

植物磷获取机制及其对全球变化的响应

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摘 要 磷是植物生长的必需元素, 而陆地生态系统普遍存在磷限制, 全球变化可能会影响土壤磷循环过程, 进一步加剧磷限制, 探讨植物磷获取策略对科学预测生态系统生产力如何适应全球变化具有重要意义。该文通过收集和梳理相关文献, 从4个方面综述植物的磷获取机制及其对全球变化的响应: 1)植物的磷饥饿响应机制; 2)植物的磷获取途径和策略; 3)土壤微生物对植物磷吸收的影响; 4)植物磷吸收对全球变化(温度升高、氮沉降和降水变化)的响应及其机制。该综述有助于深入理解全球变化背景下植物适应低磷胁迫的机理, 也可为养分资源管理实践提供理论依据。

关键词 磷循环; 微生物; 植物; 磷饥饿响应; 全球变化

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Plant phosphorus acquisition mechanisms and their response to global climate changes

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Abstract

Phosphorus (P) is an essential but limited nutrient for plant growth, and global climate changes may affect soil P cycling and further aggravate P limitations in the soil. In this review, we focused on the response of plant P acquisition strategies to climate changes and subsequent influences on ecosystem productivity. By searching and analyzing the existing literatures, we summarized the P acquisition mechanism of plants and their response to global climate changes from following aspects: 1) plant P starvation response mechanisms; 2) plant P acquisition pathways and strategies; 3) involvements of soil microorganisms in plant P utilization; and 4) responses of plant P acquisition strategies to global climate changes (e.g., warming, nitrogen deposition and precipitation changes) and the underlying mechanisms. The review is expected to deepen our understanding of plant adaptation to low-P stress under the future climate scenario, and can also provide a theoretical basis for nutrient management in agriculture.

Key words phosphorus cycling; microorganism; plant; phosphorus starvation response; global change

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磷(P)是植物生长所必需的养分, 是植物生命体内实现能量代谢、遗传变异和信息表达的重要元素(Zeng & Wang, 2015), 它能够调节糖类和淀粉的生成和转运、参与籽粒形成和成熟的过程、影响生物固氮以及根系发育等(陈家宽和陈中义, 1999), 在促进植物生长过程中发挥着至关重要的作用(Ren *et al.*, 2016)。然而, 由于大部分土壤的有效磷含量相对较低, 使得陆地生态系统普遍存在磷限制。低磷

胁迫不仅会改变植物形态外观和生理生化过程, 还可能影响植物的生长发育, 最终限制植被生产力, 影响生态系统的服务功能。因此, 探讨植物的磷获取机制一直都是相关研究领域的热点问题。

土壤磷是植物获取磷的主要来源, 分为无机磷和有机磷两类。其中无机磷又分为水溶态磷、吸附态磷和矿物态磷; 有机磷则主要是磷酸肌醇、磷脂和核酸以及微生物生物量磷(McDowell & Stewart,

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2006; Huang *et al.*, 2017)。在多种磷形态中, 能够被植物直接吸收利用的部分是水溶态磷, 但其在土壤中含量极低, 且易被铁铝氧化物等吸附固定和优先被植物利用, 容易消耗(秦武明等, 2008)。因此, 其他形态的磷转化为水溶态磷是土壤维持磷供应的重要途径, 如吸附态磷在解吸附作用下释放磷酸根, 有机磷在磷酸酶水解之后释放无机磷等(Antelo *et al.*, 2007)。探寻植物如何参与土壤磷转化并影响土壤磷的有效性, 对理解植物如何获取土壤磷至关重要。

微生物在植物磷获取过程中发挥重要作用, 能够帮助植物吸收根际之外的磷, 亦可促进难利用磷向有效磷的转化(朱倩等, 2018)。其中能够活化难利用磷的这部分微生物被称为溶磷微生物(phosphate-solubilizing microorganisms, PSMs), 主要通过以下途径参与磷的转化。一是PSMs具备分泌胞外酶的能力, 如磷酸酶、植酸酶、核酸酶、脱氢酶等(Richardson *et al.*, 2001; 吉蓉, 2013), 在酶的作用下促进有机磷水解, 进而释放可被植物利用的无机磷(包鑫等, 2014)。二是PSMs通过分泌有机酸等物质, 促进吸附态磷和蓄闭态磷的解吸附并释放磷酸根。三是微生物直接参与磷转化, 微生物在生长过程中固定了部分磷(Turner *et al.*, 2003), 在死亡后这部分磷归还至土壤, 成为植物的磷源之一。四是菌根真菌定植在植物上形成菌根共生体, 例如丛枝菌根和外生菌根, 能够有效增加植物从贫瘠土壤中获取流动性差的磷(Lambers *et al.*, 2018)。

近几十年, 全球气候变化(温度升高、降水变化及氮沉降等)对植物生长及其养分获取的影响受到越来越多的关注, 气候因子的变化将直接或间接改变植物的磷吸收策略。许多研究通过设置野外控制实验来研究全球变化对土壤磷循环的影响, 取得了较大进展, 如Zhang等(2020)研究表明了氮沉降和降水格局变化都显著改变了土壤磷组分和磷循环。梳理全球变化对植物磷吸收过程的影响, 对理解植物未来如何适应气候变化具有重要意义。

