Journal of Hazardous Materials 413 (2021) 125319

Contents lists available at ScienceDirect

Journal of Hazardous Materials

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

Review

Uranium (U) source, speciation, uptake, toxicity and bioremediation strategies in soil-plant system: A review

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ARTICLE INFO

Editor: Dr. C. LingXin

Keywords:
Uranium
Bioavailability
Accumulation
Phytotoxicity
Tolerance
Bioremediation

ABSTRACT

Uranium(U), a highly toxic radionuclide, is becoming a great threat to soil health development, as returning nuclear waste containing U into the soil systems is increased. Numerous studies have focused on: i) tracing the source in U contaminated soils; ii) exploring U geochemistry; and iii) assessing U phyto-uptake and its toxicity to plants. Yet, there are few literature reviews that systematically summarized the U in soil-plant system in past decade. Thus, we present its source, geochemical behavior, uptake, toxicity, detoxification, and bioremediation strategies based on available data, especially published from 2018 to 2021. In this review, we examine processes that can lead to the soil U contamination, indicating that mining activities are currently the main sources. We discuss the relationship between U bioavailability in the soil-plant system and soil conditions including redox potential, soil pH, organic matter, and microorganisms. We then review the soil-plant transfer of U, finding that U mainly accumulates in roots with a quite limited translocation. However, plants such as willow, water lily, and sesban are reported to translocate high U levels from roots to aerial parts. Indeed, U does not possess any identified biological role, but provokes numerous deleterious effects such as reducing seed germination, inhibiting plant growth, depressing photosynthesis, interfering with nutrient uptake, as well as oxidative damage and genotoxicity. Yet, plants tolerate U toxicity via various defense strategies including antioxidant enzymes, compartmentalization, and phytochelatin. Moreover, we review two biological remediation strategies for U-contaminated soil: (i) phytoremediation and (ii) microbial remediation. They are quite low-cost and eco-friendly compared with traditional physical or chemical remediation technologies. Finally, we conclude some promising research challenges regarding U biogeochemical behavior in soil-plant systems. This review, thus, further indicates that the combined application of U low accumulators and microbial inoculants may be an effective strategy for the bioremediation of U-contaminated soils.

1. Introduction

Uranium (U), a serious environmental contaminant, has attracted considerable attention since its chemical toxicity and radiotoxicity cause substantial damage to plants, animals, and microbes (Gao et al., 2019; Liao et al., 2020a; Wei et al., 2021). It is also highly hazardous to human health via affecting metabolic activity (Malaviya and Singh, 2012; Liang et al., 2020) causing numerous toxic effects on renal failure, neurasthenia, infertility, leukemia, and amentia (Selvakumar et al., 2018; Singh et al., 2021). In particular, U, being a radioactive metal element, is carcinogenic once it accumulates to doses > 0.05 mg U kg^{-1} body mass d^{-1} (Nie et al., 2010a, 2010b; Gao et al., 2019). However, U exposure to humans is mainly derived from the soil-crop system, as it is easily integrated into the food chain (Li et al., 2019a). Considering these potential risks, U contamination in soil has been a cause for increasing concern worldwide. A detailed understanding on the biogeochemical U behavior and better monitoring it in the environment, particularly in soil-plant systems, therefore, are urgently needed.

Uranium is extremely rare in the Earth's crust (approximately 2.5 parts per million). Yet, various anthropogenic activities, including

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https://doi.org/10.1016/j.jhazmat.2021.125319
Received 18 December 2020; Received in revised form 23 January 2021; Accepted 2 February 2021
Available online 4 February 2021

mining, milling, fuel processing, and weapon production or nuclear accidents with the ore, have resulted in elevating U background levels in the soil systems, leading to a serious threat to agricultural ecosystems (Kolhe et al., 2018; Lin et al., 2020; Coelho et al., 2020; Shu et al., 2020). Uranium phyto-uptake is not only largely dependent on soil temperature, redox potential (E_h), pH, minerals, organic matter (SOM), and microorganisms, but also plant species, root surface area, rate of root exudation, and transpiration rate (Mitchell et al., 2013; Li et al., 2019b, 2019c; Wu et al., 2020; Estes and Powell., 2020). Generally, U accumulates primarily in root systems, with only very small portions being transferred to aerial parts (Alsabbagh and Abuqudaira, 2017; Hou et al., 2018). However, potential U hyperaccumulators, such as *Salix babylonica* and *Nymphaea tetragona* Georgi, transfer and accumulate high U levels in shoot tissues (Mihalík et al., 2010; Li et al., 2019a).

Uranium does not exhibit any beneficial role in the physiological and biochemical processes of plants (Gao et al., 2019). However, a wide range of plant species take up and accumulate U (Hou et al., 2018; Gil-Pacheco et al., 2021). Generally, its accumulation in plants provokes physiological, biochemical and genetic toxic effects, such as the inhibition of plant growth (Stojanović et al., 2010), suppression of photosynthesis (Ren et al., 2019), overgeneration of reactive oxygen species (ROS) (Tewari et al., 2015), oxidation of lipid membranes (Li et al., 2019a), alteration in enzymatic activities (Imran et al., 2019), disruption of water and nutrient uptake (Lai et al., 2020a), protein oxidation (Sharma et al., 2016a, 2016b), and DNA chain breakage (Ma et al., 2020). In addition, U-induced toxicity reduces plant height and root length, leaf chlorosis, and even necrosis (Jagetiya and Sharma, 2013). Thus, a comprehensive understanding on the effects of U-induced toxicity on soil-plant systems and its related detoxification mechanisms inside plants is urgently needed.

The overgeneration of ROS is generally considered as the first plant response to abiotic stress, particularly the response to heavy metals (Berni et al., 2019; Chen et al., 2020a). Overproduction of ROS induced by U may cause various types of damage at the cellular level, including mutilation of DNA and RNA, alteration of the cell cycle and division, and inhibition of the functions of various proteins (Vandenhove et al., 2006; Gudkov et al., 2016; Gao et al., 2019, Ma et al., 2020). Plants have evolved several defense strategies to minimize ROS-induced oxidative stress, such as U sequestration in root tissue, compartmentalization in the cell wall and vacuoles, and chelation by organic molecules (Vanhoudt et al., 2011a; Saenen et al., 2013; Nie et al., 2014). As a secondary defense mechanism, the antioxidant enzyme system has been one of the most important defense strategies since it effectively scavenges the U-mediated overproduced ROS (Li et al., 2019a; Imran et al., 2019). Furthermore, various strategies to remediate U-contaminated soils have been reported, while only few studies have been applied under field conditions. Among these remediation techniques, biological strategies (plants and microorganisms) for U removal from contaminated environments have attracted increasing interest, as these technologies are quite economical, environmentally safe, and allow in situ treatment (Malaviya and Singh, 2012; Banala et al., 2020).

To date, there are only few literature reviews regarding the U behavior in soil-plant systems. In 2012, Malaviya and Singh (2012) published a comprehensive review of phytoremediation strategies for the management and remediation of U-contaminated environments, but not referring its effect on plant system. Very recently, Davies et al. (2015) have provided a mini review only referring the role of arbuscular mycorrhizal fungi as a promoter to enhance ^{238}U translocation from plant roots to aboveground tissues. To our best knowledge, the biogeochemical U behavior in soil-plant systems has not been comprehensively reviewed to date. Thus, we summarized the latest data (particularly studies published from 2018 to 2021) on U bioavailability in soil, and its accumulation, phytotoxicity, and detoxification aspects in plants. This review is divided into eight sections: (i) introduction; (ii) uranium sources and the natural levels in soils; (iii) geochemical U behavior in soil; (iv) U soil-plant transfer; (v) U toxicity symptoms in plants; (vi) plant tolerance mechanisms to U stress; (vii) bioremediation technologies; and (viii) conclusions and outlook.

2. Uranium in the environment

2.1. Occurrence, uses and sources

Uranium, being a radioactive element with an atomic number of 92 and an atomic weight of 238.03, is firstly discovered in 1789 by the German chemist Martin Heinrich Klaproth as a constituent of pitchblende (Monreal and Diaconescu, 2010). Its concentration in the Earth's crust approximately is equal to arsenic, but more abundant than silver, antimony, mercury, and cadmium. As a naturally occurring element, primordial U consists of three isotopes: ^{234}U, ^{235}U and ^{238}U (Struminska-Parulska et al., 2020). Among all U isotopes, ^{238}U accounts for approximately 99.3% and has the lowest radioactivity (Awad et al., 2021). Depleted U is a by-product during the natural U processing, while its composition is approximately the same as ^{238}U (Gao et al., 2019). Uranium mainly occurs as oxidized forms (i.e., uranyl ions (UO_2^{2+}) and pitchblende ($U_3O_8^{2+}$)) in the environment. It also remains as uranium ore, ingenious rocks, sedimentary rocks, and beach sands under natural conditions (Gavrilescu et al., 2009). To date, it has been widely used in the nuclear, pharmaceutical, and agricultural industries (Hedges, 2008).

Nuclear electricity generation has been increased the attention in many countries due to the excess consumption of nonrenewable energy sources (i.e., coal and petroleum). Uranium is one of the most important energy minerals for nuclear electricity generation (Sofranko et al., 2020). The United States has the most nuclear power plants (104 nuclear power plants) in the world, accounting for 19% of national electricity generation (Hill et al., 2008). The nuclear power of France and Belgium accounts for 76% and 54% of national electricity generation, respectively (Linnerud et al., 2011). Uranium is particularly important for its use in the military industry. It has been used to power nuclear submarines, warplanes, and aircraft carriers. Uranium is also an important raw material for preparing atomic bombs, missiles, torpedoes, and aviation bombs. Based on the perspective of the pharmaceutical and agricultural industries, U is also widely used in irradiation breeding, radiation sterilization, insect disease prevention, labeled atoms, and radiotherapy (Vanhoudt et al., 2010a; Mitchell et al., 2013; Gopal Paithankar et al., 2021).

Uranium, being the heaviest naturally-occurring element, is widely dispersed in the Earth's crust, rocks and soils at a level of approximately 1–4 ppm by weight (Gavrilescu et al., 2009). Yet, the average U concentration in plants, animals, and ocean water is approximately 10^{-7} g/g because of the low solubility of U(VI) compounds in water (Szabó et al., 2009). As shown in Fig. 1, natural U sources in soil mainly derives from atmospheric deposition and rock weathering (Gavrilescu et al., 2009; Carling et al., 2017). In addition, volcanic eruptions are another natural source, which increases the natural U expose to the environment (Luo et al., 2017). Except for natural sources, most of U deposits into soils via anthropogenic activities, such as mining and milling, nuclear leakage, improper disposal of nuclear waste, waste dump after U prospecting, the development of nuclear science and technology, and particularly in rare critical accidents of nuclear power plants occurring in recent years (Fig. 1; Malaviya and Singh, 2012; da Conceicao and Bonotto, 2017; Selvakumar et al., 2018). Among these activities, mining activities are currently the main sources of U contamination (Wang et al., 2019a). For example, the soils around U tailings reached a high I_{geo} value of U up to be greater than 3.5 (Xiao et al., 2019), indicating that the soils were heavily polluted by U. The leakage of nuclear industry wastes also poses a serious U threat to terrestrial ecosystems (Lazareva et al., 2019). In particular, the Fukushima nuclear power plant accident caused a substantial amount of U to be discharged into the soil, atmosphere, and ocean, leading to a serious contamination on the ecological environment (Mishra et al., 2019).

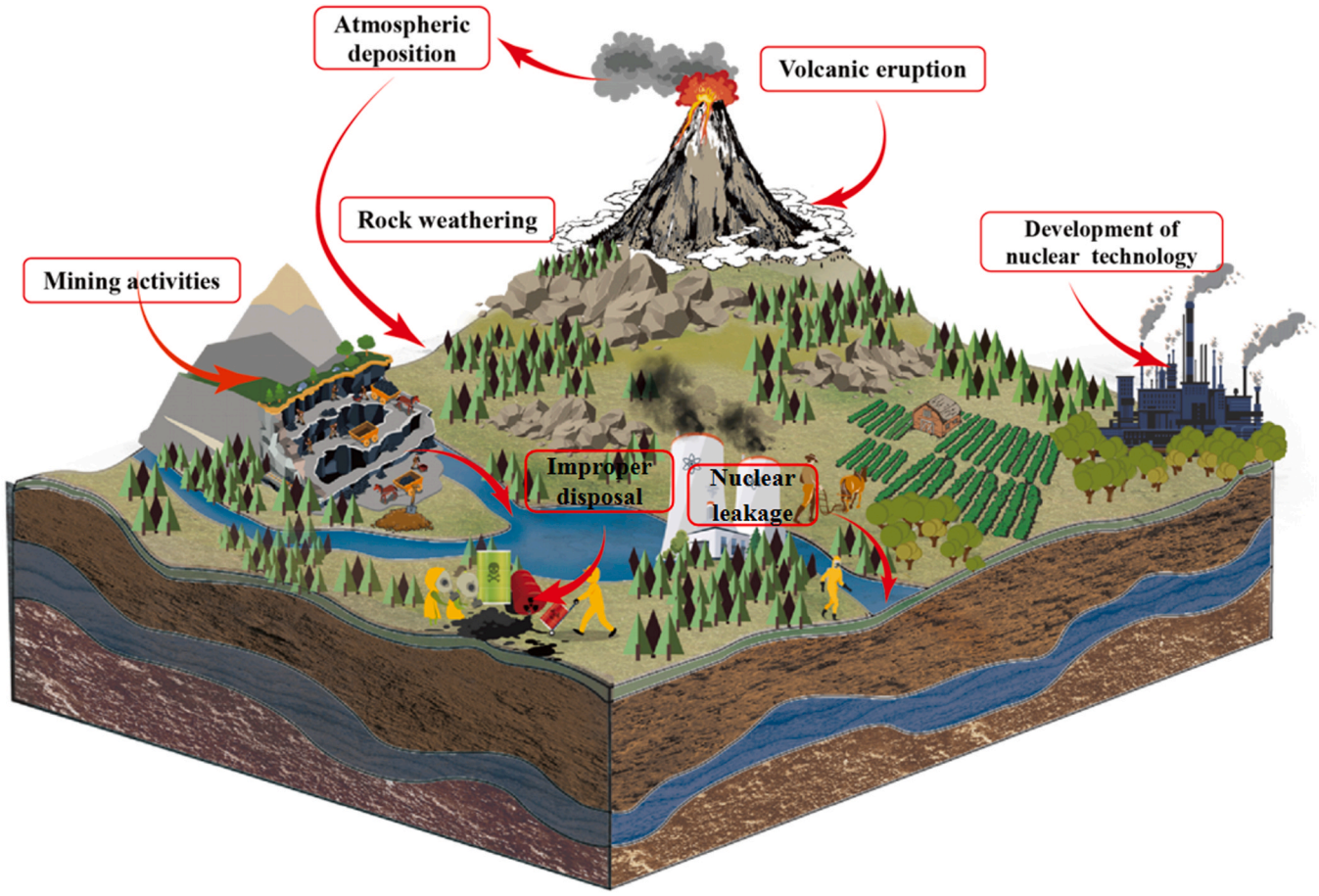

Fig. 1. Uranium (U) sources in terrestrial ecosystems.

