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SELENIUM ACCUMULATION IN
PLANTS—PHYTOTECHNOLOGICAL APPLICATIONS
AND ECOLOGICAL IMPLICATIONS

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Selenium (Se) is an essential trace element for many organisms including humans, yet toxic at higher levels. Both Se deficiency and toxicity are problems worldwide. Since plants readily accumulate and volatilize Se, they may be used both as a source of dietary Se and for removing excess Se from the environment. Plant species differ in their capacity to metabolize and accumulate Se, from non-Se accumulators (<100 mg Se/kg DW), to Se-accumulators (100–1000 mg Se/kg DW) to Se hyperaccumulators (>1,000 mg Se/kg DW). Here we review plant mechanisms of Se metabolism in these various plant types. We also summarize results from genetic engineering that have led to enhanced plant Se accumulation, volatilization, and/or tolerance, including field studies. Before using Se-accumulating plants at a large scale we need to evaluate the ecological implications. Research so far indicates that plant Se accumulation significantly affects the plant’s ecological interactions below and above ground. Selenium can protect plants from fungal pathogens and from a variety of invertebrate and vertebrate herbivores, due to both deterrence and toxicity. However, specialist (Se-tolerant herbivores), detritivores and endophytes appear to utilize Se hyperaccumulator plants as a resource. These findings are relevant for managing phytoremediation of Se and similar elements.

KEY WORDS: transgenics, phytoremediation, hyperaccumulation, plant-animal interactions, plant-microbe interactions

INTRODUCTION

Selenium (Se) is an element that naturally occurs in the earth’s crust, particularly in certain sediments such as Cretaceous shale (Kabata-Pendias 1998). Selenium is toxic at elevated levels, as may be clear from the fact that the maximal allowable Se concentration in drinking water in the USA is only 50 (µg/L). When seleniferous soils are used for agriculture, Se is mobilized and can accumulate in soils due to evapotranspiration and leach out into agricultural drainage water (Terry et al. 2000; Lin and Terry 2003). Once Se reaches surface waters it can get further concentrated through evaporation, creating levels that are toxic to biological organisms such as birds and fish (Ohlendorf et al. 1986). In addition to Se entering surface waters from seleniferous soils, the use of Se-rich coal
or oil may release Se into the environment (Hansen et al. 1998). Another source of Se toxicity is hyperaccumulator plants: these natives to seleniferous soils typically accumulate Se to levels between 0.1 and 1% of their dry weight (Beath et al. 1939). Ingestion of hyperaccumulators by mammals may lead to acute or chronic toxicity—selenosis (Draize and Beath 1935). Selenosis is a problem in many areas worldwide, particularly in the Western United States and parts of China (Wilber 1980).

While toxic at higher levels, Se is also an essential element for many organisms including mammals, many bacteria, and certain algae (Fu et al. 2002; Novoselov et al. 2002). For higher plants, however, Se has not been shown to be essential, and it is thought that essential Se metabolism may have gotten lost in this taxonomic group (Zhang and Gladyshev 2010). The reason why Se is essential for certain organisms is because they incorporate selenocysteine (SeCys) in so-called selenoproteins, which invariably have antioxidant functions. Selenium deficiency may lead to male infertility as well as enhanced susceptibility to cancer and viral infections (Diwadkar-Navsariwala et al. 2006). Like Se toxicity, Se deficiency is a problem worldwide, e.g. in the Eastern United States, Europe, Australia, and certain parts of China (Zhu et al. 2009).

The toxicity and deficiency problems associated with Se may be alleviated through the use of plants. All plants readily take up Se and accumulate it in all their organs. Some plants even hyperaccumulate Se to percent levels, as mentioned above. Plants can also convert the ingested Se into volatile forms, and release it into the atmosphere (Lewis et al. 1966). For the cleanup of Se-containing soil or water, both accumulation and volatilization are attractive plant properties. Plants may be grown as crops to reduce Se levels in soils, or in constructed wetlands to clean up agricultural or industrial wastewater (Hansen et al. 1998; Lin and Terry 2003). For battling Se deficiency, it may be feasible to use Se-containing plant material as animal feed or human food—after proper dilution to non-toxic levels, and provided no other harmful elements are present in the material. Thus, plants may be grown to clean up excess Se from one area while providing a source of essential Se for other areas, an attractive perspective. In order to optimize the capacity of plants to accumulate or volatilize Se, and to produce the most nutritious forms of Se, it is important to know the metabolic fate of Se in different plant species. Once we know pathways of Se metabolism and rate-limiting steps in these pathways we can try to speed up specific processes and tailor plants to our phytoremediation and biofortification (method of breeding or otherwise engineering plants to increase their nutritional value) needs. In the next section we will summarize our current knowledge on Se metabolism in non-hyperaccumulator and hyperaccumulator plants.

