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植物矿质养分吸收的长距离反馈调节研究进展

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摘要:植物的养分吸收能力受到局部信号和冠-根长距离反馈信号的共同调节。近年局部调节系统的研究进展较快,长距离反馈调节的研究则相对薄弱。本文从养分吸收反馈调节现象的普遍性、反馈信号的作用模式(促进/抑制)、反馈信号的鉴定、反馈信号的作用靶标等方面对该领域研究现状进行了综述,并提出了有待进一步深入研究的问题。

关键词:矿质养分吸收;反馈调节;反馈信号
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Long-distance feedback regulation of mineral nutrients uptake in plant

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Abstract: The uptake of mineral nutrients in plant relies on coordinate regulation of local and long-distance feedback signaling pathways. Recent years, the former has been investigated comprehensively, while the knowledge about the latter is limited. Although the long-distance feedback regulation involved in mineral nutrients uptake is universal, it's unclear whether feedback signals are positive or negative for regulation of nutrients uptake. Several molecules, including nutrients themselves or their metabolites, sugars, hormones, and microRNAs have been suggested function as the systemic feedback signals. However, little information is available on their target. The future research areas regarding of feedback regulation are suggested in the end.

Key words: the uptake of mineral nutrients; feedback regulation; feedback signals

土壤矿质养分的时空波动广泛存在,植物已进化出精细的局部和长距离调节系统对此做出响应,以维持体内矿质养分的稳态。局部调节包括根毛和侧根增生等根系形态结构的变化[1-6]及一些养分运输载体的诱导表达[7-9]。长距离调节则由根-冠调节和冠-根调节组成,根系感受到周围介质养分的波动后首先通过木质部向地上部传递信号,并触发一系列响应;随后地上部产生信号并由韧皮部向下运输,对根系生长和养分吸收速率进行反馈调节,使根系的吸收能力与地上部的养分需求得以匹配[10]。

植物养分吸收的局部调节和长距离调节交错重叠,精密而复杂。同一种养分的不同运输载体在缺素条件下受不同机制的介导,如拟南芥高亲和 NO_3^- 运输体 *NRT2.1* 的表达受系统反馈信号的调节,而 NH_4^+ 运输体 *AMT1.1* 的表达主要受根系局部氮状态的调节[8]。拟南芥 SO_4^{2-} 运输载体 *SULTR1.1* 的表达受局部硫饥饿的调节,而 *SULTR1.2* 主要受光合驱动的硫、氮和碳需求的控制[9]。此外,根系的同一种运输载体或同一个生长过程还受到局部信号和系统信号的双重调节,如 *NRT2.1* 的表达除了受系统反馈调节外[8],也可受 NO_3^- 局部供应的诱导[7];拟南芥 *hni* 突变体(高氮不敏感)*NRT2.1* 基因的系统反馈抑制发生缺陷,但其可正常响应 NO_3^- 的诱导[11];局部供应的 NO_3^- 可作为信号分子通过分生组织的细胞增殖促进侧根的伸长,地上部 NO_3^-

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的积累则可通过反馈信号抑制侧根分生组织的活性[2]。最近 Ruffel 等(2011)的结果表明,拟南芥根系中受 NO_3^- 有效性和分根(split-root)互作影响的基因首先对局部氮环境作出响应,稍后则处于系统调节信号的控制下;分根植株供应 NO_3^- 的一侧根系在较低的系统反馈抑制(与双侧均供应 NO_3^- 的高氮对照相比)和局部 NO_3^- 的刺激下长出较多侧根(与高氮对照相比),而不供应 NO_3^- 的一侧根系则由于缺乏局部信号的刺激侧根生长量很小。养分吸收的这种局部和系统双重调节对确保根系和地上部之间的通讯、并达到根系供应与地上部需求之间的最佳平衡非常重要[3]。

近年来,采用各种突变体进行的大量转录谱研究正在细胞水平上逐步揭示矿质养分吸收的信号通路[12-14]。已经证明,根系的 NO_3^- 运输体 NRT1.1 也是介质中 NO_3^- 的感受器,称为运输感受体[12、15、16]。NRT1.1 还具有生长素转运活性,对根系在富含 NO_3^- 区域的增殖有重要作用[17]。与局部养分信号研究取得的进展相比,人们对地上部反馈调节根系吸收能力的长距离信号及其调节机制所知甚少[18-22]。本文结合笔者在 K^+ 吸收反馈调节方面的初步工作,对几种主要矿质养分(N、P、K、S、Fe)的长距离反馈调节研究现状进行综述和展望,期望为该领域研究提供参考。

