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专论与综述

嗜热蓝细菌的固碳机制与应用潜力

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摘　要：嗜热蓝细菌作为热泉等极端高温生态系统的初级生产者，通过高效光合作用驱动碳循环。在热泉高温(>45 ℃)、矿物富集等极端条件下，其进化出独特的适应性机制：在碳同化方面，其依赖核酮糖-1,5-二磷酸羧化酶/加氧酶(Rubisco)及其羧酶体微区室，通过增强底物亲和力与 CO_2 浓缩效率，克服高温对酶活性的抑制；在能量代谢层面，重构热稳定光系统II (PSII)复合体及电子传递链，维持高温下光反应与暗反应的协同；在稳定调控方面，通过糖原动态存储、抗氧化防御及分子伴侣网络实现代谢平衡。系统解析其碳代谢与环境适应的耦合机制、羧酶体结构的动态调控特性及 PSII的高温保护机制，将为合成生物学改造高温固碳底盘细胞(如异源表达嗜热 Rubisco 或构建热稳定电子传递链)提供理论支撑，有望拓展工业高温废气的直接生物转化与含热废水的生物处理路径，助力碳中和目标下的极端环境微生物技术创新。

关键词：热泉极端生态系统；嗜热蓝细菌；碳浓缩机制；固碳潜力；碳中和

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Carbon sequestration mechanisms and potential applications of thermophilic cyanobacteria

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Abstract: Thermophilic cyanobacteria, as primary producers in extreme high-temperature ecosystems, has evolved unique adaptive mechanisms under high-temperature (>45 °C) and mineral-enriched extreme conditions in hot springs. For carbon assimilation, their dependence on ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) and its carboxysome microcellular compartment overcomes the inhibition of the enzyme activity at high temperatures by enhancing substrate affinity and CO_2 concentration efficiency. At the level of energy metabolism, the thermally stabilized photosystem II (PSII) complex and the electron transport chain are reconstructed to maintain the synergy between light and dark reactions at high temperatures. In terms of stability regulation, metabolic homeostasis is achieved through dynamic glycogen storage, antioxidant defense, and molecular chaperone networks. Systematic analysis of the carbon metabolism-environmental adaptation coupling mechanisms, carboxysome structural dynamics, and PSII thermal protection mechanisms of thermophilic cyanobacteria will facilitate synthetic biology-driven engineering of thermophilic carbon-fixing chassis cells (e.g., heterologous expression of thermophilic Rubisco or design of thermostable electron transport chains), thereby expanding the direct bioconversion of high-temperature industrial waste gas and the biotreatment of heat-containing wastewater and promoting the innovation of micro biotechnology for extreme environments in pursuit of carbon neutrality.

Keywords: extreme ecosystem of hot spring; thermophilic cyanobacteria; carbon concentrating mechanism; carbon fixation potential; carbon neutrality

在全球气候变化和生态环境持续恶化的背景下，如何有效减少大气中 CO_2 浓度已成为全球关注的核心议题。自工业革命以来，大气 CO_2 浓度已从 280 μmol/mol 快速上升至 415 μmol/mol，并可能在 21 世纪末突破 600 μmol/mol[1]。在此背景下，极端环境微生物，尤其是嗜热蓝细菌作为高效碳固定的光合原核生物，逐渐成为碳中和研究的新生物资源[2]。

蓝细菌又称蓝藻，是地球最古老的光合微生物之一，在全球碳循环和氧气产生中发挥着重要作用，贡献全球约 40%以上的初级生产力[3]。嗜热蓝细菌因能在 47−90 ℃的高温环境中利用“光-热-碳”稳定生长而被广泛关注[4]。热稳定性酶系统、高效碳浓缩机制(CO_2-concentrating mechanism, CCM)和强抗氧化体系，使得它们能在热泉等极端生态系统中保持稳定的代谢水平[5-6]。此外，嗜热蓝藻还可合成高温稳定酶类、天然色素等生物活性物质，兼具环境生态功能与资源利用潜力[7-8]。这些独特的生理代谢特征不仅体现了其对极端环境的高度适应性，也为深入

解析其固碳机制与拓展应用潜力奠定了基础。

嗜热蓝细菌的光合固碳途径、碳代谢网络及抗逆基因调控机制等成为研究热点，然而，当前嗜热蓝细菌研究多聚焦单一维度导致出现机制割裂、尺度断层和应用脱节的现象，未来亟需整合酶工程、合成生物学及生态学手段等多学科手段，优化人工固碳系统的能量转化效率，推动其在碳中和与极端环境修复中的规模化应用转化。从基础科学角度看，嗜热蓝细菌所展现出的极端环境适应策略为揭示高温胁迫下的生存机制及早期地球生命演化模式提供重要线索[9]；从应用层面，在各自适宜生长的温度范围内，其固碳效率远高于常温藻类，并且耐高温特性使其具备与工业余热资源协同利用的潜力，拓展了碳捕集与封存的应用边界[10]。本文系统综述嗜热蓝细菌的生态分布特征、代谢适应机制、核心碳代谢路径及其在碳减排和绿色制造中的潜在应用，进一步梳理并构建嗜热蓝细菌固碳的机制网与应用链，以期为后续理论研究与技术开发提供参考。

1 热泉嗜热蓝细菌的特征

1.1 热泉生境特征

热泉为嗜热微生物尤其是嗜热蓝细菌提供了重要的生境，其环境条件通常为高温、多样的 pH 值以及富集的溶解矿物。野外调查数据显示，嗜热蓝细菌的适合生长温度范围广泛，适生温度介于 47−90 ℃，并且对水体 pH 的适应范围可达 5.0−10.4[4,11]。其空间分布受地理纬度、海拔高度及地质背景的复合作用影响。例如，低纬度低海拔地区的热泉水温明显高于高纬度或高海拔地区，局部差异可达 12−18 ℃[12]。另外，不同的热泉环境也造就了多样的嗜热蓝细菌群落结构。以冰岛碳酸泉为例，因 CO_2 溶解形成酸性环境，pH 值接近 4.0，适合如湖生假鱼腥藻(*Pseudanabaena limnetica*)等嗜酸性蓝细菌生存[13]；而中国四川省的碳酸盐岩区热泉在 HCO_3^- 缓冲作用下呈中性[14]；肯尼亚马加迪湖的玄武岩热泉因硅酸盐水解形成碱性环境，适合碱性蓝细菌类群繁殖[15-16]。此外，热泉水中常富含金属离子与硫化物，如中国云南省腾冲市热泉中硫化物浓度为 10−50 mg/L[17]，日本别府热泉中铁离子浓度高达 5−20 mg/L[18]，美国黄石公园热泉中砷浓度甚至超 1 mg/L[9,19]。这些条件造就了一个对微生物选择性极强的生态位，也促使嗜热蓝细菌在化学环境梯度下形成特有的进化路径与分布特点。

