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中国荒漠与沙地生物土壤结皮研究

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摘要 生物土壤结皮广泛分布于干旱半干旱区, 其盖度占该区域地表活体覆盖的40%以上, 是联结荒漠地表生物与非生物成分的“生态系统工程师”和荒漠/沙地生态系统健康的重要标志, 也是干旱区地球表面过程研究中生物学与地球科学交叉研究的热点科学问题. 21世纪初, 相关研究绝大多数来自国外, 且集中在热带荒漠、寒漠和欧洲草原, 很少有来自中国和温性荒漠的报道. 本文评述了2000年以来中国学者在这一研究领域开展的系列创新性研究, 涉及生物土壤结皮组成、分布和演替, 对环境胁迫及全球变化的生理生态学响应, 与土壤生态、水文过程, 与维管植物和土壤动物关系, 对干扰响应和人工培养及在生态恢复实践中的应用等, 介绍了中国学者对国际生物土壤结皮研究所做的贡献.

关键词 荒漠生态系统, 生物土壤结皮, 土壤生态与水文过程, 生态恢复

生物土壤结皮(biological soil crust, BSC)是由蓝藻、绿藻、地衣、藓类和微生物, 以及相关的其他生物体通过菌丝体、假根和分泌物等与土壤表层颗粒胶结形成的十分复杂的地表覆盖体, 是荒漠生态系统的重要组成成分[1,2]. 其盖度占全球干旱、半干旱地区裸地面积的70%, 发挥着极其重要的生态系统功能. 截至2000年, 对BSC研究主要来自于美国、澳大利亚、德国、西班牙和以色列, 很少有来自中国的报道, 中国和中亚地区的研究几乎处于空白状态[3]. 基于这一现状, 中国学者从20世纪90年代末开始对BSC的形成、结构、群落组成、演替特征、时空分布和生态系统功能开展了大量的研究[4,5]. 补充和完善了国际BSC在温性荒漠区的研究不足, 填补了相关认知空白, 并从跟踪研究发展到并行研究, 促进了中国荒漠生态系统生态学和干旱区生态水文学的发展, 在国际上产生了重要影响. 本文主要评述了2000年至今我国学者在这一领域取得的重要进展, 展示了对全球BSC研究所做出的贡献.

1 BSC群落组成、分布和演替

不同于热荒漠(hot desert)和寒漠(cold desert), 发育在中国温性荒漠和沙地的BSC, 其种类组成多样, 群落多以藻类、地衣和藓类镶嵌分布. 电子显微镜扫描结果证明, 这些隐花植物在地表利用菌丝体、假根和地表的依托支撑结构及分泌的多聚糖, 束缚和胶结了土壤细小颗粒, 形成了BSC[6~13]. Hu等人[14]从微米尺度上发现了藻类在BSC中呈精细“层片”分布和发育特征, 由表及里分别为矿物质保护层(0~20 μm)、富藻层(20~1000 μm)和疏藻层(1000~5000 μm)等3层结构, 并发现随着BSC的拓殖发展, 维持BSC结构的主要胶结方式也由胞外多聚糖的黏结作用逐渐转变为蓝藻和荒漠藻的藻丝体、地衣菌丝体以及藓

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类假根对土壤颗粒的缠绕和捆绑作用[15~17].

从群落组成来看, 拓殖初期的BSC主要有蓝藻、绿藻、硅藻和裸藻, 其中以蓝藻最为丰富[18,19]. 在古尔班通古特沙漠、柴达木盆地、腾格里沙漠、科尔沁沙地和库布齐沙漠的BSC群落中已鉴定出的蓝藻分别有121, 23, 21, 23和56种, 具鞘微鞘藻(*Microcoleus vaginatus* (Vauch.) Gom.)是优势种[14,19~23], 但发育在黄土区的BSC中仅发现11种, 且无具鞘微鞘藻[24]. 此外, 利用高通量测序和土壤稀释平板法, 从细菌、真菌丰富度和多样性角度分析了不同BSC的微生物群落结构[25~27]. 与世界上的其他荒漠相比, 古尔班通古特沙漠具有较高的蓝藻-微小真菌多样性[22].

