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REVIEW ARTICLE

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An overview of fluoride stress: physiological and biochemical responses of plants

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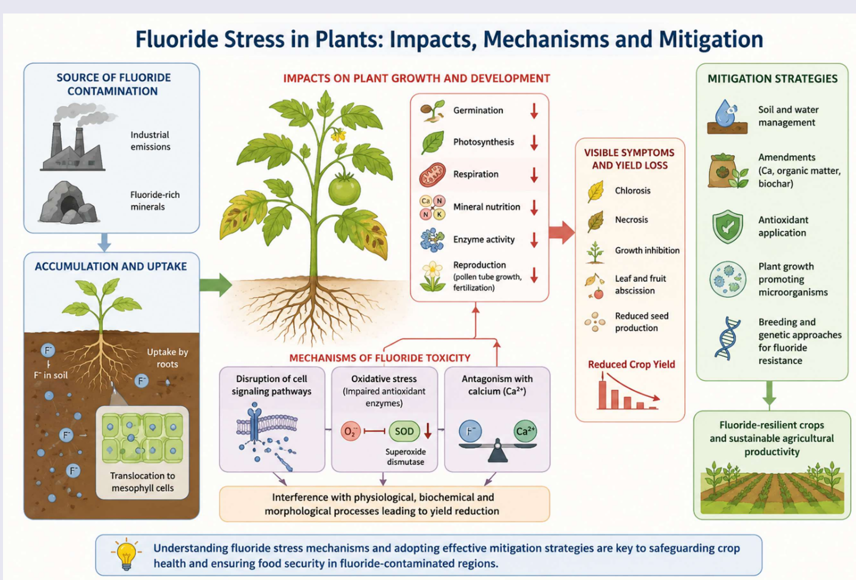
ABSTRACT

Fluoride, a hazardous air and soil contaminant, poses significant risks to agricultural productivity and plant health. Its accumulation in soil and subsequent uptake by plant roots and mesophyll cells interfere with critical morphological, physiological, and biochemical processes essential for growth and development. Fluoride toxicity affects germination, respiration, photosynthesis, mineral nutrition, enzyme activity, and reproduction, ultimately reducing crop yield. It disrupts cell signaling pathways, impairs antioxidant enzyme function (e.g., superoxide dismutase), and interacts antagonistically with calcium, a key element in fertilization and pollen tube growth. The resulting toxicity manifests as chlorosis, necrosis, growth inhibition, leaf and fruit abscission, and reduced seed production. This review provides a comprehensive evaluation of fluoride-induced stress in plants, highlighting recent advances in understanding its mechanisms and potential mitigation strategies. By synthesizing current findings, this study offers insights into developing fluoride-resistant crops and improving management practices to safeguard agricultural productivity in contaminated regions.



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Introduction

Plants face many abiotic stresses such as salinity, alkalinity,[1] fluoride toxicity,[2] micronutrient deficiency,[3] heavy metal stress,[4] drought stress,[5] and extreme temperatures. These environmental factors can significantly impact plant growth, development, and overall productivity.[6] As a result, plants have evolved various adaptive mechanisms to cope with these stressors, including osmotic regulation, ion homeostasis, antioxidant defense systems, and metabolic adjustments.[7] Additionally, advances in biotechnology have led to the development of genetically modified plants with enhanced tolerance to specific abiotic stresses, offering promising solutions for sustainable agriculture in challenging environments.[8,9] Fluoride toxicity in plants manifests as reduced growth and development, chlorosis, necrosis, leaf, flower, and fruit abscission, as well as decreased seed production.[10] While significant research has focused on abiotic stresses such as salinity, drought, and heavy metal toxicity due to their widespread impact on crop productivity, fluoride toxicity remains relatively underexplored. This disparity can be attributed to the localized nature of fluoride contamination, which is primarily associated with industrial emissions, phosphate fertilizers, and groundwater pollution in specific regions. Additionally, the physiological and biochemical effects of fluoride toxicity are often subtle and gradual, making it less immediately apparent compared to more visibly damaging stresses like drought-induced wilting or salt-induced ion toxicity. Furthermore, fluoride does not have an essential physiological role in plants, unlike elements such as sodium or chloride, which complicates its study in plant stress biology.[11] As a result, research on fluoride stress has lagged behind, despite its potential to disrupt key metabolic processes, limit crop yields, and pose food security risks in contaminated areas.[12] Addressing this gap is crucial for developing mitigation strategies and ensuring sustainable agricultural practices in fluoride-affected regions.

This review study carefully assesses the literature regarding the morphological, physiological, and biochemical impacts of fluoride toxicity on crop plants in order to better understand and minimize the detrimental effects of fluoride contamination on agricultural ecosystems.[13]

Even while its concentration is thought to be relatively modest in relation to other elements, it is yet substantial enough to add to the crust's overall makeup. It is predicted that fluoride concentrations in the mantle, which sits beneath the Earth's crust, are 200 times higher than those in the crust.[14,15]

There are several minerals that contain fluoride, but the most prevalent source is fluorite, or calcium fluoride. Cryolite, fluorspar, and apatite are some other minerals that include fluoride.[16] Weathering processes naturally release fluoride into the environment from geological formations rich in fluoride-containing minerals. Fluoride gases, including silicon tetrafluoride (SiF_4) and hydrogen fluoride (HF), are released into the atmosphere during volcanic eruptions. Downwind of volcanic vents (Figure 1), these gases may contribute to the deposition of fluoride in soil and water bodies.[17]

As fluoride-rich minerals in rocks and soil weather, fluoride ions are released into surface and groundwater systems. The rate and amount of fluoride emission are influenced by the solubility of fluoride-containing minerals, which varies with geological circumstances.[18] Surface water bodies, including lakes, rivers, and streams, can have differing fluoride concentrations based on the geology of their catchment areas. Fluoride leaching from nearby rocks and soil, as well as changes in aquifer recharge rates and flow patterns, all have an impact on groundwater fluoride levels[19] (Figure 1).

Fluoride ions are discharged into surface and groundwater systems as a result of weathering fluoride-rich materials found in rocks and soil. The solubility of fluoride-containing minerals, which varies with geological conditions, affects the pace and amount of fluoride emission.[19,20] Based on the geology of their catchment areas, surface water bodies such as lakes, rivers, and streams can have varying quantities of fluoride. Groundwater fluoride levels are affected by aquifer recharge rates and flow patterns, fluoride leaching from surrounding rocks and soil, and other factors.[21]

Fluoride levels in the environment are raised by human activities such as the burning of fossil fuels, the usage of fluoride-containing goods (such as insecticides and fluoridated water), the smelting of aluminum, and the manufacturing of phosphate fertilizer.[16]

Overview of fluoride stress on plants

Elevated fluoride ion levels in the surrounding environment can cause fluoride stress in plants, which can result in a variety of physiological, biochemical, and morphological alterations that might hinder plant

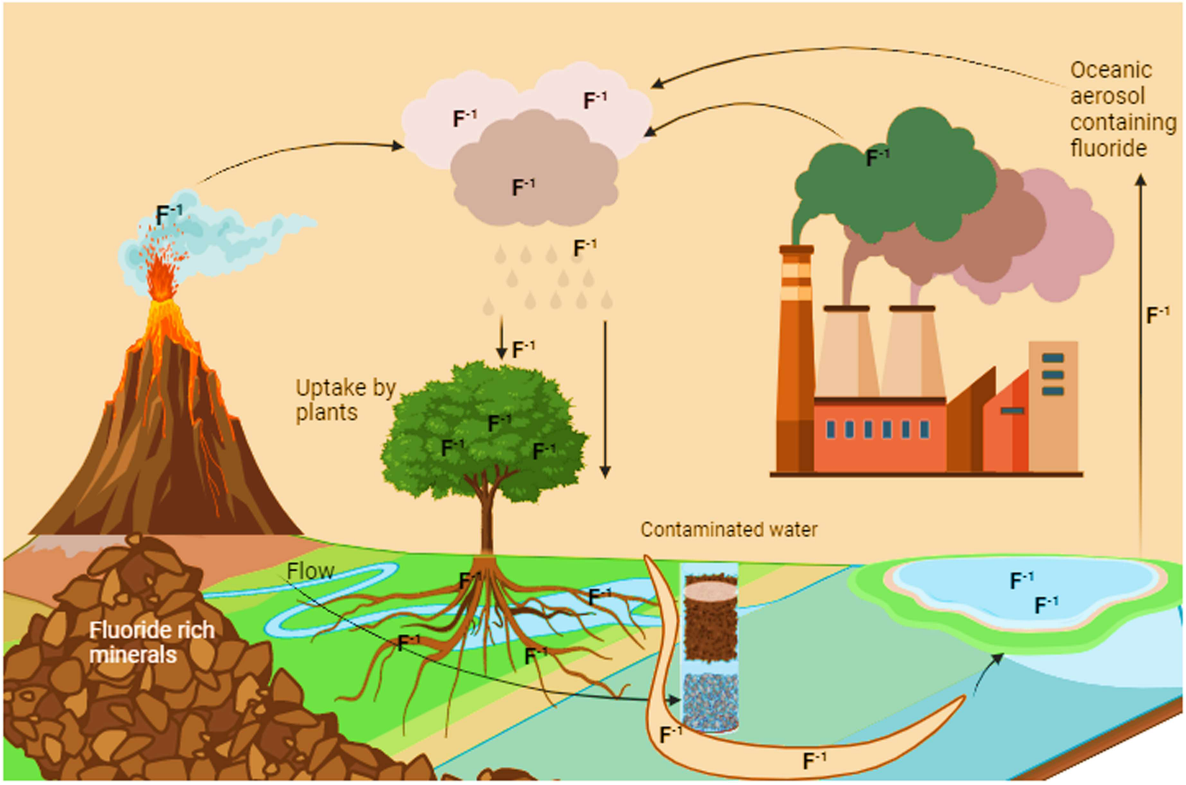

Figure 1. The dispersion and presence of fluoride in water sources, soil, and plant life.

