磷胁迫下豆科作物的基因调控

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摘　要:磷胁迫是全球耕地面临的共性问题。自然资源的局限限制了磷肥的生产,因此植物如何高效利用磷素已经成为研究热点。从基因调控的角度,包括磷胁迫诱导的EST、磷胁迫响应的转录因子、磷胁迫响应的MICRORNA以及植物激素等,综述了植物高效吸收利用磷素的机制。

关键词:磷胁迫;豆科作物;基因调控

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Genetic Control of Phosphate Stress in Legumes

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Abstract: The world's arable land is lack of phosphorus. Because of resource limitation, the manufacture of P fertilizer becomes more costly and less available. Currently, studying the mechanism of adaptive strategies that make plants highly effectively utilize P is a popular issue. Here we reported P-responsive genes improving acquisition, use, and remobilization of P, including P stress-induced ESTs, P stress-responsive transcription factors, P stress-responsive MICRORNAs, sugar signals and phytohormones. It will be useful for advanced research.

Key words: P-stress; Legumes; Genetic control

磷是植物生长和发育的必须营养元素之一,主要被根系以磷酸盐 $H_2PO_4^-$(Pi)的形态所吸收;但是磷酸盐在土壤中易被固定。据报道磷素供应不足造成世界30%以上作物生长和产量受到影响[1]。估计到2060年岩石中能够被矿化的磷储量将被消耗殆尽[1-3]。集约化种植体系中部分磷进入河流,造成湖泊和海洋污染。因此,提高植物对磷的吸收和利用为改善植株磷素营养状况,进而提高农作物的产量以及促进农业可持续性发展具有重要意义。

在磷胁迫下植物为了提高磷的吸收、利用和活化而形成了各种适应机制[1,4-5],包括根的形态和构型的变化[6-12]以及茎和花的发育变化[13]。豆科植物中,白羽扇豆(*Lupinus albus*),菜豆(*Phaseolus vulgaris*),苜蓿(*Medicago truncatula*)和大豆(*Glycine max*)是研究磷胁迫的焦点。白羽扇豆是非菌根菌寄生的植物,在磷胁迫的条件下,促进排根(cluster root)的形成,增加有机酸的分泌,提高了许多基因的表达,像酸性磷酸酶(LaSAP1)和磷的转运蛋白(LaPT1[2,14-15])等。菜豆是世界上最重要的食用豆类,菜豆的遗传多样性使其在低磷土壤也有收获[12,16]。Ramírez等分析了磷胁迫下从菜豆根中分离的几千个EST[17]。Hernández等从磷胁迫菜豆根里鉴别出约125个磷胁迫响应基因[18]。蒺藜状苜蓿,也是一种植物生物学研究的豆科模式植物,磷胁迫延迟了腋生枝和叶片的生长以及花期的出现[13]。缺磷时蒺藜状苜蓿形态变化导致了整个植株发育的迟缓或者只是磷胁迫的一个反映还有待于进一步研究。然而,目前国际上还没有统一的描述植物在磷胁迫下的生长和基因应答的标准,这使得不同实验室的结果难以比较。

磷匮乏时主根缩短,侧根上须根和根毛密度增加;根干重的分配比也增加[4,11,19-20]。磷胁迫时大多数牧草根重减少32%~86%,磷浓度降低[11]。然而由于根的构型差异,某些牧草作物并没有因为磷胁迫而减少根重[11]。同样,在磷充分和胁迫的情况下28 d的蒺藜状苜蓿幼苗根的构型没有差异,而侧

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根的长度和数目在磷胁迫的条件下减少了[13]。相反,紫花苜蓿(Medicago sativa)在缺磷的条件下,根构型发生了变化。

从分子遗传,生物化学,生理学和形态学上就植物磷胁迫问题进行了总结[1-2,20-21,5]。综述磷胁迫下豆科作物生物学研究,包括白花羽衣扇豆,菜豆,蒺藜状苜蓿和大豆。另外模式植物拟南芥(*Arabidopsis thaliana*)和水稻(*Oryzasativa*)也为理解植物对磷胁迫的反响和适应性提供了大量有价值的依据[22-26]。

