

# 土壤有机碳对外源氮添加的响应及其机制

李 嵘<sup>1,2</sup> 常瑞英<sup>1\*</sup>

<sup>1</sup>中国科学院水利部成都山地灾害与环境研究所山地表生过程与生态调控重点实验室, 成都 610041; <sup>2</sup>中国科学院大学, 北京 100049

**摘 要** 土壤有机碳库是陆地生态系统碳库的重要组成, 在全球碳循环中发挥着重要的作用。受元素化学计量平衡调控作用, 氮输入的增加将会对土壤有机碳库产生重要影响。然而, 目前关于陆地生态系统碳库对氮添加的响应主要集中在植被碳库, 对土壤碳库研究较少, 且研究结论争议较大, 尤其对其响应机制缺少系统梳理。该文作者通过对已有文献进行梳理, 认为生态系统类型、土壤碳变化的检测方法、土壤深度, 以及土壤稳定性碳和易变碳含量的差异可能是造成当前研究土壤碳汇增量(每克氮输入所增加的碳)差异的重要原因。氮添加条件下土壤有机碳的积累机制可能包括3个方面: 1)氮添加增加了凋落物输入, 促进了碳积累; 2)氮添加减少土壤碳输出, 尤其是抑制了稳定性碳的分解; 3)促进土壤腐殖质及稳定性碳的形成。此外, 该文结合当前研究中存在的不足, 提出今后需加强对深层土壤碳、土壤可溶性有机碳的淋溶及吸附, 以及不同土壤碳组分对氮添加的响应研究, 并通过改进检测方法减少氮添加条件下碳储量的测量误差。

**关键词** 外源氮添加, 易变碳, 稳定性碳, 土壤固碳, 化学计量平衡

**引用格式:** 李嵘, 常瑞英 (2015). 土壤有机碳对外源氮添加的响应及其机制. 植物生态学报, 39, 1012–1020. doi: 10.17521/cjpe.2015.0098

## Effects of external nitrogen additions on soil organic carbon dynamics and the mechanism

LI Rong<sup>1,2</sup> and CHANG Rui-Ying<sup>1\*</sup>

<sup>1</sup>Key Laboratory of Mountain Surface Processes and Ecological Regulation, Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu 610041, China; and <sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China

### Abstract

What would be the impact of external nitrogen additions on soil carbon, an issue still under debating, as reported experimental results were either positive, negative or neutral. Several factors may be related to these seemingly controversial results: differences in ecosystem types and soil properties, soil carbon detection methods, soil depths, and contents of soil labile and recalcitrant carbon that affect the responses to nitrogen additions, all could cause discrepancies and variations in carbon sequestration. The several processes that contribute to enhance soil organic carbon storage include increasing litter input, decreasing soil carbon output, particularly, by suppressed decomposition of recalcitrant carbon, promoting soil humification and formation of recalcitrant carbon storage. However, there are still many uncertainties associated with these issues. To improve our understanding, the research about carbon in deep soil layers, dissolved organic carbon leaching and accumulation, and the effect of labile and recalcitrant soil C ratios on N addition responses, should be further investigated in the future studies.

**Key words** external nitrogen addition, labile carbon, recalcitrant carbon, soil organic carbon sequestration, stoichiometric balance

**Citation:** Li R, Chang RY (2015). Effects of external nitrogen additions on soil organic carbon dynamics and the mechanism. *Chinese Journal of Plant Ecology*, 39, 1012–1020. doi: 10.17521/cjpe.2015.0098

氮素是生物必需的大量元素, 对调控生态系统结构和功能, 维持生态系统的健康和稳定具有重要意义。自工业革命以来, 由于人类活动, 如化肥、化石燃料使用等, 全球范围内的氮生产及大气活性氮沉降均大幅增加(Galloway *et al.*, 2008; Cui *et al.*,

2013)。据测算, 全球表面平均大气氮沉降从工业革命前的 $0.5 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ 增加到当前的 $10 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$  (Erisman *et al.*, 2008), 而我国当前的大气氮沉降远高于全球平均水平, 约为 $21.1 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$  (Liu *et al.*, 2013), 并且仍将持续增加(Galloway *et al.*, 2008;

Liu *et al.*, 2013)。大气氮沉降增加作为当前全球变化的一个重要方面, 伴随着大气CO<sub>2</sub>浓度增加和气温升高, 对生态系统结构、功能和服务产生了深刻影响(Mack *et al.*, 2004; Suding *et al.*, 2005; Magnani *et al.*, 2007; Bowman *et al.*, 2008; Janssens *et al.*, 2010)。

全球表土0–100 cm土壤有机碳库约为1 500 Pg, 100–300 cm土壤有机碳库约842 Pg (Jobbágy & Jackson, 2000), 北极冻土区0–300 cm土壤有机碳库约1 672 Pg (Tarnocai *et al.*, 2009), 全球0–300 cm土壤有机碳库共计约4 014 Pg, 为植被碳库(500 Pg)的8倍、大气碳库(750 Pg)的5倍。受元素化学计量平衡调控作用, 外源氮添加会对土壤有机碳库产生影响, 进而影响全球碳平衡。自20世纪90年代起, 关于氮添加对陆地生态系统碳库影响的研究大量涌现, 特别是近十几年来, 对氮添加条件下碳库的变化方向、变化程度及机制研究, 以及氮添加对碳循环过程的影响研究取得了长足进展(Reay *et al.*, 2008)。例如, Magnani等(2007)对欧洲多年的碳通量数据进行系统分析, 证实氮添加可显著提高森林生态系统碳库, 该研究引起了广泛关注(主要针对碳库响应程度), 进一步推动了氮添加对陆地生态系统碳库的影响研究。目前国内外关于陆地生态系统碳库对氮添加响应的研究主要集中在植被碳库, 对土壤碳库的研究较少, 对其响应机制仍缺少系统梳理。本文对当前土壤碳库对氮添加响应存在的争论、影响因素及响应机制进行了探讨, 对当前研究的不足进行了分析, 并提出今后需要关注的重点。

