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Selenium uptake, translocation, subcellular distribution and speciation in winter wheat in response to phosphorus application combined with three types of selenium fertilizer

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Abstract

Background Selenium (Se) deficiency causes a series of health disorders in humans, and Se concentrations in the edible parts of crops can be improved by altering exogenous Se species. However, the uptake, transport, subcellular distribution and metabolism of selenite, selenate and SeMet (selenomethionine) under the influence of phosphorus (P) has not been well characterized.

Results The results showed that increasing the P application rate enhanced photosynthesis and then increased the dry matter weight of shoots with selenite and SeMet treatment, and an appropriate amount of P combined with selenite treatment increased the dry matter weight of roots by enhancing root growth. With selenite treatment, increasing the P application rate significantly decreased the concentration and accumulation of Se in roots and shoots. P₁ decreased the Se migration coefficient, which could be attributed to the inhibited distribution of Se in the root cell wall, but increased distribution of Se in the root soluble fraction, as well as the promoted proportion of SeMet and MeSeCys (Se-methyl-selenocysteine) in roots. With selenate treatment, P_{0.1} and P₁ significantly increased the Se migration coefficient, which could be attributed to the enhanced proportion of Se (IV) in roots but decreased proportion of SeMet in roots. With SeMet treatment, increasing the P application rate significantly decreased the Se concentration in shoots and roots but increased the proportion of SeCys₂ (selenocystine) in roots.

Conclusion Compared with selenate or SeMet treatment, treatment with an appropriate amount of P combined with selenite could promote plant growth, reduce Se uptake, alter Se subcellular distribution and speciation, and affect Se bioavailability in wheat.

Keywords Winter wheat, Phosphorus, Selenium, Uptake, Translocation, Subcellular distribution, Se species

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Background

Selenium (Se) is an essential microelement for humans and animals and plays important roles under oxidative stress-related conditions and in immune system support and disease prevention [1, 2]. In recent decades, hidden hunger caused by Se deficiency has been commonly found worldwide [3], resulting in health disorders such as muscle syndrome, Keshan disease, liver disease, cognitive impairment and many cancers [4, 5]. Excessive Se intake is also harmful, resulting in health disorders such as hair loss, nervous system disorders and paralysis [6]. The World Health Organization suggests a daily intake of Se of 50–55 µg for adults. However, it has been estimated that the Se intake amount of approximately 0.7 billion people in the world is lower than the recommended value [7]. Studies have also shown that 72% of soil is Se deficient in China [8]. Therefore, Se-enriched fertilizers were applied to improve Se contents in edible plant parts and increase Se intake for humans living in Se-deficient areas [9–11].

It is well known that Se availability is influenced by pH, Eh, and Se species in soil [12, 13]. Se exists in soil in four oxidation states (-II, 0, IV and VI) [14], of which selenide (-II) and Se (0) are difficult for plant roots to absorb. Selenite (IV) is the main form of Se in acidic and neutral soils (pE + pH < 7.5), but selenate (VI) mainly exists in oxidized and alkaline soils (pE + pH > 15). Plants can uptake both selenite and selenate, most of which is converted into selenocystine (SeCys₂) and selenomethionine (SeMet) [15]. Compared to selenite and selenate, organic Se is safe and beneficial for plants [16-18]. SeMet can be absorbed by plants through amino acid transporters [17]. The translocation and metabolism of selenate, selenite and organic Se showed differences after absorption in plants [19, 20]. Furthermore, different forms of Se influence Se concentration, species and distribution [21]. For example, selenite mainly accumulates in roots, but selenate accumulates in shoots [11, 22, 23]. SeMet is the dominant organic Se in plants, and it is translocated from roots to shoots via peptide transporter (NRT1.1B) in plants [24, 25]. Organic Se can be absorbed into the phloem and then translocated to grains via the stem, while most inorganic Se is translocated through the xylem to grains [26].

It has been reported that selenite is absorbed by roots via passive diffusion or phosphate transporters [11, 23]. Studies have demonstrated that the translocation of selenite between different plant organs is promoted by phosphorus (P) application [27]. P fertilizer increased the Se concentration in the soil and then promoted Se absorption and accumulation in rice [28]. However, several studies have shown that there is an antagonistic effect between phosphate and selenite. Therefore,

the interaction of phosphate and selenite still needs to be verified. Generally, phosphate has little effect on the uptake of selenate due to their chemical dissimilarities. P starvation had no effect on selenate uptake but decreased selenate concentration in the xylem sap of selenatetreated plants in hydroponic experiments [11]. Some studies reported that P application increased the utilization of selenate and then increased the Se contents in plants [29, 30]. Compared with the numerous studies on inorganic Se, few studies have focused on the uptake of organic Se influenced by P application in plants.

Generally, inorganic Se (selenite and selenate) and selenoamino acids (SeMet, SeCys₂ and Se-methyl-selenocysteine (MeSeCys)) are present in plants [13, 22, 31]. Compared with inorganic Se, organic Se is safer to human health. Studies have noted that different Se sources, P nutrient states and crop varieties have a significant influence on Se species in plants [13, 20, 32, 33]. Selenite can be quickly assimilated in roots and then converted into organic Se (SeMet, SeCys or Selenomethionine selenoxide (SeOMet)); however, selenate can be detected in shoots due to its quick mobility during xylem transport [11]. Studies have demonstrated that P deficiency increased the proportion of MeSeCys in rice, but MeSeCys was not detected when P was added to the nutrient solution [13]. The most abundant organic Se is SeMet in wheat and rice, while the main Se species in Indian mustard roots are dimethyl selenide (DMeSe) and SeMeCys. However, SeCys₂ and SeMet combine with the protein fraction, affecting the normal structure of the protein and leading to toxicity [20, 34]. Therefore, the study of the proportion of Se species and subcellular fractions in plants is required to assess Se biofortification.

The objectives of this hydroponic study were to investigate (1) the interactive effects of P combined with three types of Se fertilizer on the absorption, transport and distribution of Se in wheat and (2) the subcellular fraction and speciation of Se in response to P combined with Se treatment. Our findings will improve our understanding of the interaction of P and Se in plants and our ability to more effectively regulate the nutritional quality of winter wheat grain via the application of P and Se fertilizers in agricultural practice.

Results

P concentration and accumulation in wheat

Se and P application the interaction between Se and P had significant effects on P concentration and accumulation in shoots and roots, except for the P concentration and accumulation in roots influenced by Se fertilizers (p < 0.01; Table S1).

Compared with $P_{0.01}$, $P_{0.1}$ and P_1 significantly increased the P concentration and accumulation in shoots and

roots with selenite and SeMet treatment (Fig. 1). With selenate treatment, $P_{0.1}$ and P_1 significantly increased the P concentration and accumulation in shoots but decreased the P accumulation in roots compared to $P_{0.01}$.

For $P_{0.01}$, the root P concentration and accumulation with selenate treatment were higher than those with selenite and SeMet treatment (Fig. 1). For $P_{0.1}$, the P concentrations in shoots with SeMet and selenate treatment were higher than those with selenite treatment, but the P accumulation in roots showed the opposite result. For P_1 , the highest shoot P concentration and accumulation were obtained with SeMet treatment, but the highest root P concentration and accumulation were obtained with selenite treatment.

Se concentration and accumulation in wheat

Se and P application and the interaction between Se and P had significant effects on Se concentration and accumulation in shoots and roots (p < 0.01; Table S2).

With selenite treatment, the Se concentration and accumulation in shoots and roots significantly decreased with increased P application (Fig. 2). Compared with $P_{0.01}$, $P_{0.1}$ and P_1 increased the Se concentration in shoots and roots with selenate treatment. With SeMet

For each P application rate, Se concentrations and accumulation in shoots and roots with SeMet treatment were significantly higher than those with selenite and selenate treatment (Fig. 2).

P and Se translocation and distribution in wheat

Se and P application and the interaction between Se and P had significant effects on the P and Se migration coefficients, except for the P migration coefficient influenced by P application (p < 0.01; Table S3).

With selenate and SeMet treatment, $P_{0.1}$ and P_1 significantly increased the P migration coefficient compared to $P_{0.01}$ (Fig. 3A). Compared with $P_{0.01}$, $P_{0.1}$ and P_1 significantly increased the Se migration coefficient with selenate treatment (Fig. 3B). For $P_{0.01}$, the P migration coefficient with selenate treatment was lower than that with selenite and SeMet treatment, but for $P_{0.1}$ and P_1 , the P migration coefficient had the opposite result (Fig. 3A). For each P application rate, the Se migration coefficient with selenate treatment was significantly higher than that with selenite and SeMet treatment (Fig. 3B).



Fig. 1 P concentration and accumulation in shoots (A and C, respectively) and roots (B and D, respectively) of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application



Fig. 2 Se concentration and accumulation in shoots (A and C, respectively) and roots (B and D, respectively) of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application



Fig. 3 P (A) and Se (B) migration coefficient from root to shoot in tissues of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

With selenate and SeMet treatment, $P_{0.1}$ and P_1 significantly increased the distribution of P in shoots compared to $P_{0.01}$ (Fig. 4A). For $P_{0.01}$, the distribution of P in shoots with selenite treatment was higher than

with selenate and SeMet treatment, but the opposite result was observed for $P_{0,1}$ and P_1 . With selenite and selenate treatment, the distribution of Se in shoots first increased and then decreased with increasing P



Fig. 4 Relative distribution of P (A) and Se (B) of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

application (Fig. 4B). For each P application rate, the distribution of Se in shoots with selenate treatment was higher than that with selenite and SeMet treatment.

