

Fluoride Accumulation in Tea Plants: Soil-Plant Interactions, Health Risks and Mitigation Strategies

Xin Wang^{1,†}, Jiali Tian^{2,†}, Nayab Gull³, Imran Ahammad Siddique^{4,5}, Yizhi Zhou², You Li², Chengwen Shen², Minghan Wang^{1,2,*}, Huaqin Xu^{1,*} and Yi Xu^{6,7}

¹ Hunan Provincial Key Laboratory of Rural Ecosystem Health in Dongting Lake Area, College of Environment and Ecology, Hunan Agricultural University, Changsha 410128, China

² Key Laboratory of Tea Science of Ministry of Education, Hunan Agricultural University, Changsha 410128, China

³ Department of Crop and Soil Sciences, Washington State University, NWREC, Mount Vernon, WA 98273, USA

⁴ Department of Agroecology, Aarhus University, 8830 Tjele, Denmark

⁵ Department of Soil Science, Bangladesh Agricultural University, Mymensingh 2202, Bangladesh

⁶ Jiangsu Provincial University Key Laboratory of Agricultural and Ecological Meteorology, School of Ecology and Applied Meteorology, Nanjing University of Information Science & Technology, Nanjing 210044, China

⁷ Collaborative Innovation Center on Forecast and Evaluation of Meteorological Disasters (CIC-FEMD), Nanjing University of Information Science & Technology, Nanjing 210044, China

* Correspondence: wmh19960228@163.com (M.W.); xhuaqin1972@163.com (H.X.)

† These authors contributed equally to this work.

How To Cite: Wang, X.; Tian, J.; Gull, N.; et al. Fluoride Accumulation in Tea Plants: Soil-Plant Interactions, Health Risks and Mitigation Strategies. *Glob. Environ. Sci.* **2026**, *2*(2), 172–192. <https://doi.org/10.53941/ges.2026.100012>

Publication History

Received: 26 February 2026

Revised: 5 April 2026

Accepted: 16 April 2026

Published: 23 April 2026

Keywords

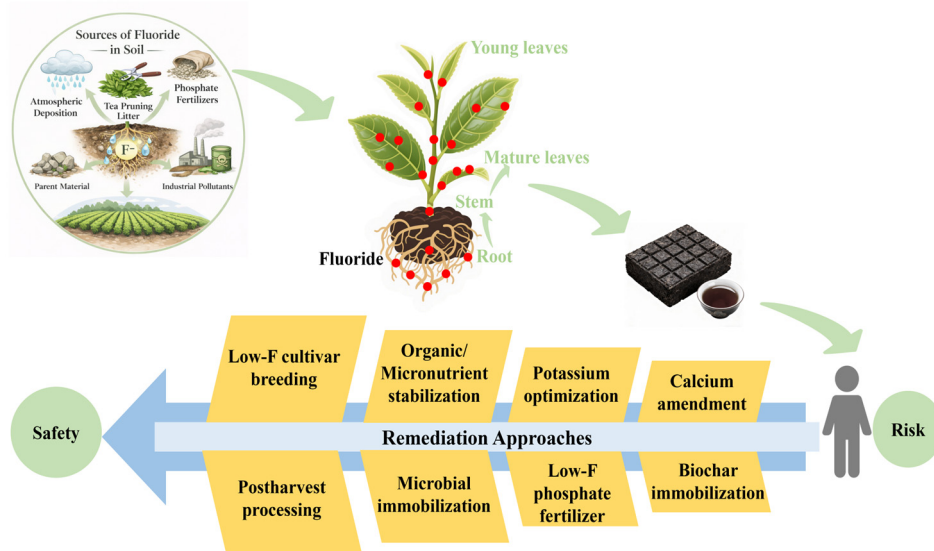
fluorine;
tea leaves;
soil chemistry;
bioaccumulation;
brick tea

Highlights

- Tea plants hyperaccumulate fluoride (F) from acidic soils, posing significant health risks through brick tea consumption.

Abstract: *Camellia sinensis* (tea plant) is a notable fluoride (F) accumulator, with mature leaves typically containing 2000–3000 mg F kg⁻¹, significantly higher than common crops like rice and wheat. This accumulation links soil geochemistry with dietary F exposure and associated fluorosis risk. However, the processes governing F mobility in soils and its transfer to tea plants remain insufficiently explored. This review summarizes current knowledge on F accumulation in tea production systems, focusing on the geochemical forms and bioavailability of F in tea-growing soils. We examine the roles of soil acidity, mineral composition, and organic matter in regulating F mobility. Mechanisms of F uptake, translocation, and preferential accumulation in mature leaves are discussed based on recent physiological and molecular studies. Human exposure risks from tea consumption, particularly in high-F soil regions, are evaluated. We review integrated mitigation strategies, including soil amendments, nutrient management, low-F cultivars, and optimized processing techniques. Among these, nutrient-based management, especially using low-F phosphate fertilizers and optimized potassium supply, is a promising approach for reducing F accumulation in tea plants. Targeted nutrient regulation can effectively limit F mobility and uptake, offering a sustainable strategy for mitigating F exposure through tea consumption. These findings emphasize the importance of soil chemical conditions in controlling F transfer from soil to tea plants and provide a scientific foundation for developing effective strategies to reduce F accumulation in tea production systems.

- Advanced analytical techniques reveal F speciation and real-time transport dynamics in soil-tea plant systems.
- Soil pH, organic matter, and exchangeable ions critically regulate F bioavailability and uptake in tea plantations.
- Key transporters (CsFEX, CsALMT6, ABC proteins) mediate F absorption, and translocation in tea plants.
- Precision fertilization can effectively reduce F accumulation without compromising tea quality.



1. Introduction

Fluoride (F) is a naturally occurring element widely distributed in soils, waters, and geological materials [1]. At low exposure levels, F can help prevent dental caries, but excessive intake may lead to dental and skeletal fluorosis, posing a significant public health concern in many regions worldwide [2]. Because the margin between beneficial and harmful exposure is relatively narrow, regulatory intake guidelines have been established; for adults, the tolerable upper intake level (UL) is 10 mg/day [3]. Nevertheless, chronic endemic fluorosis remains widespread, affecting approximately 200 million people across 28 countries, including China, the United States, Brazil, South Africa, and India, mainly through drinking water and dietary exposure [4]. China remains one of the countries most seriously affected, with nearly 41 million cases of dental fluorosis and 2.6 million cases of skeletal fluorosis [5]. Beyond drinking water, F exposure may also come from foods and beverages, especially tea and some seafood and vegetables [6]. Among dietary sources, tea has emerged as a critical contributor to F exposure because *Camellia sinensis* has an exceptional capacity to accumulate F. Mature and especially old tea leaves may accumulate F to levels above 2000 mg/kg, far exceeding those found in staple crops such as rice and wheat [7,8]. Some brick tea products prepared mainly from older leaves have been reported to contain F at or above 800 mg/kg [8].

Tea is one of the most widely consumed non-alcoholic beverages, with more than 3 billion regular consumers [9]. Tea is cultivated on a vast scale globally, especially in China [10], and the continued expansion of the tea industry further amplifies the relevance of tea as a dietary F exposure pathway [11]. In tea plants, approximately 98% of F is concentrated in the leaves, particularly in mature ones, and is readily released into

infusions during brewing [12]. Regular consumption of tea, especially high-F products made from mature leaves, may substantially increase daily F intake and pose potential health risks to consumers [13]. Therefore, controlling F accumulation in tea leaves is essential for reducing dietary F exposure and protecting human health.

Against this background, increasing attention has been paid to the soil-plant processes that regulate F accumulation in tea. The number of publications on F in tea plants has grown rapidly in recent years (Figure 1a), and most of these studies are concentrated in environmental, food, toxicological, and public health disciplines (Figure 1b). This growing interest reflects the critical role of soil F in determining F levels in tea leaves [14]. Globally, soil F typically ranges from 20 to 500 mg F/kg with an average of 321 mg F/kg [15]. In China, background soils average 453 mg F/kg, and soils in endemic fluorosis regions can reach up to 800 mg F/kg [16]. In addition, anthropogenic activities, particularly phosphate fertilizer application, can further increase soil F concentrations in some tea-growing areas [17].

However, total soil F concentration alone does not determine plant uptake; its geochemical fractionation and bioavailability are equally important. Soil F is mainly partitioned into five geochemical fractions: water-soluble (Ws-F), exchangeable (Ex-F), Fe/Mn oxide-bound (Fe/Mn-F), organically bound (Or-F), and residual (Res-F) [14]. Soil pH and soil organic matter (SOM) are critical factors controlling F adsorption. Under comparable conditions, paddy soils with higher SOM tend to have greater F adsorption capacity than upland soils, thereby reducing F mobility and bioavailability, even when total soil F concentrations remain high [18]. This is particularly relevant for tea plantations, which are typically established on acidic soils. In such soils, high concentrations of soluble Al favor the formation of soluble

Table 1. Fluoride contents and exposure risks in various commercial teas and tea drinking.

F Concentration	F Source	Location	Tea Types	Results	References
1028.4 mg/kg	tea leaves	Xizang, China	brick tea	dental fluorosis in children was 24.4% and the detection rate of skeletal fluorosis in adult was 7.1%	[32]
786.2 mg/kg	tea leaves	Sichuan, China	brick tea	dental fluorosis in children was 19.79%	[33]
750.0 mg/kg	tea leaves	Qinghai, China	brick tea	dental fluorosis in children was 22.56% and the detection rate of skeletal fluorosis in adult was 6.88%	[34]
417.0 mg/kg	tea leaves	Xinjiang, China	brick tea	dental fluorosis in children was 4.47%, and the detection rate of skeletal fluorosis in adult was 2.75%	[35]
540.0 mg/kg	tea leaves	Gansu, China	brick tea	-	[36]
192.0 mg/kg	tea leaves	Ningxia, China	brick tea	-	[37]
1.2 mg/L	tea drinks	Jordan	-	81.11% of girls and 76.43% of boys present with severe dental fluorosis	[38]
20mg/L	tea drinks	Georgia, USA	brewed orange-pekoe and pekoe-cut black tea	skeletal fluorosis	[39]
3.3 mg/L	tea drinks	Ireland	black tea	skeletal fluorosis	[40]
12 mg/L	tea drinks	Valparaiso, Chile		22.1% had risk of dental fluorosis	[41]
2.65 mg/L	tea drinks	Poland	black tea	not high enough to cause a risk of fluorosis	[42]
2.68 mg/L	tea drinks	Sri Lanka	black tea	Chronic Kidney Disease	[43]

3. Fluoride Sources in Soil-Tea Plant Systems

3.1. Natural Sources of Fluoride

Soil F primarily originates from geogenic processes associated with parent material composition and mineral weathering [46]. The weathering of F-bearing minerals, including fluorite (CaF_2), apatite ($\text{Ca}_5(\text{PO}_4)_3(\text{F},\text{OH},\text{Cl})$), biotite ($\text{K}(\text{Mg},\text{Fe})_3\text{AlSi}_3\text{O}_{10}(\text{F},\text{OH})_2$), and amphibole ($\text{Ca},\text{Na})_{2-3}(\text{Mg},\text{Fe},\text{Al})_5(\text{Al},\text{Si})_8\text{O}_{22}(\text{F},\text{OH})_2$), is an important natural source of soil F. The rate of F release from these minerals is influenced by specific soil properties such as pH, redox conditions, calcium activity, ionic strength, and water content, as well as by climatic factors including temperature and precipitation [47,48]. Soil formation processes, especially the weathering and erosion of parent materials, further contribute to F enrichment in soils (Figure 2). For example, volcanic-derived soils often exhibit elevated F concentrations because of the inherently high F content of volcanic ejecta [49]. F may also leach from rocks and minerals into groundwater, and subsequent capillary rise or irrigation with F-rich groundwater can increase soil F levels [50]. In addition, atmospheric deposition associated with volcanic emissions can deliver fluorine to soils over extensive areas [51].

3.2. Anthropogenic Sources of Fluoride

Anthropogenic activities can substantially increase F inputs into agricultural systems, especially in tea-growing regions. These inputs arise from both industrial emissions and agricultural practices. Major anthropogenic sources include coal combustion, phosphate fertilizer production and use, and emissions from aluminium and related industrial processes, all of which can release F into the surrounding environment through atmospheric deposition

or direct agricultural inputs [52]. In tea plantations without obvious industrial contamination, agricultural inputs often represent the most direct and manageable pathway of F input, with phosphate fertilizers being a particularly important source [53]. Because phosphate fertilizers are produced from F-rich phosphate rock, they can introduce substantial F into agricultural systems [54]. However, the F content of commercial phosphate fertilizers varies considerably depending on the quality of raw materials and processing technology. For instance, single superphosphate (SSP) typically contains 1.5–2.0% F by weight [55]. In contrast, potassium dihydrogen phosphate (MKP) and monoammonium phosphate (MAP) generally contain lower concentrations of residual F than raw phosphate rock [56]. Analyses of phosphate fertilizers marketed in India found total F contents ranging from about 0.14% to 1.33% (*w/w*) across different products, including diammonium phosphate (DAP), with some individual samples exceeding 1% F (*w/w*) [57]. Similar variability has also been reported in commercial phosphate fertilizers from China [56]. This variability reflects incomplete F removal during acidulation and subsequent processing. Field evidence further indicates a significant positive relationship between soil F accumulation and phosphatic fertilizer use [58]. Intensive phosphorus fertilization can increase *W*-F in soil and may, in some cases, also promote soil acidification, thereby enhancing F mobility and bioavailability [59]. Concurrent urea application may aggravate this process by sustaining soil acidification and increasing dissolved F and Al concentrations, which facilitates F migration, including in the form of Al-F complexes, from soil to tea plants [60]. Organic amendments, particularly livestock manures derived from F contaminated feed, further contribute to soil F accumulation [61].

