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Foliar Application of Nano-Selenium Enhances Tea Quality and Selenium Biofortification by Promoting Theanine Synthesis and Nitrogen Metabolism

Qingxue Guo^{1,2} | Zhenghao Wu¹ | Yuxin Xiao² | Helena Korpelainen³ | Chunyang Li¹

¹Zhejiang Key Laboratory of Horticultural Crop Quality Improvement, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou, China | ²College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou, China | ³Department of Agricultural Sciences, Viikki Plant Science Centre, FI-00014 University of Helsinki, Finland

Correspondence: Chunyang Li (lily12@zju.edu.cn)

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ABSTRACT

Selenium (Se) biofortification improves crops' nutritional value, while nano-selenium (nano-Se) offers enhanced bioavailability over traditional Se fertilisers. The quality of tea (*Camellia sinensis*) depends critically on nitrogen (N) metabolism and amino acid balance, particularly of theanine. This study assessing growth and quality, elucidating molecular mechanisms and evaluating long-term persistence explored the effects of nano-Se on tea through three different experiments. The results showed that nano-Se significantly increased the chlorophyll content, photosynthetic parameters and non-structural carbohydrates, indicating an enhanced photosynthetic capacity. Nitrogen uptake and metabolism were promoted, along with an increased leaf nitrogen content, NO₃⁻ accumulation and upregulation of ammonium transporter genes, thus providing further evidence. Theanine significantly increased in roots and leaves and upregulated theanine transporter genes, while polyphenol and catechin contents decreased, lowering the polyphenol-to-amino acid ratio of tea. The benefits of nano-Se persisted across three harvest times, with a sustained selenium content and an increased root theanine level, although leaf theanine and quality improvements varied. Overall, nano-Se promoted theanine accumulation via a coordinated regulation of N transporters and biosynthetic genes, while concurrently enhancing photosynthesis and Se biofortification. Its long-lasting efficacy positions nano-Se as a sustainable strategy for producing high-quality, Se-enriched tea, particularly in Se-deficient regions.

1 | Introduction

Tea (*Camellia sinensis* (L.) O. Kuntze) is a globally significant crop cultivated in tropical and subtropical regions, valued for its rich array of bioactive metabolites, including amino acids, catechins, caffeine, polyphenols and flavonoids. These compounds contribute to tea's widespread use as a beverage and in dairy and bakery products (Ye et al. 2023), while also conferring health benefits, such as reducing the risk of chronic diseases like cardiovascular disease and diabetes (Luo et al. 2024). The quality of tea is primarily determined by its metabolite profile, with amino

acids, particularly theanine, contributing to the umami flavour and polyphenols influencing astringency and bitterness (Wang et al. 2024). The balance between these compounds significantly affects tea's sensory attributes, nutritional value and market appeal. Consequently, strategies to enhance tea quality, especially by increasing the amino acid content, are critical for improving tea production and consumer satisfaction.

Selenium (Se) is an essential trace element that plays a vital role in human health, including antioxidant, anti-diabetes, anti-depression and anti-cancer effects (Ekumah et al. 2021). People in

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Se-deficient areas suffer a weakened immune system and health problems like Keshan disease (Natasha et al. 2018). After uptake and accumulation by different crops, Se can be transformed into organic compounds like selenoamino acids and selenoproteins (Wang et al. 2024). The edible parts of crop plants, like leaves, roots, fruits and flowers, are the main source of dietary Se for humans and animals, and many countries are working to increase Se levels in a variety of agricultural products (Broadley et al. 2010; Guo et al. 2023). Tea, as a widely consumed beverage, represents a promising vehicle for Se biofortification, particularly in areas with low Se availability. Tea plants are known for their ability to accumulate selenium. As a result, their leaves contain Se in organic forms, such as amino acids, proteins and polysaccharides. Se-enriched tea leaves are potentially more beneficial for health than regular tea leaves, due to the combined effects of their active ingredients and selenium (Wang et al. 2024).

Beyond its nutritional benefits to humans, Se application has been shown to enhance plant growth, stress resistance and quality in various crops (Elkelish et al. 2019; Teixeira et al. 2021; Guo et al. 2023). Selenium promotes nutrient uptake, including nitrogen (N), phosphorus and potassium (Teixeira et al. 2021; Guo et al. 2023), which supports chlorophyll synthesis, photosynthesis-related protein synthesis and photosynthetic efficiency (Alves et al. 2020; Guo et al. 2023). Meanwhile, Ježek et al. (2011) have reported significantly increased levels of phenylalanine, aspartic acid, glutamic acid, threonine and tyrosine after Se application in potato tubers. It is suggested that Se could be used as a regulator to manipulate the concentrations of amino acids that are essential for crop quality. Recent studies have found a marked increase in theanine, glutamate, proline and arginine levels in tea plants under Se application through adjustments in the GS-GOGAT pathway and promotion of gene expression related to amino acid and protein metabolism (Liu et al. 2021; Li et al. 2021, 2024). As a non-proteinogenic amino acid, theanine is synthesised in tea plant roots before being moved to shoots through the vascular system. The biosynthesis of theanine starts with the production of its precursors (glutamate and ethylamine), culminating in the catalysis by theanine synthetase (Ye et al. 2023). Therefore, it is postulated that Se will influence N metabolism in amino acids, particularly theanine synthesis and transportation, which improves tea quality.

Traditional Se fertilisers, such as selenite and selenate, are commonly used, but they often suffer from low bioavailability due to binding with soil components like metal oxides and organic matter (Guo et al. 2023). In contrast, nano-selenium (nano-Se) offers advantages, including higher bioavailability and reduced environmental impact, making it a promising tool for sustainable tea cultivation (Zhao et al. 2020). Recently, Liu et al. (2025) reported elevated tea quality due to effects on amino acids and Se content after nano-Se application. However, the mechanisms underlying these improvements, particularly the role of nano-Se in nitrogen uptake and metabolism, remain underexplored. Additionally, while short-term effects of Se application on tea quality have been documented (Li et al. 2024; Liu et al. 2025), the persistence of these effects across multiple seasons has received little attention.

To address the existing knowledge gaps, this study conducted three experiments to investigate the effects of nano-Se on tea

growth, quality and underlying molecular mechanisms, with a focus on nitrogen metabolism and amino acid synthesis. We proposed the following hypotheses: (1) nano-Se enhances tea quality by promoting nitrogen uptake and metabolism, leading to increased amino acid levels, particularly for theanine, thereby improving the flavour and nutritional value of tea; (2) nano-Se upregulates key genes involved in ammonium and amino acid transport, facilitating theanine synthesis and translocation; (3) the beneficial effects of nano-Se on tea quality and nitrogen metabolism persist across multiple harvest times, supporting its potential as a sustainable, long-term strategy for tea production.

2 | Results

2.1 | Effects of Nano-Se on Growth and Compounds of Two Tea Cultivars

Nano-selenium significantly influenced leaf chlorophyll pigments and photosynthetic traits of both tea cultivars. The Se application significantly increased the contents of chlorophyll a, chlorophyll b, total chlorophyll and carotenoid (Table S1). Similarly, photosynthetic traits significantly increased with higher P_n , G_s and T_r under nano-Se application compared to the control treatment (Table S2). Both tea cultivars had different photoresponse curves with significantly higher maximum photosynthetic rates and light saturation points under nano-Se spray than under control conditions (Table S2). The contents of leaf soluble sugar, root sucrose and root starch of both tea cultivars were higher under Se application (Figure 1).