growth and development.[2] In order to mitigate the adverse consequences of fluoride stress on agricultural output and ecosystem health, it is imperative to comprehend the impacts of this stress on plants.

Fluoride (F) concentrations that are too high in soil or solution culture can negatively impact a number of plant growth and development processes, such as germination, root and shoot growth, chlorophyll degradation, and grain yield loss.[22,23] Symptoms like chlorosis, leaf tip burn, and necrosis are how these impacts show up. Elevated levels of fluoride within plant cells cause disturbances to physiological cycles, impede the movement of nutrients, and reduce water consumption, which in turn affects the establishment, growth rate, and photosynthetic activities of seedlings.[24] Additionally, higher F levels lead to more reactive oxygen species (ROS) being produced, which damages membranes. Although a great deal of study has been done on how salinity (NaCl) affects plant germination and emergence, nothing is known about how F-contaminated seeds affect plant development at this point.

A small number of plant species, to varying degrees, have been the subject of studies examining the effects of F on germination, including rice, gram seed, tomato, wheat, maize, soybeans, sorghum, and beans. The entire range of fluoride's (F) impact on different elements of plant physiology and metabolism has not been fully explored, but it is absorbed by plant roots and transported inside the plant. Although it is well known that F contamination greatly reduces plant production, its effects on the morphological traits, mineral content, and metabolic functions of plants have not been thoroughly studied. It has long been known that fluoride (F) is a metabolic inhibitor, interfering with a number of metabolic processes essential to the growth and development of plants.[25] In conclusion, although it is widely known that F pollution has a negative impact on plant growth and yield, there is still much to learn and understand about the specific interactions and processes that occur at the morphological, mineral, and metabolic levels of plants. Fluoride (F) has long been recognized to be a metabolic inhibitor, interfering with several metabolic pathways necessary for plant growth and development.

Fluoride uptake and storage in plants

Plants absorb and accumulate fluoride (F) through a slow process that ultimately results in harmful reactions in the plants (Table 1). Plants are primarily exposed to F through two primary pathways: first, F

Table 1. Characteristics of plants and their tendency to accumulate fluoride ions (F^-).

S. No.	Characteristic	Plant species	F− accumulation patterns	References
1	Stage of growth	*Camellia sinensis* L. (tea plant)	Higher accumulation in old mature leaves compared to young leaves, roots, and stems	[27]
2	Developmental stage	*Brassica juncea* (Chinese mustard)	Post-flowering stage shows greater accumulation than the flowering and pre-flowering stages	[11]
3	Seasonal variation	*Camellia sinensis* L. (tea plant)	Accumulation is highest in summer followed by autumn and spring	[28,29]
4	Organ-level accumulation	*Oryza sativa* L. *Solanum tuberosum*	Varies among species, with roots showing higher accumulation compared to leaves in some cases, while in others, leaves exhibit higher accumulation than roots	[28]
5	Subcellular localization	*Camellia sinensis* L. (tea plant)	Predominantly stored in the cell wall and cell protoplast, with vacuoles containing 98.0% of the protoplast's fluoride (negligible free F^-)	[27]
6	Plant genotype influence	*Salix viminalis* L.	Variations observed in the accumulation between roots and leaves, depending on the genotype	[29]

deposited on leaves enters through stomata, and second, F diffuses passively into the roots through the soil and water.[26]

Previous research has shown that soil-derived F uptake is not as substantial as that from atmospheric air. After absorption, F enters the shoots through apoplastic and symplastic routes via xylem tissues. Furthermore, some of F is also transferred across biological membranes by hydrogen fluoride (HF), a tiny, neutral molecule that diffuses across cell membranes about seven times more quickly than fluoride ions (F). But our understanding of the exact mechanisms underlying F uptake into plant cells is still lacking.[30]

Depending on how much F moves from the soil to the roots and subsequently into the shoots, different plant sections accumulate varied amounts of this element. F accumulation is often highest in the roots and lowest in the leaves, seeds, and shoots. The distribution of F within the plant is reflected in this differential accumulation pattern, which also implies that different plant tissues are susceptible to F toxicity to differing degrees.[31]

Objectives of the review article

The review article's goals regarding fluoride toxicity in plants include a thorough analysis of all the different facets associated with fluoride pollution and effects on plant health. First and foremost, the review seeks to offer a comprehensive grasp of the sources of fluoride pollution in the environment, with an emphasis on the effects on plant. It then aims to explore the morphological, physiological, and biochemical responses of plants to fluoride stress in order to clarify the fundamental processes of fluoride toxicity. In addition, the review intends to appraise the significance of fluoride stress on agricultural output as well as the effects it has on numerous stages of plant growth and development, from germination to reproductive stages. It also seeks to investigate how environmental stressors like salinity and heavy metal pollution interact with fluoride stress and affect plant physiology and ecosystem dynamics as a whole.

Effect of fluoride stress on growth parameters

Plants and their numerous sections are affected by high internal fluoride (F) concentrations in almost all physiological and metabolic processes. In particular, plants are greatly influenced by high F levels during crucial growth stages like seed germination and early seedling growth.[22] Plants that are exposed to high levels of F have shortened root-shoot length, decreased vigor, and hindered seed germination responses. Additionally, unbalanced nutrient intake brought on by F toxicity may result in fewer seeds being produced.[32] Furthermore, excessive F concentrations inhibit biomass accumulation, which is essential for the healthful development of plants. Essentially, the disturbance of these growth characteristics indicates the severe adverse impacts of F toxicity on critical developmental processes, which in turn jeopardize the general growth and yield of plants.[33]

Fluoride stress reduces water intake and prevents the embryo's cell division and expansion, which both have an impact on plant germination. As a result, the metabolic activity required for germination decreases. When plants are treated with fluoride, similar results have been shown in radish, wheat, mung beans, and Bengal gram.[34] By suppressing the activity of the phytase enzyme, fluoride can also prevent the dephosphorylation of phytin molecules, which is necessary for germination. Furthermore, deficits in essential nutrients caused by fluoride can further hinder plants' ability to respond to development. Fluoride also reduces the production of DNA, RNA, and proteins, which stops cell division and elongation and eventually stunts growth. Because of their enormous surface area and stomata, leaves and green stems are more vulnerable to fluoride deposition, which exacerbates the effects of fluoride stress on plant growth.[35]

Effect of fluoride stress on photosynthesis

Fluoride (F) adversely affects photosynthesis by disrupting multiple structural and biochemical components of the photosynthetic apparatus (Table 2). Chloroplasts serve as the primary sites of fluoride accumulation, making them particularly susceptible to fluoride-induced damage.[24] Fluoride exposure reduces the concentrations of essential photosynthetic pigments, including chlorophyll *a*, chlorophyll *b*, carotenoids, and anthocyanins, thereby limiting light-harvesting efficiency and overall photosynthetic performance.[2] Additionally, fluoride decreases the availability of Fe^{2+}, an essential cofactor for chlorophyll biosynthesis, while enhancing chlorophyll degradation through increased chlorophyllase activity, ultimately accelerating pigment loss.[28] Beyond pigment degradation, fluoride interferes with the photochemical phase of photosynthesis by inhibiting the Hill reaction and reducing electron transport, particularly at photosystem II (PSII). Replacement of Cl^{-} ions by fluoride within the oxygen-evolving complex impairs water photolysis, leading to reduced electron flow and enhanced generation of reactive oxygen species (ROS). These alterations are accompanied by chloroplast disorganization, granal distortion, reduced stomatal conductance, and restricted CO_2 assimilation, collectively diminishing photosynthetic efficiency.[36] Furthermore, fluoride suppresses the activity of key carbon assimilation enzymes, including sucrose synthase and ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO), thereby limiting carbon fixation and carbohydrate production.[37]

Although the inhibitory effects of fluoride on photosynthesis have been consistently documented, the severity of damage varies considerably among plant species and depends on fluoride concentration, exposure duration, and nutrient status. Such variability suggests that differences in antioxidant capacity, chloroplast stability, and nutrient homeostasis may contribute to species-specific fluoride tolerance.

