

土壤–根系–微生物系统中影响氮磷利用的一些关键协同机制的研究进展^①

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摘 要: 根际是养分进入作物系统的门户, 也是土壤–根系–微生物相互作用的微域。根际界面过程决定了氮磷养分的供应强度和有效性, 最终影响了氮磷养分的利用效率和作物生产力。近年来, 国内外在揭示农田土壤–根系–微生物系统中不同界面的养分转化、吸收和运输机制方面取得了一些新进展。在不同时空尺度上分析了影响土壤氮磷转化微生物组成的影响因子; 研究了丛枝菌根系统形成的信号机制及其对氮磷吸收的基因调控机制; 从信号网络、根系质子分泌和根构型的角度系统揭示了作物根系应对根际环境氮磷养分供应的形态和生理响应机制。未来针对根际氮磷高效利用问题, 需要深入研究土壤–根系–微生物不同界面的协同机制和调控原理, 在根际微域和土壤团聚体尺度开展微生物食物网及其关键功能微生物分布格局和演替规律的研究; 揭示根构型对根系–微生物协同结构和功能的影响, 研究养分缺乏条件下根内质子分泌和关键转运蛋白对根系生长和养分吸收的调控机制; 针对粮食作物, 研究根系–微生物对话中已知信号物质(如独脚金内酯和 N-酰基高丝氨酸内酯)和新的信号物质(小 RNA)的网络作用机制及其对多养分协同代谢的影响; 最后, 针对不同气候、土壤、作物类型区, 提出提高氮磷利用效率的根际生物调控途径和措施。

关键词: 土壤–根系–微生物系统; 协同机制; 氮磷养分; 转化和代谢; 信号网络

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我国近 30 年来的粮食增长主要依赖大量水肥和农药投入, 2012 年我国化肥用量(纯量)达 5 839.8 万 t, 单位面积化肥用量是世界水平的 3 倍、发达国家的 2 倍。单位养分投入产出粮食(折算为水稻当量)仅 14 kg/kg, 远低于美国的 40 kg/kg^[1], 当季氮肥平均利用率不足 30%^[2]。养分资源低效利用不仅增加农业投入, 而且导致土壤质量退化、诱发以氮磷为主的农业面源污染乃至区域生态环境安全问题^[3]。2007 年的全国污染源普查发现我国耕地总氮和总磷损失分别达到 160 万 t 和 10.8 万 t。因此, 提高肥料利用率和作物单产, 控制农业集约化过程中的面源污染, 是保障我国粮食安全和促进农业可持续发展必须完成的双重任务^[4]。

目前在土壤学、植物营养学和微生物学的交叉领域, 研究重心转向调控地下生物系统的措施综合提高养分利用率, 通过遗传育种方式筛选养分高效利用的作物品种, 利用外源物质添加促进根系活力和微生物活性, 充分利用植物根系与土壤微生物之间的相互促

进作用, 加速土壤养分循环和植物吸收, 提高作物系统的养分利用率, 降低传统的物理和化学调控措施的使用成本和环境风险。

土壤–作物系统中养分转化和循环涉及不同的界面过程, 土壤、根系和微生物之间通过物质和信息的交换形成复杂的交互作用关系, 根际是集中体现土壤–作物系统互作的特殊微域, 根际土壤微生物是土壤–根系间养分转化和转运的调节器。从促进养分转化和传输角度, 土壤–根系–微生物系统中的协同作用体现在不同时间和空间尺度上。在微生物系统内部, 不同微生物的组成比例(如氨氧化细菌和氨氧化古菌比例、硝化微生物和反硝化微生物比例、食细菌线虫和氮转化微生物比例)影响了土壤氮转化过程。在根系–微生物界面上, 共生(菌根真菌)和非共生体系也影响了氮磷养分的吸收。在茎–根–微生物–土壤的多界面上, 植物/微生物源信号网络以及同化产物的传输影响了养分的转化和吸收(图 1)。

