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生态生理学研究

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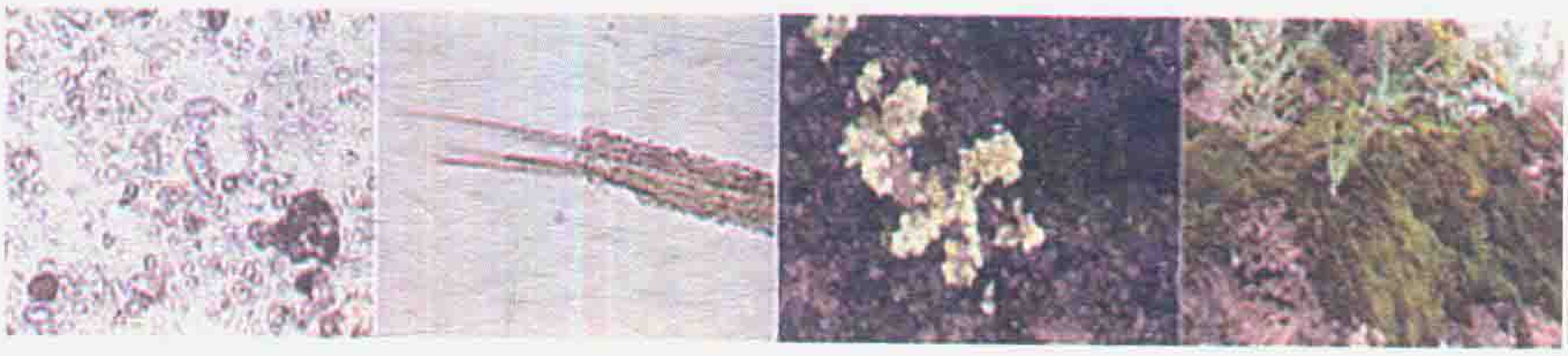

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高等教育出版社·北京
HIGHER EDUCATION PRESS　BEIJING

内容简介

生物土壤结皮是荒漠生态系统的重要组成成分，对荒漠系统生态和水文过程发挥着重要的影响，维持着荒漠生物地球化学循环和生态系统的健康和可持续发展。然而，生物土壤结皮的这些功能主要取决于组成其群落的生物体及多样性，它们对环境胁迫和气候变化具有高度的敏感性。本书全面阐述了这些结皮群落组成成分对非生物因子和生物因子等胁迫和干扰的生态生理响应，以及适应对策和机理，是正确认知和评估未来荒漠生态系统对全球变化响应和实现可持续生态系统管理的前提，是荒漠生态系统恢复与重建的重要科学依据。

本书可为生态学、土壤学、生理学、微生物学、水文学和全球变化研究者以及从事防沙治沙、荒漠生态恢复和生态系统管理的人员提供重要的参考。

图书在版编目（CIP）数据

中国荒漠生物土壤结皮生态生理学研究 / 李新荣，回嵘，赵洋著 . -- 北京：高等教育出版社，2016.12
ISBN 978-7-04-046979-0

Ⅰ. ①中… Ⅱ. ①李… ②回… ③赵… Ⅲ. ①荒漠 - 生态系统 - 土壤结皮 - 生理学 - 研究 - 中国 Ⅳ. ① P941.73 ② S152.4

中国版本图书馆 CIP 数据核字（2016）第 296644 号

策划编辑 关 焱 李冰祥 责任编辑 殷 鸽 关 焱 封面设计 刘晓翔
插图绘制 于 博 黄云燕 责任校对 刘春萍 责任印制 田 甜

出版发行 高等教育出版社 咨询电话 400-810-0598
社 址 北京市西城区德外大街 4 号 网 址 http://www.hep.edu.cn
邮政编码 100120 http://www.hep.com.cn
印 刷 固安县铭成印刷有限公司 网上订购 http://www.hepmall.com.cn
http://www.hepmall.com
开 本 787mm × 1092mm 1/16 http://www.hepmall.cn
印 张 28 版 次 2016 年 12 月第 1 版
字 数 550 千字 印 次 2016 年 12 月第 1 次印刷
购书热线 010-58581118 定 价 268.00 元

物 料 号 46979-00
审 图 号 GS（2016）2529 号
ZHONGGUO HUANGMO SHENGWU TURANG JIEPI SHENGTAI SHENGLIXUE YANJIU

序

生态文明建设是中国特色社会主义事业的重要内容，加大自然生态系统和环境保护力度是推进生态文明建设的重要举措。所谓自然生态系统是在一定时间和空间范围内，依靠自然调节能力维持的相对稳定的生态系统。我国北方广泛分布的荒漠、沙地和农牧交错带是承受风沙危害最严重的地区，是风沙治理、生态重建和恢复与生态文明建设的核心地区之一。生物土壤结皮作为干旱、半干旱荒漠自然生态系统中最重要的地表生物覆盖体，在维系荒漠自然生态系统稳定和持续发展中具有重要意义。

生物土壤结皮是由真菌界的地衣、细菌界的蓝细菌以及植物界的苔类、藓类和藻类为优势的微型生物与沙土颗粒缠绕在一起所形成的皮壳状结构。生物土壤结皮作为荒漠地区最重要的地表生物覆盖体，在遏制地表风蚀和水蚀，稳定地表环境，阻止就地起沙以切断沙尘暴沙源，促进荒漠和沙区土壤微生物及微小动物的繁衍、生存以改善土壤物质转化，如固氮中的硝化与反硝化作用、腐殖质的分解与合成等方面发挥着重要作用。同时，生物土壤结皮还能够保持土壤深层水分以利于相应数量维管植物的定居和生存，从而在维系荒漠自然生态系统的稳定和持续发展中具有重要意义。

