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干旱下植物根系分泌物及其介导的根际激发效应研究进展

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摘 要 根系分泌物是植物与土壤进行物质能量交换和信息传递的重要媒介, 同时也是植物响应外界环境变化的主要形式, 在土壤碳库动态中发挥着重要作用。伴随着全球气候变化而频繁发生的极端干旱事件对植物地上地下生长过程都产生了深刻的影响, 然而, 由于根-土界面交互作用的复杂性, 以及根系分泌物收集手段与装置的不完善, 人们对干旱条件下根系分泌物及其介导的根际激发效应的响应及机制的认知尚存在较大的局限性。基于此, 该文结合国内外生态学领域的研究前沿动态, 论述了干旱下植物根系分泌物数量及组分的动态变化, 重点阐述了根系分泌物介导的根际激发效应及其机制, 在此基础上展望了未来根系分泌物研究中的重点关注方向, 以期为未来全球气候变化条件下土壤碳汇的评估提供科学依据。

关键词 干旱胁迫; 根系分泌物; 根际激发效应; 土壤微生物; 土壤养分

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Effects of drought on plant root exudates and associated rhizosphere priming effect: review and prospect

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Abstract

Root exudates play an important role in soil carbon balance, acting as an important medium for material and energy exchange and information transfer between plant roots and soil, and also the crucial forms for plant response to environmental changes. Frequent extreme drought events accompanied with global climate change have imposed a profound impact on both above- and below-ground plant growth processes. However, significant limitation exists in understanding the responses of root exudates and their mediated rhizosphere priming effect to drought due to the complexity of root-soil interface interactions and the limitation in devices and methods for collecting root exudates. This paper reviews the effects of drought on the quantity and quality of plant root exudates, with emphasis on the rhizosphere priming effect mediated by root exudates under drought stress. The future research focuses on root exudates was also discussed. This study will provide suggestion for soil carbon sink assessment under the future climate change.

Key words drought stress; root exudates; rhizosphere priming effect; soil microorganisms; soil nutrient

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根际微生态系统是植物根系-土壤-微生物紧密联系构成的整体，其中根系分泌物是根际区域活动的重要影响因素(张福锁和申建波, 1999)。根系分泌物是指在植物生长过程中，通过根系主动或被动向根际区域释放的各类有机化合物，其中一类是初级代谢产物，包括糖类、氨基酸类和有机酸类等，另一类是次级代谢产物，包括类黄酮、酚类和萜类等(吴林坤等, 2014; Gargallo-Garriga et al., 2018)。根际沉积是植物通过根系向根际释放大量的光合作用固定碳，这些释放的有机化合物被称为根际沉积物(Preece & Peñuelas, 2016; Liu et al., 2019)。根系分泌物在根际微生态系统结构与功能方面起到至关重要的作用：在总体上，根系分泌物在促进根际与土壤物质循环和信息传递的同时，满足植物不同生长阶段的营养需求，促进植物生长和发育(Mommer et al., 2016; Canarini et al., 2019; Zhao et al., 2021)；但对于不同的根系分泌物组分，其生理作用又有所不同，例如：有机酸类化合物有助于植物定向选择微生物群落(Allard-Massicotte et al., 2016)，酚类化合物通过影响抗氧化活性进而增强植物耐盐性(毛梦雪和朱峰等, 2021)。此外，根系分泌物中的草酸通过诱导微生物和β-1,4-N-乙酰葡糖氨糖苷酶活性可以间接提高潜在氮矿化速率，是根际微生态系统中植物增强养分获取的重要机制(Pan et al., 2016)；糖类和氨基酸等也是根际微生物的重要碳源，有助于提高根际微生物的分解活性和胞外酶活性，加快土壤有机质(SOM)的周转速率，从而影响根际土壤碳循环过程(图1) (Kuzyakov, 2010; Drake et al., 2011; Phillips et al., 2011)。

