ISSN 1000-0933
CN 11-2031/Q

生态学报

Acta Ecologica Sinica

第 34 卷 第 2 期 Vol.34 No.2 2014

中国生态学学会
中国科学院生态环境研究中心 主办
科学出版社 出版

中国科学院科学出版基金资助出版

生 态 学 报

(SHENGTAI XUEBAO)

第 34 卷 第 2 期　　2014 年 1 月　(半月刊)

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期刊基本参数:CN 11-2031/Q * 1981 * m * 16 * 288 * zh * P * ￥90.00 * 1510 * 29 * 2014-01

封面图说:高原盐湖——中国是世界上盐湖分布比较稠密的国家,主要分布在高寒的青藏高原以及干旱半干旱地区的新疆、内蒙古一带。尽管盐湖生态环境极端恶劣,但它们依然是陆地特别是高原生态系统中十分重要的组成部分。微微型浮游植物通常是指粒径在 0.2—3 μm 之间的光合自养型浮游生物。微微型浮游植物不仅是海洋生态系统中生物量和生产力的最重要贡献者,也是盐湖生态系统最重要的组成部分。研究显示,水体矿化度是影响微微型浮游植物平面分布及群落结构组成的重要因子,光照、营养成分和温度等也会影响盐湖水体中微微型浮游植物平面分布及群落结构组成(详见 P282)。

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DOI: 10.5846/stxb201303060361
周进,陈国福,朱小山,陈璐,蔡中华.赤潮过程中"藻-菌"关系研究进展.生态学报,2014,34(2):269-281.
Zhou J, Chen G F, Zhu X S, Chen L, Cai Z H.A review of the relationship between algae and bacteria in harmful algal blooms.Acta Ecologica Sinica,2014,34(2):269-281.

赤潮过程中"藻-菌"关系研究进展

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摘要:微生物对促进海洋物质循环,维持水生环境的生态平衡具有重要作用。在赤潮事件中,基于微生物(尤其是细菌)的多样性和重要性,它们与藻类之间的相互关系成为了研究的热点。过去 20 年里,人们从不同角度对"藻-菌"间的关系进行了探索,包括物理学过程、生物学过程、环境过程以及化学过程。就化学过程而言,它作为一种较早出现的技术,在以往的研究中带给人们许多认识藻菌关系的方法。随着学科的渗透,化学法有了拓展与延伸,为人们认识藻菌关系带来了新的契机。从化学生态学领域来梳理"藻-菌"关系中涉及的现象和行为,包括菌对藻的有益面、菌对藻的有害面、以及藻类应答细菌行为的化学途径;并从信号语言(群体感应、化感作用)的角度来阐释两者之间的互生或克生关系。通过文献综述的方式来解读藻菌关系的互作过程和机理,为认识赤潮的发生和防控方法提供借鉴。

关键词:化学生态学;"藻-菌"关系;群体感应;化感作用;赤潮

A review of the relationship between algae and bacteria in harmful algal blooms

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Abstract: Marine microbes play important roles in the marine ecological system. They influence the climate, mediate primary production, participate in biogeochemical cycles, and maintain ecological balance. The microbes that make up harmful algal blooms (including bacteria, archaea, microbial eukaryotes and their associated viruses) are being studied closely by scientists. Because of high diversity and complexity, the interaction between algae and bacteria has become the concern of many researchers. Over the past 20 years, people have explored the relationships between algae and bacteria from different perspectives, including the physical, biological, environmental and chemical processes involved. Chemical ecology offers many methods to study and understand the relationships between algae and bacteria. Researchers have observed many different interactions between alage and bacterial, including competition, mutualism and parasitism. These microbes, which exist as free-living forms as well as securely attached to algal cells, have now been demonstrated to modulate (either positively or negatively) algal growth rates and transitions between life history stages, influence toxin production, and even induce the rapid lysis of algal cells. However, given the complex array of interactions that have evolved between them, some ecological functions and related mechanisms have not yet been fully elucidated. Biotic interactions play an important role in community regulation. Though some of the chemical response mechanisms can be clearly attributed to either the alga or to its

基金项目:973 前期专项资助项目(2012CB426504);国家自然科学基金资助项目(41106087);国家海洋公益性资助项目(201205020-9;201305021-1);广东省自然科学基金资助项目(S2012010010855); 环境模拟与污染控制国家重点联合实验室专项基金资助项目(13K10ESPCT);深圳市基础研究资助项目(20130314165552); 南山区创新研发资助项目(KC2013JSCX0003A)
收稿日期:2013-03-06; **修订日期**:2013-08-26

