



## 木质素在海洋中的生物转化及其对海洋碳循环的影响

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**摘要:** 微型生物参与的海洋碳汇是海洋重要的储碳途径, 可调节全球气候变化。木质素是地球上第二大光合而成的碳库, 其在海洋中的生物地球化学过程与海洋碳循环密切相关。异养微生物所主导的代谢活动是木质素生物转化的主要途径。近年来, 迅速发展的高通量测序技术与传统微生物技术相结合, 在探索自然生境中木质素代谢菌群, 发现木质素代谢新物种, 挖掘相关功能基因等方面已取得一系列成果。然而绝大多数的研究主要集中于陆地生态系统, 对于海洋生态系统的研究仍较少。陆源有机碳在海洋中的转化过程仍是一个“谜”, 故解析海洋木质素碳转化是海洋碳循环研究的重要任务。本文综述了参与海洋木质素转化的功能微生物、木质素代谢机理以及微生物碳代谢活动与海洋碳汇过程的内在联系, 为今后的研究提供参考。

**关键词:** 木质素, 微生物代谢, 海洋, 碳汇, 微生物碳泵

海洋是地球上最大的碳库, 可吸收人为碳排放, 调节全球气候变化<sup>[1]</sup>。据统计, 全球每年约有 0.43 Gt 的颗粒有机碳(particulate organic carbon, POC)通过河川径流汇入海洋<sup>[2]</sup>。随后, POC 可经由生物泵(biological pump, BP)的垂直沉降作用输送至深海, 也可经由微型生物碳泵(microbial carbon pump, MCP)将其转化为惰性溶解有机碳(refractory dissolved organic carbon, RDOC)在海洋中存储上千年(图 1)<sup>[3]</sup>。故陆源 POC 的生物地球化学过程对于海洋碳汇乃至全球碳循环影响深远<sup>[4]</sup>。木

质素是地球上丰富的陆源有机碳, 以不同化学键交联的氧代苯丙醇为单位, 由不同的醚键和碳-碳键连接而成的高分子芳香族杂聚物。它主要来源于陆地维管植物细胞壁<sup>[5]</sup>, 具有较高的化学稳定性和较强的抗降解能力。一直作为陆源有机碳生物标志物, 用于研究陆源有机碳在海洋中的输入、迁移和埋藏过程<sup>[5]</sup>。但近来研究指出, 木质素在海洋中的稳定性和低降解性可能被过分夸大<sup>[4,6]</sup>, 除去光降解和热降解等非生物因素外, 异养微生物的代谢活动是其生物降解的主要途径<sup>[7]</sup>。微生物所

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参与的 MCP 可将木质素转化为潜在 RDOC, 进入数千年甚至上万年周转的地球化学循环, 长期封存在海洋中, 故微生物驱动的木质素代谢活动是海洋碳汇的重要组成部分。然而目前对于海洋生态系统中微生物代谢木质素过程的研究极为有限, 为克服上述困难, 本文综述了目前参与木质素代谢的关键微生物菌群及其代谢机理, 尤其是海洋微生物代谢途径, 为后续海洋生态系统中微生物驱动木质素的生物地球化学过程以及海洋碳汇的研究提供参考。

## 1 参与木质素代谢的海洋微生物

国内外研究者已经陆续从不同海洋环境样品中筛选和分离到参与木质素代谢的海洋微生物群落。与陆地生态系统中真菌主导的木质素生物降解有所不同<sup>[8]</sup>, 这些群落以细菌和古菌为主<sup>[9-10]</sup>, 可能是由海洋特殊生境(寡营养、高盐)所造成。

迄今发现的海洋木质素降解细菌主要可分为三大类: 放线菌门、变形菌门和厚壁菌门(图 2)<sup>[11]</sup>。日本海洋科技中心 Yukari Ohta 教授团队<sup>[12]</sup>基于纯培养和质谱技术对深海沉积物和沉木样品中的菌株进行分离和功能筛选, 发现其中 208 个菌株能够代谢木质素衍生的芳香化合物, 主要分属于厚壁菌门、放线菌门和变形菌门。Ohta 据此推测海洋环境中可能富含参与木质素代谢的微生物, 能够通过氧化和非氧化途径对木质素进行代谢。