Nano-selenium increased the nitrogen content of both tea cultivars. Leaves had significantly higher nitrogen contents when compared to no-Se treatment, increments being 16.56% and 19.8%, respectively (Figure 2). Nano-Se spray significantly affected root NO_3^- , leaf NH_4^+ and leaf NO_3^- (Figure 2b,c). The NH_4^+ content in the roots and leaves of 'Longjing 43' were significantly lower after Se application than under no-Se treatment. The leaf NO_3^- content of both tea cultivars was significantly higher under Se application than without Se (Figure 2c). Nano-Se was also an important factor in influencing enzyme activities of nitrogen metabolism (Figure 2d,e). The nitrate reductase (NR) activity of roots was higher, whereas that of leaves was significantly lower under Se application than without Se in both tea cultivars. Leaf glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH) activities of both tea cultivars were also significantly promoted by Se application (Figure 2e).

Nano-Se application significantly affected tea qualities (Figure 3). After Se application, Se contents in roots, stems and leaves of both tea cultivars were significantly higher than without Se (Figure 3a). The nano-Se application did not impact root and leaf amino acid contents of either tea cultivar compared to the Se treatment (Figure 3b). However, theanine contents of roots and leaves in both tea cultivars were significantly promoted by Se application, with 46.32% and 49.64% increases detected in the roots of 'Longjing 43' and 'Zhongcha 108' when compared to the no-Se treatment, respectively. Similarly, the leaf theanine content of 'Longjing 43' and 'Zhongcha 108' increased 42.89% and 57.22% relative to the

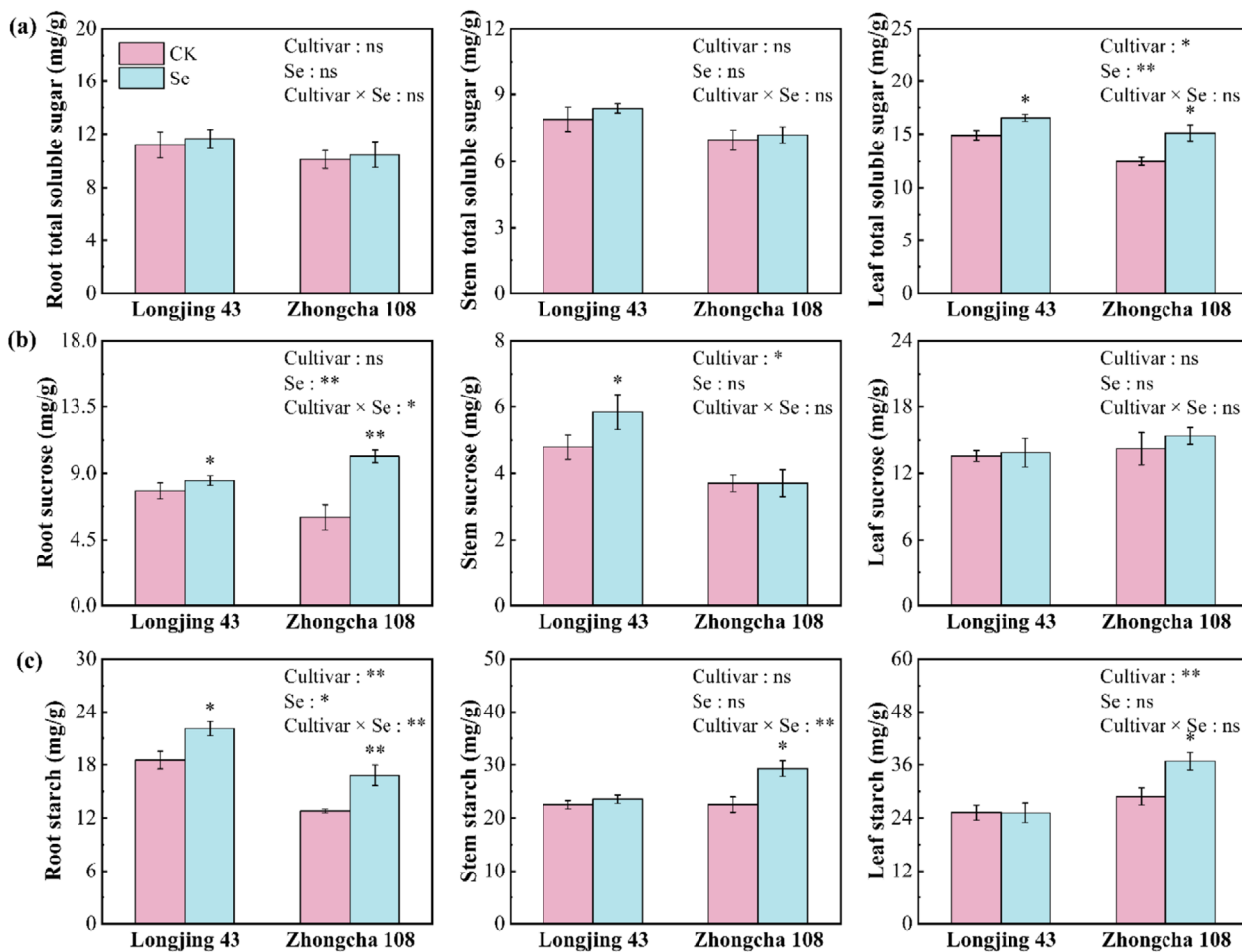


FIGURE 1 | Effects on non-structural carbohydrate contents (dry weight). (a) Soluble sugar content (b), sucrose content (c) and starch content in Longjing 43 and Zhongcha 108 plants (mean \pm SE, $n = 5$), respectively. CK: Control group; Se: Selenium application; Cultivar: Tea cultivars. Two-way ANOVA analysis was used to test cultivar, Se and their interaction effects. An independent samples t test was used to compare differences between CK and Se application for each tea cultivar. * $0.01 < p \leq 0.05$; ** $p \leq 0.01$.

no-Se application, respectively (Figure 3b). After nano-Se application, tea polyphenol and catechin contents were significantly lower than those in treatments without Se in both tea cultivars (Figure 3b), which led to a greatly declined ratio between tea polyphenols and amino acids (Figure 3c).

3 | Effects of Nano-Se Application on Transcriptome Profiles

After nano-Se application, there were a total of 2686 differentially expressed genes (DEGs) in tea roots, including 1695 up-regulated genes and 991 down-regulated genes. In tea leaves, there were 2640 DEGs, including 1055 up-regulated genes and 1585 down-regulated genes (Figure S1). Kyoto Encyclopedia of Genes and Genomes (KEGG) annotation assigned the 875 DEGs from tea roots to 50 distinct pathways. The functional analysis highlighted a significant involvement in pathways related to ATP-binding cassette (ABC) transporters (23 DEGs), endoplasmic reticulum protein processing (54 DEGs), amino acid metabolism (82 DEGs) and carbohydrate metabolism (123 DEGs) (Figure S1a). The KEGG pathway enrichment analysis of the 809 DEGs identified in tea leaves revealed their involvement in 50 distinct pathways. Notably, 31 DEGs were annotated to ABC

transporter pathways, while 52 DEGs were associated with signal transduction mechanisms. Additionally, 107 DEGs representing the largest functional cohort were linked to ribosome biogenesis and function, and 45 DEGs participated in amino acid metabolism (Figure S1b).

In the roots, pathways, such as amino acid biosynthesis (ko01230) and plant hormone signal transduction (ko04075), were up-regulated following nano-Se treatment (Figure 4a). In the leaves, arginine and proline metabolism (ko00330), nitrogen metabolism (ko00910) and alanine, aspartate and glutamate metabolism (ko00250) pathways were up-regulated, while glutathione metabolism (ko00480) and phenylpropanoid metabolism (ko00360) pathways were down-regulated (Figure 4b). In the transcriptome analysis, the differentially expressed genes in the theanine biosynthesis pathway included glutamate synthase (GOGAT, EC 1.4.1.14), glutamate dehydrogenase (GDH, EC 1.4.1.4) and arginine decarboxylase (ADC, EC 4.1.1.19). Following nano-Se treatment, all differentially expressed genes were up-regulated, indicating an enhanced expression of enzymes critical for theanine production (Figure 5a). Meanwhile, the theanine transporter genes (*CsAAP1*, *CsAAP5* and *CsAAP6*) and the ammonium transporter genes (*CsAMT1.1*, *CsAMT1.2* and *CsAMT3.1*) were significantly up-regulated by nano-Se application (Figure 5b,c).

