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More insight into the concept of iron plaque formation and its characteristics in rice (*Oryza sativa* L.)

Introduction

Rice (*Oryza sativa* L.) is the second most widely cultivated cereal crop, and around half of the world's population depends on rice consumption (Bazrkar Khatibani et al., 2019). However, the enhanced concentration of toxic metal(loids) in paddy soil due to anthropogenic activities has stimulated their increased accumulation in rice (Norton et al., 2014; Clemens, Ma, 2016), posing a significant negative impact on human health via the food chain pollution.

As a typical semi-wetland plant, rice is characterised by releasing oxygen (O₂) from the root surface in the rhizosphere when growing in a saturated or anaerobic environment; this induces the oxidation of ferrous (Fe²⁺) to ferric (Fe³⁺) and subsequently their precipitates as Fe oxides on the outermost cell layers of the root (Sundby et al., 1998; Hu et al., 2014). Iron oxide deposits are known as irregular porous coatings on the roots of hydrophytes (Tripathi et al., 2014). According to the literature reviewed by Khan et al. (2016), several studies have analysed the iron plaque (IP) deposits by employing various techniques, including X-ray diffraction and energy-dispersive X-ray microanalysis. These deposits consisted mainly of a mixture of lepidocrocite [g-FeO(OH)], goethite [α-FeO(OH)], and ferric phosphate (FePO₄), in which manganese (Mn) and Fe usually

co-occur (co-precipitate/adsorb). Under laboratory conditions, Bacha and Hossner (1977) reported a ratio of Fe (43): Mn (1) in the IP of rice roots. Either amorphous or crystalline in structure, IP is composed dominantly of 63% ferrihydrite [$(\text{Fe}^{3+})_2\text{O}_3 \times 0.5 \text{H}_2\text{O}$], 32% goethite, and 5% of siderite (FeCO_3) (Hansel et al., 2001). The latter is only formed on microsites where CO_2 concentration from respiration is high due to insufficient efflux (Hansel et al., 2001). Seyfferth et al. (2010) showed that IPs are not evenly distributed on rice roots. Predominantly mature roots show a high level of IP, while thin immature roots show minimum IP formation (Seyfferth et al., 2010, 2011). In contrast, the lowest and highest incorporation rate of rice root sections into IP coating from (oxyhydr) oxides (ferrihydrite 81–100%) sources were attributed earlier to the root base and root tips, respectively (Liu et al., 2006). Fe hydroxides' mineralogy in IP of rice root showed that ferrihydrite was the main constituent of IP (Seyfferth et al., 2011). Frommer et al. (2011) showed that the accumulation of Mn and Fe highly depends on the root thickness. Based on their observation, Fe accumulation near fine immature roots ($< 100 \mu\text{M}$) was more discernible than at thick mature roots ($\sim 500 \mu\text{M}$) compared with Mn. A recent study on primary roots by Zandi et al. (2020) showed that root surface plaque deposition was predominantly built of Fe, regardless of root sections. The unique accumulation pattern of IPs was later attributed to Fe's kinetics and thermodynamics, Mn redox transformations, and the extent of root aeration (Khan et al., 2016). The disparities in observations may emanate from genotypic differences in the roots' oxidising capacities and the biogeochemical conditions used in these studies.

Root IP may also contain a variety of other metals and metalloids such as aluminium (Al), arsenic (As), cadmium (Cd), chromium (Cr), mercury (Hg), nickel (Ni) and lead (Pb) (Tripathi et al., 2014). This feature can indicate the involvement of IP in the adsorption of both anions and cations (Liu et al., 2004a; Yang et al., 2020) and thus introduce it as an essential barrier for heavy metal uptake and accumulation (Hossain et al., 2009a, b; Hu et al., 2014; Sun et al., 2016; Xia et al., 2020; Zandi et al., 2020). It should be pointed out that sequestration mechanisms of heavy metals on IP remain mostly unknown. Growing evidence suggested that dissolved organic carbon (DOC) and sulphur (S) could participate in the precipitation of Fe hydroxides on the root surface (Liu, Huang, 2003; Sun et al., 2016; Yang et al., 2016). They probably modify Fe hydroxide's surface properties and molecular structures in IP, thus influencing the binding mechanisms of heavy metals to IP. The speciation of S has also been shown to affect and improve the barrier feature of IP against Cr uptake and accumulation in rice roots (Zandi et al., 2020). Furthermore, after being reduced in upper plant parts, S by-products can chelate Cr and Cd, and thereby actively reduce their mobility and toxicity in roots and shoots (Zhang et al., 2013; Cao et al., 2018; Yamazaki et al., 2018; Zandi et al., 2021). Among different biotic or abiotic factors involved in IP formation and development, root-released O_2 is speculated to show a strong involvement (Khan

et al., 2016; Huang et al., 2020). The physical barrier of IP has been ascribed to the proportion of roots coated by iron oxides (Xia et al., 2020), the composition type of iron oxides (Amaral et al., 2017) and the ability to develop new roots (Zandi et al., 2021).

This review primarily aimed at providing more insight into the intrinsic features of iron oxide plaques, the influencing factors on their root surface build-up, and their key role in growth parameters and heavy metal sequestration and immobilisation in rice as a semi-wetland plant.

Characterisation of iron plaque

Wetlands sediments are composed of iron (Fe) elements. Ferrous ion (Fe^{2+}) is a unique species in anoxic sediment pore water capable of donating electrons (Tripathi et al., 2014). Ferric ion (Fe^{3+}) is an electron acceptor Fe species available dominantly in oxic pore water. In addition to the Fe plaque, Mn plaque may also be formed on hydrophyte roots through oxidisation of Mn^{2+} by root-released O_2 (Hu et al., 2007). The formation process of IP (Fig. 1) primarily refers to the following chemical reactions (Amaral et al., 2017):



The concentration gradient is an essential factor in triggering the depletion of Fe^{2+} from bulk sediment and its further movement into the hydrophyte rhizosphere. In the rhizosphere, root-released O_2 oxidises Fe^{2+} to Fe^{3+} that subsequently precipitates as FeOOH (or iron oxyhydroxide) and accumulates on the root surface of hydrophyte and soil particles as IP (Fig. 1) (Hu et al., 2007; Yang et al., 2014).

The interior root penetration of iron deposition (plaque distribution) varies among species. These differences in penetration may result from the dissimilar potential of various species in oxidising rhizosphere because of their variant characteristics of root radial oxygen loss (ROL), root respiration and/or variance in the extent of soil oxygen demands (St-Cyr, Crowder, 1989). Inner parts of rice roots viz. epidermis, hypodermis and exodermis coated with iron spots/stains, were detected so far (Pereira et al., 2014). Internal iron hydroxide precipitation is possible at low ROL. In addition to the typical root plaque formation, shoot bases and rhizomes of hydrophytes also can partially be covered by IP (Povidisa et al., 2009).

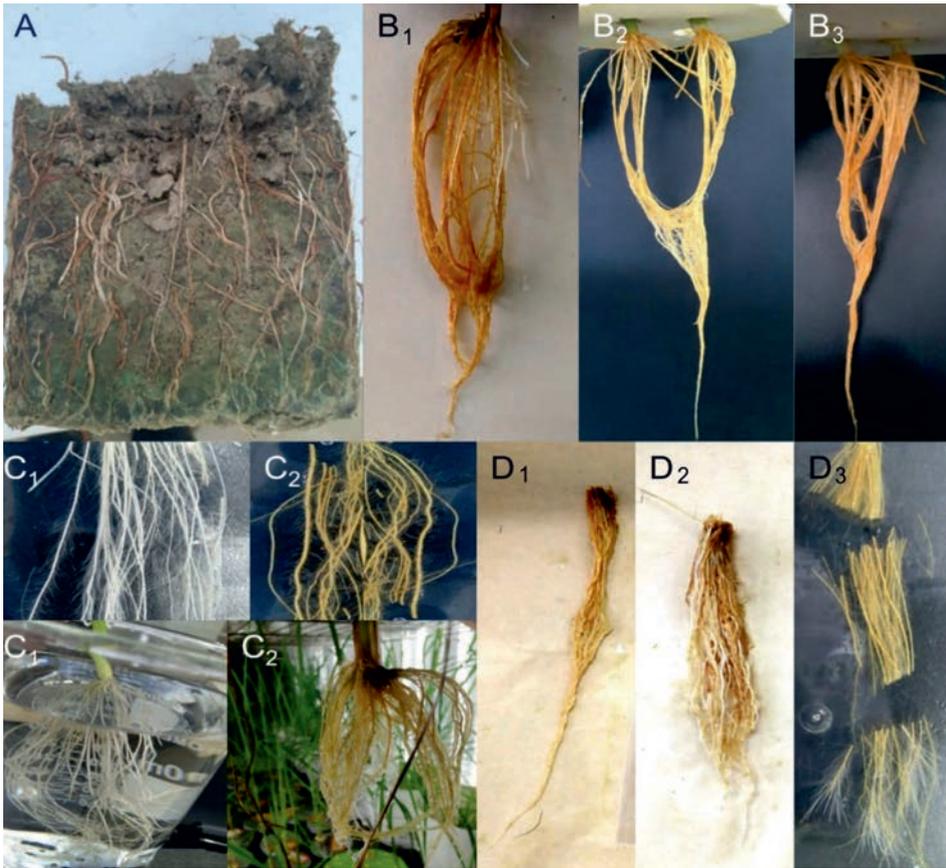


Fig. 1. Iron plaque formation in *Oryza sativa* L.; A – roots (cv. Xiangzaoxian 31) and rhizosphere; B₁₋₃ – roots of different rice cultivars (B₁ – cv. Hashemi, B₂ – cv. Lemont, B₃ – cv. Xiangzaoxian 31); C₁₋₂ – roots of rice seedlings cv. Xiangzaoxian 31 (upper row) and cv. Hashemi (lower row) before and after iron plaque induction, respectively, under laboratory conditions; D₁₋₃ – roots of rice seedlings cv. Kazemi (D₁), cv. Hashemi (D₂) and cv. Xiangzaoxian 31 (D₃) after harvest (Photo. P. Zandi and X. Xia)

The conception of iron plaque formation: influencing factors

The formation of IP occurs during the oxidation of ferrous (Fe^{2+}), formed during periods of anaerobic soil conditions, to ferric (Fe^{3+}) iron (or iron oxyhydroxides) and the precipitation of resultant ferric oxide on the outer surface of roots (Khan et al., 2016). Many physicochemical characteristics of soils and/or sediments including organic matter, soil texture, soil redox potential (Eh) (Syu et al., 2013), soil pH (Zhang et al., 2019a), soil water management (Zhang et al., 2019b), Fe/ Mn availability (Shi et al., 2004), phosphorus (P) (Hu et al., 2005), selenium (Se) (Huang et al., 2020), As (Lee et al., 2013) and S supply (Hu et al., 2007), root-released O_2 (radial oxygen loss-ROL) (Huang et al., 2020), root exudates (Becker, Asch, 2005; Wu et al., 2014), root enzymatic activates (Lee

et al., 2007), microbial activities (Neubauer et al., 2007; references therein; Huang et al., 2012a), plant genotypes (Syu et al., 2014) and plant age affect IP formation (Fig. 2).