已有研究表明植物获取磷是一个复杂的过程。在低磷条件下, 植物如何感受养分胁迫? 通过何种途径增加磷获取? 与土壤微生物如何协作? 如何响应全球变化? 针对以上问题, 本文综述已有相关研究, 从1)植物的磷饥饿响应; 2)植物的磷获取途径; 3)土壤微生物对植物磷吸收的影响; 4)植物磷吸收对

全球变化(温度升高、氮沉降和降水变化)的响应及其机制等4个方面进行探讨, 以期对未来磷循环研究提供理论支持。

1 植物磷饥饿响应

土壤中磷的缺乏会使植物发生磷饥饿响应(phosphorus starvation responses, PSR), 具体表现在磷转运子表达变化, 细胞代谢途径和根系分泌物改变, 以及根系的形态和构型的调整等方面(李锋等, 2004; 图1)。在磷饥饿响应过程中, 植物首先感知磷缺乏, 然后产生信号级联来启动和协调适应反应(Vance *et al.*, 2003; Franco-Zorrilla *et al.*, 2004; Ticconi & Abel, 2004)。研究表明, 这些适应性反应受基因表达变化调控(Amtmann *et al.*, 2005), 当植物生长受到磷限制时, 成千上万个基因的表达会发生改变(Wang *et al.*, 2002; Wasaki *et al.*, 2003; Wu *et al.*, 2003)。这些基因被分为“早期”基因和“晚期”基因, “早期”基因反应迅速且短暂, 通常在植物面临磷饥饿的几小时之内反应, “晚期”基因在植物长时间处于磷饥饿时会改变植物形态、生理和代谢(Hammond *et al.*, 2003)。已有研究发现, 磷饥饿响应基因有很大一部分受磷酸盐饥饿反应调控因子(如拟南芥(*Arabidopsis thaliana*)中的PHR1 (phosphate starvation response regulator 1))及其同源物(如水稻(*Oryza sativa*)中的PHR2)的调控(Wang *et al.*, 2014b)。当植物受到低磷胁迫时, PHR1会从调控基因和负调控因子SPX1、SPX2的复合物中迅速解离出来, 对磷饥饿响应基因进行调控(González *et al.*, 2005)。“早期”转录反应包括一般应激相关蛋白(如几丁质酶和过氧化物酶)的编码基因表达的增加(Wang *et al.*, 2002; Hammond *et al.*, 2003), 也包括编码各种转录因子(如HD-ZIP、WRKY转录因子、MYB-CC转录因子、bHLH DN结合蛋白)的基因表达的改变(Rubio *et al.*, 2001; Wang *et al.*, 2002; Hammond *et al.*, 2003; Todd *et al.*, 2004)、核糖体调节因子(如At4和TPS家族)的改变(Burleigh & Harrison, 1999), 以及细胞内信号级联的其他组成部分(如蛋白激酶和蛋白磷酸酶)的变化(Wang *et al.*, 2002; Hammond *et al.*, 2003)。“晚期”转录反应主要是适应性反应, 它能促进植物对土壤磷的吸收, 提高植物体内磷的再利用(Hammond *et al.*, 2004)。例如在根系中, 编码PHT1磷转运蛋白家族成员(Smith