Se subcellular fraction and distribution in wheat

Se and P application and the interaction between Se and P had significant effects on the subcellular fraction of Se in shoots and roots (p < 0.01; Table S4).

With selenite treatment, the Se concentration in each fraction of the three tissues all showed a significant decrease with increasing P application rates (Table 1). However, there were no pronounced differences in the Se concentrations in each fraction of shoots and roots between different P application rates with selenate treatment. With SeMet treatment, P_{0.1} and P₁ significantly decreased Se concentrations in shoot cell organelles and in root cell walls.

For all the treatments, the proportion of Se in the cell wall of shoots and roots was higher than that in the cell organelle and soluble fractions, except for that for P_1 -selenite (Fig. 5). With selenite treatment, the Se proportion in the cell wall of shoots increased, but the Se proportion in the soluble fractions of shoots decreased with increasing P application rates (Fig. 5A); however, $P_{0,1}$ and P_1 decreased the Se proportion in the cell wall of roots but increased the Se proportion in the soluble fractions of roots compared to $P_{0.01}$ (Fig. 5B). With selenate and SeMet treatment, an increase in the P application

Table 1 Subcellular fractions of Se in tissues of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

Treatment		Cell wall	Cell organelle	Soluble fraction	Cell wall	Cell organelle	Soluble fraction
Se species (2 µmol·L ⁻¹)	P (mmol·L ⁻¹)	Shoot			Root		
Selenite	0.01	8.27±0.08b	$0.62 \pm 0.04c$	4.99±0.74c	$9.46 \pm 0.32d$	$2.30 \pm 0.27 b$	3.50±0.23b
	0.1	$2.62 \pm 0.06c$	$0.21 \pm 0.02d$	$0.68 \pm 0.02 ef$	$0.85\pm0.03f$	0.27 ± 0.02 de	$0.46 \pm 0.08c$
	1	$0.56 \pm 0.09 d$	0.08 ± 0.01 d	$0.06 \pm 0.00 f$	$0.02\pm0.00 f$	$0.02 \pm 0.00e$	0.06 ± 0.04 d
Selenate	0.01	1.80 ± 0.05 cd	$0.31c \pm 0.04cd$	$1.32 \pm 0.03 d$	$2.67 \pm 0.11e$	0.59 ± 0.07 cd	$0.46 \pm 0.05 ef$
	0.1	1.77 ± 0.05 cd	0.31 ± 0.03 cd	$1.54 \pm 0.03 d$	$2.47 \pm 0.18e$	0.57 ± 0.05 cd	$0.60 \pm 0.05e$
	1	1.81 ± 0.17 cd	0.30 ± 0.02 cd	$1.55 \pm 0.20d$	$2.46 \pm 0.07e$	0.47 ± 0.03 cd	$0.65 \pm 0.03e$
SeMet	0.01	$28.3 \pm 1.20a$	8.45±0.06a	$8.65 \pm 0.32a$	$31.7 \pm 0.95a$	2.84±0.17a	4.73±0.26b
	0.1	$27.3 \pm 0.84a$	$7.06 \pm 0.48 b$	7.96±0.51ab	$19.5 \pm 0.89 b$	$2.78 \pm 0.24a$	$4.61 \pm 0.30 b$
	1	$26.9 \pm 1.85a$	$7.10 \pm 0.14 b$	$7.40 \pm 0.23 b$	$15.9 \pm 1.39c$	$2.73 \pm 0.15a$	$3.56 \pm 0.07c$

Values are the means of three independent replicates (\pm sd). For each trait, values followed by different letters are significantly different from each other according to two-way ANOVA followed by least significant difference (LSD) multiple comparison (p < 0.05)



Fig. 5 Proportion of subcellular distribution of Se in shoots (A) and roots (B) of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

rate had no significant influence on the proportion of Se. For each P application rate, the Se proportion in the cell wall of shoots with selenite treatment was higher than that with selenate and SeMet treatment (Fig. 5A); the Se proportion in the soluble fraction of roots with selenite treatment was higher than that with selenate and SeMet treatment, but the opposite result was observed for the Se proportion in the cell wall of roots (Fig. 5B).

Se species

Se application had significant effects on Se (IV), Se (IV), SeCys₂, MeSeCys and SeMet concentrations in shoots and roots (P < 0.01; Table S5); P application had significant effects on Se (IV), MeSeCys and SeMet concentrations in shoots as well as Se (IV), SeCys₂, MeSeCys and SeMet concentrations in roots (P < 0.01); the interaction between Se and P had significant effects on Se (IV), Se (IV), MeSeCys and SeMet concentrations in shoots as well as Se (IV), Se (IV), SeCys₂, MeSeCys and SeMet concentrations in roots (p < 0.01 or p < 0.05).

With selenite treatment, Se (IV) was detected only in roots, and increasing P application rates significantly reduced the concentrations of SeCys₂, MeSeCys and SeMet in shoots and roots as well as Se (IV) concentrations in roots (Table 2). With selenate treatment, $P_{0.1}$ and P_1 decreased Se (IV) concentrations in shoots but increased those in roots compared to $P_{0.01}$. With SeMet treatment, P_{0.1} and P₁ significantly decreased the shoot and root SeMet concentrations but significantly increased the root SeCys₂ concentrations.

The most abundant Se species were SeMet and MeSe-Cys in most cases (Fig. 6). With selenite treatment, the proportion of MeSeCys and SeMet in roots gradually increased, but the SeCys₂ proportion in roots decreased with increasing P application rates. With selenate treatment, an increase in P application increased the Se (VI) and MeSeCys proportions in each tissue but decreased the shoot SeMet proportion. With SeMet treatment, the SeMet proportion in shoots and roots was reduced, but the SeCys₂ proportion in each tissue increased with increasing P application rate.

Dry matter weights

Se and P application and the interaction between Se and P had significant effects on the dry matter weight in the shoots and roots of winter wheat (P < 0.01; Table S6).

Compared with $P_{0.01}$, $P_{0.1}$ and P_1 significantly increased the dry matter weights of shoots under selenite and SeMet treatments (Table 3). Both P application rates ($P_{0,1}$) and P_1) decreased the dry matter weights of roots in the selenate and SeMet treatments, respectively; however, in the presence of selenite, the dry matter weights of roots in the $P_{0,1}$ treatment were higher than those in the $P_{0,01}$ and P₁ treatments.

As P was applied at 0.01 mmol L^{-1} , the dry matter weight of shoots and roots in the selenate treatment was higher than that in the selenite and SeMet treatments; at $P_{0,1}$, the dry matter weight of shoots and roots showed selenite > SeMet > selenate treatment; however, at P_1 , the dry matter weight of shoots and roots in the selenite and SeMet treatments was significantly higher than that in the selenate treatment.

Root morphology parameters

Se and P application and the interaction between Se and P had significant effects on the root length, surface,

Treatment		Se (IV)	Se (VI)	SeCys ₂	MeSecys	SeMet
Se species (2 µmol·L ⁻¹)	P (mmol·L ⁻¹)	Shoot				
selenite	0.01	ND	ND	1.36±0.08b	3.59±0.33b	25.6±1.06d
	0.1	ND	ND	$0.78 \pm 0.03 bc$	$1.41 \pm 0.42c$	$7.31 \pm 0.22e$
	1	ND	ND	$0.21 \pm 0.05c$	$0.44 \pm 0.10c$	$3.28\pm0.38f$
selenate	0.01	ND	$3.44 \pm 0.37a$	$0.54 \pm 0.03c$	$0.42 \pm 0.04c$	$3.47 \pm 0.40 f$
	0.1	ND	$4.12 \pm 0.42a$	$0.55 \pm 0.03c$	$0.67 \pm 0.25c$	$3.35 \pm 0.56 f$
	1	ND	$0.09 \pm 0.01 f$	$0.51 \pm 0.12c$	$0.79 \pm 0.46c$	$3.57 \pm 0.12 f$
SeMet	0.01	$1.23 \pm 0.11a$	ND	$3.33 \pm 0.82a$	13.2±0.45a	90.6±1.45a
	0.1	1.15±0.11a	ND	$3.26 \pm 0.30a$	12.7±0.79a	54.4±0.01b
	1	$1.42 \pm 0.12a$	ND	$3.71 \pm 0.57a$	$12.5 \pm 1.23a$	41.4±0.13c
Se species (2 µmol·L ⁻¹)	P (mmol·L ^{−1})	Root				
selenite	0.01	1.69±0.05bc	ND	$10.9 \pm 0.68a$	$3.08 \pm 0.34 d$	$16.3 \pm 0.31 d$
	0.1	0.71 ± 0.03 cd	ND	1.85±0.16c	1.13 ± 0.10 de	$6.30 \pm 0.49 e$
	1	0.21 ± 0.01 d	ND	0.58 ± 0.01 d	$0.66 \pm 0.02e$	$3.15 \pm 0.18 ef$
selenate	0.01	ND	$0.64 \pm 0.10 b$	ND	0.79 ± 0.04 de	$1.64 \pm 0.09 f$
	0.1	ND	$1.04 \pm 0.13 b$	ND	1.04±0.05de	$1.23 \pm 0.09 f$
	1	ND	$2.14 \pm 0.46a$	ND	2.01 ± 0.10 cd	$1.19 \pm 0.11 f$
SeMet	0.01	2.54±0.18ab	ND	1.90 ± 0.07 cd	$25.3 \pm 1.14a$	$65.3 \pm 3.40a$
	0.1	2.72±0.72ab	ND	$6.29 \pm 0.39 b$	$17.2 \pm 0.85b$	52.5 ± 0.90 b
	1	$3.49 \pm 0.78a$	ND	10.5±0.83a	16.8±0.78b	38.3±4.30cd

Table 2 Se species in tissues of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

Values are the means of three independent replicates (\pm sd). For each trait, values followed by different letters are significantly different from each other according to two-way ANOVA followed by least significant difference (LSD) multiple comparison (p < 0.05). ND indicates that the value was below the detection limit. Se (IV), selenite; Se (VI), selenate; SeCys₂, selenocystine; MeSeCys, Se-methyl-selenocysteine; SeMet, selenomethionine



Fig. 6 Proportion of Se species in shoots (A) and roots (B) of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application. Se (IV), selenite; Se (VI), selenate; SeCys₂, selenocystine; MeSeCys, Se-methyl-selenocysteine; SeMet, selenomethionine

volume, tip number and forks, except for the average root diameter influenced by P application (p < 0.01 or p < 0.05; Table S7).

