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·专题论坛·

水稻根系铁膜形成及对磷吸收的影响

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摘要 水稻(*Oryza sativa*)是全球重要的粮食作物。合理施肥是保障水稻持续稳产的必要农艺措施。磷是水稻生长必需的营养元素之一，主要通过水稻根系吸收。而水稻长期生长在淹水环境中，其根系表层形成富含铁氧化物的胶膜，并在水稻根际磷的迁移和转化过程中扮演关键角色。该文综述了生物和非生物因素对水稻铁膜形成和转化的影响，探讨了铁膜对磷吸收及转运的影响，并对后续研究提出建议，旨在为阐明水稻根际铁磷互作机制提供理论依据。

关键词 水稻，土壤，铁膜，磷营养，根际

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水稻(*Oryza sativa*)作为全球最重要的粮食作物之一，养育着全世界50%以上的人口(Elert, 2014; Ma, 2016; Sha et al., 2023)。目前，水稻产量的提升主要依赖于基因改良(Li et al., 2019a, 2019b, 2020; Yoon et al., 2020)和肥料施用(Cai et al., 2023; Huang et al., 2023)等技术措施。磷(P)是植物生长发育不可或缺的营养元素，既是植物体内多种重要化合物的组成成分(Shen et al., 2011)，也参与各种代谢过程(Xing et al., 2021)。植物主要通过吸收土壤中的无机磷酸盐来获取磷(Richardson and Simpson, 2011; Zhu et al., 2016)。然而，由于土壤具有强烈的磷吸附能力，尤其是在富含铁(Fe)和铝等氧化物的情况下，磷容易形成难溶性磷酸盐沉淀，导致植物对磷的利用率较低，这成为限制水稻产量提高的主要因素之一(Fan et al., 2023)。因此，为确保粮食安全和节约资源，深入研究水稻对磷的吸收与利用至关重要(Yan et al., 2021)。

研究表明，在低磷环境中，植物通过调整根系结构来适应磷饥饿，其中包括改变根冠比、根伸长和增加根毛等(Shen et al., 2011)。同时，在某些物种中还出现特殊根，如丛枝菌根(Lynch and Brown, 2008; Shen et al., 2011)。此外，植物根际发生的化学变化对于提高土壤中磷的生物利用度至关重要，其中包括根系分泌质子酸化根际土壤、羧酸盐渗出溶解结合态磷以及根系分泌植酸酶或磷酸酶等(Zhang et al., 2010)。水稻为典型的半湿地型植物，除以上机制外，还通过调控根表铁膜的形成来促进磷吸收。水稻通过根系的通气组织向根际土壤供氧，促进土壤中金属元素的氧化。例如，将水稻根际的Fe(II)氧化为Fe(III) (Sundby et al., 1998)，导致在根的最外层细胞形成红棕色氢氧化铁沉淀物，即铁膜(图1)。铁膜是一种两性物质，具有很强的物理化学吸附能力(Antoniadis et al., 2017)，使得根际土壤中的营养元素更容易沉积在根表面形成营养库源，促进营养元素的迁移和转化(Chen et al., 2021)。本文旨在深入阐述水稻根系铁膜形成的影响因素，明确铁膜与水稻磷吸收利用之间的关系，为水稻生产中铁与磷的循环转化提供理论支持。

1 铁膜形成的影响因素

水稻根系铁膜的形成是由于在淹水厌氧条件下，水稻根系泌氧(radial oxygen loss, ROL)导致土壤中的Fe^{2+}被氧化为Fe^{3+}，并与氢氧化物结合，在根的最外层细胞形成多孔且不规则的氢氧化物沉积物。土壤环境和植物自身都会对铁膜的物理化学性质产生影响，包括生物和非生物因素(图2)。

