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蓝藻群体颗粒驱动元素地球化学循环研究进展

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摘要：在天然淡水和半咸水水体中，水华蓝藻常以群体颗粒的形态存在。在蓝藻群体颗粒中聚集着大量异养细菌，和蓝藻共同构成了具有独特生态功能的基本单元。与蓝藻单体细胞相比，蓝藻群体颗粒呈现出许多独有的特性，如内部丰富的有机质、急剧的氧化还原梯度、密切的种间互作关系等等。这些特质使得蓝藻群体颗粒在水体中成为元素地球化学循环的反应热点。同时，在蓝藻群体颗粒中也存在着远比单细胞藻类-浮游细菌之间更为密切的种间互作。本综述围绕蓝藻群体颗粒的这些特点，结合当前的研究进展，重点阐述蓝藻群体颗粒中的生物、生理、化学过程，讨论其驱动宏观生态现象的微观机制。未来蓝藻群体颗粒组学研究和多组学微生态数据库的构建或成为探索蓝藻群体颗粒中生命过程及揭示蓝藻水华暴发机制的突破口之一。

关键词：水华蓝藻，蓝藻群体颗粒，藻-菌互作，元素地球化学循环

蓝藻(蓝细菌)是目前已知最古老的产氧生物，根据化石证据可追溯到35亿年前[1]。在淡水和低盐度的水体中，蓝藻在适宜的环境中大量增殖，可造成蓝藻水华现象，极大地扰动水体生态系统功能[2]。近半个世纪以来，全球范围内由于人类活动的影响导致水体富营养化，造成在包括中国太湖、巢湖、美国五大湖、波罗的海等水体中产毒蓝藻如微囊藻 *Microcystis*、节球藻 *Nodularia*、束毛藻 *Trichodesmium* 等成为优势种，形成有害蓝藻水华[3–7]。同时，伴随着全球变暖及二氧化碳水平的持续升高，蓝藻水华发生的频率、强度和持续时间也进一步增加，更多水体或面临蓝藻水华的威胁[8–10]。

不同于真核藻类如硅藻、甲藻等，或超微型的原绿球藻 *Prochlorococcus*、聚球藻 *Synechococcus*，许多水华蓝藻在自然水体中不以单体形态存在，而是由成千上万个蓝藻细胞或藻丝聚集形成群体颗粒状的结构。这些藻细胞由不

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定形的多糖胶被包裹，大量异养细菌聚集在群体颗粒内部、藻细胞表面胶被中或群体周围的无定形粘液中[11–13]，形成了具有独特结构与功能的蓝藻群体颗粒(cyanobacterial aggregates)[7,14]。常见的能够形成群体颗粒的蓝藻来自微囊藻属、长孢藻属 *Dolichospermum*、束丝藻属 *Aphanizomenon*、节球藻属、束毛藻属等。蓝藻群体颗粒一般肉眼可见，其大小可以达到 3–5 mm[15]。群体颗粒的形成不仅有利于蓝藻在水体中占据最佳深度、抑制竞争藻类的生长[16–24]，也能够增强蓝藻对环境胁迫和浮游生物牧食的抵御力[25–29]。此外，大量研究表明，群体状态与单体状态的蓝藻在其介导的物质元素周转等过程中有着截然不同的生理生态特性。在天然水体中，蓝藻群体颗粒而非单体蓝藻，是水华蓝藻行使其生态功能的基本单元。

1 蓝藻群体颗粒中的微生物群落

蓝藻作为水体中初级生产力的主要贡献者，为异养细菌提供了赖以生存的资源。在蓝藻群体颗粒中，更是有着独特的生物、物理和化学条件，和单体蓝藻相比，更利于特定微生物类群的聚集和定殖。现有研究普遍认为，群体颗粒中的蓝藻与许多附生细菌形成共生关系，蓝藻水华的发展、维持和凋亡等过程都受到藻际细菌的调控[30]。在蓝藻群体颗粒中，蓝藻主导生物量，而藻际细菌也可以占到 50%以上的丰度，且有着复杂的群落构成。藻际细菌中的主要类群在门水平上一般是比较保守的，其中出现频率、丰度通常比较高的有拟杆菌门 *Bacteroidetes*、变形菌门 *Proteobacteria*、放线菌门 *Actinobacteria*、疣微菌门 *Verrucomicrobia* 等[31–34]。值得注意的是，蓝藻群体颗粒中的细菌群落和真核藻类的藻际以及植物根际中的细菌群落都有很高的相似度，尤其是其中的一些代表性类群如黄杆菌纲 *Flavobacteriia*、假单胞菌目 *Pseudomonadales* 等的一些成员，在真核藻际和根际中都有发现[35]。从进化的角度来看，这也说明光合生物和异养细菌的互作关系具有一定的统一性。在地球的演化历史中，蓝藻与异养细菌共同存在了超过 20 亿年，与真核藻类和植物相比，蓝藻与藻际细菌经历了更久的共进化历程。因此，解析蓝藻与藻际细菌之间的关系，或能为更高等的光合生物和异养细菌之间的关系提供进化上的思路和启示。

