International Journal of Ecology 世界生态学, 2024, 13(2), 255-261
Published Online May 2024 in Hans. https://www.hanspub.org/journal/ije
https://doi.org/10.12677/ije.2024.132034

Hans汉斯

植物–丛枝菌根真菌共生的研究进展

黄静娴

浙江师范大学生命科学学院，浙江 金华

收稿日期：2024年4月8日；录用日期：2024年5月6日；发布日期：2024年5月24日

摘　要

植物与丛枝菌根真菌(Arbuscular Mycorrhizal Fungi, AMF)共生是自然界中最常见的共生现象之一。菌根共生促进植物磷营养吸收，同时植物以脂肪酸和糖的形式给菌根真菌提供其发育所需的碳源。菌根真菌在根的皮层细胞中形成高度分支的树形结构，称为丛枝。丛枝是共生体间双向营养交换的中介，被认为是共生体的核心功能单位。提高菌根共生介导的营养吸收对植物本身的生长具有重大意义。本文概述了植物和丛枝菌根真菌建立共生的过程，并总结了在共生关系中起关键作用的重要蛋白，为丛枝菌根共生的研究提供理论基础。

关键词

丛枝菌根真菌，菌根共生，丛枝

Research Progress on Plant-Arbuscular Mycorrhizal Fungi Symbiosis

Jingxian Huang

College of Life Sciences, Zhejiang Normal University, Jinhua Zhejiang

Received: Apr. 8th, 2024; accepted: May 6th, 2024; published: May 24th, 2024

Abstract

Symbiosis between plants and arbuscular mycorrhizal fungi (AMF) is one of the most common symbiosis phenomena in nature. Mycorrhizal symbiosis promotes phosphorus nutrient absorption by plants, and at the same time, plants provide mycorrhizal fungi with carbon sources needed for their development in the form of fatty acids and sugars. Mycorrhizal fungi form highly branched tree-like structures called arbuscules in the cortical cells of the roots. Arbuscules are the mediators of two-way nutrient exchange between symbionts and are considered to be the core functional unit of symbionts. Improving mycorrhizal symbiosis-mediated nutrient uptake is of great signi-

文章引用: 黄静娴. 植物-丛枝菌根真菌共生的研究进展[J]. 世界生态学, 2024, 13(2): 255-261.
DOI: 10.12677/ije.2024.132034

ficance to the growth of the plant itself. This article outlines the process of establishing symbiosis between plants and arbuscular mycorrhizal fungi, and summarizes the important proteins that play a key role in the symbiotic relationship, providing a theoretical basis for the study of arbuscular mycorrhizal symbiosis.

Keywords

Arbuscular Mycorrhizal Fungi, Mycorrhizal Symbiosis, Arbuscules

1. 菌根共生概述

丛枝菌根真菌(Arbuscular Mycorrhizal Fungi, AMF)可以和三分之二以上的植物建立共生关系，包括谷类和豆类等重要作物。在共生期间，菌根真菌为植物提供大量生长所需的营养元素，作为交换，植物给予菌根真菌营养代谢所需的碳源，例如脂肪酸和糖[1]。从中古时代开始，这种互利互惠的共生关系就促进了陆地植物从无根配子体向有根孢子体的进化[2]。转录组数据分析显示菌根真菌体内存在硝酸盐与磷酸盐相关还原酶和转运体的编码基因[3] [4]，解释了菌根真菌为何能为宿主植物提供矿质营养这一关键问题[5]。