1.2 热泉嗜热蓝细菌的分布特征

在热泉生态系统独特的环境条件下，作为主要初级生产者的嗜热蓝细菌群落形成了明显的温度梯度分布特征。在水温超过 45 ℃的热泉中，常见包括嗜热聚球藻属(*Thermosynechococcus*)、嗜热鞘丝藻属(*Thermoleptolyngbya*)、泽丝藻属(*Limnothrix*)、席藻属(*Phormidium*)、念珠藻属(*Nostoc*)和伪枝藻属(*Scytolyngbya*)等[20]。当水温升高至 60 ℃以上时，*Thermosynechococcus*、*Thermoleptolyngbya* 和斯塔尼尔氏菌属(*Stanieria*)成为优势类群[6,20-21]；在接近 90 ℃的沸泉中，可检测到如热隐球藻属(*Aphanocapsa thermalis*)和盖式眉藻属(*Calothrix geitleri*)等极端嗜热蓝细菌[4]。同时，嗜热蓝细菌的分布还受到了营养物质和硫化物浓度的影响。研究表明，嗜热蓝细菌通常需要较高的氮磷浓度才能维持基本的生命活动。例如，当氮源充足时聚球藻属(*Synechococcus*)中的铅色聚球藻(*Synechococcus lividus*)在 74 ℃的高温下仍能生存[13]；而硫化物浓度较高的热泉内，硫化物氧化细菌能与嗜热蓝细菌共同抵抗不利环境[22]。此外，地理隔离和热泉环境使得同种嗜热蓝细菌在不同热泉群落中展现出了不同特点。*Thermoleptolyngbya* 作为全球热泉广泛分布的嗜热蓝细菌在不同地区热泉甚至局部地理尺度上均表现出了不同的形态和生理特征[23]。由此可见，热泉环境特征的差异造成了嗜热蓝细菌群落结构的多样化，而其自身也在极端环境压力下产生了个性化的适应机制。

1.3 嗜热蓝细菌的适应机制

嗜热蓝细菌群落展现出不同分布特征的原因除了热泉环境差异外，还有嗜热蓝细菌自身为应对极端环境所产生的适应机制。一方面，嗜热蓝细菌内部差异化的基因表达使得不同种属的嗜热蓝细菌展现出了各具特色的适应策略。嗜热蓝细菌的基因组不仅具有较高的鸟嘌呤(guanine, G)和胞嘧啶(cytosine, C)含量以保持高温下 DNA 三维构象稳定性及遗传信息的完整性[24]，还富含黄素氧还蛋白基因、铁胁迫诱导蛋白基因、热休克蛋白基因等与耐热功能相关的遗传物质[25]。这些基因层面的调控机制为嗜热蓝细菌提供了基础可靠的耐热能力。另一方面，嗜热蓝细菌的适应机制还体现在其对环境胁迫的动态响应。在高温胁迫下嗜热蓝细菌外部的胞外聚合物(extracellular polymeric substances, EPS)和生物膜结构表现出强大的适应性，这些结构所具有的抗脱水、抗氧化和金属螯合等功能，有助于其在热泉生态系统中形成稳定的群落结构[26]。这些特征使得嗜热蓝细菌具备高温下稳定维持光合作用与细胞结构完整性的能力，其中多数种类可在 50−70 ℃维持代谢活性，个别类群还可在 80 ℃以上仍保持生命活动[27]。此外，嗜热蓝细菌的群体防御机制也对其自身抵御极端环境做出了贡献。嗜热蓝细菌群体可通过 EPS 形成具有光合层-代谢层-保护层结构的生物垫，表层的光合层中的嗜热蓝细菌通过产氧光合作用提供能量并分泌 EPS 作为黏合剂；中层的代谢层通过异养细菌与蓝细菌共生分解有机物并固定氮素，形成营养循环网络[28]；底层的保护层通过矿物质沉淀与 EPS 形成的胶鞘层包裹减缓热量传递并维持渗透压平衡[29]。同时，嗜热蓝细菌还会通过群体感应(quorum sensing)调控协调群体行为，分泌群体特异性代谢产物抑制竞争微生物[30]。这些环境响应机制表明嗜热蓝细菌的适应性不仅依赖基因的静态表达，还涉及其对环境变化的动态调控。由此可见，嗜热蓝细菌结构与生理机制已进化为可适应多重胁迫的策略，并在热泉生境中展现出显著的温度适应性、环境敏感性和生态功能多样性，为其后续固碳机制与资源化利用提供有用的生物材料。