蓝藻群体颗粒中的细菌群落结构受到生物和非生物因素的双重影响。首先，蓝藻本身的影响是毋庸置疑的。例如，Louati 等发现，法国某湖泊中与不同优势水华蓝藻相关联的微生物群落具有显著差异；其中，固氮长孢藻的群体颗粒中 γ-变形菌和疣微菌门占比相对较高，而非固氮的微囊藻群体颗粒中 α-变形菌占比较高[36]。Zhu 等基于太湖的调查发现了类似的现象，且微囊藻群体颗粒中的细菌群落多样性显著高于长孢藻群体颗粒[37]。Te 等发现热带水库中拟浮丝藻 *Planktothricoides* 水华期间细菌群落结构受到藻次生代谢产物 2-甲基异莰醇和 β-紫罗兰酮的影响[34]。Sison-Mangus 等报道了产毒的真核拟菱形藻 *Pseudo-nitzschia* 水华中厚壁菌门 *Firmicutes* 占主导，而不产毒拟菱形藻水华中 γ-变形菌占主导[38]。张军毅、Shi 等均报道，对于微囊藻属的不同藻种，其所形成的群体颗粒中细菌群落组成也显著不同[39–41]；尤其是水华微囊藻 *M. flos-aquea* 和惠氏微囊藻 *M. wesenbergii* 群体颗粒中的菌群结构更为保守，前者中浮霉菌门 *Planctomycetes*、假单胞菌属 *Pseudomonas* 等更为

富集，而后者中芽单胞菌门 *Gemmatimonadetes*、沙雷氏菌属 *Serratia* 等更为富集[40–41]。另外，在蓝藻生长的不同阶段，其群体颗粒中也有着不同的细菌群落结构。如底栖蓝藻 *Phormidium* 群落中的异养细菌早期以 α-和 β-变形菌为主，而鞘氨醇杆菌门 *Sphingobacteria* 和黄杆菌门在中晚期迅速增加[42]。微囊藻群体颗粒在不同季节和水华发展阶段也伴随其附生菌群结构的改变。例如，在玄武湖秋季的微囊藻水华衰退期，γ-变形菌大幅上升[43]；太湖秋季微囊藻水华期拟杆菌的相对丰度相比于夏季显著增加[39]；基于时间序列的网络分析进一步揭示了与微囊藻相关联的细菌类群随季节的变化趋势，如 4 月前水华初期的微囊藻与 β-变形菌、*Cerasicoccaceae* 等呈现一致的分布趋势，在 4 月至 6 月水华发展期与疣微菌门的 *Xiphinematobacter* 呈现一致的分布，在 7 月至 10 月水华暴发中后期微囊藻与 *Cerasicoccaceae*、伯克氏菌目 *Burkholderiales* 紧密相关，在 10 月之后的衰退期与放线菌目 *Actinomycetales* 和黄单胞菌科 *Xanthomonadaceae* 等类群相关[44]。这些研究表明蓝藻宿主及其生长周期和代谢特性对藻际细菌群落起到决定性作用。