磷元素对作物的生长发育和产量都至关重要。土壤中的磷以有机磷酸盐(Po)和无机磷酸盐(Pi)的形式存在，其中大部分不能直接被植物吸收利用。菌根共生期间，以植物磷酸盐饥饿反应为中心的网络可以直接调节植物对磷酸盐的获取，暗示寄主植物对磷酸盐的需求可能是开启植物和菌根真菌共生的初始动机[6]。磷饥饿条件下，增加植物对磷酸盐的吸收是菌根共生的主要优势[7]。研究显示菌根真菌在根外菌丝中分泌的磷酸盐转运蛋白可能参与植物从土壤基质中吸收磷酸盐的过程[8]。受菌根共生诱导表达的植物磷酸盐转运基因在多个宿主植物中被发现，并且越来越多的证据表明，共生期间菌根真菌表达的很大一部分蛋白质在磷酸盐运输中起作用[9]。苜蓿中的磷酸盐转运蛋白 MtPT4 是菌根共生所必需的，MtPT4 (Phosphate Transporter 4)功能缺失导致菌根真菌无法在根内定植，阻断了磷从丛枝到皮质细胞的运输[10]。百脉根 LjPT3 (Phosphate Transporter 3)在根皮层含丛枝细胞中表达，利用 RNAi 干扰敲低 LjPT3 表达的转基因株系对磷元素摄取量减少[11]。

据统计，植物体内 90%以上完成其生命活动必需的磷来自菌根真菌的贡献[12]，同时菌根真菌消耗了高达 20%的陆生植物每年光合作用产生的碳，约 50 亿吨[13]。因此，菌根共生不仅对植物本身的生长发育具有重大意义，影响陆地植被初级生产力的同时也对陆地生态系统的磷循环和碳循环有重要贡献[14]。

2. 菌根共生关系的建立过程

2.1. 早期的信号交流

植物与菌根真菌物理接触之前相互释放的分子信号开启了一段共生关系的建立。在共生早期，植物根际释放以独角金内酯为主的化学信号，等待真菌感知、识别并释放分子信号回应[15] [16]。独角金内酯是一种由植物根系产生的激素，其生物合成受到严格调节[17]。独角金内酯不敏感型突变体中检测到编码

独角金内酯生物合成的基因 *CCD*7 和 *CCD*8 大量表达，表明独角金内酯的生物合成存在反馈调节[18] [19]。独角金内酯以及合成类似物 GR24 在极低浓度下也能诱导丛枝菌根真菌的孢子萌发以及菌丝伸长[20]。除了作为植物与菌根真菌交流必不可少的化学信号，它和自身代谢的产物还可以抑制植物分枝[21] [22]。在低磷条件下，植物根际也会分泌出独角金内酯等不稳定的化学分子以完成磷酸盐饥饿响应相关的生命活动[23]。

已有报道表明在宿主植物和菌根真菌早期非物理接触的交流过程中，独角金内酯可能不是唯一重要的信号分子。例如玉米和水稻中的转运蛋白 NOPE1 (No Perception 1)是菌根共生早期信号识别所必需的。接种菌根真菌后，NOPE1 突变体根内几乎观察不到定植产生的结构，并且 NOPE1 突变体的根际分泌物不能使菌根真菌开启自身的转录翻译[24]。NOPE1 被推测可能转运一种植物来源的乙酰氨基葡萄糖分子，该分子主要在菌根真菌体内传导信号以促进共生关系的建立[25]。

感知并识别植物分泌的化学信号后，菌根真菌诱导孢子萌发同时分泌关键的化学分子，从而找到附近寻求共生的宿主植物[25] [26]。用独角金内酯类似物 GR24 处理后，菌根真菌的 NADH 脱氢酶活性与 ATP 含量迅速增加、参与线粒体代谢和菌丝生长的基因表达上调，不需要相关基因表达就能在几分钟内激活其自身的氧化代谢[27]。菌根真菌分泌的脂壳寡糖(Lipochito Oligosaccharides, LCOs)已被证实是与宿主植物共生早期信号交流的关键因子[26] [28]。除了分泌 LCOs 外，菌根真菌还分泌壳寡糖(Chitosan Oligosaccharide, COs) [29]。COs 和 LCOs 统称为 Myc 因子(Myc Factor)，Myc 因子可触发植物体内与菌根共生相关的生命活动，例如早期共生相关基因的转录激活[30]、根部表皮细胞核发生钙振荡[31]、侧根形成[32] [33]等，同时激活下游共生信号通路(Common Symbiosis Signaling Pathway, CSSP) [29] [34]。