With selenite treatment, the total root length, surface area, tip number and fork first increased and then decreased as P application increased, but $P_{0.1}$

Table 3 Shoot and root dry matter weights of winter wheat (*Triticum aestivum* cv. Bainong 207) seedlings as an effect of P and Se application

Treatment		Shoot/(g, DW)	Root/(g, DW)	
Se species (2 µmol·L ⁻¹)	P (mmol·L ⁻¹)			
Selenite	0.01	$0.39 \pm 0.01 f$	0.27±0.01bc	
	0.1	$0.88 \pm 0.05a$	$0.29 \pm 0.01 b$	
	1	0.68 ± 0.00 bc	0.22 ± 0.01 d	
Selenate	0.01	$0.53 \pm 0.02 de$	$0.34 \pm 0.01a$	
	0.1	0.60 ± 0.01 cd	0.20 ± 0.01 de	
	1	$0.51 \pm 0.02e$	$0.19 \pm 0.02e$	
SeMet	0.01	$0.50 \pm 0.01 e$	0.26 ± 0.00 bc	
	0.1	$0.73 \pm 0.01 b$	0.22 ± 0.01 de	
	1	$0.77 \pm 0.03 b$	0.25 ± 0.00 cd	

Values are the means of three independent replicates (\pm sd). For each trait, values followed by different letters are significantly different from each other according to two-way ANOVA followed by least significant difference (LSD) multiple comparison (p < 0.05)

and P_1 decreased the root volume and average diameter (Table 4). The root length, surface area, volume, tip number and fork significantly decreased with increasing P application rates with selenate treatment. With SeMet treatment, the total root length, surface area, volume, average diameter and fork first increased and then decreased with increasing P application, but $P_{0.1}$ and P_1 significantly increased the root tip numbers.

For $P_{0.01}$, the total root length, surface area, tip number and forks with selenate treatment were higher than those with selenite and SeMet treatment (Table 4). For $P_{0.1}$ and P_1 , the total root length, tip number and forks with selenite treatment were higher than those with selenate and SeMet treatment; however, for $P_{0.1}$, the root volume and average diameter with SeMet treatment were higher than those with selenite and selenate treatment.

Photosynthesis

Se and P treatments and the interaction between Se and P had significant effect on net photosynthetic rate (P_n) , stomatal conductance (G_s) , intercellular CO₂ concentration (C_i) and transpiration rate (T_r) (p < 0.01; Table S8).

Compared with $P_{0.01}$, $P_{0.1}$ and P_1 significantly increased P_n , G_s , C_i and T_r with each Se fertilizer, with the highest values for $P_{0.1}$ with both selenite and SeMet (Table 5).

For $P_{0.01}$, G_s and T_r with selenate treatment were significantly higher than those with selenite and SeMet treatment, and *Ci* with selenate and SeMet treatment was significantly higher than that with selenite treatment (Table 5). For $P_{0.1}$ and P_1 , G_s , C_i and T_r with SeMet treatment were significantly higher than those with selenite and selenate treatment, but P_n with selenite treatment was significantly higher than that with selenite treatment was significantly higher than that with selenate and SeMet treatment for $P_{0.1}$.

Discussion

P and Se uptake, translocation and distribution

The mechanisms of uptake and transport of selenite, selenate and SeMet are different in plants [11, 35]. Selenite, selenate and SeMet are absorbed in plants via P transporters, sulfur (S) transporters and aquaporins, respectively [17, 23, 36–38]. In this study, at the same P application level, the Se concentration of each wheat organ with SeMet treatment was higher than that with selenite and selenate treatment (Fig. 2), which is in agreement with the results of Ali et al. [39], Huang et al. [40] and Eich-Greatorex et al. [41], who pointed out that the

 Table 4
 Root morphology parameters of winter wheat (Triticum aestivum cv. Bainong 207) seedlings as an effect of P and Se application

Treatment		Total root length	Surface area (cm ²)	Volume (cm ³)	Average diameter	Tip numbers	Forks	
Se species (2 µmol·L ⁻¹)	P (mmol·L ⁻¹)	(mm)			(mm)			
Selenite	0.01	782±4.55c	66.9±0.37c	$0.44 \pm 0.02 b$	0.27±0.01b	976±5.79d	1810±0.41g	
	0.1	993±9.04a	$84.4 \pm 3.02a$	$0.42 \pm 0.00 b$	$0.23 \pm 0.00 f$	$1856 \pm 3.67a$	$3486 \pm 4.90a$	
	1	$725 \pm 5.89e$	$54.8 \pm 1.22 f$	$0.33 \pm 0.01 e$	0.24 ± 0.00 de	1448±7.79b	$2523 \pm 9.09 d$	
Selenate	0.01	$895 \pm 4.53b$	$71.0 \pm 2.39b$	$0.42 \pm 0.01 \text{b}$	0.24 ± 0.00 de	1414±7.41b	$2887 \pm 5.72 b$	
	0.1	791±5.62c	$59.0 \pm 1.17e$	0.37 ± 0.02 cd	0.24 ± 0.01 de	$1210 \pm 4.99c$	$2363 \pm 6.94e$	
	1	$645 \pm 4.02g$	$53.0 \pm 2.22 f$	0.35 ± 0.02 de	$0.26 \pm 0.00 \text{bc}$	$1020 \pm 6.94 d$	$1983\pm12.4 \mathrm{f}$	
SeMet	0.01	764±8.76d	$62.5 \pm 0.73 d$	$0.39 \pm 0.01c$	$0.26 \pm 0.00 \text{bc}$	$750\pm2.83f$	$1949 \pm 7.76 g$	
	0.1	887±6.88b	70.7±0.06b	$0.54 \pm 0.01a$	$0.30 \pm 0.01a$	$830 \pm 4.90e$	$2748 \pm 7.41c$	
	1	$671 \pm 5.62 f$	$54.4 \pm 0.73 f$	0.35 ± 0.01 de	0.25 ± 0.00 cd	1243±8.83c	1686±6.94i	

Values are the means of three independent replicates (\pm sd). For each trait, values followed by different letters are significantly different from each other according to two-way ANOVA followed by least significant difference (LSD) multiple comparison (p < 0.05)

Treatment		Net photosynthetic rate	Stomatal conductance	Intercellular CO ₂	Transpiration rate
Se species (2 µmol·L ⁻¹)	P (mmol·L ⁻¹)	(μmol CO ₂ m ⁻² s ⁻¹)	(mol H ₂ O m ⁻² s ⁻¹)	concentration (μmol CO ₂ m ⁻²)	(mol H ₂ O s)
Selenite	0.01	7.73±0.36d	0.03±0.01f	$65.2 \pm 4.56 f$	0.45±0.10e
	0.1	13.4±0.16a	$0.13 \pm 0.00c$	$381 \pm 10.2b$	2.13±0.08c
	1	11.0±0.65c	$0.09 \pm 0.00e$	331±7.17e	$1.34 \pm 0.10d$
Selenate	0.01	$8.54 \pm 0.36d$	$0.08 \pm 0.00e$	$355 \pm 10.5 d$	$1.31 \pm 0.07 d$
	0.1	10.4±0.37c	$0.12 \pm 0.00d$	383±9.81b	1.87±0.06c
	1	10.0±0.71c	$0.15 \pm 0.01c$	$383 \pm 6.90b$	$2.00 \pm 0.29c$
SeMet	0.01	7.61 ± 0.40 d	$0.04 \pm 0.01 f$	$365 \pm 10.8 cd$	0.58±0.11e
	0.1	12.0±0.15b	$0.22 \pm 0.01a$	$407 \pm 3.48a$	$3.22 \pm 0.18a$
	1	10.7±0.33c	$0.20 \pm 0.00 b$	$403 \pm 2.08a$	$2.81 \pm 0.04 b$

Table 5 Photosynthetic characteristics of winter wheat (*Triticum aestivum* cv. Bainong 207) seedlings as an effect of P and Se application

Values are the means of three independent replicates (\pm sd). For each trait, values followed by different letters are significantly different from each other according to two-way ANOVA followed by least significant difference (LSD) multiple comparison (p < 0.05)

uptake rate of SeMet in rice roots was significantly higher than that of inorganic Se based on Se concentrationdependent kinetics. This might be related to the fact that organic selenium has higher biological activity and absorption efficiency than inorganic selenium [42]. Some studies pointed that foliar spraying of selenite had higher Se concentration than selenate due to selenite can rapidly convert to organic forms [21, 43]. However, other studies showed that the Se concentration in each tissue of wheat with selenate treatment was higher than that with selenite treatment because selenate had greater bioavailability than selenite [30, 44, 45]. Wang et al. [33] noted that the Se concentration of tomato relative to Se application rate, when Se application rate was 0.0175-0.2998 $mg \cdot L^{-1}$, selenate treatment was tenfold greater than that with selenate treatment in hydroponic experiments, but the opposite result was observed in other Se concentrations. Luo et al. [46] demonstrated that mycorrhizal inoculation improved the valid absorption area of roots and promoted the increased uptake of Se. In our study, Se concentration of shoots and roots with selenite treatment was higher than that with selenate treatment (Fig. 2A and B), this result might be attributed to an appropriate amount of P combined with selenite treatment altered root morphological parameters compared to that with selenate treatment (Table 4). The current results suggested that the difference in Se concentration between selenite, selenate and SeMet can be explained by their different uptake mechanisms, Se application level and Se application methods [11, 46, 47].

