Effects of Foliar Selenium Application on Selenium Distribution and Accumulation in Subcellular Fractions of Rice Leaves (Postprint)

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Abstract

Foliar selenium application is an effective agronomic biofortification strategy for increasing selenium content in crops. Investigating the distribution, accumulation characteristics, and influencing factors of selenium in rice leaf components can provide support for improving the utilization efficiency of foliar-applied selenium and reducing the ecological and environmental risks of selenium. This study utilized detached leaf culture technology to compare the effects of different selenium forms, concentrations, treatment durations, and different surfactant carriers on the distribution and accumulation of selenium in subcellular fractions of rice leaves. The results showed that: (1) Selenium was mainly distributed in the cell wall of rice leaves, followed by chloroplast and mitochondrial fractions, with the cytosol being the least; (2) Within several hours of foliar selenium fertilizer application, the absorption capacity of leaves for sodium selenite was significantly higher than that for nano-selenium, selenomethionine, and selenium-enriched yeast, being 1.25 times, 1.32 times, and 5.43 times higher, respectively, and its translocation capacity was approximately 1.26 times higher than the other three; (3) The optimal selenium application rate per rice leaf was 0.008 mg, at which point the selenium content in chloroplasts and mitochondria reached its maximum value; (4) 3–7 h after foliar selenium application was the critical time point for leaf absorption and translocation of selenium; (5) Compared with cyclodextrin and alkyl glucoside, the addition of rhamnolipid at a concentration of 30 $mg \cdot L^{-1}$ to exogenous selenium could better promote selenium absorption by rice leaves, increasing the absorption content by 80%. These results lay a foundation for subsequent understanding of the translocation mechanism of selenium in leaves and also provide support for future optimization of selenium formulations, establishment of scientific selenium application systems, and reduction of selenium ecological and environmental risks.

Full Text

Abstract

Foliar selenium spraying is an effective agronomic fortification strategy for increasing crop selenium content. Investigating the distribution, accumulation characteristics, and influencing factors of selenium in rice leaf fractions can provide crucial support for improving the utilization efficiency of foliar selenium application while reducing associated ecological and environmental risks. This study employed leaf in vitro culture techniques to compare the effects of different selenium forms, concentrations, treatment durations, and surfactant carriers on selenium distribution and accumulation in rice leaf subcellular fractions. The results demonstrated that: (1) Selenium was predominantly distributed in rice leaf cell walls, followed by chloroplast and mitochondrial fractions, with the lowest concentrations in the cytosol. (2) Within hours of application, sodium selenite exhibited significantly higher leaf uptake capacity compared to nano-selenium, selenomethionine, and yeast selenium—1.25-fold, 1.32-fold, and 5.43-fold higher, respectively—and its translocation capacity was approximately 1.26-fold greater than the other three forms. (3) The optimal selenium application rate was 0.008 mg per leaf, which maximized selenium content in chloroplasts and mitochondria. (4) The critical window for selenium uptake and translocation in leaves occurred 3–7 hours after foliar application. (5) Compared with cyclodextrins and alkyl glycosides, adding rhamnolipids at 30 $mg \cdot L^{-1}$ to exogenous selenium more effectively promoted selenium uptake in rice leaves, increasing absorbed content by 0.8-fold. These findings establish a foundation for understanding selenium transport mechanisms in leaves and provide support for optimizing selenium formulations, establishing scientific application protocols, and mitigating selenium-related ecological and environmental risks.

Keywords: selenium, rice, subcellular distribution, foliar spray, surfactant

Introduction

Selenium is an essential trace element for humans and animals. Human selenium deficiency can lead to over 40 diseases including cardiovascular and cerebrovascular disorders and hypertension syndrome, while animal selenium deficiency causes selenium-vitamin E deficiency diseases. Plants represent the primary dietary source of selenium for humans, and producing selenium-enriched crops such as rice constitutes an effective approach to preventing human selenium deficiency. Current agronomic biofortification methods primarily include soil selenium fertilization and foliar selenium spraying. Compared with soil application, foliar spraying offers higher selenium utilization efficiency because soil selenium bioavailability is strongly influenced by soil properties such as redox potential, pH, and organic matter content. Additionally, selenite exhibits high affinity for soil iron oxides, hydroxides, and organic matter, which reduces its bioavailability. Selenium is also prone to leaching through soil runoff, potentially contaminating groundwater and creating environmental risks while wasting se-

lenium resources. Foliar application provides higher bioavailability by enabling direct contact with leaf surfaces, allowing selenium to penetrate through the cuticle/stomata or aqueous pores before translocating to grains, thereby substantially improving biological utilization while reducing environmental contamination risks. Consequently, foliar selenium application has gained widespread adoption in agriculture.