同时，蓝藻群体颗粒中的细菌群落必然也受到非生物因素的影响。对于淡水湖泊如太湖，温度、氮、磷等营养盐浓度、太阳辐射和风速的变化都能够影响蓝藻群体颗粒上的微生物群落构成[45–48]。基于波罗的海更大范围的研究揭示，盐度和温度的变化是影响蓝藻和藻际细菌群落的最重要因素[49–51]。不可否认的是，此类在较大区域尺度上、以及之前所述的在较长时间尺度上完成的调查结果必然反映的是环境因子、蓝藻类型(或基因型)及其生长周期对藻际细菌群落的共同作用。若要真正地区分生物因子和非生物因子的影响，一方面可以通过对单一来源的蓝藻群体颗粒在室内控制条件下进行研究；另一方面，也可以通过数据整合来探究不同类型的蓝藻群体颗粒之间细菌群落或功能上的系统差异，寻找蓝藻藻际细菌是否存在某种模式结构。例如，Cook 等通过对全球 12 个湖泊中铜绿微囊藻群体颗粒的分析，发现所有的群体颗粒中均存在变形菌、拟杆菌、梭菌 *Clostridia*、弯曲菌 *Campylobacteria*、芽单胞菌 *Gemmatimonadetes*，以及我们目前还不甚了解的 *Negativicutes*、*Phycisphaerae*、*Ignavibacteria* 等门类。而在不同的湖泊中，尽管这些藻际细菌在相对丰度上存在差异、但在功能上却较为保守，且不受到空间距离的限制；这说明微囊藻群体颗粒中存在着一套共同的细菌功能、或形成一个相互作用组[52]。Li 等通过长期培养获得了 6 组不同来源的微囊藻的稳定群体颗粒、并基于宏基因组分箱得到了一系列藻际丰度较高的细菌基因组草图，同时揭示了滇池微囊藻群体颗粒中的特有细菌如红细菌 *Rhodobacter* spp.、生丝单胞菌 *Hyphomonadaceae* spp.和惠氏微囊藻群体颗粒中的特有细菌如黄杆菌 *Flavobacterium* spp.[53]。这些研究对发现蓝藻群体颗粒中微生物群落构成和功能方面的共性和特性提供了重要价值。

正是由于蓝藻群体颗粒中的藻-菌关系相较于单体状态的蓝藻-浮游细菌之间更加紧密和复杂，我们认为，从系统的角度来发掘藻-菌之间可能存在的互作机制及其受生物和非生物因子的调控机制是未来研究蓝藻群体颗粒中藻-菌关系的重要手段之一。

2 蓝藻群体颗粒中的微观化学环境

与单体状态的蓝藻细胞相比，蓝藻群体颗粒中的微观化学环境、尤其是氧化还原环境更为复杂。一方面，由于氧气在颗粒内细胞之间存在扩散限制，因此在群体颗粒内部会形成一定的氧化还原梯度；另一方面，外界环境的变动如昼夜更替等，又会使群体颗粒内的氧化还原梯度发生复杂的或周期性的变化。尽管对于蓝藻群体颗粒，从微观水平来研究其化学环境在方法学上存在一定的困难，近年来，尤其是针对波罗的海水华蓝藻群体颗粒微观尺度的研究已有了一些报道。例如，基于微探针、纳米二次离子质谱(nanoSIMS)等技术，Eichner、Klawonn、Ploug等对束毛藻[54–55]、节球藻[56–57]、束丝藻[58]群体颗粒内的氧化还原条件进行了微观尺度的表征。这些研究均发现在光照条件下群体颗粒中心的氧气浓度显著高于其表面的浓度，而在黑暗条件下呈现相反的趋势。对于直径超过 1 mm 的蓝藻群体颗粒，黑暗中即使处于饱和溶氧的水体环境，厌氧生境在颗粒内部仍得以存在[57,59]。随着溶氧降低，更小直径的群体颗粒中也将产生厌氧生境；尤其在温度较高的夏季，伴随呼吸作用的加强，小颗粒中产生厌氧生境的机率进一步增加。相应的，蓝藻群体颗粒内的氧气浓度梯度可达 50–100 μmol/(L·mm)[55–57]。这些证据定量地揭示出蓝藻群体颗粒内氧化还原条件的变化，且直接证明了群体颗粒结构的形成促成了厌氧微生境的发生，为蓝藻群体颗粒所介导的一系列厌氧生化过程提供了必要条件。以上研究也表明，微观尺度下群体颗粒中的蓝藻及藻际微生物所面临的化学环境的变化可能远远大于水体中所测得的宏观波动；而正是由于这些复杂的微生境的存在，使得多样的元素循环过程能够在群体颗粒中发生。尽管目前对于淡水湖泊中蓝藻群体颗粒微生境的针对性研究比较缺乏，但我们推测湖泊蓝藻群体颗粒内部也会产生相似的氧化还原梯度。值得注意的是，不同群体形态的蓝藻群体颗粒所呈现的氧化还原梯度或有明显区别。例如，群体中细胞聚集状态较为致密的水华微囊藻、鱼害微囊藻和具有明显胶鞘的惠氏微囊藻，相比较于聚集程度较为松散的史密斯微囊藻或薄片状结构的片状微囊藻[60–62]，前者可能更容易形成较明显的氧化还原梯度，而后者与外界的化学物质交换可能更为充分。