随着测序技术和数据分析方法的飞速发展, 基于宏基因组和单细胞测序技术来探索环境中微生物的群落结构、组成及功能, 正逐步揭开海洋中木质素代谢菌群的神秘面纱。美国田纳西大学 Terry Hazen 教授团队<sup>[13]</sup>结合鸟枪法宏基因组学和 16S rRNA 基因序列分析技术, 发现  $\gamma$ -变形菌纲和  $\alpha$ -变形菌纲是东地中海海平面下 50 m 处海水环境中参与木质素代谢的主要菌群, 并指出其中参与

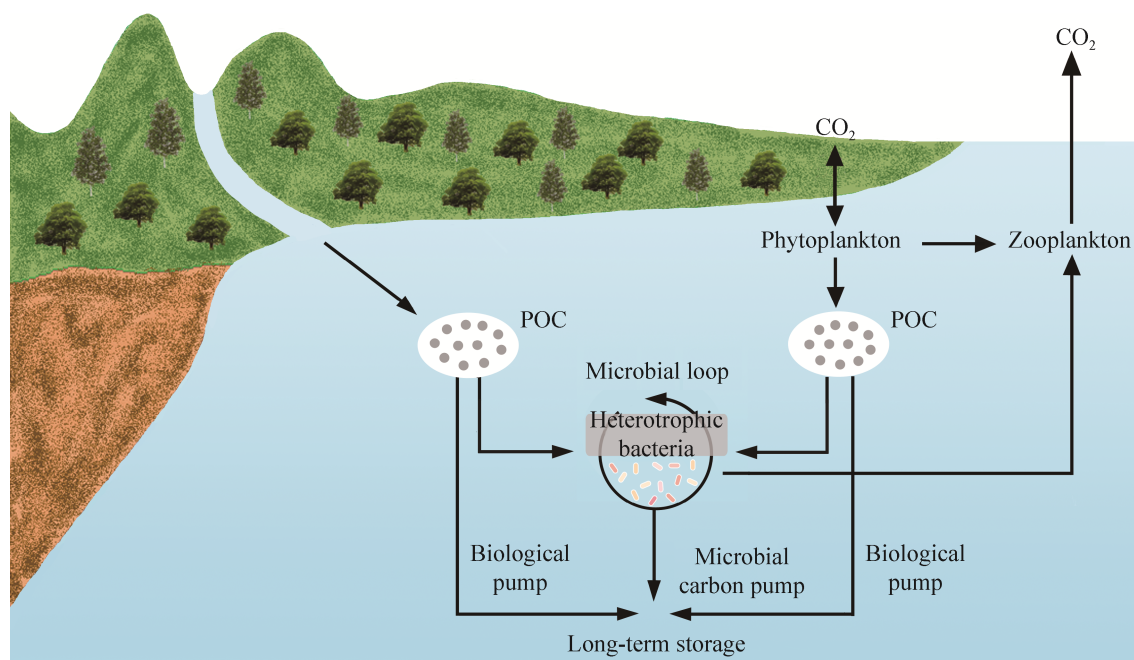


图 1. 微生物介导的陆源颗粒有机碳在海洋中的转化简图<sup>[14-15]</sup>

Figure 1. Microbial transformation of terrestrial particulate organic carbon in the ocean<sup>[14-15]</sup>.

苯乙酰 CoA、香草酸和阿魏酸分解代谢途径的相关基因丰度较高，尤其是来自于假单胞菌属 (*Pseudomonas*) 和海单胞菌属 (*Marinomonas*) 的苯乙酰 CoA 代谢途径相关基因。日本理化学研究所 Keiji 团队<sup>[16]</sup>从被尿囊素污染的海域中分离、筛选到能够以木质素或其衍生物为唯一碳源直接合成聚羟基脂肪酸酯(PHA)的 *Oceanimonas doudoroffii* 菌株。笔者所在团队<sup>[17-19]</sup>也发现能代谢木质素的 *Pseudomonas putida* 菌株，且该菌株能够以木质素

为碳源合成 PHA。结合系统生物学方法, 团队进一步揭示了该菌株木质素代谢及转化至 PHA 的分子机理。PHA 作为微生物储碳的一种有效方式, 木质素至 PHA 的生物转化可减少异养微生物通过呼吸作用所排放的  $\text{CO}_2$ , 是海洋增汇的理想途径<sup>[20]</sup>。