近年来，生物土壤结皮在维系荒漠自然生态系统的稳定性和持续发展中的重要意义已越来越被学界所认可。然而，人类对于生物土壤结皮中微型生物的种类组成、结构、形成条件、演替规律及其生态功能机理还缺乏足够认识，这既是务必探明的科学问题，又是荒漠自然生态系统重建与恢复急需解决的实际问题，有待生物学、生态学等多学科的合作与综合研究。

《中国荒漠生物土壤结皮生态生理学研究》是继《荒漠生物土壤结皮生态与水文学研究》之后，李新荣研究员和他所在的中国科学院沙坡头沙漠试验研究站研究团队的又一力作。该书在上一本的基础之上，总结了研究团队自1999年至今十余年的研究成果。全书重点研究了生物土壤结皮群落中不同的微型生物类别、优势种分布格局对非生物因子(干旱、UV-B增强、增温、降水节律变化、沙埋和大气氮沉降等)、生物因子(维管植物覆盖度、土壤种子库和土壤微生物类群等)变化和干扰(生物入侵和火烧等)的响应，以及各种胁迫对特定生物土壤

结皮群落组成、结构和功能的改变，突出回答了为什么生物土壤结皮能够发挥诸多复杂的生态和水文功能，以及其在干旱、半干旱荒漠生态重建和恢复中的重要作用。作者认为，未来环境变化，特别是气候变化会直接通过改变生物土壤结皮群落的组成(优势种的相互替代)和分布格局而影响其多样的生态功能，进一步导致荒漠生态系统功能变化的不确定性，进而提出生物土壤结皮维系荒漠自然生态系统中的沙地植被，特别是人工植被系统稳定性持续发展的观点。此外，作者通过十余年的长期定位研究，提出了利用以生物土壤结皮繁育拓殖为主的综合固沙模式，并在沙化土地恢复的实践中得到验证。

本书的出版必将在推动我国沙漠化治理和风沙区生态恢复与重建等相关科学领域的理论创新和实践应用方面有所启示和借鉴；为相关科学领域的科教人员及师生提供重要的参考。谨以此为序与读者共勉。

中国科学院院士，中国菌物学会名誉理事长
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2016年8月16日于北京中关村

绪论

我国是一个受风沙危害和沙漠化十分严重的国家，风沙危害和沙漠化区域主要分布在东经75°~125°和北纬35°~50°范围，横跨半湿润、半干旱、干旱和极端干旱区等不同生物气候带。其中年降水量大于250 mm的东部沙地和农牧交错带以及年降水量小于200 mm的贺兰山以西的沙漠与绿洲、沙漠与荒漠草原过渡区是沙漠化和风沙危害最为严重的地区，也是进行无灌溉植被建设和构建国家北方生态屏障的关键区域。为了有效遏制风沙危害，防止沙化土地进一步扩张，国家先后在风沙危害区启动了“三北”防护林建设、退耕还林和京津风沙源治理等一批以人工植被建设作为主要生态修复措施的重大生态建设工程。近60年来，我国沙区植被建设取得了举世瞩目的成就，有效遏制了沙漠化的发展，促进了局地生境恢复。在充分肯定成绩之时，笔者发现实践中还存在许多问题。无论是在降水较多的东部沙区还是降水较少的贺兰山以西沙区，都不同程度地存在局地地下水下降以及固沙植被衰退和死亡的现象，直接影响了沙区的生态恢复和防风固沙效益的可持续性。实践中出现的这些问题从一定角度反映了理论研究的滞后，包括对许多科学问题没有给予应有的重视。例如，在进行植被恢复和流沙固定过程中，对固沙植被区形成的生物土壤结皮的生态功能没有给予应有的重视，或出现认识上的片面性，一些地方甚至认为破坏生物土壤结皮可以增加降水入渗，改变土壤水分状况。从恢复生态学和生态系统生态学的角度来看，这种认识恰似盲人摸象，存在着很大的局限性和片面性。

生物土壤结皮（biological soil crust, BSC），是指由隐花植物（非维管植物）如蓝藻、绿藻、地衣、藓类和土壤中微生物以及相关的其他生物体，通过菌丝体、假根和多聚糖分泌物等与土壤表层微小颗粒胶结形成的十分复杂的复合体，是干旱、半干旱荒漠地表景观的重要组成之一，其存在是该区域生态系统健康的重要标志之一。大多数荒漠生态系统是由非生物因素（abiotic factor）调控和胁迫的系统，特别是受水分的限制，地表不可能支撑大面积、相对均一且连续分布的高等植物群落，植物群落斑块状的分布为BSC的拓殖和覆盖提供了空间和适宜的生态位，使BSC的覆盖在干旱区占地表活体覆盖面积的40%以上，在有些地区甚至达到70%以上。仅从其分布的面积就可以看出它们的重要性。

