

## Research Advances on Mechanisms of Plant Uptake of Perfluoro/Polyfluoro Compounds and Their Interactions: Postprint

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### Abstract

Perfluorooctanoic acid (PFOA) and perfluorooctane sulfonate (PFOS) are typical per- and polyfluoroalkyl substances (PFAS) that are widely applied due to their excellent surface activity, extremely high stability, and other physicochemical properties, but they typically enter the environment during their production, use, and disposal, causing contamination. Soil is an important sink for PFAS. After being taken up, translocated, and accumulated by plants, PFAS in soil can biomagnify through the food chain and cause harm. Given the high persistence of PFAS in the environment, the pollution risks and potential hazards they pose in soil-crop systems have attracted increasing attention. However, current understanding of the mechanisms and effects of plant uptake and accumulation of PFAS remains unsystematic. A review of relevant literature reveals that PFAS can affect plant growth and development, metabolism, and gene expression, while conversely, plants can also influence the environmental chemical behavior of PFAS through their uptake, translocation, and accumulation. This article briefly introduces the physicochemical properties, applications, and hazards of PFAS, and systematically elaborates the mechanisms and effects of plant uptake and accumulation of PFAS from the following aspects: plant influences on PFAS distribution in soil, plant absorption of PFAS from soil and their subsequent translocation and accumulation within plants, differences in PFAS uptake and accumulation among different plant species and crop varieties, effects of PFAS on plant metabolism and growth and development, and plant responses to PFAS stress. This review helps to comprehensively understand the interactions between plants and PFAS, and provides plant-based solutions for the remediation and utilization of PFAS-contaminated soils.

## Full Text

### Preamble

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#### Research Progress on the Mechanisms of Plant Uptake of Per/Polyfluoroalkyl Substances and Their Mutual Impacts

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**Abstract:** Perfluorooctanoic acid (PFOA) and perfluorooctane sulfonate (PFOS) are typical per/polyfluoroalkyl substances (PFAS) that have been widely applied due to their excellent surface activity and high stability. However, they inevitably enter the environment during production, use, and disposal, causing contamination. Soil serves as a major sink for PFAS, and PFAS absorbed, translocated, and accumulated by plants can be enriched through food chains, posing significant risks. Given their high persistence in the environment, the pollution risks and potential hazards of PFAS in soil-crop systems have attracted increasing attention, yet current understanding of the mechanisms and effects of plant uptake and accumulation of PFAS remains unsystematic. Literature review indicates that PFAS affect plant growth, development, metabolism, and gene expression, while plants reciprocally influence the environmental chemical behavior of PFAS through absorption, translocation, and enrichment. This paper briefly introduces the physicochemical properties, applications, and hazards of PFAS, and systematically elaborates on the mechanisms and effects of plant uptake and accumulation of PFAS from several perspectives: plant influence on PFAS distribution in soil, plant absorption of PFAS from soil and its translocation and accumulation within plants, differences in PFAS uptake and accumulation among plant species and crop varieties, PFAS effects on plant metabolism and growth, and plant responses to PFAS stress. This review provides comprehensive insights into plant-PFAS interactions and offers plant-based solutions for the remediation and utilization of PFAS-contaminated soils.

**Keywords:** perfluorooctanoic acid, perfluorooctane sulfonate, per/polyfluoroalkyl substances, environmental chemistry, plant, interaction

