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专论与综述

# 东北农田黑土固碳微生物研究进展

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**摘　要：**我国东北黑土地正在面临着不断退化的危机。碳循环是保障农田肥力和生产力的关键所在。作为土壤碳循环的驱动者，微生物在调节土壤碳平衡中发挥着重要作用。本文概述了黑土的分布、基本特征及退化的核心问题。首先综述了东北农田黑土固碳微生物的转化途径及群落组成。固碳微生物通过已发现的 6 种固碳途径进行碳固定，采用固碳功能基因 *cbbL*，基于高通量测序技术发现东北农田黑土固碳微生物主要为变形菌门和蓝细菌门。其次，论述了耕作制度、施肥、秸秆还田和冻融对黑土微生物固碳的影响。最后，从提高作物产量、减少农业面源污染、降低温室气体排放等方面分析了固碳微生物对农业及生态环境的贡献。黑土固碳微生物对于黑土养分恢复和作物产量的提升具有不可或缺的作用，但相关研究比较薄弱，因此应深入挖掘黑土固碳微生物资源，利用学科交叉融合揭示固碳微生物的生态过程与功能结构变化，构建基于微生物碳循环的黑土管理措施，以加强黑土地的保护与利用。

**关键词：**东北黑土；碳循环；黑土地保护；固碳微生物

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# Research advances of carbon-fixing microorganisms in the black soil of northeast China

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**Abstract:** The black soil in northeast China is facing the threat of continuous deterioration. The carbon cycle plays a critical role in the maintenance of soil fertility and productivity in farmland, where microorganisms regulate the carbon balance in soil. This review summarizes the distribution, characteristics, and degradation of black soil. Firstly, it describes the transformation pathways and community composition of carbon-fixing microorganisms in the black soil in farmland. These microorganisms employ six pathways to fix carbon. The high-throughput sequencing with the carbon fixation gene *cbbL* as the probe reveals that the carbon-fixing microorganisms in the black soil of northeast China mainly belong to *Proteobacteria* and *Cyanobacteria*. Secondly, the review discusses the effects of tillage systems, fertilization, straw return, and freezing-thawing on microbial carbon fixation in black soil. Finally, the contributions of carbon-fixing microorganisms to agriculture and the environment are expounded from increasing crop yields, reducing agricultural non-point source pollution, and reducing greenhouse gas emissions. While these microorganisms are crucial for nutrient recovery and crop yield improvement, research remains to be carried out. The protection and utilization of black soil necessitates a deeper understanding of the microbial resources involved in carbon fixation. Interdisciplinary studies should be carried out to reveal the ecological processes and function and structure changes of these microorganisms, and a black soil management scheme focusing on microbial carbon cycling should be formulated for the protection and utilization of black soil.

**Keywords:** black soil in Northeast China; carbon cycle; black soil protection; carbon-fixing microorganisms

东北黑土是世界四大黑土区之一，总面积达109 万 km$^2$，耕地面积 18.53 万 km$^2$，覆盖大兴安岭、三江平原以及松辽平原。东北农田黑土素以肥力高著称，土壤腐殖质层最厚可达 70–100 cm，土壤结构疏松多孔[1]，机械组成均匀[2]，pH 值为 5.5–6.5，是自然条件下最肥沃、最稀缺的土壤资源，大豆、玉米、水稻都是农田黑土的重要作物[3-4]，在我国粮食安全中具有不可替代的作用。

随着长期集约耕作和过度开发利用，黑土地正面临严重退化，土壤有机碳储量显著下降，土

壤侵蚀严重，影响农田生态功能和健康生产[5]，土壤碳源/汇的问题也成为学术界的热门话题。微生物驱动土壤物质转化，可以通过合成代谢实现固碳功能，其群落组成变化会直接影响土壤有机碳的固定[6]。研究发现固碳微生物广泛存在于多种生态环境中，目前主要利用分子生物学技术如 DNA 分子指纹图谱、qPCR、基因芯片和高通量测序等技术对黑土固碳微生物的丰度、群落组成及多样性进行分析，功能基因丰度越高微生物固碳潜力也越大[7]。此外，微生物的固碳途径也会受到环境因素的影响[8]。