BSC的演替规律是判断沙漠化发生、发展与逆转趋势的重要依据。以往判别沙漠化发生、发展和逆转趋势需要许多指标来综合判别，在实践应用中存在很多困难，而且需要训练有素的专业技术人员来完成，无论是理论研究还是在实践中会产生很多不确定性。例如，在利用大尺度研究中常用的植被指数和局地尺度的植被盖度作为沙漠化程度的判别指标时，会带来很多误差和误导。一个区域植被的盖度和植被指数有显著的季节差异，如何获取合理时段的数据本身就很困难。此外，在受风沙危害频繁的地区或沙漠化地区，植被盖度高低并不能说明生态恢复的好坏或沙漠化逆转的程度。在沙化草地，通常降水较多的年份会带来很高的植被盖度，可是这要看植被的基本组成是什么，在这种情况下往往是大量的一年生植物种群大爆发，表面上植被盖度很高，根据遥感图像或实地调查很容易误认为生态恢复明显，沙化得到遏制。但是当次年是一个干旱年时，这些一年生的草本植物不见了踪迹，地面风蚀依旧，沙化土地并未因一时的高植被盖度而得到修复。

BSC在沙化土地或流沙固定中存在有规律的发展和演替，当采取人为措施使流动沙丘表面达到相对稳定状态时，BSC在沙面就开始了拓殖、定居和发展。沙面得到固定，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，土壤微生物（如细菌）的增殖和蓝藻的拓殖使沙面在4～5年后形成了以蓝藻为优势的蓝藻结皮；大量的绿藻等旱生、超旱生的荒漠藻在BSC中逐渐占优势地位，形成荒漠藻结皮；此后，地表出现了大量的地衣结皮和地衣、蓝藻和荒漠藻的混生结皮；这些BSC的形成为藓类结皮逐渐在地势平缓或水分相对较好的局部开始大量拓殖创造了条件，50年后形成了高等植物和BSC隐花植物镶嵌分布的稳定格局特点。

在干扰程度较高的区域或常处于受干扰状态环境的BSC的演变阶段通常处在以蓝藻占优势地位的BSC状态，干扰会明显地减少地衣和藓类的物种多样性和多度；相对干燥、稳定的地表景观多为地衣为主的BSC覆盖；相对潮湿的土表或有利于集结雨水（包括凝结水）的微地形则有利于藓类结皮的拓殖和繁衍。由此可见，当一个固沙植被系统或沙化草地系统中BSC以蓝藻为优势，说明该系统处于不稳定或退化阶段，沙漠化发展趋势明显；当固沙植被系统或沙化草地系统中BSC以藓类和地衣为优势，说明该系统处于相对稳定阶段，土地沙化得到了遏制，生态处于恢复的趋势。这些简单易行的办法在过去并未得到应有的重视。

BSC抵御着风蚀和水蚀，维持了土壤的稳定性，对沙丘有持续的固定作用。大量的研究表明，BSC的存在增加了土壤的稳定性。风洞实验进一步验证了其抵抗风蚀的作用，BSC本身的形成机理就揭示了这一功能产生的机制。BSC中菌类和蓝藻等产生的菌丝体能够利用所分泌的多糖黏结小于0.25 mm的颗粒使之团聚成为稳定的大于0.25 mm的微团聚体，其过程是土壤微生物和藻类等把非结晶黏胶状的有机物密切地黏结在一起，而有机物又将矿物细粒进一步黏结，形成球状表面团聚。这样既借助于菌丝体将土壤细粒紧实地黏结，又通过微生

物分泌物的黏结，促使土表的稳定性增强而避免风蚀和水蚀。BSC特殊的结构和其复杂的组成有效地缓解了雨滴对土表的溅击，控制了径流的发生和发展。这在土质结构紧密、容重大的黄土高原和钙含量高的荒漠灰钙土生境中尤为明显。此外，尽管BSC有阻止降水入渗的作用，但观测和模拟发现BSC存在的区域只有当昼夜降水强度达到40 mm时，才有地表产流，而在沙区这种降水事件十分罕见。BSC对缓解干旱、半干旱区脆弱生境土壤侵蚀的贡献得到了广泛的认可，除减少水土流失，还减少了直接关系到人类生存环境的沙尘暴的危害。BSC能够大量捕获大气降尘，为系统输入养分，促进沙区土壤成土过程，有效地改变了荒漠系统非生物因素的胁迫，为土壤生物繁衍创造了生境。BSC在沙面一旦拓殖发展，在没有人为干扰的情况下，就会发展到与其气候相关联的演替阶段，而且能够稳定持续，使沙子不再流动，也为其他物种在固沙区的拓殖、发展提供生境，因此，BSC也被称为荒漠/沙漠的“生态系统工程师”（ecosystem engineer）。

BSC维系了荒漠系统生物多样性。BSC为大量的沙区微小生物提供了生境，维持了荒漠系统生物多样性。研究表明，微小节肢动物的数量在有BSC存在的土表层最高。对位于腾格里沙漠东南缘的沙坡头地区4种不同生境的土壤动物多样性所做的比较研究认为，土壤动物的生物量和密度与BSC的发育阶段呈正相关关系。自然发育未受干扰的地衣、藓类结皮覆盖的土壤中，土壤动物的生物量和密度明显地高于BSC发育早期阶段土壤类型中的。BSC在土表的盖度、BSC的生物体（蓝藻、其他藻类、地衣和苔藓等）组成的差异与荒漠昆虫多样性和优势种组成密切相关。BSC盖度高且发育良好的植被区昆虫以草原和荒漠化草原指示种占优势，而BSC覆盖较低的植被区昆虫种类以流沙、荒漠指示种占优势地位。

