

赵康,张磊,李凯凯,等.干旱区土壤自养微生物研究进展[J].中国沙漠,2022,42(5):177-186.

干旱区土壤自养微生物研究进展

赵康^{1a}, 张磊^{1a}, 李凯凯^{1b}, 王斐², 张丙昌^{1b}

(1. 山西师范大学 a. 生命科学学院, b. 地理科学学院, 山西 太原 030000; 2. 山西农业大学 资源与环境学院, 山西 太原 030000)

摘要: 微生物自养固碳是维持干旱区土壤微生物群落结构及异养活动的重要过程,并影响地表生物结皮的演替及生态功能。近年来,土壤微生物组学的广泛应用,拓展了蓝细菌及真核藻类土壤自养微生物功能群研究,揭示了非蓝细菌类原核微生物向土壤输入有机质的可能。基于此,本文综述了干旱区土壤蓝细菌及藻类的分布及功能特征,并总结了环境因子的调控作用,重点总结了近几年对非蓝细菌自养微生物功能群及其生态功能的探索,最后对干旱区土壤自养微生物功能群研究的发展进行了总结与展望,以期深入理解干旱区土壤微生物群落的形成及发展机理提供理论基础,并为良好生物结皮的构建提供科学依据。

关键词: 自养微生物; 生物固碳循环; 生物土壤结皮; 无机化能营养; 干旱区土壤

文章编号: 1000-694X(2022)05-177-10

DOI: 10.7522/j.issn.1000-694X.2022.00033

中图分类号: S154.36

文献标志码: A

0 引言

微生物的有机质输入过程是维持干旱区土壤微生物群落及功能的重要因素。这些自养微生物驱动了细菌、真菌及土壤动物的代谢过程,影响土壤微生物群落演替,加速生物土壤结皮(以下简称生物结皮)中碳、氮、磷等养分转化水平^[1-2],并促进地表生物结皮的形成、发展及理化性质(温度、碳、氮养分)的有序变化^[3-4]。蓝细菌及藻类被认为是干旱区土壤有机质输入的关键类群,并驱动地表生物结皮的形成与发展。近几年的研究表明,营化能及光能营养的微生物,如H₂氧化微生物、氨氧化微生物及不产氧光合细菌广泛分布于干旱的土壤中^[5]。这些不同能量获取类型的微生物具有编码生物固碳循环的基因,是潜在的自养微生物^[6-8]。本文从干旱区土壤自养微生物功能群出发,总结了干旱区土壤蓝细菌、藻类群落随地表生物结皮演替的变化规律及其对环境因子的响应,重点综述了近年来围绕土壤非蓝细菌类原核自养微生物的研究进展,以期加深对干旱区土壤微生物群落及功能维持机制的认识。

1 光合自养微生物驱动半干旱生物结皮的形成及演替

生物结皮是干旱、半干旱地区土壤表层的典型覆盖物。它们是由蓝细菌、藻类、细菌、真菌、地衣和藓类及土壤颗粒形成的有机复合体,在生态系统的物质循环、能量流动、植被演替和生态修复中发挥着重要的生态功能^[9-12]。自养微生物群落的演替是生物结皮形成及发展的主要特征^[13]。根据生物结皮中主要的光合自养型生物,可将生物结皮分为藻结皮、地衣结皮及藓类结皮^[14-15]。土壤发展至藻结皮阶段即可改变干旱、半干旱生态系统地表水文过程,显著减小水流渗透及其对土壤的侵蚀能力^[16-18],显示出生物结皮在干旱区生态修复中的价值。蓝细菌及藻类是干旱区土壤主要的光合自养微生物类群,它们对生物结皮演替的作用主要体现在:①作为初级生产者调控微生物异养过程,②胶结土壤颗粒、促进生物结皮结构的形成。目前,蓝细菌及藻类在干旱区土壤及生物结皮中的分布特征及其驱动机制已经被系统研究,并已经应用于荒漠生物结皮的构建^[19-21]。如在中国库布齐、腾格里

收稿日期:2021-12-07; 改回日期:2022-03-02

资助项目:国家自然科学基金项目(U2003214);山西省基础研究计划项目(20210302124361);山西省高等学校科技创新项目

作者简介:赵康(1988—),男,山东淄博人,博士,主要从事干旱区土壤微生物生态学的研究。E-mail: zhaokang@sxnu.edu.cn

通信作者:张丙昌(E-mail: zhangbc@sxnu.edu.cn)

及古尔班通古特沙漠的有效实践;通过接种蓝细菌及藻类能够在短期内显著提高土壤叶绿素 a 含量及生物结皮盖度(14%—48%),并促进地衣及藓类结皮的形成^[11,22-24]。

1.1 蓝细菌群落随生物结皮形成及发展的演替规律

干旱、半干旱生态系统蓝细菌及藻类的不断生长能够粘连土壤颗粒形成藻结皮。同时,藻结皮具有远高于裸土阶段的 CO₂ 净固定速率^[25-26],促进了微生物的异养过程,加速土壤碳氮养分转换^[3]。因此,蓝细菌及藻类被认为是生物结皮形成及发展的关键^[27-28]。以形成生物结皮的蓝细菌的功能差异,可将其分为三大类群:①丝状蓝藻,例如 *Microcoleus* (微鞘藻);②适应结皮环境并具有较高碳、氮循环速率的蓝细菌,如通常为单细胞的 *Chroococcidiopsis* (拟甲色球藻)、*Scytonema* (伪枝藻)及 *Stigonema* (真枝藻);③偶见蓝细菌类^[28]。其中,丝状蓝细菌因其不断生长的藻丝能够粘连土壤颗粒,因此被认为是生物结皮结构形成的关键^[28-29]。

在生物结皮形成前,干旱、半干旱土壤中即有蓝细菌类微生物的定殖^[30-31]。而此时,丝状蓝细菌如 *Microcoleus* 及 *Schizothrix* (裂须藻)等是土壤中蓝细菌群落的主要组成部分,其通过不断生长的束状藻丝连接形成的网状结构稳定土壤颗粒^[29]。同时,这些早期定殖的丝状蓝细菌能够为 *Scytonema*、*Tolypothrix* (单歧藻)及 *Nostoc* (念珠藻)等具有较高固氮速率蓝细菌的定殖创造条件^[32]。随着 *Scytonema*、*Tolypothrix* 及 *Nostoc* 等蓝细菌的定殖,土壤表层伪枝藻素等有机质的累积形成深色遮光层。此时生物结皮发育至深色藻结皮阶段^[32]。深色藻结皮的形成使得生物结皮的理化性质(如温度)发生显著的变化,并对生物结皮中生物群落的组成产生潜在影响^[4]。