BSC群落中地衣多样性的研究主要集中在腾格里沙漠和古尔班通古特沙漠. 异色杆孢衣(*Bacidia heterochroa* (Müll. Arg.) Zahlbr.)、安奈污核衣(*Porina aenea* (Wallr.) Zahlbr.)、黑白黑瘤衣(*Buellia alboatra* (Hoffm.) Branth.)、美丽黑瘤衣(*Buellia venusta* (Körb.) Lettau (I, VI)), *Endocarpon deserticola* sp. nov.和*E. unifoliatum* sp. nov., *Fulgensia desertorum* (Tomin) Poelt, *Rinodina bischoffii* (Hepp) A. Massal 和 *Seirophora orientalis*为全球新种[28~31]; 古尔班通古特沙漠固定沙丘中发现坚韧胶衣(*Collema tenax* (Sw.) Ach.)、红磷网衣(*Lecidea decipiens* (Hedw.) Ach.)、荒漠黄梅(*Xanthoparmelia deserborum* Hale.)和藓生双缘衣(*Diploschisttes muscorum* (Scop.) R. Sant)是优势种[17].

BSC群落中藓类多样性与降水量呈明显的正相关关系. 与中国其他荒漠和沙区相比, 毛乌素沙地与科尔沁沙地BSC中藓类多样性和盖度相对较高[5,32,33]; 发育在腾格里沙漠固定沙丘的BSC中藓类植物共16种, 以真藓(*Bryum argenteum* Hedw.)为优势种[34], 在古尔班通古特沙漠藓类多样性相对低, 主要有真藓、细叶真藓(*B. capillare* Hedw.)、无齿紫萼藓(*Grimmia anodon* Bruch & Schimp)和垫状紫萼藓(*G. pulvinate* (Hedw.) Sm.)[17,35].

此外, 我国学者从不同尺度上探明了决定BSC空间分布的关键因子. 在微小尺度上, 微地形是形成和维持BSC群落多样性的关键因子[36]; 在中小尺度上BSC群落的盖度和多样性受大气降尘累积、光照、土壤湿度和土壤养分的影响[37~41]; Li等人[5]认为在景观尺度上(不同气候带的沙区)降水决定了BSC的优势种群的空间分布, 在区域尺度上(某一沙区)土壤属性决定了BSC的优势种群分布, 而在局地尺度上(具体研究样地)干扰和植被盖度对BSC的分布起着重要的作用.

Li等人[36,37]提出了沙面大气降尘的不断沉积是BSC拓殖和发展的重要物质基础的观点, 认为温性荒漠BSC的演替遵循着从“藻结皮、藻-地衣混生BSC、地衣BSC、地衣-藓混生BSC和藓类BSC”的演替规律[19,42~44]. 腾格里沙漠人工固沙植被区BSC的长期监测表明, 固沙植被建立初期, 大量的降尘累积再经雨滴的打击, 在沙面形成一层黏粒和粉粒含量较高的物理结皮, 随之细菌、真菌、放线菌和蓝藻的拓殖使沙面形成藻BSC, 而后出现地衣BSC和地衣-蓝藻-绿藻的混生BSC, 随着表层土壤肥力和持水能力的提高, 最终形成了以藓类为优势种的BSC[19,34,37,42,45].

2 BSC对环境胁迫、全球变化的生理生态学响应

尽管组成BSC的生物体能够在极端环境下生存, 但其对全球变化和各种胁迫非常敏感. 我国学者从生理生态学角度研究了其对降水、UV-B辐射、氮素、盐分、温度和光照等非生物因子变化的响应, 揭示了BSC适应极端环境的生理生态学机制, 丰富了BSC研究的内涵.

