

# 根际激发效应的发生机制及其生态重要性

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**摘要** 土壤激发效应是指由各种有机物质添加等处理所引起的土壤有机质周转强烈的短期改变。根际是激发效应最主要也是最重要的发生部位。根际激发效应能够反映生态系统土壤碳氮周转的速度, 并影响植物、土壤微生物等对养分的获取和竞争, 维持生态系统各组分间的养分平衡。虽然对根际激发效应的产生机制已取得一定程度的认知, 但是对根际激发效应在土壤碳氮转化过程中的作用机理及其生态重要性依然缺乏足够的理解。该文在论述激发效应的研究历史和主要发生部位的基础上对最新研究进展进行了综合分析, 提出了一个具体的根际激发效应的发生机制, 深入剖析了影响根际激发效应的生物与非生物因素, 并阐释了根际激发效应的生态重要性, 对未来根际激发效应的研究方向进行了展望。

**关键词** 胞外酶, 根际沉积物, 根际激发效应, 土壤微生物

## Mechanisms of rhizosphere priming effects and their ecological significance

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### Abstract

Priming effects are defined as “strong short-term changes in the turnover of soil organic matter caused by moderate treatments of the soil”. Rhizosphere is the most important place, where the priming effects take place. Rhizosphere priming effects reflect the turnover rate of soil carbon and nitrogen, and affect the acquisition of nutrients by plants and microorganisms, as well as their competition for nutrients, thus maintaining nutrient balance among the various components of an ecosystem. Although there has been a general understanding on the occurrence of rhizosphere priming effects, the mechanisms underlying their role in soil carbon and nitrogen transformations and their ecological significance are still not fully comprehended. This paper provides a synthesis of the latest advancement in studies of the rhizosphere priming effects. On the basis of reviews of research history and identification of the hotspots, we first put forward a mechanism underlying the occurrence of rhizosphere priming effects, and then examined the biotic and abiotic factors influencing the rhizosphere priming effects. The ecological significance and outlooks of research in the rhizosphere priming effects were discussed and clarified.

**Key words** exoenzyme, rhizodeposition, rhizosphere priming effect, soil microorganisms

土壤是陆地生态系统最大的有机碳库, 库的大小主要受到有机物质输入和土壤有机质分解过程的共同调节(Lal, 2004)。传统的观点一直认为, 土壤有机质分解过程主要依赖于碳库的大小、温度和湿度等非生物因子(Kuzyakov *et al.*, 2000)。近年来, 随着对土壤激发效应(priming effect)的深入研究, 发现激发效应是土壤中一个普遍存在的自然现象, 主要是由根系分泌物输入和凋落物分解等过程相互作用引起的(Kuzyakov, 2010)。尽管土壤有机质的稳定性

很强(Lützow *et al.*, 2006), 但土壤激发效应可以加速它的分解。在全球尺度上, 植物-土壤间相互作用的根际过程控制着陆地生态系统CO<sub>2</sub>总释放量的50% (Schimel, 1995; Cheng *et al.*, 2013; Hopkins *et al.*, 2013), 并影响生态系统多个养分循环过程(Chapin *et al.*, 2012)。

一些模型模拟研究认为, 在全球气候变化背景下, 随着大气CO<sub>2</sub>浓度和温度升高, 将会有更多的碳储存在植物生物量和土壤有机碳库中(Joos *et al.*,

2001; Gerber *et al.*, 2004), 同时也会增加根系分泌物和凋落物的输入(Paterson *et al.*, 1997; Macdonald *et al.*, 2011; Phillips *et al.*, 2011), 加速土壤有机质分解, 从而对大气CO<sub>2</sub>浓度产生正反馈(Kuzyakov, 2010; Sayer *et al.*, 2011; Bengtson *et al.*, 2012)。这表明激发效应可以通过改变土壤有机碳库的大小而影响全球变化的进程, 因此阐明激发效应的发生机制将有助于深入理解生态系统地下过程对未来气候变化的响应与适应机理, 并将有助于改进陆地生态系统的过程模型, 准确地评估全球变化对陆地生态系统的深远影响。

因为根际是土壤激发效应发生的最主要部位, 所以本文就根际激发效应的研究历史、主要发生部位、发生机制和影响因素进行了详细的阐述, 在此基础上提出了根际激发效应的生态重要性, 并对未来根际激发效应研究进行了展望, 以期更好地从理论上探寻土壤碳、氮循环的内在机制, 推动对陆地生态系统地下过程的深入认识。

## 1 土壤激发效应的研究历史

激发效应最早发现于1926年(Löhnis, 1926), 随后采用了 Bingeman 等(1953)所建议的术语——priming effect, 之后被Kuzyakov等(2000)定义为“由各种有机物质添加等各种处理所引起的土壤有机质周转强烈的短期改变”。

尽管20世纪40年代同位素技术的发展和完善为激发效应的研究提供了重要的方法基础, 但是直到20世纪80年代和90年代, 激发效应才引起学者们的进一步关注, Jenkinson等(1985)和Kuzyakov等(2000)的两篇综述分别论述了激发效应在土壤氮转化和有机碳转化方面的研究进展, 提出了新的研究方向, 推动了激发效应在土壤碳、氮转化方面的研究。近年来, 多篇综述进一步综合分析了激发效应的机制(Blagodatskaya & Kuzyakov, 2008; Kuzyakov, 2010; Cheng *et al.*, 2013; Dijkstra *et al.*, 2013), 使激发效应研究成为当前土壤生态学研究的一个重要组成部分和生长点(Kuzyakov, 2010)。