1.2 干旱区土壤及生物结皮中的真核藻类

以往对干旱区土壤藻类的研究大多以形态学的角度展开,关注藻类在生物结皮中的分布特征。*Klebsormidiophyceae* (链丝藻)、*Zygnematophyceae* (双星藻)、*Chlorophyceae* (绿藻)、*Trebouxiophyceae* (共球藻)、*Ulvophyceae* (石莼)、*Diatomea* (硅藻)、*Eustigmatophyceae* (真眼点藻)及 *Xanthophyceae* (黄藻)是生物结皮中常见的藻类^[28,33-34]。以形成生物结皮中藻类功能的差异,可将其分为四大类群:

①生物结皮促生藻类;②附生藻类;③与地衣共生藻类及④适应水生环境的藻类。其中,生物结皮促生藻类,如 *Zygogonium* (膝接藻)及 *Klebsormidium* (克里藻)通常为丝状或具有分泌黏性物质的特性,能够粘连土壤颗粒,是生物结皮形成的主要藻类^[28]。基于藻类形态学的研究发现,藻类群落随生物结皮的形成及发展发生有规律的变化。古尔班通古特沙漠土壤及初级阶段生物结皮中的藻类主要为 *Fragilaria* (脆杆藻)及 *Amphora* (双眉藻),而在藓类结皮阶段, *Palmellococcus* (集球藻)是藻类群落的主要构成物种。同时,藻类生物量也随着生物结皮的演替表现出先升高后降低的趋势,其生物量的最大值出现在地衣结皮阶段^[35]。

1.3 土壤水热条件影响蓝细菌及藻类的群落组成及固碳能力

研究表明温度及水分条件是影响生物结皮中蓝细菌群落组成的关键;年降水量、年均气温、土壤温湿度调控生物结皮中蓝细菌的群落组成^[19,36-38]。在温度及水分条件的影响下,干旱区土壤中蓝细菌的群落组成往往由 *Microcoleus vaginatus* 及 *Microcoleus steenstrupii* 主导的群落发育为 *Chroococcidiopsis* 及 *Nostoc* 等固氮蓝藻群落^[39]。这可能由于随着地表生物结皮的形成及发展,温度的升高抑制了 *M. vaginatus* 的生长^[40-41]。除此之外,温度的上升往往会导致蓝细菌相对丰度的降低^[42-43]。对干旱区土壤中藻类群落的研究表明,其群落构成亦受温度及水分条件的调控。如南美干旱、半干旱土壤中藻类的研究表明,水分条件的改善提高了土壤藻类物种多样性^[44]。南北极土壤中的藻类群落结构(主要为 *Chlorophyceae*、*Trebouxiophyceae* 及 *Xanthophyceae*)受到降水、土壤有机质、氮、硫及磷含量的影响^[45]。

除此之外,水分条件也是影响干旱区土壤光合固碳过程的重要因素。这主要取决于生物结皮是否形成以及蓝细菌及藻类对水分的响应差异。干旱区生物结皮的碳交换过程取决于降水的强度及维持湿润的时间^[46-47]。单次降水事件首先导致了生物结皮 CO₂ 释放速率的短暂升高,随后生物结皮才出现活跃的 CO₂ 净固定状态,并且这种活跃的 CO₂ 净固定状态会随着生物结皮中水分的减少而逐渐降低,直至恢复到降水前水平^[48-49]。因此,蓝细菌及真核藻类的群落组成及其固碳能力都受到土壤水热条件的调控。

2 干旱区土壤非蓝细菌类原核自养微生物研究进展

干旱区土壤中, Actinobacteriota(放线菌)、Proteobacteria(变形菌)及 Chloroflexota(绿弯菌)是微生物群落的优势种, 并且这些微生物通常被认为是专性异养微生物, 以分解有机质满足生长需求^[50-52]。然而, 由于初级生产力的匮乏及高温、干旱、强紫外等环境胁迫, 这些细菌如何维持它们的能量及有机质需求成为焦点。最近基于土壤基因组学的研究表明, 干旱区土壤微生物能够进行诸如氨氧化、 H_2 氧化及不产氧光合过程等多种能量代谢途径^[5, 53]。同时, 这些微生物能够潜在地耦合生物固碳循环合成有机质^[6, 8, 53]。这对于维持低有机碳输入的生态系统的生产力及生物多样性至关重要^[30, 38, 54]。尤其在生物结皮形成之前, 这些适应寡营养、干旱、极端高温的自养微生物可能通过其有机质输入功能缓解环境胁迫, 为蓝细菌及藻类的定殖创造必要的微环境, 促进微生物群落的演替^[3, 30, 55]。

2.1 以生物固碳循环为基础的自养微生物生态学研究

目前, 土壤自养微生物生态学研究的最直接手段是以编码特定生物固碳过程的关键基因展开。自20世纪40年代卡尔文循环被发现至今, 已有7种生物固碳过程被发现, 卡尔文循环、还原性三羧酸循环、3-羟基丙酸循环、还原性乙酰辅酶A途径、3-羟基丙酸/4-羟基丁酸途径、二羧酸/4-羟基丁酸途径以及新近发现的反向甘氨酸裂解途径, 并且被微生物广泛利用^[8, 56]。现有的研究大多以卡尔文循环展开, 鲜有研究涉及其他6类生物固碳循环。

卡尔文循环(CBB)被认为是分布最广泛的生物碳固定循环, 编码 *RubisCO* 酶(卡尔文循环限速酶)的基因成为研究自养微生物群落分布特征最常用的指示基因。自然界中具有催化活性的 *RuBisCO* 酶为 form I 和 form II^[57], 通常分别采用 *cbbL* 及 *cbbM* 基因指示能够进行卡尔文固碳循环的自养微生物类群。已知的能够利用 CBB 循环固定 CO_2 的微生物在分类系统中隶属藻类、光合自养及化能自养型的古菌、蓝细菌^[58]、好氧及兼性好氧的 α -、 β -及 γ -Proteobacteria^[8, 38, 55, 59-60]、进行铁硫氧化的 Firmicutes(厚壁菌门)、Chloroflexi(绿弯菌门)^[57, 61]、部分 *Mycobacterium*(分枝杆菌)^[62-63] 及 *Pseudonocardia*

