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增温对生物土壤结皮微生物群落组成及其呼吸作用的影响

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摘要　生物土壤结皮作为干旱区土壤表层主要的覆盖者,生存于其中的微生物在调节旱区碳循环的气候敏感性方面发挥着重要作用。目前气候变暖对生物结皮微生物群落及其呼吸作用的研究结论尚有分歧。为了更加准确预测未来干旱地区的碳收支,本文归纳了模拟气候变暖的增温试验中不同试验周期、不同季节和不同类型的生物结皮碳排放规律,并结合微生物丰度和有机碳的变化分析了引起碳排放差异的内在原因。短期增温(低于2 a)导致生物结皮中苔藓或地衣丰度显著性降低,从而增加土壤有机碳含量,碳排放量是否同步增加取决于土壤含水量。长期增温(大于5 a)降低了微生物对温度和湿度的敏感性,微生物丰度和组成趋于稳定,从而使有机碳含量和净碳排放量保持相对稳定。已有的研究结果揭示了生物结皮碳排放规律和原因,但微生物参与的内在调控机制仍不明确。因此,今后需重点探究结皮微生物碳代谢对增温的响应机制,为评估干旱区碳平衡提供重要理论依据。

关键词　生物土壤结皮;增温;微生物群落组成;有机碳;净碳排放量

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干旱区约占全球陆地总面积的45%,在调节全球生物地球化学循环和地表水平衡等方面发挥着重要的生态作用[1-2]。随着全球工业化进程加快,温室气体排放量增速,预计到22世纪初全球平均温度将增加1.4～4.5 ℃(IPCC, 2021),而干旱区是最容易受到气候变化影响的地区之一[3-4]。了解干旱区如何响应持续的气候变化,对于制定有效的生态系统可持续发展策略至关重要。

干旱区生物土壤结皮(biological soil crusts,简称生物结皮)覆盖面积可达70%以上[5],是干旱区生态系统中的重要组成部分。生物结皮主要是由蓝藻优先拓殖荒漠生境,随后其他细菌、地衣、苔藓等相继生长其上,胶结和捆绑土壤颗粒,从而在沙土表面形成的一层易剥离的生物土壤复合层[6]。结皮微生物除了具有稳定沙土和提高土壤肥力等功能外,在调节碳循环中也发挥着重要作用[7-10]。据估计,生物结皮年累积碳释放总量约占干旱地区的42%～66%[11-12]。气候变化会使干旱区微生物多样性和丰度降低,从而导致代谢功能丧失和有机碳含量下降[13]。对于结皮微生物而言,对增温和增温引起的土壤湿度降低更加敏感[14-15]。研究表明即使升温0.34 ℃,也会导致荒漠土壤中微生物呼吸敏感性变化比其他生态系统中的更大[16],增温会使结皮中的优势物种快速死亡并降低碳代谢速率[17]。演替后期结皮微生物丰度的下降,将导致土壤稳定性、保水性和碳储量降低[18-19],从而导致土地荒漠化问题加剧。因此,为了准确预测未来干旱地区的碳收支,本文以增温对生物结皮微生物群落组成和呼吸作用为重点,探讨不同试验周期、不同地区、不同类型结皮中,优势生物、细菌种类和丰度的变化规律,以及微生物变化所引起的有机碳和碳排放量的改变,并分析导致这些变化的潜在原因,旨在为预测未来旱地功能

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和了解气候变化对全球碳循环的扰动提供参考依据。

1 生物结皮微生物群落组成和丰度对增温的响应

依据演替先后顺序，将生物结皮分为蓝藻结皮、地衣结皮和苔藓结皮，3种类型结皮的优势生物分别为蓝藻、地衣和苔藓[20]。除了这些优势生物外，结皮中还存在着丰富的细菌，它们是土壤有机质降解、异养呼吸、发酵等代谢途径的重要参与者[10,21]。增温会改变这些微生物的组成和丰度，这些变化不仅决定着生物结皮储存和释放的碳含量，也影响着生物结皮在干旱区的覆盖面积，关系着生态系统的恢复与保护。因此，我们重点分析生物结皮中优势生物和细菌的组成、丰度对增温的响应。

