外生菌根共生: 共生真菌多样性及菌根形成的分子机制

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摘要 大约2%的维管植物能够与17~18个目约280个属的真菌形成外生菌根关系. 外生菌根关系的形成、宿主植物的专一化和宿主转移等事件可能是共生真菌物种分化的重要驱动力. 比较基因组学研究发现, 外生菌根真菌丢失了大量与植物细胞壁物质降解相关的基因. 在外生菌根形成过程中, 真菌与宿主植物之间借助多样化的信号分子完成相互识别, 并且外生菌根真菌能够借助分泌效应蛋白抑制宿主植物的防御反应, 促进菌根形成. 本文对外生菌根真菌的多样性和分布规律, 以及外生菌根形成的分子机制等方面进行了综述, 并据此对后续研究提出展望.

关键词 外生菌根, 专一性, 物种分化, 信号分子, 比较基因组

真菌与植物均是自然生态系统的重要组成部分. 超过90%的维管植物与真菌形成菌根共生(mycorrhizal symbiosis)关系^[1]. 在这一共生关系中, 真菌为植物提供水分和氮、磷等矿质元素, 植物则为真菌提供碳水化合物^[2]. 化石证据显示, 早在四亿年前, 真菌与植物的共生关系即已存在^[3]. 这一共生关系的获得可能在植物从水生到陆生的过程中发挥了重要作用^[4,5]. 不同的植物和真菌类群能够形成类型多样的菌根共生关系^[2]. 根据宏观形态和解剖特征, 菌根分为丛枝菌根(arbuscular mycorrhiza)、外生菌根(ectomycorrhiza)、内外生菌根(ectendomycorrhiza)、兰科菌根(orchid mycorrhiza)、浆果鹃类菌根(arbutoid mycorrhiza)、水

晶兰类菌根(monotropoid mycorrhiza)和欧石楠类菌根(ericoid mycorrhiza)七种类型^[2]. 其中, 丛枝菌根、外生菌根、兰科菌根和欧石楠类菌根是较为常见的四种类型^[6]. 鉴于内外生菌根、浆果鹃类菌根和水晶兰类菌根常具有外生菌根的部分典型特征, 兼且形成这三种菌根类型的真菌多为外生菌根真菌类群, 这三种类型也被视作外生菌根的特殊形态^[7]. 近年来, 分子生物学的快速发展, 尤其是基因组和转录组测序技术在菌根共生关系研究中的应用, 为认识共生真菌的多样性、分布规律及菌根形成的分子机制等提供了全新的视角. 本文主要针对外生菌根这一重要的菌根类型的研究进展进行评述.

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1 主要外生菌根真菌类群及其地理分布特征

大约2%的维管植物能够与真菌形成外生菌根关系^[1]。尽管这一比例极低,但能够形成外生菌根的植物[诸如松科(Pinaceae)、壳斗科(Fagaceae)和龙脑香科(Dipterocarpaceae)等]大多是不同森林生态系统中的建群树种,因而这一共生关系对森林生态系统具有广泛的影响^[2,6]。据统计,目前已知担子菌门(Basidiomycota)和子囊菌门(Ascomycota)内共计17~18个目82~86个单系分支(lineages; 约含280属)^[7-9]超过20000种^[6]真菌能够与250~300属6000~7000种绿色植物^[10]形成外生菌根(图1)。以上特征表明这一共生关系可能经历多次起源^[10,20],代表了一种趋同演化(convergent evolution)形式^[6]。