根系分泌物的数量和组分会随着植物生长环境的变化而改变(张锡洲等, 2007)，如水分条件(Preece & Peñuelas, 2016; Preece et al., 2021)、温度(Xu et al., 2015; 马志良, 2020; 吴晨等, 2021)、土壤养分状况(Lu et al., 2018b; Sun et al., 2021; Jiang et al., 2022)和大气CO_2浓度(Jia et al., 2014; 李月明等, 2022)等。大量研究表明，根系分泌物的释放是植物响应环境胁迫的一种重要调控机制(Williams & de Vries, 2020)。同时，根系分泌物可以提高植物资源利用效率，促进植物与微生物群落之间的相互作用，从而缓解环境胁迫带来的不利影响(Chai & Schachtman, 2022)，增强植物在逆境中的适应能力和生存力(Phillips et al., 2011; Karlowsky et al., 2018)。

在气候变暖背景下，全球范围内的水文循环发生了剧烈改变，极端干旱气候事件发生的频率和强

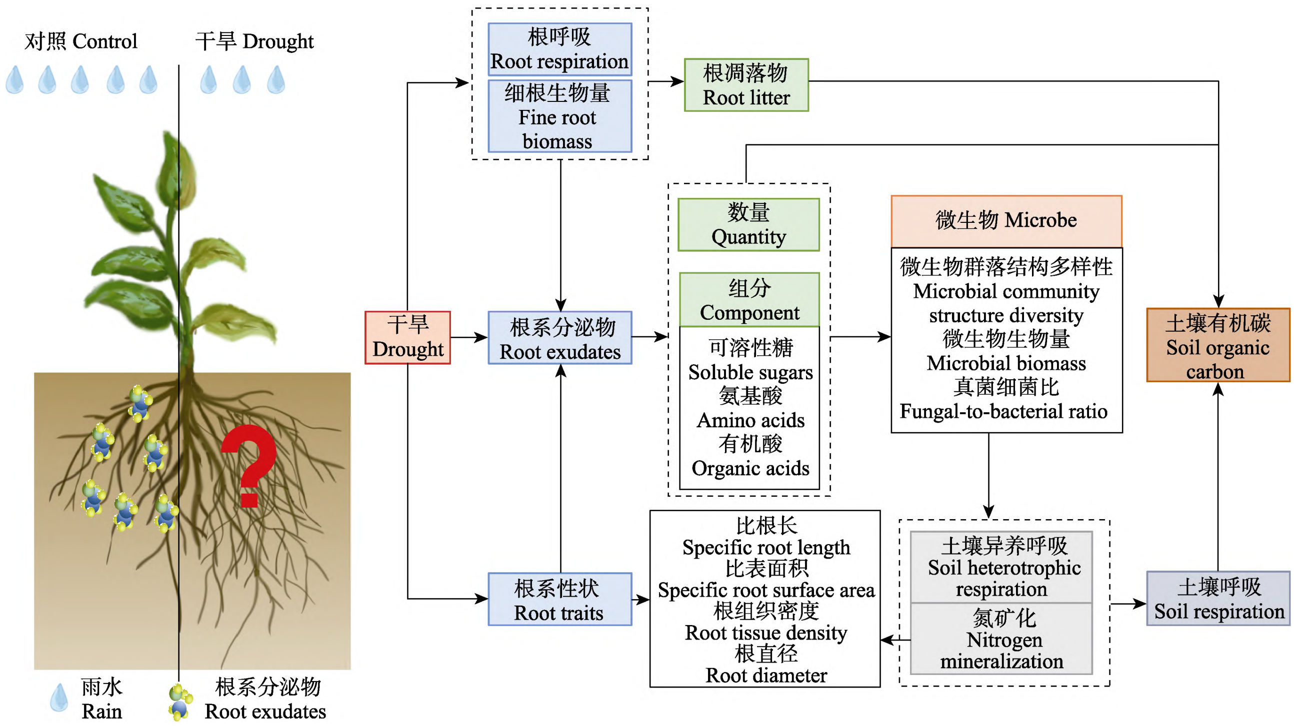

图1 根系分泌物及其介导的根际激发效应对干旱的响应。
Fig. 1 Response of root exudates and their mediated rhizosphere priming effect to drought.