1 磷胁迫诱导的 EST

近些年来,国际上先后报道了四种豆科作物(蒺藜状苜蓿,大豆,菜豆和白羽扇豆)中发现的25 000多 cDNA 插入片断和 ESTs。微阵列和宏阵列分析表明磷胁迫提高了植物磷转运蛋白、有机酸合成酶、紫色酸性磷酸酶、MATE 家族、转录因子、信号传导和防御等同源基因的转录量[14-15,17,22,26-28]。通过评估微阵列和宏阵列的数据,利用已经公开的的 EST 顺序进行生物信息分析,Graham 等鉴定了52 个备选基因并把这些基因分成 22 个组,它们在这 4 个豆科作物和拟南芥中都普遍表现出对磷胁迫的反响[29]。被鉴定的转录产物涉及多种重要的功能,包括 MYB 和 WRKY 转录因子、信号传导蛋白、转运蛋白、紫色酸性磷酸酶。目前的研究目标包括:(1)使用磷诱导的 EST 作辅助标记选择能够提高低磷抗性的基因类型;(2)探讨磷胁迫诱导基因的功能意义;(3)鉴定那些可能提高磷效的候选基因。

2 豆科作物磷胁迫应答转录因子

拟南芥和水稻研究表明营养胁迫激活或者抑制基因表达[27,30]。转录因子是基因表达重要调节子并且在生物过程中起到重要的作用,包括调节生物和非生物的植物反应[30-33]。拟南芥有 6%(大约1800)的基因和转录因子相关,包括约 72WRKY 基因家族,600 多锌指蛋白和 133 个 MYB 调控因子[34-37]。微阵列分析中,拟南芥 333 个转录基因中约 30% 在磷胁迫下有 2 倍以上正/负调控作用[27]。Müller 等和 Mission 等也报道了拟南芥中 80 个磷胁迫应答转录因子基因[26-28]。下面分别介绍几个磷胁迫诱导转录因子。

2.1 转录因子 bHLH

近年来一个与水稻磷胁迫相关的 bHLH 转录因子(*OsPTF*1)被鉴定出来[23]。通常,*OsPTF*1 是水稻茎的组成表达,但是磷饥饿也诱导了该基因根内表达[23]。磷缺失时,*OsPTF*1 在转基因水稻内的过表达提高了磷的吸收[23]。转基因水稻增加了总根长和根表面积,根重和茎重提高了 30%[23]。*OsPTF*1 启动子融合了 GUS 的转基因水稻,磷限制时侧根、主根伸长区和叶片显现出很强的 GUS 染色[23]。

2.2 转录因子 HD-Zip 和 MYB 家族

另外两个与磷信号应答基因表达相关的转录因子是大豆同源框 HD-Zip 蛋白[32]和拟南芥的 MYB 转录因子[31]。HD-Zip 蛋白与液泡内糖蛋白酸性磷酸酶的 5′-CATTAATTAG-3′结合[32];拟南芥 MYB 基因的顺序和莱因衣沼(*Chlamydomonas reinhardtii*)磷匮乏应答基因 *PHR*1 相似,结合顺序是 5′-GNATATNC-3′[31]。

2.3 转录因子 WRKY 超家族

磷胁迫下的白羽衣扇豆、菜豆、大豆、蒺藜苜蓿的一组转录因子 EST 顺序和 WRKY 家族具有同源性,该基因家族是植物所特有的[34]。它们在各种胁迫包括病害、伤口及老化时起正调控作用[34]。*WRKY*75 位于核内[38],微陈列分析显示拟蓝芥转录因子 *WRKY*75 在磷饥饿时有正调控作用[28]。然而,在磷胁迫和磷充足的情况下 *WRKY*75 沉默突变体侧根数目、长度和根毛的数目都增加了,这表明根的构型可能和磷胁迫无关。*WRKY* 基因家族可能即是转录的激活物又是抑制物,但是它们的结合位点可能是不同的 *W*-盒。今后应该重点该研究转录因子是否能够提高植物对磷匮乏的耐性。