Per/polyfluoroalkyl substances (PFAS) are synthetic compounds in which C-H bonds on the carbon skeleton are replaced by C-F bonds. Due to their unique properties—including excellent thermal stability, chemical stability, high surface activity, extremely low surface tension, and both oil- and water-repellency—PFAS have found widespread applications across various industrial sectors (such as aviation, automotive, construction, electronics, and textiles) and consumer products (such as firefighting foams, floor polishes, shampoos, non-stick coatings, carpets, and pesticides) (Evich et al., 2022). Since their invention in the 1950s, more than 4,700 PFAS have been marketed (Cousins et al., 2019), with perfluorooctanoic acid (PFOA) and perfluorooctane sulfonate (PFOS) as typical representatives. Moreover, certain PFAS can transform into PFOA or PFOS after release into the environment, making them the most frequently detected PFAS in environmental matrices (Wang et al., 2017). The C-F bond is a strong covalent bond (3.6 eV, 116 kcal · mol<sup>-1</sup>), and the presence of multiple adjacent C-F bonds renders PFAS highly resistant to hydrolysis, photolysis, and biodegradation (Milinovic et al., 2015). Consequently, PFOA and PFOS are extremely stable in the environment, with the half-life of PFOS estimated to exceed 41 years at 25°C (Beach et al., 2006). PFAS have been widely detected in water bodies and soils, with soil representing the ultimate and largest sink for these compounds (Choi et al., 2017; Wang et al., 2018; [Figure 1: see original paper]).

[Figure 1: see original paper] indicates PFAS.

**Fig.1** The main sources and distributions of soil PFAS

PFAS in soil can be absorbed and accumulated by plants, subsequently enriching in animals and humans through food chains (Ren et al., 2022; Xing et al., 2023). Numerous studies have demonstrated severe hazards of PFAS to animals and humans: the half-lives of PFOS and PFOA in the human body are approximately 9 years and 4 years, respectively. PFOA accumulates most in the liver, followed by blood, lungs, and kidneys, and has been reported to cause hepatotoxicity, nephrotoxicity, immunotoxicity, neurotoxicity, carcinogenicity, and developmental and endocrine disruption (Naomi & Yoichi, 2003; Li et al., 2017; Zhong et al., 2020; Bartell & Vieira, 2021). Therefore, the U.S. Environmental Protection Agency (EPA) has classified PFOA as a Persistent, Bioaccumulative, and Toxic (PBT) substance, representing an emerging persistent organic pollutant (POP) (Liu et al., 2022). PFOA and related compounds were listed in the Stockholm Convention on Persistent Organic Pollutants (POPs) in 2019 (Xiang et al., 2020b). With advances in toxicological research and risk assessment technologies, international organizations such as the European Food Safety Authority (EFSA) and EPA have substantially lowered the reference doses (RfDs) for PFOA and related compounds. For instance, EFSA's latest regulations set RfDs at 0.8 ng · kg<sup>-1</sup> · d<sup>-1</sup> for PFOA and 1.8 ng · kg<sup>-1</sup> · d<sup>-1</sup> for PFOS, far lower than previous values and even 50 times lower than the RfD for microcystin (40 ng · kg<sup>-1</sup> · d<sup>-1</sup>), a major hepatocarcinogenic factor (EFSA, 2018).

Given their hazardous nature, PFOA and PFOS have been gradually banned or

restricted globally (UNEP, 2019). However, to meet market demands, alternative compounds have been produced and used, primarily including short-chain and novel compounds such as perfluorobutanoic acid (PFBA), perfluorobutanesulfonic acid (PFBS), hexafluoropropylene oxide dimer acid (HFPO-DA, GenX), and chlorinated polyfluoroalkyl ether sulfonic acid 6:2Cl-PFESA (F-53B) (Chen et al., 2023; Liu et al., 2023). Currently, besides PFOA and PFOS, their alternatives are also ubiquitously detected in the environment, and existing research indicates these alternatives exhibit comparable or even higher bioaccumulation potential and toxicity than traditional compounds (Chen et al., 2023; Davis et al., 2023).

Plants serve as a critical intermediate bridge for PFAS entry into animals and humans, yet systematic understanding is lacking regarding how plants influence PFAS distribution in soil, how plants absorb PFAS from soil and translocate/accumulate them within tissues, differences in PFAS uptake and accumulation among plant species and crop varieties, PFAS effects on plant metabolism and growth, and plant responses to PFAS stress. This review synthesizes recent research progress on the mechanisms and mutual impacts of plant uptake and accumulation of PFAS, providing insights for future development of low-accumulation or hyperaccumulation plant varieties through molecular breeding to ensure food safety and enable phytoremediation of PFAS-contaminated soils.