1 养分吸收的长距离反馈调节现象普遍存在

嫁接和分根是研究矿质养分长距离反馈调节的常用方法,养分感受和信号系统发生缺陷的突变体也为探明养分稳态的反馈调节提供了手段。

尽管有少量相反的报道[23],但绝大多数研究证明矿质养分吸收的长距离反馈调节现象是普遍存在的。

分根试验显示,拟南芥一侧根系处于 NO_3^- 饥饿状态时,另一侧供应 NO_3^- 根系的 NO_3^- 内流速率和 *AtNRT2.1* 转录丰度上调,以满足植株对 N 的需求[8]。将分根试验与转录谱检测相结合,发现蒺藜苜蓿 NO_3^- 和 NH_4^+ 的吸收及根瘤 N_2 的固定均受到系统反馈调节,且每一种 N 源都有其特异的系统调控网络[24]。用 *pNTR2.1:LUC* 作为报告基因,在拟南芥中筛选到三个对高氮不敏感的突变体(*hni*),分根试验结果表明,高氮条件下 *hni* 突变体的 *NRT2.1* 系统反馈抑制发生缺陷[11]。后续研究证明,高氮条件下 NRT2.1 的转录下调与依赖 HNI9(编码一个进化上保守的 RNA 聚合酶 II 复合体组分 AtIWS1)的组蛋白 H3 赖氨酸27 三甲基化(histone H3 lysine 27 trimethylation)增加有关[25]。NO_3^- 系统信号的传递速度很快,在数小时内即可诱导根系 NO_3^- 吸收(*AtNRT3.1*)和同化(*AtNIR1*,硝态氮还原酶 1)基因的表达[3]。

向部分根系供 Pi,植株可能通过提高其养分吸收速率(与整根供 Pi 相比)部分或全部补偿缺 Pi 部分根系的损失[26-27]。植株对 Pi 的需求通过供 Pi 部分根系得到满足后,缺 Pi 部分根系 Pi 转运蛋白的表达不再受低 Pi 诱导[28-30]。*Mt4* 是蒺藜苜蓿根系的 Pi-饥饿诱导基因(PSI),在分根试验中部分根系供 Pi 后发生系统下调[31]。*pho1* 突变体根系的木质部 Pi 载入发生缺陷,地上部的 Pi 水平较低[31],导致其根系 *Mt4* 基因在充足供 Pi 时也不发生下调[32-33]。*Grevillea crithmifolia*(银桦)的排根起始和生长以及根系的 Pi 净吸收速率也均受到系统反馈调节[34]。

Claassen 和 Barber(1977)将分根试验、K^+ 浓度梯度试验、K^+ 饥饿不同时间试验的结果综合起来进行计算,发现地上部[K^+]与根系 K^+ 的最大吸收速率(Imax)关系密切($R^2=0.74$),提示地上部 K^+ 状况可能对根系的 K^+ 吸收具有反馈调节作用。向大麦幼苗的一条种子根供 K^+,其余 4～5 条种子根进行缺素处理,前者的 K^+ 吸收能力与整根供 K^+ 相比大幅增强[35]。该文作者推测,地上部需求驱动的根系 K^+ 吸收能力变化可能与 K^+ 向木质部的载入有关,这一假设此后得到证实[36-37]。20 世纪 90 年代后,关于 K^+ 吸收的研究集中在 K^+ 通道和运输载体的鉴定及细胞水平调控网络的探究上[14],对长距离反馈调节则较少涉及。笔者课题组采用钾高效棉花品种鲁棉研 22 和钾低效品种中棉所 41 进行自身嫁接和互相嫁接,发现无论砧木是哪个品种,鲁棉研 22 作为接穗时其叶片含钾量高于以中棉所 41 为接穗的嫁接组合,暗示地上部对棉花根系的 K^+ 吸收可能具有反馈调节作用[38]。笔者最近的棉花分根试验表明,一侧根系处于缺 K^+ 状态,另一侧供 K^+ 部分根系的 Imax 较供 K^+ 对照(两侧根系均供 K^+)增加近 1 倍;如果分根处理 3 d 后去掉缺 K^+ 侧根系,则供 K^+ 侧根系的吸收能力在 3 d 后基本恢复到供 K^+ 对照的水平[39],清晰地展现了根-冠-根之间长距离信号传递对棉花 K^+ 吸收的调节作用。

