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极端干旱对土壤微生物群落和功能的影响研究进展

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摘要:随着现代社会的快速发展和人类活动的日益增多,极端气候如干旱和高温等事件越来越频繁地出现。干旱和高温的同时发生容易形成极端干旱,不仅会改变土壤基本理化性质及功能,还会影响土壤微生物群落的组成和结构,同时对微生物介导的土壤微生物过程及生物地球化学循环产生深远影响,因此了解极端干旱如何影响土壤微生物群落及其功能显得至关重要。本文从个体到群落的角度综述了极端干旱对土壤微生物的影响及微生物对极端干旱的响应,包括极端干旱对微生物 DNA 及细胞完整性造成的伤害、对细菌群落和真菌群落组成的影响、对土壤微生物介导的碳氮循环功能的影响以及极端干旱下根际分泌物对根际微生物功能的影响,最后从交叉学科原位研究角度和分子组学角度对相关机理进行了展望。

关键词:极端干旱;土壤微生物响应;微生物群落;微生物功能

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极端气候的产生对全球农业生产产生了负面影响^[1],而且其影响程度在未来很可能持续加剧^[2]。在这些极端事件中,干旱与高温通常同时发生,容易形成长期的极端干旱,而且可能成为生态系统功能变化的重要驱动力^[3]。研究显示,全球干旱地区的面积已达到总陆地面积的 45%,由于气候

变化造成干旱加剧,预计全球干旱地区面积将在 21 世纪末上升到 68%,而干旱地区面积的扩张又会进一步造成局部地区的高温^[4]。土壤是一种能够支持植物生产和保持其健康的复杂体系^[5]。土壤微生物群落在土壤-植物体系的养分循环中扮演着重要的角色^[6],其活动是植物群落组成和生产力的关键驱动因素^[7]。但是,极端气候对土壤微生物活性及多样性造成了较大的扰动,也对微生物参与的土壤生态服务功能造成了较大的影响^[8]。高温和干旱事件会对土壤微生物群落产生累加、协同或抑制的作用,虽然这 2 个因素在极端干旱条件下同时出现^[9-10],但是结合高温和干旱这 2 种因素的综合研究仍然不够系统^[11-12]。因此,全面深入地了解高温干旱对微生物行为及其生态系统功能的影响具

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有重要意义。

极端干旱通常定义为土壤含水量小于 2%, 同时表层土壤(0 ~ 5 cm) 温度高于 45 ℃ 的干旱条件^[12]。极端干旱通过改变微生物生理而以非常直接的方式影响微生物群落。微生物利用各种生理策略来应对气候变化, 一些微生物种群快速生长, 而另一些则死亡^[13-14], 从而导致了微生物群落组成的转变^[12]。另一方面, 极端干旱也会引起土壤理化性质的变化^[15], 从而通过改变微生物栖息地环境来间接改变微生物群落^[16-17], 以致进一步影响到土壤元素循环及植物的生长。

在过去的几十年中, 有大量涉及极端干旱对土壤微生物的生理、丰度、群落组成及多样性影响的研究^[18], 这些研究也包括干旱对土壤呼吸的影响^[19]以及干旱^[20]和温度因素对药物、农业和食品工业的影响等^[21]。然而, 在全球极端气候变化条件下, 关于干旱和高温因素对土壤微生物个体与群落、土壤生态系统功能的影响, 以及土壤微生物对高温干旱的响应等方面, 尚未有系统的阐述。本研究综述了极端干旱对土壤微生物从个体细胞水平到群落系统水平的影响, 主要包括: (1) 极端干旱对土壤微生物细胞的直接影响; (2) 极端干旱对土壤微生物的间接影响; (3) 极端干旱条件下土壤微生物群落结构和多样性的改变; (4) 极端干旱对土壤微生物生态功能的影响。