通过对BSC在形态结构、生理生化和分子调控等方面应答脱水-复水过程的研究, 探明了BSC利用雨水、凝结水和融雪等水资源, 应对干旱胁迫的生存策略[11,46~53]; 明确了冬季降雪的湿润作用能够刺激BSC产生较高的光合和呼吸速率[54~57]; 发现BSC群落中对齿肋赤藓(*Syntrichia caninervis*)由上至下吸收水分的新模式[58~61]; 证实了水分胁迫也是保护BSC避免高强度UV-B辐射[62]、高温[63]和盐胁迫[64]伤害的一种策略.

研究表明, UV-B辐射增强显著地降低了BSC中藻类光合活性和生长速率, 并导致细胞氧化和DNA链损伤[65~68]. 虽然UV-B辐射通过减少叶绿素含量的间接途径和对光合系统影响的直接途径抑制着藻BSC净光合速率[69,70], 但BSC中的藻类可凭借外源抗坏血酸、半胱氨酸和胞外聚合物来缓解UV-B对光合活性和DNA链破坏作用[65~67]. 同样, UV-B辐射强度增加和辐射时间延长, 也显著抑制了BSC中藓类光合速率, 并造成了细胞膜的损伤, 导致抗氧化酶系统的紊乱[71~73]. BSC中藓类的细胞和叶绿体超微结构在遭受UV-B辐射后的损伤佐证了UV-B辐射对上述指

标的影响[74]，但BSC生物体在抵御UV-B辐射所造成伤害的过程中也发展了一系列的防御机制，如趋避迁移、积累UV-B吸收物质、修复DNA损伤等[71,75~78].

实验证明，氮添加对BSC生物量、碳氮代谢、渗透调节物质和抗氧化酶活性都产生显著影响[79]. 低浓度的氮对BSC生长具有正效应，高浓度的氮则具有明显的负效应. 对藻类和地衣的正效应在氮素浓度大于1 g N m^{-2} a^{-1}时减弱，而藓类在大于0.3 g N m^{-2} a^{-1}时正效应可能减弱，甚至出现负效应[79,80]. Wang等人[81]还发现氮添加改变了BSC中微生物群落的多样性和群落结构.

BSC中藻类对盐胁迫具有一定的耐受和抵抗能力[82]，而外源添加的多糖可以提高荒漠藻的抗盐特性，反之，盐胁迫可以调控荒漠藻的糖代谢，促使多糖合成[83,84]. 荒漠藻也具有适应高温和高光强的特性，这一特性可促进其胞外多糖的合成[85,86]. 模拟升温可促进藻类和藓类结皮固氮活性的提高，有利于BSC的氮固定[87]. 此外，低温黑暗条件有利于BSC活性的恢复，而光照则抑制恢复[88]. Wu等人[89]通过模拟不同强度的光合有效辐射，揭示了地衣BSC对高强度光合有效辐射的适应性与其自身特殊结构和光合色素的累积有关. 此外，模拟实验证明增温和减雨改变了BSC群落组成、结构和群落学特征进而影响BSC的生态水文功能，直接关系到荒漠生态系统功能的改变和可持续发展[90].

3 BSC与土壤生态系统过程

BSC的拓殖和发展是荒漠和沙地土壤生态健康的重要标志[90]. 我国学者的研究表明，BSC促进了沙面土壤形成，改善了土壤理化和生物学属性[5,9,91~94]. 对比演替初期与后期BSC覆盖的浅层土壤，发现黏粉粒含量由初期的3.0%~5.0%增加到后期的8.0%~25.0%，土壤团聚体(>250 μm)[12,13,32,34,45,93,95~97]、有机质含量、全氮、全磷和全钾含量明显增加[13,34,97,98]；其次，BSC通过对沙面矿物质的腐蚀作用，以及风蚀水蚀物质的沉积使土壤的细小颗粒物累积和养分的富集，促进了在沙面土壤形成[13,19,34,42,91~93,99,100]，证明了BSC的存在提高了土壤脲酶、转化酶、过氧化氢酶和脱氢酶活性，同时发现土壤氧化酶的恢复速率快于水解酶[12,93,101~104]. Li等人[105]预测了草地沙化后土壤恢复到天然植被区土壤所需的时间，首次回答了干旱区BSC参与的土壤属性恢复的时间.