However, current foliar selenium application in agricultural production suffers from relatively poor absorption efficiency. Emese et al. reported that foliar application of 100 $\mathrm{g \cdot mL^{-1}}$ selenium fertilizer to carrot leaves resulted in only approximately 10% translocation efficiency to fruits, with the majority retained in roots (2%) or leaves (50–80%). Increasing grain selenium content therefore requires either higher application rates or synergistic interactions with other elements, which may lead to excessive selenium application and heightened environmental risks. Investigating selenium uptake and distribution processes is thus critical for achieving precise selenium application, improving absorption efficiency, and ensuring safe selenium levels.

Most research on selenium uptake and distribution has focused on staple crops such as rice and wheat, employing subcellular distribution techniques to observe selenium localization in plant leaves. However, these studies have typically examined single factors such as selenium forms, concentrations, or environmental conditions like light and temperature, without comprehensive integration, limiting their utility for selenium-enriched rice production. Concentration, elemental speciation, and surfactant properties are all critical factors influencing foliar absorption and subcellular distribution. Inorganic and organic selenium differ in structure and physicochemical properties, resulting in varying leaf absorption efficiencies. As essential components of foliar fertilizers, surfactants increase contact area between aqueous solutions and leaf surfaces, promoting adhesion and retention on hydrophobic wax layers, thereby enhancing foliar fertilizer uptake opportunities and improving utilization efficiency. Therefore, systematic investigation of how different selenium forms, concentrations, application timing, and fertilizer carriers affect selenium distribution and accumulation in plant leaf subcellular components is necessary.

This study utilized excised leaf culture to examine foliar selenium application in rice, addressing two primary questions: (1) How do selenium form, concentration, and application duration affect selenium distribution and accumulation in rice leaf subcellular fractions? (2) How do different carriers influence selenium uptake and accumulation in rice leaves? The findings provide valuable insights for improving selenium fertilizer absorption efficiency and conserving selenium resources in agricultural production.

Materials and Methods

1.1 Experimental Materials

Rice variety: Xiangfei, a japonica conventional rice with a growth period of approximately 156 days, plant height of 100–105 cm, robust root system, tough stems, high lodging resistance, non-premature senescence, compact plant architecture, strong tillering ability, and high disease resistance to rice blast, false smut, and sheath blight. The thousand-grain weight is 26.2 g, with excellent grain quality and taste.

Reagents: Sodium selenite (Na_2SeO_3, Guangzhou Huayu Trading Co., Ltd.), selenomethionine ($C_5H_{11}NO_2Se$, Yuanye Bio-Technology Co., Ltd.), nano-selenium (Se, Xi' an Ruixi Biotechnology Co., Ltd.), yeast selenium (Boersen Bio-Technology Co., Ltd.), cyclodextrin ($C_{42}H_{70}O_{35}$, Sinopharm Chemical Reagent Co., Ltd.), rhamnolipids ($C_{58}H_{106}O_{22}$, Xi' an Ruijie Biotechnology Co., Ltd.), alkyl glycosides ($C_{16}H_{32}O_6$, Yuanye Bio-Technology Co., Ltd.), EDTA ($C_{10}H_{16}N_2O_8$, BBI Life Sciences Co., Ltd.), dithiothreitol ($C_4H_{10}O_2S_2$, Shanghai Macklin Biochemical Technology Co., Ltd.), Tris ($C_4H_{11}NO_3$, Beijing Solarbio Science & Technology Co., Ltd.), sucrose ($C_{12}H_{22}O_{11}$, Guangzhou Huayu Trading Co., Ltd.).