有关土壤激发效应的研究有很多, 但大部分集中在欧美国家。相比之下, 国内这方面研究起步较晚, 初期的研究多为介绍性和综述性的工作(朱祖祥, 1963; 陈春梅等, 2006; 黄文昭等, 2007), 以及我国学者在国外做的部分工作(尚卫辉等, 2008)。在

这些研究的带动下, 近年来国内有关激发效应的研究日趋增多, 开始探究激发效应的发生机制及其影响因素(李紫燕等, 2008; Zhang & Wang, 2012; Qiao *et al.*, 2013; 王若梦等, 2013; Zhang *et al.*, 2013)。

尽管当前对激发效应的研究已取得一定的进展, 但是对激发效应在土壤碳氮转化过程中的作用机理及其生态重要性依然缺乏足够的了解(Billings *et al.*, 2010; Kuzyakov, 2010; Blagodatskaya & Kuzyakov, 2013)。因此, 在当前和未来一段时间内, 深入研究激发效应的产生与维持机制及其生态学意义, 仍是土壤生态学研究领域的核心内容之一(Kuzyakov, 2010; Cheng *et al.*, 2013)。

## 2 土壤激发效应的发生部位

土壤有机质的转化过程在土壤微生物活性热区(hotspots)较为强烈, 这些活性热区通常也是激发效应的重要发生部位(Kuzyakov, 2010)。土壤中微生物活性热区主要有根际(rhizosphere)、碎屑周际(detritusphere)、动物通道(drillosphere)和其他的生物间隙(biopores)(Kuzyakov, 2010; Nannipieri *et al.*, 2003)(图1)。

碎屑周际(图1)主要由大分子量和结构复杂的物质(凋落物或碎屑)组成, 通过真菌分解释放小分子有机物质, 以不连续有机质输入方式进入土壤(Blagodatskaya & Kuzyakov, 2008; 马承恩等, 2012)。动物通道(图1)是土壤动物活动强烈的区域, 通过动

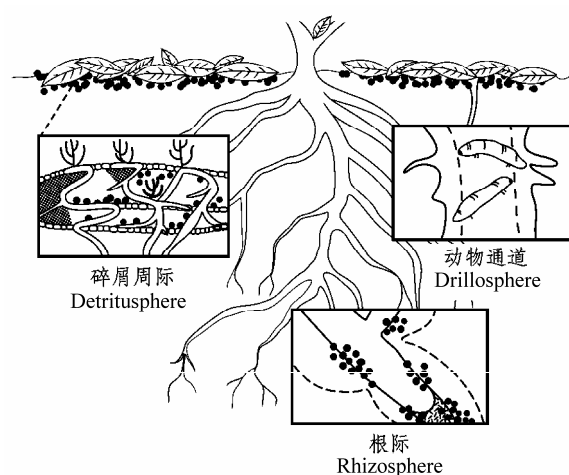


图1 土壤激发效应的主要发生部位: 碎屑周际、根际和动物通道(参照Beare *et al.*, 1995和Kladivko, 2001)。

Fig. 1 The hotspots of priming effects: detritusphere, rhizosphere and drillosphere (after Beare *et al.*, 1995 and Kladivko, 2001).

物代谢活动和食物链等影响地下过程(Alphei *et al.*, 1996; Bityutskii *et al.*, 2012)。目前有关碎屑周际和动物通道的激发效应的研究很少, 尚未有一般性的结论(Kuzyakov, 2010)。

根际(图1)是土壤中根系周边的狭小区域, 距离根系表面1–3 mm (Jones *et al.*, 2004; Kuzyakov & Xu, 2013), 受植物根系与微生物活动的强烈影响(Herman *et al.*, 2006)。植物通过根系分泌物和根系凋落物等向根际输入易于土壤微生物利用的含碳有机物(根际沉积物), 包括碳水化合物、有机酸、激素、维生素、死亡细胞和植物根系分泌的少量其他物质(Dijkstra & Cheng, 2007a), 改变了根际的营养环境(Toberman *et al.*, 2011), 提供了大量可利用的碳和能量, 促进了微生物数量及其活性, 因此根际区域土壤微生物数量通常是非根际区域的19–32倍以上(Bodelier *et al.*, 1997), 根际区域土壤微生物活性是非根际区域的10倍以上(Kuzyakov, 2010)。根际激发效应可增加3–5倍或减少10%–50%的土壤有机质的分解速率(Kuzyakov, 2002), 根际是土壤激发效应最重要的发生部位(Kuzyakov, 2010; Cheng *et al.*, 2013), 因此本文主要阐述根际激发效应的发生机制及其生态重要性。