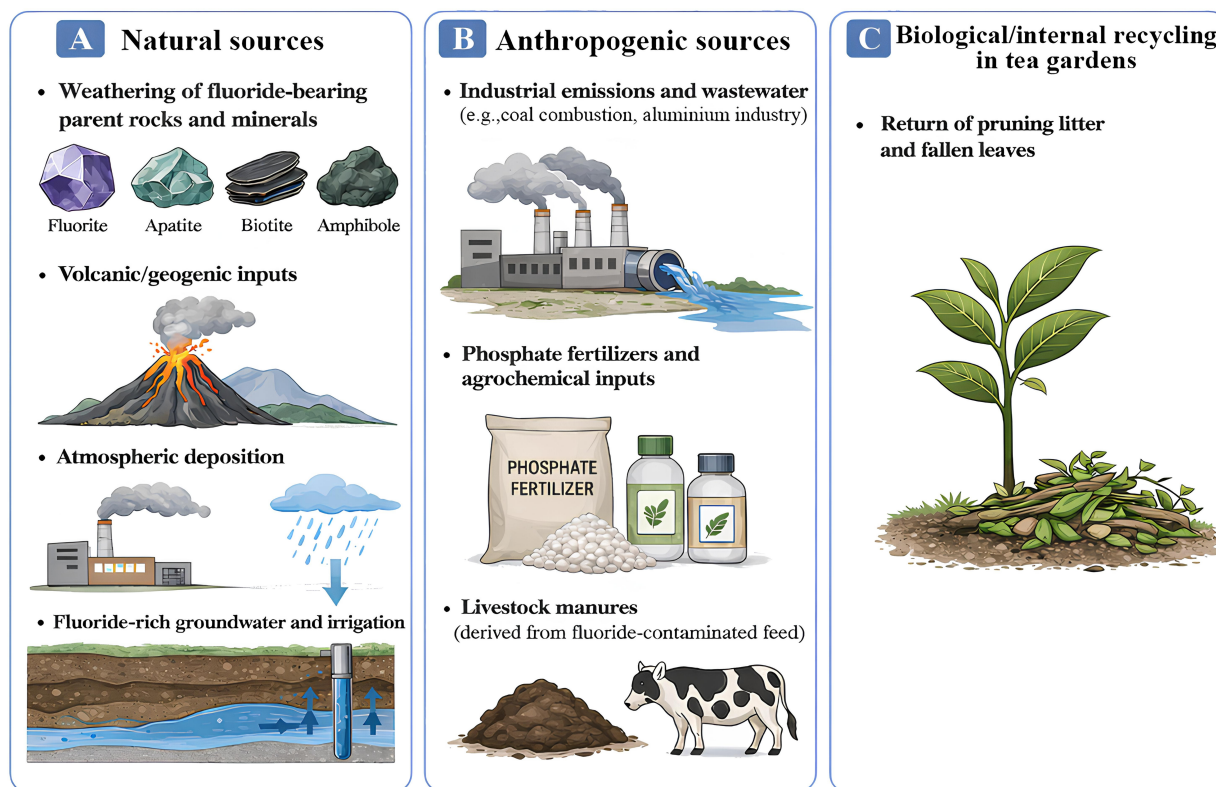


Figure 2. Sources of fluoride in tea gardens.

3.3. Biological Contributions to Soil Fluoride

Tea plants absorb F from the soil and return part of it to the soil during senescence and litter decomposition, thereby sustaining an internal biological F cycle in tea plantation ecosystems [62]. Because mature tea leaves accumulate substantial amounts of F, pruned litter and fallen leaves can become an important source of F re-entry to surface soils. In uncontaminated tea plantations, this biological circulation of F has been reported to be positive, with annual inputs of $8.336 \text{ kg ha}^{-1}\text{y}^{-1}$ and outputs of $4.163 \text{ kg ha}^{-1}\text{y}^{-1}$ [62].

Decomposition of pruned tea litter can further increase soil F availability, and this process is influenced by both microbial activity and litter quality, including nitrogen content, lignin, and cellulose. Recent research has identified two broad decomposition phases [63]. During the initial rapid-release phase (0–120 days), approximately 26–33% of total litter F is released, likely due to the mineralization of relatively labile organic fractions under favorable temperature and moisture conditions. This initial phase followed by a slower phase (120–360 days), during which an additional 2–9% of F is released as decomposition shifts toward more recalcitrant compounds such as lignin and microbial activity gradually declines. These findings indicate that litter-derived F release is not constant, but instead depends strongly on decomposition stage and environmental conditions.

Therefore, in tea plantations, pruned litter should be considered not only as an organic matter resource but also as a recurrent internal source of F. Management practices such as regulating the amount of pruning residue returned to the soil, adjusting residue incorporation timing, or converting litter into biochar may help reduce F recirculation while maintaining soil quality. More broadly, F dynamics in tea plantation soils reflect the combined effects of geological background, anthropogenic inputs, and biological recycling, highlighting the need for integrated management strategies that simultaneously address external F inputs and internal F recycling.

4. Geochemical Speciation and Analytical Characterization of Fluoride in Soil and Tea Plant Systems

4.1. Geochemical Fractions of Soil Fluoride

Soil F exhibits complex speciation, partitioning into five principal geochemical fractions: water-soluble fluoride (Ws-F), exchangeable fluoride (Ex-F), Fe/Mn oxide-bound fluoride (Fe/Mn-F), organically bound fluoride (Or-F), and residual fluoride (Res-F) [64,65]. Bioavailability follows the hierarchy $\text{Ws-F} > \text{Ex-F} > \text{Fe/Mn-F} > \text{Or-F} > \text{Res-F}$, with Ws-F and Ex-F being highly bioavailable and readily accessible for uptake by plants. Notably, Fe/Mn-F and Or-F can be transformed into more

bioavailable forms under certain soil conditions, particularly with shifts in soil pH or SOM content [66].

Although these fractions describe the geochemical partitioning of F in soils, plant uptake is governed more directly by the dissolved F species present in soil solution. In soil solution, F occurs mainly as free F^- and inorganic complexes. Under acidic conditions, HF and HF_2^- may become relatively more important, whereas complexation with metals, especially Al, can strongly influence F mobility and bioavailability [67]. Because tea plants are typically cultivated in acidic soils (pH 4.0–6.5), high concentrations of soluble Al^{3+} favor the formation of soluble Al–F complexes [19]. Accordingly, tea plants are thought to absorb F mainly as soluble Al–F complexes and free F^- , with Al–F complexes likely representing the dominant absorbed form under acidic tea-soil conditions.

4.2. Advanced Analytical Methodologies

4.2.1. X-ray Fluorescence Spectroscopy

X-ray fluorescence (XRF) spectroscopy is a rapid, non-destructive, and environmentally benign technique widely used for elemental analysis of soils. Wavelength-dispersive XRF (WD-XRF) is particularly useful for rapid screening of F-contaminated soils [68]. Oh et al. [69] showed that WD-XRF combined with pellet preparation provides reliable and reproducible measurements of total F, with better analytical performance than traditional methods such as alkaline fusion and aqua regia extraction. However, XRF also has important limitations. Portable XRF is susceptible to background interference in complex matrices, such as soils with high clay or organic matter contents, which can lead to substantial quantitative errors at low F concentrations. In addition, WD-XRF relies heavily on Ca–F calibration and may require extra matrix correction when Ca content deviates substantially from calibration conditions, thereby increasing analytical complexity.

4.2.2. Nuclear Magnetic Resonance Spectroscopy

^{19}F Nuclear Magnetic Resonance (NMR) spectroscopy is a powerful technique for characterizing F-containing species, including inorganic complexes and fluorinated organic compounds. Early studies by Morita et al. [70] and Nagata et al. [71,72] showed that F in tea infusions occurs mainly as free F^- and Al–F complexes. Quantitative speciation analysis using ^{19}F NMR combined with Geochem-PC modeling further indicated that Al/F molar ratios < 1 favor the formation of Al–F complexes [73]. The main limitation of ^{19}F NMR is its relatively low sensitivity, which often requires F concentrations higher than those typically encountered in natural samples. In addition, the method requires specialized instrumentation and expertise, and analysis of complex matrices may be complicated by signal broadening and peak overlap, which can obscure specific metal–F complexes.

4.2.3. X-ray Photoelectron Spectroscopy

X-ray photoelectron spectroscopy (XPS) provides detailed surface chemical information on elemental bonding environments, elemental composition, and chemical states within the outermost approximately 1–10 nm of a sample [74]. Cai et al. [75] used XPS to investigate F distribution on tea leaf surfaces and observed clear spatial differences. F occurred mainly as AlF_3 on the adaxial (upper) surface, whereas MgF_2 was the dominant form on the abaxial (lower) surface, with minor amounts of CaF_2 also detected. The major limitation of XPS is its extreme surface sensitivity, meaning that the information obtained may not be representative of the bulk chemical composition of tea leaf tissues. Additionally, the high cost of instrumentation and relatively low sample throughput (approximately 2–4 h per sample) limit its applicability in large-scale studies.

5. Determinants of Fluoride Mobility and Bioavailability in Tea Plantation Soils

F mobility and bioavailability in tea plantation soils are governed by dynamic sorption-desorption equilibria. Key regulatory factors include soil type, soil pH, SOM, exchangeable cations, and elemental interactions [14,65,76]. These parameters collectively influence F speciation, retention, and mobility, thereby regulating the amount of F available for root uptake by tea plants.

5.1. Soil Types

Soil type, especially parent material and associated mineralogical properties, strongly influences F occurrence and bioavailability. For example, soils derived from granite parent materials often contain higher total F concentrations than soils developed from other geological sources [77]. However, higher total F does not necessarily imply higher bioavailability. F in soils is preferentially associated with the colloid or clay fraction, and its mobility is strongly controlled by soil sorption capacity, which depends on factors such as pH, the type of soil sorbents present, and salinity [48]. Comparative studies further show that paddy soils, although they may contain relatively high total F, often exhibit lower F bioavailability than some upland soils because their finer texture and higher SOM enhance F adsorption and reduce mobility. Huang et al. [18] also demonstrated that paddy soil had a stronger F adsorption capacity than loessal soil and brown soil, indicating that F retention differs among soil types and is controlled by their associated properties rather than by soil texture alone. More generally, differences in F retention among soils cannot be explained simply by total clay content or cation exchange capacity (CEC) alone. A study of 95 Australian soils showed that F sorption was more closely related to the contents of Fe/Al hydrous oxides and kaolinite than to differences in pH, electrical conductivity, or organic carbon [78].

5.2. Soil pH

Soil pH is a key regulator of F adsorption because it affects surface charge, ligand exchange, and the stability of metal-F species in soil [67]. Under acidic conditions, protonation of reactive soil surfaces and dissolution of F-bearing phases can promote the transformation of Fe/Mn-F and Or-F into Ws-F [79]. However, the relationship between Ws-F and pH is not linear. In a moderately acidic range (pH 4.56–5.77), Ws-F has been reported to increase with pH, likely because OH⁻/F⁻ exchange becomes more pronounced [80]. Under stronger acidity, by contrast, decreasing pH enhances Al³⁺ release and favors the formation of soluble Al-F complexes, which can alter F mobility and speciation [81]. Although Al³⁺ is highly rhizotoxic to most plant species, tea (*C. sinensis*) is an acid-adapted species with a relatively high tolerance to soluble Al, making the pH-dependent behavior of F in tea soils distinct from that in many other plant–soil systems [82].

5.3. Soil Organic Matter

SOM, particularly its dissolved fraction (DOM), is an important regulator of F bioavailability because it can modify adsorption surfaces, interact with metal cations, and influence the stability of Fe/Mn oxides in soil [65,83]. Through these processes, SOM may promote the redistribution of F from more labile pools, such as Ws-F, into less mobile fractions, including Fe/Mn-F and Or-F, thereby reducing F mobility and bioavailability. Low-molecular-weight DOM components can further affect soil aggregation and organo-mineral associations, creating additional reactive surfaces for F retention [84]. Comparative adsorption studies have shown that soils with higher SOM generally exhibit stronger F adsorption capacity [18]. Organic amendments can alter F fractionation and reduce F mobility in soil. For example, peat and weathered coal were reported to decrease Ws-F in simulated high-F yellow soil and calcareous soil, with peat being more effective than weathered coal [85]. In addition, recent incubation experiments showed that organic manures can lower F bioavailability by shifting F from more available pools toward organically bound and residual fractions [86]. These findings suggest that SOM affects F behavior primarily through adsorption regulation, fraction redistribution, and retention, rather than through direct complexation with F alone.

5.4. Soil Exchangeable Ions and Other Factors

The geochemical behavior of F is differentially regulated by exchangeable ions, with their effects varying according to ion type. In tea garden soils, exchangeable H⁺ and Na⁺ have been reported to be positively associated with Ws-F, indicating that soil acidification and Na-related desorption can increase mobile F [87]. By contrast, Ca²⁺

often suppresses F mobility by enhancing F adsorption and/or favoring the formation of less soluble Ca-F phases [18,48]. Consistent with this, comparative adsorption experiments showed that, under acidic conditions, soils with higher Ca²⁺ contents exhibited stronger F adsorption capacity [18]. More broadly, Na-dominated cation exchange can promote F enrichment by lowering Ca activity, whereas the effects of Mg²⁺ and K⁺ appear to be more variable and dependent on overall soil chemistry rather than following a universal positive relationship [88]. In acidic tea soils, soluble Al³⁺ further modifies F behavior by stabilizing Al-F complexes in soil solution, thereby influencing F mobility and availability at the soil-root interface [60].