The formation of IP may arise (or result) from neutrophilic Fe²⁺ oxidising bacteria (Neubauer et al., 2007, 2008). The discovery of both lithotrophic Fe-oxidising bacteria (FeOB) and Fe-reducing bacteria (FeRB) (King, Garey, 1999) on the root surface of many wetland plants indicate that plaque-associated microbes may directly influence IP formation. The FeOB could contribute substantially to the formation of IP (Neubauer et al., 2007, 2008). Such bacteria have been shown to account for over 40–60% of Fe (III) mineral precipitation on roots of wetland hydrophytes under microoxic (~5–30 μM O₂) conditions (Neubauer et al., 2002; Maisch et al., 2019).

There is a general agreement that the reductive dissolution of IP results from rice root decay mediated by FeRB (Wang et al., 2009; Huang et al., 2012a). Root surface microbial Fe (III) reduction often results in rapid decomposition and subsequent release of crystalline iron minerals and their associated toxic metal(loids) to the immediate rhizosphere (Weiss et al., 2004, 2005). This event usually leads to some notable environmental problems.

While biological oxidation of Fe²⁺ may occur naturally, its biotic oxidation from ROL is likely to be of greater significance (Tripathi et al., 2014; Huang et al., 2020). The local conditions dramatically impact the extent and importance of biological oxidation at the root interface. Based on the heterogeneous distribution of soil oxygen due to microbial behaviour, root distribution, and soil morphology, paddy soils' Eh and/or conditions vary (Yamaguchi et al., 2014). Maisch et al. (2019) indicated that ROL central role in ferric iron mineral formation is not only limited to the root surface but also to the whole soil matrix, where it expands potential microoxic living niches for microaerophilic Fe(II) oxidisers (microFeOx) throughout the entire rhizosphere.

Soil moisture regime has been suggested to affect the amount of iron plaque formed on rice roots (Liu et al., 2010). This amount was found much lower under lower soil moisture contents than under submerged conditions (Chen et al., 2008). Continuous flooding conditions in paddy fields significantly increase the abundance of iron-reducing bacteria (e.g., *Latescibacteria*, *Desulfuromonadales*, and *Geobacteraceae*) under anaerobic rhizospheric conditions, leading to less IP formation around rice roots (Zhang et al., 2019b). However, because the availability of Cd, zinc (Zn), copper (Cu), and other metals in the rhizosphere has decreased, the absence or reduced formation of root plaques cannot promote their presence in rice grains (Xu et al., 2013; Eduardo et al., 2014; Zhang et al., 2019b). In a continuously flooded culture, changes in the soil pH (increase) and Eh (decrease) tend to increase the formation of hydrous oxides of Fe, Mn, aluminium (Al) and other metals in flooded soils with a high affinity for metal adsorption on them (more immobilisation), leaving less soil-available metal concentration for uptake in plant roots (Eduardo et al., 2014; Li et al., 2015).

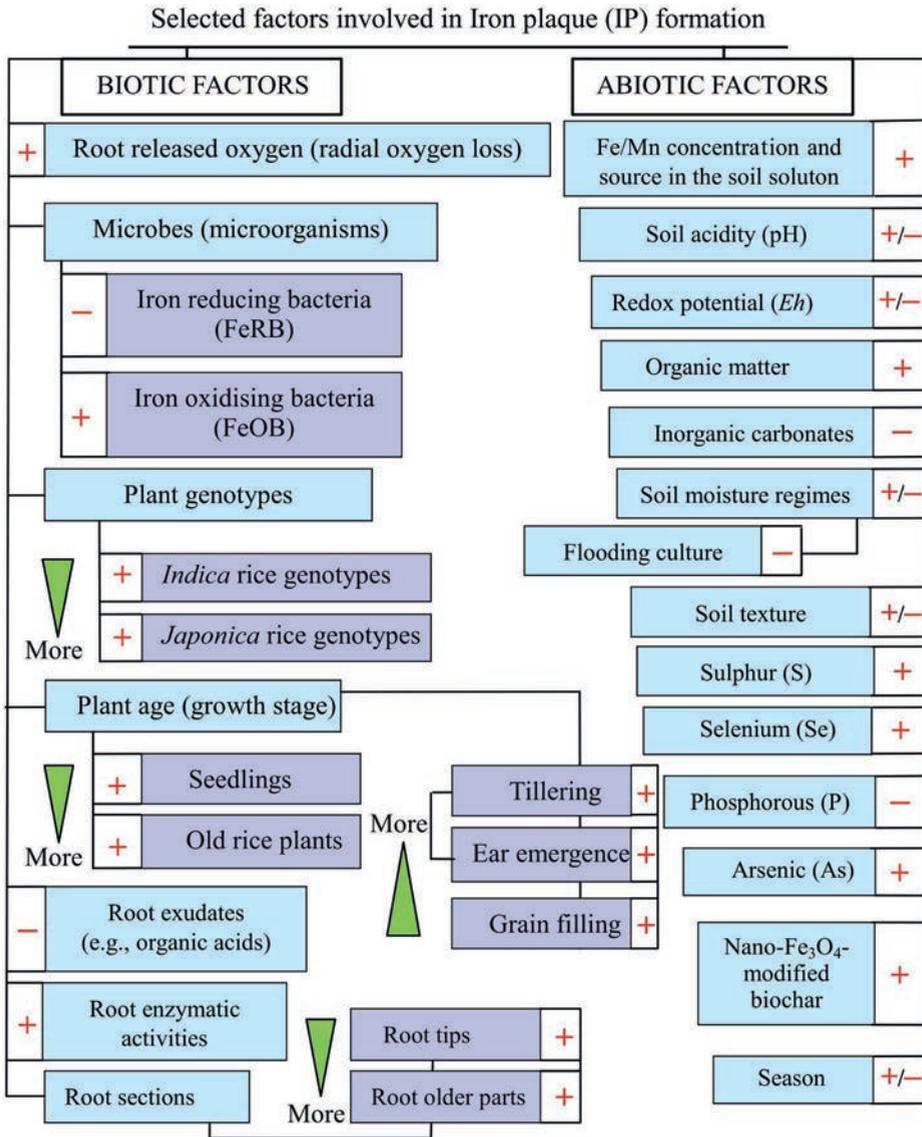


Fig. 2. Comparison of factors affecting iron plaque formation in rhizosphere where rice roots environment is located; +, - and +/- are respectively indicative of positive, negative or conditional impacts on iron plaque formation; More explanations are in the text (Courtesy of word diagram: P. Zandi)

Elemental S (S₀) could induce the formation of Fe and Mn plaques on the root surface and mineral particles in the rhizosphere (Hue et al., 2007; Yang et al., 2014). On the other hand, sulphate (SO₄²⁻) minerals significantly impacted IP's formation and barrier function compared to S₀ minerals (Hu et al., 2007). Different concentrations of Fe plaque were formed on rice roots depending on the amount of S content in soil

solution (Fan et al., 2010; Sun et al., 2016). A sufficient S supply has been suggested to play a central role in iron oxide formation and suppression of potentially toxic metals uptake and bioavailability in rice (Hu et al., 2007; Khan et al., 2016; Sun et al., 2016; Yang et al., 2016; Zandi et al., 2021). Excessive addition of S supply reduced the proportion of oxidised iron minerals through extra rhizosphere Fe^{2+} depletion via binding with monosulfide (S^{2-}) to form pyrite (FeS/FeS_2) minerals. The resultant precipitates of FeS/FeS_2 in bulk soil have been reported to diminish the mass flow of Fe^{2+} (and/or Mn^{2+}) ions from bulk soil to the rhizosphere zone, leading to less IP formation on root surfaces (Hu et al., 2007; Fun et al., 2010; Sun et al., 2016). Moreover, the abundance of S^{2-} ions in rhizosphere soil could also deplete more oxygen owing to S^{2-} oxidation. Figure (3) briefly illustrates S cycling and its relationship with IP formation in submerged conditions.

In several studies, authors have demonstrated that the absence of P in the rhizosphere (P deficiency) enhances the oxidising capacity of roots and consequently leads to more IP formation (Chen et al., 2008; Hussain et al., 2009b; Fu et al., 2010, 2014). Se-mediated enhancement of IP formation was attributed to its function in elevating the ROL of rice roots (Huang et al., 2020). ROL is assumed to be the most important driving force in the formation of plaques (St Cyr, Crowder, 1989; Xu, Yu, 2013; Yang et al., 2014). Wetland plant species, including rice cultivars, are differed based on their ROL oxidising capability (Deng et al., 2009; Yao et al., 2011). Rice roots porosities, aerenchyma structure and exodermis layer are three main controlling factors for molecular oxygen transfer and radial oxygen loss (Yamada et al., 2005; Wu et al., 2011; Yamauchi et al., 2013).

Among these, aerenchyma tissues enable the transport of oxygen to the roots under hypoxia conditions, and high root porosity tends to ROL from root to rhizoplane (Kirk et al., 2014; Huang et al., 2020). There is a general agreement that rice seedlings with their weak aerenchyma structure in their primary roots are more susceptible to paddy fields' anaerobic conditions than older rice plants. There were significant disparities in ROL, IP formation and As/Cd accumulation in roots of rice plants among plant growth stages studied, the lowest occurred at the grain-filling period (Wang et al., 2013). Some studies reported a significant difference among various rice cultivars in IP formation, regardless of whether they were grown in hydroponic, glass beads or soil culture (Liu et al., 2006; Wu et al., 2012; Lee et al., 2013; Syu et al., 2014).

In a comparison study by Zhang et al. (2021), it was demonstrated that nano- Fe_3O_4 -modified biochar (BC-Fe) was more efficient in IP formation and Cd immobilisation in rice roots than ferrous sulfate (FeSO_4), or chelated iron (EDTA-Fe). They have also shown that biochar loaded with nanoparticles of Fe could significantly raise the proportion of crystallised IP on rice roots by up to 31.8%–35.9%. It has been reported that As feeding can accelerate the formation of plaque on hydrophilic plants'

roots (Lee et al., 2013). The underlying mechanism in accelerated IP formation under As feeding conditions has been earlier attributed to As stress-induced formation of superoxide anion (H_2O_2 , O_2^-) in different plant parts, which later tend to form more plaque by diffusing free radicals and O_2^- out of the root (Mishra et al., 2011).