分根试验也广泛用于研究缺 Fe 响应的调节机

制。车前草[40]、黄瓜[41]、拟南芥[42-43]、番茄(*Lycopersicon esculentum*)[44]和木本植物小金海棠[45]等植物的部分根系处于缺 Fe 条件下时，可诱导另一部分供 Fe 根系的 Fe(III)还原酶活性和/或质子分泌增强。豌豆耐低铁基因型(Santi)作为接穗可以诱导不耐低铁基因型(Parafield)砧木的缺铁响应，使其 Fe(III)还原酶活性维持在较高水平[46]。拟南芥 *frd3* 突变体的木质部 Fe 装载(由 Fe(III)柠檬酸盐螯合物介导)发生缺陷，在充足供 Fe 条件下叶片仍处于缺 Fe 状态[47]，此时根系中的缺铁响应也不能下调[48-50]，提示来自于地上部的缺 Fe 信号在持续调节根系吸铁基因的表达。

植株去顶或去叶后，发现根系的一些缺素响应减弱或消失[3,41,51,56]，说明根系的吸收能力依赖于地上部对缺素的响应，并受到冠－根信号的介导。

2　长距离反馈信号的作用模式尚不明确

虽然已经证明了地上部可以发送长距离冠－根信号调控根系的缺素响应，但地上部是在缺素条件下发出促进信号/需求信号、还是在养分充足条件下发出抑制信号/供应信号尚未得到一致的结论。

通过监测根系形态、运输载体的转录水平和养分的内流速率，不少研究发现植株的部分根系受到缺素胁迫后地上部可能向另一部分正常供应养分的根系发出促进信号，引起该部分根系吸收能力的补偿性上调，如拟南芥局部供应 NO_3^- 后的 *AtNRT2.1* 表达、NO_3^- 的内流[8,24]及侧根伸长速率等[2]、番茄局部供应 Pi 后的 *LePt1* 和 *LePt2* 表达[28]、油菜局部供应 SO_4^{2-} 后的 APS3 ATP 硫酸化酶水平[52]、蒺藜苜蓿局部供应 N_2 后的根瘤数目和重量等[53]。

也有报道指出，向分根系统的一侧增加 NO_3^- 供应，可导致缺素侧根系 NO_3^- 吸收的补偿性下调，这种系统控制被认为由植株高氮状态激发的长距离抑制信号介导[21,54]。Chiou 和 Lin(2011)也认为，分根植株缺 Pi 部分根系的 PSI 基因上调受到抑制，很可能由来源于供 Pi 部分根系的系统抑制子介导[13]。

最近，Ruffel 等(2011)的拟南芥分根试验表明，植物至少存在两种遗传上独立的系统信号，以分别报告植株的氮供应和需求状况。他们发现，分根处理 2-4 d 后，供 N(NO_3^-)部分根系的侧根长度最长，其次为低 N 对照(双侧根系均不供 N)，分根植株缺 N 侧和高 N 对照(双侧根系均供 N)的侧根长度最短。Ruffel 等(2011)推测，分根处理供 N 侧与高 N 对照的差异由一个系统 N－需求信号(促进信号)造成，该信号发源于缺 N 侧，供 N 部分根系在长距离 N－需求信号和局部 NO_3^- 供应的刺激下长出大量侧根；而分根处理缺 N 侧与低 N 对照的差异则与一个系统 N－供应信号(抑制信号)有关，该信号发源于供 N 侧，对缺 N 部分根系的侧根生长起到抑制作用[3]。

地上部控制根系缺 Fe 响应的信号机制得到较多研究。Vert 等(2003)曾提出拟南芥地上部调控根系 Fe 吸收机制的促进模型和抑制模型[43]。促进模型(the promotive model)是指在缺 Fe 条件下叶片产生促进信号传递至根系，诱导 Fe 吸收基因的表达，在 Fe 充足条件下则不产生信号；抑制模型(the repressive model)是指在供 Fe 充足条件下地上部产生抑制信号，传递至根系后抑制 Fe 吸收响应，在缺 Fe 条件下则不产生信号。