## 1 氮添加对土壤有机碳库的影响研究

### 1.1 土壤有机碳库对氮添加的响应及争论

生态系统碳循环与氮素存在耦合关系, 碳积累与氮素供给密切相关(Luo *et al.*, 2006; Kirkby *et al.*, 2013)。碳氮耦合作用在植被的光合生产、生长与分配过程以及土壤养分的循环过程中均发挥着重要作用。目前普遍认为氮添加可促进植被净初级生产力增加及植被生长, 提高植被碳储量(Magnani *et al.*, 2007; Reay *et al.*, 2008; Xia & Wan, 2008; LeBauer & Treseder, 2008; Janssens & Luyssaert, 2009; Thomas *et al.*, 2010)。不同植被类型及气候条件下的植被碳汇增量(此处将每克氮素输入所增加的碳量暂称为碳汇增量)为30–200 g C (de Vries *et al.*, 2008; Sutton *et al.*, 2008; Reay *et al.*, 2008; Thomas *et al.*, 2010;

Templer *et al.*, 2012)。Magnani等(2007)研究认为每增加1 g氮输入, 可促使森林生态系统增加约470 g C。de Vries等(2008)则认为Magnani等(2007)的研究高估了该值, 重新估算的碳汇增量为30–70 g C, 其中植被碳库增量为20–40 g C, 土壤碳库增量为10–30 g C。

相对于植被碳汇, 目前关于土壤碳汇对氮添加的响应争议较大。Mack等(2004)研究发现氮添加改变了苔原地区植物群落组成并促进了凋落物分解, 从而使土壤有机碳储量减少, 抵消了氮添加下的植被碳汇增量, 导致生态系统碳储量减少。同样, Cleveland和Townsend (2006)研究发现, 氮添加促进土壤呼吸而减小土壤有机碳库储量。Nadelhoffer等(1999)则认为氮添加对欧洲森林生态系统碳库影响较小。此外, 较多研究显示氮添加增加了土壤碳储量(de Vries *et al.*, 2006; Reay *et al.*, 2008)。例如, Zak等(2008)指出氮添加(30 kg N·hm<sup>-2</sup>·a<sup>-1</sup>)处理的森林土壤有机碳含量显著高于对照土壤, 其增幅约12%。氮添加同样可促进北欧云杉林和松树林土壤碳吸收, 其碳汇增量为11 g C (Hyyönén *et al.*, 2008)。Reay等(2008)对以往的研究进行了综述, 认为氮添加下的土壤碳库增量为7–23 g C。Meta分析的结果表明, 森林土壤在氮添加下的碳汇增量为19 g C (Janssens *et al.*, 2010); 而Lu等(2011)的结果显示森林和草地的土壤碳库变化很小。经过文献梳理和总结, 氮添加下土壤碳汇增量范围为0–30 g C, 低于植被碳汇增量(de Vries *et al.*, 2006, 2008; Reay *et al.*, 2008; Janssens *et al.*, 2010)。整体而言, 目前关于氮添加条件下土壤碳汇的变化方向与强度争议较大, 亟需对其影响因子及机理进行深入研究分析。

### 1.2 氮添加对土壤有机碳库的影响因子

土壤有机碳对氮添加的响应差异, 可能与以下因素有关:

第一, 与生态系统类型及其性质、土壤类型及氮素添加形式、时间长短及添加水平有关(Hyyönén *et al.*, 2008; de Vries *et al.*, 2008; Cusack *et al.*, 2010)。氮添加能够显著地促进农田生态系统土壤有机碳积累, 而对林地、草地、湿地及荒漠等非农业生态系统土壤碳积累的作用不明显(Lu *et al.*, 2011)。同样, 相比于温带针叶林(temperate conifer forest)和温带混合林(temperate mixed forest)及热带雨林(tropical rain forest), 氮添加对北方泰加林

(boreal forest)矿质层土壤有机碳影响更为显著(Liu & Greaver, 2010)。不同生态系统土壤有机碳对氮添加的响应差异可能与其本身的性质有关, 如土壤氮含量及碳氮元素计量关系、凋落物质量等(Waldrop *et al.*, 2004; Kirkby *et al.*, 2013)。Waldrop等(2004)发现: 在3年的氮添加( $80 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )实验中, 凋落物质量较高(C:N较低)的*Acer saccharum*林0–20 cm土壤碳下降了20%, 而凋落物质量较低(C:N较高)的*Quercus velutina*林在同一深度的土壤碳则显著提高了10%。此外, 不同氮添加形式对土壤有机碳具有不同影响, 氨态氮对土壤有机碳累积的促进作用明显高于硝态氮(Lu *et al.*, 2011), 其原因可能是氨态氮促进土壤pH值和微生物酶活性的降低, 不利于土壤有机碳的矿化(Min *et al.*, 2011)。微生物群落与土壤有机碳对氮添加的响应存在临界阈值, 长期施氮会使受氮限制的生态系统发生氮饱和,  $\text{NO}_3^-$ 大量淋溶, 土壤酸化、大量土壤阳离子流失并产生铝毒(Tietema, 1998), 对微生物活性产生不利影响(Lovell & Hatch, 1997; Wallenstein *et al.*, 2006); 而短期施氮可促进土壤碳积累。但也有研究表明: 短期氮添加可能会增加或降低土壤微生物生物量, 或者对其无影响(Dijkstra *et al.*, 2005; Liu *et al.*, 2007), 从而对土壤碳库产生不同影响。适量施氮可促进土壤碳积累, 但过量施氮可能会使有机质分解作用强于其累积, 从而降低土壤碳储量(Soussana *et al.*, 2004)。例如, 低氮添加( $10 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )促进土壤碳积累, 而中氮( $20 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )和高氮添加( $40 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )反而会降低土壤碳储量(Fang *et al.*, 2014)。