Table 2. Effects of fluoride stress on 20 different plants and the observed toxicity effects.

Plant species	Fluoride stress concentration	Toxicity effects	References
Rice (*Oryza sativa*)	10–30 mg/L	Reduced root length, chlorosis, and reduced biomass	[38]
Wheat (*Triticum aestivum*)	150–350 ppm	Leaf necrosis, stunted growth, reduced chlorophyll content	[2,13,14]
Maize (*Zea mays*)	100, 200 ppm	Root tip browning, reduced photosynthesis, and leaf curling	[39]
Barley (*Hordeum vulgare*)	0.025% in nutrient solution	Decreased germination, growth inhibition, and oxidative stress	[40]
Soybean (*Glycine max*)	375 mg/kg	Chlorosis, decreased nitrogen fixation, and membrane damage	[41]
Tomato (*Solanum lycopersicum*)	50 ppm	Fruit yield reduction, leaf necrosis, oxidative stress	[32]
Spinach (*Spinacia oleracea*)	5–10 mg/L	Chlorophyll degradation, reduced leaf area, necrosis	[42]
Pea (*Pisum sativum*)	25–200 ppm	Inhibited seedling growth, chlorosis, oxidative damage	[43]
Mustard (*Brassica juncea*)	5–10 mg/L	Leaf yellowing, reduced biomass, and altered enzymatic activities	[42]
Radish (*Raphanus sativus*)	280 mg/kg	Root deformation, reduced germination, oxidative stress	[44]
Cucumber (*Cucumis sativus*)	1–20 mM	Leaf curling, reduced fruit size, necrosis	[45]
Cauliflower/cabbage	20 mg/L	Chlorosis, stunted growth, decreased yield	[46]
Moong (*Vigna radiata* L.)	2.5–25 mM	High ROS, chlorophyll loss	[47]
Guar (*Cyamopsis tetragonoloba* L. Taub)	10–60 mM	Upregulation and changes in gene expression pattern	[47]
Sugarcane (*Saccharum officinarum*)	100–500 ppm	Reduced sugar content, leaf necrosis, and root growth inhibition	[48]
Lettuce (*Lactuca sativa*)	10–30 mg/L	Chlorosis, reduced leaf area, necrosis	[49]
Bean (*Phaseolus vulgaris*)	200 mg/kg	Reduced nodulation, leaf necrosis, oxidative stress	[22]
Sunflower (*Helianthus annuus*)	0.2–5 mM	Reduced seed germination, chlorosis, and decreased photosynthesis	[50]
Chickpea (*Cicer arietinum*)	2.5–10 mg/L	Reduced germination, leaf necrosis, and altered metabolic activities	[51]
Sorghum vulgare	0–8 ppm	Reduced germination and growth of aerial parts	[52]

However, the molecular mechanisms governing these adaptive responses remain insufficiently understood and warrant further investigation. Representative studies describing the photosynthetic responses of different plant species to fluoride stress are summarized in Table 2.

Effect of fluoride toxicity on respiration rate

Cellular respiration is a fundamental metabolic process that provides ATP required for plant growth, nutrient uptake, maintenance, and adaptation to environmental stresses. Fluoride toxicity disrupts respiratory metabolism by altering the activity of key enzymes involved in energy production, thereby reducing metabolic efficiency and impairing normal physiological functions. However, the extent of respiratory inhibition varies considerably depending on plant species, tissue type, developmental stage, duration of exposure, and the amount of fluoride accumulated within plant tissues.[53] One of the primary effects of fluoride is the inhibition of several respiratory enzymes, including ascorbate oxidase, polyphenol oxidase, succinate dehydrogenase, malate dehydrogenase, and peroxidase, resulting in reduced respiratory activity and ATP production.[11] Because glycolytic enzymes differ in their sensitivity to fluoride, plants may exhibit shifts in carbon metabolism, with increased reliance on the pentose phosphate pathway (PPP) during prolonged fluoride exposure.[54]

Evidence also suggests that fluoride-induced metabolic adjustments activate alternative respiratory pathways associated with oxidative stress tolerance. Increased activities of glucose-6-phosphate dehydrogenase, cytochrome oxidase, catalase, and peroxidase have been reported in fluoride-stressed tissues, indicating that enhanced PPP activity may help generate reducing equivalents (NADPH) required for antioxidant defense and cellular repair.[26] These metabolic responses suggest that plants attempt to compensate for impaired respiration by reallocating carbon flux toward protective pathways.

Although respiratory inhibition is a common consequence of fluoride toxicity, the underlying regulatory mechanisms remain poorly understood. Future studies integrating physiological, biochemical, and molecular approaches are required to clarify how fluoride reprograms respiratory metabolism and contributes to stress adaptation in different plant species.

Fluoride stress on ATPase enzymes

ATPases are membrane-associated enzymes that play indispensable roles in cellular energy metabolism by maintaining ion gradients, membrane potential, intracellular pH, and ATP homeostasis. Consequently, impairment of ATPase activity under fluoride stress has profound implications for plant growth, nutrient transport, and stress adaptation. Fluoride has been shown to inhibit ATP synthase and plasma membrane H^+-ATPases, thereby disrupting ATP generation and reducing the energy available for active transport and other ATP-dependent physiological processes.[55] Furthermore, fluoride-induced damage to plasma and tonoplast membranes compromises membrane integrity, exacerbating ion imbalance and reducing transport efficiency.

Experimental evidence indicates that fluoride suppresses plasma membrane ATPase activity in species such as *Beta vulgaris*, suggesting that ATPases are important cellular targets of fluoride toxicity. The inhibitory effect appears to be influenced by Mg^{2+} availability because fluoride readily forms Mg–F complexes that interact with ATPase catalytic sites, thereby restricting ATP hydrolysis and enzyme activity. This interaction highlights the close relationship between fluoride toxicity, magnesium homeostasis, and membrane-associated energy metabolism.[56] Similar reductions in plasma membrane ATPase activity have also been reported following prolonged fluoride exposure, supporting the hypothesis that membrane ATPases are highly susceptible to fluoride-induced oxidative and structural damage.[57,58]

Although and metabolic dysfunction, the precise molecular mechanisms regulating ATPase sensitivity under fluoride stress remain largely unresolved. Current evidence suggests that ATPase inhibition is not solely a consequence of direct fluoride binding but may also result from oxidative membrane damage, altered ion homeostasis, and disruption of cellular signaling networks.[59,60] Future studies integrating structural biology, membrane physiology, and molecular genetics are therefore needed to clarify the regulation of ATPases under fluoride stress and to identify potential targets for improving fluoride tolerance in crop plants. Recent reviews likewise emphasize that molecular mechanisms governing fluoride uptake, transport, and cellular responses in plants remain insufficiently understood, underscoring the need for further mechanistic investigations.

Role of reactive oxygen species (ROS) in fluoride stress

Reactive oxygen species (ROS) play a central role in fluoride-induced phytotoxicity by acting as both signaling molecules and mediators of oxidative damage. Under normal physiological conditions, ROS are continuously generated at low levels in chloroplasts, mitochondria, and peroxisomes during aerobic metabolism and are efficiently scavenged by enzymatic and non-enzymatic antioxidant systems.[11] Fluoride-induced inhibition of photosynthetic carbon fixation reduces the availability of oxidized $NADP^+$, promoting electron leakage from photosystem I to molecular oxygen through the Mehler reaction and generating superoxide radicals ($O_2{\bullet}^-$). In addition, peroxisomes contribute substantially to ROS production through xanthine oxidase-mediated oxidation of xanthine and hypoxanthine, as well as membrane-associated electron transport chains.[35,61] The overproduction of ROS subsequently triggers lipid peroxidation, protein oxidation, nucleic acid damage, membrane destabilization, and enzyme inactivation, ultimately impairing cellular metabolism and plant growth. Although ROS accumulation is generally regarded as a hallmark of fluoride toxicity, emerging evidence suggests that ROS also function as important signaling molecules regulating stress perception, antioxidant defense, and metabolic adaptation. The balance between ROS production and scavenging therefore determines whether ROS act as beneficial signaling intermediates or become cytotoxic.[62] The major ROS generated under fluoride stress, their cellular sources, biological effects, and corresponding antioxidant defense mechanisms are summarized in Table 3.