In addition to exchangeable ions, rhizospheric organic acids can further modify F mobility under specific soil chemical conditions. Low-molecular-weight organic acids such as citric acid and malic acid may enhance F bioavailability by competing with F for sorption sites on variable-charge minerals and by complexing Al and other metal cations, thereby suppressing the formation of less soluble F-associated phases and promoting F desorption into soil solution [89]. Xu et al. [90] showed that low-molecular-weight organic acids reduced F adsorption and enhanced the desorption of previously adsorbed F, and that the magnitude of this effect depended on acid identity, pH, and acid concentration. In their study, oxalic and malonic acids were more effective than citric and malic acids, and the inhibition of F adsorption became more pronounced at higher pH and with increasing organic-acid addition [90]. Wang et al. [89] further demonstrated that citric and malic acids enhanced F release from tea rhizosphere soils under acidic conditions typical of tea plantations (pH 4.0–6.0). Therefore, in rhizospheric systems, organic acids tend to increase soluble F when ligand exchange, sorption-site competition, and metal complexation dominate the local geochemical environment.

6. Fluoride Dynamics in Tea Plants

6.1. F Uptake Mechanisms in the Tea Plant

Under conditions without substantial atmospheric F input, F uptake in *C. sinensis* occurs predominantly through the root system and depends largely on the Ws-F fraction in the soil [23]. Root uptake of F shows clear concentration dependence. At relatively low external F concentrations (0.1–10 mg/L), uptake is predominantly active and follows Michaelis-Menten-type kinetics, whereas passive uptake becomes increasingly important only at higher concentrations (50–100 mg/L) (Figure 3) [91]. Because the Ws-F concentration in most major tea-growing soils is generally below the threshold for passive uptake, F absorption by tea roots under field conditions is considered to rely mainly on active transport [92].

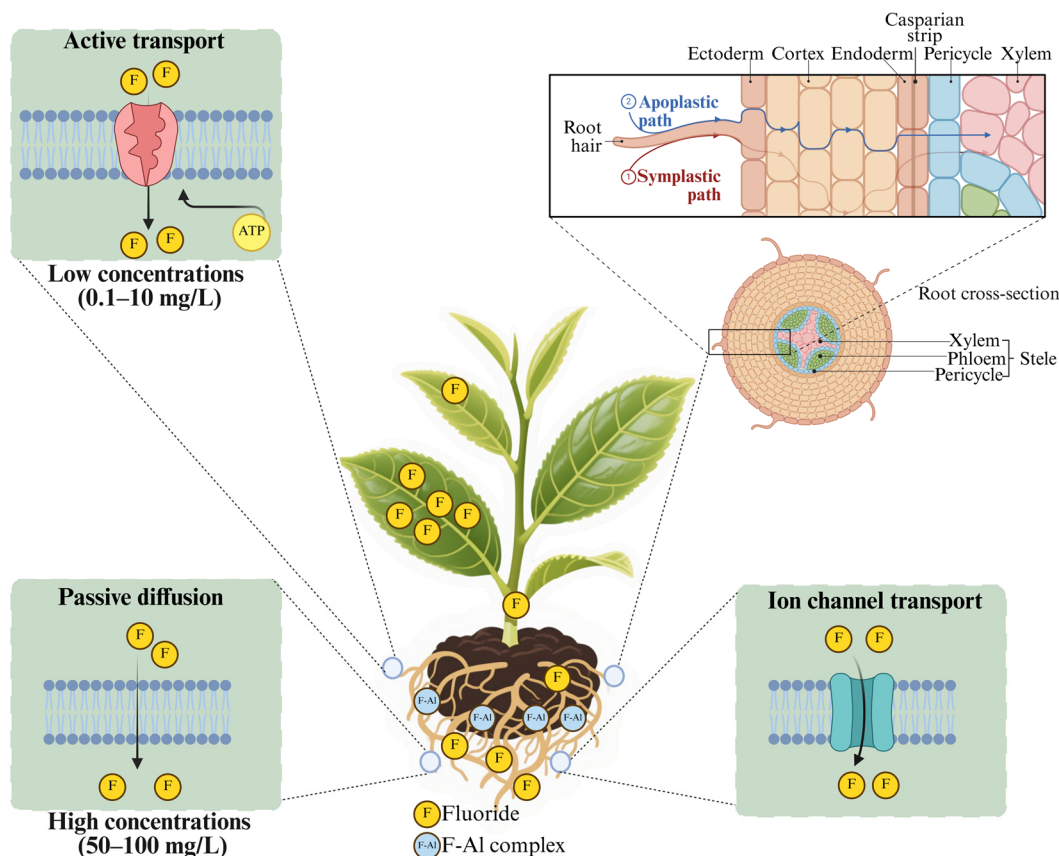


Figure 3. Schematic diagram of fluoride absorption of the tea plant roots.

Active F uptake appears to be closely associated with the proton motive force generated by plasma membrane H^+ -ATPase [93,94]. In addition, Ca^{2+} -ATPase-related RLK/ Ca^{2+} signaling has been implicated in regulating the root uptake response [93,94]. Molecular evidence suggests that F exposure induces the expression of receptor-like kinase (RLK) genes, which may activate Ca^{2+} -ATPase and thereby facilitate F uptake in tea roots [94]. By contrast, H^+ -ATPase is thought to provide the proton motive force required for active uptake, although its direct molecular role in F transmembrane transport in tea plants remains to be clarified.

In addition to active transport, passive F influx in tea roots appears to occur mainly through an anion-channel pathway. Available evidence indicates that aquaporins and cation channels are not the major routes, whereas anion channels, likely including Cl^- -related plasma membrane anion channels, play a more important role in passive F-entry [20]. At the same time, several F-related transport systems have been reported in tea plants, including CLCF-type F/ H^+ antiporters, FEX-family proteins, and ABC transporters. Among them, CsFEX1 and CsFEX2 are involved in F transport, whereas transporters such as CsCL667 appear to function mainly in F efflux, homeostasis, and stress alleviation rather than direct root influx [95,96].

Coexisting ions strongly modify F uptake and subsequent translocation. Low concentrations of Al^{3+} can promote F retention in roots but reduce its accumulation in leaves [18], whereas Ca^{2+} generally suppresses F

uptake by decreasing the Ws-F pool through precipitation or complexation and by altering root cell wall properties and membrane permeability [48]. Chloride may also competitively inhibit F uptake, suggesting that F and other monovalent anions may share, at least in part, overlapping transport pathways.

6.2. Radial Transport and Long-Distance Translocation

After entering the root, F is thought to move radially toward the stele before being loaded into the xylem and transported upward [97]. Two major pathways have been proposed for this radial movement: (i) the apoplastic pathway, in which F moves through the cell wall continuum and intercellular spaces via diffusion and convection, and (ii) the symplastic pathway, in which F enters cells through membrane transport proteins and then moves between adjacent cells through plasmodesmata (Figure 3) [98]. Recent evidence further suggests that the plasma membrane transporter CsNPF2.3, expressed in epidermal, cortex, and xylem parenchyma cells, may participate in the retrieval of F^- from the apoplast and in uptake from the soil solution [99]; however, whether tea roots exhibit a distinct apoplastic bypass of the Casparian strip remains unresolved.

Following root uptake, F is not immediately transported to the shoot. Positron-emitting tracer imaging showed that F was transiently retained in the roots for approximately 1.5 h before its upward movement became apparent [100]. Subsequent long-distance transport occurs

mainly through the xylem, and no F signal was detected in the leaves during the first 8 h after uptake. These observations indicate that transient root retention precedes xylem-mediated root-to-shoot transport.

Although xylem is the dominant route for upward F transport, limited remobilization from old leaves to developing tissues may also occur [101]. Mature leaves therefore function as the major F reservoirs in tea plants [101]. However, the extent and physiological significance of phloem-mediated redistribution remain insufficiently characterized.

6.3. Molecular Regulators of Fluoride Transport and Tolerance

A growing number of molecular regulators have been implicated in F transport and tolerance in tea plants.

Key examples include the F exporter proteins CsFEX1 and CsFEX2, whose expression increases in response to F exposure and helps reduce intracellular F accumulation [102,103]. In addition, ABC transporters such as CsCL667 and CLC family members including CsCLC1–3 have been implicated in F⁻/Cl⁻ transmembrane efflux [104,105]. Under F stress, potassium supplementation upregulates CsFEX expression while downregulating CsHAK-related genes [26,106], indicating that potassium status may influence F handling in tea roots. Other regulators include CsNPF2.3, which is positively associated with root-to-leaf F transport efficiency, and CsALMT6, which enhances F tolerance by limiting F accumulation (Figure 4) [99,107]. Taken together, these findings suggest that coordinated transport processes and potassium-related regulatory pathways may be promising targets for reducing F uptake and accumulation in tea plants.

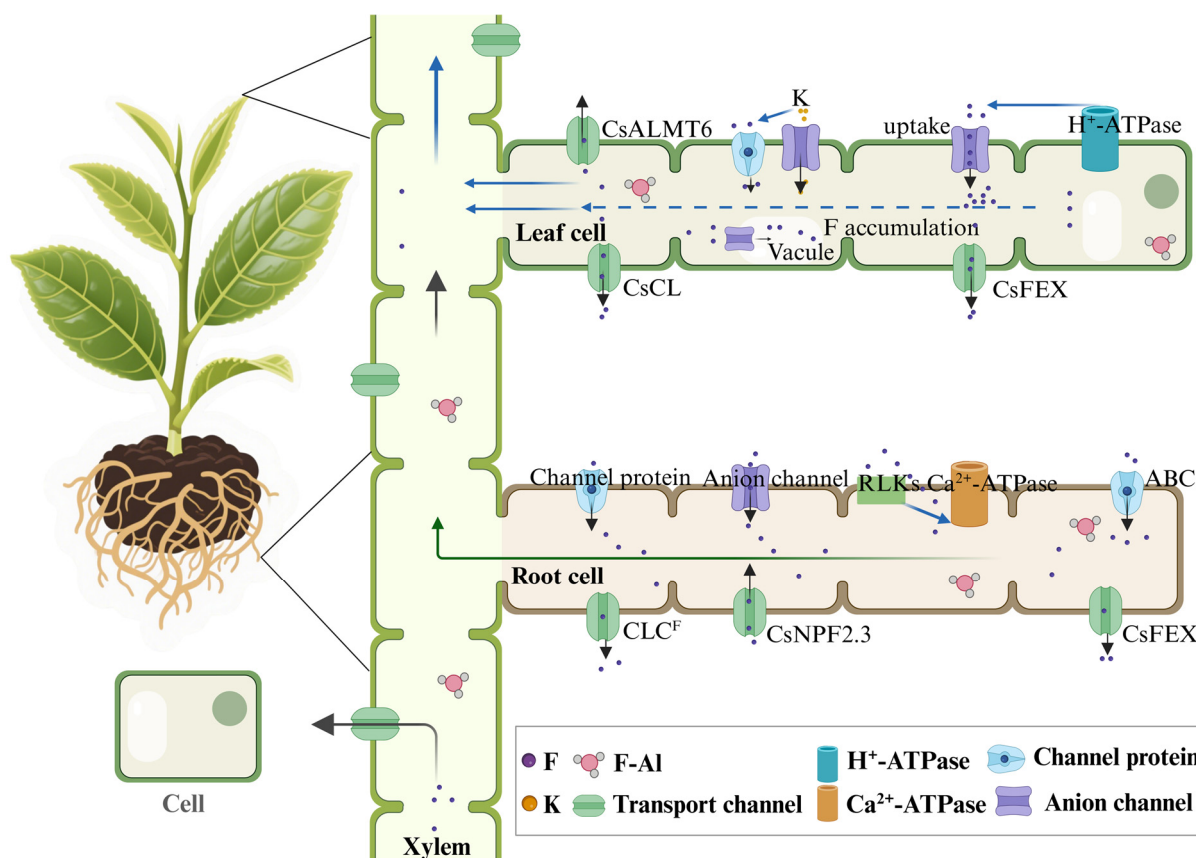


Figure 4. Channels and transport proteins responsible for fluoride uptake and movement across cellular and vascular tissues in tea plants. The schematic diagram in this figure was created using templates from BioRender.com.

6.4. Organ-, Developmental-, and Seasonal Distribution Patterns

F distribution in *C. sinensis* shows clear organ-specific and developmental gradients. In general, leaves accumulate substantially more F than roots or stems. Within aboveground tissues, F abundance follows the order: mature leaves > young leaves > shoots > branches > stems [108]. Mature leaves are the primary sinks for F

accumulation and may retain the vast majority of total plant F [109].

Seasonal variation also affects F accumulation in tea plants. Wen et al. [110] reported that F content in young leaves increased progressively from spring to autumn, whereas mature leaves showed a decreasing trend, suggesting possible redistribution of F within the plant. Cai et al. [111] further showed that F concentrations in summer tea leaves were markedly higher than those in

spring and autumn leaves, with summer tea consistently exhibiting the highest F concentration.

