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Review

Advances in bioremediation strategies for PFAS-contaminated water and soil

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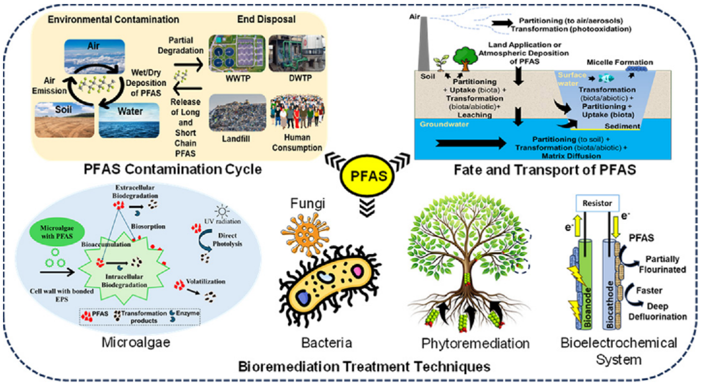
HIGHLIGHTS

- PFAS is prevalent in soil, water and air, posing significant threats to all life forms.
- Phytoremediation coupled with bacterial, fungal and microalgal-based approaches are promising.
- Microbial composition and cationic complexation govern biotransformation of PFAS.
- Bioelectrochemical systems combine synergy of electrochemistry with bioremediation.

GRAPHICAL ABSTRACT



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ABSTRACT

Per- and poly-fluoroalkyl substances (PFAS) are emerging contaminants, posing adverse impacts on water and soils due to their persistence, chemical transformations, and bioaccumulation. With over 15,000 different PFAS compounds being identified globally, their toxic effects and half-life spanning from 72 h to 8.5 years in humans are a serious concern. Bioremediation has emerged as an environmentally-friendly and cost-effective approach for PFAS degradation. However, there is still limited understanding of PFAS interactions with microorganisms and the roles of promising microbes in transforming PFAS into non-toxic end products. The knowledge about biotransformation of PFAS is essential to ameliorate the adaptation of microorganisms to local matrix and environment as well as to strengthen the natural enzymatic pathways and activities at a commercial scale, which is a major challenge. This review aims to address these gaps by providing a comprehensive analysis of recent developments in the bioremediation of PFAS-contaminated soil and water systems. The review focuses on the capabilities of phytoremediation, bioelectrochemical systems, and microbial species, including bacteria, fungi, and microalgae. Additionally, this study offers an in-depth overview of PFAS sources, their physicochemical characteristics, and their environmental fate and transport. Furthermore, it examines microbial metabolic activity, the formation of degradation intermediates, the role of co-metabolism, and the behaviour of microorganisms

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Phytoremediation
Mycoremediation

under PFAS stress as well as highlights future research directions. The key findings from this review include: 1) microbial community composition, field application, presence of co-substrate and cationic complexation govern biotransformation and fate of PFAS, 2) long chain PFAS are more susceptible to accumulate in the roots due to high hydrophobicity, and 3) algae-bacteria symbiotic relationships reduce microalgae growth inhibition and stimulates PFAS removal. Overall, this review emphasizes the potential of bioprocesses for large-scale PFAS bioremediation, contributing to environmental protection and mitigating the risks associated with PFAS contamination.

Abbreviations

ASA	Ascorbic acid
AEC	Anion exchange capacity
AFFF	Aqueous film forming foam
APX L	Ascorbate peroxidase
ATS	Algal Turf Scrubber
BCF	Bioconcentration factor
BES	Bioelectrochemical system
CAT	Catalase
CEC	Cation exchange capacity
Cyt *b*6f	Cytochrome *b*6f Complex
EC	Emerging contaminant
EtFOSA	Ethyl Perfluorooctane Sulfonamide
EtFOSAA	N-Ethyl Perfluorooctane Sulfonamidoacetic Acid
EtFOSE	Ethyl Perfluorooctane Sulfonamide Ethanol
FHxS	Perfluorohexane Sulfonate
FOSA	Perfluorooctane Sulfonamide
FOSE	Fluorooctane Sulfonamide Ethanol
FT	Fluorotelomers
FTAL	Fluorotelomer Aldehyde
FTCA	Fluorotelomer carboxylic acid
FTOH	Fluorotelomer alcohol
FtTAoS	Fluorotelomer thioether amido sulfonate
FTUCA	Fluorotelomer unsaturated carboxylic acid
GAC	Granular activated carbon
GAPDH	Glyceraldehyde-3-phosphate dehydrogenase
GPX	Glutathione peroxidase
GSH	Glutathione
GSR	Glutathione reductase (NADPH)
GST	Glutathione S-transferase
HFPO-DA	Hexafluoropropylene oxide dimer acid
i-PFAS	Ionic per and polyfluoroalkyl substances
Koc	Organic carbon-normalized distribution coefficient
MDC	Microbial desalination cell
MDHA	Monodehydroascorbic acid
MEC	Microbial electrolysis cells
MeFBSAA	N-Methyl Perfluorobutanesulfonamidoacetic Acid
MeFBSE	Methyl Perfluorobutanesulfonamido Ethanol
MES	Microbial electrochemical systems
NAPL	Non-aqueous phase liquid
NDH-1	Nicotinamide adenine dinucleotide (NAD) + hydrogen (H) dehydrogenase-1
NdhH	Nicotinamide adenine dinucleotide phosphate hydrogen dehydrogenase subunit H
PFAA	Perfluoroalkyl acids
PFAS	Per- and poly-fluoroalkyl substances
PFBA	Perfluorobutanoic acid
PFBS	Perfluorobutane sulfonic Acid
PFBSI	Perfluorobutanesulfonyl Iminium
PFCA	Perfluoroalkyl carboxylic acid
PFDA	Perfluorodecanoic Acid
PFDoDA	Perfluorododecanoic Acid
PFDoDS	Perfluorododecane sulfonic Acid
PFDS	Perfluorodecane sulfonic Acid
PFHpA	Perfluoroheptanoic Acid
PFHpS	Perfluoroheptane sulfonic Acid
PFHxA	Perfluorohexanoic Acid
PFHxS	Perfluorohexane sulfonate
PFMeUPA	Perfluoro-5-methylundecanoic Acid
PFNA	Perfluorononanoic acid
PFNS	Perfluorononane sulfonic Acid
PFOA	Perfluorooctanoic acid
PFOS	Perfluorooctane sulfonate
PFOSI	Perfluorooctane Sulfonyl Iminium
PFPeA	Perfluoropentanoic Acid
PFPeDA	Perfluorotetradecanoic Acid
PFPeS	Perfluoropentane sulfonic Acid
PFSA	Perfluoroalkyl sulfonic acid
PFTeDS	Perfluorotetradecane sulfonic Acid
PFTrDA	Perfluorotridecanoic Acid
PFTrDS	Perfluorotridecane sulfonic Acid
PFUnDA	Perfluoroundecanoic Acid
PFUnDS	Perfluoroundecane sulfonic Acid
PRDX6	peroxiredoxin 6, 1-Cys peroxiredoxin
PS I	Photosystem I
PS II	Photosystem II
PsaD	Photosystem I protein D
PVDF	Polyvinylidene fluoride
RAPIMER	Renewable Artificial Plant for In-situ Microbial Environmental Remediation
ROS	Reactive oxygen species
SOD	Superoxide dismutase
SOD1	Superoxide dismutase - Fe-Mn family
SOM	Soil Organic Matter
sPQ	Plastoquinone
TALEN	Transcription activator-like effector nucleases
TBA	Thiobarbituric acid
TFA	Trifluoroacetic acid
WWTPs	Wastewater treatment plants
ZFN	Zinc-finger nucleases

1. Introduction

Per- and poly-fluoroalkyl substances (PFAS) are synthetic fluorinated organic chemicals widely found in soil, water, and air, posing significant hazards to all life forms (Podder et al., 2021; Zhou et al., 2024). Polyfluoroalkyl substances contain both carbon-fluorine (C-F) and carbon-hydrogen (C-H) bonds, while perfluoroalkyl substances consist solely of C-F bonds (Zhou et al., 2024). The strong C-F bonds in PFAS enhance their resistance to degradation and heat, making them valuable for commercial and industrial applications (e.g., food packaging, leather goods, fabrics, surfactants, cookware, and processing aids) (Feng et al., 2024; Thapa et al., 2024). Due to their widespread production, gradual release into the environment, persistence, and ability to accumulate in living organisms (Ling, 2024; Thapa et al., 2024), as well as recent evidence of negative health impacts, PFAS have become a global environmental concern (Ling, 2024). A total of more than 15,000 variations of PFAS have been identified globally (Pervez et al., 2024), with hexafluoropropylene oxide dimer acid (HFPO-DA), perfluorooctane sulfonate (PFOS), perfluorooctanoic acid (PFOA), and perfluorohexane sulfonate (PFHxS), being particularly concerning (Thapa et al., 2024). This has led to the establishment of drinking water standards in the USA: 4 parts per trillion (ppt) for both PFOA and PFOS, whereas 10 ppt each for three PFAS chemicals: perfluorononanoic acid (PFNA), PFHxS, and HFPO-DA (commonly known as Gen X). Moreover, EPA's hazard index of 1 was designated for mixtures comprising two or more of PFHxS, PFNA, PFBS, and HFPO-DA (EPA, 2024).

The occurrence, migration, and ultimate fate of PFAS in the natural surroundings are shown in Fig. 1. These persistent chemicals can contaminate our food chain when plants take them up from water used for irrigation, affecting vegetables, meat, milk, fruits, and cereals (Ling, 2024). PFAS contamination in soil and sediment disrupts the communities of microorganisms that live there, impacting the health of entire soil ecosystem (Abou-Khalil et al., 2022; Ehsan et al., 2024). The accumulation of PFAS in the bottom layers of aquatic environments (benthic zone) further threatens these habitats (Ehsan et al., 2024). Even marine animals like polar bears, whales, seals, dolphins, and porpoises can have concerningly high levels of PFOS (up to 1900 ng/g) (Thapa et al., 2024), highlighting the persistence and detrimental effects of PFAS (such as reproductivity toxicity, hormonal disorder, neurotoxicity, immunotoxicity, hepatotoxicity, pulmonary toxicity) throughout the food chain (Mahinroosta and Senevirathna, 2020).

PFAS migration from air to water bodies and soil occurs via both dry and wet deposition (Wang et al., 2023). During dry deposition, dust particles containing attached ionic PFAS (i-PFAS) settle due to gravity. Once deposited, these particles can be further transported by wind, erosion, or vegetation. Wet deposition, however, is the primary mechanism for removing PFAS from the atmosphere and depositing them onto the Earth's surface, particularly topsoil (Wang et al., 2023). A study by Shimizu et al. (2021) reported an annual PFAS flux of 30 $\mu g/m^3$ via wet deposition, which is nearly 21 times higher than the 1.4 $\mu g/m^3$ reported for dry deposition. This finding underscores the effectiveness of precipitation in removing both particle-bound and gaseous PFAS from the atmosphere. The combination of long-range atmospheric transport and wet deposition can lead to the widespread presence of PFAS, even in remote regions like the Arctic and Antarctic (Wang et al., 2023). Moreover, elevated levels of deposited PFAS in soil ultimately result in leaching into drinking water sources and aquatic ecosystems, contributing to widespread water contamination, a growing concern globally (Ahmed et al., 2020b). Despite significant efforts, current PFAS treatment technologies, including adsorption, advanced oxidation, and membrane filtration, remain limited by cost, scalability, and incomplete degradation.

Excessive exposure to PFAS has been linked to numerous health issues, including an increased risk of cancer, compromised immune function, cell damage, liver damage, elevated cholesterol levels, obesity, neurological disorders, and adverse pregnancy outcomes (Ehsan et al., 2024; Thapa et al., 2024; Zhou et al., 2024). Between 1951 and 2002, an estimated 2600 to 5000 tonnes of PFAS, including C4 - C14 compounds, were released into the environment (Nazmul et al., 2024). Alarmingly, projections suggest an additional 5510 tonnes may be discharged between 2015 and 2030 (Nazmul et al., 2024). The situation is further exacerbated by the complex environmental behavior of PFAS. “Precursor” PFAS compounds can partially degrade into shorter/different chain PFAS, creating ongoing environmental risks (Ling, 2024). For instance, the degradation of some side-chain fluorinated polymers and gases generates highly mobile and persistent perfluoroalkyl acids (PFAAs) such as trifluoroacetic acid (TFA) (Ling, 2024). As a result, even when certain PFAS compounds are no longer in commercial use, their degradation products can persist in the environment through biological processes, photolysis (breakdown by sunlight), and oxidation (Ling, 2024). Understanding these transformation mechanisms is crucial for developing strategies to mitigate PFAS contamination, particularly in engineered environments like soil remediation sites.

The growing public concern over significant exposure risks to PFAS necessitates urgent mitigation measures to remove these contaminants from the environment (Ehsan et al., 2024; Shahsavari et al., 2021). Currently, several traditional physical and chemical treatment techniques are available for PFAS removal, including adsorption, incineration, advanced oxidation processes, electrochemical oxidation, sonochemical degradation, hydrothermal, supercritical, and plasma treatment (Berhanu et al., 2023). Adsorption is a promising method for PFAS removal from wastewater due to its simple design, adsorbent's resistance to toxic substances, high efficiency, and ease of operation (Wanninayake, 2021). However, as adsorption concentrates PFAS from the liquid phase to the solid phase, it requires a sustainable solution for disposing of or regenerating the spent adsorbent material through effective degradation of the adsorbed PFAS (Wanninayake, 2021). Major drawbacks of adsorption include high operational and maintenance costs, substantial energy demands for regeneration, and the need for offsite residual management (Wanninayake, 2021).

