Science of the Total Environment 952 (2024) 175995

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Selenium availability in tea: Unraveling the role of microbiota assembly and functions

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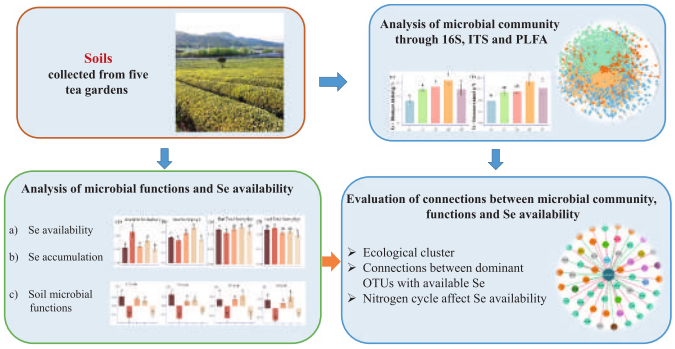
HIGHLIGHTS

- The tea cultivar Fenglǜ improved the soil available Se content.
- The microbial structure and functions were differently shaped by tea cultivars.
- Soil NH_4^+, NO_3^- and functional genes *amoA1* were positively related with available Se.
- Dominant microbes positively related with available Se were enriched in the Fenglǜ tea garden.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Abasiofiok Mark Ibekwe

Keywords:
Selenium availability
Microbiota assembly
Nitrogen cycling
Selenium-rich tea
Inter-kingdom network

ABSTRACT

Tea (*Camellia sinensis* (L.) O. Kuntze) plants have a strong ability to accumulate selenium (Se). However, the question of how tea plants affect Se availability has received little attention. In this study, five tea cultivars, including Soubei (SB), Aolǜ (AL), Longjing43 (LJ), Zhaori (ZR) and Fenglǜ (FL), were chosen for the study. Quantitative Microbial Ecology Chip and high-throughput sequencing were used to explore the effects of five tea cultivars on soil functions, microbial community structures and Se availability. The results showed that the total soil Se content in the FL garden was lower compared to LJ and SB gardens, whereas available Se was highest in the FL garden. Based on the Bray-Curtis distances, tea cultivar was the main factor affecting bacterial and fungal community structures. The abundance of functional genes concerning carbon, nitrogen, phosphorus and sulfur cycling processes varied among tea gardens. The higher soil NH_4^+ and NO_3^- contents, and higher abundance of functional genes like *nifH*, *amoA1* and *narG*, whereas lower total nitrogen in the FL garden than in the AL and LJ tea gardens demonstrated that the FL tea plants induced microbes to accelerate soil nitrogen cycling processes. Dominant microbes that positively related with functional genes like *nifH*, *narG*, and *amoA1* were also positively related with the available Se content. In conclusion, tea cultivars could regulate soil functions through affecting microbial community structures and then affecting the soil Se availability. The soil nitrogen cycle processes are suggested to be closely related with Se transformation in tea gardens.

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https://doi.org/10.1016/j.scitotenv.2024.175995
Received 3 July 2024; Received in revised form 30 August 2024; Accepted 1 September 2024
Available online 3 September 2024

1. Introduction

Selenium (Se) is a trace element with a unique role in the human health, mainly acquired through different foods. It has been found that Se participates in diverse cellular metabolic processes and exhibits a series of functions as an antioxidant, anti-diabetes, anti-depression and anti-cancer agent (Ekumah et al., 2021). However, the Se distribution is very uneven, and people in low Se areas suffer from Se deficiency, leading to a weakened immune system and health problems, like Keshan and Kashin-Beck diseases (Natasha et al., 2018). To improve daily Se uptake, many countries and regions, for instance, Finland, United Kingdom and China, are working to increase the Se content of diverse agricultural products by applying various selenium fertilizers (Broadley et al., 2010; Wen, 2021; Guo et al., 2023). While the application of Se fertilizers is a promising approach, the effectiveness of this strategy largely depends on the bioavailability of Se (Guo et al., 2023; Yuan et al., 2023).

The bioavailability of Se in soil is a key factor influencing plant uptake and accumulation (Guo et al., 2023). While plants can absorb soluble Se forms, such as selenate and selenite, a significant portion of Se in soil exists in insoluble forms unavailable for plant uptake (Dinh et al., 2019). Therefore, understanding the factors that influence Se availability in soil is crucial for developing strategies to increase the Se content in plants. Soil properties, including pH, the organic matter content, and metal ion concentrations, are known to influence Se availability (Dinh et al., 2017, 2019; Zhai et al., 2021). Additionally, recent studies have highlighted the significant role of soil microorganisms in transforming Se between soluble and insoluble forms (Liang et al., 2020; X. Luo et al., 2022; Guo et al., 2023). Specific microbial species have been shown to either increase or decrease Se availability through processes like reduction and oxidation. Fungal species (*Aureobasidium pullulans*, *Mortierella humilis*, *Trichoderma harzianum* and *Phoma glomerata*) are able to reduce selenate and selenite to Se nanoparticles (Liang et al., 2020). A heterotrophic bacterium *Bacillus megaterium* can oxidize elemental Se to selenite (Sarathchandra and Watkinson, 1981). A recent study also clearly demonstrated that four strains of bacteria (*Dyella* spp. LX-1 and LX-66, and *Rhodanobacter* spp. LX-99 and LX-100) can dramatically increase soluble Se in soil (X. Luo et al., 2022). Overall, most studies have focused on several isolated and cultured bacterial or fungal species, but the connections between Se availability and soil microbial communities have not been much studied.

