

RESEARCH

Open Access



Effects of sodium selenate on energy metabolism of amaranth inoculated with *Glomus mosseae* based on targeted metabolomics

Xiuqin Huang^{1,2}, Yunmei Lu^{1,2}, Mao Mu^{1,2}, Yaling Zhao³, Xuejun Tian^{1,2} and Renhua Huang^{1,2*}

Abstract

Background Selenium (Se) deficiency poses significant health risks to human populations globally, necessitating effective biofortification strategies. Amaranth (*Amaranthus retroflexus*), a nutrient-dense vegetable with demonstrated capacity for Se accumulation in seleniferous soils, represents a promising biofortification vehicle. Critically, arbuscular mycorrhizal fungi (AMF) enhance rhizospheric Se mobilization, yet their synergistic effects on plant energy metabolism remain unexplored.

Results This pot study investigated the influence of exogenous selenium (Se) treatment on energy metabolism in amaranth colonized by the arbuscular mycorrhizal fungus *Glomus mosseae*. Using LC–MS/MS-based targeted metabolomics with OPLS-DA and KEGG analysis, we identified 14 differentially expressed metabolites (8 up-/6 down-regulated) in Se-exposed plants. These metabolites mapped to glycolysis, TCA cycle, pentose phosphate pathway, electron transport chain, and amino acid/pyruvate metabolism. Activity assays of key enzymes, including PGI, SDH, G6PDH, 6PGDH, and CCO, revealed potential multi-pathway perturbations in energy metabolism under Se treatment.

Conclusions Based on these results, it can be concluded that selenium addition significantly affected amaranth energy metabolism.

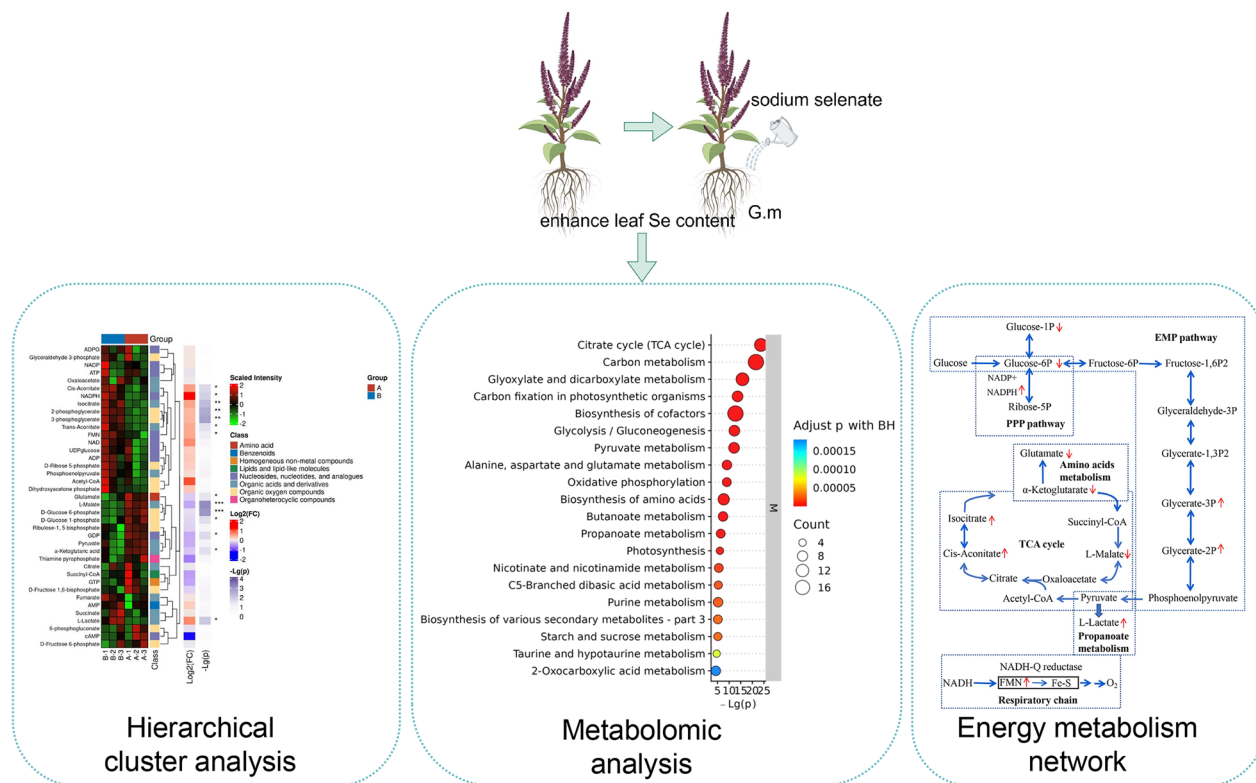
Keywords Selenium, Amaranth, Targeted metabolomics, Energy metabolism

*Correspondence:

Renhua Huang
hrh510@21cn.com

Full list of author information is available at the end of the article

Graphical Abstract



Introduction

Selenium (Se) is an essential trace element for humans, with deficiency linked to various diseases and impaired immune function [1, 2]. While dietary supplementation can mitigate Se deficiency, plant-based biofortification offers a sustainable strategy to enhance Se intake through agronomic practices [3, 4]. This approach, however, is constrained by the biphasic effects of Se on plants. Moderate concentrations can enhance antioxidant defenses, whereas excessive levels cause phytotoxicity, manifested as growth inhibition and oxidative damage. These dose-dependent responses highlight the importance of species-specific optimization.

Amaranthus retroflexus, a nutrient-dense leafy vegetable rich in essential amino acids, vitamins, and lipids [5, 6], has emerged as a promising candidate for Se biofortification due to its capacity to accumulate Se when cultivated in Se-enriched soils [6]. Recent studies have shown that arbuscular mycorrhizal fungi (AMF) further enhance Se uptake in crops such as wheat, maize, and rice [7–10]. For instance, inoculation with *Glomus mosseae* enhanced shoot selenium accumulation in selenite-treatment maize [8], while co-application of AMF and selenium facilitated

the biotransformation to organic selenium species in rice grains [9].

Plant nutrient uptake often involves active transport processes that require substantial energy expenditure. A critical knowledge gap remains in understanding how Se affects plant energy metabolism, which is fundamental to growth, stress responses, and biofortification efficiency. Respiration, a central component of energy metabolism, encompasses the Embden–Meyerhof–Parnas (EMP) pathway, the tricarboxylic acid (TCA) cycle, the cytochrome pathway, and the pentose phosphate pathway (PPP) [11, 12]. Key enzymes such as phosphoglucose isomerase (PGI, glycolysis) [13], succinate dehydrogenase (SDH, TCA cycle) [13, 14], and cytochrome c oxidase (CCO, electron transport chain) [14] regulate energy flux, while glucose-6-phosphate dehydrogenase (G6PDH) controls PPP activity [15]. Although evidence indicates that Se influences plant growth and redox balance, its impact on respiratory pathways and energy homeostasis remains largely unexplored.