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1.1 生物因素对铁膜形成的影响

影响铁膜形成的生物因素一般包括微生物(Wei et al., 2021)、根系分泌物(Armstrong and Armstrong, 2001)、水稻基因型(Syu et al., 2014; Khan et al., 2016)以及酶活性(Wu et al., 2014)等。植物根部通常会分泌有机酸、磷酸酶、阴离子及质子等来改变土壤中金属离子的吸附效应(Shaw and Burns, 2003; 王昕等, 2017; 黄亚男和傅志强, 2018; 申建波等, 2021)。根系分泌物通过降低ROL以及pH值来减少铁膜的形成(Armstrong and Armstrong, 2001; Zhang et al., 2019; Tao et al., 2020; Xiao et al., 2021)。此外, 植物体内抗坏血酸过氧化物酶、谷胱甘肽还原酶和过氧化物酶的活性可抑制ROL, 进而降低Fe(II)的氧化(Wu et al., 2014), 减少铁膜的形成。植物的根系分泌物、ROL以及土壤中营养物质为微生物的生存及繁殖提供了有利条件, 如铁还原细菌(Fe(III)-reducing bacteria, FeRB)和铁氧化细菌(Fe(II)-oxidizing bacteria, FeOB) (Wei et al., 2021),在许多湿地植物的根部表面都能发现矿质营养细菌FeOB (Emerson et al., 1999)和FeRB (King and Garey, 1999)。这表明与铁氧化还原相关的微生物可能直接影响铁膜的形成, 而植物根际高有机质含量和氧化还原条件有利于招募FeOB和FeRB定植, FeOB将Fe^{2+}氧化为Fe^{3+}, 进而增加铁膜的数量。除外部因素, 不同基因型水稻形成的铁膜量也不相同, 籼稻基因型比杂交基因型根表形成的铁膜更多(Wu et al., 2016), 铁膜量与水稻根系外皮层选择性、ROL的变化及生长环境的铁含量密切相关(Khan et al., 2016)。