Plant species or genotypes affect the composition, structure and function of soil microbial communities through their influence on soil properties and recruitment of diverse microbes (Henneron et al., 2020; Liu et al., 2022). The plants supply a substantial amount of photosynthesis-derived compounds, including carbohydrates, amino acids and organic acids, to fuel the presence of numerous bacterial and fungal species (Zhalnina et al., 2018). Different compounds released by plant species or genotypes harbor diverse soil microbial communities with further effects on nutrient cycling processes (Zhalnina et al., 2018; Henneron et al., 2020). Several studies have found that the Se transformation is affected by microbes related to the cycling of nutrients like nitrogen (N), carbon (C) or phosphorus (P). Tugarova et al. (2014) revealed that a nitrogen fixation bacterial strain *Azospirillum brasilense* was capable to reduce selenite. It is expected that plant species or genotypes with different impacts on soil nutrient cycles will also affect the Se availability through changing soil microbial communities.

Tea (*Camellia sinensis* (L.) O. Ktze.) is an economically important woody perennial plantation crop, which is widely spread throughout tropical and subtropical areas (Wang et al., 2024). Tea beverages with diverse secondary metabolites, including theanine, flavanones and polyphenols, are popular around the world (Jeyaraj et al., 2014). Tea plants have a strong ability to accumulate Se that is effectively metabolized into selenoamino acids, selenoproteins and Se-polyphenols (Wang et al., 2024). The uptake and metabolism of Se can improve tea quality, not only the Se content but also, e.g., phenol and amino acid contents (Wang et al., 2024). The Se-rich tea appears highly promising due to its distinctive value as blending taste and wellness. In this study, we firstly investigated differences in Se accumulation by testing five tea cultivars. Then, the impact of each tea cultivar on available soil Se was tested. When differences were found, the effects of tea cultivars on soil microbial communities and nutrient cycling were explored. Given the interconnectedness of plants, microbial communities, and nutrient cycling, we hypothesize that different tea cultivars differentially impact the availability of Se in tea gardens by influencing the composition and function of their associated soil microbial communities.

2. Materials and methods

2.1. Soil collections and selenium measurements

The experiment was conducted in Fusheng town (29°56′N, 120°41′E), Zhejiang Province, China. Five tea cultivars, namely Soubei (SB) (133.3 ha), Aolǜ (AL) (20 ha), Longjing43 (LJ) (53.3 ha), Zhaori (ZR) (8 ha) and Fenglǜ (FL) (16.7 ha), are famous for matcha production and also wildly grown. Six 10 m × 10 m plots were set up in each tea garden (except 20 m × 20 m in the SB tea garden). Then we divided each plot into four subplots (5 m × 5 m). At the beginning of April 2022, buds, leaves and branches of tea plants were collected from each subplot and then pooled into on sample. Tea plants strongly impose their effects on soil microbial traits and functions on topsoil layers (Wang and Ye, 2020). A soil core sampler (diameter 70 mm) was used to collect soil and roots at the soil depth of 0–5 cm and 5–10 cm. On each subplot, one soil sample was collected at each soil depth and then pooled into one sample. Coarse roots (diameter $\geq$ 2 mm) and fine roots (diameter $<$ 2 mm) were separated in each sample. All plant and soil samples were brought back to the laboratory. The fine roots were scanned and analyzed by the WinRhizo system (Régent Instrument, Inc., Québec, Canada) to determine root architecture, including specific root length and root density. Then, the buds, leaves, branches and fine roots were dried at 75 °C for 80 h and grounded into powder.

One part of fresh soil samples (10 g) was extracted with 2 M KCl, and the extractions were used to measure soil NH_4^+ and NO_3^-. Another part of soil samples was air-dried to test pH, soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), available phosphorus (AP), total Se and available Se. A soil-water suspension (1:2.5 *w/v*) was used for pH determination. SOM and AP were tested by the potassium dichromate external heating method and the molybdenum-antimony colorimetric method after extraction with sodium bicarbonate, respectively. TN and TP were tested by the Kjeldahl method and ultraviolet spectrophotometer, respectively.

To test the total Se, 0.5 g air-dried soil was first digested by 6 ml HCl and 2 ml HNO_3 through a microwave digestion procedure. The liquid was transferred and deionized water was added to 50 ml. To test available Se, 5.0 g air-dried soil was extracted with 50 ml 0.1 M KH_2PO_4 and then shaken for 80 min at 30 °C. KH_2PO_4 extractions provide an estimate of Se that is available for uptake (Zhao et al., 2005; Favorito et al., 2017). The filtrate was used to measure available Se. The plant sample (0.2 g) was digested by 3 ml HNO_3 and 1 ml H_2O_2. The liquid was transferred and deionized water was added to 25 ml for testing the plant Se content. The total Se, available Se content in soil and plant Se content were measured by Agilent 8900 ICP-MS/MS (Angilent, USA).

2.2. Bacterial and fungal communities

Soil microbial communities were quantified using a phospholipid fatty acid (PLFA) analysis and high-throughput sequencing. Free-dried soil samples were used to extract lipids following the method by Bligh and Dyer (1959). The phospholipids were purified by methanol through silica column fractionation and then diluted by hexane and transferred to gas chromatography vials for analysis with Agilent 7890B (Agilent, USA). The fatty acid 19:0 was used as the internal standard. The

biomarkers iso-, anteiso-(i13:0, i14:0, i15:0, a15:0, i16:0, i17:0 and a17:0) and 10Me-(10Me17:0 and 10Me18:0) were attributed to Gram-positive bacteria (G+ bacteria) (R. Luo et al., 2022); biomarkers 17:1ω8c, 18:1ω5c, 18:1ω7c, cy17:0 and cy19:0 were attributed to Gram-negative bacteria (G− bacteria) (R. Luo et al., 2022); and 16:1ω5c, 18:1ω9c and 18:3ω6c were used for fungi (Joergensen, 2022; Q. Guo et al., 2024). The biomarker 16:1ω5 in PLFA was used as a proxy for the AMF biomass (Willers et al., 2015; Ven et al., 2020). The biomarkers 14:0, 16:0, 17:0, 18:0 and 20:0 were used as non-specific markers present in all microorganisms (Joergensen, 2022). The sum of all selected biomarkers was used to characterize the total microbial biomass.

