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Regulation of Selenium Bioavailability in Soil-Plant Systems: Current Understanding and Future Directions

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Abstract

This review focuses on selenium (Se) bioavailability in soil-plant systems. As an essential micronutrient with antioxidant, anti-cancer, and antiviral properties, Se must be maintained at optimal dietary levels since deficiency or excess poses health risks. Globally, 500–1,000 million people live in Se-deficient regions, while seleniferous areas face Se toxicity risks, underscoring the need for proper Se management. The bioavailability of Se in soil-plant systems dictates its transfer into the food chain and thus impacts human Se status. However, the definition of Se bioavailability remains debated, and total soil Se content is a poor predictor of bioavailability compared to Se speciation and fractionation. This study aims to clarify the biogeochemical processes governing Se bioavailability, including adsorption-desorption, redox transformations, and plant-microbe interactions. We highlight the roles of soil pH, redox potential (Eh), and organic matter in Se speciation, analyze plant-mediated mechanisms such as root exudate-driven solubilization and specific transporter-mediated uptake, and propose agronomic and biotechnological strategies to optimize Se cycling in both deficient and contaminated environments. By integrating geochemical, physiological, and molecular insights, this work bridges the gap between theoretical understanding and practical Se management.

Keywords

Selenium Bioavailability; Soil Properties; Plant Uptake; Redox Potential; Rhizosphere Processes; Regulatory Strategies.

1. Introduction

1.1. Research Background and Significance

Selenium (Se), an essential micronutrient for human and animal health, exhibits significant antioxidant, anti-cancer, and anti-viral properties (Lyons et al., 2005). Its dual role as both a nutrient and a toxin underscores the importance of maintaining optimal dietary intake, as deficiency or excess can lead to severe health consequences, including Keshan disease, Kashin-Beck disease, and selenosis (Rayman, 2012; Fordyce, 2013). Globally, approximately 500–1,000 million people reside in Se-deficient regions, exemplified by the northeast-southwest low-Se belt in China, where soil Se scarcity directly impacts dietary Se intake (Figure 1). Conversely, seleniferous soils in regions like Enshi County, China, pose risks of Se toxicity, highlighting the delicate balance required in Se management.

The bioavailability of Se in the soil-plant system governs its transfer into the food chain, making it a critical determinant of human Se status (Dinh et al., 2018). Plants serve as both mitigators of Se deficiency through biofortification and regulators of environmental Se toxicity via phytoremediation (Bañuelos et al., 2015; Gupta & Gupta, 2016). However, the dynamic interplay of soil physicochemical properties, microbial activity, and plant physiological processes complicates the prediction and regulation of Se bioavailability.

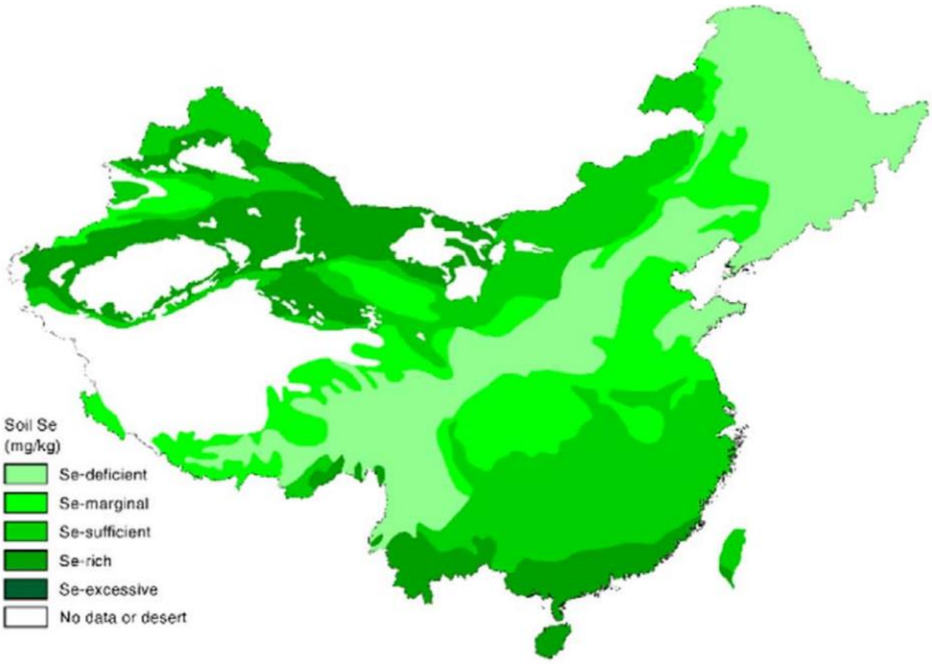

Figure 1. Distribution pattern of soil selenium concentration in China (Dinh et al., 2018).