目前对碳循环相关微生物研究比较广泛，但是对于东北农田黑土人们更关注黑土面临的退化问题，而对土壤中固碳微生物相关研究还缺乏总结和梳理。因此，本文基于前人的研究结果对我国东北农田黑土碳循环功能微生物分子机制以及调控过程进行综述。针对黑土有机质含量下降的“瓶颈”问题，全面探究黑土微生物固碳能力以及分子机制，为全面评价东北黑土区的生态效应、黑土地温室气体减排、现代绿色循环农业可持续发展提供理论依据和技术支撑。

## 1 农田黑土固碳微生物驱动的固碳过程及其微生物群落

### 1.1 黑土微生物固碳过程

土壤 $CO_2$ 固定主要是通过从大气中吸收 $CO_2$ 并将其引入土壤中来增加土壤有机碳储存的过程。研究表明，团聚体作为微生物的主要栖息地是土壤碳固存的主要场所，土壤团聚体的稳定性可改善土壤结构，保持有机碳的稳定性[9]，黑土中土壤活性有机碳组分包括微生物量碳、水溶性有机碳、易氧化有机碳和颗粒有机碳等作为反映土壤肥力与质量变化的早期预测指标，活性碳库的各组分含量与土壤微生物活性之间存在关联，也可能增加土壤碳排放量[10]，除外部因素外，土壤微生物群落在碳循环中起着重要作用。

土壤微生物既可通过分解代谢向大气释放碳，也可通过合成代谢将外源碳转化成某种物质形式储存于土壤中。其活性被认为是土壤中碳储存潜力差异的主要驱动因素[11]。微生物参与的碳循环代谢主要包括 3 个基本过程：碳固定(无机碳转化为有机碳)、甲烷代谢(产甲烷和甲烷氧化)、碳降解(有机物质的分解)[12]。碳循环代谢具体过程如图 1 所示。固碳微生物可以通过已存在的 6 种途径进行固定(表 1)，其中卡尔文循环是第一个报道的碳固定途径[15]。卡尔文循环是微生物参与的 $CO_2$ 固定过程最重要的途径[20]，核酮糖-1,5-二磷酸羧化酶/加氧酶(RubisCO)催化其底物的羧基化和氧化，是卡尔文循环进行 $CO_2$ 固定的关键酶。土壤有机碳与 RubisCO 酶活性之间的关系呈极显著正相关[21]。

### 1.2 固碳微生物群落

近年来东北黑土微生物固碳能力得到广泛关注[22-25]。*cbbL*、*cbbM* 基因是 RubisCO 酶的编码基因，作为固碳相关的生物标志物用于分析不同生态环境中固碳微生物群落多样性以及固碳能力[26]，研究表明东北农田土壤中细菌 *cbbL* 丰度范围可达 $2.4\times10^7$–$1.9\times10^8$ copies/g[27-28]。目前发现东北黑土区碳代谢微生物在门水平上包括变形菌门(*Proteobacteria*)、蓝细菌门(*Cyanobacteria*)、放线菌门(*Actinobacteria*)、绿弯菌门(*Chloroflexi*)、酸杆菌门(*Acidobacteria*)[25,29-30]，在纲水平上包括 α-变形菌纲(*Alphaproteobacteria*)、β-变形菌纲 (*Betaproteobacteria*) 和 γ-变形菌纲(*Gammaproteobacteria*)等[31]，其中硫氧化菌属(*Thioalkalivibrio*)、硫杆菌属(*Thiobacillus*)、芽孢杆菌属(*Bacillus*)、土微菌属(*Pedomicrobium*)和鞘脂单胞菌属(*Sphingomonas*)为优势菌属[30]。此外，还有部分真菌也参与碳循环过程，如丛枝菌根真菌(arbuscular mycorrhizal fungi)及其菌丝分泌物能

