丛枝菌根中养分转运、代谢、利用与调控研究的最新进展

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摘要: 丛枝菌根(AM)是球囊菌门(Glomeromycota)真菌与植物根系形成的互惠共生体。AM真菌与植物之间的养分转运、代谢、利用与调控是两者建立共生体的基础, 也是两者互惠互利的重要生理机制。关于菌根共生体中碳氮养分转运与代谢特点已有较多报道, 而关于丛枝菌根养分转运、代谢、利用与调控研究最新进展尚缺乏全面、系统的论述。本文旨在介绍AM真菌与寄主植物间养分交换的种类与时空特征的基础上, 探讨AM共生体的养分转运、代谢和利用特点及其调控机制; 分析当前研究存在的主要问题与研究动向和展望, 以期为加强该领域研究、阐明AM真菌与寄主植物共生的生理机制, 为生物共生学研究和发展提供可借鉴的思路。

关键词: AM真菌; 共生; 信号分子; 养分代谢与调控

丛枝菌根(arbuscular mycorrhiza, AM)真菌属于专性活体营养共生真菌, 侵染超过80%的陆生维管植物的根系形成互利共生体, 是分布最为广泛的菌根类型。AM真菌与植物的互利共生是建立在营养物质互换的基础之上: 寄主植物将通过光合固定的碳源输送给AM真菌, 作为菌丝生长和孢子发育所需的碳骨架和能量, 以完成真菌的生活史; 同时, AM真菌帮助寄主植物吸收矿质养分, 促进植物生长发育(赵青华等2014; 杨应等2017), 提高植物适应性和抗逆性(马通等2015)。与AM真菌形成共生关系后, 寄主植物分配AM真菌自身4%~20%的光合产物即碳水化合物(Smith和Read 2008)和相当量的脂质(Luginbuehl等2017), AM真菌则将其所吸收的绝大部分矿质养分供给寄主(Smith和Read 2008)。因此, AM共生体中的养分转运、代谢与利用深刻影响着共生真菌与寄主植物之间的库源关系, 调控着养分分配与利用、物质循环与能量流动以及共生体系的发生发展。另外, AM真菌与寄主之间的离子运输和碳素分配过程中还涉及双方之间的信号传导(Ramos等2011)。深入、全面和系统了解AM共生体中养分转运、代谢、利用与调控机制, 对于诠释AM真菌与寄主植物共生的生理机制, 促进生物共生学研究和发展具有重要的理论价值和实际意义。

1 AM真菌与寄主植物间养分转运的种类与形态

1.1 寄主植物转运给AM真菌的有机养分

寄主植物光合产物在源–库间运输的主要形式是蔗糖, 植物蔗糖/单糖转运体负责将蔗糖及单糖(如葡萄糖、果糖)转运至共生体界面, 再由AM真菌单糖转运体负责将单糖运输至菌丝内, 并通过代谢转化为糖原(glycogen, Gly)、三酰甘油(triacylglycerol, TAG)及海藻糖后被菌丝体利用。除了糖类之外, 寄主也转移AM真菌脂质如2-单酰甘油(2-monoacylglycerol, 2-MAG)或脂肪酸(Jiang等2017; Luginbuehl等2017)。寄主植物的糖类和脂质供给对真菌碳经济的相对贡献仍未知, 但AM真菌表现为脂肪酸缺陷体(Wewer等2014; Tang等2016), 利用三酰甘油作为主要的流动性碳库, 推测脂质的供给量可能占据相当比例的碳源。

1.2 AM真菌转运给寄主植物的矿质养分

AM真菌根外菌丝从土壤吸收无机氮(包括NH_4^+、NO_3^-)和无机磷(Pi), 分别转化成易于运输的精氨酸(Arg)和多聚磷酸盐(poly-P), 两者可协同转运至根内菌丝共生体界面, 然后再分解为NH_4^+或Pi后供植物根细胞吸收。单寄主培养试验中对寄主的根外菌丝鉴定发现poly-P的电荷平衡也可通过无机离子如K^+、Mg^{2+}而无需Arg^+来中和(Smith和Smith 2011)。土壤中20%~40%的氮以蛋白化合物的形式存在, AM真菌可以胞外分泌蛋白酶和肽酶

收稿 2018-08-01 修定 2018-10-24
资助 国家自然科学基金(31471946)和中科院“百人计划”(A315021449)。
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分解蛋白化合物为小肽和单个氨基酸再吸收。有机磷是土壤中常见的磷源, AM真菌胞外分泌的磷酸酶可断裂磷脂键释放Pi供根系吸收。目前AM共生体中对K、Mg、Ca、Zn及S等吸收作用的研究很少, 但以往的放射性同位素示踪试验表明, AM真菌的菌丝可以转运Ca、Zn和S等元素(Cooper和Tinker 1978; 唐振尧等1989)。

2 AM真菌与寄主植物养分转运的时空特征

丛枝结构的形成是确定AM真菌侵染根系形成AM的必要条件。通常认为, 丛枝是真菌与植物进行营养物质交换的主要场所(Harrison 2012), 并且加强了双方之间的营养物质交换(Gutjahr和Parniske 2017), AM真菌侵染植物根系形成丛枝结构, 并演化形成双向界面, 即由根皮层细胞质膜延伸包围丛枝形成的丛枝周膜(periarbuscular membrane, PAM)与丛枝真菌质膜及两膜之间的丛枝周腔(periarbuscular space)构成的共生体界面(Harriso等2002), 丛枝周膜使丛枝与根皮层细胞质隔开, AM真菌−寄主植物之间信号物质的交流与营养物质的转运要跨过两膜和约100 nm宽的丛枝周腔(Balestrini和Bonfante 2014)。