1.2 Rice Cultivation

Rice seeds were sterilized in 10% H_2O_2 solution for 30 minutes and rinsed 3-5 times with deionized water. After rinsing, seeds were germinated in a plant incubator at 28 °C for 3-4 days before transplanting to nursery trays. Seedlings were grown at 25 °C for 21 days with nitrogen-phosphorus-potassium fertilization (urea 91 $mg \cdot kg^{-1}$, calcium superphosphate 200 $mg \cdot kg^{-1}$, potassium chloride 40 $mg \cdot kg^{-1}$) to ensure adequate nutrition. After 21 days, fully expanded third leaves were excised at the leaf base for subcellular experiments.

1.3 Experimental Design

Excised leaf experiments treat leaves as independent systems for studying foliar uptake and translocation of exogenous substances. This study employed excised rice leaves, cutting them at the ligule and placing them in EDTA solution, which collects phloem exudate and reflects selenium migration to other organs after leaf absorption. Experiments examined selenium form, concentration, time, and surfactant effects.

1.3.1 Effects of Selenium Form on Selenium Translocation and Accumulation in Leaves Uniformly positioned, similarly sized third leaves were selected. The cut ends were immersed in 2 mL of 25 $mmol \cdot L^{-1}$ EDTA solution, while the upper surfaces remained exposed to air. Ten microliters of 1,000 $mg \cdot L^{-1}$ selenium solution (as sodium selenite, selenomethionine, nano-selenium, or yeast selenium) was applied to a fixed position on the exposed leaf

surface. Leaves were removed after 7 hours (preliminary experiments confirmed complete absorption by this time), and the application site was rinsed with 6 mL water. Both rinse water and EDTA solution were retained for analysis. The entire process was conducted under dark conditions (EDTA collection of phloem sap requires darkness). All treatments had three replicates.

1.3.2 Effects of Sodium Selenite Concentration on Selenium Translocation and Accumulation in Leaves To ensure droplet application at a consistent position (seedling leaves are relatively narrow), selenium concentration was increased while application volume was decreased. Preliminary experiments confirmed that high concentrations caused no leaf damage at small volumes [Figure 1: see original paper].

The experimental design involved applying 10 L of sodium selenite solution at concentrations of 0, 200, 400, 600, 800, and 1,000 $mg \cdot L^{-1}$ to fixed leaf positions, with other procedures identical to Section 1.3.1.

1.3.3 Temporal Characteristics of Selenium Migration and Accumulation in Leaves To establish systematic temporal patterns, an exponential time gradient was employed. Preliminary experiments confirmed that leaves in EDTA solution remained viable for 28 hours. The experimental design involved applying 10 L of 1,000 $mg \cdot L^{-1}$ sodium selenite solution to fixed leaf positions, with leaf harvest at 0, 1, 2, 3, 5, 7, 9, 14, and 28 hours. Other procedures followed Section 1.3.1.

1.3.4 Effects of Surfactant Concentration and Type on Selenium Migration and Accumulation in Leaves Environmentally friendly surfactants commonly used in agriculture—cyclodextrin, rhamnolipids, and alkyl glycosides—were selected. Based on critical micelle concentrations, solutions were prepared with cyclodextrin at 20, 40, 60, 80, and 100 $mg \cdot L^{-1}$; rhamnolipids at 10, 20, 30, 40, and 50 $mg \cdot L^{-1}$; and alkyl glycosides at 20, 40, 60, 80, and 100 $mg \cdot L^{-1}$. Leaves were placed in 2 mL of 25 $mmol \cdot L^{-1}$ EDTA solution, and 10 L of surfactant-containing sodium selenite solution (Se, 800 $mg \cdot L^{-1}$) was applied to fixed positions. Leaves were removed after 7 hours, and application sites were rinsed with 6 mL distilled water. Rinse water was retained for analysis. The entire process was conducted under dark conditions. All treatments had three replicates.

1.4 Sample Pretreatment and Analysis

Subcellular fractionation: Rinsed leaves were blotted dry. Subcellular separation followed the method of Su et al. (2014). Briefly, leaves were ground in 2 mL extraction buffer at 4 °C using a porcelain mortar. The extraction buffer consisted of: sucrose (0.25 $mol \cdot L^{-1}$) + Tris-HCl (50 $mmol \cdot L^{-1}$, pH = 7.5) + dithiothreitol (1.0 $mmol \cdot L^{-1}$). The homogenate was transferred to a 10 mL centrifuge tube and centrifuged at 600 × g for 10 min at 4 °C; the precipitate

represented the cell wall fraction (F1). The supernatant was transferred to a new tube and centrifuged at 1,000 × g for 20 min; the precipitate represented the chloroplast fraction (F2). The supernatant was again transferred and centrifuged at 10,000 × g for 20 min; the precipitate represented the mitochondrial fraction (F3), and the final supernatant represented the cytosolic fraction (F4).