第二, 土壤有机碳对氮添加的响应受不同环境因子与土壤深度的影响。森林土壤有机碳库在氮添加下随纬度的增高而增加, 随年平均温度的增加而降低, 而草地土壤有机碳库在不同环境因子(如温度、纬度及降水)条件下则无显著变化(Lu *et al.*, 2011)。不同深度土壤在理化性质及稳定机制等方面均存在明显差异(Salom *et al.*, 2010), 从而影响碳库对氮添加的响应程度与响应速率。研究显示: 氮添加可以显著增加土壤表层0–5 cm有机碳储量, 但对下层土壤有机碳含量影响不明显(Morell *et al.*, 2011)。但也有研究认为下层土壤碳同样对氮素添加响应敏感(Mack *et al.*, 2004; Rumpel & Kögel-土壤 Knabner, 2011)。因此, 仅考虑表层土壤而忽略下层

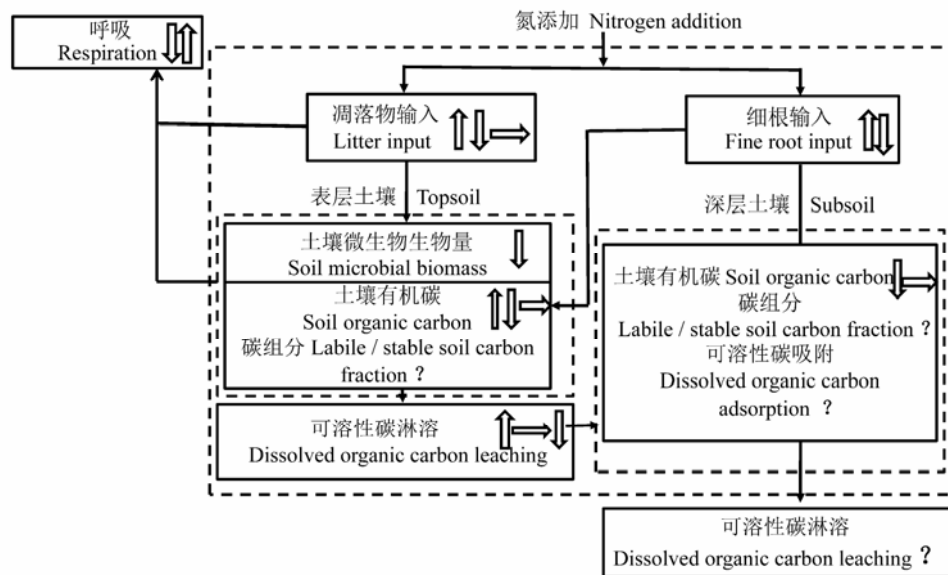
有机碳变化, 可能会对生态系统土壤有机碳积累速度的估算产生误差。VandenBygaart和Angers (2006)认为对农田生态系统土壤固碳研究至少需要考虑整个耕作层土壤碳变化, 甚至还有学者提出需要考虑土壤母质层, 即C层以上或1 m深度土壤碳的变化(Hamburg, 2000)。

第三, 氮添加对土壤有机碳影响的差异还可能与不同土壤碳组分, 即易变碳与稳定性碳的差异性响应有关。Neff等(2002)发现, 氮添加( $10 \text{ g N} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ )促进了较易分解的轻组土壤碳的分解, 而增加了较难分解的重组土壤碳的稳定性。并且, 不同土壤碳组分对氮添加的响应时间也存在差异。例如, 易变碳可能在短期内就对氮添加做出响应, 促使土壤易变碳库减少(Dijkstra *et al.*, 2005), 而稳定性碳对氮添加响应较为缓慢(Cusack *et al.*, 2010)。土壤易变碳与稳定性碳的分布和格局与植被和土壤类型以及土壤深度密切相关, 二者对氮添加的差异性响应可能也是造成不同生态系统和土壤深度碳库对氮添加响应差异的一个重要原因。

第四, 不同的土壤碳变化检测方法可能导致不同的结果。Khan等(2007)指出传统的配对样地(paired site)对比方法, 是通过对比施肥与未施肥样地的土壤碳库的变化来检测土壤碳, 无法避免土壤空间异质性引起的误差, 可能会高估氮添加的土壤固碳效应。连续观测(retrospective)方法, 即对同一块施肥样地的土壤碳进行连续检测, 虽然避免了配对样地对比法可能存在的土壤异质性差异所引起的误差, 但无法有效地剔除土壤碳在自然演替中所发生的变化, 需要结合配对样地的检测来减小误差。易检且精度较高的土壤碳变化检测方法的应用对于准确评估土壤碳对氮添加的响应具有重要的作用。

## 2 氮添加对土壤有机碳库的影响机理

氮添加对土壤有机碳库的影响依赖于碳输入与分解矿化过程的动态平衡(Mack *et al.*, 2004; Trumbore, 2006), 包括植物生长、碳吸收及光合产物的分配、凋落物分解、土壤有机质周转和土壤呼吸等过程。当前氮添加对土壤有机碳库影响的研究也主要围绕以上相关过程展开。本文对氮添加下的土壤有机碳库、碳循环过程及其相关研究进行了梳理(图1), 将氮添加对土壤碳积累与稳定性的响应机理总结为



**图1** 氮添加对土壤有机碳库及碳循环过程的影响。实心箭头表示土壤碳输入、输出与土壤碳库之间的相互作用。空心箭头表示氮添加作用。向上、向下和平行箭头表示正作用、负作用和作用不显著。“?”表示相关研究很少,需要进一步深入。  
**Fig. 1** Effects of soil nitrogen additions on soil organic carbon storage and cycle. Solid arrows indicate interaction of the input and output of soil organic carbon, and the soil organic carbon storage. Hollow arrows indicate the effect of nitrogen additions. Upward, downward, and parallel arrows show positive, negative, and insignificant effects. The question mark indicates little research was done, or an unanswered question.

