

# 盐碱土壤微生物多样性与生物改良研究进展

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**摘要:** 盐碱土壤是全球生态系统的重要组成部分, 其环境健康与可利用性涉及生态安全和人类生存。土壤微生物在土壤形成、能量转移、养分动员与循环、植被重建和生态系统长期稳定中发挥着重要作用, 地理环境、土壤组分和理化性质及立地植物等均强烈地影响着土壤微生物的多样性与分布, 反过来微生物可被用于盐碱土壤的改良, 其中输入有机质对改良效果具有决定性价值, 而具有特殊适应性的被长期“驯化”的“本土”微生物成为盐碱土壤改良的首选。从盐碱土壤微生物多样性与功能、影响其多样性的主要因素及微生物应用于土壤改造等方面的研究进展进行了分析, 总结出土壤特性造就微生物类群-微生物改变土壤微环境-微生物与土壤共同演化的生态循环模式, 以期为盐碱土壤微生物的生态功能与应用提供参考。

**关键词:** 盐碱土壤; 微生物多样性; 影响因素; 盐碱土壤改良

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## Advances on Microbial Diversity and Biological Improvement of Saline-alkali Soil

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**Abstract:** Saline-alkali soil is an important part of the global ecosystem, and its health and availability are interrelated to the safety of ecology and survival of our human. Soil microorganisms play an important role in soil formation, energy transfer, nutrient mobilization and recycling, vegetation reconstruction and long-term ecosystem stability. Their diversity and distribution are strongly influenced by the geographical environment, composition, physical and chemical properties of soils and plants living on. The microorganisms also could be used as biological additive to improve the saline-alkali soils, conversely. And the input of organic matter is one of decisive value to it. The indigenous microbes with special adaptability that have been domesticated for a long time become the first choice for this work. For the purpose to provide useful information on their ecological functions and application potentials, we analyzed the advances on diversity and function of microbes in saline-alkali soils, the major diversity-affecting factors as well as their application in soil transformation, and then summarized an ecological cycle mode of soil characteristics determine the microbial communities - the microorganisms change soil microenvironment - microbes and soil are in co-evolution.

**Key words:** saline-alkali soil; microbial diversity; regulatory factors; saline-alkali soil improvement

土壤盐碱化是全球生态系统与可持续发展的重要威胁, 全世界有  $1.0 \times 10^9 \text{ hm}^2$  土地受盐碱的影

响<sup>[1]</sup>, 并以每年 10% 的速度递增<sup>[2]</sup>。尽管盐碱会对生命造成严重损害, 但土壤中仍活跃着大量且

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多样的微生物<sup>[3-4]</sup>,其在土壤形成、有机质分解、生物地球化学循环和植物营养等方面起着重要作用<sup>[5-6]</sup>,特别在生态系统稳定性中起着核心作用<sup>[7]</sup>,并可用于盐碱土壤的改良<sup>[8]</sup>,是全球生态安全的重要保障之一。

区别于其他生物,微生物占据了地球上所有生物和非生物的生态位<sup>[9]</sup>,而与其他环境一样,土壤微生物也是生态选择和进化适应的结果,其类群结构、多样性分布等与环境因子密切相关,极端环境造就了独特的微生物群落<sup>[10]</sup>,而长期的胁迫“驯化”使不同环境本土类群具备了特殊的生物学特性<sup>[11]</sup>,进而对土壤结构进行重塑<sup>[12]</sup>,形成了土壤特性造就微生物类群-微生物改变土壤微环境-微生物与土壤共同演化的生态循环。

## 1 盐碱土壤微生物多样性与功能

土壤系统的空间复杂性和生境的异质性促进了微生物类群的生态位分配,使其呈现极高的多样性,据估计占地球生物多样性的四分之一<sup>[13]</sup>,每克土壤含有多达 $10^9$ – $10^{10}$ 个细胞,其中 $10^5$ – $10^6$ 个为“独特的分类群”<sup>[14]</sup>。土壤微生物多样性受土壤类型、理化性质、地理位置、立地植物等的影响,其中pH是主要因素,塑造了耕地<sup>[15]</sup>、森林和草原<sup>[16]</sup>等环境的特殊微生物组成。