Digestion and determination: EDTA solutions and subcellular fractions (F1–F4) were digested according to GB 5009.93-2017. Weighed samples were placed in crucibles with 10 mL of concentrated nitric acid + perchloric acid (9:1) and digested overnight at room temperature. The following day, samples were heated on an electric hotplate until yellow fumes dissipated and solutions became clear and transparent with white fumes. The temperature was then increased to 180 °C and heating continued until the volume was reduced to 1–2 mL. After cooling, 5 mL of 50% hydrochloric acid was added and samples were heated at 80 °C for 1 minute. The digests were diluted to 25 mL with 1% citric acid in volumetric flasks, left to stand overnight, and the supernatant was transferred to 10 mL centrifuge tubes for analysis. Rinse water from Section 1.3 and the prepared samples were analyzed using atomic fluorescence spectrometry (SK-2003A).

Quality control: Certified reference material (GBW10022 garlic powder) and digestion blanks were included as controls during digestion, following the same procedure as samples. Selenium standard solutions were analyzed during measurement to ensure quality control.

1.5 Data Analysis

Statistical analysis was performed using Microsoft Office Excel 2016 and SPSS 20.0 (IBM, USA). Data comparisons employed one-way analysis of variance (ANOVA, LSD, $P < 0.05$). Figures were prepared using GraphPad Prism 9 (GraphPad Software, USA).

Results

2.1 Effects of Selenium Form on Selenium Distribution and Accumulation in Rice Leaf Subcellular Fractions

[Figure 2: see original paper]

Selenium form did not alter its subcellular distribution pattern, with concentrations consistently following the order: cell wall > organelles > cytosol. However, significant differences existed among selenium forms: cell wall selenium content ranked sodium selenite > nano-selenium > selenomethionine > yeast selenium; organelle selenium content ranked sodium selenite nano-selenium > selenomethionine > yeast selenium, with selenomethionine showing F2 > F3 while other treatments showed no significant difference between F2 and F3; cytosolic selenium content ranked sodium selenite > selenomethionine yeast selenium > nano-selenium. Sodium selenite treatment resulted in significantly higher EDTA

selenium content and lower rinse water selenium compared to other treatments, indicating that after 7 hours, relatively more selenium had translocated to other organs, demonstrating the highest absorption and translocation efficiency for sodium selenite.

2.2 Effects of Sodium Selenite Concentration on Selenium Distribution and Accumulation in Rice Leaf Subcellular Fractions

[Figure 3: see original paper]

Selenium was not detected in rinse water at concentrations of 0–800 mg · L^{-1}. Cell wall selenium content increased continuously with concentration. Chloroplast and mitochondrial selenium content increased when selenium application rates were 0–0.008 mg per leaf, then plateaued. Cytosolic selenium increased rapidly at 0.004–0.008 mg per leaf, then increased slowly thereafter. EDTA selenium content increased significantly with sodium selenite application rate, with the greatest increase between 0.006 and 0.008 mg per leaf. The continuous increase in cell wall selenium indicated that higher application rates resulted in more selenium retained in cell walls, while translocation rates to other organs remained relatively stable and generally increased. Leaf surface selenium residue was only detected at 0.01 mg per leaf.

2.3 Temporal Changes in Selenium Distribution and Accumulation in Rice Leaf Subcellular Fractions

[Figure 4: see original paper]

At the experimental concentration, selenium residue appeared on leaf surfaces. Rinse water selenium decreased rapidly after application, slowing after 3 hours and stabilizing after 9 hours. EDTA selenium remained unchanged for 0–3 hours, then increased rapidly from 3–7 hours, with no significant change thereafter, indicating complete leaf surface absorption by 7 hours and completion of internal migration and export to other organs. Within leaves, selenium was predominantly distributed in cell walls, followed by chloroplasts and mitochondria, with minimal content in the soluble fraction. All subcellular fractions showed increasing selenium content over time: stable during 1–3 hours, rapid increase during 3–7 hours, slow increase after 7 hours, and stabilization after 9 hours.