应当指出，影响土壤动物的因素很多，如植被类型。BSC也在一定程度上影响着这些生境因子。例如，BSC通过对降水入渗的影响，对土壤水分起到再分配的作用。而土壤湿度直接影响着许多土壤微生物的活性与分布，间接地影响着土壤动物的食物链关系。BSC中的一些生物体及其分泌物是土壤动物的直接食物来源，如一些藻类所分泌的多聚糖物质，还有一些土壤动物直接采食BSC组成生物体。此外，藓类的孢蒴还是一些动物的食物来源。地衣和一些藻类对UV-B辐射的抵御作用、BSC对土壤温度的影响、对土壤养分（碳、氮等）的供给、对地上维管植物养分的供应、对地表稳定性的维持（抵御风蚀和水蚀作用）等，直接或间接地为土壤动物的繁衍和生存提供了适宜的生存环境，即BSC的存在很大程度上改善了相关生物的生境，维持了健康和可持续的荒漠系统。

土壤食物链的营养结构在土壤养分循环中十分重要。土壤初级生产者是BSC中的地衣、藓类、绿藻和蓝藻，这些生物体连同植物体一起既被土壤生物取食又被其分解。在分解过程中，早期增殖的酵母和细菌被线虫和原生动物（protozoa）所取食，而螨（mites）又控制着线虫的数量。真菌主导了后期的分解作用，而它则被线虫、跳虫（collembolan）和螨所取食。因此，

BSC是其他土壤食物链成分的重要食物来源。例如，细菌是蓝藻结皮的主要分解者和消费者，真菌比细菌更能克服难于分解的物质，放线菌则以蓝藻作为食物来源；原生动物包括变形虫、纤毛虫和鞭毛虫，它们和线虫在土壤食物链中以BSC中的蓝藻和其他某些藻类为食；微小节肢动物以某些藻类、真菌、蓝藻（尤其是具鞘微鞘藻）、细菌及其他无脊椎动物和植物碎片为食。

BSC“生态系统工程师”的作用连接了极端荒漠生境中非生物因素和生物因素，使极端风沙环境变得“生机勃勃”。此间BSC起着载体的作用，例如，大量的蚂蚁在有BSC覆盖的沙丘得到了繁衍，BSC不仅为它们创造了生存的环境，BSC特殊的结构确保了蚁穴不被沙埋，而且提供了重要的食物来源，如BSC生物体分泌的多聚糖。在没有降水的季节，BSC还可以利用它们对吸湿凝结水的“捕获能力”为这些微小的无脊椎动物提供珍贵的水分。因此，BSC的存在可以使原来单一的沙漠人工固沙系统转变为复杂的、多样物种参与的生态系统，为沙漠治理和沙区生态持续发展做出了贡献。

BSC促进了人工固沙系统的持续发展，使固沙成果得到巩固。BSC通过改变土壤性状而影响高等植物的萌发、定居和存活。BSC对土壤性质的改变包括改变土壤表面的粗糙度、土壤质地、温度、养分的有效性、有机质和水分等。就机理而言，BSC可以通过改变以下方面来影响高等植物的萌发、定居和存活：① 改变土壤表面的微地形。在热带荒漠，由于缺少土壤冻融，土壤表面粗糙度的改变较小，其中蓝藻结皮能使土壤表面光滑化，而地衣和藓类的生长增加了土表的粗糙度。但藓类的发育在温带荒漠特殊的地貌条件下，如在固定沙丘丘间低地，也使土表光滑化。相反，在寒冷荒漠地区，由于地表和各种BSC受到土壤侵蚀，土表的粗糙度明显增加，以至于土表高度能隆升15 cm。这些相对大的地形变化特征可捕获风和水带来的种子、有机质、土壤微粉粒和水分。② 通过影响种子的捕获间接地影响参与萌发与定居的种子数量。当土壤表面光滑时，其对种子的捕获（seed entrapment）量很低，而在那些因BSC存在而显著增加地表粗糙度的生境（已有BSC发育和冻胀丘），种子的捕获量则很高。种子在这些蓝藻形成的光滑BSC表面停留的能力很弱。进行干扰试验使这些BSC粗糙化，种子在土表停留的能力显著增强。与热带荒漠光滑土相比较，温带和寒区荒漠地表经常出现的是地衣－藓类结皮以及植物凋落物。冻胀丘土壤以有限的物理和化学板结为特征。这种粗糙的地表除了可捕获种子外，还可以捕获有机质、水分和土壤细颗粒，使土壤微生境肥力提高。③ 影响高等植物养分。BSC对土壤表面化学性质的改变与相关植物种子组织体中主要生命元素的含量变化密切相关。BSC的存在总的来说提高了植物对镁、钾、铜和锌的吸收，而同时减少了植物对铁的吸收。④ 影响种子本身的生物学特性。种子萌发对水分的需求存在差异。在空气干燥的荒漠，许多种子要求一定的植被覆盖和土壤来保持充分的湿度从而进行萌发。土表很小的裂缝和断裂微地形对小颗粒种子植物萌发已足够，但对大颗粒种子则需要额外土壤或凋落物的覆盖。一些缺少特殊穿透结构的植物种子，通常是一年生的，生长于土壤－土

表干扰相对较大的地区，它们的萌发在那些凋落物较少、BSC完整稳定以及土表干扰较低的地区就会受到抑制。土壤的流动性也是制约种子萌发的一个重要因素。种子通常有其适合的埋藏深度，增深和变浅都会有碍于萌发。增加土壤氮肥能够刺激一些植物种的种子萌发。一些植物种子的萌发可能是因BSC的存在而被激发。此外，BSC能够阻止外来种的入侵，维持系统的稳定性，这对未来全球变化背景下荒漠生态系统生物安全有着十分重大的意义。