2.2. 菌根真菌的菌丝延伸和分支

识别到植物根际分泌的独角金内酯，菌根真菌的氧化代谢被激活，促进菌丝延伸和分支以增大与宿主植物根部表皮接触的机会[27] [35]，推动共生关系的建立。菌丝主要在细胞内生长，偶尔也在细胞间生长[36]。接触到宿主植物的根部表皮后，菌根真菌的菌丝分化出一种叫做菌丝足的附着结构，为进入植物根内细胞做准备[37]。为了适应真菌结构并推进共生，植物根部细胞会主动为真菌菌丝准备好胞内环境。菌丝足形成 4~5 小时后，宿主植物根部细胞会形成一个预穿透装置(Prepenetration Apparatus, PPA) [38]。PPA 是一种亚细胞结构[39]，它预先决定了菌根真菌在植物根部细胞中的生长路径，引导真菌菌丝如何从一个细胞穿透到另一个细胞[40]。只有在这个“跨细胞通道”完整形成后，菌根真菌的菌丝才能持续生长、延伸，直至穿透表皮细胞，向植物根皮层生长。越来越多的证据表明，常见的共生相关基因作用于 PPA 形成的上游，因为在 symrk/ccamk 突变体中无法形成 PPA [41] (图 1)。

2.3. 丛枝发育

菌根真菌的菌丝在植物根皮层细胞中延伸并分支，产生的灌木状结构称为丛枝。丛枝被认为是菌根真菌和宿主植物之间进行营养交换的主要场所[39]。丛枝的形态不是特定的，形成的具体形态随着真菌种类和宿主植物的基因型变化[9]。围丛枝膜(Periarbuscular Membrane, PAM)是菌根真菌和植物进行营养物质和信号交换的界面[36]。特异性定位在围丛枝膜上的磷酸盐转运蛋白 PT4 (Phosphate Transporter 4)是介导植物和菌根真菌在围丛枝膜进行营养物质交换的转运蛋白之一[42]。

丛枝发育达到它所能生长的最大形态后便被诱导降解。丛枝的降解始于分支菌丝的塌陷，随后整个丛枝与细胞质分离，四周塌陷直至消失[43]。PT11 (Phosphate Transporter 11)和 GFP 的融合蛋白在发育成熟的丛枝内表达，数小时后，水稻根皮层细胞中便检测不到融合蛋白的表达，表明丛枝降解是一个快速的过程[44]。

3. 丛枝发育阶段的基因表达

在没有丛枝形成和仅有丛枝主干形成的细胞中，*BCP*1 受诱导表达[45]。*SbtM*1 的表达模式与 *BCP*1 相似[46]，*SbtM*1 位于外质体和丛周间隙中[47]。丛枝的分支形成之前，*BCP*1 和 *SbtM*1 的基因表达受抑制[48] (图 1(a))。丛枝的发育过程可细分为五个阶段。第一阶段是 PPA 形成，需要常见的共生基因 *CCaMK* 和 *CYCLOPS* [49]。第二阶段菌根真菌细胞进入植物根皮层，第三阶段称为“Birdsfoot”[50]，由于真菌菌丝分支在这个阶段的形状类似于鸟脚的脚趾。第二和第三阶段需要 *VAPYRIN*/*PAM*1。*VAPYRIN*/*PAM*1 突变体的共生表型显示植物根皮层细胞内完全没有菌丝进入[51]。第四阶段丛枝发育成熟，从鸟足期开始由菌丝不断分支发展而来。*PT*4 [10]和 *OsPT*13 [52]是菌丝分支所必需的，它们延缓丛枝向第五阶段的降解发展(图 1(b~c))。