**What can Plants do with Se, and how are Hyperaccumulators Different?**

Selenium is chemically similar to sulfur (S), and enzymes that function in S-related pathways generally readily metabolize Se analogs of their S substrates (Anderson 1993). This non-specific Se metabolism leads to incorporation of Se in all S metabolites, replacing S with Se. As shown in Figure 1 (and reviewed by Sors et al. 2005) selenate (the most abundant bioavailable form of Se in soils) is taken up via sulfate transporters, reduced to selenite and selenide, and combined with O-acetylserine to form selenocysteine (SeCys). SeCys can be further metabolized to Se-cystathionine, Se-homocysteine, and selenomethionine (SeMet), respectively.
Both SeCys and SeMet can get non-specifically incorporated into proteins, replacing Met and Cys. This is particularly toxic in the case of SeCys, since the thiol residue of Cys is generally important for protein structure and function. SeCys can also be broken down into selenide and alanine, or it can be methylated to methyl-SeCys. This latter mechanism is particularly active in hyperaccumulator species, which accumulate Se mainly as methyl-SeCys (Neuhierl et al. 1999; Freeman et al. 2006a). Storing Se as methyl-SeCys is an important mechanism of Se tolerance since methyl-SeCys does not get incorporated into proteins.

In hyperaccumulators methyl-SeCys can be further metabolized to dimethyldiselenide (DMDSe) which is volatile. Non-hyperaccumulators also volatilize Se, via a different pathway: they volatilize dimethylselenide (DMSe) using SeMet as a starting point (Terry et al. 2000). When supplied with selenate, non-hyperaccumulators accumulate Se mainly as selenate with a minor fraction (~5%) as organic Se (C-Se-C) (de Souza et al. 1998), and the highest Se levels are found in the vascular tissues (Freeman et al. 2006a). Hyperaccumulators, on the other hand, accumulate Se mainly as methyl-SeCys (a C-Se-C compound) in their leaf hairs or in the vacuoles of epidermal cells (Freeman et al. 2006a). Thus, cellular metabolism and tissue sequestration patterns are different between non-hyperaccumulators and hyperaccumulators.

Hyperaccumulators are also different in that they preferentially take up selenate over sulfate and tend to translocate more Se to the shoot; thus hyperaccumulators have a higher Se/S ratio than non-accumulators, and a higher shoot/root Se concentration ratio (Galeas et al. 2007). Selenium partitioning also appears to be different between hyperaccumulators and non-hyperaccumulators. Hyperaccumulators partition Se preferentially to young leaves and reproductive tissues (flowers, seeds) while non-accumulators do not. Hyperaccumulators show a different seasonal flux in Se levels over the year compared to non-accumulators. In addition, seasonal flux in Se levels is different than S fluxes in hyperaccumulators (Galeas et al. 2007). Therefore, hyperaccumulators appear to be able to distinguish selenate from...
sulfate and perhaps organic selenocompounds from their sulfur analogues, while non-accumulators cannot.

Not only can hyperaccumulators discriminate between Se and S, but they show different accumulation and partitioning for Se and S. It is intriguing to speculate what could be the underlying mechanisms for these phenomena. Perhaps hyperaccumulators have evolved specialized transporters for various selenocompounds, from transporters that originally transported S homologues (e.g., after a gene duplication event). While there is circumstantial evidence for Se-specific metabolism, at this point there is no direct evidence of any Se-specific transporters or enzymes in hyperaccumulators. The finding that hyperaccumulators contain higher levels of S as well as Se compared to non-hyperaccumulators suggests that hyperaccumulators also appear to have constitutive upregulation of certain non-specific S/Se transporters and enzymes (Verbruggen et al. 2009).