BSC为人工固沙系统提供了碳和氮，提高了系统的生产力。荒漠生态系统是一个土壤养分十分贫瘠的系统，BSC的存在对荒漠系统的能流和物流、养分循环产生了重要影响和贡献，有益于系统生物生产力的提高。

BSC中固氮的藻类主要由一些具异形细胞类（如鱼腥藻属、眉藻属、念珠藻属、裂须藻属和伪枝藻属）和一些非异形细胞类（如鞘丝藻属、微鞘藻属、颤藻属和单歧藻属）组成。地衣中具有固氮作用的主要是胶衣属（*Collema*）。以上所有的种类都可在我国沙漠BSC群落中见到。有研究表明，以地衣胶衣属为优势种的黑色BSC具有最高的固氮速率（13 kg hm^{-2} a^{-1}），以具鞘微鞘藻为优势种的浅色BSC固氮速率为1.4 kg hm^{-2} a^{-1}，而介于深色和浅色之间的是以葛仙米（*Pogostemon auricularius*）和伪枝藻（*Scytonema myochrous*）为优势种的BSC，其固氮速率为9 kg hm^{-2} a^{-1}。影响地衣和蓝藻结皮中单个种的固氮速率的主要因子是它们自身的生物学特性、土壤水分、温度和光照。另外，无论是自由生长的还是作为地衣中藻类的组成部分，它们能够固定大气中的氮，通常会有利于高等植物的生长。藓类的分解是土壤中营养元素的来源之一，特别是氮和磷，可以增加维管植物的存活率。由BSC固定的氮可以被周围的高等植物和另外的生物体如真菌、放线菌和细菌利用。大约70%由蓝藻和蓝藻－地衣固定的养分被立即释放到土壤环境中，而这些养分对相关的生物体包括高等植物、藓类和其他微生物群是有效的。研究证实，BSC的存在增加了200%的土壤环境氮含量，是荒漠土壤和植物的主要氮素来源之一。当然，BSC也可能通过反硝化作用和挥发过程造成氮的损失，尽管很少有具体的实验数据来支持这一过程。

BSC中的生物体通过光合作用、呼吸、分解和矿化作用对荒漠系统的碳循环起着直接或间接的作用，是干旱、半干旱地区荒漠系统碳的主要贡献者。它们通过调节分解和矿化率，进而调节着养分的有效性和初级生产力。因此，BSC中的微生物种群在荒漠生态系统的养分循环和能流中起着至关重要的作用。BSC通过其组成生物体中的蓝藻、地衣、绿藻和藓类的光合作用进行碳的固定，但许多因素影响着BSC对碳的贡献，如湿度决定着生物体光合作用的有效性，甚至在一些情况下如通过呼吸促使土壤碳的损失。即便如此，BSC对干旱荒漠系统碳循环的贡献也是不容置疑的。笔者在腾格里沙漠南缘的研究表明，以蓝藻为优势的BSC每年的固碳量是11.36 g C m^{-2}，而以地衣－藓类为优势的BSC每年的固碳量可达到26.75 g C m^{-2}。尽管这些数字是惊人的，但一直没有引起注意。

由以上5个方面不难看出BSC在干旱区生态恢复和沙化治理中的重要性和功能的多样性，因此，保护了我们脚下的BSC就是保护了土地不被沙化。这一理念在美国、以色列和澳大利亚的沙化土地治理和生态系统管理中已得到广泛的认可。认识到BSC的重要性，对我国沙区生态恢复和沙化土地治理将产生积极的影响，有利于形成全新的沙化治理理念，形成新的恢复和治理技术体系，进一步促进我国的防沙治沙事业。

有关BSC的功能（生态与水文功能）在笔者《荒漠生物土壤结皮生态与水文学研究》一书中有详尽的研究分析、实验验证和理论探讨，然而这些功能主要取决于形成BSC群落的种类组成、物种多样性和格局特点，这些种类组成的时空格局变化必然会导致BSC在荒漠/沙地生态系统中功能的改变，使生态恢复与重建的成效和持续性受到影响。因此，深入了解BSC群落中各功能群对环境中生物与非生物胁迫的响应，认知BSC群落组成物种多样性对干扰、气候变化的适应和响应规律，即对BSC生态生理学的研究是荒漠/沙地生态系统管理和BSC服务功能调控的理论依据和重要前提条件。

本书是沙坡头站研究组对国内荒漠BSC研究成果的总结和提升。全书共分5章，第1章论述了BSC研究进展以及中国沙区BSC群落种的多样性和空间分布格局规律，提出了BSC空间分布格局的理论假说；第2章阐述了影响BSC拓殖和发展的环境与生态因子，并重点介绍了影响BSC生态生理的非生物因子和生物因子；第3章集中阐述BSC对水分、光照、温度、UV-B辐射、CO_2浓度、风沙、N沉降、火烧、增温与降水减少等的生态生理响应；第4章集中阐述BSC与维管植物的关系，以及土壤微生物与BSC的相互作用；第5章从BSC的人工培养方法以及人工结皮的特征等方面对BSC人工培养及其在沙区的应用进行全面论述。从这本专著中，我们可以了解中国荒漠生物土壤结皮研究的历史和现状，当前研究的主要内容、前沿和热点，以及未来的主要研究方向。