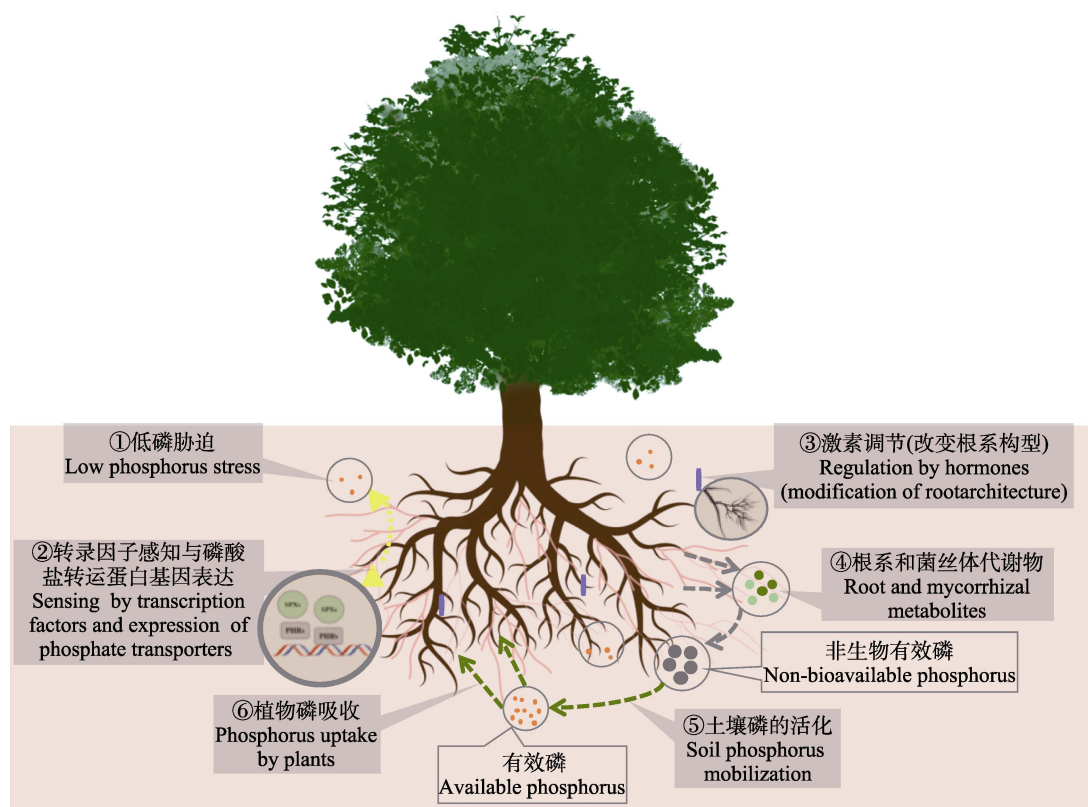


图1 植物的磷饥饿响应。

Fig. 1 Phosphorus starvation responses in plants.

et al., 2003; Wasaki *et al.*, 2003)、胞内和胞外RNA酶(Wasaki *et al.*, 2003)、磷酸酶(Stenzel *et al.*, 2003; Wasaki *et al.*, 2003)等基因的表达在磷饥饿过程中都逐渐增加。通过对十字花科植物根部的相关研究发现, 参与植物PSR相关的调控因子可能会影响植物微生物之间的磷养分竞争, 而微生物定植在植物体上会帮助植物积累磷, 影响PSR转录因子的表达水平, 同时刺激植物发生PSR (Castrillo *et al.*, 2017)。

根系分泌物是植物受磷胁迫的一种信号传递物质, 能够有效地帮助植物与土壤之间进行信息传递和物质交换(Chiou & Lin, 2011)。研究表明, 低磷环境会刺激植物根系分泌一系列代谢物, 包括初级代谢物(如糖类、氨基酸和有机酸)和次级代谢物(如酚类、黄酮类化合物、萜类化合物), 这些分泌物一方面可为微生物生长提供能量, 一方面作为信号物质调控植物根系和土壤微生物的相互作用(尹华军等, 2018)。如低磷条件下植物分泌的有机酸和酚类物质会显著增加, 如柠檬酸和酸性磷酸酶分泌增多促进了植物对磷的吸收和利用(许仙菊和张永春, 2018; 李靖怡, 2020)。张治宏等(2020)发现低磷处理下的菖

蒲(*Acorus calamus*)、菱(*Trapa bispinosa*)、苦草(*Vallisneria spiralis*)和荇菜(*Najas peltatum*)根系分泌的有机酸量均明显高于对照组。除有机酸外, 一些植物面对低磷胁迫时还会分泌质子, 如番茄(*Lycopersicon esculentum*)、鹰嘴豆(*Cicer arietinum*)、蚕豆(*Vicia faba*)通过增加质子的分泌来活化土壤难溶态磷, 从而提高了磷利用效率(Gardner *et al.*, 1982; 张恩和等, 2004; 张瑜等, 2015)。此外, 根系分泌物与微生物关系密切, 初级代谢产物还会影响微生物多样性, 改变微生物群落结构, 进而影响土壤磷转化和磷有效性。同时土壤微生物也会影响根系分泌物的产生, 如通过释放特定化合物刺激根系代谢物如氨基酸等的变化(Lambers *et al.*, 2018), 进而影响植物磷吸收。

除了根系分泌物以外, 菌根共生体的菌丝体也会向土壤中分泌代谢物(Toljander *et al.*, 2007)。然而低磷条件下菌丝体代谢产物如何影响植物磷吸收仍知之甚少。Filion等(1999)证实根内球藻的菌丝分泌物影响土壤微生物的生长和组成; 最近的一项研究还发现, 丛枝菌根真菌分泌的果糖也具有信号功能,

会直接触发溶磷细菌中磷酸酶基因的表达(Zhang *et al.*, 2019)。这些结果表明菌丝体分泌物在植物获取土壤磷过程中扮演着重要角色。但前人大多聚焦根系分泌物, 而菌丝体分泌物对磷循环影响的研究较少。