在地理分布上,根据外生菌根真菌组成的相似性,全球可以分为北温带、南方地区(Austral regions, 含澳大利亚、新西兰和南美洲南部)和热带地区三个主要的外生菌根真菌分布区^[8]。其中, /austropaxillus这一支系的真菌仅在南方地区分布, /descolea这一支系也主要分布于南方地区,但可能在历史时期经由东南亚传播至亚洲温带地区,故此在亚洲温带地区也有分布^[8]。热带地区也分布有一些少量地区特有的外生菌根真菌,诸如/atheliales1, /hydropus和/xenasmatella等支系^[9]。北温带地区的外生菌根支系真菌最为丰富,包含了大量南方和热带地区没有分布的真菌类群(详见文献^[8]中Figure 2)。全球范围的土壤真菌组成分析显示,外生菌根真菌分布的热点区域为北温带,这可能与松科这一最古老的外生菌根树种主要分布于北温带紧密联系^[21]。

2 共生关系对外生菌根真菌物种形成和演化的影响

在所有菌根类型中,外生菌根涉及的真菌类群最为丰富(图1)。已有研究表明,共生关系的形成可能为一些外生菌根真菌的快速分化提供了驱动力^[22]。针对蜡蘑属(*Laccaria*)真菌的研究显示,该属真菌的基部类群由单个物种(多态蜡蘑, *L. ambigua*)组成。同位素分析显示该种可能为腐生类型。除基部类群外,该属的所有物种均可形成外生菌根。在该属物种转为外生菌根的营养类型后,其物种多样化速率(diversification rate)

有了显著提升,表明共生关系的形成可能推动了该属的早期分化^[22]。然而,多态蜡蘑的营养类型仅是依据同位素分析进行推论的结果,这一结论需要得到菌根解剖或基因组数据来进行验证。另一方面,诸如牛肝菌科(Boletaceae)和鹅膏科(Amanitaceae)等类群均包含了大量的外生菌根真菌和较少的腐生(或寄生)物种^[23,24],对这些类群的真菌开展演化研究无疑能够为认识这一问题提供新的佐证。

除菌根关系的形成外,宿主转移(host switch)可能是外生菌根真菌多样化的驱动力之一。针对松塔牛肝菌属(*Strobilomyces*)的研究显示,该属起源于非洲,非洲地区该属物种的主要共生树种隶属于豆科(Fabaceae)和龙脑香科^[25,26]。该属由非洲传播至东南亚,随后传播至东亚及大洋洲,经历了宿主植物由龙脑香科到东亚及北温带其他地区的松科/壳斗科和大洋洲的假山毛榉科/桃金娘科(Nothofagaceae/Myrtaceae)的转变。分析显示,自龙脑香科到松科/壳斗科的宿主转移显著加速了松塔牛肝菌属的多样化速率^[25,26]。这可能与松科/壳斗科广泛分布于北温带,能够为共生真菌提供多样化的生境有关。针对红菇科(Russulaceae)的研究同样显示宿主转移驱动了该科真菌的多样化^[27]。相较于其他支系(lineage),与松科植物共生的支系具有更高的物种分化速率,推测可能在地质历史时期山体隆升过程中松科植物形成了海拔梯度分布模式,为真菌占据不同生态位并完成物种分化提供了可能^[27]。

对一些同域分布的外生菌根真菌物种,宿主植物的专一化可能是其物种形成和维持的驱动力之一。以色钉菇属(*Chroogomphus*)为例,色钉菇(*C. rutilus*)和灰紫色钉菇(*C. purpurascens*)是两个同域分布的物种,且均与松属(*Pinus*)树种共生,但是前者主要与双维管束松亚属(*Pinus* subgen. *Pinus*)植物共生,而后者则主要与单维管束松亚属(*Pinus* subgen. *Strobus*)植物共生^[28]。有趣的是,在生长于松属植物球果上的腐生真菌类群中,一些同域分布的物种体现出明显的基质(substrate)专一性。例如,在球果伞属(*Strobilurus*)中,拟厚囊球果伞(*S. luchuensis*)和厚囊球果伞(*S. pachycystidiatus*)在我国西南地区为同域分布,但前者以双维管束松亚属球果为基质,而后者以单维管束松亚属球果为基质^[29]。共生真菌与腐生真菌相似的宿主/基质专一性特征背后的机制值得进一步研究。