Previous studies have shown that Se absorption and accumulation in plants are affected by P application [11, 45]. In our study, an increase in the P application rate significantly reduced Se concentration and accumulation in

shoots and roots with selenite treatment (Fig. 2). Zhang et al. [23] and Li et al. [38] demonstrated that increasing the P application rate significantly decreased the expression of P transporters in roots and further decreased Se concentrations in plants. Liu et al. [48] also noted that P_{3,1} and P₃₁ significantly inhibited Se absorption and decreased the Se concentration of wheat compared with $P_{0.31}$, which is consistent with our results, possibly because P application inhibited the uptake of selenite. With selenate treatment, P_{0.1} and P₁ increased the Se concentration in shoots and roots (Fig. 2A and B). Previous studies demonstrated that selenate uptake by plants via sulfate (S) transporters due to the similar chemical properties between selenate and sulfate [49, 50]. Schmittgen et al. [51] indicated that -S significantly upregulated the expression of Sultr1;1 compared to +S treatment and increased Se accumulation in grain. However, Zhang et al. [30] noted that P fertilizer activated organic matter-bound Se and increased the Se concentration and accumulation of wheat with selenate treatment, but significantly inhibited Se uptake with selenite treatment due to antagonism between the absorption of P and Se [45], this is consistent with the results of our study. Previous studies showed that SeMet are absorbed in plants be found to be an energydependent symport process involving H⁺ transport [25, 52]. The present results showed that an increase in P application rates decreased the Se concentration in shoots and roots with SeMet treatment (Fig. 2A and B), which might be related to the dilution effect by an increase in plant growth as a result of increased P application rates or P involved in energy metabolism process. Therefore, the effect of P application on Se concentration and accumulation depended on the type of Se fertilizer, but further verification of this possibility is still needed [53].

The translocation factor is used to characterize the transfer ability of nutrient elements in plants [54]. Previous studies have shown that the migration of Se from roots to shoots is closely related to the type of Se [55]. Selenate has a stronger mobility, but a small amount of selenite is transported in the xylem of plants [56, 57]. The Se migration coefficient with selenate treatment was 40-90 % higher than that with selenite treatment [39], selenite readily accumulates in roots, selenate is more easily transported from root to shoot, and 70 % of the total Se is present in the straw of rice [58–60]. The present results showed that the Se migration coefficient with selenate treatment was significantly higher than that with selenite and SeMet treatment at the three P application rates (Fig. 3B), resulting in most Se being distributed in the roots with selenite treatment, while more Se was found in the shoots with selenate treatment (Fig. 4B), which is in agreement with the findings of Wang et al. [22]. Additionally, a high P application rate (P_1) reduced the Se migration coefficient with selenite treatment (Fig. 3B). Zhang et al. [23] showed that P transporters (OsPT6) are involved in Se migration from roots to shoots in rice, and P application decreased the Se translocation coefficient. Lazard et al. [61] also demonstrated that there is competition between P and selenite ions for both Pi transport systems by studying the corresponding kinetic parameters. In contrast, the migration coefficient and distribution of P and Se in shoots increased with increasing P application rates with selenate treatment (Figs. 3 and 4), which suggested that P and selenate had synergistic effects on the uptake of P and Se in plants. This might be because P application enhanced transpiration and further promoted selenate translocation in plants [62].

Subcellular distribution of Se

The compartmentalization effect of metals and metallike elements in cells can greatly affect the level of free heavy metal ions in cells, thus affecting the movement of ions in plants [63, 64]. Se can be considered both a nutrient and toxic to plants because the gap between beneficial and toxic levels is narrow [65, 66]. Roots have a known series of important functions for defending against toxic elements, including binding elements to cell walls or sequestering them in vacuoles, and then inhibiting the translocation of these elements to shoots [67, 68]. In our study, the subcellular distribution of Se in each part of wheat occurred in the order of cell wall > cell soluble fraction > cell organelles with the three Se fertilizers, regardless of P application (Fig. 5B). Su et al. [69] found that the cell wall and vacuole (soluble fraction) can sequester more metal ions to limit the movement of ions in plants. A previous study demonstrated that the cell wall plays an important role in Se binding [67]. In the wheat roots, an increase in P application decreased the Se concentration in each fraction and the distribution of Se in the root cell wall but increased that in the root soluble fraction with selenite treatment (Table 1 and Fig. 5B). Our results are consistent with the findings of Wang et al. [13], who noted that compared with P-normal treatment, P deficiency combined with -P+Se treatment increased the proportion of Se distributed in the root cell wall but reduced the Se distribution in the root soluble fraction. These results indicated that increasing the P supply could inhibited the transmembrane transportation of Se to reduce cell wall-bound Se and then decreased the Se migration coefficient from roots to shoots in wheat [70]. In contrast, an increase in P supply level increased the distribution of Se in the shoot cell wall and cell organelles and decreased the shoot soluble fraction, which is consistent with the results of Liu et al. [48]. Winkel et al. [71] indicated that increasing distribution of Se in the cell organelle is related to enhance metabolism of Se. Therefore, this result may also indicate that an increase in the P supply level may promoted Se metabolism. However, P application had no obvious influence on the subcellular distribution of Se with SeMet and selenate treatment (Table 1, and Fig. 5), which might be because the uptake pathway of selenate is via sulfate transporters and that of SeMet is via aquaporins, respectively, but not phosphate transporters [17]. Li et al. [11] also indicated that P application significantly inhibited the influx of selenite, and had no significant effect on Se uptake with selenate treatment, whereas S-starved treatment increased Se uptake and translocation by 9.5-fold in the presence of selenate.

Se species

It is well known that Se is chemically similar to S [72], and Se is converted into organic forms through the S metabolic pathway after being absorbed by plant roots [73, 74]. Selenate is first converted into selenite via two enzymes known as ATP sulfurylase (APS) and APS reductase (APR) in plants [75], and then selenite is converted into selenide and SeCys by sulfite reductase (SiR) and cysteine synthase; some SeCys can be converted into SeMet by a series of enzymes [66, 76]. In our study, the main Se species in wheat was SeMet (Table 2, Fig. 6), which is consistent with the results of previous studies [77, 78]. However, different Se fertilizers had significant effects on Se species in plants. For example, SeMeCys was dominant when selenite was supplied, but Se (VI) was dominant with selenate addition in Brassica rapa [79]. SeMet was the major form of Se in the roots and shoots of rice with SeNPs or selenite treatment [80]. Our study showed that Se(VI) (20.8-45.8 %) and SeMet (22.5-55.0 %) were the main species in the roots and shoots of wheat when selenate was applied (Fig. 6), which is consistent with the results of Li et al. [11] and Li et al. [81]. This might be related to the fact that selenate is not completely converted into organic Se as a result of the high uptake rates or storage of Se in vacuoles [20, 82]. Selenite was quickly metabolized to organic Se (SeCys₂, MeSeCys and SeMet) after absorption in roots and then transported to shoots in the form of organic Se [37], which might be the reason that Se (IV) was detected only in roots (Table 2). Oliveria et al. [83] also showed that inorganic Se was most likely transformed in root chloroplasts because selenoamino acids are known to exist in the chloroplasts of plant roots by genetic control. With SeMet treatment, SeMet and MeSeCys accounted for more than 79.0 % of the total Se, but low concentrations of Se (IV) and SeCys₂ were detected in roots and shoots (Fig. 6). This is consistent with the results of Wang et al. [52], who showed that SeMet and MeSeCys were the dominant species in organic Se-treated wheat.

In the present study, increasing the P application rate promoted the transformation of Se species with three types of Se fertilizers (Table 2, Fig. 6). With selenite treatment, an increase in P application elevated the proportion of SeMet, but decreased the proportion of SeCys₂ (Fig. 6B), this result was consistent with the result of Wang et al. [13], who showed that additional P under P-deficient condition induced a strong reduction in the proportion of SeMet but increased the proportion of Se (VI) and SeCys₂ in the roots of rice. Moreover, the proportion of Se (VI) was increased, but the proportion of SeMet in shoots and roots was decreased by P application with selenate treatment (Fig. 6). A previous study suggested that little selenate was assimilated into organic forms due to selenate was highly mobile in xylem transport [11]. Therefore, it was speculated that an increase in P application increased Se migration coefficient with selenate treatment due to selenate can rapidly mobile (Fig. 3B). However, with SeMet treatment, increasing the P supply decreased the proportion of SeMet but increased the proportion of SeCys₂ in roots and shoots (Fig. 6). SeCys₂ can be converted into MeSeCys via methylation and SeMet by a series of enzymes (i.e., cystathionine-γ -synthase, cystathionine- β -lyase, and Met synthase) [76], and P plays an important roles on protein synthesis and energy metabolism. Our study showed that P application had different influences on the proportion of Se species in each organ with three types of Se sources, which was probably due to their different uptake mechanisms, and altered the bioavailability of Se [13, 17]. However, further studies on how Se metabolism is mediated by P application are still needed.