(假诺卡氏菌)物种^[6]。这些自养微生物除了能够利用光能进行固碳循环, 还能够利用诸如 H_2 及硫的代谢过程获取能量^[5, 64]。

目前, 鲜有涉及其他6类生物固碳循环的微生物生态学研究。基于微生物宏基因组的研究表明, 温带荒漠生物结皮中编码一氧化碳脱氢酶的基因(*coxL*)丰度远高于编码 *RubisCO* 酶的 *cbbL* 基因, 表明生物结皮中自养微生物通过还原性乙酰辅酶A途径固定 CO_2 的潜能^[65]。现有的研究通常以 *aclB*、*porCDAB* 及 *acsB* 等基因来定量研究环境样本中的自养微生物类群^[66]。如表1所列, 这些基因能够指示环境样本中隶属于 *Helicobacter*(螺旋菌)、*Hydrogenobacter*(氢杆菌)及 *Rhodospirillum*(红螺菌)等能够进行还原性三羧酸循环的自养微生物^[67]; *Ruminococcus*(瘤胃球菌)、*Blautia*、*Clostridium*(梭菌)、*Aminobacter*(氨基杆菌)及 *Bradyrhizobium*(慢生根瘤菌)等能够利用还原性乙酰辅酶A途径固定 CO_2 的自养微生物^[68-69]; *Nitrosopumilus*、*Crenarchaeum*、*Rhodospirillum* 及 *Bacteroides* 等能够进行3-羟基丙酸循环/4-羟基丁酸循环的自养微生物^[70-71]; 以及隶属于 Proteobacteria、Actinobacteria 及 Firmicutes 等能够进行3-羟基丙酸循环途径的自养微生物^[72]。而在获取维持生物固碳循环的能量方面, 这些微生物也表现出了多样性。

2.2 微生物 H_2 氧化过程与生物固碳循环的潜在耦合

干旱土壤中, 微生物的 H_2 氧化过程被认为是最主要的能量获取途径^[53, 73]。这种化能过程曾被认为是微生物休眠阶段主要的获能方式, 在辅助微生物休眠过程中发挥关键的作用^[74]。能够进行 H_2 氧化过程的微生物隶属于 Actinobacteria、Proteobacteria、Chloroflexi、Firmicutes 及 Euryarchaeota(广古菌)^[69, 75-76]。这些类群中的部分微生物同样具有编码包括卡尔文循环(IE型 *RubisCO*)等固碳循环关键酶的基因^[6, 53, 77], 能够潜在地将能量获取途径与生物固碳循环耦合, 完成自养过程。例如, 基于 $^{14}CO_2$ 标记培养的研究表明, 微生物在黑暗培养的条件下仍能够向沙漠土壤固定 CO_2 , 并且可能与微生物的 H_2 氧化获能过程存在密切的关联^[53]。而具有高 H_2 亲和力和脱氢酶(group 1h [NiFe]-hydrogenases)的微生物类群可能在极端环境的碳输入及微生物群落结构维持中发挥关键的作用^[54, 65, 78-79]。干旱、半干旱的荒漠及南极土壤中, 能够进行 H_2 氧化的微生物类群

表 1 生物固碳循环指示基因及其对应的自养微生物类群

Table 1 Functional genes of different autotrophic CO ₂ fixation pathways and corresponding microbial groups								
生物固碳循环	还原性乙酰辅酶 A 途径		3-羟基丙酸双循环	3-羟基丙酸循环/ 4-羟基丁酸循环		还原性三羧酸循环		
功能基因	<i>acsB</i>	<i>coxL</i>	<i>pcc/acc</i>	<i>hcd</i>	<i>accA</i>	<i>aclB</i>	<i>oorA</i>	<i>porA</i>
门	Firmicutes	Proteobacteria	Proteobacteria	Thaumarc	Thaumarchaeota	Aquificae	Aquificae	Chlorobi
	Euryarchaeota	Actinobacteria	Actinobacteria	haeota	Firmicutes		Thermotogae	Proteobacteria
			Chloroflexi		Proteobacteria		Proteobacteria	Firmicutes
			Deinococcus-		Bacteroidetes		Firmicutes	Thermotogae
			Thermus					Euryarchaeota
属			Firmicutes					
			Euryarchaeota					
			Bacteroidetes					
	<i>Blautia</i>	<i>Aminobacter</i>		<i>Cenar-</i>	<i>Nitrosopumilus</i>	<i>Perse-</i>	<i>Helicobacter</i>	<i>Chlorobaculum</i>
	<i>Marvinbryantia</i>	<i>Bradyrhizobium</i>		<i>chaeum</i>	<i>Thermoanaero-</i>	<i>phonella</i>	<i>Hydrogeno-</i>	<i>Helicobacter</i>
	<i>Syntrophococcus</i>	<i>Burkholderia</i>		<i>Nitro-</i>	<i>bacter</i>		<i>bacter</i>	<i>Clostridium</i>
	<i>Acetitomaculum</i>	<i>Mesorhizobium</i>		<i>sopumilus</i>	<i>Rhodospirillum</i>		<i>Thermotoga</i>	<i>Thermotoga</i>
		<i>Mycobacterium</i>			<i>Erythrobacter</i>		<i>Thermoanaero-</i>	<i>Archaeoglobus</i>
		<i>Stappia</i>			<i>Rhodobacter</i>		<i>bacter</i>	<i>Pyrococcus</i>
	<i>Clostridium</i>	<i>Stenotrophomonas</i>			<i>Bacteroides</i>		<i>Geobacter</i>	<i>Methanococcus</i>
	<i>Methanoregula</i>	<i>Xanthobacter</i>					<i>Desulfovibrio</i>	
							<i>Campylobacter</i>	

广泛存在(每克土重基因拷贝数可达10⁹)并活跃地表达编码一氧化碳脱氢酶及脱氢酶的基因,表明通过此途径进行有机质碳输入的可能^[6,54,80]。

2.3 氨氧化微生物的生物固碳循环

营化能自养的氨氧化古菌及氨氧化细菌广泛分布于干旱、半干旱土壤中,影响生物结皮中碳氮养分水平^[81-82]。这些隶属于Proteobacteria、Crenarchaeota(泉古菌)及Thaumarchaeota(奇古菌)类的微生物一度被认为是专性自养微生物^[7,83],能够耦合氨氧化过程及3-羟基丙酸循环/4-羟基丁酸循环固定大气CO₂^[8,84-85]。目前,生物结皮中氨氧化细菌或古菌的研究大多关注其对生物结皮的氮循环过程的影响,鲜有研究涉及其CO₂固定功能。研究表明,氨氧化细菌及古菌在沙漠裸沙中指示每克土重基因拷贝数可达10⁵,并且其在表层(0—2 cm)土壤的丰度远高于(>20倍)生物结皮^[86-87]。而在裸沙中,隶属于Clostridiaceae及Proteobacteria的微生物可进行活跃的生物固氮作用^[88-89],为氨氧化过程输入底物。随着干旱区土壤表层生物结皮的形成及发展,氨氧化古菌也可能受到细菌、真菌的强烈竞争而导