To quantify soil functional genes related to the cycling processes of C, N, P and S, the abundance of seventy-one biogeochemical cycling genes were tested using a qPCR-based chip named Quantitative Microbial Ecology Chip QMEC on the WaferGen Smart-Chip Real-time PCR platform. Details of the 36 primer pairs, DNA extraction and quantification, primer validation and HT-qPCR processes were described in Zheng et al. (2018). The abundance of functional genes was calculated and normalized in relation to the 16S rRNA gene according to Zheng et al. (2018).

The ALFA-SEQ Magnetic Soil DNA Kit was used to extract soil DNA. After testing its concentration and purity, the 16S rRNA gene and the ITS fragment were amplified using specific primers (799F: AACMGGATTAGATACCCKG and 1193R: ACGTCATCCCCACCTTCC for bacteria; ITS3-F: GCATCGATGAAGAACGCAGC and ITS4-R: TCCTCCGCTTATTGATATGC for fungi) (Beckers et al., 2016; McKay et al., 1999). Detailed information about the amplification processes is provided in Supplementary materials. Raw data generated from sequencing were quality-filtered and merged by FASTQ (version 0.14.1, https://github.com/OpenGene/fastp). During the clustering, the chimera sequences and singleton OTUs were removed at the same time. The remaining sequences were clustered into operational taxonomic units (OTUs) using the UPARSE algorithm at 97 % similarities. The taxonomic assignment of the 16S rRNA gene and ITS fragment sequencies was performed based on the SILVA database and UNITE database, respectively. The raw reads were deposited into the NCBI Sequence Read Archive database under the accession code PRJNA1101723.

2.3. Statistical analysis

The Wilcoxon test was used to test differences in the total Se, available Se, abundance of functional genes and microbial α diversity among the five tea gardens with package 'ggpubr' (Kassambara, 2023). One-way ANOVA analysis was used to compare differences in soil traits like pH, NH_4^+ and NO_3^-. The Principle Coordinate Analysis (PCoA) was used to test the beta-diversity of bacterial and fungal communities based on Bray-Curtis distances through the "adonis" function in the 'vegan' package in R (Oksanen et al., 2017). Package 'ggClusterNet' was used to construct the inter-kingdom bacterial-fungal network after removing OTUs with a relative abundance <0.01 %, and Spearman's $r > 0.6$ was selected with package 'igraph' to visualize the network (Wen et al., 2022). The microbial taxa that presented high correlations with each other were strongly co-occurring within the inter-kingdom bacterial-fungal network community. The highly connected and identifiable taxa form ecological clusters that represent important ecological units. The modules (ecological clusters) of the network were used to calculate the relative abundance of each module by averaging the standardized relative abundances (z-score) of the functional genes of nutrient cycles (Fan et al., 2021). Dominant species were selected from the ecological clusters with the relative abundance >0.05 and Spearman's correlation $r > 0.8$, significant at $P < 0.001$. The connections between dominant OTUs with available Se were tested with package 'Hmisc' and visualized by 'pheatmap' (Kolde, 2019; Harrell, 2023).

3. Results

The chemical properties of the soil varied among the five tea gardens (Table S1). The TN level was lower, whereas NH_4^+ and NO_3^- amounts were much higher in the FL garden than in the other tea gardens. The soil in AL, LJ and SB gardens had much higher TP, SOM and AP compared to FL and ZR gardens (Table S1). The specific root length (SRL) of FL was much higher than that of the other tea cultivars at 0–5 cm soil depth, while SRL of SB was lower than that of the other tea cultivars at 5–10 cm soil depth (Fig. S1). The LJ cultivar had a lower root density than the ZR cultivar at 0–5 cm and 5–10 cm (Fig. S1).

The amount of available Se in the soil of the FL garden was higher than that in AL, LJ and ZR gardens at 0–5 cm and 5–10 cm soil depth. However, the total Se content of soil in the FL garden was lower than that in LJ and SB (Fig. 1). The total Se of FL leaves was significantly higher than that of ZR, and the total Se of FL branches was much higher than that of AL and LJ. However, the total Se of FL roots was significantly lower than that of LJ, SB and ZR (Fig. 1).

The tea cultivar type significantly affected the structure of soil microbial communities based on the PLFA, 16S and ITS results (Fig. 2a–d). The FL soil had a lower G+, G-, AMF, bacterial, fungal and total microbial biomass than the soil in the SB garden (Figs. S2 and S3). Acidobacteria, Proteobacteria and Actinobacteria of bacteria at the phylum level, and Mortierellomycetes and Leotiomycetes of fungi at the class level were the main components of microbial communities (Tables S2–S5). The available Se content was significantly positively correlated with the bacterial beta-diversity but negatively correlated with the fungal beta-diversity (Fig. 2e, f).

The abundance of functional genes concerning C, N, P and S cycling processes varied among the tea gardens (Fig. 3a, Tables S6 and S7). The soil in the FL gardens had much more functional genes related with C degradation (such as *lig*, *cex* and *amyA*), carbon fixation (such as *korA*, *accA* and *smtA*) and N cycling (such as *narG*, *amoA1* and *gdhA*) than soils in AL and LJ tea gardens (Tables S6, S7). The functional gene compositions of each variety were distinct from each other (Fig. 3b). The soil N and P cycling potential (Z score) in FL and ZR gardens were much lower than that in other tea varieties (Fig. 3c). The available Se was strongly connected with soil NH_4^+ and NO_3^- levels (Fig. S4). There was no obvious connection with different soil functions (Fig. S5), whereas a further analysis found that the available Se content was positively related with genes *yedZ*, *phoX*, *nifH*, *narG*, *cdh* and *amoA1* (Fig. 4).

