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植物—土壤反馈研究进展

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摘　要: 该文综述了植物—土壤反馈研究的定义、途经、方法和国内外的研究现状以及存在的问题。植物—土壤反馈是指植物改变根际土壤的生物和非生物特征,同时被改变的也能提高或降低该植物的生长,形成正的或负的反馈,从而影响植物群落组成及植物间相互作用。植物—土壤反馈研究对于理解植物群落演替、生态系统多样性与生产力形成与维持机制,认识生态系统对气候变化和生物入侵等全球生态事件的响应具有重要的理论意义。外来物种快速生长和繁殖及其可能的负反馈可能会导致本地种被竞争排除,未来气候变化可能导致物种组成发生变化及生物多样性丢失,但资源互补和植物—土壤反馈效应则可能使植物群落具有较高的生产力和多样性。因此,未来植物—土壤反馈关系应该加强以下几方面研究:(1)开展不同生态系统植物—土壤反馈关系的比较研究;(2)植物—土壤及土壤—植物等群落水平的反馈研究;(3)特别是要加强分子和基因工具在植物土壤—反馈关系中的应用,揭示植物—土壤反馈关系的分子机理。

关键词: 植物, 土壤, 反馈关系

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Advance in plant and soil feedback

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Abstract: This paper reviewed the definition, research approaches and methods of plant-soil feedback and its research progress and problems. Plant-soil feedbacks involve two-step processes: plant changes the abiotic and biotic conditions of its associated soil; these changes in soil conditions may increase or decrease the growth of conspecifics, resulting in posi-

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tive or negative plant-soil feedbacks, respectively. Plant-soil feedbacks can affect plant performance and plant-competitive interactions, ultimately affecting community composition and diversity. Role of feedback in the succession process in the plant is uncertain. Growth enhancement of exotic and less negative feedback may result in that local species are competitively excluded, future climate change may cause changes in species composition and biodiversity loss, but resource complementarity and not too strong plant-soil feedbacks effects may lead to high productivity and diversity of mixed plant community. The key issues and further tasks of plant-soil feedback study were suggested as follows: (1) Design the experiment of plant-soil feedback in different ecosystems; (2) There were strong need to study reciprocating effects of plant and soil; using the molecular or genetic mean in plant-soil feedback; (3) Study on the mechanism of plant-soil feedback as a ecological factor.

Key words: plant, soil, feedback

植物—土壤反馈研究对于理解植物群落演替、生态系统多样性与生产力形成与维持机制,认识生态系统对气候变化和生物入侵等全球生态事件的响应具有重要的理论意义。研究植物—土壤反馈关系是认识植物和土壤生态学的核心。早期文明的玛雅人、罗马人和北京人已经发现土壤的不同会影响农业的产量(Leigh, 2004)。2000 年以前的欧洲和亚洲人就发现果树移栽到同种个体或同类个体生长过的土地上就会出现生长受限的情况(Leigh, 2004)。现在研究认为植物—土壤相互作用是土壤起源的基本驱动因子(Dokuchaev, 1879;Wardle et al,2004),并能预示陆地植物的进化(Selosse & Le Tacon, 1998;Putten et al, 2013;Simberloff et al, 2013)。同时,研究者们认为植物—土壤相互作用不仅仅涉及许多生态学过程,而且也是对全球变化最敏感的生态反应之一(Bardgett et al, 2010)。

人为活动引起的全球变化影响着植物—土壤反馈,反过来这些反馈关系的变化也可能改变这些人为活动引起变化的程度和生态学过程(Wardle et al,2004; Putten et al, 2013)。正确理解植物—土壤反馈理念能帮助我们预测不同环境条件下的植物群落组成和生产力的变化,并有助于减缓人为活动导致的全球性变化的后果,提升生态系统服务的可持续性。

1 植物—土壤反馈关系的概念

在牛津字典中反馈被定义为"修改、调整或控制一个过程或者系统,通过过程的结果影响这一过程的起因"。在生态学上,植物—土壤反馈是指植物影响根际土壤的生物和非生物特征,这种影响反过来影响其自己或其它物种的行为(Ehrenfeld et al, 2005)。即植物—土壤反馈包括两个方面,首先植物改变了它周围的土壤环境(Chanway et al, 1991);其次,植物引起的土壤环境的改变反过来又能够影响其自身或其它物种的行为(Bever et al, 1997;Thrall et al, 1997)。