2.2. Uranium levels in soil

Since it largely varies in the contamination source, soil presents a significant difference in the background U concentration, leading to unambiguous and significant efforts in the treatment, storage and safe disposal of nuclear waste at the repository. The average U concentration in the Earth's crust has been estimated to be 2.7 mg kg^{-1} (Taylor, 1996), which is much lower than that under natural conditions (Table 1). For example, the average U concentrations in the soils of Poland and Canada are 0.79 mg kg^{-1} and 1.2 mg kg^{-1}, respectively (Vodyanitskii, 2011). The U concentration in the soddy-gley soils is 0.2–0.9 mg kg^{-1} in the polar Urals (Vodyanitskii, 2011).

Table 1
Natural/background value of U in soils of different countries (mg kg^{-1}).

Country	U contents (mg kg^{-1})	References
Chile	0.79	Cabral Pinto et al., 2014
Germany	1.9	Utermann and Fuchs, 2008
Switzerland	2.25 (arable soil)	Bigalke et al., 2017
Switzerland	1.93 (grassland)	Bigalke et al., 2017
England	2.6	Vodyanitskii., 2011
Spain	13.5	Santos-Francés et al., 2018
Japan	1.74	Sahoo et al., 2011
USA	3.5	Bern et al., 2019
Portugal	25.1	Neiva et al., 2014
India	11	Vodyanitskii., 2011
Poland	0.79	Vodyanitskii., 2011
Europe	2.46 (subsoil)	Plant et al., 2003
Europe	2.37 (topsoil)	Plant et al., 2003
Canada	1.2	Vodyanitskii., 2011
China	3.13	Xu et al., 1993

Currently, U-contaminated soils have been globally reported, but largely varies with the study area. In Sichuan Province, China, the soil surrounding the U mining area contained an average U concentration of 19.62 mg kg^{-1} (Li et al., 2020). This pollution load index is greater than 5, suggesting that the soils are highly contaminated by U because of increased mining activities. Similarly, the soil U concentrations near a U ore field had an average value of 32.3 mg kg^{-1} in Xiazhuang City, Guangdong Province, China. In particular, soils surrounding the Cunha Baixa uranium mine (Central Portugal) had a high ecological risk due to the high U concentration of 109.2 mg kg^{-1} (Antunes et al., 2008). In addition, Kumar et al. (2011) indicated comparatively high levels of U in the soils near thermal power plants and cement factories (Bathinda, Punjab state, India), leading to a chemical risk in the groundwater. Recently, in France, soil U concentrations from the wetlands of Rophin sites significantly ranged from 8.9 to 3560 mg kg^{-1}, which of its accumulation tendency occurred at the interface with topsoil layers being characterized by a high SOM content (Martin et al., 2020). However, except of China, Portugal, India, France, and America, U-contaminated soils has been less studied, possibly as, U contamination is less occurred in other countries. In Switzerland, there is no U contamination in the agricultural soils and the drinking water wells in the canton of Bern (Bigalke et al., 2018).

3. Speciation and bioavailability of U in soil

Uranium speciation and bioavailability drive its biogeochemical behavior in the soil-plant system, which plays a key role in risk assessment and soil remediation studies (Bone et al., 2017; Selvakumar et al., 2018). The BCR sequential extraction technique fractionates heavy metal chemical fractions (e.g., exchangeable, reducible, oxidizable, and

residual phases) in soils (Quevauviller 2002). In general, the exchangeable phase of heavy metals is used to assess the extent of bioavailability in soil-plant systems, while the residual phase represents relatively stable heavy metal forms (Zhang et al., 2014). Since the majority of U fractions are associated with the residual fraction, the exchangeable U fraction is the lowest (Vandenhove et al., 2014; Hu et al., 2020), indicating a low U bioavailability in soil. However, these U fractions can be converted to the exchangeable fraction through a number of reactions through adsorption, desorption, precipitation, and U–ligand complex formation (Gavrilescu et al., 2009; Selvakumar et al., 2018), thus increasing the U-induced ecological risk. The U fraction conversion is also strongly dependent on soil chemical properties (e.g., E_h, soil pH, and SOM), which alter its mobility and bioavailability in soil-plant systems (See more detailed discussion below; Zhou and Gu, 2005; Papanicolaou et al., 2010; Bone et al., 2017). In addition, these dynamic reactions are easily affected by soil microbial activity (Tan et al., 2020a, 2020b).

3.1. Influences of soil chemical properties on U speciation and bioavailability

3.1.1. Effects of E_h on U speciation and bioavailability

Since U is a redox-sensitive metal, redox conditions play an outstanding role in controlling its dynamic in soil environments (Saunders et al., 2016; Rinklebe and Shaheen, 2017; Rinklebe et al., 2020). Uranium occurs in different chemical forms (such as +III, +IV, +V and +VI) in the environment. In aqueous media, only U(IV) and U(VI) are stable, but U(VI) exhibits a higher toxicity than other valences (Gao et al., 2019). The conversion of U species determines its sensitivity to environmental redox conditions. Under oxidative conditions, uranyl (UO_2^{2+}) forms highly mobile compounds, while U^{4+} is oxidized to stable uranyl oxide (UO_2) under reductive conditions (Vodyanitskii, 2011). This conversion alters the biogeochemical U behavior in the soil-plant system. The sediment E_h gradually decreased with increasing flooding time and the U(VI) concentration of decreased, whereas the U(IV) concentration gradually increased under a flooding E_h experiment (Liao et al., 2020b). This finding likely results from that U sorption on the sediment increases with decreasing sediment E_h (Liao et al., 2020b). Indeed, U reduction is a complex process because E_h largely depends on pH (Wang et al., 2020a). Specifically, at pH = 4, U reduction begins at E_h < +100 mV and is favored due to the stabilization of the U(IV) oxidation state with the formation of both $U(OH)_4$ and $U(OH)_5^-$. However, at pH = 8, a negative E_h is required for U(VI) reduction (Papanicolaou et al., 2010). The reduction from U(VI) to U(IV) also depends strongly on the carbonate/phosphate concentration. Thus, an increase in the carbonate/phosphate concentration in solution favors the formation of U (VI)-carbonate/phosphate complexes and hence stabilize the oxidation state of U(VI) (Papanicolaou et al., 2010; Liao et al., 2020b). Furthermore, U(VI) easily reduces to U(IV) in the presence of electron donors, including organic compounds (Gavrilescu et al., 2009; Vodyanitskii, 2011). Thus, large amounts of dissolved organic carbon may be responsible for reducing U(VI) to U(IV) in soils.

3.1.2. Effects of soil pH on U speciation and bioavailability

The pH governs U equilibrium among solubility, adsorption, and desorption in soils (Shaheen et al., 2019; Fu et al., 2019), suggesting that soil pH is one of the most important factors to govern U dynamics in soils (Crawford et al., 2017; Dlamini et al., 2019). Uranium displays a higher mobility in alkaline soils than that in acidic soils, indicating that U is mobilized and released into soil solution with increasing pH (Selvakumar et al., 2018). This effect is attributed to the enhanced oxidation of U (IV) (sparingly soluble) to U(VI) (soluble) under alkaline conditions (Wang et al., 2018a).

Numerous studies have well indicated this pH-induced effect on U mobility and bioavailability via interacting with soil compositions (Echevarria et al., 2001, Wu et al., 2017; Yu et al., 2020). Soil mineral particles present a higher sorption of U(VI) at a lower pH, while this sorption substantially decreases with increasing pH (Echevarria et al., 2001). This finding is also valid in aerated environments within the range of pH 4 ± 9 (Echevarria et al., 2001), especially in the cultivated soils rich in Fe/Al (hydr)oxide minerals (Cumberland et al., 2016). Recently, Yu et al. (2020) found that the percentage of U(VI) adsorbed on montmorillonite colloids increased obviously at pH = 4.0–7.0 and then decreased with an increasing pH value. Indeed, the adsorption of U ions on montmorillonite mainly occurs through ion exchange with a permanent negative charge and complexation with Si–O– and Al–O– groups, which strongly depends on the solution pH (Yu et al., 2020). Similarly, the deprotonation of the surface functional groups on soil humic substances occurs at an elevated pH, thereby leading to a decrease in the adsorption capacity of soil U(VI) (Zhou and Gu, 2005). This decreasing sorption capacity is also partly attributed to the formation of uranyl–carbonate complexes (Li et al., 2014). The aforementioned studies indicate a complex interplay between pH and the geochemical U behavior in soils, influencing the U mobility, availability, and ecotoxicity. In addition, the pH also affects soil microbial activities, indirectly altering U mobility and bioavailability in soil-plant systems (Salome et al., 2017). Yet, this internal mechanism is not well known. Thus, the mobility and bioavailability of U is higher at alkaline pH, leading to its uptake by plants and threatening the agricultural system and human health.

3.1.3. Effects of SOM on U speciation and bioavailability

Soil organic matter (SOM), originating from the decomposition of plant, animal, and microbial material, has a high affinity for U ions to increase its adsorption ability (Tinnacher et al., 2013; Bone et al., 2017). SOM surfaces contain various functional groups (e.g., carboxylic, hydroxyl, phenolic, aliphatic, aromatic, and aromatic groups), determining the bonding capabilities of SOM to U ions (Cumberland et al., 2016). Thus, SOM adsorption properties to U are very complex due to its complex chemical and structural nature in soils (Stockdale and Bryan, 2013).

Increasing SOM content alters soil E_h to promote U(VI) reduction (Gavrilescu et al., 2009). Importantly, humic substances are the main component of SOM to facilitate electron transfer from microbial metabolism products to U(VI), promoting the formation of sparingly soluble oxides (UO_2) (Vodyanitskii et al., 2019). In addition, the electronegativity of SOM and soil colloids increase U(VI) retention due to their sorption interaction between negatively charged SOM and uranyl forms (Li et al., 2014). Increased sorption of uranyl species into SOM is mainly attributed to an increase in the soil ionic exchange capacity (Gavrilescu et al., 2009). As been reported by Rout et al. (2016), uranyl forms strong bonds with SOM, even at low pH levels, leading to that a part of the total U(VI) is converted to be less mobile U(IV) to decrease the U bioavailability in soils. This effect results from the SOM compositions (i.e., C and Ca content), promoting U−C−Ca formation to increase U adsorption and incorporation with $CaCO_3$ in soils (Bone et al., 2020). Clay colloid minerals, also control on U sorption via promoting U and C to form ternary surface complexes (Dublet et al., 2017), while this underlying mechanism is still required for further investigation via EXAFS spectroscopic analysis. Uranyl ions are adsorbed strongly by soil Fe oxides, probably bounding as inner-sphere complexes with Fe oxides (Izquierdo et al., 2020). Similarly, soil colloids such as humic acid, ferric, and bentonite colloids also significantly affect U(VI) mobility and bioavailability since their electronegativity results in ready complexation with uranyl in solution, thereby forming the colloid-uranyl complex (Li et al., 2013, 2014; Vodyanitskii et al., 2019). Yet, Wang et al. (2013) reported that the association of insoluble U(IV) with Fe oxides and organic matter colloids enhance the solubility and mobility of U(IV), thus increasing the risk of U(IV) contamination in natural environments. This finding is likely attributed from that U(IV) bound to amorphous Al-P-Fe-Si aggregates in the soil is labile; thus, it may be transferred from the Al-P-Fe-Si aggregates in soil to the mobile Fe and OM colloids (Wang

et al., 2013).