2 高温环境下嗜热蓝细菌的高效碳固定机制

2.1 CO_2 浓缩机制优化

热泉高温环境中常伴随 CO_2 气体脱离，导致水体中液相 CO_2 浓度相对较低。为维持高效光合碳同化，嗜热蓝细菌保留多种无机碳转运系统，构建 CO_2 浓缩机制(图 1)。通过涵盖 *Thermosynechococcus*、*Synechococcus*、*Leptolyngbya* 等 17 株嗜热蓝细菌的比较基因组分析，揭示其普遍具备五类无机碳转运系统(BicA, SbtA, BCT1, NDH-1_3, NDH-1_4)，特别是 NDH-1_3 与 NDH-1_4 型 CO_2 摄取系统在所有嗜热蓝细菌中广泛存在，显示出该机制对热环境的普适性[31]。这些转运系统与淡水或低盐蓝细菌(如典型 β-蓝细菌)中 CO_2 转运系统高度相似，而与海洋蓝细菌如原绿球藻属(*Prochlorococcus*)和束毛藻属(*Trichodesmium*)显著不同，后者往往仅保留单一转运模块甚至完全缺失 CCM 相关基因[32-33]。这一差异表明，嗜热蓝细菌所处的低盐、高温、CO_2 挥发强烈的生态环境对 CCM 系统的完整性提出了更高要求。嗜热蓝细菌的 CCM 不仅依赖碳酸氢根转运体(如 BicA、SbtA、BCT1)，还包括高表达的碳酸酐酶(carbonic anhydrase, CA)和 Rubisco 的空间隔离结构——羧酶体，形成完整的细胞级 CO_2 浓缩通路[34]。其核心在于通过膜转运和酶解耦联，实现胞内 CO_2 的局部富集，提高 Rubisco 羧化/氧化选择性，降低光呼吸效应。如图 1 所示，嗜热蓝细菌不仅可以通过多种离子运输方式维持细胞内外的离子梯度，从而支持 CO_2 的跨膜运输；还通过调节细胞膜上的离子通道和转运蛋白，维持细胞内 pH 的稳定；这些机制有助于嗜热蓝细菌维持胞内 CO_2 浓度，从而对抗外界环境 pH 的波动[35]。羧酶体

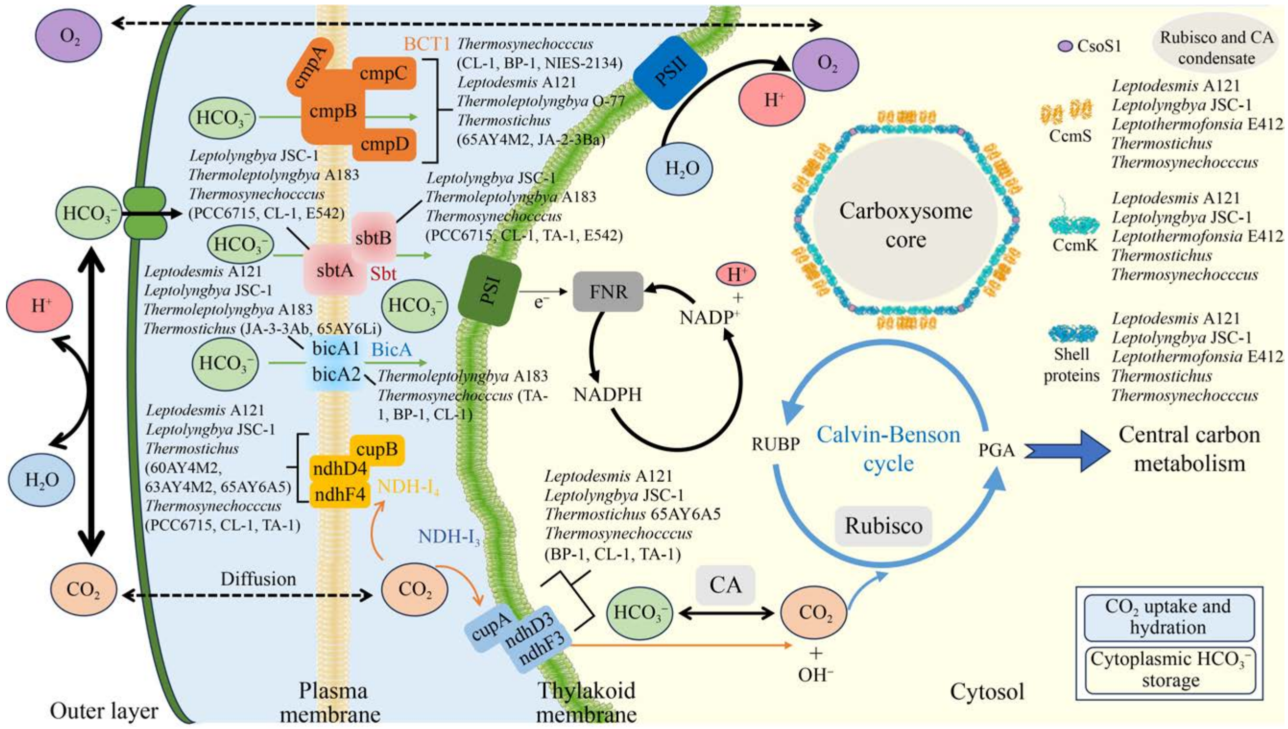

图 1 不同热泉生态系统中嗜热蓝细菌无机碳运输机制与羧酶体差异[31] CO_2 和 HCO_3^-通过扩散或特定蛋白(BCT1、Sbt、BicA、NDH-I$_3$、NDH-I$_4$)实现跨膜运输；嗜热蓝细菌的羧酶体由壳蛋白、CcmS、CcmK 等蛋白质组成；碳酸酐酶参与了胞内 CO_2 和 HCO_3^-之间的转化并显著提高胞内 CO_2 的浓度，为卡尔文循环提供充足原料；在 PSII主导光解水与 ATP 形成，PSI负责产生 NADPH 为卡尔文循环提供动力。

Figure 1 Comparative analysis of inorganic carbon uptake mechanisms and carboxysomal structural variations in thermophilic cyanobacteria across distinct hot spring ecosystems[31]. CO_2 and HCO_3^- are transported across the membrane by diffusion or specific proteins (BCT1, Sbt, BicA, NDH-I$_3$, NDH-I$_4$); The carboxysome of thermophilic cyanobacteria consists of proteins such as chitin, CcmS, CcmK, etc.; Carbonic anhydrase participates in the intracellular conversion between CO_2 and HCO_3^- and significantly increases the intracellular concentration of CO_2, which provides sufficient raw materials for the Calvin-Benson cycle; In PSII dominates the photolysis of water and ATP formation, PSI is responsible for the production of NADPH to provide power for the Calvin-Benson cycle.