盐碱严重制约土壤微生物的组成,研究发现其多样性随盐浓度的增加呈线性下降,高盐会致多样性降低而相对丰度增加<sup>[17]</sup>,细菌类群在盐浓度3.5%–4.5%与4.5%–5.5%之间相似,但与1.5%–2.0%和7.5%–8.5%间显著不同,其中 $\gamma$ -变形菌门(Gammaproteobacteria)相对丰度与盐含量呈显著负相关, $\beta$ -变形菌门(Betaproteobacteria)和硬壁菌门(Firmicutes)则呈显著正相关,但放线菌门(Actinobacteria)与盐和pH均无相关;盐单胞菌属(*Halomonas*)、史密斯氏菌属(*Smithella*)、假单胞菌属(*Pseudomonas*)和丛毛单胞菌属(*Comamonas*)分别与盐浓度1.5%–2.0%、3.5%–4.5%、4.5%–5.5%和7.5%–8.5%关系密切<sup>[18]</sup>,显示丛毛单胞菌属具有更强的耐盐性。

微生物类群对土壤酸碱度的响应不同,细菌丰度和多样性及类群结构与pH显著相关,而真

菌则受pH和C/N的共同影响<sup>[19]</sup>。盐渍土中细菌多样性低而古菌比例高,而非盐渍土中细菌比例高<sup>[20]</sup>。盐杆菌纲(Halobacteria)、腈基降解菌纲(Nitriliruptoria)、Rhodothermi、 $\gamma$ -变形菌纲和 $\alpha$ -变形菌纲(Alphaproteobacteria)细菌显示出对高盐的偏好性<sup>[17]</sup>;电导率(electrical conductivity, EC)为58–93 dS/m的盐渍土中古菌占主导地位,而高于或低于此范围则细菌占优势;盐碱土壤中变形菌门(Proteobacteria)、拟杆菌门(Bacteroidetes)和芽单胞菌门(Gemmatimonadetes)是最丰富的类群,非盐碱土壤中占据前3位的是变形菌门、酸杆菌门(Acidobacteria)和放线菌门,且盐渍土中门/类的标准差远高于非盐碱土,显示盐渍土中微生物类群变异更大<sup>[20]</sup>。

土壤微生物通过固氮或溶磷等为植物提供营养,对营养缺乏生态系统更加重要。如菌根真菌和固氮细菌可为草原植物每年提供5%–20%的氮素营养,在温带和北方森林高达80%,同时还可提供75%的磷元素<sup>[21]</sup>。即便在贫瘠的南极沙漠土壤中,其微生物被认为是重要的氮输入源<sup>[22]</sup>。衡量土壤氮有效性的指标:土壤净氮矿化率(Nmin)随土壤微生物生物量、总氮和年均降雨量的增加而显著增加,但随土壤pH的升高而降低,而年均降水量、土壤pH和土壤总氮均通过土壤微生物影响Nmin<sup>[23]</sup>。

土壤微生物类群会改变植物对开花时间的选择<sup>[24]</sup>,有益土壤微生物可加速植物开花而促进繁殖<sup>[25-26]</sup>,以此影响植物对生境的选择和适应。此外土壤放线菌对土壤生物缓冲、土壤环境的生物控制有重要作用<sup>[27]</sup>。据估计,地球上大约有20 000种植物完全依赖微生物共生体来生长和生存,表明土壤微生物是地球植物物种丰富度的重要调节剂<sup>[21]</sup>。

## 2 影响盐碱土壤微生物多样性的因素

土壤是地球上微生物最多多样化的环境<sup>[28]</sup>,1 g土壤可包含超过10 000个基因组<sup>[29]</sup>,显示土壤微生物具备巨大的功能潜力。