Thermal treatment, such as incineration, involves heating soil up to 1000 °C to degrade and vaporize PFAS (Ahmed et al., 2020a; Mahinroosta and Senevirathna, 2020). Furthermore, certain PFAS compounds with high melting points exhibit significant resistance to thermal treatment. Additional drawbacks of thermal methods include the high temperatures required, potential damage to soil structure, and the large capital investment needed for large-scale PFAS-contaminated sites (Mahinroosta and Senevirathna, 2020). Hydrothermal treatment is another thermal treatment technique for PFAS removal in sludge, which operates at high pressure (10–15 MPa) and temperature (250–350 °C) and transforms organic matter in sludge into liquid biocrude oil (Zhou et al., 2024). This process is more economical due to 50 % low energy consumption than other thermal techniques. The efficiency of this

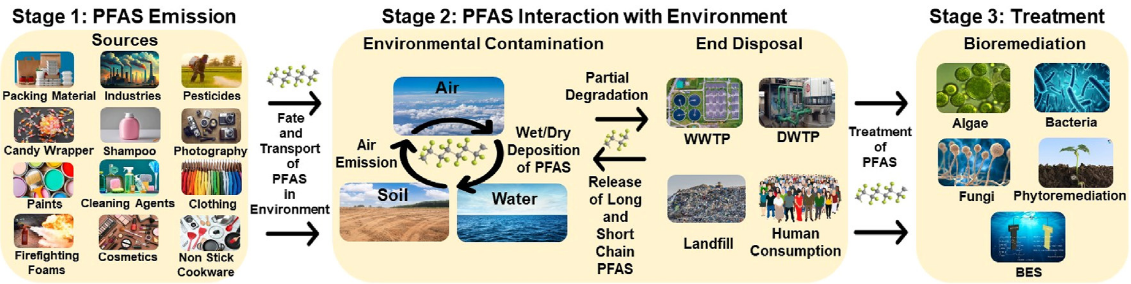


Fig. 1. PFAS occurrence, distribution, and exposure pathways to living organisms (Adapted from Ehsan et al., 2024; Ji et al., 2020), where WWTP: Wastewater Treatment Plant, PFAS: Per- and poly-fluoroalkyl substances, BES: Bioelectrochemical System, DWTP: Drinking water treatment plant.

process is dependent on PFAS structure and therefore, its practical feasibility on a large scale is restricted due to its inefficiency in treating diverse PFAS types (Boshir et al., 2020).

Additionally, advanced oxidation processes (AOPs) such as chlorination, ultraviolet (UV) radiation, UV/H_2O_2, ozonation, and potassium permanganate have proven to be largely ineffective for total PFAS degradation and generally result in the formation of less amount of shorter chain PFAS compound (Ahmed et al., 2020a). This is because the highly electronegative fluorine atom resists oxidation reactions. Replacing the fluorine atom from PFOA and PFOS with another oxidant is thermodynamically unfavorable due to fluorine's high reduction potential of 3.6 V, making it a strong oxidizing element (Ahmed et al., 2020a; Berhanu et al., 2023). Compared with traditional AOPs, plasma treatment technology which utilizes plasma electrical discharge has been proven to be effective for PFAS removal from ground and surface water. This process exhibits high efficiency, but is expensive than AOPs and generates greenhouse gases and hazardous end products (Boshir et al., 2020; Wanninayake, 2021). Furthermore, in recent years, electrochemical oxidation has received significant research interest for PFAS removal, due to its potential to treat diverse persistent micropollutants. However, this technique is not effective for removing shorter chain PFAS. Besides, complications associated with frequent corrosion of electrodes and generation of toxic by-products such as perchlorate, hydrogen fluoride, bromate, and chlorine gas in the presence of organics, inorganics, such as Cl^-, are possible drawbacks (Wanninayake, 2021). Besides, PFAS degradation was found to be enhanced at supercritical water treatment when temperature and pressure are more than 350 °C and 22.1 MPa, respectively, but the exorbitant energy demand restricts its practical implementation at large scale (Boshir et al., 2020; Mutanda et al., 2023).

In comparison, PFAS pollutants in the environment can be sustainably addressed through biological treatment, which leverages the inherent capabilities of living microorganisms and their enzymes to break chemical bonds in PFAS, producing harmless byproducts (Berhanu et al., 2023). Bioremediation involves using biological systems (either introduced or natural) to eliminate contaminants (Berhanu et al., 2023). Microbial species cleave the C-F bond in PFAS compound either by (i) oxidation i.e. introducing oxygen across the C-F bond or (ii) reduction i.e. electron addition across the C-F bond (Shahsavari et al., 2021; Upadhyay et al., 2023). This method requires low capital investment, causes less disruption to water and soil ecosystems, and is known to remove persistent organic pollutants (POPs) effectively (Zhang et al., 2022). However, the diversity and unique properties of PFAS may require microbial evolution to degrade these compounds, which is vital for maintaining ecological balance (Berhanu et al., 2023; Hu et al., 2014). Biological degradation, utilizing algae, bacteria, fungi, phytoremediation, and bioelectrochemical systems, transforms or defluorinates organic compounds through various metabolic pathways (Fig. 1) and is a cost-effective solution for in-situ PFAS remediation (Berhanu et al., 2023).

Bacterial species such as *Gordonia, Acidimicrobium, Pseudomonas* can degrade PFAS under both anaerobic and aerobic conditions, though aerobic biotransformation is more commonly reported (Zhang et al., 2022). Microalgae such as *Scenedesmus*, *Chlorella*, and *Chlamydomonas* are also capable of PFAS degradation and can thrive in extreme environmental conditions such as low light, saline stress, unfavorable temperature or pH and nutrients limitation (Zhou et al., 2022; Sharma et al., 2024). These microalgae exhibit short reproduction times, fast growth rates, and high adaptability to various wastewater types (Zhang et al., 2022). In aquatic systems, symbiotic relationships between microalgae and bacteria can enhance PFAS removal (Wu et al., 2022). Fungi also play a critical role in breaking down complex organic compounds into simpler molecules (Zhang et al., 2022). Bioelectrochemical systems (BESs) use exoelectrogens to treat recalcitrant compounds while generating bioelectricity (Ji et al., 2020). Phytoremediation leverages plant roots to uptake and degrade PFAS, offering an economical and reliable in-situ removal method for both aquatic and soil environments (Zhang et al., 2022). Effective bioremediation depends on understanding of PFAS sorption behavior, fate, and transport in soils to release them from surfaces (LaFond et al., 2023).

Furthermore, the bibliometric analysis using VOS Viewer software revealed that from 2008 to 2024, only 179 studies on “PFAS” and “bioremediation” were published in the Scopus database. In contrast, 417 studies were found when focusing broadly on PFAS removal (Fig. S1). This discrepancy shows that most studies (Connor et al., 2022; Nazmul et al., 2024) emphasize PFAS emission, distribution, detection, and toxicity, while sustainable, economical bioremediation strategies remain underexplored, despite strict regulations in Europe and USA (Zhang et al., 2022). Fluorinated chemicals challenge microbial metabolism (Upadhyay et al., 2023; Wackett, 2022), making it crucial to identify microbes capable of degrading PFAS. However, microbial interactions with PFAS are not well understood. We hypothesize that, to develop and strategize effective bioremediation methods for addressing PFAS contamination, it is important to understand microbial degradation pathways with a focus on microbial response, metabolic activity, and self-adaptation mechanism under PFAS stress conditions. Therefore, to fulfill the existing gaps in the published literature, the objective of this review is to critically explore recent advancements in PFAS bioremediation techniques, including fungi, microalgae, bacteria, phytoremediation, and bioelectrochemical systems. The novelty lies in examining bioremediation for both soil and aquatic environments, including the role of co-metabolism in PFAS removal. The study discusses PFAS sources and impacts (Section 1), followed by their properties and classification (Section 2), environmental transport (Section 3), and performs an in-depth assessment of bioremediation strategies, degradation pathways, and dynamic behaviour of microorganisms at varying PFAS exposure concentrations and under different environmental conditions (Section 4). It also addresses post-treatment opportunities and future research directions, providing valuable insights into sustainable PFAS treatment.

2. Characteristics and classification of PFAS with a focus on bioremediation

Understanding the physicochemical properties of PFAS is crucial for effective bioremediation (Sharma et al., 2024). The vast diversity of PFAS molecules, with different weights, charges, and chain structures, presents a challenge for using a single treatment technique (Ji et al., 2020). Because the applicability and efficiency of a treatment method depends on the specific type of PFAS molecule (Mahinroosta and Senevirathna, 2020), considering their key characteristics is essential for designing a cost-effective treatment strategy (Zhou et al., 2024).

As categorized in Fig. S2, PFAS are either non-polymer or polymer substances. Perfluoroalkyl carboxylic acids (PFCAs) and perfluoroalkyl sulfonic acids (PFSAs) are the prominent subcategories within the non-polymer group, attracting significant regulatory and scientific attention (Lyu et al., 2022). In the polymer category, PFAS compounds are formed from monomers and are classified into fluoropolymers, side-chain fluorinated polymers, and polymeric perfluoropolyethers (Phong et al., 2020). These polymers can break down into terminal PFAA products, acting as PFAA precursors. These precursors can have various functional groups, including alcohol, epoxide, sulfide. (Phong et al., 2020).

Among the various types of PFAS chemicals, perfluoroalkyl acids (PFAAs) are concerning (Phong et al., 2020; Thapa et al., 2024). The number of carbon atoms in a PFAS molecule is particularly important for their transport and fate. PFAAs have the formula of C_nF_{2n-1}-R, where “n” defines the chain length ($n \geq 1$) and R is the attached group (Mahinroosta and Senevirathna, 2020; Phong et al., 2020). Longer carbon chains (PFCA ($C_nF_{2n+1}COOH$) $\geq$ C8, PFSAs $\geq$ with C $\geq$ 6) (Gagliano et al., 2020; Thapa et al., 2024; Veciana et al., 2022) bioaccumulate rapidly and require specialized remediation due to stronger adsorption (Gagliano et al., 2020). Conversely, shorter PFCAs ($\leq$C7) (Phong et al., 2020) exhibit greater mobility and high water solubility, adversely impacting biodegradation pathways, thus posing long-term ecological endangerment concerns (Brendel et al., 2018; Gagliano et al., 2020; Li et al., 2020). Studies suggest a correlation between increasing chain length and higher log K_d (distribution coefficient) values (Feng et al., 2024). Higher log K_d values indicate strong binding to soil, potentially hindering microbial access (Mahinroosta and Senevirathna, 2020). Besides chain length, the terminal functional group (e.g., -COOH in PFCAs, $-SO_3H$ in PFSAs) influences biodegradation (Feng et al., 2024; Gagliano et al., 2020; Thapa et al., 2024). These groups impact stability, environmental fate, and the initial attack points for microbial biodegradation (Berhanu et al., 2023).

Polyfluoroalkyl substances comprise C-H bonds, forming weak chains that are susceptible to biodegradation (Shahsavari et al., 2021). As per published literature, biodegradation of precursors arises in the non-fluorinated part of the structure. Though defluorination in PFAS precursors has been noticed in C-F bonds in case of FTOH, this process is restricted to polyfluoroalkyl substances and not observed in perfluoroalkyl substances (Behnami et al., 2024). The compounds with more fluorinated carbons demonstrate higher resistance towards biodegradation (Behnami et al., 2024).

Under aerobic conditions, Che et al. (2021) investigated the structure reactivity relationship and noticed that the replacement of F atom with one or two H atoms in the α position can decline the microbial defluorination efficiency. For instance, microbial defluorination reached 85 % in case of 3,3,3, trifluoropropionic acid whereas no removal was observed for 2,2 difluoropropionic acid and 2,2,3,3 tetrafluoropropionic acid when treated with wastewater treatment plant (WWTP) sludge. Therefore, it has been reported that in PFAS molecule, C-H bonds and sp^2 C-F bonds at the α and β position, respectively are pivotal for microbial defluorination via β oxidation pathways. The presence of non-fluorinated carbons and the position of functional groups can also influence biotransformation pathways (Berhanu et al., 2023). Besides, studies have observed that unsaturated PFAS removal efficiency was higher in aerobic conditions than anaerobic conditions, indicating that process conditions also exhibit a crucial role in biotransformation of PFAS (Zhou et al., 2024). The presence of non-fluorinated carbons and the position of functional groups can also influence biotransformation pathways (Berhanu et al., 2023).

For the same carbon chain length, due to the presence of an additional CF_2 bond, the PFSAs are generally more hydrophobic and tend to bioaccumulate more than PFCAs (Gagliano et al., 2020; Veciana et al., 2022). Long chain PFASs such as PFCAs with ≥ C8 and PFSAs with ≥ C6 show greater inertness and lipophilic characteristics. As shown in Table S1, increasing C-F chain length leads to an increase in octanol water partition coefficient (log K_{ow}) value, indicating greater hydrophobicity (Veciana et al., 2022). For PFAS with same functional group, longer chains can be adsorbed more easily due to their higher hydrophobicity, while shorter chain exhibits greater water solubility with a low tendency to sorb, leading to greater mobility in the environment (Gagliano et al., 2020; Ji et al., 2020; Veciana et al., 2022). In other words, short chain PFAS have lower bioaccumulation potential than long chain PFAS. Consequently, toxic effect of long chain PFAS with sulfonate group on biota is significantly higher than short chain PFAS (Phong et al., 2020). Thus, concern about bioaccumulation led to substitution of long chain PFAS with short chain PFAS for industrial applications (Phong et al., 2020). However, despite low bioaccumulation potential, increased human exposure and adverse health effects attributable to the presence of short chain PFAS in drinking water is also a major apprehension (Gagliano et al., 2020; Podder et al., 2021). Therefore, the European Commission has aimed to completely restrict the usage of all types of PFAS by 2030 (Podder et al., 2021).

A summary of the PFAS characteristics and their influence on the sorption of PFAS on soil and sediments is mentioned in Table S2. Ecosystems contain both branched and linear PFAS. However, branched PFAS degrades much faster than linear PFAS because the stability of perfluoro carbanions is in the order of 3 ° > 2 ° >1 ° for branched and linear structural isomers (Hoomissen and Vyas, 2017; Sima and Jaffé, 2021). In soil, the organic carbon-normalized distribution coefficient (K_{oc}) of branched PFAS is 10 times lower than that of linear isomers (Sima and Jaffé, 2021). This difference in sorption behavior leads to a higher degree of accumulation in plants and living organisms for linear PFAS. The bioconcentration factor for linear PFAS is roughly 10 times higher compared to branched PFAS (Sima and Jaffé, 2021). Due to the complex characteristics of PFAS, their removal presents a major challenge. Therefore, it is crucial to assess and monitor the sources and sorption behavior of PFAS in soil, sediment, and the aqueous medium. This information is vital for formulating suitable action plans and making well-informed decisions for PFAS removal strategies.