以下3个主要方面。

## 2.1 增加土壤凋落物输入促进土壤有机碳积累

一些研究显示施氮可显著增加植被凋落物量 (Bradley *et al.*, 2006; Adamek *et al.*, 2009), 且凋落物量随氮添加水平增加而增加。例如, 樊后保等(2007)研究指出: 高氮添加( $240 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )显著增加森林凋落物量( $2599.5 \text{ kg} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ ), 而中氮( $120 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )和低氮( $60 \text{ kg N} \cdot \text{hm}^{-2} \cdot \text{a}^{-1}$ )对凋落物量增加的促进作用不明显。但也有研究发现: 尽管氮添加可以促进植被生产力增加, 但地上叶片与地下根系凋落物输入对氮添加并无明显的正反馈作用(Zak *et al.*, 2008; Janssens *et al.*, 2010)。此外, 氮添加可以增加叶片和细根氮含量(Giardina *et al.*, 2003; Xia & Wan, 2008; Zak *et al.*, 2008; Yuan & Chen, 2012), 可能促进叶片和细根凋落物的分解(Waldrop *et al.*, 2004; Knorr *et al.*, 2005; Parton *et al.*, 2007; Hobbie *et al.*, 2012), 而不利土壤碳的积累。然而, 有研究显示氮添加只在初期促进凋落物分解, 主要包括水溶性物质和非木质性纤维素的分解, 随着中后期难分解的木质素含量的增多, 氮添加抑制了凋落物的分解(Carreiro *et al.*, 2000)。

## 2.2 抑制土壤呼吸作用与土壤稳定性碳分解

氮添加通过抑制土壤呼吸作用与土壤稳定性碳

的分解而促进土壤碳的积累, 这也是目前被广泛接受的解释(Zak *et al.*, 2008; Reay *et al.*, 2008; Janssens & Luyssaert, 2009; Cusack *et al.*, 2010; Ramirez *et al.*, 2012)。

土壤呼吸是影响土壤碳输出的重要方面。研究认为氮添加可降低土壤微生物呼吸(Janssens & Luyssaert, 2009; Janssens *et al.*, 2010), 并通过减少植物碳的地下分配和减小根系碳而减弱根际微生物呼吸(Phillips & Fahey, 2007)。但也有观点认为氮添加可促进生态系统土壤呼吸(Cleveland & Townsend, 2006; Jassal *et al.*, 2010), 加速土壤有机质分解, 而不利土壤碳的积累。

氮添加不仅对土壤微生物呼吸产生影响, 而且可以促使土壤微生物群落结构发生改变(Waldrop *et al.*, 2004; Carreiro *et al.*, 2000)。土壤微生物对陆地生态系统土壤碳矿化过程及营养元素循环具有重要影响, 由土壤微生物活动、植物根系分泌物和动植物残体腐解过程所产生的土壤酶, 包括游离酶、胞内酶和胞外酶等的活性与土壤有机质的分解合成以及土壤供应植物养分的能力密切相关(关松荫, 1986)。研究认为氮添加可改变土壤细菌与真菌组成比例(Demoling *et al.*, 2008; Ramirez *et al.*, 2012), 并通过影响水解酶和氧化还原酶的活性而影响稳定性碳的

分解,如促进纤维素和多糖类有机质的分解,抑制木质素等其他难分解有机质的分解(Carreiro *et al.*, 2000; Hobbie *et al.*, 2012; Ramirez *et al.*, 2012)。此外,分子生物学的发展为微生物生态学的研究提供了新的手段。Cusack等(2010)利用磷脂脂肪酸分析和 $^{13}\text{C}$ 核磁共振技术对热带雨林的研究发现,氮添加通过影响水解酶及氧化酶活性促进土壤中活性碳的分解。此外,高通量测序技术、RT-PCR技术、PCR-DGGE技术、基于rDNA指纹图谱等的应用,也将有助于深入认识氮添加下土壤有机碳变化的微生物学机制。

此外,有研究认为土壤微生物的碳利用效率(CUE)与土壤碳积累有关(Six *et al.*, 2006)。微生物的碳利用效率是指用于微生物生物量积累的碳与微生物所吸收的碳之比(del Giorgio & Cole, 1998)。CUE越高表明微生物用于自身有效生长的碳越多,反之则表明有更多的碳用于微生物呼吸和分泌物的产生,从而导致碳损耗,不利于土壤碳积累。土壤微生物的碳利用效率受多种因素影响,如高温和水分胁迫可通过影响微生物活动和呼吸作用而降低CUE(Conant *et al.*, 2011; Manzoni *et al.*, 2012)。氮添加则可通过影响微生物的合成代谢与分解代谢影响CUE。研究认为,氮添加可提高微生物CUE,减弱微生物呼吸作用(Blagodatskaya *et al.*, 2014),从而促进土壤碳积累(Thiet *et al.*, 2006; Manzoni *et al.*, 2012),也可通过影响土壤胞外酶活性降低稳定性碳分解(Ågren *et al.*, 2001)。

### 2.3 促进土壤腐殖质和稳定性碳形成增加土壤有机碳积累

氮添加可促进腐殖质的形成,促进分解残物向稳定性碳的转变,增加稳定性碳积累(Moran *et al.*, 2005; Whittinghill *et al.*, 2012)。氮元素与较难分解的凋落物残体(如木质素等)结合形成更难分解的杂环类物质(如吡啶等)和酚类是氮添加促进难分解碳形成的一个机制(Berg, 2000; Janssens *et al.*, 2010)。而氮添加对团聚体(aggregate, 即土壤碳的物理保护)的促进作用可能不明显(Janssens *et al.*, 2010)。尽管氮添加对稳定性碳库的促进作用在短期内可能对土壤总有机碳库影响不显著,但其长期作用明显(Reid *et al.*, 2012)。土壤稳定性碳是影响土壤有机碳库稳定与积累的重要因素,加强对土壤稳定性碳的研究对于从机理上深入认识氮添加对土壤有机碳库的影