As mentioned above, while many animals and bacteria, as well as certain green algae (Fu et al. 2002) have been shown to require Se as a trace element, to this date there is no convincing evidence for the presence of selenoproteins in higher plants, and thus plants do not appear to need Se as an essential element (Anderson 1993). Nevertheless, Se has been shown to be beneficial for the growth of many plant species, both non-accumulators and hyperaccumulators (Pilon-Smits et al. 2009). This may be because Se enhances plant antioxidant capacity, either directly due to antioxidant activity of selenocompounds or to induction of plant antioxidants by Se (Hartikainen 2005). Hyperaccumulators show the strongest positive growth response to Se of all plants tested (Broyer et al. 1972), yet no physiological requirement for Se has been demonstrated.

Hyperaccumulators do, however, appear to have an ecological need for Se in their natural habitat, as suggested by the fact that they occur exclusively on seleniferous soils (Beath et al. 1939). From such soils, hyperaccumulators bioconcentrate Se from a few mg Se/kg up to levels of 10,000 mg/kg, thus 1000–10,000 fold. There is also evidence that hyperaccumulator roots show positive chemotropism for Se by seeking and directing their root growth toward Se-rich pockets (Goodson et al. 2003; Galeas et al. 2007). Seasonal fluxes of Se in hyperaccumulators indicate that these perennials store Se in their roots during the winter, translocate Se in the spring to the developing leaves, and remobilize it from older leaves to younger leaves and reproductive tissues in the summer. In the fall, the Se is stored in the seeds and the remainder remobilized to the root (Galeas et al. 2007). Thus, Se hyperaccumulators appear to accumulate and remobilize Se on purpose. The functional significance of hyperaccumulation may in part be a growth-promoting physiological effect but, more importantly, appears to be protection from herbivores and pathogens (Galeas et al. 2007; Quinn et al. 2008), as we describe in one of the next sections. But first we will summarize results from genetic engineering approaches to study and manipulate Se metabolism in plants.

**Use of Genetic Engineering to Study and Manipulate Se Fluxes in Plants**

Several approaches have been used to study and manipulate Se (and S) metabolism in plants (Figure 2). These have been reviewed recently (Pilon-Smits and LeDuc 2009) and will be summarized here. The first enzyme of the sulfate/selenate assimilation pathway, ATP sulfurylase (APS), was overexpressed in Indian mustard (*Brassica juncea*), resulting in increased Se tolerance and accumulation, and enhanced reduction of selenate to organic Se (Pilon-Smits et al. 1999). Overexpression in Indian mustard of cystathionine-γ-synthase
Figure 2  Overview of genetic engineering approaches that have been used to modify plant Se tolerance, accumulation and/or volatilization. Overexpression of the key enzyme of sulfate/selenate assimilation, ATP sulfurylase, led to enhanced Se tolerance and accumulation in *Brassica juncea*. Overexpression of cystathionine-γ-synthase, the first enzyme involved in the conversion of (Se)Cys to volatile DMSe/DMS led to enhanced Se volatilization, reduced accumulation and enhanced tolerance in *B. juncea*. Introduction of SeCys methyltransferase from hyperaccumulator *Astragalus bisulcatus* in *B. juncea* or *Arabidopsis thaliana* led to enhanced Se accumulation, tolerance and volatilization, and introduction of a mouse selenocysteine lyase into *B. juncea* or *A. thaliana* resulted in enhanced Se accumulation and tolerance.

(CγS), the first enzyme mediating the conversion of SeCys to volatile Se resulted in enhanced Se volatilization, reduced Se accumulation, and enhanced Se tolerance (van Huysen et al. 2003). Since both APS and CγS function in sulfate assimilation, these results confirm that Se is metabolized via S pathways. The results also show that these enzymes are rate-limiting for selenate reduction and volatilization, respectively. In other studies, enzymes with novel activities were introduced and their effects on Se metabolism studied. In one study, selenocysteine lyase (SL) from a mouse was introduced, which specifically breaks down SeCys (but not Cys) into alanine and selenide. This led to enhanced Se tolerance and accumulation in *Arabidopsis thaliana* and Indian mustard (Pilon et al. 2003; Garifullina et al. 2003). Later, overexpression of an *A. thaliana* homologue of the mouse SL gene (AtepNifS) gave similar results (Van Hoewyk et al. 2005). In another study, a SeCys methyltransferase (SMT) from a hyperaccumulator species (*Astragalus bisulcatus*) was introduced into *A. thaliana* and Indian mustard, which led to enhanced Se tolerance, accumulation and volatilization (Ellis et al. 2004; LeDuc et al. 2006).