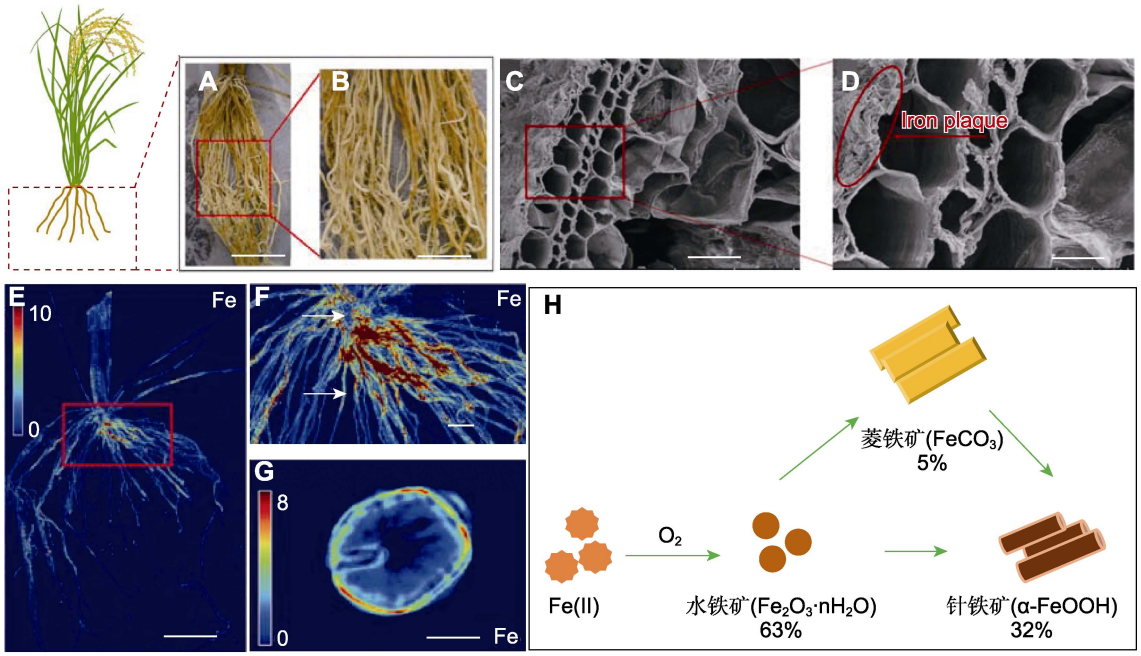


图1 水稻根表铁膜形貌及组分表征

(A), (B) 新鲜的水稻根部光学图像(Seyfferth et al., 2010); **(C), (D)** 水稻根横切面扫描电镜图(Tian et al., 2023); **(E), (F)** 水稻根部X-射线荧光(XRF)图像, **(E)**中红色方框及**(F)**中箭头均指示铁膜(Seyfferth et al., 2010); **(G)** X-射线断层扫描(XRT)图像(Seyfferth et al., 2010); **(H)** 铁膜形成过程及组分(Hansel et al., 2001)。**(A)** Bar=5 cm; **(B)** Bar=2 cm; **(C)** Bar=25 μm; **(D)** Bar=10 μm; **(E)** Bar=20 mm; **(F)** Bar=6 mm; **(G)** Bar= 200 μm

Figure 1 Morphology and component characterization of iron plaque on rice root surface

(A), (B) Optical image of fresh rice root (Seyfferth et al., 2010); **(C), (D)** Scanning electron microscope image of rice root cross-section (Tian et al., 2023); **(E), (F)** X-ray fluorescence (XRF) images of rice roots, the red-outlined box in **(E)** and the arrows in **(F)** both represent iron plaques (Seyfferth et al., 2010); **(G)** X-ray tomography (XRT) images (Seyfferth et al., 2010); **(H)** Formation and composition of iron plaque (Hansel et al., 2001). **(A)** Bar=5 cm; **(B)** Bar=2 cm; **(C)** Bar=25 μm; **(D)** Bar=10 μm; **(E)** Bar=20 mm; **(F)** Bar=6 mm; **(G)** Bar=200 μm

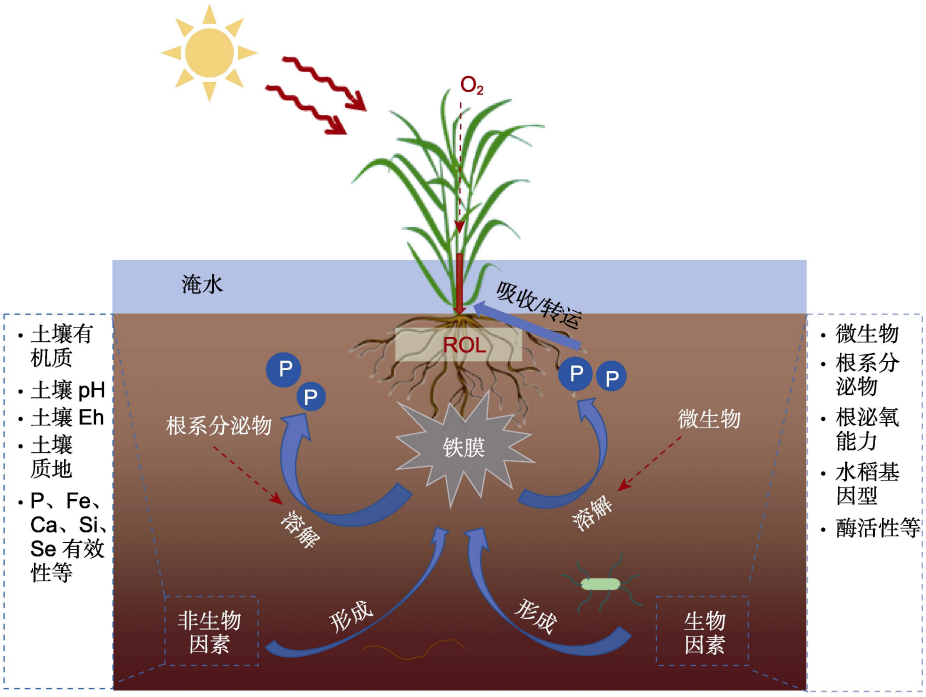


图2 水稻根际生物(微生物和根系分泌物等)及非生物(土壤pH和氧化还原电位(Eh)等)因素对根表铁膜形成的影响
在根系泌氧(ROL)等因素的调控下，根系附近铁(II)被氧化后在根表沉积形成铁(III)膜，铁膜对根际磷(P)养分具有富集效应，并随着根系分泌物或微生物对铁膜结合态磷的溶解效应，磷素被释放出来以供水稻吸收利用。