3.2. Influences of soil microbial activity on U speciation and bioavailability

Microbial interactions with U ions, such as reduction, adsorption, and precipitation, lead to changes in U chemical speciation, which controls U mobility and bioavailability in the soil-plant system (Fig. 2; Nevin et al., 2003; Selvakumar et al., 2018). Numerous types of microbes have been identified to reduce U(VI) to U(IV), including *Thermoterrabacterium ferrireducens* (Khijniak et al., 2005), *Shewanella oneidensis* MR-1 (Sheng et al., 2011), *Thermus scotoductus* SA-01 (Cason et al., 2012), *Bacillus* sp. dwc-2 (Li et al., 2017), *Shewanella putrefaciens* (Xie et al., 2018), and *Stenotrophomonas* Br8 (Sánchez-Castro et al., 2020). Here, it has been proposed three potential explanations for microbial U(VI) reduction. First, U-reducing microorganisms contain various U(VI) reductases, including membrane-bound, periplasmic and intracellular enzymes (Lakaniemi et al., 2019). Second, these microorganisms transfer electrons to U(VI) through the cytochromes via acetate and lactate groups of the electron transport chain, enzymatically promoting the reduction of aqueous U(VI) to insoluble U(IV) (Orellana, et al., 2013; Mtimunye and Chirwa, 2014). Furthermore, some proteins in microbes including oxidoreductase, thioredoxin, and thioredoxin reductase obtaining electrons from nicotinamide adenine dinucleotide (NADH), can carry out two electron reduction of U(VI) to U(IV) (Li and Krumholz, 2009). Yet, the mechanisms of microbial U(VI) reduction are likely different due to microbial species. Microorganisms including bacteria, fungi, and unicellular algae have the capability of biosorption to U(VI) (Bader et al., 2018; Banala et al., 2021). The reason for its biosorption capability may relate to the composition of the microbial cell wall (Banala et al., 2021). Microbial cells generally have a high surface-to-volume ratio, thus promoting the absorption of U(VI) in the soil solution to microbial cell surfaces (Li et al., 2014). Meanwhile, various functional groups (i.e., hydroxyl, carbonyl, amine, phosphoryl, and sulfhydryl groups) on the microbial cell wall enhance the biosorption capability to U(VI) (Selvakumar et al., 2018; Banala et al., 2021). In addition, microorganisms also have the potential to precipitate U(VI) via complexing with inorganic ligands such as phosphates through a phosphorylase process and form a U–phosphate insoluble precipitate (Lakaniemi et al., 2019; Banala et al., 2020). However, the underlying mechanism by which U precipitation occurs in microbes is not well recognized and still requires for further investigation.

4. Uranium acquisition, translocation, and accumulation in plants

4.1. Uranium uptake by plants

Uranium uptake by plants has recently been received the attention of the global community due to the extensive application of U and its compounds in the nuclear industry, and its adverse effects on plant growth, microbial reproduction, and human health (Jha et al., 2016; Gao et al., 2019). Thus, quantifying the amounts of U uptake by plants from the soil matrix has become a main concern, particularly in remediation studies (Favas et al., 2014). Plants are increasingly considered as an important tool to remediate U-contaminated soils in situ because they have the ability to absorb and accumulate U in an efficient and eco-friendly manner (Qi et al., 2019; Hu et al., 2021). Generally, plants absorb both U(IV) and U(VI) via epidermal root cells, while its specific molecular mechanism remains still unknown (Baumann et al., 2014; Lai et al., 2021). Most U cations (such as UO_2^{2+}) are taken up by roots mainly via the same carriers or ion channels with the essential elements such as calcium, iron and magnesium (Croteau et al., 2016). Anionic species of U, such as $UO_2(CO_3)_2^{2-}$ and $UO_2PO_4^-$, might cross cell membranes via anionic channels as analogs for bicarbonate or phosphate, as anion channels on membranes are often large and nonselective (Simkiss and Taylor, 1995; Croteau et al., 2016). As shown in Table 2, the ability of plants to absorb U mainly depends on the plant species due to the difference in their accumulation functions. For example, water lily, wild ramie, and mustard are potential U hyperaccumulators since they absorb

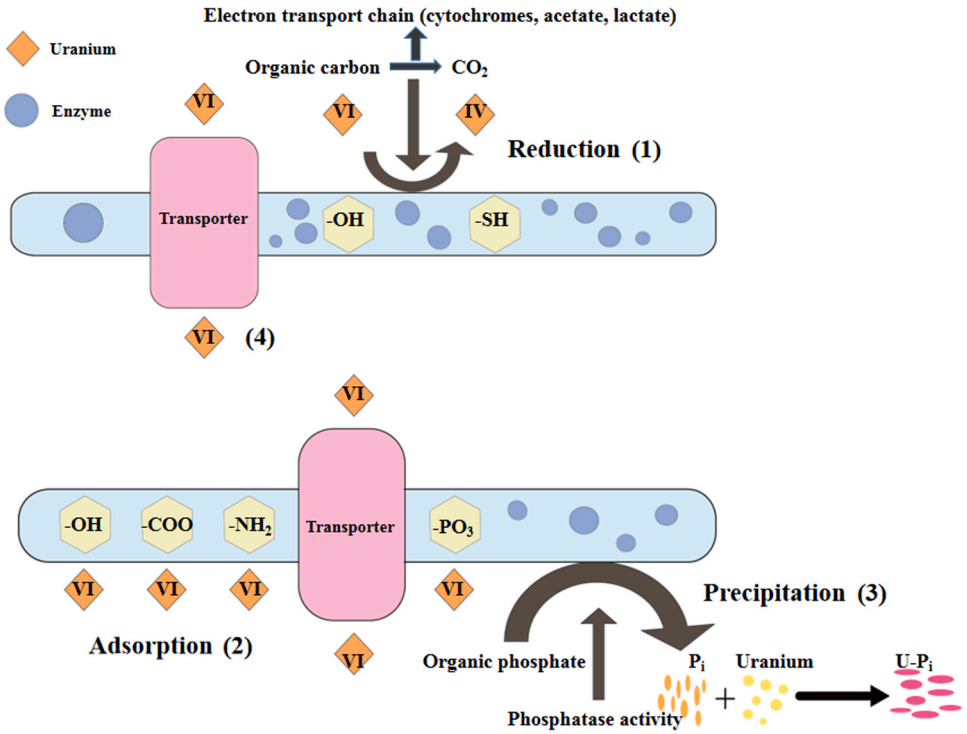

Fig. 2. Known mechanisms on the microbial interactions with U ions using reduction, adsorption, and precipitation. Note: (1) the reduction of U(VI) via cytochromes, acetate, and lactate; (2) various anions such as hydroxyl, carbonyl, amine, phosphoryl, and sulfhydryl groups present in the cell wall enhance the sorption of U(VI); (3) U(VI) complexes with phosphates through a phosphorylase process; and (4) U(VI) pass cell membranes via transporters.

Table 2
Uranium uptake by different plant species. (data is collected from academic articles published from 2010 to 2020).

Plant Species	Root (mg kg^{-1})	Aerial tissue (mg kg^{-1})	Notes	References
Water lily	1538	3446	55 mg L^{-1} U (VI) (Hydroponic experiment)	Li et al., 2019a
Arrowhead Plant	527	36	3 mg L^{-1} U (VI) (Hydroponic experiment)	Chao et al., 2019
Leptochloa fusca	408	15	200 mg kg^{-1} U (VI, $UO_2(NO_3)_2{\cdot}6H_2O$) (Pot experiment) (13 mg kg^{-1} in leaves)	Ahsan et al., 2017
Bamboo-willow	328.18	173.12	25 mg kg^{-1} U (VI, $UO_2(NO_3)_2{\cdot}6H_2O$) (Pot experiment) (All plants were ashed and weighed)	Sha et al., 2019
Scrobic	275.44	27.34		
Macleaya cordata	577.37	132.74		
Sesbania rostrata	20.61	23.74	80 mg kg^{-1} U (VI) (Pot experiment)	Ren et al., 2019
Macleaya cordata	36.8	12.5	18 mg kg^{-1} U (VI) (Pot experiment)	Hu et al., 2019
Mustard	7145	~380	47.74 mg kg^{-1} U (VI) (Pot experiment)	Qi et al., 2014
Sunflower	136	4.08	82 mg kg^{-1} U (VI, UO_3) (Pot experiment)	Meng et al., 2018
Indian mustard	277	19.1		
Italian ryegrass	~800	~290	150 mg kg^{-1} U (VI, $UO_2(CH_3COO_2)_2{\cdot}2H_2O$) (Pot experiment)	Qi et al., 2019
Ryegrass	~980	~600		
Orchard grass	~820	~280		
Broad bean	5309.82	0.24	25 μmol L^{-1} U (VI) (Hydroponic experiment)	Liu et al., 2020
Sunflower	~315	~5.8	318 mg kg^{-1} U soil (Field experiment, harvesting times is 4 weeks)	Alsabbagh and Abuqudaira, 2017
Bidens pilosa	721.46	661.36	480 μmol L^{-1} U (VI) (Hydroponic experiment)	Imran et al., 2019
Wild ramie	21.85	35.88	7.98 mg kg^{-1} U (VI) (Pot experiment)	Wang et al., 2018b
Wild stonecrop	~800	~1600	100 μmol L^{-1} U (VI, $UO_2(CH_3COO_2)_2{\cdot}2H_2O$) (Hydroponic experiment)	Du et al., 2016
Oilseed rape	~4900	~230		
Mustard	~3000	~340		
Garden peas	2327.5	11.16	25 μmol L^{-1} U (VI) (Hydroponic experiment)	Gupta et al., 2020
Bean	1243.48	4.15	500 mg L^{-1} U (VI) (Hydroponic experiment)	Yang et al., 2015
Arabidopsis thaliana	~10100	~3.8	25 μmol L^{-1} U (VI) (Hydroponic experiment)	Tewari et al., 2015
Sunflower	16.05	0.21	15 mg kg^{-1} U (VI) (Pot experiment)	Chen et al., 2020b
Mustard	37.77	1.82	15 mg kg^{-1} U (VI) (Pot experiment)	Chen et al., 2020a
Zebrina	20.91	1.23	15 mg kg^{-1} U (VI) (Pot experiment)	Chen et al., 2019
Maize	32.01	3.50	50 mg kg^{-1} U (VI) (Pot experiment)	Stojanović et al., 2010
Willow	16	69	480 mg kg^{-1} U (Pot experiment; 15 mg kg^{-1} in leaves of willow)	Mihalík et al., 2010
Sheep sorrel	9.0	2.8	146 mg kg^{-1} U soil (Field condition)	Favas et al., 2016
Antirrhinum majus	7.6	0.4	132 mg kg^{-1} U soil (Field condition)	
Common rush	250	1.1	250 mg kg^{-1} U soil (Field condition)	
Toad rush	36.1	2.5	135 mg kg^{-1} U soil (Field condition)	
Bent grass	6.8	0.3	96.5 mg kg^{-1} U soil (Field condition)	
Sweet potato	2216	6.67	25 μmol L^{-1} U (VI) (Hydroponic experiment)	Lai et al., 2021
Purple sweet potato	5712	3.48	25 μmol L^{-1} U (VI) (Hydroponic experiment)	Lai et al., 2021

and translocate the high levels of U to aerial parts (Qi et al., 2014; Wang et al., 2018b; Li et al., 2019a). Sunflower is a variety of metal hyper-accumulators, while unexpectedly, it does not show a strong uptake of U in the shoot tissues. This finding has been confirmed by several studies (Rizwan et al., 2016; Alsabbagh and Abuqudaira, 2017; Meng et al., 2018; Farid et al., 2018). In addition, U speciation in soil solution may also be an important factor influencing U uptake by plants. As reviewed above, this process also relates to the soil properties, such as soil pH, SOM, and mineral elements (Favas et al., 2016).

Uranium mainly exists as UO_2^{2+} and $[UO_2OH]^+$ in soil solution, and plants absorb U through an active transport process requiring energy expenditure or through passive uptake, such as facilitated diffusion (Gavrilescu et al., 2009; Muscatello and Liber, 2010; Wu et al., 2020). The addition of phosphate fertilizers to U-contaminated soils efficiently reduces U uptake by plants (Rufyikiri et al., 2006). This decrease attributes to the phosphorus presence in soil solution as negatively charged phosphate ions, such as $H_2PO_4^-$ and HPO_4^{2-}, which react readily with U ions to form uranyl phosphates with low solubility or precipitation products such as autunite (Rufyikiri et al., 2006; de Boulois et al., 2008; Edayilam et al., 2020). In addition, soil types and its properties control plant U uptake via affecting U bioavailability. A greater U uptake by plants is observed in calcareous soils than in natural soil because UO_2^{2+} complexes with carbonates, forming highly mobile anionic complexes (Shahandeh and Hossner, 2002). Indeed, soil properties (mineralogy, pH, and organic matter) also largely affect U uptake in ryegrass via governing U bioavailability, presenting a log-log relationship between plant U uptake and the sum of U species (such as UO_2^{2+}, uranyl carbonate complexes, and $UO_2PO_4^-$) in the soil solution (Duquène et al., 2010). Uranium uptake by plants is dependent on pH since it affects the chemical forms and bioavailability of U and the physiological characteristics of the plant, such as nutrient uptake, organic acid exudation, and enzyme activity (Vandenhove et al., 2006; Duquène et al., 2006; Saenen et al., 2013; Favas et al., 2016). Arbuscular mycorrhizal fungi also participates in the biochemical U cycling in the soil-plant system by mobilizing U in soils and improving plant resistance to U stress, thus promoting U uptake by plants (Malaviya and Singh, 2012; Zhang et al., 2019a). Uranium uptake by plant roots is greatly affected by Ca and carbonate contents in soils (El Hayek et al., 2018). As discussed above, the formation of uranyl-carbonate and ternary uranyl-calcium-carbonate complexes results in the decrease the U bioavailability in soil, in turn decreasing plant uptake (El Hayek et al., 2018). Importantly, root activity, particularly the continuous release of organic acids in the rhizosphere, has a positive effect on U uptake by plant roots. Root exudation of a model organic acid, citrate, increases the size of extractable U pool in the soil due to the formation of UO_2-citrate$^-$ (Henner et al., 2018; Wu et al., 2020). In addition, CO_2 pressure also partly influences the kinetics of U uptake by plants, while it is quite complicated. This effect likely results from that the dissolved CO_2 in the soil solution has a strong affinity for the UO_2^{2+} cation, therefore indirectly affecting U bioavailability in the soil-plant system (Trenfield et al., 2011; Boghi et al. 2018).