Given that nutrient uptake in plants depends on energy-intensive active transport, we hypothesize that Se absorption in amaranth is energy dependent. This

study investigates the effects of Se treatment and AMF inoculation on energy metabolism in *A. retroflexus*. Using targeted metabolomics, we characterized shifts in energy-related metabolites and pathways. By elucidating how Se modulates respiratory metabolism, this work aims to advance the mechanistic understanding of Se–plant interactions and provide insights into optimizing Se biofortification while maintaining plant vigor. These findings are expected to inform sustainable production of Se-enriched vegetables and to bridge agronomic practices with human nutritional needs.

Materials and methods

Preparation of the tested materials

The pot experiment was conducted in a climate-controlled greenhouse at Jingchu University of Technology (day/night: 30 °C/23 °C; RH 50–70%; 14-h photoperiod with supplemental lighting). Soil was collected from a vegetable garden in the Dongbao Area, Jingmen City, Hubei Province, China. After removing grass roots, the soil was air-dried, crushed, homogenized, and passed through a 5-mm sieve. It was then mixed with perlite and sterilized using high-pressure steam in an autoclave at 121 °C for 2 h under moist heat. The treated soil was stored in the dark for one week prior to use.

The soil had the following properties: cation exchange capacity (CEC) 10.87 cmol kg^{−1}, pH 6.23 (soil/water=1:2.5), soil organic matter (SOM) 32.34 g kg^{−1}, total nitrogen (TN) 1.84 g kg^{−1}, total phosphorus (TP) 0.67 g kg^{−1}, total potassium (TK) 17.04 g kg^{−1}, total sulfur (TS) 0.35 g kg^{−1}, and total selenium 0.25 mg·kg^{−1}. Soil treatment was performed as described previously [6]. The AM fungus *Glomus mosseae* was provided by the Microbiology Laboratory, Institute of Plant Nutrition and Resources, Beijing Academy of Agriculture and Forestry Sciences. The AMF inoculum was propagated using white clover (*Trifolium repens* L.). After removing the aboveground parts of the plants, the soil containing roots and fungal propagules (15 propagules/g) was used as the mycorrhizal inoculum [16]. A non-mycorrhizal control inoculum was prepared under the same conditions.

Pot experiment and harvest

Pot experiments were designed. The amaranth seeds were sown into a 1-L plastic pot, where 300 g of sterilized soil and 50 g of mycorrhizal fungi inoculants were supplied, then covered with an additional 50 g of sterilized soil, as the non-selenium treatment. The other experiment used 300 g of selenium-treated soil and 50 g of mycorrhizal fungi inoculants, which contained *G. mosseae* with selenium concentrations of 0.5, 1, 2, and 5 mg kg^{−1}, also covered with 50 g sterilized soil, as the selenium treatment. For both experiments, only one amaranth (*Amaranthus*

retroflexus) plant was allowed to grow in each pot. Each treatment group included 10 pots, for a total of 50 pots. The experiments were carried out in a sunlit glasshouse with a day/night temperature of 30/23 °C and 50–70% relative humidity. After a period of 40 days, three or four mature leaves from the amaranth plant were harvested.

Assessment of arbuscular mycorrhizal colonization

Mycorrhizal colonization was assessed using a modified ink-vinegar staining protocol [17]. Roots were cleared in 10% KOH (80 °C, 25 min), neutralized with 1% HCl (1 h), and stained in ink–acetic acid solution (blue-black writing ink:acetic acid=1:20 (v/v); 60 °C, 10 min). Destaining was performed in sterilized 5% acetic acid overnight until pale blue. Roots were mounted in 50% glycerol and examined under a compound light microscope.

Plant properties analyses

The seedlings of amaranth plants were collected from each experimental treatment to measure their plant height and fresh weight. Plant height was measured using a ruler. The seedlings were collected and washed, and fresh weight was measured using an electronic balance. The selenium concentration was determined using inductively coupled plasma mass spectrometry (ICP-MS). A total of 0.1 g of dried amaranth leaf powder was weighed and placed into a digestion tube, followed by the addition of 8 mL HNO₃ and 2 mL H₂O₂. The mixture was vortexed thoroughly and digested in a graphite digestion system at 180 °C for 2 h until the sample was evaporated to near dryness. After digestion, 5 mL of ultrapure water was added to the digestate, which was reheated until the solution became clear and colorless. The cooled digestate was filtered through a 0.45-μm membrane. Total selenium concentrations in the leaves were determined using ICP-MS.

Enzyme activity assay

Respiratory enzyme activities were quantified spectrophotometrically following Li et al. [18]. Phosphoglucose isomerase (PGI) was assayed in leaf homogenates (1 g fresh weight in 5 mL 0.05 M Tris–HCl, pH 7.4) centrifuged (5,000 g, 30 min); the supernatant (0.5 mL) was incubated with 10 mM glucose-6-phosphate (30 °C, 5 min), terminated with 10% TCA, color-developed with resorcinol/HCl (80 °C, 8 min), and measured at 520 nm. Succinate dehydrogenase (SDH) was determined using mitochondrial extracts centrifuged (10,000 g, 15 min, 0 °C) in sucrose-phosphate–EDTA buffer; the reaction mixture (0.1 mL extract+0.4 M sodium succinate+DCIP/PMS electron acceptors) was incubated for 15 min, stopped with 0.25 M HCl, and read at 600 nm. Glucose-6-phosphate

Table 1 Colonization rate, plant height, fresh weight and Se concentration of amaranth grown in selenate-spiked soils inoculated with *Glomus mosseae* for 40 days (mean ± SD, n = 3)

Treatments	Colonization rate (%)	Plant height (cm)	Fresh weight (g)	Se concentration in leaves (ug g ⁻¹ FW)
Gm	33.33 ± 5.77 ^b	6.92 ± 0.38 ^a	4.400 ± 0.426 ^{ab}	0.021 ± 0.003 ^e
Gm + 0.5 mg kg ⁻¹ Se	53.33 ± 5.77 ^a	6.08 ± 0.83 ^a	4.063 ± 0.373 ^{ab}	0.501 ± 0.035 ^d
Gm + 1 mg kg ⁻¹ Se	56.67 ± 5.77 ^a	5.92 ± 1.18 ^a	3.487 ± 0.206 ^b	0.913 ± 0.027 ^c
Gm + 2 mg kg ⁻¹ Se	63.33 ± 15.28 ^a	6.96 ± 0.56 ^a	5.161 ± 1.144 ^a	3.478 ± 0.016 ^a
Gm + 5 mg kg ⁻¹ Se	60.00 ± 10.00 ^a	6.29 ± 1.05 ^a	4.610 ± 0.151 ^{ab}	2.925 ± 0.048 ^b

Gm, *Glomus mosseae*. In each column, different letters indicate significant differences (*P* < 0.05) among treatments