2.4 Effects of Different Surfactants on Selenium Distribution and Accumulation in Rice Leaf Subcellular Fractions

[Figure 5: see original paper]–[Figure 7: see original paper]

Surfactant application did not alter the characteristic distribution of selenium primarily in cell walls and minimally in cytosol. Cyclodextrin addition significantly increased F4 selenium content with no significant change in F1; F2+F3 selenium reached maximum values at 20 mg · L^{-1} and 80 mg · L^{-1}, with 20 mg · L^{-1} showing significant differences from other concentrations while 80 mg · L^{-1}

showed no significant differences. Rhamnolipid addition caused F1 and F2+F3 to increase initially then plateau, both reaching maximum values at 30 $mg \cdot L^{-1}$; F4 selenium increased slowly, peaking at 40 $mg \cdot L^{-1}$. Alkyl glycoside addition did not affect F1 selenium content, while F4 showed fluctuating trends and F2+F3 reached maximum selenium content at 40 $mg \cdot L^{-1}$. Comparing optimal concentrations and internal leaf selenium content among the three surfactants, rhamnolipids required the lowest concentration and achieved the highest internal selenium content, making it the optimal choice.

Discussion and Conclusion

Selenium utilization efficiency after leaf entry can be assessed through selenium content in various leaf subcellular fractions. Subcellular components extracted via differential centrifugation include cell walls, chloroplasts and mitochondria, and cytosol. The cell wall constitutes the first barrier for element entry into leaves and can transport required nutrients to organelles through transmembrane movement. Organelles contain chloroplasts, mitochondria, and other sites of normal physiological activity. Research indicates that chloroplasts and mitochondria are interdependent organelles in plant cells, playing critical roles in metabolism, energy status, and redox state. Plastid genes in chloroplasts and mitochondria largely participate in nutrient synthesis in grains, including protein synthesis, enzyme activation, metabolite production, and electron transport chain maintenance, demonstrating that chloroplasts and mitochondria are essential components for converting nutrients into grain-usable forms after leaf entry. The cytosol comprises the liquid contents of leaf cells, containing various solutes and intracellular structures that fill cellular space and support organelle function.

Selenium form significantly affects leaf selenium content. Among four selenium forms (sodium selenite, sodium selenate, zinc selenite, and selenomethionine), sodium selenite showed the best enrichment effect in rice seedling leaves, while selenomethionine performed worst. In functional leaves during the booting stage, selenium accumulation ranked sodium selenate > sodium selenite > nano-selenium > selenomethionine > yeast selenium. Our study found that within hours of foliar application, selenium accumulation in excised seedling leaves ranked sodium selenite > nano-selenium > selenomethionine > yeast selenium, consistent with previous findings that inorganic selenium outperforms organic forms. Results showed that sodium selenite and nano-selenium applications resulted in significantly higher organelle selenium accumulation compared to selenomethionine and yeast selenium, indicating that inorganic and nano-selenium migrate more readily to functional organs for plant utilization. This occurs because inorganic and nano-selenium exhibit greater stability in binding proteins or polysaccharides, facilitating leaf entry and grain utilization. Analysis of cytosolic, EDTA, and leaf surface residual selenium revealed that sodium selenite demonstrated significantly higher leaf absorption and translocation capacity, confirming its superior suitability for rice foliar application.

Exogenous selenium concentration significantly affects subcellular selenium accumulation. Previous studies reported that low concentrations promote mitochondrial and cytoplasmic selenium content while high concentrations inhibit it, with chloroplast selenium showing fluctuating trends and cell wall selenium continuously increasing. Our results differed somewhat. Although high concentrations were applied, the 10 L volume resulted in a maximum application rate of 0.01 mg per leaf. As exogenous selenium concentration increased, all subcellular fractions showed increasing selenium content. However, when application exceeded 0.008 mg per leaf, chloroplast and mitochondrial selenium content plateaued, indicating that 0.008 mg sodium selenite per leaf represents the absorption capacity limit for rice leaf organelles. At 0.01 mg per leaf, rinse water contained 0.18 $mg \cdot L^{-1}$ selenium, representing residual selenium after subtracting leaf-absorbed amounts, indicating saturation and cessation of absorption. Therefore, 0.008 mg sodium selenite per leaf is the optimal application rate, maximizing utilization by organelles such as chloroplasts and mitochondria to provide optimal exogenous selenium for grain development.