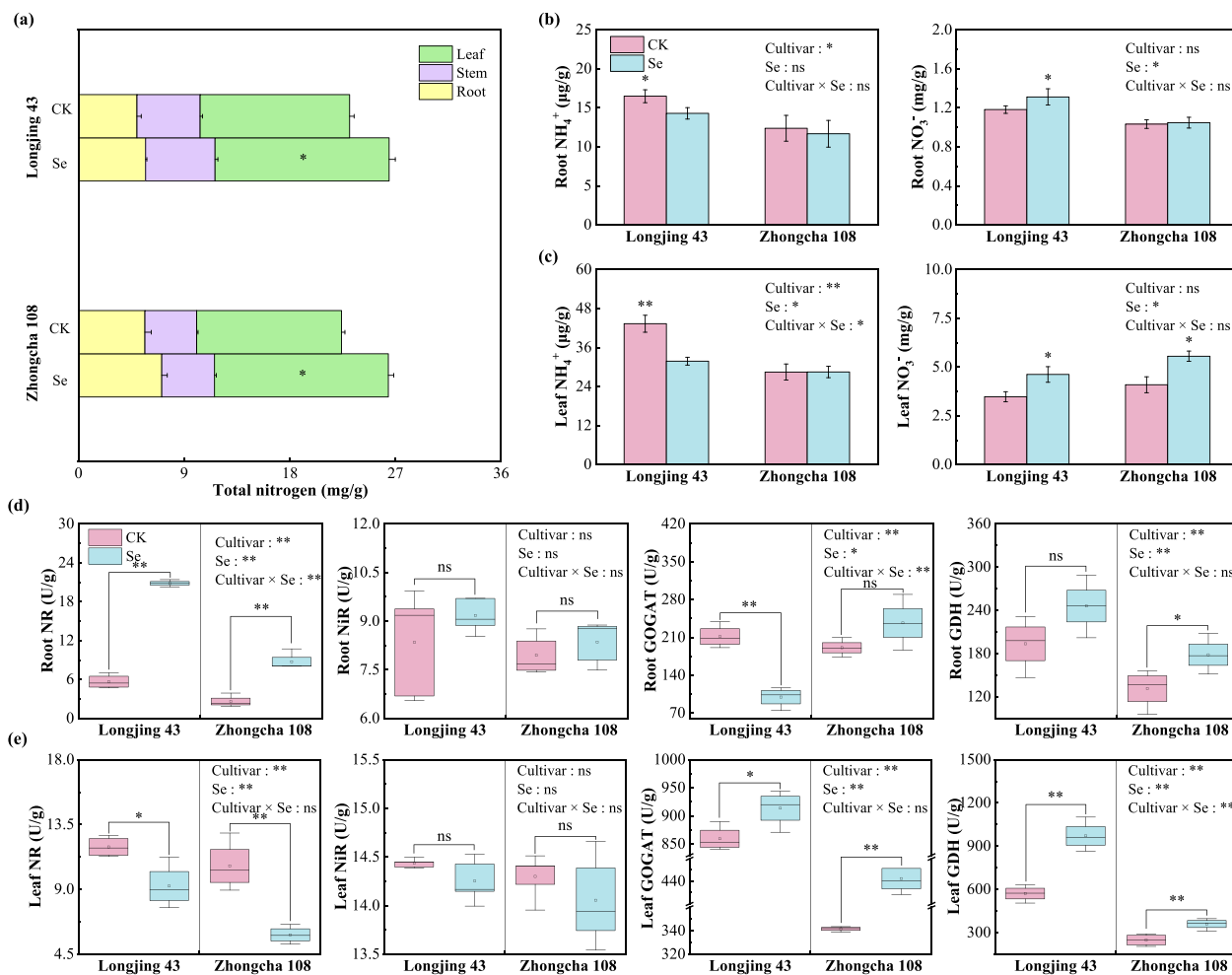


FIGURE 2 | Effects of nano-selenium treatments on total nitrogen, ammonium and nitrate contents and enzyme activities in Longjing 43 and Zhongcha 108 (mean \pm SE, $n = 5$). (a) Total nitrogen content in plants (dry weight), (b) root ammonium and nitrate contents; (c) leaf ammonium and nitrate contents, (d) root enzyme activity, (e) leaf enzyme activity. CK: Control group; Se: Nano-Se application; cultivar: Tea cultivars, root NH_4^+ : Root ammonium; root NO_3^- : Root nitrate; leaf NH_4^+ : Leaf ammonium nitrogen; leaf NO_3^- : Leaf nitrate; NR: Nitrate reductase; NiR: Nitrite reductase; GOGAT: Glutamate synthetase; GDH: Glutamate dehydrogenase. Two-way ANOVA analyses were used to test the effects of cultivar, nano-Se and their interactions. Independent samples *t*-test analyses were performed to test differences between control and nano-Se application at $p \leq 0.05$. ns, no significant difference; * $0.01 < p \leq 0.05$; ** $p \leq 0.01$.

4 | Persisting Effects of Nano-Se Application on Tea Quality in Long-Term Experiment

Contents of *Chl a*, *Chl b*, total chlorophyll pigments and P_n across the three harvested times were continuously higher under nano-Se application than in the treatment without Se (Tables 1 and S3). Both the old and young expanded leaves were greener after nano-Se application than those under control conditions (Figure S2). Nano-Se application also greatly impacted photosynthesis curves at different harvest times by increasing the maximum net photosynthetic rate and light saturation point (Figure S3). The nano-Se application showed persistently increasing effects on tea plant nitrogen contents across different harvest times. In particular, the leaf nitrogen content was continuously significantly higher under Se application than without Se (Figure 6). Similarly, nano-Se application continuously increased the leaf NO_3^- content and GOGAT activity during the long-term experiment (Figure 6).

Tea plants had significantly higher Se contents under nano-Se applications than without Se during the long-term experiment (Figure 7a). Nano-Se application significantly increased the theanine content of tea roots across three harvest times (Figure 7b). The amino acid and theanine contents of tea leaves were significantly higher under Se application than without Se at the first harvest time. However, the contents of polyphenol and catechin (TP/AA) significantly declined (Figure 7b), which led to a significantly lower ratio of tea polyphenol and amino acid in summer and autumn (Figure 7c).

5 | Discussion

Selenium (Se) is increasingly recognised as a beneficial element for plant physiology and human nutrition, with its application in crop biofortification gaining attention (Schiavon and Pilon-Smits 2017; Guo et al. 2023). This study investigated