高度分化的丛枝赋予了共生体一个广大的互作界面, 由于共生体界面的表面积增加, 定殖丛枝结构的细胞的表面积多达无丛枝定殖细胞的7倍, 这对于养分转运极为重要。AM真菌在菌根共生体中充当一个附加的碳库, 依靠与植物专性共生获取植物光合有机碳, 并转运至根内菌丝(intraradical mycelium, IRM)或/和根外菌丝(extraradical mycelium, ERM)供其生长、发育和产孢(Smith和Read 2008), 以及作为自身其他器官结构的构建物质和能量来源, 这往往提高寄主植物的光合能力以供应“增加的库强”。同时, 高效的AM共生互作还依赖AM真菌吸收转运土壤中的无机和/或有机养分给寄主植物: AM真菌利用直径更小的根外菌丝扩大了根系吸收面积和土壤利用空间, 通过自身或诱导寄主分泌有机酸、土壤酶等活化和增强养分有效性(Shu等2014), 以及诱导共生体界面营养分子转运体表达以提高养分的转运效率(Koltai和Kapulnik 2010)。

丛枝在寄主细胞中发育成熟后寿命仅1~3天便开始衰老消亡, 同时寄主细胞又恢复原来状态可被新的丛枝再次侵染定殖。为了维持共生效率, 寄主植物细胞可以引发衰老丛枝的消解过程(Gutjahr和Parniske 2017)。以往认为丛枝消解时才释放养分给寄主植物, 而事实上丛枝器官是一边输入碳素养分一边输出矿质养分, 这与植物的幼叶发育早期一边输入植物储藏的有机养分、一边生长并合成新的碳素养分并输出可谓十分相似。AM真菌根外菌丝高效获取和转移难利用养分至膜运输体系的交换界面并被植物吸收, 因此, 共生双方成员在共生体界面发生养分代谢的“重定向”和细胞局部“程序”改变(包括膜运输功能的分化和极化)以完成养分的大量运转, 通过活细胞荧光成像显示丛枝周膜至少包含“丛枝分枝域”和“丛枝主干域” (Pumplin和Harrison 2009)。AM共生体双方养分交换的膜运输体系(即从土壤吸收养分的真菌质膜位点和传送养分至丛枝周膜)包括运输机制、选择性、亲和性和调控功能不同的转运体和离子通道(表1)。共生体界面养分和/或代谢物的吸收与交换依赖膜转运体, 膜转运体可以直接运转矿质养分或小分子有机物(位于界面两膜上的H^+-ATPase活性指示膜转运活力), 它们的表达或调控决定了AM真菌−植物之间互作及适应土壤养分变化的结果(Casieri等2013)。

3 AM共生体的养分转运与代谢特点

3.1 共生体中的碳转运与代谢

在大多植物中, 有机碳以蔗糖形式通过韧皮部筛管分子/伴胞复合体从叶源转运到根库。AM共生体作为强的碳库, 从寄主植物的光合组织源吸取碳(Rich等2017), AM真菌定殖增加了寄主植物的根库强度以从韧皮部卸载更多蔗糖, 同时伴随叶片和定殖根系几种蔗糖转运体(sucrose transporters, SUTs)的表达增加(Boldt等2011; Doidy等2012), 蔗糖在韧皮部卸载和外运至丛枝细胞过程中受SUTs的严格调控并伴随蔗糖的分解(转化为葡萄糖和果糖), 由于AM真菌无蔗糖分解酶活性, 蔗糖分解在寄主植物细胞中进行(Schubert等2004)。变形球囊霉(*Glomus versiforme*)定殖使寄主根皮层细胞中的己糖转运体(Mtst1)表达量增加了2~4倍, 地上部茎叶中的表达量也有所提高(Harrison 1996),

表1 寄主植物和AM真菌内的专性转运体及离子通道

Table 1 Symbiosis-specific transporters and ion channels from host plants and AM fungi