Plaque formation has been generally reported to have negative associations with organic matter, inorganic carbonates (CO_3) and *Eh*, and a positive association with extractable Fe in the substrate (Batty et al., 2000). Iron immobilisation in the presence of inorganic carbonates (e.g., FeCO_3) is a typical phenomenon in wetlands. High organic matter content in soil matrix has been found to bind iron and make it less available for cycling (Perret et al., 2000; Weiss et al., 2003). The relationship between the root plaques and the concentrations of organic matter in sediments has been linked to the degree of organic matter decomposition and the creation of anoxia (reducing) conditions around the root surface. Syu et al. (2013) suggested that the *Eh* of the soil and the extent of Fe^{2+} released into soil solution are determined by two factors, the content of

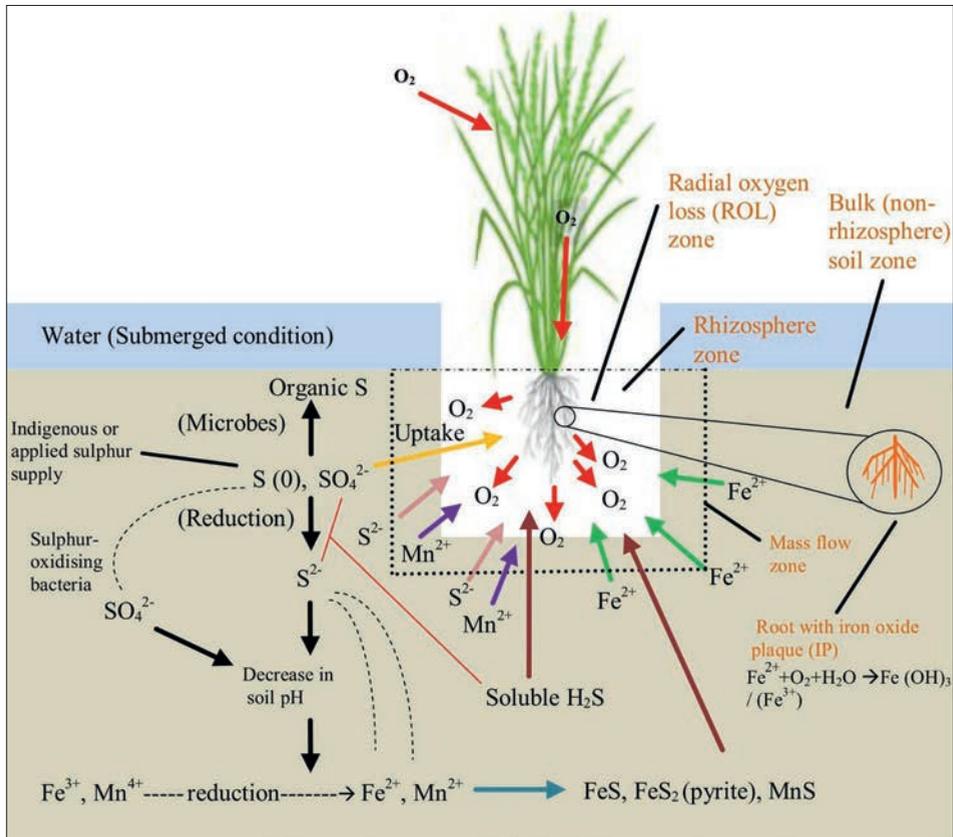


Fig. 3. Conceptual model illustrating sulphur cycling and iron plaque formation under the influence of submerged conditions. (Courtesy of conceptual model: P. Zandi)

iron oxides and organic matter in flooding soils. They further concluded that soil iron budget alone is not sufficient to form IP on roots of hydrophytes in flooding conditions but when coincides with high contents of organic matter elevates the extent of Fe^{2+} ions release into soil solutions which further are oxidised to form Fe^{3+} on root surfaces (Syu et al., 2013, 2014).

Amongst the leading factors affecting the extent of IP formation are organic matter and clay composition of soil texture. Soils with low clay contents are better candidates for IP deposition on roots than soils with high clay contents. This report rests on the speculation that the low clay soils boundless iron, making it more available in solution than the higher clay soils. It is generally accepted that organic matter contents in clay soils with iron reservoir characteristics (Bacha, Hossner, 1977) are more than in sandy soils (Dou et al., 2016). St-Cyr, Crowder (1989) stated that soil organic matter usually counterbalances the effect of low/high clay contents on IP formation. In other words, clay minerals compete with organic matter for iron adsorption. Organic matters can instead adsorb iron desorbed from clay colloids to bound carbonates in paddy soils rich in organic matter. The binding of iron and carbonates has been proposed as a prerequisite step in the formation of plaques. Overall, it may be concluded that the effect of clay content on IP formation depends significantly on the amount of soil organic matter and the positive correlation between clay and carbonate-bound iron, which can be achieved on the condition that organic matter proportion in the soil is constant.

A sufficient amount of Fe^{2+} (or Mn^{2+}) present in the soil sediment is required for plaque formation (Yang et al., 2011; Jia et al., 2018; Singha et al., 2019). The degree of iron deposition on roots has been related to iron concentration in solution (Taylor et al., 1984) and to the dominant form of iron. Taylor et al. (1984) demonstrated that chelated iron, whether it is in oxidised (Fe-EDDHA-ferric-ethylenediamine di (o-hydroxy-phenyl acetic acid), Fe-EDT (a-ferric-ethylenediaminetetraacetic acid) or reduced (Fe-BPDS-ferrous-4,7-di[4-phenylsulfonate] 1,10-phenanthroline) states, had little chance to produce root plaques compared with Fe^{2+} in solution. Their finding supported the contention that supplying the soil culture medium with Fe^{3+} , Fe^{3+} chelates, or Fe^{2+} chelates results in less extensive plaque formation. However, at lower solution culture pH values (<4), ferric iron could produce more plaques compared with ferrous iron. At these lower pH values, significant concentrations of Fe^{3+} ions were suggested to maintain in a soluble/ colloidal state and plants had utilised their reduction at the solution-root interface for plaque generation. Of different soil iron fractions, the fraction at which iron is bound to carbonates has been central for the formation of root iron plaques. In contrast to hydroponic studies, showing a positive association between IP formation and Fe^{2+} in solution (Bacha, Hossner, 1977; Taylor et al., 1984), the exchangeable iron fraction in soil samples was not necessarily related to IP accumulation. The underlying reason for this might be that iron oxyhydroxide plaques are not directly produced from

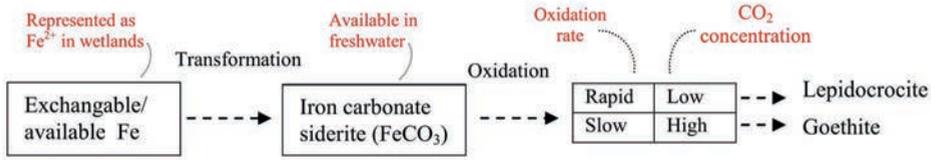


Fig. 4. Conceptual word diagram illustrating the relationship between iron-bound-to-carbonates (Siderite) and iron plaque formation in the rhizosphere (Courtesy of conceptual word diagram: P. Zandi)

Fe^{2+} after oxidation but rather from iron carbonate siderite (FeCO_3) that resulted from exchangeable iron transformation (Fig. 4). Siderites are subsequently oxidised by the oxidation potential of rhizosphere and rhizospheric CO_2 concentration to goethite ($\alpha\text{-FeOOH}$) or lepidocrocite ($\gamma\text{-FeOOH}$).

The extent of Fe and/or Mn plaque formed on roots increases in proportion to the concentration of organic matter responsible for creating an anoxic environment in which these elements (after being reduced) are oxidised to form Fe and Mn oxides on root surfaces (Syu et al., 2013, 2014). Mn and Fe plaques are positively correlated to each other (Ye et al., 2003). In an earlier study by Crowder and Coltman (1993), it was shown that the amount of IP formed on the root surface was fully consistent with the amount of pH and Mn^{2+} in the rhizosphere. Similar to the results of Taylor et al. (1984), the formation level of Fe oxide plaque on rice roots remained higher upon increasing the pH value, as indicated by Zhang et al. (2019a).

Soil pH impact on IP deposition on root surfaces in the rhizosphere can be considered from two aspects: direct control of iron concentration in solution and dissolution of precipitated root iron and the indirect influence of root oxidising capacity. In other words, the pH of the soil can control the net oxidising capacity of the roots and hence cause the precipitation of iron in the rhizosphere. Earlier reports showing that the IP formation elevated linearly as the soil pH ranged between 3 and 4.6 in *Typha latifolia* L. (Taylor et al., 1984) or 3 and 5.3 in *Oryza sativa* L. Probably, the given pH ranges diminished the solubility rate of Fe^{3+} on the roots, leaving more root iron deposition. As with iron plaque reduction (lower IP accumulation) at pH above 5, it is speculated to have been occurred by soluble iron depletion due to Fe^{2+} oxidation in the culture solution (Taylor et al., 1984; St-Cyr, Crowder, 1989). These researchers found a positive correlation between lower IP accumulation and lower carbonate-bound iron fractions under rhizosphere pH of more than 5, suggesting the iron-bound to carbonate fraction to be the precursor to IP formation on the roots.

The relative quantities and reactivities of the reductants and oxidants in the rhizosphere portray the extent to which the net oxidative and reductive nature of the rhizosphere is determined. As the soil pH decreases, phenolic compounds as Fe^{3+} reductants are released into the immediate rhizosphere as a result of suberin and lignin decomposi-

tion/hydrolysis in root outer cell layers (endodermis and exodermis). In addition, at low pH, rice roots lose much of their oxidising power that will tend to lower the oxidation of Fe^{2+} in the solution, leading to negligible IP deposition. On the other side, at higher soil pH values, the oxidative capacity of the rhizosphere increases the possibility of IP accumulation to a degree (of pH) at which there is no iron available in the solution.

In addition to the concentration and form of Fe, the soil *Eh* was also characterised as a driving component for plaque formation. The impact of *Eh* on plaque formation depends primarily on its influence on iron concentration in soil solution (Taylor et al., 1984). An increase in the soil *Eh* may not restrict the plaque formation process until the soil solution iron is not decreased. On the other side, very negative *Eh* has been found to initiate an increase in soil oxygen demand more than the oxidising power of roots, resulting in the mitigation or absence of plaques. The *Eh* value decreases with depth in the submerged soil profile (Schmidt et al., 2011). Plaques are mostly found on roots near the surface of submerged soil where the *Eh* value is neither too high nor too low to prevent plaque formation. Christensen et al. (1998) proved that IP is formed in sediment with relatively low *Eh* because high concentrations of reduced Mn and Fe diffuse towards the surface of roots where they eventually were oxidised due to root oxygen release.

The oxidising capacity of plant roots, as a biotic factor, is an essential factor in controlling IP formation (Xu, Yu, 2013; Cheng et al., 2014; Huang et al., 2020). In addition to this, root plaque formation may also be influenced, as outlined above, by root exudates, root enzymatic activities and hydrophyte genotypes (Tripathi et al., 2014). Based on the studies conducted so far, there has been a general belief over the possible implication of root-released O_2 on Fe oxidation in the rhizosphere (Khan et al., 2016; Huang et al., 2020). Although root-released O_2 has been introduced as the primary cause of iron oxide plaque formation in wetland plants, in some exceptions (e.g., *Menyanthes trifoliata* L. and *Molinia caerulea* (L.) Moench), root enzymatic activity could play a decisive role in oxidising ferrous iron in the rhizosphere. Root exudates (organic acids, phytosiderophores, etc.) have a high capacity in the reductive dissolution of iron oxides (Lee et al., 2007) and mobilisation of iron in the rhizosphere (Wu et al., 2014). The flow rate of oxygen through the aerenchyma system is substantially associated with plant characteristics and environmental conditions (temperature and humidity) (Colmer, 2003; Yamauchi et al., 2013; Amaral et al., 2017). Rice cultivars with higher ROL rates showed a higher potential in root plaque formation (Cheng et al., 2014). However, in some cases, there has been strong evidence of the more appreciable effect of root enzymatic activity on oxidising Fe(II) for ROL scavenging (Becker, Asch, 2005; Wu et al., 2014).