度显著增加(Su et al., 2018), 对植物生长、养分吸收及土壤碳循环产生了强烈影响(Pretzsch et al., 2020; Zeng et al., 2023)。近年来人们围绕植物(尤其是农作物)的耐旱性和抗旱性开展了大量的研究, 但却在很大程度上忽视了根系对干旱胁迫的反应(图1) (de Vries et al., 2019)。事实上, 根系是植物水分管理的关键, 根系分泌物作为植物-土壤-微生物交互作用的重要“媒介”, 对植物的耐旱性和存活率有着重要影响(Hartmann et al., 2018; Williams & de Vries, 2020)。其次, 土壤水分的变化也将改变根际碳分配, 包括根生物量以及根系分泌物等根际碳过程, 抑制根际沉积碳分解, 最终影响陆地生态系统的土壤碳平衡(图1) (周国逸等, 2020; Wang et al., 2021a, 2021b)。然而, 关于根际碳过程及其调控因素的研究还较为匮乏, 限制了我们对干旱条件下土壤碳库动态的评估(Sulman et al., 2014; Guenet et al., 2018)。长期以来, 受制于根际微生态系统的复杂性, 以及根系分泌物收集手段与装置尚不完善等因素, 目前对植物根际过程如何响应干旱胁迫缺乏系统的认知(Oburger & Jones, 2018; 尹华军等, 2018)。基于此, 本文通过搜集整理国内外关于干旱条件下根系分泌物及其介导的根际激发效应(RPE)的研究, 在梳理相关结论的基础上, 厘清干旱胁迫下根系分泌物的变化规律, 深化对植物关键地下碳过程的认识, 为今后开展气候变化背景下生态系统地下碳过程的研究提供参考和借鉴。

1 干旱对植物根系分泌物的影响

1.1 根系分泌物数量

光合作用固定的碳, 约30%被分配至地下用于植物养分获取的碳投资(Pausch & Kuzyakov, 2018)。干旱发生时, 植物可以通过改变根系分泌物输入来响应水分亏缺的环境压力, 从而对植物的适应性和生存力产生积极影响(Karlowsky et al., 2018)。虽然目前已有一些研究探讨了干旱对根系分泌物数量的影响, 但结果尚存在一定的分歧(表1)。Sanaullah等(2012)在为期40天的干旱盆栽实验中发现, 干旱条件下根系分泌物的输入增加。有研究发现, 随着土壤含水量的减少, 植物根系分泌速率增加(Brimecombe et al., 1999; Henry et al., 2007; Canarini et al., 2016), 当植物临近枯萎点时根系分泌物输入土壤的速率最快(Brunn et al., 2022)。也有研究表明, 干旱显著降低了根系分泌物输入速率和部分酶活性(图1) (Staszel et al., 2022; Jiang et al., 2023); 而在对大豆(*Glycine max*)和欧洲赤松(*Pinus sylvestris*)的两项研究中却发现干旱胁迫并未对其根系分泌物输入数量造成显著影响(Canarini et al., 2016; Preece et al., 2021)。此外, 根系分泌物的输入数量也受到干旱强度的调控, Preece和Peñuelas (2016)的研究结果指出, 在中度干旱条件下根系分泌物总量增加, 但在极端干旱条件下根系分泌物总量的变化具有不确定性。由此可见, 植物根系分泌物数量对干旱胁迫的响应还存在较大不确定性, 亟需开展广泛而深入的研究。

1.2 根系分泌物组分

在特定干旱强度下, 植物不仅改变根系分泌物输入总量, 还可能改变根系分泌物组分, 调整根际微生物群落的结构和数量及胞外酶活性(Tan et al., 2021), 进而影响土壤有机碳分解速率和养分循环(图1) (Phillips et al., 2011; Karlowsky et al., 2018; de Vries et al., 2019)。有研究发现水分限制会使得植物根系分泌物中某些化合物浓度升高(Calvo et al., 2017, 2019; Cesari et al., 2019), 但不同物种所具有的独特生理生态特征(如植物生长策略、根系形态等)导致不同类型植物根系分泌物组分对干旱胁迫的响应程度和方向存在差异。例如, 在干旱期间不同的农作物根系分泌物具有不同的表现: 向日葵(*Helianthus annuus*)根系能够释放更多的糖类、脯氨酸、氨基酸类等内源性物质来应对干旱胁迫(Canarini et al., 2016); 敏感型御谷(*Pennisetum glaucum*)的酚酸、木酚素和类黄酮浓度增加, 有助于土壤微生物群落适应土壤水分的变化(Ghatak et al., 2022)。对于木本植物, Jiang等(2023)研究发现常绿阔叶林优势树种在极端干旱下根系分泌物中葡萄糖和氨基酸的分泌速率分别降低了30.8%和35.0%, 而有机酸的分泌速率提高。Gargallo-Garriga等(2018)研究发现, 干旱条件下冬青栎(*Quercus ilex*)根系分泌物主要由次生代谢物(如乳酸、丙酮酸、脱落酸和葡萄糖等)组成, 而水分恢复后分泌物主要由初级代谢物(如天冬氨酸、天冬酰胺、精氨酸和缬氨酸等)组成。而草本植物在响应干旱时, Ulrich等(2022)的研究结果显示, 格兰马草(*Bouteloua gracilis*)根系分泌物中蔗糖、苹果酸、葡萄糖、甜菜碱和富马酸等部分代谢物浓度在干旱下升高, 而戊酸、3-羟基丁