4.2. *Uranium sequestration in plant roots*

The accumulation and distribution of U in plants varies substantially among plant species in terms of plant U tolerance mechanisms (Nie et al., 2015; Lai et al., 2020a). In most plant species, U is retained in root systems, and its transfer from plant roots to shoots is generally limited (Laurette et al., 2012; Qi et al., 2019). Indeed, U concentration in plant tissues exhibits the following decreasing trend: roots > leaves > stems > flowers/fruits (Favas et al., 2016). Nevertheless, in *Leptochloa fusca* L. and *Calluna vulgaris* (L.) Hull plants, U concentrations in different plant tissues occurred in the following order: roots > stems > leaves (Favas et al., 2016; Ahsan et al., 2017). In plant root cells, the majority of U is

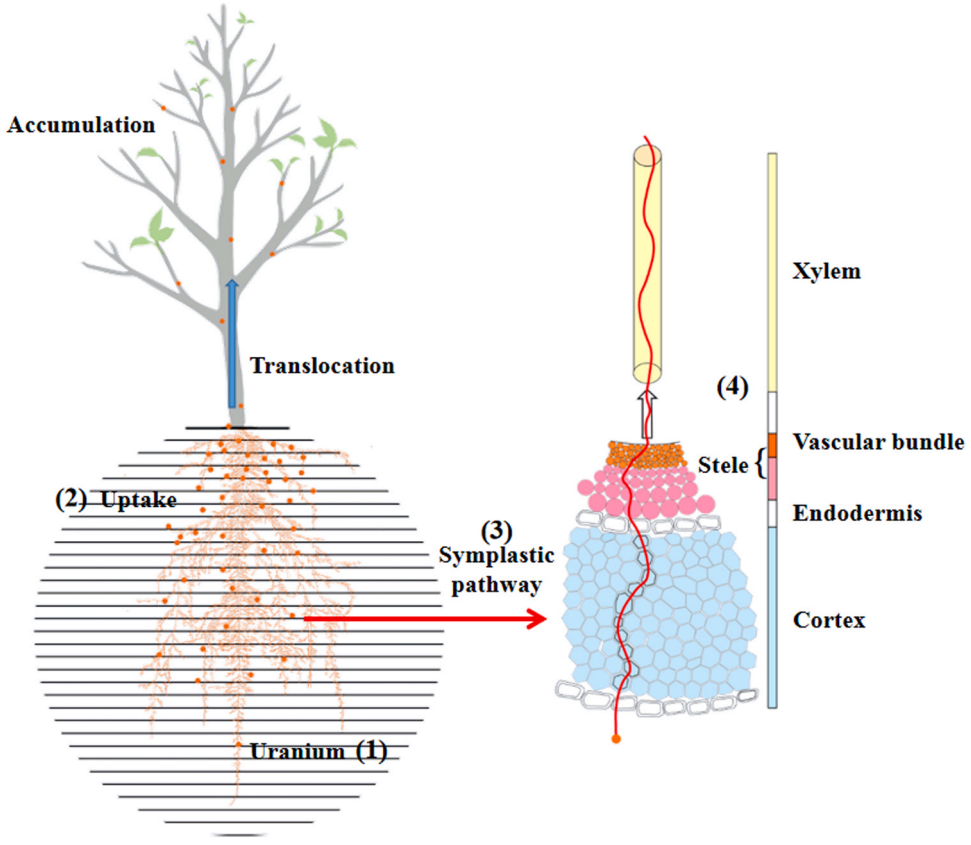

Fig. 3. Mechanism on U ions transport from roots to aerial parts. Note: (1) Plant grown with U contaminated soil. (2) U uptake takes place plant roots. (3) Transport of U was through symplastic pathway. (4) A series of cells of the cortex, endodermis, stele and xylem for the translocation of U is shown.

located in the cell wall fraction, followed by the organelle fraction, while the lowest amount U is associated with the cytosol-containing fraction (Nie et al., 2014, 2015). Similarly, root cell walls and vacuoles (soluble components) are the main distribution sites of U ions, indicating that the chemical forms of U in the plant roots are insoluble and oxalate compounds (Lai et al., 2021). Plant cell walls are principally composed of polyose (including cellulose, hemicellulose and pectin) and protein, providing negatively charged sites on their surfaces to bind UO_2^{2+} ions and restrict their transport across the cytomembrane (Nie et al., 2014; Huang et al., 2017). Moreover, P groups on the root cell walls are key coordination sites for U complexation, precipitation and mineralization, which are responsible for the majority of U sequestration in root systems, thus restricting U transfer from roots to aerial parts (Straczek et al., 2010; Laurette et al., 2012; Nie et al., 2015; Baker et al., 2019). Thus, U sequestration in the root may result from the propensity of U to bind to cell walls and the biotransformation of U inside plant roots to alleviate U phytotoxicity.

4.3. Root-shoot transport of U

After the penetration of U into root parts, it accumulates in roots, or may be translocated to aboveground plant tissues. In most plant species, only a small portion of root U is transported to the aerial parts of the plant, such as *Zea mays* L. (Stojanović et al., 2010), *Arabidopsis thaliana* (Saenen et al., 2013), *Nicotiana tabacum* L. (Soudek et al., 2014), *Helianthus annuus* L. (Alsabbagh and Abuqudaira, 2017), *Brassica juncea* L. (Meng et al., 2018), *Macleaya cordata* (Hu et al., 2019), *Vicia faba* L. (Lai et al., 2020a), *Pisum sativum* L. (Gupta et al., 2020) and *Encelia farinosa* A. Gray ex Torr. (Wetle et al., 2020), and *Ipomoea batatas* L. (Lai et al., 2021). However, some studies have showed a high rate of U translocation towards the aerial parts of the plant, including *Salix babylonica* (Mihalík et al., 2010), *Sesbania rostrata* (Ren et al., 2019), and *Nymphaea tetragona* Georgi (Li et al., 2019a). Indeed, plant U uptake depends not only on the potential U bioavailability in soil, but also on transporter gene expression in plants (Vanhoudt et al., 2010b; Doustaly et al., 2014; Wu et al., 2020). Doustaly et al. (2014) have identified three transporter genes (*IRT1, FRO2 and FIT1*) involving U uptake and translocation in *Arabidopsis thaliana* being treated with 5- and 50-mM uranyl. Furthermore, U also binds to other metal transporters in plants, but the molecular mechanism of U translocation is not still well known and requires further investigation (Dinocourt et al., 2015). In particular, uranyl ions combine with phosphate groups in a soil solution, resulting in low U translocation in the plants; in contrast, the formation of UO_2-lactate$_2$ promotes U transport from the roots to the shoots (Wu et al., 2020). In addition, transpiration also drives U transport within plant tissues (Aranjuelo et al., 2014; Wu et al., 2020).

Generally, U is absorbed by roots and then translocated from the root tissues into the aboveground parts via symplastic movement (Fig. 3; Straczek et al., 2010; Wu et al., 2020). Its transport is governed via three processes: i) U sequestration inside root cells, ii) symplastic transport into stele, and iii) release into xylem (Sheoran et al., 2010; Mihalík et al., 2012; Pentyala and Eapen, 2020). In xylem, U is transported through the symplastic pathway, as special U-chelates are formed (such as UO_2-citrate$^-$ and UO_2-lactate$_2$) (Wu et al., 2020). In roots, U is water-insoluble in most plants, thus resulting in low U transport to aerial parts (Zhao et al., 2010; Wu et al., 2020). Moreover, the movement of U ions from root symplasts into xylem vessels is generally a tightly controlled process mediated by U transporters and is probably driven by transpiration (Aranjuelo et al., 2014; Berthet et al., 2018). Symplastic transport of U ions occur in xylem after these ions cross the casparian strip, which is an active transport process (Pentyala and Eapen, 2020). Meanwhile, U transport is further regulated by membrane transport proteins due to the selectively permeable plasma membrane of the cells (Rufyikiri et al., 2004; Berthet et al., 2018). However, to date, only a few studies have reported that high U transporter gene expression increases the rate of U translocation from roots to aerial parts. Thus, future studies on U transport in plants should focus on the molecular mechanisms to provide a theoretical basis for phytoremediation of U-contaminated soils.

4.4. Potential U hyperaccumulator plants

Phytoextraction, a promising phytoremediation technique, uses the selected hyperaccumulator plants that accumulate extraordinarily high amounts of heavy metals in the harvested regions (aerial regions) of the plant (Sheoran et al., 2010; Hou et al., 2017). Thus, the identification of hyperaccumulators is a key step for the remediation of metal-contaminated soils. This process has been ongoing over the last three decades (Zhang et al., 2002; Krzciuk and Gałuszka, 2015; Wu et al., 2018). In March 2020, the Global Hyperaccumulator Database has reported 759 species of metal hyperaccumulators (i.e., 82 families) around the world (Manara et al., 2020). Among these species, most are identified as hyperaccumulators of nickel (523), copper (53), cobalt (43), cadmium (43), and manganese (42) (Reeves et al., 2018; Manara et al., 2020). However, the identification of U hyperaccumulators lags substantially relative to hyperaccumulators of other heavy metals.

Hyperaccumulator plants mainly exhibit three characteristics: (i) large accumulation (shoot bioconcentration factor > 1); (ii) high translocation (translocation factor > 1); and (iii) strong tolerance (growth process without showing symptoms of toxicity) (Liu et al., 2019; Ge at al., 2020). Ideally, hyperaccumulator plants should have a rapid growth cycle with a large aboveground biomass (Liu et al., 2019). Furthermore, metal concentration thresholds in plant have become an important criterion for the identification of metal hyperaccumulators. It has been well accepted that thresholds of heavy metal hyperaccumulation in plants are a dry weight aerial tissue above 10, 000 mg kg^{-1} for manganese, 3000 mg kg^{-1} for zinc, 1000 mg kg^{-1} for lead, nickel, or arsenic, 300 mg kg^{-1} for copper and cobalt, or above 100 mg kg^{-1} for cadmium (Reeves et al., 2018; Manara et al., 2020). However, this thresholds on U has still not yet been determined, thus lacking a known reference standard for the identification of U hyperaccumulators. As known, the aerial parts of plants accumulating large amounts of U are far fewer in number than that of plants accumulating large amounts of other heavy metals, such as nickel, copper, cobalt, manganese, zinc, and cadmium (Reeves et al., 2018). Recently, it has been reported that Wild ramie (*Boehmeria nivea*) accumulates high amounts of U in the shoots (shoot bioconcentration factor > 4), and its translocation factor is > 1.5 (Wang et al., 2018b). This finding indicates that *Boehmeria nivea* may be considered a potential U hyperaccumulator. In this regard, other identified potential U hyperaccumulators can be considered such as *Salix babylonica* (Mihalík et al., 2010), *Sesbania rostrata* (Ren et al., 2019), and *Nymphaea tetragona* Georgi (Li et al., 2019a). The mechanisms on potential U hyperaccumulators in the aerial parts depend on the following four processes: (i) increasing U bioavailability in the soil rhizosphere to further enhance U uptake in roots via releasing root exudates, (ii) reducing U accumulation in root cell walls and vacuoles, (iii) increased U root-to-shoot translocation via efficient xylem loading, and (iv) improving plant resistance to U stress via its chelation in the shoot cytosol and/or compartmentalization in leaf/stem vacuoles (Li and Zhang, 2012; Malaviya and Singh, 2012; Manara et al., 2020).

4.5. Effects of chemical accelerators on promoting U accumulation by plants

Some chemical accelerators, such as chelating agents, plant growth regulators, and plant growth-promoting rhizobacteria, can transform non-bioavailable U into bioavailable fractions in soil or alleviate U phytotoxicity, thereby improving U accumulation by plants (Hu et al., 2019; Qi et al., 2019; Chen et al., 2020a). Applying chelating agent such as S, S-ethylenediamine disuccinic acid (EDDS), oxalic acid (OA) and citric acid (CA), increases U bioavailability in U-contaminated soils, which promotes U uptake and translocation in soil-plant systems (Chen

et al., 2020b; Hu et al., 2021). These effects may be attributed to the fact that chelating agents can hinder the sorption of U by soil to form chelant-U complexes with uranyl ions due to their negatively charged hydroxyl or carboxyl groups. This processes thus, enhances the bioavailable U contents in soil, leading to increases in the capability of plants to absorb and transfer the U (Hu et al., 2019; Chen et al., 2020b). Moreover, there are two possible mechanisms behind the plant uptake of chelant-U complexes. The first possibility is that chelant-U complexes are directly absorbed by roots. Second, the complexes are dissociated prior to their uptake in soil-plant systems (Chen et al., 2020b). The specific processes are still unknown and require for further investigation. Yet, this effect induced by CA is much more significant effects on the uptake and translocation of U than that of EDDS and OA. Applying CA promotes U solubilization in U-contaminated soil through releasing the adsorbed U from the solid phases into soil solution, thus increasing shoot U uptake and its translocation (Hu et al., 2019). Generally, phosphate group in rhizosphere soils decreases U bioavailability in soil-plant systems via combining with U ions. Nevertheless, under CA treatments, U mainly existed as UO_2-citrate^{-} in soils and it avoided U combination with phosphate, which easily could be absorbed by roots and translocated to the shoot of plants (Hu et al., 2021).