Grusak 和 Pezeshgi(1996)将豌豆突变体 *dgl*(正常供铁条件下根部缺铁响应机制仍然处于激活状态，导致植株体内的 Fe 超量积累)和野生型 DGV 共同嫁接在野生型砧木上，发现充足供 Fe 时野生型砧木的 Fe(III)还原速率也能在 *dgl* 突变体接穗的诱导下得到提高，他们认为这种现象是由 *dgl* 突变体向下传递的促进信号所致[55]。Enomoto 等(2007)的去叶试验也证明地上部在缺 Fe 条件下向根系传递促进信号，他们发现烟草根系编码 Fe 运输载体的基因 *NtIRT1* 和编码 Fe(III)还原酶的基因 *NtFRO1* 在缺 Fe 条件下被诱导，但去掉叶片 3 h 后它们的表达快速下降，并逐渐降低到充足供 Fe 下的水平[56]。

拟南芥 *opt3-2* 突变体韧皮部中的肽－Fe 螯合物运输存在缺陷[57]。García 等(2012)向处于缺 Fe 状态的野生型植株叶面喷施 $FeSO_4$，发现根系的 Fe(III)还原酶活性下降数倍，吸铁基因的表达几乎被阻断；但 *opt3-2* 突变体的 Fe(III)还原酶活性和吸铁基因表达仍然维持在与缺 Fe 处理相当的水平。他们据此推断，叶面施 Fe 后产生了特异的抑制信号以阻止根系的缺 Fe 响应，而非减弱或阻断了地上部的促进信号向根系传递[58]。

Lucena 等(2006)对 Fe 吸收反馈调节的促进模型和抑制模型进行了整合，提出地上部既可向根系发出促进信号(乙烯或促进乙烯合成的物质，如生长素或乙烯前体 ACC)，也可发出抑制信号(与韧皮部中的 Fe 有关)；根系可将两类信号进行整合，最终决定是诱导还是抑制吸铁基因的表达[59]。

3 长距离反馈信号的鉴定取得一定进展

3.1 养分或它们的同化物/代谢物信号

Ruffel 等(2011)采用拟南芥硝酸还原酶(NR)双突变体(*NIA1* 和 *NIA2* 基因)进行分根试验,发现该突变体在处理 8 h 后仍然表现出正常的 N 调节响应[3];与野生型相比,NR 缺陷突变体的侧根生长对 NO_3^- 的系统抑制响应也得到加强[2]。这些结果表明,NO_3^- 自身(而不是其同化物)介导了早期转录水平上的 N 调节及此后对侧根生长的系统抑制。在韧皮部运输的 N 的下游代谢物氨基酸,也可能是反映植株 N 状态、调节根系 N 获取和同化的冠-根负反馈信号[21,60-62],它们的生理功能已得到验证[63],然而早期研究未发现韧皮部中氨基酸流量或组成与根系 NO_3^- 吸收速率的相关性[64]。谷氨酸盐是植物体内 N 运输的主要形式,通常发现于韧皮部和木质部汁液中[65],且参与高 N 对侧根伸长的抑制[66],最有可能是 NO_3^- 吸收的候选反馈信号[62]。Beuve 等(2004)还发现 GABA(伽玛氨基丁酸)可能是一种调控油菜 NO_3^- 吸收的信号物质[67],Kinnersley 和 Lin(2000)在浮萍上也发现了 GABA 的这种作用[68]。然而,N 同化产物直接参与系统 N 调节的证据至今尚不充分[69]。

分根试验表明,缺 Pi 侧根系 PSI 基因的上调受到抑制,很可能由供 Pi 侧运输而来的 Pi 介导[28,32,70]。拟南芥 *PHO2* 基因编码一个位于叶片韧皮部的 Pi 转运蛋白,*pho2* 突变体的 Pi 吸收能力和根-冠转运能力提高,导致地上部的 Pi 过量积累,暗示 Pi 的负反馈调节功能缺失[71]。*pho1* 突变体根系木质部的 Pi 载入发生缺陷,地上部的 Pi 水平较低,其根系中 PSI 的下调同时受到破坏[32-33]。但 Pi 本身可能不负责这种系统下调,因为在蒺藜苜蓿的分根系统中,缺 Pi 部分根系 *Mt4* 的下调早于 Pi 浓度的上升,而且 Pi 流量的减少不影响系统抑制[32]。当然,也可能是根系和地上部之间 Pi 的动态循环(而不是 Pi 浓度自身)为反馈调节提供了信号[35]。