1.2. Core Issues and Objectives

The concept of Se bioavailability remains contentious, with definitions ranging from Van Leeuwen's (1995) "portion available for biological action" to Alexander's (2000) "accessibility for assimilation." This ambiguity hinders the development of standardized assessment methods, particularly in heterogeneous soil-plant systems. Existing studies emphasize that total soil Se content poorly predicts bioavailability, as speciation (e.g., Se(IV), Se(VI), organic Se) and fractionation (e.g., adsorbed, precipitated) dominate its mobility (Christophersen et al., 2013; Tolu et al., 2014).

This review focuses on elucidating the biogeochemical processes controlling Se bioavailability, including adsorption-desorption, redox transformations, and plant-microbe interactions. Key objectives include: (1) clarifying the roles of soil pH, redox potential (Eh), and organic matter in Se speciation; (2) analyzing plant-mediated mechanisms such as root exudate-driven solubilization and transporter-specific uptake (e.g., OsPT2 in rice); and (3) proposing agronomic and biotechnological strategies to optimize Se cycling in both deficient and contaminated environments (Zhang et al., 2014). By integrating geochemical, physiological, and molecular insights, this work aims to bridge the gap between theoretical understanding and practical Se management.

2. Chemical Behaviors and Speciation Transformation of Selenium in Soil

2.1. Occurrence Forms and Dynamic Processes of Selenium

Selenium exists in multiple oxidation states in soil, including selenate (Se(VI)), selenite (Se(IV)), elemental selenium (Se^0), and selenide (Se(-II)) (El-Ramady et al., 2014; Kabata-Pendias, 2011). The distribution of these species is governed by soil pH and redox potential (Eh). In oxidizing alkaline soils, selenate (Se(VI)) predominates due to its high mobility, while selenite (Se(IV)) is more stable in neutral or acidic soils, where it readily adsorbs onto iron/aluminum oxyhydroxides (Kabata-Pendias, 2011; He et al., 2018). Under reducing conditions, Se(IV) is further reduced to insoluble elemental selenium (Se^0) or metal selenides (e.g., $FeSe_2$), which significantly limits bioavailability (Masscheleyn et al., 1991; Nakamaru & Altansuvd, 2014).

Adsorption-desorption processes play a critical role in regulating Se mobility. Selenite forms strong inner-sphere complexes with Fe/Al oxides via ligand exchange, while selenate is weakly

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adsorbed through outer-sphere electrostatic interactions (Peak, 2006; He et al., 2018). Clay minerals, particularly montmorillonite, selectively adsorb Se(IV) at edge sites through bidentate inner-sphere complexes (Charlet et al., 2007). Organic matter (OM) enhances Se solubility by forming ternary complexes with metals (e.g., Fe^{3+}-OM-Se), as low-molecular-weight organic acids (LMWOAs) compete with Se for adsorption sites (Dinh et al., 2018; Supriatin et al., 2016).

2.2. Key Transformation Mechanisms

Redox Reactions: Microbial activity drives the reduction of Se(VI) to Se(IV) and subsequently to Se^0. Bacteria such as *Thauera selenatis* and *Sulfurospirillum barnesii* mediate these transformations under anaerobic conditions. Nitrate inhibits Se(VI) reduction, maintaining Se in its oxidized state. Conversely, oxidation of Se^0 to Se(IV) occurs slowly in aerobic environments, mediated by manganese oxides or microbial activity (Scott & Morgan, 1996).

Methylation and Demethylation: Biomethylation of Se produces volatile dimethylselenide (DMSe), reducing soil Se content. Organic amendments (e.g., rice straw) enhance microbial methylation, promoting Se volatilization (Zhang & Frankenberger, 2003). Conversely, demethylation releases inorganic Se back into the soil solution, increasing bioavailability.

Dissolution-Precipitation Equilibrium: Selenium solubility is influenced by precipitation with sulfides or metals. For instance, Se(IV) co-precipitates with Fe^{3+} under acidic conditions to form $FeSeO_3$, while Se-S precipitates (e.g., Se^0-S^0) dominate in sulfide-rich environments at pH 4–7 (Jung et al., 2016; Geoffroy & Demopoulos, 2011).