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epibiont, in many cases the producers, as well as the mechanisms triggering the biological behaviour, remain ambiguous. Chemical ecology brings new opportunities to explore the interactions between algae and bacteria. This paper reviews the relationships between algae and bacteria from a chemical ecology viewpoint, including both benefical and negative effects on the algae. Positive algae-bacteria interactions include phytohormone production, morphogenesis of microalgae triggered by bacterial products, specific antibiotic activities affecting epibionts and the elicitation of oxidative burst mechanisms. Deleterious algae-bacteria interactions include induction of algal diseases, growth inhibition, an influence on algal metabolism and production of antibiotic compounds. The mechanisms concerning the algal response to bacteria from a chemical signal perspective (such as, quorum sensing and allelopathy) are also addressed. Signal molecules are considered to play a potentially important role in structuring phytoplankton communities and affect the population dynamics of harmful algae species. Future work should focus on three research aspects. 1) how microbes and their secondary metabolites regulate their ecological division and social characterization with chemical signals in the phycosphere environment. 2) analysis of the secondary metabolites of algae and bacteria *in situ* in the algal-bacterial symbiotic system possibly using a new method called desorption electrospray ionization mass spectrometry (DESI-MS). 3) Coupled application of chemical and molecular biological methods to study the interaction of alage and bacterial. Some new tools should be widely applicable, such as bioinformatics, metagenomic technology and development of online monitoring instruments. The aim of this paper is to interpret the complex ecological interaction and the related mechanisms between planktonic algae and bacteria in a new way. This review can provide a reference for readers to understand red tide processes and help develop novel ways to prevent or control harmful algal blooms.

Key Words: chemical ecology; algae-bacteria relationship; quorum sensing; allelopathy; harmful algae blooming

生态行为的出现几乎都是以生物化学反应为基础而实现的,生态过程也相伴着各种化学规律。以化学方法为基础求得对宏观生态现象透彻理解的分枝科学被喻为化学生态学(Chemical Ecology)[1]。它通过鉴定载带信息的天然化学物质,阐明这些信息物质的受体和它们在生物群体内或群体间的传导作用;以及化学信息对生物的进化、行为及生态的影响。在陆地生态系统,化学生态学的研究方法已进入森林、农田、湿地、虫害防治等领域,并应用到对生态系统的人为控制和改造中[2]。与陆地生态系统相比,化学生态学在海洋生态系统的研究尚处于起步阶段[3]。但新近的研究让人们认识到:海洋生物的起源和进化相对原始,在长期的环境适应中依靠物理防御的作用是有限的,因而在竞争激烈的生存状态下势必依赖于以次生代谢产物为主的化学防御体系[4]。聚焦于信号通讯机制的化学方法,在研究拥有社会结构属性的海洋生态学中将大有可为;而基于化学方法来研究典型的海洋生态问题也逐渐成为新的研究热点[5]。

赤潮作为一类严重的海洋生态灾难,已成为人们日益关注的共性问题。在赤潮的研究中,聚焦于"藻-菌"关系这一核心,人们从化学生态学层面认识到化学信号是两者交流与通讯的一种重要手段[6]。越来越多的研究发现宿主与微生物、细菌与细菌之间的信号交流方式,包括防御素、信息素、引诱剂以及其它信号分子等。这些化学信号中有些是通用的、有些是种属特异性的[7]。Steinberg 等研究证实藻菌共生环境中,由化学方法所介导的各类行为,如受精、孢囊萌发以及捕食都在一定程度上依赖于化学感应[8]。Elleuche 和 Pöggeler 报道藻际微生物的繁殖行为受宿主的调控[9]。其它由化学语言调节的微生物行为,如趋化运动、粘附能力、群集运动以及生物膜的形成也都被相关工作所证实[10-12]。如能深入了解赤潮事件中的化学行为,将为透彻的认识赤潮过程提供裨益。

据此,本文以化学生态学为切入点,尝试总结目前存在的藻菌行为和相互关系,并梳理"藻-菌"之间的互作过程及相应机制,以期更好的理解细菌与藻类的种群多样性、生理多样性和生态功能多样性,为后续研究赤潮的形成机制和防控方法提供借鉴。

1　菌对藻的促进作用

海洋细菌作为重要的分解者,以多样化的代谢活动参与海洋中物质转化和分解过程,是生物地球化学循环的一个重要参与者。细菌对藻类提供的有利面主要集中在营养改善(生源要素的提供、生长因子的转化)、信息素调节和协同保护[13-14]。对生源要素的改善中,最为典型的是固 N 作用[15-18]。除 N 源外,细菌也充当了其它生源要素的加工者。例如,1)细菌可以将三价铁还原为溶解度较高的二价铁,为藻类提供生长所需的铁元素[19];2)有些细菌具有高水平的 5′-核苷酶,它们可以迅速地水解 ATP 类 5′-核苷酸,还原产生无机磷供海洋藻类使用[20];3)某些细菌能产生特定的有机物质,如胞内磷脂或胞外糖肽,以促进浮游藻类的生长[21];4)海洋中存在着大量的维生素(如 VB_{12})产生菌,它们通过接受 cAMP 途径上的 X1 信号而行使产 VB_{12}的功能,对海洋藻类的生长是必不可少的[22]。另外,过量的溶解氧会抑制藻细胞的光合作用,使其转向光呼吸从而阻碍藻的生长,细菌对藻细胞周围环境中高浓度溶解氧的利用,也为藻的生长提供了一个还原性较强的生长环境[23]。