Dry matter weight, root morphological parameters and photosynthesis of wheat

Studies demonstrated that root growth and photosynthesis of plant play a vital role in the growth and yield of crops, root and photosynthesis are closely related to the uptake of nutrient elements and organic matter accumulation, respectively [84]. Studies showed that plants can adjust their root length, volume, surface area, average diameter, tip numbers and forks to adapt to different P conditions [85], and P starvation decreased ATP synthase activity because P is the substrate for ATP synthesis in the chloroplast stroma and also significantly decreased the photosynthesis of barley [86]. Our results showed that an increase in P application had significant effect on root morphological parameters and photosynthesis of winter wheat in each Se sources (Tables 4 and 5). Loudari et al. [87] noted that an adequate amount of P significantly increased the photosynthetic parameters and biomass in wheat. Although Se is not an essential element for plants, it is beneficial for plant growth and photosynthesis [88]. Se application increased photosynthetic pigments content, including chlorophyll a, chlorophyll b and carotenoid, and then enhanced photosynthesis [89]. Roda et al. [90] analysed the transcriptome of rice flag leaves and found that selenite application promoted vitamin biosynthesis and metabolism, which are involved in photosynthesis in rice. Low-dose selenite treatment (0.5 and 1 mg kg^{-1}) stimulated plant growth by enhancing root activities, but high Se levels (50 and 100 mg·kg⁻¹) decreased root activity [91]. Different Se species as well as their application rates affect the crop yield and biomass of plants [33, 92, 93]. Previous studies showed that 2 $mg \cdot kg^{-1}$ Se (VI) significantly inhibited wheat plant growth and decreased plant height compared to 0.5 $mg \cdot kg^{-1}$ Se (IV) treatment [94]. Li et al. [32] pointed that selenite application can improve the root activity of lettuce and increase the root fresh weights and root length, but selenate has no significant influence on root activity. However, some studies indicated that P nutritional status significantly affects plant growth under different Se application conditions [30, 95]. In our study, P application rate had different effects on wheat growth with different Se fertilizers (Table 3). These may indicate that the effect of Se fertilizer on the growth of plant is closely related to the type of Se, Se application levels and P conditions [22].

In the present study, an increase in P application promoted plant growth and increased the dry matter weight in shoots and roots with selenite treatment, where the highest value appeared under the $P_{0.1}$ treatment, this may be because an appropriate amount of P combined with selenite significantly promoted the uptake of nutrient elements and organic matter accumulation, and then promoted plant growth by improved photosynthesis and root morphology parameters (the total root length, surface area, tip numbers and forks) of winter wheat (Tables 4 and 5), which is in agreement with the results of Nie et al. [95], who pointed out that P application increased the biomass of shoots, and P combined with selenite promoted root growth [49]. Qin et al. [96] also noted that selenite application significantly altered root morphological parameters and photosynthesis with Cd treatment, and then remitted Cd toxicity. However, P_{0.1} and P_1 significantly decreased the dry matter weight in roots with selenate treatment (Table 3). Previous studies indicated that P starvation caused a large number of crown roots, a high lateral root density, and a large number of adventitious roots with a shallow root growth angle, but sufficient P application had exactly the reverse effect [97, 98]. It was revealed that P is critical in promoting plant growth in agricultural practices, and selenate application had no obvious effect on the root morphological parameters when P was combined with selenate compared to that with selenite and SeMet, which may be because P plays a leading role in root growth. Therefore, increasing P application decreased the dry matter weight in roots through inhibited root morphology parameters (Tables 3 and 4). Our results also showed that photosynthesis $(P_n \text{ and } G_s)$ and root morphological parameters with selenite and SeMet treatment were higher than those with selenate treatment when P was supplied at 0.1 mmol· L^{-1} (Table 5). This may be because selenite and SeMet application can increased the photosynthetic pigment and altered root activity of plants when Se application level was 2 μ mol·L⁻¹, but the opposite result was observed for selenate. The reason for this difference may be that the selenate application level was too high for winter wheat in our experiment, resulting in plant toxicity, decreased plant organic matter accumulation and the dry matter weight of roots (Table 3) [89, 99, 100]. Zhang et al. [30] pointed that compared with no P fertilizer treatment, P fertilizer treatment significantly increased wheat biomass with selenate treatment (1 or 2 mg·kg⁻¹) in a pot experiment. The reasons for these different results may be related to the differences in Se and P application rates and cultivation methods [22, 38]. This result showed that an appropriate amount of P combined with selenite can promote winter wheat growth compared with selenate and SeMet treatment, and also pointed out that different Se sources have different responses to the dry matter weight of wheat under the same Se application level [32, 49, 101].

Conclusion

We first reported that the effects of the uptake, translocation and subcellular distribution and species of Se in wheat by P application with three types of Se fertilizers. With selenite treatment, although increased P application decreased Se uptake and translocation, an appropriate amount of P promoted wheat growth, photosynthetic and altered the Se species fraction, and then has significantly influence on Se bioavailability in wheat. P fertilizer application should be balanced in actual production. With selenate treatment, an increase in P application promoted Se uptake and translocation, but P combined with selenate application inhibited root growth of winter wheat, it caused toxicity to plant growth when Se application level was 2 μ mol·L⁻¹ in this experiment. With SeMet treatment, increased P application decreased Se concentration of winter wheat, this might be related to the dilution effect by an increase in plant growth, but significantly increased photosynthesis and the dry matter weight of shoots. The proportion of Se species in winter wheat was related to the Se sources and P application rate. Therefore, we should consider rational application of P fertilization and the types of Se fertilizer in soil in field agricultural production. Our results provided critical reference on the effective agricultural production of Se-enriched wheat. However, further studies are needed to elucidate the transformation of Se species by P application.

Materials and methods

Plant materials and treatment

A hydroponic experiment was conducted in a greenhouse with controlled environmental conditions of approximately 14/10 h of light/dark, 22/18 °C air temperatures, approximately 500 μ mol m⁻² s⁻¹ photon flux density, and 65 % relative humidity.

Winter wheat (*Triticum aestivum cv.* Bainong 207, purchased from Henan Agricultural High Tech Group Co., Ltd.) seeds were germinated in deionized water at 25 °C for four days after sterilization in 5 % (v/v) NaClO solution for 15 min. Then, uniform wheat seedlings were transplanted into a plastic container containing 2 L nutrient solutions as described previously by Arnon et al. (1940), which consisted of 945 mg L⁻¹ Ca(NO₃)₂·4H₂O, 607 mg·L⁻¹ KNO₃, 493 mg·L⁻¹ MgSO₄·7H₂O, 20 mg·L⁻¹ EDTA-Fe, 2.86 mg·L⁻¹ H₃BO₃, 1.81 mg·L⁻¹ MnCl₂·4H₂O, 0.22 mg·L⁻¹ ZnSO₄·7H₂O, 0.08 mg·L⁻¹ CuSO₄·5H₂O, and 0.02 mg·L⁻¹ (NH₄)₆Mo₇O₂₄·4H₂O.

Experimental design

P was added to the solutions as $NaH_2PO_4 \cdot 2H_2O$ at three rates: 0.01, 0.1 and 1 mmol·L⁻¹. Se was added as Na_2SeO_3 , Na_2SeO_4 and SeMet at one rate of 2 µmol·L⁻¹. Each treatment was performed in triplicate. Seedlings were supplied with full-strength nutrient solutions until sampling, except for the quarter-strength and halfstrength solutions supplied during the first and second weeks, respectively. The solution was renewed every three days to ensure a sufficient nutrient concentration. A solution of 5 % HCl was used to soak all vessels for one week, and then deionized water was used to wash those vessels more than three times. After cultivation for 21 d, the roots and shoots of 14 seedlings were separated, dried at 70 ± 5 °C, and analysed for dry weights and concentrations of P and Se. The leaves, stems, and roots of the other six seedlings were immediately frozen in liquid nitrogen and then stored at -20 °C for further subcellular fractionation and Se speciation analysis.

Analysis of the root morphology

Three 14-d-old seedlings in each treatment were analysed in terms of their root morphological characteristics. According to the method of Nie et al. [102], the root length, root surface area, root volume, average root diameter, root tip number and forks were measured using the root imaging analysis software WinRHI-ZO Version 2009 PRO (Regent Instruments, Quebec City, Canada).

Analysis of the photosynthetic parameters

According to the method of Shi et al. [103], three uniform seedlings of each treatment were selected for photosynthetic parameter analysis. The net photosynthetic (P_n) , stomatal conductance (G_s) , intercellular CO₂ concentration (C_i) and transpiration rate (T_r) in the leaves of 21-d-old seedlings were measured from 9:00 to 11:00, and the 3rd fully expanded leaf was selected using the LI-6400XT photosynthetic-fluorescence assay system (USA, LI-COR).

Analysis of the P concentration of wheat

According to the method of Bao. [104], after being digested with H_2SO_4 -HClO₄, the vanadate-molybdate-yellow colorimetric method was used to estimate the plant phosphorus concentration.