Although F uptake by roots is an active and regulated process, its subsequent movement to the shoot occurs largely through the xylem. Higher summer transpiration rates may therefore contribute to higher root-to-leaf F delivery, but this explanation remains tentative and should not be viewed as the sole cause of seasonal variation. Seasonal F accumulation is likely influenced by multiple interacting factors, including root uptake capacity, xylem transport, leaf developmental stage, and environmental conditions.

These seasonal patterns also raise the possibility that climate-related factors may influence F accumulation in tea plants [112,113]. The IPCC Sixth Assessment Report indicates that the frequency and intensity of hot extremes have already increased in most land regions and are projected to rise further with continued global warming [112]. Tea cultivation is widely recognized as highly vulnerable to climate variability, particularly extreme heat, drought, and rainfall anomalies [113,114]. Because F translocation in tea occurs primarily through the xylem, with transpiration acting as the driving force, warmer growing conditions and more frequent heat events could enhance root-to-leaf F delivery when soil moisture is sufficient, thereby increasing the risk of leaf F accumulation [111]. Conversely, under combined heat and drought stress, stomatal closure may constrain transpiration and partly limit xylem-mediated F transport [115,116]. Thus, the influence of climate change on F accumulation in tea plants is likely to be nonlinear and to depend on interactions among heat stress, soil moisture availability, and stomatal regulation [117]. Future field studies should explicitly quantify how warming, heatwaves, vapor pressure deficit, and drought jointly affect F uptake, xylem transport, and seasonal accumulation in tea plantations.

6.5. Subcellular Sequestration and Cell-Wall Immobilization

At the cellular level, the cell wall is a major site of fluoride immobilization in tea leaves [118]. In particular, the pectin-rich fraction appears to play a central role in F fixation. Available evidence suggests that F is closely associated with amino and carboxyl groups in cell-wall

pectin, while metal-ion-mediated interactions may also contribute to its retention within the wall [24,118].

Pectin is the principal F-binding component within the cell wall, accounting for 56–71% of cell-wall-associated F [119]. At the subcellular level, both the cell wall and the soluble fraction serve as major F storage pools, whereas the relative proportion of these two fractions varies with cultivar and F treatment [120]. F detected in the soluble fraction likely reflects intracellular compartmentalization, possibly through vacuolar sequestration.

7. Factors Affecting Fluoride in Tea Infusion and Their Food Safety Implications

F levels in tea infusions are determined by both plant-intrinsic factors and postharvest conditions. From leaf selection at harvest to processing and brewing, each step can influence F release into the final beverage and thus, affect potential human exposure.

7.1. Leaf Selection and Harvest Season

Leaf age and harvest season play critical roles in determining F accumulation in tea materials. Senescent leaves contain 3–5 times more F than apical buds or young leaves (Figure 5) [121]. Therefore, high-quality teas are typically produced from young shoots consisting of a bud and one or two leaves, with lower F content, thereby contributing to a milder flavor profile and lower potential F intake. In contrast, mature leaves (the fourth leaf and older), which generally contain more F, are more commonly used in commercial brick teas and some tea-bag products because of their greater biomass, wider availability, and suitability for bulk processing and mechanical packaging [122].

Seasonal variation further modulates F accumulation. Under comparable conditions, spring harvests (March–April) generally yield leaves containing 35–50% less F than summer or autumn harvests [123]. This seasonal difference is particularly important for non-fermented teas, for which early spring shoots are often selected for premium products. In contrast, many brick dark teas are manufactured from older, coarser leaves and stems or branches rather than tender shoots, which contributes to their distinctive sensory characteristics and relatively high F content [124].

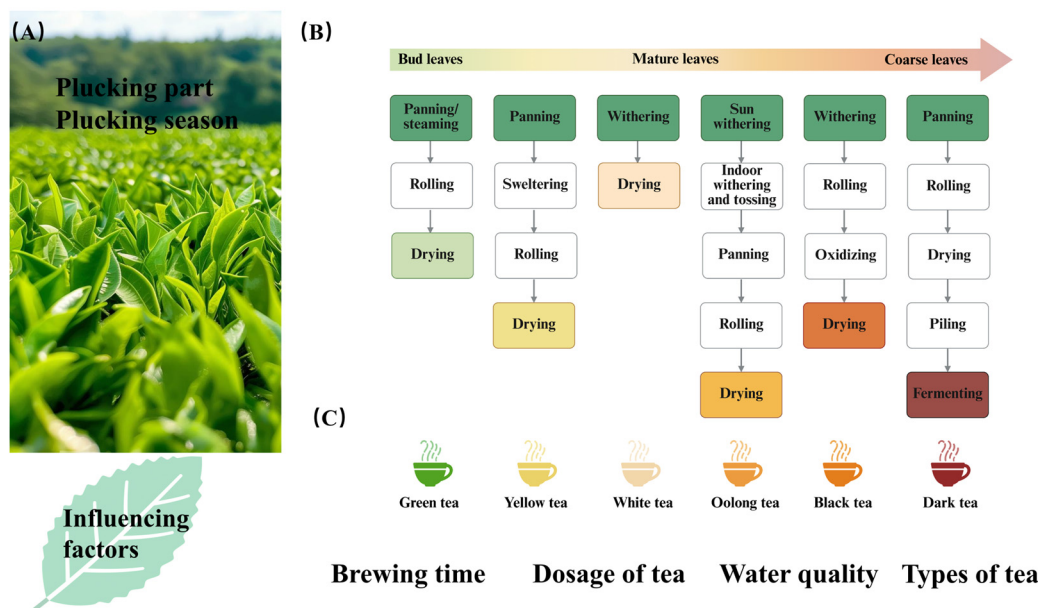


Figure 5. Factors influencing the fluoride content of tea infusions: (A) plucking part; (B) types of tea; (C) brewing methods.

7.2. Processing Technology and Fluoride Dynamics

After harvest, F migration can be further influenced by processing steps, which alter leaf structure and thereby affect the subsequent release of F during brewing. In minimally processed white tea, gentle drying better preserves cellular integrity, which may restrict F release during infusion, although direct evidence for this mechanism remains limited [125].

By contrast, in rolled tea products, mechanical disruption increases the accessibility of F to water; accordingly, a brief water rinse (1–2 min, room temperature) can remove part of the readily extractable F while largely retaining major bioactive compounds [126,127]. Karak and Bhagat. [128] found that infusion F concentrations vary significantly by tea type, with black teas generally exceeding green teas in F release.

7.3. Brewing Process

Brewing conditions strongly influence F transfer into tea infusions. Leaf fragmentation increases surface area and thereby promotes extraction [12]. Accordingly, powdered teas exhibit substantially higher F release than whole leaves, although the effects of particle size remain insufficiently characterized. During infusion, 96–99% of total tea F becomes water-soluble, with extraction efficiency governed by water chemistry, duration, tea variety, and leaf-to-water ratio [129]. Extending brewing from 5 to 15 min increases F extraction from black tea by 12–36%, compared to 0.3–15.8% in green tea and 5.7–9.6% in white tea [130]. Brick tea shows a particularly strong dependence of F release on brewing time and repeated infusions. In addition, the percentage of F extracted decreases as the leaf-to-water ratio increases, likely because less water is available per unit tea and the

infusion reaches extraction equilibrium more rapidly under solvent-limited conditions [131].

Collectively, these findings indicate that leaf maturity, harvest season, processing methods, and brewing practices all influence F exposure from tea consumption, with important implications for food safety, especially in populations with frequent intake of brick tea or strong infusions.

8. Management Strategies for Mitigating F Bioaccumulation in *Camellia sinensis*

8.1. Source Control: Modulating Soil Fluoride Bioavailability

8.1.1. Soil Amendment Strategies

Source control through soil amendment is a primary strategy for mitigating F bioavailability, based on the principle that F uptake depends strongly on its chemical form in soil. Among different soil F fractions, Ws-F is the most readily available for tea plant uptake. Accordingly, amendment strategies generally aim to convert soluble F into less bioavailable forms.

Calcium-containing amendments are among the most widely studied options for reducing F mobility in tea soils. Calcium sources such as agricultural lime (CaCO₃), gypsum (CaSO₄), calcium nitrate [Ca(NO₃)₂], and dolomite can reduce F bioavailability by promoting CaF₂ precipitation, increasing soil pH, and lowering exchangeable Al³⁺ [132]. Fung and Wong. [133] showed that CaCO₃, Ca(OH)₂, and CaO reduced F accumulation in leaves by 23–41% relative to the control (374 mg/kg), with stronger effects at higher application rates. Similarly, Ruan et al. [76] reported that 500 mg/kg Ca(NO₃)₂ decreased leaf F accumulation, likely through CaF₂ precipitation and displacement of Al³⁺ from exchange sites, thereby reducing the pool of bioavailable F.

Biochar amendments provide complementary benefits through porous structures that immobilize F via electrostatic interactions, ion exchange, and surface complexation (Figure 6) [134]. Their generally alkaline nature can also increase soil pH, reduce exchangeable Al, and, under suitable conditions, favor stabilization of F in less bioavailable forms [27]. However, because tea is an acid-adapted crop, this benefit is limited to an appropriate pH range; excessive alkalinization may instead increase Ws-F. Therefore, the long-term response of tea plants depends on maintaining soil pH within the suitable acidic range rather than continuously increasing pH [27]. Gao et al. [65] reported that 0.5–5.0% (w/w) charcoal or bamboo charcoal reduced soil Ws-F by 23–29% and decreased young-leaf F by 35–37% (from 156.73 mg/kg to 98.6–102.5 mg/kg). Likewise, Wang et al. [27] found that biochar application reduced F accumulation in tea plants and altered soil F fractions, although the effect was strongly dose-dependent: lower amendment rates favored fixation of Ws-F, whereas excessive application increased soil pH and, under some conditions, enhanced F solubility.

Tea-residue-derived biochar is particularly attractive because it enables reuse of tea-processing waste while also reducing F uptake by tea plants. In our previous work, applying tea-residue-derived biochar at 0.5% (w/w), together with heavy shading for 12 days before the autumn harvest, reduced F content in tea leaves by 30.0–39.1%

[135]. Recent evidence further supports this potential. Yi et al. [136] showed that calcium-modified biochar prepared from dark tea residues reduced young-leaf F from 252.22 to 124.96 mg/kg (48.6%) and soil Ws-F from 15.91 to 10.99 mg/kg. These effects were attributed to multiple mechanisms, including adsorption of Ws-F in rhizosphere soil, improved nutrient availability, and beneficial shifts in the bacterial community. In contaminated systems, Li et al. [137] further found that 5% AlCl₃-modified biochar reduced root F by 33–77% across tea-growing regions in Hubei Province, suggesting that modified biochar may remain effective under complex pollution conditions.

However, because tea plants are F hyperaccumulators, the environmental fate of endogenous F during pyrolysis of tea residues requires explicit consideration. Direct mass-balance studies on F partitioning during pyrolysis of high-F tea residues are still lacking, and it therefore cannot be assumed that F originally present in tea biomass is permanently sequestered in the resulting biochar. Evidence from agricultural-waste pyrolysis indicates that fluorine can be redistributed among pyrolysis products and that higher temperatures promote its release, with gaseous fluorine-bearing species becoming increasingly important above 500 °C [138]. Other studies of fluorine-bearing wastes similarly show that fluorine can volatilize during thermal conversion, with HF and SiF₄ detected among the released species [139].

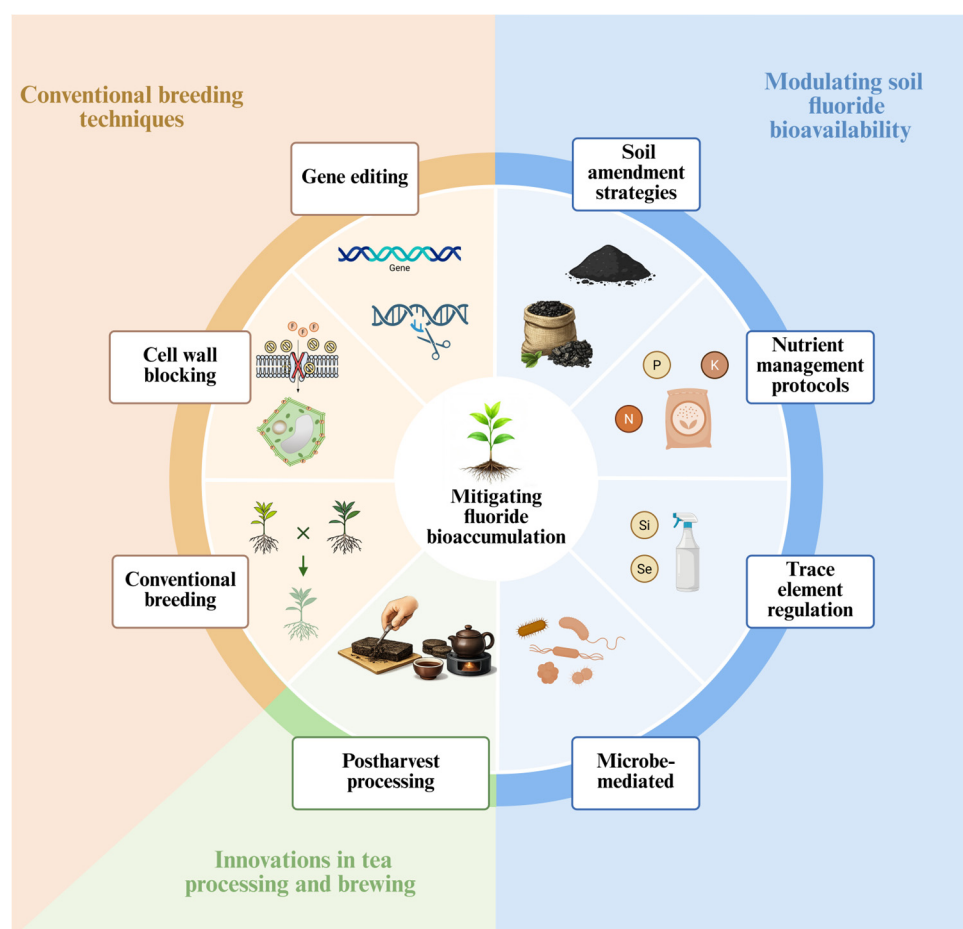


Figure 6. Holistic measures to reduce fluoride in tea leaves.