作为嗜热蓝细菌 CO_2 浓缩机制的核心结构，不仅能形成局部高浓度的 CO_2 环境，从而提高光合作用效率；还可通过其壳蛋白的结构特性保护 Rubisco 免受重金属离子的毒性影响[36]。嗜热蓝细菌通过高效的 CCM 将胞内积累的 CO_2 浓度提升到外界环境的 500−1 000 倍。

2.2 Rubisco 的热适应与表达调控优势

嗜热蓝细菌的CCM 显著提高了Rubisco 的催化效率，CCM 和 Rubisco 的协同作用使得光合作用效率得以提升。Rubisco 作为 CO_2 固定的关键酶，在高温环境中面临活性损失和氧化应激的双重挑战。嗜热蓝细菌中的 Rubisco 一般属于 Form IB 型，封装于 β-羧酶体中，通过多层级分子机制维持高温稳定性[37]。首先，Rubisco 在高温下的催化常数(k_{cat})与 CO_2 亲和力(K_m)表现出双重适应性。例如，嗜热细长聚球藻(*Thermosynechococcus elongatus*) BP-1 中 Rubisco 在 65 ℃的 V_{max} 较中温菌株提升约 30%，而 K_m (CO_2)降低了 40%，反映其对高温胁迫的酶学响应[38]。其次，结构生物学研究揭示了 Rubisco

大亚基间通过残基替换(如 G261 被替换为 E261)、界面氢键重构和疏水堆积增强构象稳定性；CcmK 等壳蛋白通过特异互作形成稳定的β-羧酶体结构，有效隔离 Rubisco 和 CA，提高局部 CO_2 浓度并抑制氧合反应[39]。此外，Rubisco 激活酶(rubisco activase, RCA)和热休克蛋白(heat shock protein, HSP)等辅助因子也在调节 Rubisco 组装与稳定中发挥重要作用[40]。例如，在高温条件下的 RCA 表达显著提升，协助 Rubisco 维持高效催化活性。pH 是影响嗜热蓝细菌固碳能力的重要环境因子之一，研究表明，嗜热蓝细菌的 Rubisco 通过增强二级结构的稳定性从而在偏碱性环境中具有更高的活性，尤其是在高温高 pH 条件下，其光合作用效率显著提高[37]；当 pH 过高时，嗜热蓝细菌将通过增强其蛋白质的电荷分布或改变其表面电荷特性，使其在碱性环境中仍能保持活性[38]。同时，Rubisco 还通过增强与 Ca^{2+}、Mg^{2+}等金属离子的结合能力或改变构象，减少金属离子对其活性的不利影响[41]。

2.3 光系统与电子传递链的热稳定性

在嗜热蓝细菌的光合固碳过程中光系统起到了至关重要的作用，光系统通过光能吸收与电子传递为 Rubisco 提供所需的 ATP 和 NADPH。嗜热蓝细菌在高温环境下仍能维持 70%−85%的光合效率，其关键在于光系统结构和能量传递链的热稳定性重构[42]。在 45 ℃以上的热泉环境中，具备较强热稳定性 Fe-S 簇的 PSI 成为主导光系统，可替代 PSII完成电子传递，维持还原力供应[43-44]。同时，NDH-1 复合体在嗜热蓝细菌内高度表达，其 NDH-1L 和 NDH-1MS/MS’亚型分别参与 CO_2浓缩和 ATP/NADPH 产量调节。该系统通过调控质子跨膜转运与循环电子流的比例，实现能量耦合效率的提升[45]。胞内昼夜节律系统(KaiABC 复合体)进一步通过温度补偿机制调节光暗期能量分配。在高温光周期中，ATP 优先并主要供给卡尔文循环，光周期 Rubisco 表达与活化占 ATP 使用的 80%，而暗周期则转向抗氧化与糖异生储能代谢(如海藻糖合成等)，实现代谢节律与光合作用的动态耦合，为系统稳定运行提供保障[46-48]。此外，热泉金属离子的存在可能改变嗜热蓝细菌的代谢途径，例如通过提供电子供体或受体，影响其光合作用或化能合成的效率。例如，在热泉中，金属离子(如 Fe^{3+}、Ca^{2+}、Zn^{2+})可能作为催化剂，促进氨基酸的聚合反应，从而影响固碳过程[49]。然而，金属离子的毒性也可能对嗜热蓝细菌产生负面影响。例如，当热泉内 pH 值降低时，某些金属离子(如 Cu^{2+}、Zn^{2+})的毒性会显著增加，从而抑制嗜热蓝细菌的生长和固碳能力[50]。这表明在热泉环境中金属离子浓度和 pH 值对嗜热蓝细菌的固碳机制具有双重影响。

2.4 抗氧化胁迫与碳代谢稳态维持

高温常伴随活性氧(reactive oxygen species, ROS)积累，这将干扰嗜热蓝细菌的光合固碳过程、抑制其固碳酶活性、破坏其光合电子传递链[51]，嗜热蓝细菌因此进化出多层次抗氧化系统以维持固碳过程的代谢稳态。胞外多糖不仅形成物理隔离屏障，还富含酚羟基和羧基等活性基团，具备高效金属螯合和抗氧化能力[52-53]。同时，嗜热蓝细菌胞内还含有丰富的非酶抗氧化剂(如谷胱甘肽、抗坏血酸)及热稳定酶系统，在高温下其表达显著上调[52,54]。例如，嗜热菌株表达的超氧化物歧化酶(superoxide dismutase, SOD)在 60 ℃时仍保有 90%以上的活性，其酶半衰期也大幅延长。在分子调控层面，嗜热蓝细菌通过提高基因组 G+C 含量、完成 *hsp* 家族扩增(*hsp*70 表达量提升超 20 倍)以及完善抗氧化转录模块(如 *isiA-fldA* 协同表达)形成系统性抗热应激的响应网络[23,55]。结合热休克因子(heat shock element, HSE)介导的快速响应机制，嗜热蓝细菌能在几分钟内迅速调整蛋白质折叠与 ROS 清除机制，维持细胞功能稳定[56]。除高温外，pH 值的偏离和金属元素的累积也会导致嗜热蓝细菌 ROS 的积累，进一步损伤细胞结构，嗜热蓝细菌中富含的酚类化合物、类胡

萝卜素和类黄酮等非酶类抗氧化剂同样可以清除由 pH、强紫外光等条件产生的 ROS[57]。嗜热蓝细菌通过多种机制维持在热泉重金属环境中的稳态：研究发现嗜热蓝细菌可通过金属离子结合蛋白螯合重金属离子，减少其对细胞的毒性，同时还可以通过水平基因转移(horizontal gene transfer, HGT)保留源自古生菌和细菌的重金属耐受基因提高其抗金属毒性能力[58]。

