensitive ones showed a preference for nitrate.[9] We also note that rice is more Al-tolerant and shows a stronger preference for ammonium than other crops, while those crops that show a preference for nitrate, such as wheat and barley, are generally Al-sensitive. Tea trees also showed a preference for ammonium and enhanced growth in response to Al.[15,16] Thus, it seems that the ammonium/nitrate preference is associated with regulating Al tolerance in rice.

Why are two separate traits, Al tolerance and ammonium/nitrate preference, closely linked in plants? Is it a simple correlation, or something more complex? Acid soils are characterized by greater quantities of ammonium and potentially toxic Al compared with neutral soils, which generally contain more nitrate

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and less Al.[17] Therefore, we speculate that plants may have evolved some intercrossed mechanisms to adapt to Al toxicity and N nutrition collaboratively in acid soils. A recent microarray analysis of Al-responsive genes showed that genes encoding a nitrate transporter and nitrate reductase were upregulated in Al-tolerant wild-type rice but not in an Al-sensitive mutant.[6] This finding suggested that Al tolerance in rice is related to N uptake and assimilation. Moreover, functional disruption of the two nitrate transporters NRT1.8 and NRT1.5 decreased and increased cadmium tolerance, respectively, in *Arabidopsis thaliana*,[18,19] indicating an important role of nitrate in regulating metal tolerance. These results suggested that N processes such as N uptake and metabolism might be involved in regulating Al tolerance in rice. Several N intermediate products, nitrate, glutamate and NO, function as signaling molecules in regulating root growth and Al toxicity.[20-22] The rice varieties with different ammonium/nitrate preferences may have different types and amounts of N signaling molecules, which could result in differences in Al tolerance among rice varieties. As to the exact mechanism by which N regulates Al tolerance in rice, it remains to be investigated.

In our previous research, we observed that Al enhanced growth of ammonium-supplemented rice, but inhibited growth of nitrate-supplemented rice,[9] consistent with the results of similar studies on grasses and tropical trees.[11,23] Although toxic at high levels, Al at low levels can benefit the growth of some plant species, especially those native to acid soils.[24] Al can be used to increase antioxidant enzyme activity, prevent iron toxicity and deter herbivory in acid soils, all of which results in beneficial effects of Al on plant growth.[24] According to our results, we propose that another possible mechanism by which Al promotes growth is to improve ammonium utilization in the plant. There are two possible explanations for this mechanism: one is that competition among $Al^{3+}$, ammonium and ammonium-induced protons alleviates the toxic effects of ammonium and protons; the other is that Al affects the activity of N metabolic enzymes. Al activated chloroplastic glutamine synthetase in wheat and enhanced the expression of a gene encoding glutamine synthetase in rice.[25,26] However, in another study, Al inhibited the activity of nitrate reductase and glutamine synthetase, but enhanced the activities of other N metabolic enzymes in rice.[27] In spite of these inconsistent results, these reports suggest that Al might be involved in regulating N metabolism. More research is needed to explore in detail how Al affects N metabolism.

Based on the results of our own research and other studies, we propose that N signaling molecules produced during N uptake and assimilation may be involved in the Al tolerance of rice, and the regulation of N metabolism by Al may be one factor in the beneficial role of Al in some plants. The interactive regulation of N and Al seems to facilitate the growth of plants in acid soils.

## Disclosure of Potential Conflicts of Interest

The authors have no potential conflicts of interest to declare.

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