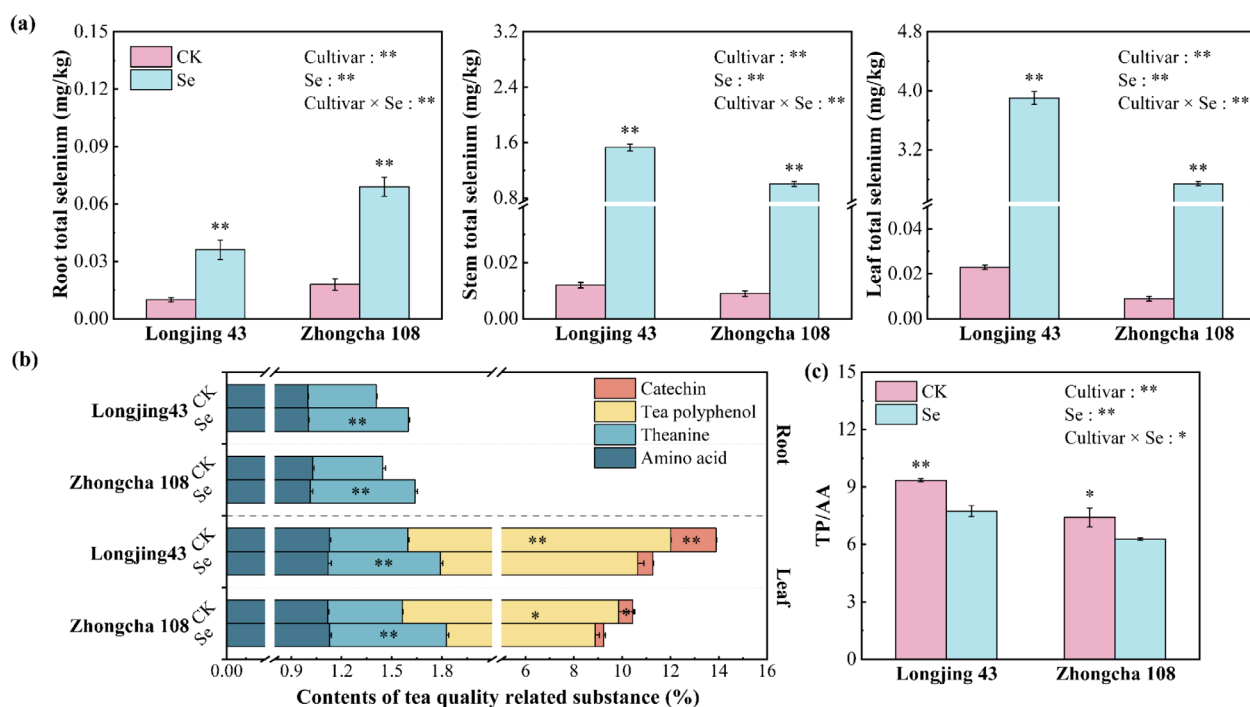


FIGURE 3 | Effects of nano-Se application on total selenium contents and tea quality characters in Longjing 43 and Zhongcha 108 plants (mean ± SE, $n = 5$, dry weight). (a) Total selenium content in roots, stems and leaves, (b) tea quality, including amino acid, theanine, tea polyphenol and catechin, (c) tea polyphenol and amino acid ratio (TP/AA). CK: Control group; Se: Nano-Se application; Cultivar: Tea cultivars. Two-way ANOVA analyses were used to test the effects of cultivar, nano-Se and their interactions. Independent samples *t*-test analyses were performed to test differences between control and nano-Se application at $p < 0.05$. ns, no significant difference; * $0.01 < p < 0.05$; ** $p < 0.01$.

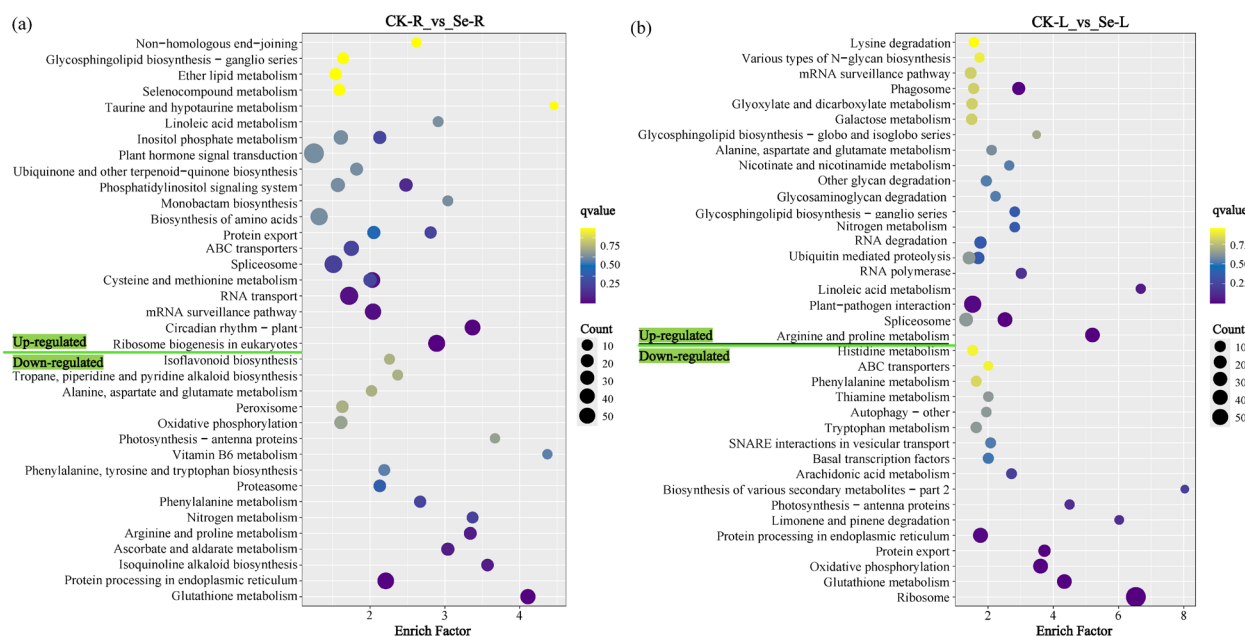


FIGURE 4 | KEGG enrichment analyses of DEGs between control and nano-Se treatments. (a) KEGG enrichment in tea roots between control and nano-Se treatments. (b) KEGG enrichment in tea leaves between control and nano-Se treatments. Rich factor represents the ratio of DEGs enriched in a given KEGG pathway to all genes annotated to that pathway in the background genome. The higher the enrichment factor, the more significant the enrichment level of DEGs in this pathway is. The colour of the circle represents *qvalue*. The smaller the *qvalue* is, the more reliable the enrichment significance of DEGs in this pathway is. The size of the circle indicates the number of genes enriched in the pathway.

the effects of nano-selenium (nano-Se) on tea growth, quality and nitrogen metabolism through a series of experiments. Our findings demonstrated that nano-Se significantly enhances

photosynthetic capacity, nitrogen uptake and theanine content, leading to improved tea quality, with some effects persisting across multiple harvest times. These results provide insights