3 热泉嗜热蓝细菌的碳代谢网络与极端环境适应机制

在高温、低溶解态 CO_2、高光强等极端环境下，热泉嗜热蓝细菌通过重塑碳代谢通路，构建了一套高度热稳定、能量耦合紧密的碳流调控体系。

3.1 稳定表达的碳代谢关键生物大分子

嗜热蓝细菌利用复杂的碳代谢网络将固定的无机碳转化为具有热稳定性且功能明确的生物大分子，这些生物大分子是嗜热蓝细菌适应热泉极端环境的基础。嗜热蓝细菌内常见的碳代谢生物大分子包括：稳定的光合色素蛋白、关键代谢酶、分子伴侣以及细胞结构蛋白，其共同维系了细胞膜完整性、蛋白质构象稳定性以及遗传物质的复制表达。以光合色素蛋白为例，藻蓝蛋白(phycocyanin, PC)和别藻蓝蛋白(allophycocyanin, APC)不仅在高温下维持结构稳定，还能有效参与能量捕获与传递[59]。如 *Thermosynechococcus* sp. HN-54 的 PC 在 50 ℃水浴 5 h 后仍保持 90%以上活性[60]。PSII的稳定性也依赖于特有的 *Psb*27/28 复合体和 D1 蛋白修复机制。分子伴侣如 HSP_{60}、HSP_{70} 和 GroEL 通过 RNA 温度计(RNA thermometer, RNAT)调控表达，快速响应热胁迫，协助蛋白正确折叠[42]。细胞膜脂肪酸组成也发生优化：饱和脂肪酸与支链脂肪酸比例升高，增强膜刚性与热稳定性[61]。另外，嗜热蓝细菌含有一种有铁离子结合功能的 DNA 保护蛋白，不仅能帮助嗜热蓝细菌克服热泉环境中重金属离子毒性，还能通过芬顿反应抑制自由基的产生从而保护光系统免受氧化损伤[62]。嗜热蓝细菌所含有的带有正电荷的多胺与负电荷的多聚磷酸盐(polyphosphates, polyP)不仅可以保护细胞免受氧化损伤，还能作为热泉 pH 与重金属离子的缓冲剂[63]。

3.2 适应多重胁迫的光合碳同化路径

嗜热蓝细菌的光合碳同化途径在热稳定生物大分子的协同作用下能平稳运行。相较于中温蓝细菌，嗜热蓝细菌在 50−65 ℃环境下仍可维持 70%−85%的碳同化效率，这归功于光合作用的多级耦合强化[7]。从光反应到卡尔文循环的全过程体现出热稳定性、能量分配优化和分子进化适应的协同作用(图 2)。在光反应阶段，PSII核心 D1 蛋白更新速率提升至 3−4 次/h，PSI 通过 Fe-S 簇维持稳定电子流，使 ATP 和 NADPH 输出分别达到 8−12 mmol/(g·h)与 4−6 mmol/(g·h)[65]。同时，NDH-1L 型循环电子流系统显著提升 ATP/NADPH 比(达 1.94)，优化能量供需关系[66]。在暗反应中，Rubisco 与磷酸核酮糖激酶(phosphoribulokinase, PRK)等关键酶表现出高热稳定性与高催化效率，50 ℃条件下 *Thermosynechococcus elongatus* 的 PRK 的 V_{max} 提升至 320 nmol/(L·s)[67]。海藻糖合成途径通过整合碳代谢网络调控，优化碳源分配以提升生物热稳性[68]。如图 2 所示，面对热泉多种的 pH 和重金属离子的胁迫，嗜热蓝细菌的抗氧化系统得到了充分的激活。它们通过类囊体吸收来自间质中的 H^+，在形成跨膜质子梯度的同时，为光化学反应的进行与抗氧化酶的产生提供还原力[69]。热泉极端环境下的 HGT 使得某些嗜热蓝细菌获得并表达固氮基因，其碳同化路径与氮同化机制紧密相连，光合作用产生的 ATP 和 NADPH 为氮转运和同化提供能量与还原力[64]。