Impact of fluoride toxicity on the anti-oxidative enzyme system

The excessive accumulation of reactive oxygen species (ROS) under fluoride stress activates a complex antioxidant defense system that protects plant cells against oxidative damage (Figure 2). Because the mechanisms of ROS generation have already been discussed (Section 2.6), this section focuses on the antioxidant responses that maintain cellular redox homeostasis under fluoride exposure. The effectiveness of this defense system largely determines the degree of fluoride tolerance exhibited by different plant species. Among the enzymatic antioxidants, superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), ascorbate peroxidase (APX), and glutathione reductase (GR) constitute the primary detoxification machinery against fluoride-induced oxidative stress.[66,67] SOD catalyzes the conversion of superoxide radicals ($O_2{\bullet}^-$) into hydrogen peroxide (H_2O_2), which is subsequently detoxified by CAT and APX to prevent excessive H_2O_2 accumulation.[68,69] Meanwhile, POX contributes to H_2O_2 scavenging while participating in lignification and cell wall strengthening, whereas GR maintains intracellular glutathione in its reduced form, thereby sustaining the ascorbate–glutathione cycle and overall cellular redox balance.[70,71] The activities of antioxidant enzymes under fluoride stress, however, are highly species-dependent and are influenced by fluoride concentration, exposure duration, tissue type, and nutrient availability.[72] Moderate fluoride exposure frequently induces antioxidant enzymes as an adaptive response, whereas prolonged or

Table 3. Major reactive oxygen species generated under fluoride stress, their cellular sources, biological effects, and plant defense responses.

Reactive oxygen species	Major site of generation	Primary cause under fluoride stress	Cellular damage	Plant defense response	References
Superoxide anion ($O_2{\bullet}^-$)	Chloroplasts (PSI), mitochondria	Electron leakage through the Mehler reaction	Protein oxidation, membrane damage	Converted to H_2O_2 by SOD	[63]
Hydrogen peroxide (H_2O_2)	Chloroplasts, peroxisomes, mitochondria	Dismutation of $O_2{\bullet}^-$ and oxidase reactions	Oxidative stress, lipid peroxidation	Detoxified by CAT and APX	[64]
Hydroxyl radical (•OH)	Cytoplasm and organelles	Fenton reaction in the presence of transition metals	Severe DNA, protein, and lipid damage	No enzymatic detoxification; prevented by antioxidant systems	[64]
Singlet oxygen ($^1O_2$)	Chloroplast thylakoid membranes	Overexcitation of PSII under fluoride stress	Chlorophyll degradation and membrane injury	Carotenoids and tocopherols quench $^1O_2$	[65]

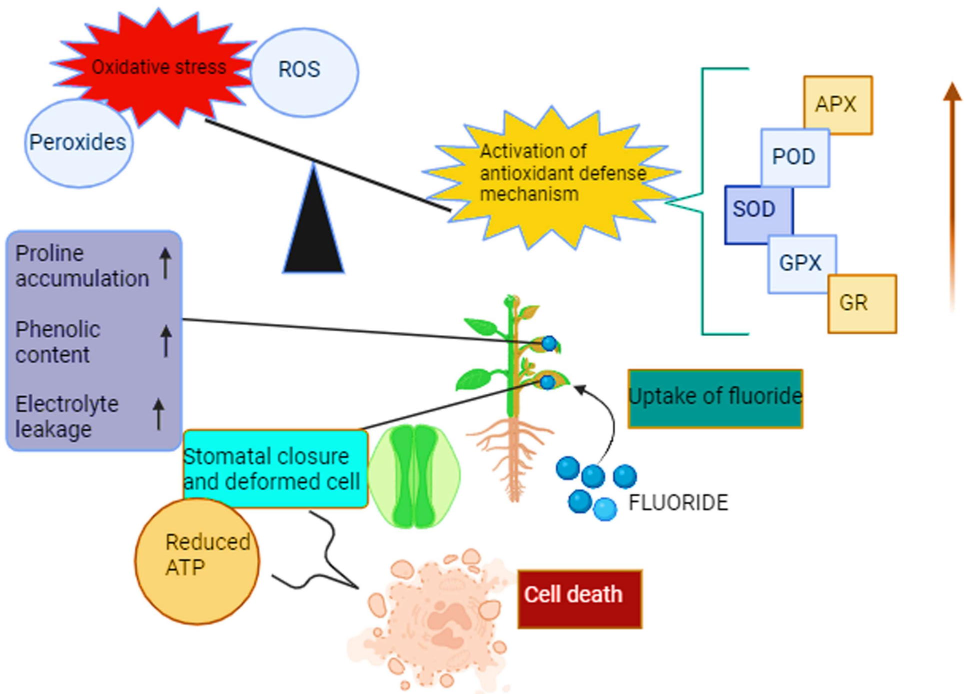

Figure 2. Fluoride's adverse effects on plants: toxicity and ramifications.

excessive fluoride accumulation may overwhelm the antioxidant system, resulting in enzyme inhibition and enhanced oxidative damage.[73] These contrasting responses indicate that antioxidant activation represents a dynamic defense mechanism rather than a universal indicator of fluoride tolerance.[73] Although numerous studies have reported alterations in antioxidant enzyme activities under fluoride stress, relatively little is known about the molecular regulation of these enzymes or their interaction with signaling pathways governing stress adaptation. Future investigations integrating transcriptomics, proteomics, metabolomics, and functional genomics are therefore needed to clarify the regulatory networks controlling antioxidant responses and to identify biomarkers associated with fluoride tolerance.

Impact of fluoride toxicity on anabolic processes

Anabolic metabolism encompasses the biosynthesis of carbohydrates, proteins, nucleic acids, lipids, and other cellular constituents that are essential for plant growth and development. Fluoride toxicity disrupts these biosynthetic pathways primarily by reducing ATP production, impairing carbon assimilation, disturbing nutrient homeostasis, and inducing oxidative stress, thereby limiting the availability of energy and metabolic precursors required for cellular biosynthesis.[74] The suppression of anabolic metabolism under fluoride stress extends beyond photosynthesis. Reduced carbohydrate production limits substrate availability for the synthesis of structural polysaccharides, while inhibition of protein synthesis restricts the formation of metabolic enzymes and structural proteins required for growth. Fluoride-induced deficiencies of essential nutrients such as Fe, Mg, Ca, and *P* further impair chlorophyll biosynthesis, amino acid metabolism, nucleic acid synthesis, and membrane formation, thereby reducing overall metabolic activity.[75] In addition, oxidative damage to cellular macromolecules diverts metabolic resources from biosynthetic processes toward cellular repair and antioxidant defense, further suppressing plant growth and biomass accumulation.

Although photosynthesis provides the primary carbon source for anabolic metabolism, increasing evidence suggests that fluoride-induced inhibition of biosynthetic pathways cannot be explained solely by reduced photosynthetic efficiency. Instead, fluoride exerts coordinated effects on cellular energy metabolism, nutrient utilization, enzyme activities, and redox homeostasis, collectively restricting plant anabolic capacity. Nevertheless, the molecular regulation of anabolic pathways under fluoride stress remains poorly understood, and future studies employing transcriptomic, proteomic, and metabolomic approaches are needed to identify the key regulatory networks involved in metabolic adaptation and fluoride tolerance.[76] Although fluoride-induced suppression of anabolic metabolism has been consistently reported, the relative contribution of impaired energy metabolism, nutrient imbalance, and oxidative stress to the inhibition of individual biosynthetic pathways remains unclear. Future studies integrating physiological, transcriptomic, proteomic, and metabolomic approaches are therefore required to elucidate the regulatory mechanisms underlying fluoride tolerance.