致其丰度逐渐减少^[86]。

2.4 不产氧光合过程与生物固碳循环的耦合

不产氧光合细菌是干旱、半干旱土壤除蓝细菌及藻类之外能够利用光能的微生物类群。这些隶属于Proteobacteria、Chloroflexi、Acidobacteria(酸杆菌)及Gemmatimonadetes(芽单胞菌)^[90-92]的微生物占生物结皮中可培养微生物的0.1%—5.9%^[30,93]。不产氧光合细菌通过细菌叶绿素(Bacteriochlorophyll)或视紫红质(Rhodopsin)捕获光能,并耦合异养或自养过程进行种群增长^[92,94]。营自养型的光合不产氧细菌主要通过卡尔文循环或3-羟基丙酸途径固定CO₂^[8,94]。而现有的研究表明,不产氧光合细菌能够使生物结皮的有机质有效积累,并能够有效维持微生物的异养过程^[30,95]。

不产氧光合细菌能够在37℃条件下生长^[93,96],而这些条件往往限制了蓝细菌及藻类的增殖,造成其在裸沙微生物群落组成中较低的相对丰度^[97-98]。因此,这些适应干旱、高温及高盐的环境的微生物也被认为在温带荒漠生物结皮的形成过程中发挥重要作用^[30]。除此之外,部分不产氧光合细菌兼具

固氮及活化磷的功能,可能为藻类等的生长创造有利条件,促进生物结皮的发展^[99-100]。

3 自养微生物对土壤碳输入及微生物群落的影响

迄今,我们仍无法确切地评估特定自养微生物类群与土壤有机质输入过程之间的联系。以往关于自养微生物有机质输入过程的研究或从宏观水平出发研究自养微生物整体的CO₂固定速率^[25-26,101];或从纯细菌生理过程出发,揭示纯细菌进行的固碳循环及其潜在的有机质固定效应^[102-103];亦或从生物固碳循环关键功能基因出发,探索自养微生物的分布特征及其对土壤有机质固定的潜在影响^[38,104],尚无研究对不同自养微生物类群的有机质输入能力进行系统分析。

生物结皮CO₂通量监测及土壤¹³CO₂同位素标记的研究表明,早期发育阶段的生物结皮整体能够以70—120 μmol·m⁻²·min⁻¹的速率固定CO₂^[25,101,105],并能够以18—29 mg·kg⁻¹·d⁻¹的速率向高寒草表层土壤(0—2 cm)输入有机质(以CO₂计)^[38]。在寡营养的土壤中,土壤自养微生物往往表现出了较高的净固碳速率^[38]。纯培养细菌生理学的研究也发现越来越多的微生物能够通过无机化能过程获取能量,维持种群生长,如*Acidithiobacillus ferrooxidans*及*Chloroflexus aggregans*等^[73]。基于微生物功能基因的研究表明,化能自养微生物是纳米比热带沙漠生物结皮中活跃表达固碳基因的自养微生物类群^[106]。新近的研究也表明,荒漠土壤及生物结皮在黑暗条件下能够吸收外源添加的¹³CO₂,并且¹³CO₂固定速率与H₂氧化细菌存在正相关关系^[53]。

微生物群落结构的规律性演替是生物结皮最典型的特征。随着干旱区地表生物结皮的形成与发展,微生物总量及多样性逐渐增加^[86,107-108],这主要与生物结皮不断增长的有机质输入能力有关^[31]。由于藓类及维管植物的匮乏,早期发育阶段生物结皮微生物群落结构的维持及变异可能更依赖于自养微生物的有机质输入。如对古尔班通古特沙漠生物结皮的研究发现,真核藻类及地衣真菌能够有效指示生物结皮的多功能性特征的转变^[109]。现有的研究表明,生物结皮微生物群落结构主要受到确定性(环境及种间关系)过程的影响^[31]。其中以土壤有机质为主的环境因子只决定了微生物群落变异的13%—23%^[110],凸显出了种间关系对生物结皮

微生物群落结构的影响。对毛乌素沙漠生物结皮微生物网络分析表明,*Microcoleus*为藻结皮阶段微生物群落的模块枢纽(Module hubs),是微生物群落的关键物种^[2]。然而在裸沙中,Firmicutes细菌处于微生物群落结构的核心(Keystone microbes),并与Actinobacteria及Acidobacteria微生物存在正关系,即潜在的共生关系或生态位的重叠^[2,111]。迄今,这些关键物种对微生物群落结构维持的内在机理尚未被完全揭示。现有的研究表明,微鞘藻是早期发育阶段生物结皮中的主要光合自养微生物,而部分隶属于厚壁菌门的微生物也具有H₂氧化等化能营养的潜力^[19,73,78]。

4 展望

土壤自养微生物功能群作为干旱区土壤微生物群落的重要组成部分,驱动了干旱区土壤微生物异养过程。随着土壤微生物组学技术的发展及广泛应用,越来越多的非蓝细菌类原核微生物被发现具有潜在的生物固碳能力,这极大拓展了我们对干旱区土壤微生物群落维持的理解。迄今,土壤自养微生物功能群及其潜在的生态学功能尚未被系统揭示。这首先体现在自养微生物功能群固碳过程的调控机制尚未被清晰阐述。目前已知的自养微生物功能群中,大部分是混合营养型微生物,存在自养以及异养过程的转化。因此,环境因子(水分、有机质等)的变异可能导致微生物的营养过程的转变。除此之外,自养微生物对土壤异养过程的影响过程尚未被系统阐述;干旱区土壤自养微生物的存在是否驱动了土壤微食物网的形成及演替还不明确。对这些问题的探索将有助于我们理解维持干旱区土壤生态功能的内在机制,为干旱区的生态修复提供理论依据。

参考文献:

- [1] Guan P T, Zhang X K, Yu J, et al. Soil microbial food web channels associated with biological soil crusts in desertification restoration: the carbon flow from microbes to nematodes [J]. Soil Biology & Biochemistry, 2018, 116: 82–90.
- [2] Zhou H, Gao Y, Jia X H, et al. Network analysis reveals the strengthening of microbial interaction in biological soil crust development in the Mu Us Sandy Land, northwestern China [J]. Soil Biology & Biochemistry, 2020, 144: 107782.
- [3] Maier S, Tamm A, Wu D, et al. Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts [J]. ISME Journal, 2018, 12 (4):