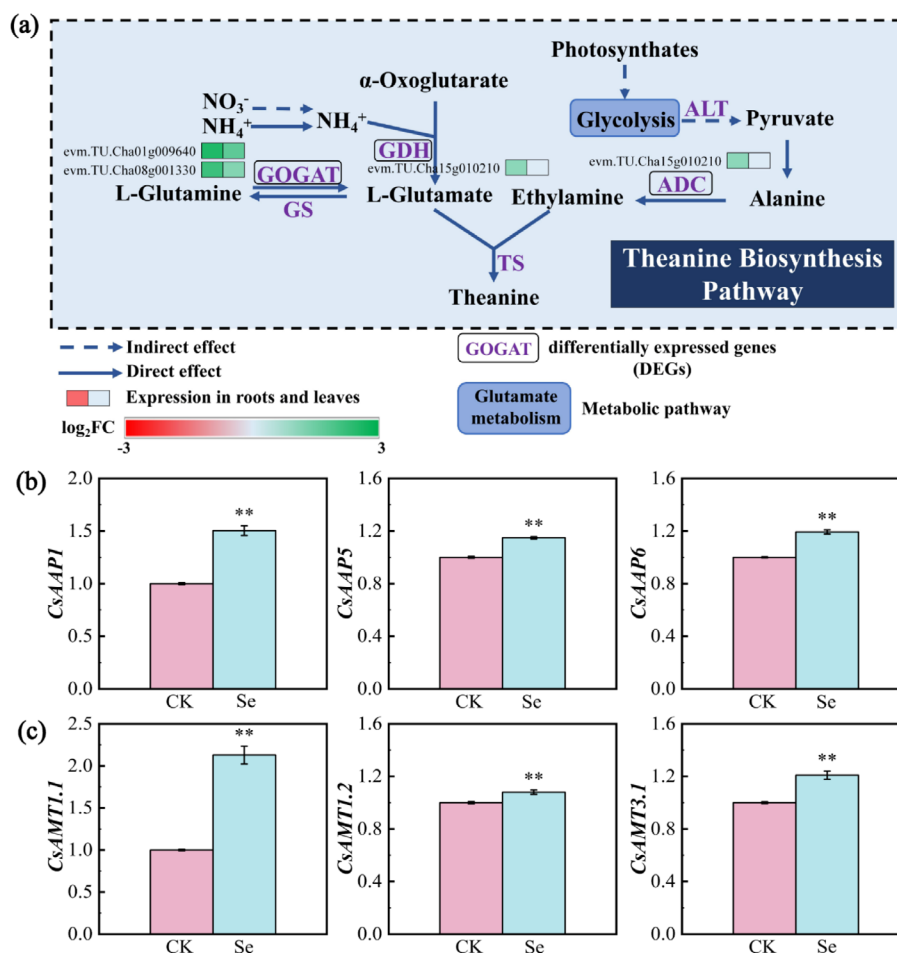


FIGURE 5 | Nano-Se effects on nitrogen uptake, metabolism and transport. (a) Effects of nano-Se application on theanine biosynthesis pathway in tea roots and leaves. Solid and dashed arrows represent direct and indirect effects. The purple font within a black border represents the relevant genes, and the black font within a blue background represents the relevant pathways. evm.TU.Cha01g009640 represents the gene ID, and the box to the right of the gene ID indicates the expression of the gene in the root and leaf (\log_2 Fold). GOGAT: Glutamate synthase; GDH: Glutamate dehydrogenase; ADC: Arginine decarboxylase; ALT: Alanine aminotransferase. (b) The expression of theanine transporters CsAAPs in tea leaf. (c) The expression of ammonium transporters CsAMTs in tea leaf.

TABLE 1 | Effects of nano-Se treatment on chlorophyll pigment contents across different harvest times.

Harvest time	Treatment	Chl a/(mg/g)	Chl b/(mg/g)	Chl/(mg/g)	Chl a/b	Car/(mg/g)
First	CK	1.314 ± 0.089	0.433 ± 0.034	1.747 ± 0.122	3.044 ± 0.045*	0.275 ± 0.015
	Se	1.796 ± 0.078**	0.769 ± 0.115*	2.565 ± 0.192**	2.446 ± 0.184	0.259 ± 0.022
Second	CK	0.792 ± 0.114	0.214 ± 0.038	1.006 ± 0.152	3.771 ± 0.103*	0.240 ± 0.019
	Se	1.855 ± 0.131**	0.775 ± 0.164*	2.630 ± 0.291**	2.650 ± 0.306	0.328 ± 0.042**
Third	CK	0.426 ± 0.041	0.120 ± 0.013	0.546 ± 0.053	3.569 ± 0.106*	0.131 ± 0.009
	Se	0.755 ± 0.093*	0.239 ± 0.032*	0.995 ± 0.125*	3.183 ± 0.077	0.205 ± 0.019**
<i>p</i>	<i>P</i> Time	**	**	**	**	**
	<i>P</i> Se	**	**	**	**	*
	<i>P</i> Time × Se	**	ns	**	ns	ns

Note: The values presented in the table represent the mean ± standard error ($n=5$); ns, no significant difference; * $0.01 < p \leq 0.05$; ** $p \leq 0.01$. Abbreviations: Car, content of carotenoid; Chl, total chlorophyll; Chl a, content of chlorophyll a; Chl a/b, ratio of chlorophyll a to chlorophyll b; Chl b, content of chlorophyll b; CK, control group; Se, nano-Se treatment group.

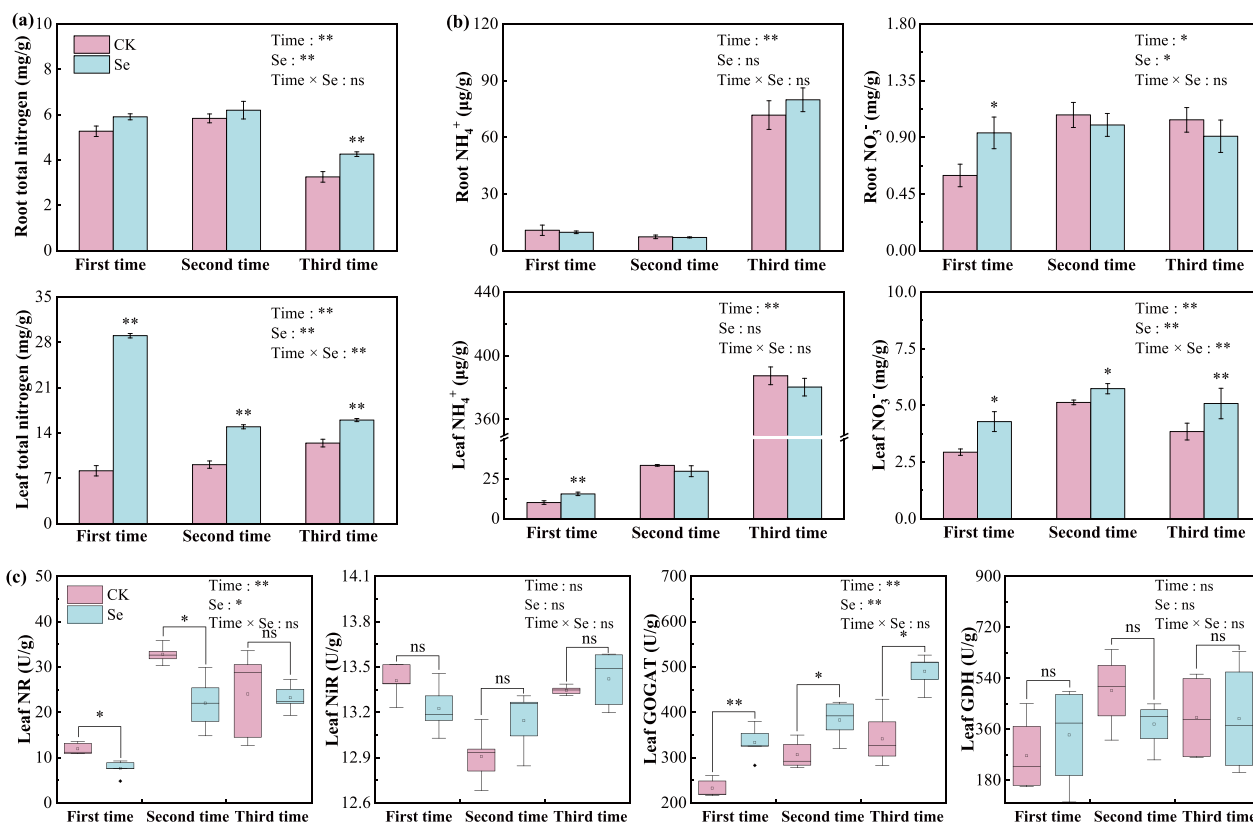


FIGURE 6 | Effects of nano-Se treatment on total nitrogen, ammonium and nitrate contents and enzyme activities across different harvest times (mean \pm SE, $n = 5$). (a) Total nitrogen contents in roots and leaves (dry weight), (b) ammonium and nitrate contents in roots and leaves, (c) leaf enzyme activity. CK: Control group; Se: Nano-Se application. NR: Nitrate reductase; NiR: Nitrite reductase; GOGAT: Glutamate synthetase; GDH: Glutamate dehydrogenase. Independent samples t -test analyses ($p \leq 0.05$): Ns, no significant difference; * $0.01 < p \leq 0.05$; ** $p \leq 0.01$.

into the physiological and molecular mechanisms underlying nano-Se's benefits and highlight its potential as a sustainable tool for tea production.