### 1.1 Effects of Different Soil Conditions on Plant Uptake of PFAS

Soil serves as an important sink for PFOA in the environment, and its properties significantly influence plant uptake. Miao et al. (2017) investigated PFOA sorption on soils collected from 10 locations in China with different compositions, revealing that sorption followed pseudo-second-order reaction kinetics and reached saturation in approximately 24 hours. PFOA sorption positively correlated with soil organic carbon content and mineral composition, with hydrophobic interactions between fluorinated carbon chains and soil organic matter representing the primary mechanism. PFOA sorption in soil was highly irreversible, suggesting that adding organic carbon to contaminated soils could reduce plant-available PFOA and effectively decrease PFOA concentrations in crops.

Soil organic matter (SOM) adsorbs PFOA and PFOS, thereby affecting plant uptake. Lee et al. (2021) studied the effects of granular activated carbon (GAC) addition on PFOA and PFOS sorption and uptake in lettuce grown in soils with different SOM contents. The maximum sorption capacities of GAC for PFOA and PFOS were  $9.091 \text{ mg} \cdot \text{g}^{-1}$  and  $27.778 \text{ mg} \cdot \text{g}^{-1}$ , respectively, which decreased to  $5.208 \text{ mg} \cdot \text{g}^{-1}$  and  $17.241 \text{ mg} \cdot \text{g}^{-1}$  after adding 0.04% humic acid. In soil with 2.6% SOM, the plant uptake factors (PUFs) for PFOA and PFOS in lettuce were 0.629 and 0.252, respectively, but significantly decreased to 0.006 and 0.005 after adding 1% GAC. Similarly, in soil with 4.0% SOM, PUFs were 0.353 and 0.108, respectively, decreasing to 0.079 and 0.023 after GAC addition, reducing PFAS concentrations in lettuce by 4.3 to 155-fold. These results demonstrate that soil organic matter content significantly inhibits plant uptake of PFOA and

PFOS, suggesting that increasing soil organic matter could reduce crop PFAS accumulation and ensure agricultural product safety.

Soil composition and physicochemical properties affect plant uptake of PFAS. Knight et al. (2021) collected 20 different soil types from multiple locations in Australia to investigate the aging and plant uptake of PFOA, PFOS, and perfluorohexanesulfonic acid (PFHxS) over six months. Using multiple linear regression, they modeled sorption coefficients for these compounds and bioaccumulation factors in common bean (*Phaseolus vulgaris*) as functions of soil physicochemical properties. Results showed that sorption coefficients were influenced by soil organic carbon, pH, and various cations ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$ ,  $\text{K}^+$ , and oxalate-extractable  $\text{Al}^{3+}$ ), while bioaccumulation factors did not correlate strongly with any single soil property but were negatively correlated with soil sorption coefficients. No significant aging of PFOA, PFOS, or PFHxS was observed during the experimental period, consistent with their long environmental half-lives.

During growth, plant roots secrete organic acids, sugars, and proteins into soil, resulting in significantly higher dissolved organic carbon (DOC) in rhizosphere soil compared to unplanted soil (Yu et al., 2021). Under PFOS treatment, DOC concentrations in the rhizosphere of low-accumulating crop varieties (LACV) were lower than those of high-accumulating varieties (HACV). DOC can desorb PFOS from soil particles, increasing its bioavailability to plant roots, thus root uptake of PFOS positively correlates with DOC concentration—one mechanism underlying differential accumulation between HACV and LACV lettuce varieties (Yu et al., 2021). Xiang et al. (2018) reported similar findings for PFOA in HACV and LACV lettuce.