Analysis of the Se concentration of wheat

According to the method of Nie et al. [105], approximately 0.5 g of plant samples (shoot or root) was digested with HNO_3 - $HClO_4$ (4:1) at 180 °C. The digest was then restored to volume with 6 mol·L⁻¹ HCl, cooled, filtered and brought to volume with deionized water. The Se concentration was determined by hydride generation atomic fluorescence spectrometry (HG-AFS-8220, Beijing Titan Instruments Co., China).

Subcellular fraction separation

According to the methods described by Wan et al. [63], approximately 0.4 g of frozen samples (shoot or root) was homogenized in 10 mL of extraction buffer containing 1.0 mM dithioerythritol, 250 mM sucrose, and 50 mM Tris–HCl (pH 7.5). The homogenate was centrifuged at $300 \times \text{g}$ for 10 min, and the residue constituted the cell wall fraction (F1). The supernatant was then centrifuged at $20,000 \times \text{g}$ for 30 min, and the precipitate and the supernatant were taken as the organelle fraction (F2) and the soluble fraction (F3), respectively. The soluble fraction was diluted to 50 mL with 5 % HNO₃ (GR) prior to elemental determination. All steps were performed at 4 °C.

Se speciation determination

According to the methods described by Wang et al. [106], 0.05 g of the samples (shoot or root) was placed in 15 mL centrifugal tubes with 5 mL Tris-HCl. After ultrasonication for 30 min, 50 mg cellulase and 20 mg protease K were added. The mixture was incubated in an oscillation box with horizontal shaking (250 r·min⁻¹) at 50 °C ± 2 °C for 18 h. After adding 20 mg protease K, the mixture was then incubated in an oscillation box with horizontal shaking (250 r·min⁻¹) at 37 °C \pm 2 °C for 18 h. The hydrolysate was centrifuged at 10,000 r·min⁻¹ for 30 min, and the supernatant was filtered through a 0.22 μ m cellulose nitrate filter (Millipore, Billerica, MA, United States). Subsequently, the filtrate was stored at -80 °C for Se speciation analysis using high-performance liquid chromatography-ultraviolet treatment-hydride generationatomic fluorescence spectrometry (HPLC-UV-HG-AFS; SA-50, Ji tian Instruments Co., Beijing, China).

Data analysis

All data were statistically analysed by two-way ANOVA with LSD multiple comparison at a 5% level (p < 0.05) using SPSS 18.0.

Supplementary Information

The online version contains supplementary material available at https://doi. org/10.1186/s12870-023-04227-6.

Additional file 1: Table S1. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the P concentration and accumulation of winter wheat (Triticum aestivum cv Bainong 207) grown under greenhouse conditions. Table S2. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the Se concentration and accumulation of winter wheat (Triticum aestivum cv Bainong 207) grown under greenhouse conditions. Table S3. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the P and Se migration coefficient of winter wheat (Triticum aestivum cv Bainong 207) grown under greenhouse conditions. Table S4. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the subcellular fractions of Se in tissues of winter wheat (Triticum aestivum cv Bainong 207) grown under greenhouse conditions. Table S5. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on Se species in tissues of winter wheat (Triticum aestivum cy Bainong 207) grown under greenhouse conditions. Table S6. Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the dry

matter weight of winter wheat (*Triticum aestivum* cv Bainong 207) grown under greenhouse conditions. **Table S7.** Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the root morphology of winter wheat (*Triticum aestivum* cv Bainong 207) grown under greenhouse conditions. **Table S8.** Two-way analysis of variance (ANOVA) of the effects of Se, P treatment as well as their interactions on the photosynthetic parameter of winter wheat (*Triticum aestivum* cv Bainong 207) grown under greenhouse conditions.

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Authors' contributions

H.E.L and Z.J.N conceived and designed the experiments. H.Z.S., H.Y.P., G.X.L., H.Y.L and C.L performed the experiments. Z.J.N and C.X.H analysed the data. C.X.H wrote the paper. All authors have read and approved the submitted manuscript.

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Availability of data and materials

The datasets generated or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Experimental research and field studies on plants (either cultivated or wild), including the collection of plant material, were performed in compliance with relevant institutional, national, and international guidelines and legislation. The experiments did not involve endangered or protected species.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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References

- 1. Rayman MP. The importance of selenium to human health. The Lancet. 2000;356(9225):233–41.
- Sors TG, Ellis DR, Salt DE. Selenium uptake, translocation, assimilation and metabolic fate in plants. Photosynth Res. 2005;86(3):373–89.
- D'Amato R, Fontanella MC, Falcinelli B, Beone GM, Bravi E, Marconi O, Benincasa P. Selenium biofortification in rice (oryza sativa l.) sprouting: Effects on se yield and nutritional traits with focus on phenolic acid profile. J Agric Food Chem. 2018;66(16):4082–90.
- Winkel LH, Johnson CA, Lenz M, Grundl T, Leupin OX, Amini M, Charlet L. Environmental selenium research: From microscopic processes to global understanding. Environ Sci Technol. 2012;46(2):571–9.
- Yin H, Qi Z, Li M, Ahammed GJ, Chu X, Zhou J. Selenium forms and methods of application differentially modulate plant growth, photosynthesis, stress tolerance, selenium content and speciation in oryza sativa I. Ecotoxicol Environ Saf. 2019;169:911–7.

- Bajaj M, Eiche E, Neumann T, Winter J, Gallert C. Hazardous concentrations of selenium in soil and groundwater in north-west india. J Hazard Mater. 2011;189(3):640–6.
- Gao J, Liu Y, Huang Y, Lin Z-q, Bañuelos GS, Lam MH-W, Yin X. Daily selenium intake in a moderate selenium deficiency area of suzhou, china. Food Chemistry. 2011;126(3):1088–93.
- Tan LC, Nancharaiah YV, van Hullebusch ED, Lens PNL. Selenium: Environmental significance, pollution, and biological treatment technologies. Biotechnol Adv. 2016;34(5):886–907.
- Chilimba ADC, Young SD, Black CR, Meacham MC, Lammel J, Broadley MR. Assessing residual availability of selenium applied to maize crops in malawi. Field Crop Res. 2012;134:11–8.
- Germ M, Stibilj V, Osvald J, Kreft I. Effect of selenium foliar application on chicory (cichorium intybus I). J Agr Food Chem. 2007;55(3):795–8.
- Li HF, McGrath SP, Zhao FJ. Selenium uptake, translocation and speciation in wheat supplied with selenate or selenite. New Phytol. 2008;178(1):92–102.
- 12. Lenz M, Lens PN. The essential toxin: The changing perception of selenium in environmental sciences. Sci Total Environ. 2009;407(12):3620–33.
- Wang Y, Wang K, Wang Q, WanY, Zhuang Z, Yu Y, Li H. Selenite uptake and transformation in rice seedlings(oryza sativa l.): Response to phosphorus nutrient status. Front Plant Sci.2020;11:874.
- Yamada H, Kang Y, Aso T, Uesugi H, Fujimura T, Yonebayashi K. Chemical forms and stability of selenium in soil. Soil Science and Plant Nutrition. 1998;44(3):385–91.
- Zhu YG, Pilon-Smits EA, Zhao FJ, Williams PN, Meharg AA. Selenium in higher plants: Understanding mechanisms for biofortification and phytoremediation. Trends Plant Sci. 2009;14(8):436–42.
- Carey AM, Scheckel KG, Lombi E, Newville M, Choi Y, Norton GJ, Price AH, Meharg AA. Grain accumulation of selenium species in rice (oryza sativa l.). Environ Sci Technol. 2012;46(10):5557–64.
- Kikkert J, Berkelaar E. Plant uptake and translocation of inorganic and organic forms of selenium. Arch Environ Contam Toxicol. 2013;65(3):458–65.
- Longchamp M, Castrec-Rouelle M, Biron P, Bariac T. Variations in the accumulation, localization and rate of metabolization of selenium in mature zea mays plants supplied with selenite or selenate. Food Chem. 2015;182:128–35.
- Wang L, Yang Y, Chen S, Ge M, He J, Yang Z, Lin P, Wu X. White matter integrity correlates with residual consciousness in patients with severe brain injury. Brain Imaging Behav. 2018;12(6):1669–77.
- Eiche E, Bardelli F, Nothstein AK, Charlet L, Gottlicher J, Steininger R, Dhillon KS, Sadana US. Selenium distribution and speciation in plant parts of wheat (triticum aestivum) and indian mustard (brassica juncea) from a seleniferous area of punjab, india. Sci Total Environ. 2015;505:952–61.
- Di X, Qin X, Zhao L, Liang X, Xu Y, Sun Y, Huang Q. Selenium distribution, translocation and speciation in wheat (triticum aestivum l.) after foliar spraying selenite and selenate. Food Chem. 2023;400:134077.
- 22. Wang M, Ali F, Qi M, Peng Q, Wang M, Banuelos GS, Miao S, Li Z, et al. Insights into uptake, accumulation, and subcellular distribution of selenium among eight wheat (triticum aestivum l.) cultivars supplied with selenite and selenate. Ecotoxicol Environ Saf. 2021;207:111544.
- Zhang L, Hu B, Li W, Che R, Deng K, Li H, Yu F, Ling H, et al. Ospt2, a phosphate transporter, is involved in the active uptake of selenite in rice. New Phytol. 2014;201(4):1183–91.
- Abrams MM, Burau RG. Fractionation of selenium and detection of selenomethionine in a soil extract. Commun Soil Sci Plant Anal. 2008;20(3–4):221–37.
- Zhang L, Hu B, Deng K, Gao X, Sun G, Zhang Z, Li P, Wang W, et al. Nrt1.1b improves selenium concentrations in rice grains by facilitating selenomethinone translocation. Plant Biotechnol J. 2019;17(6):1058–68.
- Ji Y, Huang W, Wu B, Fang Z, Wang X. The amino acid transporter aap1 mediates growth and grain yield by regulating neutral amino acid uptake and reallocation in oryza sativa. J Exp Bot. 2020;71(16):4763–77.
- Peng Q, Zhang Z, Su R, Zhang X, Lambers H, He H. Phosphorus and selenium uptake, root morphology, and carboxylates in the rhizosheath of alfalfa (medicago sativa) as affected by localised phosphate and selenite supply in a split-root system. Funct Plant Biol. 2021;48(11):1161–74.