土壤–根系–微生物系统中交互作用的强度和方

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向受到根际环境养分条件、微生物组成和根系状况的共同影响,并且受到多种信号物质的调控,目前面临的一个挑战是如何针对农田养分循环过程认知不同时空尺度上的生物协同结构和作用机制。中国科学院从2014年启动了战略性先导科技专项“土壤-微生物系统功能及其调控”^[5],其中一个重要研究内容涉及土壤-根系-微生物的协同作用机制与氮磷生物有效性。近年来一些综述分析了氮磷转化微生物的空间分布规律^[6-7];评述了植物-微生物(特别是菌根)共生机制及其养分代谢的影响^[8-9];提出了不同养分胁迫的信号作用网络^[10-12]以及不同信号对植物生长的调控机制^[13-15]。本文针对土壤-根系-微生物系统的3个界面,重点分析影响养分界面转化和传输过程的一些关键交互作用机制,并从系统尺度探讨农田氮磷养分转化的生物协同调控机制的研究框架和研究重点。

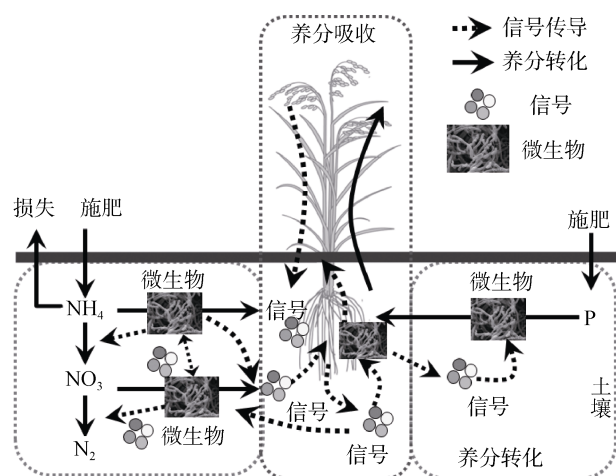


图1 土壤-根系-微生物相互作用及其对土壤养分转化和作物吸收的影响

Fig. 1 Diagram for the relationship between soil, root and microbe and its impact on soil nutrient turnover and crop uptake

1 影响土壤氮磷养分转化微生物组成的土壤、生物和环境因素

根际土壤微生物组成影响了其氮、磷转化功能^[16-17],其变化受气候、植被、土壤、耕作等因素的综合影响。在大空间尺度上,存在气候、土壤和植被类型的地带性分布,对2个地点(中亚热带祁阳、暖温带封丘)长期试验的对比研究表明,历史因素(具有不同气候和土壤类型)对微生物多样性的影响大于现代因素(种植和施肥)^[18]。然而,气候、土壤、植被对微生物群落组成空间分布的相对作用仍不清楚。基于相同土壤类型(红壤和紫色土)在2个气候区(中亚热带鹰潭、暖温带封丘)的移置试验表明,在20年的时间尺度上现代因素(气候条件和种植系统变化)

可以显著改变土壤氮转化微生物组成^[19]。

在长时间尺度上,耕作施肥通过影响土壤性质(如pH和养分)改变氮转化微生物的组成。长期平衡施肥(合理配施氮磷钾化肥、以及化肥和有机肥配施)可以提高酸性旱地土壤(红壤)中氨氧化古菌(AOA)和氨氧化细菌(AOB)数量^[20];在水稻土中主要增加了AOA的数量^[21-22];但在碱性旱地土壤(潮土)主要增加AOB数量^[23-24]。土壤pH一方面影响了土壤中氨的形态和含量,另一方面显著影响了AOB和AOA的丰度和结构变化,从而影响了土壤氨氧化过程^[25-26]。近期研究发现,酸性土壤中氨氧化古菌中的1.1b古菌主导了土壤氨氧化过程^[27]。