### 3 根际激发效应的方向与强度

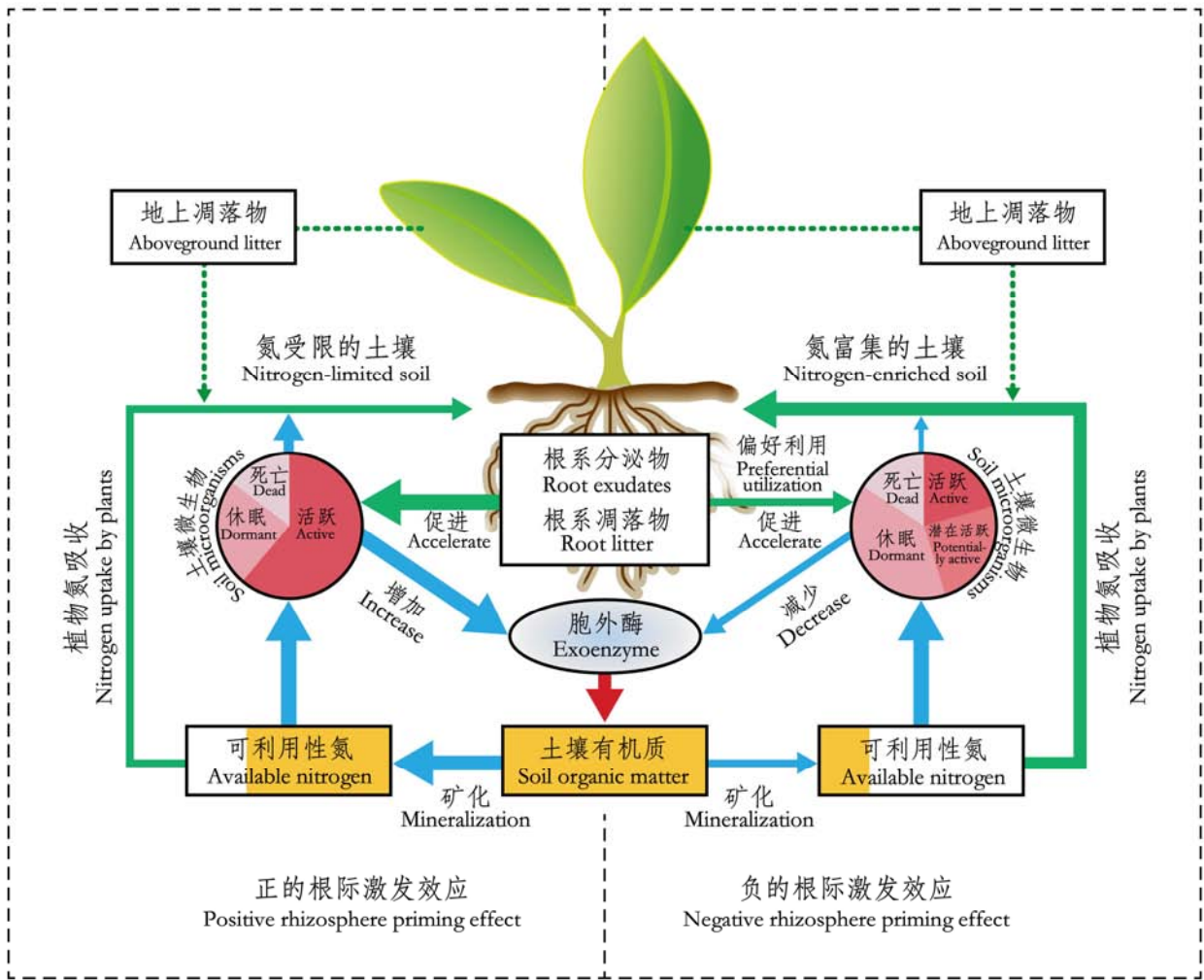
由于根系分泌物、凋落物、死亡微生物等物质输入根际, 加速或抑制了根际土壤有机质分解, 而表现为正或负的根际激发效应, 此效应的强度依赖于植物物种(Fu & Cheng, 2002; Cheng *et al.*, 2003; Bengtson *et al.*, 2012)、根系构型(Kuzyakov, 2002)、菌根(Cheng *et al.*, 2012)、光合作用(Kuzyakov & Cheng, 2001, 2004)、植物物候(Cheng *et al.*, 2003; Cheng & Kuzyakov, 2005)、土壤类型(Dijkstra & Cheng, 2007b)、土壤可利用底物的数量和质量(Blagodatskaya & Kuzyakov, 2008; Bengtson *et al.*, 2012; Guenet *et al.*, 2012; Dijkstra *et al.*, 2013; Drake *et al.*, 2013)、土壤水分(Dijkstra & Cheng, 2007a)等。研究表明, 正的根际激发效应可促进有机质矿化增加3.8倍, 而负的根际激发效能减少50%的有机质矿化(Cheng *et al.*, 2013)。

### 4 根际激发效应的发生机制

根际激发效应的产生是植物根系和微生物以

及土壤有机质之间相互作用的结果, 是由根系分泌物驱动, 通过改变微生物量及其活性来实现的, 同时受其他生物与非生物因子的调控(Kemmitt *et al.*, 2008; Kuzyakov, 2010)。虽然土壤中微生物种类繁多, 但通常仅有0.1%–2.0%的微生物处于活跃状态, 10%–40%由于能量缺乏而处于潜在活跃的状态(Blagodatskaya & Kuzyakov, 2013)。植物根系向根际区域输入易于被微生物利用的有机物质, 为“饥饿”的微生物提供碳和能量, 可在很短的时间内激活处于潜在活跃状态的微生物(de Nobili *et al.*, 2001), 改变微生物的群落结构和大小, 显著增加土壤微生物数量和活性(Fontaine *et al.*, 2003)。当土壤养分缺乏时, 微生物可“投资”1%–5%的同化产物用于产生胞外酶, 通过解聚合作用分解部分难以利用的有机质, 获取其所需养分(Burns *et al.*, 2013), 因此根际的养分状况会影响微生物对其生长和胞外酶产生之间的能量分配(Fontaine *et al.*, 2011)。此外, 微生物也可以直接分泌一些有机酸或酶, 通过化学反应改变根际养分状况(Kuzyakov *et al.*, 2002)。虽然微生物的活性及土壤养分可利用性被认为是激发效应发生的重要因素(Kuzyakov, 2010; Dijkstra *et al.*, 2013, Sullivan & Hart, 2013), 但是目前对根际激发效应的发生机制还未形成一致的结论(Kuzyakov, 2010; Sullivan & Hart, 2013)。根据近期的研究, 我们通过综合分析提出了一个具体的根际激发效应发生机制(图2)。