响及其响应机制具有重要作用。

### 3 研究不足及展望

目前研究对氮添加下土壤有机碳库积累的机制取得了一定认识,但在一些方面仍存在不足。本文对相关研究进行梳理,提出今后可能需要关注的重点。

第一,目前关于氮添加对土壤有机碳的影响研究多数集中于对表层土壤的研究,如对凋落物层或表层20 cm土壤的探究,但缺少对深层(如20–100 cm)土壤有机碳变化的探讨。深层土壤不仅具有巨大的碳储量(Jobbágy & Jackson, 2000),且一些证据表明深层土壤有机碳同样对氮素添加响应敏感(Mack *et al.*, 2004; Rumpel & Kögel-Knabner, 2011)。增加对下层土壤有机碳变化的考虑,对于准确评估土壤有机碳对氮添加的响应具有重要价值。

第二,对氮添加下地表凋落物层和表层土壤可溶性有机碳(dissolved organic carbon)淋溶研究较多,而对下层土壤可溶性有机碳淋溶及积累的监测较少。目前认为下层碳累积的机制包括以下3种: 1)根系碳输入的积累作用; 2)土壤动物的扰动作用(bioturbation)(Rumpel & Kögel-Knabner, 2011); 3)淋溶碳输入(Harrison *et al.*, 2011)。多数研究认为根系碳输入是下层土壤碳的主要来源(Lorenz & Lal, 2005; Rumpel & Kögel-Knabner, 2011),但在一些森林生态系统中,淋溶碳对下层碳积累的贡献可以达到20%(Sanderman & Amundson, 2009)。一方面根系以及淋溶碳的输入可以增加下层土壤碳的积累,但另一方面也可能造成下层碳的损失。有研究发现表层根系碳及其他活性碳的输入会促进下层土壤老碳(old carbon)的分解(Fontaine *et al.*, 2007),即所谓的激发效应(priming effect)和根际激发效应(rhizosphere priming effect) (Kuzakov, 2000, 2010; Cheng *et al.*, 2003)。然而, Salome等(2010)研究表明,下层碳可能受团聚体的物理保护(隔离了微生物的侵袭),活性碳输入不会造成下层有机碳由于激发效应产生的损失。激发效应对土壤碳的影响程度和作用时间与生态系统类型、活性碳类型、观测时间以及土壤氮供给水平等密切相关(Cheng *et al.*, 2003; Dijkstra & Cheng, 2007; Drake *et al.*, 2013)。目前对淋溶碳输入是否会引发土壤激发效应仍缺乏实证,需要结合对土壤剖面可溶性有机碳的淋溶过程的观测深入开

展研究。因此, 土壤剖面淋溶碳的相关研究对于认识土壤有机碳, 尤其是下层土壤碳在氮素添加下的变化机制具有重要作用。

第三, 以往研究更多的是将土壤碳作为一个整体, 检测其在氮添加下的变化。而根据现有的一些研究结果发现, 不同的土壤碳组分, 如稳定性碳和易变碳对氮素添加的响应在时效性与影响程度上均具有较大差异, 而微生物群落组成(如细菌和真菌比例)和不同种类酶活性的改变可能是影响不同土壤碳组分差异响应的关键。因此, 区分不同土壤碳组分以及强化土壤微生物组成和酶活性研究可以从机制上提高土壤碳对氮添加响应的认识。

第四, 土壤碳储量巨大, 但其在氮添加下的变化量相对微小。如何减小其变化量的检测误差, 是当前相关研究需重点关注的一个方面。采取连续观测法并通过严格选择采样点可减小测量误差(Ellert *et al.*, 2002; VandenBygaart & Kay, 2004)。相比于传统的样地对比法, 碳同位素( $^{13}\text{C}$ 和 $^{14}\text{C}$ )示踪方法可以更加敏感地揭示土壤碳的动态变化(de Camargo *et al.*, 1999)。碳的稳定性同位素( $^{13}\text{C}$ )示踪技术可以阐明土壤碳储量的迁移和转化, 揭示不同形成时期新老土壤有机碳对碳储量的贡献(Bernoux *et al.*, 1998)。放射性同位素( $^{14}\text{C}$ )可以反映土壤固定和释放碳的时间, 可用于研究不同时间尺度土壤有机碳的动力学机制(Trumbore, 2000)。常用的估算土壤有机碳库更新速率的方法包括以下两个方法: 1)将 $^{14}\text{C}$ 作为土壤有机碳更新速率的指示剂, 通过检测1950年以来土壤有机碳中的 $^{14}\text{C}$ 量, 推算土壤碳动力学过程(Hsieh, 1993; Trumbore *et al.*, 1996; Wang *et al.*, 1999); 2)根据大气层残留核爆 $^{14}\text{C}$ 来识别土壤有机碳库的驻留时间(MRT)(Hsieh, 1993)。如利用加速质谱仪检出土壤中 $^{14}\text{C}$ 含量在短期内的变化, 可以间接反映土壤碳的分解与更新速率。同时,  $^{15}\text{N}$ 标记在氮添加实验中的应用不仅可以有效地检验氮素的循环过程, 而且可以在较短时期内(可以假定C:N不变)通过检验不同碳库中的 $^{15}\text{N}$ 含量及碳氮比, 并结合氮平衡法(N-balance method, 测定 $^{15}\text{N}$ 在土壤中的积累量并结合土壤C:N来估算土壤碳的变化量)来检测氮添加下土壤碳变化(de Vries *et al.*, 2006; Mol *et al.*, 2009)。此外, 碳氮同位素的应用还可以有效地示踪土壤有机碳的来源和周转过程(Ehleringer *et al.*, 2000), 揭示土壤碳氮耦合变化关系, 这也必将