## 1.2 Differences Among Plant Species and Varieties in PFAS Uptake

Different plant species exhibit distinct PFAS accumulation patterns. Wen et al. (2016) investigated PFOA and PFOS uptake and translocation in seven plant species (maize, soybean, carrot, mung bean, lettuce, alfalfa, and Italian ryegrass). Root concentration factors ( $\text{C}_{\text{root}}/\text{C}_{\text{soil}}$ ) ranged from 1.37–4.68 for PFOA and 1.69–10.3 for PFOS, while translocation factors from root to shoot ( $\text{C}_{\text{shoot}}/\text{C}_{\text{root}}$ ) ranged from 0.055–0.16 for PFOA and 0.093–1.8 for PFOS. These results demonstrate interspecific variation in PFAS uptake and translocation, with protein content positively correlating with uptake/translocation and lipid content showing negative correlations, suggesting involvement of protein carriers in PFAS transport (Wang et al., 2020; Yu et al., 2021). Wang et al. (2020) studied eight common wetland plants (*Canna indica*, *Thalia dealbata*, *Cyperus alternifolius*, *Phragmites australis*, *Arundo donax*, *Pontederia cordata*, *Cyperus papyrus*, and *Alisma orientale*) using desorption electrospray ionization mass spectrometry and transmission electron microscopy with energy-dispersive spectroscopy. PFOS primarily accumulated in roots (48.8%–95.8%), whereas PFOA accumulated mainly in shoots (29.3%–77.4%). Both compounds entered root cortex via apoplastic and symplastic pathways, with subsequent transport

to vascular bundles occurring via symplastic pathways in *T. dealbata* and *P. australis*, but via both pathways in *C. indica* and *C. alternifolius*. *T. dealbata* translocated PFAS from roots to shoots primarily through cortical tissues, while *C. indica* and *C. alternifolius* utilized both cortical and vascular tissues. Studies on spring wheat, oats, potatoes, maize, rye, carrots, cucumbers, spinach, and green onions have also shown significant interspecific differences in PFAS accumulation (Stahl et al., 2009; Lechner & Knapp, 2011; Lee et al., 2020), indicating that differential accumulation is widespread among plants. summarizes PFAS distribution and concentrations in various plants for reference.

**TABLE:1** Distributions and contents of PFAS in plants

Name of plant	Location	PFAS type	Content (ng · g <sup>-1</sup> )	Literature source
<i>Medicago sativa</i>	Root	PFOS/PFOA	81.4/4 310.3	Wen et al., 2016
	Shoot	PFOS/PFOA	61.2/493.6	
<i>Vigna radiata</i>	Root	PFOS/PFOA	640.2/3 230.1	
	Shoot	PFOS/PFOA	105.5/3 500.9	
<i>Raphanus sativus</i>	Root	PFOS/PFOA	403.2/1 250.3	
	Shoot	PFOS/PFOA	72.3/2 227.4	
<i>Lolium perenne</i>	Root	PFOS/PFOA	212.4/977.8	
	Shoot	PFOS/PFOA	27.9/550.8	
<i>Glycine max</i>	Root	PFOS/PFOA	723.6/1 335.9	
	Shoot	PFOS/PFOA	39.9/123.6	
<i>Alisma orientale</i>	Root	PFOS/PFOA	11.6/117.4	Wang et al., 2020
<i>Cucumis sativus</i>	Root	PFOS/PFOA	19/796	Lechner et al., 2011
<i>Daucus carota</i>	Peeled edible parts	PFOS/PFOA	18.4/30.8	Stahl et al., 2009
	Peelings	PFOS/PFOA	16.4/29.3	
<i>Solanum tuberosum</i>	Peeled edible parts	PFOS/PFOA	194.9/356.7	
	Peelings	PFOS/PFOA	0.7/7.7	
<i>Avena sativa</i>	Peeled edible parts	PFOS/PFOA	15/17.6	Navarro et al., 2017
	Peelings	PFOS/PFOA	41.1/331.1	
<i>Lolium perenne</i>	Vegetative compartments	PFOS/PFOA	150/690	Korucu et al., 2015

Name of plant	Location	PFAS type	Content (ng · g <sup>-1</sup> )	Literature source
<i>Zea mays</i>	Vegetative compartments	PFOS/PFOA	17/54	Yoo et al., 2011
<i>Tomato</i>	Fruit	PFOS/PFOA	270/1 900	
<i>Celery</i>	Fruit	PFOS/PFOA	2.2/4.19	
<i>Lactuca sativa</i>	Shoots	PFOS/PFBS	104/126	
	Leaves	PFPeA PFHxA PFHpA PFHxS	23 100/120	