国内大量研究证实BSC是荒漠生态系统碳、氮循环的重要参与者和土壤有机碳、氮的重要来源[44,50,106~109]. 藻类BSC的碳固定和碳释放量分别为2.9~11.3和4.6~61.3 C m^{-2} a^{-1}，地衣为BSC 3.5~37.0和5.8~48.8 C m^{-2} a^{-1}，藓类为26.8~64.9和4.7~140.0 g C m^{-2} a^{-1}[47,50,106~111]. 这些量化研究填补了我们对温性荒漠碳循环的认知空白[106,108,109,112~114].

对BSC碳释放的研究认为，BSC碳释放量随着降水总量和冬季降雪量的增加而增加，但极端降水抑制了藻类和混生BSC的碳释放量而不影响藓类结皮的碳释放量[55,57]；增温显著影响BSC碳收支，增温达到2.5℃时将显著抑制BSC的光合速率，而促进碳释放速率[115]. Huang等人[110]建立了受土壤水分驱动下的固碳模型，综合计算出藻类和藓类的结皮年际固碳潜力. 水分(包括降水和非降水)决定了BSC固碳活性[114,116]，而土壤含水量和有效湿润时间决定了BSC的固碳量[106,107,117]，水分也是BSC碳释放的驱动因素[50,97,109,111,113,118~120]；另外，沙埋干扰抑制了BSC的碳固定，促进了碳释放[110]，但BSC的缺失也将导致碳释放量显著增加[121].

有关BSC氮固定，Wu等人[122]和Su等人[123]明确了其固氮活性介于2.5~62.0 μmol C_2H_4 m^{-2} h^{-1}，其中藻类BSC的平均固氮活性(28.1 μmol C_2H_4 m^{-2} h^{-1})>地衣结皮(24.3 μmol C_2H_4 m^{-2} h^{-1})>藓类结皮(14.0 μmol C_2H_4 m^{-2} h^{-1})；BSC的年固氮量介于3.7~13.2 mg m^{-2} a^{-1}，藻类>地衣>藓类BSC. BSC的氮矿化率(硝态氮、铵态氮和无机氮)则是藓类(0.14~0.83 mg kg^{-1} d^{-1})>藻类(0.06~0.58 mg kg^{-1} d^{-1})[124]，证明了BSC向荒漠生态系统氮输入并转化为土壤养分以及直接供应给荒漠植物使用的事实[122,123,125~128]. 氮固定和矿化与降水量呈显著的正相关，而对氮添加的响应因BSC类型不同而表现出明显差异[127,129]；此外，影响BSC碳循环的因子同样影响氮循环[122~124]，而轻度放牧能够促进了BSC氮固定量[130]. 在荒漠景观尺度上BSC斑块与植被斑块之间存在碳氮的“源-汇”关系，指出BSC斑块是维管植物斑块的C，N的重要输入者[91,99,100,131]. 这些研究填补了温性荒漠BSC碳、氮循环的研究空白，证明通过荒漠生态系统管理有望实现BSC的碳氮“源-汇”关系的转换[97,107,124~126].

4 BSC与土壤水文过程

BSC深刻影响着荒漠和沙区的土壤水文过程[99].

我国学者系统研究了不同演替阶段BSC对降水入渗、地表蒸发和凝结水捕获的影响及机理[58,132~139].