Figure 2 Effects of biotic (microbial, root exudates, etc.) and abiotic (soil pH, Eh, etc.) factors on the formation of iron plaque on rice root surface
Under the regulation of radial oxygen loss (ROL) and other factors, iron (II) near the root can be oxidized and deposited on the root surface to form iron (III) plaque. Iron plaque has an enriching effect on rhizosphere phosphorus (P) nutrition, and with the dissolution effect of the root exudates or microorganisms on iron plaque-bound phosphorus, phosphorus will be released for rice absorption and utilization.

1.2 非生物因素对铁膜形成的影响

影响铁膜形成的非生物因素有土壤质地(Boxma, 1972; Loeppert et al., 1984)、有机质含量(Weiss et al., 2003; Mohamed et al., 2010)、pH值(Li et al., 2012)、氧化还原电位(Eh) (Li et al., 2012)以及土壤无机离子铁(Tai et al., 2018; Singha et al., 2019)、钙(Qiao et al., 2018)、硅(Guo et al., 2007; Amaral et al., 2017)、硒(Huang et al., 2018)和磷(Liu et al., 2004)等。研究发现，黏土含量低的土壤更容易发生铁膜的沉积(Chen et al., 1980)，主要是由于黏土含量低的土壤吸附固定铁的能力相对较弱，这有利于更多的铁在根表沉积形成铁膜(Mendelssohn et al., 1995)。而黏土含量对于铁膜形成的影响很大程度上受土壤中有机质含量的影响，土壤中有机质含量高容易结合更多的铁(Weiss et al., 2003)。有机质含有芳香族化合物和丰富的反应性官能团(如苯酚、羧基和羟基)，可直接与土壤中的铁离子形成络合物，这些络合物的形成也与铁膜的生成有关(Sun et al., 2017)，因此土壤中有机质含量高会形成更多的铁膜。

铁的氧化还原进程与土壤溶液的pH值及Eh等密切相关(Li et al., 2012; Syu et al., 2013)。铁一般以Fe(II)的形态迁移至根际，在根上或根周围被氧化和沉淀，并可能形成铁膜。水稻根部形成铁膜的pH值介于3–5.3之间(Boone et al., 1983)。一般而言，低pH值会增加可溶性铁的比例(Sarkar and Wynjones, 1982)，而高pH值下铁易被氧化，会降低Fe(II)的溶解度(Zhang et al., 2012)。除pH外，Christensen等(1998)证实铁膜是在Eh相对较低的沉积物中形成，Fe(III)氧化物还原为Fe(II)时，其氧化还原电位显著升高。此外，土壤中的元素也影响铁的转化，进而影

响铁膜的形成。农田中施入适量的碳酸钙可增加土壤呼吸, 提高土壤氧含量(Guo et al., 2019), 并显著影响铁的氧化还原。例如, Qiao等(2018)研究表明, 富铁土壤中的钙改良剂可显著促进根系铁膜的形成。在田间条件下, 硅促进水稻侧根的生长发育(Isa et al., 2010), 而侧根占整株根系表面积的78%左右(Kawashima, 1988), 是根系泌氧的主要部位(Seyfferth et al., 2017), 因此施用硅可增加根系泌氧量, 促进根表面沉积更多的铁膜(Cheng, 1982; Guo et al., 2007)。硒是一种重要的非金属元素, Huang等(2018)发现在水稻分蘖期施用硒会显著诱导铁膜的形成, 硒可增强超氧化物歧化酶(superoxide dismutase, SOD)和过氧化氢酶(catalase, CAT)的活性, 在活性氧(reactive oxygen species, ROS)催化降解过程中有利于氧气的大量释放, 从而诱导铁膜的形成(Seppänen et al., 2003; Gill and Tuteja, 2010)。Huang等(2020)发现硒可提高水稻ROL, 可能是调控铁膜形成的因素之一。总之, 铁膜的形成与根际氧环境密切相关, 土壤中的元素如能增加根际氧含量, 将会加快铁的氧化及在根表的沉积。