3.3 糖异生分解与碳存储代谢的胁迫调控机制

糖异生不仅是嗜热蓝细菌碳代谢的核心途径，也是其应对高温胁迫的重要策略。在热、高盐、高光环境中，嗜热蓝细菌通过重构糖异生网

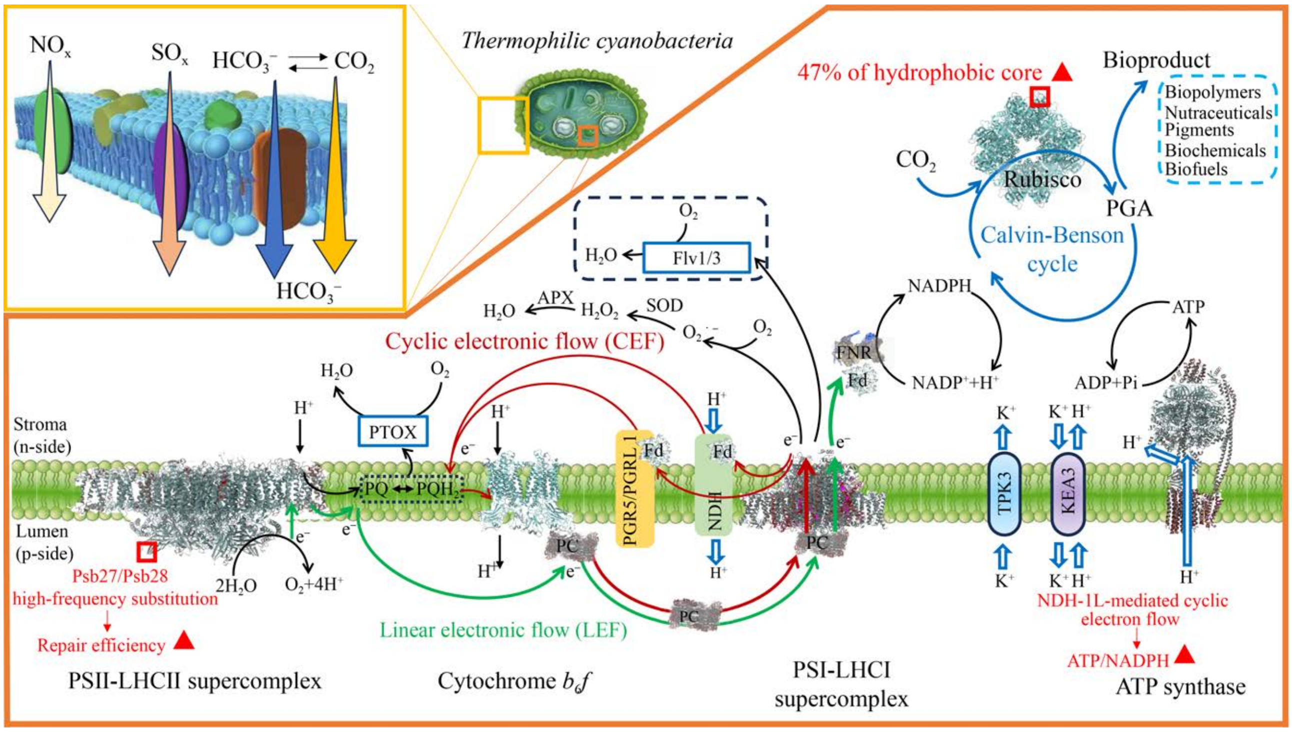

图 2 嗜热蓝细菌光合碳同化途径及调控机制[64] PSI和 PSII在膜上呈均匀分布，仅局部范围存在富集差异。PSII优先捕获高能 450 nm 蓝光(核心吸收峰 700 nm)并主导光解水与 ATP 的合成；PSI主要利用红光(核心吸收峰 680 nm)负责 NADPH 的生成；光状态转换与 CEF 途径协同调节能流分配；抗坏血酸过氧化物酶(APX)和超氧化物歧化酶(SOD)协同抵抗氧化应激；质体醌氧化还原酶(PTOX)优化对光系统的保护；红色三角形表示该通路相较常温蓝细菌提升。

Figure 2 Thermophilic cyanobacterial photosynthetic carbon assimilation pathways and regulatory mechanisms[64]. PSI and PSII are uniformly distributed on the membrane, with only localized differences in concentration. PSII preferentially captures high-energy 450 nm blue light (core absorption peak at 700 nm) and dominates water photolysis and ATP synthesis; PSI primarily utilizes red light (core absorption peak at 680 nm) to generate NADPH; Photosystem state conversion and the CEF pathway synergistically regulate energy flow distribution; Ascorbate peroxidase (APX) and superoxide dismutase (SOD) synergistically resist oxidative stress; Plastid quinone oxidoreductase (PTOX) optimizes protection of the photosystem; The red triangle indicates that this pathway is enhanced compared to mesophilic cyanobacteria.

络，有效耦合渗透保护、能量再生与碳流循环。其关键酶如 PEP 羧激酶(phosphoenolpyruvate carboxykinase，PEPCK)和蔗糖合成酶活性显著增强，例如拟胶球藻(*Gloeocapsopsis*) AAB1 的 PEPCK 活性可达 12.8 U/mg，海藻糖合成速率提升至 4.3 μmol/(g·h)[70]。三羧酸循环(tricarboxylic acid cycle，TCA)在热稳定性酶(如 α-KGDH 与柠檬酸合酶)支撑下，构建“双向代谢枢纽”，支持基础代谢、抗氧化物合成与能量供给。蔗糖高浓度反馈调控琥珀酸脱氢酶活性，诱导碳流转向糖原储存。糖原/海藻糖积累与昼夜节律联动，暗期糖异生通量受 KaiC 调节精确配合 TCA 循环需求，维持碳氮平衡、降低 ROS 水平，实现碳源回收与能量冗余控制的双重目标[71]。同时，嗜热蓝细菌在代谢条件下，不仅可通过调节膜的通透性与选择吸收机制减少 pH 和重金属的毒性影响，还能在一定条件下积累如 Mn^{2+}、Fe^{3+}等特定的金属离子来增强其抗

逆性[72]。研究表明这些具有多价态的金属离子不仅能作为抗氧化剂抵抗氧化损伤，还能激活某些糖异生和碳储存代谢途径并形成螯合金属离子的配体(如海藻糖、聚酮类等)从而降低金属毒性[73]。这些机制不仅揭示了嗜热蓝细菌在极端环境下的适应策略，也为开发与嗜热蓝细菌相关的新型材料和药物提供了理论基础和实践指导。

3.4 光呼吸途径的极端适应性与碳效率维持

在嗜热蓝细菌中，光合作用和光呼吸之间存在复杂的相互作用和联系。它们通过共享的电子传递链、代谢调控和能量代谢形成一个动态的能量网络。尽管光呼吸常被视为能量浪费，但在高温下，嗜热蓝细菌通过优化光呼吸通路与重建旁路代谢，实现碳回收效率提升和氧化胁迫缓解[74]。嗜热蓝细菌的光呼吸关键酶热稳定性得到充分增强：甘氨酸脱羧酶(glycine decarboxylase, GDC)在高温下通过疏水界面增强稳定性，保留 83%以上活性，GroEL 协助其延长半衰期至 6.5 h[75]。在此基础上，嗜热蓝细菌通过光呼吸为卡尔文循环提供充足补给：嗜热侧生藻(*Fischerella thermalis*)通过光呼吸途径有效回收 2-磷酸甘油酸，并通过酶促反应将前者转化为 3-磷酸甘油酸重新进入反应[76]。同时，通过乙醛酸循环(glyoxylate cycle)形成高温碳回收旁路，有效绕过 TCA 循环脱羧步骤，在 65 ℃通量占比可达 42%[15,42]。在动态调控方面，*NdhR* 既是转录因子，响应 α-酮戊二酸、2-磷酸甘油酸等代谢物，调控碳转运与光呼吸基因的表达，又在热泉复杂环境中充当信号分子，参与碳氮代谢平衡[77]。此外，热泉环境 pH 和重金属离子会造成嗜热蓝细菌 Rubisco 活性下降从而导致光呼吸增强[72]。为了克服这些问题，一方面，嗜热蓝细菌通过调节光呼吸途径中的关键酶(如磷酸甘油酸激酶、甘油酸脱氢酶等)来减少毒性产物[78]；另一方面，由于铁是叶绿素和 Rubisco 的必需元素，而锰是光呼吸途径中多种酶的辅因子，所以嗜热蓝细菌通过调节这些金属离子浓度和利用效率维持其代谢平衡[79]。