### 2.1 地理因素

生物地理分离和土壤母质差异是造就不同地理环境微生物多样性的主要因素,研究表明微生物群落变异中约一半可归因于栖息地和地理距离<sup>[30]</sup>。微

生物的散布需经载体运输<sup>[31]</sup>，故地理分离是地域特有微生物类群与多样性的主要驱动因子。以南北极为代表的地理因素对土壤微生物多样性的影响最具典型性，尽管极地被认为是不适合生物生存的“净土”<sup>[32]</sup>，但仍然是微生物的天堂，其微生物多样性多得“令人惊讶”，贫瘠的土壤和岩石地貌没有阻止原核生物的孕育，且季节性极端低温并不妨碍微生物定殖<sup>[33]</sup>。区别于动植物，微生物多样性无明显的纬度梯度<sup>[34]</sup>，其原核生物多样性并不符合“高等生物于高纬度呈现出低多样性”的典型趋势<sup>[35]</sup>，从72°S的哈雷特角到84°S的达尔文冰川的微生物多样性无差异<sup>[36]</sup>。但Shivaji等<sup>[37]</sup>报道，南极Schirmacher绿洲Zub湖附近土壤中细菌多样性与大陆架沉积物相似，其原因尚未知。同时极地土著微生物种群的遗传与生理特征也被重新塑造，如其特有的与细胞壁结构有关的糖基转移酶和糖基合成酶可能在进化过程中获取或保留，但这部分相关基因在热带菌株中认为被丢失<sup>[38]</sup>，而其类群<sup>[39-40]</sup>与生物学特性<sup>[41-42]</sup>及基因表达<sup>[43]</sup>也存在巨大差异，表明环境不仅造就微生物组成，还对其进化产生影响。

## 2.2 土壤理化因子

盐碱土壤的理化因子包括盐的类型，如碱性盐、中性盐等，以及各种化学离子，包括 $\text{SO}_4^{2-}$ 、 $\text{CO}_3^{2-}$ 、 $\text{Mg}^{2+}$ 、 $\text{Ca}^{2+}$ 等阴阳离子。理化因子对微生物多样性的影响具有独特性，表现为不同土壤类型的微生物类群不同，及不同微生物类群对不同盐碱或离子的耐受程度不同。

土壤盐碱是控制真菌与细菌平衡的重要因素<sup>[44]</sup>，其中细菌比真菌更易受到盐碱胁迫的影响<sup>[45]</sup>。研究显示盐度对细菌群落结构的影响强烈<sup>[46]</sup>，但也有报道认为与包括有机碳（total organic carbon, TOC）、水分、pH和P等其他因素的相关性更好<sup>[4]</sup>，而Navarro-Noya等<sup>[47]</sup>的研究表明盐碱地古菌群落结构与pH有良好相关性。Li等<sup>[48]</sup>认为当盐度恒定时，养分是构建细菌群落的关键因素，EC仅起次要作用，但Zhao等<sup>[18]</sup>认为土壤pH与盐度对细菌群落的形成同样重要。pH也是影响北极土壤微生物独特群落形成的主要因素<sup>[49]</sup>；干旱区土壤细菌群落构建也由pH主导而非水分<sup>[50]</sup>；多年冻土的微

生物群落分布也主要受土壤pH和植物多样性的调节<sup>[51]</sup>。Xie等<sup>[20]</sup>报道，盐度、酸碱度和TOC均影响原核生物类群分布，但TOC和pH显著影响盐碱土壤地表和地下的微生物类群，而EC却只影响地下。对美洲土壤的研究发现，pH 6.8的细菌丰度比pH 5.1高60%，pH 5.5土壤的细菌丰富度比pH 4.1高26%<sup>[52]</sup>。但也有认为决定微生物群落的主要因素是盐，而不是温度、pH或其他因素<sup>[53]</sup>。