土壤解磷微生物受植被和管理措施的影响,表现出明显的根际效应。研究表明,在暖温带华北平原区不同利用方式下,土壤有机磷细菌较无机磷细菌数量高,有机磷细菌主要为芽孢杆菌属和假单胞杆菌属,而无机磷细菌主要为假单胞杆菌属;磷细菌数量在菜地中最高,在农田(小麦-玉米)和林地土壤中较低,但其数量与土壤速效磷和有机质含量并无线性相关性^[28]。在不同作物系统中,花生根际的解磷细菌种群密度最高,而高粱和玉米根际最低^[29]。在热带地区,玉米根际土壤中细菌对无机磷(磷酸钙)溶解能力较强,特别是芽孢杆菌属(*Bacillus*)和伯克氏菌属(*Burkholderia*),而真菌对有机磷(磷酸铝、植酸和卵磷脂)溶解能力较强^[30]。长期平衡施肥导致土壤解磷微生物数量下降,而缺磷施肥条件下土壤磷矿化和溶解菌数量增加^[31]。

在小空间尺度上,土壤结构及其微生物食物网(包括食微动物、捕食性动物和微生物)共同影响了土壤微生物的分布及其养分转化功能。土壤团聚体是土壤结构单元,其内部的空间结构(孔隙)和有机碳及氮磷养分的分异影响了微生物群落的结构和分布^[32-33]。在土壤微生物食物网中,土壤线虫对微生物的选择性取食和携带^[34],影响了微生物数量与活性^[35-36]。在农田系统中,农业管理措施和团聚体结构共同影响了线虫组成和微生物多样性^[37]。基于中亚热带(鹰潭)长期施用猪粪的红壤旱地试验,发现团聚体线虫和微生物的协同分布方式影响了土壤的碳氮代谢,线虫对微生物的取食抑制了土壤呼吸熵(负反馈)^[38]、促进了土壤硝化强度(正反馈)^[39]。长期施用猪粪后土壤各粒径团聚体中微生物生物量和线虫总数增加,微生物生物量随团聚体粒径的增大而降低,而线虫数量的变化趋势相反;施用猪粪促进氨氧化微生物(AOB和AOA)丰度的增加,但AOA/AOB呈下降趋势,食细菌线虫专一性捕食氨氧化细菌刺激了土壤硝化强度,促进了

土壤氮素循环^[39]。

植物根系也是影响土壤微生物组成的重要因素,根系通过吸收和分泌作用改变了根际土壤的环境条件(pH、O₂分压、碳源等)^[40],进而影响氮磷养分的有效性及其转化吸收^[41]。根际环境对氮转化过程的影响较为复杂,不同植物可以促进和抑制土壤硝化作用^[42-43];植物根系通过根呼吸降低 O₂分压或者增加根分泌物刺激反硝化作用^[44-45]。基于土壤功能基因芯片(GeoChip)和分子生态网络分析方法,发现在不同的气候-土壤类型区,种植玉米增加了土壤核心氮转化功能基因丰度及其网络结构的复杂度,网络中关键基因包括固氮基因(*nifH*)、反硝化基因(*narG/nosZ*)和氨化基因(*ureC*),说明种植作物改变了土壤氮转化微生物群落的结构和功能^[46]。

总体上针对不同的气候、土壤、作物和施肥系统,根际土壤氮磷转化微生物在大空间和长时间尺度的分布格局及其演变规律仍不清楚,不同时空尺度上生物和非生物因素对微生物分布的相对重要性仍然存在争论。在农田耕作和培肥过程中,由于土壤团聚体和微生物食物网存在复杂的协同变化过程,目前仍然缺乏直接手段揭示土壤微生物群落组成与氮磷转化功能之间的定量关系,因此需要加强微观尺度上土壤氮磷转化微生物结构和功能的研究。

2 丛枝菌根系统形成及其影响氮磷养分转运的机制

丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)定殖在植物根系皮层细胞内形成丛枝结构,这种共生体系在环境养分缺乏条件下促进了植物对养分的吸收^[8,47]。AMF 菌根真菌产生的根外菌丝扩展到土壤中,在土壤团聚体中与微生物区系和微域环境形成密切联系^[48]。AMF 吸收水和氮磷等养分传输给宿主植物,宿主植物将碳水化合物以己糖的形式回馈给 AMF 作为碳源^[49]。丛枝菌根系统中养分交换形成的共生状态可以提高植物抵抗生物及非生物胁迫的能力^[9],最终调节了生态系统的物质代谢^[50]。