Different varieties within the same species also show variation in PFAS accumulation. Xiang et al. (2018) examined 20 lettuce cultivars under two PFOA concentrations, finding that three low-accumulating varieties accumulated 3.7-5.5 times less PFOA than high-accumulating varieties. Yu et al. (2018) reported similar results for PFOS, with concentration differences of 4.4-5.7 times between high- and low-accumulating varieties, demonstrating that screening for low-accumulation cultivars is an important strategy for ensuring food safety (Xiang et al., 2020b). Further analysis revealed that mechanisms underlying differential accumulation include variation in root exudation of small organic acids like oxalic acid (affecting PFAS sorption in soil), differences in root-to-shoot translocation capacity, distinct subcellular distribution patterns, and differential expression of transporter proteins (Xiang et al., 2018, 2020a; Yu et al., 2018, 2021).

### 1.3 Transport, Redistribution, and Accumulation of PFAS in Plants

After root absorption from soil, PFAS are translocated via transpiration stream to shoots where they accumulate, demonstrating transport, redistribution, and accumulation processes within plants. Wen et al. (2013) reported bioconcentration factors in hydroponically grown maize roots of 23.94 for PFOA and 75.92 for PFOS, with translocation factors to shoots of 0.241 and 0.384, respectively, indicating root enrichment with limited upward translocation. Du et al. (2020) studied <sup>14</sup>C-PFOA uptake in soil-grown cucumber, finding highest concentrations in leaves, followed by roots and stems. The root concentration factor was 11.3-17.4, with translocation factors of 0.78-0.83 to stems and 3.28-5.41 to leaves. Fan et al. (2020) treated *Arabidopsis* with 20, 50, and 100 mol · L<sup>-1</sup> PFOA, observing more pronounced growth inhibition in shoots than roots, with shoot PFOA concentrations significantly exceeding root concentrations and this disparity increasing over time. Chen et al. (2020) investigated PFOA and its alternative 2,3,3,3-tetrafluoro-2-(heptafluoropropoxy)propanoic acid (GenX) in *Arabidopsis* and tobacco, reporting root accumulation factors of 67.0 and 16.4 for

PFOA versus 29.0 and 7.7 for GenX, indicating stronger PFOA accumulation. Translocation factors for PFOA and GenX were 2.77 and 2.52 in *Arabidopsis* (greater shoot accumulation) but 0.35 and 0.58 in tobacco (greater root accumulation), demonstrating species-specific differences.

Xiang et al. (2018) compared high- and low-accumulating lettuce varieties under 0.2 and 1 mg · kg<sup>-1</sup> PFOA treatments. The HACV cultivar showed root concentration factors of 13.5 ± 2.8 and 9.3 ± 0.4, with translocation factors of 0.50 ± 0.15 and 0.64 ± 0.09, respectively. *Inco* These results indicate higher PFOA accumulation in roots than shoots for both varieties, with significantly greater concentrations in HACV. Subcellular fractionation revealed that approximately 60% of root PFOA localized to cell walls, less than 10% to cytoplasm, and the remainder to organelles, with HACV showing lower cell wall distribution than LACV. Yu et al. (2020) obtained similar results with PFOS-treated lettuce varieties, suggesting that cell wall adsorption and sequestration are important factors regulating PFAS accumulation.

Plants can also translocate PFAS from shoots to roots for excretion into soil under certain conditions. Wang et al. (2020) demonstrated that the wetland plant *A. orientale* translocated PFOA and PFOS to root vascular bundles via apoplastic and symplastic pathways, then further to stems and leaves through transpiration. When PFAS-laden plants were transferred to PFAS-free medium, PFOA and PFOS were translocated downward and excreted. Subcellular distribution in *A. orientale* roots showed PFOS primarily in cell walls (52.4%–53.7%), organelles (31.0%–33.4%), and soluble fractions (13.3%–15.4%), whereas PFOA distribution was cell walls (23.4%–25.7%), organelles (5.82%–6.21%), and soluble fractions (68.5%–70.4%), reflecting physicochemical property differences.