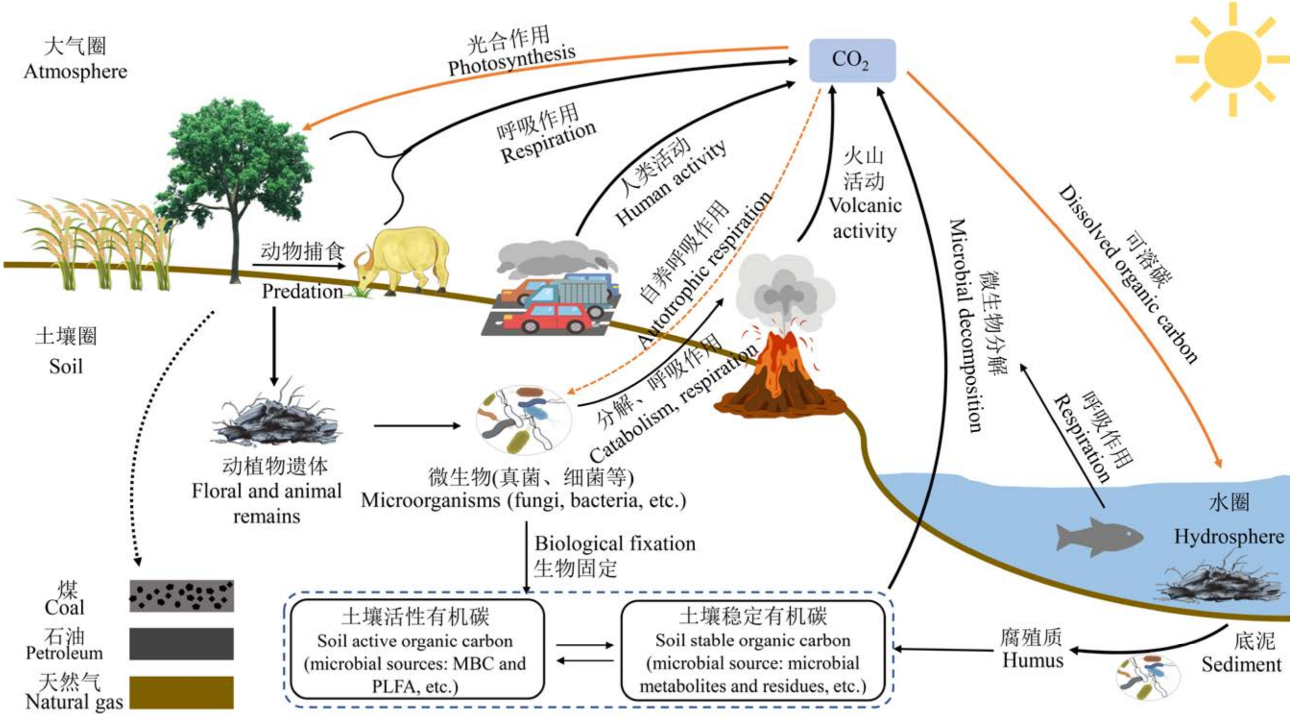

**图 1　碳循环过程示意图**[13-14]

Figure 1　Diagram of carbon cycle process[13-14].

够促进土壤有机碳(soil organic carbon, SOC)的积累和土壤团聚体的聚集[32]，对生态系统和土壤碳库的稳定有重要作用。

现阶段对土壤微生物固碳的研究引入了碳同位素技术、气相色谱/质谱、近红外光谱技术和 $^{13}C$ 核磁共振法等技术手段，这些技术已广泛用于从分子水平来分析有机质的结构特征。例如，Cheng 等[33]使用 $^{13}C$ 标记探究土壤侵蚀和沉降对东北黑土区坡田土壤有机碳动态的影响；徐香茹[9]采用 $^{13}C$ 示踪不同添加量秸秆对土壤碳组分的分配与固定。运用同位素的标记技术不仅可以测定土壤量和状态，还可以更准确把握碳的来源与动态变化。

## 2　农田黑土微生物固碳的影响因素

黑土中微生物的固碳效果并非一成不变，微生物固碳会受到不同因素的影响[34]，气候变化以及土壤状况、植被或土壤管理等的变化可能会进一步改变土壤固碳过程[35]。不同的固碳微生物因其表达不同的固碳途径，从而固碳能力也有差异，不同的影响因素相关关系见图 2。