共生体类别	营养	转运体名称	来源	参考文献
寄主植物	糖	MtSt1	蒺藜苜蓿(*Medicago truncatula*)	Harrison (1996)
		MtSut, MtHex1		Gaude等(2012)
		MtSUT1-1, MtSUT2, MtSUT4-1		Doidy等(2012)
		SUT1, SUT2, SUT4	番茄(*Lycopersicon esculentum*)	Boldt等(2011)
		SWEETs	马铃薯(*Solanum tuberosum*)	Manck-Gotzenberger和Requena (2016)
	脂质	STR/STR2	蒺藜苜蓿(*Medicago truncatula*)	Zhang等(2010); Jiang等(2017)
		STR1/STR2	水稻(*Oryza sativa*)	Gutjahr等(2012)
	磷酸	StPT3	马铃薯(*Solanum tuberosum*)	Rausch等(2001)
		MtPT4	蒺藜苜蓿(*Medicago truncatula*)	Harrison等(2002); Javot等(2007)
		MtPT4, 8		Breuillin-Sessoms等(2015)
		LePT4	番茄(*Lycopersicon esculentum*)	Nagy等(2005); Xu等(2007)
		LePT3, LePT4, LePT5		Chen等(2014)
		OsPT11	水稻(*Oryza sativa*)	Paszkowski等(2002); Yang等(2012)
		LjPT4	百脉根(*Lotus japonicus*)	Volpe等(2015)
		PhPT5	矮牵牛(*Petunia hybrid*)	Breuillin等(2010)
	铵根	AMT2;3, AMT2;4, AMT2;5	蒺藜苜蓿(*Medicago truncatula*)	Breuillin-Sessoms等(2015)
		LjAMT2;2	百脉根(*Lotus japonicas*)	Guether等(2009b)
		LeAMT4, LeAMT5	番茄(*Lycopersicon esculentum*)	Ruzicka等(2012)
		SbAMT3;1, SbAMT4	高粱(*Sorghum bicolor*)	Koegel等(2013)
		GmAMT1.4, GmAMT3.1, GmAMT4.1, GmAMT4.3, GmAMT4.4	大豆(*Glycine max*)	Kobae等(2010)
	硝酸根	NRT2	番茄(*Lycopersicon esculentum*)	Hildebrandt等(2002)
			蒺藜苜蓿(*Medicago truncatula*)	Hohnjec等(2005)
			百脉根(*Lotus japonicas*)	Guether等(2009a)
	氨基酸	LjAAPs	百脉根(*Lotus japonicas*)	Guether等(2009a)
		LjLHT1.2		Guether等(2011)
	钾	Cation/H^+ exchanger	蒺藜苜蓿(*Medicago truncatula*)	Garcia等(2017)
		K^+ transpoerter	百脉根(*Lotus japonicas*)	Guether等(2009a)
	钙	Ca^{2+} channel	蒺藜苜蓿(*Medicago truncatula*)	Benedito和Udvardi (2010)
	硫	MtSultr1;2	蒺藜苜蓿(*Medicago truncatula*)	Casieri等(2012); Sieh等(2013); Wipf等(2014)
		LjSultr1;2	百脉根(*Lotus japonicas*)	Giovannetti等(2014)
	锌/铁	Zn^{2+}-Fe^{2+} Permease	蒺藜苜蓿(*Medicago truncatula*)	Benedito和Udvardi (2010)
	金属离子	LeNramp1	番茄(*Lycopersicon esculentum*)	Ouziad等(2005)
AM真菌	糖	GpMST1	聚合菌(*Geosiphon pyriformis*)	Schüssler等(2006)
		RiMST2	球囊霉(*Glomus* sp.)	Helber等(2011)
	磷酸	GvPT	变形球囊霉(*Glomus versiforme*)	Harrison和Vanbuuren (1995)
		GiPT	根内球囊霉(*Glomus intraradices*)	Maldonado-Mendoza等(2001)
		GmosPT	摩西球囊霉(*Glomus mosseae*)	Balestrini等(2007)
		GigmPT	珠状巨孢囊霉(*Gigaspora margarita*)	Xie等(2016)
		GintPT	异形根孢囊霉(*Rhizophagus irregularis*)	Fiorilli等(2013)
	铵根	GintAMT1	根内球囊霉(*Glomus intraradices*)	López-Pedrosa等(2006)
		GintAMT2		Pérez-Tienda等(2011)
		GintAMT3		Calabrese等(2016)
	硝酸根	GiNT	根内球囊霉(*Glomus intraradices*)	Tian等(2010)
	氨基酸	GmosAAP1	摩西球囊霉(*Glomus mosseae*)	Cappellazzo等(2008)
	二肽	RiPTR2	异形根孢囊霉(*Rhizophagus irregularis*)	Belmondo等(2014)
	锌	GintZnT1	根内球囊霉(*Glomus intraradices*)	González-Guerrero等(2005)

已鉴定的SWEETs单向转运体可以运载蔗糖和单糖, 表明其可能在韧皮部卸载蔗糖和外运至根细胞中具有关键作用(Manck-Götzenberger和Requena 2016)。在AM真菌定殖的蒺藜苜蓿根系细胞中, 推定的两个蔗糖转运体MtSut和己糖转运体MtHex1都高度表达, 且不含丛枝细胞中的表达更高, 表明这些转运体不仅参与蔗糖外运至丛枝细胞, 也可从丛枝细胞中回运蔗糖至植物细胞(Gaude等2012)。同样, AM真菌也存在糖转运体, 例如聚合菌(*Geosiphon pyriformis*)的GpMST1与质子作为共转运体高亲和转运单糖(首先是葡萄糖和甘露糖, 其次是半乳糖和果糖) (Schüssler等2006)和球囊霉(*Glomus* sp.)根内菌丝表达的高亲和单糖转运体RiMST2 (Helber等2011)。AM真菌早期侵染直接引起根细胞内蔗糖合成酶、细胞壁和液泡转化酶基因表达增加(以分解蔗糖为葡萄糖和果糖, 从而增加了根碳库潜力), 在植物蔗糖(或单糖)转运体和真菌单糖转运体(如MST2)的协助下穿过共生体界面(Blee和Anderson 2002; Garcíarodríguez等2007), 最终转运至根内菌丝。