The occurrence of Fe oxide plaque, which is believed to be liable for the sequestration and immobilisation of various metal(loids) (Hansel et al., 2001; Bailey-Serres et al., 2012), is common in wetland and aquatic plant species such as *Typha latifolia*, *Phragmites australis* (Cav.) Trin. ex Steud, *Aster tripolium* L. (= *Tripolium pannonicum*

subsp. *tripolium* (L.) Greuter), and *Spartina alterniflora* Loisel.; root and rhizome surface of the *Cymodocea serrulata* (R. Brown) Ascherson & Magnus; mangrove seedlings viz., *Avicennia schaueriana* Stapf & Leechman ex Moldenke, *Laguncularia racemosa* (L.) C.F. Gaertn., *Rhizophora mangle* L. and *Oryza sativa* (Tripathi et al., 2014). These species are usually grown under partially or all-time flooded conditions. This suggests that they possess a versatile development of internal aeration (air lacunae) systems that facilitate oxygen diffusion from the atmosphere to the plant roots for root respiration by basic dispersion through the air spaces within the cortical tissue (Bedford et al., 2001). Because some parts of roots are 'leaky' (to some extent suberised), oxygen diffuses outside of roots' parts where it encounters Fe^{2+} and precipitates (mostly abiotically) as Fe^{3+} (Thomas et al., 2005). Therefore, the plant's ability to oxidise the rhizosphere is one of the critical factors underlying root iron oxide formation (Chen et al., 2007).

Some wetlands' seasonal impacts on IP accumulation were exclusively attributed to their closeness to the free-flowing water source containing carbonates. In addition to this, other factors which include ecotypic abilities in biomass and photosynthesis production for providing oxygen for ROL and iron oxidation, as well as site-specific characteristics in pH and *Eh*, were proposed as principals for site differences in root Fe deposition (St-Cyr, Crowder 1989).

Effect of rice origin on iron plaque formation

Recent studies have pointed to the significant differences among various rice cultivars and genotypes in IP formation (Wu et al., 2012; Lee et al., 2013; Cheng et al., 2014; Syu et al., 2014; Zandi et al., 2020). The amount of Fe content in root plaques of lowland rice cultivars was reported to be higher than upland rice cultivars (Pereira et al., 2014). Moreover, rice cultivars' difference with respect to IPs was attributed to exodermis selectivity, Fe nutrition solutions and variations in ROL (Khan et al., 2016). Lee et al. (2013) reported a significant variation in the amount of root plaque among various rice cultivars grown in hydroponic culture. Similarly, Syu et al. (2014) demonstrated that the degree of root plaque formation in 14 *indica* rice genotypes was remarkably lower than that of 14 *japonica* rice genotypes. The difference was ascribed to the lower oxidation capability of *indica* rice roots compared with *japonica* rice roots. According to the result by Weiss et al. (2005), plaque accumulation in different plant species is characterised by their ability to release oxygen into the rhizosphere. Such potential in a specific plant species can also be related to the age of plants (Chen et al., 2008). The duration between tillering and the ear emergence stage in rice coincided with a dramatic increase in ROL and Fe plaque (Wang et al., 2013). In another experiment on ten rice genotypes after iron treatment, it was found that the difference between genotypes in root and plaque Fe content was in close association with iron influx regulatory mechanisms in these genotypes (Asch et al., 2007). Additionally, Asch et al. (2007) demonstrated that sensitive

rice genotypes had more iron content in the root and root iron plaque than resistance rice genotypes. The amount and order of IP formation among rice cultivars studied so far were found different for hydroponic and soil cultures; thereby indicating the multilateral controlling capability of root plaques (Lee et al., 2013; Syu et al., 2013). In a glasshouse study conducted to assess rice genotypic tolerance against As-rich irrigation water, Liu et al. (2006) found the concentration of IP formation often varied among genotypes. These authors observed a similar pattern of IP formation (tip > middle > base) in the roots of different rice genotypes. In soil and hydroponic study under various aeration conditions, Wu et al. (2012) similarly found an additional mass of root plaque at different root zones among various genotypes studied. Despite higher discharge of oxygen from root tips (Nishiuchi et al., 2012), the occurrence of root plaque was more apparent in older root parts of rice plants (Williams et al., 2014). This could be explained by rapid development of immature root parts (growing root tips) (Sharma, Kaur, 2020).

Iron plaque: buffer or barrier for metal translocation?

Great endeavours towards scrutinising IP function in metal sequestration and translocation have yielded conflicting results (Tripathi et al., 2014; Khan et al., 2016; Amaral et al., 2017). Earlier experiments suggest that IP's barrier feature suppresses the uptake of elements (Christensen et al., 1998; Batty et al., 2000), while others estimate IP as a buffer/reservoir allowing the uptake of elements (Ye et al., 2001). Apparently, the entry of potentially phytotoxic metal(oids) into rice roots can be either decreased or increased based on the degree of IP formation (Tripathi et al., 2014). The heavy coating of IP may impede the uptake and concentration of Zn in sea aster and rice, Cd (Liu et al., 2007; Xu et al., 2018) and Cr (Xia et al., 2020; Zandi et al., 2020) in rice and As in rice (Liu et al., 2006). Zhou et al. (2007) concluded a direct association between the quantities of Se accumulated in plaque and the amount of IP encircled root surface. Thus, their studies demonstrated that Se concentration in shoots and roots of rice plants decreased upon increasing IP formation. According to Batty et al. (2000), under pH conditions of 6.0, IP presence lowers the content of Cu in the shoots of a robust perennial grass, common reed (*Phragmites australis*).

Moreover, *Spartina densiflora* Brong showed a higher potential to maintain essential metals around the root surface and control metal absorption by increasing root plaques' formation (Cambrollé et al., 2008). There have been reports of IP mediated reduction in Cd concentration in response to Fe fertiliser application to Cd-contaminated paddy soil (Liu et al., 2008). The extended formation of IP might be used as a trapping strategy to immobilise Cd and Cr from the rhizosphere through adsorption; however, it may not affect their uptake and translocation (Khan et al., 2016). It was found that the presence of IP constitutes a barrier to entry (acquisition) and circulation (uptake and accumulation) of both Cr(III) and Cr(VI) species in rice (Yu et al., 2017). This result was later contradicted

by Zandi et al. (2020) who reported a greater inhibitory function of IPs against Cr(VI) compared to Cr(III). Sorption experiments have shown higher net As enrichment in IP for rice seedlings treated with monomethylarsenate (MMA) compared to monomethylthioarsenite (MMTA), and no enrichment for dimethylmonothioarsenate (DMMTA) treatment (Kerl et al., 2019). Their results also showed that methylated thioarsenates (MTA) have very little binding/sorption capacity to amorphous ferrihydrite, indicating a low barrier capacity of IP for MTA.

The role of IP as a nutrient reservoir/buffer is recommended, particularly when decreasing the supply of nutrients (Khan et al., 2016). Its direct impact on exerting changes corresponding to the translocation of nutrients or toxic metal(oids) is often plant-species and element-specific (Tripathi et al., 2014). Accordingly, it has been demonstrated that IP exhibits greater affinity for selenite Se (IV) than for Ni or Cu in *Typha latifolia*; this indicates deferential affinity and sequestration capacity of IP for different ions. Ye et al. (2001) reported that root plaque could act as a Cu reservoir. This result was violated by a recent study by Peng et al. (2018) who concluded that root surface iron oxides are strong barriers against Cu oxide uptake and translocation in rice plants. Otte et al. (1989) stated that IP increased Zn and As uptake by *Aster tripolium*. Besides, P and Zn concentrations in rice plants were lower in the absence of IP than in those with IP, suggesting that IP acted as a Zn and P reservoir. Ye et al. (1997) reported that the root surface of *Typha latifolia* without IP had lower concentrations of Cu than those with IP and that the presence of IP enhances Ni translocation. As in hydroponic cultures, the degree of IP formation on root surfaces was positively correlated with net P enrichment in IP both in the field (Dwivedi et al., 2010) and pot (Liang et al., 2006) cultures. Unfortunately, there is no report in the literature on the positive/negative impact of IPs on nutrient transporters. The disparity in uptake patterns (ascending/descending) of metal(oids) in the presence of IP was strongly attributed to the amount of IP formed, the mineral composition of IPs and the type and availability of metallic ions (including anions and cations) in the growth media (Tripathi et al., 2014; Khan et al. 2016).

Role of iron plaque in sequestration and uptake of heavy metals

Root IPs have been predominately found associated with metal(loid)s sequestration (or deposition), uptake and translocation, including Pb, Cu, Zn, Cd, As, Cr, Al, Sb (Chen et al., 2006; Jiang et al., 2009; Huang et al., 2012b; Xu, Yu, 2013; Xu et al., 2015; Xia et al., 2020). This is because a noticeable amount of metals bind to the Fe plaque by complex formation due to Fe hydroxide's high affinity for different metals (Machado et al., 2005; Khan et al., 2016). In most studies, root IP reduced metal translocation to root and shoot (Xu et al., 2015). The IP that forms on the roots of aquatic plants is an indispensable sorbent of both cations and anions metal(loid)s (Chen et al., 2006; Cheng et al., 2014) and is liable for the attenuation of metal(loid) uptake into wetland plants

(Jiang et al., 2014). Reduction in IP formation due to continuous flooding conditions did not necessarily contribute to an increase in Cd and other metals accumulation in rice grains (Zhang et al., 2019b). This was ascribed to the flood-mediated reduction in root-to-shoot translocation and availability of metals in the rhizosphere (Xu et al., 2013; Zhang et al., 2019b).

What is probably the most determinative factor in controlling plaque formation is the presence of soluble soil iron and plant species capable of creating an oxidised rhizosphere (Chen et al., 2006). These Fe plaques are precipitated at the oxic-anoxic interface of the aquatic rhizosphere where oxygen from radial oxygen loss and Fe(II) from the reductive dissolution of Fe (oxyhydr)oxides intercept (Liu et al., 2006). This process may be biotic or abiotic (Seyfferth et al., 2011; Xu, Yu, 2013; Khan et al., 2016 – Fig. 2), and the type of Fe phase that forms and its potential to sorb metal(loid)s is dependent upon the solution chemistry and rate of oxidation (Yamauchi et al., 2013; Amaral et al., 2017).

Taylor, Crowder (1963) reported about the possible involvement of IP in the immobilisation of Ni and Cu in the rhizosphere of *Typha latifolia*. Zhang et al. (1998) suggested that Zn uptake might be influenced both by the presence and amount of IP precipitates on the root surface. Liu et al. (2004a) reported that about ~90% of total As was concentrated in IP on the rice root surface. The formation of IP under P deficiency conditions had a significant effect on As sequestration in IP and reduction in root to shoot translocation of As (Liu et al., 2004b; Hu et al., 2005). Cu accumulation in roots and shoots of rice plants was negatively associated with the extent of IP development (Peng et al., 2018). In other words, the physical presence of IP could dramatically reduce the amount of Cu in the abovementioned rice tissues. In a study of three rice cultivars using Cr (III) treatments, Hu et al. (2014) concluded that the degree of IP formation and Cr concentration in IP increased in the treatment with no P application.