根际激发效应的发生取决于土壤养分的可利用性, 主要与土壤氮的有效性有关(Dijkstra *et al.*, 2013; Sullivan & Hart, 2013)。根际沉积物作为根际微生物的主要能量来源, 主要是含碳化合物(Merbach *et al.*, 1999; Hütsch *et al.*, 2002), 通常其C:N高于根际微生物的C:N (Cleveland & Liptzin, 2007)。由于根系和微生物对根际可利用氮的获取, 根际通常成为碳过剩而氮受限强烈的区域(Kuzyakov *et al.*, 2002)。在氮受限的环境中, 植物会将较多的光合产物投资到地下(Dijkstra *et al.*, 2008; Phillips *et al.*, 2009, 2011), 通过增加根系分泌物输入促进微生物的生长和活性, 微生物周转加快, 导致根际有效氮被快速消耗。低的有效性氮促使微生物增加胞外酶的分泌(Fontaine *et al.*, 2003; Bengtson *et al.*, 2012; Burns *et al.*, 2013), 加速土壤有机质的分解, 释放无机氮, 从中获取所需的氮和其他养分,



**图2** 根际激发效应的发生机制: 当土壤氮受限时, 植物将较多的光合产物投资到地下, 根际微生物利用根际沉积物获取碳和能量, 增加微生物数量和活性, 促进微生物胞外酶的分泌, 分解有机质释放可利用氮, 产生正的根际激发效应(图左); 当土壤氮富集时, 减少了微生物对养分的需求, 根际微生物偏好利用根系分泌物, 减少胞外酶的分泌, 而植物也减少向地下的碳分配, 导致根际微生物数量减少和活性降低, 抑制了有机质分解, 产生负的根际激发效应(图右)。绿箭头、蓝箭头和红箭头分别代表由植物、土壤微生物和胞外酶主导的生态过程; 箭头的粗细表征通量的大小或过程的强弱。可利用性氮库中的黄色代表来自土壤有机质矿化作用产生的可利用性氮, 其色块面积大小代表来自有机质矿化作用的数量。

**Fig. 2** Mechanism of rhizosphere priming effects. At low nutrient levels (left), plants allocate more photosynthates to belowground and supply soil microorganisms with carbon and energy. As a result, microbial biomass and activities increase and enhance production of extracellular enzymes by the rhizosphere microorganisms to decompose soil organic matter and release nutrients. Therefore, a positive priming effect takes place. In contrast, at high nutrient levels (right), microorganisms have less demand for nutrients and thus preferentially utilize root exudates, leading to reduced production of extracellular enzymes. Moreover, as plants invest less photosynthates in belowground, microbial biomass and activities will decrease. As a result, the decomposition of soil organic matter slows down and a negative priming effect occurs. The green, blue, and red arrow-lines represent the ecological processes mediated by plants, soil microorganisms, and exoenzymes, respectively. The thickness of an arrow-line indicates its relative magnitude of a flux or intensity of a process. Yellow colour of the available nitrogen pool indicates mineral nitrogen derived from mineralization of soil organic matter. The area of the yellow colour represents the amount of mineral nitrogen derived from mineralization of soil organic matter.

从而导致正的根际激发效应的发生(图2), 以上微生物利用碳和能源获取难分解有机质中的氮的过程, 也被称为“nitrogen mining”机制(Craine *et al.*, 2007; Fontaine *et al.*, 2011), 在自然生态系统普遍存在。

虽然根际持续性的碳输入能促进微生物的活性, 但是在氮富集的条件下, 往往可观察到负的根际激发效应。这主要是由于在较高的氮有效性条件下, 根际微生物不需要通过分解难以利用的土壤有

机质获取氮, 而是偏好利用易于分解的根系分泌物 (Kuzyakov *et al.*, 2000; Kuzyakov & Cheng, 2004), 减少了用于分解有机质的胞外酶分泌。同时, 较高的氮有效性还会减少植物向地下的碳分配 (Phillips *et al.*, 2009, 2011), 减小根际微生物数量和活性。根际微生物量的降低、胞外酶分泌的减少, 以及微生物对根系分泌物的偏好利用均抑制了土壤有机质的矿化, 从而产生负的根本激发效应 (图2) (Fu *et al.*, 2002; Blagodatskaya & Kuzyakov, 2008; Dijkstra *et al.*, 2013), 此效应见于具有施氮肥等管理措施的农田生态系统。