图1 能够形成菌根共生关系的种子植物和真菌类群汇总。真菌的系统发育树参考^[11-13], 种子植物的系统发育树参考^[14,15]。种子植物与真菌形成的菌根共生关系主要参考^[2,9,10,16-19]

Figure 1 A summary of fungi and seed plants involved in mycorrhizal symbioses. Phylogenetic trees of fungi and seed plants follow references [11-13] and [14,15], respectively. Mycorrhizal symbioses between seed plants and fungi are summarized based on references [2,9,10,16-19]

3 外生菌根形成的分子机制

3.1 不同营养类型真菌的植物细胞壁降解酶相关基因演化规律

已有研究表明, 外生菌根真菌是由不同类型[包含白腐(white rot)、褐腐(brown rot)和土生(soil saprotrophs)]的腐生真菌多次独立演化而来^[6,30]。对于腐生真菌, 其营养物质(尤其是碳源)的获取主要来源于降解木材或土壤表面凋落物。因此, 腐生真菌对木质纤维素(lignocellulose)这一植物细胞壁的主要组成部分的降解能力对其碳源的获取至关重要。植物细胞壁降解酶(plant cell wall degrading enzyme, PCWDE)是参与真菌木质纤维素降解的一类重要碳水化合物活性酶

(carbohydrate active enzyme, CAZyme)^[30]。子囊菌门和担子菌门的基部类群包含大量能够降解纤维素(cellulose)但不能降解木质素(lignin)的土生和木腐真菌。比较基因组研究表明, 这些类群的真菌基因组内包含能够降解晶状纤维素(crystalline cellulose)的碳水化合物活性酶, 包括纤维二糖水解酶(cellobiohydrolase, GH)和相当数量的溶多糖单加氧酶(lytic polysaccharide monooxygenases, LPMO)^[30-32]。在演化过程中, 大约在2.9亿年前, 自蘑菇纲(Agaricomycetes)木耳目(Auriculariales)开始, 真菌获得一类与木质素降解相关的氧化还原酶(oxidoreductase), 最具代表性的是II类过氧化物酶(class II peroxidase, POD), 与之相伴随的是与纤维素降解相关的基因家族(包括但不限于溶多

糖单加氧酶)的扩张. 这一变化是白腐真菌既能降解木质素又能降解纤维素的基础^[31,32]. 与白腐真菌不同, 褐腐真菌仅改变木质素的结构而不对其降解, 这一过程主要通过Fenton反应(Fenton reaction)完成, 这一反应可能依赖于纤维素脱氢酶(cellulose dehydrogenase)或其他氧化还原酶(如glucose-methanol-choline家族, GMC)^[6,33]. 与白腐真菌相比, 褐腐真菌完全丢失或仅保留极少数的II类过氧化物酶、GH6和GH7以及碳水化合物结合组件1(family 1 carbohydrate binding module, CBM1)等相关基因^[6,30,33,34]. 与之相似, 在外生菌根和丛枝菌根真菌的基因组内, 植物细胞壁降解酶相关基因较之白腐真菌显著降低^[30,35-38]. 植物细胞壁降解相关基因的丢失可能导致外生菌根真菌极度依赖宿主植物为其提供碳水化合物, 并且可能丧失重新向腐生真菌过渡的可能性^[6].

3.2 外生菌根真菌与宿主植物的信号识别

在真菌与植物形成外生菌根的过程中, 共生真菌与宿主植物的信号识别极为重要. 研究发现, 宿主植物可能通过分泌类黄酮(flavonoid)来实现信号传导^[39,40], 外生菌根真菌则通过合成并分泌生长素(auxin)^[41,42]实现信号传递, 该生长素进入植物根系细胞后, 诱发植物生长素信号通路, 抑制植物根系生长并诱导侧根形成^[41,43]. 同时, 也有研究显示, 独立于调控宿主