In addition to the inevitable function of root plaques in suppressing the transfer of toxic metal(oids) in wetland-living species, the importance of those additional factors affecting the uptake process of elements, namely, plant species, ionic species and their concentrations, pH of the rhizosphere, particular Fe phases and the development of new lateral roots, should not be overlooked (Khan et al., 2016). For instance, Zandi et al. (2021) showed how newly developed lateral roots negate the benefit of IP by providing barrier-free absorption conditions. Given the fact that the whole root axis is not covered by IP, an absorption gap may be available around root tips for penetration of nutrients (Batty, Younger, 2003; Yamauchi et al., 2014). Not to mention that the redox (*Eh*) state and amount of Fe²⁺ produced, as well as the specific reactive surface area, may also be involved in the uptake of metal/oids (Tripathi et al., 2014). It should be pointed out that high-pH induced formation of IP and expression of metal transporter genes were responsible for absorption and uptake of toxic metal elements, such as Cd, Mn and Zn (Zhang et al., 2019a).

Role of iron plaque in plant growth

There are conflicting reports regarding the variable influence of IP on the growth of different plant parts during IP formation. Investigations of *Typha latifolia* growth revealed that the exposure of plaque-bearing roots to Cu, Ni, Zn, Pb, and Cd addition did not enhance growth in comparison to plaque-free roots that were exposed to the same metals. Experiments with the aquatic plant *Lobelia dortmanna* L. showed that the IPs located on the root surface did not affect the growth of root diameter (Møller, Sand-Jensen, 2008). The addition of Cu and Ni tended to decrease root length, especially when coated by IP. Despite this, the presence of IP on the roots of seedlings exposed to slightly toxic conditions of Cu and Ni improved the shoot growth of rice seedlings. In plants under excess Cu and Zn toxicity, the IP was demonstrated to positively affect the dry weight of roots and shoots and the length of leaves and roots (Tripathi et al., 2014). Additionally, plants without IP had more leaves displaying chlorosis than those bearing IP when treated with excess Cu. Thus, it may symbolise the role of IP as a barrier to both toxic and essential metals.

Conclusion

Anthropogenic activities are the main sources of recent incremental trends in contaminants loading in wetlands. It is a general belief that IP development on the root surface of hydrophytes is an initial output of ferrous iron oxidation under oxic conditions of the rhizosphere in wetlands. Amorphous and crystalline iron oxyhydroxides are fundamental factors of IP constitution and thus account for sequestration of those of nutrients and contaminants having a high binding affinity to iron oxides. The so-called sequestration may influence the uptake of nutrients and contaminants. The distribution and evenness of such sequestration are dependent on several components including bio-physicochemical properties of the rhizosphere, diffusion capability of hydrophytes roots and the nutrient and contaminants availability in soil solution. Adopting careful management of nutrients and contaminants charging can curb their excess loading in wetlands. Above all, much research is still lacking regarding the fluctuate and controversial role of IPs (as ineffectual, barrier or facilitator) concerning the plant uptake of emerging contaminants that need to be addressed.

Conflict of interest

The authors declare no conflict of interest related to this article.

References

- Amaral, D.C., Lopes, G., Guilherme, L.R.G., Seyferth, A.L. (2017). A new approach to sampling intact Fe plaque reveals si-induced changes in Fe mineral composition and shoot as in rice. *Environmental Science and Technology*, 51, 38–45. <http://doi.org/10.1021/acs.est.6b03558>

- Asch, F., Aung, T., Becker, M. (2007). Root iron plaque formation as a resistance mechanism to iron toxicity in lowland rice. In: E. Tielkes (ed.), *Utilisation of diversity in land use systems: Sustainable and organic approaches to meet human needs*. Deutcher Tropentag, October 9–11, 2007, Cuvillier Verlag: Göttingen, Kassel-Witzenhausen.
- Bacha, R.E., Hossner, L.R. (1977). Characteristics of coatings formed on rice roots as affected by iron and manganese additions. *Soil Science Society of America Journal*, 41, 931–935. <https://doi.org/10.2136/sssaj1977.03615995004100050025x>
- Bailey-Serres, J., Lee, S.C., Brinton, E. (2012). Waterproofing crops: effective flooding survival strategies. *Plant Physiology*, 160, 1698–1709. <https://doi.org/10.1104/pp.112.208173>.
- Batty, L.C., Baker, A.J.M., Wheeler B.D., Curtis, C.D. (2000). The effect of pH and plaque on the uptake of Cu and Mn in *Phragmites australis* (Cav.) Trinex. Steudel. *Annals of Botany*, 86, 647–653. <https://doi.org/10.1006/anbo.2000.1191>
- Batty, L.C., Younger, P.L. (2003). Effects of external iron concentration upon seedling growth and uptake of Fe and phosphate by the common reed, *Phragmites australis* (Cav.) Trin ex. Steudel. *Annals of Botany*, 92(6), 801–806. <https://doi.org/10.1093/aob/mcg205>
- Bazrkar-Khatibani, L., Fakheri, B.A., Hosseini-Chaleshtori, M., Mahender, A., Mahdinejad, N., Ali, J. (2019). Genetic mapping and validation of quantitative trait loci (QTL) for the grain appearance and quality traits in rice (*Oryza sativa* L.) by using recombinant inbred line (RIL) population. *International Journal of Genomics*, 3160275. <https://doi.org/10.1155/2019/3160275>
- Becker, M., Asch, F. (2005). Iron toxicity in rice-conditions and management concepts. *Journal of Plant Nutrition and Soil Science*, 168, 558–573. <https://doi.org/10.1002/jpln.200520504>
- Bedford, B.L., Leopold, D.L., Gibbs, J.P. (2001). Wetlands ecosystems. In: S.A. Levin (ed.), *Encyclopedia of Biodiversity* (Second Edition), Academic Press, pp. 384–402. <https://doi.org/10.1016/B978-0-12-384719-5.00314-2>.
- Cambrollé, J., Redondo-Gómez, S., Mateos-Naranjo, E., Figueroa, M.E. (2008). Comparison of the role of two *Spartina* species in terms of phytostabilization and bioaccumulation of metals in the estuarine sediment. *Marine Pollution Bulletin*, 56(12), 2037–2042. <https://doi.org/10.1016/j.marpolbul.2008.08.008>
- Cao, Z.Z., Qin, M.L., Lin, X.Y., Zhu, Z.W., Chen, M.X. (2018). Sulfur supply reduces cadmium uptake and translocation in rice grains (*Oryza sativa* L.) by enhancing iron plaque formation, cadmium chelation and vacuolar sequestration. *Environmental Pollution*, 238, 76–84. <https://doi.org/10.1016/j.envpol.2018.02.083>
- Chang, H-S., Buettner, S.W., Seaman, J.C., Jaffe, P.R., van Groos, P.G.K., Li, D., Peacock, A.D., Scheckel, K.G., Kaplan, D.I. (2014). Uranium immobilization in an iron-rich rhizosphere of a native wetland plant from the savannah river site under reducing conditions. *Environmental Science and Technology*, 48, 9270–9278. <https://doi.org/10.1021/es5015136>
- Chen, R.F., Shen, R.F., Gu, P., Dong, X. Y., DU, C. W., Ma, J. F. (2006). Response of rice (*Oryza sativa*) with root surface iron plaque under aluminium stress. *Annals of Botany*, 98(2), 389–395. <https://doi.org/10.1093/aob/mcl110>
- Chen, W., Chen, Z., He, Q., Wang, X., Wang, C., Chen, D., Lai, Z., (2007). Root growth of wetland plants with different root types. *Acta Ecologica Sinica*, 27(2), 450–457. [https://doi.org/10.1016/S1872-2032\(07\)60017-1](https://doi.org/10.1016/S1872-2032(07)60017-1).
- Chen, X.P., Kong, W.D., He, J.Z., Liu, W.J., Smith, S.E., Smith, F.A., Zhu, Y.G. (2008). Do water regimes affect iron-plaque formation and microbial communities in the rhizosphere of paddy rice? *Journal of Plant Nutrition and Soil Sciences*, 171, 193–199. <https://doi.org/10.1002/jpln.200700018>
- Cheng, H., Wang, M., Wong, M.H., Ye, Z. (2014). Does radial oxygen loss and iron plaque formation on roots alters Cd and Pb uptake and distribution in rice plant tissues? *Plant and Soil*, 375(1/2), 137–148. <https://doi.org/10.1007/s11104-013-1945-0>

- Christensen, K.K., Jensen, H.S., Andersen, F., Wigand, C., Holmer, M. (1998). Interferences between root plaque formation and phosphorus availability for isoetids in sediments of oligotrophic lakes. *Biogeochemistry*, 43, 107–128.
- Clemens, S., Ma, J.F. (2016). Toxic heavy metal and metalloid accumulation in crop plants and foods. *Annual Review of Plant Biology*, 67, 489–512. <https://doi.org/10.1146/annurev-arplant-043015-112301>
- Colmer, T.D. (2003). Aerenchyma and an inducible barrier to radial oxygen loss facilitate root aeration in upland, paddy and deep-water rice (*Oryza sativa* L.). *Annals of Botany*, 91, 301–309. <https://doi.org/10.1093/aob/mcf114>
- Deng, H., Ye, Z.H., Wong, M.H. (2009). Lead, zinc and iron (Fe²⁺) tolerances in wetland plants and relation to root anatomy and spatial pattern of ROL. *Environmental and Experimental Botany*, 65, 353–363. <https://doi.org/10.1016/j.envexpbot.2008.10.005>
- Dou, F., Soriano, J., Tabien, R.E., Chen, K. (2016). Soil texture and cultivar effects on rice (*Oryza sativa* L.) grain yield, yield components and water productivity in three water regimes. *PLoS ONE*, 11(3), e0150549. <https://doi.org/10.1371/journal.pone.0150549>
- Dwivedi, S., Tripathi, R.D., Srivastava, S., Singh, R., Kumar, A., Tripathi, P., Dave, R., Rai, U.N., Chakrabarty, D.P. Trivedi, K., Tuli, R., Adhikari, B., Bag, M.K. (2010). Arsenic affects mineral nutrients in grains of various Indian rice (*Oryza sativa* L.) genotypes grown on arsenic-contaminated soils of West Bengal. *Protoplasm*, 245, 113–124. <https://doi.org/10.1007/s00709-010-0151-7>
- Eduardo, M.J., Andrew, A.M., Erik, S., Rebeca, M., Daniel, B., Javier, S.L., Ángel, A., Antonio, L.P. (2014). Sprinkler irrigation of rice fields reduces grain arsenic but enhances cadmium. *Science of Total Environment*, 485–486, 468–473. <https://doi.org/10.1016/j.scitotenv.2014.03.106>
- Fan, J.L., Hu, Z.Y., Ziadi, N., Xia, X., Wu, C.Y.H. (2010). Excessive sulfur supply reduces cadmium accumulation in brown rice (*Oryza sativa* L.). *Environmental Pollution*, 158(2), 409–415. <https://doi.org/10.1016/j.envpol.2009.08.042>
- Fan, J.L., Xia, X., Hu, Z.Y., Ziadi, N., Liu, C. (2013). Excessive sulfur supply reduces arsenic accumulation in brown rice. *Plant, Soil and Environment*, 59, 169–174. <https://doi.org/10.17221/882/2012-PSE>
- Frommer, J., Voegelin, A., Dittmar, J., Marcus, M.A., Kretzschmar, R. (2011). Biogeochemical processes and arsenic enrichment around rice roots in paddy soil: results from micro-focused X-ray spectroscopy. *European Journal of Soil Science*, 62(2), 305–317. <https://doi.org/10.1111/j.1365-2389.2010.01328.x>
- Fu, Y., Yu, Z., Cai, K., Shen, H. (2010). Mechanisms of iron plaque formation on root surface of rice plants and their ecological and environmental effects: a review (in Chinese). *Plant Nutrition and Fertilizers Science*, 16, 1527–1534.
- Fu, Y.Q., Yang, X.J., Shen, H. (2014). The physiological mechanism of enhanced oxidizing capacity of rice (*Oryza sativa* L.) roots induced by phosphorus deficiency. *Acta Physiologia Plantarum*, 36, 179–190. <https://doi.org/10.1007/s11738-013-1398-3>
- Gong, J.L., Xing, Z.P., Hu, Y.H.J., Zhang, H.C., Dai, Q.G., Huo, Z.Y., Xu, K., Wei, H.Y., Gao, H., Guo, B.W. (2014). Difference of root morphological and several physiological characteristics between *indica* and *japonica* super rice varieties. *Acta Agronomica Sinica*, 40(6), 1066–1080. <https://doi.org/10.3724/SPJ.1006.2014.01066>
- Hansel, C.M., Fendorf, S., Sutton, S., Newville, M. (2001). Characterization of Fe plaque and associated metals on the roots of Mine-Waste impacted aquatic plants. *Environmental Science and Technology*, 35, 3863–3868. <https://doi.org/10.1021/es0105459>
- Hossain, M.B., Jahiruddin, M., Loeppert, R.H., Panaullah, G.M., Islam, M.R., Duxbury, J.M. (2009b). The effects of iron plaque and phosphorus on yield and arsenic accumulation in rice. *Plant and Soil*, 317, 167–176. <https://doi.org/10.1007/s11104-008-9798-7>