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表1 干旱对根系分泌物的影响研究
Table 1 Effects of drought on root exudates

研究地点 Study site	研究类型 Study type	研究对象 Study object	干旱/对照(恢复) Drought/control (recovery)	干旱时间 Drought duration	根系分泌速率变化范围 Variation range of root exudation rate	参考文献 Reference
中国浙江 Zhejiang, China	野外实验 Field experiment	木荷 *Schima superba*	减少70%的降雨/正常降雨 70% lower rainfall/normal rainfall	10 a	–0.271↓	Jiang et al., 2023
		米槠 *Castanopsis carlesii*			–0.217↓	
		苦槠 *Castanopsis sclerophylla*			–0.142↓	
		柯 *Lithocarpus glaber*			–0.034=	
德国 Germany	野外实验 Field experiment	欧洲水青冈 *Fagus sylvatica*	减少70%的降雨/正常降雨 70% lower rainfall/normal rainfall	5 a	0.071=	Brunn et al., 2022
		欧洲云杉 *Picea abies*			0.308↑	
波兰 Poland	盆栽实验 Pot experiment	无梗花栎 *Quercus petraea*	25% SWC/55% SWC	31 d	–0.665↓	Staszel et al., 2022
美国 America	盆栽实验 Pot experiment	格兰马草 *Bouteloua gracilis*	50% WHC, 25% WHC/100% WHC	30 d	0.506, 50%WHC= 3.007, 25%WHC↑	Ulrich et al., 2022
西班牙 Spain	盆栽实验 Pot experiment	欧洲赤松 *Pinus sylvestris*	10% SWC/20% SWC	14–17周 14–17 weeks	0.375=	Preece et al., 2021
		冬青栎 *Quercus ilex*			0.091↑	
英国 Britain	盆栽实验 Pot experiment	绒毛草 *Holcus lanatus*	20% WHC/60% WHC	14 d	0.783↑	de Vries et al., 2019
		酸模 *Rumex acetosa*			0.141=	
阿根廷 Argentina	培养皿 Culture dish	落花生 *Arachis hypogaea* (SEMIA6144)	Hoagland solution (–0.28 MPa)/ Hoagland solution (–0.07 MPa)	7 d	0.270↑	Cesari et al., 2019
		落花生 *Arachis hypogaea* (Az39)			0.250↑	
西班牙 Spain	盆栽实验 Pot experiment	冬青栎 *Quercus ilex*	0.3%–22.6% SWC/20%–24.7% SWC	21 d	0.213↑	Preece et al., 2018
德国 Germany	盆栽实验 Pot experiment	大麦 *Hordeum vulgare* (cv. Golden Promise)	减少33%的降雨/正常降雨 33% lower rainfall/normal rainfall	91 d	–0.251=	Calvo et al., 2017
		大麦 *Hordeum vulgare* (cv. Bambina)			–0.164=	
澳大利亚 Australia	盆栽实验 Pot experiment	向日葵 *Helianthus annuus*	40% WHC/65% WHC	14 d	2.207↑	Canarini et al., 2016
		大豆 *Glycine max*			0.495=	
加拿大 Canada	盆栽实验 Pot experiment	颤杨 *Populus tremuloides*	减少90%的水量/最佳水量 90% less water/optimum water	42 d	0.930=	Karst et al., 2017
美国 America	盆栽实验 Pot experiment	冰草 *Agropyron cristatum*	减少75%的水量/最佳水量 75% less water/optimum water	35 d	0.680↑	Henry et al., 2007