- Liu Q, Wang DJ, Jiang XJ, Cao ZH. Effects of the interactions between selenium and phosphorus on the growth and selenium accumulation in rice (oryza sativa). Environ Geochem Health. 2004;26(2):325–30.
- Dos Santos MJV, de Lima Lessa JH, de Assis MB, Raymundo JF, Ribeiro BT, Guilherme LRG, Lopes G. Selenium desorption in tropical soils by sulfate and phosphate, and selenium biofortification of mombaça grass under increasing rates of phosphate fertilisation. Crop Pasture Sci. 2021;73(2):56–66.
- Zhang D, Dong T, Ye J, Hou Z. Selenium accumulation in wheat (triticum aestivum I) as affected by coapplication of either selenite or selenate with phosphorus. Soil Science and Plant Nutrition. 2017;63(1):37–44.
- Dai Z, Imtiaz M, Rizwan M, Yuan Y, Huang H, Tu S. Dynamics of selenium uptake, speciation, and antioxidant response in rice at different panicle initiation stages. Sci Total Environ. 2019;691:827–34.
- 32. Li Y, Xiao Y, Hao J, Fan S, Dong R, Zeng H, Liu C, Han Y. Effects of selenate and selenite on selenium accumulation and speciation in lettuce. Plant Physiol Biochem. 2022;192:162–71.
- Wang M, Peng Q, Zhou F, Yang W, Dinh QT, Liang D. Uptake kinetics and interaction of selenium species in tomato (solanum lycopersicum l.) seedlings. Environ Sci Pollut Res Int. 2019;26(10):9730–8.
- Dong Z, Xiao Y, Wu H. Selenium accumulation, speciation, and its effect on nutritive value of flammulina velutipes (golden needle mushroom). Food Chem. 2021;350: 128667.
- Hu T, Liang Y, Zhao G, Wu W, Li H, Guo Y. Selenium biofortification and antioxidant activity in cordyceps militaris supplied with selenate, selenite, or selenomethionine. Biol Trace Elem Res. 2019;187(2):553–61.
- Deng X, Liu K, Li M, Zhang W, Zhao X, Zhao Z, Liu X. Difference of selenium uptake and distribution in the plant and selenium form in the grains of rice with foliar spray of selenite or selenate at different stages. Field Crop Res. 2017;211:165–71.
- Huang QQ, Wang Q, Wan YN, Yu Y, Jiang RF, Li HF. Application of x-ray absorption near edge spectroscopy to the study of the effect of sulphur on selenium uptake and assimilation in wheat seedlings. Biol Plant. 2017;61(4):726–32.
- Li J, Liu R, Zhang C, Yang J, Lyu L, Shi Z, Man YB, Wu F. Selenium uptake and accumulation in winter wheat as affected by level of phosphate application and arbuscular mycorrhizal fungi. J Hazard Mater. 2022;433: 128762.
- Ali F, Peng Q, Wang D, Cui Z, Huang J, Fu D, Liang D. Effects of selenite and selenate application on distribution and transformation of selenium fractions in soil and its bioavailability for wheat (triticum aestivum I.). Environ Sci Pollut Res Int. 2017;24(9):8315–25.
- Huang Q, Yu Y, Wang Q, Luo Z, Jiang R, Li H. Uptake kinetics and translocation of selenite and selenate as affected by iron plaque on root surfaces of rice seedlings. Planta. 2015;241(4):907–16.
- Eich-Greatorex S, Sogn TA, Øgaard AF, Aasen I. Plant availability of inorganic and organic selenium fertiliser as influenced by soil organic matter content and ph. Nutr Cycl Agroecosyst. 2007;79(3):221–31.
- 42. Kieliszek M, Blazejak S. Selenium: Significance, and outlook for supplementation. Nutrition. 2013;29(5):713–8.
- 43. Wang M, Dinh QT, Qi M, Wang M, Yang W, Zhou F, Liang D. Radicular and foliar uptake, and xylem- and phloem-mediated transport of selenium in maize (zea mays l.): A comparison of five se exogenous species. Plant and Soil. 2019;446(1–2):111–23.
- Lim TT, Goh KH. Selenium extractability from a contaminated fine soil fraction: Implication on soil cleanup. Chemosphere. 2005;58(1):91–101.
- Li YY, Yu SH, Zhou XB. Effects of phosphorus on absorption and transport of selenium in rice seedlings. Environ Sci Pollut Res Int. 2019;26(14):13755–61.
- Luo W, Li J, Ma X, Niu H, Hou S, Wu F. Effect of arbuscular mycorrhizal fungi on uptake of selenate, selenite, and selenomethionine by roots of winter wheat. Plant Soil. 2019;438(1–2):71–83.
- Li J, Loi G, Otero-Gonzalez L, Laing GD, Ferrer I, Lens PNL. Selenate and selenite uptake, accumulation and toxicity in lemna minuta. Water Sci Technol. 2020;81(9):1852–62.
- Liu H, Shi Z, Li J, Zhao P, Qin S, Nie Z. The impact of phosphorus supply on selenium uptake during hydroponics experiment of winter wheat (triticum aestivum) in china. Front Plant Sci. 2018;9:373.

- Terry N, Zayed AM, De Souza MP, Tarun AS. Selenium in higher plants. Annu Rev Plant Physiol Plant Mol Biol. 2000;51:401–32.
- Sors TG, Ellis DR, Na GN, Lahner B, Lee S, Leustek T, Pickering IJ, Salt DE. Analysis of sulfur and selenium assimilation in astragalus plants with varying capacities to accumulate selenium. Plant J. 2005;42(6):785–97.
- 51. Schmittgen TD, Livak KJ. Analyzing real-time pcr data by the comparative ct method. Nat Protoc. 2008;3(6):1101–8.
- Wang Q, Kong L, Huang Q, Li H, Wan Y. Uptake and translocation mechanisms of different forms of organic selenium in rice (oryza sativa I.). Front Plant Sci. 2022;13:970480.
- 53. Yu XZ, Gu JD. Differences in uptake and translocation of selenate and selenite by the weeping willow and hybrid willow. Environ Sci Pollut Res Int. 2008;15(6):499–508.
- Renkema H, Koopmans A, Kersbergen L, Kikkert J, Hale B, Berkelaar E. The effect of transpiration on selenium uptake and mobility in durum wheat and spring canola. Plant Soil. 2011;354(1–2):239–50.
- 55. Zayed AC, Lytle M, Terry N. Accumulation and volatilization of different chemical species of selenium by plants. Planta. 1998; 206:284±292.
- Su C, Suarez DL. Selenate and selenite sorption on iron oxides an infrared and electrophoretic study. Soil Sci Soc Am J. 2000;64(1):101–11.
- Cartes P, Gianfreda L, Mora ML. Uptake of selenium and its antioxidant activity in ryegrass when applied as selenate and selenite forms. Plant Soil. 2005;276(1–2):359–67.
- Bai B, Chen W, Zhang J, Shen Y. Growth effects and distribution of selenite in medicago sativa. Plant Soil. 2018;425(1–2):527–38.
- Boldrin PF, Faquin V, Ramos SJ, Boldrin KVF, Ávila FW, Guilherme LRG. Soil and foliar application of selenium in rice biofortification. J Food Compos Anal. 2013;31(2):238–44.
- Mazej D, Osvald J, Stibilj V. Selenium species in leaves of chicory, dandelion, lamb's lettuce and parsley. Food Chem. 2008;107(1):75–83.
- Lazard M, Blanquet S, Fisicaro P, Labarraque G, Plateau P. Uptake of selenite by saccharomyces cerevisiae involves the high and low affinity orthophosphate transporters. J Biol Chem. 2010;285(42):32029–37.
- 62. Dhillon SK, Dhillon KS. Selenium adsorption in soils as influenced by different anions. J Plant Nutr Soil Sci. 2000;163(6):577–82.
- 63. Wan Y, Wang K, Liu Z, Yu Y, Wang Q, Li H. Effect of selenium on the subcellular distribution of cadmium and oxidative stress induced by cadmium in rice (oryza sativa I.). Environ Sci Pollut Res Int. 2019;26(16):16220–8.
- Nocito FF, Lancilli C, Dendena B, Lucchini G, Sacchi GA. Cadmium retention in rice roots is influenced by cadmium availability, chelation and translocation. Plant Cell Environ. 2011;34(6):994–1008.
- Kaur N, Sharma S, Kaur S, Nayyar H. Selenium in agriculture: A nutrient or contaminant for crops? Archives of Agronomy and Soil Science. 2014;60(12):1593–624.
- Jiang H, Lin W, Jiao H, Liu J, Chan L, Liu X, Wang R, Chen T. Uptake, transport, and metabolism of selenium and its protective effects against toxic metals in plants: A review. Metallomics. 2021;13(7).
- Ding Y, Wang R, Guo J, Wu F, Xu Y, Feng R. The effect of selenium on the subcellular distribution of antimony to regulate the toxicity of antimony in paddy rice. Environ Sci Pollut Res Int. 2015;22(7):5111–23.
- Gallego SM, Pena LB, Barcia RA, Azpilicueta CE, Iannone MF, Rosales EP, Zawoznik MS, Groppa MD, et al. Unravelling cadmium toxicity and tolerance in plants: Insight into regulatory mechanisms. Environ Exp Bot. 2012;83:33–46.
- Su Y, Liu J, Lu Z, Wang X, Zhang Z, Shi G. Effects of iron deficiency on subcellular distribution and chemical forms of cadmium in peanut roots in relation to its translocation. Environ Exp Bot. 2014;97:40–8.
- Li G, Li Q, Wang L, Chen G, Zhang D. Subcellular distribution, chemical forms, and physiological response to cadmium stress in hydrilla verticillata. Int J Phytorem. 2019;21(3):230–9.
- Winkel LH, Vriens B, Jones GD, Schneider LS, Pilon-Smits E, Banuelos GS. Selenium cycling across soil-plant-atmosphere interfaces: A critical review. Nutrients. 2015;7(6):4199–239.
- 72. White PJ. Selenium metabolism in plants. Biochim Biophys Acta Gen Subj. 2018;1862(11):2333–42.
- 73. Whanger PD. Selenocompounds in plants and animals and their biological significance. J Am Coll Nutr. 2002;21(3):223–32.
- 74. Pilon-Smits EA, LeDuc DL. Phytoremediation of selenium using transgenic plants. Curr Opin Biotechnol. 2009;20(2):207–12.