Four main modules (modules 1–4) constituted the inter-kingdom bacterial-fungal network (Fig. 5a). OTUs belonging to Proteobacteria, Actinobacteria and Chloroflexi were the main components within module 1 (Fig. 5b). Only the OTU abundance in module 1 was positively related with the soil available Se content and functional potential (Z score) (Fig. 5c, d). A further analysis found that the richness was positively related with the functional genes of nitrification, denitrification, N mineralization, S reduction, S oxidation and P mineralization (Fig. S6). Many dominant bacterial and fungal OTUs within module 1 were significantly connected with the available Se content and soil functional genes (Fig. 6). For example, the relative abundance of bacterial OTU108 (belonging to the Chloroflexi phylum) and fungal OTU886 (belonging to the Mortierellomycetes phylum) was positively associated with the available Se content, and also with genes *yedZ*, *phoX*, *nifH*, *narG*, *cdh* and *amoA1*. Meanwhile, the relative abundances of OTU108 and OTU886 in the FL tea garden were higher than those in other tea gardens (Fig. 6; Table S8). OTU1574, OTU35, OTU20, OTU463, OTU 512, OTU59 and OTU414 were negatively related with available Se and with some of the above genes as well (Fig. 6b, Table S8). The relative abundances of these OTUs were significantly lower in the FL garden than in AL and LJ tea gardens (Table S8).

4. Discussion

It has been demonstrated that Se can promote tea plant growth,

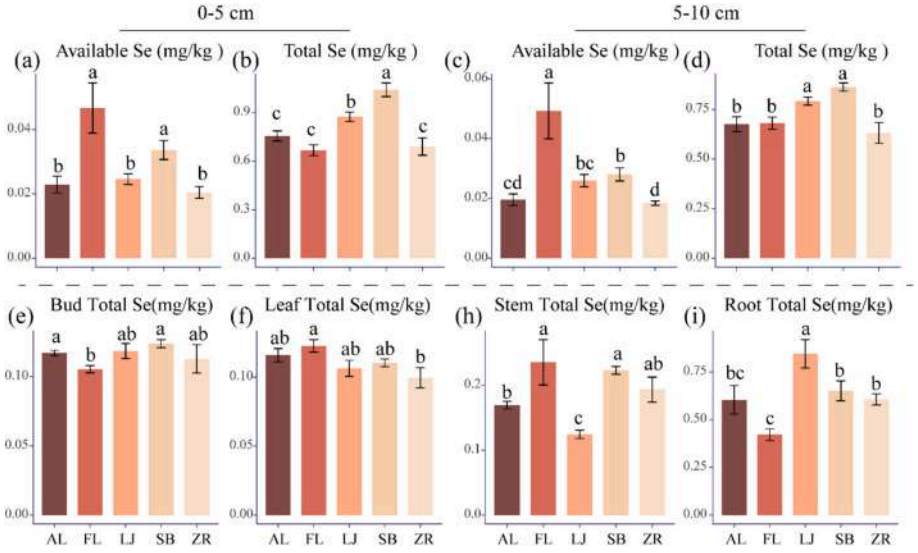

Fig. 1. Selenium (Se) contents in the soil and plant. (a–d) The total Se and available Se contents of soil on two soil layers (0–5 cm and 5–10 cm). (e–i) The total Se content in different parts of tea plants. Different letters indicate significant differences. Five tea varieties are Soubei (SB), Aolù (AL), Longjing43 (LJ), Zhaori (ZR) and Fenglù (FL).

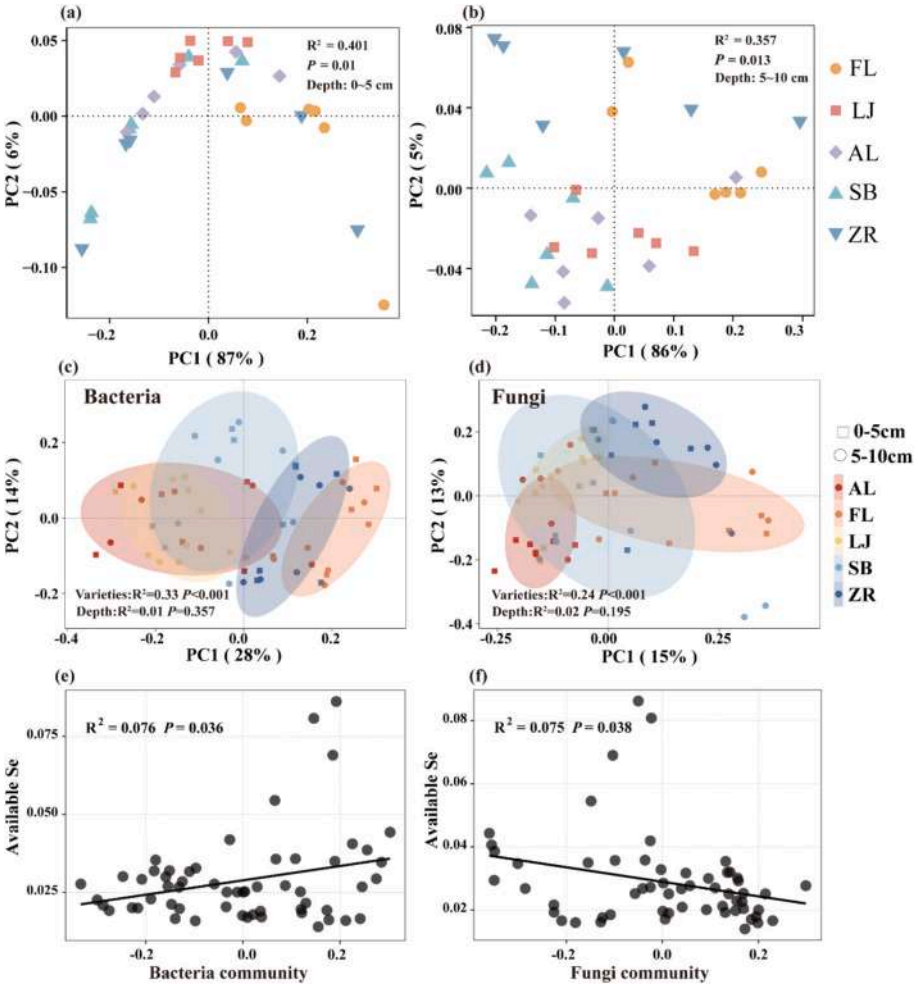

Fig. 2. Soil microbial community structure traits and their relationships with the available Se content. (a, b) The PCoA analysis based on PLFA. (c–d) The PCoA analysis based on 16S and ITS. (e–f) The bacterial and fungal community structure connected with the available soil Se content based on Bray-Curtis distances (Spearman correlation). The tea varieties are Soubei (SB), Aolù (AL), Longjing43 (LJ), Zhaori (ZR) and Fenglù (FL).