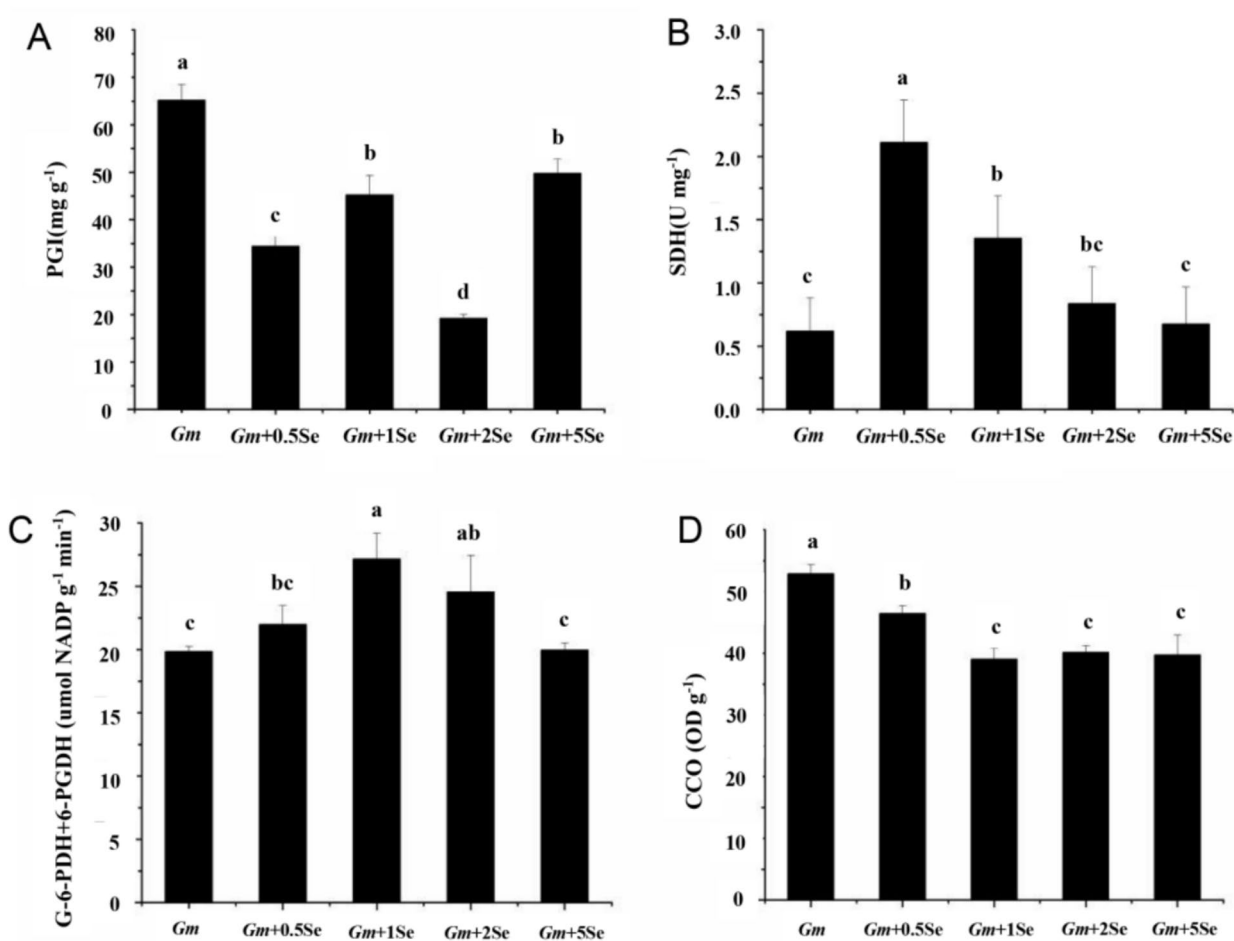


Fig. 1 Effects of different selenium concentrations on the activities of PGI, SDH, G-6-PDH + 6-PGDH and CCO in AMF-inoculated amaranth

dehydrogenase + 6-phosphogluconate dehydrogenase (G6PDH + 6PGDH) activity was monitored via NADPH production at 340 nm, and cytochrome c oxidase (CCO) at 510 nm using 3 g samples. All measurements were performed using a Shimadzu UV-1750 spectrophotometer.

UHPLC–MS assay
The LC/MS analysis was carried out using a Shimadzu Nexera X2 LC—30AD system, which was equipped with an ACQUITY UPLC BEH Amide column and a triple quadrupole mass spectrometer. The ACQUITY UPLC BEH amide column was maintained at 45 °C, and the

flow rate was set at 300 $\mu\text{L}/\text{min}$. The gradient mobile phase used for compound separation consisted of solvent A (a mixture of 20 mM ammonium acetate and 5% v/v acetonitrile with a pH of 9.45) and solvent B (100% acetonitrile).

In the mass spectrometer detection system, the optimized instrumental parameters were used. The ion source temperature was maintained at 550 $^{\circ}\text{C}$, with Ion Source Gas 1 (GAS1) and Ion Source Gas 2 (GAS2) set to 40 and 50 arbitrary units, respectively. The curtain gas (CUR) was maintained at 35 arbitrary units, and the ion spray voltage floating (ISVF) was set to -4500 V . The mass spectrometer was operated with a dwell time of 200 ms for optimal signal acquisition. For the construction of the metabolite MRM library, we first analyzed

individual metabolite standards (50 mg/mL) using LC-MS/MS to determine their optimal MRM transition parameters. Subsequently, we established the retention times for 40 energy-related metabolites by systematically measuring their specific MRM ($Q1/Q3$) transitions. To ensure accurate quantification, we prepared a series of dilutions from a reference standard containing these 40 metabolites. Calibration curves were generated using the least-squares method, correlating the peak areas of each metabolite in the serially diluted standards with their corresponding concentrations. Only calibration curves demonstrating a correlation coefficient (R^2) greater than 0.99 were deemed acceptable for quantitative analysis. The concentration of each metabolite in experimental