针对 AMF 吸收、转运和代谢氮磷过程,近年来研究者运用生物化学与分子生物学方法研究了丛枝菌根共生体中氮转运和传递的形态、真菌体内氮代谢的新途径,完善了氮代谢模型^[51-52];在 AMF 转运和代谢磷的分子基础和基因调控机制方面也取得明显进展^[53-54]。研究发现无机氮被 AMF 菌丝吸收同化为精氨酸进入内部真菌结构,然后以氨的形式传输给植物^[55]。在丛枝菌根中鉴定出了多种氮代谢相关基因

(硝酸还原酶、谷氨酰胺合成酶)^[56]和氮运输离子泵(氨离子泵)^[57]。在植物个体水平上,AMF 通过与植物共生形成的菌根网络增强了氮代谢水平,改善了植物养分供应;在种群水平和生态系统中,AMF 通过复杂的菌根网络改变植物间的营养平衡,影响土壤养分的循环过程^[58]。在磷转运方面,AMF 外生菌丝可以将无机磷转化为多聚磷酸盐,以多聚磷酸盐的形式运输到内生菌丝中;内生菌丝中的多聚磷酸盐通过水解释放无机磷到菌根细胞中,进而传递给宿主植物^[59]。多聚磷酸盐水解释放的能量,可以增强氮代谢载体精氨酸从外生菌丝到内生菌丝的转运^[60]。

AMF 侵染植物根系能诱导植物合成多种信号物质,如水杨酸、茉莉酸、类黄酮、一氧化氮、过氧化氢和 Ca²⁺等,这些信号促进了菌根共生体的形成,但对这些信号传导途径和相互关系的认识仍不系统^[61-62]。近期对可以转化磷的重要菌根真菌(如 *Glomus intraradices*, *Rhizophagus irregularis*)的全基因组分析表明,其专性共生的演变机制不是由于代谢复杂性减少,而是由于缺乏编码植物细胞壁降解酶基因所致^[63-64]。在菌根形成因子(Myc 因子)研究方面发现,脂质几丁寡糖(lipochitooligosaccharide)作为内共生信号分子刺激了丛枝菌根的形成以及植物根部的发育^[65]。在丛枝菌根抗旱胁迫作用机制方面,发现玉米丛枝菌根中的 2 个重要水通道蛋白基因(*gintaqpf1* 和 *gintaqpf2*),在酵母细胞中的克隆表明, GintAQPF1 位于细胞膜, GintAQPF2 位于细胞质和细胞内膜,转化的酵母细胞在高渗休克下细胞体积显著降低,在低渗休克下原生质体破裂更快,说明丛枝菌根可能通过这两个水通道蛋白为宿主植物输送水分^[66]。

菌根真菌对植物的侵染率与环境氮磷的水平相关^[67]。环境中无机氮源种类和浓度影响了菌根真菌菌丝的生理形态,根际微生物或者根系分泌物以及一些次生代谢产物也可以调节菌根真菌的生长和发育^[68]。在水稻中菌根生长与菌根对氮和锌的协调吸收有关,而与对碳的消耗无关^[69]。在缺磷土壤(潮土)中,长期平衡施用氮磷钾化肥降低了玉米 AMF 的多样性;长期施用含磷的有机肥可以显著增加玉米 AMF 种群的多样性和数量,但减少了外菌丝的长度;缺素(不施磷)施用氮、钾化肥对 AMF 没有显著影响^[70-71]。与常规耕作相比,免耕也可以增加玉米 AMF 数量^[72]。