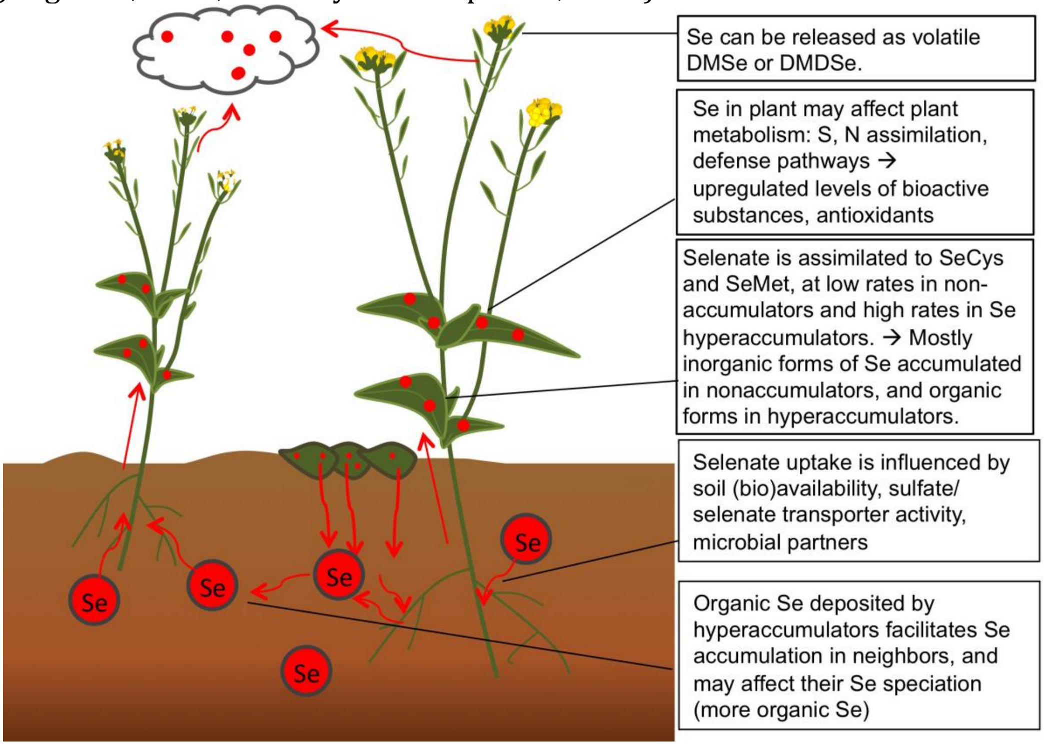

Figure 2.ProcessesrelatedtoSeinthesoil-plantsystem,relevantforSebiofortification (Mario et al., 2015).

3. Control Factors of Soil Properties on Selenium Bioavailability

3.1. Dominant Physicochemical Parameters

The bioavailability of selenium (Se) in soil-plant systems is predominantly governed by the synergistic effects of pH and redox potential (Eh) (Figure 2). Under oxidizing conditions (Eh > 200 mV), selenate (Se(VI)) predominates due to its high solubility and mobility, whereas selenite (Se(IV)) becomes the dominant species under moderately reduced conditions (Eh: 0–

200 mV) (Masscheleyn et al., 1991). In acidic and strongly reduced soils (Eh < −200 mV), Se tends to form insoluble elemental Se (Se^0) or metal selenides (e.g., $FeSe_2$), significantly reducing bioavailability (Nakamaru & Altansuvd, 2014). Alkaline soils favor Se(VI) desorption from soil colloids via electrostatic repulsion, enhancing its phytoavailability (Lee et al., 2011).

Iron/aluminum/manganese (Fe/Al/Mn) oxides critically regulate Se adsorption through inner-sphere complexation (Se(IV)) or outer-sphere electrostatic interactions (Se(VI)) (He et al., 2018). Fe oxides exhibit strong affinity for Se(IV), forming stable inner-sphere complexes on amorphous Fe hydroxides, thereby immobilizing Se in acidic soils. Conversely, Se(VI) adsorption is weaker and pH-dependent, with alkaline conditions promoting its release into soil solution (Feng et al., 2016).

3.2. Dual Roles of Organic Matter and Clay Minerals

Soil organic matter (OM) exerts dual effects on Se bioavailability. High-molecular-weight humic acids (HA) immobilize Se through complexation, whereas low-molecular-weight organic acids (LMWOAs) enhance Se solubility via competitive adsorption and ligand-promoted dissolution (Supriatin et al., 2016). For instance, dissolved organic carbon (DOC) derived from straw amendments increases Se mobility by competing with Se oxyanions for sorption sites on Fe/Al oxides (Dinh et al., 2018). However, excessive OM (>20%) may reduce bioavailable Se by promoting microbial reduction of Se(VI) to immobile Se^0 (Tolu et al., 2014).