2 铁膜对磷固定及释放的影响

磷的有效利用对于农业可持续发展至关重要。Zou等(2022)通过统计分析全球数据, 预测到2050年作物磷的利用效率需提高到68%–81%才能应对磷素对农业的限制。大量研究表明, 铁膜可作为植物根系周围磷的营养库源, 促进植物对磷的吸收(张西科等, 1997; Chen et al., 2021)。研究表明, 铁膜含量增加提高了水稻植株的磷浓度(Wang et al., 2019)。不仅如此, 不同组分的铁膜对磷的富集程度也不相同(Zhang et al., 2021)。例如, Wang等(2018)发现磷酸盐在针铁矿表面形成Fe-P沉淀的速率显著高于赤铁矿, 说明铁膜对磷的调控可能存在数量(或含量)效应。根系铁膜可将根际周围的磷富集并固定, 铁膜的厚度、含量以及根际磷浓度是驱动这些过程的主要因素(Christensen and Sand-Jensen, 1998; Fink et al., 2016), 只有厚度适宜的铁膜才能促进植物对磷的吸收(Christensen and Wigand, 1998; Batty and Younger, 2003; Xu et al., 2009)。当根系表面铁膜较厚时, 可能会成为磷转运的屏障以减少水稻对磷的吸收(Liang et al., 2006; Xu et al., 2009)。因此, 铁膜在水稻磷吸收过程中的作用存在争议。一方面, 铁膜富集根际的磷供水稻利用; 另一方面, 铁膜作为屏障阻碍水稻对磷的吸收(Fan et al., 2023)。铁膜与磷养分之间的关系尚需实验验证, 并需考虑多方面因素。

铁膜表面富集磷以后, 在土壤环境中的溶解引起磷的释放, 使其被植物吸收利用(Wang et al., 2022a, 2022b)。研究表明, 植物对铁的溶解度具有一定的调控作用, 它们可通过分泌质子、有机酸以及络合配体来改变根际环境(Graham, 1973)。研究表明, 根系分泌物增加了番茄(*Solanum lycopersicum*)和分生毛葱(*Allium cepa*)间作系统中磷的可用性(Khashi et al., 2021)。柠檬酸是根系分泌的一种有机酸, 低浓度柠檬酸能够促进磷酸铁沉淀的形成, 高浓度柠檬酸则促进沉淀溶解(Qin et al., 2013)。较高浓度的柠檬酸通过抑制磷酸铁结晶相的形成来提高磷的生物有效性(Wang et al., 2015)。抗坏血酸能加速赤铁矿还原速率, 草酸也能通过配体-金属离子直接发生电子转移作用还原Fe(III) (Lueder et al., 2020)。

植物根系分泌物不仅直接作用于被矿物固定的磷, 还能够通过影响根际环境中的微生物间接提高磷的生物有效性。根系分泌的有机酸通过直接影响分解有机磷的微生物使土壤中的有机磷矿化, 提高土壤无机磷的有效性(Wang et al., 2023a, 2023b)。根系分泌物除直接作用于微生物外, 还可调节根际细菌的群落结构, 其中酚酸和三萜在调节根际细菌群落结构中起主要作用(Badri et al., 2013; Huang et al., 2019)。此外, Fe(III)的还原溶解可能是在低氧化还原条件下增加磷释放的关键(Saleque et al., 2004; 陈琳等, 2019)。在淹水条件下, Fe(III)是厌氧微生物维持新陈代谢最常见的末端电子受体, 特别是在强风化的酸性土壤中(Sánchez-Alcalá et al., 2011)。Fe(III) 还原为Fe(II)通过生物或非生物机制进行(Li et al., 2012)。以Fe(III)-P结合态为主的矿物在异化Fe(III)还原微生物(Lovley et al., 2004)的调控下发生溶解, Fe(III)还原微生物还可通过直接(Lovley, 1995)或间接(Lovley et al., 1998)途径耦合稻田土壤中有机物的氧化来还原Fe(III) (Yu et al., 2021)。微生物的胞外分泌物也对铁膜的还原溶解产生一定影响, 如海藻酸可通过与含磷矿物的强烈相互作用阻碍磷酸铁矿物的溶解-再沉淀过程, 有利于磷酸铁以无定形的状态存在于土壤中,