因为根际土壤微生物活性和养分的可利用性常处于一种动态变化之中, 因此根际激发效应的正与负也常常交替出现。

以上根际激发效应是根际区域植物根系和微生物对资源竞争利用的结果。植物和土壤微生物几乎具有相同的养分需求, 在根际有限的资源环境中, 两者对氮的竞争尤为强烈 (Kuzyakov & Xu, 2013), 常常会引起正的根际激发效应 (图2)。但当植物和微生物同时受氮的强烈限制时, 也可能引起负的根际激发效应 (Dijkstra *et al.*, 2013)。除了根系与微生物之间的竞争, 根际微生物之间也存在着强烈的竞争, 这种竞争也会引起不同的根际激发效应。当分泌物抵达根际时, 采用r生存策略的微生物 (主要为细菌) 首先利用根际沉积物和有效氮进行快速地生长和周转 (Paterson *et al.*, 2007; Moore-Kucera & Dick, 2008), 此时产生负的根际激发效应 (Fontaine *et al.*, 2003, 2011; Shahzad *et al.*, 2012; Pascault *et al.*, 2013)。随着根际资源的快速消耗, r生存策略的微生物活性降低, 而k生存策略的微生物数量增加、活性增强。因为k生存策略的微生物主要是真菌, 它们是影响土壤有机质分解的最主要类群 (Talbot *et al.*, 2008; Fontaine *et al.*, 2011), 不仅可以通过菌丝从低有效性的底物中获取养分 (Otten *et al.*, 2001), 而且还可以分泌胞外酶分解难以被r生存策略的微生物利用的有机质 (Blagodatskaya *et al.*, 2007), 促进了土壤有机质分解, 而产生正的激发效应。

## 5 根际激发效应的影响因素

影响根际激发效应的因素有很多, 主要包括土壤微生物、植物、土壤动物等生物因素和土壤结构、养分状况、温度、水、CO<sub>2</sub>、氮沉降等非生物因素

(Kuzyakov, 2002, 2010; Blagodatskaya & Kuzyakov, 2008; Cheng *et al.*, 2013)。

### 5.1 影响根际激发效应的生物因素

因为土壤微生物是根际激发效应发生的“主角”, 所以大量研究在探寻微生物在根际激发效应中所起的作用。初始的研究集中在土壤微生物生物量在激发效应产生中的作用 (Kuzyakov *et al.*, 2000), 但由于总的微生物生物量中包含了许多处于休眠状态的微生物 (Blagodatskaya & Kuzyakov, 2013), 因此有些研究开始探讨不同土壤微生物类群在土壤有机质分解中的作用, 研究发现: 随着碳利用性的增加, 与土壤有机质分解有关的真菌、革兰氏阳性细菌、革兰氏阴性细菌活性都会增强 (Nottingham *et al.*, 2009; Bird *et al.*, 2011; Fontaine *et al.*, 2011; Garcia-Pausas & Paterson, 2011; Dijkstra *et al.*, 2013)。限于目前的研究手段, 当前大多数研究仅限于细菌、真菌和放线菌在土壤有机质分解中的作用, 初步明确了r生存策略的微生物和k生存策略的微生物在激发效应产生中的作用 (Fontaine *et al.*, 2003; Pascault *et al.*, 2013)。微生物的活性, 尤其是胞外酶的活性对根际激发效应的影响逐渐受到较多的关注, 但是尚缺乏普遍性的研究结论 (Marxsen & Witzel, 1991; Fontaine & Barot, 2005; Blagodatskaya & Kuzyakov, 2008; Burns *et al.*, 2013)。考虑到根际激发效应的产生主要是活性微生物作用的结果, 未来这方面的研究迫切需要发展量化处于活性状态各类微生物种群的新技术 (Blagodatskaya & Kuzyakov, 2013), 阐明它们在根际激发效应产生中的作用。

土壤微生物的活性受到可利用底物的制约, 在根际主要取决于根系分泌物的数量和质量 (Dijkstra *et al.*, 2013)。植物根系分泌物一般占光合产物的10% (Chapin *et al.*, 2012), 与植物营养状况密切相关 (Zhang *et al.*, 2004), 因此光合作用强度、植物生长状况、植物种类和物候期等都会改变根系分泌物的数量和质量, 从而改变根际激发效应的方向和强度 (Kuzyakov & Cheng, 2001, 2004; Kuzyakov, 2002; Gärdenäs *et al.*, 2011)。在普通光照强度下可产生正的根际激发效应, 当光照停止后根际激发效应逐渐减少为0, 而在光照恢复4天后却观察到负的激发效应 (Kuzyakov & Cheng, 2001)。不同种类植物的生长状况不同, 其光合作用的效率存在差异, 可进一步影响根际激发效应的大小和方向。

植物地上、地下部分的生长情况,尤其是根系的生长情况,也是影响根系分泌物数量和质量的重要因素,通常在根毛到根冠之间的区域根系分泌物数量最多、质量最好(Kuzyakov, 2002)。由于根尖的移动,沿根系存在不同类型的根际沉积区域,相应的微生物种群及其活性存在空间上的差异,根际激发效应的强度和方向也会随之变化。通常新生的根产生的根系分泌物比成熟的根多,从而引起较强的激发效应。此外,根系的密度也影响根际激发效应的强度和方向(Kuzyakov, 2010)。在土壤有效氮不足时,根系可以通过改变根的构型和增加细根的周转、根系分泌物等促进激发效应的发生(Hodge *et al.*, 1996; Paterson & Sim, 1999; Kuzyakov, 2002)。因为根系的生物量与根际激发强度成正比(Fu & Cheng, 2002),所以植物发达的根系有可能产生较强的根际激发效应。此外,根系与微生物的共生,如豆科植物与根瘤固氮菌或菌根等可能对激发效应产生影响,例如,研究发现在成熟期具根瘤的大豆根系比不具根瘤的根系能产生更强的根际激发效应(Zhu & Cheng, 2012);丛枝状菌根真菌能够促进土壤有机质的分解(Hodge & Fitter, 2010; Cheng *et al.*, 2013)。