目前在不同的根际养分胁迫条件下,丛枝菌根共生体中养分(碳、氮、磷)协同传输和代谢机制仍不清楚;另一方面,在根际养分满足或者过量供应作物需

求的条件下,丛枝菌根共生体的响应机制也不清楚。

3 作物根系应对根际环境氮磷养分供应的形态和生理响应机制

根际养分不足可诱导根系分泌质子、有机酸等物质活化局部养分,即根系的生物化学适应机制,该机制对植物缺磷的响应明显,但对缺氮的响应并不显著。玉米根外质子分泌有益根际养分活化^[73],而同步进行的根内质子分泌可以软化细胞壁促进根细胞伸长^[74]。在根质子分泌的网络作用途径方面,针对烟草和拟南芥研究了14-3-3蛋白在控制质子泵和养分离子通道活性的作用机制^[75-76]。近期研究表明,在低磷胁迫下,西红柿体内14-3-3蛋白TFT7能提高根尖细胞伸长区的质子外排^[77];在土壤干旱条件下,水稻根尖14-3-3蛋白累积促进生长素转运进而提高根系质子外排^[78]。因此,植物14-3-3蛋白在应对土壤环境胁迫,调控根尖分泌质子促进根系生长方面起到重要作用。

根际环境中氮磷养分匮乏通常会刺激植物根系的生长以增加吸收面积,提高养分的空间有效性,即根系的生物学形态响应机制。不同类型和品种的作物根系在土壤中的空间分布(根构型)不同,由于氮磷养分在土壤中的移动性不同,不同作物根构型对养分利用的贡献也不同。对移动性强的氮素而言,根系夹角变小、碳消耗减少及根系深扎有利于高效吸收土壤氮素^[79]。针对长期耕作施肥导致有效磷含量沿土壤剖面中逐渐下降的特征,浅根系有利于作物对表层土壤有效磷的吸收^[80]。近期发现与大豆磷效率紧密连锁的3个QTL(Quantitative Trait Loci,大豆数量性状基因座),克隆和鉴定了负责大豆根瘤磷转运的基因*GmPT5*,从遗传上证实了大豆根构型与磷效率密切相关^[81-82]。基于作物根系原位动态定量分析及三维重建平台^[83],发现玉米/大豆间作体系以及水稻的根系间存在回避和交叉生长的不同行为,影响了对磷的利用效率^[84-85]。因此,需要综合考虑生物工程技术遗传改良、磷肥的合理施用和最佳栽培模式等措施,实现作物养分(磷)高效和高产^[86]。

根系的生物学形态响应过程与植物激素(如生长素、细胞分裂素等)主导的信号转导机制密切相关,目前的研究热点是在分子水平上识别激素信号转导途径中各实体单元(即信号传导通路中的关键组分),解析其下游关系和作用机制^[10,14,87-88]。对根际植物信号物质的研究发现,环丙基-羧酸-脱氨酶可以促进根系生长和氮素吸收^[89];N-酰基高丝氨酸内酯(N-acyl-

homoserine lactones, AHLs)可以调节根系发育,但在氮素转化中的功能及调控机制仍不清楚^[90-91]。在缺磷条件下植物体内独脚金内酯含量显著增加,促进侧根和根毛发育,从而提高植物对磷素的利用^[92];独脚金内酯与植物其他激素(生长素、细胞分裂素)共同作用可以促进植物的侧枝生长,但独脚金内酯完整的合成和传导途径仍不清楚^[13]。

在低铵土壤环境下,植物根系形态可以响应硝酸盐和铵盐的供给状况^[93],局部供硝酸盐主要促进侧根伸长,而局部供铵明显促进侧根的分枝(高级侧根的发生),通过侧根的生长提高根系吸收养分的效率。植物根系生长对局部硝酸盐和铵盐的响应表现出明显的互补性,局部供铵对侧根发生的促进作用不依赖铵的营养效应,而是环境铵信号作用的结果^[94]。在铵(NH_4^+)响应信号方面,土壤铵毒抑制拟南芥根伸长并降低根向地性,这些反应可能发生在根尖的伸长区和过渡区。在根尖伸长区,主要与铵外排有关,由VTC1(维生素C缺陷1)和DPMS1(多萜醇磷酸甘露糖合酶1)控制;在根尖过渡区,主要与生长素转运分配有关,ARG1(向重性响应基因)、AUX1(生长素内流转运基因)和PIN2(生长素外排转运基因)在该过程中起到重要作用^[95-96]。而在缺氮条件下,拟南芥根维管结构中由氮反应CLE肽(CLA VATA3/ESR相关)和CLV1类富亮氨酸重复受体激酶(CLA VATA1)组成信号模块,其表达控制了根系伸长^[97]。