3. Fate, transport, and behaviour of PFAS in soil-sediments and aqueous environment

As shown in Fig. 2, the interconnected nature of soil and sediment and surface water and groundwater systems necessitates a holistic approach to

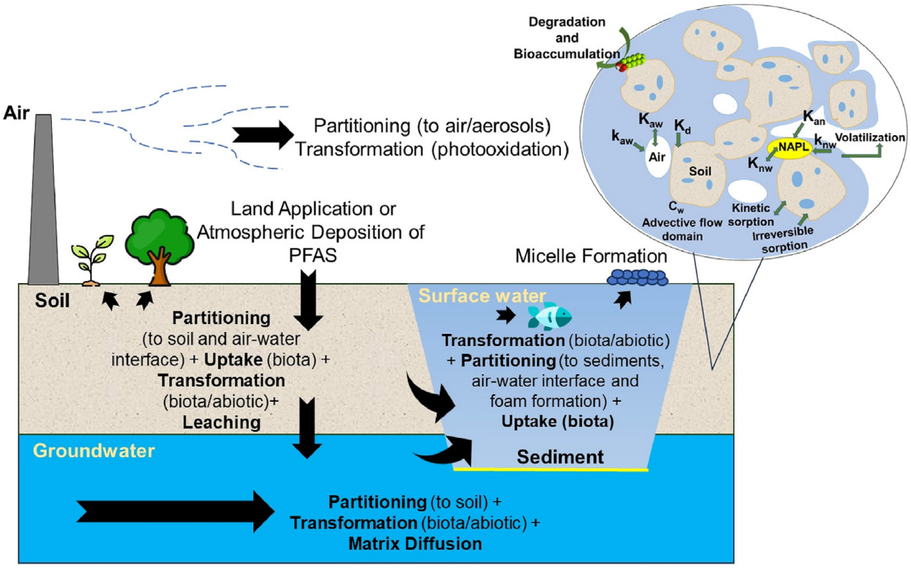


Fig. 2. Schematic illustration of PFAS interaction with environmental matrix (where k_{aw} and k_{nw} indicate interfacial sorption coefficients (cm^3/cm^2) between air-water and NAPL-water coefficient, respectively; K_{aw} and K_{nw} indicate partition coefficient between air-water and NAPL-water, respectively) (Adapted from Sima and Jaffé, 2021).

studying PFAS remediation. While soil and sediment can act as filters and reservoirs for PFAS-laden surface water, these persistent contaminants can eventually migrate and pollute groundwater, posing a long-term threat. These interactions influence the environmental fate of PFAS, which is crucial for developing PFAS bioremediation strategies and protecting our water resources (Sima and Jaffé, 2021). The key processes that govern the phase transfer of PFAS and its interaction with soil/sediments and water in soil/sediment, surface water, and ground water compartments are illustrated in Fig. 2 (Ahmed et al., 2020a). PFAS show hydrophobic partitioning to organic carbon, electrostatic interactions with charged surfaces, and a tendency to assemble at air-water interfaces. These processes increase retention in sediments and unsaturated soils, as well as groundwater retardation, resulting in varying transit rates for distinct PFAS types (Brusseau and Guo, 2021). Additionally, media-specific mechanisms include PFAS diffusion into low-permeability matrices, air transport, and leaching from soil into groundwater. The partitioning and transformation of PFAS generally occur across different environmental mediums, but the media - specific mechanisms are limited to specific habitats or transport channels (Adamson et al., 2020). Despite the recalcitrant behaviour of PFAS due to strong C-F interactions, some polyfluorinated compounds are partially degraded in soil-sediment/aqueous matrices via biological and abiotic processes (Bolan et al., 2021). Common abiotic processes that contribute to the transformation of PFAS include photolysis, hydrolysis, chemical oxidation, thermal oxidation, and ball milling (Bolan et al., 2021; Connor et al., 2022). Additionally, microorganisms can degrade PFAS precursors under both aerobic and anaerobic conditions, with the transformation rate largely depending on the microbial community structure and environmental factors such as pH, temperature, oxygen availability, and the presence of other contaminants (Bolan et al., 2021; Connor et al., 2022). This degradation impacts the temporal and regional trends of PFAS occurrence, as well as their propensity for bioaccumulation (Burkhard, 2021).

Discharged PFAS migrate to terrestrial and aquatic systems, where they are bioaccumulated by plants and subsequently transported through the food web (Ahmed et al., 2020b). PFAS absorption by plant roots occurs through both active and passive processes (Ahmed et al., 2020b). Active transport primarily involves selective adsorption via aquaporins and ion channels, allowing ionized PFAS to enter plant cells. In contrast, passive transport is driven by the diffusion of non-ionized, small-molecule PFAS, facilitated by the plant's transpiration stream (Bolan et al., 2021; Sima and Jaffé, 2021; Thapa et al., 2024). After diffusion along the root apoplast, PFAS are translocated to various plant components, including stems, shoots, and leaves. PFAS uptake has been commonly reported in wetland plants and agricultural crops (Bolan et al., 2021; Sima and Jaffé, 2021; Thapa et al., 2024). Furthermore, when edible plants and food crops, such as grains and stalks, are consumed, PFAS can accumulate in humans and animals, propagating to higher trophic levels through dietary exposure (Bolan et al., 2021). For instance, cows may ingest PFAS by consuming silage grown on contaminated agricultural fields (Bolan et al., 2021). Aquatic habitats are also at high risk, with significant PFAS bioaccumulation observed in species such as seals, whales, seabirds, and polar bears (Thapa et al., 2024). These processes influence the environmental behavior of PFAS, shaping its distribution, persistence, and potential effects on ecosystems and human health (Thapa et al., 2024). A summary of PFAS source and concentration in different environmental components is mentioned in Table S3.

PFAS in surface and groundwater mainly originate from industrial effluents, domestic wastewater, and leachate from municipal solid waste (Wang et al., 2023; Sivagami et al., 2023). Another prominent source is aqueous fire-fighting foams (AFFFs) used at fire training sites, which contain perfluorooctane sulfonamide (PFOSA), PFCAs, and PFSAs. AFFFs release large amounts of PFAS quickly, contaminating nearby surface water and surrounding areas, eventually migrating to groundwater (Venkatesh Reddy et al., 2024). Seepage of contaminated surface water is a major cause of PFAS occurrence in groundwater (Liu et al., 2017a,b; Xu et al., 2021). Liu et al., 2017a,b proposed eq. (1) to estimate the PFAS release through seepage of surface water to groundwater ($G_{seepage}$, kg/day).

$$G_{seepage} = E_{surface\ water} \times \left(1 - P_{sediment\ adsorption}\right) \times SR_{surface\ water} \quad (1)$$

where $E_{surface\ water}$ (kg/m^3) denotes the release of PFAS via surface water emission; $P_{sediment\ adsorption}$ (dimensionless) indicates the fraction of PFAS adsorbed by sediments; and $SR_{surface\ water}$(m^3/day) represents the seepage rate of PFAS from surface water.

Additionally, the use of organic fertilizer (digestate and composts), sewage sludge or biosolids in agricultural fields, and the application of industrial wastewater for irrigation, also expose surface and groundwater to PFAS (Connor et al., 2022; Sharma et al., 2024). The PFAS concentration in agricultural effluents depends on the type of applied biosolids and fertilizers. Compost produced from municipal solid waste has a PFAS concentration ranging from 28.7 to 76 μg/kg (Sharma et al., 2024). A high abundance of short chain PFAS has been reported in aquatic water bodies whereas long chain PFAS are retained in sediments (Venkatesh Reddy et al., 2024). Studies have reported that frequently detected short chain PFAS in surface water comprised of PFBS, PFBA, PFHxA, PFHpA, PFPeA, of which PFBS and PFBA hold >50 % of total concentration of short chain PFAS in the aquatic system and ranges from 0.01 to 4520 ng/L and 1.15–6280 ng/L, respectively (Li et al., 2020; Phong et al., 2020; Sharma et al., 2024).

The total PFAS concentration in groundwater and surface water is strongly influenced by upstream sources (Wang et al., 2023). Therefore, further studies should focus on developing effective, robust, economical, and advanced bioremediation techniques to eliminate PFAS on a large scale (Lenka et al., 2021). In this regard, microbial remediation, fungal based bioremediation, phytoremediation, algal-bacteria mediated degradation, and aerobic or anaerobic biotransformation of PFAS have gained significant research interest and are therefore comprehensively discussed in Section 4.

4. Bioremediation of PFAS from soil and aqueous media

Bioremediation offers a cost-effective and environmentally friendly solution for treating PFAS contaminated soil and water (Shahsavari et al., 2021). This technique has proven successful in removing various organic pollutants such as petroleum hydrocarbons, chlorinated chemicals, and pesticides (Shahsavari et al., 2021). The effectiveness of bioremediation for PFAS hinges on "biodegradation triangle"- a concept that considers PFAS composition, microbial genetics, and environmental conditions (Thapa et al., 2024). Understanding field conditions before treating PFAS contaminated soil and water is crucial for selecting effective bioremediation methods, considering factors such as PFAS characteristics, soil composition, and water conditions (detailed in Table S2). There are several bioremediation techniques, including bacterial remediation, fungal remediation (mycoremediation), phytoremediation (using plants), and microalgal remediation (Douna and Yousefi, 2022), each of which has been discussed extensively in the subsequent sections. Table 1 briefly summarizes the degradation efficiency of different classes of PFAS using various strains of microorganisms (*Acidimicrobium* sp., *Pseudomonas*, *Dehalococcoides,* etc), fungi (*Pleurotus ostreatus*, *Phanerochaete chrysosporium)*, plants (*Eichhornia crassipes, Xanthium strumarium, Polygonum salicifolium,* etc) and microalgae (*Chlorella* and *Scenedesmus* etc) under distinct environmental conditions.

4.1. Bacterial mechanisms and influencing factors

PFAS biodegradation can occur through either oxidative or reductive processes. Microorganisms can utilize PFAS as carbon source and concomitantly execute defluorination (Zhang et al., 2022). Once the C-F bond is cleaved, common degradation enzymes can break down the remaining molecules (Shahsavari et al., 2021). However, the strong C-F bond necessitates significant energy input, provided by these oxidative or

Table 1
Performance summary of PFAS removal efficiency under different bioremediation approaches.

Type of PFAS	Bioremediation	Strain	Conditions	Degradation efficiency/ Transformation Products	References
Perfluorooctanoic acid (PFOA) and perfluorooctane sulfonate (PFOS)					
PFOA and PFOS	Bacteria	*Acidimicrobium* sp. A6	pH: 4.5–5, anaerobic, 30 °C PFAS concentration: 0.1 and 100 mg/L, duration: 100 days	60 %	Huang and Jaffé (2019)
PFOA	Bacteria	*Acidimicrobium* sp. A6	pH: 4.5–5, anaerobic, 25 °C, PFAS concentration: 0.2 and 10 mg/L, duration: 150 days	More than 50 %	Huang et al. (2022)
PFOA	Bacteria	*Acidimicrobium* sp. A6	pH: 5–5.5, anaerobic, PFAS concentration: 47 mg/L, duration: 18 days	77 %	Ruiz-Urigüen et al. (2022)
PFOA	Bacteria	*Pseudomonas parafulva* YAB1	pH: 7, aerobic, 30 °C, PFAS concentration: 500 mg/L, duration: 96 days	48.1 %	Mudumbi et al. (2014)
PFOA	Fungal	*Pleurotus ostreatus*	pH: 3.8, aerobic, 22 °C, PFAS concentration: 8 mg/L, Duration: 157 days	60 %	Luo et al. (2015)
PFOA	Phytoremediation	*Eichhornia crassipes, Xanthium strumarium, Polygonum salicifolium*	Sediment pH: 7.43–8.08, fibrous root system, PFAS concentration: 1.7–38 ng/g	5–37 % BCF	Mudumbi et al. (2014)
PFOA	Algal	*C. sorokiniana*	pH: 6.93, 12 - 12 light/ dark cycle, PFAS concentration: 1 mg/L, duration: 7 days	37 %	Bah (2022)
PFOS	Bacteria	*Pseudomonas aeruginosa strain HJ4*	pH: 7, aerobic, 35 °C, PFAS concentration: 1.4–1.8 mg/L, duration: 2 days	67 %	Kwon et al. (2014)
PFOS	Bacteria	*Pseudomonas plecoglossicida 2.4-D*	pH: 7, aerobic, 28 °C, PFAS concentration: 1000 mg/L, duration: 6 days	100 % biodegradation in liquid media and 75 % degradation in 6 months in soil	Chetverikov et al. (2017)
PFOA, PFOS	Algal	*Chlorella vulgaris* and *Scenedesmus obliquus*	pH: 7, 25 ± 2 °C, 16:8 light/dark cycles, illumination: 90 ± 20 μmol photons/m^{2}s, PFAS concentration: 10 mg/L, duration: 7 days	11–16 %	Mojiri et al. (2023)
PFOA, PFOS	Algal	*Chlorella* sp.	23 ± 1 °C, 12:12 h light (5000 lx)/dark cycle, PFAS concentration: 320 mg/L PFOA and 160 mg/L PFOS, duration: 7 days	PFOA uptake: 0.89 %–0.66 %, PFOS uptake: 1.21 %–0.95 %,	Mao et al. (2023)
Perfluoroalkyl carboxylic acids (PFCAs)					
PFMeUPA ($C_6HF_9O_2$)	Bacteria	*Dehalococcoides* dominated KB1 enrichment culture.	Anaerobic, 34 °C, PFAS concentration: 20.7 mg/L, duration: 63 days	100 % biotransformation, ~10 % defluorination	Yu et al. (2020)
5:3 FTCA	Bacteria	*P. fluorescens DSM 834, Pseudomonas oleovorans*	pH: 7.0, aerobic, 30 °C, PFAS concentration: 2 mg/L, duration: 90 days	4:3 acid, PFPeA	Kim et al. (2014)
6:2 FTUCA ($C_8H_2F_{12}O_2$)	Bacteria	*Dehalococcoides* dominated KB1 enrichment culture.	Anaerobic, 34 °C, PFAS concentration: 358 mg/L, Duration: 63 days	100 % biotransformation,~1 % defluorination, - 3-fluoro 5:3 acid (82.9 %), 5:3 FTCA (17.1 %)	Yu et al., 2022b
Short-chain fluorinated carboxylic acids					
3,3,3-Trifluoropropionic acid ($C_3H_3F_3O_2$)	Bacteria	Activated sludge communities	pH: 7.0, aerobic, PFAS concentration: 6.4 mg/L, Duration: 336 days	100 % biotransformation, 84 % defluorination	Che et al. (2021)
Perfluoroalkyl phosphates (PAPs)					
monoPAPs, diPAPs (n:2 PAPs, n = 2, 6, 8)	Bacteria	WWTP activated sludge	Aerobic, PFAS concentration: 1 mg/L, duration: 92 days	6:2 FTOH	Lee et al. (2010)
Fluorotelomer alcohols and their precursor polymers					
8:2 FTOH	Bacteria	Consortium	pH: 7, aerobic, PFAS concentration: 0.75 mg/L, duration: 15 days	100 %	Dinglasan et al. (2004)