根据同位素标记代谢分析及有关基因表达证明, 植物光合碳源以己糖的形式输送到真菌的根内菌丝并代谢转化为糖原和三酰甘油后, 然后运往根外菌丝中被分解利用, 供以真菌的生长发育需要(李元敬等2014), 而且, 在这一过程中大量的糖会转变成脂肪酸, 使脂质成为AM真菌的主要碳贮存形式, 己糖合成代谢产生的海藻糖则是AM真菌体内的高能化合物贮存糖的形式之一(Bago等2003; Schliemann等2008)。

3.2 共生体中脂肪酸的转运与代谢

AM真菌异形根孢囊霉(*Rhizophagus irregularis*)和其远亲玫瑰红巨孢囊霉(*Gigaspora rosea*)基因组中缺失I型脂肪酸合酶(type I fatty acid synthase, FAS-I) (Wewer等2014; Tang等2016), 表明*FAS-I*缺失可能是AM真菌的共有特征。Jiang等(2017)也发现, 寄主植物除了供给AM真菌异形根孢囊霉糖类有机物, 也合成脂肪酸并转运至AM真菌以维持真菌定殖。同样, Luginbuehl等(2017)研究发现, 除糖类外, 脂肪酸也是植物转移给共生AM真菌的一种主要有机碳源, 转运过程中需依赖甘油-3-磷酸酰基转移酶RAM2−GRAS转录因子RAM1 (REQUIRED FOR ARBUSCULAR MYCORRHIZA 1)的直接靶向基因, 构成AM真菌脂质生产的原料, 并且RAM1对这一共生关系至关重要, 为激发脂质生物合成代谢途径所必须。百脉根(*Lotus japonicas*)中AM特异性的脂质合成基因*KASI* (β-keto-acyl ACP synthase I)和*GPAT6* (glycerol 3-phosphate acyl transferase 6)旁系同源缺失突变, 抑制脂肪酸的积累及AM真菌侵染定殖(Keymer等2017), 进一步证实了植物也转运脂质至共生AM真菌。脂肪酸由RAM2催化转变为2-MAG, 定位在丛枝周膜上的ABC转运体G家族(ATP-binding cassette transporters of the G family, ABCG)异二聚体STR (stunted arbuscule)和STR2运载2-MAG至共生体界面(Zhang等2010; Gutjahr等2012; Jiang等2017), 2-MAG可转变为TAG并沿菌丝转运, 但进一步转运吸收机制或相应的转运体尚未知。AM所需的*STR*和*STR2*在丛枝中诱导表达, *STR*和*STR2*突变导致丛枝形态发生的缺陷(Zhang等2010; Gutjahr等2012), STR/STR2与角质、木栓质和孢子花粉素的脂质前体外运体密切相关(Wu等2014; Yadav等2014)。非菌根植物拟南芥具有20多个ABCGs, 但缺失*STR*和*STR2*的直系同源(Zhang等2010), 推测与AM真菌共生的植物中进化形成了(而拟南芥丧失)诱导脂质分泌的路径。

3.3 共生体中氮的转运与代谢

土壤无机氮从AM真菌向植物细胞的转运研究结果表明, AM真菌根外菌丝从土壤中吸收的NH_4^+或NO_3^-经谷氨酰胺合成酶/谷氨酰胺-α-酮戊二酸转氨酶、天冬酰胺合成酶和尿素循环, 转化合成为Arg并以此形式储存, Arg可协同聚磷酸poly-P一起再转运至根内菌丝中, 经精氨酸酶和脲酶等催化分解生成鸟氨酸(Orn)和NH_4^+ (NH_4^+、Pi可释放到丛枝周腔并通过植物专性的转运体由根细胞吸收, Cox等1978; Govindarajulu等2005), Orn进一步分解生成谷氨酸(Glu)和腐胺(Put), 二者以某种方式进入ERM, 可提供无机氮有机转化所需的碳骨架(Jin等2005, 2012), 这种运输机制可以节约碳的消耗, 有利于AM共生体的发育和进化。此外, AM真菌根外菌丝还可以直接吸收一些有机氮或氨基酸, 以及加速茎叶等有机物质的分解以获得氮源(Leigh等2009)。

从根内球囊霉(*Glomus intraradices*)中克隆和鉴定了高亲和NH_4^+转运体GintAMT1 (López-Pedrosa等2006)、GintAMT2 (Pérez-Tienda等2011), 低亲和NH_4^+转运体GintAMT3 (Calabrese等2016), 以及一个NO_3^-转运体GiNT (NO_3^-诱导*GiNT*基因的表达) (Tian等2010)。GintAMT1在根外菌丝体中参与NH_4^+吸收, 并受低NH_4^+浓度的诱导表达, 而*GintAMT2*在根内菌丝的转录水平高于根外菌丝, 并且在氮限制条件下仍发生组成型表达(López-Pedrosa等2006), 暗示GintAMT2可能参与真菌NH_4^+代谢中“泄漏”的重吸收。当供应AM真菌根外菌丝外源NH_4^+时, AM真菌优先吸收NH_4^+ (因NO_3^-需消耗更多能量被还原为NH_4^+后再被吸收), 且GiNT的表达下调(Tian等2010)。