在低铵土壤环境下,植物也可以通过提高铵转运蛋白活性来增加单位面积根系的铵吸收能力^[98]。土壤中氮素形态在通气性较好时以硝态氮为主导,在淹水条件下(如水稻田)以铵态氮为主,植物对其吸收转运的主要载体分别为硝酸盐转运系统(NRT)和铵转运系统(AMT)。根系吸收氮磷养分后向地上部分传输以满足作物生长和产量形成的需求,这一传输过程的分子载体是由植物体内多个专一性的转运系统在不同组织部位协同完成^[99-101]。植物中对氮缺乏反应最敏感的高亲和力氮吸收系统包括吸收铵态氮的AMT和吸收硝态氮的NRT2^[102]。对于水稻,其根系中*AMT1;1*、*1;2*和*1;3*的转录可响应低铵环境^[103];通过转基因技术过量表达*AMT1;1*可显著增强水稻对低浓度铵的吸收能力,并且促进根系和地上部的生长^[104]。

在硝酸盐响应信号方面, NO_3^- 可直接作为氮信号,而硝酸盐转运体CHL1可作为感应器调控植物感受硝态氮的信号途径^[11]。在硝酸盐信号通路中,小RNA(microRNA)作为上游组分可调控其下游靶基因NRT的转录^[105]。近来研究发现养分转运蛋白也参与

对环境养分的感知及相应信号的传导过程,如拟南芥硝酸盐转运蛋白 NRT1.1 一方面负责根系对硝酸盐的吸收,另一方面参与根系对环境硝酸盐浓度的感知,并通过自身的磷酸化修饰实现对根系吸收硝态氮的调节和对局部硝酸盐供应的生长响应^[106]。

与氮相比,植物磷信号物质、磷信号感受与转导途径方面的研究尚无突破性进展,但对植物磷信号调控途径的研究进展较大。针对模式植物拟南芥,已构建了一个以转录调控因子 AtPHR1 为中心,包括其上游的 *SIZ1* 及 AtPHR1 控制的下游基因,如转运蛋白基因 *PHT1*、*PHO1*、*H1* 和 *PHO2*、*H10*,磷的再利用蛋白基因(酸性磷酸酶和 *RNS*)、调控磷体内平衡基因(*IPS1* 和 *miR399*)以及花青素合成基因等^[12]。作物中的磷信号途径远比拟南芥复杂,不仅涉及植物本身对磷的感应和传导,还包括与根际微生物的互作。目前,在水稻中已初步构建了一个以 *OsPHR2* 为中心,包括 *OsmiR399*、*OsSPX*、*OsIPS* 和 *OsPHO2* 等参与的磷信号调控网络,协同调控植株体内磷平衡、根际磷活化吸收及根际共生微生物磷吸收途径^[15]。但是总体而言,目前对植物体内养分和信号的协同传输机制认识不足^[107-108],对信号物质及其作用网络的研究亟需加强^[109]。

4 展望

在土壤学和植物营养学交叉领域,国内外针对根际土壤养分转化和固定、土壤微生物转化机制以及根系吸收养分机制开展了长期的系统研究,在根系-土壤和根系-微生物界面的养分活化和运输机制方面也从生理水平深入到分子生理水平,但目前对土壤-根系-微生物之间在氮磷养分利用过程中的协同机制并不清楚。由于施肥后氮磷养分的转化和迁移涉及土壤-微生物、土壤-根系、根系-微生物等界面,因此需要针对我国不同农区的土壤-作物系统,研究不同界面上存在哪些生物组成结构,揭示不同组成之间如何形成协同关系,分析这些协同关系如何影响氮磷养分转化和迁移,最终为提高作物氮磷利用率提出土壤-根系-微生物系统的协同调控原理和措施。