Clay minerals, particularly montmorillonite, selectively adsorb Se(IV) through bidentate inner-sphere complexes at edge sites (Charlet et al., 2007). Particle size significantly influences adsorption capacity, with clay fractions (<0.025 mm) exhibiting higher Se retention than coarser particles. This selective fixation reduces Se bioavailability in clay-rich soils, particularly under acidic conditions.

3.3. Nutrient Element Interactions

Competitive interactions between selenium and sulfur/phosphorus profoundly affect Se uptake. Sulfate (SO_4^{2-}) competes with Se(VI) for sulfate transporters (e.g., Sultr1;2 in *Arabidopsis*), inhibiting Se(VI) absorption (El Kassis et al., 2007). Similarly, phosphate (PO_4^{3-}) suppresses Se(IV) uptake by competing for phosphate transporters (e.g., OsPT2 in rice) (Zhang et al., 2014). Field studies demonstrate that sulfur fertilization reduces soil pH and enhances OM content, promoting Se immobilization via Fe/Mn oxide-bound fractions. Conversely, phosphorus application increases Se bioavailability in alkaline soils by displacing adsorbed Se(IV) from mineral surfaces (Premarathna et al., 2010).

4. Plant Factors Influencing Selenium Absorption and Translocation

4.1. Species and Genotypic Differences

Plant species and genotypes exhibit significant variations in selenium uptake efficiency and translocation mechanisms. Hyperaccumulators such as *Astragalus bisulcatus* (e.g., milkvetch) demonstrate exceptional Se accumulation capacities, with tissue concentrations exceeding 1,000 $mg \cdot kg^{-1}$, while non-accumulators like *Oryza sativa* (rice) typically accumulate <10 $mg \cdot kg^{-1}$ under similar soil conditions (Bañuelos et al., 2015; Zhang et al., 2014). This divergence stems from species-specific transporter systems. For instance, rice employs the phosphate transporter OsPT2 to actively uptake selenite [Se(IV)], whereas selenate [Se(VI)] absorption in *Arabidopsis thaliana* is mediated by sulfate transporters (Sultr1;2) (El Kassis et al., 2007; Zhang et al., 2014). These molecular mechanisms highlight the critical role of genetic determinants in Se assimilation efficiency.

4.2. Root Exudates and Rhizospheric Processes

Root exudates, particularly low-molecular-weight organic acids (LMWOAs), significantly enhance Se bioavailability by desorbing Se from soil matrices. Citrate and malate secreted by roots form soluble complexes with Fe/Al oxide-bound Se, increasing its mobility in the rhizosphere (Dinh et al., 2018). Additionally, rhizospheric microorganisms mediate Se speciation transformations. For example, sulfate-reducing bacteria (*Desulfovibrio spp.*) facilitate the reduction of Se(VI) to less mobile Se(IV) or elemental Se [Se(0)] under anaerobic conditions . Conversely, *Pseudomonas spp.* can oxidize Se(0) to bioavailable Se(IV) in aerated soils, illustrating the bidirectional microbial regulation of Se bioavailability.

4.3. Dynamic Changes During Plant Growth Stages

Selenium allocation in plants exhibits temporal specificity, with preferential translocation to reproductive organs during critical growth phases. In wheat (*Triticum aestivum*), 60–70% of absorbed Se is redirected to grains during the grain-filling stage, driven by enhanced phloem loading of selenomethionine (SeMet) (Deng et al., 2017). Similarly, foliar Se application during the booting stage in rice increases grain Se content by 2.5-fold compared to vegetative-stage applications, underscoring the importance of growth stage-specific management (Guo et al., 2013). These dynamics are regulated by physiological demands for antioxidant protection during reproductive development (Dinh et al., 2018).

5. Comprehensive Regulation Strategies for Selenium Bioavailability

5.1. Optimization of Agronomic Practices

The application of organic amendments, such as crop straw, has been demonstrated to enhance selenium bioavailability by increasing dissolved organic carbon (DOC), which promotes the solubilization of selenium through competitive adsorption and complexation reactions (Dinh et al., 2017). For instance, rice straw amendments can facilitate the reduction of selenate [Se(VI)] to elemental selenium [Se(0)] under anaerobic conditions, thereby reducing its mobility (Zhang & Frankenberger, 2003). However, the efficacy of organic amendments depends on their chemical composition and decomposition rates. For example, low-molecular-weight organic acids (LMWOAs) derived from straw mineralization enhance selenium dissolution, while high-molecular-weight humic substances may immobilize selenium through adsorption (Supriatin et al., 2016).