如果植物引起的土壤环境的改变提高了其自身的生长,这种现象称为正反馈(Ehrenfeld et al, 2005)(图 1)。正反馈可能来自于营养的获得(Chapman et al, 2006)以及根际共生体的聚集(Klironomos, 2002)等。相反,一种植物生长在其它植物生长的土壤中时比在自己生长的土壤中生长的更好,这种现象称为负反馈(Ehrenfeld et al, 2005;Kulmatiski et al, 2008)(图 1)。负反馈产生的原因可能是因为营养被固定或消耗(Berendse, 1994),或者根际捕食者或病原体聚集(Van der Putten, 2003),或者土壤碳的聚集达到某一水平等所导致的(Ehrenfeld et al, 2005)。

Klironomos(2002) 综述了 1994—2008 年 45 篇文献的 329 个实验结果,发现 28%的研究结果是正反馈,70%的结果是负反馈,正反馈提高了植物生物量的 25%,而负反馈则降低了植物生物量的 65%。这一发现表明植物—土壤反馈在生态系统结构和功能的研究中是非常重要的机制(Kulmatiski et al, 2008)。

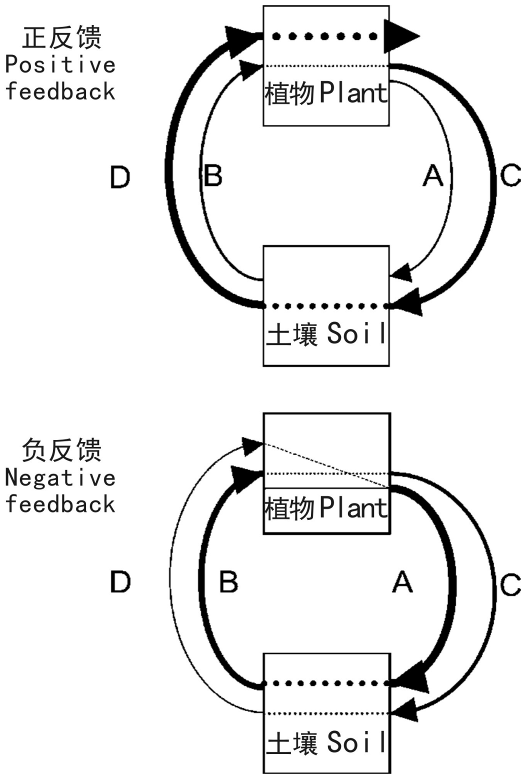

图 1　正反馈和负反馈　正反馈：**A.** 植物对土壤的积极影响；**B.** 由于植物对土壤的影响引起的土壤对植物的影响；**C.** 植物对土壤的影响进一步放大；**D.** 更加放大土壤对植物的影响。　负反馈：**A.** 植物对土壤的负面影响；**B.** 由于植物对土壤的负影响引起土壤对植物负面影响；**C.** 植物对土壤的影响进一步放大；**D.** 土壤对植物的影响会更加放大。当土壤对植物的负影响到达阈值的时候，植物土壤反馈的相互影响会回到原始的影响水平并重新开始植物土壤反馈的循环过程。

Fig. 1　Feedback in the plant-soil system　In positive feedback: **A**. An effect of plants on soil; **B**. Causes a reciprocating effect of soil on plants; **C**. Amplifies the effect of plants on soil; **D**. Further amplifies the effect of the soil on the plants. In negative feedback: **A**. An effect of plants on soil; **B**. Causes a reciprocating effect of soil on plants; **C**. Attenuates the effect of plants on the soil; **D**. Further attenuates the effect of the soil on the plants. When (D) reaches some threshold level, it allows the mutual effects to increase back to the original level (A), which then starts the cycle of decreasing effect.