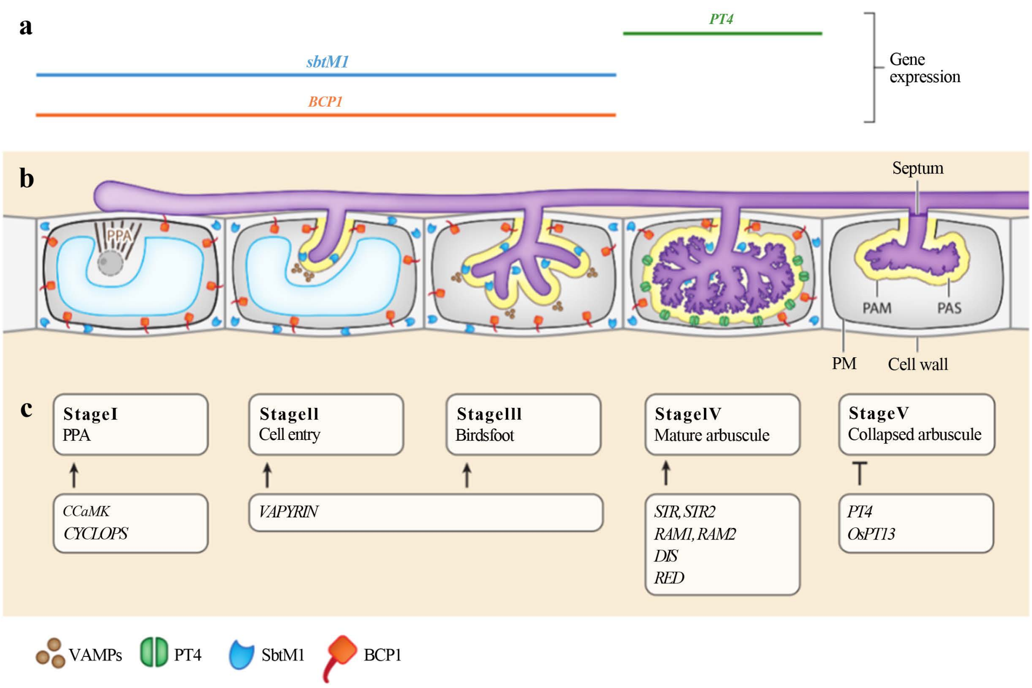

Figure 1. Genes expression at different stages of arbuscular development [49]
图 1. 丛枝发育各阶段的基因表达情况[49]

4. 结语

菌根共生是自然界众多共生关系中的一种，大多数陆生植物可与丛枝菌根真菌形成互惠共生关系。植物从真菌获取矿质养分，特别是磷和硝酸盐，同时向真菌提供有机碳。共生体之间营养物质的运输是通过植物根细胞内称为丛枝的共生结构进行的。共生关系建立的过程伴随着共生体之间信号分子的交换。菌根共生相关分子信号通路的研究提供了对共生相互作用机制的多方面理解，揭示了未来研究的潜在途径。

首先，植物和真菌之间的分子对话代表了一个丰富的探索前沿，揭示越来越多的菌根共生体的基因组蓝图和控制共生相互作用的复杂信号网络，这有望增强我们对互惠共生的理解，以阐明共生发育和营养交换动态的遗传基础。

其次，共生体对生态的影响远远超出了个体对生态系统的影响。将生态学理论与实证研究相结合，可以深入了解菌根真菌介导的养分循环、碳循环和群落动态的机制。未来的研究应侧重于将局部相互作

用扩大到生态系统水平的过程，结合全球调查、景观尺度分析和建模方法来预测环境变化对菌根功能和生态系统服务的影响。

最后，菌根共生的实际应用在可持续农业、生态系统恢复和减缓气候变化方面具有巨大的潜力。利用菌根真菌的有益特性，如养分获取效率和抗逆性，可以为提高作物生产力、土壤肥力和生态系统恢复力的策略提供信息。未来的研究可以开辟菌根生态学的新领域，为在快速变化的世界中建立可持续发展的生态系统铺平道路。

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