4 固碳潜力与应用前景

热泉嗜热蓝细菌因其高温适应性、高光合效率及碳同化能力，具备广泛的工程利用前景。当前研究与实践主要集中在工业废热协同碳捕集、极端环境生态修复、合成生物学平台构建以及资源化开发等方面，体现出其在碳中和与绿色转型背景下的重要价值。

4.1 工业废热协同碳捕集

工业废热造成的能源损耗已成为全球制造业低碳转型的核心挑战。嗜热蓝细菌在高温(>45 ℃)条件下仍能稳定生长，并具备良好的酶热稳定性及光合活性，是天然适配工业与热环境的固碳候选生物[80-81]。相较于传统中温藻类，嗜热蓝细菌可在无冷却系统控制的条件下直接耦合高温烟气或热尾水余热资源，实现能源梯级利用并显著降低综合运营成本。研究表明，*Thermosynechococcus elongatus* E542 可耐受 1.0 mol/L $NaHCO_3$ 及 376.6 mg/L NO_x、523.3 mg/L SO_2 的烟气模拟环境[7]。此外，部分嗜热蓝细菌具备促进碳酸盐沉淀能力，其 EPS 中的羧基、氨基糖等基团可络合 Ca^{2+}，诱导碳酸钙沉积，构建微生物诱导碳矿化(microbially induced carbonate precipitation, MICP)过程，实现生物-矿物协同碳封存[82-84]。

4.2 极端环境生物处理

热泉嗜热蓝细菌长期适应高温、高矿化度和重金属环境，显示出优良的耐受性和生物处理潜力(表 1)。在废水处理方面，嗜热蓝细菌不仅能吸附和沉积重金属离子(如 Fe^{3+}、Cu^{2+}、As^{3+})，其 EPS 也具有优异的吸附能力[29]。相较于常规物理/化学/生物处理，嗜热蓝细菌主导的生物处理技术绿色高效、成本较低且不易产生二次污染，已被证实可去除多种污染物(如染料、抗生素、挥发性有机物等)[2]。此外，部分蓝细菌还能合成具有抗菌活性的多肽与次级代

表 1　嗜热蓝细菌生物处理潜力

Table 1　Biotreatment potential of thermophilic cyanobacteria

类型 Type	物种 Species	应用温度 Application temperature (℃)	去除率 Removal efficiency (%)							生物量 Biomass (mg/(L·d))	脂质含量 Lipid content (mg/(L·d))	参考文献 Reference
			Chemical oxygen demand	N	P	Zn	Cu	Pb	其他 Other			
城市污水 Urban sewage	*Anabaena* sp. LS68	–	98.6	100.0	96.5			–	–	215.7	7.2	[85]
	Thermosynechococcus sp. CL-1	50.0	–	–	–	–	–	52.6	76.0 Cd	2 736.0	–	[86]
	Oscillatoria limosa	–	–	94.9	–	28.5	10.1	85.0	52.0 Cd	–	–	[87]
	Nostoc commune	–	–	97.6	–	29.0	8.5	90.0	49.0 Cd	–	–	[87]
	Synechococcus elongatus BDU13091	–	–	–	–	–	–	–	70.0 Ur	–	–	[88]
纺织废水 Textile wastewater	*Phormidium laminosum*	–	99.0	99.0	100.0	–	–	–	–	268.0	39.0	[89]
	Spirulina platensis	–	79.4	92.9	68.3		55.6	–	42.9 Se	112.2	–	[90]
	Synechococcus sp.	45.0	–	–	–		–	–	68.6 活性黑 B 染料 Reactive black B	–	–	[91]
	Phormidium sp.	48.0	–	–	–	–	–	–	92.6 拉马唑染料 Ramazolium blue	–	–	[92]
乳品废水 Dairy wastewater	*Anabaena ambigua*	–	50.0	52.9	63.1		–	–	–	11.6	–	[93]
	Arthrospira platensis	46.0	98.4	98.8	100.0	–	–	–	–	241.6	158.0	[94]
	Microcystis aeruginosa	–	–	100.0	34.0	–	–	–	–	–	–	[95]
糖业废水 Sugar wastewater	*Thermosynechococcus* sp. CL-1	50.0	–	99.0	47.0	–	–	–	–	2 296.8	92.5	[96]

–：该参数在这项研究中未提及。

–: This parameter was not mentioned in the specific reference.

谢物，有望用于控制水体致病菌，提高水质安全性[50,97-98]。

4.3 合成生物与绿色制造

嗜热蓝细菌因其独特的热稳定蛋白系统和模块化代谢网络，正在成为合成生物学研究与绿色制造体系的重要模式生物。其 Rubisco 和 RCA 等基因可外源表达于农作物中，提升其在高温、干旱环境下的光合效率与抗逆能力[99]。例如，*Thermosynechococcus* 的 Rubisco 的特异性因子(specific factor, SR)值高达 222，远高于普通植物(90−95)，显示出优异的碳固定潜力[38]。此外，嗜热蓝细菌还可作为微生物燃料电池(microbial fuel cell, MFC)阳极催化剂，在 55 ℃ 无细胞体系中实现电子流驱动氢气释放，展现其在新能源技术中的拓展性[99-100]。此外，嗜热蓝细菌具有生长速度快、易于基因操作、代谢途径丰富的特点，未来通过推动光能捕获、固碳、抗逆、系统代谢工程等方面研究的突破，开发出超越自然进化的高效光合底盘，并最终建造高版本的光驱动细胞工厂[101]。通过整合热适应启动子、HSP 蛋白表达模块及代谢通路编辑，嗜热蓝细菌有望构建广温耐受型的碳转化平台，服务合成燃料、热稳定酶、生物塑料等绿色产品生产。