植物生长素信号通路, 共生真菌可以通过释放倍半萜(sesquiterpene)促进植物侧根形成^[44]. 除此之外, 外生菌根真菌也能够分泌脂壳寡糖(lipochitooligosaccharide, LCO)^[45]. 这一类几丁衍生物(chitin-derived molecules)同时是促进丛枝菌根真菌及根瘤菌形成丛枝菌根和根瘤的信号分子^[46,47]. 脂壳寡糖能够被宿主植物识别并激活通用共生信号通路(common symbiosis signaling pathway, CSSP), 这一信号通路在固氮共生和丛枝菌根共生均普遍存在^[47,48]. 通用共生信号通路的激活可以促进宿主植物侧根形成, 并参与了丛枝菌根形成的不同阶段(如丛枝的形成)^[49,50]. 研究表明, 外生菌根真菌双色蜡蘑(*Laccaria bicolor*)分泌的脂壳寡糖同样能够部分激活通用共生信号通路(图2), 影响侧根和哈蒂氏网(外生菌根的重要特征)的形成^[45].

3.3 菌根介导的小分子分泌蛋白在外生菌根形成过程中的作用

在菌根关系形成过程中, 共生真菌涉及信号传递及营养传输和代谢等的真菌基因转录明显上调^[6,30]. 同时研究发现, 在外生、丛枝、兰科和欧石楠类菌根形成过程中, 大量物种特异性的基因得以上调, 而其中大部分为一类可分泌效应蛋白(secreted effector protein). 这类蛋白通常短于300个氨基酸, 且包含一段信号肽, 被命名为菌根介导的小分子分泌蛋白(mycorrhizal

图 2 外生菌根形成过程中宿主植物与共生真菌信号识别示意图. LCO为脂壳寡糖/壳寡糖; MiSSP为菌根介导的小分子分泌蛋白. CSSP即通用共生信号通路, 参与该通路的基因及其主要功能见文献^[47,48], MiSSP抑制宿主植物茉莉酸途径的防御反应的分子机制见文献^[6]中的Figure 4

Figure 2 Diagram showing the signal exchanges between mycosymbionts and their host plants during the development of ectomycorrhizae. LCO, lipochitooligosaccharide; MiSSP, mycorrhiza-induced small secreted protein; CSSP, common symbiosis signaling pathway. The genes involved in CSSP and their functions are summarized in references ^[47,48]. Descriptions regarding the mechanisms via which MiSSP helps fungi escape plant defenses induced by the jasmonate signaling pathway can be found in Figure 4 in ref. ^[6]

za-induced small secreted protein, MiSSP). 目前对该类蛋白的功能认识仍极为有限. 针对外生菌根的研究主要限于双色蜡蘑MiSSP7基因功能的探讨.

MiSSP7基因的产物在真菌菌丝中富集, 随后分泌到环境中. 它能够通过内吞作用(endocytosis)进入植物根系细胞的细胞核内. 基因沉默显示MiSSP7对形成哈蒂氏网极为重要^[51]. 深入研究显示, MiSSP7通过阻断宿主植物茉莉酸信号途径(jasmonate signalling pathway)使得真菌菌丝能够进入植物根系细胞间隙并形成哈蒂氏网^[52]. 在双色蜡蘑和毛果杨(*Populus trichocarpa*)形成菌根关系的过程中, 双色蜡蘑菌丝侵染植物根系细胞时会诱导植物细胞释放茉莉酸, 这一信号会被COI1蛋白感知. COI1是E3泛素连接酶复合物SCF^{COI1}的组成部分, SCF^{COI1}能够泛素化JAZ6蛋白并导致JAZ6被降解, 进而诱发植物对真菌侵染的防御反应. 然而, MiSSP7能够与JAZ6蛋白结合, 避免JAZ6被降解, 因此, 植物对真菌侵染的防御反应被抑制, 真菌得以顺利和植物形成共生关系^[52].