根系分泌速率变化范围= (干旱处理下的根系分泌速率–对照或恢复处理下的根系分泌速率)/对照或恢复处理下的根系分泌速率。SWC, 土壤含水量; WHC, 田间持水量; ↑, 升高; ↓, 降低; =, 无显著变化。
Variation range of root exudation rate = (root exudation rate under drought – root exudation rate under control or recovery) / root exudation rate under control or recovery. SWC, soil water content; WHC, water holding capacity; ↑, increase; ↓, decrease; =, no significant change.

酸、丁酸和癸酸等代谢物的浓度降低; 冰草(*Agropyron cristatum*)则表现出有机酸的分泌速率加快, 特别是苹果酸、富马酸、丙二酸、琥珀酸和草酸等(Henry et al., 2007), 以吸引有利于干旱防护的特定细菌增强植物的抗旱能力(Gagné-Bourque et al., 2016; Henry et al., 2019)。此外, 在影响根系分泌物组分响应干旱的研究中, 除物种本身外, 干旱程度也是重要的影响因素。然而, 不同的干旱程度如何影响根系分泌物组分变化的研究较为匮乏, 结论仍存在争议。Gargallo-Garriga等(2018)发现随着干旱程度的加剧, 根系分泌物会发生不可逆的变化, 以致复水6周后根系分泌物代谢组无法恢复到干旱前的正常水平。也有研究指出, 随着干旱的加剧, 根系分泌物组分呈现出增加的趋势(李敏等, 2022), 而根系分泌物组成也反映了不同干旱程度处理的生理梯度, 具体而言, 在对照水平和轻度干旱条件下的代谢化合物主要是己二酸、3-氨基丙腈和1-十六烷醇等, 而在重度干旱条件下的代谢化合物主要是蔗糖、肌醇和甘露糖等(Ulrich et al., 2022)。尽管已有研究表明植物根系分泌物组分普遍受到干旱的影响, 但对不同组分的研究还不够深入, 其中相关根际过程以及植物细胞特异性功能的调控尚不清楚, 根系分泌物组分的变化如何受到物种自身基因遗传的生理控制需要更多关注。

1.3 干旱对根系分泌物影响的调控因素

干旱对根系分泌物数量和组分的影响受一系列复杂的非生物因素(如土壤含水量、土壤养分等)和生物因素(如树种、根系形态特征等)的调控(Williams & de Vries, 2020)。从非生物因素来看, 首先, 根系分泌物对干旱胁迫的响应方向可能随着干旱胁迫的强度变化而发生改变。具体表现为在轻度或中度干旱条件下, 植物对地下部分的碳投入相对较多, 即植物倾向于将碳分配给具有资源获取功能的器官(Hagedorn et al., 2016; Staszel et al., 2022)。由于根系分泌物中的黏液有助于根系在干燥的土壤中移动, 并保持和土壤的接触, 根系分泌物数量随之增加(Vranova et al., 2013; Brunn et al., 2022)。而在重度干旱条件下, 由于调节根系养分获取性状的碳投入减少, 具体表现为比根长、比表面积减小, 导致根系分泌物数量随之降低(Wen et al., 2019; Wang et al., 2021a, 2021b)。其次, 研究表明, 土壤养分的有效性已成为衡量植物根系分泌物受干旱影响的关键指标(Preece et al., 2021), 反之, 从根系分泌物输入总量上也可以推测植物或土壤微生物的营养水平(Canarini et al., 2019)。具体而言, 为了满足在快速生长期间的营养需求, 植物可能会改变自身的根系分泌物输入模式, 以便快速调整土壤微生物的响应策略(Zhao et al., 2021), 或者通过较高的根系分泌速率刺激土壤微生物介导的养分循环, 从而提高土壤养分的有效性(图1), 营造更有利的植物生长环境(Schmidt et al., 2016; de Vries et al., 2019)。这些研究认为根系分泌物可以作为植物和土壤微生物的选择信号或养分来源, 但形成这些关系的潜在化学机制尚未得到充分求证。