3 磷胁迫响应 MICRORNAS

研究发现内生非编码的小 RNA,可能在植物和动物的发育过程中具有很重要的作用[39-42]。MicroRNA(miRNAs)是一类微小的 RNA,长约 18~32 个核苷酸的非编码 RNA,它可以通过与特定 mRNA 结合或调节特定 mRNA 的蛋白质翻译过程来调控基因的表达[39,43-45]。据推测多数已知植物的 miRNA 与几类基因表达相关,包括转录因子,说明它们在调节植物发育方面的重要性[39]。mi399 是从拟南芥和水稻里分离出来的,24 和 48 h 的磷胁迫可以诱导 mi399[46-47]。在含磷培养基内 mi399 表达量迅速降低了[25],而在磷充足的条件下却没检测到 mi399[24-25,46-47]。另外,mi399 在泛肽交联酶 E2(UBC)基因顺序有 5 个结合靶点[46-47]。磷饥饿抑制了拟南芥 UBC 基因的表达[46]。其他营养胁迫包括钾、氮对 miRNA399 的表达没影响[46]。今后要看 miRNA399 和其他 miRNA 在豆科作物磷应答基因

中是否有重要作用。

4　糖调控磷胁迫应答基因的表达

磷胁迫增加了白羽扇豆茎和根的 *LaPT*1、*MATE*、*LaSAP*1 基因表达量[48-50]。研究证明转基因白羽扇豆和紫花苜蓿(其启动子 5'-非翻译区与 GUS 报告基因融合)的 *LaPT*1、*MATE*、*LaSAP*1 基因和磷饥饿相关[49-50]。磷胁迫时转基因紫花苜蓿根显示很强的 GUS 染色,磷充足的情况下没有 GUS 染色出现。其他逆境胁迫,象氮饥饿、铝毒害、或者添加萘乙酸、*LaPT*1 和 *LaSAP*1 转基因作物里没有 GUS 染色。然而铝毒害和铁、氮和镁胁迫都提高排根 *MATE* 基因表达[50]。

白羽扇豆发芽 5 d 后,16 h 光照/8 h 黑暗光周期,很容易检测出 *LaPT*1。然而,在黑暗下生长的白羽扇豆幼苗磷转运蛋白基因表达减少了,说明了光在磷代谢过程中的重要性。糖即是代谢产物,也是植物的信号分子。羽扇豆和拟南芥的研究表明磷和糖都与磷胁迫诱导基因密切相关[49,51]。在黑暗和磷充分的条件下生长的幼苗,外源糖诱导磷转运蛋白基因表达。白羽扇豆环割研究说明缺磷时光合产物/糖在调节磷响应基因表达中重要作用[49]。环割减少了植株的排根里 *LaPT*1、*LaSAP*1 和 *LaMATE* 表达。另外,在 16 h 光照/8 h 黑暗光周期和磷胁迫条件下生长的植株,放在黑暗下 24 h,磷胁迫诱导的基因根内的表达消失了,但是重新放在光下 16 h 后其表达又恢复了[49]。研究发现在磷胁迫下白羽扇豆排根的糖感应和代谢基因,包括已糖激酶、葡萄糖合成酶、果糖激酶、焦磷酸果糖激酶-1、和 6-P 海藻糖合成酶表达提高了 2 倍[14]。连续 48 h 的黑暗抑制了糖感应和代谢基因表达;植株重新放回连续光照下,这些基因又恢复了。这些结果表明糖代谢和磷胁迫之间存在交互作用。