在为藻类提供生长因子方面,细菌的表现也十分活跃。例如转化和加工各种激素和生长促进剂。交替单胞菌(*Pseudoalteromonas porphyrae*)在大型藻海带(*Laminaria japonica*)生长中扮演生长促进剂的作用[24]。一些海洋细菌被证实能产生植物激素,Maruyama 等证实在藻菌共生系统中,与纯培养的藻类相比,细菌能产生更多的植物细胞分裂素和茁长素[25]。以往的研究也显示浒苔共生菌具有将色氨酸转变为植物激素吲哚乙酸(indole-3-acetic acid, IAA)的能力[26]。Ashen 和 Goff 进一步证实在海洋红藻(*Prionitis lanceolata*)中,植物激素的形成就与玫瑰杆菌(*Roseobacter* sp.)相关,并提出这种共生关系也利于彼此间的协同进化[27]。

细菌除了作为营养物质的提供者与加工者,对维持藻细胞个体形态也有调节作用。海洋绿藻,如石莼在无菌的纯培养体系下,将会逐渐失去其原有的典型形态,相似的现象也在红藻中发现[28-30]。随后的研究中,证实对藻类形态有维护作用的细菌也在其它种属中被相继发现,如柄杆菌(*Caulobacter* sp.),弧菌(*Vibrio* sp.),假单胞菌(*Pseudomonas* sp.),海水德莱氏菌(*Deleya* sp.),肠杆菌(*Escherichia* sp.)以及一些革兰氏阳性菌[31]。Mieszkin 等总结到在藻类的形态发生过程中,许多步骤是受微生物严格调控的,如生物膜的形成和孢囊的发生,孢囊的附着能力与生物膜的厚度成正比,并证实生物膜在构建藻类周从生物结构上有重要意义,这一生态现象的形成机制得益于生物膜的成熟结构和多样化的碳水养分[32]。在绿藻中,藻体表面的生物膜具有维护孢子体正常形变的作用[33],并且这种能力取决于生物膜的年龄;多样性分析证明调控生物膜组成的主要是变形杆菌属(Gamma-proteobacteria 和 Alpha-proteobacteria)。

协同保护上,细菌主要通过对毒物进行吸附、分解和转化,以减少或消除重金属、原油以及化学污染物对藻细胞的侵害[34-35]。

2　菌对藻的抑制作用

菌类在藻际环境中的作用多种多样,除了表现出对藻类的惠利关系外,也会表现出对藻类的抑制或拮抗,主要体现在营养竞争、毒素释放以及溶藻酶类的产生。

2.1　营养竞争

在藻-菌共生系统中,当没有外源营养物质补充下,细菌与藻竞争营养物质。这种竞争关系一方面对维持藻类生物量的平衡有着非常重要的作用,另一方面也对藻细胞产生克生效应。周名江等证明了营养竞争的普遍性、广泛性和多样性[36];郑天凌等采用流式细胞术(FCM)和镜检法测定了营养竞争条件下的海洋细菌对赤潮藻的生长和增殖的影响;表明在不同菌种、不同菌浓以及不同处理方式的抑藻效果等存在着种属特异性和差异性[37]。Haaber and Middelboe 也证实当共生环境中变形杆菌数量增加 1 倍的情况下,甲藻对营养物质的捕获能力降低三分之一,这主要是由于变形杆菌对营养物质的竞争所致[38]。国内也有学者利用这种竞争关系来改善水体环境,如在养殖区内投入光合细菌,通过竞争掉藻类营养,以达到控制富营养化和水华发生的目的[39]。

2.2　释放化学毒素

细菌可分泌毒素或类似物,通过阻断呼吸链、抑

制细胞壁合成、抑制孢囊的形成,从而有效抑制藻细胞的生长甚至杀灭藻细胞。变形杆菌门和厚壁菌门的细菌能向水环境中分泌种分子量大于 10kDa 的热不稳定物质,该物质能抑制米氏凯轮藻(*Karenia mikimotoi*)和链状裸甲藻(*Gymnodinium catenatum*)的生长[40]。斯氏假单胞菌(*Pseudomonas stutzeri*)可分泌高活性的抑藻物质环二萜,该物质可杀灭顽固的古老卡盾藻(*Chattonella marina*)[41]。Kato 等在日本 Hiroshima 海湾也发现 4 株交替单胞菌(*Alteromonas* sp.)可以杀灭古老卡盾藻,其中 1 株菌所产的甲藻生长抑制剂(dinoflagellate growth inhibitor, DGI)不仅活性高,且毒性稳定,是一种比较理想的杀藻物质[42]。雪卡毒素藻类-刚比亚藻(*Gamibierdiscus*),在培养后期会出现自亡现象,这种现象的出现可能与共生菌释放的吩嗪类毒素有关[43]。其它的研究也发现,假单胞菌(*Pseudomonas* sp.)、芽孢杆菌(*Bacillus* sp.)、蛭弧菌(*Bdellovibrio* sp.)、黄杆菌(*Flavobacterium* sp.)和腐螺旋菌(*Saprospira* sp.)均可分泌有毒物质释放于水环境中,抑制某些藻类如甲藻和硅藻的生长[44]。