(continued on next page)

Table 1 (*continued*)

Type of PFAS	Bioremediation	Strain	Conditions	Degradation efficiency/ Transformation Products	References
8:2 FTOH	Bacteria	*Pseudomonas OCW, Pseudomonas OCY4*	Aerobic, 30 °C, PFAS concentration: 100 mg/L, duration: 7 and 60 days	PFOA, 7:2 sFTOH, 8:2 FTCA	Liu et al. (2007)
8:2 FTOH	Fungal	*Phanerochaete chrysosporium*	Aerobic, 30 °C, PFAS concentration: 1.7 mg/L, duration: 28 days	70 %	Tseng et al. (2014)
6:2 FTOH	Fungal	*Gloeophyllum trabeum* *Trametes versicolor*	Aerobic, 30 °C, PFAS concentration: 3 mg/L, duration: 28 days	51 and 6 %	Merino et al. (2018)
8:2 FTOH	Bacteria	*Pseudomonas Oleovorans, Pseudomonas butanovora,*	Aerobic, 30 °C, PFAS concentration: 40 mg/L, duration: 28 days	8:2 FTUCA, 7:2 ketone, 7:2 sFTOH, PFOA, PFHxA	Kim et al. (2012)
6:2 FTOH	Bacteria	*Pseudomonas fluorescens* DSM 8341	pH: 7, aerobic, PFAS concentration: 4.125 mg/L and 100 mg/L, duration: 28, 90 and 52 days	5:3 FTCA, PFHxA, PFBA, 4:3 FTCA, PFPeA,	Kim et al. (2014)
Fluorotelomer sulfonic acids (FTSAs) and their precursors					
PFHxS	Bacteria	*Pseudomonas* strains PS27 and PDMF10	Aerobic, 27 °C, PFAS concentration: 20 mg/L, duration: 5 days	40 %	Presentato et al. (2020)
6:2 FTSA	Bacteria	Landfill leachate microcosm	pH: 7.5–7.9, aerobic, 20 °C, PFAS concentration: 232 mg/L, duration: 90 days	5:3 FTCA, PFPeA, PFBA, PFHxA, 5:2 sFTOH	Hamid et al. (2020)
6:2 FTSA	Bacteria	*Dietzia aurantiaca* J3 enrichment	pH: 7, aerobic, 30 °C, PFAS concentration: 64.23 mg/L, duration: 7 days	PFHxA, 6:2 FTCA, 5:3 FTCA, 6:2 FTUCA, PFPeA	Méndez et al. (2022)
6:2 FTAB	Bacteria	*Gordonia* sp. NB4-1Y	Aerobic, sulfur limiting, 30 °C, PFAS concentration: 34.22 mg/L, duration: 7 days	4:3 FTCA, 6:2 FTCA, 6:2 FTSA, 5:3 FTCA, PFBA, PFHxA, 6:2 FTUCA, PFPeA,	Shaw et al. (2019)
6:2 FTSA	Bacteria	*Gordonia* sp. NB4-1Y	Aerobic, sulfur limiting, 30 °C, PFAS concentration: 25.69 mg/L, duration: 7 days	99.9 %	Shaw et al. (2019)
PFBA	Phytoremediation	*Ulothrix, Potamogeton crispus*	PFAS concentration: 21.5 mg/L	40 and 73 %	Wang et al. (2019)
PFBA, PFPeA	Phytoremediation	*Maize*	PFAS concentration: 250–1000 mg/kg dw for individual PFAS Duration: 128 days	PFBA and PFPeA were the highest in maize straw and kernel	Krippner et al. (2014)
PFBA	Algal	A mixed solution of green algae *(Chlorophyta)* and diatom *(Bacillariophyta)*	PFAS concentration: 2–200 μg/L, duration: 90 days	10–15 %	Wu et al. (2022)
Perfluoroalkyl sulfonamide derivatives					
EtFOSE, MeFBSE	Bacteria	Municipal digester sludge	Anaerobic, room temperature methanogenic, PFAS concentration: 1 mg/L, duration: 108 days	2–3 % degradation of EtFOSE to EtFOSAA and PFOSI. MeFBSE breakdown to PFBSI and MeFBSAA	Lange (2018)
EtFOSE	Bacteria	Marine sediments	Aerobic, 25 °C and 4 °C, PFAS concentration: 0.0625 mg/L, duration: 120 days	PFOSi, FOSA, PFOS, EtFOSAA, FOSA aldehyde, EtFOSA aldehyde, EtFOSA, FOSE	Benskin et al. (2013)

BCF: Bioconcentration factor, PFPeA: Perfluoropentanoic Acid, PFMeUPA: Perfluoro-5-methylundecanoic Acid, FTCA: Fluorotelomer Carboxylic Acid, FTUCA: Fluorotelomer Unsaturated Carboxylic Acid, PFHxA: Perfluorohexanoic Acid, PFBA: Perfluorobutanoic Acid, PFHxS: Perfluorohexane Sulfonate, EtFOSE: Ethyl Perfluorooctane Sulfonamide Ethanol, MeFBSE: Methyl Perfluorobutanesulfonamido Ethanol, EtFOSAA: N-Ethyl Perfluorooctane Sulfonamidoacetic Acid, PFOSI: Perfluorooctane Sulfonyl Iminium, MeFBSAA: N-Methyl Perfluorobutanesulfonamidoacetic Acid, PFBSI: Perfluorobutanesulfonyl Iminium, MeFBSE: Methyl Perfluorobutanesulfonamido Ethanol, PFOSi: Perfluorooctanesulfonyl Iminium, EtFOSA: Ethyl Perfluorooctane Sulfonamide, FOSE: Fluorooctane Sulfonamide Ethanol, FOSA: Perfluorooctane Sulfonamide.

reductive pathways within the microbial cells. Both aerobic and anaerobic microorganisms can break down the C-F bond, though aerobic biotransformation appears more prevalent (Thapa et al., 2024). The effectiveness of biodegradation is further influenced by the specific bacterial composition and environmental conditions within the contaminated matrix. These factors can lead to significant variations in degradation products and rates (Douna and Yousefi, 2022). For example, studies have shown that the same contaminant can yield different degradation profiles depending on the incubation matrix. PFHxA was found to be a more significant degradation product when 6:2 fluorotelomer alcohol (FTOH) was incubated with different bacterial cultures; however, PFPeA was more abundant when incubated with soil or sediment (Just et al., 2022). Secondly, the specific bacterial community plays a crucial role in determining the biodegradation products of PFAS.

For example, in the aerobic degradation of the most investigated FTOH precursor, i.e. 6:2 fluorotelomer sulfonate (FTSA), activated sludge from a WWTP produced PFHxA, PFPeA, 5:2 ketone, and 5:2 fluorotelomer secondary alcohol (sFTOH), whereas sediment microorganisms produced 6:2 fluorotelomer carboxylic acid (FTCA) and fluorotelomer alcohol (FTOH) (Yang et al., 2022a,b).

Recently *Acidimicrobiaceae* sp. strain A6 (A6), an anaerobic autotrophic bacteria demonstrated the capability to defluorinate PFAS compounds reductively and stimulate ammonium (NH_4^+) oxidation and ferrous iron reduction (Thapa et al., 2024). Strain A6 exhibits exoelectrogenic behavior and can proliferate in microbial electrolysis cells (MECs) by using the anode as an electron acceptor instead of ferric ion (Ruiz-Urigüen et al., 2022). With an initial concentration of 47 mg/L, 77 % of PFOA was removed using a highly enriched culture of A6 during 18 days of operation. Fluoride ions and short-chain perfluorinated compounds increased in MECs with applied potential, showing that PFAS are actively biodegraded in the system (Ruiz-Urigüen et al., 2022). In another study, Huang and Jaffé (2019) investigated the potential of the same strain A6, for PFOA/PFOS degradation at varying concentrations (0.1–100 mg/L). After 100 days of incubation, a 50 % reduction of PFOA/PFOS was obtained in 100 mg/L media with four transformation products perfluoroheptanoic acid (PFHpA), PFBA, PFHxA, PFPeA, whereas a 63 % degradation was noticed at 0.1 mg/L concentration of PFOA/PFOS without the detection of intermediates or final products due to low concentrations.

Moreover, research suggests that *Pseudomonas* species also hold a promise for bioremediation of PFAS (Shahsavari et al., 2021). Studies using isolated strains of *Pseudomonas* bacteria in a controlled environment, incubating PFHxS under alkanotrophic conditions have demonstrated their ability to remove PFAS compounds from the growth medium (Presentato et al., 2020). These investigations aimed to understand the impact of bacterial cell activity (growing versus resting cells) on PFHxS removal with a short incubation period. Notably, two *Pseudomonas* strains namely PS27 and PDMF10 achieved PFAS removal efficiency of 32 % and 28 %, respectively, within 10 days under alkanotrophic conditions. While complete deflourination of PFAS molecules through biodegradation remains unconfirmed, some microorganisms can defluorinate simpler molecules with a single F atom (Huang and Jaffé, 2019). Interestingly, as a sole carbon source, certain *Pseudomonas* strains can utilize fluoroacetate under aerobic conditions which in turn benefits the biodegradation of PFAS as shown in eq. (2), where hydroxyl group is originated from water (Shahsavari et al., 2021).

$$FCH_2COO^- + OH^- \rightarrow HOCH_2COO^- + F^- \qquad (2)$$

A study carried out by Liu et al. (2010) compared the degradation efficiency of different microbial communities for 6:2 FTOH. They found that an aerobic soil microbial culture achieved a degradation efficiency of 67 %, while aerobic sewage yielded a degradation efficiency of 60 %. Notably, when using these cultures, the primary breakdown products were 6:2 fluorotelomer unsaturated carboxylic acid (FTUCA), 6:2 FTCA, and 5:3 polyfluorinated acid (5:3 Acid, $F(CF_2)_5CH_2CH_2COOH$), implying that the diversity of bacterial cultures within the ecological matrix regulates the biotransformation and fate of PFAS (Liu et al., 2017a,b). Moreover, existence of co-substrate can also influence the biodegradation pathways of PFAS. For example, under aerobic conditions, *Pseudomonas butanovora* produces five transformation products, i.e 5:2 ketone, 6:2 FTCA, PFHxA, 5:2sFTOH, and 6:2 FTUCA, whereas, in the presence of co-substrate, i.e. lactate, additional degradation products such as PFPeA, 5:3 u acid, and 5:3 acid were obtained during degradation of 6:2 FTOH, indicating that the degradation pathway of PFAS alters in the presence of co-substrate (Zhang et al., 2022).

In fact, Zhang et al. (2016) exemplify how the type of biodegradation (aerobic or anaerobic) can influence the resulting transformation products. The study investigated the biotransformation of 6:2 FTSA in both aerobic and anaerobic sediments. In aerobic river sediment, 6:2 FTSA rapidly biodegraded, with a half-life of less than 5 days. After ninety days, only 1.9 % of 6:2 FTSA remained and the key breakdown products in aerobic sediment on a molar basis were 5:3 Acid (16 %), PFPeA (21 %), and PFHxA (20 %). Conversely, 6:2 FTSA did not biodegrade in anaerobic sediment over 100 days due to a lack of sulfate reductase enzymes in anaerobic microbial consortium, indicating enzymatic desulfonation step restricted the biotransformation process. In summary, when 6:2 FTSA is present in aerobic sediments, the breakdown processes are more efficient, leading to higher production of short-chain PFCAs (like PFPeA and PFHxA) and PFSAs (like 5:3 acid), thereby suggesting that aerobic environments are more significant contributors to these specific degradation products compared to anaerobic sediments (Zhang et al., 2016).

Long-term exposure to PFAS can significantly alter the microbial diversity of soil. Recently, Xu et al. (2022) observed an increase in alpha-diversity (species richness within a sample) of soil microbial communities after 90 days of exposure to PFOS and PFOA. More PFAS-tolerant bacteria, including *Proteobacteria*, *Burkholderiales*, and *Rhodocyclales*, were enriched in soil microbial communities because of the exposure to PFAS. A lab-scale sequencing batch reactor, continuously exposed to 20 mg/L PFOA concentration, to simulate the extreme scenario of industrial wastewater or groundwater in firefighting training sites, revealed that PFOA inhibited overall microbial growth, impacting the removal of dissolved organic carbon from the wastewater. However, prolonged exposure led to a significant variation in microbial community composition, with the emergence of more PFOA-tolerant species such as *Proteobacteria*, *Acidobacteria*, and *Bacteroidetes* (Yu et al., 2018).

Over the past two decades, microbial degradation of PFAS has moved from biological inertness to the possibility of biotransformation and biodefluorination. Although progress has been made in detecting PFAS biotransformation and comprehending processes at polluted sites, the viability of microbial bioremediation in addressing PFAS in the real environment still needs further research (LaFond et al., 2023). A meticulous understanding of the defluorination reactions is essential to assess the transformation products, boost the biological activities at the contaminated sites, and for developing genetically engineered strains for PFAS degradation in complex environment (LaFond et al., 2023).

Biotransformation pathways of different PFAS classes: As PFAS structure governs the extent and type of defluorination and biotransformation reactions (Berhanu et al., 2023), examining the biodegradation pathway is critical for understanding the reactions that occur once PFAS are released into the environment. Therefore, this section briefly explains the biodegradation routes of PFAS along with product profiles based on different PFAS classes such as PFCAs, PFSAs, FTOHs, fluorotelomer-based precursors, and perfluoroalkyl sulfonamide derivatives (Berhanu et al., 2023).