除上述海洋细菌外,深海古菌也积极参与了海洋木质素代谢。上海交通大学王风平教授团队<sup>[9]</sup>通过宏基因组测序和纯培养技术相结合,从海洋沉积物中发现了一个“深古菌”新门,命名为 *Bathyarchaeota*。

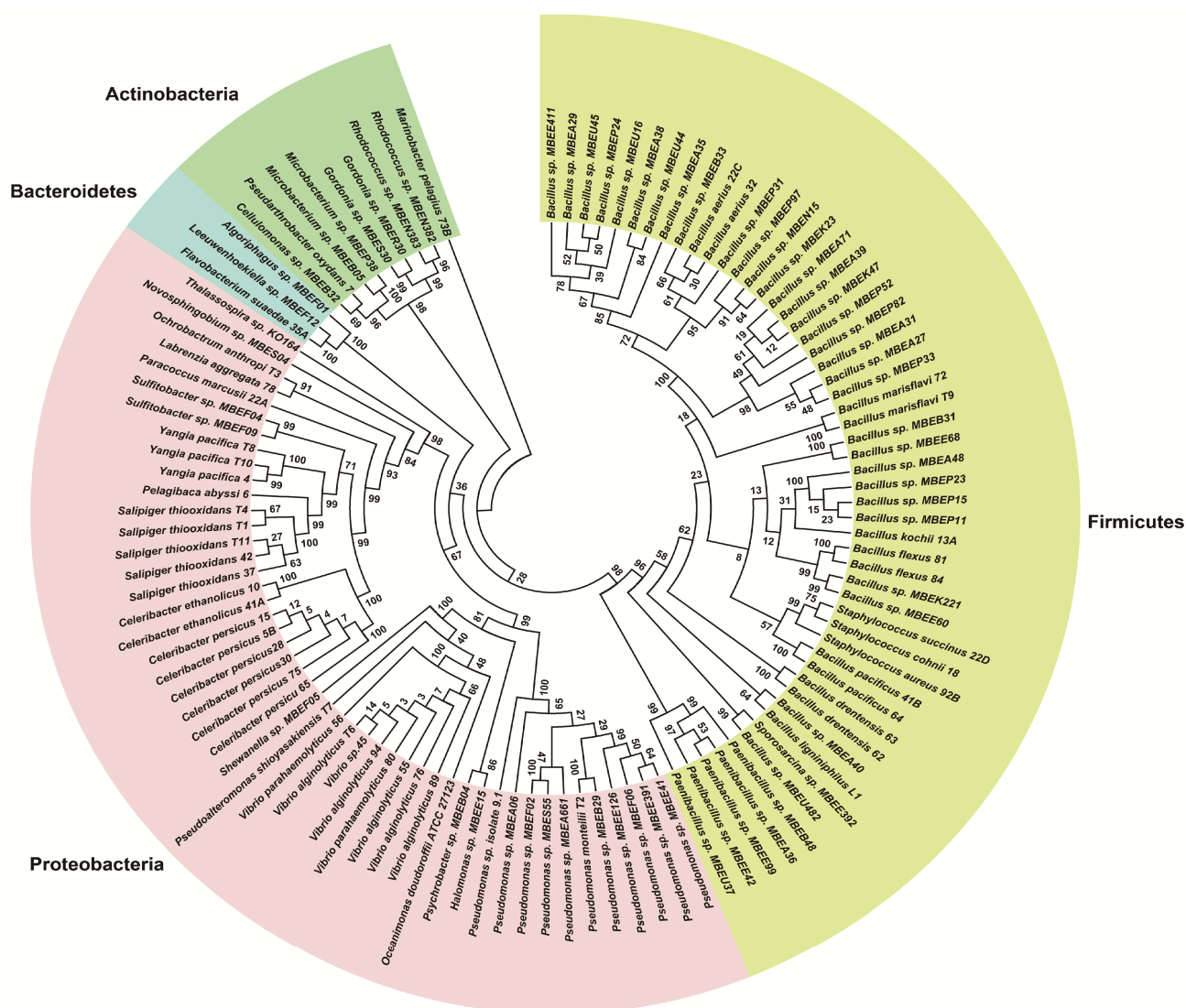


图 2. 参与木质素代谢的海洋细菌系统发育进化树

Figure 2. Phylogenetic tree of marine lignin-metabolizing bacteria.