### 2.1　耕作制度

不同的土地利用方式显著影响了黑土碳代谢微生物群落[38]，研究发现，免耕土壤平均 $CO_2$ 释放速率显著低于秋翻和常规耕作[39]。相同土壤中不同耕作处理之间固碳功能基因丰度存在差异，免耕黑土固碳基因主要与土壤可溶性有机碳含量、土壤容重呈现正相关，而常规耕作土壤固碳基因与土壤可溶性有机碳含量呈负相关[39]。研究表明，与裸地相比，轮作种植(玉米-大豆-小麦)可以显著提高土壤有机质含量及土壤微生物丰度[36]。在连作系统中，如长期单一种植玉米、大豆和小麦土壤有机碳会出现不同程度的下降(0–90 cm 土层有机碳下降率分别为 0.91%、0.97%和 0.48%)[40]，小麦连作土壤具有较高的土

表 **1** 微生物驱动的碳循环类型

Table 1 Types of carbon cycles driven by microorganisms

| 碳循环类型<br>Type of carbon cycles | 微生物<br>Microorganisms | 能量来源<br>Source | 产物<br>Product | 关键酶<br>Enzyme | 参考文献<br>References |
|---|---|---|---|---|---|
| 卡尔文循环<br>Calvin-Benson-Bassham cycle | 藻类、蓝藻、好氧变形杆菌、紫色细菌<br>Algae, cyanobacteria, *Proteus*, purple bacteria | 光能<br>Light | 3-磷酸甘油酸<br>3-phosphoglycerate | 核酮糖-1,5-二磷酸羧化酶/加氧酶、磷酸核酮糖激酶<br>RubisCO and phosphoribulokinase | [15] |
| 还原三羧酸循环<br>Reductive tricarboxylic acid (rTCA) cycle | 紫色细菌、绿硫细菌、变形杆菌、产水菌科、硝化菌<br>Purple bacteria, green sulfur bacteria, *Proteus*, *Aquificae*, nitrifying bacteria | 氢和硫<br>Hydrogen and sulfur | CoA | α-酮戊二酸合酶、柠檬酸裂解酶<br>alpha-ketoglutaric acid and citrate lyase | [16] |
| 厌氧乙酰辅酶 A<br>Wood-Ljungdahl pathway | 产甲烷菌、硫酸盐还原菌、产乙酸菌<br>Methanogenus, sulfate-reducing bacteria, acetogenic bacteria | 氢<br>Hydrogen | CoA | 乙酰辅酶 A 合酶、一氧化碳脱氢酶<br>Acetyl-CoA synthetase and carbon monoxide dehydrogenase | [17] |
| 3-羟基丙酸循环<br>3-hydroxypropionate bicycle | 绿弯菌门<br>*Chloroflexi* | 氢和硫<br>Hydrogen and sulfur | 丙酮酸<br>Pyruvic acid | 丙二酰辅酶 A 还原酶<br>Malonyl-CoA reductase | [18] |
| 3-羟基丙酸/4-羟基丁酸循环<br>3-hydroxypropionate/4-hydroxybutyrate cycle | 绿弯菌门、硫化叶菌目、古细菌、勤奋金属球菌<br>*Chloroflexi*, *Sulfolobales*, archaea, *Metallosphaera sedula* | 氢和硫<br>Hydrogen and sulfur | CoA | 乙酰辅酶 A/丙酰辅酶 A 羧化酶、4-羟基丁酰辅酶 A 脱氢酶、丙二酰辅酶 A 还原酶<br>Acetyl-CoA/propionyl-CoA carboxylase, 4-hydroxybutyryl-CoA dehydratase, malonyl-CoA reductase | [19] |
| 二羧酸/4-羟基丁酸循环<br>Dicarboxylate/4-hydroxybutyrate cycle | 古菌、极端嗜热嗜酸菌<br>Archaea, themophiles | 氢和硫<br>Hydrogen and sulfur | CoA | 4-羟基丁酰辅酶 A 脱氢酶、磷酸烯醇丙酮酸羧化酶<br>4-hydroxybutyryl-CoA dehydratase, phosphoenolpyruvate carboxykinase | [20] |