从生物因素来看, 干旱对根系分泌物输入状况的影响具有显著个体差异, 不同的物种由于系统发育历程和生活环境的差异, 可能对干旱胁迫的应对策略不同(Preece et al., 2021)。如前文所述, 物种是植物响应干旱时根系分泌物数量和组分变化的重要影响因素, 但不同植物类型响应干旱的潜在机制可能存在差异。同时, 植物的抗旱能力还受自身资源获取策略影响, 通常资源获取型的快生树种对水分含量变化较为敏感, 而资源保守型的慢生树种则相反(Ouédraogo et al., 2013)。比如, 在干旱期间快速生长的树种会及时关闭气孔, 降低光合作用速率和呼吸强度, 最终导致根系分泌物的输入总量减少, 组分也发生改变(Henry et al., 2019), 进而影响植物碳分配策略。Williams和de Vries (2020)提出了一种假说, 认为植物的特异性生长策略能够影响干旱条件下根系分泌物的输入, 具体来说, 快速生长的植物对干旱的响应更为明显, 表现为快速调整其根系分泌物的输入以吸引有益的微生物, 促进干旱后植物的再生长, 进一步影响其丰度和生态系统功能。而Jiang等(2023)的研究结果表明, 在极端干旱下生长速率较高的树种根系分泌速率比生长速率较低的树种变化更为强烈, 充分证实了上述假说。

由于物种对水分限制的敏感性不同, 各物种的根系分泌物和根系形态特征对水分限制的响应可能存在差异, 其中根系形态已成为植物抗旱性的关键影响因素(罗丹丹等, 2021)。比如浅根系的欧洲云杉(*Picea abies*)可能比深根系的欧洲水青冈(*Fagus sylvatica*)更易受到水分限制(Brunn et al., 2022), 因为浅根系树种的抗栓塞性较强, 而深根系树种会向深层土壤吸收水分, 进而缓解因干旱导致的植物水势降低(Johnson et al., 2018)。与此同时, 随着干旱的加剧, 植物通过减少根系生物量和改变根系资源获取策略, 进而降低植物根系氮吸收的能力(图1) (de Vries et al., 2016)。因此根系分泌速率通常与比根长、比表面积呈显著正相关关系(de Vries et al., 2019; Staszel et al., 2022; Jiang et al., 2023)。但是, 也有研究认为较低的比根长、较高的细根组织密度可以促使土壤无机氮的浓度升高(de Vries et al., 2016)。综上所述, 根系分泌物对干旱胁迫的响应受到植物-土壤交互作用过程中诸多生物和非生物因素的复杂调控, 目前认知上仍极度缺乏, 是未来亟需深入研究的课题。

2 干旱下根系分泌物介导的根际激发效应

2.1 干旱下根系分泌物在土壤有机碳分解中的重要作用

土壤碳库主要来源包括根系输入、凋落物分解和微生物固碳等(Callesen et al., 2003)。当土壤中碳输入的数量和质量发生改变时, 会影响SOM分解速率的现象被称为“激发效应” (Kuzyakov et al., 2000), 其中根际活动是SOM分解和养分释放的重要过程。一般来说, 植物从土壤中获得的绝大多数养分源于根际(Yin et al., 2014; Finzi et al., 2015), 同时, 根际活动所释放的根系分泌物能够提高根际微生物的底