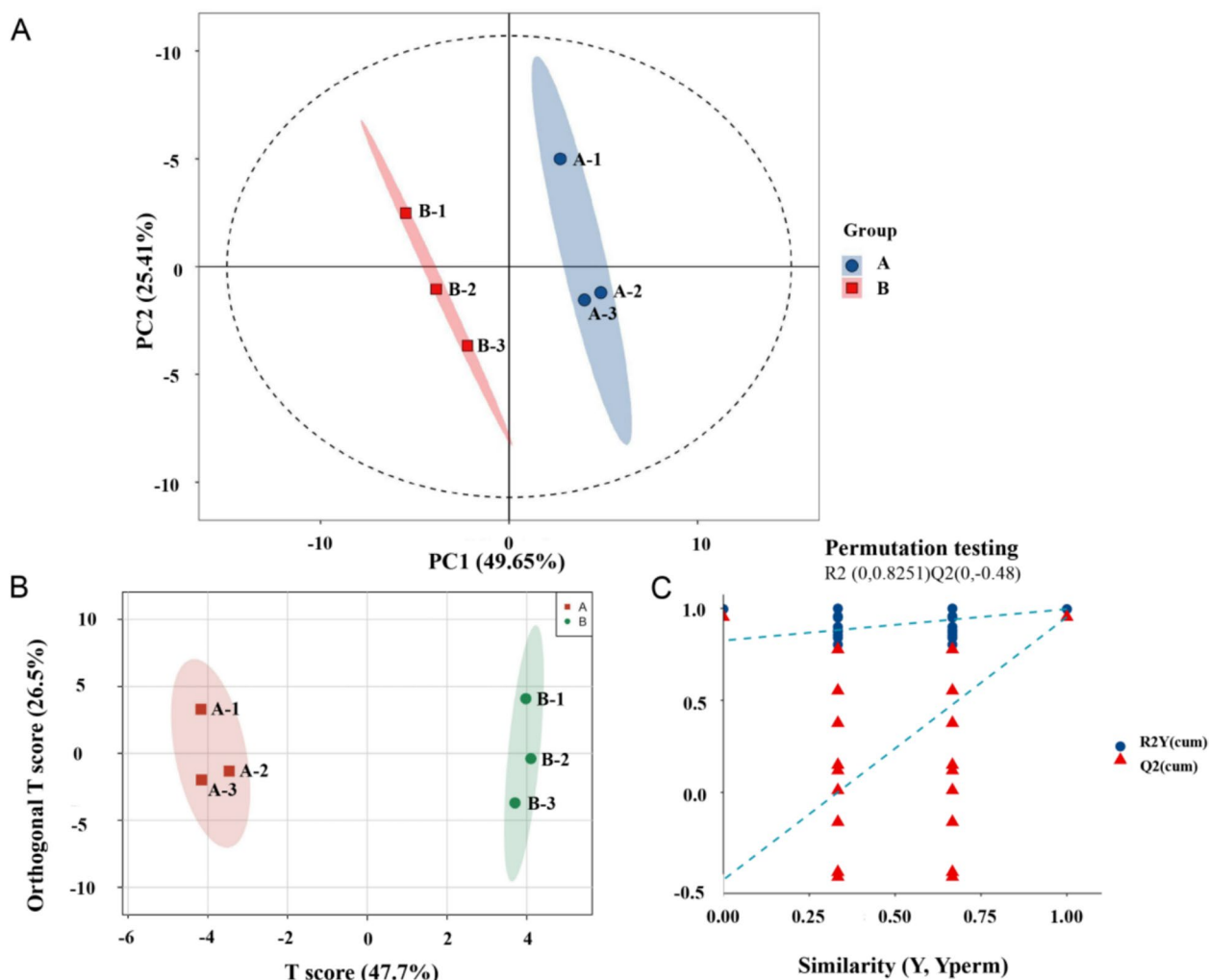


Fig. 2 Differential metabolite analysis using PCA and OPLS-DA. **A** PCA reveals metabolic divergence between control and selenium-treated groups (**A**: no-selenium control, **B**: selenate-treated (2 mg Se kg^{-1}) group, PC1: first principal component, PC2: second principal component (PC2), percentage indicates percentage of variance explained). **B** OPLS-DA validation of differential metabolites in energy metabolism. **C** Plot of OPLS-DA permutation test for B vs. A

samples was then determined by interpolation from these validated calibration curves.

Data processing and statistical analysis

Raw MRM data were processed using MultiQuant™ software (peak detection, alignment, and filtering). Differential metabolites (fold-change > 1.5, $p < 0.05$ by Student's t-test or ANOVA) were subjected to KEGG pathway analysis with Fisher's exact test enrichment. Cluster analysis was performed using R packages. Selenium content and enzyme activities (triplicate measurements) are expressed as mean ± SD. Statistical significance ($P < 0.05$)

was determined by one-way ANOVA (SPSS 22.0), and data visualization was conducted in GraphPad Prism 8.0.

Results

Impact of selenium on the growth of AMF-inoculated amaranth

AMF colonization of amaranth roots increased with selenium addition regardless of the Se concentration (Table 1 and Supplementary Fig. 1). The addition of sodium selenate did not have a notable effect on amaranth height and fresh weight compared to no selenium addition (Supplementary Fig. 2). As the selenium concentration