This uncertainty should be distinguished from the post-production F sorption capacity of tea-waste-derived biochar in aqueous systems. For example, acid-modified tea domestic waste biochar achieved a maximum F sorption capacity of 109.18 mg/g and removed 80.89–93.31% of F from real industrial wastewater [140], whereas lanthanum-modified tea waste biochar reached a theoretical maximum adsorption capacity of 47.47 mg/g and removed more than 95% of F from geothermal hot spring water [141].

Emerging engineered adsorbents also provide targeted options for F immobilization in soil. Zhao et al. [142] synthesized polyphenol-Ce composites that chelate Al³⁺ via phenolic hydroxyl groups while electrostatically adsorbing F⁻ at Ce sites. This interaction was proposed to inhibit Al-associated F complexation, thereby reducing leaf F by up to 74.8% in Sichuan tea gardens. Huang et al. [143] developed aluminum humate adsorbents with high F affinity (62.5 mg/g at pH 4–10), achieving a 53% reduction in soil-solution F and a 74.3% reduction in leaf F accumulation in field trials. These findings suggest that molecularly tailored materials may offer targeted F immobilization, although their long-term environmental compatibility, cost, and field applicability still require further evaluation.

8.1.2. Nutrient Management Protocols

Precision fertilization is a key component of tea plantation management because it optimizes plant nutrition while also influencing soil F bioavailability through changes in F solubility and ion interactions. Empirical evidence shows that both macronutrients (N, P, and K) and micronutrients (e.g., Se) can affect F chemical forms and bioavailability [59,60]. Within nutrient management, two aspects appear particularly important for F control: phosphate fertilizer source selection and potassium optimization.

First, because phosphate fertilizers themselves are an important anthropogenic source of F in tea-growing soils, nutrient-ratio optimization alone is insufficient for true source control. In addition to adjusting N/P/K ratios, the type of phosphate fertilizer should also be considered. Recent evidence from commercial phosphate fertilizers in China showed that SSP, DAP, and some NPK fertilizers contain substantially higher total and Ws-F than MKP, MAP, and water-soluble macroelement fertilizers [56]. Therefore, where agronomically and economically feasible, low-F or defluorinated phosphate fertilizers should be preferentially used, whereas high-F phosphorus sources such as SSP and some compound fertilizers should be avoided or minimized in tea plantations. This source-selection strategy is likely to provide more effective F control than nutrient-ratio adjustment alone.

Second, potassium nutrition represents a promising physiological strategy for limiting F accumulation in tea

plants. Controlled trials show that NPK co-application can induce short-term (10–20 d) reductions in Ws-F, with Ws-F showing a moderate positive correlation with nitrogen dosage [75]. More specifically, potassium plays an important role in F regulation, and potassium deficiency increases F accumulation in tea plants. Hydroponic studies using Longjing 43 seedlings showed that potassium supplementation reduced F accumulation in new shoots, with 5 mM K identified as an effective level. This effect was accompanied by increased K influx in roots, stabilization of root membrane potential, and transcriptional changes in F-related transport pathways, including upregulation of CsFEX and downregulation of CsHAKs. Potassium treatment was also associated with reduced Ca and Mg contents in some tissues, suggesting antagonistic ion interactions that may contribute to lower F accumulation [26]. Overall, these findings indicate that nutrient-based F mitigation should integrate preferential use of low-F phosphate fertilizers with optimized potassium management.

Organic amendments and micronutrient treatments may provide additional support for F mitigation. The reduction in F mobility by organic amendments is thought to be related largely to interactions involving dissolved organic matter (DOM). Specifically, dissolved organic matter (DOM) may reduce soluble F indirectly by complexing metal ions (e.g., Al, Ca, and Fe) and thereby promoting metal-mediated F retention, rather than through direct binding of F⁻ to negatively charged functional groups such as carboxyl groups [18]. Soil culture experiments further show that fermented organic sheep and soybean manures effectively reduce water-soluble and exchangeable F, with 5% soybean manure producing the strongest suppression [86]. Selenium supplementation also exerts compartment-specific effects: sodium selenite (5 mg/L) in hydroponic systems promotes root pectin and hemicellulose synthesis, enhances cell-wall F binding, and reduces leaf F accumulation by 47.8% [7]. Field trials showed that foliar selenium sprays (selenite, κ -selenocarrageenan, selenomethionine, and nano-Se) decreased leaf fluoride by 10–48% and were associated with pectin demethylation and enhanced F retention in the cell wall, particularly in mature leaves and stems [25]. Complementary foliar calcium sprays further reduced leaf F and may be associated with changes in pectin methylesterification, cell-wall carbohydrate composition, and the expression of cell-wall-related genes [24].

Taken together, these findings suggest that nutrient- and amendment-based F mitigation should not rely on a single intervention. Instead, integrated management of fertilizer sources, potassium nutrition, organic amendments, and selected micronutrient treatments may provide a more effective strategy for reducing F uptake while maintaining tea quality.

8.1.3. Microbial-Mediated Mitigation of Fluoride Bioavailability

Microbial remediation has emerged as a sustainable and relatively low-cost strategy for reducing soil F bioavailability by using native or introduced F-tolerant microorganisms to lower soluble F and thereby limit plant uptake. Metagenomic analyses of F-rich agricultural soils identified Actinobacteria and Proteobacteria as dominant phyla, with taxa such as *Streptomyces*, *Bradyrhizobium*, *Nocardioideae*, and *Pseudomonas* representing core members of F-adapted microbial communities [144]. In addition, isolated strains such as *Bacillus megaterium* (JF273850) exhibit high F tolerance and substantial F sequestration capacity, suggesting a potential role in reducing the bioavailable F pool rather than in permanently removing F from soil [145].

Mechanistically, microorganisms may reduce F bioavailability through several synergistic pathways: (1) bioaccumulation, involving adsorption of F onto cell-surface functional groups and intracellular sequestration; (2) biochemical and surface-mediated immobilization, in which extracellular polymeric substances (EPS) and other microbial metabolites modify the local microenvironment and promote F sorption or temporary stabilization, depending on pH and metal availability; and (3) indirect plant–microbe interactions, by which rhizosphere colonization improves plant vigor and tolerance under F stress [145,146]. Recent metagenomic evidence further indicates that F-rich soils harbor microbial communities enriched in F-tolerance-associated functions, supporting the ecological feasibility of microbe-based remediation under long-term F stress [144]. Overall, these findings suggest that microbial remediation may represent a promising strategy for reducing F bioavailability in contaminated soils, with potential applicability to tea plantation systems.

8.2. Strategic Breeding of Low-Fluoride Cultivars

Substantial genotypic variability in F accumulation exists among *C. sinensis* cultivars, providing opportunities to reduce soil-to-plant F transfer through varietal selection and breeding [34]. For example, Chen et al. [34] reported that leaf F content differed by up to 2.7-fold between high- and low-accumulating varieties and suggested that Zhenong 138 could be promoted as a low-F cultivar. F uptake, transport, and accumulation in tea plants are regulated by multiple genes [99,147]. Accordingly, breeding programs can exploit existing genetic diversity to identify and propagate cultivars with low F accumulation [148]. In this context, selection breeding provides a genetics-based approach for limiting excessive F accumulation in tea plants [110].

Recent studies have identified several representative low- and high-F cultivars. Yang et al. [149] identified Xiangbo Lü as a promising low-F cultivar and Zhenong

139 as a high-F cultivar, with mean bud F concentrations of 96.00 ± 13.87 and 198.65 ± 56.56 mg/kg, respectively. Wu et al. [150] found that the tea cultivar Xianggu Liaobaihao had the lowest F content, and it was suggested that it could be promoted as a low-F variety. Ma et al. [151] further selected six low-F varieties, including Zhongcha 108, for brick tea production and found that the resulting brick tea contained less than 150 mg/kg F. In addition, Wen et al. [110] evaluated seasonal F patterns across 85 cultivars and found significant varietal effects, with six cultivars—Xiaoxianghong, Huangjincha 1, Zhuyeqi, Taoyuandaye, 53–54, and Huangjincha 2—consistently showing low F levels in both young and mature leaves, making them promising candidates for commercial development.

Although genetic selection provides an eco-friendly and chemically independent strategy with potentially stable trait inheritance, its practical implementation remains constrained. Conventional breeding of tea plants is time-consuming because of their perennial growth habit, and prolonged evaluation is required to confirm trait stability. In addition, regional adaptability must be assessed through extensive field trials to ensure that low-F performance is maintained across different soil and climatic conditions.

8.3. Innovations in Tea Processing for Fluoride Mitigation

Physical processing interventions can influence F retention in made tea. Chen et al. [152] compared three traditional enzyme-deactivation methods (water-laoqing, pan-firing, and steaming) and found significant differences in F content among treatments, following the order steaming > pan-firing > water-laoqing. The lower F content under water-laoqing likely reflects transfer of a readily mobile F fraction into the processing water rather than disappearance of F. Gao et al. [128] further showed that a 60 °C water wash during rolling was an effective condition for reducing F in brick tea.

Chemical approaches have also been explored as potential F-reduction measures. Wang et al. [153] reported that adding DTF, a sheep-bone-derived F-fixing emulsion, at 0.5–10.0% immobilized 21.2–97.9% of tea F, with no obvious adverse effects on tea color, taste, pH, or polyphenol content. Lin et al. [154] identified Formula E as the most effective tested formulation, reducing F by >40%.

Biotechnological approaches have likewise been investigated for F mitigation in dark tea. In particular, ultraviolet mutagenesis has been used to generate or screen *Eurotium cristatum* strains with enhanced potential to lower free or extractable F during fermentation, rather than implying that UV irradiation itself directly removes F [155].

Collectively, these studies highlight several postharvest possibilities for reducing F in tea products. However, methods involving direct chemical additives

require particularly careful evaluation of food safety, sensory quality, regulatory acceptability, and consumer acceptance before practical application.

9. Challenges and Future Research Directions

Despite recent progress, several key knowledge gaps still limit the development of optimized F-mitigation strategies in tea systems. First, rapid and field-deployable technologies for real-time F monitoring in soils and plant tissues remain underdeveloped. Current analytical methods, such as WD-XRF and NMR, are largely confined to laboratory settings and are not readily scalable for on-site assessment. Future research should prioritize portable sensors and spectroscopic tools capable of quantifying F chemical forms and bioavailability in situ. Such tools would enable real-time evaluation of mitigation efficacy and support timely field intervention.

Second, the molecular mechanisms governing F transport and compartmentalization remain incompletely understood. In particular, the roles of key transporters, including CsFEX, CsCLC, CsALMT6, and ABC proteins, in root uptake, xylem loading, vacuolar sequestration, and inter-organ redistribution require further clarification. Multidisciplinary approaches integrating in vivo imaging, such as PET with ^{18}F tracers, transcriptomics, and heterologous expression studies will be important for elucidating these pathways and identifying genetic targets for breeding low-F cultivars.

Another major gap concerns microbial-mediated F mitigation. Although existing studies have preliminarily identified dominant F-tolerant taxa, such as Actinobacteria and Proteobacteria, and several functional strains in tea garden soils, systematic characterization of the structure, diversity, and functional potential of F-tolerant microbial communities across tea-growing regions is still lacking. In addition, the mechanisms underlying microbe–rhizosphere interactions remain unclear, particularly the pathways through which microbial metabolites, including organic acids and extracellular polymeric substances, influence F chemical transformation and root uptake in tea plants.

Finally, optimizing agronomic practices to reduce F accumulation while maintaining tea yield and quality requires moving beyond nutrient-ratio adjustment alone. Future work should jointly consider phosphate fertilizer source selection and potassium optimization as complementary components of nutrient-based F mitigation. In particular, machine learning models trained on multi-season and multi-location field datasets could integrate variables such as phosphate fertilizer type and F content, potassium application rate, organic amendments, soil type, and climate to generate site-specific fertilization protocols that minimize F input and plant uptake without compromising productivity or tea quality.

Beyond tea-specific studies, useful insights may also be drawn from F-control practices in other crop systems. For example, amendment with flue gas desulfurization gypsum has been shown to reduce F accumulation in the aboveground parts of alfalfa and ryegrass grown in acidic soils [156], nano-maghemite can mitigate F accumulation in rice seedlings [157], and exogenous silicon can alleviate F stress in wheat by reducing F uptake and suppressing root-to-shoot transport [158]. However, because species differ substantially in F uptake, transport, and tolerance, these approaches cannot be directly transferred to tea cultivation without further validation under tea-specific soil and management conditions.