These studies demonstrate that PFAS undergo transport, redistribution, and accumulation after root absorption, with significant interspecific variation. Elucidating the underlying mechanisms will enhance understanding of PFAS behavior in plants.

#### 1.4 Regulation of Plant Metabolic Pathways Under PFAS Stress

Following uptake, PFAS distribute widely in plant cells, typically inducing reactive oxygen species (ROS) production. Plants can adjust metabolism and gene expression to cope with low ROS levels, while high ROS levels cause cellular damage. Li et al. (2021a) treated hydroponic lettuce with PFOA, observing dose-dependent increases in ROS (H<sub>2</sub>O<sub>2</sub> increased 8.1%–38.7%, ·OH increased 11.3%–26.4%, ·O<sub>2</sub><sup>-</sup> increased 3.1%–22.8%). Both enzymatic antioxidants (catalase, peroxidase, glutathione peroxidase) and non-enzymatic systems (glutathione, cinnamic acid, *p*-coumaric acid, 5-O-caffeoylquinic acid, coumarin, flavonoids, flavonols, and other polyphenols) were activated. Guo et al. (2020) used high-throughput non-targeted metabolomics to study PFOS effects on *Arabidopsis* leaves after 30 days, identifying 53 significantly altered metabolites (21 upregulated, 32 downregulated). Changes in primary metabolites (amino acids,

sugars, nucleotides) provided the metabolic basis for oxidative stress responses, while secondary metabolites (indole derivatives, phenylpropanoids, flavonoids, vitamins, phytohormones) were also regulated to mitigate oxidative damage.

PFAS primarily affect plants by disrupting metabolism. Li et al. (2020a, b) co-exposed lettuce to 500, 1,000, 2,000, and 5,000 ng · L<sup>-1</sup> PFOA and PFOS (1:1 ratio) for 28 days. While biomass remained unchanged, metabolomics revealed significant alterations. In leaves, multiple metal ions decreased (Na<sup>+</sup> by 15.4%-47.8%, K<sup>+</sup> by 8.1%-10.0%, Mg<sup>2+</sup> by 14.2%-23.9%, Cu<sup>2+</sup> by 12.6%-20.2%, Fe<sup>2+</sup> by 1.8%-25.6%, Ca<sup>2+</sup> by 3.8%-21.3%, Mo<sup>6+</sup> by 10.4%-17.9%), while Zn<sup>2+</sup> increased (7.4%-24.2%), altering downstream metabolism. Amino acids, peptides, fatty acids, and lipids decreased, while purines and nucleosides increased. Phytol (14.8%-77.0%) and abscisic acid (60.7%-73.8%) decreased substantially, affecting photosynthesis and signaling. Elevated polyphenol and phenolic antioxidant levels provided defense against oxidative stress (Li et al., 2020a). In roots, key metabolites including antioxidants, lipids, amino acids, fatty acids, carbohydrates, linolenic acid derivatives, purines, and nucleosides were significantly altered. At 5,000 ng · L<sup>-1</sup> PFOA and PFOS, the tricarboxylic acid cycle was disrupted. Lettuce roots employed multiple strategies: altering membrane composition, regulating signaling molecules, enhancing inorganic nitrogen fixation, remodeling carbon-nitrogen metabolism, adjusting energy metabolism, activating antioxidant synthesis, and upregulating purine metabolism (Li et al., 2020b).