相比于成体,细菌及其毒素对藻类孢囊的抑制作用更为显著。Ma 等证实在海藻中分离的 192 株细菌中,其中有 63 种对孢囊的释放有抑制作用[45]。同样,细菌毒素也影响孢囊的产生[24, 46]。澳洲石莼中分离的 1 株铜绿假单胞菌(*Pseudoalteromonas tunicata*),能分泌一种抗藻肽抑制孢囊的萌发[47]。红藻中交替单胞菌(*Alteromonas* sp.)所产的肽成分和希万氏菌(*Shewanella* sp.)所产的两种脂肪酸(cis-9-oleic acid 和 2-hydroxymyristic acid),同样具有对藻类幼体的抑制作用[48]。

2.3 溶藻(杀藻)酶类

除了直接产生毒素,细菌也能诱导一些胞外酶来抑制有害水华。Daft 等发现 9 种从环境中分离出的粘细菌可溶解鱼腥藻(*Anabaena* sp.),束丝藻(*Aphanizomenon* sp.),微囊藻(*Microcystis* sp.)及颤藻(*Oscillatoria* sp.)。其溶藻机理是粘细菌直接与宿主细胞接触,或通过分泌可溶解纤维素的酶消化掉宿主的细胞壁,进而逐渐溶解整个藻细胞[49]。Mitsutani 等也发现静止培养的假单胞菌(*Pseudoalteromonas* A25)可以产生抑藻的高活性酶[50]。Skerratt 等进一步证实了两种细菌(*Ateromonas* sp.和 *Cytophaga* sp.)能分泌一种溶藻酶,用以抑制和杀灭藻细胞;且该菌具有趋群现象,趋群现象作为溶藻作用的一种信号,能加快溶藻过程的速度响应[51]。

3 藻际环境中的化学防御

在藻际环境中存在着多样的生物组成,彼此间为了竞争生存,存在着“菌与菌”和“藻与菌”之间的克生效应,这种借助化学手段来实现的克生效应被称为化学防御。“菌与菌”之间的防御主要通过抗生素或抗菌素的分泌来实现;而“藻与菌”之间的防御则主要通过自身的代谢产物来完成。

“菌与菌”之间的克生关系,即抗菌能力在藻际细菌中广泛存在。Wiese 等证实从白令海峡褐藻(*Saccharina latissima*)中分离的 210 株共生菌中,有半数具有抑制革兰氏阳性菌或阴性菌的能力[52]。Burgess 等报道源自大型藻表面的可培养细菌中有 35%的个体能产生抗菌物质[53]。Boyd 等也发现从 7 种海藻中分离的 280 株细菌克隆,有 21%的比例显示具有抗菌活力[54]。日本海褐藻和红藻的可培养细菌中,具有抗菌活力的菌株分别占 20% 和 33%[55]。Penesyan 等从澳大利亚近海岸红藻(*Delisea pulchra*)与绿藻(*Ulva australis*)中分离的 325 株细菌中,应用筛选法证实其中能产生抗菌素的比例占到 12%,部分细菌还具有溶藻作用[56]。上述提到的具有抗菌活力的菌株大部分属于假单胞菌(*Pseudomonas* sp.),交替假单胞菌(*Pseudoalteromonas* sp.),嗜麦芽寡养单胞菌(*Stenotrophomonas* sp.),气单胞菌(*Aeromonas* sp.),弧菌(*Vibrio* sp.),希万氏菌(*Shewanella* sp.),链霉菌(*Streptomyces* sp.)和芽孢杆菌(*Bacillus* sp.)[52]。许多芽孢杆菌是高能抗菌素的生产者,因而它能在共生系统中占据优势,成为藻体表面的优势菌[57]。一些报道的具有防污损能力的细菌也多数为芽孢菌属(*B.pumilus*, *B.licheniformis* 和 *B.subtilis*)。除了芽孢杆菌,其它细菌也存在种间克生关系,例如,假单胞菌属(*Pseudoalteromonas* sp.)中的大部分具有活性分子的产生能力[58];绿藻共生菌中的三类假单胞菌能够抑制周从环境中其它细菌或真菌的生长[59];铜绿假单胞菌(*Pseudoalteromonas tunicata*)也能通过抑制其它细菌而达到生物防污损的目的。在实现这一目的的过程中,该菌产生至少 5 种针对性的化合物,包括抗菌蛋白,极性抗幼体分

子, 抗藻肽, 抗真菌生物碱以及紫色杆菌素。这些化学物质共同组成细菌的“化学兵工厂”,以使得该菌在生存环境中具有较强的竞争力[60-65]。这些化学元素的存在使得菌类在微生物共生、竞争以及进化上具有重要意义。

在藻类抵抗细菌的化学防疫中,主要体现在藻类与生物膜之间的防疫机制上。Lu 等报道绿藻对弧菌(*Vibrio anguillarum*)有抑制作用,但并不减少整个异养细菌的数量。随后的研究推测,造成这一现象的内在机理有可能是藻类或者藻类相关的微生物所产的化学物质抑制了外周生物膜的生长[66]。Pang 等观察到当弧菌(*V. alginolyticus* 和 *V. logei*)与红藻(*Gracilaria textorii*)共生培养时,弧菌的整体数量将得到调控,维持在一个较为恒定的数量级[67]。同样,有作者报道当往红藻(*Grateloupia turuturu*)的培养体系中接入弧菌(*V.parahaemolyticus*)进行培养时,菌的生长将会受到抑制,而这种抑制与生物膜的形成有关[68]。