研究发现, BSC显著地改变降水入渗过程和土壤水分的再分配格局, 并在一定条件下可减少降水对深层土壤水分的有效补给[8,132,138,139]. 在降水量70~150 mm的古尔班通古特沙漠, 藓类、地衣和藻类BSC分别使入渗速率降低16.50%~36.10%, 33.98%~46.42%和35.92%~50.39%, 1 h累积入渗量分别降低16.10%, 28.56%和26.56%[8]; 在降水量150~200 mm的腾格里沙漠, 对入渗拦截量依次为藓类结皮>地衣结皮>藻类结皮, 三者在小于5 mm或者大于10 mm的降雨下没有显著的差异[133]; 在降水量为300~500 mm的毛乌素沙地和科尔沁沙地, BSC降低了入渗速率和下渗深度[138,140], 而在降水量450 mm的黄土高原地区, BSC的减渗效应使土壤水分浅层化, 增加了地表径流[91,141~143]. 也有研究认为, BSC对土壤水分入渗起到积极作用[34]或者无影响[144].

BSC可吸收雨滴冲溅产生的能量, 减缓地面径流或土壤侵蚀的发生[141]. 扫描电子显微镜下发现含沙土壤有足够的孔隙度以供水分的流动, 但结皮中的泥和黏土颗粒在湿润状态下膨胀后可能抑制土壤水分的入渗[139]. 如有些黏质蓝藻在降雨后其体积可以迅速膨胀, 从而关闭了土壤表面的水流途径, 而发育良好的一些藓类结皮表面不易被水沾湿, 有利于土壤表面水分的入渗. 魏江春[144]指出, 凡是以石果衣(*Endocarpon pusillum* Hedw.)和坚韧胶衣为优势的BSC有截流降水下渗作用, 而以*Psora decipens* (Hedwig) Hoffm和*Toninia* sp.为优势的BSC, 则因在表面呈现网状裂隙而有利于降水的下渗. Li等人[132]采用LISEM (limburg soil erosion model)模型验证了藻类BSC覆盖的沙丘背风坡较藓类BSC覆盖的迎风坡更容易产流. 在实验和模拟的基础上, Li等人[34,132]提出了BSC对降水入渗的影响主要取决于BSC自身的生物学特征(如孔隙度、厚度和种类组成等)、表层土壤性质(土壤初始含水率、质地组成)和区域降水特征(雨型、雨滴直径和降雨强度)的综合评价观点, 并解释了当前有关BSC影响入渗所存在的分歧与长期争论.

BSC通过改变土壤理化性质来影响地表蒸发[135,137]. 这是因为BSC通过降低地表反射率[145]和提高表层土壤的持水能力[140]而促进蒸发. 也有观点认为, BSC封闭了土壤表面而降低了蒸发[146]. 除了受到区域气候条件[135]、土壤水分状况[147]及微地形[133]等因素的影响, BSC对地表蒸发的影响还受到自身生物学特征[139], 不同类型及盖度的BSC对地表蒸发的影响也不同[137,148]. 藓类BSC具有较高的持水能力, 遇降水后其促进了蒸发, 尔后又开始抑制蒸发, 延长了水分在表土的保持时间, 对一年生植物的萌发、定居具有重要的意义[42,135,149~151].

凝结水是BSC中的隐花植物和其他微小的生物体珍贵的水资源, 决定着它们的活性[46,106,110,115,134,135,152]. 来自腾格里沙漠的长期监测发现, 藓类与藻类BSC表面获得凝结水量日均值在0.15 mm左右, 最大值接近0.50 mm d^{-1}. 流沙、物理结皮和BSC的吸湿凝结水生成总量分别占同期降水量的15.90%, 22.90%和37.90%[136]; 在古尔班通古特沙漠, 藓类、藻类和地衣BSC的表面凝结水量日均值分别为0.14, 0.11和0.09 mm d^{-1}[135]; 而在毛乌素沙地, 藓类和藻类BSC的平均凝结水量甚至可以达到0.12和0.10 mm d^{-1}[148]. 针对凝结水形成的机理, 认为BSC通过其表面的微气候环境[58,134,136]、黏附大量微生物有机组分[136]、BSC藻丝体的发育及其胞外分泌物[46]和叶片毛尖特殊的水分收集与传输系统(凹槽和疣状突起)形成凝结水[58,59]. Pan等人[52,136]指出, 吸湿凝结水在水量平衡中的重要性在于夜间生成的吸湿凝结水在日出后的蒸发过程中能够弥补土壤表层水分的散失, 有利于BSC表层水分的保持, 是表层水分在旱季不会无限降低的主要原因. 人工固沙植被建立后, BSC的形成深刻地改变了降水入渗、土壤蒸发及凝结水捕获等水文过程及沙地原有的水分平衡关系, 驱动了固沙植被在组成、结构和功能上的演变, 其解释了人工固沙植被退化的原因, 也揭示了我国沙区人工植被演变的基本规律[19].