1 极端干旱对微生物细胞的直接影响

微生物通过其半渗透性细胞壁与水紧密接触。在干旱条件下, 微生物细胞内水分的流失可能会损害细胞完整性并对细胞具有致死性^[22]。此外, 大多数微生物只能耐受 40 ℃ 以下的温度^[12]。当微生物长期暴露在极端干旱条件下时, 在核酸层面上会造成 DNA 链断裂、弯曲、超螺旋、化学修饰以及 mRNA 二级结构的改变等^[23]。另外, 极端干旱条件还可以通过烷基化或氧化等化学修饰、交联或碱基去除等方式来破坏微生物核酸, 从而改变微生物细胞的基因表达模式^[24-25]。在细胞膜结构层面上, 极端干旱去除了微生物细胞膜磷脂双分子层的水合壳, 增加了相邻脂质之间范德华力的相互作用, 造成了膜相变温度的升高, 并且促进了膜在环境相变温度下向凝胶相的转变, 相变温度较高的膜将进入凝胶相, 并与相变温度较低的膜分离, 从而导致蛋白质聚集^[22]。在再水化过程中, 如果经过干燥的膜在后高

温干旱时期的相变温度高于环境温度, 造成的膜泄漏对细胞是一种严重伤害^[26]。此外, 极端干旱造成的脱水还会诱导蛋白构象变化并限制酶效率, 导致电子传输链发生变化, 进而造成自由基积聚^[20]。脱水过程中自由基的积累可改变微生物的膜特性, 并导致细胞溶解, 这主要是因为其引起了细胞内蛋白质的变性和脂质的过氧化^[25,27]。

微生物在受到环境影响时, 可以采取多种生理适应机制, 使其能够保持活跃并生存下去^[13]。为了保护微生物的结构和细胞器的完整, 微生物采取的主要生理适应机制为 DNA 的自我修复^[24]。此外, 暴露于高温下的微生物还可以合成部分热休克蛋白^[28]。另外, 经历干旱的一些细菌可以储存大量核糖体, 从而使它们能够快速合成蛋白质^[29]。微生物还可以通过改变脂质脂肪酸成分的组成^[27]来实现膜组成的变化以维持关键特性, 例如通过快速的细胞生理调节机制来保持膜的流动性状态^[30]。为了降低土壤干旱对细胞膜和蛋白质的损伤, 微生物还可以合成细胞内渗透因子^[31]。最后, 微生物孢子形成和休眠也是其克服各种不利极端环境条件的重要策略^[32]。这些策略标志着在极端干旱等应激过程中, 细胞生长控制和细胞周期调控的最终形式的形成^[33]。

2 极端干旱对土壤微生物的间接影响

土壤具有各种各样的微环境, 这些环境提供了适合于微生物生长、活动和生存发展的广泛生态位。微生物生境特征取决于土壤的非生物特性, 例如水分、温度、pH 值、盐度、渗透平衡、土壤养分、氧气和氧化还原电位等。不同的土壤孔隙提供了不同的生境, 可以适应不同的微生物种群的生存^[34]。土壤颗粒的排列结构决定了土壤的孔隙空间大小^[35], 在该空间内部, 水分含量决定了土壤的物理通透性, 并且是控制土壤非生物因子空间异质性的关键因素之一^[36]。在变动的环境条件下, 水的运动推动了微环境特征的快速时空动态变化, 对微生物种群变化造成了重要影响^[37]。极端干旱条件对土壤微生物的影响取决于所涉及的土壤特性, 但是由于极端干旱条件本身也是土壤特性的决定因素之一, 因此极端干旱也可以通过改变土壤特性来间接影响土壤微生物群落结构。

2.1 极端干旱对土壤理化性质及微生物活动的影响

极端干旱主要通过增加和减少土壤中水分的

聚集过程来调节土壤结构^[38]。土壤结构的改变通过改变土壤的净水特性^[39]和保水能力^[40]以及其热导率^[41]来影响土壤水分的运动。更好的通气条件也可能改变土壤的氧化还原状态,这会导致一些离子在可溶与不可溶形式之间转化,改变了其生物可利用度,从而改变这些元素的化学存在形式及微生物对其利用的方式。此外,土壤含水量决定了土壤 pH 值,随着土壤溶液变得更加浓缩,它可能会使微生物暴露于渗透胁迫下^[42]。土壤 pH 值在广泛的生物地球化学条件下与微生物群落密切相关^[43]。土壤 pH 值以不同的方式影响微生物的代谢。在自然环境中,将环境 pH 值升高或降低 1 个单位会使微生物群落的代谢活性降低多达 50%^[44]。