通过宏基因组数据分析,该团队推测 *Bathyarchaeota* 具有多种代谢潜能,并通过木质素富集实验证实其中 Bathy-8 类群能够在厌氧环境下以木质素为能源,以无机碳为碳源进行生长<sup>[9]</sup>。

## 2 微生物代谢木质素机制

过去几十年里,以陆地生态系统中真菌为主导的木质素降解已得到广泛研究。真菌能够分泌多种胞外酶对木质素进行解聚<sup>[21]</sup>,如漆酶(Lac)、木质素过氧化物酶(LiP)、锰过氧化物酶(MnP)、多功能过氧化物酶(VP)、染料脱色过氧化物酶(DyP)等,通过胞外催化生成化学不稳定性木质素自由基中间体,进而引发高分子木质素内部的 C<sub>α</sub>-C<sub>β</sub> 裂解、烷基-芳基裂解、交联、去甲氧基化及环裂解等,产生低分子量芳香族化合物<sup>[22]</sup>(表 1)。与真

菌类似,细菌也拥有自己的胞外氧化酶系统,能够对木质素进行解聚,如细胞色素 P450 单加氧酶(P450s)、染料过氧化物酶(DyP)、漆酶(Lac)、锰过氧化物酶(MnP)、双加氧酶、非血红素铁酶、超氧化物歧化酶(SOD)、β-醚酶等<sup>[19,36-43]</sup>(表 1)。其中,染料过氧化物酶(DyP)普遍存在于各种细菌中。笔者所在团队解析出 *Pseudomonas putida* 中 2 个 B 型 DyP,具有独特的木质素氧化活性,能与细菌高效协同,从而极大促进细菌生长和木质素降解<sup>[19]</sup>。总之,细菌的木质素降解能力虽弱于真菌,但通常具有简单的蛋白表达系统和较强的环境适应能力,如更好的热稳定性、更广的 pH 和温度耐受范围等<sup>[11]</sup>。此外,细菌还能生产高价值产物,因而细菌介导的木质素代谢近年来逐渐受到广泛关注<sup>[17-18,44]</sup>。

目前,对细菌木质素衍生物代谢途径的研究主要集中于陆地环境中所筛选到的菌株,如来自

表 1. 陆地和海洋生态系统中真菌与细菌参与木质素代谢的酶及代谢途径比较

Table 1. Comparison of enzymes and metabolic pathways of fungi and bacteria involved in lignin metabolism in the terrestrial and marine ecosystem

Taxonomy	Lignin-degrading microorganisms	Enzymes	Pathway
Fungi	White-rot fungi	Major enzymes such as laccases (Lac),	Diaryl propane catabolic pathway,
	<i>Coriolus</i> <sup>[23]</sup> , <i>Phanerochaete</i> <sup>[24]</sup> , <i>Trametes</i> <sup>[25]</sup>	manganese peroxidases (MnP), lignin	pinoresinol pathway <sup>[35]</sup> , etc.
	<i>Bjerkandera</i> <sup>[26]</sup> , <i>Pleurotus</i> <sup>[27]</sup> , <i>Phlebia</i> <sup>[28]</sup>	peroxidases (LiP), dye-decolorizing	
	Brown-rot fungi	peroxidases (D-type DyP), versatile	
Bacteria	<i>Gloeophyllum</i> <sup>[29]</sup> , <i>Poria</i> <sup>[29]</sup> , <i>Polyporus</i> <sup>[30]</sup>	peroxidases (VP). Auxiliary enzymes	
	Soft-rot fungi	such as aryl-alcohol oxidases (AAO),	
	<i>Chaetomium</i> <sup>[31]</sup> , <i>Paecilomyces</i> <sup>[32]</sup> ,	glyoxal oxidases (GLOX), glucose	
	<i>Fusarium</i> <sup>[33]</sup> , <i>Aspergillus</i> <sup>[34]</sup>	oxidases (GIO).	
	<i>Actinobacteria</i>	Major enzymes such as laccases (Lac),	β-Aryl ether cleavage pathway,
	<i>Streptomyces</i> <sup>[45]</sup> , <i>Micrococcus</i> <sup>[46]</sup> ,	dye-decolorizing peroxidases (DyP),	biphenyl catabolic pathway, diaryl
	<i>Micromonospora</i> <sup>[46]</sup> , <i>Arthrobacter</i> <sup>[47]</sup> ,	manganese peroxidases (MnP).	propane catabolic pathway, biphenyl
	<i>Rhodococcus</i> <sup>[48]</sup> , <i>Microbispora</i> <sup>[46]</sup> ,	Auxiliary enzymes such as cytochrome	degradation pathway, vanillic acid
	<i>Nocardia</i> <sup>[49]</sup> , <i>Thermoactinomyces</i> <sup>[50]</sup>	P450, dioxygenase, non-heme enzyme,	pathway, ferulic acid degradation
	<i>Proteobacteria</i>	superoxide dismutase, β-etherase	pathway, 3-methyl-gallic acid
	<i>Acinetobacter</i> <sup>[51]</sup> , <i>Comamonas</i> <sup>[52]</sup> ,	enzyme.	pathway, benzoic acid pathway,
	<i>Pseudomonas</i> <sup>[47]</sup> , <i>Xanthomonas</i> <sup>[53]</sup> ,		oxidative cleavage of protocatechuic
	<i>Mycoplana</i> <sup>[54]</sup> , <i>Sphingomonas</i> <sup>[55]</sup>		acid, β-ketoadipate pathway,
	<i>Firmicutes</i>		phenylacetic acid pathway, phenol
	<i>Clostridium</i> <sup>[46]</sup> , <i>Bacillus</i> <sup>[56]</sup>		pathway, gentisate pathway, etc.