充足供 Fe 的蓖麻植株,其叶片 Fe 浓度和韧皮部中 Fe 复合物的水平高于缺 Fe 植株;叶面供应 Fe-EDTA 可降低根系的缺 Fe 响应(质子泌出和 Fe(III)还原酶活性提高)。因此,韧皮部中的 Fe 复合物可能控制植物根系对 Fe 有效性的响应[72]。拟南芥 *opt3-2* 突变可能影响韧皮部中 Fe-肽螯合物的运输[73];番茄 *chln* 突变导致烟草胺(NA,氨基羧酸类 Fe 螯合剂)无法合成[74],而 NA 可以与 Fe(II)形成稳定的复合体在韧皮部运输[75-77];豌豆 *dgl* 突变体在韧皮部中不形成野生型具有的 Fe-肽螯合物[78-80]。上述这些突变体根系的缺 Fe 响应在供 Fe 条件下均比较强,据此推测与肽或 NA 形成复合物的 Fe 可能作为韧皮部信号下调根系吸 Fe 基因的表达。最近的叶面 ^{57}Fe 标记试验表明,突变体 *opt3-2*、*chln* 和 *dgl* 根系中积累的 ^{57}Fe 与各自的野生型相似[58],说明韧皮部中的总 Fe 含量不是根系缺 Fe 响应的抑制信号,为上述 Fe 复合物作为信号物质的推测提供了旁证。

谷胱甘肽(GSH)是在植物中运输和储存的主要含 S 有机化合物,被认为是一种负调节 SO_4^{2-} 吸收和同化的长距离信号[52]。

3.2 地上部衍生的碳水化合物信号

Pitman(1972)的遮光试验表明,K^+ 自根系向地上部的运转量与根系中的糖浓度有关,推测地上部可能通过向根系供应能量来反馈调节 K^+ 向地上部的运输[81]。

糖类物质对 Pi 饥饿响应的调节得到很多研究的肯定。根中糖浓度的增加早于磷胁迫响应基因(PSR)的诱导[82]。在缺 Pi 条件下,采用黑暗或环割处理抑制蔗糖的生物合成和转运,使根中 PSI 的表达降低[83]。*pho3* 突变体的 *SUC2* 基因(编码一个在韧皮部表达的蔗糖运输载体)发生缺陷,在低 Pi 条件下其根系的酸性磷酸酶(ACP)活性和 PSI 基因表达减弱[84-85]。Lei 等(2011)构建了一个 *SUC2* 基因过表达的拟南芥突变体 *hps1*,其在 Pi 吸收、转运和根系构型等多方面表现出低 Pi 响应[86]。缺 Pi 白羽扇豆排根中的几个 PSR 以依赖光合作用的方式上调[82]。外源施用糖类物质对根系形态和 Pi 运输载体等 PSR 有放大作用[83-89]。

拟南芥根系中 NO_3^-(*NRT1.1* 和 *NRT2.1*)、NH_4^+(*Amt1.1*, *Amt1.2* 和 *Amt1.3*)、SO_4^{2-}(*SULTR1.1*)、PO_4^{3-}(*PHT1.4*)和 K^+(*KUP2*)运输载体的表达均具有昼夜节奏,且受到糖类物质的促进,表明光合产物可能是调节根系大量矿质元素吸收活性的共有信号[90]。此后有研究证实,氧化磷酸戊糖途径(OPPP)的果糖-6-P 代谢可产生糖信号,是调节 NO_3^-、NH_4^+ 和 SO_4^{2-} 吸收所需要的[91]。但不同的养分胁迫信息是否由地上部衍生的特异糖信号传递尚不可知。