Impact of fluoride toxicity on the catabolic processes

Fluoride toxicity disrupts catabolic metabolism by altering energy-generating pathways that are essential for maintaining plant growth, nutrient acquisition, and cellular homeostasis. Cellular respiration, a central catabolic process responsible for ATP production, is particularly sensitive to fluoride stress, although its response depends on fluoride concentration, duration of exposure, plant species, and developmental stage. Mild fluoride exposure may transiently stimulate oxygen consumption, whereas prolonged or excessive exposure generally suppresses respiratory activity and reduces metabolic efficiency.[53] Fluoride-induced alterations in respiration are associated with changes in the activity of several key metabolic enzymes. Inhibition of enzymes involved in glycolysis and the tricarboxylic acid (TCA) cycle restricts ATP generation, leading to impaired energy availability for biosynthetic and transport processes. Furthermore, respiratory responses vary among tissues due to differences in fluoride accumulation and metabolic activity, explaining the inconsistent findings reported across plant species.[77] Under fluoride stress, plants may partially compensate for reduced respiratory efficiency by redirecting carbon metabolism toward the pentose phosphate pathway (PPP). Increased activities of enzymes such as glucose-6-phosphate dehydrogenase, cytochrome oxidase, catalase, and peroxidase have been reported in fluoride-exposed tissues, indicating activation of alternative metabolic pathways that generate reducing power (NADPH) required for antioxidant defense and cellular repair. However, the molecular mechanisms regulating this metabolic reprogramming remain poorly understood and require further investigation.[78]

Interactions between fluoride toxicity and mineral nutrition

The interaction between fluoride toxicity and mineral nutrition is complex and bidirectional, as fluoride not only disrupts the uptake and utilization of essential mineral nutrients but is itself influenced by nutrient availability. Among the essential elements, calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn), manganese (Mn), phosphorus (*P*), and nitrogen (*N*) play important roles in determining the severity of fluoride toxicity through their involvement in ion transport, enzyme activation, and metabolic regulation.[79] The interaction between fluoride toxicity and mineral nutrition is complex and bidirectional, as fluoride not only disrupts the uptake and utilization of essential mineral nutrients but is itself influenced by nutrient availability. Among the essential elements, calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn), manganese (Mn), phosphorus (P), and nitrogen (*N*) play important roles in determining the severity of fluoride toxicity through their involvement in ion transport, enzyme activation, and metabolic regulation.[11] Adequate calcium nutrition stabilizes plasma membranes, preserves membrane permeability, and reduces fluoride-induced cellular damage, whereas calcium-deficient plants exhibit greater susceptibility to fluoride toxicity due to enhanced fluoride uptake and impaired membrane integrity.[80–82] Furthermore, calcium deficiency may disrupt pollen germination, pollen tube elongation, and reproductive development, thereby exacerbating fluoride-induced yield losses.

Magnesium also plays an important role because it serves as a cofactor for numerous enzymes involved in photosynthesis and energy metabolism. Fluoride can interfere with magnesium-dependent enzymatic reactions through the formation of Mg–F complexes, thereby inhibiting ATP-dependent metabolic processes and reducing enzyme activity.[53] Although several studies have suggested that fluoride primarily affects the physiological activity of magnesium rather than its tissue concentration, disruption of magnesium function may contribute to impaired photosynthesis, respiration, and overall metabolic performance.[83] Fluoride toxicity also alters the uptake and distribution of micronutrients such as iron (Fe), manganese (Mn), and zinc (Zn). Deficiencies of these nutrients frequently accompany fluoride exposure, resulting in chlorosis, reduced chlorophyll synthesis, impaired enzyme activity, and diminished photosynthetic efficiency.[84] In addition, interactions with macronutrients, including nitrogen (*N*), phosphorus (*P*), and potassium (K), indirectly influence fluoride absorption and translocation within plants. Moderate supplies of nitrogen, phosphorus, and calcium may enhance fluoride uptake because of increased root activity, whereas nutrient deficiencies or excessive calcium can reduce fluoride accumulation by restricting its mobility or promoting precipitation within the rhizosphere.[85] Collectively, these findings demonstrate that fluoride toxicity cannot be considered independently of plant mineral nutrition. Rather than acting through a single mechanism, fluoride disrupts nutrient homeostasis by modifying ion transport, membrane function, enzyme activities, and metabolic processes, ultimately reducing plant growth and productivity.[86] However, the interactions between fluoride and mineral nutrients remain highly species-specific and are influenced by soil properties, nutrient availability, and environmental conditions. Future studies integrating ionomics, molecular transport biology, and nutrient signaling are therefore required to elucidate the regulatory mechanisms governing fluoride–mineral interactions and to develop nutrient-based strategies for improving fluoride tolerance in crop plants. Figure 3 summarizes the interactions between fluoride toxicity and essential mineral nutrients, highlighting their collective effects on nutrient homeostasis, enzyme activity, photosynthesis, and plant growth.

Impact of fluoride toxicity on fruit yield

Fluoride's interference with calcium, a crucial element for fertilization, can result in various harmful effects on fruit yield and quality. Plants deficient in calcium are especially vulnerable to fluoride damage, which often manifests as leaf injury.[87] This interference can also disrupt pollen germination and growth, ultimately impacting the fertilization process. Certain fruits, such as peaches, exhibit high sensitivity to fluoride exposure. Fluoride-induced conditions like “black tip” or “suture red spot” can develop in affected fruits, characterized by premature ripening, reddening of the suture area externally and internally, and splitting of the flesh along the suture line.[88]

Prolonged exposure to heightened levels of fluoride can lead to a significant increase in the occurrence of abnormal fruit in peaches and deformation in strawberries. Moreover, fluoride has been observed to disrupt fruiting in tomatoes and beans by interfering with fertilization and seed development processes. The stage of flowering is notably sensitive to fluoride toxicity, with the carpels, responsible for seed

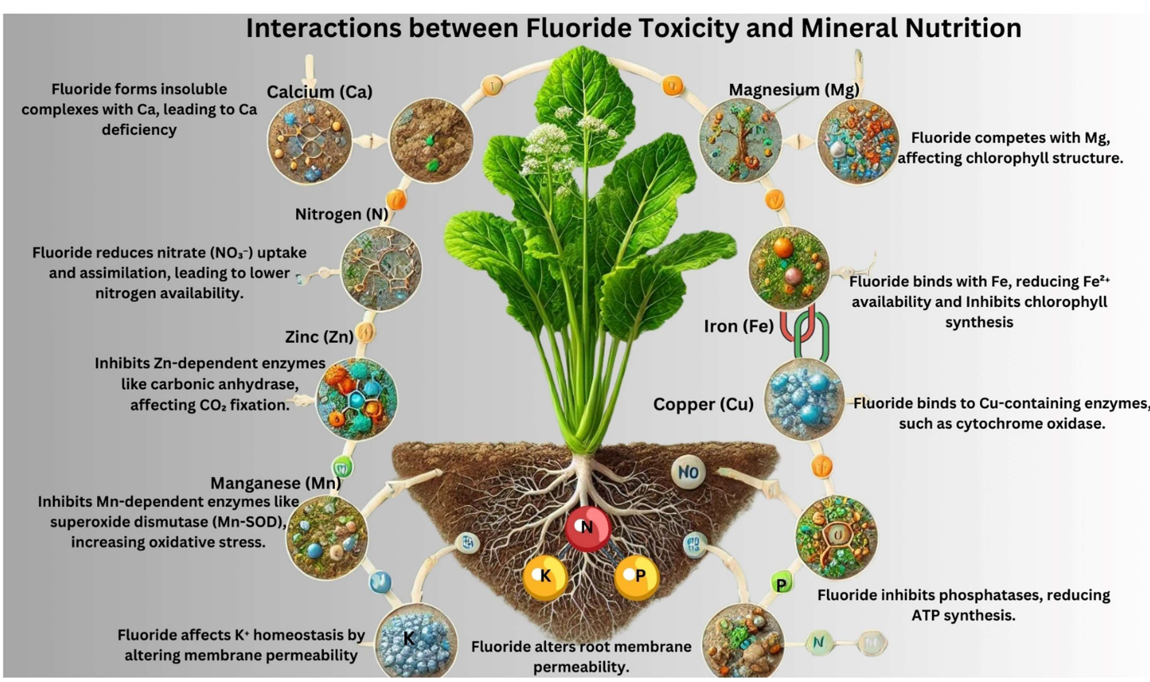

Figure 3. Highlighting the interaction of essential minerals and fluoride.

production, being more vulnerable compared to the pollen-producing anthers.[89] Exposure to fluoride during flowering alters the surface of the stigma, crucial for pollen reception, thereby affecting the growth of pollen tubes and subsequent fertilization events. The accumulation of fluoride on both the surface and within the stigma and style disrupts the normal calcium gradient, essential for guiding pollen tube growth and facilitating fertilization. This interference ultimately hampers the successful development of seeds and subsequent fruit formation.[90] The detrimental effects of fluoride on fertilization, seed formation, and fruit yield underscore the intricate interplay between fluoride exposure and vital reproductive processes in plants. These findings highlight the importance of understanding and mitigating fluoride-induced disruptions to ensure optimal plant reproductive health and yield.[90]

Potential mitigation strategies and research gaps

Addressing fluoride toxicity in crops requires a multifaceted approach, integrating soil amendments, breeding for tolerance, and biotechnological interventions.[91] Liming and phosphate fertilizers can reduce fluoride bioavailability by forming stable complexes, while organic amendments like biochar enhance soil buffering capacity.[92] Additionally, silicon and calcium supplementation have shown promise in mitigating fluoride uptake by competing with fluoride ions at absorption sites.[93] From a genetic perspective, identifying and engineering fluoride-tolerant crop varieties through molecular breeding or gene-editing technologies could offer long-term solutions.[94] However, discrepancies in fluoride toxicity thresholds across species, variations in soil interactions, and the limited understanding of plant fluoride detoxification pathways highlight significant research gaps. Future studies should focus on elucidating the molecular mechanisms of fluoride tolerance and developing sustainable management strategies for affected agricultural regions.