综上所述，蓝藻群体颗粒的结构特征及藻细胞的聚集状态可能是影响蓝藻参与元素化学循环的重要因素。已有研究发现不同大小、不同群体形态的微囊藻群体颗粒中所包含的细菌群落构成存在显著区别[33,39–41,63]，进一步说明了群体颗粒的大小和形态可能通过对微环境的影响间接影响藻际微生物群落及其元素化学循环功能。

3 蓝藻群体颗粒中的藻-菌关系

3.1 蓝藻胞外有机质利于异养细菌定殖与生长

蓝藻群体颗粒不仅为异养细菌提供了附着空间，更通过光合作用固定有机碳、合成并分泌大量以多糖为主的藻类有机质[64]。其中，胞外有机物(extracellular organic matter，EOM)直接支持着群体颗粒中异养细菌的生长[65–67]。铜绿微囊藻的 EOM 由包括多糖[68]、氨基酸[69]、多肽、蛋白质[70]、有机酸[71–72]等在内的复杂化合物组成；拟柱孢藻 *Cylindrospermopsis raciborskii* 的 EOM 中，碳水化合物、脂质、蛋白质、脂肪酸和氨基

酸等均被检测到[73]。蓝藻凋亡后，藻体内的有机质也释放到藻际空间，经过矿化、再加工，重新进入物质循环过程。相较于单体状态的蓝藻，群体颗粒或生物膜中的蓝藻 EOM 包含更广的代谢产物[74]。这些藻际 EOM 大多具有较高的生物可利用性[75]，为异养细菌提供充分的碳源和其他营养物质[76]。外界环境如光强、营养盐水平等均能够影响蓝藻 EOM 的产生和化学构成。例如，随着光照强度的适当提升，鱼腥藻的胞外多糖产量也显著提升[77]；Otero 等发现在氮限制条件下，念珠藻将过量固定的碳转移到胞外多糖[78]；Chen 等在对微囊藻的研究中也观察到了类似的结果，且随着微囊藻 EOM 中糖类物质比重的提高，对反硝化作用起到了更好的促进效果[79]；Huang 等发现沉降的及暗光缺氧条件下的微囊藻依然能够持续分泌有机碳[80]。除此之外，也有研究发现蓝藻 EOM 中的化合物可以使某些异养细菌产生趋向性运动[81–82]，进而吸引特定的异养细菌在藻际定殖，促进有益关系的形成。

3.2 藻际细菌对蓝藻的反馈作用

在海洋中，关于真核藻类与异养细菌相互关系的研究相对来说较为广泛，且已建立了若干模式体系并发现了一些明确的藻-菌合作机制[35, 83]。例如，异养细菌亚硫酸杆菌 *Sulfitobacter* 利用藻源色氨酸合成吲哚三乙酸促进硅藻生长，并提供铵氮以交换藻源碳[84]；海杆菌 *Marinobacter* 分泌光感铁转运蛋白，在黑暗中结合铁元素，并在光下释放，为藻类所利用[85]；藻际鲁杰氏菌 *Ruegeria*、盐单胞菌 *Halomonas*、沟鞭玫瑰杆菌 *Dinoroseobacter* 等为其宿主合成与提供维生素 B12[86–88]。这些研究极大地推动了我们对藻-藻际细菌这一共生体系内部微观过程的认知，其中某些互作机制可能同样也适用于蓝藻和藻际细菌。近年来，包括宏基因组、宏转录组、宏蛋白组、代谢组等在内的组学手段也有力地推进了蓝藻-异养细菌互作的研究。在海洋固氮蓝藻中，Lee 等通过多组学手段确定了束毛藻与交替单胞菌 *Alteromonas macleodii* 间的保守关联，揭示二者之间或存在包括铁、磷获取、维生素 B12 交换、联合碳分解代谢等在内的相互作用[89]；Beliaev 等通过转录组分析揭示了聚球藻和希瓦氏菌 *Shewanella* 共培养体系中，异养细菌利用藻源氨基酸的同时为藻增加了铁的可利用性[90]；在微囊藻群体颗粒中，Li 和任明磊等通过宏基因组分析发现藻际细菌可能协同进行维生素 B12 的合成、支持微囊藻的生长[53,91–92]。