- 1032–1046.
- [4] Couradeau E, Karaoz U, Lim H C, et al. Bacteria increase arid-land soil surface temperature through the production of sunscreens[J]. *Nature Communications*, 2016, 7: 10373.
- [5] Leung P M, Bay S K, Meier D V, et al. Energetic basis of microbial growth and persistence in desert ecosystems[J]. *mSystems*, 2020, 5(2): e00495–19.
- [6] Ji M, Greening C, Vanwonderghem I, et al. Atmospheric trace gases support primary production in Antarctic desert surface soil[J]. *Nature*, 2017, 552: 400–403.
- [7] Hugler M, Sievert S M. Beyond the calvin cycle: Autotrophic carbon fixation in the ocean[J]. *Annual Review of Marine Science*, 2011, 3: 261–289.
- [8] Berg I A. Ecological aspects of the distribution of different autotrophic CO₂ fixation pathways[J]. *Applied and Environmental Microbiology*, 2011, 77(6): 1925–1936.
- [9] Pointing S B, Belnap J. Microbial colonization and controls in dryland systems[J]. *Nature Reviews Microbiology*, 2012, 10(8): 551–562.
- [10] 李新荣, 张元明, 赵允格. 生物土壤结皮研究: 进展、前沿与展望[J]. *地球科学进展*, 2009, 24(1): 11–24.
- [11] 周晓兵, 张丙昌, 张元明. 生物土壤结皮固沙理论与实践[J]. *中国沙漠*, 2021, 41(1): 164–173.
- [12] 李茜倩, 张元明. 荒漠藻类结皮边缘效应下土壤肥力的灰色关联度分析[J]. *中国沙漠*, 2019, 39(3): 17–24.
- [13] Dojani S, Budel B, Deutschewitz B, et al. Rapid succession of biological soil crusts after experimental disturbance in the Succulent Karoo, South Africa[J]. *Applied Soil Ecology*, 2011, 48(3): 263–269.
- [14] Budel B, Darienko T, Deutschewitz K, et al. Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency[J]. *Microbial Ecology*, 2009, 57(2): 229–247.
- [15] 张元明, 王雪芹. 荒漠地表生物土壤结皮形成与演替特征概述[J]. *生态学报*, 2010, 30(16): 4484–4492.
- [16] Eldridge D J, Reed S, Travers S K, et al. The pervasive and multifaceted influence of biocrusts on water in the world's drylands[J]. *Global Change Biology*, 2020, 26: 6003–6014.
- [17] 肖波, 赵允格, 邵明安. 陕北水蚀风蚀交错区两种生物结皮对土壤饱和和导水率的影响[J]. *农业工程学报*, 2007, 23(12): 35–40.
- [18] 李亚红, 卜崇峰, 郭琦, 等. 毛乌素沙地藓、藻结皮生态功能对比[J]. *中国沙漠*, 2021, 41(2): 138–144.
- [19] Angeles Munoz-Martin M, Becerra-Absalon I, Perona E, et al. Cyanobacterial biocrust diversity in Mediterranean ecosystems along a latitudinal and climatic gradient[J]. *New Phytologist*, 2019, 221(1): 123–141.
- [20] Garcia-Pichel F, Lopez-Cortes A, Nubel U. Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau[J]. *Applied and Environmental Microbiology*, 2001, 67(4): 1902–1910.
- [21] Munoz-Rojas M, Roman J R, Roncero-Ramos B, et al. Cyanobacteria inoculation enhances carbon sequestration in soil substrates used in dryland restoration[J]. *The Science of the Total Environment*, 2018, 636: 1149–1154.
- [22] Wang W B, Liu Y D, Li D H, et al. Feasibility of cyanobacterial inoculation for biological soil crusts formation in desert area[J]. *Soil Biology & Biochemistry*, 2009, 41(5): 926–929.
- [23] Zhao Y, Jia R L, Wang J. Towards stopping land degradation in drylands: water-saving techniques for cultivating biocrusts in situ[J]. *Land Degradation & Development*, 2019, 30(18): 2336–2346.
- [24] 饶本强, 王伟波, 兰书斌, 等. 库布齐沙地三年生人工藻结皮发育特征及微生物分布[J]. *水生生物学报*, 2009, 33(5): 937–944.
- [25] Housman D C, Powers H H, Collins A D, et al. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert[J]. *Journal of Arid Environments*, 2006, 66(4): 620–634.
- [26] Zaady E, Kuhn U, Wilske B, et al. Patterns of CO₂ exchange in biological soil crusts of successional age[J]. *Soil Biology & Biochemistry*, 2000, 32(7): 959–966.
- [27] Buedel B, Williams W J, Reichenberger H. Annual net primary productivity of a cyanobacteria-dominated biological soil crust in the Gulf Savannah, Queensland, Australia[J]. *Biogeosciences*, 2018, 15(2): 491–505.
- [28] Weber B, Büdel B, Belnap J. Biological soil crusts: an organizing principle in drylands[M]. Switzerland: Springer International Publishing, 2016: 56–73.
- [29] Garcia-Pichel F, Wojciechowski M F. The evolution of a capacity to build supra-cellular ropes enabled filamentous cyanobacteria to colonize highly erodible substrates[J]. *Plos One*, 2009, 4(11): e7801.
- [30] Tang K, Jia L J, Yuan B, et al. Aerobic anoxygenic phototrophic bacteria promote the development of biological soil crusts[J]. *Frontiers in Microbiology*, 2018, 9: 2715.
- [31] Xu L, Zhu B J, Li C N, et al. Development of biological soil crust prompts convergent succession of prokaryotic communities[J]. *Catena*, 2020, 187: 104360.
- [32] Gao Q J, Garcia-Pichel F. Microbial ultraviolet sunscreens[J]. *Nature Reviews Microbiology*, 2011, 9(11): 791–802.
- [33] Hoffmann L. Algae of terrestrial habitats[J]. *Botanical Review*, 1989, 55(2): 77–105.
- [34] Pushkareva E, Johansen J R, Elster J. A review of the ecology, ecophysiology and biodiversity of microalgae in Arctic soil crusts[J]. *Polar Biology*, 2016, 39(12): 2227–2240.
- [35] Zhang B C, Zhang Y M, Zhao J C, et al. Microalgal species variation at different successional stages in biological soil crusts of the Gurbantunggut Desert, Northwestern China[J]. *Biology and Fertility of Soils*, 2009, 45(5): 539–547.
- [36] Zhang B C, Li R H, Xiao P, et al. Cyanobacterial composition and spatial distribution based on pyrosequencing data in the Gurbantunggut Desert, Northwestern China[J]. *Journal of Ba-*