造纸厂废水环境中的 *Sphingomonas paucimobilis* SYK-6 菌株以及来自土壤环境中的 *Streptomyces viridosporus* T7A 菌株等<sup>[57-59]</sup>。而对海洋微生物代谢木质素的研究较为缺乏, 故本文综述了陆地微生物木质素代谢途径, 并与已知的海洋微生物代谢途径相比较, 为后续海洋微生物代谢木质素途径的研究提供参考。

木质素经胞外解聚酶解聚后可得到 3 种不同结构的基本单元, 含有 2 个甲氧基的 S 型单元, 含有 1 个甲氧基的 G 型单元, 以及不含甲氧基的 H 型单元。这些木质素衍生物输送到胞内后, 经过多种外围和中心代谢途径进行开环代谢, 最后进入三羧酸(TCA)循环为细胞供能<sup>[60]</sup>(图 3)。

对香豆酸作为 H 单元的代表, 其降解途径主要可分为 CoA 依赖型  $\beta$  氧化、CoA 依赖型非  $\beta$  氧

化和不依赖于 CoA 的代谢途径(图 3)。(1) CoA 依赖型  $\beta$  氧化途径首先通过羟基肉桂酰 CoA 合成酶的催化, 将对香豆酸转化为羟基肉桂酰 CoA, 而后通过水合、氧化和裂解生成乙酰 CoA 和对羟基苯甲酰 CoA, 并进一步转化为对羟基苯甲酸<sup>[61-62]</sup>。(2) CoA 依赖型非  $\beta$  氧化前两步与 CoA 依赖型  $\beta$  氧化途径相同, 随后发生  $C_\alpha$ - $C_\beta$  断裂, 生成乙酰 CoA 和对羟基苯甲醛, 对羟基苯甲醛进一步氧化为对羟基苯甲酸<sup>[63-66]</sup>。(3) 不依赖于 CoA 的代谢途径与 CoA 依赖型非  $\beta$  氧化途径相似, 将对香豆酸转化为对羟基苯甲醛, 进而氧化生成对羟基苯甲酸, 但不形成 CoA 硫酯<sup>[67]</sup>。生成的羟基苯甲酸在对羟基苯甲酸-3-羟化酶的催化下可转化为原儿茶酸。原儿茶酸是芳香族化合物降解的重要中间产物, 可在原儿茶酸 4, 5 双加氧酶、原儿茶酸 3, 4