成为今后相关研究的重要方面。

**基金项目** 国家自然科学基金(41301219)和中国科学院“西部之光”人才培养计划西部博士资助项目。

## 参考文献

- Adamek M, Corre MD, Hölscher D (2009). Early effect of elevated nitrogen input on above-ground net primary production of a lower montane rain forest, Panama. *Journal of Tropical Ecology*, 25, 637–647.
- Ågren GI, Bosatta E, Magill AH (2001). Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia*, 128, 94–98.
- Berg B (2000). Litter decomposition and organic matter turnover in northern forest soils. *Forest Ecology and Management*, 133, 13–22.
- Bernoux M, Cerri CC, Neill C, de Moraes JFL (1998). The use of stable carbon isotopes for estimating soil organic matter turnover rates. *Geoderma*, 82, 43–58.
- Blagodatskaya E, Blagodatsky S, Anderson TH, Kuzyakov Y (2014). Microbial growth and carbon use efficiency in the rhizosphere and root-free soil. *PLoS ONE*, 9, e93282.
- Bowman WD, Cleveland CC, Halada L, Hreško J, Baron JS (2008). Negative impact of nitrogen deposition on soil buffering capacity. *Nature Geoscience*, 1, 767–770.
- Bradley K, Drijber RA, Knops J (2006). Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi. *Soil Biology & Biochemistry*, 38, 1583–1595.
- Carreiro MM, Sinsabaugh RL, Repert DA, Parkhurst DF (2000). Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. *Ecology*, 81, 2359–2365.
- Cheng WX, Johnson DW, Fu SL (2003). Rhizosphere effects on decomposition. *Soil Science Society of America Journal*, 67, 1418–1427.
- Cleveland CC, Townsend AR (2006). Nutrient additions to a tropical rain forest drive substantial soil carbon dioxide losses to the atmosphere. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 10316–10321.
- Conant RT, Ryan MG, Ågren GI, Birge HE, Davidson EA, Eliasson PE, Evans SE, Frey SD, Giardina CP, Hopkins FM, Hyvönen R, Kirschbaum MUF, Lavelle JM, Leifeld J, Parton WJ, Steinweg JM, Wallenstein MD, Wetterstedt JÅM, Bradford MA (2011). Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. *Global Change Biology*, 17, 3392–3404.
- Cui SH, Shi YL, Groffman PM, Schlesinger WH, Zhu YG (2013). Centennial-scale analysis of the creation and fate of reactive nitrogen in China (1910–2010). *Proceedings of*

- the National Academy of Sciences of the United States of America, 110, 2052–2057.
- Cusack DF, Torn MS, McDowell WH, Silver WL (2010). The response of heterotrophic activity and carbon cycling to nitrogen additions and warming in two tropical soils. *Global Change Biology*, 16, 2555–2572.
- de Camargo PB, Trumbore SE, Martinelli LA, Davidson EA, Nepstad DC, Victoria RL (1999). Soil carbon dynamics in regrowing forest of eastern Amazonia. *Global Change Biology*, 5, 693–702.
- del Giorgio PA, Cole JJ (1998). Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics*, 29, 503–541.
- de Vries W, Reinds GJ, Gundersen P, Sterba H (2006). The impact of nitrogen deposition on carbon sequestration in European forests and forest soils. *Global Change Biology*, 12, 1151–1173.
- de Vries W, Solberg S, Dobbertin M, Sterba H, Laubhahn D, Reinds GJ, Nabuurs GJ, Gundersen P, Sutton MA (2008). Ecologically implausible carbon response? *Nature*, 451, E1–E3.
- Demoling F, Nilsson LO, Bååth E (2008). Bacterial and fungal response to nitrogen fertilization in three coniferous forest soils. *Soil Biology & Biochemistry*, 40, 370–379.
- Dijkstra FA, Hobbie SE, Reich PB, Knops JMH (2005). Divergent effects of elevated CO<sub>2</sub>, N fertilization, and plant diversity on soil C and N dynamics in a grassland field experiment. *Plant and Soil*, 272, 41–52.
- Dijkstra FA, Cheng WX (2007). Moisture modulates rhizosphere effects on C decomposition in two different soil types. *Soil Biology & Biochemistry*, 39, 2264–2274.
- Drake JE, Darby BA, Giasson MA, Kramer MA, Phillips RP, Finzi AC (2013). Stoichiometry constrains microbial response to root exudation—Insights from a model and a field experiment in a temperate forest. *Biogeosciences*, 10, 821–838.
- Ehleringer JR, Buchmann N, Flanagan LB (2000). Carbon isotope ratios in belowground carbon cycle processes. *Ecological Applications*, 10, 412–422.
- Ellert BH, Janzen HH, Entz T (2002). Assessment of a method to measure temporal change in soil carbon storage. *Soil Science Society of America Journal*, 66, 1687–1695.
- Erisman JW, Sutton MA, Galloway J, Klimont Z, Winiwarter W (2008). How a century of ammonia synthesis changed the world. *Nature Geoscience*, 1, 636–639.
- Fan HB, Liu WF, Qiu XQ, Xu L, Wang Q, Chen QF (2007). Responses of litterfall production in Chinese fir plantation to increased nitrogen deposition. *Chinese Journal of Ecology*, 26, 1335–1338. (in Chinese with English abstract) [樊后保, 刘文飞, 裘秀群, 徐雷, 王强, 陈秋凤 (2007). 杉木人工林凋落物量对氮沉降增加的初期响应. 生态学杂志, 26, 1335–1338.]
- Fang HJ, Cheng SL, Yu GR, Yang XM, Xu MJ, Wang YS, Li LS, Dang XS, Wang L, Li YN (2014). Nitrogen deposition impacts on the amount and stability of soil organic matter in an alpine meadow ecosystem depend on the form and rate of applied nitrogen. *European Journal of Soil Science*, 65, 510–519.
- Fontaine S, Barot S, Barré P, Bdioui N, Mary B, Rumpel C (2007). Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, 450, 277–280.
- Galloway JN, Townsend AR, Erisman JW, Bekunda M, Cai ZC, Freney JR, Martinelli LA, Seitzinger SP, Sutton MA (2008). Transformation of the nitrogen cycle: Recent trends, questions, and potential solutions. *Science*, 320, 889–892.
- Giardina CP, Ryan MG, Binkley D, Fownes JH (2003). Primary production and carbon allocation in relation to nutrient supply in a tropical experimental forest. *Global Change Biology*, 9, 1438–1450.
- Guan SY (1986). *Soil Enzyme and Research Methods*. China Agricultural Press, Beijing. (in Chinese) [关松荫 (1986). 土壤酶及其研究法. 农业出版社, 北京.]
- Hamburg SP (2000). Simple rules for measuring changes in ecosystem carbon in forestry-offset projects. *Mitigation and Adaptation Strategies for Global Change*, 5, 25–37.
- Harrison RB, Footen PW, Strahm BD (2011). Deep soil horizons: Contribution and importance to soil carbon pools and in assessing whole-ecosystem response to management and global change. *Forest Science*, 57, 67–76.
- Hobbie SE, Eddy WC, Buyarski CR, Adair EC, Ogdahl ML, Weisenhorn P (2012). Response of decomposing litter and its microbial community to multiple forms of nitrogen enrichment. *Ecological Monographs*, 82, 389–405.
- Hsieh YP (1993). Radiocarbon signatures of turnover rates in active soil organic carbon pools. *Soil Science Society of America Journal*, 57, 1020–1022.
- Hyvönen R, Persson T, Andersson S, Olsson B, Ågren GI, Linder S (2008). Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry*, 89, 121–137.
- Janssens IA, Dieleman W, Luyssaert S, Subke JA, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G, Papale D, Piao SL, Schulze SD, Tang J, Law BE (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, 3, 315–322.
- Janssens IA, Luyssaert S (2009). Carbon cycle: Nitrogen's carbon bonus. *Nature Geoscience*, 2, 318–319.
- Jassal RS, Black TA, Trofymow JA, Roy R, Nesic Z (2010). Soil CO<sub>2</sub> and N<sub>2</sub>O flux dynamics in a nitrogen-fertilized Pacific Northwest Douglas-fir stand. *Geoderma*, 157, 118–125.
- Jobbágy EG, Jackson RB (2000). The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, 10, 423–436.
- Khan SA, Mulvaney RL, Ellsworth TR, Boast CW (2007). The

