



# 氮输入对滨海盐沼湿地碳循环关键过程的影响及机制

韩广轩\* 李隽永 屈文笛

中国科学院烟台海岸带研究所, 中国科学院海岸带环境过程与生态修复重点实验室, 山东烟台 264003; 中国科学院大学, 北京 100049

**摘要** 滨海盐沼湿地是缓解全球变暖的有效蓝色碳汇, 但是近岸海域富营养化导致的大量氮输入对盐沼湿地稳定性和碳汇功能构成严重威胁。潮汐作用下大量氮输入对盐沼湿地植物光合碳输入、植物-土壤碳分配和土壤碳输出等碳循环关键过程产生深刻影响, 进而影响盐沼湿地碳汇功能评估的准确性。该文从植物光合固碳、植物-土壤系统碳分配、土壤有机碳分解、土壤可溶性有机碳释放、盐沼湿地土壤碳库5个方面综述了氮输入对盐沼湿地碳循环关键过程的影响。在此基础上, 针对当前研究的不足, 提出今后的研究中, 需要进一步探究氮输入对盐沼湿地植物光合固碳及碳分配过程的影响、盐沼湿地土壤有机碳分解的微生物机制、盐沼湿地土壤可溶性有机碳产生和横向流动的影响、以及氮类型对盐沼湿地土壤碳库的影响。以为揭示氮输入对盐沼湿地碳汇形成过程与机制提供基础资料和理论依据, 为评估未来近岸海域水体富营养化影响下滨海盐沼湿地碳库的潜在变化提供新思路。

**关键词** 氮输入; 碳循环; 碳分配; 碳汇; 滨海盐沼湿地; 潮汐作用

韩广轩, 李隽永, 屈文笛 (2021). 氮输入对滨海盐沼湿地碳循环关键过程的影响及机制. 植物生态学报, 45, 321-333. DOI: 10.17521/cjpe.2020.0353

## Effects of nitrogen input on carbon cycle and carbon budget in a coastal salt marsh

HAN Guang-Xuan\*, LI Juan-Yong, and QU Wen-Di

CAS Key Laboratory of Coastal Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, Shandong 264003, China; and University of Chinese Academy of Sciences, Beijing 100049, China

### Abstract

Coastal salt marshes are an effective blue carbon sink to mitigate climate warming, but their ecosystem stability and carbon sink function are threatened by the large amount of nitrogen input caused by coastal eutrophication. Under the action of regular tides, the high nitrogen content in the coastal waters will have a profound effect on the key processes of carbon cycle such as plant photosynthetic carbon fixation, carbon allocation in plant-soil system, and soil carbon release in the salt marsh. This study reviewed the effects of nitrogen input on plant photosynthetic carbon fixation, carbon allocation in plant-soil system, decomposition of soil organic carbon, formation and release of soil dissolved organic carbon (DOC), and carbon sequestration in the salt marsh. Based on the shortcomings of current research, this review proposed the directions of future research, including the effects of nitrogen input on plant photosynthetic carbon fixation and carbon allocation in plant-soil system, the microbial mechanism of soil organic carbon decomposition, production and lateral exchange of soil DOC, and the potential impact of different forms of nitrogen input on soil carbon sequestration in the salt marsh. Overall, this study aims to improve the understanding of impacts of nitrogen input on the key carbon processes and the mechanisms of carbon sequestration in a salt marsh, and to provide new ideas for assessing the potential changes of carbon pools under the influence of eutrophication of coastal waters in the salt marsh wetlands.

**Key words** nitrogen input; carbon cycle; carbon allocation; carbon sink; coastal salt marsh; tidal action

Han GX, Li JY, Qu WD (2021). Effects of nitrogen input on carbon cycle and carbon budget in a coastal salt marsh. *Chinese Journal of Plant Ecology*, 45, 321-333. DOI: 10.17521/cjpe.2020.0353

滨海盐沼湿地是缓解全球变暖的有效蓝色碳汇 (即“蓝碳(Blue Carbon)”)。它是地球上最密集的碳汇之一, 其碳埋藏速率为 $(218 \pm 24) \text{ g} \cdot \text{m}^{-2} \cdot \text{a}^{-1}$ , 比森林生态系统高40倍左右(McLeod *et al.*, 2011; Macreadie

收稿日期Received: 2020-10-26 接受日期Accepted: 2021-01-18

基金项目: 国家自然科学基金(42071126)。Supported by the National Natural Science Foundation of China (42071126).