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物可利用性, 有效调控微生物群落结构及其多样性, 进而刺激或抑制SOM的分解过程(Kuzyakov, 2010)。根系输入和相关的根际微生物活动所引起土壤有机碳强烈分解的现象则被称为“根际激发效应”(Cheng et al., 2014)。研究表明由RPE引起SOM分解速率最大可提高380%, 最低可降低50% (Huo et al., 2017)。RPE的大小和方向受到根系分泌物数量和组分、微生物活性、土壤养分和土壤水分等因素调控(Murphy et al., 2017; 尹华军等, 2018)。尽管关于干旱下根系分泌物及其介导的RPE研究不少(Gargallo-Garriga et al., 2018; Karlowsky et al., 2018; de Vries et al., 2019), 根系分泌物的数量和组分及其根际微生物群落已被证实受到干旱强烈影响, 但是目前关于土壤水分调控根系分泌物输入及其介导的RPE的相关研究尚未形成一致的结论, 根系分泌物的具体化学特征及其与根际微生物群落的相互作用尚不明晰。有研究认为, 随着土壤水分含量降低, RPE也随之减弱(Wang et al., 2021b), 土壤有机碳含量在干旱早期、中期和晚期均呈现下降趋势, 其中干旱晚期土壤氧化酶活性的提高可能与土壤碳的大量流失有关(Yan et al., 2021)。也有研究指出, 土壤水分含量降低反而会增强RPE, 为了适应干旱条件, 植物产生了较高的根系活性, 导致了净氮矿化的发生和RPE的增强(图1) (Lu et al., 2018a)。从根系分泌物数量来看, 干旱条件下植物分配给根系分泌物的碳量相对较多, 意味着植物可将更大比例的碳投入根系分泌物中(Karst et al., 2017)。从根系分泌物组分来看, 相比于葡萄糖和乙酸, 干旱下根系分泌物中的草酸增多, 会诱发更强的RPE, 一定程度上促进碳的损失(Henry et al., 2007; Keiluweit et al., 2015)。综上可知, 根系分泌物在调控土壤碳库动态中扮演着一个不可或缺的角色, 虽然干旱引起的根系分泌物变化引发强烈的RPE, 影响土壤碳循环过程, 但是其强度和方向仍然具有极大的不确定性(de Vries et al., 2019)。

2.2 干旱下根系分泌物介导的激发效应机理

在土壤系统中, 土壤微生物在消耗根系分泌物的同时调控根系分泌物输入模式, 维持土壤碳库的动态平衡(Oburger & Jones, 2018; Canarini et al., 2019)。当干旱发生时, 根系分泌物与微生物群落之间的关系是否会发生变化, 根系分泌物又如何介导RPE的发生仍是当前研究中的一个重点。干旱条件下, 根际微生物群落特征取决于土壤中细菌群落对水分限制的响应, 而大量的研究已经证实干旱胁迫对根系分泌物组分及根际微生物群落的显著影响, 其中, 土壤微生物代谢周转普遍受到干旱的抑制(Karlowsky et al., 2018; 朴世龙等, 2019; Chen et al., 2022), 而干旱引起的根系分泌物变化又将间接影响根际微生物的多样性和活性(Naylor & Coleman-Derr, 2018)。然而, 根系分泌物影响微生物群落的机制却一直是未解之题。有研究认为, 干旱条件下植物可以选择特定的微生物群落(Monohon et al., 2021), 而这些特定的微生物群落组成又将反作用于根系分泌物的组成。根系分泌物通过影响微生物在土壤系统中的流动性和化学趋向性, 调控微生物对植物根系的附着能力, 进而改善干旱胁迫对植物的消极影响(Cesari et al., 2019)。这一研究观点与传统的“微生物共代谢”假说相符, 该假说认为土壤中存在较多潜在活跃的微生物(10%–40%) (Blagodatskaya & Kuzyakov, 2013), 而根系分泌物输入为微生物提供了大量可利用碳源, 并刺激微生物迅速增殖生长。由微生物所分泌的胞外酶将加速分解SOM, 表现为正的RPE (Zhu et al., 2014)。而最近的研究也指出, 在有菌、无菌或加糖环境中植物根系分泌物特征变化显著(McLaughlin et al., 2023), 其中氨基酸中氮的输入有助于促进微生物群落的生长(表现为微生物生物量碳增加)和激发(表现为土壤颗粒有机质的激发), 加速矿化相关的SOM的积累(Henry et al., 2007; Canarini et al., 2016; Chari & Taylor, 2022)。而有机化合物(如草酸)的释放则可以打破土壤矿物-有机物组合的物理保护作用, 促进土壤碳矿化, 加速碳的流失(Henry et al., 2007; Keiluweit et al., 2015)。因此, 干旱条件下植物根系分泌物数量和组分的变化可能会对根际微生物群落组成和活性产生强烈影响(Preece et al., 2018), 进而改变根系分泌物介导的RPE, 而将根系分泌物组成变化与土壤微生物群落组成和功能变化的机制联系起来将是一项具有挑战性的工作。

3 结论和展望

根系分泌物是联系根系与土壤系统最为重要的一种物质, 对根际微生态系统结构与功能起到至关重要的作用。因此, 关于根系分泌物的相关研究一直是国内外地下生态学研究者所关注的热点领域。

