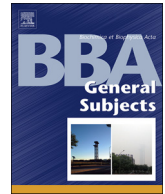




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Review

Plant selenium hyperaccumulation- Ecological effects and potential implications for selenium cycling and community structure[☆]

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ABSTRACT

Background: Selenium (Se) hyperaccumulation occurs in ~50 plant taxa native to seleniferous soils in Western USA. Hyperaccumulator tissue Se levels, 1000–15,000 mg/kg dry weight, are typically 100 times higher than surrounding vegetation. Relative to other species, hyperaccumulators also transform Se more into organic forms. **Scope of review:** We review abiotic and biotic factors influencing soil Se distribution and bioavailability, soil being the source of the Se in hyperaccumulators. Next, we summarize the fate of Se in plants, particularly hyperaccumulators. We then extensively review the impact of plant Se accumulation on ecological interactions. Finally, we discuss the potential impact of Se hyperaccumulators on local community composition and Se cycling.

Major conclusions: Selenium (hyper)accumulation offers ecological advantages: protection from herbivores and pathogens and competitive advantage over other plants. The extreme Se levels in and around hyperaccumulators create a toxic environment for Se-sensitive ecological partners, while offering a niche for Se-resistant partners. Through these dual effects, hyperaccumulators may influence species composition in their local environment, as well as Se cycling.

General significance: The implied effects of Se hyperaccumulation on community assembly and local Se cycling warrant further investigations into the contribution of hyperaccumulators and general terrestrial vegetation to global Se cycling and may serve as a case study for how trace elements influence ecological processes. Furthermore, understanding ecological implications of plant Se accumulation are vital for safe implementation of biofortification and phytoremediation, technologies increasingly implemented to battle Se deficiency and toxicity.

1. Background and scope of this review

Selenium (Se) is chemically similar to sulfur (S). Most plants inadvertently take up Se via S transporters, and the natural variation in plant Se accumulation is directly correlated with their S accumulation. However, certain plant species called Se hyperaccumulators have evolved the ability to distinguish Se from S. They concentrate and tolerate Se in their tissues at levels > 1000 mg/kg DW, and in some individuals as high as 15,000 mg/kg DW [1]. The Se levels in Se hyperaccumulator species vary greatly within and between populations of the same species growing in seleniferous soils [2–5]. The types of soils where Se hyperaccumulators are found can vary greatly as well [6,7]. Some of the earliest accounts of Se hyperaccumulators were by a chemist named O.A. Beath working at the Agricultural Experimental Station outside Laramie, Wyoming, USA. Beath's early work in documenting livestock poisoning lead him to Se hyperaccumulators [8].

Beath extensively studied Se hyperaccumulators and their habitat in Wyoming [9]. He coined several terms describing plants that accumulate differing levels of Se: he termed hyperaccumulators “indicator plants” because their presence “indicated” seleniferous soils. Tissue concentrations of 1000 mg/kg DW found in field-collected plant tissues are commonly considered hyperaccumulator levels [10]. Other characteristics hyperaccumulators have in common will be discussed in depth in Section 3.2 below.

There are around 50 known Se hyperaccumulator taxa that span 7 families, but most are within 3 families: Fabaceae, Asteraceae and Brassicaceae [11]. Judged from its occurrence within different clades, Se hyperaccumulation appears to be an evolutionarily derived trait, and non-accumulation the ancestral condition [12]. Given the seeming convergent evolution of Se hyperaccumulation across these families, what are some potential selection pressures that lead to hyperaccumulation? There are a few proposed hypotheses [13,14]. By far the

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most widely studied, as reviewed in Section 5.3, has been the elemental defense hypothesis, which states that plant accumulation of toxic trace elements like Se offers a defensive benefit against herbivory; other hypotheses are that it benefits plants via allelopathy (as reviewed in 5.1), causing toxicity to other plants, or by enhancing drought resistance (as mentioned in 3.1, 5.1) [15]. In addition to selection pressures favoring Se accumulation in plants, there may be selection pressures against the Se hyperaccumulation syndrome, for instance if hyperaccumulation is associated with reduced growth and, thus, fitness. Alternatively, while Se hyperaccumulation may give certain advantages on seleniferous soils, it may lead to reduced fitness on non-seleniferous soils. Such constraints may explain the rarity of Se hyperaccumulators in non-seleniferous areas and be a contributing factor for their low abundance in seleniferous areas (< 5% of the vegetation, Reynolds and Pilon-Smits, unpublished results).