10. Conclusions

Camellia sinensis exhibits a strong capacity for fluoride (F) accumulation, particularly in mature leaves, which are the main contributors to F exposure through tea consumption. This issue is particularly important in regions where brick tea, made from older leaves, is frequently consumed, as F transfer into infusions can be substantial. A range of mitigation strategies have shown potential to limit F accumulation in tea, including soil amendments, nutrient management, low-F cultivars, and processing optimization. Among these, nutrient-based management, especially the use of low-F phosphate fertilizers and optimized potassium supply, emerges as a promising approach to reduce F accumulation without compromising tea quality or yield. However, several challenges remain, including the lack of field-deployable F monitoring tools and incomplete understanding of the molecular and microbial mechanisms underlying F uptake and sequestration. Future research should focus on integrated, site-specific F management strategies, leveraging machine learning models and advanced technologies for real-time monitoring and precise management of F bioavailability. These efforts will be essential for developing scalable and sustainable solutions to mitigate F exposure in tea systems.

Author Contributions

X.W.: Conceptualization, Methodology, Writing—Original draft, Writing—review & editing, Visualization. J.T.: Conceptualization, Methodology, Writing—Original draft, Visualization. N.G.: Conceptualization, Writing—review & editing. I.A.S.: Conceptualization, Writing—review & editing. Y.Z.: Conceptualization, Methodology. Y.L.: Conceptualization, Methodology. C.S.: Writing—review & editing, Funding acquisition, Supervision. M.W.: Conceptualization, Writing—review & editing. H.X.: Conceptualization, Methodology, Writing—review & editing. Y.X.: Conceptualization, Writing—review & editing. All authors have read and agreed to the published version of the manuscript.

Funding

This study was financially supported by the Graduate Research Innovation Project of Hunan Agricultural University (Non-funded Program) (2024XKCB013); the project of National Key Research and Development Plan (2024YFD1200504); the project of National Natural Science Foundation of China (32372765); the project of Chenzhou National Sustainable Development Agenda Innovation Demonstration Zone Construction Project (2022SFQ48); and the project of Special Project for the Construction of Modern Agricultural Industrial Technology Systems in Hunan Province (HARS-10).

Institutional Review Board Statement

Not applicable

Informed Consent Statement

Not applicable

Data Availability Statement

Not applicable

Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the authors used ChatGPT for language refinement. After using those tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

References

1. Ghosh, A.; Mukherjee, K.; Ghosh, S.K. Sources and Toxicity of Fluoride in the Environment. *Res. Chem. Intermed.* **2013**, *39*, 2881–2915.
2. Kabir, H.; Gupta, A.; Tripathy, S. Fluoride and Human Health: Systematic Appraisal of Sources, Exposures, Metabolism, and Toxicity. *Crit. Rev. Environ. Sci. Technol.* **2020**, *50*, 1116–1193.
3. NIH Office of Dietary Supplements. Fluoride—Health Professional Fact Sheet. Available online: <https://ods.od.nih.gov/factsheets/Fluoride-HealthProfessional/> (accessed on 20 March 2026).
4. Cao, W.; Zhang, Z.; Guo, H. Spatial Distribution and Controlling Mechanisms of High Fluoride Groundwater in the Coastal Plain of Bohai Rim, North China. *J. Hydrol.* **2023**, *617*, 128952.
5. Li, Y.; Zhang, M.; Mi, W. Spatial Distribution of Groundwater Fluoride and Arsenic and Its Related Disease in Typical Drinking Endemic Regions. *Sci. Total Environ.* **2024**, *906*, 167716.
6. Waldbott, G.L. Fluoride in Food. *Am. J. Clin. Nutr.* **1963**, *13*, 393.
7. Niu, H.; Zhan, K.; Xu, W. Selenium Treatment Modulates Fluoride Distribution and Mitigates Fluoride Stress in Tea Plant (*Camellia sinensis* (L.) O. Kuntze). *Environ. Pollut.* **2020**, *267*, 115603.
8. Li, Q.S.; Lin, X.M.; Qiao, R.Y. Effect of Fluoride Treatment on Gene Expression in Tea Plant (*Camellia sinensis*). *Sci. Rep.* **2017**, *7*, 9847.
9. Miao, S.; Wei, Y.; Chen, J. Extraction Methods, Physiological Activities and High Value Applications of Tea Residue and Its Active Components: A Review. *Crit. Rev. Food Sci. Nutr.* **2023**, *63*, 12150–12168.
10. Li, W.; Cheng, H.; Mu, Y. Occurrence, Accumulation, and Risk Assessment of Trace Metals in Tea (*Camellia sinensis*): A National Reconnaissance. *Sci. Total Environ.* **2021**, *792*, 148354.
11. Jayasinghe, S.L.; Kumar, L. Causes of Tea Land Dynamics in Sri Lanka Between 1995 and 2030. *Reg. Environ. Chang.* **2023**, *23*, 127.
12. Pattaravisitsate, N.; Phetrak, A.; Denpetkul, T. Effects of Brewing Conditions on Infusible Fluoride Levels in Tea and Herbal Products and Probabilistic Health Risk Assessment. *Sci. Rep.* **2021**, *11*, 14115.
13. Zhang, D.; Xu, X.; Wu, X. Monitoring Fluorine Levels in Tea Leaves from Major Producing Areas in China and the Relative Health Risk. *J. Food Compos. Anal.* **2023**, *118*, 105205.
14. Yi, X.Y.; Qiao, S.; Ma, L.F. Soil Fluoride Fractions and Their Bioavailability to Tea Plants (*Camellia sinensis* L.). *Environ. Geochem. Health* **2017**, *39*, 1005–1016.
15. Ozsvath, L.D. Fluoride and Environmental Health: A Review. *Rev. Environ. Sci. Biotechnol.* **2009**, *8*, 59–79.
16. Zhang, C. Spatial and Vertical Distribution and Pollution Assessment of Soil Fluorine in a Lead-Zinc Mining Area in the Karst Region of Guangxi, China. *Plant Soil Environ.* **2010**, *56*, 282–287.
17. Wang, M.; Li, X.; He, W. Distribution, Health Risk Assessment, and Anthropogenic Sources of Fluoride in Farmland Soils in Phosphate Industrial Area, Southwest China. *Environ. Pollut.* **2019**, *249*, 423–433.
18. Huang, X.; Chen, K.; Wang, C. Characteristics of Fluoride Adsorption in Different Soil Types: Potential Factors and Implications for Environmental Risk Assessment. *Environ. Pollut.* **2025**, *367*, 125537.
19. Shu, W.; Zhang, Z.; Lan, C. Fluoride and Aluminium Concentrations of Tea Plants and Tea Products from Sichuan Province, PR China. *Chemosphere* **2003**, *52*, 1475–1482.
20. Zhang, L.; Li, Q.; Ma, L.F. Characterization of Fluoride Uptake by Roots of Tea Plants (*Camellia sinensis* (L.) O. Kuntze). *Plant Soil* **2013**, *366*, 659–669.
21. Peng, C.Y.; Xu, X.F.; Ren, Y.F. Fluoride Absorption, Transportation and Tolerance Mechanism in *Camellia Sinensis*, and Its Bioavailability and Health Risk Assessment: A Systematic Review. *J. Sci. Food Agric.* **2021**, *101*, 379–387.
22. Wu, Z.; Xing, A.; Chu, R. The Fluoride Exporter (CsFEX) Regulates Fluoride Uptake/Accumulation in *Camellia*

- Sinensis* Under Different pH. *Ecotoxicol. Environ. Saf.* **2024**, *278*, 116407.
23. Yang, J.; Liu, C.S.; Li, J.L. Critical Review of Fluoride in Tea Plants (*Camellia sinensis*): Absorption, Transportation, Tolerance Mechanisms, and Defluorination Measures. *Bever. Plant Res.* **2024**, *4*, e019.
 24. Luo, J.L.; Zhang, L.T.; Li, D.L. Foliar Calcium Application Reduces Fluorine Accumulation in Tea Plant by Regulating Cell Wall Structure and Gene Expression. *Front. Plant Sci.* **2025**, *15*, 1443439.
 25. Niu, H.; Zhan, K.; Cheng, X. Selenium Foliar Application Contributes to Decrease Ratio of Water-Soluble Fluoride and Improve Physio-Biochemical Components in Tea Leaves. *Ecotoxicol. Environ. Saf.* **2023**, *266*, 115568.
 26. Sun, Y.; Wu, Z.; Xing, A. Potassium Alleviates Fluoride Accumulation and Enhances Fluoride Tolerance in *Camellia Sinensis*. *Ind. Crops Prod.* **2024**, *219*, 119062.
 27. Wang, H.Y.; Hu, T.; Wang, M.H. Biochar Addition to Tea Garden Soils: Effects on Tea Fluoride Uptake and Accumulation. *Biochar* **2023**, *5*, 24.
 28. Małyszczek, A.; Kiryk, S.; Kensy, J. Identification of Factors Influencing Fluoride Content in Tea Infusions: A Systematic Review. *Appl. Sci.* **2025**, *15*, 5974.
 29. Koblar, A.; Tavčar, G.; Ponikvar-Svet, M. Fluoride in Teas of Different Types and Forms and the Exposure of Humans to Fluoride with Tea and Diet. *Food Chem.* **2011**, *130*, 286–290.
 30. Cao, J.; Zhao, Y.; Liu, J.W. Processing Procedures of Brick Tea and Their Influence on Fluorine Content. *Food Chem. Toxicol.* **2001**, *39*, 959–962.
 31. Fang, X.J. Current Research Status on the Drinking Safety of Fluoride in Brick Tea. *Hunan For. Sci. Technol.* **2011**, *38*, 85–88. (In Chinese)
 32. Gesang, Z.; Tudan, Ci, Z. Analysis of Monitoring Results for Brick-Tea Type Fluorosis in Biru County, Naqu City, Tibet, 2017. *Psychol. Mon.* **2018**, 161–162. (In Chinese)
 33. Xu, D.; Chen, J.; Yang, X. Analysis of Surveillance Results for Brick-Tea Type Endemic Fluorosis in Sichuan Province, 2016–2017. *J. Prev. Med. Inf.* **2019**, *35*, 692–696. (In Chinese)
 34. Chen, P.; Zhang, Q.; Jiang, H. Analysis of the Prevalence of Tea-Drinking Type Fluorosis in Haibei Prefecture, Qinghai Province, 2018. *Chin. J. Endemiol.* **2020**, *39*, 47–49. (In Chinese)
 35. Duan, Y.; Wang, C.; Pu, D. Analysis of Monitoring Results for Brick-Tea Type Endemic Fluorosis in Xinjiang, 2014–2016. *Chin. J. Endemiol.* **2018**, *37*, 316–318. (In Chinese)
 36. Zhang, L.; Huang, H.; Yang, J. Probabilistic Risk Assessment of Chinese Residents' Exposure to Fluoride in Improved Drinking Water in Endemic Fluorosis Areas. *Environ. Pollut.* **2017**, *222*, 118–125.
 37. Guo, B.; Li, C.; Liang, L. Investigation on Fluoride Content in Brick Tea. *Chin. J. Endemiol.* **2019**, *38*, 467–471. (In Chinese)
 38. Frayse, C.; Bilbeissi, M.W.; Mitre, D. Le Rôle de la Consommation du Thé Dans La Fluorose Dentaire En Jordanie. *Bull. Group. Int. Rech. Sci. Stomatol. Odontol.* **1989**, *32*, 39–46.
 39. Izuora, K.; Twombly, J.G.; Whitford, G.M. Skeletal Fluorosis from Brewed Tea. *J. Clin. Endocrinol. Metab.* **2011**, *96*, 2318–2324.
 40. Waugh, D.T.; Potter, W.; Limeback, H. Risk Assessment of Fluoride Intake from Tea in the Republic of Ireland and Its Implications for Public Health and Water Fluoridation. *Int. J. Environ. Res. Public Health* **2016**, *13*, 259.
 41. Sergio Gomez, S.; Weber, A.; Torres, C. Fluoride Content of Tea and Amount Ingested by Children. *Odontol. Chil.* **1989**, *37*, 251–255. (In Spanish)
 42. Szmagara, A.; Krzyszczyk, A.; Stefaniak, E.A. Determination of Fluoride Content in Teas and Herbal Products Popular in Poland. *J. Environ. Health Sci. Eng.* **2022**, *20*, 717–727.
 43. Chandrajith, R.; Bhagya, S.; Diyabalanage, S. Exposure Assessment of Fluoride Intake Through Commercially Available Black Tea (*Camellia sinensis* L.) from Areas with High Incidences of Chronic Kidney Disease with Undetermined Origin (CKDu) in Sri Lanka. *Biol. Trace Elem. Res.* **2022**, *200*, 526–534.
 44. Shang, W.J.; Shang, R.Z.; Wang, Q.H. Analysis of the Prevalence Status of Tea-Drinking Endemic Fluorosis in Gannan Prefecture. *Bull. Dis. Control Prev.* **2021**, *36*, 32–34. (In Chinese)
 45. Buzalaf, M.A.R. Review of Fluoride Intake and Appropriateness of Current Guidelines. *Adv. Dent. Res.* **2018**, *29*, 157–166.
 46. García, M.G.; Borgnino, L. *Fluoride in the Context of the Environment*; The Royal Society of Chemistry: London, UK, **2015**.
 47. Feng, G.; Li, Z.; Su, C. Provenance and Geogenic Modes of High-Fluoride Groundwater Occurred in Various Sedimentary Environments: Constraints of Hydrogeology and Hydrogeochemistry. *Appl. Geochem.* **2025**, *195*, 106624.
 48. Subbaiah, P.M.; Mohammed, Y.; Yongtae, A. Fluoride Occurrence in Environment, Regulations, and Remediation Methods for Soil: A Comprehensive Review. *Chemosphere* **2023**, *324*, 138334.
 49. Regenspurg, S.; Virchow, L.; Wilke, F. Origin and Migration of Fluoride in the Area of the Aluto Volcanic Complex (Main Ethiopian Rift). *Appl. Geochem.* **2021**, *146*, 105063.
 50. Li, D.; Gao, X.; Wang, Y. Diverse Mechanisms Drive Fluoride Enrichment in Groundwater in Two Neighboring Sites in Northern China. *Environ. Pollut.* **2018**, *237*, 430–441.
 51. Bellomo, S.; D'Alessandro, W.; Longo, M. Volcanogenic Fluorine in Rainwater Around Active Degassing Volcanoes: Mt. Etna and Stromboli Island, Italy. *Sci. Total Environ.* **2003**, *301*, 175–185.
 52. Rizzu, M.; Tanda, A.; Cappai, C. Impacts of Soil and Water Fluoride Contamination on the Safety and Productivity of Food and Feed Crops: A Systematic Review. *Sci. Total Environ.* **2021**, *787*, 147650.
 53. Fuge, R. Fluorine in the Environment, a Review of Its Sources and Geochemistry. *Appl. Geochem.* **2019**, *100*, 393–406.