PFAS also alter gene expression. Fan et al. (2020) used RNA-Seq to identify 1,131 differentially expressed genes (DEGs) in *Arabidopsis* roots and shoots under PFOA treatment, including 41 and 29 transporter genes induced in shoots and roots, respectively (12 shared). These transporters likely mediate root uptake and root-to-shoot translocation. Notably, ROS-regulating genes showed greater differential expression in shoots than roots, consistent with higher PFOA accumulation and growth inhibition in shoots. Among shoot DEGs, 57 were ROS-induced transcripts, and glutathione S-transferase genes involved in glutathione synthesis were upregulated. qRT-PCR validation confirmed that ROS stress marker genes (*GSTU9*, *GSTU24*, *UGT74E2*, *OXI1*, *AOX1A*) increased with PFOA concentration, while ROS-scavenging enzyme genes (*CAT2*, *APX1*, *sAPX*, *Fe-SOD*) were downregulated, with corresponding decreases in enzyme activities. Zhang et al. (2022) found that PFOA and PFOS inhibited *Arabidopsis* root growth by regulating auxin and abscisic acid signaling pathways, affecting hormone content and signaling, and suppressing cell division in root apical meristems. Thus, PFAS accumulation triggers changes in gene expression and metabolism, ultimately manifesting as phytotoxicity in physiological indicators and phenotypes (Yang et al., 2015; Li et al., 2021c; Zhang et al., 2022).

### 1.5 Transport Mechanisms of PFAS in Plants

Plant uptake of chemicals occurs through transmembrane diffusion and carrier-mediated transport. Concentration-dependent uptake kinetics following

Michaelis-Menten equations indicate carrier-mediated processes (Zhan et al., 2010). 2,4-dinitrophenol (2,4-DNP) uncouples oxidative phosphorylation and proton electrochemical gradients. Wang et al. (2020) found that  $0.5 \text{ mmol} \cdot \text{L}^{-1}$  2,4-DNP reduced PFOS and PFOA uptake in *A. orientale* by 14.4% and 24.1%, respectively, indicating energy-dependent, carrier-mediated transport. Glycerol and silver nitrate, aquaporin inhibitors, significantly reduced PFOS (25.3%–30.9%) and PFOA (22.3%–33.9%) uptake, suggesting aquaporin involvement. 9-anthracene carboxylic acid (9-AC) and 5-nitro-2-(3-phenylpropylamino)benzoic acid (NPPB) block slow anion channels, while 4,4'-diisothiocyanostilbene-2,2'-disulfonate (DIDS) blocks fast anion channels. Wang et al. (2020) showed that 9-AC and NPPB reduced PFOS uptake in *A. orientale* roots by 11.1% and 27.6%, respectively, while NPPB and DIDS reduced PFOA uptake by 23.9% and 16.4%, respectively. Competitive effects between PFOS and PFOA suggested shared transporters. Wen et al. (2013) demonstrated that maize root uptake of PFOS and PFOA followed Michaelis-Menten kinetics, confirming carrier-mediated transport. Metabolic inhibitors sodium azide ( $\text{NaN}_3$ ) and sodium orthovanadate ( $\text{Na}_3\text{VO}_4$ ) inhibited maize root PFOA uptake by 83% and 43%, respectively, but had minimal effects on PFOS uptake. Glycerol and silver nitrate reduced PFOS uptake by 31% and 25%, respectively, but did not affect PFOA uptake. NPPB and DIDS reduced PFOS uptake by 33% and 30%, respectively, while 9-AC reduced PFOA uptake by 28%.

Yu et al. (2021) studied PFOS uptake in HACV and LACV lettuce, finding Michaelis-Menten kinetics. Metabolic inhibitors  $\text{NaN}_3$  and  $\text{Na}_3\text{VO}_4$  had limited effects, while aquaporin inhibitor glycerol significantly reduced PFOS uptake by 32.3% in HACV and 20.1% in LACV, and silver nitrate reduced uptake by 57%–59% in both varieties. 9-AC and NPPB significantly reduced PFOS uptake in LACV by 32.0% and 24.6%, respectively, and in HACV by 11.0% and 26.1%, respectively, while DIDS only affected HACV. qRT-PCR analysis revealed significantly higher expression of aquaporin genes (*PIP1-1*, *PIP2-2*), fast anion channel genes (*ALMT10*, *ALMT13*), and slow anion channel genes (*SLAH1*, *SLAH2*) in HACV compared to LACV, with significant induction by PFOS treatment for all except *ALMT13*. These inhibitor and gene expression studies demonstrate that PFAS uptake is carrier-mediated active transport, though specific transporters remain unidentified. We are currently using CRISPR/Cas9 genome editing and overexpression technologies to generate genetic materials for candidate genes to provide definitive evidence for PFAS transport mechanisms.