Among PFCAs, PFOA is the most extensively investigated, as it is highly resistant to microbial degradation and defluorination (Berhanu et al., 2023). Structure-reactivity studies by Yu et al., 2022b, 2020) have provided insights into PFCA microbial defluorination and it was observed that an anaerobic enrichment dominated by *Dehalococcoides* (KB1) transformed and defluorinated unsaturated fluorinated carboxylic acids via reductive defluorination. This enrichment transformed over 90 % of Perfluoro-2-methyl-3-pentanoic acid (PFMeUPA) and Fluorotelomer-2-methyl-3-pentanoic acid (FTMeUPA), leading to further research into the degradation of short-chain PFCAs, revealing that in addition to double bond, the α-, β-unsaturation (-C=C-COOH) is critical to microbial degradation and defluorination (Yu et al., 2020). Structures comprising of α-, β-unsaturation such as FTCA and Fluorotelomer Unsaturated Carboxylic Acid (FTUCA), underwent over 80 % biotransformation, while their saturated counterparts were resistant to biotransformation (Berhanu et al., 2023). On the other hand, PFOS is microbially inert, as demonstrated by extensive anaerobic experiments with various microbial populations, electron donors, and co-metabolites that lasted 259 days and revealed no signs of biotransformation or defluorination (Liou et al., 2010). However, Huang and Jaffé (2019) demonstrated that A6-mediated cultures could degrade up to 60 % of PFOS, producing fluoride, sulfate, and short-chain intermediates. Similarly, Chetverikov et al. (2017) reported 75 % PFOS biodegradation in soil in 6 months by *Pseudomonas plecoglossicida*, resulting in fluoride release.

Moreover, FTOHs have been designated as the major sources of PFOA and other PFCAs in the environment. Unlike other PFAS compounds, FTOHs degrade relatively quickly, producing PFCAs and aldehydes under aerobic conditions (Berhanu et al., 2023). Fig. 3 (a) represents the aerobic and anaerobic biotransformation pathway of FTOH (Hamid et al., 2020; Zhang et al., 2013). The aerobic degradation of FTOHs starts with oxidation to fluorotelomer aldehyde (FTAL), which is then further oxidized to form FTCA, and finally converted into FTUCA, with fluoride ions being released in the process. Under anaerobic conditions, the degradation pathway for 8:2 FTOH leads to intermediates such as 7:2 olefin and terminal products like PFHxA, PFBA, PFOA, and PFHpA (Hamid et al., 2020). Besides, the most prevalent and thoroughly studied fluorotelomer-based precursors are FTSAs, as they can be emitted directly into the environment or can be produced by the microbial biotransformation of other precursor compounds, such as fluoroalkylbetaine sulfonates and fluoroalkylthioamido sulfonates. A degradation pathway where Fluorotelomer thioether amido sulfonate (FtTAoS) transforms into FTSA and then subsequently degrades into PFCAs under aerobic condition was proposed by (Harding-Marjanovic et al., 2015). This is supported by the finding of 6:2 FTCA in the degradation products of 6:2 FTSA, where FTSAs are desulfonated to FTOHs, which then defluorinate and undergo FTOH degradation.

Perfluoroalkyl phosphates (PAPs), another type of FTOH-based surfactants are also identified as FTOH precursors. In wastewater treatment plants, 6:2 mono- and di-PAPs were observed to be hydrolyzed by microbes to produce 6:2 FTOH (Lee et al., 2010). Similarly, fluorotelomer esters, such as fluorotelomer citrate ester and fluorotelomer stearate monoester commonly found in oil and water repellent textiles, can also be biotransformed into FTOHs (Dasu et al., 2012, 2013). Besides, perfluoroalkyl sulfonamide derivatives have been recognized as precursors to PFOS, with N-ethyl perfluorooctane sulfonamidoethanol (EtFOSE) being majorly investigated. A microbial biotransformation pathway was postulated by Rhoads et al. (2008) after they observed the biotransformation of volatile compound EtFOSE in activated sludge and found various intermediates, including N-ethyl perfluorooctane sulfonamido

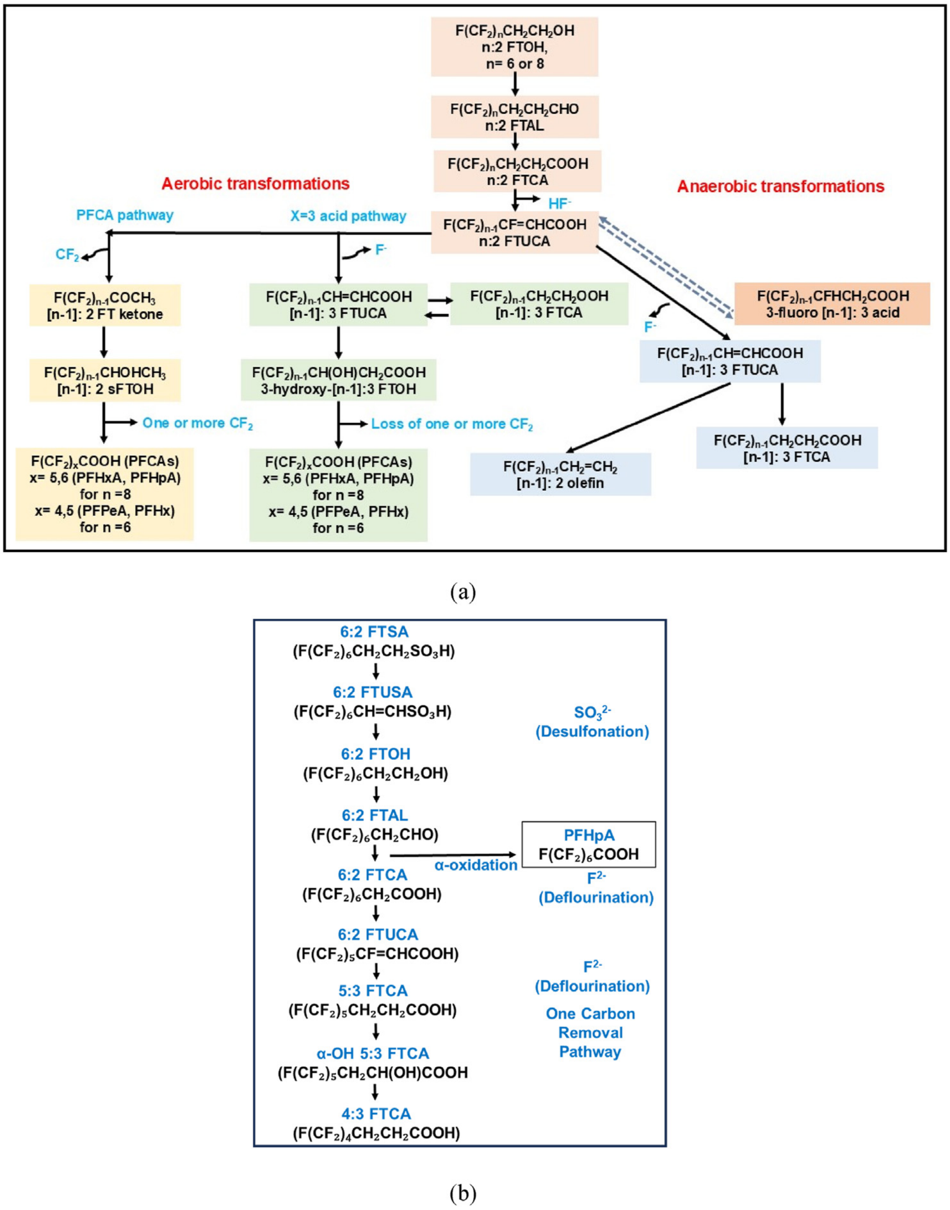


Fig. 3. (a) Consolidated microbial aerobic and anaerobic biotransformation pathway of FTOH (Zhang et al., 2013; Hamid et al., 2020). (b) Biodegradation pathway of 6:2 FTSA by RHA1 fungus under aerobic condition (Yang et al., 2022a,b), where **FTOH**: Fluorotelomer Alcohol, **FTAL**: Fluorotelomer Aldehyde, **FTUCA**: Fluorotelomer Unsaturated Carboxylic Acid, **PFCA**: Perfluoroalkyl carboxylic Acid, **PFHxA**: Perfluorohexanoic Acid, **PFHpA**: Perfluoroheptanoic Acid, **PFPeA**: Perfluoropentanoic Acid, **PFHx**: Perfluorohexane, **FTCA**: Fluorotelomer Carboxylic Acid, **FTSA**: Fluorotelomer Sulfonic Acid, **FTUSA**: Fluorotelomer Unsaturated Sulfonic Acid.

acetic acid (N-EtFOSAA) and perfluorooctane sulfonamide (FOSA) within one day and PFOS on the third day. According to the model developed in the study, 13 % of the N-EtFOSE was converted to N-EtFOSAA, 5 % sorbed to waste solids, 76 % was stripped into the atmosphere, and 6 % was released into the wastewater effluent. The degradation of N-EtFOSE to N-EtFOSAA followed a first-order rate of 0.99 ± 0.08/d and a pseudo second order rate of 0.26 ± 0.02 L/mg VSS/d, while further transformation of N-EtFOSE to N-EtFOSA proceeded at a slower rate i.e. 0.93 ± 0.08/d.

In all the aforementioned PFAS compounds, enzymes play a central role in microbial biodegradation in catalyzing the breakdown processes. However, the enzymes involved in PFAS defluorination and their mechanisms remain largely unknown (Huang et al., 2022; Huang and Jaffé, 2019). A study carried out by Wackett (2021) categorized defluorinating enzymes into five reaction types: eliminative, substitutive, hydrolytic, reductive, and oxidative, with fluoroacetate dehalogenase (FAcD) enzyme being notable for hydrolytic defluorination. Evidence of reductive defluorination is shown by C_6 unsaturated PFCAs, but the exact enzyme responsible could not be determined (Yu et al., 2020). Desulfonation is required for PFSA biodegradation before defluorination, and it is assumed to be mediated by enzymes such as haloacid dehalogenases, alkanesulfonate monooxygenases, nitriloacetate monooxygenases and cytochrome P450s (Méndez et al., 2022; Van Hamme et al., 2013). Studies have reported that defluorination of 8:2, 6:2, and 4:2 FTOHs and PAPs are linked to enzymes namely butane monooxygenases and alkane monooxygenases (Hamid et al., 2020b). In addition, several different enzymes, i.e. nylon oligomer hydrolases, fluoroglutamate dehalogenases, cyclamate sulfamatases, *trans*-3-chloroacrylate dehalogenases, azoreductases, carbaryl hydrolases, etc are associated with biotransformation and final biodefluorination of various other fluorinated compounds (Berhanu et al., 2023). However, intense and promising research on the identification of enzymes involved in PFAS biodegradation is still required to facilitate broader opportunities to enhance or expedite the defluorination rates.

4.2. *Fungal based PFAS degradation/mycoremediation*

Fungi, which constitute 75 % of soil's microbial biomass, exhibits an important role in biotransformation of PFAS (Thapa et al., 2024). Due to their demonstrated ability to biodegrade complex pollutants, including synthetic dyes, hydrocarbons, and explosives such as 2,4,6-trinitrotoluene, researchers hypothesized that these organisms could also be effective in the biodegradation of PFAS (Deshmukh et al., 2016). Fungi hold versatile enzymes with a wide range of activity, allowing them to degrade a variety of substances simultaneously. These enzymes consist of internal P450 oxidases as well as external oxidoreductases such as peroxidases and laccases (El-Gendi et al., 2022). Notably, cytochrome P450 oxidases, the primary internal enzyme in fungi, have been shown to degrade various pollutants like dioxins, polycyclic aromatic hydrocarbons (PAHs), anti-inflammatory drugs, and defluorinate 6:2 fluorotelomer alcohol (Yang et al., 2022a,b; Tomer et al., 2021). Fungal degradation of PFAS might also yield unidentified compounds associated with fungal metabolism (Merino et al., 2018). Mycoremediation of PFAS occurs via two primary routes. First, extracellular enzymes like manganese peroxidase, laccase, and lignin peroxidase secreted by fungal hyphae degrade PFAS in the surrounding environment, after which the partially degraded compounds are taken up for further metabolism within the fungal cells. Second, fungi can directly uptake PFAS, where it undergoes enzymatic reactions such as oxidation and reduction, leading to its transformation and metabolism. The resulting PFAS intermediates are either stored intracellularly or further metabolized and excreted as final degraded products (Ho et al., 2022).

Various studies have reported the potential of fungi for the biodegradation of PFAS. For instance, Tseng et al. (2014) investigated the impact of wood-rotting fungus *Phanerochaete chrysosporium* on 6:2 FTOH, which showed promising results. This fungal strain degraded 6:2 FTOH and 8:2 FTOH up to 50 % and 70 %, respectively within 28 days. The primary transformation products identified were 5:3 Acid (40 %), 5:2 FTOH (10 %), and PFHxA (4 %). Remarkably, a different fungus *Aspergillus niger*, which lacked lignolytic properties, was incapable to transform 6:2 FTOH after 35 days. The same study also found that *P. chrysosporium* could potentially degrade 20 % PFOS within 28 days.

Yang et al., 2022a,b conducted a study on the biotransformation of 6:2 fluorotelomer sulfonic acid (6:2 FTSA), a prevalent environmental pollutant, focusing on how carbon and sulfur sources impact gene expression in *Rhodococcus jostii* RHA1. The study revealed that while enzymes like alkane monooxygenase and cytochrome P450 were highly expressed, they could only defluorinate 6:2 fluorotelomer alcohol, not 6:2 FTSA, due to the presence of the sulfonate group. In sulfur-free conditions, enzymes such as alkanesulfonate monooxygenase facilitated desulfonation, and four degradation metabolites were identified. The detailed degradation pathway of 6:2 FTSA is shown in Fig. 3 (b). Initially, 6:2 FTSA was transformed to 6:2 FTUSA, and thereafter sulfonate ($S\ O^{3-}$) was liberated from 6:2 FTUSA and resulted in formation of 6:2 FTOH, which underwent further degradation and finally led to a generation of 4:3 FTCA as an end product (Kim et al., 2012, 2014). The conversion of 6:2 FTOH to 6:2 FTAL and finally to 6:2 FTCA occurs rapidly. 6:2 FTAL is the branching point to enter one of two lower pathways, as indicated in the proposed pathway. This leads to the formation of 6:2 FTUCA, α-OH 5:3 FTCA, and PFHpA in which fluoride was released because of two defluorination processes: the formation of 6:2 FTUCA and α-OH 5:3 FTCA (Yang et al., 2022a,b). After 144 h of incubation, α-OH 5:3 FTCA was found to transform into 4:3 acid and shorter PFAS via a single carbon removal mechanism (Wang et al., 2012). However, it is important to note that these experiments were carried out in a controlled laboratory setting, and the effectiveness in natural environments remains to be determined.