极端干旱还可以通过改变养分的利用率来改变微生物的活动。干燥土壤,尤其是再湿润的干燥土壤会导致生物或物理过程中有机物的利用率增加,从而增加微生物的活性^[45]。这可能是由于在干旱期间土壤微生物分泌的外切酶改变了土壤的微环境,但所产生的有机质对于微生物仍然不可利用,直到润湿使其具有生物可利用性,从而提升了这些有机质的利用率^[12,45]。此外,极端干旱条件下,有机物的“质量”可能会提高,并且可能具有高周转率使其更容易被降解,从而为微生物提供了新的营养优势^[46]。另外,极端干旱可能会加剧有机质分解,提高有机物的生物利用率^[18],从而促进了高亲和力土壤有机矿物的分解和吸收^[47],并可能在动力学上刺激微生物对不稳定碳的吸收和利用^[48]。

2.2 微生物细胞膜对极端干旱条件的响应

生物膜是由细胞生物量和细胞外聚合物组成的一种混合微生物群体。其中,后者主要成分是微生物分泌的高分子量物质以及细胞裂解和大分子水解的产物,可显著促进微生物聚集并维持微生物聚集体的稳定性。胞外聚合物是生物膜的主要成分,可在极端环境下为细胞提供碳源和能量^[49]。众所周知,各种微生物生物膜环境,例如水生附生植物和生物土壤结皮,都对微生物群落有利,可以保护它们免受极端环境的干扰^[50]。在极端环境下,胞外聚合物的产生不仅在细胞上而且在环境层面上都起着关键作用^[51]。实际上,在干旱、侵蚀、辐射和高温下的沙漠表层土壤微生态系统中,生物土壤结皮的形成、土壤稳定化和保水作用均取决于胞外聚合物的产生^[52]。

胞外聚合物能够吸收环境中的水^[26],保留土壤

养分^[53],保持了土壤中水分的运输特性以及土壤的湿润性^[54],并增加了土壤团聚体的稳定性^[55]。这意味着胞外聚合物可能在快速干湿过程中造成一定程度的水分隔离,从而保护了土壤中包埋在生物膜中的微生物^[50]。土壤胞外聚合物在土壤-微生物界面的位置及其特定的水文特征,可能对极端干旱条件下,分析土壤孔隙连通性和受水合作用影响的微生物活性之间的相互影响具有重要作用^[56]。

3 极端干旱条件下土壤微生物群落结构和多样性格局的改变

极端干旱不仅能对土壤微生物细胞产生影响,还能进一步改变土壤微生物群落的组成和结构。由于微生物群落是生态过程的重要驱动因素,了解极端干旱对土壤微生物群落的影响对于预测生态系统功能具有重要意义^[57-58]。

3.1 极端干旱对微生物群落组成的影响

虽然极端干旱对微生物群落组成产生了一定的影响,但不同微生物种类对极端干旱的响应存在较大的差异。与细菌相比,真菌在全球范围内对高温更加敏感^[59]。研究显示,大部分真菌比细菌更适合土壤低湿度条件^[60]。这种适应性差异与特定的真菌性状有关,例如,在低扩散率时,真菌菌丝比细菌更能自主运输扩散,不过度依赖水驱动运输^[61]。因此,干旱条件可能会增加微生物群落中的真菌优势^[62-63]。在细菌组中,干旱可能会对革兰氏阴性细菌影响较大,而对于革兰氏阳性细菌影响较小^[13,64]。革兰氏阳性细菌被认为比革兰氏阴性细菌更能适应高的水位渗透势^[65],因为它们具有保守的生物学特性,例如厚而坚硬的细胞壁、高渗透压调节能力^[13,66-68]和孢子形成能力^[25]。有研究者应用了这些发现,并提出了优化革兰氏阳性对革兰氏阴性和真菌对细菌的比率,作为群落抗旱性的全球指标^[69]。

极端干旱还会对微生物的丰度造成较大的影响,研究显示干旱环境的土壤微生物菌群主要由放线菌门、变形菌门、拟杆菌门、酸杆菌门和厚壁菌门为主,而海洋微生物门、衣原体门、软壁菌门和糖化菌门等不存在^[70]。进一步研究表明,在干旱土壤中,微生物结构似乎受到年平均降水量和年平均温度的强烈调控,而不是 pH 值的影响^[70]。从温度角度来说,寒冷条件下的土壤微生物主要是由变形菌门(12.1%)、放线菌门(31.8%)、拟杆菌门