Temporal allocation patterns of foliar-applied selenium reflect its absorption, transformation, and translocation dynamics in leaves. Selenium content in all fractions stabilized by 7 hours. EDTA selenium content indicates translocation capacity to other organs, showing no change during 0–3 hours, rapid increase during 3–7 hours, and stabilization thereafter. This demonstrates that during the first 3 hours, selenium did not translocate but concentrated within leaves; during 3–7 hours, significant increases in chloroplast, mitochondrial, cytosolic, and EDTA selenium indicate completion of synthesis and transformation required for grain development and initiation of export to other plant parts; after 7 hours, the process stabilized. Thus, 3–7 hours represents the optimal window for leaf selenium absorption and transformation, consistent with agricultural recommendations that foliar fertilizers should not be exposed to rainfall within 6 hours of application. Rinse water selenium residue similarly confirms 3–7 hours as the critical period for selenium transformation and translocation.

As essential foliar fertilizer components, surfactant properties and concentrations significantly affect absorption efficiency. Studies confirm that low surfactant concentrations can substantially alter leaf surface properties, overcome cuticular resistance, and improve penetration and utilization of foliar fertilizers, growth regulators, and herbicides. Identifying low-concentration, high-efficiency surfactants can reduce selenium fertilizer requirements. This study compared three environmentally friendly biosurfactants: cyclodextrin, rhamnolipids, and alkyl glycosides. Surfactant application altered organelle selenium content: cyclodextrin and alkyl glycosides showed fluctuating effects with low-concentration promotion and high-concentration inhibition; rhamnolipids peaked at 30 $mg \cdot L^{-1}$ then showed minimal change. Surfactants thus promoted selenium migration to functional organs and enhanced leaf transformation. Optimal concentrations were 20, 30, and 40 $mg \cdot L^{-1}$ for cyclodextrin, rhamnolipids, and alkyl glycosides, respectively. Comparison at optimal concentrations revealed that rhamnolipids most effectively promoted exogenous selenium entry into leaf

tissues, primarily because surfactants enhance solubilization and penetration. Lower critical micelle concentration (CMC) values result in more micelle formation and greater solubilization capacity. Rhamnolipids have a CMC of approximately 30–50 mg · L^{-1}, lower than cyclodextrin and alkyl glycosides (CMC ~100 mg · L^{-1}), making rhamnolipids the optimal choice.

As an essential human nutrient, both selenium deficiency and excess produce adverse effects, making safe and effective intake a societal priority. For selenium-enriched agricultural production, the focus is maximizing exogenous selenium utilization to produce compliant products without crop or ecological toxicity. This study reveals subcellular distribution, accumulation, and translocation characteristics in rice third leaves within hours of foliar application: sodium selenite provides optimal utilization, the optimal rate is 0.008 mg per leaf, the critical transformation period is 3–7 hours post-application, and rhamnolipid addition enhances selenium absorption while reducing required application rates, conserving selenium resources and minimizing environmental risks. These results establish a foundation for understanding selenium transport mechanisms in leaves and support future selenium formulation optimization, scientific application system development, and ecological risk reduction.

References

CEBALLOS-LAITA L, GUTIERREZ-CARBONELL E, LATTANZIO G, et al., 2015. Protein profile of Beta vulgaris leaf apoplastic fluid and changes induced by Fe deficiency and Fe resupply[J]. Front Plant Sci, 6: 145.

CHEN L, LIN Y, CHEN P, et al., 2019. Effect of iron deficiency on the protein profile of rice (Oryza sativa) Phloem Sap[J]. Chin Bull Bot, 54(2): 194-207.

DING Y, WANG R, GUO J, et al., 2015. The effect of selenium on the subcellular distribution of antimony to regulate the toxicity of antimony in paddy rice[J]. Environ Sci Poll Res, 22:

EBRAHIMI N, HARTIKAINEN H, SIMOJOKI A, et al., 2015. Dynamics of dry matter and selenium accumulation in oilseed rape (Brassica napus L.) in response to organic and inorganic selenium treatments[J]. Agric Food Sci, 24: 104-117.