然而, 当可获得NH_4^+时, NO_3^-转运体的表达将被抑制(氮分解代谢物阻遏现象), GATA转录因子在氮分解代谢物阻遏中起着关键作用, 而且对GintAMT2的分析表明其存在GATA核心序列(Pérez-Tienda等2011)。在根内球囊霉中鉴定的谷氨酰胺合成酶的两种功能同工型GiGS1和GiGS2, 前者在根外菌丝中发生组成型表达, 后者受NO_3^-的诱导表达, 表明GiGS1和GiGS2分别在氮缺乏和氮充足时对氮同化具有重要作用(Tian等2010)。此外, AM真菌细胞能够通过外排或囊泡储存过多的NH_4^+以维持胞内低NH_4^+浓度, 从而保持对NH_4^+的持续同化能力及向植物根细胞的转运(Brun 2006)。摩西球囊霉(*Glomus mosseae*)中发现了一种氨基酸转运蛋白或透性酶基因*GmosAAP1* (与质子耦合转运脯氨酸) (Cappellazzo等2008), 一些其他氨基酸如丝氨酸、甘氨酸和天冬氨酸可以竞争结合GmosAAP1转运体, 还有研究报道根内球囊霉根外菌丝也可以吸收精氨酸(Jin等2005)。小分子肽是土壤中重要的氮源, 异形根孢囊霉中一种推定的二肽转运体RiPTR2在IRM中的表达远高于ERM, 暗示这一转运体在菌丝从土壤吸收小肽和从丛枝周腔重吸收小肽过程中均发挥着作用(Belmondo等2014)。

NRT2家族中受AM诱导的NO_3^-转运体已在植物如番茄(*Lycopersicon esculentum*)、蒺藜苜蓿(*Medicago truncatula*)和百脉根等中得到鉴定(Hildebrandt等2002; Hohnjec等2005; Guether等2009a), 表明NO_3^-可通过菌根共生体吸收途径转移至植物。在低NO_3^-水平或高Pi水平时, 也发现一些AM诱导上调表达的植物NRTs, 暗示了NO_3^-的吸收不仅依赖于氮状况, 也取决于氮和其他营养之间的交互作用(Hildebrandt等2002; Garcia等2016), 但由于没有NRTs的亚细胞定位和转运活性的确切鉴定, NRTs在共生转移中的作用还仍待深入研究。许多植物中一些NPF (NRT1/PTR)家族成员可以跨膜转运NO_3^-和寡肽(Léran等2014)。对百脉根的转录组分析得出, 一些*PTR*基因呈AM诱导上调表达, 且表达水平最高的1个基因定位于含丛枝根细胞(Guether等2009a)。蒺藜苜蓿中的2个PTRs和水稻(*Oryza sativa*)中的1个NPF转运体均在丛枝细胞中特异性表达, 对水稻中的*NPF*基因在爪蟾卵母细胞中进行异源表达显示NO_3^-低亲和转录活性, 暗示其可能促进NO_3^-跨丛枝周膜转运(Chen等2018)。

植物根系含丛枝的皮层细胞中鉴定得到的许多NH_4^+转运体(ammonium transporters, ATMs)也受AM真菌存在的诱导表达。例如, 蒺藜苜蓿中的AMT2;3、AMT2;4及AMT2;5 (Breuillin-Sessoms等2015), 番茄中的LeAMT4和LeAMT5 (Ruzicka等2012), 高粱(*Sorghum bicolor*)中的SbAMT3;1和SbAMT4 (Koegel等2013), 还有大豆(*Glycine max*)中的GmAMT1.4、GmAMT3.1、GmAMT4.1、GmAMT4.3及GmAMT4.4 (Kobae等2010)。

与其他植物的AMTs不同, 百脉根中发现的LjAMT2;2可以在共生体界面运载NH_3而非NH_4^+, 这表明除NH_4^+外, NH_3也可能被AM真菌释放于共生体界面并被寄主植物吸收(Guether等2009b)。百脉根菌根中的转绿组分析揭示了3个氨基酸透性酶(amino acid permease, AAP)家族成员, 并且一种编码赖氨酸−组氨酸型的转运体基因*LjLHT1.2*在丛枝细胞中被高度诱导表达, 在酵母细胞进行异源表达表明其作为一种高亲和氨基酸转运体(Guether等2009a, 2011)。

3.4 共生体中磷的转运与代谢

植物从土壤中吸收Pi可以借助高亲和Pi转运蛋白直接从根−土界面吸收(直接途径)或根皮层细胞−丛枝共生体界面吸收(菌根途径)。菌根吸收路径中, AM真菌根外菌丝借助高亲和Pi转运蛋白和H^+-ATPase水解供能, 吸收Pi并暂时转化为poly-P (以缓冲细胞质Pi浓度), 沿菌丝(协同Arg^+, Jin等