3.3 植物激素信号

3.3.1 细胞分裂素(CK)　CK 作为 NO_3^- 系统信号的作用已得到较多研究。CK 是 NO_3^- 衍生的根 - 冠信使,可以调节地上部的生长[92-95];根系 N 吸收和同化基因的表达[95-97]及根系结构[98-101]又受到 CK 调节。因而 Krouk 等(2011)和 Kiba 等(2011)推测,NO_3^- 控制 CK 的含量,而 CK 反过来对 N 营养进行反馈调节[95,97]。Ruffel 等(2011)应用分根系统和 CK 生物合成突变体证明,CK 可介导冠 - 根系统性 N 信号,该信号可控制 N 吸收/同化和侧根生长[3]。

有研究表明,CK 可抑制 Pi 饥饿响应[102],但外源 CK 处理不能模拟恢复供 Pi 的抑制效应[70],因而对 CK 作为 Pi 长距离信号的作用提出了质疑。

3.3.2 生长素(Auxin)　与那些中途转移到低 NO_3^- 条件下的拟南芥幼苗相比,持续生长在高 NO_3^- 条件下的幼苗地上部 IAA(吲哚乙酸,主要的活性 Auxin)水平较高而根中的 IAA 含量较低[103],暗示地上部 NO_3^- 浓度较高时 IAA 的向基运输可能受抑,不能满足侧根发生对 IAA 的需求。

拟南芥 *lpr1*(抗低 Pi)突变体的侧根形成在 Pi 饥饿条件下减少,而该突变体是 Auxin 极性运输所需要的 *BIG* 的等位基因系[104],表明自上而下运输的 Auxin 可能也与根系的 Pi 饥饿响应有关。应用野生型和 Auxin 响应突变体进行的研究发现,根系中 Auxin 的重新分布激发了 Pi 饥饿诱导的根系发育[105]。但其他不依赖于 Auxin 的信号途径也参与了这些响应[104]。

大量应用突变体、去顶(去除 Auxin 产生的主要源器官)、环割(阻断 Auxin 的向基运输)、添加 Auxin 及其极性运输抑制剂的研究为 Auxin 作为系统信号参与缺 Fe 响应提供了证据。拟南芥突变体 *aux1-7* 的生长素极性运输有缺陷,该突变体的转录因子 *FIT* 及其靶标基因 Fe(III)还原酶的表达不受缺 Fe 诱导[106]。大豆缺 Fe 植株去掉茎顶端、或在初生叶下方的茎部施用 IAA 运输抑制剂 CFM,根系的 Fe(III)还原酶活性降低,恢复到与供 Fe 处理相当的水平[41]。缺 Fe 导致红三叶草根系的 IAA 积累和 Fe(III)还原酶活性的提高,而在茎部施用 IAA 运输抑制剂 TIBA 后根系的 IAA 积累减少,还原酶活性也受到显著抑制[107]。最近 Wu 等(2012)的系列试验证明,IAA 自上而下的长距离运输确实介导了根系的缺 Fe 响应,如茎环割完全抑制了根系中的 IAA 积累,同时阻止了根系中质子泌出和 Fe(III)还原酶活性的上调;去掉茎尖抑制了根中的质子泌出和 Fe(III)还原酶活性的上调,但向去顶植株的顶端补充 NAA 可以恢复这两种生理响应[108]。

Auxin 作为长距离冠 - 根信号调控根系缺 Fe 响应也受到一些质疑。去顶和施用 CFM 不能降低黄瓜缺 Fe 植株根系的 Fe(III)还原酶活性[41],烟草去顶不影响根系中 *NtIRT1* 和 *NtFRO1* 的表达[56]。Schmidt 等(2000)应用多种突变体的研究表明,主要植物激素(包括 Auxin)均未参与拟南芥的缺 Fe 响应[109]。Bacaicoa 等(2011)则推测,IAA 调节缺 Fe 响应的作用可能是次级的,而且是非必需的[110]。

3.4 新的长距离信号物质 MicroRNA

在韧皮部汁液中鉴定出 MicroRNAs(miRNAs)的事实,提示这类物质具有作为长距离信号分子的潜力[111-112]。目前,几种主要矿质养分缺乏时均发现韧皮部中有 miRNAs 上调现象。miR395、miR398 和 miR399 的表达分别在 S、Cu 和 Pi 缺乏时上调[113-116]。最近在油菜(*Brassica rapus*)韧皮部汁液中检测到了 miR395、miR398 和 miR399,而且它们的丰度在植物分别处于 S、Cu 和 Pi 饥饿时增加[108]。油菜缺 Fe 时韧皮部中的 miR158b 上调[117],拟南芥中也发现同样的现象[118]。借助谷氨酰合成酶抑制剂 MSX,Gifford 等(2008)鉴定出一个响应有机 N 的 miR167/ARF8 调节模型,该模型调节侧根起始和伸长,使根系与有机 N 进行匹配[66]。miR393/AFB3(生长素受体)模型则通过调节主根和侧根的生长对 N 作出响应[119]。但目前还没有直接证据表明 miR167 或 miR393 可以从地上部运输至根系。