基于已有研究，可以认为大多数藻际细菌为藻的生长提供了正面的影响。例如，Sher 等将原绿球藻与 250 种异养细菌进行共培养，发现绝大多数细菌能够促进藻的生长[93]；Bershova 在研究了 2166 种天然细菌分离株后，发现与蓝藻紧密相关的细菌很少表现出对藻的拮抗作用，而那些通常不与蓝藻相关的细菌更容易对蓝藻产生拮抗作用[94]。不可否认的是，某些蓝藻群体颗粒中必然也会存在与蓝藻相拮抗的异养细菌。在营养限制的条件下，附生细菌可能与蓝藻竞争氮、磷等营养盐[95–96]；有些细菌能够合成有抑藻作用的次级代谢物，如微囊藻群体颗粒中由伯克氏菌目主导编码苯甲酸盐降解通路相关酶，其代谢产物能够抑制藻类生长[91]；有的细菌能够直接产生溶藻作用，如噬纤维菌 *Cytophagia* 中的一些成员[97–98]。这些拮抗细菌的存在加速了藻细胞的更替，使得藻体内的元素和营养物质得以更快地参与蓝藻群体颗粒内的营养循环，利于其他蓝藻细

胞与细菌的生长[35,99]。此外，藻-菌关系也可能随着生长阶段或环境条件而变化。例如，硅藻藻际的交替单胞菌在氮充足的条件下不与藻竞争氮源且能够促进藻的生长，而在氮限制的条件下抑制其生长并与之竞争硝酸盐[95,100]；处于生长期的铜绿微囊藻能够从附生的假单胞菌体内获得数量可观的磷元素，而当铜绿微囊藻处于衰退期的时候，情况变为假单胞菌从铜绿微囊藻体内获取磷元素[101]。以上研究说明藻-菌关系也可能存在动态变化的过程。

值得注意的是，相较于分散的藻细胞，蓝藻群体颗粒的形成促生了一个更加紧密的藻-菌互作体系。在这个体系中，蓝藻与藻际细菌的接触频率大大提高，甚至稳定共存、互相依赖。因此，群体颗粒内的藻-菌关系可能更加符合黑皇后假说(Black queen hypothesis)的观点[102]。该假说认为，在一个体系内部，许多重要的生态功能将不可避免地“沦为”可供整个群落所使用的“公共产品”。群体的共同进化会导致一系列“公共产品”的诞生，并且在自然选择的作用下，部分类群中某些功能基因将被丢失，因此在群体水平上实现了冗余度的降低；而对于这部分类群，它们将依赖于共生的微生物来弥补这些丧失的代谢功能。在微囊藻群体颗粒中，Li、任明磊等通过宏基因组分析发现微囊藻-藻际细菌之间、甚至细菌-细菌之间都或存在一定程度上的功能互补[53, 92]。此类研究的进一步拓展或能为解析蓝藻群体颗粒内的合作模式提供更清晰的思路。最后，尽管微囊藻是淡水中最常见的蓝藻类群之一，至今其无菌的纯培养藻株仍非常难以获得，这也从侧面说明了蓝藻群体颗粒中存在更加复杂的藻-菌关系。因此，如何建立适用于群体颗粒的模式体系，既是蓝藻群体颗粒中藻-菌关系研究的难点，也是重要的突破点。

4 藻-菌关系协同驱动水体元素地球化学循环

4.1 碳循环

水华期间蓝藻通过光合作用固定无机碳，带来了水体初级生产力的巨幅提升；而有机碳异养代谢的增强进一步激发了氮、磷、硫等其他元素的地球化学循环。蓝藻群体颗粒中，附生细菌群落的结构与功能很大程度上受到蓝藻 EOM 底物的调控[103–104]。由于藻类 EOM 化学组分非常复杂，单一类群的细菌难以同时拥有能够利用所有 EOM 的物质转运及酶系统，因此，藻际有机质的周转往往由不同的微生物类群协同完成[104–107]。例如，拟杆菌门的许多成员具有分解复杂生物大分子和藻类衍生物的代谢能力[108–109]。转录组研究发现，不论对于真核藻类或蓝藻群体颗粒，拟杆菌门的黄杆菌纲对藻类 EOM 中高分子聚合物的降解均起到主导作用，可能与其编码并丰富表达 TonB-依赖性转运系统(TonB-dependent transporter，TBDT)相关组件的能力相关[104,110]；基于藻际纯培养菌株的研究也证实了一些黄杆菌菌株对聚糖及蓝藻毒素的降解能力[111–113]。拟杆菌门噬几丁质杆菌科 *Chitanophagaceae* 的细菌也能够分解纤维素和一些大分子复杂有机化合物[114–115]。另外，藻际常见的噬纤维菌纲细菌能够分解包括果胶、几丁质、琼脂等在内的有机大分子，且该类群的菌株常具有溶藻作用[116]；淡水水体中常见的放线菌门在水华期间也占有较高的相对丰度[117–118]，可能与其降解大分子有机物如植源性纤维二糖等物质