- Hossain, Z., Lopez-Climent, M.F., Arbona, V., Perez-Clemente, R.M., Gomez-Cadenas, A. (2009a). Modulation of the antioxidant system in citrus under waterlogging and subsequent drainage. *Journal of Plant Physiology*, 166, 1391–1404. <https://doi.org/10.1016/j.jplph.2009.02.012>
- Hu, Y., Huang, Y.Z., Liu, Y.X. (2014). Influence of iron plaque on chromium accumulation and translocation in three rice (*Oryza sativa* L.) cultivars grown in solution culture. *Chemistry and Ecology*, 30(1), 29–38. doi:10.1080/02757540.2013.829050
- Hu, Y., Li, J.H., Zhu, Y.G., Huang, Y.Z., Hu H.Q., Christie, P. (2005). Sequestration of As by iron plaque on the roots of three rice (*Oryza sativa* L.) cultivars in a low-P soil with or without P fertilizer. *Environmental Geochemistry and Health*, 27, 169–176. <https://doi.org/10.1007/s10653-005-0132-5>
- Hu, Z.Y., Zhu, Y.G., Li, M., Zhang, L.G., Cao, Z.H., Smith, F.A. (2007). Sulphur(S)-induced enhancement of iron plaque formation in the rhizosphere reduces arsenic accumulation in rice (*Oryza sativa* L.) seedlings. *Environmental Pollution*, 147, 387–393. <https://doi.org/10.1016/j.envpol.2006.06.014>
- Huang, G., Ding, C.F., Li, Y., Zhang, T., Wang, X. (2020). Selenium enhances iron plaque formation by elevating the radial oxygen loss of roots to reduce cadmium accumulation in rice (*Oryza sativa* L.). *Journal of Hazardous Materials*, 122860. <https://doi.org/10.1016/j.jhazmat.2020.122860>
- Huang, H., Zhu, Y., Chen, Z., Yin, X., Sun, G. (2012a). Arsenic mobilization and speciation during iron plaque decomposition in a paddy soil. *Journal of Soils and Sediments*, 12, 402–410. <https://doi.org/10.1007/s11368-011-0461-1>
- Huang, Y.C., Chen, Z., Liu, W.J. (2012b). Influence of iron plaque and cultivars on antimony uptake by and translocation in rice (*Oryza sativa* L.) seedlings exposed to Sb(III) or Sb(V). *Plant and Soil*, 352, 41–49. <https://doi.org/10.1007/s11104-011-0973-x>
- Jia, X., Otte, M.L., Liu, Y., Qin, L., Tian, X., Lu, X., Jiang, M., Zou, Y. (2018). Performance of iron plaque of wetland plants for regulating iron, manganese, and phosphorus from agricultural drainage. *Water*, 10(1), 42. <https://doi.org/10.3390/w10010042>
- Jiang, F.Y., Chen, X., Luo, A.C. (2009). Iron plaque formation on wetland plants and its influence on phosphorus, calcium and metal uptake. *Aquatic Ecology*, 43(4), 879–890. <https://doi.org/10.1007/s10452-009-9241-z>
- Jiang, X., Teng, A., Xu, W., Liu, X. (2014). Distribution and pollution assessment of heavy metals in surface sediments in the Yellow Sea. *Marine Pollution Bulletin*, 83(1), 366–375. <https://doi.org/10.1016/j.marpolbul.2014.03.020>
- Kerl, C.F., Bllaran, T.B., Planer-Friedrich, B. (2019). Iron plaque at rice roots: no barrier for methylated thioarsenates. *Environmental Science and Technology*, 53(23), 13666–13674. <https://doi.org/10.1021/acs.est.9b04158>
- Khan, N., Seshadri, B., Bolan, N., Saint, C.P., Kirkham, N.B., Chowdhury, S., Yamaguchi, N., Lee, D.Y., Li, G., Kunhikrishnan, A., Qi, F., Karunanithi, R., Qiu, R., Zhu, Y.G., Syu, C.H. (2016). Root iron plaque on wetland plants as a dynamic pool of nutrients and contaminants. *Advance in Agronomy*, 138, 1–96. <https://doi.org/10.1016/bs.agron.2016.04.002>
- King, G.M., Garey, M.A. (1999). Ferric iron reduction by bacteria associated with the roots of rice seedlings (*Oryza sativa*). *Applied and Environmental Microbiology Journal*, 14, 375–385. <https://doi.org/10.1128/aem.65.10.4393-4398.1999>
- Kirk, G.J.D., Greenway, H., Atwell, B.J., Ismail, A.M., Colmer, T.D. (2014). Adaptation of rice to flooded soils. In: U. Lüttge, W. Beyschlag, J. Cushman (eds.), *Progress in Botany*, 75. Berlin, Heidelberg: Springer, pp. 215–253. https://doi.org/10.1007/978-3-642-38797-5_8
- Lee, C.H., Hsieh, Y.C., Lin, T.H., Lee, D.Y. (2013). Iron plaque formation and its effect on arsenic uptake by different genotypes of paddy rice. *Plant and Soil*, 363, 231–241. <https://doi.org/10.1007/s11104-012-1308-2>

- Lee, S.O., Tran, T., Jung, B.H., Kim, S.J., Kim, M.J. (2007). Dissolution of iron oxide using oxalic acid. *Hydrometallurgy*, 87, 91–99. <https://doi.org/10.1016/j.hydromet.2007.02.005>
- Li, Z., Wu, L., Zhang, H., Luo, Y., Christie, P. (2015). Effects of soil drying and wetting drying cycles on the availability of heavy metals and their relationship to dissolved organic matter. *Journal of Soils and Sediments*, 1, 1510–1519. <https://doi.org/10.1007/s11368-015-1090-x>
- Liang, Y., Zhu, Y.G., Xia, Y., Li, Z., Ma, Y. (2006). Iron plaque enhances phosphorus uptake by rice (*Oryza sativa* L.) growing under varying phosphorus and iron concentrations. *Annals of Applied Biology*, 149(3), 305–312. <https://doi.org/10.1111/j.1744-7348.2006.00095.x>
- Liu, C., Gong, X., Chen, C., Yang, J., Xu, S. (2015). The effect of iron plaque on lead translocation in soil-*Carex cinerascens* kukenth system. *International Journal of Phytoremediation*, 18(1), 1–9. <https://doi.org/10.1080/15226514.2015.1021954>
- Liu, C., Huang, P.M. (2003). Kinetics of lead adsorption by iron oxides formed under the influence of citrate. *Geochimica et Cosmochimica Acta*, 67, 1045–1054. [https://doi.org/10.1016/S0016-7037\(02\)01036-0](https://doi.org/10.1016/S0016-7037(02)01036-0)
- Liu, H., Zhang, J., Christie, P., Zhang, F. (2008). Influence of iron plaque on uptake and accumulation of Cd by rice (*Oryza sativa* L.) seedlings grown in soil. *Science of the Total Environment*, 394(2–3), 361–368. <https://doi.org/10.1016/j.scitotenv.2008.02.004>
- Liu, H.J., Zhang, J.L., Zhang, F.S. (2007). Role of iron plaque in Cd uptake by and translocation within rice (*Oryza sativa* L.) seedlings grown in solution culture. *Environmental and Experimental Botany*, 59, 314–320. <https://doi.org/10.1016/j.envexpbot.2006.04.001>
- Liu, W.J., Chen, L.N., Wang, Y. (2010). Dynamics of As species in the interface of soil and rice roots under three water regimes. In: J-M. Xu, P.M. Huang (eds.), *Molecular environmental soil science at the interfaces in the Earth's Critical Zone*. Germany: Springer Science and Business Media, pp. 164–166. https://doi.org/10.1007/978-3-642-05297-2_50
- Liu, W.J., Zhu, Y.G., Smith, F.A., Smith, S.E. (2004a). Do iron plaque and genotypes affect arsenate uptake and translocation by rice seedlings (*Oryza sativa* L.) grown in solution culture? *Journal of Experimental Botany*, 55, 1707–1713. <https://doi.org/10.1093/jxb/erh205>
- Liu, W.J., Zhu, Y.G., Hu, Y., Williams, P.N., Gault, A.G., Meharg, A.A., Charnock, J.M., Smith, F.A. (2006). Arsenic sequestration in iron plaque, its accumulation and speciation in mature rice plants (*Oryza sativa* L.). *Environmental Science and Technology*, 40(18), 5730–5736. <https://doi.org/10.1021/es060800v>
- Liu, W.J., Zhu, Y.G., Smith, F.A., Smith, S.E. (2004b). Do phosphorus nutrition and iron plaque alter arsenate (As) uptake by rice seedlings in hydroponic culture? *New Phytologist*, 62, 481–488. <https://doi.org/10.1111/j.1469-8137.2004.01035.x>
- Liu, X., Zhao, Z., Hu, C., Zhao, X., Guo, Z. (2016). Effect of sulphate on selenium uptake and translocation in rape (*Brassica napus* L.) supplied with selenate or selenite. *Plant and Soil*, 399, 295–304. <https://doi.org/10.1007/s11104-015-2699-7>
- Machado, W., Gueiros, B.B., Sebastiao, D., Lisboa-Filho, L., Lacerda, D. (2005). Trace metals in mangrove seedlings: role of Iron plaque formation. *Wetlands Ecology Management*, 13(2), 199–206. <https://doi.org/10.1007/s11273-004-9568-0>
- Maisch, M., Lueder, U., Laufer, K., Scholze, C., Kappler, A., Schmidt, C. (2019) Contribution of microaerophilic iron(II)-oxidizers to iron(III) mineral formation. *Environmental Science and Technology*, 53, 8197–8204. <https://doi.org/10.1021/acs.est.9b01531>
- Mishra, S., Jha, A.B., Dubey, R.S. (2011). Arsenite treatment induces oxidative stress, upregulates antioxidant system, and causes phytochelatin synthesis in rice seedlings. *Protoplasma*, 248, 565–577. <https://doi.org/10.1007/s00709-010-0210-0>
- Møller, C.L., Sand-Jensen, K. (2008). Iron plaques improve the oxygen supply to root meristems of the freshwater plant, *Lobelia dortmanna*. *New Phytologist*, 179(3), 848–856. <https://doi.org/10.1111/j.1469-8137.2008.02506.x>