不同盐碱土壤可“驯化”出独特的微生物类群。新疆玛纳斯河流域4种盐碱类型土壤中碳酸盐型土壤细菌多样性和丰度均显著高于其他3个，变形菌门、拟杆菌门和放线菌门是硫酸-氯化物盐型、氯化-硫酸盐型和硫酸盐型土壤的优势菌门，硬壁菌门、变形菌门和放线菌门为碳酸盐型土壤的优势菌门<sup>[54]</sup>。Liu等<sup>[55]</sup>对我国北方高盐沉积物和盐渍化土壤研究显示，高盐沉积物中变形菌门占比达57%~95%，拟杆菌门也比盐碱土中更丰富，放线菌门在盐碱土壤中丰度更高，而厚壁菌门仅存在于高盐样品中。废弃盐渍化农田复垦会显著影响细菌多样性和丰度，对复垦10年和15年的盐渍土研究显示，经长期驯化和演变，再生土壤的细菌群落趋于稳定<sup>[11]</sup>。Xie等<sup>[20]</sup>报道，盐渍土壤中古菌和细菌分别占52.8%和47.2%，与非盐渍土中的6.8%和93.2%差异巨大；与非盐渍土相比，盐渍土的微生物复杂程度较低，但古细菌比例较高。

土壤阴离子也对其微生物组成产生影响，盐渍土壤中细菌多样性与 $\text{Cl}^-$ 、 $\text{SO}_4^{2-}$ 、 $\text{Mg}^{2+}$ 、 $\text{Na}^+$ 和 $\text{Ca}^{2+}$ 呈显著负相关，而群落结构与 $\text{SO}_4^{2-}$ 和AP呈高度正相关；变形菌门、拟杆菌门和蓝细菌门（Cyanobacteria）与 $\text{CO}_3^{2-}$ 显著负相关，放线菌门与 $\text{CO}_3^{2-}$ 和 $\text{K}^+$ 显著负相关，酸杆菌门与 $\text{CO}_3^{2-}$ 和 $\text{K}^+$ 显著正相关<sup>[11]</sup>，显示碳酸盐型土壤对细菌多样性及类群的影响更大。

## 2.3 立地植物

土壤微生物与植物多样性密切相关，其功能与组成随植物多样性的变化而变化<sup>[56]</sup>，植物多样性通过增加生态系统生物量而调控土壤性质和微生物多样性。试验证实，植物多样性的增加通过养分可及性和土壤理化状态的巩固强烈地影响着土壤微生物群落结构<sup>[57-59]</sup>，根源有机质输入是土壤微生物群落

特性的主要驱动因素<sup>[60-61]</sup>, 植物丰度提高则微生物丰度增加<sup>[62-63]</sup>, 细菌和真菌的生物量及真/细菌比值也显著增加, 而真菌随根系生物量增加的幅度大于细菌<sup>[61]</sup>。

立地植物类型直接影响着土壤微生物的多样性, 如以油松 (*Pinus tabulaeformis*) 对黄土高原天然草地进行造林改造后, 土壤优势菌群由变形菌门向放线菌门转变, 而优势真菌类群由子囊菌门 (Ascomycota) 向担子菌门 (Basidiomycota) 转变; 认为是草地造林后土壤氮的减少导致了微生物群落结构和功能的变化<sup>[45]</sup>。艾比湖盐渍土中藜科 (*Chenopodiaceae*) 植物盐穗木 (*Halostachys caspica*)、盐节木 (*Halocnemum strobilaceum*) 和盐爪爪 (*Kalidium foliatum*) 相关细菌多样性低于白花丹科 (Plumbaginaceae) 的大叶补血草 (*Limonium gmelinii*) 和茄科 (Solanaceae) 的黑果枸杞 (*Lycium ruthenicum*), 盐穗木和盐节木的细菌群落组成与大叶补血草和黑果枸杞差异巨大<sup>[48]</sup>, 显示植物类群显著影响着土壤微生物的组成。