植物根系构型的变化是植物磷饥饿响应的另一个特征, 如根和根毛的伸长和增多、菌根真菌感染率增加等(刘灵等, 2008; Lynch, 2011)。研究发现, 磷饥饿下根系生长和结构的适应性变化受根和地上部分之间碳水化合物分配的影响, 这可能与植物激素、糖类信号物质的产生有关(Phillips *et al.*, 2004)。与缺磷响应类似, 生长素外部供应的改变会抑制初生根生长、促进侧根生长和根毛形成, 引起根表型的变化(Raghothama, 1999)。如磷饥饿时侧根的形成与转录调节因子(ARF19)调控的生长素变化有关, 而生长素通过赤霉素(GA)介导的生长抑制因子(DELLA蛋白: RGA和GAI)来影响根的生长(Nacry *et al.*, 2005)。植物磷饥饿会降低GA的生物活性, 促进DELLA蛋白的积累(Fu & Harberd, 2003), 抑制了初生根的生长, 并促进了根毛的生长(Jiang *et al.*, 2007)。还有研究发现, 初生根分生组织的停滞可能会触发糖的积累(Canarini *et al.*, 2019)。当根尖分生组织衰竭时, 分生组织细胞的共质体连接遭

到破坏(可能是由于胼胝体沉积), 根分泌物减少(Shishkova *et al.*, 2008), 糖向根尖的持续运输会导致根系糖浓度的短暂增加。因此, 根系糖浓度可作为指示根系结构变化的一种信号分子(Canarini *et al.*, 2019)。

2 植物磷获取途径

植物主要通过两种途径吸收土壤磷, 一是根表皮和根毛直接吸收, 另一种是通过菌根途径吸收土壤磷(Smith *et al.*, 2004; Shi *et al.*, 2021; 图2)。多数研究表明, 在低磷胁迫条件下, 植物通过增加根毛数量和长度、根系变细变长等方式, 扩大根系吸收面积以获取更多的磷(Lynch, 2011)。如低磷胁迫下大豆(*Glycine max*)的总根长、根表面积显著增加(孔令剑等, 2018); 棉花(*Gossypium* sp.)幼苗通过增加侧根数、比根长、分枝密度、根长密度和根毛长度, 同时降低根的平均直径, 促进根的伸展, 扩大根覆盖面积, 增加了磷的获取范围(Zhang *et al.*, 2021)。然而, 在对驴食豆(*Onobrychis viciifolia*)新品系幼苗生长及生理特性的研究中, 低磷胁迫显著降低了驴食豆的根体积、根表面积、根长和根尖数(江海慧等, 2020)。除形态外, 根系还会发生生理上的变化。如

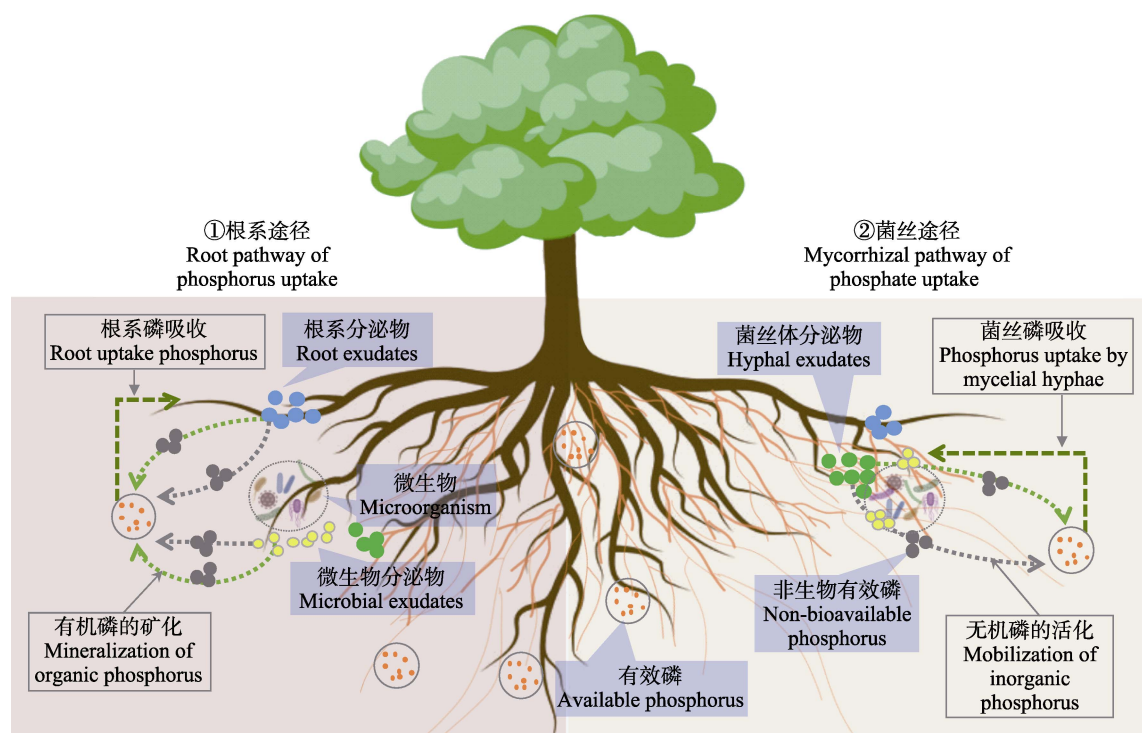


图2 植物的磷吸收途径。

Fig. 2 Pathways of plant phosphorus acquisition.