- Neubauer, S.C., Emerson, D., Megonigal, J.P. (2002). Life at the energetic edge: Kinetics of circumneutral iron oxidation by lithotrophic iron-oxidizing bacteria isolated from the wetland-plant rhizosphere. *Applied and Environmental Microbiology Journal*, 68, 3988–3995. <https://doi.org/10.1128/AEM.68.8.3988-3995.2002>
- Neubauer, S.C., Emerson, D., Megonigal, J.P. (2008). Microbial oxidation and reduction of iron in the root zone and influences on metal mobility. In: A. Violante, P.M. Huang, G.M. Gadd (eds.), *Biophysico-chemical processes of heavy metals and metalloids in soil environments*. New Jersey, USA: John Wiley and Sons, Inc, Hoboken, pp. 339–372.
- Neubauer, S.C., Toledo-Dur'án, G.E., Emerson, D., Megonigal, J.P. (2007). Returning to their roots: iron-oxidizing bacteria enhance short-term plaque formation in the wetland-plant rhizosphere. *Geomicrobiology Journal*, 24, 65–73. <https://doi.org/10.1080/01490450601134309>
- Nishiuchi, S., Yamauchi, T., Takahashi, H., Kotula, L., Nakazono, M. (2012). Mechanisms for coping with submergence and waterlogging in rice. *Rice*, 5, 2. <https://doi.org/10.1186/1939-8433-5-2>
- Norton, G.J., Douglas, A., Lahner, B., Yakubowa, E., Lou Guerint, M., Pinson, S.R.M., Tarpley, L., Eizenga, G.C., Zhao, F.-J., Rafiqul Islam, M., Islam, S., Duan, G., Zhu, Y., Salt, D.E., Meharg, A.A., Price, A.H. (2014). Genome wide association mapping of grain arsenic, copper, molybdenum and zinc in rice (*Oryza sativa* L.) grown at four international field sites. *PLoS ONE*, 9(2), e89685. <https://doi.org/10.1371/journal.pone.0089685>
- Otte, M.L., Rozema, J., Koster, L., Haarsma, M.S., Broekman, R.A. (1989). Iron plaque on roots of *Aster tripolium* L. interaction with zinc uptake. *New Phytologist*, 111(2), 309–317. <https://doi.org/10.1111/j.1469-8137.1989.tb00694.x>
- Peng, C., Chen, S., Shen, C., He, M., Zhang, Y., Ye, J., Liu, J., Shi, J., (2018). Iron plaque: a barrier layer to the uptake and translocation of copper oxide nanoparticles by rice plants. *Environmental Science and Technology*, 52(21), 12244–12254. <https://doi.org/10.1021/acs.est.8b02687>
- Pereira, E.G., Oliva, M.A., Siqueira-Silva, A.I., Rosado-Souza, L., Pinheiro, D.T., Almeida, A.M. (2014). Tropical rice cultivars from lowland and upland cropping systems differ in iron plaque formation. *Journal of Plant Nutrition*, 37, 1373–1394. <https://doi.org/10.1080/01904167.2014.888744>
- Perret, D., Gaillard, J.F., Dominik, J., Atteia, O. (2000). The diversity of natural hydrous iron oxides. *Environmental Science and Technology*, 34, 3540–3546. <https://doi.org/10.1021/es0000089>
- Povidisa, K., Delefosse, M., Holmer, M. (2009). The formation of iron plaques on roots and rhizomes of the seagrass *Cymodocea serrulata* (R. Brown) ascherson with implications for sulphide intrusion. *Aquatic Botany*, 90, 303–308. <https://doi.org/10.1016/j.aquabot.2008.11.008>
- Schmidt, H., Eickhorst, T., Tippkötter, R. (2011). Monitoring of root growth and redox conditions in paddy soil rhizotrons by redox electrodes and image analysis. *Plant and Soil*, 341, 221–232. <https://doi.org/10.1007/s11104-010-0637-2>
- Seyfferth, A.L., Webb, S.M., Andrews, J.C., Fendorf, S. (2011). Defining the distribution of arsenic species and plant nutrients in rice (*Oryza sativa* L.) from the root to the grain. *Geochimica et Cosmochimica Acta*, 75(21), 6655–6671. <https://doi.org/10.1016/j.gca.2011.06.029>
- Seyfferth, A.L., Webb, S.M., Andrews, J.C., Fendorf, S. (2010). Arsenic localization, speciation, and co-occurrence with iron on rice (*Oryza sativa* L.) roots having variable Fe coatings. *Environmental Science and Technology*, 44, 8108–8113. <https://doi.org/10.1021/es101139z>
- Sharma, R., Kaur, R. (2020). Physiological and metabolic alterations induced by phthalates in plants: possible mechanisms of their uptake and degradation. *Environmental Sustainability*, 3, 391–404. <https://doi.org/10.1007/s42398-020-00141-x>
- Shi, K., Zhang, F.S., Liu, X.J., Zhang, X.D. (2004). Effects of different periods applied Fe²⁺ and concentrations on Fe and Cd contents in iron plaque on rice root. *Journal of Agro-Environment Science*, 23, 6–12.

- Singha, K.T., Sebastian, A., Prasad, M.N.V. (2019). Iron plaque formation in the roots of *Pistia stratiotes* L.: importance in phytoremediation of cadmium. *International Journal of Phytoremediation*, 21(2), 120–128. <https://doi.org/10.1080/15226514.2018.1474442>
- St-Cyr, L., Crowder, A.A. (1989). Factors affecting iron plaque on the roots of *Phragmites-Australis* (Cav) Trin Ex Steudel. *Plant and Soil*, 116, 85–93. <https://doi.org/10.1007/BF02327260>
- Sun, L., Zheng, C., Yang, J., Peng, C., Xu, C., Wang, Y., Feng, J., Shi, J. (2016). Impact of sulfur (S) fertilization in paddy soils on copper (Cu) accumulation in rice (*Oryza sativa* L.) plants under flooding conditions. *Biology and Fertility of Soils*, 52, 31–39. <https://doi.org/10.1007/s00374-015-1050-z>
- Sundby, B., Vale, C., Cacador, I., Catarino, F., Madureira, M.J., Caetano, M. (1998). Metal-rich concretions on the roots of salt marsh plants: mechanism and rate of formation. *Limnology and Oceanography*, 43, 245–252. <https://doi.org/10.4319/lo.1998.43.2.0245>
- Syu, C.H., Jiang, P.Y., Huang, H.H., Chen, W.T., Lin, T.H., Lee, D.Y. (2013). Arsenic sequestration in iron plaque and its effect on As uptake by rice plants grown in paddy soils with high contents of As, iron oxides, and organic matter. *Soil Science and Plant Nutrition*, 59, 463–471. <https://doi.org/10.1080/00380768.2013.784950>
- Syu, C.H., Lee, C.H., Jiang, P.Y., Chen, M.K., Lee, D.Y. (2014). Comparison of As sequestration in iron plaque and uptake by different genotypes of rice plants grown in As-contaminated paddy soils. *Plant and Soil*, 374(1/2), 411–422. <https://doi.org/10.1007/s11104-013-1893-8>
- Taylor, G.J., Crowder, A.A. (1963). Uptake and accumulation of copper, nickel, and iron by *Typha latifolia* grown in solution culture. *Canadian Journal of Botany*, 61, 1825–1830. <https://doi.org/10.1139/b83-193>
- Taylor, G.J., Crowder, A.A., Rodden, R. (1984). Formation and morphology of an iron plaque on the roots of *Typha latifolia* L. grown in solution culture. *American Journal of Botany*, 71(5), 666–675. <https://doi.org/10.2307/2443363>
- Thomas, A.L., Guerreino, M.C., Sodek, L. (2005). Aerenchyma formation and recovery from hypoxia of the flooded root system of nodulated soybean. *Annals of Botany*, 96(7), 1191–1198. <https://doi.org/10.1093/aob/mci272>
- Tripathi, R.D., Tripathi, P., Dwivedi, S., Kumar, A., Mishra, A., Chauhan, P.S., Norton, G.J., Nautiyal, C.S. (2014). Roles for root iron plaque in sequestration and uptake of heavy metals and metalloids in aquatic and wetland plants. *Metallomics*, 6, 1789–1800. <https://doi.org/10.1039/c4mt00111g>
- Wang, X., Yao, H., Wong, M.H., Ye, Z. (2013). Dynamic changes in radial oxygen loss and iron plaque formation and their effects on Cd and As accumulation in rice (*Oryza sativa* L.). *Environmental Geochemistry and Health*, 35, 779–788. <https://doi.org/10.1007/s10653-013-9534-y>
- Wang, X.J., Chen, X.P., Yang, J., Wang, Z., Sun, G. (2009). Effect of microbial mediated iron plaque reduction on arsenic mobility in paddy soil. *Journal of Environmental Science-China*, 21(11), 1562–1568. [https://doi.org/10.1016/s1001-0742\(08\)62456-0](https://doi.org/10.1016/s1001-0742(08)62456-0)
- Weiss, J.V., Emerson, D., Backer, S.M., Megonigal, J.P. (2003). Enumeration of Fe(II)-oxidizing and Fe(I-II)-reducing bacteria in the root zone of wetland plants: Implications for a rhizosphere iron cycle. *Biogeochemistry*, 64, 77–96. <https://doi.org/10.1023/A:1024953027726>
- Weiss, J.V., Emerson, D., Megonigal, J.P. (2004). Geochemical control of microbial Fe(III) reduction potential in wetlands: comparison of the rhizosphere to non-rhizosphere soil. *FEMS Microbiology Ecology*, 48(1), 89–100. <https://doi.org/10.1016/j.femsec.2003.12.014>
- Weiss, J.V., Emerson, D., Megonigal, J.P. (2005). Rhizosphere iron(III) deposition and reduction in a *Juncus effusus* L.-dominated wetland. *Soil Science Society of America Journal*, 69(6), 1861–1870. <https://doi.org/10.2136/sssaj2005.0002>
- Williams, P.N., Larsen, M., Lehto, N.J., Oburger, E., Wenzel, W., Glud, R.N., Davison, W., Zhang, H. (2014). Localised flux maxima of arsenic, lead, and iron around root apices in flooded lowland rice. *Environmental Science and Technology*, 48(15), 8498–8506. <https://doi.org/10.1021/es501127k>