2005)转运至根内菌丝, poly-P水解释放Pi, 再通过共生体界面被吸收进入植物(Smith和Smith 2011)。

Pi跨质膜进入植物细胞需借助Pi转运体的质子−去质子化并伴随着构象变化, 质膜上的H^+-ATPase可以为包围丛枝的丛枝周膜提供能量, 研究揭示了存在于蒺藜苜蓿和水稻中的一种H^+-ATPase HA1对于共生界面中Pi的吸收至关重要(Krajinski等2014; Wang和Schultze 2014)。受AM真菌侵染诱导的植物Pi转运蛋白基因属Pht1家族, 不同植物中Pht1家族成员的数量呈现差异, 在AM真菌侵染的植物中一个或多个Pht1家族成员的表达水平发生上调或抑制, 也有少数基本上不变化。植物体内AM诱导的Pi转运体有: 蒺藜苜蓿中的MtPT4和MtPT8 (Harrison等2002; Javot等2007; Breuillin-Sessoms等2015), 水稻中的OsPT11 (Paszkowski等2002), 马铃薯(*Solanum tuberosum*)中的StPT3 (Rausch等2001), 及番茄中的 LePT3、LePT4及LePT5 (Xu等2007; Nagy等2005; Chen等2014)。受AM诱导的Pi转运体与Pi的菌根吸收方式相关, 受AM抑制的Pi转运体与直接吸收方式相关(Casieri等2013), AM真菌侵染的植物根系通常伴随其他(特别是参与直接吸收途径的) Pi转运体的下调表达, 这表明在AM共生体中Pi吸收的菌根途径抑制了直接途径, 例如, AM真菌侵染的水稻中参与Pi直接吸收途径的*OsPT2*、*OsPT6*表达下调, 而*OsPT11*突变体中*OsPT2*、*OsPT6*的表达没有发生变化(Yang等2012)。Volpe等(2016)发现Pi转运体LjPT4和MtPT4在寄主植物形成菌根前介导了根系对磷水平的早期反应, 表明它们均参与了Pi吸收的直接途径和菌根途径。对AM诱导的Pi转运体的启动子分析鉴定得到了2个保守的顺式作用原件MYCS和P1BS, 它们为AM诱导的Pi转运体启动子的转录激活所必需(Chen等2011)。miR339作为系统性Pi缺乏信号, 在AM中, 提高的mi339转录能够保持PHO2的低水平表达和活性以增加Pi吸收及维持AM真菌-植物共生(Branscheid等2010)。先前对番茄miRNAs的表达鉴定发现, miR395的表达仅受AM诱导, 与Pi水平无关, 而miR172的表达受高Pi水平或AM的诱导, 表明它们可能在Pi吸收直接途径和菌根途径之间的联结中发挥作用(Gu等2010)。此外, 蒺藜苜蓿中的Mt4 (一种非编码RNA)和一种Pi缺乏诱导的酸性磷酸酶基因在AM真菌定殖时迅速下调表达(Smith等2011), 因此, 通过鉴定不同表达模式的有关调控元件, 有助于阐明直接途径和菌根途径之间的交互作用。此外, 蔗糖介导的糖信号和Pi缺乏反应相关联, 如菜豆(*Phaseolus vulgaris*)开始出现Pi缺乏时, 光合碳同化物蔗糖的积累引发miR399的表达, 糖和miRNAs作为潜在的信号分子调控根系Pi吸收(Liu等2010)。

AM真菌Pi转运体GvPT (*G. versiforme*)和GiPT (*G. intraradices*)通常定位在根外菌丝上(Harrison和van Buuren 1995; Maldonado-Mendoza等2001), 而GmosPT (*G. mosseae*)和GigmPT (*Gigaspora margarita*)通常定殖在根外菌丝和丛枝细胞表达(Benedetto等2005; Balestrini等2007; Xie等2016), 它们协助磷从土壤中转运至根外菌丝或丛枝周腔。基因敲除*GigmPT*导致AM真菌定殖水平降低, 而且GigmPT也可能同时起着Pi转运和感受的作用(Xie等2016)。Fiorilli等(2013)研究表明, AM真菌的高亲和Pi转运蛋白基因*GintPT*在其整个生活史的主要阶段持续表达, 与寄主蒺藜苜蓿的共生保证了*GintPT*在根外菌丝体中的高水平表达, 且*GintPT*和植物共生专性Pi转运蛋白基因*MtPT4*的表达对磷状况变化的反应很敏感。

3.5 共生体中其他离子的转运

百脉根丛枝细胞中的一种推定的植物K^+转运体表达增加了44倍(Guether等2009a), 同样, AM真菌侵染诱导蒺藜苜蓿质膜上AtCHX20 (K^+/H^+转运体)直系同源基因上调表达, 使寄主植物在钾素限制时增强了钾吸收, 但与氮和磷不同, 钾的有效性对AM真菌的侵染没有影响(Garcia等2017)。推定的蒺藜苜蓿中的MtSultr1;2 (Casieri等2012; Sieh等2013; Wipf等2014)和百脉根中的LjSultr1;2 (Giovannetti等2014) S转运体分别在S缺乏和S足量时受AM的诱导表达。转录分析蒺藜苜蓿AM诱导的转运体发现一种Zn^{2+}-Fe^{2+}透性酶和一种Ca^{2+}通道(源自TRP-CC家族)上调表达(Benedito和Udvardi 2010), 并且从根内球囊霉分离的一种推定的Zn转运体(GintZnT1), 可能发挥向寄主转运Zn的作用(González-Guerrero等2005)。此外, AM共生除了增加寄主对金属离子的吸收(在金属元素缺乏时), 也具有抗毒性保护机制, 例如, AM真菌的侵染定殖

