Recent progress on aluminium/silicon interactions in higher plants

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Introduction

Aluminium (Al) toxicity is an important factor in decreasing plant growth in both naturally occurring acid soils and in soils that are affected by acidic precipitation. The amelioration of Al toxicity by silicon (Si) under some circumstances is now a well established fact. It is nearly 25 years since the first paper in the "modern era" addressing Al/Si interactions in plants was published.[1] This paper, together with observations suggesting that Si could reduce Al toxicity in animal systems, led to a flurry of activity by plant scientists in the 1990s, which we documented in two reviews.[2,3] At the "2nd Silicon in Agriculture" conference in Japan in 2002, I was able to report that we knew more about the amelioration of Al toxicity by Si than we did about the effects of Si on any other abiotic stress.[4] Here we will confine our discussion to work on Al/Si interactions in higher plants in the last decade.

The Chemistry of Al/Si Interactions

The chemistry of Al/Si interactions in solution, at least in simple solutions, has become clearer in the last ten years. The use of equilibrium speciation models (e.g. EQ3NR), can predict the behaviour of Al and Si in growth solutions.[5] For example, the addition of 1000 µM Si to 100 µM Al solutions caused a reduction in Al^{3+} content between pH 4.0 and 5.0. At pH 4.0 Al^{3+} fell from 92.4 to 83.3% in the presence of Si; and at pH 5.00 the fall was from 54.6 to 17.7%. These falls were attributed to the formation of hydroxyaluminosilicate (HAS) species. HAS are believed to be non-toxic to plants, and their formation is thought to be at least partly responsible for the amelioration of Al toxicity by Si.

Uptake of Al and Si

There has been further advancement in determining the range of Al and Si contents in plants. In 1995 we asserted that, "very high Si accumulation and very high Al accumulation are mutually exclusive",[2] and there has been little to change this assumption. Comparing an analysis of Al accumulator plants[6] with a meta-analysis of the silicon contents of the shoots 735 plant species[7] strongly suggests that there are no extreme accumulators of both elements. The nearest to an exception so far reported is *Faramea marginata*, an Al accumulator in the Rubiaceae, which uses HAS to detoxify Al in its leaves, but it is only a moderate Si accumulator.[8] In the last decade there has been considerable progress in isolating transporters for both Si[9] and Al[10], but as yet the significance of this work to Al/Si interactions is unclear.

Amelioration of Al Toxicity by Si

There have been relatively few papers in the last ten years where the amelioration of Al toxicity by Si has been investigated at the whole plant level, probably because this had been intensively studied in the 1990's. However, we were able to demonstrate amelioration in a conifer[5], and probably the most comprehensive study ever was conducted on maize.[11]

Al/Si Codeposition

It is now clear that codeposition of Al with Si in solid phytoliths is a relatively widespread phenomenon in higher plants. The two areas where such codeposition has been most studied are in roots and in conifer needles.[12] In roots Al is often codeposited with Si in epidermal and cortical cells. Codeposition in the shoots of higher plants depends on two factors occurring together: the plant must have the capability to transport both Al and Si in reasonable quantities; and Al must be available for uptake from the soil.

Is there an *in planta* Component to Amelioration Effects?

Although it is now obvious that bulk external solution effects, and the formation of non-toxic HAS are often a key component in amelioration effects, it is equally certain that *in planta* phenomena are also often involved. In addition to the deposition of Al within phytoliths, there have also been cases where soluble HAS have been invoked in detoxification of Al in the leaves of *Faramea marginata*[8] and in the apoplast of the maize root apex.[11] Another approach has been to investigate Al/Si interactions in plant suspension cultures of Norway spruce.[13] Again the results strongly suggested that the formation of HAS in the cell walls led to increased Al tolerance.

Conclusions

There is little doubt that there has been less work on Al/Si interactions in the last ten years. The reasons for this are not entirely clear, but may be related to difficulties in applying work carried out in simple solutions in the laboratory to much more complex field situations. Although Si is sometimes invoked as one factor in decreasing Al toxicity in soil experiments, it is frequently one among many.[14] It may also be that workers in this area reached the limits of the available technology. With the discovery of both Al and Si transporters in plants a new phase of investigations into Al/Si interactions should be possible.

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