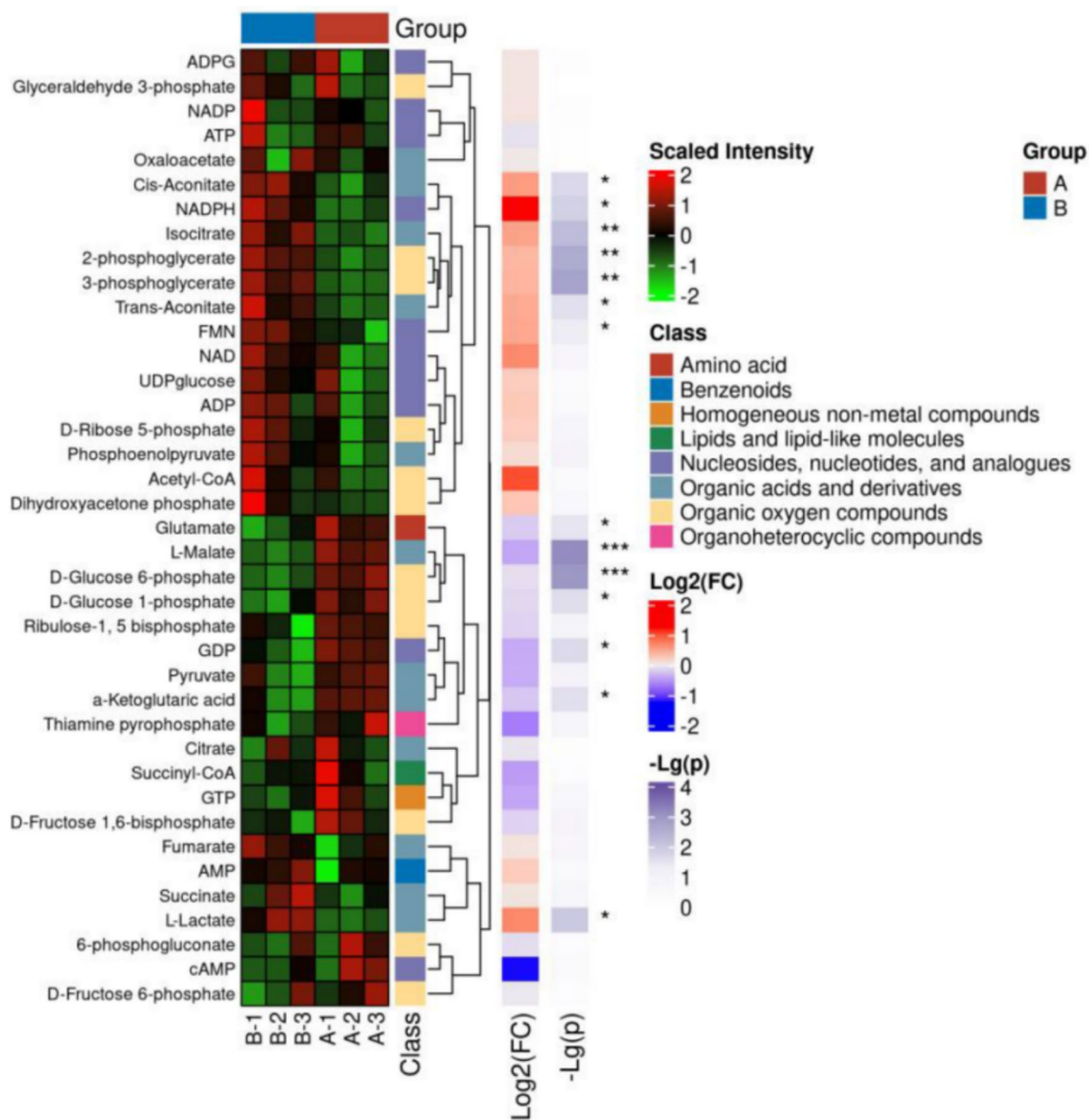


Fig. 3 Results of hierarchical clustering of differential metabolites in the compared treatments (A no-selenium control, B selenate-treated at 2 mg Se kg⁻¹) (only the top 50 VIP values are plotted)

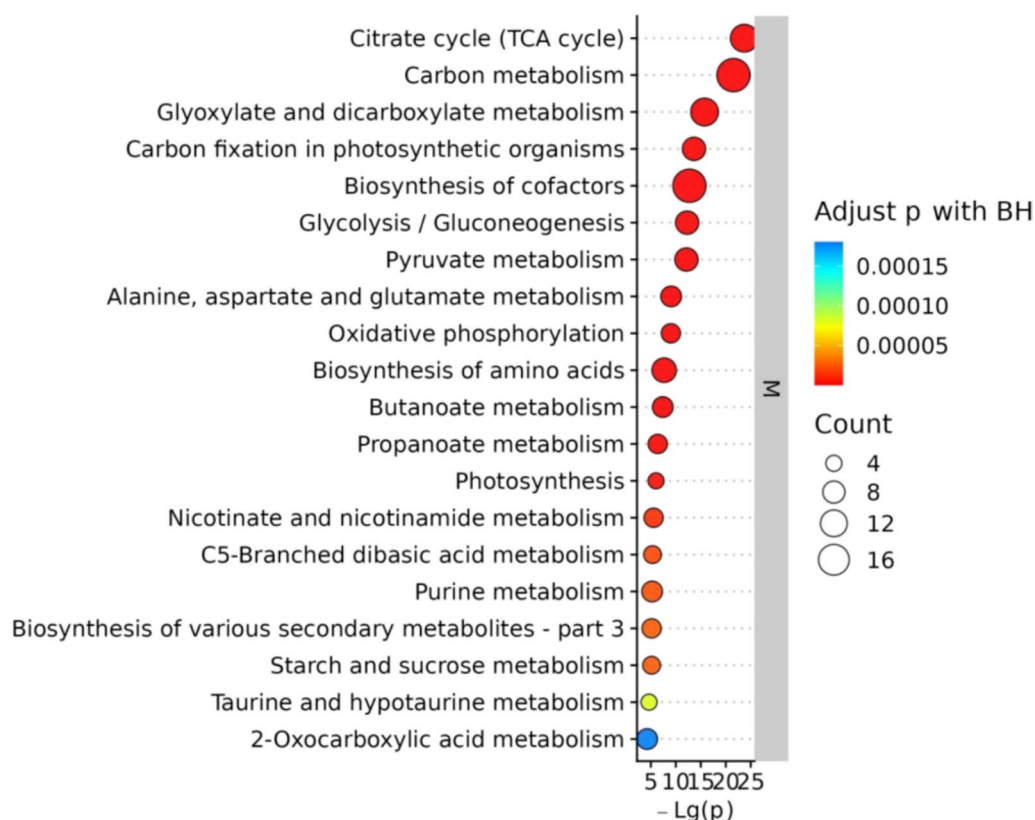


Fig. 4 Bubble plot of KEGG enrichment of differential metabolites under 2 mg kg⁻¹ selenium treatment (Top20) compared with the no-selenium control

increased up to 2 mg kg⁻¹, the selenium concentration in leaves increased significantly (Table 1). The results indicated that soil application of Se at the concentration of 2 mg kg⁻¹ is sufficient for amaranth growth and provides enough selenium in amaranth leaves.

Impact of selenium on the functionality of key enzymes in the respiratory metabolic pathway

To investigate the effects of different selenium concentrations on the activities of essential enzymes in the respiratory pathway, we tested four crucial enzymes. The PGI activity was significantly reduced at all four selenium concentrations compared to no selenium addition (Fig. 1A). The PGI activity was reduced by 70.6% at a selenium concentration of 2 mg kg⁻¹ and 23.6% at a selenium concentration of 5 mg kg⁻¹ compared to no selenium addition ($P < 0.05$).

Regarding SDH activity, there was a 3.41-fold increase at selenium concentration of 0.5 mg kg⁻¹ and a 2.19-fold increase at 1 mg kg⁻¹ compared with the no-Se control (Fig. 1B). The SDH activity was highest at a selenium concentration of 0.5 mg kg⁻¹, and gradually decreased with increasing selenium concentration.

The addition of selenium increased G-6-PDH+6-PGDH activity compared to no selenium addition (increases were 1.11-fold at selenium concentration of 0.5 mg kg⁻¹, 1.37-fold at 1 mg kg⁻¹ and 1.24-fold at 2 mg kg⁻¹) (Fig. 1C). The G-6-PDH+6-PGDH activity first increased and then decreased, reaching the optimum at 1 or 2 mg kg⁻¹.

The CCO activity decreased with the selenium addition compared to the no-selenium control (Fig. 1D), with the lowest activity ($P < 0.05$) recorded at the range of Se concentrations of 1–5 mg kg⁻¹.

In summary, the data on the enzyme activities suggest that the soil addition of selenium alters energy metabolism in amaranth.