1.1 优势生物

不同优势生物对增温的响应和适应性存在差异。为了更准确评估气候变暖对它们的影响，研究者围绕丰度和物种丰富度变化开展了长期增温试验。根据试验地点和样品不同将这些研究分为3类：(1)腾格里沙漠：苔藓结皮和地衣结皮，增温范围0.5～2 ℃；(2)西班牙中东部：苔藓和地衣混合结皮，增温范围2～3 ℃；(3)科罗拉多高原：蓝藻、苔藓和地衣混合结皮，增温范围2～4 ℃。增温对这3种类型中优势生物的影响不同(表1)。在第1种类型中，自然条件下，优势生物组成和生物量(用叶绿素含量指示)，以及结皮覆盖度在十几年里未发生明显变化，经增温处理后，苔藓生物量下降了约69%，导致苔藓结皮平均覆盖度显著($P<0.05$)降低了17%～37%，而地衣生物量和地衣结皮覆盖度下降幅度很小，苔藓和地衣物种丰富度无变化[22-24]。第2种类型中苔藓、地衣物种丰富度和结皮覆盖度的变化更复杂。依据初始覆盖度值，分别将低于20%和高于50%的混合结皮称为低覆盖度生物结皮(low biocrusts cover, LBC)和高覆盖度生物结皮(high biocrusts cover, HBC)[25-27]。LBC总覆盖度在自然条件下显著($P<0.05$)增加，增温使LBC总覆盖度小幅度增加或降低，但LBC中地衣结皮覆盖度和地衣种类经增温后降低。HBC总覆盖度在对照组和增温处理组中的下降幅度大于20%，增温处理组降低幅度高于对照组，这主要是由于地衣结皮覆盖度大幅度降低，地衣种类和相对丰度也减少，苔藓结皮覆盖度略有增加。第3种类型中，自然条件下苔藓结皮覆盖度呈波动增加，增温后其覆盖度急剧减少了约15%～20%，而具鞘微鞘藻结皮覆盖度增加了25%～30%，地衣结皮覆盖度小范围降低[28-29]。

表1 增温引起的优势生物丰度变化情况

Table 1 Changes in abundance of dominant organism caused by warming

类型 Type	试验地点 Experimental location	年均降雨量和温度 Mean annual rainfall and temperature	丰度变化 Abundance variations	参考文献 Reference
苔藓结皮和地衣结皮 Moss biocrusts and lichens biocrusts	腾格里沙漠 Tengger Desert	186 mm 8.6 ℃	苔藓生物量约下降了69%，地衣生物量降幅小，二者物种丰富度无变化	[22-24]
苔藓和地衣混合结皮 Lichen - moss crusts	西班牙中东部 East-central Spain	315～349 mm 14.6 ℃	地衣种类和相对丰度大幅度降低，苔藓相对丰度略增、种类无变化	[25-27]
苔藓、地衣和蓝藻混合结皮 Cyanobacteria-lichen-moss crusts	科罗拉多高原 Colorado Plateau	269 mm 13.0 ℃	蓝藻相对丰度急剧增加，苔藓相对丰度急剧降低，地衣相对丰度略降	[28-29]

导致不同地区优势生物变化规律差异的原因很可能与土壤湿度有关。在腾格里沙漠和西班牙中东部的增温试验是通过开顶箱增温，而科罗拉多高原是红外辐射器增温。开顶箱对土壤含水量的影响相对较小，而红外辐射器可降低30%的土壤含水量[30]。科罗拉多高原年降雨量高于腾格里沙漠，其土壤湿度也较高，经增温后2个地区的土壤湿度很可能相差不大，且低于西班牙地区。因此，我们猜测影响优势生物丰度变化的第1个原因为土壤湿度，在相对干燥的条件下，增温导致苔藓相对丰度大幅度下降，而在相对湿润的土壤，增温导致地衣相对丰度和物种种类降低。Finger-Higgens等[31]在科罗拉多高原开展的23 a自然增温观测试验表明，地衣种类和生物量下降，从而导致地衣结皮平均覆盖度下降，而苔藓结皮覆盖度小幅度增加，这一结果验证了我们的假设。第2个原因是优势生物之间的竞争关系，当苔藓或地衣丰度降低时，蓝藻将抢占空出来的生态位[32]。地衣和苔藓存在时，它们占据了蓝藻绝大