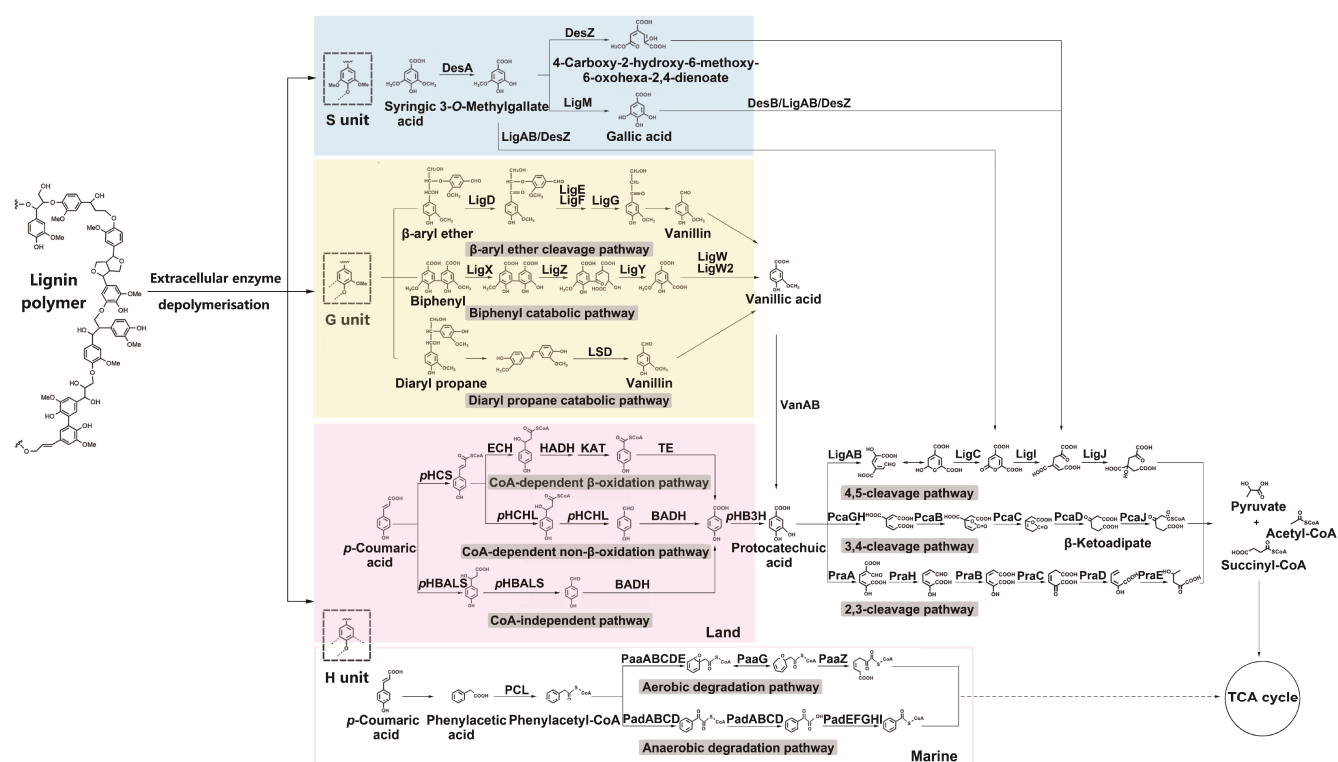


图 3. 木质素三种基本结构单元代谢途径示意图

Figure 3. Metabolic pathways of three basic structural units of lignin.

双加氧酶及原儿茶酸 2,3 双加氧酶的催化下分别在苯环的 4, 5 位、3, 4 位或 2, 3 位间进行开环<sup>[68-70]</sup>。其中, 原儿茶酸 3,4 双加氧酶广泛存在于细菌中, 原儿茶酸经 3,4 开环裂解后能够进入  $\beta$ -酮己二酸芳香族分解代谢途径, 最终进入 TCA 循环为细胞供能<sup>[71]</sup>。

G 单元木质素衍生体以  $\beta$ -芳基醚、联苯、二芳基丙烷等为代表(图 3)。(1)  $\beta$ -芳基醚首先通过脱氢酶氧化生成相应的酮, 而后经以谷胱甘肽为辅因子的  $\beta$ -醚酶的还原性醚裂解反应, 转化为中间体香草酸, 经甲基化进一步转化为原儿茶酸进入中心代谢途径<sup>[72-74]</sup>。(2) 联苯在木质素中的含量仅次于芳基醚寡聚体。它首先在脱甲基酶的催化下进行脱甲基化, 随后由双加氧酶催化苯环断裂, 裂解产物在水解酶作用下发生 C-C 键断裂, 形成 5-羧基香草酸, 经脱羧酶催化脱羧为香草酸后进一步转化, 生成原儿茶酸, 进入中心代谢途径<sup>[75-76]</sup>。(3) 二芳基丙烷被某种未知酶催化生成甲醛和 Lignostilbene, 随后在双氧酶的作用下进一步氧化为香草醛, 进入中心代谢途径<sup>[77-78]</sup>。

