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

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Arsenic (As) disturbs the primary metabolism of an organism, which is detrimental [1]. For that reason, organisms have evolved various mechanisms of As tolerance such as extrusion, intracellular compartmentalization, repression of transporters, and a high tolerance to reactive oxygen species and it is important to understand the mechanisms to conquer its toxicity.

An As-hyperaccumulator, *Pteris vittata*, is a type of plant that is able to accumulate 100 times more As than normal plants or organisms that use the normal mechanisms mentioned above for As tolerance. The fern not only tolerates As in very high concentrations, but also predominantly accumulates it in the form of arsenite (AsIII), which is a more toxic form of the As oxyanion. The accumulation level of non-hyperaccumulators differs from those of non-hyperaccumulating organisms. However, each of the known mechanisms for As tolerance have been observed in various degrees or in certain parts of As-hyperaccumulators, and it is not clear which strategy or combination thereof is most effective for the tolerance of As by a plant.

In ancient times, when the primitive earth had no oxygen and was under reductive conditions, it was assumed that bacteria first developed and acquired a tolerance to AsIII, which predominates under reductive conditions. Tolerance is achieved by exporting such toxic AsIII from a single cell. For example, in *Sinorhizobium meliloti*, AsIII is excreted from the cell via aquaglyceroporin, AqpS [2], and the tolerance system for arsenate (AsV), such as AsV reductase is considered to be acquired under latter oxidative conditions. Unlike bacterium, eukaryotic cells have no intercellular organs, such as plastids or vacuoles (lysosomes), in which to compartmentalize As. In the *Saccharomyces cerevisiae* system, AsIII is conjugated using a thiol compound, glutathione (GSH), and either sequestered into the vacuolar lumen as an As-(GS)3 complex or excreted from the cell by AsIII transporters as with bacteria [3].

For plants, inorganic As species AsV and AsIII, and organic forms of As such as MMA and DMA, are available from the soil [4]. Of those, AsV is the dominant species incorporated into plants via the phosphate (Pi) transport pathway, as AsV is a chemical analogue of Pi. The subsequent metabolism of AsV by terrestrial plants has been studied [5]. Similar to *S.cerevisiae*, after the incorporation of AsV into the cell, AsV is transformed to AsIII by AsV reductase. AsIII is simply excreted from the cell via aquaporin [6,7] or conjugated either by GSHs or phytochelatins in the plant [8]; then, it is likely sequestered into the vacuolar lumen by glutathione-S-transferase [9]. In a similar manner, several plants produce thiol compounds for the detoxification of AsIII [10,11] or repress the AsV uptake system by the roots [5,11]. In aquatic plants, an increase in thiol compounds has been observed in response to As exposure and a similar mechanism could be considered for As detoxification [12,13].

However, in the As-hyperaccumulating plants, the role of thiol 1 compounds for AsIII detoxification is considered to be very small [8,14]. As species in those plants and the behavior of As in the plant body is distinct from that in other plants. Normally, As accumulation in plants mostly range from 5-100 (Kabata-Pendias and Pendias, 1992) and mostly less than 1 mg/kg in the leaf. In those particular plants, As accumulation was 100 times more than normal plants with an accumulation of the most-toxic AsIII found at the shoot [15].

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 Pi transporters, pht1:1 and pht1:4 [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

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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 1 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.

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