- Wu, C., Ye, Z., Li, H., Wu, S., Deng, D., Zhu, Y., Wong, M. (2012). Do radial oxygen loss and external aeration affect iron plaque formation and arsenic accumulation and speciation in rice? *Journal of Experimental Botany*, 63(8), 2961–2970. <https://doi.org/10.1093/jxb/ers017>.
- Wu, C., Ye, Z., Shu, W., Zhu, Y., Wong, M. (2011). Arsenic accumulation and speciation in rice are affected by root aeration and variation of genotypes. *Journal of Experimental Botany*, 62(8), 2889–2898. <https://doi.org/10.1093/jxb/erq462>.
- Wu, L.B., Shhadi, M., Gregorio, G., Matthus E., Becker M., Frei, M., (2014). Genetic and physiological analysis of tolerance to acute iron toxicity in rice. *Rice*, 7(1), 1–12. <https://doi.org/10.1186/s12284-014-0008-3>
- Xia, X., Yang, J., Yan, Y., Wang, J., Hu, Y., Zeng, X. (2020). Molecular sorption mechanisms of Cr(III) to organo-ferrihydrite coprecipitates using synchrotron-based EXAFS and STXM Techniques. *Environmental Science and Technology*, 54(20), 12989–12997. <https://doi.org/10.1021/acs.est.0c02872>
- Xu, B., Wang, F., Zhang, Q., Lan, Q., Liu, C., Guo, X., Cai, Q., Chen, Y., Wang, G., Ding, J. (2018). Influence of iron plaque on the uptake and accumulation of chromium by rice (*Oryza sativa* L.) seedlings: insights from hydroponic and soil cultivation. *Ecotoxicology and Environmental Safety*, 162, 51–58. <https://doi.org/10.1016/j.ecoenv.2018.06.063>
- Xu, B., Yu, S. (2013). Root iron plaque formation and characteristics under N₂ flushing and its effects on translocation of Zn and Cd in paddy rice seedlings (*Oryza sativa* L.). *Annals of Botany*, 111(6), 1189–1195. <https://doi.org/10.1093/aob/mct072>
- Xu, B., Yu, S., Ding, J., Wu, S., Ma, J. (2015). Metal-dependent root iron plaque effects on distribution and translocation of chromium and nickel in Yellow Flag (*Iris pseudacorus* L.). *International Journal of Phytoremediation*, 17(1–6), 175–181. <https://doi.org/10.1080/15226514.2013.876965>.
- Xu, J.Z., Wei, Q., Yu, Y.M., Peng, S.Z., Yang, S.H. (2013). Influence of water management on the mobility and fate of copper in rice field soil. *Journal of Soils and Sediments*, 13, 1180–1188. <https://doi.org/10.1007/s11368-013-0716-0>
- Yamada, H., Takeda, C., Mizushima, A., Yoshino, K., Yonebayashi, K. (2005). Effect of oxidizing power of roots on iodine uptake by rice plants. *Soil Science and Plant Nutrition*, 61, 141–145. <https://doi.org/10.1111/j.1747-0765.2005.tb00018.x>
- Yamaguchi, N., Ohkura, T., Takahashi, Y., Maejima, Y., Arao, T. (2014). Arsenic distribution and speciation near rice roots influenced by iron plaques and redox conditions of the soil matrix. *Environmental Science and Technology*, 48, 1549–1556. <https://doi.org/10.1021/es402739a>
- Yamauchi, T., Shimamura, S., Nakazono, M., Mochizuki, T. (2013). Aerenchyma formation in crop species: A review. *Field Crops Research*, 152, 8–16. <https://doi.org/10.1016/j.fcr.2012.12.008>.
- Yamazaki, S., Ueda, Y., Mukai, A., Ochiai, K., Matoh, T. (2018). Rice phytochelatin synthases OsPCS1 and OsPCS2 make different contributions to cadmium and arsenic tolerance. *Plant Direct*, 2, 1–15. <https://doi.org/10.1002/pld3.34>
- Yang, J., Liu, Z., Wan X., Zheng, G., Yang, J., Zhang, H., Guo, L., Wang, X., Zhou, X., Guo, Q., Xu, R., Zhou, G., Peters, M., Zhu, G., Wei, R., Tian, L., Han, X. (2016). Interaction between sulfur and lead in toxicity, iron plaque formation and lead accumulation in rice plant. *Ecotoxicology and Environmental Safety*, 128, 206–212. <https://doi.org/10.1016/j.ecoenv.2016.02.021>
- Yang, J., Xia, X., Liu, J., Wang, J., Hu, Y. (2020). Molecular mechanisms of chromium (III) immobilization by organo-ferrihydrite co-precipitates: The significant roles of ferrihydrite and carboxyl. *Environmental Science and Technology*, 54(8), 4820–4828. <https://doi.org/10.1021/acs.est.9b06510>
- Yang, J.X., Tam, N.F.Y., Ye, Z.H. (2014). Root porosity, radial oxygen loss and iron plaque on roots of wetland plants in relation to zinc tolerance and accumulation. *Plant and Soil*, 374(1–2), 815–828. <https://doi.org/10.1007/s11104-013-1922-7>
- Yang, L.F., Li, Y.W., Yang, X.Y., Xiao, H., Peng, H., Deng, S. (2011). Effects of iron plaque on phosphorus up-

- take by *Pilea cadierei* cultured in constructed wetland. *Procedia Environmental Science*, 11, 1508–1512. <https://doi.org/10.1016/j.proenv.2011.12.227>
- Yao, F., Shen, G.X., Li, X.L., Li, H.Z., Hu, H., Ni, W.Z. (2011). A comparative study on the potential of oxygen release by roots of selected wetland plants. *Physics and Chemistry of the Earth*, 36, 475–478. <https://doi.org/10.1016/j.pce.2010.11.001>
- Ye, Z.H., Cheung, K.C., Wong, M.H. (2003). Cadmium and nickel adsorption and uptake in cattail as affected by iron and manganese plaque on the root surface. *Communications in Soil Science and Plant Analysis*, 34, 2763–2778. <https://doi.org/10.1081/CSS-120025202>
- Ye, Z.H., Baker, A.J.M., Wong, M.H., Willis, A.J. (1997). Zinc, lead and cadmium tolerance, uptake and accumulation by *Typha latifolia*. *New Phytologist*, 136(3), 469–480. <https://doi.org/10.1046/j.1469-8137.1997.00759.x>
- Ye, Z.H., Cheung, K.C., Wong, M.H. (2001). Copper uptake in *Typha latifolia* as affected by iron and manganese plaque on the root surface. *Canadian Journal of Botany*, 79, 314–320. <https://doi.org/10.1139/b01-012>
- Zandi, P., Yang, J., Xia, X., Barabasz-Krasny, B., Możdżeń, K., Puła, J., Bloem, E., Wang, Y., Hussain, S., Hashemi, S.M., Rózanowski, B., Li, Q. (2021). Sulphur nutrition and iron plaque formation on roots of rice seedlings and their consequences for immobilisation and uptake of chromium in solution culture. *Plant and Soil*, 462, 365–388. <https://doi.org/10.1007/s11104-021-04870-8>
- Zandi, P., Yang, J.J., Xin, X., Yu, T., Li, Q., Możdżeń, K., Yaosheng, W. (2020). Do sulfur addition and rhizoplane iron plaque affect chromium uptake by rice (*Oryza sativa* L.) seedlings in culture solution? *Journal of Hazardous Materials*, 388, 121803. <https://doi.org/10.1016/j.jhazmat.2019.121803>
- Zhang, J.-Y., Zhou, H., Zeng, P., Wang, S.-L., Yang, W.-J., Huang, F., Huo, Y., Yu, S.-N., Gu, J.-F., Liao, B.-H., (2021). Nano-Fe₃O₄-modified biochar promotes the formation of iron plaque and cadmium immobilization in rice root. *Chemosphere*, 276, 130212. <https://doi.org/10.1016/j.chemosphere.2021.130212>
- Zhang, Q., Chen, H., Huang, D., Xu, C., Zhu, H., Zhu, Q. (2019b). Water managements limit heavy metal accumulation in rice: Dual effects of iron-plaque formation and microbial communities. *Science of the Total Environment*, 687, 790–799. <https://doi.org/10.1016/j.scitotenv.2019.06.044>
- Zhang, Q., Chen, H., Xu, C., Zhu, H., Zhu, Q. (2019a). Heavy metal uptake in rice is regulated by pH-dependent iron plaque formation and the expression of the metal transporter genes. *Environmental and Experimental Botany*, 162, 392–398. <https://doi.org/10.1016/j.envexpbot.2019.03.004>
- Zhang, W., Lin, K.F., Zhou, J., Zhang, W., Liu, L., Han, X. (2013). Spatial distribution and toxicity of cadmium in the joint presence of sulfur in rice seedling. *Environmental Toxicology and Pharmacology*, 36, 1235–1241. <https://doi.org/10.1016/j.etap.2013.10.007>
- Zhou, X.B., Shi W.M., Zhang, L.H. (2007). Iron plaque outside roots affects selenite uptake by rice (*Oryza sativa* L.) grown in solution culture. *Plant and Soil*, 290, 17–28. <https://doi.org/10.1007/s11104-006-9072-9>

Poglądy na koncepcję powstawania blaszki żelazowej i jej cechy charakterystyczne u ryżu siewnego (*Oryza sativa* L.)

Streszczenie

Trwały i bioakumulacyjny charakter toksycznych metali(oidów) (TM) jest głównym problemem związanym z ich obecnością w środowisku. Skażenie TM w glebie i osadach zwiększa potencjalne ryzyko utraty zdrowia człowieka, przez narażenie na skażenie łańcucha pokarmowego. Odkładanie płytki tlenku żelaza na korzeniach hydrofitowych (np. ryżu) jest wynikiem różnych czynników biotycznych i abiotycznych. Promieniowa utrata tlenu (ROL) odgrywa kluczową rolę w utlenianiu żelaza w ryzosferze, a następnie wytrącaniu nisko- lub wysoko krystalicznych i/lub amorficznych minerałów żelaza na powierzchni korzeni. Biorąc pod uwagę, że każdy gatunek rośliny ma unikalną zdolność tworzenia utlenionej ryzosfery w warunkach beztlenowych gleby, obecność żelaza w ryzosferze ma ogromne znaczenie. Grupy funkcyjne (-OH) i specyficzne powierzchnie re-

agujące w blaszkach żelaza mają wysokie powinowactwo do adsorpcji różnych metali śladowych (toksycznych/nietoksycznych), wpływając na ich wchłanianie i akumulację w roślinach. W akumulacji różnych pierwiastków ważną rolę odgrywają płytki żelaza (IP). Gatunki roślin o niskim IP na swoich korzeniach mogą lepiej akumulować metale ciężkie, niezależnie od tego, czy IP jest barierą, czy buforem. Rośliny jadalne o wysokim IP są lepszymi fito-remediatorami potencjalnie fitotoksycznych metali(oidów) i mogą być bezpieczniejsze do spożycia przez ludzi. Niniejszy przegląd podsumowuje obecną wiedzę dotyczącą czynników związanych z tworzeniem i funkcjami płytki żelaza w zarządzaniu transportem metali w systemie korzeniowym.

Key words: iron oxide plaque, paddy fields, radial oxygen loss, toxic metals immobilisation

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