2　反馈发生的途径

植物—土壤之间可通过物理、化学和生物途径进行相互作用。

2.1 物理反馈

植物和土壤之间的物理反馈途径包括通过改变土壤水分、温度和土壤结构(Gao et al, 2003; Pugnaire et al, 1996)等物理条件产生反馈途径。土壤水分控制着植物个体，种群和群落以及地下微生物群落的许多生态特征(Gao et al, 2003; Pugnaire et al, 1996)。反过来,植物通过生长、庇荫、蒸腾和水分提升等作用影响着土壤的水分变化(Ehrenfeld et al, 2005)和温度(Raich & Tufekciogul, 2000; Eviner, 2004; Sturm et al, 2005),并通过植物的根系生长和活动改变根际土壤的结构(Eviner & Chapin III, 2002; Garcia et al, 2005; Rillig, 2004)等物理特征。

2.2 化学反馈

植物通过根和根际土壤微生物活动改变土壤有机物,从而对土壤养分起聚集作用(Martens, 2000; Angers & Caron, 1998)。植物可以提高或降低土壤的 pH(Binkley & Giardina, 1998; Inkley et al, 1989)、改变土壤的氧含量(Cronk & Fennessy, 2016)、阳离子浓度(Larcher, 2003; Mengoni et al, 2004)、碳(Berendse, 1998; Su, 2004; Schlesinger et al, 1990; Schlesinger & Pilmanis, 1998)和氮(Eviner & Chapin, 1997; Eviner et al, 2006)等化学特征,反过来,这些土壤特征的改变又能决定植物的生长和分布(Inkley et al, 1989; Su, 2004)。一些研究发现在干旱半干旱生态系统,灌木或多年生丛生禾草能够引起土壤碳的聚集(Binkley & Giardina, 1998; Inkley et al, 1989)。例如,在中国的荒漠草地,当灌木取代草本后,土壤碳呈现明显的空间异质性;当沙生草本取代灌木后土壤碳的异质性随后降低(Cheng et al, 2004)。

2.3 生物反馈

土壤微生物对植物引起的改变非常敏感。大量研究表明植物能提高其根际土壤微生物的生物量(Burke et al, 2002; Kourtev et al, 2003; Ravit et al, 2003)。一般认为,植物对微生物的这种影响能改变微生物的功能,从而直接影响植物的生长(Hamilton & Frank, 2001)。例如植物物候(Innes et al, 2004; Kuzyakov, 2010; Lu & Conrad, 2005)、土壤肥力(Innes et al, 2004; Ibekwe et al, 2010; Kennedy et al, 2004; Bardgett & Wardle,

2003）、生物量（Kuske et al, 2003）、植物的净初级生产力（Eisenhauer et al, 2011；Martínez-García et al, 2011；Lin et al, 2011；Kivlin & Hawkes, 2011）、碳输入（Radford et al, 2010；Suding et al, 2008；Nemergut et al, 2008）及植物群落多样性等都会影响到土壤微生物的种类或结构。甚至有些根际微生物的遗传物质（Lugtenberg et al, 2002）也会因根的分泌物不同而发生改变 。除了土壤微生物，植物也通过土壤无脊椎动物（Strauss & Agrawal, 1999）、根际共生体或病原体、寄生生物等与土壤产生反馈关系。大量的研究表明病原体和寄生生物能够驱动演替过程中的物种替代（Fester et al, 1999）、影响幼苗在母株附近的定植（Klironomos, 2002）、促进外来物种的入侵（Klironomos, 2002）、或者改变群落的结构和竞争关系（Van der Putten et al, 2005；Knevel et al, 2004；Beckstead & Parker, 2003）。

3 反馈研究的方法

植物—土壤反馈包括特定物种对土壤的影响以及改变了物种对土壤的反应（Ehrenfeld et al, 2005；Bever, 1994）。因此植物—土壤反馈的研究可以通过将试验植物栽到某一土壤中即将该植物栽培到自己生长的的土壤中或栽培到其它植物生长的土壤中，从而开展比较研究。如果是一种植物生长在自己或其它植物生长过的土壤中开展研究叫直接或个体的植物—土壤反馈研究；而当两个物种被栽培在自己或其它植物生长过的土壤中开展的研究，可以用来评价间接的植物—土壤反馈关系（Mills & Bever, 1998；Reynolds et al, 2003）。单个的植物—土壤反馈关系提供了植物和土壤之间的关系（正的或负的）。相反，成对的植物—土壤反馈关系可以用来描述物种间的竞争排除或共存。理论模型证明研究成对的植物—土壤反馈关系比研究直接反馈的方向和程度更重要（Bever, 2003；Eppinga et al, 2006），但目前这方面的研究还很少（Kulmatiski et al, 2008）。