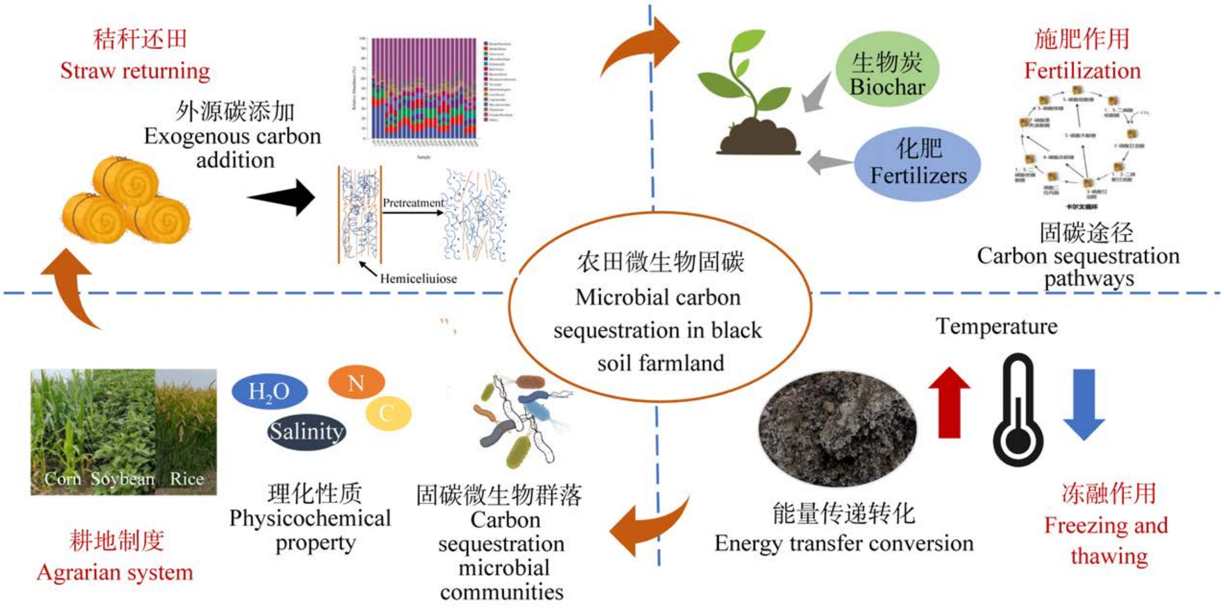

**图 2　黑土有机碳固定影响因素示意图**[10,25,34-37]

Figure 2　Diagram of factors affecting organic carbon sequestration in black soil[10,25,34-37].

壤有机碳矿化速率，其次是大豆连作，玉米连作的土壤有机碳矿化速率最低[41]。此外土壤性质会影响固碳微生物类群的变化[42]，微生物的分布可能会受到土壤温度、盐度和土壤养分等因子的制约[43]，如潮湿的条件可能有利于有机物的积累影响微生物分布[44]。

## 2.2　施肥措施

施肥可以通过改变土壤各活性碳库组分含量与土壤微生物活性影响土壤碳排放量[10]。研究发现通过施用生物炭会增加一些固碳功能微生物的相对丰度，如芽孢杆菌属(*Bacillus*)和土微菌属(*Pedomicrobium*)等，但却降低了慢生根瘤菌(*Bradyrhizobium*)相对丰度[45]。根据相关研究，长期单施化肥条件下，玉米生育期黑土碳排放量显著高于不施肥处理 37.36%[10]。此外，长期有机肥与无机肥配施和无机肥配施秸秆处理也显著增加了土壤呼吸及异养呼吸碳累积排放量，分别提高了 56.32%–86.54%和 70.01%–100.93%[46]。

微生物固碳途径也同样受到施肥的影响，研究表明，在东北黑土区化学和有机肥料组合施用显著降低了参与还原乙酰辅酶 A 途径和 CO 氧化的基因丰度，同时增加了还原三羧酸(reductive tricarboxylic acid, rTCA)循环的基因丰度[47]；李亚男[31]的研究中也发现了施用化肥增加了 C4-二羧酸循环代谢途径，而抑制了二羧酸/4-羟基丁酸循环。

## 2.3　秸秆还田

秸秆还田是提升农田土壤有机质的有效措施，秸秆可为土壤微生物提供丰富的碳源和养分，不仅提高土壤自养固碳微生物多样性[48-49]，同时使黑土中固碳微生物(如酸杆菌门和绿弯菌门)的相对丰度产生变化[25]。秸秆还田处理下，碳循环过程中新碳形成速率高于老碳分解速率从而提升 SOC 含量[50]，同时使土壤呼吸总量增加 4.38%[51]。研究表明，随着秸秆覆盖的增加，变形菌门(*Proteobacteria*)和拟杆菌门(*Bacteroidetes*)在碳固定代谢中的作用增强，土壤碳固定功能基因的总丰度降低[52]。此外，秸秆的掺入使不同