- sic Microbiology, 2016, 56(3): 308–320.
- [37] Giraldo-Silva A, Fernandes V M C, Bethany J, et al. Niche partitioning with temperature among heterocystous cyanobacteria (*Scytonema* spp., *Nostoc* spp., and *Tolypothrix* spp.) from biological soil crusts[J]. Microorganisms, 2020, 8(3): 396.
- [38] Zhao K, Kong W D, Wang F, et al. Desert and steppe soils exhibit lower autotrophic microbial abundance but higher atmospheric CO₂ fixation capacity than meadow soils[J]. Soil Biology & Biochemistry, 2018, 127: 230–238.
- [39] Yeager C M, Kornosky J L, Morgan R E, et al. Three distinct clades of cultured heterocystous cyanobacteria constitute the dominant N₂-fixing members of biological soil crusts of the Colorado Plateau, USA[J]. Fems Microbiology Ecology, 2007, 60(1): 85–97.
- [40] Garcia-Pichel F, Loza V, Marusenko Y, et al. Temperature drives the continental-scale distribution of key microbes in topsoil communities[J]. Science, 2013, 340(6140): 1574–1577.
- [41] Fernandes V M C, Lima N M, Roush D, et al. Exposure to predicted precipitation patterns decreases population size and alters community structure of cyanobacteria in biological soil crusts from the Chihuahuan Desert[J]. Environmental Microbiology, 2018, 20(1): 259–269.
- [42] Steven B, Gallegos-Graves L V, Yeager C M, et al. Dryland biological soil crust cyanobacteria show unexpected decreases in abundance under long-term elevated CO₂ [J]. Environmental Microbiology, 2012, 14(12): 3247–3258.
- [43] Steven B, Kuske C R, Gallegos-Graves L V, et al. Climate change and physical disturbance manipulations result in distinct biological soil crust communities[J]. Applied and Environmental Microbiology, 2015, 81(21): 7448–7459.
- [44] Samolov E, Baumann K, Budel B, et al. Biodiversity of algae and cyanobacteria in biological soil crusts collected along a climatic gradient in Chile using an integrative approach[J]. Microorganisms, 2020, 8(7): 1–28.
- [45] Rippin M, Borchhardt N, Williams L, et al. Genus richness of microalgae and Cyanobacteria in biological soil crusts from Svalbard and Livingston Island: morphological versus molecular approaches[J]. Polar Biology, 2018, 41(5): 909–923.
- [46] Ferrenberg S, Reed S C, Belnap J. Climate change and physical disturbance cause similar community shifts in biological soil crusts[J]. Proceedings of the National Academy of Sciences of the United States of America, 2015, 112(39): 12116–12121.
- [47] Rodriguez-Caballero E, Belnap J, Budel B, et al. Dryland photoautotrophic soil surface communities endangered by global change[J]. Nature Geoscience, 2018, 11(3): 185–189.
- [48] Cable J M, Huxman T E. Precipitation pulse size effects on Sonoran Desert soil microbial crusts[J]. Oecologia, 2004, 141(2): 317–324.
- [49] Reed S C, Coe K K, Sparks J P, et al. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility[J]. Nature Climate Change, 2012, 2(10): 752–755.
- [50] Cary S C, McDonald I R, Barrett J E, et al. On the rocks: the microbiology of Antarctic dry valley soils[J]. Nature Reviews Microbiology, 2010, 8(2): 129–138.
- [51] Makhallanyane T P, Valverde A, Gunnigle E, et al. Microbial ecology of hot desert edaphic systems[J]. Fems Microbiology Reviews, 2015, 39(2): 203–221.
- [52] Angel R, Soares M I M, Ungar E D, et al. Biogeography of soil archaea and bacteria along a steep precipitation gradient[J]. Isme Journal, 2010, 4(4): 553–563.
- [53] Bay S K, Waite D W, Dong X Y, et al. Chemosynthetic and photosynthetic bacteria contribute differentially to primary production across a steep desert aridity gradient[J]. Isme Journal, 2021, 15: 3339–3356.
- [54] Lynch R C, Darcy J L, Kane N C, et al. Metagenomic evidence for metabolism of trace atmospheric gases by high-elevation desert Actinobacteria[J]. Frontiers in Microbiology, 2014, 5: 698.
- [55] Zhao K, Zhang B C, Li J N, et al. The autotrophic community across developmental stages of biocrusts in the Gurbantunggut Desert[J]. Geoderma, 2021, 388: 114927.
- [56] Figueroa I A, Barnum T P, Somasekhar P Y, et al. Metagenomics-guided analysis of microbial chemolithoautotrophic phosphate oxidation yields evidence of a seventh natural CO₂ fixation pathway[J]. Proceedings of the National Academy of Sciences of the United States of America, 2018, 115(1): 92–101.
- [57] Tabita F R, Hanson T E, Li H Y, et al. Function, structure, and evolution of the *RubisCO*-like proteins and their *RubisCO* homologs[J]. Microbiology and Molecular Biology Reviews, 2007, 71(4): 576–600.
- [58] Codd G A, Marsden W J N. The carboxysomes (polyhedral bodies) of autotrophic prokaryotes[J]. Biological Reviews of the Cambridge Philosophical Society, 1984, 59(3): 389–422.
- [59] Cannon G C, Bradburne C E, Aldrich H C, et al. Microcompartments in prokaryotes: carboxysomes and related polyhedra[J]. Applied and Environmental Microbiology, 2001, 67(12): 5351–5361.
- [60] Tabita F R, Satagopan S, Hanson T E, et al. Distinct form I, II, III, and IV *RubisCO* proteins from the three kingdoms of life provide clues about *RubisCO* evolution and structure/function relationships[J]. Journal of Experimental Botany, 2008, 59(7): 1515–1524.
- [61] Berg I A, Keppen O I, Krasil'nikova E N, et al. Carbon metabolism of filamentous anoxygenic phototrophic bacteria of the family Oscillochloridaceae[J]. Microbiology, 2005, 74(3): 258–264.
- [62] Caldwell P E, MacLean M R, Norris P R. Ribulose biphosphate carboxylase activity and a Calvin cycle gene cluster in *Sulfobacillus* species[J]. Microbiology-SGM, 2007, 153: 2231–2240.
- [63] Lee J H, Park D O, Park S W, et al. Expression and regulation of ribulose 1, 5-bisphosphate carboxylase/oxygenase genes in *Mycobacterium* sp strain JC1 DSM 3803[J]. Journal of Micro-