© 1994-2021 China Academic Journal Electronic Publishing House. All rights reserved. http://www.cnki.net

*et al.*, 2019)。究其原因,一方面,滨海盐沼植被群落光合固碳、凋落物及根系分泌物等碳输入量极大;另一方面,滨海盐沼长期处于厌氧状态导致土壤有机质分解缓慢,同时,周期性潮汐携带大量的 $\text{SO}_4^{2-}$ 阻碍甲烷( $\text{CH}_4$ )产生,从而降低盐沼湿地 $\text{CH}_4$ 的产生和排放(Choi & Wang, 2004)。此外,由于滨海盐沼湿地不断向下沉积,土壤碳库很难达到饱和,其固定的碳可以储存在土壤中数千年(Radabaugh *et al.*, 2018)。另外,模型模拟表明,气候变暖和海平面上升可能使得盐沼湿地能够更迅速捕获和埋藏大气中的碳,因此盐沼湿地碳汇功能在减缓全球气候变化和实现“碳达峰”和“碳中和”目标方面扮演着重要角色。

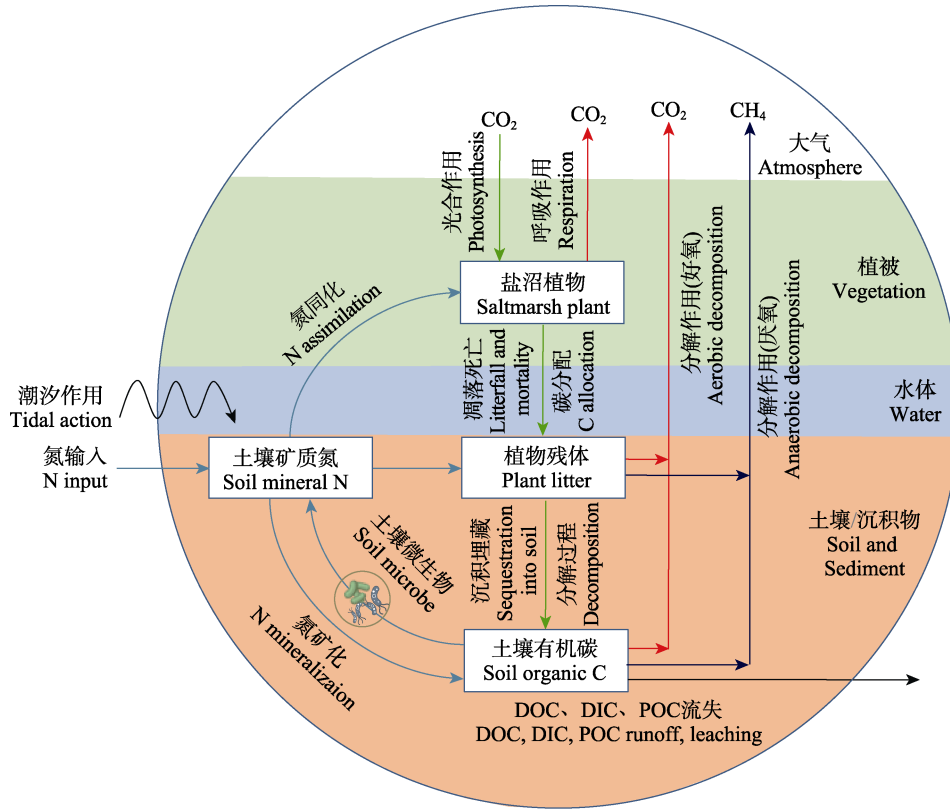
滨海盐沼湿地碳交换包含垂直方向上的 $\text{CO}_2$ 和 $\text{CH}_4$ 交换和横向方向上的可溶性有机碳(DOC)、可溶性无机碳(DIC)、颗粒有机碳(POC)交换(图1)(韩广轩, 2017)。一方面,滨海盐沼湿地生态系统作为大气 $\text{CO}_2$ 库,通过植物叶片的光合作用固定大气中的 $\text{CO}_2$ 合成有机质,即植被的总初级生产力(GPP),再通过根际沉积作用和植物残体传输到土壤中;另一方面,滨海盐沼湿地作为碳源,通过植物呼吸、微生物呼吸作用分解凋落物等有机质,从而释放 $\text{CO}_2$ 和 $\text{CH}_4$ 。此外,潮汐及地表径流作用还会将盐沼湿地中的可溶性和颗粒态的有机质淋溶和迁移到临近水体中。滨海盐沼湿地地处陆海过渡带,周期性潮汐作用下的干湿交替及其伴随的剧烈的物质交换过程是控制和维持滨海盐沼湿地碳循环关键过程和碳汇功能的特异性机制(韩广轩, 2017)。潮汐作用将近海水体中的营养盐等物质带入滨海盐沼湿地生态系统中,从而导致其养分元素化学计量关系的改变,最终影响滨海盐沼湿地生态系统有机碳周转和固定过程(Penning, 2012; 韩广轩, 2017)。例如,某些滨海盐沼输入的硝酸盐形式的氮超过 $500 \text{ kg} \cdot \text{km}^{-2} \cdot \text{a}^{-1}$ ,这种外源氮的输入可能是滨海盐沼固碳功能降低以及生态系统稳定性减弱的重要原因(Pardo *et al.*, 2011; Penning, 2012)。