54. Vithanage, M.; Bhattacharya, P. Fluoride in the Environment: Sources, Distribution and Defluoridation. *Environ. Chem. Lett.* **2015**, *13*, 131–147.
55. O'Hara, P.J.; Cordes, D.O. Superphosphate Poisoning of Sheep: A Study of Natural Outbreaks. *N. Z. Vet. J.* **1982**, *30*, 153–155.
56. Li, H.; Ma, X.; Huang, X. Fluoride Contents in Commonly Used Commercial Phosphate Fertilizers and Their Potential Risks in China. *Environ. Monit. Assess.* **2023**, *195*, 1051.
57. Ramteke, L.; Sahayam, A.; Ghosh, A. Study of Fluoride Content in Some Commercial Phosphate Fertilizers. *J. Fluorine Chem.* **2018**, *210*, 149–155.
58. Kundu, C.M.; Mandal, B. Agricultural Activities Influence Nitrate and Fluoride Contamination in Drinking Groundwater of an Intensively Cultivated District in India. *Water Air Soil Pollut.* **2009**, *198*, 243–252.
59. Li, T.; He, J.G.; Zhou, Z. The Effect of Phosphate Fertilizer on Fluoride Accumulation in Tea Leaves Based on Ecological Environment Analysis. *IOP Conf. Ser. Earth Environ. Sci.* **2021**, *696*, 012024.
60. Long, H.; Jiang, Y.; Li, C. Effect of Urea Feeding on Transforming and Migrating Soil Fluorine in a Tea Garden of Hilly Region. *Environ. Geochem. Health* **2021**, *43*, 5171–5182.
61. Jiang, J.L.; Zhong, N. Research Progress on Toxicity of Fluoride in Environment and Feed to Livestock and Poultry. *Feed Ind.* **2005**, 25–32. (In Chinese)
62. Zheng, D.X.; Qi, S.Q. *Mineral Elements in Tea Plant and Tea Orchards of China*, 1st ed.; China Environmental Science Press: Beijing, China, 2012; pp. 211–220. (In Chinese)
63. Yang, J. Pruned Litter Decomposition Primes Fluorine Bioavailability in Soils Planted with Different Tea Varieties. *Sci. Total Environ.* **2023**, *903*, 166250.
64. Gan, C.; Jia, Y.; Yang, J. Remediation of Fluoride Contaminated Soil with Nano-Hydroxyapatite Amendment: Response of Soil Fluoride Bioavailability and Microbial Communities. *J. Hazard. Mater.* **2021**, *416*, 124694.
65. Gao, H.J.; Zhang, Z.Z.; Wan, X.C. Influences of Charcoal and Bamboo Charcoal Amendment on Soil-Fluoride Fractions and Bioaccumulation of Fluoride in Tea Plants. *Environ. Geochem. Health* **2012**, *34*, 551–562.
66. Chen, W. Effect of Nitrogen Fertilizer on Fluorine Species and Soil pH in Fluorine-Contaminate Soil. In Proceedings of the 2010 4th International Conference on Bioinformatics and Biomedical Engineering, Chengdu, China, 18–20 June 2010; pp. 1–4.
67. Xie, Z.M.; Wu, W.H. Migration and Transformation of Fluoride in the Environment and Its Ecological Effects. *Chin. J. Environ. Eng.* **1999**, 40–53. (In Chinese)
68. Jeong, S.; Kim, D.; Kim, Y.T. A Rapid Screening of Fluorine Contents in Soil with a Consideration of Chemical Binding by Wavelength Dispersive X-ray Fluorescence Spectrometry. *Spectrochim. Acta B* **2018**, *149*, 261–266.
69. Oh, S.Y.; Kim, H.; Yoon, H.O. Fluorine Contamination, Mobility, and Risks in Soils at a Phosphate-Gypsum Waste Landfill: A New Analytical Method and Comparison with Previous Methods. *Environ. Geochem. Health* **2024**, *46*, 170.
70. Morita, A.; Horie, H.; Fujii, Y. Chemical Forms of Aluminum in Xylem Sap of Tea Plants (*Camellia sinensis* L.). *Phytochemistry* **2004**, *65*, 2775–2780.
71. Nagata, T.; Hayatsu, M.; Kosuge, N. Identification of Aluminum Forms in Tea Leaves by ²⁷Al NMR. *Phytochemistry* **1992**, *31*, 1215–1218.
72. Nagata, T.; Hayatsu, M.; Kosuge, N. Aluminum Kinetics in the Tea Plant Using ²⁷Al and ¹⁹F NMR. *Phytochemistry* **1993**, *32*, 771–775.
73. Yang, Y.; Liu, Y.; Huang, C.F. Aluminium Alleviates Fluoride Toxicity in Tea (*Camellia sinensis*). *Plant Soil* **2016**, *402*, 179–190.
74. Wepasnick, K.A.; Smith, B.A.; Bitter, J.L. Chemical and Structural Characterization of Carbon Nanotube Surfaces. *Anal. Bioanal. Chem.* **2010**, *396*, 1003–1014.
75. Cai, H.M.; Peng, C.Y.; Chen, J. X-ray Photoelectron Spectroscopy Surface Analysis of Fluoride Stress in Tea (*Camellia sinensis* (L.) O. Kuntze) Leaves. *J. Fluorine Chem.* **2014**, *158*, 11–15.
76. Ruan, J.Y. The Impact of pH and Calcium on the Uptake of Fluoride by Tea Plants (*Camellia sinensis* L.). *Ann. Bot.* **2004**, *93*, 97–105.
77. Lahermo, P.; Backman, B. The Occurrence and Geochemistry of Fluorides with Special Reference to Natural Waters in Finland. *Tutkimusraportti* **2000**, *149*, 1–40.
78. Wehr, J.B.; Dalzell, S.A.; Menzies, N.W. Predicting and Modelling Availability of Fluoride in Soil from Sorption Properties. *Soil Use Manag.* **2022**, *39*, 521–534.
79. Zhang, Y.L.; Liao, W.Y.; Wang, Y.J. Effect of Nitrogen Fertilizer on Combined Forms and Transformation of Fluorine in Tea Garden Soil. *J. Agric. Resour. Environ.* **2015**, *32*, 436–442. (In Chinese)
80. Li, C.L. Effects of Fluoride on Physiology and Biochemistry of Tea Seedlings and Its Mechanism. Ph.D. Thesis, Hua Zhong Agricultural University, Wuhan, China, **2011**. (In Chinese)
81. Lu, L.J.; Zong, L.G.; Luo, M. Fluoride Content in Tea Leaves of Typical Tea Plantations in Jiangsu and Its Influencing Factors. *J. Anhui Agric. Sci.* **2006**, *34*, 2183–2185. (In Chinese)
82. Lili, S.; Mengshi, Z.; Xiaomei, L.; et al. Aluminium Is Essential for Root Growth and Development of Tea Plants (*Camellia sinensis*). *J. Integr. Plant Biol.* **2020**, *62*, 984–997.
83. Doig, L.E.; Liber, K. Influence of Dissolved Organic Matter on Nickel Bioavailability and Toxicity to *Hyalella azteca* in Water-Only Exposures. *Aquat. Toxicol.* **2006**, *76*, 203–216.
84. Chen, H.M. *Behavior of Chemicals in Soil and Environmental Quality*; Science Press: Beijing, China, 2002. (In Chinese)
85. Wang, K.Y.; Yang, L.; Zhao, T.Y. Effects of Organic Materials on Environmental Behavior of Water-Soluble Fluoride in Soils. *Ecol. Environ.* **2007**, *16*, 879–882. (In Chinese)
86. Chen, K.; Ma, X.Z.; Wang, C.X. Organic Manures Reduce the Bioavailability of Fluoride in Soil via Different Mechanisms. *Environ. Pollut.* **2024**, *363*, 125142.

87. Zheng, D.X.; Sha, J.Q. Fluorine in Soils of Fujian Tea-Growing Areas. *Chin. J. Soil Sci.* **1994**, *5*, 230–233. (In Chinese)
88. Feng, B.X.; Men, Q.N.; Gan, L.M.; et al. Determination of Fluorine Speciation in Tea Garden Soils and Main Factors Affecting Fluorine Content in Tea Leaves in Ziyang Area, Shaanxi Province. *Rock Miner. Anal.* **2024**, *43*, 166–176. (In Chinese)
89. Wang, L.; Tang, J.; Xiao, B.; et al. Enhanced Release of Fluoride from Rhizosphere Soil of Tea Plants by Organic Acids and Reduced Secretion of Organic Acids by Fluoride Supply. *Acta Agric. Scand. Sect. B–Soil Plant Sci.* **2013**, *63*, 426–432.
90. Xu, R.; Wang, Y.; Zhao, A.; et al. Effect of Low Molecular Weight Organic Acids on Adsorption and Desorption of Fluoride on Variable Charge Soils. *Environ. Geochem. Health* **2006**, *28*, 141–146.
91. Peng, C.Y.; Chen, J.; Cai, H.M. Study on Absorption Kinetics Characteristics of Fluoride in Tea Plants. *Chin. J. Trop. Crops* **2013**, *34*, 495–500. (In Chinese)
92. Wang, Y.M.; Chai, R.S.; Gao, H.J. Apparent Characteristics of Active Transmembrane Uptake of Fluoride by Tea Plant Roots. *J. Agro-Environ. Sci.* **2016**, *35*, 1473–1479.
93. Xu, J.; Guang, M.; Shi, S.; et al. Physiological and Molecular Mechanisms of Transmembrane Fluoride Absorption by Tea Plant Roots. *J. Tea Sci.* **2019**, *39*, 365–371. (In Chinese)
94. Xing, A.; Wu, Z.; Xu, X.; et al. Research Progress on the Characteristics and Mechanisms of Fluoride Accumulation in Tea Plants. *J. Tea Sci.* **2022**, *42*, 301–315. (In Chinese)
95. Stockbridge, R.B.; Robertson, J.L.; Kolmakova-Partensky, L. A Family of Fluoride-Specific Ion Channels with Dual-Topology Architecture. *eLife* **2013**, *2*, e01084.
96. Guang, M. Molecular Mechanism of ABC Transporter Protein Mediated Transmembrane Absorption and Transport of Fluorine in Tea Plant Roots. Master's Thesis, Anhui Agricultural University, Hefei, China, 2020. (In Chinese)
97. Gadi, B.R.; Kumar, R.; Goswami, B. Recent Developments in Understanding Fluoride Accumulation, Toxicity, and Tolerance Mechanisms in Plants: An Overview. *J. Soil Sci. Plant Nutr.* **2021**, *21*, 209–228.
98. Kumar, K. Effects of Fluoride on Respiration and Photosynthesis in Plants: An Overview. *Ann. Environ. Sci. Toxicol.* **2017**, *2*, 43–47.
99. Niu, H.; Wang, J.; Liao, Z. Root-Specific Expression of CsNPF2.3 Is Involved in Modulating Fluoride Accumulation in Tea Plant (*Camellia sinensis*). *Hortic. Res.* **2025**, *12*, uhae267.
100. Niu, H.L.; Peng, C.Y.; Zhu, X.D. Positron-Emitting Tracer Imaging of Fluoride Transport and Distribution in Tea Plant. *J. Sci. Food Agric.* **2020**, *100*, 3554–3559.
101. Li, L.X.; Du, X.; He, C.L. Absorption and Accumulation Characteristics of Fluorine in Nutrient Liquid Cultured Tea Plant. *J. Sichuan Agric. Univ.* **2008**, *26*, 62–66. (In Chinese)
102. Song, J.; Hou, C.; Guo, J. Two New Members of CsFEXs Export Fluoride Coupled Proton Gradients and Participate in Reducing the Fluoride Accumulation in Low-Fluoride Tea Cultivars. *J. Agric. Food Chem.* **2020**, *68*, 8568–8579.
103. Zhu, J.; Xing, A.; Wu, Z. CsFEX, a Fluoride Export Protein Gene from *Camellia Sinensis*, Alleviates Fluoride Toxicity in Transgenic Escherichia Coli and Arabidopsis Thaliana. *J. Agric. Food Chem.* **2019**, *67*, 5997–6006.
104. Luo, B.; Guang, M.; Yun, W. *Camellia Sinensis* Chloroplast Fluoride Efflux Gene CsABC9 Is Involved in the Fluoride Tolerance Mechanism. *Int. J. Mol. Sci.* **2022**, *23*, 7756.
105. Xing, A.; Ma, Y.; Wu, Z. Genome-Wide Identification and Expression Analysis of the CLC Superfamily Genes in Tea Plants (*Camellia sinensis*). *Funct. Integr. Genom.* **2020**, *20*, 497–508.
106. Huang, X.; Wang, P.; Liu, S. An RNA-Seq Transcriptome Analysis Revealing Novel Insights into Fluorine Absorption and Transportation in the Tea Plant. *Botany* **2020**, *98*, 249–259.
107. Li, Q.; Zhang, R.; Hu, X. Aluminum-Activated Malate Transporter Family Member CsALMT6 Mediates Fluoride Resistance in Tea Plants (*Camellia sinensis*). *Hortic. Res.* **2024**, *12*, uhae080.
108. Tang, Q.; Zhao, X.M.; Du, X. Effects of Fluorine Stress on Growth, Physiological-Biochemical Characteristics and Quality of Tea Leaves. *Plant Nutr. Fertil. Sci.* **2011**, *17*, 186–194. (In Chinese)
109. Sha, J.Q.; Zheng, D.X. Study on Fluoride Content in Fresh Tea Leaves of Fujian Tea Plants. *J. Tea Sci.* **1994**, *14*, 37–42. (In Chinese)
110. Wen, X.; Wang, Y.; Wang, S. Fluorine Accumulation Characteristics of 85 Tea Tree (*Camellia sinensis*) Varieties and Its Potential Risk Assessment. *Ecotoxicol. Environ. Saf.* **2024**, *283*, 116785.
111. Cai, H.; Zhu, X.; Peng, C.; et al. Critical Factors Determining Fluoride Concentration in Tea Leaves Produced from Anhui Province, China. *Ecotoxicol. Environ. Saf.* **2016**, *131*, 14–21.
112. IPCC. *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: Cambridge, UK, 2021.
113. Omer, A.A.A.; Zhang, C.H.; Liu, J.L.; et al. Comprehensive Review of Mapping Climate Change Impacts on Tea Cultivation: Bibliometric and Content Analysis of Trends, Influences, Adaptation Strategies, and Future Directions. *Front. Plant Sci.* **2024**, *15*, 1542793.
114. Huang, F.; Lei, Y.; Duan, J.; et al. Investigation of Heat Stress Responses and Adaptation Mechanisms by Integrative Metabolome and Transcriptome Analysis in Tea Plants (*Camellia sinensis*). *Sci. Rep.* **2024**, *14*, 10023.
115. Wang, Z.; Slot, M.; Wang, C. Decoupling of Stomatal Conductance, Transpiration, and Photosynthesis in Terrestrial Plants under Elevated Temperature: A Meta-Analysis. *Nat. Commun.* **2026**, *17*, 1528.
116. Lu, Y.; Zheng, J.; Hu, H.; et al. Determination of Critical Crop Water Stress Index of Tea under Drought Stress Based on