The different Indian mustard transgenics were tested for their Se phyto-extraction capacity on Se-polluted sediment in the field. The APS transgenics showed 4–5-fold higher Se accumulation in the field than wildtype plants (Bañuelos et al. 2005) and the SL and SMT plants showed ~2-fold higher Se accumulation (Bañuelos et al. 2007). Combining APS and SMT (by crossing the transgensics, obtaining double-transgenics) even resulted in 9-fold higher Se accumulation in laboratory studies; these have not yet been tested in the field (LeDuc et al. 2006). In summary, it is possible to manipulate Se metabolism in plants and obtain plants with more favorable properties for Se phytoremediation, via phyto-extraction and phyto-volatilization as well as enhanced tolerance. If Se is the only pollutant accumulated by the plant, the resulting Se-containing plant material may also have enhanced nutritional value, if diluted with low-Se food to healthy levels (Lyons et al. 2003).
Plant Herbivore and Higher Trophic Level Interactions

Plant Se accumulation may affect the plant’s ecological interactions, as outlined in Figure 3. Better knowledge of these ecological effects of Se accumulation by plants may shed light on the functional significance of Se accumulation, selection pressures that have driven the evolution of hyperaccumulation, as well as practical implications of growing Se-rich plants for phytoremediation. Multiple explanations have been proposed for the functional significance of Se hyperaccumulation, such as metal tolerance, drought resistance, plant allelopathy, and as a defense against herbivores and pathogens—also known as the elemental defense hypothesis (Boyd et al. 2007). Selenium concentrations in Se accumulators and hyperaccumulators are toxic to a wide variety of herbivores and pathogens. Most research investigating the functional significance of hyperaccumulating plants has lent support to the elemental defense hypothesis (for a review see Boyd et al. 2007). Brassica juncea, often used for elemental phytoremediation, was shown to be protected from fungal pathogens in leaves because of elevated Se levels (Hanson et al. 2003, 2004). Other plant herbivores such as aphids, white cabbage butterfly larvae, and prairie dogs (native to the Western United States and coevolved with Se hyperaccumulator) were also deterred by elevated Se levels (Quinn et al. 2008). In large scale phytoremediation field trials Bañuelos et al. (2002) found that B. juncea with elevated Se was protected from cabbage looper larvae (Trichoplusia ni) and that saltbrush with elevated Se (Atriplex spp.) was protected from beet armyworm larvae (Spodoptera exigua); both of these generalist Lepidoptera herbivores are important agriculture pests that feed on a variety of crop species. Stanleya pinnata (a Se hyperaccumulating plant), with elevated Se suffers less Orthoptera, Lepidoptera and prairie dog herbivory than S. pinnata with low-Se concentrations (Freeman
et al. 2006b, 2007, 2009; Quinn et al. 2008). *Astragalus bisulcatus*, another Se hyperaccumulating species, is also protected from a variety of herbivores and is toxic to livestock (Rosenfield and Beath 1964; Quinn et al. 2008). Many generalist herbivores avoided high-Se plants in choice laboratory studies, possibly using pungent volatile Se as a cue to identify toxic high-Se plants. A field study in 2008 provided more support for the elemental defense hypothesis by demonstrating that Se hyperaccumulating plants harbored fewer arthropods and fewer arthropod species than comparable non-Se hyperaccumulating plants growing in the same seleniferous habitat (Galeas et al. 2008). Selenium hyperaccumulation plants also store Se in tissue and organs that are venerable to attacks, possibly as a defensive strategy. *Stanleya pinnata* stores Se in the periphery of leaves and in epidermal cells; *A. bisulcatus* stores Se primarily in trichomes, which are often associated with a defensive function.