4.4 嗜热蓝细菌综合应用潜力

嗜热蓝细菌不仅具备高效碳捕集与抗逆性，其快速生长、产脂潜力及藻蓝蛋白、类胡萝卜素等高附加值产物赋予其多元资源化开发前景[102-104]。现有研究表明嗜热蓝细菌及其代谢产物可用于生物能源、生物肥料、天然色素、食品添加剂、医药原料等领域(图 3)[105-124]。例如，*Thremosynechococcus elongatus* BP-1 具有种类丰富的多糖，其分子量、糖醛酸含量等结构特征在抗病毒活性、糖尿病治疗等领域展现出了较强潜力[45,116]。在农业与环境领域，嗜热蓝细菌被探索用于土壤改良、固氮调节、生物肥料、废水处理等，具备微生态修复和资源循环功能[119-124]。例如，有学者使用 *Synechococcus* sp. MA19 生产出的聚 β-羟基丁酸酯可替代工业塑料，以减少传统塑料制品潜在的微塑料污染[121]。同时，其基因组中的 CRISPR-Cas 系统及天然质粒为基因工程提供了可用工具[2]。通过代谢工程、高通量筛选与生物反应器集成优化，未来可推动嗜热蓝细菌向更高效、可规模化、资源复合利用方向发展，为“碳中和”与“零排放”目标提供微生物解决路径。

5 总结与展望

热泉嗜热蓝细菌作为典型的极端环境光合原核生物，凭借其卓越的高温适应能力和高效碳固定机制，在应对全球气候变化、实现碳中和目标中展现出独特优势。本文从热泉生态系统的环境特征出发，系统梳理了嗜热蓝细菌的种群组成与生理适应机制，重点剖析了其在高温胁迫下构建碳浓缩机制、Rubisco 结构热适应、光电系统稳定性维持以及碳代谢网络重塑等关键生物学过程。研究显示，热泉生态系统以高温(47−90 ℃)、高矿物含量(硫化物、金属离子)为典型特征，形成对微生物选择性极强的极端环境，嗜热蓝细菌因此形成了适应极端环境的生态特征与适应机制。一方面，嗜热蓝细菌形成了结构与功能协同的物理屏障，通过胞外聚合物与金属、矿化物螯合构建出抗氧化抗脱水结构。同时，由 SOD、过氧化氢酶-过氧化物酶(catalase-peroxidase, KatG)、谷胱甘肽等组成的抗氧化系统与热休克蛋白形成敏感响应网络以维持代谢热稳态。在基因层面，高 G+C 含量基因组、RNAT 及 KaiABC 实现代谢动态分配。另一方面，嗜热蓝细菌的固碳机制与中温蓝细菌相比也存在显著不同。嗜热蓝细菌所具有的多模块无机碳运输载体与羧酶体协同构建出 CO_2 浓缩机制，显著提高极端环境下的羧化效率。通过提高饱和脂肪酸/支链脂肪酸的比例、完成光合色素蛋白氢键重构、优化光呼吸旁路、增强甘氨酸脱羧酶的热稳定性等层面的协同作用提升碳回收效率。转录因子通过分子信号调

图 3　嗜热蓝细菌的资源综合化利用途径

Figure 3　Integrated resource utilization pathway of thermophilic cyanobacteria.

控光呼吸基因的表达，实现碳流在光/暗期的精准分配。

在理论层面，嗜热蓝细菌作为极端环境中的生产者，是揭示地球环境变迁与探索生命起源的重要原核生物，未来应通过分子机制解析突破羧酶体自组装动态、光系统复合体的热稳定界面等生物学瓶颈，通过单细胞测序解析高温条件下核心基因簇(如 CCM 操纵子、热休克蛋白家族)的表达阈值与调控网络，借助分子动力学与量子化学计算，建立光合色素蛋白在高温下的激子-震动耦合模型，揭示非相干能量传递的量子相位同步机制。从应用角度出发，工业余热的利用效率低且前期投资高，而嗜热蓝细菌具备较高的工业适配性与环境弹性，在高温碳捕集、污染治理、生物材料制造等方向展现出广阔前景。其可直接耦合工业废热、富含 N/P 的尾水以及烟气资源，支撑构建“热-碳协同”的高温固碳体系，推动构建“自净城市”，同时具备抗重金属、降解有机污染物及合成高附加值天然产物的多重功能，适用于极端生态系统的生物处理与资源回收。合成生物学与代谢工程的发展也为其异源表达平台构建和精准路径

调控提供了新机遇。另外，本研究团队发现[125]，嗜热蓝细菌作为未经人工改造的极端微生物，其产物相较于常温蓝细菌而言具有更高的稳定性，产生的活性物质中不仅具有产量高、多胺及多聚磷酸盐，还富含高 polyP 聚合度、高浓度和高纯度的稳定体活性颗粒生物材料，未来不仅可满足食品、日化等领域的应用要求，还能满足临床医疗等严格条件，具有极大的实际应用价值和商业前景。

然而，尽管嗜热蓝细菌具有巨大的应用前景与优势，但至今仍未能广泛应用，许多瓶颈问题亟待处理。一方面，嗜热蓝细菌的关键酶在高温下具有初始高活性，但长期运行中的结构稳定性不足使得处理效率的持续性受到较大影响。另一方面，现有生物反应器设计存在着气体传质效率低、工艺适配性差的问题，使其难以兼顾嗜热蓝细菌的生长需求与工业废气与废水的特性。未来需通过合成生物学、反应器工程及工艺优化多学科交叉突破，推动其从实验室研究走向工业化实践。着重提升嗜热蓝细菌高温酶稳定性、开发低能耗培养系统及开展复合菌群协同机制研究，以释放其在环境治理中的潜力。

总体而言，嗜热蓝细菌的研究已从基础生物学向工程应用快速转化，其碳固定机制与热适应策略为碳中和提供了“微生物解决方案”。未来通过解析光合-代谢-环境互作的分子语言、开发“光-热-碳”协同技术体系、构建极端环境生物技术标准将成为研究焦点。随着合成生物学与人工智能的交叉融合，嗜热蓝细菌有望在2030年前实现规模化应用，为全球碳循环调控与绿色制造开辟新范式。

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