Recently, PFOA decomposition was found to be feasible via enzyme catalyzed oxidative humification reaction (ECOHR) which is carried out by natural extracellular enzymes released by brown rot fungi (*Aspergillus niger*) and white rot fungi (*Phanerochaete chrysosporium*), such as laccases (LaC), MnP and LiP, etc (Grgas et al., 2023). The PFAS degradation in ECOHR occurs either via one of the two routes (i) decomposition of double bond due to radical action followed by fermentation (ii) Kolbe's decarboxylation with subsequent sequential conversion of $-CF_2$ units to carbon dioxide (CO_2) and fluoride ions (Grgas et al., 2023). A study carried out by Luo et al. (2015) attained 50 % decomposition of PFOA in 152 days with first order rate constant of 0.0044/day upon addition of 1-hydroxybenzotriazole and laccase obtained from *Pleurotus ostreatus*. The degradation mechanism includes Kolbe's decarboxylation cycle and radical rearrangement with no detection of any shorter carbon chains PFCAs as degradation products. Moreover, Luo et al. (2018) noted that in the presence of Ca^{2+} and Mg^{2+}, a 62 % PFOA degradation was observed in 152 days using laccase induced ECOHR with 0.0066/d as a degradation rate constant. It was found that Mg^{2+} and Ca^{2+}, stimulate a bridging effect to reduce the distance between negatively charged PFOS and laccase, thereby elevating the reactivity of laccase-released radicals with PFOS. Thus, the result suggests that the PFOS complexation with cations enhances its degradation efficiency via ECOHR pathway.

Merino et al. (2018) investigated the degradation of 6:2 FTOH by fungi isolated from both pristine and PFAS-contaminated environments. This study compared two known wood-decaying fungal strains (*Gloeophyllum trabeum*) with six fungal isolates from a PFAS-contaminated site. All the fungal strains favored the production of 5:3 Acid up to 51 % of the initial 6:2 FTOH, over more stable PFCAs, which only reached up to 12 % of the total degradation products. These results suggest that fungi, particularly those adapted to PFAS-contaminated environments, may be suitable for bioremediating sites with fluoroalkyl-contaminated compounds like 6:2 FTOH. Furthermore, the preferential degradation of 6:2 FTOH into 5:3 Acid highlights the potential role of fungi in degrading PFAS precursors in the environment.

In summary, fungi's internal and extracellular enzymatic systems make them suitable for bioremediation applications. Although fungal bioremediation has immense potential, some limitations and obstacles need to be addressed before introducing the technology on a commercial and industrial scale such as selection of right fungal strains, ensuring stability and activity of ligninolytic enzymes, optimizing environmental conditions, and determining economic feasibility. Also, it is imperative to investigate the fungal enzymes responsible for the PFAS degradation, their metabolic activity and degradation pathways as well as toxicity of the intermediate products. Furthermore, future studies should explore the effectiveness and long-term stability of carriers for ligninolytic enzymes and fungal cells for PFAS bioremediation (Torres-Farradá et al., 2024).

4.3. Phytoremediation

Plants offer a promising potential for removing PFAS from contaminated environments through a process called phytoremediation (Kavusi et al., 2023). Plants can accumulate PFAS using various parts, including roots (rhizofiltration), shoots (caulofiltration), and even seedlings (blastofiltration), thereby removing these contaminants from polluted water and soil matrices (Greger and Landberg, 2024). Phytoremediation relies on three main mechanisms: phytoextraction, phytodegradation/rhizodegradation, and phytovolatilization (Kavusi et al., 2023). Phytoextraction utilizes the natural tendency of plants to accumulate contaminants in their biomass above ground, which can be harvested and disposed of properly (Jacob et al., 2018). This strategy requires regular biomass collection to ensure a continuous elimination of soil pollutants. Phytodegradation involves the breakdown of organic pollutants by plant enzymes released from roots or through metabolic processes within plant tissues (Kavusi et al., 2023). The roots absorb the hydrophobic organic pollutants and transform them into less toxic chemicals in plant tissues during phytodegradation (Kavusi et al., 2023). Similarly, rhizodegradation refers to the degradation of contaminants into other forms within the rhizosphere. This microorganism-rich soil zone around the roots plays a crucial role in degrading synthetic organic contaminants by releasing enzymes such as laccases, peroxidases, cytochrome P450, dehalogenases, and monooxygenases, contributing to soil decontamination (Pathak et al., 2024). Rhizospheric microbes can reduce PFAS uptake by plants, monitored through the bioconcentration factor (BCF), the ratio of PFAS concentration in plants to soil, and the translocation factor (TF), the ratio of PFAS concentration in shoots to roots (Pathak et al., 2024). To enhance PFAS removal, specific bacterial strains can be introduced as inoculants at contaminated sites and the population of these bacterial strains can be enriched by altering the pH and nitrogen concentration in the soil (Kavusi et al., 2023). On the other hand, phytovolatilization refers to the uptake of contaminants by roots, their conversion into a gaseous form, and further release into the environment (Kavusi et al., 2023).

The efficacy of phytoremediation for PFAS relies on the chain length of the PFAS molecule and its interaction with soil particles (soil sorption behaviour). PFAS with low K_{ow} (0.5–5) and shorter carbon chains are more suitable for this technique due to their high root uptake (Bolan et al., 2021). In other words, more hydrophilic PFAS are easily sorbed onto the root surface as compared to hydrophobic PFAS which experiences high retardation in the soil matrix (Wang et al., 2023). Upon PFAS uptake, transpiration, which involves water movement through the plant further distributes these PFASs to leaves, stems, shoots, and flowers, leading to bioconcentration in different tissues. Long-chain PFAS tend to be more hydrophobic and have lower bioconcentrations as they are readily absorbed by roots (Jiao et al., 2021). However, some studies suggest that longer carbon chain PFAS can accumulate in roots by adsorption due to their increased hydrophobicity (Kavusi et al., 2023; Shahsavari et al., 2021).

A PFOSA spiked soil was investigated by Zhao et al. (2018) to understand its biodegradation, absorption, and metabolism in wheat (*Triticum aestivum* L.) and earthworms (*Eisenia fetida*). The research demonstrated that soil bacteria degraded PFOSA into the highly stable PFOS, which has the equivalent perfluorinated carbon chain length as PFOSA. Despite that, wheat roots and earthworms demonstrated higher bioaccumulation potential for PFOSA than PFOS and both degraded PFOSA into PFOS. Roughly 52 % of the PFOS in wheat roots originated from PFOSA biodegradation, whereas in earthworm around 73.6 % of PFOS came from soil, while 26.4 % originated from PFOSA transformation. Interestingly, shorter-chain perfluoroalkane sulfonates such as perfluorohexane sulfonate (PFHxS) and perfluorobutane sulfonate (PFBS) were found in wheat shoot and root due to PFOSA degradation but not observed in soil or earthworms, thereby suggesting that wheat displayed significantly different PFOSA degradation pathway as compared to earthworms and soil microbes (Zhao et al., 2018). Thus, the result signifies that indirect exposure of PFOSA could be a major contributor of PFSAs in the environment.

Furthermore, a recent study by Li et al. (2022) explored a promising approach known as biomimetic nano-framework derived from plants for remediation of PFAS. This framework, called the Renewable Artificial Plant for In-situ Microbial Environmental Remediation (RAPIMER), offers a synergistic solution by combining highly efficient adsorption with fungal biotransformation. RAPIMER exhibited a strong adsorption capacity for two types of PFAS compounds (PFOA and PFOS) and achieved adsorption equilibrium within 30 and 45 h, respectively. The adsorption quantity per gram sorbent ranged between 3529 mg/g and 4151 mg/g for PFOA and PFOS respectively, making it one of the highest recorded adsorption rates among the numerous sorbents in the literature. Following adsorption, RAPIMER acted as a delivery system, providing the pollutants and necessary substrates for the fungus *Irpex lacteus* to facilitate in-situ biodegradation of PFAS. Moreover, the use of inexpensive lignocellulosic materials in its production makes RAPIMER an economical and sustainable solution for PFAS remediation (Li et al., 2022).

Based on phytoextraction, Tien-Chi and Wu (2021) studied the influence of four fertilizer treatments on the accumulation of PFAS in various plants. The study found that PFASs were primarily transported and deposited in leaves, in comparison with other plant compartments. Hemp exhibited the highest amount of PFASs in its tissues, i.e. 14.3 μg/plant, while it was 12.9 μg/plant for sunflower and 8.3 μg/plant for mustard. Interestingly, despite having the lowest overall PFAS uptake, mustard leaves had the highest PFAS concentration of 1.2 μg/g dry weight compared to stem and roots of the plant (Douna and Yousefi, 2022). Also, the addition of nutrient fertilizer and microbe fertilizer reduced the concentration of PFAS in plant tissue due to the increased sorption of PFASs onto the fertilizer. Overall, hemp appeared to be a potential choice for phytoremediation of PFAS-contaminated soil (Tien-Chi and Wu, 2021).

Aquatic vegetation also holds promise for PFAS remediation. A study by Greger and Landberg, demonstrated the rapid removal of PFAS from heavily contaminated lake water using various wetland plants (Greger and Landberg, 2024). The study evaluated seventeen surface and one submerged plant species, with *Carex rostrata*, *Elodea canadensis*, and *Eriophorum angustifolium* exhibiting the highest PFAS uptake due to greater biomass per unit volume, depicting that PFAS removal depends on the amount of absorbing biomass instead of plant species. It is worth to note the influence of both laccases and the peroxidases present in the medium surrounding the plants which aided in the degradation the PFAS and increased their derivatives. Laccases degraded 5 % of PFPeA, PFBA, PFHxS, PFHxA and PFOS in 24 h, while peroxidases degraded 2 % of PFHxA, PFPeA and PFHxS. Also, PFAS initially accumulated mainly in the roots, and over time, it translocated to the shoots, leading to higher concentrations in shoots than roots. Notably, the breakdown of PFAS happens primarily in the water itself, with the resulting metabolites subsequently being absorbed by the plants and accumulating in their roots and shoots, indicating that wetland plants can be utilized as promising approach for purifying PFAS contaminated water (Greger and Landberg, 2024).

Despite the fact that phytoremediation is an efficient bioremediation technique for PFAS removal, its precarious use may pose a huge threat to human health. According to Brown et al. (2020), humans typically are exposed to PFAS by consuming edible plants that contain PFAS. Monte Carlo simulation revealed that young children had the highest daily exposure to individual PFASs in vegetables (1–2 years > adults >3–5 years > 6–11 years > 12–19 years). Hence, PFAS bioaccumulation within edible crops or vegetables has been a major concern (Xiang et al., 2018). Cultivating crops with low PFAS accumulation is a crucial strategy to lower the risk associated with growing crops in contaminated soil (Xiang et al., 2020). Recently, genetic modification has been utilized to create crop cultivars with low PFAS accumulation levels (Xiang et al., 2018). Three cultivars of loose-leaf lettuce were found by Xiang et al. (2018) to have low levels of PFOA accumulation. In comparison to high-PFOA cultivars, the concentrations of PFOA in the shoots of low-PFOA cultivars were 3.7–5.5 times lower. Based on the acceptable daily PFOA consumption (1.5 μg/kg/d), the identification of low PFOA cultivars should help ensure food safety even when grown in extremely polluted soils (1 mg/kg). The study found that low-PFOA cultivars had a higher distribution of PFOA in their cell walls and organelles of roots, lower desorbing fractions of PFOA in the rhizosphere soil, and lower bioconcentration factors than high-PFOA cultivars. These factors are important in limiting uptake of PFOA and their translocation to shoots from soil (Xiang et al., 2020). Further research should examine and understand the molecular processes governing the low accumulation of PFAS in plant species to eliminate the exposure risk and maintain a balance in the global food system (Kavusi et al., 2023).

At present, the conventional method for disposing of PFAS-enriched plant biomass after phytoremediation involves burying it in landfills or incineration. However, these methods raise concerns since PFAS compounds may leach from decomposing plants in landfills, potentially contaminating surface or groundwater, and incineration demands substantial energy input (Kavusi et al., 2023). Consequently, more research is needed to find safer disposal methods for this biomass. Recently, there has been growing interest in using biochar made from plant biomass and hydrothermal liquefaction for long-term waste management (Gong et al., 2018). Biochar, produced through plant biomass pyrolysis can serve as an efficient sorbent for dye removal and to minimize the leaching of PFAS from contaminated soils, which in turn offers a sustainable way to recycle plant waste post-phytoremediation (Sørmo et al., 2021). However, conducting a life cycle analysis is essential to assess and mitigate any potential negative environmental impacts associated with this process in the future.

4.4. Microalgal based PFAS degradation

In recent times, microalgae have emerged as an efficient technique for bioremediating wastewater contaminated with PFAS (Gondi et al., 2022). These organisms offer a two-fold approach to tackle PFAS through biodegradation mechanism. One strategy involves metabolic degradation, where microalgae utilize PFAS molecules as a carbon source or electron donor to fuel their own growth and energy needs. Alternatively, enzymes within the microalgae, which primarily focus on breaking down other substrates can incidentally degrade PFAS molecules as well, in a process called co-metabolism (Sutherland and Ralph, 2019). Microalgal biodegradation or phycoremediation of PFAS is a complex enzymatic process involving two key stages. The first stage, Phase I, focuses on transforming PFAS molecules to make them more water-soluble, by adding or removing a hydroxyl group using hydrolysis, oxidation, or reduction processes. This is achieved by cytochrome P450 enzymes, such as monooxygenase, dioxygenase, hydroxylase, carboxylase, and decarboxylase. The second stage, Phase II, involves detoxification and protection. Enzymes called glutathione-S-transferases attach glutathione to the modified PFAS compound, further enhancing its solubility and protecting the microalgae from potential harm caused by degradation products (Douna and Yousefi, 2022). The various removal mechanisms involved in the microalgal remediation of PFAS are shown in Fig. S3. Bioaccumulation refers to the accumulation of contaminants within a cell's cytoplasm from the environment (Hena et al., 2021). Biosorption is the adsorption to the cell wall and is influenced by cell wall composition which has a role in electrostatic attraction, chelation, and complexation, and its rate is affected by factors such as dissolved oxygen, PFAS concentration, pH, and hydraulic retention time (HRT) (Abdolali et al., 2014) whereas biodegradation indicates metabolic breakdown of contaminants (Gondi et al., 2022). Microalgae also degrade PFAS via photolysis and volatilization (Hena et al., 2021).