双子叶植物的根际激发效应比单子叶植物强烈(Cheng & Kuzyakov, 2005)。C<sub>3</sub>植物和C<sub>4</sub>植物因为生理上的差异引起根系分泌物的组成和质量不同,也会导致根际激发效应的差异(Fu *et al.*, 2002)。与禾本科的春小麦(*Triticum aestivum*)相比,豆科植物大豆(*Glycine max*)引发了较高的激发效应(Cheng, 2009)。近来的研究还发现,作物混种的不同搭配也会产生不同的根际激发效应(Pausch *et al.*, 2013)。然而,以上都是初步的结果,还需要进行大量的研究来明确植物类型对根际激发效应的影响,比如低等植物——蕨类、苔藓,和高等植物不同类群——裸子植物、被子植物等根际激发效应间的差异,相同科属的物种之间根际激发效应的差异也需要进一步调查。

植物在不同的物候期,根系分泌物的数量和组成存在差异,也会影响根际激发效应的强度和方向。春季植物生长旺盛,对氮的需求量较大,此时植物分配较多的光合产物到根际,产生正的根际激发效应;在夏季或秋季至植物成熟期后,植物对氮需求减少,根系生长和根系分泌物量也逐渐下降,从而导致较低的或负的根际激发效应。对于一年生植

物,在生长初期,根际激发效应不明显或为负的根际激发效应;而在生长盛期则产生明显的正的根际激发效应(Kuzyakov *et al.*, 2001; Warembourg & Esterlich, 2001);在开花期根际激发效应可达到最大值(Cheng & Kuzyakov, 2005; Cheng *et al.*, 2013; Pausch *et al.*, 2013)。根际沉积物的季节性变化对一年生植物的影响比对多年生植物的影响明显(Gärdenäs *et al.*, 2011)。

原生动物的线虫、节肢动物等土壤动物是地下食物链的重要组分,它们可以通过释放分泌物(Lavelle *et al.*, 1995; Bitvutskii *et al.*, 2012)、捕食根际微生物和啃食植物根系,影响微生物与植物对养分的竞争,改变微生物的群落结构和周转(Alphei *et al.*, 1996; Dijkstra *et al.*, 2013),从而影响根际激发效应的方向和强度。

## 5.2 影响根际激发效应的非生物因素

土壤结构、养分、水分、pH、温度以及大气CO<sub>2</sub>浓度和氮沉降等非生物因素通过影响微生物活性及根系分泌等过程,直接或间接地影响根际激发效应的方向和强度(Blagodatskaya & Kuzyakov, 2008; Cheng, 2009; Kuzyakov, 2010; Zhu & Cheng, 2011; Cheng *et al.*, 2013; Dijkstra *et al.*, 2013)。

土壤的结构和质地(Blagodatskaya & Kuzyakov, 2008; Cheng *et al.*, 2013; Zhang *et al.*, 2013)、矿质性质(Rasmussen *et al.*, 2007)等均可对根际激发效应产生影响。因为土壤有机质的累积和矿化常依赖于土壤团粒结构大小,大团粒结构(macroaggregates)中的碳通常比小团粒结构(microaggregates)中的碳易于分解(Six & Jastrow, 2002),意味着不同团粒结构对有机质具有不同的保护作用而产生不同的激发效应(Blagodatskaya & Kuzyakov, 2008)。例如,在中等大小团粒(1–2 mm)中观察到正的激发效应,而在0.25–1 mm的团粒中观察到负的激发效应(Degens & Sparling, 1996)。这可能是由于不同微生物类群的需求定位不同,通常真菌偏向于利用大团粒结构内的资源,而细菌优先利用小团粒结构的资源(Guggenberger *et al.*, 1999)。

土壤的养分含量决定根际激发效应的方向和强度(Kuzyakov *et al.*, 2000),其中氮和磷是影响植物和微生物生长的最重要的两个大量元素。土壤中可利用性氮含量直接影响微生物活性及根系与微生物对养分的竞争。虽然有研究认为土壤中较高的氮

有效性可以引起较强的根际激发效应(Azam *et al.*, 1993; Nyborg *et al.*, 1995; Soon, 1998), 但更多的研究认为土壤的低氮有效性更能促进正的根际激发效应发生(Fontaine *et al.*, 2003, 2011; Zhang & Wang, 2012; Dijkstra *et al.*, 2013), 而高的氮输入会抑制激发效应的发生(Nottingham *et al.*, 2012)。尽管研究表明根际激发效应可能与磷的有效性有关(Nottingham *et al.*, 2012), 但更多研究认为微生物可以直接固持土壤中的无机磷或通过分泌胞外酶水解有机磷中的磷离子基团, 很少促进有机质的分解(Dakora & Phillips, 2002; George *et al.*, 2011; Dijkstra *et al.*, 2013)。因此, 根际激发效应主要与氮的有效性相关, 而与磷的有效性的关系不显著(Dijkstra *et al.*, 2013; Sullivan & Hart, 2013)。

土壤水分可以直接改变微生物活性和植物的生长状况, 影响根际的激发效应, 通常较高的土壤含水量能产生更强烈的根际激发效应(Dijkstra & Cheng, 2007a)。植物的蒸腾作用能使根际发生干湿交替, 短时间和高频率的干湿交替可以促进土壤有机质矿化(Fierer & Schimel, 2003; Dijkstra & Cheng, 2007a; Cheng, 2009)。Cheng (2009)指出大豆的根际激发效应比小麦强烈, 可能是由于大豆比小麦具有持续、更高的蒸腾速率。土壤水分还能通过影响土壤微生物和植物对氮素的竞争(Lodge *et al.*, 1994)、根系分泌物的含量(Gorissen *et al.*, 2004)、酶活性(Bell & Henry, 2011; Geisseler *et al.*, 2011; Burns *et al.*, 2013)等对根际激发效应产生影响。