Conclusion

Fluoride toxicity poses a significant global challenge, impacting both plant and animal health. While extensive research has focused on its effects on animals and human health, the implications for crop plants require greater attention. Understanding the physiological, biochemical, and molecular mechanisms underlying fluoride tolerance is crucial for developing effective mitigation strategies. The adverse effects of fluoride contamination in air and soil on crop growth and yield have serious implications for global agriculture.

To address this challenge, future research should focus on identifying key molecular pathways involved in fluoride detoxification and tolerance, leveraging biotechnological advancements such as CRISPR-based gene editing and transgenic approaches to develop fluoride-resistant crop varieties. Additionally, the application of beneficial microbes, biochar, and soil amendments like calcium and silicon could offer practical strategies for minimizing fluoride uptake in plants. Integrating these approaches will contribute to the development of sustainable agricultural practices in fluoride-affected regions, ensuring long-term food security and environmental stability. Recent advances in transcriptomics, proteomics, metabolomics, and functional genomics have opened new opportunities to unravel the molecular mechanisms underlying fluoride uptake, transport, detoxification, and stress adaptation. Future research integrating these multi-omics approaches with CRISPR/Cas-mediated genome editing and molecular breeding will facilitate the identification of key genes, transporters, signaling pathways, and regulatory networks associated with fluoride tolerance, thereby accelerating the development of fluoride-resilient crop cultivars.

Disclosure statement

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Author contributions

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Data availability statement

Data included in study/supplementary material/referenced in study.

Ethics approval

The ethical statement is not applicable in this study as this is a review paper, and we are using secondary published information.

Consent for publication

Not applicable.

References

1 Saleem A, Zulfiqar A, Ali B, Tufekci ED, Rahimi M, Mostafa RM. Alkaline and acidic soil constraints on iron accumulation by rice cultivars in relation to several physio-biochemical parameters. BMC Plant Biol. 2023;23(1):397. doi: 10.1186/s12870-023-04400-x.

2 Zulfiqar A, Fatima R, Ahmed S, Saleem A, Sardar R, Ahmad MN, Yasin NA. Mechanistic insights into the interaction of fluoride resistant bacteria with wheat roots toward enhancing plant productivity by alleviating fluoride stress. Fluoride. 2023;56(3).

3 Saleem A, Zulfiqar A, Ali B, Naseeb MA, Almasaudi AS, Harakeh S. Iron sulfate (FeSO4) improved physiological attributes and antioxidant capacity by reducing oxidative stress of *oryza sativa* L. Cultivars in alkaline soil. Sustainability. 2022;14(24):16845. doi: 10.3390/su142416845.

4 Teoh YJ, Cheng WH, Wider W, Krishnan K, Yap CK, Chen Q, Jiang LL, Lei TMT, Tanee T, Sudmoon R, Lee SY. Heavy metal accumulation in paddy plants and health risks: insights from southern Peninsular Malaysia and global research trends. Asian J Agric Biol. 2025. 2024135. doi: 10.35495/ajab.2024.135.

5 Ali S, Balal RM, Javaid MM. Assessment of drought tolerance capacity of tuberose (Polianthes tuberosa L.) on the basis of various growth and physio-chemical indicators. Asian J Agric Biol. 2024;(2):2023278. doi: 10.35495/ajab.2023.278.

6 Afra JM, Habibi E, Fathi A, Saleem A, Ghadimi F, Khazainezhad S, Rezazadeh R, Danafar T, Kheyri Y, Nozari F. Influence of chemical fertilizers and animal manure on morphological traits of medicinal plants in Northern Iran. Res Crop Ecophysiol. 2022;17(2):86–101.

7 Alshegaihi RM, Saleem MH, Ali B, Aziz H, Fahad S, Alataway A, Dewidar AZ, Elansary HO. Silicon and titanium dioxide mitigate copper stress in wheat (*triticum aestivum* L.) through regulating antioxidant defense mechanisms. J Plant Growth Regul. 2023;43:1–17. doi: 10.1007/s00344-023-11204-8.

8 Saleem A, Zulfiqar A, Ahmed Z. Effect of 2-(phenylsulfonyl) hydrazine carbothioamide on photosynthetic pigments in wheat (*Triticum aestivum* L.) varieties. J Plantarum. 2020;2(1):1–9.

9 Saleem A, Zulfiqar A, Alamoudi SA, Ashkan MF, Alhomaidi E. Plant growth-promoting bacteria improve *triticum aestivum* L. growth and photosynthetic activity in sulfonamide-contaminated soil. Turk J Agric For. 2022;46(6):822–837. doi: 10.55730/1300-011X.3045.

10 Saleem A, Zulfiqar A, Fahad S. Elevated expression of YSL genes and enhanced physiological responses in rice subjected to iron application. J Plant Growth Regul. 2024;43:1–19. doi: 10.1007/s00344-024-11249-3.

11 Panda D. Fluoride toxicity stress: physiological and biochemical consequences on plants. Int J Biores Environ Agric Sci. 2015;11(2):70–84.
12 Han J, Kiss L, Mei H, Remete AM, Ponikvar-Svet M, Sedgwick DM, Roman R, Fustero S, Moriwaki H, Soloshonok VA. Chemical aspects of human and environmental overload with fluorine. Chem Rev. 2021;121(8):4678–4742. doi: 10.1021/acs.chemrev.0c01263.
13 Zulfiqar A, Mushtaq I, Ahmed S, Ali M, Saleem A, Sadar R, Ahmad MN. Fluoride resistant bacteria alleviate fluoride stress in *triticum aestivum* L. through modulating gas exchange characteristics and enhanced plant growth. Fluoride. 2022;55(3):280–294.
14 Mushtaq I, Zulfiqar A, Ali M, Saleem A. Effect of sodium fluoride on the growth and productivity of *triticum aestivum* L. in the presence of fluoride resistant bacteria. The Presence of Fluoride Resistant Bacteria. 2021.
15 Chen Y, Zhang Y, Liu Y, Guan Y, Eiler J, Stolper EM. Water, fluorine, and sulfur concentrations in the lunar mantle. E&PSL. 2015;427:37–46. doi: 10.1016/j.epsl.2015.06.046.
16 García MG, Borgnino L. Fluoride in the context of the environment. In: Fluorine: chemistry, analysis, function and effects; 2015. p. 3–21. The Royal Society of Chemistry.
17 Pashkevich DS, Mamaev AV. Production of hydrogen fluoride by processing fluorine-containing wastes and by-products of modern industries. WIT Trans Ecol Environ. 2019;231:111–123.
18 Ozsvath DL. Fluoride and environmental health: a review. Rev Environ Sci Bio/Technol. 2009;8:59–79. doi: 10.1007/s11157-008-9136-9.
19 Wambu EW, Agong SG, Anyango B, Akuno W, Akenga T. High fluoride water in bondo-rarieda area of siaya county, Kenya: a hydro-geological implication on public health in the lake Victoria basin. BMC Public Health. 2014;14(1):1–8. doi: 10.1186/1471-2458-14-462.
20 Zulfiqar A, Naseer S, Saleem A, Sabar M, Ahmed S, Sardar R, Shahzadi F, Raza Q. Genetic diversity studies for grain iron and zinc content analysis for elite rice (*Oryza sativa* L.) genotype by using SSR markers. J Food Compos Anal. 2023;115:104816. doi: 10.1016/j.jfca.2022.104816.
21 Brindha K, Elango L. Fluoride in groundwater: causes, implications and mitigation measures. In Fluoride properties, applications and environmental management. 2011;(Vol. 1), p. 111–136.
22 Chahine S, Melito S, Giannini V, Seddaiu G, Roggero PP. Fluoride stress affects seed germination and seedling growth by altering the morpho-physiology of an African local bean variety. Plant Growth Regul. 2024;102(2):339–350. doi: 10.1007/s10725-023-01064-3.
23 Rizzu M, Tanda A, Cappai C, Roggero PP, Seddaiu G. 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. doi: 10.1016/j.scitotenv.2021.147650.
24 Gadi B, Kumar R, Goswami B, Rankawat R, Rao SR. Recent developments in understanding fluoride accumulation, toxicity, and tolerance mechanisms in plants: an overview. J Soil Sci Plant Nutr. 2021;21(1):209–228. doi: 10.1007/s42729-020-00354-3.
25 Yadu B, Chandrakar V, Keshavkant S. Responses of plants to fluoride: an overview of oxidative stress and defense mechanisms. Fluoride. 2016;49(3):293.
26 Baunthiyal M, Bhatt A, Ranghar S. Fluorides and its effects on plant metabolism. Int J Agric Technol. 2014;10:1–27.
27 Gao L, He J, Hu J, Li Y. Large enhancement in polarization response and energy storage properties of poly (vinylidene fluoride) by improving the interface effect in nanocomposites. J Phys Chem C. 2014;118(2):831–838. doi: 10.1021/jp409474k.
28 Mondal NK. Effect of fluoride on photosynthesis, growth and accumulation of four widely cultivated rice (*Oryza sativa* L.) varieties in India. Ecotoxicol Environ Saf. 2017;144:36–44. doi: 10.1016/j.ecoenv.2017.06.009.
29 Telesinski A, Śnioszek MA, Smolik B, Malinowska K, Mikiciuk M, Cichocka J. Fluoride uptake in hydroponic culture by different clones of basket willow, Salix viminalis L. Fluoride. 2011;44(4):255–259.
30 Li L. The biochemistry and physiology of metallic fluoride: action, mechanism, and implications. Crit Rev Oral Biol Med. 2003;14(2):100–114. doi: 10.1177/154411130301400204.
31 Hong B-D, Joo RN, Lee KS, Lee DS, Rhie JH, Min SW, Song SG, Chung DY. Fluoride in soil and plant. Korean J Agric Sci. 2016;43(4):522–536.
32 Ahmad MA, Bibi H, Munir I, Ahmad MN, Zia A, Mustafa G, Ullah I, Khan I. Fluoride toxicity and its effect on two varieties of solanum lycopersicum. Fluoride. 2018;51(3):267–277.
33 Alim H, Ahmad MA, Munir I, Khan I, Mustafa G, Ullah I, Ahmad MN, Khan H, Yasinzai M, Zia A, et al. The effect of different concentrations of the fluoride ion on the growth and nutritional value of two elite genotypes of *triticum aestivum*. Fluoride. 2017;50(1):143.
34 Baunthiyal M, Ranghar S. Physiological and biochemical responses of plants under fluoride stress: an overview. Fluoride. 2014;47(4):287–93.
35 Asthir B, Tak Y. Fluoride-induced changes in carbon and nitrogen metabolism in two contrasting cultivars of *triticum aestivum* L. Fluoride. 2017;50(3):334–342.
36 Sahariya A, Bharadwaj C, Emmanuel I, Alam A. Fluoride toxicity in soil and plants: an overview. Asian Jo Adv Res. 2021;4(1):573–581.