FAN J, WANG R, HU HQ, et al., 2016. Effect of selenate and selenite on selenium uptake and subcellular distribution in leaves of flue-cured tobacco[J]. Chin Tobacco Sci, 37(4): 37-41.

HU C, NIE Z, SHI H, et al., 2023. Selenium uptake, translocation, subcellular distribution and speciation in winter wheat in response to phosphorus application combined with three types of selenium fertilizer[J]. BMC Plant Biol, 23(1): 224.

KÁPOLNA E, HILLESTRøM P R, LAURSEN K H, et al., 2009. Effect of foliar application of selenium on its uptake and speciation in carrot[J]. Food Chem,

115(4): 1357-1363.

KOVALCHUK N M, SIMMONS M J, 2021. Surfactant-mediated wetting and spreading: Recent advances and applications[J]. Current Opinion Colloid Interface Sci, 51: 101375.

LAKIN H W, 1972. Selenium accumulation in soils and its absorption by plants and animals[J]. GSA Bull, 83(1): 181-190.

LI G, MAO HJ, GONG ZQ, et al., 2011. Solubilization of diesel and polycyclic aromatic hydrocarbons by certain kinds of surfactants[J]. Res Environ Sci, 24(7): 775-780.

LI H, JI G, WANG Y, et al., 2018a. WHITE PANICLE3, a novel nucleus-encoded mitochondrial protein essential for proper development and maintenance of chloroplasts and mitochondria in rice[J]. Front Plant Sci, 9: 762.

LI X, YUE C, WANG B, et al., 2011. Effect of surfactant on boron absorption of soybean and peanut plants[J]. Guizhou Agric Sci, (7): 107-111.

NIE X, YANG X, HE J, et al., 2023. Bioconversion of inorganic selenium to less toxic selenium forms by microbes: A review[J]. Front Bioengin Biotechnol, 11: 1167123.

RAYMAN MP, 2000. The importance of selenium to human health[J]. The lancet, 356: 233-241.

SHI L, 2021. Effects of foliar application of selenium on arsenic accumulation characteristics in rice[D]. Shenyang: Shenyang University: 241-313.

SU Y, LIU J, LU Z, et al., 2014. Effects of iron deficiency on subcellular distribution and chemical forms of cadmium in peanut roots in relation to its translocation[J]. Environ Exp Bot, 97:

WAN Y, WANG K, LIU Z, et al., 2019. Effect of selenium on the subcellular distribution of cadmium and oxidative stress induced by cadmium in rice (Oryza sativa L.)[J]. Environ Sci Poll Res, 26: 16220-16228.

WANG B, 2011. Research on the permeability of cuticle and screening for efficient surfactant[D]. Zhengzhou: Zhengzhou University: 31-126.

WANG C, LI B, LI H, et al., 2010. Effects of Se, Zn and their interaction on the subcellular distribution of selenium in spring tea leaves[J]. Acta Hortic Sin, 37(5): 794-800.

WANG K, WANG Y, WAN Y, et al., 2021. The fate of arsenic in rice plants (Oryza sativa L.): Influence of different forms of selenium[J]. Chemosphere, 264: 128417.

YANG H, YANG X, NING Z, et al., 2022. The beneficial and hazardous effects of selenium on the health of the soil-plant-human system: An overview[J]. J Hazardous Mat, 422:

WANG YP, 2020. Effects of exogenous selenium biological fortification method on rice selenium enrichment and selenium forms in grain[D]. Nanning: Guangxi University: 132-209.

ZHANG LH, ZHAO W, YU FY, et al., 2012. Physiological characteristics of selenium uptake by excised leaves of rice[J]. J Soil Sci, 49(1): 189-193.

ZHANG Q, 2020. Synthesis of amphiphilic hydroxypropyl-β-cyclodextrin and its paclitaxel-loaded micelles[D]. Harbin: Northeast Forestry University: 23-131.

ZHU J, ZHAO P, NIE Z, et al., 2020. Selenium supply alters the subcellular distribution and chemical forms of cadmium and the expression of transporter genes involved in cadmium uptake and translocation in winter wheat (Triticum aestivum)[J]. BMC Plant Biol, 20:

ZHU YG, 2003. Micro-interfacial processes in soil-plant systems and their environmental impacts[J]. J Environ Sci, 23(02): 205-210.

Note: Figure translations are in progress. See original paper for figures.