Tang等(2013)发现低磷胁迫下, 白羽扇豆(*Lupinus albus*)根系对质子、柠檬酸和酸性磷酸酶的分泌增多。但不同植物分泌物的种类和数量会有不同, 可见, 不同植物的磷获取机制可能存在差异, 仅关注根系的形态和生理变化无法全面揭示植物应对低磷胁迫的策略。

陆地上超过95%的植物可以和菌根真菌形成菌根共生体, 而菌根是植物获取土壤磷的另一个重要途径。由于菌丝可以达到植物根系触及不到的土壤区域, 可帮助植物扩大磷吸收面积(曹庆芹等, 2011)。因此在缺磷条件下, 植物更易与菌根真菌建立菌根共生体来增强自身从土壤中获取磷的能力(Raven *et al.*, 2018)。如接种丛枝菌根真菌摩西管柄囊霉(*Funneliformis mosseae*, FM)和地表球囊霉(*Glomus versiforme*, GV)后, 南美蟛蜞菊(*Sphagneticola trilobata*)的磷含量分别增加了36.6%和40.7%, 这表明菌根共生体能促进植物的生长, 提高土壤难溶性磷的吸收效率(李琴等, 2020)。刘云龙等(2021)在研究丛枝菌根真菌对豆科作物磷吸收影响的实验中, 也证实了接种丛枝菌根真菌显著提高了大豆地上部分的磷含量和磷吸收量。此外, 不同菌根类型(外生菌根和丛枝菌根)促进植物磷吸收的机制也不相同(Rosling *et al.*, 2016)。如外生菌根主要通过分泌磷酸酶来水解土壤中的有机磷(Häussling & Marschner, 1989), 而丛枝菌根分泌磷酸酶的能力相对较弱(Joner *et al.*, 2000)。外生菌根真菌还可以产生低分子量有机酸和螯合剂以促进矿物磷的风化和无机磷释放(Plassard & Dell, 2010), 因此外生菌根植物通常具有比丛枝菌根真菌植物更强的土壤磷获取能力。

3 土壤微生物对植物磷获取的影响

土壤PSMs与难溶性磷的活化密切相关, 它们能够将难溶性磷转化为可溶性磷供植物吸收利用, 从而提高植物对土壤磷的利用率(滕泽栋等, 2017; 图2)。微生物溶磷机理十分复杂, 不同微生物类群的溶磷机理不同。其中微生物对难溶性无机磷盐的溶解机制主要包括: 1)通过质子或分泌有机酸进行溶磷; 2)产生特定螯合物来溶解难溶性无机磷酸盐(吴鹏飞等, 2008); 3)释放 H_2S 与磷酸铁进行反应产生硫酸亚铁和可溶性磷酸盐等(孙合美等, 2016)。微生物对有机磷的转化主要通过释放水解酶, 如植酸

酶、核酸酶和磷酸酶等进行(滕泽栋等, 2017)。

PSMs对无机磷的溶解与小分子有机酸的分泌有关, 主要是葡萄糖酸、草酸、酮基葡萄糖酸、苹果酸、柠檬酸等(Marra *et al.*, 2015; Sane & Mehta, 2015), 不同微生物类群合成的有机酸种类和含量不同, 溶磷效果也存在差异。如唐岷宸等(2020)从农田土壤中筛选出解磷能力最强的X-P18菌株, 并使用16S rDNA技术对该菌株进行了分析, 鉴定其为贝莱斯芽孢杆菌(*Bacillus velezensis*), 并通过测定发酵液中小分子有机酸种类发现其溶磷机理是分泌乙酸及其他少量小分子有机酸。有研究报道, 欧文氏菌(*Erwinia*)对矿物态磷的高效溶解作用, 其原理是葡萄糖脱氢酶(GDH)催化葡萄糖氧化后产生葡萄糖酸(Liu *et al.*, 1992), 而葡萄糖酸对磷矿石进行溶解后释放大量的无机磷(Goldstein, 1994)。但是, 骆韵涵等(2020)从罗源湾红树林根际土壤中分离溶磷菌, 筛选出洋葱伯克霍尔德菌(*Burkholderia cepacia*, NR113645.1), 发现其溶磷效果不佳, 原因可能与菌液中主要以丙酮酸、乳酸、乙酸和丁二酸等为主, 而葡萄糖酸量极低有关。部分溶磷微生物还可将葡萄糖酸进一步氧化为2-酮基葡萄糖酸, 其具有更强的溶磷效果(Goldstein, 1986)。然而一些微生物的GDH相关基因突变失活后就不能再溶解难溶性无机磷, 但可在吡咯喹啉醌(yr-roloquinoline quinone, PQQ)为辅基的条件下参与无机磷的溶解(Babu-Khan *et al.*, 1995)。例如有人发现土壤细菌恶臭假单胞菌(*Pseudomonas putida*) KT2440可以通过分泌葡萄糖酸来溶解难溶性土壤磷酸盐, 同时还需要PQQ作为辅酶(An & Moe, 2016)。张健(2014)在分子水平上阐明了草酸青霉菌(*Penicillium oxalicum*) BK可通过提高编码苹果酸合成反应的催化酶基因表达, 增加苹果酸的分泌和积累, 从而缓解磷胁迫。何迪等(2020)发现草酸青霉菌HB1主要是通过分泌氢质子酸解含磷矿物来进行溶磷的, 结果也表明其对磷酸钙和磷矿粉都有较好的溶解效果。