- Versini A, Di Tullo P, Aubry E, Bueno M, Thiry Y, Pannier F, Castrec-Rouelle M. Influence of se concentrations and species in hydroponic cultures on se uptake, translocation and assimilation in non-accumulator ryegrass. Plant Physiol Biochem. 2016;108:372–80.
- 76. Gupta M, Gupta S. An overview of selenium uptake, metabolism, and toxicity in plants. Front Plant Sci. 2016;7:2074.
- Poblaciones MJ, Rodrigo S, Santamaria O, Chen Y, McGrath SP. Agronomic selenium biofortification in triticum durum under mediterranean conditions: From grain to cooked pasta. Food Chem. 2014;146:378–84.
- Hu T, Li H, Li J, Zhao G, Wu W, Liu L, Wang Q, Guo Y. Absorption and biotransformation of selenium nanoparticles by wheat seedlings (triticum aestivum I.). Front Plant Sci. 2018;9:597.
- Yu Y, Liu Z, Luo LY, Fu PN, Wang Q, Li HF. Selenium uptake and biotransformation in brassica rapa supplied with selenite and selenate: A hydroponic work with hplc speciation and rna-sequencing. J Agric Food Chem. 2019;67(45):12408–18.
- Wang K, Wang Y, Li K, Wan Y, Wang Q, Zhuang Z, Guo Y, Li H. Uptake, translocation and biotransformation of selenium nanoparticles in rice seedlings (oryza sativa I.). J Nanobiotechnol. 2020;18(1):103.
- Li HF, Lombi E, Stroud JL, McGrath SP, Zhao FJ. Selenium speciation in soil and rice: Influence of water management and se fertilization. J Agric Food Chem. 2010;58(22):11837–43.
- Drahoňovský J, Száková J, Mestek O, Tremlová J, Kaňa A, Najmanová J, Tlustoš P. Selenium uptake, transformation and inter-element interactions by selected wildlife plant species after foliar selenate application. Environ Exp Bot. 2016;125:12–9.
- Oliveira L. The development of chloroplasts in root meristematic tissue of secale cereale I. Seedlings New Phytol. 1982;91:263–75.
- Peng B, Liu X, Dong X, Xue Q, Neely CB, Marek T, Ibrahim AMH, Zhang G, et al. Root morphological traits of winter wheat under contrasting environments. J Agron Crop Sci. 2019;205(6):571–85.
- 85. Huang G, Zhang D. The plasticity of root systems in response to external phosphate. Int J Mol Sci. 2020;21(17).
- Carstensen A, Herdean A, Schmidt SB, Sharma A, Spetea C, Pribil M, Husted S. The impacts of phosphorus deficiency on the photosynthetic electron transport chain. Plant Physiol. 2018;177(1):271–84.
- Loudari A, Mayane A, Zeroual Y, Colinet G, Oukarroum A. Photosynthetic performance and nutrient uptake under salt stress: Differential responses of wheat plants to contrasting phosphorus forms and rates. Frontiers in Plant Science. 2022; 13.
- Jiang C, Zu C, Lu D, Zheng Q, Shen J, Wang H, Li D. Effect of exogenous selenium supply on photosynthesis, na(+) accumulation and antioxidative capacity of maize (zea mays l.) under salinity stress. Sci Rep. 2017;7:42039.
- Bai B, Wang Z, Gao L, Chen W, Shen Y. Effects of selenite on the growth of alfalfa (medicago sativa I. Cv. Sadie 7) and related physiological mechanisms. Acta Physiologiae Plantarum. 2019;41(6).
- Roda FA, Marques I, Batista-Santos P, Esquivel MG, Ndayiragije A, Lidon FC, Swamy BPM, Ramalho JC, et al. Rice biofortification with zinc and selenium: A transcriptomic approach to understand mineral accumulation in flag leaves. Front Genet. 2020;11:543.
- Kong L, Wang M, Bi D. Selenium modulates the activities of antioxidant enzymes, osmotic homeostasis and promotes the growth of sorrel seedlings under salt stress. Plant Growth Regul. 2005;45(2):155–63.
- Dinh QT, Cui Z, Huang J, Tran TAT, Wang D, Yang W, Zhou F, Wang M, et al. Selenium distribution in the chinese environment and its relationship with human health: A review. Environ Int. 2018;112:294–309.
- Kaur M, Sharma S. Influence of selenite and selenate on growth, leaf physiology and antioxidant defense system in wheat (triticum aestivum l.). J Sci Food Agric. 2018;98(15):5700–10.
- 94. Wang M, Zhou F, Cheng N, Chen P, Ma Y, Zhai H, Qi M, Liu N et al. Soil and foliar selenium application: Impact on accumulation, speciation, and bioaccessibility of selenium in wheat (triticum aestivum I.). Front Plant Sci. 2022;13:988627.
- Nie ZJ, Li JF, Zhao P, Liu SL, Fang XZ, Liu HE. Effects of phosphors combined with selenium application on absorption and translocation of phosphors and selenium in winter wheat seedlings. Southwest China Journal of Agricultural Sciences. 2019;32(1):122–7.

- Qin X, Nie Z, Liu H, Zhao P, Qin S, Shi Z. Influence of selenium on root morphology and photosynthetic characteristics of winter wheat under cadmium stress. Environ Exp Bot. 2018;150:232–9.
- He J, Jin Y, Du YL, Wang T, Turner NC, Yang RP, Siddique KHM, Li FM. Genotypic variation in yield, yield components, root morphology and architecture, in soybean in relation to water and phosphorus supply. Front Plant Sci. 2017;8:1499.
- Sun B, Gao Y, Lynch JP. Large crown root number improves topsoil foraging and phosphorus acquisition. Plant Physiol. 2018;177(1):90–104.
- Yao XQ, Chu JZ, YWG. Effects of drought stress and selenium supply on growth and physiological characteristics of wheat seedlings. Acta Physiologiae Plantarum. 2009;31(5):1031–6.
- Sabatino L, Ntatsi G, Iapichino G, D'Anna F, De Pasquale C. Effect of selenium enrichment and type of application on yield, functional quality and mineral composition of curly endive grown in a hydroponic system. Agronomy. 2019;9(4):207.
- 101. Lee S, Woodard HJ, Doolittle JJ. Effect of phosphate and sulfate fertilizers on selenium uptake by wheat (triticum aestivum). Soil Science and Plant Nutrition. 2011;57(5):696–704.
- Nie Z, Zhao P, Wang J, Li J, Liu H. Absorption kinetics and subcellular fractionation of zinc in winter wheat in response to nitrogen supply. Front Plant Sci. 2017;8:1435.
- Shi Z, Yang S, Han D, Zhou Z, Li X, Liu Y, Zhang B. Silicon alleviates cadmium toxicity in wheat seedlings (triticum aestivum l.) by reducing cadmium ion uptake and enhancing antioxidative capacity. Environ Sci Pollut Res Int. 2018;25(8):7638–46.
- 104. Bao SD. Soil chemical analysis. Beijing: China Agriculture Press; 2002.
- Nie Z, Zhu J, Li J, Liu H, Zhao P, Gao W, Qin S, Li C, et al. Phosphorus application alters concentrations and proportions of organic se forms in the grain of winter wheat. J Plant Nutr Soil Sci. 2020;183(3):282–91.
- 106. Wang TL, Zhou XH, Liu JX, Wei H, Zhang D, Guo J, Jia B, Li HZ et al. Determination of selenium species in se-enriched high-fat crops by high performance liquid chromatography-hydridegeneration-atomic fluorescence spectrometry. J Chin Cereals and Oils Assoc. 2022.

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