丁香酸是 S 型木质素的单体模型化合物。已知能够有效降解丁香酸的微生物较少, 可能是由

于 S 型木质素单元的芳香环含有 2 个甲氧基, 包围了酚羟基, 使得甲氧基在降解竞争中占据优势地位, 其与苯环连接键最先发生断裂, 然而甲氧基与苯环连接键的键能较高, 较难发生断裂, 因此 S 型比 H 型和 G 型木质素降解更为困难<sup>[79-80]</sup>。有关细菌 S 型木质素降解途径的研究主要集中于 *Sphingomonas* sp. SYK-6。丁香酸首先被依赖于四氢叶酸依赖型脱甲基酶脱甲基化为 3-甲基没食子酸, 3-甲基没食子酸可以直接开环裂解进入原儿茶酸 4,5-裂解途径; 也可以以没食子酸或 4-羧基-2-羟基-6-甲氧基-6-氧-2,4-己二烯酸(CHMOD)为中间体进行代谢, 最终进入原儿茶酸的 4,5-裂解途径<sup>[81-83]</sup>(图 3)。

此外, 有限的研究显示, 海洋微生物存在其独特的代谢途径, 可能是由于其独特的生境所造成(表 2 和图 3)。对于来自东地中海的海水样品进行宏基因组分析显示, 海洋生境中的微生物可以通过苯乙酰 CoA 途径进行木质素分解代谢, 以代替陆地上经典的  $\beta$ -酮己二酸芳香族分解代谢途径<sup>[13]</sup>。与  $\beta$ -酮己二酸代谢不同, 苯乙酰 CoA 途径无需经过开环, 可直接通过 CoA 与芳香族化合物连接, 经环-环氧化或芳香族 CoA 硫酯的还原后实

表 2. 陆地与海洋生态系统中参与细菌木质素代谢的酶及代谢通路比较

Table 2. Comparison of enzymes and metabolic pathways involved in bacterial lignin metabolism in the terrestrial and marine ecosystems

Ecosystem	Lignin-degrading microorganisms	Characteristic enzymes	Characteristic pathway
Land	<i>Sphingomonas paucimobilis</i> <sup>[56]</sup> , <i>Rhodococcus jostii</i> <sup>[49]</sup> <i>Burkholderia multivorans</i> <sup>[84]</sup> , <i>Pseudomonas putida</i> <sup>[48]</sup> <i>Bacillus amyloliquefaciens</i> <sup>[57]</sup> , <i>Comamonas serinivorans</i> <sup>[53]</sup> , <i>Streptomyces viridosporus</i> <sup>[46]</sup> , <i>Nocardia autotrophica</i> <sup>[50]</sup>	Oxidative enzymes, etc.	Oxidative cleavage of protocatechuic acid, $\beta$ -ketoadipate pathway, etc.
Marine	<i>Bacillus ligniniphilus</i> <sup>[85]</sup> , <i>Pseudomonas deceptionensis</i> <sup>[86]</sup> , <i>Pseudomonas putida</i> <sup>[17]</sup> , <i>Thalassospira</i> sp. <sup>[87]</sup> , <i>Oceanimonas doudoroffii</i> <sup>[16]</sup>	Oxidative enzymes, phenylacetyl-CoA ligase (PCL), etc.	Phenylacetic acid pathway, etc.

现环活化,能降解包括芳香族氨基酸及木质素类苯丙烷化合物在内的多种芳香族化合物<sup>[88-89]</sup>。此外,相比于依赖于双加氧酶的 $\beta$ -酮己二酸,苯乙酰 CoA 途径所产生的 CoA 硫酯能够更好地被细胞利用,尤其适用于处于海洋寡营养生境中的微生物,且 CoA 硫酯可以进入好氧和厌氧两种途径,使得兼性厌氧微生物在氧气波动或低氧条件下具有较高灵活性<sup>[90]</sup>,故苯乙酰 CoA 途径可能更适用于海洋生境中木质素代谢。