(11.7%) 和酸杆菌门(15.4%) 组成, 高温条件下的土壤微生物是由厚壁菌门(8.6%)、放线菌门(36.8%)、变形菌门(23.8%) 和酸杆菌门(5.5%) 组成。同样地, 尽管放线菌是干旱土壤中的优势门, 但随着年平均降水量的增加, 其相对丰度显著降低。这些观察结果强调了温度和水分对干旱土壤中某些微生物类群相对丰度的影响。

有些研究认为, 放线菌是干旱土壤中的优势门, 与土壤相对湿度的降低呈正相关^[71-72]。也有研究认为, 当土壤湿度降低时, 变形菌、蓝藻菌和黑体菌与其正相关^[70]。将微生物丰度与年平均温度的增加对比, 可以观察到变形菌门和厚壁菌门丰度增加, 而酸杆菌门和拟杆菌门丰度减少^[70]。相反, 寒冷条件下内蒙古草原上拟杆菌门的丰度很高^[73]。同样, Kumar 等研究表明, 拟杆菌门在寒冷环境中占优势, 但在研究的较冷地区则不占优势^[74]。有趣的是, 研究发现极端干旱条件下细菌群落内部观察到了更多的拟杆菌, 这个门类微生物在 28 d 50 °C 试验中表现出耐热性^[75]。这表明, 拟杆菌门在寒冷环境和高温干旱环境中都能生长旺盛, 具有较好的极端环境适应性。

3.2 细菌群落和真菌群落对极端干旱的响应差异

生态网络分析是研究微生物群落对扰动反应的一种新方法^[76]。土壤微生物群落形成了高度复杂的生态网络, 其中包括共存类群之间的多种相互作用, 而且越来越多的证据表明, 这些网络的特性可以影响它们对极端气候的反应。例如, 最近的一项研究显示, 干旱对细菌的影响大于对真菌的影响^[77], 这与土壤细菌群落比真菌群落抗旱能力弱的预期相一致^[62,78-79]。然而, 也有研究发现, 细菌共生网络在理论上具有在扰动下稳定性较低的特性, 如高连通性和中心性, 而真菌网络具有稳定性较高的特性, 如负相关性较少, 从而使微生物生态共生网络趋于稳定^[80-83]。另一个重要的发现是, 对干旱反应最灵敏的主要细菌类群高度集中并在生态网络中相互连接, 这表明它们是细菌网络结构变化的主要驱动因素^[77]。尽管在解释共生网络时需要谨慎^[84-85], 但它可以提供关于微生物类群间的相关性和时空结构以及面对极端气候等扰动时微生物群落的稳定性的重要信息^[77,86]。

细菌和真菌群落如何适应干旱胁迫呢? 细菌群落对干旱的适应力和恢复力取决于该群落的组成以及它们是否或如何适应干旱胁迫。一般来说,

革兰氏阳性细菌有内在的抗旱能力, 因为它们有厚厚的细胞壁起到限制脱水的作用^[87], 这与前述一致。相比之下, 革兰氏阴性硝化菌或甲烷氧化菌对脱水更敏感, 受干旱影响较大, 会被弱化部分功能^[13]。暴露在干旱胁迫下的细菌群落能够通过更灵敏的感应胁迫、溶质合成和休眠等反应机制^[88] 以更好地应对干旱^[89]。在干旱很少发生的地方, 细菌群落更容易受到干旱的影响, 因为它们不能预先适应土壤湿度的极端范围^[89]。

真菌是土壤微生物群落的另一个重要组成部分。真菌被认为比细菌更能适应水分胁迫, 并且能够通过多糖的分泌在自己周围创造一个保护环境来防止脱水^[90]。当土壤水分受限时, 底物扩散限制可能会迫使土壤真菌菌丝网络扩张, 有助于真菌对水分和养分的吸收^[91], 而且真菌群落组成的变异性更高, 具有高可塑性的种群周转率使得真菌能快速对干旱做出响应^[92]。另一方面, 土壤水分变化通过植物群落间接影响真菌, 真菌群落中大量的菌根和腐生真菌强烈依赖植物物种^[93-94]。腐生真菌更易受到资源可用性的影响, 如植物根系分泌物输入量及化学特性^[95]。像细菌一样, 真菌也以多元醇^[96] 而不是氨基酸的形式积累渗透物质。在极端水分胁迫下, 真菌细胞的碳和氮可分别增加 30% ~ 40% 和 20%^[13,97]。干湿交替和长期干旱也可能增加真菌与细菌的比率^[98], 真菌群落比例较大的土壤更能保持养分^[99]。