In summary, multiple factors influence plant uptake and accumulation of PFAS at different levels, reflecting the diversity and complexity of these mechanisms. PFAS accumulation depends not only on PFAS physicochemical properties (chain length, functional groups), soil characteristics (composition, mineral content, organic matter, pH), and plant traits (root protein content, exudation, subcellular distribution, translocation efficiency) but also on interactions among these factors. Conversely, PFAS affect plant metabolism, gene expression, and growth ([Figure 2: see original paper]). Beyond experimental studies, machine learning and artificial intelligence can help identify patterns in complex

systems. Xiang et al. (2023) extracted data from literature published between 2007–2022 to develop machine learning models that accurately predict root concentration factors (RCFs) for PFAS (including branched isomers), providing a tool for rapid assessment of root uptake in complex PFAS-soil-plant systems to ensure food safety. Since translocation mechanisms differ from root uptake mechanisms and many plant shoots serve as food sources, developing similar models to predict root-to-shoot translocation factors is equally valuable.

[Figure 2: see original paper] indicates PFAS; indicates soil; indicates soil organic matter; indicates dissolved organic carbon; indicates transporters in cell membrane; indicates the transportation direction of PFAS.

**Fig.2** A schematic diagram of the mutual influence between plants and PFAS

PFAS are widely used due to their excellent physicochemical properties but inevitably enter the environment during production, application, and disposal. Their persistence, toxicity, and bioaccumulation classify them as emerging POPs. Soil represents the largest PFAS sink, and plants interact closely with soil. Plants absorb PFAS through roots, translocate them via apoplastic and symplastic pathways to shoots, and distribute them throughout cells. At sufficient concentrations, PFAS induce oxidative stress, disrupt metabolism, remodel gene expression profiles, and ultimately alter growth phenotypes. Current research focuses on PFAS effects on plant development, distribution in plants, and impacts on physiology, biochemistry, metabolism, and gene expression.

As discussed, PFAS uptake and translocation are carrier-mediated active processes, but the specific carriers and channel proteins remain unidentified—representing a key future research direction. High/low-accumulation crop varieties with similar genetic backgrounds provide ideal materials for elucidating molecular mechanisms. Clarifying these mechanisms will have important theoretical significance and practical applications, enabling development of low-accumulation varieties for food safety (Xiang et al., 2020b) and hyperaccumulation varieties for phytoremediation (Li et al., 2021b). Additionally, plants influence PFAS soil distribution not only by secreting organic acids, sugars, and proteins (DOC) but also indirectly through microbial recruitment and enrichment. These interactions and mechanisms warrant further investigation.

Rational utilization and remediation of PFAS-contaminated soils are critical concerns. For low-contamination soils, widespread screening of crop varieties can identify low-accumulation cultivars for safe food production. For heavily contaminated soils, appropriate remediation measures are essential. Among remediation technologies (physical, chemical, microbial, and phytoremediation), phytoremediation is promising due to its environmental friendliness, low cost, effectiveness, and lack of secondary pollution. Key challenges include identifying suitable plants with high biomass and hyperaccumulation capacity. Additionally, phytoremediation is slow and requires long periods, making integrated approaches valuable. Combining phytoremediation with microbial or nanotech-

nological methods has shown success in heavy metal remediation (Yulikasari et al., 2024; Zhao et al., 2024), and exploring such combined technologies represents an important direction for PFAS pollution control.

In conclusion, in-depth research on plant-PFAS interactions and rational utilization/remediation of contaminated soils will provide strong scientific support for environmental protection and ecological security related to PFAS.

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