在气候变化背景下多种气候灾害可能同时发生, 给土壤碳平衡和人类可持续发展带来多重风险(Zeng et al., 2023), 其中干旱事件对植物根系分泌物及其所介导的土壤碳过程的影响不容忽视。然而, 目前关于干旱对根系分泌物影响的研究相对较少, 各项研究结果也存在较大的差异(表1)。我们对于干旱条件下根系分泌物输入介导的RPE更是缺乏系统的认识。未来亟需从以下几个方面开展深入研究:

(1)关注不同干旱强度下根系分泌物数量及组分的变化。研究发现, 在不同干旱强度下根系分泌物的响应方向可能不同。目前围绕干旱对根系分泌物影响的研究大多处于某一特定干旱强度下(表1), 关于干旱梯度下的系统研究还比较匮乏, 尤其是根系分泌物介导的RPE的作用机制有待深入探讨。未来需要开展更多的干旱梯度模拟实验研究来突破相关的瓶颈, 以便确定是否存在引起根系分泌物变化的干旱阈值, 阐明在不同干旱强度下根系分泌物的响应趋势及其对土壤碳循环过程的调控机制, 深化我们对植物抵御气候变化策略的认识。然而, 鉴于植物根系分泌物的收集技术和分析方法的限制(尹华军等, 2018), 如何完善根系分泌物收集技术和装置是至关重要的问题, 例如, 如何将人工培养(水培装置)条件下获得的根系分泌物与野外原位(自然土壤环境)收集的进行定性和定量的比较, 仍然存在许多值得探索的地方(Williams & de Vries, 2020)。此外, 也需要在选择根系分泌物收集方法时考虑如采样环境(土壤或水培)、采样位置(单个根段、整个根系或整株植物)、植物年龄(幼苗或成树)、采样时间(1–4 h)等因素(Oburger & Jones, 2018; de Vries et al., 2019; Brunn et al., 2022)。

(2)开展多种类型植物的根系分泌物强化研究。目前的研究虽然已得到了一些重要的研究成果, 但是, 现有结果表明, 由于实验研究对象的物种特异性和研究区域的气候条件差异等因素, 导致干旱下各类型植物根系分泌物对干旱胁迫的响应机制仍存在较大的差异, 尚未形成系统的认知(表1) (Canarini et al., 2016; de Vries et al., 2019; Jiang et al., 2023)。如何解释各项研究结论之间的分异将是评估根系分泌物变化的一大难点, 并且将根系分泌物数量和组分的变化与土壤碳过程的微生物调控机制联系起来是一项极具挑战性的工作。未来需要广泛开展多种类型植物的根系分泌物系统研究, 通过总结归纳不同物种、不同生长环境、不同干旱强度及干旱持续时间下根系分泌物的变化趋势及其调控机制, 将有助于阐明气候变化条件下根系分泌物及其所介导的RPE响应特征, 为农业育种、森林保护及土壤碳汇管理提供科学指导。

(3)完善气候变化多因子对根系分泌物的交互效应研究。干旱事件的发生并不是单一的, 可能伴随着温度升高、营养匮乏等多因子同时发生, 而干旱与多气候因子(如增温、氮沉降等)的交互效应仍然具有非常大的不确定性(周贵尧等, 2020)。不同的研究区域气候背景存在差异, 可能某种特定的实验处理背后还伴随着其他气候因子的影响。有研究表明, 在生长季内增温处理下根系分泌物输入速率显著增加, 增温处理导致土壤含水量显著降低, 同时形成一定的干旱胁迫(马志良, 2020), 其中增温和干旱的交互效应对根系分泌物输入速率的影响程度尚不清楚。还有研究发现, 施加氮肥后可以逆转干旱对地下碳分配的影响, 即在根系中保留了更多的碳, 在土壤中则相反, 这表明养分限制的缓解可以调控植物根系生长和根际碳分配方面的权衡(Wang et al., 2021b)。未来还需要开展多因子交互实验, 厘清多种气候因子交互影响下植物根系分泌物变化的机制, 以便更好地研究根系分泌物介导的RPE对未来气候变化的响应, 进一步预测土壤碳库动态的变化趋势。

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