5.1 | Nano-Se Enhances Photosynthetic Capacity and Carbon Metabolism

Several studies have suggested that Se application can potentially increase the growth and production of various crop species (Zhang et al. 2014; Hussain et al. 2025). One of the most important reasons is that Se application can largely promote chlorophyll content and then increase photosynthetic ability (Mozafariyan et al. 2017; Alves et al. 2020). The improved photosynthesis will supply sufficient carbon for the growth of roots, shoots and other edible parts. In our first experiment, we also found a greater promotion of the chlorophyll content and photosynthetic ability of tea plants after nano-Se application (Tables S1, S3). Ren et al. (2022) have found an upregulation of sugar transporter genes of tea plants in response to Se application. Enhanced photosynthesis likely provided here more carbon assimilates, as evidenced by increased root sucrose and starch contents (Figure 1).

A large proportion of DEGs related to functions, including carbon metabolism, starch and sucrose metabolism and carbon fixation, which may reflect complex underlying pathways that explain how tea plants regulate carbon flux under the influence of nano-Se application (the second experiment, Figure S1).

The beneficial effects of nano-Se on improving tea photosynthetic traits persisted during the long-term experiment (Table 1, Figure S3). The sustained increase in the chlorophyll content and photosynthetic parameters across the three harvest times in the long-term experiment (Table 1, Figure S3) indicated that nano-Se has a lasting impact on tea plant vigour, likely by enhancing carbon availability for metabolic processes (Zhang et al. 2024). Some studies have reported that exogenous Se application enhances plants' resistance to various stresses (Sharma and Dietz 2006; Malik et al. 2012; Guo et al. 2023). Previous studies have also reported that Se enhances plants' resistance to abiotic stresses, such as cold stress in tea plants, by regulating the proline content and antioxidant enzyme activities (Malik et al. 2012; Liu et al. 2021). Future research should explore whether nano-Se improves tea plants' resilience to environmental stressors, such as drought or temperature fluctuations, which are critical for tea production.

5.2 | Nano-Se Application Increased Nitrogen Uptake and Influenced Nitrogen Metabolism

The present study demonstrated that a foliar application of nano-Se significantly enhanced nitrogen metabolism and assimilation in tea plants, as evidenced by physiological, biochemical, transcriptional and enzymatic data. Different studies have reported that Se application promotes nutrient concentrations, including nitrogen, in diverse species

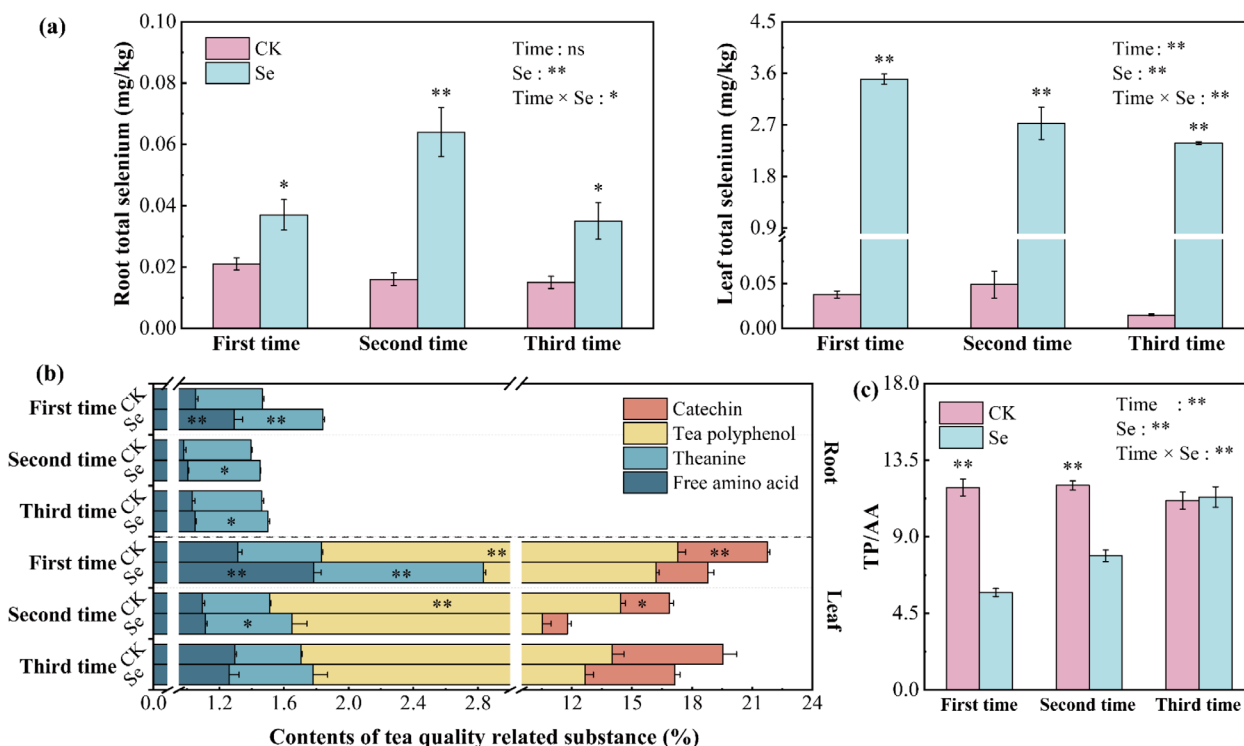


FIGURE 7 | Effects of nano-Se application on the total selenium content and tea quality across different harvest times (dry weight). (a) Total selenium contents in roots and leaves, (b) tea quality including amino acids, theanine, tea polyphenols and catechins, (c) tea polyphenol and amino acid ratio (TP/AA). CK: Control group; Se: Nano-Se application; time: Harvest time. Two-way ANOVA analyses were used to test the effects of harvest time, nano-Se and their interactions. Independent samples *t*-test analyses were performed to test differences between control and nano-Se application at $p \leq 0.05$. ns, no significant difference; * $0.01 < p \leq 0.05$; ** $p \leq 0.01$.

(Mozafariyan et al. 2017; Zhu et al. 2017; Wen et al. 2021). In our study, nano-Se application led to a significant increase in the leaf nitrogen content, alongside upregulating the expression of ammonium transporter genes, *CsAMT1.1*, *CsAMT1.2* and *CsAMT3.1* (Figures 2, 4, 5), which demonstrated that nano-Se enhances the tea plant's ability for ammonium uptake and N accumulation. Tea plants have a preference for NH_4^+ over NO_3^- . Ruan et al. (2016) found that the presence of NH_4^+ can promote NO_3^- influx in tea plants, probably due to reduced, potentially toxic effects of superfluous NH_4^+ . The lower activity of leaf NR suggested that nano-Se prioritised NH_4^+ assimilation, resulting in a higher NO_3^- accumulation in tea leaves (Figure 2). The upregulation of the glutamine synthetase-glutamate synthase (GS-GOGAT) pathway, particularly the increased GOGAT and glutamate dehydrogenase (GDH) activities, further supports the view of enhanced nitrogen assimilation (Figures 2, 5). These metabolic changes likely provide precursors for amino acid synthesis, particularly for theanine, which is critical for tea quality.

One of the primary objectives of this study was to investigate whether nano-Se application enhances the amino acid content in tea plants, as amino acids are critical for tea quality. However, the impact of nano-Se on the total amino acid content was inconsistent. The theanine content significantly increased in roots and leaves of both cultivars in the first experiment (Figure 3) and in roots across all three harvest times (July, October, April) in the long-term experiment (Figure 7). In contrast, the total amino acid content of leaves only increased significantly at the

July harvest (Figure 7). Liu et al. (2025) have reported an increase in the amino acid content in tea plants treated with nano-Se, attributing it to enhanced nitrogen availability mediated by the rhizosphere microbiota. In contrast, Li et al. (2024) found no significant increase in the amino acid content following a selenite fertiliser application. This discrepancy may result from nitrogen allocation to other metabolic processes, such as protein synthesis or storage, rather than free amino acid accumulation (Liu et al. 2020). Our transcriptomic analysis revealed the upregulation of pathways related to alanine, aspartate, glutamate, arginine and proline metabolism (Figure 4), indicating that nano-Se enhances the synthesis of specific amino acids critical for theanine production. The upregulation of theanine transporter genes (*CsAAP1*, *CsAAP5*, *CsAAP6*) further suggested that nano-Se facilitated theanine transport from roots to leaves, contributing to its accumulation in edible parts (Figure 5). These findings partially support our hypothesis that nano-Se enhances tea quality through increased amino acid levels, particularly in relation to theanine, but suggest that the total amino acid accumulation may be influenced by other factors, such as cultivar or environmental conditions at different harvest times.