At present, studies have primarily focused on *Chlorella* and *Scenedesmus* species for PFAS removal. A study by Mao et al. (2023) examined the effects of PFOA and PFOS on *Chlorella* sp. and found that concentrations <40 mg/L for PFOA and <20 mg/L for PFOS stimulated algal growth, while concentrations from 80 to 320 mg/L hindered it. The study also revealed that *Chlorella* sp. cells can bioaccumulate PFOA and PFOS, but this process can impede photosynthesis, cause oxidative stress, and limit algal growth. PFOS exhibited greater toxicity and bioaccumulation potential compared to PFOA (Mao et al., 2023). Similarly, Mojiri et al. (2023) examined the ability of *Chlorella vulgaris* and *Scenedesmus obliquus* to remove varying amounts of PFAS mixture (PFOS and PFOA) i.e., 0–10 mg/L over extended exposure periods. Their findings indicated that increasing both PFAS concentration and exposure time led to decreased chlorophyll concentration, cell viability, and protein content of both algae. At 10 mg/L concentrations of the PFOS and PFOA mixture with a long exposure time of 7 days, the cell viability (16 %), chlorophyll content (1.9 mg/L), and protein content (9 %) were comparatively higher in case of *Chlorella vulgaris* as compared to *Scenedesmus obliquus*, indicating

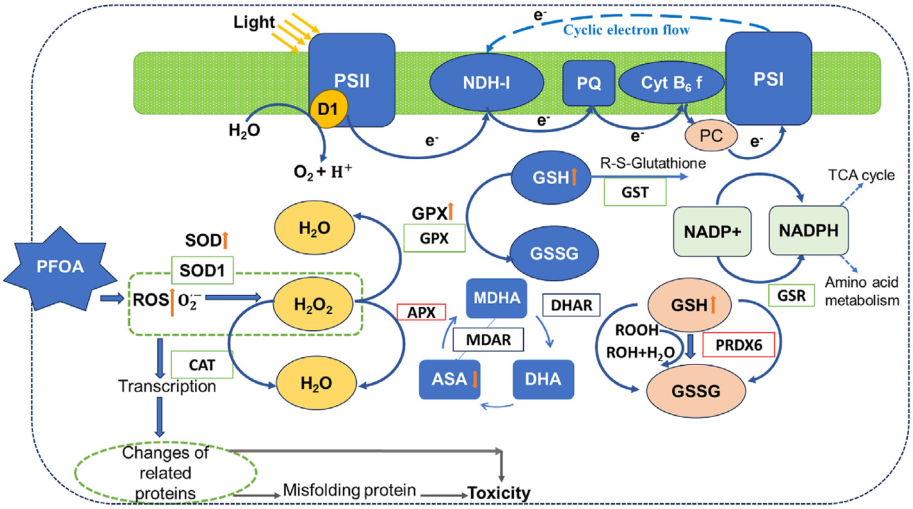


Fig. 4. Sequential physiological and genetic responses of *Microcystis aeruginosa* to PFOA exposure (Adapted from Hu et al., 2023; Liu et al., 2021) where APX L: ascorbate peroxidase, CAT: catalase, PRDX6: peroxiredoxin 6, 1-Cys peroxiredoxin, GPX: glutathione peroxidase, GSR: glutathione reductase (NADPH), GST: glutathione S-transferase, SOD1: Superoxide dismutase - Fe-Mn family, sPQ: Plastoquinone, Cyt b_6f: Cytochrome b_6f Complex, PSII: Photosystem II, PSI: Photosystem I, NDH-1: nicotinamide adenine dinucleotide (NAD) + hydrogen (H) dehydrogenase-1, ASA: ascorbic acid, GSH: glutathione, MDHA: monodehydroascorbic acid.

high susceptibility of *Scenedesmus obliquus* to PFAS exposure. The result of the study suggests that removal of PFAS by microalgae is species-specific. Therefore, the selection of microalgae strains is also a crucial step for the effective removal of PFAS (Hena et al., 2021).

Recently in an investigation by Hu et al. (2023), the effect of PFOA on cyanobacterium *Microcystis aeruginosa* and its adaptive responses were reported. It was observed that PFOA initially suppressed the growth of *Microcystis aeruginosa*, and inhibition was maximum after 2 days, but the PFOA induced inhibition decreased after 12 days of exposure and it stabilized over time. The maximum inhibition rates were 15.9 %, 16.9 %, 27.5 %, and 25.8 % at 1, 10, 25, and 50 mg/L PFOA exposure, respectively. As the concentration of PFOA increased, activity of superoxide dismutase (SOD) and photosystem II (PSII) increased, but respiration, nicotinamide adenine dinucleotide (NAD) + hydrogen (H) dehydrogenase-1 (NDH-1) activity, and total carbohydrate content decreased. Fig. 4 depicts the sequential physiological and genetic responses of *Microcystis aeruginosa* to PFOA exposure. Microalgae *Microcystis aeruginosa* upon PFAS stress generates excessive reactive oxygen species (ROS) ($O_2^{\cdot-}$) which can impair the cellular components (Hu et al., 2023). Subsequently, as a defensive response to PFAS stress, *Microcystis aeruginosa* exhibits a series of oxidative stress tolerance mechanisms. In the antioxidant defensive process, a SOD enzyme is generated, which reacts with reactive oxygen species (ROS) (O_2^{-}) and produces hydrogen peroxides (H_2O_2) and O_2 (Hu et al., 2023). This catalytically generated H_2O_2, if not eliminated, can engender oxidative damage to microalgal cells. In this regard, genes for catalase (CAT), glutathione peroxidase (GPX), and L-ascorbate peroxidase (APX) demonstrate a critical role in anti-oxidant biological process by repairing ROS damage and stimulating H_2O_2 decomposition reaction into monodehydroascorbic acid (MDHA) and H_2O (Hu et al., 2023). Moreover, 1-cys peroxiredoxin (PRDX6) gene utilizes glutathione (GSH) as a substrate to reduce the phospholipids hydroperoxides to alcohols to safeguard the cells from oxidative destruction. In addition, GSH initiates detoxification by integrating with the ROS damaged cellular components, thereby regarded as an important gene in glutathione-abscorbate cycle (GSH-ASA) in microalgae that exhibits an anti-oxidant effect against PFOS pollutants (Hu et al., 2023). Self-adaptation of microalgae towards PFAS exposure is mediated through antioxidant pathways along with photodamage healing (Hu et al., 2023). The microalgal D1 protein overcompensation leads to upregulation of various downstream photosynthesis related proteins such as photosystem I protein D (PsaD), nicotinamide adenine dinucleotide phosphate hydrogen dehydrogenase subunit H (NdhH), and Glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and thereby facilitate the recovery of the photosystem from PFAS induced damage (Hu et al., 2023). The PSII receptor side is resistant to PFOS stress and the flow of electrons in PSII remains balanced, while photosystem I (PSI) repairing is complex and requires prolonged time (Hu et al., 2023). Around the PSI, the active NDH-1-dependent cyclic electron transport (NDH-CET) ejects the excited electrons into the stromal portion of the cyt b_6f complex or PQ pool to decrease the ROS production thus indicating that, under PFAS exposure, self-adaptation mechanisms of microalgae depend on the various metabolic processes (Hu et al., 2023). In summary, cyanobacterium performed self-adaptation to high PFOA concentration through antioxidant pathways, energy distribution among photosystems, and the repair of PSI and NDH complexes. This observation is consistent with Li et al. (2021) who reported that upon exposure to a PFOA alternative, GenX for 96 h, the coping strategy of *Chlorella pyrenoidosa* was upregulation of the genes linked to photosynthesis and glutathione-ascorbate cycle.

Moreover, Latała et al. (2009) examined the toxicity of PFCA compounds on three microalgae species and found that blue-green algae *Geitlerinema amphibium* and diatoms *Skeletonema marinoi* are more vulnerable to PFCAs than green algae *Chlorella vulgaris*, perhaps due to variations in cell wall structure. Furthermore, researchers investigated the utilization of *Synechocystis* sp. PCC6803, a photosynthetic cyanobacterium, for phycoremediation of PFAS in wastewater (Xiang et al., 2020). *Synechocystis,* tested for the first time in PFAS-enriched water, showed resilience and negligible short-term toxicity to PFOA and PFOS at concentrations of up to 0.5 mg/L and 4 mg/L, respectively. Long-term research in continuous and batch systems found no significant toxicity up to 1 mg/L doses. Fractionated biomass study revealed that PFOS is internalized into cells and that there are potential PFOA transformation routes. Bioinformatic investigation revealed transporters and enzymes involved in PFAS sequestration and transformation, implying future metabolic engineering opportunities (Marchetto et al., 2021).

Besides, the effectiveness of an Algal Turf Scrubber (ATS) system for removing various types of PFAS was investigated by Lopes Viticoski (2019). Based on their initial concentration, the amount of PFOA, PFOS, HFPO-DA, and PDHA in the algal biomass was found to be 1.2 %, 1.2 %, 0.26 %, and 0.76 %, respectively. It was noticed that the mass balance failed to account for 35–92 % of the initial concentration of PFOS and PFOA. Preliminary experiment findings suggested that the mass loss observed in the ATS system could be attributed to PFAS sorption onto the building components of the ATS system (Lopes Viticoski, 2019). Furthermore, a study by Bah (2022) aimed to assess the effectiveness of biosorption using microalgae to treat PFAS contaminated water supplies. The algae species investigated was *Chlorella sorokiniana*, which showed no substantial growth inhibition in solutions with 1 ppm PFOA and PFOS levels. Microalgae in the absence of PFAS showed a linear growth rate of 0.15 g/L/d, while in the presence of PFOA and PFOS, the growth rate reduced to 0.12 g/L/d. Over two weeks, *C. sorokiniana* showed a higher removal efficiency for PFOA of 37 % as compared to PFOS, i.e. 20 %. This is because PFOA interacted with the microalgae surface more strongly than PFOS, as affinity constant (K_a) value for PFOA (0.305) is greater than PFOS (0.0069). This led to high adsorption capacity of microalgae for PFOA i.e 556 μg PFAS/g *C. sorokiniana* than PFOS (435 μg PFAS/g *C. sorokiniana*) (Bah, 2022).

Furthermore, the elimination of PFAS using algae-bacteria symbiotic relationships is worth noting. Algae and bacteria form these relationships through mutualism (partners of different species benefit each other), symbiosis (both the partners are benefited, or one partner are benefited and the other is harmed), and parasitism (one species benefits at the expense of the other) (Fuentes et al., 2016). According to Shen et al. (2011) the formation of algae-associated biospheres (phycosphere) aids in contaminant remediation without the use of flocculants. While studies have extensively explored the ability of bacteria-algae symbiotic systems to remove common contaminants like heavy metals (Chandrashekharaiah et al., 2022), research on the removal capability of PFAS in such systems is limited. In this regard, Wu et al. (2022) constructed a synthetic symbiotic environment between bacteria and algae to monitor for possible PFAS degradation. A significant correlation ($R^2 = 0.822$, $p < 10^{-4}$) was observed between carbon chain lengths and removal rates in the study. Longer carbon chain lengths of PFASs improved microbial community successions ($p < 0.05$), leading to a higher removal rate. Algal-bacteria symbiosis showed that algae acted as bacterial growth hosts and during algal metabolisms, the key photosynthetic pigments such as chlorophyll-a and carotenoids were resistant to oxidative stress generated by PFASs. An increase in PFAS concentration led to an increase in chlorophyll-a and carotenoids content in microalgae. Therefore, growth of microalgae enhanced during PFAS loading, whereas bacterial growth was inhibited, resulting negative biomass correlation between two communities, while their symbiotic influence led to an increased PFAS removal. The two PFAS that had the greatest impact on bacterial metabolisms in the phycosphere (microenvironment around algae where interactions between algae and microorganisms occur, influencing nutrient exchange and ecosystem dynamics) was PFBA (10–15 %) and PFTeDA (10–16 %), whereas PFPeA (13–24 %) and PFDoA (10–11 %) had the greatest impact on the free-living biosphere (organisms that live independently in their habitats without a symbiotic interaction with a host). The study shows that the symbiotic relationship between the algae-bacteria system is effective for PFAS removal. To expedite the PFAS removal in symbiotic ecosystem, further research should focus on investigating the type of metabolite released in the system during PFAS removal and briefly explore the mechanism of interaction at proteomic, transcriptomic, and genomic levels.

End use of microalgae biomass and future directions: PFAS remediation, yet questions remain about their fate post-treatment. Notably, under stress conditions such as high salinity or nutrient limitations, microalgae can accumulate lipids, potentially enhanced by PFAS-induced stress (Sajjadi et al., 2018; Yang et al., 2022a,b). This lipid accumulation suggests a dual benefit: remediation coupled with biofuel production. Thermal conversion methods like gasification, liquefaction, and pyrolysis show promise for extracting biofuels from lipid-rich algae biomass, benefiting from high operating temperatures (250–1000 °C) that can also aid in PFAS destruction (Krishnan et al., 2022). Gasification, performed at 400–1000 °C, generates syngas through partial oxidation of biomass. Thermochemical liquefaction converts wet biomass into bio-crude oil at temperatures (250–380 °C) under high pressure (5–20 MPa) with the help of a catalyst. Pyrolysis which is conducted at 300–700 °C has also demonstrated promising results, producing higher-quality bio-oil from algae than from lignocellulosic materials. Lipid-rich biomass has been shown to yield higher heat balances and bio-oil quantities. Direct combustion, which involves burning biomass at temperatures above 800 °C in the presence of air, is another method for energy extraction (Sarwer et al., 2022). However, associated challenges such as long reaction times, low conversion efficiency, and high production costs in case of thermal conversion methods need to be addressed for the commercial viability of this technology (Krishnan et al., 2022). Although this method can be applied to microalgae treated PFAS with melting points below 1000 °C, however for PFAS compounds with higher melting points, the effectiveness and applicability of the thermal technique can be a major constraint. Therefore, further studies should employ advanced genetic tools, genome sequences, and high-throughput analytical techniques to modulate the metabolic pathways and strengthen the defensive response to PFAS stress condition to enhance algal characteristics for bioremediation and biofuel applications (Ng et al., 2017).

4.5. *Bioelectrochemical degradation pathway*

Microbial electrochemistry offers a promising alternative to traditional PFAS remediation methods as these conventional treatment methods are chemical and energy intensive, time consuming and difficult to control. Furthermore, interference of co-contaminants, shortage of electron donor/acceptor availability and formation of toxic by-products further limits their application (Wang and Ren, 2013). Bioelectrochemical systems (BES) combine the synergistic effects of electrochemistry with microbes to degrade PFAS compounds (Meegoda et al., 2022; Verma et al., 2023).