使番茄中一种广谱金属离子转运体LeNramp1表达下调, 暗示了AM真菌保护寄主植物在重金属胁迫下避免受金属毒害的潜在防御作用(Ouziad等2005)。

4 共生体中的养分转运、交换与代谢调控及其利用

4.1 共生体中养分转运、交换与代谢的调控

寄主植物和AM真菌之间的养分交换是受膜转运体和H^+-ATPase介导的严格调控的过程, AM共生体之间的养分交换遵循“自由市场”模式, 植物和真菌双方控制各自的供给, 根据互惠补偿策略来维持碳和氮/磷之间的“公平交易” (Bücking和Shachar-Hill 2005; Fellbaum等2012)。在两种真菌的共侵染试验中, 与合作性弱的真菌(*G. aggregatum*)相比, 寄主植物向合作性强的真菌(*G. intraradices*)分配更多的碳源(Kiers等2011), 寄主植物能以AM真菌提供的养分量区别选择真菌合作者, 并分配以较高量的光合产物。寄主植物分配给AM真菌的碳主要依赖于菌根中的氮水平, 共生体中碳和氮的化学计量关系控制着它们之间的养分交换(Olsson等2005)。

有研究指出, 寄主植物的碳源供给充当一个关键的诱因刺激真菌的氮和磷输送, 并且高碳水平下AM真菌可以识别和优先分配给“高相容”寄主氮/磷, 共生体界面可利用性碳源激发AM真菌吸收氮并向植物输送, 且增加的氮输送受AM真菌基因表达的严格调控, 如果直接供给AM真菌的根外菌丝体以外源碳源(真菌不单独依赖于寄主提供的碳源), 那么氮的吸收和输送便受到抑制(Fellbaum等2012, 2014)。与此类似, AM真菌向寄主植物的磷输送也高度依赖于植物的碳源供给(Hammer等2011), 而且碳源的量和种类调节着磷从真菌向寄主植物的运输和代谢(Bücking和Shachar-Hill 2005), AM真菌还可以向寄主植物选择性地输送磷(Kiers等2011)。马铃薯体内组成型过表达蔗糖转运体(SoSUT1)时, 仅在土壤高磷水平下增加AM真菌侵染(Gabriel-Neumann等2011)。球囊霉单糖转运体RiMST2 (具有广泛的底物)与植物共生专性Pi转运体MtPT4的表达紧密相关, 基因沉默抑制*RiMST2*表达, 导致菌根受损、丛枝畸形及*MtPT4*的表达下调, 也暗示了碳与磷交换的紧密相关(Helber等2011)。

转录组分析表明, 高Pi水平抑制类胡萝卜素和SLs合成酶基因表达, SLs合成的减少使孢子萌发直接受到抑制, 但高Pi水平没有影响根系对AM真菌的Ca^{2+}峰反应(Coline等2013), 表明Pi并未影响通过共生信号途径的共生前信号转导, 但也有研究指出, 高Pi水平显著抑制了共生前信号转导过程, 如产生Ca^{2+}峰细胞的比例和峰均值(Giulia等2013)。据报道, Pi使矮牵牛(*Petunia hybrid*)共生专性Pi转运体基因*PhPT5*的表达下调而可能降低了AM真菌定殖, 因*PhPT5*的表达下调先于AM真菌定殖的降低。有趣的是, 高Pi水平也阻碍STR/STR2 (介导向AM真菌的脂质转运)表达(Breuillin等2010)。综上可知, Pi添加减少了源自AM真菌的Pi流量, 反过来导致寄主植物输送给AM真菌的碳源量也变少。

Pi缺乏或氮缺乏诱导合成SLs的基因表达上调而促进孢子萌发和菌丝分枝及AM真菌定殖(Bonneau等2013)。*Mtpt4*或*Ospt11*突变体根系形成大量早熟性退化丛枝(Javot等2007; Yang等2012), 在氮限制情况下, *Mtpt4*突变体和*Mtpt4*/*Mtpt8*双突变体丛枝的早熟性消解均受阻是依赖共生体界面中ATM2;3介导的氮输送, 暗示了通过共生体界面运输至根皮层细胞的Pi可能直接或间接引发一种信号, 进而调控寄主植物的碳源流向真菌或抑制寄主植物防御反应, 而运送到皮层细胞的氮可以绕过Pi转运介导的信号, 也充当一种信号以维持丛枝发育(Breuillin-Sessoms等2015)。这些结果表明, 丛枝寿命取决于本身至少氮和磷元素的输送, 寄主植物可能会通过这一信号感知丛枝传输养分效率并整合自身的营养状况作出应答反应。在某些养分特别是氮缺乏时, 可激发明显的AM促生信号以拮抗高Pi水平的抑制作用(Nouri等2015)。因此, 氮缺乏和Pi缺乏反应路径之间交互作用机制的阐明, 有助于揭示植物在AM中或养分限制时如何调控内源细胞进程。

4.2 共生体中养分的利用

AM真菌提供寄主植物明显数量的氮和磷(特别是养分可利用性低的土壤), 对寄主植物氮和磷吸收的贡献超过80% (van der Heijden等2015), 氮吸收贡献较磷虽略低, 但菌丝体可以固定相当量的氮(Hodge和Fitter 2010), 大多植物依赖菌根共生