根际激发效应的大小也受土壤pH的影响(Rukshana *et al.*, 2012, 2013)。一般土壤pH为5–8之间时微生物和胞外酶有较高的活性(Blagodatskaya & Anderson, 1998), 此时可产生较强的根际激发效应(Blagodatskaya & Kuzyakov, 2008)。土壤pH还能通过影响植物根系的生长和伸长(Edwards & Scott, 1974)、菌根的共生(Read & Perez-Moreno, 2003)、根际微生物的组成(Blagodatskaya & Kuzyakov, 2008; Rukshana *et al.*, 2012)而影响根际激发效应的方向和强度。

尽管很多研究证实温度能够加速土壤有机质的分解(Trumbore *et al.*, 1996; Holland *et al.*, 2000), 但是有关温度对根际激发效应影响的研究并不多见。已有的研究表明, 根际激发效应能够增加土壤有机质分解对温度的敏感性(Zhu & Cheng,

2011; Thiessen *et al.*, 2013), 但也有研究发现温度升高降低了根际激发效应(Kuzyakov *et al.*, 2007)。为了深入理解全球变化对陆地生态系统所带来的深远影响, 亟待深入研究根际激发效应对温度的敏感性及其机制。

许多研究表明, CO<sub>2</sub>浓度升高能促进植物的光合作用和净初级生产力(Amthor, 1995), 增加植物对地下的碳分配(de Graaff *et al.*, 2006; Phillips *et al.*, 2011), 并对根际分泌物的组成、数量和质量产生影响(Kuzyakov, 2002), 从而促进了根际激发效应(Phillips *et al.*, 2012; Dijkstra *et al.*, 2013)。同时, CO<sub>2</sub>浓度升高增加了植物和微生物对氮的获取(Drake *et al.*, 2013), 降低了根际氮素的可利用性(Gill *et al.*, 2002; Reich *et al.*, 2006), 改变了植物根系和微生物对氮的竞争, 从而可间接影响根际激发效应的发生(Phillips *et al.*, 2011, 2012)。

大气氮沉降可以增加土壤氮的可利用性。在土壤氮富集的条件下, 氮沉降会降低植物对地下的碳分配(Liljeroth *et al.*, 1994; Phillips *et al.*, 2009), 改变微生物群落(Treseder, 2008; Liu & Greaver, 2010), 抑制微生物活性(Liu *et al.*, 2010), 进而降低根际激发效应(Kuzyakov, 2002)。在氮受限的土壤中, 氮沉降反而能改善微生物和植物的养分状况, 促进有机质的分解, 可能增加根际激发效应。因此, 氮沉降对根际激发效应的影响与土壤养分状况有关。

## 6 根际激发效应的生态学意义

根际激发效应是土壤中普遍存在的一个自然过程, 是植物根系和根际微生物与土壤有机质相互作用的结果, 经历了漫长的时间过程, 尤其对具有共生作用的植物与微生物的协同进化有着更重要的意义。可以认为根际激发效应是植物和土壤微生物在进化过程中形成的资源获取策略(Cheng *et al.*, 2013)。在植物和根际微生物与土壤有机质的漫长的相互作用中, 植物和土壤微生物在根际形成了既竞争又互惠的关系, 植物侧重于氮素等养分的获取, 而微生物侧重于碳和能源的获取(Kuzyakov & Xu, 2013), 两者的相互作用推动了陆地生态系统的演替和发展, 使地球生命支持系统趋于更加稳定。

在大多数陆地生态系统中, 大部分氮被固定在土壤有机质中, 植物生长受到氮素的限制(LeBauer & Treseder, 2008), 土壤有机质中可利用氮的释放

需经微生物的矿化作用,然而土壤微生物因为碳和能源的缺乏,大部分处于非活跃状态(Blagodatskaya & Kuzyakov, 2013)。在生态系统中植物和土壤微生物的共存必须解决两者各自所面对的矛盾,而在漫长的进化过程中,植物和微生物成功地解决了这个难题。在氮受限的环境中,植物通过根系向根际分泌有机物质,为根际微生物提供碳和能量,激活处于休眠和潜在活跃状态的微生物生产胞外酶,加速有机质分解,释放土壤有机质所固定的养分,为微生物和植物提供可利用性氮,缓解植物和土壤微生物对氮的竞争,最终导致正的根际激发效应。在可利用氮富集的生态系统中,微生物与植物对氮素的竞争很小,此时植物虽然减少了对地下的投资,但是根系分泌物的输入导致微生物对其偏好利用,并固持了多余的氮素,从而使养分不会因为淋溶等过程而流失(Kuzyakov & Xu, 2013),但结果却产生了负的根际激发效应。正是根际这种微生物和植物的相互作用,通过根际激发效应改变土壤碳、氮可利用性,调节了养分的可利用性,并可能长期地影响土壤有机质的累积和释放,维持根际养分的正常周转,对生态系统养分循环发挥着极为重要的作用。