针对土壤-微生物以及土壤-根系界面,需要在不同气候、土壤、作物类型区,结合原位观测、同位素标记、稳定性同位素核酸探针和高通量测序技术,针对氮磷的转化-运输-利用过程,开展根际微域以及土壤团聚体中微生物食物网及其关键功能微生物分布格局和演替规律的研究。针对根系-微生物界面,研究作物根构型对氮磷协同吸收的影响,揭示根系-微

生物协同结构形成的分子机制,同时研究根内质子分泌调控根系生长促进土壤氮磷养分利用的机制。特别是针对氮磷养分的关键转运蛋白,如介导根系吸铵和局部供铵促进根系生长的 *AMT* 型铵转运蛋白,深入研究养分转运蛋白的生物学功能及其对环境养分变化的响应,揭示根际养分缺乏条件下的作物根系的应答机制及其调控节点。

针对主要的粮食作物(如水稻、玉米、小麦等),构建根际土壤和植物信号物质发现和鉴定的代谢组学研究方法和技术体系,深入研究根系-微生物对话中影响氮磷转化、吸收和代谢的已知信号的作用机制,挖掘新的信号物质,揭示作物体内和微生物群落中信号物质的传导与应答网络机制,识别不同养分管理水平下信号调控机制对作物利用氮磷养分的影响。

基于上述过程机理的研究,在不同气候、土壤、作物类型区建立生物调控措施的田间试验,从激发土著生物功能、接种有益生物和调控植物根系功能 3 个方面,系统研究不同施肥(碳源和养分)、耕作灌溉、微生物菌剂、作物品种和栽培措施对土壤微生物-根系协同结构形成及其养分转化利用的影响,提出提高氮磷利用效率的根际生物调控途径,集成适应不同气候、土壤和作物类型区的土壤生物功能综合管理体系。

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Advances in Key Coordinative Mechanisms in Soil–Root–Microbe Systems to Affect Nitrogen and Phosphorus Utilization

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Abstract: Rhizosphere is not only the gateway for soil nutrients entering plants, but also the microzone for the interaction among plant, soil and microorganisms. Rhizosphere determines the supply strength and effectiveness of nitrogen and phosphorus, which in turn affects the nutrient use efficiency and crop productivity. The recent progress of research on the synergy transformation and transportation of nutrients in soil-root-microbe systems was reviewed. The factors driving the change of microbial community composition relative to the turnover of nitrogen and phosphorus were investigated at different spatial-temporal scales. The signal network regulating the formation of arbuscular mycorrhizal systems and the genetic control mechanisms to affect the translocation of nitrogen and phosphorus were studied. The ecophysiological response mechanisms of the roots adapting soil nutrient conditions were revealed by signal networks, root exudates regulating root growth, and the relationship between crop root architecture and nitrogen and phosphorus use efficiency. In the future, we need to deepen our knowledge of soil-root-microbial synergy mechanisms at the differently interfaces by studying: 1) the distribution pattern and succession law for microbial food web and its key function groups in rhizospheres and soil aggregates; 2) the impacts of root architecture on the functions of root-microbe coordination system, and the regulatory mechanisms for root proton secretion and nutrient transport proteins on root growth and nutrient uptake under the nutrient deficient conditions; and 3) the signaling networks and their impacts on nutrient use for known signals (such as strigalactone and N-acyl-homoserine lactones (AHLs) and new signal substances (such as microRNA). Finally, the biological regulatory pathways and countermeasures should be proposed to increase the utilization efficiency of nitrogen and phosphorus under different climate, soil and crop regimes.

Key words: Soil-root-microbe system; Synergy mechanism; Nitrogen and phosphorus; Metabolism and translocation; Signal network