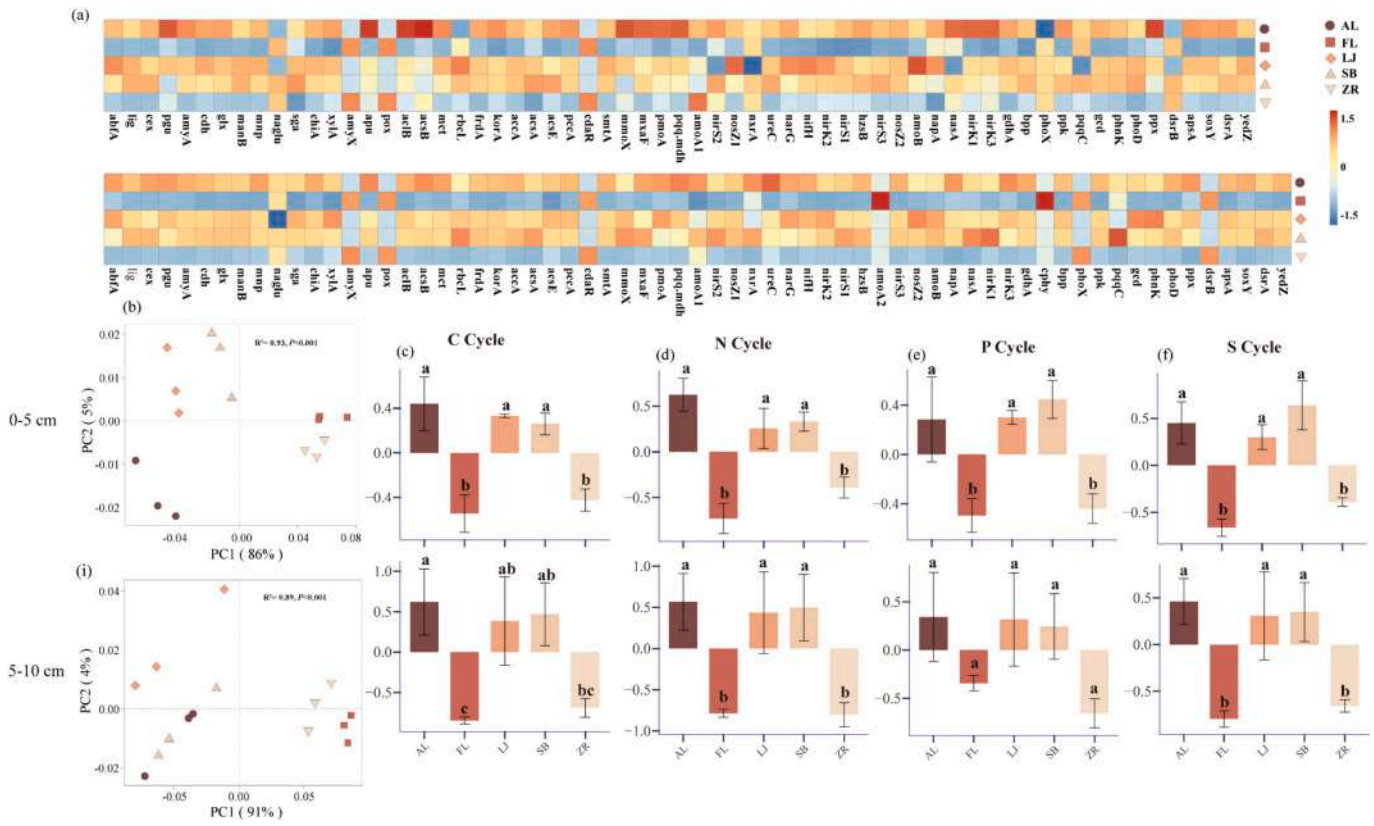

Fig. 3. The effects of tea cultivars on soil functional traits related to carbon, nitrogen, phosphorus and sulfur cycles on two soil layers (0–5 cm and 5–10 cm). (a) The heatmaps of diverse functional genes (z-score) on each soil layer. (b) The Principle Coordinate Analysis on soil microbial functions on each soil layer. (c–f) The potential soil functions (z-score) in different tea gardens on each soil layer. Different letters indicate significant differences. The tea varieties are Soubei (SB), Aolù (AL), Longjing43 (LJ), Zhaori (ZR) and Fenglù (FL).