从而提高其被还原溶解的可能性(Ge et al., 2022)。

3 铁膜对植物根系磷吸收的影响

水稻的磷吸收主要通过主动吸收机制进行，这一过程受到多种因素的综合影响，其中包括根结构、磷转运蛋白以及根际微生物等(图3) (周志高等, 2005; Li et al., 2010; Lazali and Bargaz, 2017; Kuppe et al., 2022)。磷可能通过水稻根系表面磷转运蛋白直接被吸收，也可能通过铁膜进入植物根系，水稻根表面的铁膜多孔且不规则，这成为磷进入根系的一个关键环节。研究表明，铁在调节根际磷的有效性中起主导作用，根表铁膜则在其中扮演着关键角色，通过化学吸附作用从根系附近的土壤和孔隙水中富集和积累磷(Wang et al., 2019)，从而增加根表附近的磷含量，这有利于水稻根系对磷的转运及吸收。研究表明，水稻根系形成的铁膜数量与根表面积显著相关，较大的根表面积为土壤溶液中铁离子的沉淀提供额外的空间(Jiang et al., 2009)，也为磷提供更多的吸附位点。此外，研究表明根系铁膜可减少O_2从根表释放(Møller and Sand-Jensen, 2008; Li et al., 2019a, 2019b)，从而使更多的O_2到达根尖(Møller and Sand-Jensen, 2008)，这有利于新根生长(Yu et al., 2021)。

植物根系的改变也可能是磷缺乏引起相关基因的表达(段海燕等, 2002)。例如，Giri等(2018)发现磷缺乏时OsAUX1通过将生长素从根顶端转运到分化区促进根伸长，增加了磷的可吸收性(Wang et al., 2023a, 2023b)。Mora-Macías等(2017)还发现植物根系分泌的苹果酸可激活根顶端分生组织耗尽过程来抑制初级根生长，从而促进侧根增殖，以增加植物根系接触磷的表面积。

植物根系通过磷转运蛋白从土壤中吸收正磷酸盐(Raghothama, 1999)。研究表明，过表达磷转运蛋白OsPht1;8 (OsPT8)导致水稻在低至中磷淹水土壤中的磷吸收增多(Jia et al., 2011; Wu et al., 2011)，原因是OsPT8在根外一系列组织中表达，这种转运蛋白的过表达(或OsPHR2过表达)可能通过增大单位面积内磷转运蛋白的密度使根系在土壤溶液中的磷吸收率增高。此外，在磷缺乏条件下，水稻可通过上调根系中磷转运蛋白(OsPht1;3和OsPht1;6)表达提高磷的生物有效性(Ai et al., 2009; Chang et al., 2019)。

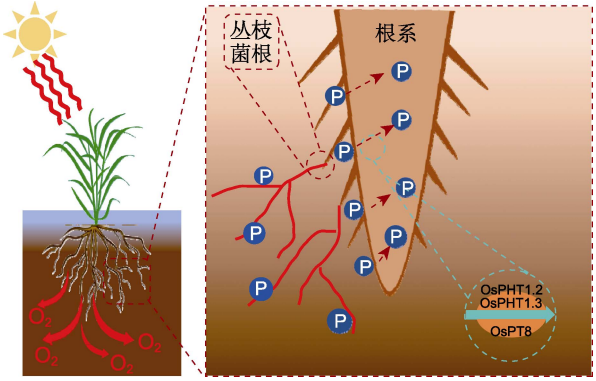


图3 水稻根系磷吸收相关机制示意图
水稻根系通过根表直接获取磷养分，或通过铁膜及丛枝菌根等间接获取磷养分，再通过转运蛋白吸收。

Figure 3 Schematic diagram of phosphorus absorption related mechanism in rice roots
Rice roots acquire phosphorus nutrients directly through the root surface or indirectly through the iron plaque, and arbuscular mycorrhizae, and absorb them through transporters.