37 Banerjee A, Roychoudhury A. Differential regulation of defence pathways in aromatic and non-aromatic indica rice cultivars towards fluoride toxicity. Plant Cell Rep. 2019;38:1217–1233. doi: 10.1007/s00299-019-02438-6.
38 Chakrabarti S, Patra PK. Biochemical and antioxidant responses of paddy (*Oryza sativa* L.) to fluoride stress. Fluoride. 2015;48(1):56.
39 Aslam A, Nawaz H, Khan A, Ghaffar R, Abbas G. Effect of exogenous application of citric acid on growth of maize (*Zea mays* L.) under sodium fluoride stress. Fluoride. 2023;56(4 Pt 1):329–350.
40 Dawood MF, Tahjib-Ul-Arif M, Sohag AAM, Abdel Latef AAH. Fluoride mitigates aluminum-toxicity in barley: morpho-physiological responses and biochemical mechanisms. BMC Plant Biol. 2022;22(1):287. doi: 10.1186/s12870-022-03610-z.
41 Bustingorri C, Balestrasse KB, Lavado RS. Effects of high arsenic and fluoride soil concentrations on soybean plants. 2015
42 Chakrabarti S, Patra PK. Effect of fluoride on superoxide dismutase activity in four common crop plants. Fluoride. 2013;46(2):59–62.
43 Verma KK, Singh M. Influence of fluoride phytotoxicity in germinating seedlings of pisum sativum: modeling of morpho-physiological traits. Vegetos. 2022;35(3):736–746. doi: 10.1007/s42535-021-00333-8.
44 Chen Y, Wang S, Nan Z, Ma J, Zang F, Li Y, Zhang Q. Effect of fluoride and cadmium stress on the uptake and translocation of fluoride and cadmium and other mineral nutrition elements in radish in single element or co-taminated sierozem. Environ Exp Bot. 2017;134:54–61. doi: 10.1016/j.envexpbot.2016.11.002.
45 Chandra P, Vishnoi N, Singh D. Assessment of fluoride contamination of water and soil and its phytotoxic effect on the growth parameters in selected vegetable crops. Glob J Appl Environ Sci. 2012;2(1):55–65.
46 Gan C-D, Cui S-F, Yang J-Y. Foliar application of ca in alleviation of atmospheric fluoride stress on leafy vegetable and reduction of potential dietary health risk. Water Air Soil Pollut. 2024;235(9):566. doi: 10.1007/s11270-024-07381-1.
47 Sharma K, Verma K, Meena AK. Biochemical and molecular behaviour of cluster bean and mung bean against fluoride stress. Pharma Innov J. 2023;12(3):1973–1976.
48 Verma KK, Song X, Huang H, Singh M, Xu L, Wu J, Khan ZH, Zhang B, Li Y. Mathematical modeling of climate and fluoride effects on sugarcane photosynthesis with silicon nanoparticles. Plant Physiol Biochem. 2023;204:108089. doi: 10.1016/j.plaphy.2023.108089.
49 Almeida Rodrigues A, de Fátima Sales J, Carvalho Vasconcelos Filho S, Carlos Costa A, Lino Rodrigues C, Alves da Silva A, Domingos M, Müller C. Morphoanatomical, physiological, and biochemical indicators in *Lactuca sativa* L. germination and growth in response to fluoride. Plants. 2022;11(23):3406. doi: 10.3390/plants11233406.
50 Saleh AA, Abdel-Kader DZ. Metabolic responses of two helianthus annuus cultivars to different fluoride concentrations during germination and seedling growth stages. Egypt J Biol. 2003;5(1):43–54.
51 Sachan P, Lal N. Effect of sodium fluoride on germination, seedling growth and photosynthetic pigments in *Cicer arietinum* L. and *Hordeum vulgare* L. MOJ Ecol Environ Sci. 2018;3(1). doi: 10.15406/mojes.2018.03.00103.
52 Fina BL, Lupo M, Dri N, Lombarte M, Rigalli A. Comparison of fluoride effects on germination and growth of zea mays, glycine max and sorghum vulgare. J Sci Food Agric. 2016;96(11):3679–3687. doi: 10.1002/jsfa.7551.
53 Johnston NR, Strobel SA. Principles of fluoride toxicity and the cellular response: a review. Arch Toxicol. 2020;94(4):1051–1069. doi: 10.1007/s00204-020-02687-5.
54 Waugh DT. Fluoride exposure induces inhibition of sodium-and potassium-activated adenosine triphosphatase (Na+, K+-ATPase) enzyme activity: molecular mechanisms and implications for public health. Int J Environ Res Public Health. 2019;16(8):1427. doi: 10.3390/ijerph16081427.
55 Baunthiyal M, Sharma V. Response of fluoride stress on plasma membrane H+-ATPase and vacuolar H+-ATPase activity in semi-arid plants. Indian J Plant Physiol. 2014;19:210–214. doi: 10.1007/s40502-014-0103-x.
56 Banerjee A, Roychoudhury A. Fluorine: a biohazardous agent for plants and phytoremediation strategies for its removal from the environment. Biol Plant. 2019;63(1):104–112. doi: 10.32615/bp.2019.013.
57 Wang R, Gong W, Chen X, Zheng M, Cui Y, Liang C, Hu J, Ji Y. Fluoride induces spermatogonial apoptosis via IP3R-MCU-Mediated mitochondrial calcium overload. Biol Trace Elem Res. 2026;204(4):2841–2855. doi: 10.1007/s12011-025-04860-2.
58 Patial B, Thakur R. Exploring the impacts of fluoride-induced thyroid toxicity: a comprehensive review. Biol Trace Elem Res. 2026;204(4):2594–2619. doi: 10.1007/s12011-025-04840-6.
59 De Luca V, Verdoliva V, Supuran CT, Capasso C. Hyaluronic acid-palmitate nanoparticle delivery of carbonic anhydrase inhibitors impairs growth and early metabolism in *Escherichia coli* through β-and γ-carbonic anhydrase-associated processes. Int J Mol Sci. 2026;27(2):621. doi: 10.3390/ijms27020621.
60 Buragohain K, Nath R. Microbial remediation of groundwater fluoride contamination: prospect for environmental clean-up. Water Air Soil Pollut. 2026;237(4):221. doi: 10.1007/s11270-025-08931-x.
61 Banerjee A, Singh A, Roychoudhury A. Spermidine application reduces fluoride uptake and ameliorates physiological injuries in a susceptible rice cultivar by activating diverse regulators of the defense machinery. Environ Sci Pollut Res. 2019;26:36598–36614. doi: 10.1007/s11356-019-06711-9.
62 Meng H, Ommati MM, Li J, Heidari R, Zhao W, Wang H, Zhou B. Fluoride toxicodynamics and interactions with co-contaminants: mechanistic insights with implications for agricultural systems and food safety. J Agric Food Chem. 2026;74:20126–20143. doi: 10.1021/acs.jafc.6c01386.