Metabolite pattern analysis

Differential metabolite profiling reveals selenium-induced metabolic shifts

To investigate selenium-induced metabolite differences, principal component analysis (PCA) and orthogonal partial least squares-discriminant analysis (OPLS-DA) were performed on amaranth leaf samples from the no-selenium control group and the selenate-treated group

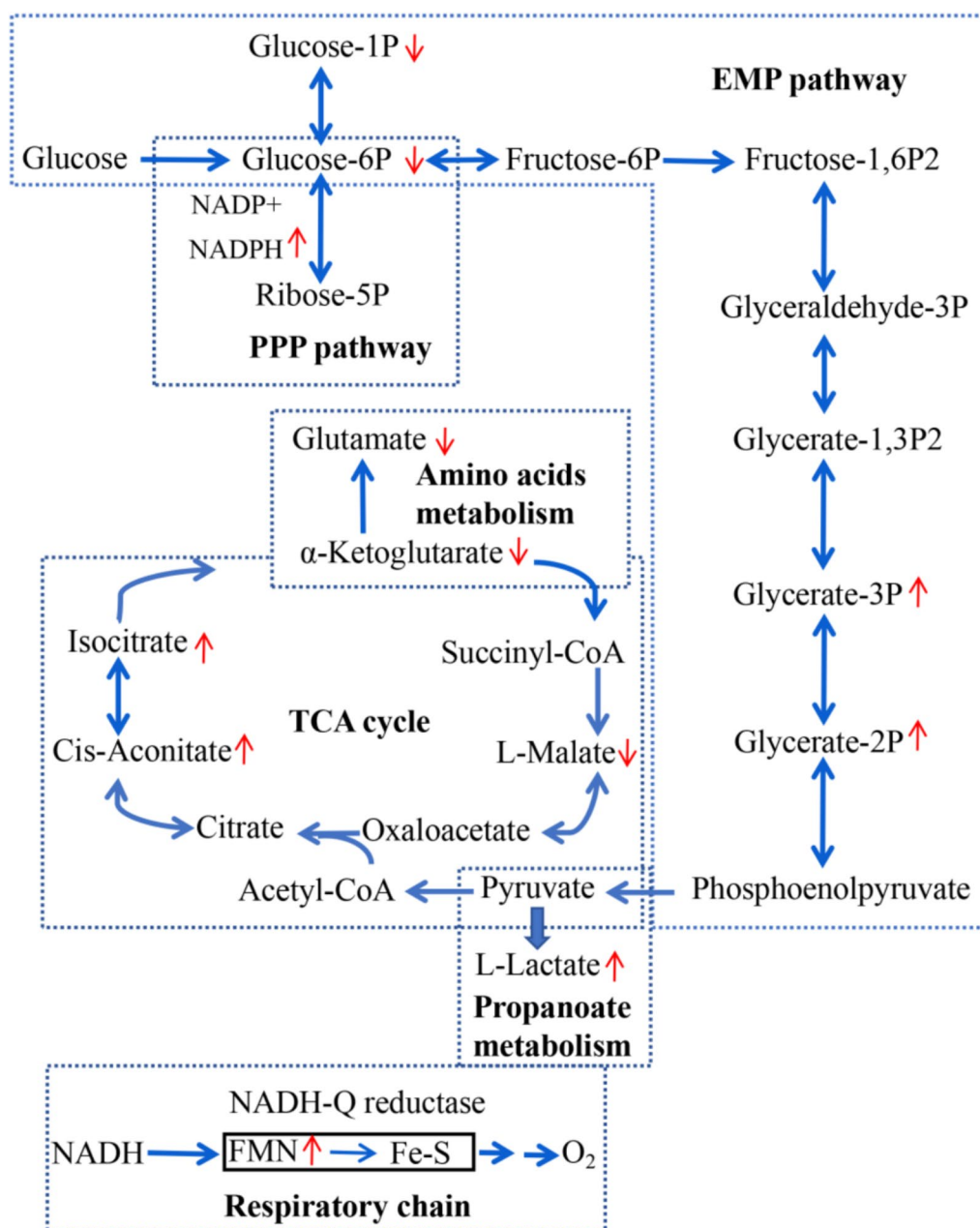


Fig. 5 Network visualization of energy metabolism in amaranth. “↓” indicating down-regulation, “↑” indicating upregulation

(2 mg Se kg⁻¹). PCA revealed a clear separation between the two groups along the PC1 axis (explaining 49.65% of the total variance; cumulative PC1+PC2: 75.06%, Fig. 2A), with control samples positioned to the right of the origin and treated samples to the left, indicating distinct metabolic profiles. The subsequently constructed OPLS-DA model effectively filtered non-classification noise and confirmed clear group discrimination (control: left of origin; treated: right of origin, Fig. 2B). Validation parameters ($R^2/Q^2 \approx 1$, $Q^2 > 0.5$) and permutation testing

(Q^2 intercept = -0.475) demonstrated model robustness without overfitting, verifying that differential metabolites predominantly mapped to energy metabolism pathways (Fig. 2C). These metabolomic shifts indicate potential perturbations in energy metabolism pathways.

Differential metabolite identification and screening

A total of 14 differential metabolites were identified using fold-change > 1.5 or < 1/1.5, and $P < 0.05$ (Table S1). The differential metabolites selected were

the marker variables for treatment separation. Eight differential metabolites were upregulated, and six differential metabolites were down-regulated in the selenate-treated at 2 mg Se kg⁻¹ group compared to the no-selenium control. Hierarchical cluster analysis (HCA) was conducted on the top 50 differential metabolites with the highest VIP values, which mainly included energy metabolites such as organic acids, nucleotides, and organic oxides (Fig. 3).

The KEGG enrichment pathway analysis of differential metabolites

The results of the metabolic pathway analysis are shown in the bubble diagram (Fig. 4). The names of KEGG metabolic pathways were ordered from top to bottom according to the magnitude of the Rich Factor. A larger value on the horizontal axis indicates a greater likelihood of an enriched result rather than a random result. The size of each bubble corresponds to the number of enriched metabolites. The redder the color of the bubble, the more significant the enrichment. Our metabolomic analysis revealed that the three major energy pathways enriched in differential metabolites were citrate cycle (ath00020), carbon metabolism (atg12000), and glyoxylate and dicarboxylate metabolism (ath00630).

Basic energy metabolism network analysis

The results of 2 mg kg⁻¹ selenium treatment on amaranth energy metabolism network are shown in Fig. 5. In the EMP pathway, selenium treatment caused a significant decrease in D-glucose 1-phosphate (0.91-fold) and D-glucose 6-phosphate (0.94-fold), and caused a significant increase ($P < 0.05$) in 3-phosphoglycerate (1.33-fold) and 2-phosphoglycerate (1.31-fold). In the TCA cycle, selenium treatment caused a significant increase ($P < 0.05$) in *cis*-aconitate (1.50-fold) and isocitrate (1.44-fold), and a significant decrease ($P < 0.05$) in α -ketoglutarate (0.86-fold) and L-malate (0.75-fold). In the PPP pathway, selenium treatment caused a significant upregulation ($P < 0.05$) of NADPH (2.36-fold). In the electron transport chain, selenium treatment caused a significant upregulation of FMN (1.41-fold) ($P < 0.05$). In amino acid metabolism, selenium treatment caused a significant down-regulation ($P < 0.05$) of glutamate (0.87-fold). In pyruvate metabolism, selenium caused significant upregulation ($P < 0.05$) of pyruvate conversion to L-lactate (1.63-fold). These results indicated that differential metabolites were involved in the glycolytic pathway, TCA cycle, pentose phosphate pathway, electron transport chain, amino acid metabolism, and pyruvate metabolism. The findings proved that selenium treatment would affect the intensity of

amaranth energy metabolism by inhibiting amino acid metabolism and enhancing pyruvate metabolism.