部分生存空间，也限制了蓝藻向地表移动获得光的机会。当增温导致地衣或苔藓丰度下降时，对土壤湿度和营养条件要求更低的蓝藻开始大量生长。在科罗拉多高原混合结皮中，蓝藻结皮初始覆盖度高于晚期结皮[28-29]，而在其他的研究中，晚期结皮中只存在着少量的蓝藻结皮，晚期结皮覆盖度降低时蓝藻也能占据少部分区域。我们推测相同微区内蓝藻结皮覆盖度越高，与苔藓或地衣的竞争越激烈，蓝藻将占据更多的缺失区域。地衣种类的不同也会影响增温的结果。西班牙地区地衣结皮主要物种为 *Diploschistes diacapsis*，该物种有时很容易从土壤中分离[33]，增温加速了其菌丝体的分离并通过风扩散到其他地方[26]；*D. diacapsis* 对温度较为敏感，2 a 的增温即可导致其覆盖度下降约 10%[34]。总之，增温所引起的优势生物组成和丰度的变化受土壤湿度、物种竞争强弱和物种种类等因素的相互作用。

1.2　细　菌

与优势生物相比，细菌群落组成与相对丰度受增温的影响较小。经 2 a 或 6 a 的 2 ℃增温处理后，通过扩增子测序获得的细菌相对丰度数据表明，无论是在门还是属水平，只有少数物种相对丰度发生变化，但蓝藻结皮的覆盖度改变[35-36]。在全球范围内，虽然生物结皮中细菌的种类和相对丰度存在差异，但主要的细菌为蓝细菌门、放线菌门、变形杆菌门、酸杆菌门和拟杆菌门[37-40]，这些细菌大部分为革兰氏阴性菌。Maestre 等[27]检测磷脂脂肪酸 cy17∶0 与 16∶1ω7 的比值，该比值反映了革兰氏阴性菌所经历的生理应激程度，增温 2 ℃后的 16 个月和 53 个月该值增加，这反映了微生物生理活性发生了变化。除蓝藻外的细菌多位于结皮下层，表层的蓝藻、地衣和苔藓起到了一定的缓冲作用[41]。另外，优势生物覆盖度的变化影响着土壤中营养物质的含量，结皮中的细菌长期生存于营养物质相对紧缺的条件下，具有快速响应营养物质变化的潜力。因此，增温使细菌群落组成和相对丰度处于动态平衡状态。

2　生物结皮呼吸作用对增温的响应

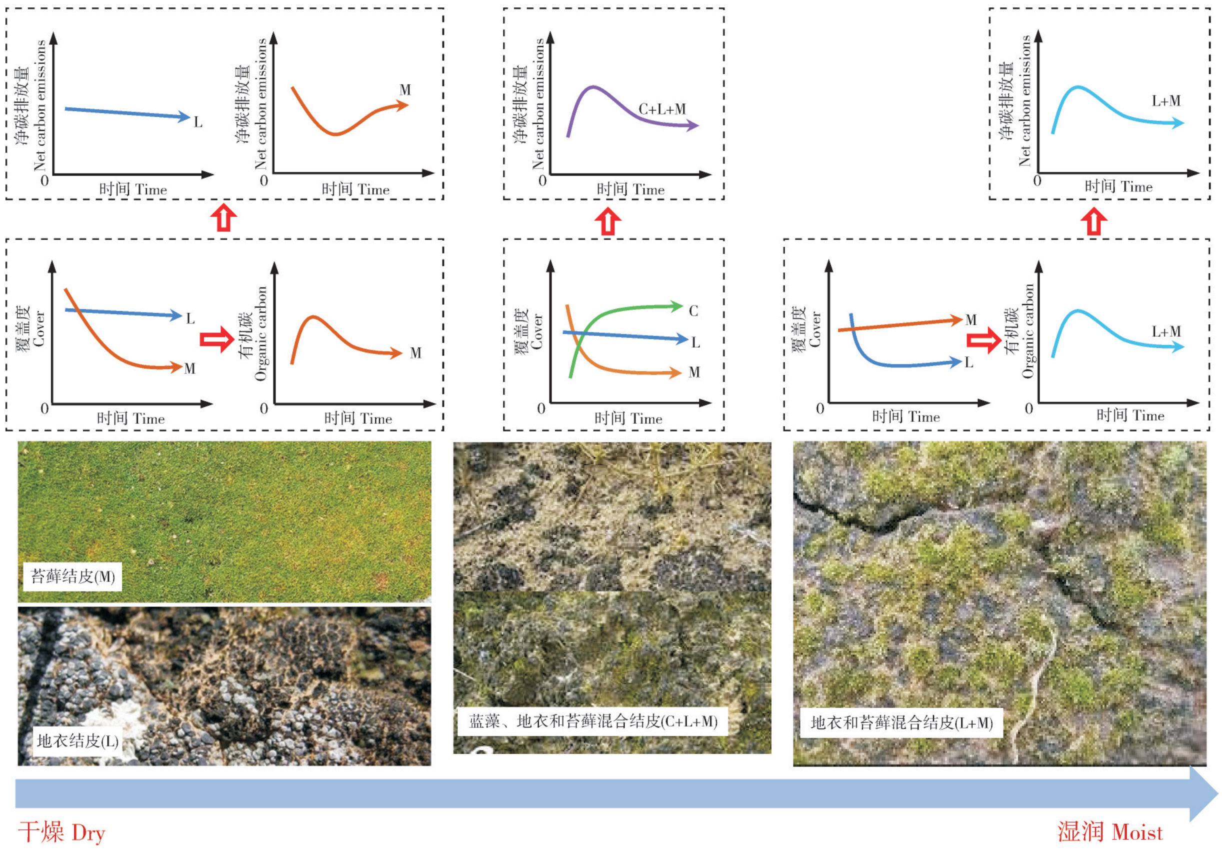
生物结皮呼吸作用的强弱关系着干旱地区总碳排放量[11-12]。目前大部分增温试验中的呼吸速率是指单位时间内净 CO_2 排放量，即总呼吸作用产生的 CO_2 减去光合作用吸收的 CO_2[42]。结皮中呼吸作用的底物包括光合作用产生和外源输入的有机碳，有机碳含量的变化影响着呼吸作用和净碳排放量。其中，颗粒态有机碳（particulate organic carbon，POC）和矿物结合态有机碳（mineral-associated organic carbon，MAOC）常用于评估土壤有机碳（soil organic carbon，SOC）对气候变化的响应[43-44]。因此，下文将从土壤有机碳（POC 和 MAOC）和净碳排放量含量变化间接分析增温对生物结皮呼吸作用的影响。