土壤中有机磷一般不能被植物直接吸收利用, 而是要通过酸性磷酸酶、碱性磷酸酶、肌醇六磷酸酶等水解酶对有机磷进行分解后才能供植物吸收(陈哲等, 2009)。Torriani和Ludtka (1985)首次证实了大肠杆菌(*Escherichia coli*)中有关有机磷的溶解基因的存在。Thaller等(1994)根据分子大小将酸性磷酸酶分为A、B、C三类, 从革兰氏阴性杆菌(Gram

negative bacillus)中分离克隆了酸性磷酸酶基因,由 *acpA*、*phoC*和*napA*等基因编码的酸性磷酸酶在pH 6.0时表现出了较强的溶磷活性。在农田土壤中筛选出的有机磷细菌GN1,在不同磷源培养条件下基因表达差异明显,长期低磷胁迫激发了GN1大量磷代谢基因的表达,导致碱性磷酸酶活性持续升高(廖梓鹏, 2017)。来自动物排泄物和有机肥的肌醇六磷酸盐,在肌醇六磷酸酶作用下水解后才可被植物利用(陈哲等, 2009)。已有研究从部分细菌中分离克隆出肌醇六磷酸酶基因(*phy*),并证实了接种含有*phyA*基因的微生物明显提高了植物对肌醇六磷酸盐的利用能力(Asea *et al.*, 1988)。

长期以来,根系形态构型的改变、菌根真菌与植物的共生关系被认为可以有效改善磷的转运,然而随着对细菌与植物的关联研究越来越深入,发现内生菌也能够促进非结瘤植物在低营养环境中的生长(Santi *et al.*, 2013)。有研究表明,磷酸盐一旦进入植物体内,很容易与植物中普遍存在的钙和其他金属离子发生反应,形成不溶性磷酸盐,而内生菌能够根据植物需求重新释放磷酸盐(Varga *et al.*, 2020),这说明了内生菌在植物磷的利用中起着重要作用。在植物组织内,内生菌还能够从宿主中获取养分,因此面临的营养限制较少,并且不易受到环境胁迫(Gaiero *et al.*, 2013)。Emami等(2020)报道了溶磷细菌对提升植物磷利用率的作用,对小麦(*Triticum aestivum*)同时接种根际细菌和内生细菌后,两个小麦品种的磷效率指数分别提高29.5%和18.7%,可能是接种细菌后有机酸含量和酶活性的增加提高了小麦的磷利用率。由此可见,无论是内生菌还是内生菌与根际微生物对植物的共同作用,都对植物磷吸收有着重要意义。

4 全球变化对植物获取磷的影响

4.1 温度升高对土壤磷转化和植物磷吸收的影响

全球变暖会影响土壤磷循环过程,进而影响植物磷获取策略。温度变化改变了土壤水、气、热、肥等条件,直接或间接影响土壤磷转化和磷的有效性(McGill & Cole, 1981)。增温主要通过以下4个方面调节土壤磷循环相关的生物和化学过程(贝昭贤等, 2018)。

一是增温改变植物的磷吸收能力。如Zhou等(2021)对青藏高原高寒草甸进行了为期8年的增温

实验,发现地上和地下植物生物量中磷浓度都显著增加,表明了增温条件下植物对磷的动员和同化能力提升; Rui等(2012)也观察到增温使得青藏高原草甸生态系统两种主要植物鹅绒委陵菜(*Potentilla anserina*)和麻花艽(*Gentiana straminea*)叶片中磷浓度显著增加。但Wang等(2021)的研究具有相反的结果,对青藏高原草场进行连续增温3年后发现,植物磷浓度下降了14.3%–49.4%; Yang等(2019)发现增温条件下亚热带杉木(*Cunninghamia lanceolata*)幼苗中的磷含量无显著变化。据此,推测增温对植物磷吸收能力的影响因植被类型、增温时长等存在差异。

二是增温改变了土壤养分状况、pH等理化性质,影响土壤磷循环(Yang *et al.*, 2019; 付倩等, 2020)。由于土壤活性有机碳是微生物最主要的碳源,有机碳含量变化将直接影响微生物活性,进而影响土壤磷的转化(张恩平等, 2014)。此外,有机碳含量高的土壤有利于降低土壤矿物对磷的固持,使得土壤磷更容易被植物和微生物利用(陈智等, 2010)。因此,土壤有机碳含量通常与磷有效性呈正相关关系(杨昊天等, 2018)。增温可能会促进土壤有机碳分解,降低有机碳含量并影响磷的有效性。如王子龙等(2021)设置了不同水平的增温处理,发现温度升高导致冻结期黑土有机碳含量显著降低。增温还会改变土壤养分计量比来影响土壤磷周转。如增温提高了南亚热带季风常绿阔叶林土壤的硝化速率,增加了土壤氮有效性(赵建琪等, 2019),有效氮含量的增加可能会改变氮磷养分平衡,加剧土壤磷限制(Zhang *et al.*, 2013)。