体得以生存和生长。菌根共生对植物养分利用效率(特别在养分受限的环境中)起着重要作用, 寄主植物与AM真菌之间的养分交换增强养分可利用性而促进了寄主植物生长, 合理利用共生菌的有利特性可以显著减少肥料的施用; 但AM真菌也通过植物激素的调控显著影响寄主植物的生长、开花、根型及抗逆(Ruizlozano等2012; Selosse等2014)。AM真菌除了提高植物生长, 由于AM共生增加植物体内养分含量进而也改善了植物品质(赵青华等2014)。值得注意, AM真菌还能明显减少养分损失(由于养分的高效吸收而降低了因淋洗或反硝化导致的养分损失)。例如, AM真菌分别减少24%氮和31%磷的土壤淋洗损失(Bender等2015); 由于影响土壤细菌群落反硝化过程而间接减少了N_2O的释放(Bender等2014); 并且, AM真菌也使有机养分的淋洗损失减少(Bender等2015), 这与先前关于AM真菌可以获取有机养分的研究结论相符。AM真菌在生态系统中影响各种生态过程(van der Heijden等2015; Powell和Rillig 2018), 例如调控矿质养分和碳循环、土壤团聚体形成、凋落物分解、幼苗存活、及与其他生物的相互作用。

5 研究动向与展望

AM共生体的构建需要AM真菌−寄主植物根系之间的信号识别, AM真菌释放Myc因子被寄主植物受体识别后激活通用共生信号途径, 寄主植物根系分泌的SLs可诱发AM真菌孢子萌发、菌丝生长及分枝并向根系趋向性生长。一旦菌丝接触根系表面, 即可形成附着胞, 随后, 植物根表皮细胞发生一系列变化(包括核移动和微管、内质网的变化)而形成侵入前器官以引导菌丝侵入根皮层细胞。在AM共生双方发生物理接触之前, RAM2参与了早期的信号事件(Wang等2012), 并且RAM2诱导表达通过Myc因子信号识别路径且依赖GRAS转录因子RAM1 (Gobbato等2012), 在已建立的丛枝细胞中RAM2启动子被高度诱导, 暗示了其在丛枝细胞中也发挥着某种功能(Gobbato等2013)。AM共生互作还赖以双方在根细胞内分化产生新的共生界面及持续的养分交换(Chen等2018), 伴随多个基因(参与营养的转移、同化和分配)的转录调控和不同营养之间互作反馈机制的调节。此外, DELLA是GA信号路径的主要调控者, 也是光和其他激素的“共同通讯中心点”, 在AM真菌-植物共生中发挥着关键作用, 这使寄主植物能够整合发育和营养信号以调控双方互惠关系(Gutjahr 2014; Yu等2014; Jin等2016)。最近发现丛枝消解的重要转录调控因子MYB1, 且消化水解酶的启动表达需要MYB1与转录因子NSP1、DELLA的互作(Gutjahr和Parniske 2017), 激素、转录调控因子及它们之间复杂的“交叉对话”仍待深入研究。此外还应重视土壤−真菌界面和真菌−植物界面转录组和代谢组网络的整合分析以进一步揭示AM真菌介导的营养信号调控网络。

AM真菌通过增加根系吸收面积、土壤空间利用率和促进难利用的矿质元素的流动性, 来提高寄主植物对营养元素(如氮、磷)的吸收率; 反之, 寄主植物提供真菌生长所需的碳源, 其中脂质也是一种主要的碳源形式。在寄主植物和AM真菌之间运输不同物质基质的其他转运体还待进行鉴定, 特别是糖和脂质的共生转运体。AM真菌促进土壤中氮磷等养分流动循环而且也是重要的碳汇, 不仅AM共生体中的氮/磷转运蛋白和相关同化酶的表达水平状况引起氮、磷吸收及供给能力的变化, 而且AM真菌-植物的关系也受非生物因子, 如水分、土壤养分及pH等的制约(Hoeksema等2010), AM真菌−寄主植物之间共生关系与寄生关系的转变很大程度上取决于自然或人工生态系统中土壤养分的供应状况(Corrêa等2015), 鉴于田间土壤养分水平的变异性, 未来研究中还应当考虑到不同的土壤养分梯度或变异的影响, 及碳与矿质养分互换的动态分析。

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Recent advances in the studies of nutrient transportation, metabolism, utilization and regulation in arbuscular mycorrhizas

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Abstract: Arbuscular mycorrhizas (AM) are mutualistic associations between Glomeromycota fungi and host plant roots. The processes involving transportation, metabolism, utilization and regulation of both inorganic and organic nutrients are the foundation of the symbionts, which are the critical physiological mechanisms of the mutual relationship between the AM fungi and host plants. The characteristics of the transportation and metabolism of nitrogen or carbon have been well documented in the literature. However, the latest progress on comprehensive and systematic review in relation to the studies of nutrient transfer, metabolism, utilization and regulation in AM associations remain unavailable. This review aims to introduce the nutrient-exchange forms and spatiotemporal characteristics between AM fungi and host plants, and summarize the characteristics of nutrient transport, metabolism and utilization and their regulatory mechanism in AM associations. The advances and prospects of the studies in this research topic are discussed. This study may enhance our understanding of the physiological mechanisms of the mutualisms between AM fungi and host plants, and promote future study in this research area.

Key words: arbuscular mycorrhiza (AM) fungi; symbiosis; signal molecules; nutrient metabolism and regulation

Receive 2018-08-01 Accepted 2018-10-24

This work was supported by the National Natural Science Foundation of China (31471946) and the Chinese Academy of Sciences "Hundred Talent Program" (A315021449).

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