2.1　有机碳含量

增温后有机碳含量增加或降低很可能与生物结皮类型有关。田畅[45]对蓝藻结皮和苔藓结皮进行 2 a 的 1～2 ℃增温后，蓝藻结皮覆盖度升高了 9.53%，POC 含量显著（$P<0.001$）降低了 30.14%，MAOC 含量降幅小；苔藓结皮覆盖度降低了 5.73%，POC 和 MAOC 含量分别显著（$P<0.001$）增加了 22.53% 和 36.49%。由于 MAOC 比 POC 更不容易分解[43]，POC 具有更快的周转速率，更容易受到环境变化的影响[46-47]。在短期增温试验中，蓝藻结皮覆盖度的增加伴随着微生物生物量的增加，再加上温度升高使微生物分解和呼吸速率增加[48]，从而加速结皮中 POC 的分解。微生物残体是 MAOC 主要组成物质[49]，苔藓的死亡直接增加了 MAOC 的含量，进而增加 POC 含量。Díaz-Martínez 等[50]对地衣和苔藓混合生物结皮的增温试验结果表明，9 a 的 2～3 ℃增温使高覆盖度生物结皮（HBC）POC 和 MAOC 含量无明显变化。HBC 覆盖度在前 5 a 降低，之后保持稳定（图 1），虽然 5 a 后增温组与对照组的有机碳含量无显著性差异，但覆盖度的不同表明两组处理中碳输入和碳输出含量不同，即碳平衡状态不同。综上，有机碳在短期试验中的变化取决于结皮覆盖度的变化，而在长期试验中有机碳含量趋于稳定。

2.2　净碳排放量

很多研究报道了增温对生物结皮净碳排放的影响，但是促进还是抑制仍存在争议。在腾格里沙漠开展的野外短期（低于 2 a）增温试验（0.5～2 ℃）结果表明，增温抑制了生物结皮累积净碳排放[51-54]；而在科罗拉多高原和西班牙中东部地区，短期增温（2～4 ℃）导致净碳排放量显著（$P<0.05$）增加[55-57]（图 1）。干旱区域的光合作用和呼吸作用，都受土壤湿度和温度的影响[58-59]。理论上小幅度的变暖会提高细胞内多种酶活性，从而促进代谢活动的进行；而变暖引起的土壤干燥度降低又会抑制微生物活性[60]（表 2）。Sun 等[61]通过 Meta 分析整合了全球已发表的文献，探究了增温试验对生物结皮净碳排放量的影响，结果表明：在相对湿润的地区，升温增加了生



C：蓝藻结皮 Cyanobacteria crusts；L：地衣结皮 Lichen crusts；M：苔藓结皮 Moss crusts.