5 BSC与维管植物和土壤动物的关系

由于水分限制, 干旱半干旱区植被往往呈现BSC斑块与维管植物斑块镶嵌分布的特点[4,36]. 大部分学者认为BSC的存在有利于维管植物的生存与繁衍. 据Zhang等人[153]报道, BSC显著提高了5种植物对N的吸收, 增加了地上和地下的生物量. Li等人[150]和Su等人[151,154]的研究表明, 藻类和藓类BSC显著地提高了植物的萌发率和存活率. Zhao等人[155]用同位素示踪的方法证明BSC可以促进C_3植物对碳的吸收. 也有研究认为, 在多风的环境中, 大多数维管植物种子很难在光滑的BSC表面停留, 间接地降低了种子

的萌发机会[150]. Xiao等人[156]的研究发现在藓类BSC增加了油蒿(*Artemisia ordosica* Kraschen)的死亡率. 相反, 植被盖度和地表凋落物的增加会导致BSC的死亡[33].

许多报道认为, BSC对维管植物的影响机制在于BSC通过改变土壤性状(地表粗糙度、土壤温度、湿度、养分含量等)来影响维管植物的种子萌发、定居和存活[150,157~163], 并改变了浅层土壤的水分含量, 导致植被组成中浅根系的草本物种丰富度和生物量增加, 深根系的木本植物盖度和生物量降低, C_4植物增加[117,133,164,165].

荒漠和沙丘严酷的环境威胁着动物的生存, BSC的存在改变了土壤生境, 为微小土壤动物的生存提供了适宜的生境和食物来源. 沙面BSC和表层土壤厚度的增加有效地保护了蚁穴不被沙埋所破坏[166~168], 增加了昆虫多样性[149]. Liu等人[169,170]认为BSC的存在增加了土壤微生物丰富度和生物量, 而细菌、真菌等微生物又分别被植食性和肉食-杂食性线虫所取食[171~173]. 垫刃科(*Tylenchidae*)和滑刃线虫属(*Bursaphelenchus*)的线虫可能会直接取食蓝藻, 也有可能取食藓类和绿藻[172]. 线虫丰富度的增加会引来更多的杂食-肉食动物[174,175]. 拟步甲科(*Tenebrionidae*)昆虫对藓类结皮有取食作用, 石蛃(*Microcoryphia*)对地衣结皮有取食作用[176]. 以上研究证明, BSC不仅为微小土壤动物提供生存生境, 还直接参与荒漠生态系统食物链的构成[90].

另外, 土壤微小动物也影响了BSC, 如土壤线虫表皮上会携带一些细菌, 还有一些细菌会通过线虫的消化系统被排泄出来, 在线虫扩散的过程中促进了细菌的繁殖与拓殖, 间接地促进了BSC的拓殖[172]. 有研究发现, 掘穴蚁(*Formica cunicularia* Latr.)筑穴会使土壤中出现通道, 增加土壤孔隙度, 从而削弱了BSC对降雨的截留作用[166,167].

6 BSC对干扰的响应

由于自身矮小, 隐花植物对风蚀、沙埋、水蚀、火烧和放牧踩踏等干扰十分敏感. 风蚀会直接引起隐花植物机械损伤, 加快水分丧失, 从而抑制BSC光合和呼吸生理活性、生物量累积、生长和无性繁殖能力[177], 但BSC增强了土表抗风蚀的能力, 其存在可显著增加临界起沙摩擦速度[8,138,178,179].