Discussion

Selenium serves as an essential trace element that promotes plant growth and enhances stress resistance [19–21]. Our results demonstrate that 2 mg kg⁻¹ selenate treatment did not significantly alter amaranth biomass, which is consistent with reports of selenium's growth-neutral effects in rice [9]. Pakchoi growth was promoted at lower selenite concentrations ($\text{Se} \leq 1 \text{ mg L}^{-1}$) while it was inhibited at higher selenite concentrations ($\text{Se} \geq 2.5 \text{ mg L}^{-1}$) [19]. Optimal selenium concentration not only promotes earlier bud break in tea plants, but also significantly increases their biomass, thereby improving tea yield [20]. Based on a comparative study of AMF-inoculated and non-inoculated maize treated with 20 mg kg⁻¹ selenite, AMF inoculation significantly enhanced the biomass of inoculated plants [11]. Previous research has also demonstrated that AMF can significantly increase the biomass of edible amaranth [6]. This result is in agreement with numerous studies demonstrating that AMF increases plant biomass and enhances selenium uptake in plants [7–10].

Selenium affects energy metabolism in organisms. For instance, selenium can regulate glycolysis in pig skeletal muscle by modulating its redox status [22]. At present, research on the effects of selenium on energy metabolism in plants remains limited. Our previous work showed that selenium treatment decreased ATP levels and energy charge and reduced the activities of phosphoglucose isomerase and cytochrome c oxidase [6]. These results suggest that selenium may regulate plant energy metabolism, thereby influencing selenium uptake. Notably, targeted metabolomics in this study revealed that selenium regulated energy metabolism in *Glomus mosseae*-colonized amaranth. Excessive selenium supply may negatively affect the expression and activity of proteins involved in energy metabolism in primary insulin target tissues of pigs [23]. Selenium may regulate energy metabolism in amaranth to modulate selenium uptake, maintaining stable biomass while significantly increasing leaf selenium content. The abundant NADPH in seedlings contributes to enhanced plant growth, and a positive correlation exists between NADPH content and plant antioxidant capacity [24]. NADPH content in the PPP pathway was significantly increased after selenium addition, which could be attributed to selenium addition increasing the activity of G-6-PDH+6-PGDH, thereby enhancing the PPP pathway, which is the main pathway for cellular production of reducing power (NADPH). Similarly, in the EMP pathway, the content of glucose 1-phosphate and glucose 6-phosphate was significantly

down-regulated by selenium addition, possibly due to a decrease in PGI activity, and also due to the enhancement of the PPP pathway exacerbating the depletion of glucose 6-phosphate. In the EMP pathway, selenium addition caused an increase in the content of 3-phosphoglycerate and 2-phosphoglycerate, probably because ribulose 5-phosphate formed by the PPP pathway produces 3-phosphoglycerate, which in turn produces 2-phosphoglycerate. The EMP pathway was enhanced by the selenium addition so that the content of 3-phosphoglycerate and 2-phosphoglycerate also increased. The metabolic pathway for the conversion of pyruvate to L-lactate was also enhanced. In the TCA cycle, selenium treatment significantly increased the content of *cis*-aconitate and isocitrate and down-regulated the content of α -ketoglutarate and L-malate. Glutamine reacts with α -ketoglutaric acid to form glutamate, which could explain the significant decrease in glutamate content. On the NADH-Q reductase complex of the electron transport chain, the electrons on NADH are first transferred to the FMN cofactor to form FMNH₂, and the electrons on the cofactor FMNH₂ are transferred to the iron-sulfur center (Fe-S). Selenium is chemically similar to sulfur and will replace sulfur in proteins. Sodium selenate is primarily absorbed into plants via sulfate transporters located on the roots [25]. Thus, some of the electrons on the cofactor FMNH₂ may not be transferred to the iron-sulfur center, which may explain the increase in FMN content with the addition of selenium and also suggests that selenium addition may perhaps reduce NADH-Q reductase activity. In addition, the CCO activity in the electron transport chain was reduced, which further corroborates that selenium addition attenuates electron transport chain.

Collectively, these data suggest that 2 mg kg⁻¹ Se reconfigures amaranth energy metabolism through PPP upregulation, EMP/TCA modulation, and electron transport inhibition. This metabolic remodeling, rather than growth suppression, facilitates selenium biofortification in mycorrhizal amaranth. Future research will be dedicated to elucidating the underlying mechanisms by which selenium modulates energy metabolism to enhance the selenium uptake capacity of AMF-inoculated amaranth. We also intend to explore whether Se-induced NADPH overproduction drives glutathione-mediated stress tolerance [24], a connection implied by our pathway analysis.

Conclusions

In conclusion, our study provides evidence that sodium selenate at 2 mg kg⁻¹ increases Se concentration in AMF-inoculated amaranth. This finding provides a theoretical basis for cultivating selenium-enriched amaranth.

The AM fungus *Glomus mosseae* may influence selenium uptake through its involvement in energy metabolism in AMF-inoculated amaranth.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40538-025-00845-4>.

Supplementary file 1.

Acknowledgements

Not applicable.

Author contributions

Conceptualization, R.H. and X.H.; data curation, Y.L. and M.M.; formal analysis, X.H.; investigation, Y.L.; resources, M.M.; writing—original draft preparation, X.H. and M.M.; writing—review & editing, R.H. and Y.L.; visualization, X.H.; supervision, M.M.; project administration, Y.L.; funding acquisition, R.H., X.H., X.T., Y.Z. and Y.L. All authors have read and agreed to the published version of the manuscript.

Funding

This research was supported by the Doctoral Fund of Jingchu University of Technology (YY202201, YY202404); the Funding from Guangxi Key Laboratory of Agro-Environment and Agric-Products Safety (GKLAEP52024-05); the Hubei Provincial Education Department Project (B2023224); the Jingmen Key Science and Technology Plan Projects (2023YFZD014); Grants from the Natural Science Foundation of Guangdong Province (2023A151110814); the Guangdong Province Key Laboratory of Microbial Signals and Disease Control (MSDC2023-18); and the Young and Middle-aged Leading Science and Technology Innovation Team by the Education Department of Hubei Province (T2023032).

Data availability

No datasets were generated or analyzed during the current study.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

¹College of Food and Biology, Jingchu University of Technology, Jingmen 448000, China. ²Hubei Provincial Key Laboratory of Drug Synthesis and Optimization, Jingchu University of Technology, Jingmen 448000, China. ³Guangxi Key Laboratory of Agro-Environment and Agric-Products Safety, Guangxi University, Nanning 530004, China.

