Arsenic efflux and its role in As tolerance in As-hyperaccumulators

Masayoshi Hatayama*
Graduate School of Environmental Studies, Tohoku University, Japan

The efflux of arsenic (As) is a critical step in the detoxification of As in plants. In hyperaccumulator species, the efflux of As is primarily mediated by thiol transferases, such as glutathione-S-transferase. This process is crucial for the survival of these plants under As-stress conditions. The efflux of As from the root cell is known to be effective for AsIII detoxification, which is a dominant As species in the shoot of hyperaccumulator plants.

Since much toxic AsIII is a dominant As species in the shoot, compartmentalization of AsIII in the shoot cell is considered one of the possible mechanisms of detoxification of AsIII in P. vittata. Energy dispersive X-ray microanalyses (EDXA) of frond cells has shown that a part of As is localized in the subcellular compartment, which corresponds to a vacuole in epidermal cells [16]. For gametophytes, AsIII was clearly localized in the vacuolar lumen, whereas AsV was possibly moved into the cytosol [17]. Further, the AsIII membrane transport protein, (tonoplast intrinsic protein) TIP, which directly transports AsIII into the vacuolar lumen, was isolated and characterized [18]. However, the expression of the AsIII transporter was limited to root tips when exposed to As and no expression was observed in the shoot. Thus, the compartmentalization of AsIII into the vacuole might not be the best of the adaptive strategies for As tolerance by the frond cell of P. vittata.

AsIII efflux from the root cell is known to be effective for AsIII detoxification. The role of AsIII efflux for As detoxification is significant in the A. thaliana root. In this plant, AsV taken up by the roots almost exits the root as an AsIII species within 24 hrs [19]. Additionally, a membrane transport protein of the aquaporin family, which is responsible for AsIII efflux in the root of A. thaliana, is localized 1 on the plasma membrane of root tips [18]. It might be possible that AsV, which was taken up by Pt transporters, pH1:1 and pH1:4 [20] in A. thaliana were efficiently reduced to AsIII in the root cells and excreted to the external environment. For As-hyperaccumulators, AsIII efflux was also observed, but at a lower rate by comparison with non-hyperaccumulators such as A. thaliana [21,22]. Additionally, the excretion of AsV has been observed in As hyperaccumulators. However, AsV efflux is also lower in As-hyperaccumulators. The low efflux of AsIII and AsV contributes to the As accumulation in the plant and most of the incorporated As is efficiently translocated (loaded) to the shoot. The idea of As efflux from a cell can be extended to shoot cells, not only to the root. AsIII efflux is conserved among various plants such as rice [23], tomatoes [24], and rootless duckweed [25]. If As is excreted from the shoot cell, this could be helpful for As detoxification. This speculation is supported by the results from the suspension cell culture of P. vittata. A callus exhibited approximately three times more As accumulation than A. thaliana callus [26]. However, maximal accumulation of the cell cultures in this study seemed to be around 1,000 mg/kg DW, while the entire plant of P. vittata can accumulate a maximum of 22,630 mg/kg DW of As [15]. Based on this observation, As tolerance by the pinna cells is lower than the maximum accumulation exhibited by the entire plant. It is also clear that high tolerance to...
oxidative stress is one of the significant factors for AsIII tolerance in *P. vittata*. Singh et al. found a higher tolerance from oxidative damage for *P. vittata* than for other non-hyperaccumulating ferns when exposed to As [27], which was not as high as expected, however, based on the differences in As accumulation between the hyperaccumulators [15] and non-hyperaccumulators.

When we consider the AsIII efflux from the pinna cell, it seems there is no AsIII efflux to the apoplastic space, since there is no significant accumulation in the cell wall and in the apoplastic fluid [16]. Thus, the efflux of AsIII to the phloem of the companion cell is suggested. There are a few reports of the phloem transport of As. In the Castor bean, As was detected in the phloem sap [28], and, in rice, the phloem transport of As from the flag leaf to the grain was observed [29], but the As species accumulated in those examples were not AsIII. Also, there is a difference in As accumulation between the young and the mature frond. The lower As-accumulation in the frond could be a sink for the As expected from the source frond. Further research at the cellular level and in the behavior of As at the whole plant level should be conducted in the future.

**References**