Since elevated Se protects plants from a wide range of generalist herbivores it likely provides a niche for Se tolerant species. A population of diamondback moth (*Plutella xylostella*) collected from a population of *S. pinnata* was shown to have developed Se tolerance and readily accumulated high concentrations of Se. Another population of diamondback moth, collected from a non-seleniferous habitat, developed slower and suffered 100% mortality rates when fed Se enriched plant material. The Se sensitive diamondback moth accumulated toxic SeCys, which is easily incorporated into important S proteins, while the Se tolerant diamondback moth accumulated MeSeCys, which is not as toxic because it is not as easily incorporated into proteins. This finding, of a Se-tolerant and Se-accumulator herbivore, raises the question, how does Se affect multiple trophic levels? Do specialist herbivores of Se hyperaccumulators form a portal of Se into the local ecosystem? An example of Se movement across trophic levels was found in the Se tolerant population of diamondback, which harbored the parasitic wasp *Diadegma insulare*. This parasitic wasp accumulated Se to similar levels as its host, and the Se tolerance of the parasite was explained by the accumulation of methylselenocysteine, similar to the host plant and the diamondback moth (Freeman et al. 2006b). In a different study on the effects of Se at higher trophic levels, the generalist predator *Podisus maculiventris*, developed slower and had higher mortality rates when fed Lepidoptera larvae with elevated Se compared to *P. maculiventris* fed with low-Se Lepidoptera larvae (Vickerman and Trumble 2003). Thus, it appears that Se accumulating plants are protected from generalist herbivores but offer a niche to Se-tolerant specialist herbivores. Similarly, Se-tolerant herbivores may be protected from generalist predators or parasites but offer a niche to Se-tolerant predators or parasites.

These findings have important implications for the management of Se phytoremediation. Owing to its toxicity and deterrence, Se can be used as a natural pesticide when growing Se-rich plants. However, it is likely that some species will develop Se tolerance creating a gateway for Se to enter other components of the ecosystem.

**Effects of Plant Se on Plant–Pollinator Interactions**

To date little is known about how elevated Se effects plant pollinator interactions. As more studies demonstrate that Se is toxic to generalist herbivores concern has increased about the potential of Se toxicity to pollinators, particularly honeybees. Flowers of many plants readily accumulate Se. *Brassica juncea* flowers grown with Se accumulate 250 mg Se kg⁻¹, compared to 350 mg Se kg⁻¹ in the same plants leaves. Selenium hyperaccumulators *S. pinnata* and *A. bisulcatus* store more Se in flowers than in leaves, and flowers can contain upwards of 1% Se. Since these concentrations of Se are toxic to many herbivores
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it may be assumed that they are also toxic to pollinators. A recent article published in an online affiliate of the Discovery Channel expressed concern about the effects increased Se concentrations in pollen and nectar have on bees used for pollination in the seleniferous central valley of California, USA (Reily 2009). Plant-pollinator studies are needed to investigate the effect of Se on pollinator visits and pollinator health. It is possible that Se deter generalist pollinators, which would affect the seed production of the Se-rich crop but not neighboring crops. It is also possible that Se does not deter pollinator visits, and that the Se has a toxic effect on the generalist pollinators. This would reduce pollinator abundance and therefore crop productivity throughout the area. Another possibility is that pollinators are not deterred and that the levels accumulated in the pollinators is low enough to not be harmful or to even protect the pollinator from disease or predation. Also, similar to what was found for specialist herbivores, it is possible that Se-tolerant pollinators exist or evolve that can forage on high-Se plants, enjoying reduced competition and perhaps profiting from the accumulated Se. In the future Se-pollinator interactions may shed light on these questions and may even provide a model to study symbiotic relationships. Preliminary studies have shown that honeybee and other pollinator visits are the same in frequency and duration on *B. juncea* with elevated Se compared to *B. juncea* with low Se (Quinn and Pilon-Smits unpublished results). The effects of Se on plant-pollinator interactions deserves further exploration and will provide managers of Se phytoremediation sites with valuable information.

**Effects of Plant Se on Plant-Microbe Interactions**

Selenium accumulation in plants can be affected by belowground interactions with microbes (de Souza et al. 1999; Di Gregorio et al. 2006). Plant-microbe interactions in Se hyperaccumulators can range from pathogenic to symbiotic (Rogerson 1957; Wangelin and Reeves 2007), and such interactions appear to be strongly influenced by the distribution and accumulation of Se across the plant tissues. The difference in distribution and levels of selenium across the plant determines the type of microbial interactions and contributes to the development of different microbial niches (Figure 4). Each niche is determined by the ability of a microbe to metabolize and tolerate the levels of selenium in a particular part of the plant. Belowground interactions may involve root endophytic fungi (filamentous, dark septate and mycorrhizal fungi), root surface (rhizoplane) fungi, rhizospheric fungi and bacteria, and nitrogen fixing bacteria associated with root nodules. Aboveground interactions may involve endophytic fungi (found inside shoots and reproductive organs), leaf surface fungi, and leaf litter decomposers.