Received: 3 June 2025 Accepted: 15 August 2025

Published online: 01 September 2025

References

- Chang C, Yin R, Wang X, et al. Selenium translocation in the soil-rice system in the Enshi seleniferous area, Central China. *Sci Total Environ.* 2019;669:83–90. <https://doi.org/10.1016/j.scitotenv.2019.02.451>.
- Koseoglu E, Kutuk B, Nalbantoglu OU, et al. Arsenic and selenium measurements in nail and hair show important relationships to Alzheimer's disease in the elderly. *J Trace Elem Med Biol.* 2021. <https://doi.org/10.1016/j.jtemb.2020.126684>.

3. Zhang H, Zhao Z, Zhang X, et al. Effects of foliar application of selenate and selenite at different growth stages on Selenium accumulation and speciation in potato (*Solanum tuberosum* L.). Food Chem. 2019;286:550–6. <https://doi.org/10.1016/j.foodchem.2019.01.185>.
4. Francini A, Quattrini E, Giuffrida F, et al. Biofortification of baby leafy vegetables using nutrient solution containing selenium. J Sci Food Agric. 2023;103(11):5472–80. <https://doi.org/10.1002/jsfa.12622>.
5. Baraniak J, Kania-Dobrowolska M. The dual nature of amaranth—functional food and potential medicine. Foods. 2022;11(4):618. <https://doi.org/10.3390/foods11040618>.
6. Mu M, Lu Y, Liao H, et al. Effect of inoculation with arbuscular mycorrhizal fungi on the energy metabolism of selenite-rich amaranth. J Basic Microbiol. 2024;64(3): e2300424. <https://doi.org/10.1002/jobm.202300424>.
7. Durán P, Acuña JJ, Jorquera MA, et al. Enhanced selenium content in wheat grain by co-inoculation of selenobacteria and arbuscular mycorrhizal fungi: a preliminary study as a potential Se biofortification strategy. J Cereal Sci. 2013;57(3):275–80. <https://doi.org/10.1016/j.jcs.2012.11.012>.
8. Yu Y, Zhang S, Wen B, et al. Accumulation and speciation of selenium in plants as affected by arbuscular mycorrhizal fungus *Glomus mosseae*. Biol Trace Elem Res. 2011;143(3):1789–98. <https://doi.org/10.1007/s12011-011-8973-5>.
9. Chen X, Zhang Z, Gu M, et al. Combined use of arbuscular mycorrhizal fungus and selenium fertilizer shapes microbial community structure and enhances organic selenium accumulation in rice grain. Sci Total Environ. 2020. <https://doi.org/10.1016/j.scitotenv.2020.141166>.
10. Zhang Z, Li B, Liu Y, et al. Arbuscular mycorrhizal fungal inoculation increases organic selenium accumulation in soybean (*Glycine max* (Linn.) Merr.) growing in selenite-spiked soils. Toxics. 2022;10(10): 565. <https://doi.org/10.3390/toxics10100565>.
11. Heidarvand L, Millar AH, Taylor NL. Responses of the mitochondrial respiratory system to low temperature in plants. Crit Rev Plant Sci. 2017;36(4):217–40. <https://doi.org/10.1080/07352689.2017.1375836>.
12. Nunes-Nesi A, Carrari F, Gibon Y, et al. Deficiency of mitochondrial fumarate activity in tomato plants impairs photosynthesis via an effect on stomatal function. Plant J. 2007;50(6):1093–106. <https://doi.org/10.1111/j.1365-3113X.2007.03115.x>.
13. Zhou Y, Yan K, Qin Q, et al. Phosphoglucose isomerase is important for *Aspergillus fumigatus* cell wall biogenesis. MBio. 2022;13(4): e0142622. <https://doi.org/10.1128/mbio.01426-22>.
14. Chumyam A, Shank L, Uthaibutra J, et al. Effects of chlorine dioxide on mitochondrial energy levels and redox status of 'Daw' longan pericarp during storage. Postharv Biol Technol. 2016;116:26–35. <https://doi.org/10.1016/j.postharvbio.2016.01.002>.
15. Lin Y, Lin H, Chen Y, et al. The role of ROS-induced change of respiratory metabolism in pulp breakdown development of longan fruit during storage. Food Chem. 2020;305: 125439. <https://doi.org/10.1016/j.foodchem.2019.125439>.
16. Zheng FL, Liang SM, Chu XN, et al. Mycorrhizal fungi enhance flooding tolerance of peach through inducing proline accumulation and improving root architecture. Plant Soil Environ. 2020;66(12):624–31. <https://doi.org/10.17221/520/2020-PSE>.
17. Vierheilig H, Schweiger P, Brundrett M. An overview of methods for the detection and observation of arbuscular mycorrhizal fungi in roots. Physiol Plant. 2005;125(4):393–404. <https://doi.org/10.1111/j.1399-3054.2005.00564.x>.
18. Li L, Lv F-y, Guo Y-y, et al. Respiratory pathway metabolism and energy metabolism associated with senescence in postharvest broccoli (*Brassica oleracea* L. var. *italica*) florets in response to O₂/CO₂ controlled atmospheres. Postharvest Biol Technol. 2016;111:330–6. <https://doi.org/10.1016/j.postharvbio.2015.09.032>.
19. Li D, Zhu Z, Xu Z, et al. Effects of selenium on the growth and nutrient absorption of pakchoi. J Plant Nutr Fertil. 2003;9(3):353–8. <https://doi.org/10.11674/zwjyf.2003.0319>.
20. Xiang J, Rao S, Chen Q, et al. Research progress on the effects of selenium on the growth and quality of tea plants. Plants. 2022;11(19):2491. <https://doi.org/10.3390/plants11192491>.
21. Hasanuzzaman M, Fujita M. Selenium pretreatment upregulates the antioxidant defense and methylglyoxal detoxification system and confers enhanced tolerance to drought stress in rapeseed seedlings. Biol Trace Elem Res. 2011;143(3):1758–76. <https://doi.org/10.1007/s12011-011-8998-9>.
22. Zhang J, Tang C, Zhang K. PSIV-B-35 late-breaking: integrating target metabolomic and global proteomic analyses reveals a selenium shift energy metabolism by regulating the redox state in skeletal muscle of pigs. J Anim Sci. 2019;97(Supplement_3):329–30. <https://doi.org/10.1093/jas/skz258.659>.
23. Pinto A, Juniper DT, Sanil M, et al. Supranutritional selenium induces alterations in molecular targets related to energy metabolism in skeletal muscle and visceral adipose tissue of pigs. J Inorg Biochem. 2012;114:47–54. <https://doi.org/10.1016/j.jinorgbio.2012.04.011>.
24. Alipour S, Wojciechowska N, Stolarska E, et al. NAD(P)-driven redox status contributes to desiccation tolerance in *acer* seeds. Plant Cell Physiol. 2020;61(6):1158–67. <https://doi.org/10.1093/pcp/pcaa044>.
25. Shibagaki N, Rose A, McDermott JP, et al. Selenate-resistant mutants of *Arabidopsis thaliana* identify Sultr1;2, a sulfate transporter required for efficient transport of sulfate into roots. Plant J. 2002;29(4):475–86. <https://doi.org/10.1046/j.0960-7412.2001.01232.x>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.