- the Intercellular CO₂ Concentration. *Agronomy* **2024**, *14*, 2154.
117. Grossiord, C.; Buckley, T.N.; Cernusak, L.A.; et al. Plant Responses to Rising Vapor Pressure Deficit. *New Phytol.* **2020**, *226*, 1550–1566.
 118. Liu, S.Y.; Zhu, X.J.; Fang, F.X. Fluorine Subcellular Distribution and Its Combining Characteristics with Cell Wall in Tea Leaves (*Camellia sinensis*). *J. Tea Sci.* **2018**, *38*, 305–312. (In Chinese)
 119. Luo, J.L. Study on Fluoride Enrichment Mechanisms in Tea Leaf Cell Walls. Ph.D. Thesis, Huazhong Agricultural University, Wuhan, China, 2020. (In Chinese)
 120. Peng, C.Y. Study on Fluoride Enrichment Patterns, Subcellular Distribution, and Morphological Forms on Tea Leaf Surfaces. Master's Thesis, Anhui Agricultural University, Hefei, China, 2013. (In Chinese)
 121. Zhang, L.L.; Peng, L.; Wang, Y. Correlation between Fluoride Ion Enrichment in Fresh Tea Leaves and Growth Period. *Tea Fujian* **2021**, *43*, 17–19. (In Chinese)
 122. Wong, M.H.; Fung, K.F.; Carr, H.P. Aluminium and Fluoride Contents of Tea, with Emphasis on Brick Tea and Their Health Implications. *Toxicol. Lett.* **2003**, *137*, 111–120.
 123. Yang, X.D.; Zong, Q.W.; Wu, Y.J. Analysis of Fluoride Content in Anhui Tea. *Food Sci.* **1995**, 59–61. (In Chinese)
 124. Zheng, W.J.; Wan, X.C.; Bao, G.H. Brick Dark Tea: A Review of the Manufacture, Chemical Constituents, and Bioconversion of the Major Chemical Components During Fermentation. *Phytochem. Rev.* **2015**, *14*, 499–523.
 125. Jakubczyk, K.; Gutowska, I.; Antoniewicz, J. Evaluation of Fluoride and Selected Chemical Parameters in Kombucha Derived from White, Green, Black and Red Tea. *Biol. Trace Elem. Res.* **2021**, *199*, 3547–3552.
 126. Chun, X.Y.; Chen, Y.Q.; Ni, D.J. Effects of Washing on Fluoride Content and Main Quality Components in Brick Tea Rolling Leaves. *Hubei Agric. Sci.* **2011**, *50*, 2453–2455. (In Chinese)
 127. Gao, F.J.; Lu, J.L.; Liang, Y.R. Study on Fluoride Reduction Measures in Tea. *J. Xinyang Agric. Coll.* **2002**, 36–38. (In Chinese)
 128. Karak, T.; Bhagat, R.M. Trace Elements in Tea Leaves, Made Tea and Tea Infusion: A Review. *Food Res. Int.* **2010**, *43*, 2234–2252.
 129. Anjana, B. Unveiling the Presence of Fluoride in Commercial Tea Infusion: Factors Influencing Its Release and Its Adsorptive Elimination by Indigenously Developed Nano-adsorbents. *Sci. Total Environ.* **2024**, *914*, 169810.
 130. Esfehiani, M.; Ghasemzadeh, S.; Mirzadeh, M. Comparison of Fluoride Ion Concentration in Black, Green and White Tea. *Int. J. Ayurvedic Med.* **2018**, *9*, 263–265.
 131. Luo, S.H.; Jia, H.Y.; Tong, X.C. Study on Leaching Patterns of Fluoride in Brick Tea. *J. Tea Sci.* **2002**, *22*, 38–42. (In Chinese)
 132. Jing, T.; Li, J.; He, Y. Role of Calcium Nutrition in Plant Physiology: Advances in Research and Insights into Acidic Soil Conditions—A Comprehensive Review. *Plant Physiol. Biochem.* **2024**, *210*, 108602.
 133. Fung, K.; Wong, M. Application of Different Forms of Calcium to Tea Soil to Prevent Aluminium and Fluorine Accumulation. *J. Sci. Food Agric.* **2004**, *84*, 1469–1477.
 134. Kumar, R.; Sharma, P.; Yang, W. State-of-the-Art of Research Progress on Adsorptive Removal of Fluoride-Contaminated Water Using Biochar-Based Materials: Practical Feasibility Through Reusability and Column Transport Studies. *Environ. Res.* **2022**, *214*, 114043.
 135. Shen, C.W.; Xu, H.Q.; Wang, M.H. A Method for Reducing Fluoride Accumulation in Tea, **2025**.
 136. Yi, C.; Zhou, C.; Mo, Y.; et al. Study on the Mechanism of Modified Biochar in Reducing Fluoride Content in Tea Leaves and Improving Soil Environment. *J. Agric. Food Res.* **2026**, *27*, 102769.
 137. Li, X.; Qi, Y.; Zhang, X. Influence of Modified Biochar on Soil Fluoride and Cadmium Speciation and Their Bioavailability to Tea Seedling (*Camellia sinensis* L.). *Soil Sediment Contam.* **2024**, *33*, 612–633.
 138. Du, S.; Wang, X.; Shao, J.; et al. Releasing Behavior of Chlorine and Fluorine During Agricultural Waste Pyrolysis. *Energy* **2014**, *74*, 295–300.
 139. Li, W.H.; Ma, Z.Y.; Yan, J.H.; et al. Evolution and Distribution Characteristics of Fluorine during the Incineration of Fluorine-Containing Waste in a Hazardous Waste Incinerator. *J. Zhejiang Univ.-Sci. A* **2019**, *20*, 564–576.
 140. Aboulsoud, Y.I. Biosorptive Removal of Fluoride from Wastewater Using Tea Domestic Waste Biochar. *Environ. Dev. Sustain.* **2025**, *27*, 16451–16468.
 141. Zhang, M.; et al. Preparation of Lanthanum-Modified Tea Waste Biochar and Its Adsorption Performance on Fluoride in Water. *Materials* **2024**, *17*, 766.
 142. Zhao, S.; Liu, Y.; Ma, J. Influence of Fertilizers on Fluoride Accumulation in Tea Leaves and Its Remediation Using Polyphenol–Ce Adsorbents. *RSC Adv.* **2015**, *5*, 6085–6091.
 143. Huang, C.; Zhang, H.; Zeng, W. Enhanced Fluoride Adsorption of Aluminum Humate and Its Resistance on Fluoride Accumulation in Tea Leaves. *Environ. Technol.* **2018**, *40*, 3236–3245.
 144. Pramanik, K.; Sen, A.; Dutta, S. Microbial Populations Under Fluoride Stress: A Metagenomic Exploration from Indian Soil. *World J. Microbiol. Biotechnol.* **2025**, *41*, 221.
 145. Pal, K.C.; Mukhopadhyay, P.; Chatterjee, S. A Study on Fluoride Bioremediation via a Novel Bacterium *Bacillus Megaterium* Isolated from Agricultural Soil. *J. Earth Syst. Sci.* **2022**, *131*, 183.
 146. Mohammed, J.N.; Mohammed, A.; Muhammad, I.L. Role of Plant Growth Promoting Rhizobacteria in Remediation of Fluoride Toxicity. In *Fluoride and Fluorocarbon Toxicity: Sources, Issues, and Remediation*; Springer Nature: Singapore, **2024**.
 147. Pan, J.; Xing, A.; Zhu, J. Gene Expression Analysis in Leaf of *Camellia Sinensis* Reveals the Response to Fluoride. *Acta Physiol. Plant.* **2021**, *43*, 111.
 148. Tadeo, K.; Ronald, K.; Vereriano, T. Genetic Diversity and Structure of Ugandan Tea Germplasm and Its Implication in Breeding. *Genet. Resour. Crop Evol.* **2024**, *71*, 481–496.

149. Yang, P.; Liu, Z.; Zhao, Y. Comparative Study of Vegetative and Reproductive Growth of Different Tea Varieties Response to Different Fluoride Concentrations Stress. *Plant Physiol. Biochem.* **2020**, *154*, 419–428.
150. Wu, M. Study on Fluoride Accumulation Characteristics and Fluoride Reduction Measures in Tea. Master's Thesis, Zhejiang University, Hangzhou, China, 2011. (In Chinese)
151. Ma, L.; Zheng, P.; Li, C. Preliminary Study on Processing Suitability of Different Low-Fluoride Varieties of Dark Brick Tea. *Hubei Agric. Sci.* **2012**, *51*, 5739–5741. (In Chinese)
152. Chen, Y.; Ni, D.; Chun, X. Effects of Different Enzyme Deactivation Methods on Fluoride Content in Raw Materials of Dark Brick Tea. *Hubei Agric. Sci.* **2011**, *50*, 1193–1195. (In Chinese)
153. Wang, L. Preliminary Study on DTF Tea Fluoride-Reducing Agent for Tea Fluoride Reduction. *Chin. J. Control Endem. Dis.* **2003**, *18*, 17–19. (In Chinese)
154. Lin, Z.; Shu, A.; Jiang, Y. Preliminary Report on Technology for Reducing Fluoride Content in Brick Tea. *Chin. Tea* **2002**, *24*, 16–17. (In Chinese)
155. Xu, Y.; Zhao, Y.; Liu, S. Research Progress on Reducing Fluoride Content in Dark Tea Using Eurotium Cristatum. *Acta Agric. Jiangxi.* **2011**, *23*, 125–127. (In Chinese)
156. Álvarez-Ayuso, E.; Giménez, A.; Ballesteros, J.C. Fluoride Accumulation by Plants Grown in Acid Soils Amended with Flue Gas Desulphurisation Gypsum. *J. Hazard. Mater.* **2011**, *192*, 1659–1666.
157. Banerjee, A.; Roychoudhury, A. Maghemite Nano-Fertilization Promotes Fluoride Tolerance in Rice by Restoring Grain Yield and Modulating the Ionome and Physiome. *Ecotoxicol. Environ. Saf.* **2021**, *215*, 112055.
158. Sogarwal, A.; Kumari, N.; Sharma, V. Silicon Alleviates Fluoride Induced Oxidative Damage in Wheat Cultivars by Improving Antioxidants Defense System and Reducing Fluoride Uptake. *Silicon* **2023**, *15*, 5121–5132.