图1 增温对生物结皮覆盖度、有机碳和净碳排放量的影响

Fig. 1 Effects of warming on biocrusts coverage，organic carbon and net carbon emissions

表2 增温引起的净碳排放量变化情况

Table 2 Changes of net carbon emissions caused by warming

试验周期 Experimental period	类别 Categories	净碳排放量变化 Changes of net carbon emissions	参考文献 Reference
短期 Short-term (<2 a)	不同地区 Different regions	腾格里沙漠生物结皮累积碳排放被抑制，而在科罗拉多高原和西班牙中东部地区，累积碳排放量显著增加	[51-57]
	不同季节 Different seasons	生长季节碳排放量变化大于非生长季节	[58,61-62]
	不同类型 Different types	苔藓结皮年累积碳排放量降低幅度大于地衣结皮	[53-54]
长期 Long-term (>5 a)		生物结皮累积碳排放量在后期与对照组无明显差异	[22,42]

物结皮净碳排放量，而在干燥条件下则抑制。腾格里沙漠的年降雨量占另外2个地区年降雨量的比例为53%～69%（表1），这表明腾格里沙漠相对干燥，增温引起的土壤湿度进一步下降，从而降低了生物结皮净碳排放量；而另外2个地区相对湿润且年均气温较高，这些地区的生物结皮对温度敏感性较低，升温会促进碳排放。因此，增温导致的不同地区净碳排放量差异是由气候条件不同引起的，特别是气温和降雨量。

同一地区不同季节的降水量变化特征导致了净碳排放量的季节变化差异。腾格里沙漠80%以上的年降水量集中在夏季和秋季，这2个季节为结皮的生长季节，另外2个地区的生长季节为春季和冬季。由表2可见，在生长季节，生物结皮累积碳排放量远高于非生长季节，且增温引起的波动更大[42,58,61]。土壤呼吸的季节性变化与降水、温度和土壤含水量密切相关[11,60]。生物结皮中的苔藓、地衣和藻类等在土壤水分含量极低时进入休眠状态，当环境中出现少量可用水时快速恢复至活跃状态[6]。在生长季节，结皮微生物获得水分的机会和时间都增加。在中等

温度和水分含量下，生物结皮光合活性趋于最大值，而呼吸活性呈线性增加趋势[58,62]。这些结果表明降水量差异引起的呼吸速率不同是决定净碳排放量增加与否的主要因素。

不同类型生物结皮的净碳排放量对增温的响应也不同。在相同地区，净碳排放量随着演替而增加：蓝藻结皮＜地衣结皮＜苔藓结皮。这是由于演替后期土壤有机碳含量丰富，苔藓自养呼吸和微生物异养呼吸都较高[22,63]。经增温处理后，苔藓结皮年累积碳排放量下降幅度大于地衣结皮，蓝藻结皮的波动较小[53-54,64]（表2）。激活和维持苔藓的代谢活动所需水分含量高于地衣和蓝藻，而增温缩短了土壤湿润时间[65]，更强烈地抑制了苔藓结皮的呼吸作用。与苔藓相比，地衣对水分的依赖性更小[66]，保持土壤水分能力较差[3]，从而使其对温度和湿度的敏感性较弱。

与短期试验不同，在这些地区开展的长期（大于5 a）增温试验都表明生物结皮累积净碳排放量在后期与对照组无明显差异[22,42,56]（表2）。Dacal等[56]通过分析土壤湿度在增温试验中的变化，指出温度升高是调节生物结皮呼吸短期变化的主要驱动力，长期变化主要由热适应性决定。土壤呼吸热适应性是干旱地区特有的属性[16]。在长期试验的前几年，由于增温会抑制地衣或苔藓的生长，导致生物结皮覆盖度发生变化，但6 a之后趋于稳定[22-26]。虽然稳定后的结皮覆盖度低于对照组，但优势生物丰度的显著降低同时影响着光合作用和呼吸作用，从而影响土壤有机碳含量，经长期增温后呼吸作用对温度不敏感，有机碳含量也无明显变化，这些因素的共同作用使结皮净碳排放量趋于稳定（图1）。