三是增温改变土壤微生物群落组成和活性,进而影响土壤磷周转。研究表明,温度升高能够增加某些特异性微生物的丰度,从而可能直接促进根际磷的溶解和植物对磷的吸收(Jin *et al.*, 2015)。例如Drigo等(2010)发现根际土壤中具有溶磷功能的假单胞菌的丰度在CO₂浓度升高的条件下增加; Smith等(2004)发现温度升高增加了宿主植物根部的碳分配,这刺激了丛枝菌根真菌丰度的增加,菌丝网络扩大,有助于宿主植物对磷的获取。这表明,温度的升高可能有利于这些溶磷微生物的生长,改变微生物及其活性。但这种效应的大小取决于土壤中含磷化合物和植物的种类,而植物种类又决定其根际溶磷微生物的种类和丰度(Wenzel *et al.*, 1994)。如增温改变了北方森林交错带微生物群落结构,具体表现在变

暖显著改变了细菌群落组成(如酸杆菌增加了11%, 放线菌增加了29%, 拟杆菌减少了29%)和外生菌根真菌群落的结构(以担子菌的变化为主, 其丰度减少了47%)(van Nuland *et al.*, 2020); 但Fang等(2020)在中国黄土高原半干旱草原上的田间实验发现, 升温导致微生物代谢速率下降, 但未改变微生物的生物量。同时, 不可忽略的是, 增温诱导的微生物生物量和活性的增加将意味着这些微生物可能会与植物争夺更多的磷, 从而导致磷固化, 进一步影响植物对磷的吸收。

四是增温通过改变土壤磷酸酶活性调节有机磷矿化速率, 影响土壤有效磷含量(贝昭贤等, 2018)。不少研究发现增温可以提高土壤磷酸酶活性, 如Rui等(2012)发现酸性和碱性磷酸单酯酶的活性都因变暖而升高, 与此同时, 土壤有机磷矿化因温度和磷酸酶活性的增加而增加; 高CO₂浓度诱导的升温下, 白毛羊胡子草(*Eriophorum vaginatum*)根际土壤中磷酸酶活性增加了254%, 使得在草丛中每年释放的磷增加了40%以上(Moorhead & Links, 1997)。但也有相反的结果, 如刘朝阳(2020)发现在农田土壤中, 酸性磷酸酶活性随温度升高呈下降趋势; 还有研究发现增温未显著影响高山草甸土壤的磷酸酶活性(Wang *et al.*, 2014b)。不同的研究结果表明增温对土壤磷转化酶的影响机制相对复杂, 仍需要更为深入的研究探索其潜在机制。

4.2 氮沉降对土壤磷转化和植物磷吸收的影响

化石燃料的大量使用导致全球范围内氮沉降持续增加, 高额的氮输入可能改变土壤氮有效性、引起土壤酸化, 进而影响土壤磷转化(陈立新等, 2012)。首先, 氮沉降可能会刺激植物生长, 增加磷需求, 诱导植物的磷饥饿响应并驱动土壤不同磷组分之间的转化(Crowley *et al.*, 2012; Fan *et al.*, 2018)。如庞丽等(2014)发现氮沉降显著增加了马尾松(*Pinus massoniana*)苗高、生物量以及磷吸收效率等, 其原因是促进了根系生长和增加了表层土壤根系分布比例。Long等(2016)研究表明氮沉降可能会增强半干旱草原植物对磷的吸收, 且随着氮沉降的增加, 磷限制对于植物生长的限制不如预期那么重要。其次, 氮沉降还会影响凋落物的产量及其养分归还(陈美领等, 2016)。如张蔷等(2021)以杜鹃(*Rhododendron simsii*)灌丛为研究对象进行了为期两年的模拟氮沉降实验, 结果显示低氮、中氮和高

氮处理样地的凋落物产量均高于对照样地; 在东北针叶林中也发现了类似的结果(Yan *et al.*, 2018)。再者, 氮沉降还会影响凋落物分解速率, 有不少研究发现氮沉降会减少微生物以获取氮为目的的凋落物分解, 延缓了凋落物养分的归还, 可能会影响土壤磷的来源(Carreiro *et al.*, 2000)。