综上所述,在海洋环境中,木质素的转化对于海洋碳库起着重要调节作用。除沉降到深海,长期埋藏在海底外,木质素还可经微生物转化成各种芳香族化合物。而这些芳香族化合物可能是潜在的 RDOC,有助于海洋增汇。

### 3 木质素代谢研究前景

已知海洋环境中存在多种木质素代谢微生物,但相较于陆地生态系统,对于海洋环境中木质素代谢微生物的认知仍然有限<sup>[11-12]</sup>。纯培养和高通量测序是目前研究海洋木质素代谢菌所采用的主要手段。纯培养是微生物研究的基石,微生物的生理或生态功能假说均需通过纯培养进行验证,但自然界中约有99%的微生物难以在现有实验条件和技术下进行培养。此外,分离培养工作量大,操作繁琐,通量低,大大限制了我们对海洋木质素代谢菌的认知。故发展快速、简便的适用于木质素代谢菌筛选和培养的新方法迫在眉睫。本课题组已基于木质素代谢菌的生理参数构建模型,建立了一种木质素利用菌快速筛选的方法,目前正在评审中。与此同时,宏基因组测序技术克服了依赖培养的微生物研究模式,直接以环境中微生物群体基因组为研究对象,借助于高

通量测序和生物信息学技术获得新基因、新物种,探索自然生境中的微生物群落结构及功能<sup>[91]</sup>。但受限于现有测序和数据分析技术,使得在研究木质素代谢微生物群落方面具有以下几个难点。首先,对木质素降解基因认知不足,依赖于现有的公共基因组数据库对木质素代谢菌基因组功能注释成为一大难题。因此,构建针对木质素代谢的功能基因数据库,填补木质素代谢菌功能基因的空白是当前急需解决的难题。本课题组前期已构建一个专门用于宏基因组数据中氮循环功能基因挖掘的氮循环功能基因数据库 NCycDB,以解决搜索效率低、基因家族同源性低以及参与氮循环基因的测序序列覆盖率低等问题<sup>[92]</sup>。该工作为今后建立木质素降解基因数据库奠定了良好基础。其次,参与木质素代谢基因的相关丰度可能较低,通过宏基因组技术极易忽视与之相关的低丰度基因,从而增加了数据分析的难度。借助现有的 Geochip 技术<sup>[93]</sup>开发针对木质素代谢的微阵列芯片,可将所有已知木质素代谢功能基因探针集中在芯片上,大大提高了目的基因的检测灵敏度,简化了数据分析的困难,两者相结合将能够更全面、准确地挖掘出参与木质素代谢的微生物功能基因。此外,结合宏转录组测序、宏蛋白质组以及质谱技术等可分别从转录水平、蛋白水平以及代谢物水平解析参与木质素代谢的成员、代谢途径及功能基因等。借助随机矩阵理论也有助于进一步探究菌株间、基因间的相互联系。同时,通过解析不同环境因子下参与木质素代谢的微生物群落结构和组成,将有助于发现环境因子对于微生物代谢调控的影响及微生物对于环境变化的应对策略。

探索海洋木质素代谢微生物,认知木质素在自然界中所参与的碳循环过程,为深入理解以木

质素为代表的陆源 POC 在海洋碳汇中所发挥的作用以及海洋碳循环机制提供参考。

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# Biotransformation of lignin in the ocean and its impact on marine carbon cycle

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**Abstract:** Microbial carbon sequestration in the ocean plays an important role in marine carbon storage to alleviate the global climate change. Lignin is the second most abundant carbon pool formed by photosynthesis on earth. The biogeochemical process in the ocean, which is mediated by heterotrophic microorganisms, is closely related to the marine carbon cycle. In recent years, the rapidly developing high-throughput sequencing technology, together with the traditional microbial technology, provides insights into the lignin-degrading microbial community, novel lignin-metabolizing microbial species, and functional genes in open environments. However, numerous studies focused on the terrestrial ecosystem, rather than marine ecosystem. The biogeochemical process of such terrestrial organic carbon in the ocean remains elusive. Therefore, analyzing the marine lignin transformation is essential in the study of marine carbon cycle. This article reviews not only the marine microbes involved in the lignin conversion, the mechanism of lignin metabolism and the links between microbial carbon metabolism and marine carbon sink, but also provides further ideas in the future.

**Keywords:** lignin, microbial metabolism, marine, carbon sink, microbial carbon pump

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