的能力有关[110]。

变形菌门的许多成员具有高效降解可溶性有机物(dissolved organic matter，DOM)的能力，且参与了藻际元素循环的多个环节[119–121]。不同于拟杆菌门，变形菌门中尤其是 α-和 γ-变形菌对有机物的摄取更多依赖于 ABC (ATP-binding cassette) 和 TRAP (tripartite ATP independent periplasmic)转运系统，而非 TBDT 系统[99]。海洋中的玫瑰杆菌 *Roseobacter* (α-变形菌)主要利用的碳源为藻源性小分子 DOM，且参与有机硫化物的周转，已有研究证实了其对藻源 EOM 的趋化作用[99,122]。淡水中，伯克氏菌目的成员能够降解芳香族化合物[123–124]，且参与包括硝酸盐还原在内的氮循环过程；假单胞菌目的成员具有降解一系列蓝藻残体和胞外复合物中高分子量化合物的能力[33]；鞘脂单胞菌目 *Sphingomonadales* 中的细菌也能够分解一些藻源性有机质及蓝藻次级代谢产物[125]。综上所述，藻类 EOM 所包含的复杂的底物多样性使得藻际异养细菌能够通过功能上的区分，在群体颗粒中获得各自相应的生态位，这既是微生物群落多样性得以维持的基础，同时也对水体中的碳循环过程起到了重要的调节作用。

4.2 氮循环

蓝藻群体颗粒无疑是水体中氮过程发生的热点。首先，固氮蓝藻往往在氮限制、尤其在 N/P 比较低的水体中勃发，为异养细菌和其他藻类提供氮源[15]。水体中的铵态氮则对固氮反应有着强烈的抑制作用[126]。在波罗的海，由于夏季水体中强烈的氮限制，其水华蓝藻多由固氮蓝藻如节球藻、束毛藻、束丝藻等所主导[15]。淡水湖泊中，固氮长孢藻与非固氮微囊藻的更替在太湖中反复出现[44]；而在滇池中，固氮束丝藻与微囊藻的更替更为典型[127]。尽管固氮过程是厌氧的生物化学反应，但由于固氮作用一般限于异形胞中，因此在有氧的水体中也能够发生[128]。Ploug 等基于微观尺度的表征发现束丝藻的固氮作用仅在日间发生，而在夜晚无固氮作用；并且只有在大于 5 μm 的群体颗粒中才能够检测到固氮作用[58]，进一步表明了群体颗粒的结构对氮循环功能的影响。Klawonn 等揭示了束毛藻昼夜不同的氮过程，同样证明其日间具有更高的固氮速率[59]。通过同位素示踪，研究发现束丝藻所固定的铵氮中约 35%被释放到周围的水体中，为其他微生物所利用[58]。而在淡水的微囊藻群体颗粒内部，宏基因组和宏转录组研究均表明固氮基因及其表达丰度极低[39,129]。

除固氮作用之外，蓝藻群体颗粒也是其他氮过程、尤其是还原性氮过程发生的热点，主要包括反硝化、硝酸盐异化还原成铵(dissimilatory nitrate reduction to ammonium，DNRA)和厌氧氨氧化作用(anaerobic ammonium oxidation，Anammox)等。蓝藻水华期间，随着外源性氮负荷的增加，湖泊水体中氮的脱除速率也显著增加[130]。Chen、许海和肖琳等通过一系列野外及室内的控制实验，都证明蓝藻群体颗粒上发生的反硝化作用是水柱中脱氮的主要过程[131–133]。蓝藻水华期间，蓝藻群体颗粒中反硝化细菌的丰度显著增加[134]；尤其是水华暴发中后期，反硝化细菌的丰度可增加至非藻华期的 100 倍[135]；在水华末期的微囊藻群体颗粒中，我们的研究发现反硝化细菌可能在群体颗粒中异养细菌类群中占据绝对主导地位。在水华末期蓝藻堆积的水体，由于大量蓝藻残体被降解，导致溶氧趋近于零，因

此反硝化作用得以持续发生；而对于非水华末期的健康蓝藻群体颗粒，Klawonn 等揭示了硝酸盐还原作用主要在夜间发生，硝酸盐浓度在群体颗粒的中心降至最低[59]，与群体颗粒中的氧化还原条件相符合。另外，基于实验室培养(未发表)以及功能基因丰度[39]，蓝藻群体颗粒中的厌氧氨氧化作用对水体脱氮的贡献可能远小于反硝化作用。DNRA 作用相关基因在蓝藻群体颗粒中也被发现存在[39]。我们团队通过培养实验发现极度氮限制的厌氧条件下，微囊藻群体颗粒中的反硝化作用逐渐减弱，而 DNRA 作用逐渐增强(未发表)。Zhu 等通过宏基因组分析也表明 DNRA 相关基因在微囊藻群体颗粒中比在长孢藻群体颗粒中更为富集[37]。