植物还与促进植物生长的各种真菌衍生物相互作用来提高磷的利用率(Etesami et al., 2021)。丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)是最常见的与植物互作的真菌(Sharma et al., 2013; Etesami, 2020)。AMF一般通过与根表皮和根毛连接促进磷的直接吸收，或者通过与根内菌丝体相连增加根系对磷的吸收(Smith and Smith, 2011)，其中共生界面由丛枝或菌丝团提供(通过表达菌根中特定细胞的磷酸盐转运蛋白从界面质外体吸收磷) (Tisserant et al., 2012; Fiorilli et al., 2013)，而且有证据表明菌丝途径帮助植物获取磷是可行的(Smith and Smith, 2011)。

4 研究展望

水稻根系铁膜形成及对磷吸收的影响是农业和植物营养学研究的重要领域。由于铁膜在土壤与水稻根际交界处占据关键的生态位，其对土壤磷的转化、植物磷缺乏反应及磷获取等相关过程具有重要作用。为全面了解铁膜形成及对磷养分的影响，在已有研究的基础上，仍有以下问题需要重点关注。

(1) 深入研究水稻根系铁膜的形成机制。以往研究多关注土壤环境等单因子对铁膜形成的影响，但是

在复杂的根际环境下, 环境因素与根系泌氧、分泌物等多因素对铁膜形成的作用机制仍不清楚。铁膜的形成及形态变化与水稻的生长状况及栽培中的农艺措施(如水分管理)密切相关, 需进一步明确不同农艺措施对水稻关键生育期根际环境生物及非生物因素的影响, 以及铁膜形成及转化的主要调控因子及机制。

(2) 系统分析铁膜形成与磷素吸收之间的相互关系, 探究铁膜如何影响根际土壤中磷的有效性、磷在根内的运输及其调控机制。利用现代分析技术, 解析铁膜与磷结合的精细结构以及铁膜结合态磷释放的原位动力学过程及机制, 明确根际微生物及分泌物等对该过程的调控作用。建立数学模型, 用于模拟铁膜形成和磷吸收的动态作用, 评估铁膜为植物提供养分的贡献比例, 为预测和管理水稻养分变化提供理论依据。此外, 铁膜还可以作为植物抵御重金属胁迫的天然屏障(Zhao et al., 2010; Khan et al., 2016; Meng et al., 2024), 其抑制重金属和促进磷吸收的耦联机制仍需进一步研究。

(3) 运用分子生物学和生物信息学技术, 对不同水稻品种铁膜形成过程的分子机制差异进行分析, 明确铁膜形成及磷吸收相关基因、转运子及代谢过程的联系, 进而通过遗传工程手段培育出有利于铁膜形成及增强磷吸收的水稻品种。

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Iron Plaque Formation and Its Effects on Phosphorus Absorption in Rice Roots

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Abstract Rice (*Oryza sativa*) is a globally important cereal crop, and the rational application of fertilizers is necessary agricultural practice to ensure its sustainable and stable yield. Phosphorus is one of the essential nutrients for rice, primarily absorbed through the rice roots. Since rice is mostly grown in flooded conditions, the root surface of rice generally forms iron plaques rich in iron oxides, which play a crucial role in the migration of inorganic phosphorus in the rhizosphere of rice. This paper reviews the impact of biotic and abiotic factors on the formation of iron plaques in rice and discusses the effect of iron plaques on the absorption and transport of phosphorus in plant nutrition. Furthermore, we discuss the prospects of future research on iron plaques, aiming to provide clues for our further understanding of the interactions between iron and phosphorus in the rhizosphere of rice.

Key words rice, soil, iron plaque, phosphorus nutrition, rhizosphere

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