生态系统间土壤轻组分有机碳含量在不同土壤深度存在差异，且差异随着剖面深度的增加而降低[53]，SOC 含量及其变异大小也随土壤深度的增加而显著降低[23]。

### 2.4 冻融作用

冻融作用是东北黑土区常见的自然现象，冻融循环中会导致土壤中的水分、温度和气体等因素发生变化，进而引发土壤能量传递和转化等复杂性过程。研究表明，低幅冻融循环(–5–5 °C)和高幅冻融循环(−10–10 °C)下土壤的 $CO_2$ 排放量分别是恒温培养的 1.64 倍和 3.18 倍[37]。冻融交替作用会降低土壤中微生物残体碳的累积[54-55]。此外，随着温度的升高，冻土层(0–40 cm)碳循环相关微生物丰度显著提高[56]。宋媛等[57]通过 $^{13}C$ 标记模拟春季解冻期(单向冻融)可显著改变土壤 $CO_2$ 释放速率及微生物群落结构。

## 3 固碳微生物对农业及生态环境的贡献

### 3.1 固碳微生物驱动土壤生产力的提升

提升黑土耕地土壤肥力是粮食增产增收的前提，也是维护国家粮食安全的重要保证。根据研究，东北黑土中矿物结合态有机碳的比例最高，其次是占全国耕地面积 1/5 的水稻土和南方红壤，而西北的灰漠土的比例最低[39]。目前，东北黑土土壤碳汇约为 4 Gt，占全国土壤碳汇的 5%[40,58]。

土壤有机碳含量低是限制作物增产的重要因素，土壤有机碳的增产作用存在的最优阈值并不是固定的，而是与气候、土壤以及作物类型有关，玉米的平均最优土壤有机碳含量水平为 43.2−43.9 g/kg，而小麦为 12.7−13.4 g/kg、水稻为 31.2−32.4 g/kg[59]。邱建军等[60]对东北黑土地区的研究表明，土壤有机碳的含量会引起粮食作物的变化，在阈值范围内(有机碳含量为 44–46 t/hm$^2$)农田土壤每固定 1.0 tC/(hm$^2$·a)有机碳，粮食作物产量可平均提升约 0.7 t/hm$^2$，这意味着作物通过土壤固碳可以实现更大的增产空间。

保护性耕作等农业管理措施通过直接改变有机碳输入或间接改变微生物的环境条件来影响耕作层土壤的碳循环过程，合理的施肥方式如有机无机配施较单施化肥使土壤中相关养分均出现显著提高[61]。现代农业中常常利用化肥与秸秆还田相结合增加黑土有机质含量[62]，还通过利用秸秆等农业废弃物为主要原料育苗[49,63]，与微生物协同作用下能提高作物素质并节约成本。

此外，微生物在环境中生长并不是靠单一元素周转而存活的，生物地球化学元素循环例如碳、氮、磷、硫等，存在复杂的耦合关系，微生物可增加土壤的有机碳、氮、钾和土壤呼吸水平[64]。微生物在分解有机碳过程中可以释放出氮素，从而提高土壤中的氮素含量；氮沉降的增加可以促进土壤碳积累，同时有机碳源的输入也会影响氮转化过程[65-66]，这种相互作用关系可以促进土壤的肥力和生态系统的稳定性[67]。

东北黑土区有机培肥是改善东北黑土区农田土壤碳含量的有效途径，有机无机配施处理主要通过增加碳向土壤稳定库及粒径较小的团聚体的分配，从而增强了土壤对碳的固持能力，相关研究表明此措施下土壤有机碳年增加量为 0.35−0.47 g/kg，同时全氮含量增加 46.3%−84.2%，玉米产量稳定系数达到较高水平[68-69]。