硝化作用是有机体中氮素回收再利用的关键步骤，其与反硝化作用相配合也是有机氮脱除的主要方式。对于非固氮蓝藻而言，藻与氨氧化菌之间的关系主要是对铵态氮的竞争作用[136–137]。基于组学分析也发现微囊藻群体颗粒中硝化过程相关基因的丰度很低[37,39]。Shi 等比较了不同大小蓝藻群体颗粒中微生物的群落构成，也发现在较大的群体颗粒中与硝化作用相关的微生物类群丰度最低[63]。因此，硝化作用发生的主要区域可能主要是蓝藻群体颗粒的表面或外部，且水体中浮游的硝化菌群所介导的硝化作用或有着更大贡献。江海洋等通过室内模拟实验，表明微囊藻水华期间铵态氮的硝化作用主要发生在日间[138]。另有研究揭示微囊藻水华期间水体中的氨氧化作用由氨氧化古菌转为氨氧化细菌所主导[135]。而对于固氮蓝藻而言，固氮作用生成的铵态氮能够为藻际氨氧化菌所利用。Tuomainen 等在波罗的海节球藻水华中检测到了硝化作用基因的存在[139]；而 Klawonn 等发现固氮束毛藻藻际硝化作用依然微弱，说明异养细菌和氨氧化菌之间也存在强烈的对铵态氮的竞争作用[59]。

4.3　磷循环

磷是浮游植物生长、细胞内能量代谢及信号传导等过程所必需的关键营养元素[140]，而水体中的初级生产力常常受到磷的限制[141–142]。水环境中磷的主要形态包括溶解性无机磷(dissolved inorganic phosphorus，DIP)和溶解性有机磷(dissolved organic phosphorus，DOP)，一般认为前者是细菌和浮游植物的首选磷源[143–144]。已有的研究表明，海洋蓝藻对于磷限制已进化出一系列适应机制。如，原绿球藻和聚球藻通过合成含有硫和糖的膜脂取代磷脂膜来适应低磷环境[143]；一些蓝藻的基因组中编码了高亲和力磷酸盐结合蛋白基因 *pstS* 以增加对磷的捕获[144]。许多微生物也能够从 DOP 中获取磷，且这种能力在一些海洋蓝藻和浮游植物中也被发现[145–147]。如，磷酸结合蛋白(PstS 和 SphX)和 2 个碱性磷酸酶(PhoA 和 PhoX)的编码基因在束毛藻基因组中均保守存在[148]。其中，碱性磷酸酶可以介导 DOP 的水解，增加蓝藻对磷的吸收[145]。在微囊藻群体颗粒中，宏转录组研究发现无机磷的摄取由微囊藻主导，而有机磷的代谢主要由变形菌表达，说明变形菌在颗粒内部磷的循环再利用方面可能起到重要作用[110]。Hudson 等认为浮游生物群落对磷的内部再生是湖泊浮游生物的主要磷来源[107]。也有研究发现，水华蓝藻对聚磷菌具有富集作用，因此藻际细菌也可能通过磷的高效捕获促进蓝藻的生长[134]。另外，Yuan 等观察到铜绿微囊藻与其附生假单胞菌之间存在磷的循环利用[96]。这些现象或许可以解释为什么某些蓝藻可以在看似营养盐有限的条件下仍以高生物量存在。