5.3 | Nano-Se Improves Tea Quality and se Biofortification

The quality of tea is primarily determined by its chemical composition, particularly by the balance between polyphenols (including catechins) and amino acids. Polyphenols, especially

catechins, contribute to the astringency and bitterness of tea, while theanine is responsible for the umami taste and sweetness (Bhattacharyya et al. 2012; Guo et al. 2021). The ratio of tea polyphenols to amino acids (TP/AA) is a crucial indicator of tea quality, a lower ratio generally indicating a better quality due to a more favourable balance between astringency and umami (Guo et al. 2021). The nano-Se application significantly decreased the content of polyphenols and catechins and the TP/AA ratio in tea leaves in the first experiment (Figure 3b,c). The increased theanine content, driven by the enhanced GS-GOGAT activity and upregulation of GOGAT, GDH and arginine decarboxylase (ADC) genes, underscores nano-Se's role in improving tea's sensory and nutritional quality (Figure 5). Meanwhile, the high bioavailability of nano-Se also led to a significant Se accumulation in tea roots, stems and leaves across all three harvest times (Figure 3), supporting its potential for producing Se-enriched tea, particularly in Se-deficient regions.

5.4 | Effects of Nano-Se on Tea Quality Persist a Long Time

One important aim of this study was to reveal how long the positive effect of the nano-Se application lasts. We found that the persistence of nano-Se's effects on the tea quality varied, although tea plants accumulated significantly higher N contents across all three harvest times. The root theanine content remained elevated at all three harvests, while the leaf theanine content significantly improved only at the July harvest (Figure 7). By reducing the polyphenol (including catechins) content, tea plants kept lower TP/AA at the initial two harvest times. This variation may be influenced by environmental factors, such as temperature, light intensity, or day length, which differ across the sampling times and affect plant metabolism. These findings suggest that the timing of nano-Se application is critical for optimising its effects on tea quality.

With progress in nanotechnology-driven agriculture, the foliar application of selenium nanoparticles has become an innovative approach for selenium biofortification in crops (Hussain et al. 2020; Liu et al. 2025; Wang et al. 2025). Nano-Se can enter plant leaves through stomata into the substomatal cavity due to its small size relative to stomatal apertures, and it can also penetrate the leaf cuticle directly for leaf absorption (Wang et al. 2025). Then, they are mainly transformed to selenocysteine, selenomethionine and methylselenocystein, which are important for human health (Wang et al. 2024, 2025). Our results demonstrated that nano-Se application significantly increased the Se content in roots and leaves of both tea cultivars in the first experiment, and Se can accumulate within tea plants for a long time. The Se increment is driven by nano-Se's high bioavailability, enabling efficient uptake and accumulation (Wang et al. 2025). The sustained increase in Se contents across all harvest times highlights nano-Se's efficacy for long-term biofortification to produce Se-rich tea.

This study demonstrates that nano-Se is a promising tool for enhancing tea quality and Se biofortification, with significant effects on nitrogen metabolism, theanine synthesis and photosynthetic capacity. The sustained effects on the root theanine

and Se content across July, October and April harvests underscore nano-Se's potential for long-term improvements in tea production. However, the inconsistent increase in the total amino acid content of leaves and the lack of significant quality improvements at the last harvest suggest that nano-Se's impact is time-dependent. Future research should optimise the timing and frequency of nano-Se application to maximise its benefits on tea quality across different harvest times. Additionally, investigating the interaction between nano-Se and environmental factors, such as light or temperature variations at different sampling times, could provide insights into its efficacy under diverse conditions. The potential of nano-Se to enhance tea plants' resilience to abiotic and biotic stresses, as reported in other crops (Guo et al. 2023), also warrants further exploration. Finally, consumer studies are needed to evaluate the sensory and health benefits of Se-enriched tea produced with nano-Se, ensuring its market viability.

6 | Materials and Methods

6.1 | Materials and Experimental Design

6.1.1 | Effects of Nano-Se on Tea Growth and Quality

Two widely cultivated tea (*Camellia sinensis*) cultivars, 'Longjing 43' and 'Zhongcha 108', were used in this experiment. Sixty healthy seedlings (30 per cultivar) were planted individually in pots containing 7 kg of homogeneous soil and provided with adequate water. After five months of growth, 20 seedlings per cultivar were selected for the experiment, which consisted of four treatments, combining two nano-selenium (nano-Se) levels (0 and 10 mg l⁻¹) and two cultivars, with five replicates per treatment. A previous study found that 10 mg l⁻¹ of nano-Se had significant impacts on tea growth (Liu et al. 2025). Each replicate comprised two pots, with one seedling per pot. Selenium nanoparticles with their sizes ranging from 50 nm to 150 nm were synthesised by reducing selenium dioxide with ascorbic acid in the presence of chitosan. Briefly, 20 mM SeO₂ solution was mixed with 1% chitosan solution under stirring. Then, 1% ascorbic acid solution was added gradually, and the reaction was maintained at 25°C with stirring for 3 h, yielding a transparent red solution (Yu et al. 2024). For the selenium-treated group, nano-Se was applied as a foliar spray twice, with a 7-day interval between applications. The solution was evenly sprayed from top to bottom onto all leaves of each plant until the leaves were fully saturated but not dripping. Each plant received approximately 35 mL of solution for each foliar spray.

6.1.2 | Mechanisms of Nano-Se Effects on Tea Quality

To investigate the mechanisms underlying nano-Se's effects on tea quality, a second experiment was conducted using the 'Longjing 43' cultivar. Twenty healthy seedlings were planted in pots as described above. After five months, 10 seedlings were selected and subjected to the same nano-Se foliar spray protocol (0 and 10 mg l⁻¹, two applications with a 7-day interval), with five replicates per treatment. Tea leaves and fine roots were harvested, immediately frozen at -80°C and stored for

RNA extraction. Transcriptome sequencing and quantitative real-time PCR (qRT-PCR) were performed to analyse the expression of genes related to ammonium transporters (*CsAMTs*) and amino acid transporters (*CsAAPs*).

6.1.3 | Persistence of Nano-Se Effects on Tea Quality

To evaluate the long-term effects of nano-Se, 40 healthy 'Longjing 43' seedlings were planted in pots as described above. After six months, 30 seedlings were selected and randomly divided into two groups. One group received nano-Se foliar spray (10 mg l⁻¹, two applications with a 7-day interval) in mid-June, while the control group received an equivalent volume of water. Samples were collected at three time points: July, October and April of the following year. At each time point, five replicates were harvested for analysis.

6.2 | Data Collection Methods

6.2.1 | Photosynthetic Characters and Non-Structural Carbohydrates

Before sample harvesting, the net photosynthetic rate was measured using a portable photosynthesis measuring system (LI-6800; Li-Cor, USA). The measured leaf was illuminated at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD) for at least 5 min before the gas exchange measurement. The leaf temperature, relative humidity and CO₂ concentration were maintained at 26°C, 60% and 400 \pm 5 $\mu\text{mol mol}^{-1}$. Then, the photoresponse curve was measured at 1800, 1700, 1600, 1400, 1200, 1000, 750, 550, 400, 200, 100, 50, 20, 10 and 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD. Chlorophyll pigments were quantified using 80% acetone at absorbance wavelengths of 645, 663 and 470 nm.