### 3.2 固碳微生物对温室气体排放的影响

大气中 $CO_2$ 是主要的温室气体之一，土壤碳循环是调节土壤物质动态和土壤与大气之间气体交换的基本生物地球化学循环[70-71]。微生物在调节气候变化方面至关重要，但它们很少成为气候变化研究的重点。“双碳”目标为农业绿色发展提出了新要求和新目标。黑土在减缓和适应气

候变化的工作中发挥关键作用，在东北黑土中除了植被光合作用、凋谢物分解作用，土壤中固碳微生物也是土壤碳固定的重要因素之一。

微生物回收和固定 $CO_2$ 气体的生物固碳方法逐渐成为解决“温室效应”这一重大环境问题的焦点[72-73]。固定 $CO_2$ 的微生物主要为自养菌，其中土壤中固碳菌是重要的一个方面[74-75]，数据显示深度为 1 m 土壤内的有机碳储量为 1 505 Pg (1 Pg=$10^{15}$ g)，其储量约是土壤表层植物(620 Pg C)中的 2.43 倍，也是大气圈碳储量(867 Pg C)的 1.71 倍[76-77]。研究表明，土壤中 $CO_2$ 的固定量可以达到 4.52 g/kg 干土[78]，微生物固定的碳含量可占总有机碳的 0.12%−0.59%[79]。

为了应对气候变化并可持续地从碳循环中受益，微生物利用自然能源固定大气中温室气体的能力是未来可持续发展的一个有效途径。面对温室气体不断加剧的挑战，通过提高土壤有机碳固定水平对于缓解大气温室气体和气候变化有重大的贡献。

## 4 总结与展望

固碳微生物对于黑土养分恢复和作物产量的提升具有不可或缺的作用。卡尔文循环作为自养生物固碳的主要途径，RubisCO I 型的大亚基由 *cbbL* 基因编码，其作为固碳标志物已广泛用于土壤环境中固碳微生物的种群结构及多样性；固碳微生物可以吸收无机碳并将其转化成有机物，黑土中固碳微生物可能会受到耕作制度、施肥、秸秆还田和冻融等因素的影响。土壤微生物作为碳循环过程的主要驱动者与作物生产和生态环境关系密切，给土壤提供养分提高作物产量的同时降低温室气体，在“碳达峰、碳中和”背景下对实现黑土地保护具有重要意义。

现有研究更关注于黑土退化问题的研究，但是缺少对黑土中固碳微生物的深入挖掘。为加强黑土地保护，全面系统了解黑土固碳微生物物种类型、分布和作用机制，以及其对土壤环境和作物生产的影响至关重要。利用微生物对黑土碳循环进行调节也将成为研究的主要方向，未来应在 3 个方面进行深入研究。

(1) 深入挖掘东北黑土区固碳微生物资源。立足于东北寒区挖掘低温环境下固碳功能微生物菌群，利用微生物之间的协同作用开发适用于黑土地人工高效碳固定功能菌剂，为解决寒区微生物资源匮乏的问题提供菌种与基因资源；在分子水平上研究固碳微生物基因改造，以提高微生物的固碳能力及非固碳菌向固碳功能菌株的转化，并建立基于东北黑土的微生物资源数据库共享平台，实现资源开放并建立资源网络，对于促进东北地区甚至全国农业可持续发展具有意义。

(2) 前沿技术交叉融合全面解读固碳微生物生命过程。现阶段对土壤有机碳变化速率及潜力估算结果中存在不确定性，目前使用的同位素示踪技术可以揭示土壤微生物的生态过程与功能结构变化，但想要更加系统地阐明微生物生命活动过程及其对土壤中有机碳循环的影响变化，仍需要其他测试技术相辅，综合利用地理信息系统(geographic information system, GIS)、遥感、人工智能、大数据等前沿技术交叉融将成为土壤碳管理的一个新趋势，更加全面地评价我国东北黑土生产对生态环境的综合影响，巩固其生态地位。

(3) 构建基于微生物有机碳循环的黑土管理策略。设计适用于东北黑土地耐低温且活性好的专用型复合微生物肥料(菌肥)有效改良土壤状况，通过农业生产调控固碳菌群的构成及活性。建立智能监测与感知体系对区域土壤的养分状况制定专门的用养模式，并研发自动精准施肥设施智能调节和控制农田施肥，在保护黑土地的同时提高作物产量。

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