在本书文字录入、准备、书稿校对等工作过程中，得到了研究组贾荣亮、李计红、王进、谭会娟、潘颜霞、刘艳梅、黄磊、苏延桂、陈应武、冯丽、张鹏、张亚峰、虎瑞等博士的大力支持，在此一并表示衷心感谢。

感谢中国科学院微生物研究所魏江春院士在百忙中为本书作序鼓励。

感谢中国科学院西北生态环境资源研究院、中国科学院沙坡头沙漠试验研究站和高等教育出版社的领导和编辑，没有他们的支持和努力，本书很难在较短的时间里问世。

本书中的研究得到了国家自然科学基金重点项目（项目号：41530746、40930636）、面上项目（项目号：41271061）和中国科学院寒区旱区环境与工程研究所“生物环保固沙技术在防沙治沙中的应用”项目（项目号：HHS-TSS-STS-1505）的支持。

生物土壤结皮的研究还存在许多未知的前沿科学问题，加之我们学识所限，书中遗漏和不妥之处在所难免，恳请读者不吝指正。

Introduction

Within China, a large area stretching from 75°–125° E and 35°–50° N is severely threatened by sand storms and desertification. This area spans semi-humid, semi-arid, arid, and extremely arid bioclimatic regions. The most vulnerable regions within the area are located in Northern China, and include the eastern desert and the transition region between agriculture and pasturage interlaced, where annual precipitation is more than 250 mm, and the transition regions between desert and oasis, desert and desert grassland, which are west of Helan Mountain and have an annual precipitation less than 200 mm. These extremely vulnerable regions make up the key target regions for construction of an ecological screen against desertification in the north of China through population without irrigation vegetation. To effectively contain the destruction caused by sand storms and prevent further desert expansion, the Chinese government has successively launched a batch of significant ecological restoration projects. These projects have focused on vegetative restoration, such as construction of the "Shelter Forest System Programme in Three-North Regions of China", "Grain for Green Project", and "Beijing-Tianjin Dust Storms Sources Control Project". Through the last 60 years, the Chinese government has implemented remarkable measures to curb desertification and promote restoration of vegetative ecosystems in desert regions. While fully recognizing these impressive achievements, it is also important to acknowledge that continued efforts are essential to the prevention of further desertification. Both the eastern desert regions, with their relatively high precipitation, and the desert region west of Helan Mountain, with its low precipitation, to different extents, suffer from declines in groundwater levels, and degeneration and death of sand fixing vegetation. These changes have directly affected the ecological restoration of these desert regions and the capacity to minimize the effects of wind and sustainably promote sand fixing. These problems, from a certain perspective, reflect a lack of theoretical knowledge, and need for more scientific research on desertification issues and restoration. For example, in the course of vegetation restoration for fixation of moving sand dune, few studies have investigated the ecological functions of biological soil crust (BSC), which are formed by sand fixing vegetation. The result is an overall poor understanding of how to best restore vegetation to promote BSC formation. Some managers even attempt to enhance permeation of precipitation and improve soil moisture status by destroying the BSC. With large knowledge gaps, restoration of these ecosystems is like "groping in the dark", which obviously has great limitations.

BSC make up a key component of the arid and semi-arid desert surface landscape and provide an important indicator of regional ecosystem health. They are made up of a complex composite of cryptogams (non-vascular plants), such as cyanobacteria, green algae, lichens, mosses, microorganisms in the soil, and other related organisms that bond with fine particles on the surface of soil via mycelia, rhizoids, and polysaccharides. Most desert ecosystems are controlled and limited by abiotic factors, such as moisture limitations, which prevent the event and continuous coverage with higher plant communities. The distribution of plant community patches within desert ecosystems provides space and appropriate ecological niches for BSC. The importance of BSC to arid ecosystems is evident in their immense distribution area. Within arid regions covered with living organisms, BSC account for more than 40% (and in some regions more than 70%) of the surface area.

The succession stages of BSC provide a useful basis for diagnosis of desertification trends. Before research increased our understanding of BSC, it was necessary to quantify a wide range of indicator variables in order to assess ecosystem desertification status and trends. Therefore, assessments of the status of desert ecosystems were impractical in application, requiring highly trained professional technicians, and possessing considerable uncertainty both for restoration and research applications. For example, using the vegetation index (commonly applied for large spatial scale quantification) and the vegetation coverage (used for small spatial scale quantification) to identify the degree of desertification introduces large errors and contributes to misleading conclusions. Vegetation coverage and index of a region vary independently with season. Therefore, data for these two indices is unreliable when collected over long time periods. Furthermore, vegetation coverage is a poor indicator of ecological restoration and/or desertification status in regions that are frequently hit by sand storms or experienced desertification. Vegetative indices may vary with environmental factors, for example, in desertificated grasslands, vegetation coverage is usually very high during high precipitation years, but low during low precipitation years. During high precipitation years, annual plant populations within desertificated grasslands spread like an outbreak. Remote sensing images or field investigations would quantify vegetation coverage as very high, and conclude that the ecosystem has been restored and desertification has been curbed. However, during a subsequent arid year, the same annual plants will disappear and the surface of the ecosystem will again be subject to wind erosion. Using only vegetative coverage as an assessment of ecosystem restoration, the temporary high vegetative coverage makes a non-restored ecosystem appear to be restored during a high precipitation year.