- myth of nitrogen fertilization for soil carbon sequestration. *Journal of Environmental Quality*, 36, 1821–1832.
- Kirkby CA, Richardson AE, Wade LJ, Batten GD, Blanchard C, Kirkegaard JA (2013). Carbon-nutrient stoichiometry to increase soil carbon sequestration. *Soil Biology & Biochemistry*, 60, 77–86.
- Knorr M, Frey SD, Curtis PS (2005). Nitrogen additions and litter decomposition: A meta-analysis. *Ecology*, 86, 3252–3257.
- Kuzyakov Y, Friedel JK, Stahr K (2000). Review of mechanisms and quantification of priming effects. *Soil Biology & Biochemistry*, 32, 1485–1498.
- Kuzyakov Y (2010). Priming effects: Interactions between living and dead organic matter. *Soil Biology & Biochemistry*, 42, 1363–1371.
- LeBauer DS, Treseder KK (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.
- Liu LL, Greaver TL (2010). A global perspective on below-ground carbon dynamics under nitrogen enrichment. *Ecology Letters*, 13, 819–828.
- Liu WX, Xu WH, Han Y, Wang CH, Wan SQ (2007). Responses of microbial biomass and respiration of soil to topography, burning, and nitrogen fertilization in a temperate steppe. *Biology and Fertility of Soils*, 44, 259–268.
- Liu XJ, Zhang Y, Han WX, Tang AH, Shen JL, Cui ZL, Vitousek P, Erisman JW, Goulding K, Christie P, Fangmeier A, Zhang FS (2013). Enhanced nitrogen deposition over China. *Nature*, 494, 459–462.
- Lorenz K, Lal R (2005). The depth distribution of soil organic carbon in relation to land use and management and the potential of carbon sequestration in subsoil horizons. *Advances in Agronomy*, 88, 35–66.
- Lovell RD, Hatch DJ (1997). Stimulation of microbial activity following spring applications of nitrogen. *Biology and Fertility of Soils*, 26, 28–30.
- Lu M, Zhou XH, Luo YQ, Yang YH, Fang CM, Chen JK, Li B (2011). Minor stimulation of soil carbon storage by nitrogen addition: A meta-analysis. *Agriculture, Ecosystems and Environment*, 140, 234–244.
- Luo YQ, Field CB, Jackson RB (2006). Does nitrogen constrain carbon cycling, or does carbon input stimulate nitrogen cycling? *Ecology*, 87, 3–4.
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin III FS (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, 431, 440–443.
- Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007). The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, 447, 849–851.
- Manzoni S, Taylor P, Richter A, Porporato A, Ågren GI (2012). Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. *New Phytologist*, 196, 79–91.
- Min K, Kang H, Lee D (2011). Effects of ammonium and nitrate additions on carbon mineralization in wetland soils. *Soil Biology & Biochemistry*, 43, 2461–2469.
- Mol Dijkstra JP, Reinds GJ, Kros H, Berg B, de Vries W (2009). Modelling soil carbon sequestration of intensively monitored forest plots in Europe by three different approaches. *Forest Ecology and Management*, 258, 1780–1793.
- Moran KK, Six J, Horwath WR, van Kessel C (2005). Role of mineral-nitrogen in residue decomposition and stable soil organic matter formation. *Soil Science Society of America Journal*, 69, 1730–1736.
- Morell FJ, Cantero-Martínez C, Lampurlanés J, Plaza-Bonilla D, Álvaro-Fuentes J (2011). Soil carbon dioxide flux and organic carbon content: Effects of tillage and nitrogen fertilization. *Soil Science Society of America Journal*, 75, 1874–1884.
- Nadelhoffer KJ, Emmett BA, Gundersen P, Kjånaas OJ, Koopmans CJ, Schleppi P, Tietema A, Wright RF (1999). Nitrogen deposition makes a minor contribution to carbon sequestration in temperate forests. *Nature*, 398, 145–148.
- Neff JC, Townsend AR, Gleixner G, Lehman SJ, Turnbull J, Bowman WD (2002). Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature*, 419, 915–917.
- Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, Fasth B (2007). Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, 315, 361–364.
- Phillips RP, Fahey TJ (2007). Fertilization effects on fineroot biomass, rhizosphere microbes and respiratory fluxes in hardwood forest soils. *New Phytologist*, 176, 655–664.
- Ramirez KS, Craine JM, Fierer N (2012). Consistent effects of nitrogen amendments on soil microbial communities and processes across biomes. *Global Change Biology*, 18, 1918–1927.
- Reay DS, Dentener F, Smith P, Grace J, Feely RA (2008). Global nitrogen deposition and carbon sinks. *Nature Geoscience*, 1, 430–437.
- Reid JP, Adair EC, Hobbie SE, Reich PB (2012). Biodiversity, nitrogen deposition, and CO<sub>2</sub> affect grassland soil carbon cycling but not storage. *Ecosystems*, 15, 580–590.
- Rumpel C, Kögel-Knabner I (2011). Deep soil organic matter—A key but poorly understood component of terrestrial C cycle. *Plant and Soil*, 338, 143–158.
- Salom C, Nunan N, Pouteau V, Lerch T, Chenu C (2010). Carbon dynamics in topsoil and in subsoil may be controlled