Adding plant growth regulators (such as indole-3-acetic acid, gibberellin A3 and 24-epibrassinolide) increases the shoot U uptake in *Brassica juncea* L.; and an increase in the activities of antioxidant enzymes indicates that these enzymes improve the plant tolerance to U stress (Chen et al., 2020a). Soil microbes also drive U uptake. For example, both rhizobial and arbuscular mycorrhizal fungi significantly increase U accumulation and biomass of *Sesbania rostrata* (Ren et al., 2019). This results from that adding arbuscular mycorrhizal fungi significantly increases phytochelatin synthase gene expression compared to the control; and it also increase the contents of succinic acid, malic acid, and citric acid in the root exudates of the inoculated plants (Dupré de Boulois et al., 2008; Ren et al., 2019). In addition, Qi et al. (2019) have reported that a plant growth-promoting bacterial mixture (M_4 and M_{12}) significantly improves U absorbing capability in three grass species (*Lolium perenne* L., *Lolium multiflorum* Lam., and *Dactylis glomerata* L.), increasing their biomass. Indeed, five bacterial mixtures have the ability to produce siderophores. Siderophore production directly and indirectly promotes plant rhizosphere growth, releasing U from insoluble to soluble phases to further increase U bioavailability in the soil-plant system (Gaonkar and Bhosle, 2013; Qi et al., 2019). However, studies of an increase in plant U uptake induced by biochar are limited. A potential explanation for this finding is that biochar may immobilize heavy metals in soil and thus decreases their uptake by plant roots (Liu et al., 2021; Palansooriya et al., 2020; Qi et al., 2021).

5. Toxic effects of U on plants

Uranium is a well-known toxic metal to plants. Its exposure induces toxic effects on several physiological and biochemical processes in plants, such as seed germination, root and shoot growth, photosynthesis, and nutrient uptake (Tables 3 and 4; Fig. 4) (Stojanović et al., 2010; Sachs et al., 2017; Imran et al., 2019). In addition, U toxicity induces plants to accumulate large amounts of ROS, thus resulting in lipid peroxidation and genotoxicity (such as damage to the DNA structure and blocking mitosis). These toxic effects on plants mainly depend on plant species, dose of U, and environmental conditions.

5.1. Seed germination

Uranium toxicity toward seed germination is an initial physiological effect on plants. For example, U treatment (1 mmol L^{-1}) markedly decrease the maize germination rate during the early phase of seed germination (2–4 days), while the inhibitory effect is eliminated in the next phase (5–7 days) (Nie et al., 2010a, 2010b). Plant seeds alleviate U

Table 3
Toxic effect of U on plant growth. (Data is collected from research articles published after 2006).

Plant species	Toxicity effect	U exposure level	References
Arabidopsis	The shoots and roots biomass were decreased by 25.04% and 39.92%, respectively. The root length was also reduced.	50 μM U (VI) ($UO_2(NO_3)_2{\cdot}6H_2O$)	Misson et al., 2009
Duckweed	The shoot and root growth were significantly inhibited.	50 μM U (VI) ($UO_2(NO_3)_2{\cdot}6H_2O$)	Mkandawire et al., 2007
Cabbage	The plant height, shoot and root dry wight decreased.	0.1 mg L^{-1} U (VI)	Xie and tang, 2014
Duckweed	The fresh weight was decreased by 31.82–94.89%.	5–150 μM U (VI)	Horemans et al., 2015
Wheat	The root and shoot dry biomasses did not significantly vary.	25 μM U (VI)	Laurette et al., 2012
Broad bean	The root length and shoot dry wight decreased, and roots darkened.	25 mg L^{-1} U (VI)	Lai et al., 2020a
Radish	The root length and root dry mass significantly decreased.	10–2560 mg kg^{-1} U (VI)	Hou et al., 2018
Cabbage	The stem height and root length significantly decreased.	640–2560 mg kg^{-1} U (VI)	Hou et al., 2018
Cucumber	The root length and root dry mass significantly decreased.	1280–2560 mg kg^{-1} U	Hou et al., 2018
Spinach	The root length and root dry mass significantly decreased.	160–2560 mg kg^{-1} U	Hou et al., 2018
Arabidopsis	The leaf area, fresh and dry weight significantly decreased.	50 μM U (VI)	Vanhoudt et al., 2014
Maize	The plant height, roots and shoots dry mass was reduced 13.85%, 32.12% and 31.01%, respectively.	500 mg kg^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Stojanović et al., 2010
Broad bean	The shoots and roots biomass were decreased by 11.63% and 9.09%, respectively.	25 μmol L^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Liu et al., 2020
Dwarf beans	The shoot height, leaf, root and shoot fresh weight significantly reduced, and roots started to turn yellowish.	1000 μM U (VI)	Vandenhove et al., 2006
Arabidopsis	The leaf surface area and shoot and root fresh weight decreased.	25 μM U (VI) ($UO_2(NO_3)_2{\cdot}6H_2O$)	Tewari et al., 2015
Sunflower	The root and shoot biomass reduced after 10 weeks of cultivation.	156 mg kg^{-1} U (Field condition)	Alsabbagh and Abuqudaira, 2017
Ramie	The shoot biomass was reduced 6.77%, but the shoot heights and root lengths slightly increased.	125 mg kg^{-1} U (VI)	Wang et al., 2018b

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Table 3 (*continued*)

Plant species	Toxicity effect	U exposure level	References
Ryegrass	The plant height and shoot dry mass significantly reduced.	150 mg kg^{-1} U (VI)	Qi et al., 2019
Orchard grass	The plant height and shoot dry mass significantly reduced.	100–150 mg kg^{-1} U (VI)	Qi et al., 2019
Sesbania rostrata	The dry weight of shoots and roots significantly decreased.	150–300 mg kg^{-1} U (VI)	Ren et al., 2019
Arabidopsis	Fresh weight of leaves significantly reduced.	25–100 μM U (VI)	Saenen et al., 2015a
Azolla	The growth inhibition for Azolla is decreased by 50.31%.	10 mg L^{-1} U (VI)	Pan et al., 2015
Garden peas	The shoot and root biomasses decreased.	50 μmol L^{-1} U (VI)	Gupta et al., 2020
Sweet potato	The root length, root and shoot biomasses decreased.	25 mg L^{-1} U (VI)	Lai et al., 2021

toxicity via regulating antioxidant defense systems, leading to the restoration of plant cell function (Nie et al., 2010a, 2010b). This effect also depends on U concentration in soils. Low levels of U promoted seed germination, but when the soil U concentration was greater than 320 mg kg^{-1}, the germination of seeds from three vegetables (tomato, kohlrabi, and radish) was obviously inhibited (Hou et al., 2018). Similar phenomena were also reported in several other studies (Sheppard et al., 1992; Nie et al., 2010a, 2010b; Butler et al., 2016; Aicha et al., 2019). This finding does not suggest that low levels of U (< 20 mg kg^{-1}) does not harm the seeds of these vegetables, while its results from plant self-resistance against injury (Hou et al., 2018). Two potential explanations for these phenomena have been proposed. The first possibility is that low levels of U stimulate the activity of some enzymes that promote seed germination and cause seeds to sprout quickly (Nie et al., 2010a, 2010b). Second, low U levels reduce the transpiration efficiency of the plant seeds and improve its water use efficiency, thus promoting seed germination (Hou et al., 2018). When the U levels increase up to the maximum limit of the seed tolerance, its metabolism is disturbed. Thus, the absorption of some mineral elements is hindered, and the DNA structure of the plant cells is damaged, resulting in decreasing seed germination rate (Hou et al., 2018; Gao et al., 2019; Chen et al., 2020c). Moreover, the specificity of resistance to U among different plant species is worth noting (Gao et al., 2019). For instance, cucumber still maintains a certain germination rate (~80%) upon treatment with high U levels (1280 mg kg^{-1}), while the germination rates of tomato, kohlrabi and cabbage are all less than 10% upon the same U treatment (Hou et al., 2018).

5.2. Root growth

Since U preferentially accumulates in plant roots, root growth is not surprisingly adversely affected by its stress. Uranium-induced inhibition on root growth has been observed in different plants, such as *Arabidopsis thaliana* at 50–500 μmol L^{-1} U in solution (Misson et al., 2009), *Zea mays* L. at 250–1000 mg kg^{-1} U in agricultural soil (Stojanović et al., 2010), *Lolium perenne* L. at 150 mg kg^{-1} U in agricultural soil (Qi et al., 2019), *Dactylis glomerata* L. at 100–150 mg kg^{-1} U in agricultural soil (Qi et al., 2019), *Vicia faba* L. at 20–25 μmol L^{-1} U in solution (Liu et al., 2020), and *Pisum sativum* L. at 50 μmol L^{-1} U in solution (Gupta et al., 2020) (Table 3). These findings likely suggests that this effect on roots repossess the U concentration due to their different species. Yet, the extent of this effect on roots is characterized by its physiological characteristic change. Recently, Zhang et al. (2020a) reported that 25 μmol L^{-1} U in solution caused a significant decrease in both root biomass and total root

Table 4
The physiological response of plants to U toxicity. (References are collected from academic articles published after 2010).

Plant species	Growth parameters	U exposure level	References
Arabidopsis	The CAT, APX, GR and lipid peroxidation increased, while the SOD activity maintained stable.	10 μM U (VI) ($UO_2(NO_3)_2{\cdot}6H_2O$)	Vanhoudt et al., 2010a
Perennial ryegrass	The soluble protein decreased, but the MDA increased.	5 mg kg^{-1} U (IV, U_3O_8)	Rong et al., 2020
Water hyacinth	The SOD, POD, CAT decreased, but the MDA increased.	50 mg L^{-1} U (VI)	Li et al., 2015
Wheat Seedling	The chlorophyll a and b decreased, and the carotenoid content maintained stable.	50 mg L^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Chen et al., 2012
Broad bean	The H_2O_2, O_2^- and MDA increased, but the SOD and POD decreased.	25 μM U (VI) ($UO_2(NO_3)_2{\cdot}6H_2O$)	Chen et al., 2020c
Arabidopsis	H_2O_2 and NO, and MDA of shoots and roots increased.	25 μM U (VI)	Tewari et al., 2015
Arabidopsis	The SOD and CAT of leaves increased, but the GPX decreased.	25 μmol L^{-1} U (VI)	Vanhoudt et al., 2011b
Broad bean	The photosynthesis rate, stomatal conductance, and stomatal conductance decreased significantly, but the leaf intercellular CO_2 parameters was not obvious.	0–25 μmol L^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Zhang et al., 2020a
Bidens	The efficiency of photosynthesis and SOD decreased, but the soluble protein, CAT and POD increased.	40–1000 μmol L^{-1} U ($C_4H_6O_6U$)	Imran et al., 2019
Macleaya cordata	The POD and APX concentrations decreased, but SOD and CAT increased.	18 mg kg^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Hu et al., 2019
Sesbania rostrata	The photosystem II efficiency decreased significantly.	150–300 mg kg^{-1} U (VI)	Ren et al., 2019
Spinach	The concentrations of SOD decreased.	10–2560 mg kg^{-1} U (VI)	Hou et al., 2018
Tomato	The concentrations of SOD increased.	40–2560 mg kg^{-1} U (VI)	Hou et al., 2018
Pea	Total chlorophylls content of leaves decreased significantly, but the carotenoid contents have not changed markedly.	0–0.5 μmol L^{-1} U ($UO_2(NO_3)_2$)	Tawussi et al., 2017
Leptochloa fusca	The total chlorophylls (chlorophyll a+b) content of leaves decreased.	200 mg kg^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Ahsan et al., 2017
Azolla	The CAT, POD and SOD contents increased markedly.	1–5 mg L^{-1} U (VI)	Pan et al., 2015
Water lily	The carotenoids, chlorophyll a and b content decreased, but the SOD, POD, CAT, and MDA content increased.	30 mg L^{-1} U ($UO_2(CH_3COO)_2{\cdot}2H_2O$)	Li et al., 2019a
Arabidopsis	The ascorbate, stomatal conductance, chlorophyll a and b content decreased, but	50 μmol L^{-1} U ($UO_2(NO3)_2{\cdot}6H_2O$)	Aranjuelo et al., 2014

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Table 4 (*continued*)

Plant species	Growth parameters	U exposure level	References
	the MDA content increased.		
Arabidopsis	The carotenoids, chlorophyll a and b content of leaves decreased, but the lipid peroxidation increased.	50 μmol L^{-1} U ($UO_2(NO3)_2{\cdot}6H_2O$)	Vanhoudt et al., 2014
Garden peas	The total chlorophyll and carotenoid concentration decreased, but H_2O_2, MDA and CAT content increased.	25 μmol L^{-1} U ($UO_2(NO_3)_2$)	Gupta et al., 2020
Sweet potato	The photosynthesis rate, transpiration rate, stomatal conductance, and intercellular CO_2 concentration decreased.	0–25 μmol L^{-1} U ($UO_2(NO_3)_2{\cdot}6H_2O$)	Lai et al., 2021

Note: H_2O_2, hydrogen peroxide; O_2^-, superoxide anion; NO, nitric oxide; MDA, malondialdehyde; CO_2, carbon dioxide; CAT, catalase; APX, ascorbate peroxidise; GR, glutathione reductase; SOD, superoxide dismutase; POD, Peroxidase; GPX, guaiacol peroxidase.

length in *Vicia faba* L., with the roots appearing black, indicating that U at this concentration was severely toxic to plant roots. This finding is potentially because U affects cell viability in the primary root apex of the plant and modulates mitotic activity in the root (Serre et al., 2019; Zhang et al., 2020a). Meanwhile, U destroys the root microstructure and interferes with plant auxin metabolism (Chen et al., 2020c). Moreover, under U stress, root cell shape, size, organelle distribution and cell wall structure change significantly, which causes the root tip necrosis, thereby aggravating U toxicity to roots (Lai et al., 2021). Another explanation for the substantial U-induced decrease in root biomass is that U may induce overproduction of H_2O_2 and the synthesis of NO, resulting in membrane lipid peroxidation and a disruption of membrane integrity (Li et al., 2019a; Serre et al., 2019).