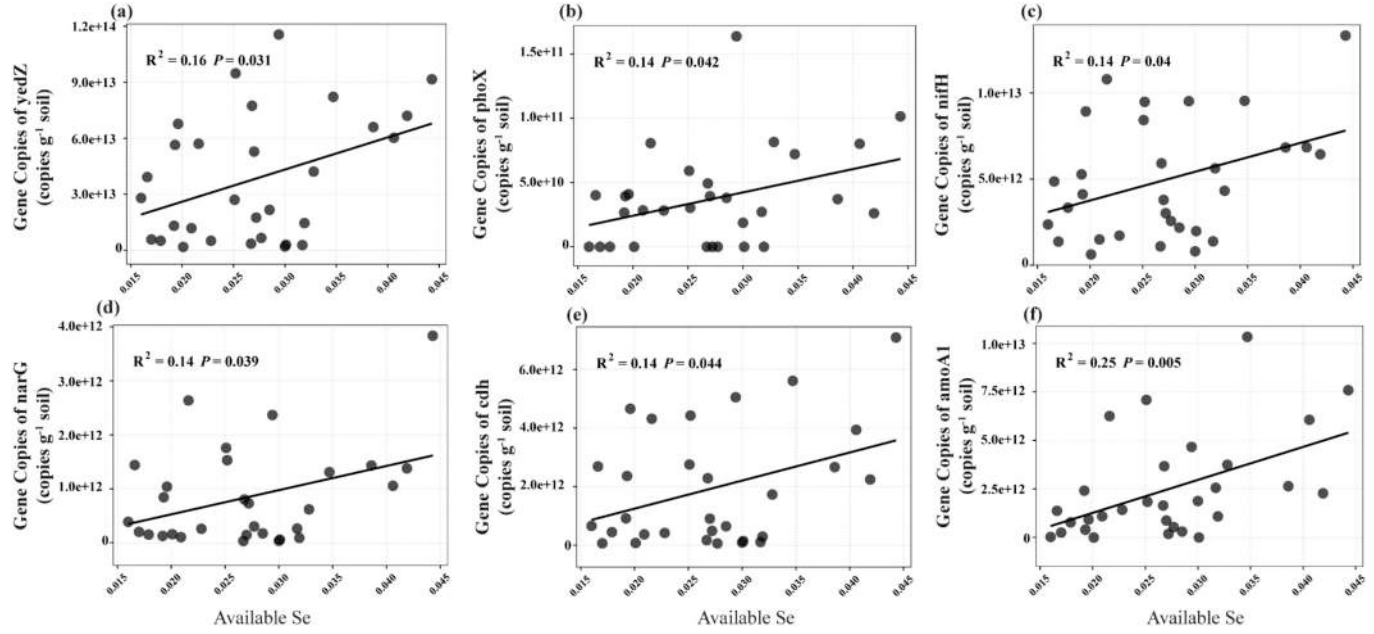

Fig. 4. The relationships between functional gene abundances and available Se contents. Only significant connections are displayed (Spearman correlation). (a) Relationship between functional gene yedZ and available Se content. (b) Relationship between functional gene phoX and available Se content. (c) Relationship between functional gene nifH and available Se content. (d) Relationship between functional gene narG and available Se content. (e) Relationship between functional gene cdh and available Se content. (f) Relationship between functional gene amoA1 and available Se content.

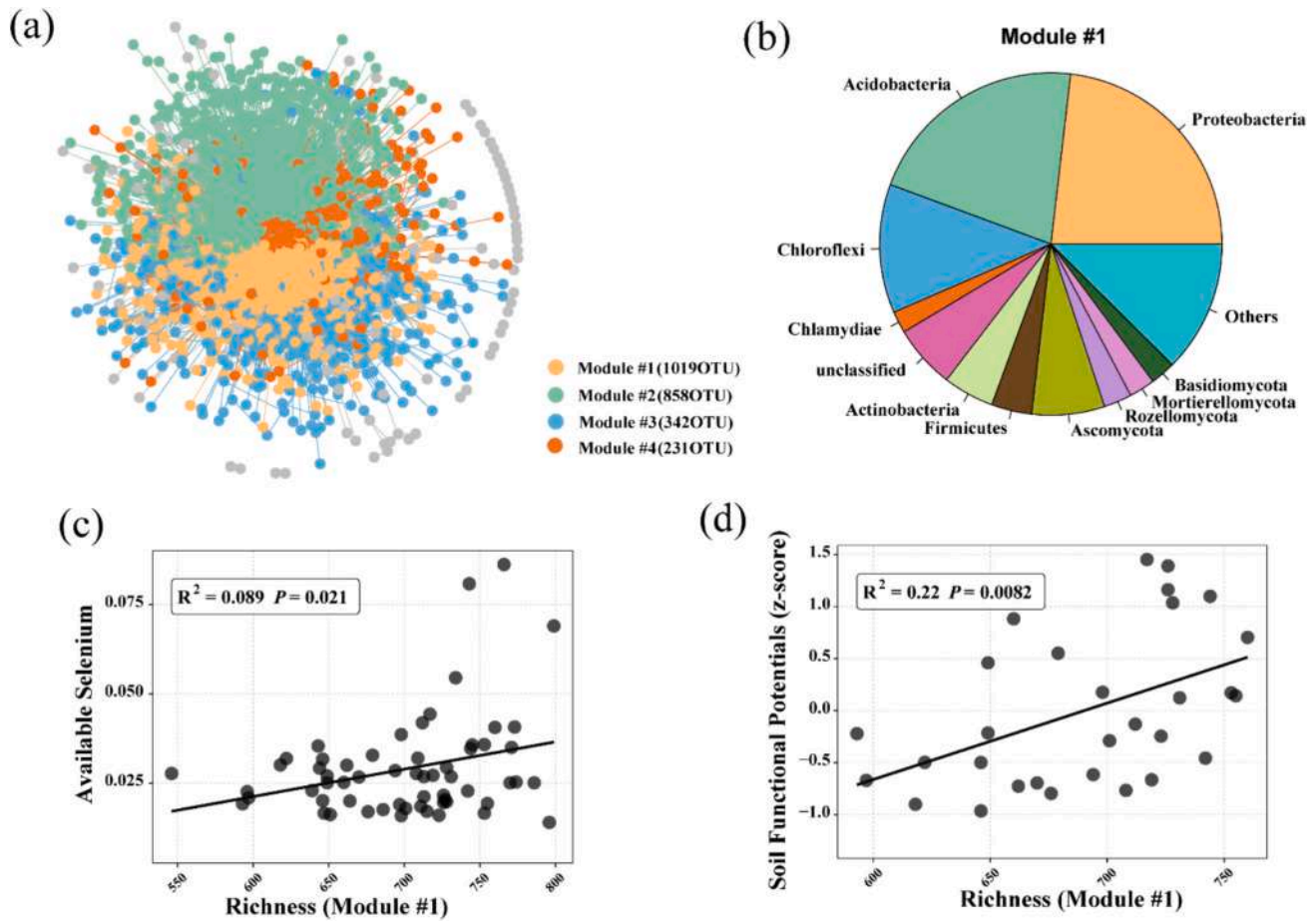

Fig. 5. The inter-kingdom bacterial-fungal network. (a) Four modules (ecological clusters) are within the network. (b-d) Only the abundance of OTUs in module 1 has significant connections with available Se contents and potential soil functions (z-score).