63 Liu R, Wang S, Song J. New progress in the production, oxidative damage, and scavenging mechanisms of reactive oxygen species in plants under abiotic stress. Front Plant Sci. 2026;17:1774033. doi: 10.3389/fpls.2026.1774033.
64 Ul Islam SN, Asgher M, Khan NA. Hydrogen peroxide and its role in abiotic stress tolerance in plants. In Gasotransmitters signaling in plant abiotic stress: gasotransmitters in adaptation of plants to abiotic stress. 2023. p. 167–195. Cham: Springer International Publishing. doi: 10.1007/978-3-031-30858-1_9.
65 Tano DW. Characterization of chloroplast quality mechanisms during singlet oxygen stress. The University of Arizona; 2022.
66 Iftikhar F, Zulfiqar A, Kamran A, Saleem A, Arshed MZ, Djalovic I, Vara Prasad PV, Soufan W. Antioxidant responses in chromium-stressed maize as influenced by foliar and root applications of fulvic acid. Sci Rep. 2025;15(1):1289. doi: 10.1038/s41598-024-84803-4.
67 Zulfiqar A, Gul B, Saleem A, Islam A, Ali MF, Nawaz M, Al-Ghamdi AA, Rizwana H, Abdelsalam M. Salicylic acid mitigates cadmium stress in wheat: experimental insights into growth and biochemical parameters. Scientifica. 2024;2024(1):6887694. doi: 10.1155/sci5/6887694.
68 Ighodaro O, Akinloye O. First line defence antioxidants-superoxide dismutase (SOD), catalase (CAT) and glutathione peroxidase (GPX): their fundamental role in the entire antioxidant defence grid. Alex J Med. 2018;54(4):287–293. doi: 10.1016/j.ajme.2017.09.001.
69 Vašková J, Vaško L, Kron I. Oxidative processes and antioxidative metaloenzymes. In: Antioxidant enzyme. Vol. 2; 2012. p. 19–58.
70 Verma H, Sakhre AS, Singh VP. Assay of Peroxidase (POX) activity. In Manual of ICAR Sponsored Training Programme for Technical Staff of ICAR Institutes on physiological techniques to analyze the impact of climate change on crop plants. 2017. p. 92.
71 Kunert KJ, Foyer CH. The ascorbate/glutathione cycle. In: Adv Bot Res. Vol. 105. Elsevier; 2023. p. 77–112. doi: 10.1016/bs.abr.2022.11.004.
72 Alonazi M, Al-Daihan S, Aldbass AM, Bhat RS. Antioxidant defense and growth responses of *Vigna radiata* L. sprouts under sodium fluoride stress. Fluoride. 2025;58(9):1–10.
73 Angwa LM, Jiang Y, Pei J, Sun D. Antioxidant phytochemicals for the prevention of fluoride-induced oxidative stress and apoptosis: a review. Biol Trace Elem Res. 2022;200(3):1418–1441. doi: 10.1007/s12011-021-02729-8.
74 Dawood MF, Tahjib-Ul-Arif M, Sohag AAM, Abdel Latef AAH. Fluoride mitigates aluminum-toxicity in barley: morpho-physiological responses and biochemical mechanisms. BMC Plant Biol. 2022;22(1):1–17. doi: 10.1186/s12870-022-03610-z.
75 Sharma R, Kaur R. Insights into fluoride-induced oxidative stress and antioxidant defences in plants. Acta Physiol Plant. 2018;40:1–14. doi: 10.1007/s11738-018-2754-0.
76 Luo J, Ni D, Li C, Du Y, Chen Y. The relationship between fluoride accumulation in tea plant and changes in leaf cell wall structure and composition under different fluoride conditions. Environ Pollut. 2021;270:116283. doi: 10.1016/j.envpol.2020.116283.
77 Chlubek D, Poland S. Fluoride and oxidative stress. Fluoride. 2003;36(4):217–228.
78 Barbier O, Arreola-Mendoza L, Del Razo LM. Molecular mechanisms of fluoride toxicity. Chem Biol Interact. 2010;188(2):319–333. doi: 10.1016/j.cbi.2010.07.011.
79 Bhatnagar A, Kumar E, Sillanpää M. Fluoride removal from water by adsorption—a review. Chem Eng J. 2011;171(3):811–840. doi: 10.1016/j.cej.2011.05.028.
80 Ahmad MN, Zia A, van den Berg L, Mahmood R, Dawar KM, Alam SS, Riaz M, Ashmore M. Effects of soil fluoride pollution on wheat growth and biomass production, leaf injury index, powdery mildew infestation and trace metal uptake. Environ Pollut. 2022;298:118820. doi: 10.1016/j.envpol.2022.118820.
81 Choudhary S, Rani M, Devika OS, Patra A, Singh RK, Prasad SK. Impact of fluoride on agriculture: a review on it's sources, toxicity in plants and mitigation strategies. Int J Chem Stud. 2019;7(2):1675–1680.
82 Brennan E, Leone I, Daines RH. Fluorine toxicity in tomato as modified by alterations in the nitrogen, calcium, and phosphorus nutrition of the plant. Plant Physiol. 1950;25(4):736–747. doi: 10.1104/pp.25.4.736.
83 Wei M, Ye Y, Ali MM, Chamba Y, Tang J, Shang P. Effect of fluoride on cytotoxicity involved in mitochondrial dysfunction: a review of mechanism. Front Vet Sci. 2022;9:850771. doi: 10.3389/fvets.2022.850771.
84 Yadav A, Kumari N, Kumar R. Fluoride distribution, contamination, toxicological effects and remedial measures: a review. Sustain Water Resour Manag. 2023;9(5):150. doi: 10.1007/s40899-023-00926-y.
85 Yadav S, Yadav J, Kumar S, Singh P. Metabolism of macro-elements (calcium, magnesium, sodium, potassium, chloride and phosphorus) and associated disorders. In Clinical applications of biomolecules in disease diagnosis: A comprehensive guide to biochemistry and metabolism. 2024. p. 177–203. Singapore: Springer Nature Singapore. doi: 10.1007/978-981-97-4723-8_8.
86 Kumar S, Shenoy S, Swamy RS, Ravichandiran V. Fluoride-induced mitochondrial dysfunction and approaches for its intervention. Biol Trace Elem Res. 2024;202(3):835–849. doi: 10.1007/s12011-023-03720-1.
87 Moirana RL, Mkunda J, Perez MP, Machunda R, Mtei K. The influence of fertilizers on the behavior of fluoride fractions in the alkaline soil. J Fluor Chem. 2021;250:109883. doi: 10.1016/j.jfluchem.2021.109883.
88 Kumar YS, Rushi VR, Subbaiah PV, Deekshitha D, Kavitha P. Chapter-3 fluoride effect and its impact on humans & agricultural crops. In Fluoride effect and its impact on humans & agricultural crops. 2021. p. 39–65 kinik Publications.

89 Davison AW, Weinstein LH. Some problems relating to fluorides in the environment: effects on plants and animals. In: Advances in Fluorine Science. Vol. 1; 2006. p. 251–298. doi: 10.1016/S1872-0358(06)01008-6.
90 Treshow M. Fluorides as air pollutants affecting plants. Annu Rev Phytopathol. 1971;9(1):21–44. doi: 10.1146/annurev.py.09.090171.000321.
91 Selvam R, Kalaiyarasi G, Saritha B. Heavy metal contamination in soils: risks and remediation. In: Soil Fertility and Plant Nutrition. Vol. 141; 2024.
92 Li H, Ma X, Huang X, Ji W, Chen K, Xu S, Gao P. Fluoride contents in commonly used commercial phosphate fertilizers and their potential risks in China. Environ Monit Assess. 2023;195(9):1051. doi: 10.1007/s10661-023-11623-w.
93 Koley R, Mondal NK. Synthesis of calcium-based nanofertilizer and its efficacy towards reduction of oxidative stress and fluoride uptake in rice (*Oryza sativa* L.). Plant Nano Bioly. 2024;9:100087. doi: 10.1016/j.plana.2024.100087.
94 Kumar R, Sinha R, Sharma PK, Ivy N, Kant N, Jha A, Gupta PK, Singh RK, Ghosh A, Prasad PVV. Bioaccumulation of fluoride in plants and its microbially assisted remediation: a review of biological processes and technological performance. Processes. 2021;9(12):2154. doi: 10.3390/pr9122154.