4 展望

4.1 外生菌根真菌的多样性及时空分布规律

过去二十年来, 研究者在不同地区基于分子证据对不同植被类型和不同树种开展了外生菌根真菌多样性研究. 研究范围覆盖古热带(包括非洲大陆、马达加斯加、塞舌尔群岛和东南亚等)^[21,53]、新热带(如南美洲)^[54,55]、北温带^[56~58]和寒温带^[59~61]等. 尽管如此, 外生菌根真菌多样性的研究仍存在明显的地区局限性. 一些地区, 如非洲大陆和东亚等地, 仍是外生菌根真菌研究的薄弱地区. 在中国, 目前已有的研究主要集中在地上子实体的调查分析^[62,63]和零星的基于分子鉴定的菌根研究^[59,64~71]. 加强这些薄弱地区的研究, 无疑有助于更加全面地认识共生真菌的多样性.

外生真菌的分布受到非生物和生物因素的共同影响, 显示出环境过滤(environmental filtering)效应^[72]. 因此, 外生菌根真菌常显示出一定程度的时空分布规律: 在时间尺度上, 植物群落的不同演替(succession)阶段^[73,74]和不同生长季节^[61]对外生菌根菌的群落组成均有影响. 然而, 也有相反的例证表明, 在不同植物群落的演替阶段, 外生菌根菌的组成较为均一^[75]. 在空间尺度上, 土壤成分、海拔及宿主和非宿主植物均是外生菌根真菌群落组成的重要影响因素^[76]. 开展共生真菌的时空分布规律研究, 能够为认识共生真菌与环境生物和非生物之间的相互作用提供新视角.

4.2 外生菌根形成过程中植物-真菌的相互识别的分子机制

如前所述, 外生菌根形成过程中, 宿主植物与共生真菌的信号识别是基础, 然而目前对这一机制的了解仍需进一步加强. 基于双色蜡蘑的研究发现, 生长素、倍半萜和脂壳寡糖都能作为共生真菌的信号分子^[41,44,45]. 这些信号分子彼此间是否存在协同作用以促进菌根形成值得深入研究. 同时, 外生菌根真菌包含了許多亲缘关系亲疏各异的类群, 不同真菌类群是否采用相同的信号分子值得更进一步探讨. 此外, 鉴于外生菌根、丛枝菌根和根瘤形成过程中均涉及通用共生信号通路, 其他的菌根类型(诸如兰科菌根和欧石楠类菌根)是否也利用相似的信号通路同样值得进行探讨. 共生真菌分泌的MiSSP能够抑制宿主植物的防御反应, 促进外生菌根形成. 然而, 目前对外生菌根真菌MiSSP的功能研究仅限于双色蜡蘑的MiSSP7, 以上结论仍需更多研究案例来支持. 值得关注的是, 多数MiSSP均具有物种特异性^[30], 且大量MiSSP的功能尚未研究, 这些MiSSP如何参与到外生菌根形成过程, 是否与共生真菌-植物的专一性相关, 仍有待进一步探索.

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Ectomycorrhizal symbioses: Diversity of mycobionts and molecular mechanisms that entail the development of ectomycorrhizae

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Approximately 2% of vascular plants are involved in ectomycorrhizal symbioses with about 280 genera of higher fungi from 17–18 fungal orders. The development of ectomycorrhizal symbiosis, host specificity, and host-switch events appear to be key drivers for the speciation of ectomycorrhizal fungi. Comparative genomics indicates that ectomycorrhizal fungi have lost a set of genes that control the decay of organic matter contained in plant cell walls. During the formation of ectomycorrhizae, mycobionts and host plants require diversified signaling molecules to induce their bilateral communication; at the same time, mycobionts can release some mycorrhizal-induced small secreted proteins, which can help them escape plant defenses and thereby enable them to colonize plant roots. We present a review on the diversity and geographical distribution pattern of ectomycorrhizal fungi and on molecular mechanisms contributing to the development of ectomycorrhizae. Based on this, we also suggest several future prospects.

ectomycorrhiza, specificity, speciation, signaling molecules, comparative genomics

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