除了针对生物膜的作用,藻类自身释放的代谢产物也是重要的抗菌方式。由于藻类缺乏细胞免疫反应,且处于开放的微生物环境中,因而可以推测藻类具有产生活性次生代谢产物的基本机制,以抵御细菌性微生物的侵袭[69]。藻类的这种抗菌能力早在 1917 年就被发现,并逐渐引起人们的关注。所产生的化合物种类较多,主要包括脂肪酸、酚类、炔烃、萜类、香豆素、羰基化合物以及多糖;这些物质具有消除和控制病原微生物的作用[70-71]。虽然有许多文献报道了藻类的代谢产物具有抗菌活性,然而这些物质在生态层面所起的作用却较少提及,只有少数研究人员调查了几种藻类的代谢产物对藻类腐生菌、寄生虫和病原体的影响,发现抗菌代谢产物的功能体现具有选择性[72-73]。

从生态学的角度看,藻类的抗菌机制也许通过影响共生环境、抑制非成熟分解以及直接抵抗病原生物来实现[72]。这些所需的化学物质有可能是持续表达的,也有可能是由于微生物的存在、或者微生物信号的存在而诱导产生的[74]。这种诱导防疫能够节约代谢成本、降低自我毒性的风险、并具有较强的环境适应性[75]。最近关于诱导防疫机制用来抵抗微生物的研究已逐渐引起人们的关注,Vairappan 等首次证实了源自红藻(*Laurencia majuscula*)的高选择性卤代抗菌化合物,这些化合物的浓度在宿主疾病爆发期增加了 1.2 倍,对 6 种病原细菌具有明显的抑制作用[76]。有趣的是,在另外一个红藻物种(*Laurencia obtusa*),它所积累的卤代化合物与细菌生物膜有关,作者认为这一过程直接参与了抑制细菌污损的过程[77]。

除了分泌抗菌化合物,藻类也具有类似高等植物的非特异性防疫机制,即氧爆发作用[78]。氧爆发通过细胞与细胞间的识别而发生,通过藻细胞膜对入侵生物的信号分子进行识别而完成[79]。常见的非特异性宿主反应诱导物包括寡糖、糖蛋白和糖肽。最近研究发现,其它成分如茉莉酸甲酯和自由脂肪酸也被证实在大型褐藻(*Laminaria digitata*)中能启动氧爆发[80]。事实上,多糖类所诱导的防御机制在大型海藻中已经被证实了,这主要是由于病原菌、附生菌以及内生菌释放的酶类对藻细胞壁的多糖层有降解作用[81]。一个明显的例子在褐藻(*L. Digitata*)中得以发现,孢囊皮层细胞的海藻酸钠低聚糖引起了明显的氧爆发反应,以调控附生细菌的快速繁殖[82]。随后 Küpper 等调查了 45 种褐藻中寡糖与氧爆发的关系,发现 15 株呈现阳性反应,这些藻株富含褐藻胶,且具有较为复杂的形态结构[81]。但也有证据显示巨型红藻(*Solieria chordalis*)通过连续释放过氧化氢,以防止细菌生物膜的形成和藻类附生植物的定植[78]。除了藻类所产生的诱导物,Küpper 等发现革兰氏阴性菌的小分子肽,也被作为藻类的外源诱导物,参与藻细胞的非特异性防疫过程[79, 83]。

4　群体感应及其在藻菌关系中的作用

群体感应(QS)是细菌之间的密度调节信号,被视为细菌的通讯语言,它在菌株特性、生物膜的形成、生态系统的发生以及环境适应性上具有十分重要的作用[84]。QS 系统由自诱导分子、感应分子及下游调控蛋白组成。根据细菌合成的信号分子和感应机制的不同,QS 系统主要包括革兰氏阴性菌的 LuxR/AI-I 系统、革兰氏阳性菌中寡肽介导的 QS 系统,以及 LuxS/AI-2 系统[85-86]。至今,已经确认了包括 AI-1 和 AI-2 在内的多种信号分子,如酰基高丝氨酸内酯类化合物(AHLs),寡肽类化合物、芳香醇类化合物、二酮哌嗪类化合物(DKP),2-庚基-3-羟基-4-喹啉(PQS)以及呋喃硼酸二酯等[87-88]。这些信号