近些年，植物—土壤反馈研究逐渐增加。但植物—土壤反馈研究的实验方法还不太成熟（Kulmatiski & Kardol, 2008）。例如，植物土壤反馈研究一般分为两步：第一步获得植物影响过的土壤；第二步用植物影响过的土壤栽培同种或其他种植物。第一阶段的土壤可以用自然出现的植物培养的土（一些自然状态下生长的单种植物斑块），也可以用实验栽培植物培养的土。用自然单种植物斑块获得第一阶段土壤能消除第一阶段对时间的要求，同时也能更多地反应自然的土壤条件，但这一方法却不能消除取样点间土壤的异质性差异（Troelstra et al, 2001；Ellis & Weis, 2006 ）。在第二阶段，可做物种水平和群落水平对土壤反应的测量。在这一方法中，目标物种的反应是以单个物种，多个单个物种，单个物种在群落中反应来体现的。研究方法比较单一，新的研究方法和研究技术还很少应用到植物—土壤反馈研究中。

另外，目前关于植物—土壤反馈的研究多集中于个体水平，群落水平的反馈试验做得相对较少（De Deyn et al, 2004；Kulmatiski et al, 2006；Kardol et al, 2007）。植物在自然条件下是长在群落里的，所以群落水平的植物—土壤反馈研究可能更重要（Kulmatiski et al, 2008）。

4 植物土壤反馈研究的现状

从 20 世纪 90 年代起，国外学者开始在森林（Van Breemen & Finzi, 1998；Binkley & Giardina, 1998）、草原（Burke et al, 1998）、沼泽（Young & Harvey, 1996）、沙丘（Putten et al, 1993；Putten & Troelstra, 1988）、苔原（Sturm et al, 2005）和弃耕地（Kardol et al, 2007, 2006）等不同生态系统做了大量有关植物—土壤反馈方面的工作，但在不同生态系统内植物—土壤反馈关系及不同群落的植物—土壤反馈关系的比较研究还很少（Tmartijn et al, 2006）。近年来，植物—土壤反馈研究在解释群落演替以及外来种入侵和全球变化的机制等方面成为一个研究热点（Putten et al,2016；Bailey & Schweitzer, 2016）。

4.1 气候变化

植物可能通过改变生理特性、物候、基因组成或地理分布对全球气候变化和 CO_2 增加做出反应

(Kardol et al, 2016)。未来气候变化可能导致物种组成发生变化(Parmesan & Yohe, 2003; Walther et al, 2002)及生物多样性丢失(Thomas et al, 2005)。物种组成的变化可能打破一些原有的营养关系,甚至当宿主和寄生者都扩大了适合度,它们原有的关系可能变得不那么紧密(Menéndez et al, 2008; Teste et al, 2016)。这种单个物种适合度的变化可能对地下群落产生影响(Kowalchuk et al, 2002; Porazinska et al, 2003)。另外,温度升高,土壤微生物呼吸增强,均能增加土壤氮的矿化(Rustad et al, 2001),从而可能提高初级生产力并影响食草动物的特征(Bezemer et al, 1998)。

基于不同的影响,多个地下地上营养关系可能改变。例如,CO_2 增加将会降低植物叶片质量,增加活性碳向土壤的输入(Van Groenigen et al, 2006)。这些变化将要影响植物和捕食者的关系并会影响地下食物网发生显著的改变(Mikola et al, 2001),从而改变地上地下生态系统的相互作用。

4.2 群落演替

在群落演替方面已经有关于植物—土壤反馈的研究(Kulmatiski & Kardol, 2008)。关于植物—土壤反馈在群落演替过程中的作用,研究者提出了两个对立的假说。Reynolds et al (2003)基于模型的假说认为,演替在早期是正反馈而晚期是负反馈。这个假说认为,在演替早期共生体(如固氮微生物)对植物的生长是必须的。因此,导致演替早期的正反馈。另外,在一开始的演替阶段,因为土壤条件很严酷,寄主密度低,这些都是病原体所不喜欢的条件,所以负反馈机制是不太重要的。当寄主达到一定密度,并改变了非生物环境,使条件有利于土壤病原体。这时就会使负反馈的作用越来越强并驱动演替过程中的物种替代(Reynolds et al, 2003)。有学者通过概念模型提出植物群落动态将会从多物种共生群落逐渐演变为单优势种群落,在演替后期特殊的植物—土壤反馈作用在混合植物群落中将会导致连续的负反馈作用,这也能解释为什么单一物种植物群落的生产力小于混合植物群落(Putten et al, 2013)