5.3. Shoot growth

As shown in Table 3, U also affects plant shoot growth, while its toxicity differs among plant species. Uranium-induced reductions in shoot growth have been reported in *Arabidopsis thaliana* at 1–100 μmol L^{-1} U in solution (Vanhoudt et al., 2011b), *Lemna minor* L. at 5–150 μmol L^{-1} U in solution (Horemans et al., 2015), *Boehmeria nivea* at 125 mg kg^{-1} in agricultural soil (Wang et al., 2018b), *Lolium multiflorum* Lam. at 100–150 mg kg^{-1} in agricultural soil (Qi et al., 2019), and *Pisum sativum* L. at 20–50 μmol L^{-1} U in solution (Gupta et al., 2020), and *Ipomoea batatas* L. at 25 μmol L^{-1} U in solution (Lai et al., 2021; Table 3). In *Zea mays*, the 1000 mg kg^{-1} U treatment in soil reduced the plant

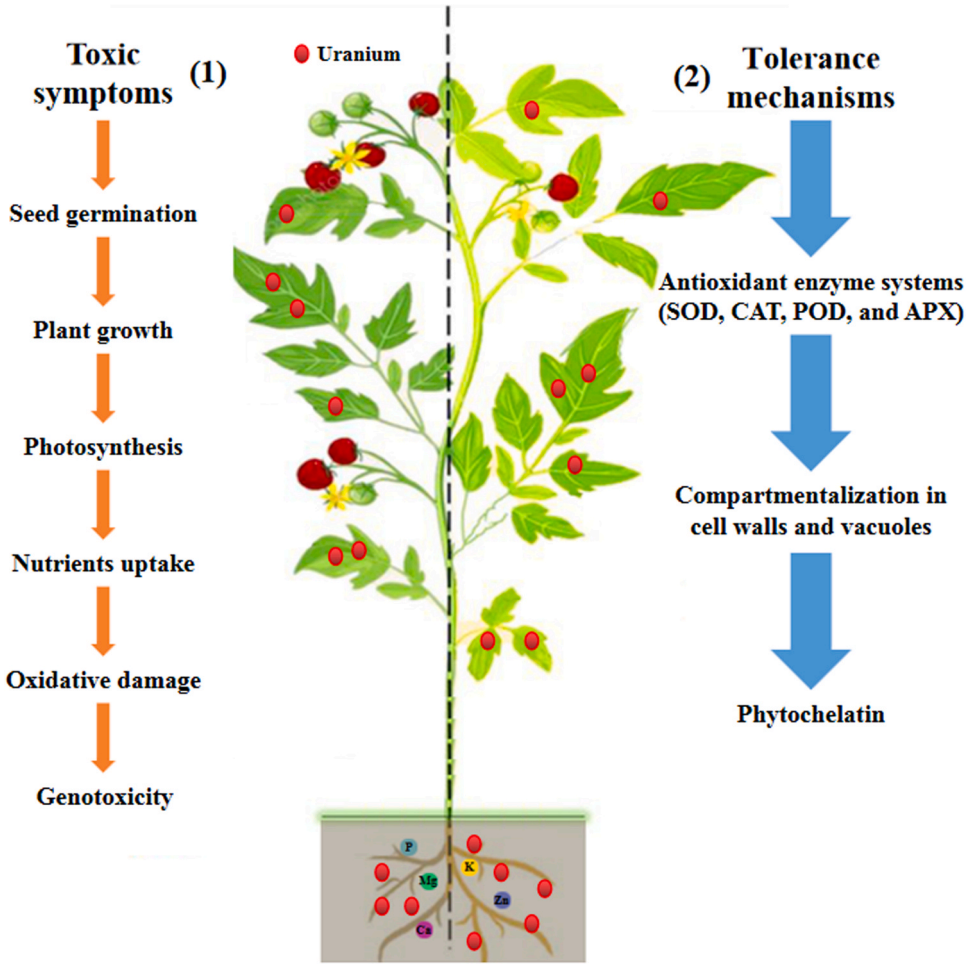

Fig. 4. Uranium toxicity to plants and tolerance mechanisms. Note; (1) The toxic effects on plants mainly include seed germination, plant growth, photosynthesis, nutrient uptake, oxidative damage, and genotoxicity. (2) Plants have evolved a number of defense strategies such as antioxidant enzymes, compartmentalization, and phytochelatin to enhance the U tolerance.

height by 46.94% and shoot dry mass by 58.23%, and the percentage of surviving plants by 23.3% (Stojanović et al., 2010). These decreases induced by U is attributed to both decrease of shoot cell division and inhibition of photosynthesis (Serre et al., 2019; Zhang et al., 2020a). This is also confirmed by Horemans et al. (2015), who found that the fresh weight of *Lemna minor* L. was decreased by 94.89% under the condition of 150 μmol L^{-1} U, and the medial lethal dose was 29.5 μmol L^{-1}. Uranium-induced stress inhibits root growth and development, leading to decreases in the absorption and transport of water and mineral elements via roots (Malaviya and Singh, 2012; Lai et al., 2020a). Another reason behind U-induced decreasing shoot growth is possible that U exposure causes a slightly shorter cell cycle and interferes with the homeostasis of essential elements (Rajabi et al., 2021). Moreover, U toxicity interferes with photosynthesis, transpiration, respiratory metabolism, carbon metabolism, and plant hormone synthesis, thereby inhibiting plant shoot growth (Vanhoudt et al., 2014; Gao et al., 2019; Lai et al., 2020b; Zhang et al., 2020a).

5.4. Photosynthesis

Photosynthesis is already known to be affected by abiotic stress, particularly heavy metal stress, resulting in a decrease in plant growth, delaying in plant development, and even, in some cases, plant death (Berthet et al., 2018; Chen et al., 2020b; Chi et al., 2020). Uranium toxicity decreases the leaf area, stomatal conductance, transpiration rate, and chlorophyll efficiency. These stresses are strongly dependent on U concentration, plant species, and other environmental conditions (Zhang et al., 2020a). Decreases in the chlorophyll content (such as chlorophyll-*a*, chlorophyll-*b*, and carotenoid) induced by U stress, have been reported in various plant species, such as *Triticum aestivum* L. (Chen et al., 2012), *Arabidopsis thaliana* (Vanhoudt et al., 2014), *Pisum sativum* L. (Tawussi et al., 2017), *Leptochloa fusca* L. (Ahsan et al., 2017), *Nymphaea tetragona* Georgi (Li et al., 2019a), *Bidens pilosa* L. (Imran et al., 2019), and *Pisum sativum* L. (Gupta et al., 2020). Uranium inhibits photosynthesis by damaging the hydration photo-oxidation process, decreasing photosynthetic pigment contents and altering the protein composition of photosynthetic membranes (Gao et al., 2019; Gupta et al., 2020; Zhang et al., 2020a). In addition, U-induced ROS overproduction and lipid peroxidation damaged the chloroplast structure and inhibited the expression of genes involving photorespiration pathway, resulting in a decrease in leaf chlorophyll content (Gupta et al., 2020). Recently, Zhang et al. (2020a) also reported a significant decrease in the photosynthetic parameters (photosynthesis rate, stomatal conductance, and stomatal conductance) of *Vicia faba* L. upon treatment with increasing U concentrations (0–25 μM U(VI)). The decrease in the photosynthetic parameters was also confirmed that the photosynthetic carbon metabolism pathway of the plants was damaged by U toxicity (Lai et al., 2021). The reason may be attributed to that U stress significantly inhibited the expression of genes involving in water photolysis, the electron transport chain and ATP synthesis in the chloroplast thylakoid membrane, resulting in the inhibition of ATP formation and blockade of electron transport chain. Meanwhile, many genes involving Calvin cycle were also significantly inhibited by U toxicity, which reduced carbon fixation in plants, thus leading to a decrease in chlorophyll a and b contents (Zhang et al., 2020a).

5.5. Nutrient metabolism

Heavy metals affect mineral nutrient metabolism by disturbing nutrient composition and regulating nutrient uptake, distribution, and transport, thus inducing phytotoxicity in the soil-plant system (Seneviratne et al., 2019; Lai et al., 2020b). Uranium also interferes with plant mineral nutrition in a complex manner (Vanhoudt et al., 2011c; Lai et al., 2020a). Several previous studies have documented U(VI) interference with essential nutrients, such as nutrient uptake and transport (P, K, Mg, Zn, Ca and Zn) in *Trifolium subterraneum* L., cv. Mount Barker (Rufyikiri et al., 2004), (P, K, Na, Ca, Mg, Fe, Zn, Cu, Mn) in both *Arabidopsis thaliana* (Vanhoudt et al., 2011c) and *Vicia faba* L. (Lai et al., 2020a), and (P, K, Cu, Zn, Ca, Zn) in *Pisum sativum* L. (Tawussi et al., 2017). Thus, the uptake and transport of some essential nutrients are inhibited by U stress in the soil-plant system, resulting in an imbalance in mineral nutrient metabolism. This is potentially because U accumulation occurs in the cell wall of plants to significantly damage plasmodesmata, which is an important transport channel for mineral nutrients, sugar, amino acids, and organic acids (Nie et al., 2015; Lai et al., 2020a). This damage exerts adverse effects on the metabolism of mineral elements in plants. Being a nonessential element, U is easily adsorbed and retained in the root system to further damage the root development, leading to a decrease in its nutrient uptake via roots (Vanhoudt et al., 2011a, 2011c). Moreover, it also interferes with nutrient metabolism in plants through the competitive binding of U ions to common carriers of mineral elements and the reduction in transpiration under U stress (Aranjuelo et al., 2014; Richter et al., 2016). A high U level exerts a significant inhibitory effect on the expression of transporter genes involving the uptake and transport of nutrient elements in plants, which may also result from the abnormal mineral nutrition metabolism in these plants (Lai et al., 2020a, 2021).

5.6. Oxidative damage

Under U stress, the main ROS species in plants are hydrogen peroxide (H_2O_2), superoxide (O_2^-), hydroxyl radicals (·OH), and nitric oxide (NO) (Tewari et al., 2015; Serre et al., 2019; Chen et al., 2020c). These ROS species mainly occur in numerous plant organelles, including chloroplasts, mitochondria, peroxisomes, and the endoplasmic reticulum (Vanhoudt et al., 2011b). Under normal conditions, ROS is associated with various physiological activities of plants, including defense against pathogens, induction and sensing of apoptosis, and adaptation to stress conditions. Yet, increased ROS production also causes an imbalance between ROS generation and ROS scavenging, further leading to oxidative damage in living cells (Vanhoudt et al., 2011a; Gagnaire et al., 2013). Uranium-induced overproduction of ROS has been reported in many plant species, such as *Armoracia rusticana* exposed to 500 μmol L^{-1} U (VI) (Soudek et al., 2011a), *Arabidopsis thaliana* exposed to 25 μmol L^{-1} U (VI) (Tewari et al., 2015), *Pisum sativum* L. exposed to 50 μmol L^{-1} U (VI) (Gupta et al., 2020), and *Vicia faba* L. exposed to 25 μmol L^{-1} U (VI) (Chen et al., 2020c).

Generally, increased ROS generation results in oxidative damage upon their interaction with various active biomacromolecules, including proteins, lipids, DNA, and enzymes. These interactions, in turn lead to lipid peroxidation, enzyme inactivation, inhibition of the electron transport system, gene overexpression and even cell death (Johnson et al., 2011; Saenen et al., 2015a; Maleki et al., 2017). Like other heavy metals, U is well documented to induce ROS overproduction by interacting with biomolecules inside plant cell, therefore interrupting normal cell metabolism (Li et al., 2019a; Kolhe et al., 2020a). U-induced ROS overproduction reduces the photosynthetic and transpiration rates, and decreases jasmonic acid and salicylic acid contents in *Arabidopsis thaliana* (Aranjuelo et al., 2014). After U exposure, large amounts of O_2^- and H_2O_2 in *Vicia faba* L resulted in the destruction of the cellular structure (Chen et al., 2020c). This finding may be attributed to the overproduction of ROS that causes chromosomal aberrations and the generation of micronuclei in plant cells (Wang et al., 2019b; Chen et al., 2020c). Moreover, plant growth has consistently been shown to be sensitive to overproduction of ROS induced by U stress (Vanhoudt et al., 2011b; Saenen et al., 2015a; Tewari et al., 2015).