- biology, 2009, 47(3): 297–307.
- [64] Greening C, Berney M, Hards K, et al. A soil actinobacterium scavenges atmospheric H_2 using two membrane-associated, oxygen-dependent NiFe hydrogenases[J]. Proceedings of the National Academy of Sciences of the United States of America, 2014, 111(11): 4257–4261.
- [65] Li J Y, Jin X Y, Zhang X Y, et al. Comparative metagenomics of two distinct biological soil crusts in the Tengger Desert, China[J]. Soil Biology & Biochemistry, 2020, 140: 107637.
- [66] 刘洋炎, 王尚, 厉舒祯, 等. 基于功能基因的微生物碳循环分子生态学研究进展[J]. 微生物学通报, 2017, 44(7): 1676–1689.
- [67] Campbell B J, Cary S C. Abundance of reverse tricarboxylic acid cycle genes in free-living microorganisms at deep-sea hydrothermal vents [J]. Applied and Environmental Microbiology, 2004, 70(10): 6282–6289.
- [68] Gagen E J, Denman S E, Padmanabha J, et al. Functional gene analysis suggests different acetogen populations in the Bovine Rumen and Tammar Wallaby forestomach[J]. Applied and Environmental Microbiology, 2010, 76(23): 7785–7795.
- [69] King G A. Molecular and culture-based analyses of aerobic carbon monoxide oxidizer diversity [J]. Applied and Environmental Microbiology, 2003, 69(12): 7257–7265.
- [70] Yakimov M M, La Cono V, Denaro R. A first insight into the occurrence and expression of functional *amoA* and *accA* genes of autotrophic and ammonia-oxidizing bathypelagic Crenarchaeota of Tyrrhenian Sea [J]. Deep-Sea Research Part II, 2009, 56(11): 748–754.
- [71] Offre P, Nicol G W, Prosser J I. Community profiling and quantification of putative autotrophic thaumarchaeal communities in environmental samples [J]. Environmental Microbiology Reports, 2011, 3(2): 245–253.
- [72] Diaz M R, Van Norstrand G D, Eberli G P, et al. Functional gene diversity of oolitic sands from Great Bahama Bank[J]. Geobiology, 2014, 12(3): 231–249.
- [73] Islam Z F, Welsh C, Bayly K, et al. A widely distributed hydrogenase oxidises atmospheric H_2 during bacterial growth [J]. ISME Journal, 2020, 14: 2649–2658.
- [74] Liot Q, Constant P. Breathing air to save energy—new insights into the ecophysiological role of high-affinity NiFe-hydrogenase in *Streptomyces avermitilis* [J]. Microbiologyopen, 2016, 5(1): 47–59.
- [75] Gadkari D, Schrick K, Acker G, et al. *Streptomyces-thermoautotrophicus* sp. nov., a thermophilic CO-oxidizing and H_2 -oxidizing obligate chemolithoautotroph [J]. Applied and Environmental Microbiology, 1990, 56(12): 3727–3734.
- [76] Weber C F, King G M. Volcanic soils as sources of novel CO-oxidizing *Paraburkholderia* and *Burkholderia*: *Paraburkholderia hiiakae* sp. nov., *Paraburkholderia metrosideri* sp. nov., *Paraburkholderia paradisi* sp. nov., *Paraburkholderia peleae* sp. nov., and *Burkholderia alpina* sp. nov. a member of the *Burkholderia cepacia* complex [J]. Frontiers in Microbiology, 2017, 8: 207.
- [77] King G M, Weber C F. Distribution, diversity and ecology of aerobic CO-oxidizing bacteria [J]. Nature Reviews Microbiology, 2007, 5(2): 107–118.
- [78] Greening C, Biswas A, Carere C R, et al. Genomic and metagenomic surveys of hydrogenase distribution indicate H_2 is a widely utilised energy source for microbial growth and survival [J]. ISME Journal, 2016, 10(3): 761–777.
- [79] Khdhiri M, Hesse L, Popa M E, et al. Soil carbon content and relative abundance of high affinity H_2 -oxidizing bacteria predict atmospheric H_2 soil uptake activity better than soil microbial community composition [J]. Soil Biology & Biochemistry, 2015, 85: 1–9.
- [80] Cordero P R F, Bayly K, Leung P M, et al. Atmospheric carbon monoxide oxidation is a widespread mechanism supporting microbial survival [J]. ISME Journal, 2019, 13(11): 2868–2881.
- [81] Delgado-Baquerizo M, Maestre F, Eldridge D J, et al. Microsite differentiation drives the abundance of soil ammonia oxidizing bacteria along aridity gradients [J]. Frontiers in Microbiology, 2016, 7: 505.
- [82] Abed R M M, Lam P, Beer D D, et al. High rates of denitrification and nitrous oxide emission in arid biological soil crusts from the Sultanate of Oman [J]. ISME Journal, 2013, 7(9): 1862–1875.
- [83] Francis C A, Roberts K J, Beman J M, et al. Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean [J]. Proceedings of the National Academy of Sciences of the United States of America, 2005, 102(41): 14683–14688.
- [84] Verhamme D T, Prosser J I, Nicol G W. Ammonia concentration determines differential growth of ammonia-oxidising archaea and bacteria in soil microcosms [J]. ISME Journal, 2011, 5(6): 1067–1071.
- [85] Zhang L M, Hu H W, Shen J P, et al. Ammonia-oxidizing archaea have more important role than ammonia-oxidizing bacteria in ammonia oxidation of strongly acidic soils [J]. The ISME Journal, 2012, 6: 1032–1045.
- [86] Zhao L N, Liu Y B, Yuan S W, et al. Development of archaeal communities in biological soil crusts along a revegetation chronosequence in the Tengger Desert, north central China [J]. Soil & Tillage Research, 2020, 196: 104443.
- [87] 刘鑫, 荣晓莹, 张元明. 古尔班通古特沙漠生物土壤结皮对氨氧化微生物生态位的影响 [J]. 生物多样性, 2021, 29(1): 43–52.
- [88] Strong C L, Bullard J E, Burford M A, et al. Response of cyanobacterial soil crusts to moisture and nutrient availability [J]. Catena, 2013, 109: 195–202.
- [89] Pepe-Rannek C, Koechli C, Potrafka R, et al. Non-cyanobacterial diazotrophs mediate dinitrogen fixation in biological soil crusts during early crust formation [J]. ISME Journal, 2016, 10(2): 287–298.
- [90] Salka I, Cuperova Z, Masin M, et al. Rhodoferritin-related pufM