4.4 硫循环

海水中由于硫酸根离子的大量存在，一般认为硫元素不是限制异养细菌生长的关键因子。但近年来的研究发现，一些海洋中广泛存在的细菌类群如 SAR11、SAR86 等不具有硫酸盐同化还原途径，而是完全依赖于对环境中可溶性有机硫(dissolved organic sulfur，DOS)的摄取[149–150]。DOS 如二甲基巯基丙酸(dimethylsulfoniopropionate，DMSP)、2,3-二羟基丙烷-1-磺酸酯(2,3-dihydroxypropane-1-sulfonate，DHPS)等多源自于藻类的代谢产物[151–153]。藻类光合作用产生的能量支持了无机硫酸盐的同化还原过程，而其所生成的有机硫化物中约 50%被释放到了水体中[154]。这些还原性的 DOS 相较于高价态的硫酸盐更易于被异养细菌所利用，且其中的碳骨架也能够成为异养细菌的碳源[152]。因此，藻-菌之间 DOS 的释放与利用也是海洋碳循环的一个重要支路[155]。相应的，在一些典型的藻际细菌中发现了有机硫的代谢通路[99]。反过来，异养细菌为藻类提供的维生素 B12 是多数藻类中甲硫氨酸合成不可或缺的辅因子，而甲硫氨酸正是 DMSP 合成的起始底物[154,156]。一些其他的含硫化合物如 DHPS 的代谢途径在异养细菌基因组中发现的频率相对较低，这些专化性较强的物质可能是某些藻类吸引特定细菌类群的策略之一[157]。然而，相较于真核藻类，基于蓝藻-藻际细菌之间含硫物质交换的研究还比较欠缺。有研究报道一些聚球藻和原绿球藻也能够产生包含硫酯的囊泡并排出体外[158]。Li 等基于宏基因组手段揭示了铜绿微囊藻、水华微囊藻、惠氏微囊藻群体颗粒中，藻和多个细菌类群都能够进行硫酸盐的同化还原，且其中的 α-和 β-变形菌同时具有氧化硫代硫酸盐的能力[53]。然而，由于淡水湖泊中硫酸盐浓度相对较低，我们认为异养细菌对硫的摄取可能在一定程度上也依赖于藻源 DOS。迄今为止，对淡水水体硫循环的关注大多围绕蓝藻水华期间所产生的硫化氢和挥发性有机硫化物，因为这些物质是水体异味的主要来源，硫化氢的形成也与湖泛的发生有着密切关系。水华期间硫化氢和挥发性有机硫化物的产生大多是源于死亡藻体中含硫有机质的厌氧分解[159]。Yang 等检测到活体铜绿微囊藻也能够产生挥发性硫化物如二甲基硫醚(dimethyl sulfide，DMS)、二甲基三硫醚(dimethyl trisulfide，DMTS)；有趣的是，这些物质的合成受到假单胞菌 *P. pseudoalcaligenes* 的影响，且在微囊藻不同的生长阶段或存在不同的效应[160]。这项研究为蓝藻群体颗粒中藻、菌共同参与有机硫的代谢与调控提供了实验证据。

5 展望

对于大多具有群体性状的蓝藻，其群体颗粒而非单体状态的蓝藻细胞，是行使生态功能的基本单元。多年来，人们已经认识到自然水体中蓝藻群体颗粒存在的普遍性；未来，更需要从群体的角度来解析蓝藻群体颗粒如何参与元素地球化学循环、进而影响宏观生态过程。一方面，需要构建更多的模式体系进行藻-菌关系研究，寻找藻-菌作用的效应物，以建立在蓝藻群体颗粒这个内部紧密联系的体系中藻-菌甚至菌-菌之间互作的桥梁；另一方面，基于蓝藻群体颗粒组学的数据分析和挖掘能够帮助我们寻找蓝藻群体颗粒中反复出现的规律或模式，并以此构建多组学微生态数据库，这将是探索水体生态系统生命和化学过程的关键所在，也是揭示蓝藻水华暴发机制的突破口之一。

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Biogeochemical cycling processes associated with cyanobacterial aggregates

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Abstract: In natural freshwater and low-salinity waters, bloom-forming cyanobacteria often live in the form of cyanobacterial aggregates. Many heterotrophic bacteria colonize in the cyanobacterial aggregates, subsequently they constitute the fundamental unit with unique ecological functions. Compared with single-celled cyanobacteria, cyanobacterial aggregates exhibit many unique characteristics, e.g., rich organic matter, steep redox gradient, and complex inter-specific interactions. These properties enable cyanobacterial aggregates to become the hotspot for elemental biogeochemical cycling in aquatic ecosystems. Meanwhile, the inter-specific interactions within cyanobacterial aggregates are far more intense compared to those between single-celled algae and free-living bacteria. This review introduces current research progress on these aspects, with a focus on the biological, physiological and chemical processes within cyanobacterial aggregates, and discusses the micro-mechanisms of the macro-phenomena. In the future, the omic research of cyanobacterial aggregates and the construction of multi-omic microecological databases may become the key for exploring life processes within cyanobacterial aggregates and for revealing the mechanisms of cyanobacterial bloom outbreak.

Keywords: bloom-forming cyanobacteria, cyanobacterial aggregates, cyanobacteria-bacteria interactions, elemental biogeochemical cycling

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