然而,一些实验并不支持 Reynolds 等的概念模型。在原生演替(Putten et al, 1993; Putten & Troelstra, 1988)和次生演替(Kardol et al, 2006)的早期都发现了负反馈。在原生演替早期负反馈被证实源于线虫的寄生(Putten et al, 1993)。在次生演替中,早期物种的负反馈与物种的快速生长及弱的抗病能力有关(Coley et al, 1985; Poorter, 1989)。Zhang et al(2016)通过对植物根系分解在植物土壤反馈中作用时发现演替初期根系凋落物分解短期内产生负反馈作用,随着时间增加会慢慢变为正反馈作用。另外,Kardol et al (2007)发现次生演替的晚期出现正的植物—土壤反馈关系并指出正反馈来源于共生真菌的促进作用。

4.3 外来种入侵

植物土壤反馈作为一种机制在解释外来植物的丰富度和物种维持方面也引起人们的注意(Reinhart & Callaway, 2006)。入侵种之所以能够入侵成功是因为一般人们预期引入生境的土壤是天敌和病原体缺乏的(Putten et al, 2013)。因为在入侵的土壤中食根天敌和病原体还没进化为专一性、而共生体却是普遍的(Callaway & Aschehoug, 2000)。有学者在加拿大研究发现,相比于本地物种对植物—土壤的正反馈作用,外来物种对于这种反馈作用并不敏感(Crawford & Knight, 2016; Schittko et al, 2016)。这种结果暗示了外来种之所以变成入侵种可能并不是都是因为正反馈作用(当然也不排除其在原生长地的反馈作用不敏感)。研究认为不是所有的外来者或入侵者都能从病原体缺乏中获益,但是从病原体缺乏中获益的外来种却更有可能成为成功的入侵者(Reynolds et al, 2003)。如果入侵者能保留或聚集有益的土壤条件,外来物种相比本土物种会产生显著的正反馈 (Klironomos, 2002; Reinhart & Callaway, 2006; Agrawal et al, 2005),导致本地种被竞争排除 (Bever et al, 1997; Bever, 2003)。

4.4 物种多样性与生产力

到目前为止,有关植物—土壤—反馈与物种多样性对生产力影响的实验也相对较少。有学者通过对这方面研究发现植物多样性对生产力的影响可能是由于混播群落水平对土壤病原菌以及养

分水平的响应(Putten et al，2013)。有研究发现单作植物群落生产力要相对低于混播植物群落，但是进行土壤灭菌作用之后就会获得较高的生产力(Putten et al，2013)。他们认为土壤致病菌可能是引起单作植物群落生产力降低的原因,因此解释了物种多样性与生产力之间的正相关关系。这个结果对于植物多样性的功能研究方面提供了一个新的观点,他们认为这种生产过剩现象并不只是由于资源互补效应引起,还有可能是由于这种不太强的植物—土壤反馈作用导致混合植物群落出现这种现象(Putten et al，2013)。Kulmatiski et al(2008)通过模型模拟研究发现负反馈作用将导致生产过剩,正反馈作则导致生产不足。实验结果强调了复合试验设置的重要性,而且要对比较群落水平的植物—土壤反馈作用与个体水平的差异(Putten et al，2013；Hufkens et al，2016)。

5 存在问题与建议

目前,大量的植物—土壤反馈研究多是在单一生态系统内开展的,缺乏不同生态系统之间的比较研究。特别是植物—土壤反馈研究多是在温室或盆栽条件下植物个体在幼苗或中等大小下单种栽培完成的。事实上,植物生长在自然界,植物之间的相互影响更为重要。

为了更好地评价物种对土壤物理、化学和生物特征的影响,应该研究某个自然单元内多个相互作用的植物对土壤的影响及其反馈。另外,新的科学方法和技术在探索自然生态系统中的植物—土壤反馈研究中应用很少,如加强分子基因工具以及元素示踪技术的引入能加强我们对隐藏在明显反馈背后的机制的理解。再者,植物—土壤反馈研究的理念还有待于进一步加强。研究植物—土壤反馈的变化强度和方向可以用来解释演替和入侵现象,并能够帮助理解生态系统如何应对气候变暖和物种多样性变化。在未来通过将植物—土壤反馈理念整合到生态学理论中,对于怎样确定一个通用的生态学模型以及植物—土壤反馈怎样影响生物进化等方面都具有重要的意义。

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