miR399 对 Pi 饥饿响应的调节得到最系统和广泛的研究。miR399 在缺 Pi 组织中特异上调[114,120-122],直接引起一种泛素结合 E2 酶基因 *PHO2* mRNA 的裂解,从而促进 Pi 吸收和向地上部的运输。过表达 miR399 的拟南芥和水稻在地上部过量积累 Pi,在充足供 Pi 条件下出现 Pi 中毒现象[120,124]。由于在油菜和南瓜的韧皮部汁液中也检测到 miR399[123,126],因此推测长距离信号系统在不同植物种类中可能是保守的。采用嵌合基因(启动子 - 报告基因)的分析表明,miR399 和 *PHO2* 主要在维管组织中表达[121]。嫁接研究证明,野生型与过表达 miR399 的拟南芥或烟草互相嫁接,接穗中的 miR399 能通过嫁接位点向野生型砧木移动并抑制砧木中 *PHO2* 的表达,从而激活 Pi 的吸收和运输[123,127]。着生菌根的苜蓿植株,其叶片中成熟

miR399 及其前体含量均高于无菌根植株[125]，并且部分成熟 miR399 可被转运至菌根中组成 miR399-PHO2 信号途径。

由于 miR399 既可以在地上部表达、也可以在根系表达，它在冠－根之间移动的生物学意义曾受到质疑。但时间动态分析表明，Pi 缺乏条件下 miR399 在地上部的表达早于根系，因此它的系统移动确实属于 Pi 缺乏的早期响应[127]。

4 长距离反馈信号的作用靶标得到初步研究

地上部产生的系统反馈信号需要由根系感受器接收，然后引发一系列生理生化反应乃至根系形态变化对养分缺乏作出响应。但反馈信号的调控靶标、相关调控网络的上、下游组分研究总体上比较薄弱，目前仅有一些初步进展。

上文提到的 *PHO2* 被鉴定为 miR399 的下游靶标[121-122]。Pi 缺乏条件下，miR399 的上调抑制了 *PHO2* 的表达，解除了 PHO2 对 Pi 吸收的抑制。*pho2* 突变体的 Pi 吸收和运输受到促进，导致地上部过量积累 Pi 出现 Pi 中毒现象[71, 121]。已知 miR399 在 Pi 饥饿信号途径中的上游元件可能为转录因子 PHR1[122]，同为反馈信号的蔗糖也位于 miR399 的上游[128]。PHO2 的下游分子元件尚不清楚，推测泛素介导的蛋白质水解或功能修饰可能参与其中[13]。

此外，有研究表明，Cu 饥饿反馈信号 miR398 的上调介导了 Cu/Zn-SOD mRNA 的降解[116]，S 饥饿反馈信号 miR395 通过调节 ATP 硫酸化酶和低亲和 SO_4^{2-} 运输载体 *SULTR2. 1* 的表达影响 SO_4^{2-} 的同化和分配[113]。*AtNRT2. 1* 基因是 N 系统反馈信号的一个主要靶标[3, 63, 129, 130]，至少部分在转录水平上受到高 N 供应的抑制[7, 8]。

5 研究展望

至今，人们对养分长距离反馈调节机制的了解还很有限。已知的养分/代谢物信号是直接调控根系吸收能力还是通过激发其他次级信号发挥调节作用尚不可知。此外，笔者推测抑制信号和促进信号共存比较接近反馈调节的本质，但目前缺乏足够的试验证据。

因此，鉴定潜在的长距离信号物质、揭示其作用模式仍然是养分吸收反馈调节领域需要面对的长期挑战，应用养分感受或信号传导途径发生缺陷的突变体有望加快这方面的进展。另外，反馈信号的产生部位、运输机制、作用靶标及此后的调控网络都是该领域未来的研究重点。

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