陆源氮通过地表径流进入近海,导致近岸海域富营养化日益加剧(Deegan *et al.*, 2012; Xu *et al.*, 2020),是目前全球海岸带面临的最为严重的一个环境问题。在潮汐作用下,大量氮必然会进入盐沼等滨海湿地生态系统,并被盐沼植被截留,进而改变其光合碳输入、植物-土壤碳分配、土壤有机碳分解和土壤可溶性有机碳释放等碳循环关键过程(Hu

*et al.*, 2016; 韩广轩, 2017; Herbert *et al.*, 2020),并对其碳汇功能产生广泛且深刻的影响(图1)。相比工业化之前,近海水体氮负荷持续加重,全球范围内由陆地向海洋输出的氮至少增加了10倍,且主要以无机氮(DIN)为主要氮类型(Deegan *et al.*, 2012; Breitburg *et al.*, 2018)。监测及模拟结果表明,2000–2050年间,中国沿海总氮输入量将增加30%–200%(Strokal *et al.*, 2014; Wang *et al.*, 2018)。因此,阐明氮输入对盐沼湿地碳循环关键过程的影响机制,将有助于揭示氮输入对盐沼湿地蓝色碳汇形成过程与机制的影响,并为预测近岸海域富营养化背景下盐沼湿地碳库的潜在变化趋势提供科学依据。

## 1 氮输入对盐沼湿地植物光合固碳的影响

氮被认为是限制陆地生态系统净初级生产力的最重要的一种营养元素,植物可以从土壤中以无机物(如硝酸盐和铵盐)或有机物(如尿素、氨基酸和肽)的形式通过根部获得氮(Jones & Kielland, 2012; Kiba & Krapp, 2016)。最新的研究表明,全球超过50%的天然陆地生态系统受到氮限制(Du *et al.*, 2020)。氮被生物固定到土壤之后,非常容易通过淋溶或挥发从生态系统中移除,例如以溶解性有机氮(DON)和DIN形式的氮流失(Vitousek *et al.*, 2002)。从植物组织到植物个体,再到整个群落的组成部分,氮利用效率均存在较大的差异(Wang *et al.*, 2019)。氮输入一方面通过改变植株整体生物量以及植株地上和地下间、叶片和木质组织间生物量的分配等,进而影响植株的氮利用效率(Iversen *et al.*, 2010; Wang *et al.*, 2019)。例如,氮是光捕获组织及植物生物量的重要组分,氮在叶片光合酶中占很大比例,因此叶片氮含量与光合能力之间普遍存在正相关关系(Chapin III *et al.*, 2011; Mao *et al.*, 2018)。适量增加土壤氮有效性能提高植物叶片生物量及叶片氮含量,进而通过3种途径提高植物生物量:增加 $\text{CO}_2$ 的吸收、通过改变 $\text{CO}_2$ 同化作用及气孔导度提高叶片的水分利用效率、减少光消耗(Guerrieri *et al.*, 2011)。另一方面,长期氮输入可能对植物群落演替产生影响,从而影响植被群落的氮吸收利用效率(Wang *et al.*, 2019)。通常提高氮有效性能显著降低植物和群落的氮吸收利用效率,这种现象主要有三方面的原因:(1)解除氮限制后,其他环境因子(例如土壤水分、温度、光照强度等)变得更为关键,限制