The degradation mechanisms and reaction pathways in BES vary based on the composition of the microbial community, electrode materials, specific PFAS compounds and operational conditions (Meegoda et al., 2022; Verma et al., 2023). Typical electrochemical systems use stepwise defluorination to degrade PFAS via direct oxidation or indirect oxidation mediated by oxidants such as hydroxyl radicals (•OH), superoxide radicals ($\bullet\ O_2^-$), hydroperoxyl radicals ($\bullet H\ O_2$) (Fang et al., 2017). In BES systems, electroactive bacteria oxidize organic substrates at the anode and facilitate electron transfer to the cathode for PFAS degradation reactions, while cathodic microbial reactions involve the reductive defluorination of PFAS directly or through intermediates. In some systems, PFAS molecules can also undergo direct or indirect oxidation at the anode, where electroactive biofilms enhance and sustain the oxidation reactions. PFAS transformation pathways involve complete defluorination by radicals or intermediate formation (e.g., •OH radicals or carboxylates), breaking down PFAS into non-toxic products, or coupled microbial-electrochemical reactions that enhance defluorination through microbial metabolites produced during electrochemical reactions as shown in eq. (3) (Saratale et al., 2017).

$$\text{PFAS} \rightarrow \text{Microbial Metabolite} + \cdot\text{OH} / \cdot\text{H} \rightarrow \text{Degraded by products} + \text{F}^- \tag{3}$$

To optimize microbial interaction and PFAS contaminant breakdown, BESs require meticulously engineered reactor designs and electrode architectures to increase the electroactive surface area, maximize microbial metabolism, and expedite the electron transfer rate. Various BES reactor configurations, including single chamber, dual chamber and multiple electrode assemblies utilized in the remediation of organic pollutants can also be used for PFAS bioelectrochemical remediation. Among BES, microbial fuel cells (MFCs) facilitate PFAS degradation by oxidizing organic substrates and generating electricity. Microbial electrolysis cells (MECs) enhance PFAS breakdown by applying an external voltage, producing hydrogen or other valuable compounds. Microbial desalination cells (MDCs) can simultaneously treat PFAS pollutants in wastewater and desalinate wastewater (Douna and Yousefi, 2022).

One of the first endeavors integrating biocompatible electroactive materials with PFAS-degrading microbial communities for efficient bioremediation of PFAS was conducted by Che et al. (2023). Using *E*-perfluoro (4-methylpent-2-enoic acid) (PFMeUPA) as a model PFAS molecule, Che et al. reported that a hybrid system consisting of enriched anaerobic microbial consortium and biocompatible cobalt-phosphorus (Co-P) alloy cathode leads to a faster and deeper release of F⁻ from the decomposition of PFMeUPA, resulting in fluoride formation of 17.4 ± 2.4 μM in the cathode chamber. The observed increase in defluorination could be because (i) the source compound or biodefluorination products could be directly defluorinated through electrochemical reactions; and (ii) the microbial defluorination could be augmented at the electricity-driven material-microbe interface (Yu et al., 2020, Yu et al., 2022b).

A study by Lee et al. (2024) investigated the possibility of PFOA degradation by enhancing the activity of anammox granules by injecting Fe (III) and applying electric potential. It was observed that reactor operated with electric potential of +0.4 V Vs. Ag/AgCl and Fe (III) injection showed a PFOA removal efficiency of 51 % in 14 days, majorly due to biodegradation by anammox granules. Furthermore, the reactor initially generated current of 282 μ A/s and it reached maximum up to 562 μ A/s after 3 days indicating application of external potential and addition of Fe (III) resulted in current generation via electron transfer and both stimulated effective degradation of PFOA (Lee et al., 2024). The most likely mechanism for PFCAs chain shortening and accompanying F⁻ release is proposed as Decarboxylation-Hydroxylation-Elimination-Hydrolysis (DHEH) mechanism. PFOA degrades by DHEH pathway through the following four steps (Refer eqs. (4)–(7)) (Bentel et al., 2019):

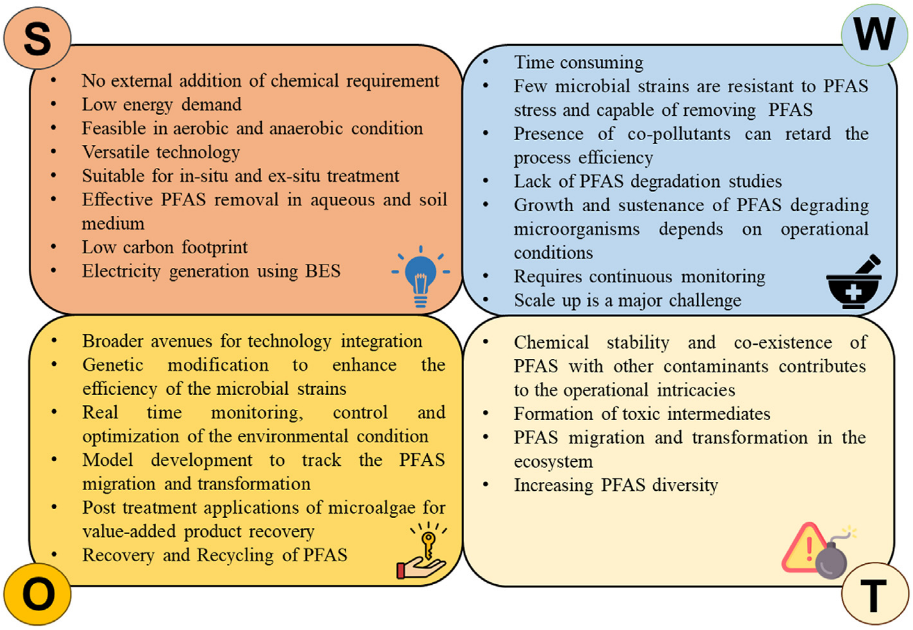
$$\text{Decarboxylation} : C_7F_{15}COO^- \rightarrow \bullet C_7F_{15} + CO_2 + e^-_{aq} \tag{4}$$

$$\text{Hydroxylation} : \bullet C_7F_{15} + \bullet\ OH \rightarrow C_7F_{15}OH \tag{5}$$

$$\text{Elimination} : C_7F_{15}OH \rightarrow C_7F_{14}O + HF \tag{6}$$

$$\text{Hydrolysis} : C_7F_{14}O + H_2O \rightarrow C_6F_{13}COO^- + HF + H^+ \tag{7}$$

Another study by Blotevogel and Mahendra (2021) investigated the synergistic treatment of PFAS contaminants by combining electrolytic degradation with electrobiostimulation (Blotevogel and Mahendra, 2021). The fungal species *Trametes versicolor* was cultivated to treat AFFF-spiked water with PFOS as the main PFAS species. Although no significant improvement in the rate constant (0.0040 min^{-1}) was observed compared to the untreated AFFF sample (0.0039 min^{-1}), the current density decreased by 20 %–100 mA/cm^2 at a constant applied potential of 30 V. This reduction was likely due to the fungal degradation of more readily biodegradable AFFF components, which led to 20 % lower energy consumption for the overall electrochemical treatment



- No external addition of chemical requirement
- Low energy demand
- Feasible in aerobic and anaerobic condition
- Versatile technology
- Suitable for in-situ and ex-situ treatment
- Effective PFAS removal in aqueous and soil medium
- Low carbon footprint
- Electricity generation using BES

- Time consuming
- Few microbial strains are resistant to PFAS stress and capable of removing PFAS
- Presence of co-pollutants can retard the process efficiency
- Lack of PFAS degradation studies
- Growth and sustenance of PFAS degrading microorganisms depends on operational conditions
- Requires continuous monitoring
- Scale up is a major challenge

- Broader avenues for technology integration
- Genetic modification to enhance the efficiency of the microbial strains
- Real time monitoring, control and optimization of the environmental condition
- Model development to track the PFAS migration and transformation
- Post treatment applications of microalgae for value-added product recovery
- Recovery and Recycling of PFAS

- Chemical stability and co-existence of PFAS with other contaminants contributes to the operational intricacies
- Formation of toxic intermediates
- PFAS migration and transformation in the ecosystem
- Increasing PFAS diversity

Fig. 5. Strength weakness opportunities and technology (SWOT) analysis of bioremediation treatment of PFAS.

process. Although their experiments were unable to confirm or eliminate biodefluorination, biomineralization, or biotransformation of highly persistent PFAAs, they demonstrated that several AFFF components, including hydrocarbon surfactants, are readily biodegradable.

Bioelectrochemical systems (BESs) are emerging as a potential technique for destroying PFAS in contaminated soils and water, which is preferable to removal and disposal. Destructive technologies that are effective for PFAS, including electrochemical treatment, can be expensive. Despite the promising results with BES, issues such as surface fouling, concentration effects, and mass transfer limitations must be addressed. Ongoing research focuses on improving reactor designs, electrode materials, and operational conditions to increase efficiency and scalability. Integrating BES with other treatment technologies can improve overall remediation efficacy. BES has the potential to significantly reduce environmental impact, but further research is required to fully comprehend the underlying mechanics and develop more cost-effective solutions for real-world applications.

5. Strength weakness opportunities and technology (SWOT) analysis

A SWOT analysis (Fig. 5) was conducted based on ongoing advancements in bioremediation technology. This analysis highlights key challenges, the current technology readiness level, and potential opportunities for bioremediation of PFAS to evolve into a sustainable and competitive solution. The primary goal of bioremediation is PFAS mineralization; however, this is not always feasible. Therefore, the focus should be on maximizing defluorination rates while minimizing the production of toxic intermediates. In some cases, the defluorination rate may not reliably indicate PFAS removal, as shorter-chain PFAS can be more toxic than their parent compounds. Thus, future research should consider both the toxicity of intermediates and defluorination efficiency to assess the treatment's safety and effectiveness. Additionally, research should explore cost-effective solutions for PFAS recovery and recycling at an industrial scale to generate financial returns, which could attract investment for scale-up trials. In this context, the SWOT analysis serves as a valuable tool for policymakers, researchers, and industries, guiding strategic decisions to advance technology and reduce the PFAS footprint in the ecosystem.

6. Conclusion and future research directions

The pervasive presence of diverse PFAS in the environment has prompted the urgent need for effective strategies and advanced technologies for large-scale mitigation and removal. In most contaminated sites, PFOA and PFOS account for 80 % of the total PFAS concentration (Thapa et al., 2024). PFAS contamination levels vary across soil and water matrices depending on land use, and these compounds undergo chemical transformations based on environmental conditions. A key strategy for PFAS degradation is the breakdown of the highly stable C-F bonds. While bioremediation has emerged as a cost-effective treatment approach, its slow degradation rates necessitate the combination of various bioremediation techniques to accelerate PFAS removal. Microorganisms can utilize PFAS as a carbon source and defluorinate these compounds, yet the concentration, toxicity, and bioavailability of PFAS significantly influence microbial community dynamics, ultimately impacting the rate and efficiency of degradation. Certain microbes have been reported to tolerate PFOS concentrations as high as 1000 mg/L and PFOA concentrations of 50 mg/L (Zhang et al., 2022). However, complete mineralization of PFAS has yet to be achieved, likely due to limitations in microbial enzymatic reactions required to break the chemical bonds, presenting a significant challenge for large-scale applications. Moreover, the production of other polyfluorinated compounds during incomplete degradation, such as the accumulation of PFCAs is a serious concern and thereby, requires effective strategies to catalyze complete defluorination reaction. Therefore, the assessment and identification of various diverse species along with enzymatic mechanism and material chemistry need to be studied to increase the PFAS removal efficiency. Additionally, PFAS biodegradation is a slow process, often taking weeks or months, with limited degradation efficiency. To overcome these challenges, integrating bioremediation with physicochemical processes or leveraging the microbe-plant-PFAS interaction could offer a more promising approach for PFAS degradation. Recent studies suggest that coupling PFAS-degrading bacteria with phytoremediation in constructed wetlands can enhance microbial degradation of PFAS (Shahsavari et al., 2021). However, further research is needed to assess the long-term effectiveness of this method and to explore sustainable disposal options for PFAS-enriched plant biomass.

Additionally, fungal biotransformation of certain PFAS, such as 6:2 FTOH, has shown to be more effective compared to bacterial biotransformation. Therefore, active research is needed to explore the efficiency of mixed cultures of bacteria and fungi to assess how cooperative interactions influence PFAS removal. Microalgae, while demonstrating limited PFAS uptake, also warrant further investigation, particularly regarding their long-term exposure to PFAS and the efficacy of mixed microalgal species in removing different PFAS compounds. Moreover, in bioelectrochemical systems (BES), synergistic interactions between electricity-driven materials and microbes have demonstrated greater versatility in treating saturated fluorinated structures. Although the degradation of the parent PFAS compounds is often partial, bioelectrochemical defluorination promotes the formation of less toxic end products containing C-H bonds, which are more amenable to further biodegradation under aerobic conditions. As more defluorinating microbial strains and enzymes are identified, BES systems could be enhanced by coupling them with various biocatalysts to further accelerate PFAS destruction (Che et al., 2023). Present studies have focused on the limited PFAS types, therefore more research is indispensable to understand the degradation pathway and efficiency of bioremediation techniques in removing diverse varieties of PFAS.

Future studies should also focus on employing metagenomics and metatranscriptomics to investigate the effects of PFAS stress on microbial communities in different environmental matrices and to elucidate the mechanisms of PFAS bond cleavage, thereby revealing the stepwise biodegradation pathways. Additionally, exploring the development of engineered proteins through genetic reprogramming to enhance PFAS remediation offers a promising avenue. Some potential future directions in bioremediation include: (i) utilizing molecular and organism-scale models for PFAS pre-screening (Carla Ng, 2019), (ii) developing robust synthetic biofilms with diverse microbial communities for use in bioreactors (Garza, 2024), (iii) investigating insect-mediated bioconversion using black soldier fly larvae (BSFL) for PFAS biotransformation and metabolism (Heather Bischel, 2022), and (iv) studying the role of reactive oxygen species (ROS) in activating plant stress responses under PFAS exposure (Difazio, 2024). By advancing such emerging bioremediation strategies, researchers can develop more efficient and sustainable solutions for PFAS removal and overall environmental management.

CRediT authorship contribution statement

Ayushman Bhattacharya: Writing – review & editing, Writing – original draft, Conceptualization. **Jesna Fathima:** Writing – original draft. **Sunith Varghese:** Writing – original draft. **Pritha Chatterjee:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Venkataramana Gadhamshetty:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization.

Data availability

The data used in the review paper for the discussion are available within the article and in the supplementary material.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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