4 极端干旱对微生物功能的影响

微生物群落组成及其与物种的相互作用是生态系统功能的关键驱动力^[100]。极端干旱引起的微生物组成变化可能会影响土壤功能, 进而影响土壤所提供的服务^[101]。极端干旱造成的土壤条件的变化会影响微生物的功能, 如二氧化碳排放、有机质降解、养分循环和固氮等^[12,18,63,102-103]。在这些功能里面, 涉及土壤碳氮循环及微生物-植物相互作用等方面更值得被关注。

4.1 极端干旱条件对微生物参与土壤碳氮循环的影响

极端干旱显著地影响了土壤微生物群落的结构和功能, 从而改变土壤微生物介导的碳氮转化。由于干旱通常与高温同时发生, 因此了解土壤中碳氮循环与水与温度相互作用至关重要^[104]。极端干旱主要通过降低土壤水分来影响土壤碳氮循环, 所

以土壤碳氮循环对土壤水分的变化较为敏感^[105]。干旱期间较低的水位渗透势和减少底物扩散可以抑制微生物的生长,增加微生物的死亡率,诱导微生物休眠,从而造成微生物群落组成发生变化^[105-106]。同时,干旱会降低微生物的活性,例如降低呼吸作用^[105]。干旱也会降低参与蛋白质解聚的细胞外酶活性,但是其对微生物摄入和生产总氨基酸的影响仍未能确定^[107]。在干旱期间,有机化合物可以集中在剩余的土壤溶液中,并可能增加底物酶解作用的能力^[108]。此外,在干燥条件下,细胞外酶的活性可能比微生物细胞更高^[109]。干旱会降低 NO_3^- 产生量和增加 NH_4^+ 的吸收。氮矿化的减少导致微生物氮素利用效率总体减少。虽然干旱可能会刺激微生物采取策略来保护氮,例如生产含氮的渗透压化合物^[105],但干旱对氮矿化和硝化的影响很大程度上取决于生态系统和土地管理类型^[104,110]。研究显示,干旱降低了 2 个草地中微生物生物量中的氮浓度,显著提高了蛋白质解聚速率,这是蛋白酶催化的胞外过程^[111],这与在温带荒地中观察到的动态变化相反。在温带荒地中,蛋白质解聚速率不受干旱的影响^[112]。总体而言,干旱能够增加微生物中碳氮比,这种现象与以前的研究结果^[63]一致,表明干旱对微生物氮循环的影响可能比碳循环更大。

温度升高通常会增加微生物的活性,但也会增加维护成本和微生物能量需求^[113]。如果微生物将更多的碳分配给呼吸,而不是增加其生物量,则会降低微生物的碳利用率^[114],这可能会导致土壤碳的整体损失^[115]。较高的温度可使蛋白质在热力学上以更快的速度分解为适合微生物吸收的有机氮形式,从而刺激微生物生长^[116],尽管它们也可能会加速酶的失活^[117]。还有研究显示,随着温度的升高,微生物对氮的矿化作用和硝化作用比吸收无机氮的作用更强烈,从而导致土壤中无机氮的净增加^[118-119]。总体而言,微生物的碳和氮循环过程对环境条件的变化反应不同,微生物的碳循环对温度变化更敏感,而氮循环受水的可利用性更强烈。

在干旱期间,表层土壤中常出现多个干湿交替的情况,因为这些地区有一些间歇降雨,但不足以使土壤完全重新湿润并打破干旱。研究发现,重复的干湿交替循环增加了有机质的氮矿化和周转^[120]。多次干湿交替会降低氮含量和脲酶活性,增加溶解的有机碳^[121]。草地土壤干湿交替后,

可提取有机碳立即增加 80%,微生物生物量碳下降^[122]。然而,重湿后并没有发现土壤氮总溶解浓度增加的证据^[123]。矿化率增加导致的氮和碳的淋洗可能在 2~3 d 后消退^[124],或者在最初的重新润湿后持续 10 d^[125]。Butterly 等测定的重新润湿后溶解氮增加,持续 4 d 后恢复到与干燥前相同的水平^[126]。