increase tea quality and enhance plants' resistance to environmental stresses (Liu et al., 2021; Ren et al., 2022; Guo et al., 2023). In this study, we discovered that different cultivars vary in their abilities to acquire and transport Se along the soil-plant continuum since, for example, the root Se content of the LJ tea cultivar was much higher, whereas its stem Se content was lower compared to other tea cultivars (Fig. 1). The Se uptake largely depends on its availability to tea plants. In this study, we firstly hypothesized that the five tea cultivars differently impact the Se availability. Our results showed that the total Se content in the FL tea garden was much lower but the available Se was higher compared to LJ and SB gardens, particularly at 5–10 cm soil depth (Fig. 1). Our study demonstrated that different tea varieties differently impact Se availability and the FL tea plants have a higher ability to transform insoluble Se to a soluble fraction compared to other tea varieties.

Earlier studies have confirmed a higher Se availability in the plant rhizosphere than in bulk soil (Chen et al., 2010; Oram et al., 2011), for example, via oxidation of reduced Se within the rhizosphere (Oram et al., 2011), which has demonstrated the potential role of plants in controlling Se transformation. One way for plants to control soil nutrient forms is to affect soil chemical traits (Dinh et al., 2017; Zhai et al., 2021). Previous studies have found that increasing pH can increase Se solubility by facilitating desorption (or oxidization) of Se from metals and organic matter (Natasha et al., 2018; Dinh et al., 2019). However, the small range of pH and the presence of no clear relationship among the five tea gardens indicated that pH was not the main factor affecting the Se solubility (Table S1). By contrast, the contents of NH_4^+ and NO_3^- were positively related with the available Se (Fig. S4). Dinh et al. (2019) have suggested that high NO_3^- dislodges Se anions from the surface of soil particles, leading to an increase in the selenate concentration in soil and also promoting Se uptake. Phosphate exhibits a higher affinity to soil colloids than selenite (Rydén et al., 1987) and increasing phosphate could decrease Se sorption leading to an increased Se availability in alkaline soil (Shahid et al., 2018; Peng et al., 2021; Li et al., 2022). By contrast, we found a significant negative relationship between AP and available Se in acid soil (Fig. S4). Phosphorus-solubilizing bacteria increase the soil AP content in tea gardens, whereas their promotion of the Se availability depends on the tea varieties (J. Guo et al., 2024). Therefore, the results implied that soil conditions, plant species and other factors have a complex influence on the available Se content.

Another way how plants affect Se bioavailability is through influencing soil microbial functions (Guo et al., 2023), and one of the aims of this study was to explore connections between available Se and potential soil functions. It was clear that the type of the tea cultivar was a crucial factor affecting nutrient cycle functions, and the expression of genes related to C, N, P and S greatly varied among cultivars (Figs. 2 and 3). The *phoX*, *yedZ* and *cdh* genes related to organic P mineralization, S oxidation and C hydrolysis (Zheng et al., 2018) had marginally significant connections with available Se (Fig. 4). Meanwhile, *nifH*, *narG* and *amoA1* related to N fixation, denitrification and nitrification (Zheng et al., 2018) were strongly connected with available Se (Fig. 4). The NH_4^+ and NO_3^- contents in the FL tea garden were much higher, whereas the total nitrogen was lower when compared to others (Table S1). Many genes related to N cycling, including N fixation, nitrification and denitrification, were enriched in the FL garden compared to other gardens (Tables S6 and S7). It was demonstrated that the FL tea cultivar accelerated N cycling processes and accumulated more NH_4^+ and NO_3^- than the other tea cultivars. Lei et al. (2022) found that a Se application up-regulated *nifH* and nitrification genes (*amoA*, *nxrA*), and down-regulated