Belowground interactions between hyperaccumulators and microbes are affected by the levels of Se in the soil and the distance of the microbe from the plant. Microbes in bulk soils with no litter or no influence from the rhizosphere of a hyperaccumulator are often exposed to Se levels between 1 and 4 mg/kg DW. Microbes in bulk soils influenced by litter from a hyperaccumulator are often exposed to average selenium levels between 10 and 25 mg/kg DW, while the rhizospheric soil can range from 20 to 200 mg/kg DW (Valdez-Barillas and Pilon-Smits, unpublished results). Inside the root, hyperaccumulators are capable of concentrating Se up to 500 mg/kg DW in lateral roots and 2500 mg/kg DW in the tap root, with higher levels in the epidermis and cortex, and lower levels in the pith. These root accumulation levels indicate that root surface fungi and root endophytic fungi that can utilize root resources of Se accumulating plants likely have evolved high Se tolerance. Indeed, rhizospheric fungi from Se hyperaccumulator habitat were significantly
more Se-tolerant than rhizosphere fungi from a non-seleniferous habitat Se tolerant, and a particular rhizospheric fungus (Aspergillus leporis) from hyperaccumulator habitat showed no growth inhibition when growing in 1,200 mg/kg Na_2SeO_4 while the same species isolated from a non-seleniferous habitat showed 50% growth reduction when growing in 30 mg/kg Na_2SeO_4 (Wangeline et al. 2011).

The level of tolerance to Se by microbes is dependent on the ability of a microbe to assimilate, accumulate, and detoxify selenium through elemental reduction or volatilization (Hassoun et al. 1995; Chasteen and Bentley 2003; Vallini et al. 2005; Stolz et al. 2006). Microbes assimilate selenium into seleno-enzymes using the similar pathways for sulfur (Bradfield et al. 1970; Cypionka 1987; Stolz et al. 2006; Lechenne et al. 2007). When exposed to 30 mg/kg NaSeO_4 or NaSeO_3, selenium sensitive fungi can initially reduce most of the selenium and accumulate 90% of it as organic Se and selenite. Selenium tolerant fungi will accumulate between 60 and 70% of the Se as organic selenium, 15–30% as elemental selenium and 5–10% as selenite. Selenium reduction and greater volatilization are among the many mechanisms that selenium tolerant fungi use differently compared to selenium sensitive fungi.

Based on their metabolic capacities, microbes may affect plant uptake of selenium by changing the concentration and chemical speciation of Se in the soil. For instance, microbes may volatilize may volatilize soil Se, break down or accumulate organic Se in the rhizosphere, and can reduce plant Se availability by reducing it to elemental Se (Figure 5). Rhizospheric microbes may also induce plant root hair formation and enhance plant sulfate/selenate uptake as a result of increased serine/O-acelyserine concentrations in the rhizosphere (de Souza et al. 1998).

Plant-microbe aboveground interactions range from pathogenic to mutualistic. Selenium accumulation in leaves and stems has been shown to reduce the growth and infection of pathogenic fungi sensitive to Se (Hanson et al. 2003). However, Se-tolerant fungi are

**Figure 4** Selenium accumulation in different plant tissues creates a niche for different microbial associations. Diagram represents average Se levels found in bulk soil, rhizosphere, and plant tissues of the hyperaccumulator Astragalus bisulcatus collected from a population in Fort Collins, Colorado, USA.
capable of colonizing the surface of leaves and flowers of hyperaccumulators, as was reported for the fungi *Albugo cruciferarum* in *Stanleya viridiflora* and *Albugo candida* in *Stanleya pinnata* (Rogerson 1957). Moreover, fungal decomposers in a seleniferous area were shown to be capable of capitalizing litter resources from hyperaccumulator material with Se levels up to 600 mg/kg (DW) (Quinn et al. 2010). Also, Se-tolerant endophytic fungi (fungi that leaves inside plant tissues), have been isolated from hyperaccumulator species, and are also capable of colonizing the apoplasm of leaves, stems, flowers, and seeds of hyperaccumulators without showing signs of pathogenicity. Leaves, flowers and seeds of hyperaccumulators can accumulate as much as 10,000 mg/kg (DW) Se. Current studies are focused on understanding the effects of these endophytic and rhizospheric fungi on plant uptake and metabolism of Se.

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