The ecological impact of Se hyperaccumulation on the local environment is another fascinating area of inquiry. Se in soils is generally low as compared to the dramatically concentrated Se in the root and shoot of Se hyperaccumulators [16]. Concentration of Se to toxic levels, coupled with the relocation of the Se to locations accessible to more organisms (aboveground, in tissues, at soil surfaces) may have striking influences on the biotic environment. The presence of Se at toxic concentrations in Se hyperaccumulator tissues may dramatically affect the biotic interactions these plants have with herbivores, pollinators, other plants and microbes (both within the plant and in its external area of influence). These biotic interactions may have a powerful influence on the ecosystems where hyperaccumulators grow, altering species composition, favoring the Se tolerant taxa. The redistribution of Se by hyperaccumulators also likely creates a more heterogeneous environment. Environmental heterogeneity has long thought to increase species richness [17,18]. The importance of Se hyperaccumulators' influence on local Se cycling as well as impacts on broader Se cycling is an area lacking study. We will review the current literature on ecological aspects of plant Se accumulation and discuss a potential role of plant Se hyperaccumulators in Se cycling, both locally and more broadly. In addition to concentrating Se by 2–3 orders of magnitude, Se hyperaccumulators completely transform inorganic environmental selenate to methyl-selenocysteine (methyl-SeCys, different from non-hyperaccumulator vegetation (see Sections 3.1, 3.2). This change in Se speciation likely changes its bioavailability and movement in the food chain [19]. The overall change in spatial Se distribution, concentration and forms of Se due to the presence of Se hyperaccumulators may have positive or negative effects on local biota, depending on particular species' tolerance/sensitivity and utilization of Se. These collective effects may constitute selection pressures on species, influencing species composition and distribution in seleniferous areas and possibly more broadly. We will conclude this review by discussing the potential importance of Se hyperaccumulators on local community composition and possible influences further away.

2. Overview of Se distribution and cycling through the abiotic and biotic realm

2.1. Global Se cycling

There is relatively little known about the contribution of terrestrial vegetation in Se cycling, nor of the relative contribution of hyperaccumulators. Here we will summarize current knowledge about global Se cycling; for in-depth coverage of the subject please refer to recent reviews by Sharma [20] and Winkel [21].

The origin of Se in soils varies greatly. Dependent on the redox condition of the location Se is found in four different oxidation states: selenate Se(VI), selenite Se(IV), elemental selenium Se(0), and selenide Se(-II). Se(-II) can occur as organic selenium compounds, usually proteins containing the amino acids selenocysteine and selenomethionine, or as metal selenide mineral, typically with aluminum and iron is

sediments and rocks. Primary forms found in waters are selenate and selenite as they are soluble, but all of the other forms have been found associated with particulates in some waters as well [22]. Atmospheric Se originates from natural and anthropogenic sources; it is estimated that around 40% of total atmospheric Se is of anthropogenic origins [23]. Mining and refining of metals, and coal combustion account for 70–90% of anthropogenic Se emissions [23]. Natural sources of Se include particulate matter from sea spray and dust and volatilization from organisms; ocean microorganisms are considered the primary emitters of volatile Se [23]. Airborne inorganic Se can be either from natural or anthropogenic sources and can be H_2Se , Se and SeO_2 , but these are thought to quickly become particulate matter in the atmosphere [23]. For an in-depth review of current knowledge of atmospheric Se, see Wen and Cargnan 2007 [23].

Parent rock material, as opposed to deposition, is thought to be the main source of Se in soils worldwide but in certain areas like Western UK and South East China deposition from the atmosphere can be a major factor as well [21]. The concentration of Se in soils ranges from 0.01 to 100 $\mu g/g$. Se may be released to soils by both natural weathering from parent rock material, biogenic processes, and human activity [24]. Certain minerals have higher Se concentrations, including sulfide minerals where Se readily substitutes for sulfur (S), iron oxides of sediments which strongly bind Se, and phosphatic minerals [25]. Selenium concentrations are generally greater in shales than in other rock types and particularly in black shales (carboniferous) which can reach 600 $\mu g Se/g$ [22]. Shales are the main source of soil Se in Ireland, China and the Western USA [21].

Weathering of minerals and run-off from irrigation are the main contributors of Se to fresh water. Soil Se levels are strongly correlated to the soil parent material, and if the geology of an area is diverse, soil Se distribution can be highly variable [22]. Anthropogenic sources of Se contribute a significant amount of Se to soils. The use of phosphatic minerals in agriculture may be particularly relevant to Se cycling; these minerals are mined for agricultural applications, and so applied directly to crop plants [24]. Mining and the refining and burning of fossil fuels are other anthropogenic sources of Se [21]. For an overview of Se cycling between earth and atmosphere, and contributions of different processes, see Fig. 1.

2.2. Selenium in Western US habitats: from the soil to the plant interface

In this section, an overview is given of the origin and cycling of Se in soils in the Western United States, where the vast majority of reported Se hyperaccumulator plant species occur [10,26]. For a more extensive review of processes governing the forms of Se in soils in general, please refer to Fernández-Martínez & Charlet 2009 [19].

Much of the work documenting Se in soils of the Western United States started in connection to livestock poisoning caused by vegetation growing on seleniferous soils (Beath et al. 1935; Trelease & Martin 1936). The primary source of Se in soils of the Western United States is soil parent material (rocks), from which the Se is released via weathering and leaching, becoming more bioavailable in the process [24]. Selenium in parent material in the Western U.S. mainly originates from volcanic activity during the Cretaceous period (145–66 MYA). Therefore, seleniferous soils in the Western US were present long before the evolution of plant Se hyperaccumulation. For instance, the genus *Stanleya*, which contains the hyperaccumulator *Stanleya pinnata*, likely arose < 5 MYA [28].

Because Se adsorbs firmly to clay, some of the highest Se levels are found in sedimentary rocks high in clay content such as the Pierre and Niobrara formations, both sedimentary shales of the Cretaceous period. [19,29]. These formations are the main Se containing formations found throughout the Western United States [24]. There are other, earlier formations deposited by volcanic activity during the Permian and Triassic era that also contain high levels of Se, but they are much less common; the important commonality is that the Se was deposited due

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