的存在可调节细菌自身的群体行为,以实现某种生态行为[89-90]。

在藻-菌共生系统中,人们发现了藻类生理行为与细菌 QS 的相关性。Krysciak 等在海绵共栖细菌中发现了一系列五肽类化合物 DKPs,他认为海绵细胞和共栖细菌可以利用这种信号分子进行相互感应,使得细菌在海绵体表形成生物膜,促进共栖关系的建立[91]。Natrah 等推测海洋微生物次级代谢产物(其中包括 QS)对浮游植物的增殖有促进作用[92]。此外,Geng 和 Robert 也从微食物环的角度证实了 QS 的存在有利于细菌在藻类表面形成生物膜,生物膜的构建能提供给藻细胞所需的生命元素(如 VB_{12}、硫化物 DMSP、嗜铁素等),而这些微量元素是藻类本身所不能合成的[93]。绿藻的游动孢子与鳗弧菌(*Vibrio anguillarum*)的相互关系证实绿藻对细菌的 QS 信号非常敏感[94]。进一步的研究发现细菌中的 AHL 分子影响了藻类孢子体对钙离子的吸收,进而影响其附着能力[95]。此外,有研究表明红藻(*Acrochaetium* sp.)生活史的完成和幼体的释放严格受 AHL 分子的调控,而这种 AHL 分子由藻类的共生菌所产生[96]。大型海藻石莼的共生菌中,具有 AHLs 生产能力的鳗弧菌对孢囊的成功附着有协助作用;且相比于短链 AHLs,孢子体受长链 AHLs 的影响更甚[93]。Weinberger 等的试验也证明在所测试的 7 种 AHLs 中,N-butanoyl-丝氨酸内酯(C4-HSL)在 100 μmol/L 剂量下能诱导红藻(*Acrochaetium* sp.)孢子的产生与释放[96]。Jones 等使用 16s RNA 分析了自然条件下墨西哥湾裸甲藻(*Karenia brevis*)赤潮发生区和非发生区的菌类组成,发现共栖菌群在发生区和非发生区存在明显差异,并推测这种结构演替的出现可能受细菌自身代谢产物 QS 的调节[97]。Paul 和 Pohnert 在总结藻际微生物与藻类相互作用的工作中,强调微生物具有很强的社会属性,它调节藻类的生长、改变其生理状态、影响其生态过程;这些功能的实现依赖于细菌生物量的形成和结构的建立,菌群 QS 便是其中的推动力之一[98]。

QS 介导的行为除了带给藻类直接的有利因素外,藻类也通过自身的一些方式获得间接的利益。例如藻类通过抑制细菌的种群数量来减少自身的有害效应,这种抑制效应通过干扰 QS 系统的发生来实现[99]。过去 10 年间,不少研究证实海藻能够产生 QS 抑制剂或者其类似物,用以抑制或者钝化 QS 信号的产生[93,100]。以澳大利亚红藻(*Delisea pulchra*)为例,该藻能产生呋喃酮(一种 N-acyl homoserine lactones 的类似物),这种小分子化合物能和细菌的 AHL 受体蛋白竞争性结合,并且促进这些受体分子的降解,以此来抑制外周菌的生长与生物膜的形成[101]。除了红藻产生的呋喃酮以外,不少细菌和真核生物也能产生环二肽(cyclic dipeptides),它能模拟 AHL 分子影响 QS 所介导的调控行为[102-103]。最近,Kanagasabhapathy 等的研究发现,褐藻(*Colpomenia sinuosa*)的一种共生杆菌具有分泌群体感应抑制剂(QSI)或者类似物的能力,以此来抵抗或抑制其它竞争性菌类在褐藻表面的附着[100]。

除此之外,研究者们通过自然发掘和人工合成,已得到多种群体感应抑制剂,包括 QS 降解酶、呋喃酮类化合物、吡咯酮类化合物、二酮呱嗪类化合物、HSL 类化合物以及 AIP 类化合物等[8,104]。其中最有成效的是革兰氏阴性菌 AHL 介导的群感效应抑制剂。与传统的化学药剂相比,QSI 对细菌的抑制机理有所不同,前者在于杀灭生物个体,而后者在于破坏微生物的生存环境和通讯机制,具体体现在下调致病基因的表达、解除生物膜对病原菌的保护、以及竞争性抑制信号分子 AI 与受体的结合从而干扰 QS 体系[84]。应用 QSI 进行微生物的防控,不易产生耐药性,亦不会导致二次污染,体现环境友好性。

上述关于群体感应的研究实例带给笔者两点启示,一是细菌在藻类生态学中的重要作用有可能受 QS 信号的调节;二是针对 QS 信号开发的 QS 抑制剂是阻断藻菌关系、抑制藻类生长的可能方法。因此,聚焦于 QS 信号的研究,将对认识藻华和赤潮防控提供新的视角。

5 化感作用及其在藻菌关系中的作用

1937 年,Molisch 首次提出“化感作用”一词,将其定义为:所有植物(包括微生物)之间的促进或抑制的生物化学作用。1996 年,国际化感学会(International Allelopathy Society)给化感作用做了新的定义:由植物、细菌、病毒和真菌所产生的二次代谢产物(其中酚类和类萜化合物较为常见),这些产物影响农业和自然生态系统中生物的生长和发育。在赤潮过程中,涉及到发生、发展、演替、衰退、消亡

等过程,每一阶段的驱动力都来自于系统中生物的多样性和功能的多样性,生物间的相生相克导演了上述过程的出现。就化感作用而言,涉及的作用主要包括两个方面:菌对藻的抑制以及藻细胞间的相互拮抗。