3　总结与展望

本文总结了生物结皮微生物群落组成及其呼吸作用经增温后所发生的变化，并探讨了引起这些变化的潜在机制，如图1所示。在短期增温过程中，土壤含水量是决定结皮中优势生物组成和丰度以及净碳排放量变化的主要因素。短期增温会导致相对干燥地区结皮中苔藓丰度急剧下降，而相对湿润地区结皮中地衣丰度和种类大幅度降低，优势生物丰度降低会使土壤有机碳含量增加；由于干燥地区呼吸作用被抑制，净碳排放量与有机碳含量的变化存在延迟效应，而在湿润地区，二者同步变化。经长期增温后，结皮覆盖度不可逆性降低，结皮中微生物对温度和湿度的敏感性降低，结皮优势生物和细菌相对丰度、组成趋于稳定，从而使有机碳含量和净碳排放量保持相对稳定。已有的这些研究结果很少涉及生物结皮光合活性和细菌代谢活性的变化。为进一步深入探究结皮微生物参与的碳代谢对增温响应的内在机制，今后的研究可以从以下几个方面展开。

1）在开展长期试验时，增加检测碳排放量的时间点。已有的长期增温研究大多只检测了其中几年中十几天的生物结皮碳排放量。相同地区，土壤温度和湿度在不同月份和不同年份中存在差异，隔几年采样不便于精确判断碳排放发生变化的转折点；每个月份中存在着一定的降水事件，通过每个月固定日期的碳排放量计算年累积碳排放量会存在偏差。为了更加准确地反映增温试验中碳排放规律，需每年进行多次监测，且监测时间应综合考虑天气的影响。

2）同时检测生物结皮净呼吸速率和光合速率，分别探究结皮作为“碳源”和“碳汇”对增温的响应。目前大部分研究只关注于增温对生物结皮净碳排放量的影响，但不同地区苔藓、地衣、蓝藻和细菌等种类不同，再加上不同的气候条件，不同地区生物结皮的光合速率和呼吸速率存在较大差异，净碳排放量对增温的响应主要受光合作用还是呼吸作用的影响仍需阐明，这将有助于解释不同区域净碳排放量存在差异的内在原因。

3）开展增温对生物结皮中碳分配影响的研究。结皮中微生物种类众多，且微生物在促进碳循环的过程中发挥着重要作用。增温导致的苔藓或地衣丰度降低，不仅影响着结皮中的总输入量碳，二者的残体也为其他异养微生物提供了有机质，从而使结皮中原有的碳分配规律发生改变，并随着时间的推移达到新的平衡状态。在今后的研究中，可以通过稳定同位素标记法探究增温对碳元素在微生物之间转换的影响，以及微生物代谢活性的变化，并阐明碳元素在结皮中保存和输出的具体含量和存在形式，为评估在气候变化条件下干旱地区在全球碳循环中的贡献提供数据支持。

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Effects of warming on composition and respiration of microbial community in biological soil crusts

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Abstract Biological soil crusts are the main cover of the soil surface in arid areas, in which the microorganisms play an important role in regulating the climate sensitivity of carbon cycling in dry areas. At present, there are still disagreements in the studies on the effects of climate warming on the microbial communities and their respiration in biological soil crusts. This article summarized the emission patterns of carbon in biological soil crusts in different experimental cycles, seasons, and types of biological soil crusts through the warming experiments of simulating climate warming to more accurately predict the carbon balance in arid areas in the future. The intrinsic reasons for the differences in carbon emissions were analyzed by combining changes in microbial abundance and organic carbon. The results showed that short-term warming (below 2 year) led to a significant decrease in the abundance of moss or lichens in the biological soil crust, thereby increasing the content of organic carbon in soil, with a synchronous increase in the emissions of net carbon depending on the content of moisture in soil. Long-term warming (greater than 5 year) reduced the sensitivity of microorganisms to temperature and humidity, and the abundance and composition of microorganisms tended to stabilize, resulting in relatively stable content of organic carbon and the emissions of net carbon. The existing results reflect the patterns of and reasons for carbon emissions in biological soil crusts, but the underlying regulatory mechanisms involved by microorganisms are still unclear. Therefore, it is necessary to focus on studying the response mechanism of the carbon metabolism of microorganisms in biological soil crusts to warming in the future. It will provide important theoretical basis for evaluating carbon balance in arid areas.

Keywords biological soil crusts; warming; the composition of microbial community; organic carbon; emission of net carbon

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