- gene cluster dominates the aerobic anoxygenic phototrophic communities in German freshwater lakes[J]. *Environmental Microbiology*, 2011, 13(11): 2865–2875.
- [91] Achenbach L A, Carey J, Madigan M T. Photosynthetic and phylogenetic primers for detection of anoxygenic phototrophs in natural environments[J]. *Applied and Environmental Microbiology*, 2001, 67(7): 2922–2926.
- [92] 杨素萍, 林志华, 崔小华, 等. 不产氧光合细菌的分类学进展[J]. *微生物学报*, 2008, 48(11): 1562–1566.
- [93] Csotonyi J T, Swiderski J, Stackebrandt E, et al. A new environment for aerobic anoxygenic phototrophic bacteria: biological soil crusts[J]. *Environmental Microbiology Reports*, 2010, 2(5): 651–656.
- [94] Zarzycki J, Brecht V, Muller M, et al. Identifying the missing steps of the autotrophic 3-hydroxypropionate CO₂ fixation cycle in *Chloroflexus aurantiacus*[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2009, 106(50): 21317–21322.
- [95] Bryant D A, Costas A M G, Maresca J A, et al. *Candidatus Chloracidobacterium thermophilum*: an aerobic phototrophic acidobacterium[J]. *Science*, 2007, 317(5837): 523–526.
- [96] Csotonyi J T, Swiderski J, Stackebrandt E, et al. Novel halophilic aerobic anoxygenic phototrophs from a Canadian hypersaline spring system[J]. *Extremophiles*, 2008, 12(4): 529–539.
- [97] Johnson S L, Budinoff C R, Belnap J, et al. Relevance of ammonium oxidation within biological soil crust communities[J]. *Environmental Microbiology*, 2005, 7(1): 1–12.
- [98] Lee K C, Archer S D J, Boyle R H, et al. Niche filtering of bacteria in soil and rock habitats of the Colorado plateau desert, Utah, USA[J]. *Frontiers in Microbiology*, 2016, 7: 1489.
- [99] Chauhan H, Bagyaraj D J, Selvakumar G, et al. Novel plant growth promoting rhizobacteria-prospects and potential[J]. *Applied Soil Ecology*, 2015, 95: 38–53.
- [100] Hallenbeck P. Modern topics in the phototrophic prokaryotes: environmental and applied aspects[M]//Yurkov V, Hughes E. *Aerobic Anoxygenic Phototrophs: Four Decades of Mystery*. Switzerland: Springer International Publishing, 2017: 193–214.
- [101] Lan S, Ouyang H, Wu L, et al. Biological soil crust community types differ in photosynthetic pigment composition, fluorescence and carbon fixation in Shapotou region of China[J]. *Applied Soil Ecology*, 2017, 111: 9–16.
- [102] Gourion B, Delmotte N, Bonaldi K, et al. Bacterial *RubisCO* is required for efficient *bradyrhizobium/aeschynomene* symbiosis[J]. *PloS One*, 2011, 6(7): e21900.
- [103] Grostern A, Alvarez-Cohen L. *RubisCO*-based CO₂ fixation and C-1 metabolism in the actinobacterium *Pseudonocardia dioxanivorans* CB1190[J]. *Environmental Microbiology*, 2013, 15(11): 3040–3053.
- [104] Guo G X, Kong W D, Liu J B, et al. Diversity and distribution of autotrophic microbial community along environmental gradients in grassland soils on the Tibetan Plateau[J]. *Applied Microbiology and Biotechnology*, 2015, 99(20): 8765–8776.
- [105] Miralles I, Ladron de Guevara M, Chamizo S, et al. Soil CO₂ exchange controlled by the interaction of biocrust successional stage and environmental variables in two semiarid ecosystems[J]. *Soil Biology & Biochemistry*, 2018, 124: 11–23.
- [106] Leon-Sobrinho C, Ramond J B, Maggs-Kolling G, et al. Nutrient acquisition, rather than stress response over diel cycles, drives microbial transcription in a hyper-arid Namib Desert soil[J]. *Frontiers in Microbiology*, 2019, 10: 1054.
- [107] Zhang B C, Zhang Y Q, Li X Z, et al. Successional changes of fungal communities along the biocrust development stages[J]. *Biology and Fertility of Soils*, 2018, 54(2): 285–294.
- [108] Liu L C, Liu Y B, Zhang P, et al. Development of bacterial communities in biological soil crusts along a revegetation chronosequence in the Tengger Desert, northwest China[J]. *Biogeosciences*, 2017, 14(16): 3801–3814.
- [109] Xu L, Zhu B J, Li C N, et al. Increasing relative abundance of non-cyanobacterial photosynthetic organisms drives ecosystem multifunctionality during the succession of biological soil crusts[J]. *Geoderma*, 2021, 395: 115052.
- [110] Su Y G, Chen Y W, Padilla F M, et al. The influence of biocrusts on the spatial pattern of soil bacterial communities: a case study at landscape and slope scales[J]. *Soil Biology & Biochemistry*, 2020, 142: 107721.
- [111] Deng Y, Zhang P, Qin Y J, et al. Network succession reveals the importance of competition in response to emulsified vegetable oil amendment for uranium bioremediation[J]. *Environmental Microbiology*, 2016, 18(1): 205–218.

A review on autotrophic microorganisms research in dryland soils

Zhao Kang^{1a}, Zhang Lei^{1a}, Li Kaikai^{1b}, Wang Fei², Zhang Bingchang^{1b}

(1. a. School of Life Science / b. School of Geographical Sciences, Shanxi Normal University, Taiyuan 030000, China;

2. College of Resource and Environment, Shanxi Agricultural University, Taiyuan 030000, China)

Abstract: Microbial CO₂ fixation is an important autotrophic process for maintaining soil microbial community structure and heterotrophic processes in arid areas, which affects the succession and ecological function of biological soil crusts. In recent years, the extensive application of soil microbial genomics has expanded the community of autotrophs, which used to be dominated by cyanobacteria and algae. These results supported the possibility of non-cyanobacteria prokaryotes to import organic matter into soils. In this text, the distribution characteristics of cyanobacteria and algae and the regulation mechanism of environmental factors in dryland soil were reviewed. Moreover, the exploration of non-cyanobacterial autotrophs and their ecological functions in dryland soil in recent years were summarized characterizing by the coupled microbial energy metabolism pathways and biological carbon sequestration cycles. Finally, soil microbial autotrophs in dryland soils were summarized and prospected in order to provide a theoretical basis for understanding the formation and development mechanism of soil microbial community, and to provide a scientific basis for the construction of biological soil crusts.

Key words: autotrophic microorganisms; biological carbon sequestration pathway; biological soil crust; chemolithotrophy; dryland soils