The extent and nature of ROS induced under heavy metal stress mainly depend on the nature (redox ability) and concentrations of the heavy metals (Farooq et al., 2019). Redox-active metals, including lead, chromium, and vanadium, can participate in Fenton reactions, thus promoting ROS production in plants (Terrón-Camero et al., 2019). Being a redox-active metal, U is associated with ROS production in plants

through two pathways: (i) the Fenton reaction ($H_2O_2 + Fe^{2+} \rightarrow \cdot OH\ OH^- + Fe^{3+}$) and (ii) the Haber–Weiss reaction ($O^{2-} + H_2O_2 \rightarrow \cdot OH + OH^- + O_2$) (Song et al., 2016; Abdel-Rahman et al., 2017). According to previous studies, UO_2^{2+} ions are reduced to UO_2^+ ions by H_2O_2 via Fenton-type reactions ($2UO_2^{2+} + H_2O_2 \rightarrow 2UO_2^+ + 2H^+ + O_2$) (Nakajima and Ueda, 2007; Nakajima et al., 2009). In addition, ROS overproduction may be reduced by various antioxidants, such as catalase (CAT), peroxidase (POD), superoxide dismutase (SOD) and ascorbate peroxidase (APX) (Hu et al., 2019; Chen et al., 2020a).

Lipid peroxidation induced by metal stress is a major indicator for evaluating oxidative damage to plants (Chen et al., 2020b). The overproduced ROS attack hydrogen atoms of fatty acid chains, resulting in the generation of aldehydes and lipid radicals (Yalcinkaya et al., 2019). To date, numerous studies have reported that U-induced oxidative stress is capable of provoking damage to the function and integrity of the cell membrane, leading to an increase in lipid peroxidation in plants (Vanhoudt et al., 2011b; Aranjuelo et al., 2014). As reported by Vanhoudt et al. (2014), the level of lipid peroxidation in *Arabidopsis* significantly increased upon treatment with 50 μmol L^{-1} U, while the plant water content, dry weight, and photosynthetic efficiency significantly decreased, suggesting that U induced oxidative damage in the plants.

5.7. Genotoxicity

Being an indicator of cellular dysfunction, genotoxicity represents the toxicity to DNA damage and chromosomal aberrations (Iqbal, 2016). Despite that U genotoxicity in animals and humans has been extensively studied, it is less studied on the effects of U-induced genotoxic and mutagenic on plants (Gao et al., 2019; Chen et al., 2020c). Short-term U exposure (24–72 h) indirectly damages the DNA structure via inducing the ROS overproduction in plants (Özdemir et al., 2012; Chen et al., 2020c). The DNA replication fork is the basic structure of DNA replication in plant cells; and its formation requires the participation of multiple proteins, but it is easily altered by various abiotic stresses. Recently, Chen et al. (2020c) found that U stress significantly downregulated the expression of related genes (*ORC, CDC45, MCM, CCNA,* and *CCNB1*) in *Vicia faba* L., suggesting that DNA replication was inhibited via preventing the formation of replication forks. Moreover, their downregulation resulted in the cell remaining in intermitosis, thereby decreasing the mitotic index and delaying cell proliferation (Chen et al., 2020c). Upon DNA damage, a series of DNA repair systems promote the repair of damaged DNA through processes requiring the participation of multiple genes (Feng et al., 2017). However, U stress leads to the downregulation of 13 related genes (e.g., *RBX1*, *PCNA*, *RAD54*, *MSH6*, *BLM* and *RPA1*), thus preventing damaged DNA from being repaired (Chen et al., 2020c). Uranium genotoxicity in plant cells also induces chromosomal aberrations, represses antioxidant enzymes, inhibits cell division, induces cell cycle arrest and alters the structure of the cell wall (Özdemir et al., 2012; Saenen et al., 2015a; Zhang et al., 2020). Özdemir et al. (2012) observed U-induced aberrations in mitotic division in root tip cells of various plant species (*Cicer arietinum* L., *Phaseolus vulgaris* L., *Vigna anguiculata* L. and *Phaseolus coccineus* L.). This is probably because U induced degradation of the microtubule cytoskeleton, governing plant cell division under normal conditions (Özdemir et al., 2012). Uranium exposure significantly changes the genes expression via decreasing *CAT1* and *CAT2* expression, which causes a decrease in total CAT enzyme activity but an increased lipid peroxidation (Saenen et al., 2015a). In addition, the expression of related genes of cell wall structure proteins (fasciculin like arabinogalactan protein) is interfered by U stress, which is one of the mechanisms of cell wall damage, leading to the inhibition in root growth (Lai et al., 2021).

6. Plant defense system against U toxicity

Plants have evolved a number of defense strategies to scavenge overproduction of ROS and enhance the tolerance against a long-term U exposure stress. As shown in Fig. 4, these defense strategies (i.e., phytochelatins, compartmentalization, and antioxidant enzymes) operate separately or cooperate with each other to alleviate U-induced phytotoxicity (Nie et al., 2015; Gupta et al., 2020).

6.1. Antioxidant enzymes

Upon the exposure of U stress to plants, the activity of the antioxidant enzyme system is enhanced to scavenge overproduced ROS and combat adverse effects (Hu et al., 2019). Meanwhile, the activation or suppression of antioxidant enzymes in plants to eliminate U-induced oxidative damage primarily depends on both plant species and their ROS types (Hou et al., 2018).

Superoxide dismutase (SOD) plays a central role in regulating the ROS concentration since it converts ROS species into oxygen and hydrogen peroxide ($O_2\cdot^- + O_2\cdot^- + 2H + \rightarrow 2H_2O_2 + O_2$) (Gill and Tuteja, 2010). Uranium-induced SOD activation is due to an increase in O_2^- levels or a direct action on SOD. Uranium-induced increase in SOD activity has been reported in several plant species, such as *Arabidopsis thaliana* (Vanhoudt et al., 2011a), *Eichhornia crassipes* (Li et al., 2015), *Lycopersicon esculentum* Mill. (Hou et al., 2018), *Nymphaea tetragona* Georgi (Li et al., 2019a), and *Pisum sativum* L. (Gupta et al., 2020). Interestingly, Chen et al. (2020c) observed a significant increase in the SOD activity of *Vicia faba* L. after 24 h of 25 μM U(VI) exposure, while SOD activity significantly decreased by the same treatment at 48–72 h. Here, the SOD activity variably responses to U stress, which may be attributed to chromosome fracture and hysteresis and accelerated apoptosis in the plants after 48 h of U exposure (Chen et al., 2020c). CAT activity promotes the H_2O_2 detoxification produced by SOD ($H_2O_2 \rightarrow H_2O + 1/2O_2$) (Anjum et al., 2016). Its activity upregulation with U exposure has been verified by several studies (Saenen et al., 2015b; Imran et al., 2019). For example, Hu et al. (2019) reported that an 18 mg kg^{-1} U treatment as a form of $UO_2(NO_3)_2{\cdot}6H_2O$ markedly increased CAT activity in the leaves of *Macleaya cordata*. Imran et al. (2019) also examined *Bidens pilosa* L. being exposed to 120 μM U(VI), revealing that both CAT and POD activities increased, while SOD activity was reduced by U treatment. The balance between CAT and POD or SOD is crucial for maintaining the steady-state level and normal physiological processes in cells via rapidly converting $O_2\cdot^-$ and H_2O_2, which is of vital importance in detoxifying U toxicity (Hu et al., 2019). In addition, POD and APX activities also showed significant increases in plants under U stress (Hu et al., 2019; Li et al., 2019a). Nevertheless, underlying their molecular mechanisms are still limited.

6.2. Compartmentalization

Uranium compartmentalization in the cell walls and vacuoles is responsible for the adaptation tolerance and detoxification mechanism for U in plant cells (Misson et al., 2009; Nie et al., 2014; Moll et al., 2020). In *Spirodela punctata* cells, the proportion of U concentrations was approximately 8:2:1 in the cell wall, organelle, and cytosol fractions after treatment with 200 mg L^{-1} U for 120 h; however, the increased proportion of U concentrations in the cell wall fraction was significantly lower than U concentrations in the organelle and cytosol fraction as the initial U content increases (Nie et al., 2015). A possible explanation may be that U was first bound to the cell wall instead of the organelle and cytosol, thus improving the tolerance of plant cells to U stress (Nie et al., 2015). Similarly, Nie et al. (2014) also observed that the cell wall of *Phaseolus vulgaris* L. exhibited a preferential affinity for U. This finding is that the cell wall of the plants has intrinsically high contents of phytic acid and organic acid, leading to interfacial reactions with UO_2^{2+} ions (Nie et al., 2014). Thus, cell wall is the most important accumulation site of U, which plays an important role in enhancing U tolerance via preventing U ions from entering the cellular environment (Lai et al., 2021). This also weakens U translocation from roots to shoots in plants (Nie

et al., 2014; Nie et al., 2015). In plant cells, the vacuole is a prominent organelle to occupy as much as 90% of the total cell volume in some cell types. Meanwhile, the compartmentalization of xenobiotics in the vacuole is essential for adaptation to environmental stresses, so that it is an important protector to avoid U toxicity to the cells (Misson et al., 2009; Shitan and Yazaki, 2020). For example, Misson et al. (2009) observed that under U stress, *Arabidopsis thaliana* largely sequestered U, and its chemical speciation was transformed from soluble to insoluble in the vacuole.

6.3. Phytochelatin

Phytochelatins (PCs) are the most vital type of metal chelators with the general structure (γ-Glu-Cys)n-Gly. These PCs are rich in thiol moieties which have positive effect on U and chelation other metals, thereby alleviating the adverse effects of U stress in plants (Pal and Rai, 2010; Yu et al., 2021). In the process of metal detoxification, PCs form complexes with metals (Yadav, 2010). Once being formed, PC–metal complexes are transported through the tonoplast and compartmentalized in metabolically inactive sites (Yadav, 2010; Sharma et al., 2016). To date, numerous studies have reported the production of PC–metal complexes and their sequestration in the vacuole to increase plant tolerance (Fischer et al., 2014; Gonçalves et al., 2016; Dubey et al., 2018). Nevertheless, it is still limited on the studies of PC–U complexes in plants relative to other metals such as chromium, cadmium, lead, copper, and mercury (Yadav, 2010; Saenen et al., 2013; Saenen et al., 2015c; Yu et al., 2021). Glutathione (Glu) is a precursor of the formation of PC-metal complexes in plants (Yadav, 2010). For example, Saenen et al. (2013) observed a significant increase in the total Glu concentrations in the roots of *Arabidopsis thaliana* plants after exposure to 25 mM U, suggesting an increased capacity to produce PC–U complexes. Ren et al. (2019) reported that under U stress, the inoculation of arbuscular mycorrhizae increased PC gene expression in *Sesbania rostrata*, alleviating the effect of U stress on plant growth and promoting U transfer from the roots to the shoots. Thus, the formation of PC–U complexes enhances plant tolerance to U stress via reducing the levels of free cellular U ions in plants (Saenen et al., 2015c). In contrast, other studies found that a large group of metal elements including U, did not induce PC production in plants (Pradines et al., 2005; Soudek et al. 2011b). These PC responses to U stress may be attributed to the following three factors: i) biological differences in the selected plants, ii) differences in treating U concentrations, and iii) different environmental conditions. In addition, organic acids also are against metal tolerance of plants by forming complexes with metals (Sytar et al., 2013). To date, numerous reports have described the formation of organic acid–U complexes for enhancing U accumulation in plants (Qi et al., 2014; Hu et al., 2019; Sha et al., 2019; Ren et al., 2019; Wu et al., 2020). Thus, U ions form a bond with organic acid groups, improving plant resistance to U toxicity (Lai et al., 2020a). Regretfully, it is less investigated on the roles of organic acids in U detoxification and tolerance in plants.

7. Bioremediation strategies

Bioremediation is a process using biological metabolism to reverse environmental pollution and protect human health (Chen et al., 2021a). For U-contaminated soils, bioremediation strategies mainly involve phytoremediation and microbial remediation (Fig. 5). Phytoremediation is the use of plants to remove or to stabilize U in contaminated sites, while microbial remediation is the reduction of soluble U(VI) to insoluble U(IV) or the adsorption of U ions by microorganisms (Malaviya and Singh, 2012; Lakaniemi et al., 2019; Yan et al., 2021).

7.1. Phytoremediation

Phytoremediation in U-contaminated soils has been widely used worldwide, as it is inexpensive, simple to operate, and eco-friendly (Wang et al., 2020b). This process mainly occurs through phytoextraction and phytostabilization (Fig. 5). Phytoextraction in highly U-contaminated refers to U uptake via plant roots and further translocation and accumulation in aerial parts (Pentyala and Eapen, 2020).