The development and evolution of BSC in desertificated or sand fixed areas follows regular trends. After restorative stabilization of moving sand dune surfaces, colonization of BSC will begin, and the crusts will settle and develop on the sand surface. Surface sand colonization will fix the sand allowing accumulation of dust. When rain falls on the accumulated dust, it forms a physical crust with a high content of clay and silt particles on the sand surface. Within four to five years, the sand surface will become colonized with bacteria, soil microbes, and cyanobacteria, forming a crust dominated by cyanobacteria. Considerable xeric and super-xeric desert algae, such as green algae, will then gradually become dominant in BSC, forming a desert algae crust. Finally, crusts will become populated with lichen, resulting in mixed BSC of lichen, cyanobacteria and desert algae. This mixed BSC provides conditions favorable for large amounts of moss to colonize the crust in relatively flat areas and areas with relatively high moisture content. Within 50 years, this BSC development process will give rise to a stable distribution pattern of higher plants and BSC cryptogams.

In highly disturbed regions, the diversity of BSC is reduced through reductions in abundance of lichen and moss, resulting in BSC dominated by cyanobacteria. In relatively dry and stable regions, BSC tends to be dominated by lichen. Whereas, in humid regions or small areas that collect rainfall or condensation, moss crusts tend to proliferate. Therefore, domination of sand-fixing vegetation system or desertificated grassland BSC with cyanobacteria suggests the system is at an unstable or degenerative stage, and desertification is occurring. Otherwise, when the BSC of sand-fixing vegetation system or desertificated grassland is dominated by moss and lichen, the system is likely at a relatively stable stage and desertification has been curbed allowing restoration of the ecosystem. These simple and easy indicators have not attracted due attention in past restoration efforts.

BSC resists wind and water erosion and maintains the stability of soil and fixed sand dunes. Several studies have shown BSC to enhance soil stability. Wind tunnel experiments have shown BSC to resist wind erosion. The mechanisms driving these functions stem from the processes leading to the formation of BSC. Fungi and cyanobacteria within BSC secrete saccharine, and mycelium (generated by fungi and cyanobacteria) binds particles smaller than 0.25 mm into stable micro-aggregates. Through this process, soil microbes, algae, etc., tightly bind to non-crystalline sticky organic matter and the organic matter further binds fine mineral particles to form spherical surface aggregates. Through these processes, mycelium tightly binds the soil particles, and secretions produced by the soil microbes strengthen the stability of the sand surface, stabilizing it against wind and water erosion. The special structure and complex composition of BSC can effectively attenuate the splash caused by rainfall and alleviate the erosion caused by runoff. Such effects are especially obvious in the Loess Plateau, where the soil structure is compact and dense, and within grey desert habitats, where calcium content is high. Despite the capacity of BSC to prevent permeation of precipitation, monitoring and simulation studies have shown that only when cumulative 24-hour precipitation reaches 40 mm and surface runoff occurring, which is rare in desert regions. Reductions to soil erosion within arid and semi-arid vulnerable habitats covered with BSC have been widely recognized. In addition to reducing water damage and soil loss, BSC can reduce the destructive impacts of sandstorms, which are directly caused by anthropogenic alterations to the environment. BSC can capture large amounts of dust, which infuses the system with nutrients and promotes the formation of soil in desert regions. These actions change the impacts of abiotic stressors and create a habitat for the reproduction of soil organisms within desert regions. In the absence of artificial disturbance, once the BSC has developed on the sand surface, it will progress to a stage compatible with the climate, and persist, acting to stop sands from moving, and provide a habitat for the colonization with and development of other species in the sand-fixing regions. Therefore, BSC is often considered the "ecosystem engineer" of the desert.

BSC is important to the maintenance of biological diversity within desert ecosystems. It provides habitat for huge communities of microorganisms. Research has shown that the greatest abundances of micro-arthropods on the earth's surface are found within BSC. A study comparing soil microorganism diversity among four different habitats within the Shapotou region at the southeastern edge of Tengger Desert, found both the biomass and density of soil organisms to positively correlate with the developmental stage of the BSC. That is, the biomass and density of soil organisms within lichen- and moss-dominated BSC, which had developed naturally with no disturbances, were clearly higher than biomass and densities within BSC at earlier developmental stages. The BSC coverage of a region and the composition of the BSC (*e.g.*, cyanobacteria, algae, lichen, and/or moss) are closely related to the diversity and dominant species of insects within a desert. When the soil surface around vegetation has a high coverage of later developmental stage BSC, the dominant insects tend to be indicator species of grasslands and desertificated grasslands; whereas vegetation with relatively low soil surface BSC coverage tends to be dominated with insects indicative of quicksand and deserts.

It should be pointed out that many habitat factors, including vegetation type, influence soil organism composition. BSC, to a certain extent, can indirectly influence soil organisms through impacts on habitat factors. For example, by influencing precipitation permeation, BSC can re-allocate soil moisture. Soil moisture directly influences the activity and distribution of many soil microbes and indirectly influences food chain relationships among soil organisms. Some BSC organisms and their secretions, for example the saccharine secreted by some BSC algae, are a food source for other soil organisms. Additionally, spores of some mosses are a food source for soil organisms. The lichen and some algae from BSC resistance to UV-B radiation, increasing soil temperature and supply of soil nutrients (*e.g.*, carbon and nitrogen), supply of nutrients to the vascular plants above the ground, and maintenance of earth's surface stability (resistance to wind and water corrosion) will directly or indirectly provide a suitable living environment for the reproduction and survival of soil animals. Namely, BSC plays important roles in maintaining habitats for desert organisms and the health and sustainability of desert ecosystems.