研究发现外源磷和糖调节拟南芥根的构型和生长[51-52]。限制磷和蔗糖的拟南芥幼苗鲜重减少了 10 倍[51]。在缺磷培养介质中加入蔗糖后拟南芥植株侧根的密度明显提高。缺磷培养基中没有蔗糖,拟南芥幼苗侧根密度降低了 50%;磷充分而缺少蔗糖的培养基中侧根密度降低了 5 倍[51]。这些研究表明了蔗糖代谢和/或者蔗糖感应和磷胁迫信号的交互影响。植物糖和/或者糖代谢水平调节着茎中磷水平的系统信号传递及磷应答基因。最近 Müller 等利用微阵列分析也证明了磷吸收和糖之间的交互作用[26]。蔗糖正负调控拟南芥叶子中 640 多个基因[26]。另外,磷和蔗糖协同作用提高了约 150 个基因的表达[26],这表明了磷代谢过程中磷和糖共同调节基因表达。白羽扇豆的磷应答基因,*MATE*、*LaSAP*、*LaPT*1 与糖感应和糖代谢相关的基因具有相似的表达模式[49],糖才能使许多磷应答基因最大表达。

5　植物激素和磷胁迫适应性

植物生长素(IAA)调节植物生长和根的发育,包括磷胁迫诱导的排根[53]。Nacry 等证明磷饥饿期间,拟南芥的主根和幼侧根 IAA 浓度增加了[52]。没有 IAA 时拟南芥只有主根生长[51]。无论磷营养状况和糖的有效性,外源 IAA 促进了拟南芥侧根形成且抑制了主根的延长[19,51]。磷充分而无蔗糖时 IAA 对侧根的形成有显著作用[51]。磷充分时外源生长素对白羽扇豆和磷匮乏对排根形成的影响很相似[53]。磷匮乏时生长素运输抑制剂显著降低了排根的生成。这些结果有力说明了生长素有效利用率调控着白羽扇豆排根生成。

*NAC*1 基因在拟南芥主根和侧根里表达水平很高,而在茎杆和叶片里表达水平较低[54]。生长素没有刺激 *NAC*1 沉默的转基因植物侧根的生成[54]。这些证实了生长素和 *NAC*1 基因表达对拟南芥侧根生成的协同作用。

磷胁迫刺激多种植物乙烯生成,包括菜豆[55]、羽衣扇豆[53]和拟南芥[56]。磷胁迫下,乙烯刺激了主根和侧根的延长但是没有影响侧根的密度而刺激了根毛密度和长度增加[20,57]。值得注意的是菜豆、羽衣扇豆和蒺藜苜蓿在磷胁迫下都增加了根毛密度和长度。大约 40 个基因被认为和根毛生长发育有关[57]。综合这些结果说明根对磷胁迫的适应过程中,乙烯具有重要作用。

细胞分裂素在根生长和磷胁迫中的作用还没有明确。通常认为细胞分裂素负调控根生长而正调控茎叶生长[58-59]。细胞分裂素氧化酶(CKX)过表达降低了分裂素的含量,促进了根的生长,包括侧根和不定根[60]。磷和氮的匮乏降低了细胞分裂素含量[20],同时促进了侧根的形成。外源细胞分裂素抑制了拟南芥磷胁迫诱导基因的表达[61]。在磷胁迫下,羽衣扇豆排根中 *CKX* 基因表达增加了 3 ~ 5 倍[1]。另外,缺磷的条件下,外源分裂素抑制了白羽扇豆排根的形成,增加了排根中激动素的含量[62]。Aloni 等认为磷充分条件下植株侧根产生的机制与生长素、分裂素和乙烯有关[59]。那些调节主根细胞分裂素量的因素使得侧根萌生位点的乙烯和

生长素增加了,从而出现新的侧根。这些假设和前人的结论相同,低浓度磷抑制初生根根尖生长,减少根尖生长点的优势,增加了侧根的形成。显然营养胁迫下植物激素调节根的发育可塑性。然而,植物是如何使得磷胁迫信号、植物激素平衡和基因诱导协调而调节植物生长的,还有待于深入研究。了解植物对磷吸收机制,提高土壤磷的利用效率对经济和环境友好型农业发展具有深远的意义。

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