5.1　化感作用介导的菌对藻的抑制

与前面所述的细菌抑藻的方式不同,微生物存在另外一种特殊的机制,以直接或间接抑制藻类的生长而表现出杀藻效应,即化感机制。最近有研究者从藻际细菌中提取了几种特异性杀藻的化感物质,如 1-羟基吩嗪,它能强烈抑制蓝藻和绿藻的生长;杀藻机理的探索中发现它是通过阻断呼吸链和光合作用来实现的[105]。袁峻峰等从绿裸藻(*Euglena viridis*)水华中分离的优势菌种-中性柠檬酸菌(*Citrobacter intermedius*),它的分泌物对斜生栅藻(*Scenedesmus obliquus*)、粉核小球藻(*Chlorellapyrenoidosa*)、羊角月牙藻(*Selenastrum capricormutum*)、水华鱼腥藻(*Anabaena flosaquae*)和易变鱼腥藻(*Anabaena vqriabilis*)的生长有促进作用;而对银灰平裂藻(*Merismopedia glauca*)、莱茵衣藻(*Chlamydononasreinhardii*)和铜绿微囊藻(*Microcystis aerugiuosa*)的生长具有抑制作用[106]。中性柠檬酸菌的胞外分泌物能促进粉核小球藻细胞个体的生长,对其它藻类主要是影响细胞的大小。其他研究者也发现,从厦门西部海域分离到的几株海洋细菌,在一定条件下具有显著的抑制塔玛亚历山大藻(*Alexandrium tamarense*)生长和产毒的能力,化感物质发挥了很大的作用[107]。在实际应用中,郑天凌等指出如果能从分子水平揭示化感物质作用的机制,探明化感物质基因,利用基因工程手段定向构建高效抑藻菌或活性物质高产菌并应用到赤潮的实际防治中,那将是微生物防治赤潮的一种全新思路[37]。

5.2　化感作用引发的藻间拮抗

微藻间的拮抗作用,通常认为在同一水体中生活着较丰富的浮游植物种群。在藻华形成过程中,其中某种藻类逐渐占据生态位(ecological niche)成为优势种群,从而形成较为单一藻种的水华。这一现象涉及多个复杂的过程,其中种间竞争是重要原因之一。陈德辉等研究表明,微囊藻和栅藻共培养条件下,微囊藻对栅藻的抑制能力相对而言是栅藻对微囊藻抑制能力的 7 倍[108]。高亚辉等研究发现,海洋微藻在生长过程中会不断向周围环境中释放多种化感产物,如酸、酚、酯、萜、毒素、挥发性物质以及抑制和促进因子等。这些产物是海水中化学物质的一个重要来源,它们在海洋生态系统碳循环、微食物环、藻-菌、藻-藻的相互作用中起着重要作用[109]。而正是这些化感产物的存在,在浮游植物与微生物之间的动力学变化中起到了重要作用。

以化感物质介导的藻间拮抗作用有可能是藻华种群演替的重要原因之一。有报道称从 35 种不同微藻培养液的提取物中筛选杀藻化合物,发现海洋蓝藻(*Nodularia harveyana* 和 *Nostoc insulate*)的提取物具有很强的细胞毒性和很广的作用谱,且培养液中的杀藻物质分别为吲哚生物碱(9-Hpyfido-3,4-b-indole)和 4,4′-二羟基联苯(4,4′-dihydroxybiphenyl)[110]。如把四尾栅藻(*Scenedesmus quadrwauda*)的培养液经过滤后培养板星藻(*Pediastrum boryanum*),后者不能生长;但如果把培养液用蒸馏水稀释或煮沸,则会失去抑制作用。这个试验表明栅藻能分泌某种物质来抑制板星藻的生长[111]。小球藻(*Chlorella vulgar*)能分泌一种抗生素-小球藻素来抑制菱形藻(*Nitzschia frustulum*)的生长;多甲藻(*Peridinium polonicum*)能分泌一种抗生素(glenodinin)来抑制栅藻、杜氏藻(*Dunaliella* sp.)的生长[112]。Pratt 发现,中肋骨条藻(*Skeletonema costatum*)引起的赤潮和金黄滑盘藻(*Olisthodiscus luteus*)赤潮常是交替发生的[113]。骨条藻的滤液有促进金黄滑盘藻增殖的作用,而金黄滑盘藻的滤液却明显地阻碍了骨条藻的增殖,这是硅藻与黄藻间的化感作用所致。张冬鹏等认为,链状亚历山大藻(*Alexandrium catenella*)和锥状施氏藻(*Scrippsiella trochoidea*)的存在可能对拟菱形藻的生长有促进作用,这种促进作用的机理或许可以依赖化感作用来解释。拟形菱藻可能分泌有关的化学物质抑制亚历山大藻和锥状施氏藻的生长,而亚历山大藻与锥状施氏藻的存在反而有促进拟菱形藻生长的作用[112]。但是,这种相生相克作用只有在高浓度营养条件下才能表现出来,其原因尚需作进一步的探讨。其它研究中,钟恢明等研究了实验条件下原甲藻(*Prorocentrum donghaiense*)与中肋骨条藻(*Skeletonema costatum*)种间的相互作用,发现中肋骨条藻与原甲藻共培养时的种间相互作用,可以由细胞间的直接接触进行,而并不需要通过介质来完