因此,根际激发效应的强度和方向能够反映生态系统土壤碳、氮动态过程和系统内养分的盈亏。尽管根际激发效应可通过影响植物、微生物等对养分的获取策略和竞争关系维持生态系统碳、氮循环和生态系统各组分间的养分平衡,但是在不同的生态系统是否存在差异,以及养分平衡的阈值如何,尚需进一步研究(Kuzyakov, 2010)。

## 7 对根际激发效应的展望

综上所述,我们已经对根际激发效应的发生机制、发生部位、方向与强度,以及影响因素等有了一定程度的认知,但是大多数研究仍然侧重于有机物质输入对碳分解或氮矿化的影响,很少研究涉及对碳和氮平衡的评估(Qiao *et al.*, 2013),因而缺乏对根际激发效应生态重要性的综合评价。因此,未来有关根际激发效应的研究应当侧重于以下几个方面:

(1)加强不同生态系统根际激发效应的原位研究。尽管激发效应已经被确认为是生态系统普遍存在的一个自然现象,但是由于研究方法的限制,目前大多数根际激发效应的研究是在温室内进行的

(Kuzyakov, 2010),所获得的认识能否真实地反映生态系统原位的真实情况,还需要加强野外原位控制实验,以及长期的观测和数据积累。特别是从物种水平、群落水平和生态系统水平上深刻揭示根际激发效应相应的发生过程与机理。

(2)通过研究根际激发效应过程中的碳平衡与养分平衡,综合评价根际激发效应过程中植物和微生物各自的收益,阐明根际激发效应的生态重要性。尽管植物和微生物有相似的养分需求,但是两者还是存在一定的差异,前者更多地受养分限制,后者则主要受碳和能源的限制(Kuzyakov, 2002)。根据进化理论,根际激发效应很可能是植物和土壤微生物对土壤环境的一种适应策略。植物通过根系分泌物为根际微生物提供了碳和能源,而根际微生物通过加速土壤有机质的降解回报植物以矿质养分。因此,植物会根据自身需求和不同的养分条件,调节根系分泌物的输出,通过影响微生物活动来控制根际激发效应的发生(Liljeroth *et al.*, 1994; Kuzyakov *et al.*, 2001, 2002)。因此,我们可以通过调控根际激发效应的大小和方向,研究不同根际激发效应过程中植物和根际微生物各自的养分获取以及碳的分配与利用,从而量化根际激发效应的生态重要性。尽管大多数生态系统受氮素限制,但是磷和铁等大量元素也时常短缺。因此,在评价根际激发效应过程中植物和土壤微生物各自的收益时,需要同时关注植物和土壤微生物对碳、氮、磷等养分的获取,才能全面评价根际激发效应的生态学意义。

(3)探明根际来源的碳在土壤中的去向,综合评价根际激发效应对土壤有机碳的深远影响。尽管很多研究已经揭示根际激发效应能够促进土壤原有有机质的分解(Kuzyakov, 2010),但是引发根际激发效应的这部分碳并没有完全被微生物分解释放到大气,依然有一部分残留在土壤而弥补因激发效应引起的碳损失(Fontaine *et al.*, 2004a, 2004b; Hamer & Marschner, 2005; Ohm *et al.*, 2007; Qiao *et al.*, 2013)。因此,这部分碳在土壤中的去向至关重要,如果根际激发效应促进了土壤中的原有有机碳,而残留的根源性碳滞留在易分解碳库中,那么土壤有机碳的增加可能是一种假象,随着可利用碳库的消耗,这部分碳还是很快被释放到大气中,因而根际激发效应对土壤有机碳的影响依然较大。相反,如果这部分碳进入了难分解的碳库,那么根际激发效



应并没有因促进土壤有机碳的分解而影响土壤有机碳的截留(Qiao *et al.*, 2013)。

(4)继续深化研究根际激发效应的微生物学机制。活的有机体和死的有机物之间的相互作用在根际激发效应的产生中具有重要的作用(Kuzyakov, 2010),特别是根际微生物的活性一直被认为是根际激发效应产生的驱动者。然而,由于土壤中微生物种类繁多,而且大量微生物处于休眠状态(Morita, 1990; Stenström *et al.*, 2001; Blagodatskaya & Kuzyakov, 2013),究竟是哪些类群的微生物参与了根际激发效应?通过什么方式参与的?胞外酶在根际激发效应的产生中到底起什么样的作用?有关研究目前依然缺乏充分的实验数据。近年来,随着微生物分子技术的迅速发展,阐明根际激发效应的微生物学机制及其控制因素已经成为本领域内的核心科学问题。

(5)根际激发效应与全球变化。土壤有机质分解对温度的敏感性是预测陆地生态系统碳循环对全球变暖影响的关键环节(Craine *et al.*, 2013),但目前的研究尚未达成一致的认识(von Lützwow & Kögel-Knabner, 2009; Conant *et al.*, 2011),而根际激发效应具有改变土壤有机碳的巨大潜势而对气候变暖产生正的反馈,因此根际激发效应对温度的敏感性更值得关注(Cheng *et al.*, 2013)。特别是在全球变化背景下,大气CO<sub>2</sub>浓度增加和气温升高同时发生,而大气CO<sub>2</sub>浓度增加又能潜在地促进根际激发效应,因此阐明根际激发效应、大气CO<sub>2</sub>浓度增加和气温升高之间的相互作用是探究陆地生态系统对气候变化响应的重要前提。目前已经有研究开始探讨根际激发效应对温度的敏感性(Zhu & Cheng, 2011; Thiessen *et al.*, 2013),但仍需要大量研究去破解其内在的机制,为生态系统过程模型的精确模拟预测提供基石。

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