沙埋作为沙区一种常见的物理胁迫, 除了对BSC产生机械压迫外[180], 还降低了BSC生境中光和水分(包括凝结水)等资源的有效性[152,181]. 沙埋对BSC的影响因沙埋厚度、时间和BSC类型而异: 浅层沙埋促进BSC生长, 而较厚的沙埋降低BSC的PSII光化学效率、叶绿素a和胞外多糖含量, 长时间的深层沙埋导致BSC死亡[180,182]; 具鞘微鞘藻可通过向上移动的方式耐受厚度不超过1 cm的沙埋[181], 而藓和地衣所能耐受沙埋厚度明显大于藻. 通过降低呼吸碳损失和向上生长等机制, 藓类和地衣结皮可耐受1~4 mm厚度的沙埋[183]. 沙埋还可改变BSC中真菌群落物种组成[25]和覆盖土壤温室气体通量[120].

针对BSC对土壤水蚀的响应, Zhao等人[143]利用模拟单滴降雨, 从能量的角度分析了BSC抗击水滴冲击的作用, 发现随着BSC的演替, 其覆盖土壤抗水蚀能力显著提高. 火烧在我国荒漠地区属于人为控制和预防的特殊因子, 发生概率小, 但偶尔发生的火烧显著改变了BSC物种组成, 增加了蓝藻的盖度, 减少了地衣和藓类的盖度[177]. 火烧也增强了藓BSC的斥水性[184], 抑制了坚韧胶衣的固氮功能[185]. 放牧动物踩踏降低了BSC物种丰富度、盖度和地表稳定性[33,130,186], BSC的破坏增加了外来种入侵的机会[159,160], 并可能改变荒漠生态系统的功能[99].

7 BSC的人工培养及其在生态恢复实践中的应用

作为荒漠生态系统的重要组成, BSC的形成和发育是生态系统健康的主要标志之一, 其在防治沙化、维护荒漠生态系统的稳定性和生态修复等方面所发挥的独特作用引起了广泛关注[4], 但BSC自然形成往往需要几年甚至几十年[19,32,42,187,188]. 因此, 如何通过人工培育和扩繁技术, 加快沙区生态恢复和重建的进程是荒漠化防治的重大实践需求[177].

Chen等人[189]、Wang等人[190]和Lan等人[88,191]在库不齐沙漠成功分离、培养了具鞘微鞘藻和爪哇伪枝藻(*Scytonema javanicum* Born et Flah), 通过掌握人工藻结皮的生理特性[192]、耐胁迫能力[77]和外在土壤水分、温度、光照和养分供应等环境条件[189]及其在沙丘的分布规律[193], 确定了最佳光照、温度和养分条件[88,194], 建立了工厂化生产流程和沙面接种技术体系[195]. 在腾格里沙漠, 研究者从本地BSC中分离、培养了3种蓝藻(*Nostoc* sp., *Phormidium* sp.和*Scytonema* *arcangeli* Bornet ex Flahault), 同时配合使用固沙剂和高吸水性聚合物在流沙进行接种, 1年后土壤硬度明显增加, 新生BSC碳水化合物含量、蓝藻生物量、微生物生物量、土壤呼吸、碳固定和有效量子产率可达到发育20年自然BSC的50%~100%[196]. 此外, 根据所筛选的藓类植物芽、茎、叶碎片无性繁殖能力证明了人工培养藓结皮的可行性[197,198], 并分别确定了古尔班通古特沙漠刺叶墙藓(*Tortula desertorum* Broth.)[198]、腾格里沙漠和毛乌素沙地真藓(*Bryum argenteum* Hedw.)[90,197]、黄土高原土生对齿藓(*Didymodon vinealis* (Brid.) Zand)[199,200]人工培养的最佳温湿度、营养液及浓度、基质和野外接种方法.