氮沉降对土壤微生物组成和功能的影响也会影响土壤磷的转化, 如有研究发现氮添加降低了草地土壤溶磷细菌的丰度, 改变了溶磷细菌的群落组成, 最终导致有机磷矿化的增加和结合态无机磷溶解的减少(Widdig *et al.*, 2019)。而与细菌相比, 真菌通常具有更强的溶磷功能(林启美等, 2001)。已有研究发现氮沉降改变了土壤真菌细菌比(F:B), 如氮添加后长白山温带森林有机层土壤的F:B显著升高(杨静怡等, 2020); 与之相反, 氮沉降降低了红椎(*Castanopsis hystrix*)人工幼林土壤的真菌生物量和F:B(洪丕征等, 2016)。也有研究发现氮添加没有改变F:B, 但随着氮添加水平升高丛枝菌根真菌的比例显著增加, 且长期的氮添加极大地增加了细菌应激指数, 并增强了和磷矿化有关的特定酶活性, 从而可能对植物的磷获取造成影响(Wang *et al.*, 2018)。以上结果表明, 施氮水平、植被类型和季节变化等均可能影响土壤微生物对氮沉降的响应模式, 这一差异还可能改变土壤磷转化过程和土壤有效磷含量, 进而影响植物的磷吸收策略。

4.3 降水变化对土壤磷转化和植物磷吸收的影响

降水格局的改变是全球变化的重要内容, 会对植物生产力和土壤养分循环产生重大影响(Ruiz-Lozano *et al.*, 1995)。首先, 降水的变化会影响土壤水分条件, 而土壤中水分含量又会影响土壤氧化还原条件, 从而对土壤中磷的吸附与释放产生影响, 改变土壤磷的有效性(张宝贵和李贵桐, 1998)。如Dijkstra等(2012)观察到土壤水分状况对于磷的有效性十分关键, 土壤有效磷含量随降水增加而减少, 植物中的磷含量也随土壤水分增加而增加(Hou *et al.*, 2018)。而大量的降水控制实验发现, 隔离降水降低了植物的磷吸收, 主要体现在植物生长速率下降, 植物磷含量降低等方面(Munns, 1993; He & Dijkstra, 2014; Fan *et al.*, 2021)。一方面, 干旱胁迫可能会限制植物光合能力和生长, 降低磷需求; 另一方面水分限制会引起植物根系形态和功能变化, 影响根系磷获取能力(Dunham & Nye, 1976)。如陈

佳瑞等(2021)通过盆栽控水实验发现,随着干旱的加剧,紫丁香(*Syringa oblata*)、黄刺玫(*Rosa xanthinal*)、连翘(*Forsythia suspensa*) 3种灌木的叶片及茎的磷含量呈降低趋势,认为可能与干旱影响植物磷吸收和在不同器官中的分配有关。另外,水分是影响营养物质运输的重要介质,降水增多也会对植物的磷吸收造成影响,有研究发现增雨有利于水分对营养物质的运输,可以提高植物的磷含量,促进植株生长(张慧等, 2020)。

此外,降水变化也会通过影响土壤微生物进而影响植物对磷的吸收。降水变化的扰动会影响土壤磷的可用性,并可能导致植物和微生物对磷的吸收发生变化(Dijkstra *et al.*, 2015)。如降水增加可以显著促进土壤微生物的生长(Nielsen & Ball, 2015),而微生物的增加会促使植物和微生物之间的磷养分竞争加剧(Dijkstra *et al.*, 2015)。许多研究都表明了土壤微生物生物量随着降水量的增加而增加(Cregger *et al.*, 2012; Bell *et al.*, 2014),如增雨显著增加了内蒙古草原生态系统细菌丰度、Shannon-Wiener多样性指数、Chao 1指数和Faith系统发育多样性指数; Xu等(2022)发现降水增多还显著增加了丛枝菌根真菌丰度。而植物与微生物对于磷的整体竞争随着干旱而减少,因为干旱会抑制植物和微生物的生长,两者对磷的需求减少(Dijkstra *et al.*, 2015)。有研究发现水分与土壤微生物磷含量呈极显著的正相关关系,水分减少抑制了微生物活性及其对磷的固持(贝昭贤等, 2018)。Kaisermann等(2017)发现干旱对细菌和真菌群落组成产生了遗留影响,降低了同种土壤中的植物生长速率,并对植物与土壤微生物养分竞争产生了影响。综上,降水变化不仅通过影响土壤微生物数量和功能,改变土壤磷周转过程和磷有效性,还会通过影响植物生长来改变植物的磷需求。因此,降水格局变化可能会改变磷的供需平衡,影响植物磷吸收。

5 问题和展望

植物获取土壤磷的机制十分复杂,特别是分子水平上植物如何感受低磷胁迫并作出响应的调控机制仍有待深入研究。虽然在农田生态系统中,已对植物磷饥饿响应的基因表达、信号物质合成等做了有益探索,但在森林生态系统中是否存在类似调控机制还缺乏研究。

植物与土壤微生物的相互作用,如植物根系病害、豆科植物结瘤、菌根共生关系以及植物根系与微生物之间的非侵入性共生关系等均可能影响植物获取土壤磷的策略。目前已对拟南芥、水稻等植物的PHRs调控网络及其信号机制做了有益探索,但尚不清楚不同类型植物的关键调控因子是否相同,未来研究应继续验证和探索。

全球变化对植物磷获取策略的影响是一个综合多因素的过程,但当前控制实验多关注单因子变化对磷转化的影响。亟需开展气温升高、氮沉降、水分变化等多因子交互实验,揭示全球变化对植物磷获取策略及陆地生态系统磷循环的影响机制。

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