立地植物与土壤微生物是一个生态共同体。释放到土壤的根分泌物的数量和质量取决于植物的种类与功能<sup>[64]</sup>、年龄<sup>[65]</sup>和土壤条件<sup>[66]</sup>等, 反过来土壤微生物也可影响根分泌物的数量和组成<sup>[67]</sup>, 显示其相互作用的机制尚未被揭示。但也有研究认为植物多样性与土壤微生物间没有直接联系<sup>[68]</sup>, 土壤细菌多样性主要由非生物和空间因子决定, 植物的功能性状对土壤细菌多样性的调节能力优于植物多样性<sup>[69]</sup>。此外, 一些科学家<sup>[70-71]</sup>认为植物多样性与微生物群落和功能间的关系是混合的, 原因是二者均会受多种非生物和生物因子的影响<sup>[64, 72]</sup>。

### 3 微生物对盐碱土壤的改造

生物改良是盐碱土壤利用的研究热点, 目前采用的技术包括增加土壤有机质和施加微生物肥料以改善土壤微生物群落结构等。

生物炭是生物质在无氧或微氧条件下低温热转化的产物, 具有提高土壤碳含量、保水、有益于土壤微生物栖息与活动的功能而备受关注。研究认为早在数百年前亚马逊印第安人就会将生物炭和有机质掺入土壤, 创造出肥沃的黑土<sup>[73]</sup>, 据此研究者采用多种措施增加生物炭以对盐碱土壤进行改造, 如

对苏打型盐碱地添加玉米秸秆生物炭可显著减少盐和碱对土壤功能的影响<sup>[74]</sup>; 源于加拿大一枝黄花 (*Solidago canadensis* L.) 的生物炭可改善沿海盐碱地土壤的交换性钠胁迫并显著影响小白菜 (*Brassica chinensis* L.) 和微生物的生长和生物多样性<sup>[75]</sup>; 吴丹等<sup>[76]</sup>利用浒苔生物炭用于滨海盐碱土修复, 证实其可增强微生物活性和改善土壤营养可利用性, 土壤有机质提高 42.64%, 并分别使土壤蔗糖酶、脲酶及过氧化氢酶活性提高 2.39、1.18 和 1.50 倍。生物炭还可增强土壤团聚体的稳定性并导致微生物群落结构改变<sup>[77]</sup>, 还对土壤微生物具有“启动效应”, 提高或降低土壤原生有机碳的分解速率<sup>[78]</sup>, 从而促进土壤改良。

微生物肥料是依据特定需要将活的微生物菌株制作成的生物制剂, 其功能主要是通过微生物的生命活动增加植物营养供应或提供包括植物激素等调节因子<sup>[79]</sup>, 或拮抗土壤中的植物病原菌等<sup>[80]</sup>。盐碱土壤中有益根围微生物可提高植物蛋白质和光合色素合成而促进植株生长和生物量的增加<sup>[81]</sup>, 具有 ACC - 脱氨酶活性的微生物可诱导植物对盐和干旱的耐受<sup>[82-83]</sup>。给盐渍化土壤施用微生物菌肥可使土壤中  $\text{Na}^+$ 、 $\text{Cl}^-$  显著下降而  $\text{K}^+$ 、 $\text{SO}_4^{2-}$  上升<sup>[84]</sup>; 菌肥还可降低燕麦根区土壤 pH 和 EC, 有效提高土壤含水量、微生物生物量及土壤酶活性<sup>[85]</sup>。盐碱土壤微生物也被证实具有改良功能, 一株分离自盐碱环境的可耐受 pH 12 和 20% 盐浓度、被鉴定为马氏芽孢杆菌 (*B. marmarensis*) 的菌株可使盐碱土壤中的蔗糖酶、脲酶和碱性磷酸酶活性分别提高 23.2%、68.8% 和 106.5%, 并可使小麦的株高、鲜重和干重分别提高 21.8%、57.9% 和 41.7%, 小麦根系超氧化物歧化酶、过氧化物酶和过氧化氢酶活性分别增长 109.6%、17.8% 和 50%, 丙二醛含量减少 39.8%, 显示该菌株对盐碱土壤具有显著改良作用并可促进立地植物的生长<sup>[86]</sup>; 同样, 一株分离自盐碱地的被鉴定为海水盐单胞菌 (*H. aquamarina*) 的菌株降碱能力为 8.7%、产 IAA 的能力为 8.97 mg/L, 在盐胁迫下可提高小麦的发芽率和幼苗的根长<sup>[87]</sup>; 一株分离自土壤的贝莱斯芽孢杆菌 (*Bacillus velezensis*) 菌株 FKM10 能够抑制土壤中的植物真菌病原体, 可通过促进养分吸收、改变土壤微生物群落结构及