- by different regulatory mechanisms. *Global Change Biology*, 16, 416–426.
- Sanderman J, Amundson R (2009). A comparative study of dissolved organic carbon transport and stabilization in California forest and grassland soil. *Biogeochemistry*, 92, 41–59.
- Six J, Frey SD, Thiet RK, Batten KM (2006). Bacterial and fungal contributions to carbon sequestration in agroecosystems. *Soil Science Society of America Journal*, 70, 555–569.
- Soussana JF, Soussana JF, Loiseau P, Vuichard N, Ceschia E, Balesdent J, Chevallier T, Arrouays D (2004). Carbon cycling and sequestration opportunities in temperate grasslands. *Soil Use and Management*, 20, 219–230.
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 4387–4392.
- Sutton MA, Simpson D, Levy PE, Smith RI, Reis S, van Oijen M, de Vries W (2008). Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, 14, 2057–2063.
- Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009). Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, 23, GB2023.
- Templer PH, Mack MC, Chapin FS III, Christenson LM, Compton JE, Crook HD, Currie WS, Curtus CJ, Dail DB, D'Antonio CM, Emmett BA, Epstein HE, Goodale CL, Gundersen P, Hobbie SE, Holland K, Hooper DU, Hungate BA, Lamontagne S, Nadelhoffer KJ, Osenberg CW, Perakis SS, Schleppi P, Schimel J, Schmidt IK, Sommerkorn M, Spoelstra J, Tietema A, Wessel WW, Zak DR (2012). Sinks for nitrogen inputs in terrestrial ecosystems: A meta-analysis of  $^{15}\text{N}$  tracer field studies. *Ecology*, 93, 1816–1829.
- Thiet RK, Frey SD, Six J (2006). Do growth yield efficiencies differ between soil microbial communities differing in fungal: Bacterial ratios? Reality check and methodological issues. *Soil Biology & Biochemistry*, 38, 837–844.
- Thomas QR, Canham CD, Weathers KC, Goodale CL (2010). Increased tree carbon storage in response to nitrogen deposition in the US. *Nature Geoscience*, 3, 13–17.
- Tietema A (1998). Microbial carbon and nitrogen dynamics in coniferous forest floor material collected along a European nitrogen deposition gradient. *Forest Ecology and Management*, 101, 29–36.
- Trumbore SE (2000). Age of soil organic matter and soil respiration: Radiocarbon constraints on belowground C dynamics. *Ecological Applications*, 10, 399–411.
- Trumbore SE (2006). Carbon respired by terrestrial ecosystems—Recent progress and challenges. *Global Change Biology*, 12, 141–153.
- Trumbore SE, Chadwick OA, Amundson R (1996). Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, 272, 393–396.
- VandenBygaart AJ, Kay BD (2004). Persistence of soil organic carbon after plowing a long-term no-till field in southern Ontario, Canada. *Soil Science Society of America Journal*, 68, 1394–1402.
- VandenBygaart AJ, Angers DA (2006). Towards accurate measurements of soil organic carbon stock change in agroecosystems. *Canadian Journal of Soil Science*, 86, 465–471.
- Waldrop MP, Zak DR, Sinsabaugh RL, Gallo M, Lauber C (2004). Nitrogen deposition modifies soil carbon storage through changes in microbial enzymatic activity. *Ecological Applications*, 14, 1172–1177.
- Wallenstein MD, McNulty S, Fernandez IJ, Boggs J, Schlesinger WH (2006). Nitrogen fertilization decreases forest soil fungal and bacterial biomass in three long-term experiments. *Forest Ecology and Management*, 222, 459–468.
- Wang Y, Amundson R, Trumbore S (1999). The impact of land use change on C turnover in soils. *Global Biogeochemical Cycles*, 13, 47–57.
- Whittinghill KA, Currie WS, Zak DR, Burton AJ, Pregitzer KS (2012). Anthropogenic N deposition increases soil C storage by decreasing the extent of litter decay: Analysis of field observations with an ecosystem model. *Ecosystems*, 15, 450–461.
- Xia JY, Wan SQ (2008). Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, 179, 428–439.
- Yuan ZY, Chen HYH (2012). A global analysis of fine root production as affected by soil nitrogen and phosphorus. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3796–3802.
- Zak DR, Holmes WE, Burton AJ, Pregitzer KS, Talhelm AF (2008). Simulated atmospheric  $\text{NO}_3^-$  deposition increases soil organic matter by slowing decomposition. *Ecological Applications*, 18, 2016–2027.

责任编辑: 杨元合 责任编辑: 王 蔚