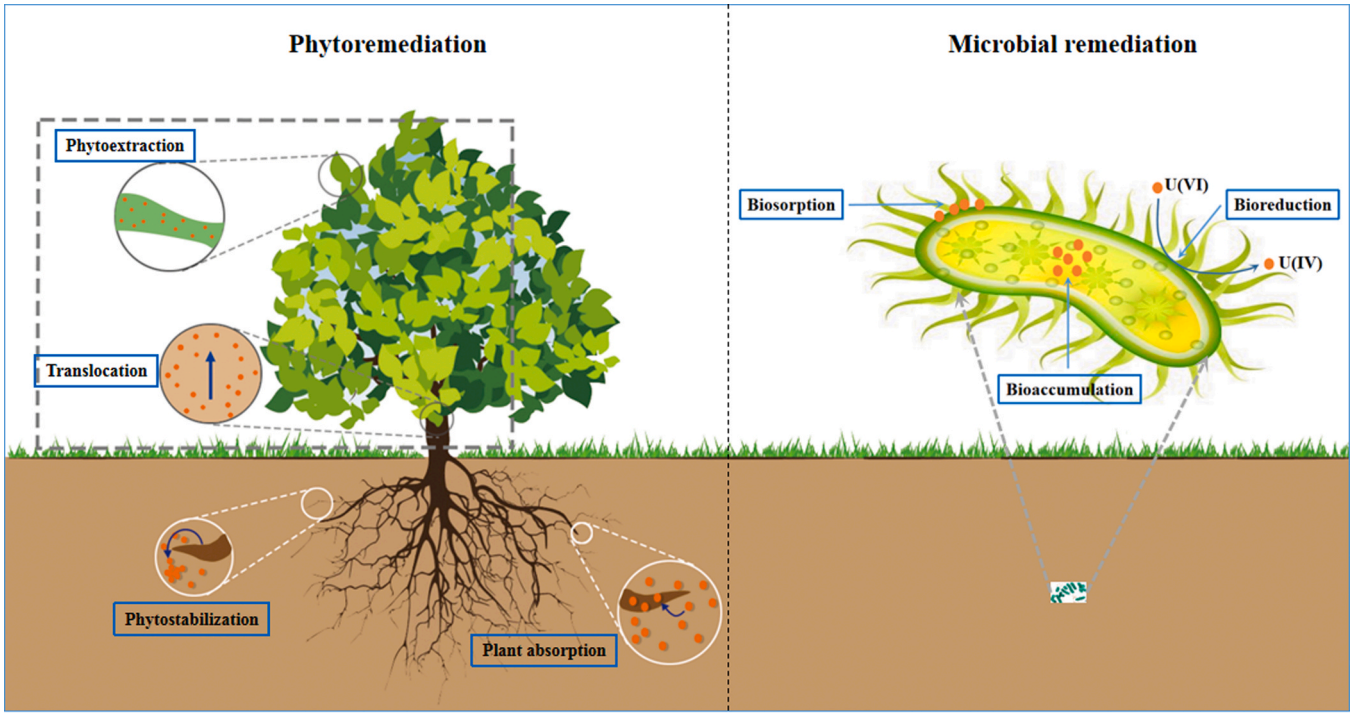

Fig. 5. Bioremediation strategies for U-contaminated soils. The interactions between plants, microorganisms and U ions are exploited in bioremediation strategies, phytoremediation and microbial remediation, which can remove or stabilize U in contaminated soils.
(Adapted from Hou et al., 2020).

Phytoextraction of U mainly involves four processes: i) bioavailable U enter plant roots through cellular membrane; ii) little fraction of U taken up by the roots becomes immobilized in cell wall and vacuole; iii) mobile U in roots enter the xylem; iv) most U is translocated from roots to aerial parts. And the selected plants for this medium generally possess following characteristics: i) a rapid growth rate, ii) high biomass, iii) strong U tolerance, iv) large amounts of U accumulation in the aerial parts; v) easy cultivation and harvest; vi) wide geographic distribution; and vii) repulsion to herbivores to avoid food chain contamination (Gavrilescu et al., 2009; Li et al., 2019a). Such as an use of mustard (*Brassica juncea var. Tumida*) to remediate U (47.75 mg kg^{-1})-contaminated soil was assessed by (Qi et al., 2014), finding that shoot U concentration reached up ~380 mg kg^{-1} and exhibiting a strong capacity to extract U from soils. Similarly, bamboo-willow (*Salix* sp.) also can accumulate large amounts of U (173.12 mg kg^{-1}) in the aboveground parts upon treatment 25 mg kg^{-1} U, significantly remediating U-contaminated soils (Sha et al., 2019). Phytoextraction efficiency of U is related to the following factors; i) U bioavailability in rhizosphere soil, ii) the expression of U transporters, and iii) the plant biomass and growth cycle (Hu et al., 2019; Lai et al., 2021). However, phytoextraction produces a large number of biomass containing high amounts of U, which limits its wide application. To minimize secondary pollution, several treatment methods of U enriched biomass, such as biodegradation, incineration, and compression landfill (Jing et al., 2020). In addition, some assistive measures have been used to improve the efficiency of U phytoextraction through applying chelating agents (Hu et al., 2021), plant growth-promoting bacteria (Qi et al., 2019), plant growth regulators (Chen et al., 2021b), and intercropping with various plants (Chen et al., 2018).

Phytostabilization involves the use of plants to take up or immobilize high contaminant levels in the soil (Bolan et al., 2014). The objective of this technique is to reduce the mobility and bioavailability of metal contaminants in soil-plant system, thereby restricting its entry into the food chain (Bolan et al., 2014; Ashraf et al., 2019). Low-accumulator plants are curial to U phytostabilization, as they absorb and accumulate high U levels in the roots via not only root uptake, but also adsorption onto the root surface (Gavrilescu et al., 2009). In phytostabilization, the ideal characteristics of U low-accumulators are: i) to possess large production of root biomass, ii) greater ability to stagnate U in the roots, and iii) able to tolerate elevated levels of U (Favas et al., 2019; Wetle et al., 2020). Broad bean (*Vicia faba* L.) has been considered as an excellent U low-accumulator, as it exhibits the ability of high root accumulation and low translocation (Liu et al. 2020; Lai et al., 2020a; Chen et al., 2020c). Broad bean has a well-developed root system with strong U tolerance, so it may acquire U from contaminated site and accumulate U in cell wall of the root (Malaviya and Singh, 2012; Lai et al., 2020a). For most plant species, U mainly accumulates in root systems via binding U ions by root cell wall, decreasing U bioavailability in soil-plant systems, as discussed above in this review. Once plant return into soil over its decomposition, soil organic matter also sequesters U and renders it largely unavailable for plant uptake and translocation, facilitating U phytostabilization in the soil-plant system (Gavrilescu et al., 2009). In this regard, despite that biochar amendment immobilizes heavy metals in contaminated soils while improving soil quality and significantly reduces plant uptake and translocation of metal contaminants (El-Naggar et al., 2020; Palansooriya et al., 2020), regretfully, it is currently limited on the studies of U phytostabilization by applying biochar materials.

7.2. Microbial remediation

Among all various remediation strategies, microbial remediation technology has been considered as a promising approach (Yin et al., 2019; Zhang et al., 2019b). The benefits of microbial U remediation are the following aspects: i) U is immobilized in situ without above-ground exposure; ii) non-native microorganisms are not required; and iii) the remediation processes are low cost, high efficiency, and excellent stability (Banala et al., 2020). Microorganisms have the ability to adsorb, precipitate, and redistribute U using their enzymatic processes or through cell surface components, thereby decreasing the concentration of bioavailable U in the environment (Newsome et al., 2014; Selvakumar et al., 2018; Lakaniemi et al., 2019). To date, a wide range of microorganisms have been identified from contaminated sites that can remove or immobilize the U(VI) (Kolhe et al., 2020b; Pinel-Cabello et al., 2021; Banala et al., 2021). Indeed, the potential mechanisms on U–microbe interactions include bioreduction and biosorption (Lakaniemi et al., 2019; Zhang et al., 2020b).

Bioreduction process of U(VI) to U(IV), makes insoluble U precipitate and sequester it from contaminated site (Shukla et al., 2020; Loreggian et al., 2020). Currently, many studies have reported the reduction of soluble U(VI) to insoluble U(IV) using microorganisms such as iron-reducing bacteria (i.e., *Geobacter (G.) metallireducens* GS-15 and *Shewanella (S.) oneidensis*) (Lovley et al., 1991), sulfate-reducing bacteria (i.e., *Desulfovibrio (D.) desulfuricans*) (Lovley et al., 1992), and indigenous bacterial community (i.e., *Desulfovibrio* sp. and *Geobacter* sp.) (Maleke et al., 2015). In particular, Lakaniemi et al. (2019) found a U (VI) removal efficiency of more than 99% within 37 h in a packed-bed bioreactor containing *Desulfovibrio* and *Desulfuricans*. Generally, the reduction of U(VI) to U(IV) needs two electrons. Nevertheless, recent studies indicated that a single electron reduction system was the most likely mechanism of reduction (Banala et al., 2020). This mechanism was resulted from that after adding *G. sulfurreducens*, U(VI) initially diminished to U(V) via one electron and then to U(IV) via disproportionation (Banala et al., 2020). Furthermore, adding low concentrations of electron donors, particularly acetate, into the surface soil, increase the activity of U-reducing microorganisms, promoting the removal of soluble U(VI) from contaminated sites (Selvakumar et al., 2018). For instance, Anderson et al. (2013) found that adding acetate as an electron donor in U-contaminated sites resulted in the growth of *Geobacter* sp. to reduce U(VI). Microorganisms are able to absorb U because of their cell surface containing specific functional groups including hydroxyl, carbonyl, amine, and phosphoryl (Wang et al., 2019c; Zhang et al., 2020b; Gong et al., 2021). Recently, Kolhe et al. (2020a) reported an excellent sorption capacity of marine yeast *Yarrowia lipolytica* for uranyl removal, showing a biphasic uranium binding pattern with a maximum loading capacity of 37.5 mg U g^{-1} dry weight of cells. In addition, the bioreduction and biosorption of U are also substantially affected by various factors (e.g., temperature, soil pH, SOM, and U chemical speciation), as these factors and their effects are important when designing efficient microbial remediation strategies (Beazley et al., 2011; Li and Zhang, 2012; Lakaniemi et al., 2019; Banala et al., 2020). However, the specific mechanisms still require further investigation to enhance the U remediation efficiency.

8. Concluding remarks and future perspectives

With its resource global use and further being returned into terrestrial environment, U pollution constantly increases in soils, leading to its toxic effects on plants, microbes and animals. This review highlights U source, speciation, toxicity and detoxification in the soil-plant systems, as well as possible bioremediation strategies. Uranium mainly exists as a form of U(VI) in soil, being much more stable than other chemical valences of U such as U(IV) and U(III). Generally, U speciation easily influences its mobility, bioavailability, phyto-uptake and toxicity. Soil chemical properties (e.g., E_h, soil pH, and SOM contents) and microbial activity further govern U speciation and behavior in soil-plant system. Plant roots absorb U as a form of UO_2^{2+} and $[UO_2OH]^+$. Yet, U soil-plant transfer depends not only on U bioavailability, but also on the related transporter proteins in soil-plant system. It mainly accumulates in roots, while only few is translocated to shoot tissues. Potential U hyperaccumulators, however, transfer high levels of U to aerial parts.

Once being exposed to a certain level, U adversely affects plant

physiological and genetic processes, such as plant seed germination, growth, photosynthesis, nutrient uptake and genotoxicity. Its accumulation also induces overgeneration of ROS in plants, further resulting in lipid peroxidation and even cell apoptosis. To mitigate U-induced toxicity, plants have evolved various defense strategies such as antioxidant enzyme systems, compartmentalization and phytochelatins. In addition, bioremediation technologies (i.e., phytoremediation and microbial remediation) are promising approaches to decontaminate U contaminated soils, owing to their low-cost, environmental friendliness, and ability to be applied over large areas.

Based on the published data, especially from 2018 to 2021, the coming research gaps need to be further explored as the below six points. First, U speciation and bioavailability in soil-plant systems are affected by multiple factors including temperature, E_h, soil pH, and SOM. Yet, their coupling interactions among these factors are still limited. Second, biochar is characterized by a high surface area, surface charge, functional groups such as carboxyl and carbonyl or hydroxyl and etc. These properties increase interactions with soil minerals, OC, pH, nutrients, and contaminants. Biochar induced interactions may variably affect the bioavailability and mobility of U in soils. Yet, it is less investigated on the effect of biochar on the geochemical U behavior in soil, and its uptake and translocation in the soil-plant system. Third, U accumulation in plant substantially differs with its species. Yet, it is still not clear on the mechanisms of U uptake and translocation at the molecular level, especially its transporter genes expression in plant cells. Fourth, unlike other heavy metals, it is not yet well defined regarding the concentration threshold in plant shoots with U hyperaccumulators. Currently, there are only few plant species being identified to hyperaccumulate U in their shoot tissues, so it still needs more works to focus on identification of potential U hyperaccumulators. Fifth, it also needs more exhaustive research to improve knowledge referring U detoxification and tolerance strategies. Meanwhile, the threshold lethal quantity of U based on its chemical speciation and exposure duration should be further deeply explored. Sixth, future studies should pay more attentions on the combined application of U low accumulators and microbial inoculants to enhance their remediation efficiency in U contaminated soils.

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.

Acknowledgments

This work was financially supported by the Key R & D Program of Gansu Province, China (17YF1NA065); the Gansu Special Project for Guiding Innovation and Development of Science and Technology, China (2018ZX-09); Z. Li is supported by Fonds National de la Recherche Scientifique' and Chargé de recherches of Belgium.

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