成[114]。郑迪和段舜山报道了球藻滤液对雨生血球藻(*Haematococcus pluvialis*)的生长具有化感促进效应,雨生血球藻滤液对普通小球藻同时存在化感促进或抑制效应[115]。杨翠云等报道海洋卡盾藻与甲藻之间不仅存在化感效应,同时也存在营养盐竞争[116]。杨维东的报道显示利玛原甲藻(*Prorocentrum lima*)与赤潮藻间存在交互抑制作用,可能会通过分泌化感物质、细胞间接触抑制等途径抑制其它藻的生长[117]。

6 结语

成熟的"藻-菌"共生系统应该是菌群保护藻类免受生物污损等现象的干扰,藻类则为细菌提供生存场所和必要的营养物质,这种共生关系是得益于化学过程的介导[118]。然而,考虑到藻菌间化学交互和化学生态过程的复杂性,一些科学问题依旧需要在后续的工作中得以揭示,未来的工作重点或许可集中在以下几个方面:

(1)微生物及其代谢产物如何通过化学信号调整自身的生态分工和社会学属性。赤潮的发生、发展和消亡过程,藻际微生物的组成与结构是相异的,这种差异的存在在一定程度上具有时空的必然性;而必然性背后的机理,以及藻类生物与周从微生物是否具有相互选择性以形成不同赤潮阶段的藻菌共生体,或许是未来科学问题的一个聚焦点。

(2)共生系统中藻和菌代谢产物的原位分析(溯源、产物鉴定)。精准判断化合物的来源与归属,是理解化学交互作用的前提。解吸电喷雾电离质谱(desorption electrospray ionization mass spectrometry, DESI-MS)或许能带给人们新的曙光,它可以灵敏、高效的定位和探测化合物产生的源头[119]。

(3)化学方法与分子生物学的耦合应用。除了化学方法,还需要使用分子生物学方法和生物信息学的方法来理解藻菌共生系统,如宏基因组技术的应用和实时在线监测仪器的开发。2013 年美国 Woods Hole 海洋研究所 Anderson 团队研发了一款可用于水下分析藻类和微生物 DNA 的在线仪器,可实时获得藻菌数量和多样性数据,为观测藻菌关系的动力学过程带来了曙光[120]。正如 Anderson 教授本人所说:学科的渗透与融合将给化学生态学研究带来新的裨益,未来的藻菌关系将是化学、生物学、信息科学交织的舞台[120]。

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国内邮发代号:82-7,国外邮发代号:M670

标准刊号:ISSN 1000-0933　　CN 11-2031/Q

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编辑部主任　孔红梅　　**执行编辑**　刘天星　段　靖

生　态　学　报
(SHENGTAI　XUEBAO)
(半月刊　1981 年 3 月创刊)
第 34 卷　第 2 期　(2014 年 1 月)

ACTA ECOLOGICA SINICA
(Semimonthly, Started in 1981)
Vol. 34　No. 2 (January, 2014)

编　　辑	《生态学报》编辑部 地址:北京海淀区双清路 18 号 邮政编码:100085 电话:(010)62941099 www. ecologica. cn shengtaixuebao@ rcees. ac. cn
主　　编	王如松
主　　管	中国科学技术协会
主　　办	中国生态学学会 中国科学院生态环境研究中心 地址:北京海淀区双清路 18 号 邮政编码:100085
出　　版	科学出版社 地址:北京东黄城根北街 16 号 邮政编码:100717
印　　刷	北京北林印刷厂
发　　行	科学出版社 地址:东黄城根北街 16 号 邮政编码:100717 电话:(010)64034563 E-mail:journal@ cspg. net
订　　购	全国各地邮局
国外发行	中国国际图书贸易总公司 地址:北京 399 信箱 邮政编码:100044
广告经营许可证	京海工商广字第 8013 号

Edited	by	Editorial board of ACTA ECOLOGICA SINICA Add:18, Shuangqing Street, Haidian, Beijing 100085, China Tel:(010)62941099 www. ecologica. cn shengtaixuebao@ rcees. ac. cn
Editor-in-chief		WANG Rusong
Supervised	by	China Association for Science and Technology
Sponsored	by	Ecological Society of China Research Center for Eco-environmental Sciences, CAS Add:18, Shuangqing Street, Haidian, Beijing 100085, China
Published	by	Science Press Add:16 Donghuangchenggen North Street, Beijing 100717, China
Printed	by	Beijing Bei Lin Printing House, Beijing 100083, China
Distributed	by	Science Press Add:16 Donghuangchenggen North Street, Beijing 100717, China Tel:(010)64034563 E-mail:journal@ cspg. net
Domestic		All Local Post Offices in China
Foreign		China International Book Trading Corporation Add:P. O. Box 399 Beijing 100044, China

ISSN 1000-0933　CN 11-2031/Q　国内外公开发行　国内邮发代号 82-7　国外发行代号 M670　定价 90.00 元