One part of the harvested materials was dried at 75°C for 72 h and ground into powder. For the non-structural carbohydrate analysis, 0.05 mg of fine powder was extracted in 80% ethanol at 80°C and centrifuged. The residues were hydrolysed with 9.2 M HClO₄ and then used to measure starch after centrifugation according to Yemm and Willis (1954). The supernatant was then used to measure soluble sugars using the anthrone reagent at 625 nm (Yemm and Willis 1954), and sucrose was determined according to the method of Green et al. (1994).

6.2.2 | Amino Acids, NH₄⁺, NO₃⁻ and Enzyme Activities

The theanine content was determined by high-performance liquid chromatography (HPLC). Briefly, 0.15 g of fine powder was extracted with 50% ethanol at 70°C for 20 min and centrifuged at 4500 rpm for 10 min. The supernatant was mixed with a 50 $\mu\text{g ml}^{-1}$ L-norvaline internal standard, boric acid buffer, deionised water and a fluorescent colour-developing reagent to prepare the sample solution. An Agilent ZORBAX Eclipse AAA column (150 \times 4.6 mm, 3.5 μm) was used at 40°C with a gradient flow rate of 1.0 mL min⁻¹, using mobile phase A (disodium hydrogen phosphate) and mobile phase B (acetonitrile methanol water). The injection volume was 10 μL .

The nitrogen (N) concentration was measured for 0.1 g of dried powder using the semi-micro Kjeldahl method. The free amino acid content was determined by the ninhydrin method: 0.1 g of dried powder was homogenised in 5 mL of ultrapure water, extracted at 100°C for 5 min and the supernatant was mixed with phosphate buffer and 2% ninhydrin, with absorbance measured at 570 nm. Fresh leaf and root samples stored at -80°C were used to measure NH₄⁺ and NO₃⁻ contents following Luo et al. (2015). Activities of nitrate reductase (NR), nitrite reductase (NiR), glutamate synthase (GOGAT) and glutamate dehydrogenase (GDH) were quantified using assay kits (Solarbio, Beijing, China). Enzyme activities were measured in five biological replicates, with three technical replicates per sample.

6.2.3 | Tea Polyphenols, Catechin and Total se Content

Tea polyphenols were quantified using the Folin-Ciocalteu method (Mao et al. 2023). Dried powder samples were extracted with 70% methanol at 70°C, and the supernatant was mixed with 10% Folin-Ciocalteu reagent and 7.5% Na₂CO₃, with absorbance measured at 765 nm. The total Se content was determined by digesting 0.2 g of plant material with HNO₃-H₂O₂ and analysing it using an Agilent 8900 ICP-MS/MS (Agilent, USA).

The catechin content was measured by HPLC following Zhou et al. (2022). Briefly, a fine powdered tea sample (0.2 g) was extracted with 70% methanol in a 70°C water bath for 10 min. After cooling to room temperature, the mixture was centrifuged for 10 min. The supernatant was collected, and the residue was re-extracted with an additional 70% methanol under identical conditions. The combined supernatants were diluted to a final volume of 10 mL with 70% methanol and filtered through a 0.45 μm membrane to obtain the stock solution. Chromatographic separation was performed on a C18 reversed-phase column (250 mm \times 4.6 mm, 5 μm) maintained at 35°C. The chromatographic conditions followed Zhou et al. (2022).

6.2.4 | Transcriptome Sequencing and Analysis

Tea roots and leaves under control and nano-Se application in the second experiment were chosen for sequencing. Transcriptome sequencing and data analysis utilised the reference tea genome (<https://bigd.big.ac.cn/gwh/Assembly/1086/show>) (Wang et al. 2020) and were completed by Biomarker Technologies Co. LTD (Beijing, China) at HiSeq 2000 (Illumina, San Diego, California USA). The filtration of raw reads was performed in the BMK cloud (www.biocloud.net). Subsequently, the cleaned reads were aligned to the reference genome using Hisat 2 (v2.2.1, <https://daehwankimlab.github.io/hisat2/>). Reads with multiple mismatches were excluded from the annotation process, while only reads with perfect matches and one mismatch were further analysed and annotated based on the reference genome. A normalised expression level was calculated using the fragments per kilobase of exon per million mapped fragments (FPKM) normalisation method. To identify differentially expressed genes (DEGs) between control and nano-Se treatments in the second

experiment, the DeSeq package was used within R (v 4.4.0). Stringent values of false discovery rate (FDR) ≤ 0.01 and fold change (\log_2 FC) ≥ 2 (p value 0.05) as a threshold were used to identify significant differences in gene expression between different treatments. KEGG functions of DEGs were annotated in the BMK cloud (www.biocloud.net).

6.2.5 | Real-Time Quantitative PCR (RT-qPCR) Analysis

Total RNA was extracted from tea plant tissues using TRIzol Reagent by TaKaRa Bio (Dalian, China), followed by first-strand cDNA synthesis with the PrimeScript II 1st Strand cDNA Synthesis Kit (TaKaRa Bio) according to the manufacturer's protocol. RNA concentration and purity were determined using a NanoDrop 2000 spectrophotometer (Thermo Fisher Scientific, USA). RT-qPCR amplification was performed in a CFX96 Real-Time PCR Detection System (Bio-Rad Laboratories, Hercules, USA) using SYBR Green chemistry (Premix Ex Taq, TaKaRa Bio). The reaction conditions were as follows: initial denaturation at 95°C for 30 s, 95°C for 5 s (denaturation), primer-specific annealing for 35 s (temperature optimised per gene) and 72°C for 35 s (extension), amplification for 40 cycles. The reference gene β -actin was used for normalisation. Primer specificity was confirmed by a melt curve analysis and agarose gel electrophoresis of PCR products. Relative gene expression was calculated via the $2^{-\Delta\Delta C_t}$ method. All primer information of CsAMTs and CsAAPs is in Table S4.

6.2.6 | Statistical Analyses

The two-way ANOVA analysis was used to explore the effects of tea cultivar or harvest time, nano-Se and their interactions on various parameters. After that, the independent samples t -test was used to compare control and nano-Se treatments in the first and third experiments. In the second experiment, the independent samples t -test was also used to compare gene expression levels of CsAMTs and CsAAPs between control and nano-Se treatments, respectively. Statistical analyses were performed using SPSS 26.0. Graphs were generated using Origin 2022. The KEGG classification maps and KEGG enrichment graphs were constructed on the BMK Cloud Platform (www.biocloud.net).

Author Contributions

Qingxue Guo: conceptualisation; data curation; formal analysis; investigation; methodology; visualisation; writing – original draft. **Zhenghao Wu:** data curation; investigation. **Yuxin Xiao:** data curation; investigation. **Helena Korpelainen:** validation; writing – review and editing. **Chunyang Li:** conceptualisation; funding acquisition; methodology; project administration; resources; supervision; validation; writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the [Supporting Information](#) of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** pbi70491-sup-0001-DataS1.zip. **Figure S1:** Statistics of differentially expressed genes (DEGs) and KEGG classification in roots and leaves of 'Longjing 43' plants between control and nano-Se treatments. **Figure S2:** Picture of 'Longjing 43' leaves. **Figure S3:** Light response curves and photosynthetic characteristics of Longjing 43 plants across three harvest times. **Table S1:** Effects of nano-Se application on the photosynthetic pigment contents of Longjing 43 and Zhongcha 108 (mean \pm SE, $n = 5$). **Table S2:** Photosynthetic characters of Longjing 43 and Zhongcha 108 plants before and after nano-selenium application (mean \pm SE, $n = 5$). **Table S3:** Effects of nano-Se application on photosynthetic characteristics of Longjing 43 across three harvest times (mean \pm SE, $n = 5$). **Table S4:** Primer information for RT-qPCR analysis. **Table S5:** Data used to compare differences in Se treatments between tea varieties. **Table S6:** Data used to compare persistent effects on tea quality. **Table S7:** Data of RT-qPCR.