减少真菌多样性而促进湖北海棠 (*Malus hupehensis* Rehd.) 的生长<sup>[88]</sup>。但目前这类研究尚处于探索阶段, 尽管已取得一定进展, 但鉴于盐碱土壤成分的复杂性和微生物菌株适应性与代谢特性的差异, 尚难以获得具有普适性的菌株用于土壤改良。为此, 加强对不同盐碱土壤本土微生物特性与代谢特性的研究, 是其应用于土壤改良的基础。

盐碱土壤改良必然会对其微生物多样性产生影响, 不同改良方法其影响亦不同, 其中客土法因携带原位微生物而可在短时间内显著改变其类群<sup>[89]</sup>; 土壤有机质的增加会明显改变微生物类群与丰度, 如 Jiang 等<sup>[90]</sup>分析了 4 种不同施肥制度对滨海盐渍土微生物的影响发现, 有机质输入可使土壤细菌丰度增加 3 倍, 但同时导致细菌多样性降低, 其中受影响最为显著的是变形菌门、拟杆菌门和厚壁菌门。随盐碱土壤的改良, 其盐度和 pH 必然相应下降, 故此其微生物类群亦相应改变<sup>[18, 46]</sup>, 而伴随复垦等改良措施的实施, 微生物类群与结构也会显著改变<sup>[11]</sup>。无论是生物的或是非生物的改良, 均会导致微生物间的相互关系向良性发展, 而什么样的类群能够代表土壤健康, 须根据不同地域和盐碱土壤的理化性质分别对待, 尚无统一的标准可供参考。

#### 4 展望

土壤微生物是盐碱地生态系统重要的调控者, 其群落组成的变化先于土壤可检测理化性质, 故成为环境胁迫或生态演化的早期预警指标<sup>[91]</sup>。盐碱土壤微生物类群与结构首先受土壤性质特别是含盐量和 pH 的影响, 随之而建立的微生物群落, 其代谢过程特别是产物的积累会改变微环境, 从而进一步改变微生物类群, 在此进程中土壤有机质具有决定作用, 此亦是盐碱土壤改良的物质基础。尽管对盐碱土壤微生物多样性的影响因子报道较多, 而将微生物应用于盐碱地的改良尝试也才刚刚起步, 对哪些微生物可用于改良哪种类型的盐碱土还缺乏足够的认识。全面了解盐碱土壤微生物多样性和群落组成及其生存机制是将其应用于土壤改良的第一步, 获得纯培养菌株并对其生物学特性及代谢生理进行深入研究是了解其应用潜力的重要一环, 但目前仍有 99% 的微生物处于未培养状态, 严重限制了其资

源的开发利用。尽管有科学家提出可以人为设计微生物群落来优化预期功能<sup>[92]</sup>, 但仍需首先了解常见和罕见微生物在不同生态系统类型中的功能<sup>[93]</sup>。随着生物学技术与方法的创新和进步, 盐碱地微生物研究越来越受到全世界科学家的重视, 以宏基因组学及宏代谢组学等为代表的现代“组学”技术为开发和利用未培养微生物资源提供了可能, 而与相应的有机质输入相关的微生物类群与功能解析必将为其应用于盐碱土改良提供更多理论与技术支持, 其中“本土”微生物以其因长期“驯化”所获得的特殊适应性成为盐碱土壤生物改良的首选。

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