在同一研究中,微生物生物量碳随着每次干湿交替的发生而降低,在 5 个循环后为潮湿对照中测量的 60%。Mikha 等也观察到,反复干燥和湿润循环导致碳量的减少^[127]。同样,增加湿润和干燥循环次数会减少干燥再湿润事件中的氮矿化^[128],凋落物分解随着再湿润频率的增加而减少^[129]。在反复的水土流失事件中,土壤中碳和氮的损失分别高达 18% 和 10%^[130],这是每年土壤养分损失的重要部分。

4.2 极端干旱条件下根系分泌物对微生物功能的影响

土壤微生物对植物多样性和生产力的贡献可能是其在生态系统功能中,特别是在农业系统中最重要的作用之一^[131-132]。在根际这样的土壤微生物活动“热点”区域中,微生物在不同时空尺度上参与了土壤-植物体系的各种过程^[5]。另外,已经有研究显示,植物可以直接或间接控制和介导土壤中尤其是微生物圈的多营养相互作用^[5,133],植物群落组成差异影响微生物生物量和分解代谢活动,从而对干湿扰动的恢复力存在抗性差异^[134]。随着植物通过碳输入获得更多的资源,微生物群落结构对全球变化干扰的适应力会增加,这可能会刺激胞外聚合物的产生和生物膜的发育^[56]。研究显示,极端干旱条件下,土壤微生物的多样性与植物的多样性存在显著正相关^[135],因此植物与土壤微生物之间存在着相互反馈的协同抗旱机制。

根系分泌物是植物与微生物间的主要交流途径,在生态系统对环境变化的响应中发挥着关键作用。植物发育会影响根系分泌物的组成,进而通过优先吸收特定代谢产物影响根际细菌群落^[136]。微生物群落的变化也可以促进植物的生长和物候变化,例如拟南芥中香豆素的渗出刺激了致病菌诱导和促进生长的根瘤菌的存在^[137]。也有研究显示,根系分泌物选择的土壤微生物增加了土壤氮的利用率,进而延迟了开花时间^[138]。另外,根系分泌物也可能反映干旱后植物再生和生态系统恢复情况^[139-140],例如,有研究记录了干旱恢复期间向日

葵和大豆根系分泌物渗出速率和组成的差异响应^[141]。而在冬栎中,分泌物的代谢特征取决于干旱或恢复的不同阶段^[142]。还有一些植物通过微生物影响根部基因的表达以促进干旱保护,例如,干旱期间玉米得益于与丛枝菌根真菌(arbuscular mycorrhizal fungi)的共生关系,丛枝菌根真菌通过减少根中水通道蛋白相关基因的表达来调节水分流失^[143]。此外,植物还可以通过根系分泌物选择特定的细菌来增强抗旱能力,例如,干旱能增加玉米中有机酸的渗出,特别是苹果酸(以及富马酸、丙二酸、琥珀酸和草酸)^[144],它是枯草芽孢杆菌(*Bacillus subtilis*)的一种有效的化学吸引剂^[145],枯草芽孢杆菌是有益的细菌种类,研究显示其可增加植物的抗旱性^[146]。这些研究表明,不同生长策略的植物根系分泌物不同,根系分泌物可以选择有益的土壤微生物群落,以不同的方式降低极端干旱对植物的胁迫并保证植物的正常生长。

5 总结与展望

极端干旱(干旱与高温同时存在的条件)对土

壤微生物介导的生物地球化学循环及其陆地生态系统生态服务功能产生了较大的影响。为了应对极端干旱,土壤微生物动员了从个体到群落的应对策略(图1),包括DNA的自我修复、合成热休克蛋白、维持细胞膜的流动性、分泌胞外聚合物以及合成生物膜等措施。从群落角度而言,真菌比细菌更容易耐受极端干旱条件,革兰氏阳性菌比阴性菌也具有更高的极端干旱耐受性。放线菌门、拟杆菌门、变形菌门等门类的微生物是极端干旱环境下微生物的主要门类。土壤微生物所介导的碳循环对温度变化更敏感,而氮循环受水的影响更大。植物根际分泌物也能够选择有益的土壤微生物群落,根际微生物能够以不同的方式降低极端干旱对植物的胁迫,并保证营养和水分的运输。虽然本文梳理了极端干旱对土壤微生物从个体到群落以及功能方面的影响,但是其相关机制仍然不甚清楚,为了更加系统地研究极端干旱对土壤微生物群落与功能的影响机制,还需要从以下几个方面进行进一步的研究:(1)在极端干旱对土壤微生物群落的影响上,应该考虑进行原位研究,比较微生物群落对不