The soil food chain structure is very important to soil nutrient circulation. The primary nutrient producers in desert soils are lichen, moss, green algae and cyanobacteria, which are all found within the BSC. Soil organisms depend on these BSC organisms and plant materials for their nutritional supply. During process of decomposition, yeasts and bacteria at early developmental stages of BSC are consumed by nematodes and protozoa, while mites control the quantity of nematodes. Fungi become the dominant decomposers in later stage BSC, and are eaten by nematodes, collembolan, and mites. Therefore, the components of the BSC are important food sources for other organisms making up the soil food chain. For example, bacteria within algae crust are the dominant decomposer and consumer. Materials that are not decomposable by bacteria can often be decomposed by fungi. Actinomycetes consume cyanobacteria as a food source; Nematodes and protozoa, including amoebas, ciliates, and flagellates, feed on cyanobacteria and algae in BSC; micro-arthropods feed on algae, fungus, cyanobacteria (especially *Microcolus vaginatus*), bacteria, other invertebrate animals, and plant fragments.

The "ecosystem engineer" functions of BSC, it plays a role of a carrier and connects biotic and abiotic processes to facilitate life and diversity in extreme desert habitats. For example, many ant species reproduce in sand dunes covered with BSC. BSC provides a stable habitat with important food sources, such as the saccharine secreted by BSC organisms, which is secured from destruction through sand movement. The high capacity for BSC to capture water through absorption and condensation also provides precious moisture for tiny invertebrate animals during the dry season. Therefore, BSC can transform simple artificially produced sand-fixing desert ecosystems into complex, multiple species ecosystems that contribute to desertification control and the sustainable development of desert ecology.

BSC facilitates the sustainable development of artificial sand-fixing ecosystems and consolidates the benefits of sand fixing. By altering soil properties, such as surface roughness, texture, temperature, nutrient availability, organic matter content, and moisture, BSC can influence the seeds germination, settlement and survival of higher plants. The mechanisms through which BSC alters ecosystems include: i) In tropical deserts,where land surface disturbances through freezing and thawing do not occur, the soil surface can remain extremely smooth. For example, land surfaces of areas with algae crusted soil tend to be smooth, whereas the growth of lichen and moss in the BSC can introduce irregularities to the land surface. Notably, moss-dominated BSC in temperate deserts form a special exception, and can contribute to areas of smooth land surface in lowlands between sand-fixing dunes. However, in cold desert regions, the actions of soil erosion and diverse BSC, contribute to roughening of the land surface, and can raise the surface by as much as 15 cm. By increasing the roughness of the soil surface, BSC can facilitate entrapment of seeds, organic matter, fine soil particles, and moisture from wind and precipitation. ⅱ) By influencing the entrapment of seeds, BSC can indirectly influence the quantity of seeds that successfully germinate and settle. Smooth land surfaces are poor at entrapping seeds. In habitats where the land surface is rough due to the influences of BSC and frost heaving, seed entrapment rates are very high. Cyanobacteria-dominated BSC does not introduce irregularities to the soil surface, which results in poor seed retention. Interfere test will roughen these BSCs and the seed entrapment on the earth’s surface will be enhanced obviously. Tropical desert soils tend to be extremely smooth compared to temperate and cold desert soils, which are usually covered by lichen-moss crust and plant litter. Soils experiencing frost heaves are characterized by limited physical and chemical hardening. This kind of rough land surface can trap, not only seeds, but also organic matter, moisture and fine soil particles, and enhance the fertility of the soil micro-habitat. ⅲ) BSC can influence the nutrients available to higher plants. Studies have shown the changes to soil chemical properties caused by BSC to correlate with changes in the biological element contained within the seed tissues of plants growing within the same area. Generally speaking, the existence of BSC can enhance the absorption of Mg, K, Cu and Zn, and reduce the absorption of Fe by plants. ⅳ) BSC can influence the biological properties of seeds. The conditions which required to retain sufficient moisture for seed germination vary with desert type. In a desert with dry air, seeds often require specific vegetation coverage and soil to retain adequate moisture for germination. Tiny crevices and fractured micro-habitat within the land surface tend to trap enough moisture for germination of tiny seeds, but large seeds require extra soil and plant litter coverage. Plant seeds lacking a special penetration structure are usually annual species, and tend to be restricted to regions with relatively high land surface disturbance. Germination for these species would be inhibited in the regions with small amounts of plant litter, complete and stable BSC and relatively low land surface disturbance. Soil mobility is another important factor constraining seed germination. Most seeds are influenced by burying depth, with too deep or shallow depths hampering germination. Enhancement of the nitrogen fertility of soil can stimulate seed germination for some plants. Germination of some species’ seeds can be stimulated through to the existence of BSC. Additionally, BSC can guard against the invasion of alien species, and thus maintain the stability of the system. This protection is becoming an increasingly significant advantage of BSC in desert ecosystems under the context of global changes.

BSC enhances the productivity of desert ecosystems through providing carbon and nitrogen to nutrient poor soils. BSC contributes to the flow of energy and materials and nutrient circulation within the desert ecosystem, which enhances the biological productivity of the system.

The nitrogen fixing cyanobacteria in BSC are mainly comprised of heterocyst cells (*e.g.*, *Anabaena, Calothrix, Nostoc, Schizothrix, Scytonema*) with a few non-heterocyst cells (*e.g.*, *Lyngbya, Microcolus,*