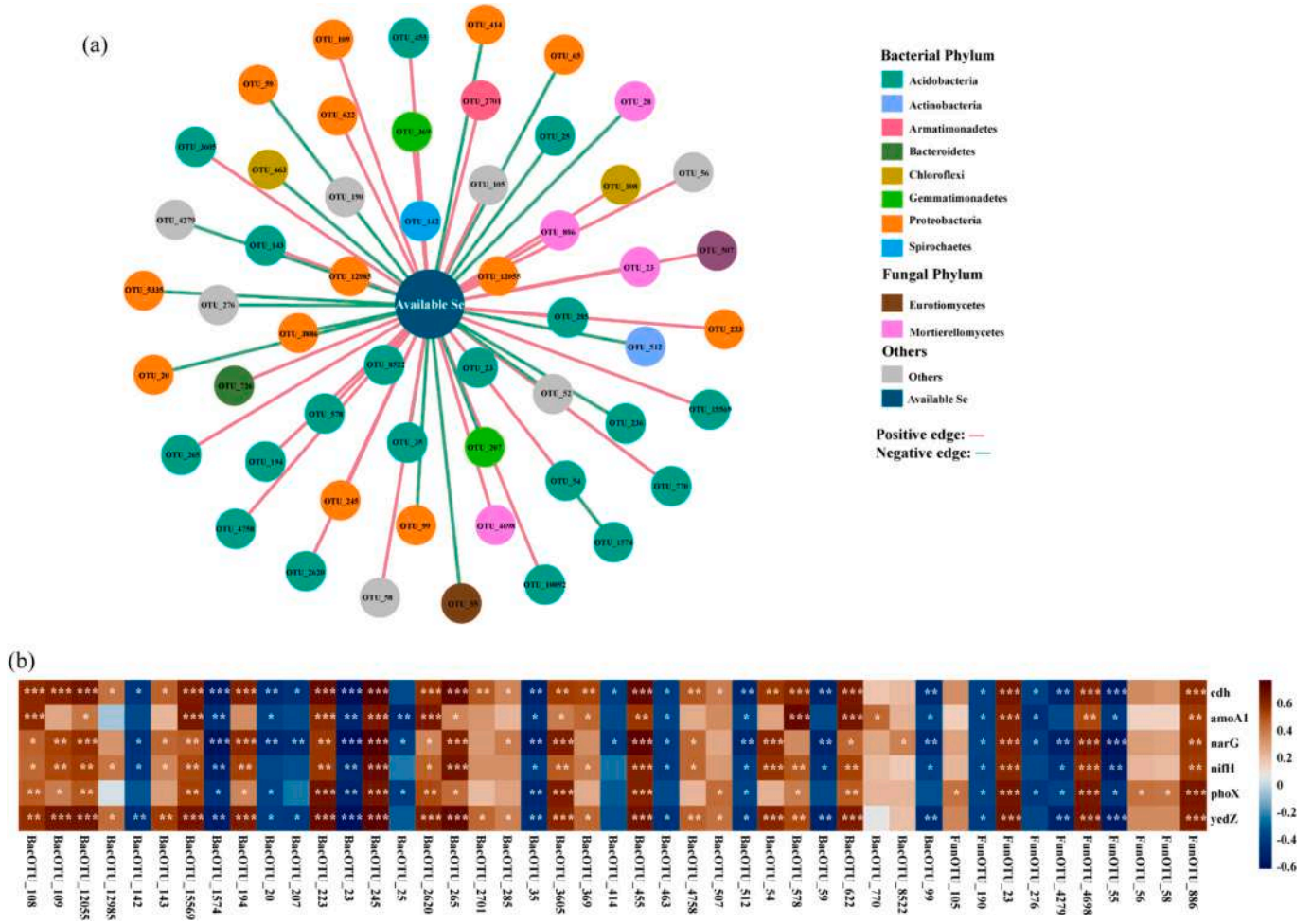

Fig. 6. The abundance of dominant OTUs closely connected with soil functions. (a) The relationships between available soil Se and dominant OTUs within the module 1. (b) The relationships between soil functional genes and dominant OTUs within the module 1. *: $0.01 \leq P < 0.05$. **: $0.001 \leq P < 0.01$. ***: $P < 0.001$.

denitrification genes (*narG*, *nirS*). It has been mentioned that the nitrate ion (NO_3^-) is structurally similar to SeO_3^{2-} and the functional groups of denitrification can also use the latter one in the biochemical process (Tugarova et al., 2014; Lei et al., 2022). The close connections with *nifH* and *amoA1*, and also with NH_4^+ and NO_3^- contents observed in this study suggest that the functional microbe groups of N fixation and nitrification may participate in the Se transformation.

Diverse bacterial and fungal species display their ability to transform Se to different valent states by reduction/oxidation and methylation/demethylation, thus affecting its bioavailability (Sarathchandra and Watkinson, 1981; Lindblom et al., 2014; Khoei et al., 2017; Eswayah et al., 2019; Guo et al., 2023). Selenium-oxidizing bacteria have a Se oxidation ability through oxidizing Se(0) to SeO_3^{2-} or SeO_4^{2-} in different environments, which would increase soluble Se fractions in soil (Sarathchandra and Watkinson, 1981; R. Luo et al., 2022; X. Luo et al., 2022). Arbuscular mycorrhizal fungi (*Funneliformis mosseae* and *Glomus versiforme*) have been found to increase available Se forms and to facilitate plants' Se uptake (Li et al., 2020). In general, the oxidation rate of a bacteria-oxidizing species is much lower than the reduction or methylation rates (Guo et al., 2023). However, most studies have utilized culture-based methods. Microbial communities rather than functions or activities of individual organisms are important for Se transformation in natural environments. Biological cycling of different nutrients are driven and determined by cooperation of different functional microbial groups. Closely connected species constitute modules of microbial networks, and these groups are important for soil functions (Fig. 5). In the present study, the inter-kingdom bacterial-fungal network provided strong evidence that species richness of module 1 was closely associated with Se availability and potential soil functions. Dominant OTUs within the module 1 that were positively related with available Se and functional genes were also enriched in the FL tea garden (Table S8). Meanwhile, OTUs that were negatively related with the Se availability and functional genes declined. It was demonstrated that the FL tea cultivar increased microbial species to enhance soil nutrient cycling functions (particularly N cycling) and Se availability, but decreased some species that hampered cycling functions. Different effects on these functional groups were probably the main reason for the divergent structure of bacterial and fungal communities among different tea gardens.

Previous studies have well demonstrated that plants can regulate soil nutrient cycling functions and microbial communities through releasing root exudates (Coskun et al., 2017). Recent studies have revealed that root exudates can increase Se bioavailability by reducing Se adsorption while promoting desorption (Dinh et al., 2017; Zhou et al., 2018). However, the amount and composition of root exudates in the five tea cultivars and their crucial roles in affecting Se bioavailability need further exploration. In summary, this study found that tea plants could regulate the structure of microbial communities, especially through constructing groups of highly connected microbes closely related with potential soil functions. Different tea cultivars had different abilities to enrich or reduce dominant microbial species within ecological clusters, thus affecting the available Se content. Based on the connections between NH_4^+, NO_3^- and functional genes, and the available Se, it is proposed that microbial groups driving nitrification processes may have a

strong influence on transforming less soluble Se forms to soluble fractions. Therefore, a tea cultivar with a high ability to promote N availability is suggested to increase Se availability. Such Se-rich tea appears highly promising due to its distinctive value of blending taste and wellness. Understanding how tea plants affect soil Se availability is important for promoting tea quality and production.

Funding

This work was supported by the Talent Program of the Zhejiang University (0022112).

CRediT authorship contribution statement

Qingxue Guo: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yuxin Xiao:** Investigation, Data curation. **Yuanjing Zhu:** Investigation, Data curation. **Helena Korpelainen:** Writing – review & editing, Validation. **Chunyang Li:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175995.

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