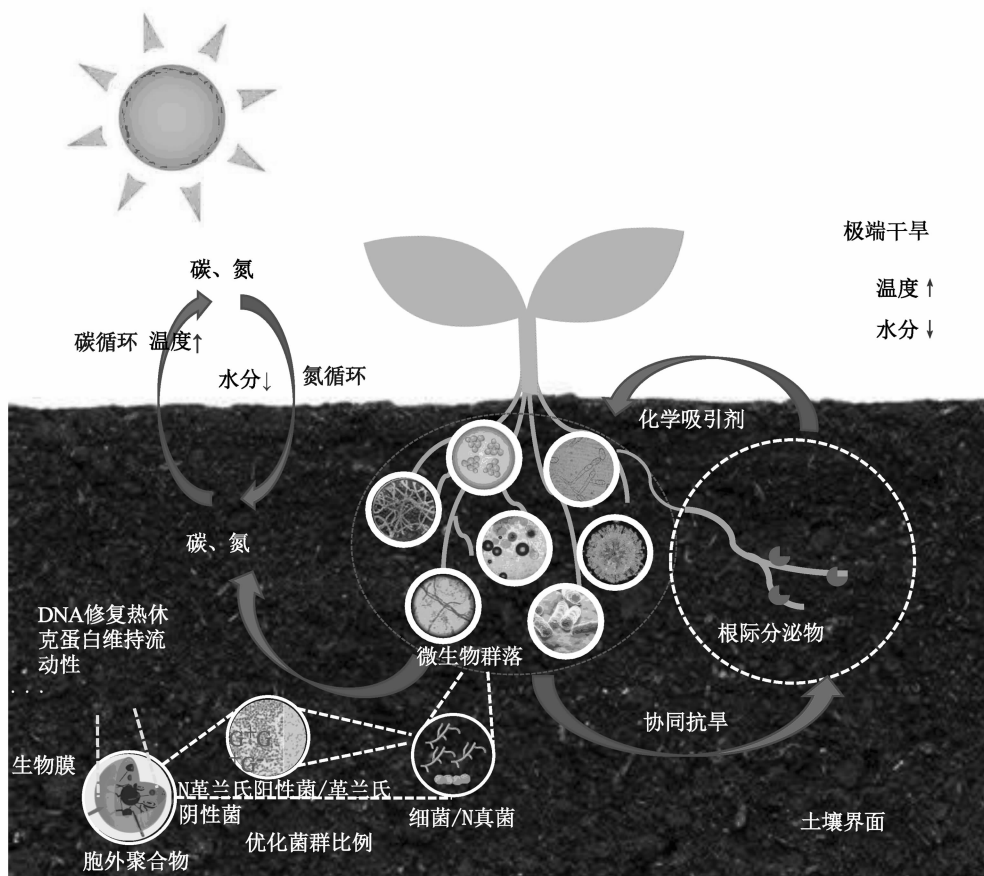


图1 极端干旱对土壤微生物群落和功能的影响示意图

同纬度和不同土地土壤中极端气候事件的反应,并讨论高温和干旱综合影响的模型效果。(2)有必要开展极端干旱条件下土壤微生物结构功能的稳定性状、共耐受性和微生物抗性和恢复性的相关性方面的研究。(3)元转录组学和代谢组学可以提供定量信息来反映具有相同功能的微生物群落,可以通过识别分类单元功能基因的表达来反应环境干扰。虽然转录组学和代谢组学为在极端干旱环境下将土壤微生物群落结构的稳定性与微生物群落的功能联系起来提供了新的补充工具,但是极端干旱环境下土壤中潜在的功能基因的分布仍然是一个挑战。(4)积极开展跨学科的合作,进一步研究极端干旱发生前后根际及其寄主的物理化学特性与植物和微生物相互作用机制,对理解土壤微生物的农业生态功能有重要意义。

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