Selenium fertilization strategies should consider speciation and application timing. Foliar application of selenate [Se(VI)] during the reproductive growth stage (e.g., grain filling in wheat) significantly improves selenium translocation to edible parts due to higher mobility of Se(VI) compared to selenite [Se(IV)] (Deng et al., 2017). Conversely, soil incorporation of nano-sized selenium particles (e.g., Se^0) shows promise for sustained release, reducing leaching losses and enhancing long-term bioavailability.

5.2. Soil-Plant System Regulation

Water management plays a critical role in modulating selenium redox dynamics. Flooding-induced reducing conditions promote the reduction of Se(VI) to immobile Se(IV) or Se(0), effectively lowering selenium bioavailability in contaminated soils (Masscheleyn et al., 1991). Conversely, intermittent drainage in seleniferous soils can maintain aerobic conditions, favoring Se(VI) dominance and phytoavailability.

Nutrient interactions, particularly sulfur (S) and phosphorus (P), require strategic management. Sulfate (SO_4^{2-}) competes with Se(VI) for root uptake via shared transporters (e.g., Sultr1;2 in *Arabidopsis*), necessitating balanced S fertilization to mitigate antagonistic effects (El Kassis et al., 2007). Co-application of nitrogen (N) and phosphorus (P) fertilizers enhances selenium assimilation by improving root exudation of organic acids (e.g., citrate), which desorb selenium from Fe/Al oxide surfaces.

5.3. Biofortification and Phytoremediation Technologies

Selenium hyperaccumulators, such as *Astragalus bisulcatus*, exhibit exceptional selenium sequestration capacities (up to 15,000 mg kg^{-1} in shoots), making them ideal for phytoremediation of seleniferous soils (Bañuelos et al., 2015). Genetic engineering of non-accumulators (e.g., rice) to overexpress selenium transporters (e.g., OsPT2 for Se(IV) uptake) offers a targeted approach for biofortification (Zhang et al., 2014).

Microbial inoculants, including *Pseudomonas* spp. and *Thauera selenatis*, enhance selenium reduction and volatilization, reducing soil selenium loads by 30–50% in field trials (Eswayah et al., 2016). These bacteria utilize selenium oxyanions as terminal electron acceptors, converting them to volatile dimethylselenide [$(CH_3)_2Se$] under aerobic conditions.

6. Conclusion

The bioavailability of selenium (Se) in soil-plant systems is governed by a complex interplay of soil geochemical properties, plant physiological mechanisms, and microbial-mediated transformations. Soil pH and redox potential (Eh) synergistically regulate Se speciation, with Se(VI) dominating in alkaline/oxidizing conditions and Se(IV) immobilized under acidic/reducing regimes. Iron/aluminum/manganese oxides exert critical control through inner-sphere complexation of Se(IV), while organic matter (OM) exhibits dual roles—low-molecular-weight organic acids enhance Se solubility, whereas humic substances promote adsorption. Plant-microbe interactions at the rhizosphere interface, such as root exudate-driven Se desorption and microbial reduction of Se(VI) to Se(0), significantly influence Se mobility. Furthermore, interspecies variations in Se uptake efficiency, exemplified by the OsPT2 phosphate transporter-mediated Se(IV) absorption in rice, highlight the importance of plant genetic traits in biofortification strategies.

Despite advancements, critical knowledge gaps persist. First, the development of multiscale models integrating geochemical speciation data, plant physiological parameters, and microbial functional genomics remains imperative for predicting Se dynamics under field conditions. Second, standardized protocols for Se speciation analysis—particularly HPLC-ICP-MS methodologies—require refinement to address matrix interference challenges in complex soil-plant systems. Third, climate change-induced alterations in soil moisture regimes and carbon cycling may perturb Se bioavailability patterns, necessitating long-term adaptive management strategies. Field validation of microbial inoculants (e.g., *Pseudomonas* spp. for Se reduction) and nano-Se fertilizers must prioritize ecological safety and agronomic efficacy. Lastly, harmonizing global Se deficiency/toxicosis mitigation efforts with United Nations Sustainable Development Goals demands interdisciplinary collaboration across soil science, nutrition epidemiology, and policy-making sectors.

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