上述人工培养的藻和藓类材料在田间接种后, 显著增强了固沙功能[9,190,196,201,202], 改善了沙面土壤的水文[141,203]和理化属性[191,202,204,205], 为我国干旱和半干旱地区沙化土地修复提供了有力的技术支撑, 有望推广至全球其他类似地区, 甚至可能用于月球和火星表面尘埃的控制[206].

8 展望

随着全球环境变化和干旱区可持续发展研究的不断深入, BSC作为干旱区荒漠和沙地生态系统的重要组成, 在国际上受到了前所未有的重视. 其研究的视野开始从局地向区域和全球(陆地)尺度方向转变. 研究手段和思路已从传统的野外观测和控制实验向利用分子生物学进行机理探索、大尺度的模型模拟和多学科交叉研究发展. 研究内容从BSC时空分布、组成、结构和功能到多尺度的生态系统和景观过程与机理研究, 其中, BSC对全球干旱区生物地球化学循环的驱动机理、对全球旱地生物多样性的维持、对重要生态过程的影响, 如对全球旱地C、N循环, 旱区生物入侵、沙尘暴和水分平衡的影响, 以及对荒漠与沙地生态系统稳定性维持的多功能和互馈机理是未来研究的重点. 此外, 强化BSC群落的多元生态系统功能对全球变化的响应和利用BSC促进荒漠生态系统恢复的研究, 尤其是在沙化土地治理中的应用研究是国际BSC研究者的共识.

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Summary for "中国荒漠与沙地生物土壤结皮研究"

Researches in biological soil crust of China: A review

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Biological soil crust (BSC), a complicated assemblage of cyanobacteria, green algae, diatoms, lichens, mosses, soil microbes and other related microorganisms cemented with soil particles with special architecture, covers more than 40% and even as much as 70% living surface in arid and semi-arid regions. Being an important ecosystem engineer and indicator of desert ecosystem health, BSC plays vital roles in linking the surficial biotic and abiotic components in arid and semi-arid regions and the related studies become a hotspot in the biological-geographic crossing studies in the earth surface process. However, most studies related to BSC came from abroad and mainly focused on hot desert, cold desert, polar and tundra as well as European grassland at the beginning of this century, little information available from Chinese temperate and central Asia desert. In this paper, we reviewed the research achievements in BSC by Chinese researchers since 2000 in the following aspects: (1) The composition, distribution and succession of BSC across Chinese temperate deserts, in particular, the responses of crustal species distribution pattern to climatic, soil properties and vascular plant cover at different spatial scales; (2) eco-physiological responses of BSC to environmental stress, climatic change as well as to natural and anthropological disturbances, large changes in rainfall regimes, UV-B radiation, nitrogen addition, salt and other stresses could result in the conversion of BSC types and further contribute to the changes in the structure and functioning of desert ecosystems; (3) the critical roles of BSC in the soil ecological and hydrological processes, including the dramatic influences of BSC on soil stability, C and N cycling, and other physiochemical properties, as well as infiltration, dew entrapment, soil surface evaporation and soil moisture; (4) the relationships between BSC and vascular plants and soil animals, such as the responses and underlying mechanisms of seed retention, germination, establishment and survival of vascular plants to the succession of BSC, and BSC creating a suitable niche and food web for soil animal and microorganisms, maintaining soil biodiversity; and (5) the cultivation and inoculation of components within BSC as new material applied for soil fertilization and desertification reversal, 6 cyanobacteria and 3 moss species inhabiting BSC were selected from different desert areas and successfully cultured in laboratory and then identified to enhance the stability, fertility and other physiochemical properties of the upper sand soil after their inoculation in the field. Finally, based on the analysis of the new trends in research vision, means and ideas of the international BSC study, we pointed out the key points for future research in BSC.

desert ecosystem, biological soil crusts, soil eco-hydrology processes, ecological restoration

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