**图1** 潮汐作用下氮(N)输入对盐沼湿地碳(C)循环关键过程的影响。周期性潮汐作用将近岸富营养水体中的氮带入滨海盐沼湿地生态系统中, 改变盐沼湿地土壤营养元素的化学计量关系, 进而对盐沼植物的光合作用及光合产物分配、植物呼吸作用、土壤有机碳分解、可溶性有机碳(DOC)流失等碳循环关键过程产生重要影响。DIC, 可溶性无机碳; POC, 颗粒有机碳。

**Fig. 1** Effect of nitrogen (N) input under tidal action on key processes of carbon (C) cycle in a salt marsh. Periodic tides bring N from nearshore eutrophic water into coastal salt marsh ecosystems, changing the stoichiometric relationship of soil nutrient elements in salt marsh wetland. The exogenous N input could have important impacts on the key processes of carbon cycle, such as photosynthesis and respiration of plants, distribution of photosynthetic products, decomposition of soil organic carbon and loss of dissolved organic carbon (DOC). DIC, dissolved inorganic carbon; POC, particulate organic carbon.

了植株的生长(Harpole *et al.*, 2016; Wang *et al.*, 2018); (2)高浓度NH<sub>4</sub><sup>+</sup>的潜在阳离子毒性可能限制植物的生长(Wei *et al.*, 2013); (3)氮添加引起群落内部的物种更替。此外, 植物光合作用对氮的响应还取决于植物本身的性能。例如, 某些莎草属(*Cyperus*)的植物对氮较为敏感, 即使较低的氮负荷也会对其光合能力产生负面影响; 但一些氮利用效率较高、生存能力较强的物种则更能适应氮负荷较高的生境, 并提高自身的光合能力和生产力(Mao *et al.*, 2018; Shen *et al.*, 2019)。

氮输入对盐沼湿地植物光合固碳影响并非简单的线性变化, 存在阈值效应, 主要受时间尺度、氮输入类型和水平的影响(Vivanco *et al.*, 2015; Peng *et al.*, 2019; Xiao *et al.*, 2019; Herbert *et al.*, 2020)。大部分生态系统都会受到氮的限制, 因此外源氮输入能通过提高植被的氮利用效率显著提高植物光合固碳能力, 刺激植物地上或者地下部分生长, 进而增

加土壤碳输入(Fernández-Martínez *et al.*, 2014; Herbert *et al.*, 2020)。但是, 达到一定阈值后, 继续加氮可能抑制这种正效应, 甚至产生金属毒害作用从而抑制植物正常生长(Bubier *et al.*, 2007; Peng *et al.*, 2019)。就盐沼湿地而言, 特别是新生湿地, 通常是氮限制, 因此短期内大量氮输入可能会提高其植物光合固碳能力。例如, 加氮能通过改变植株密度、促进土壤磷流动以及增大微域环境CO<sub>2</sub>浓度等途径增加植物光合固碳能力(Wu *et al.*, 2015)。但是长期大量氮输入可能导致生态系统逐渐走向氮饱和, 甚至导致生态系统从氮限制转变为磷限制, 从而降低植物光合固碳能力对氮输入的响应(Chen *et al.*, 2017; Peng *et al.*, 2019)。

## 2 氮输入对盐沼湿地植物-土壤系统碳分配的影响

氮输入不仅从整体上影响植物光合固碳能力,

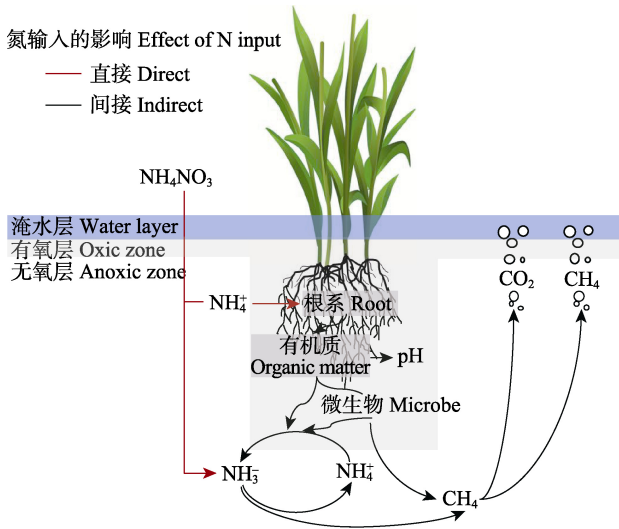
还能影响植物光合产物在植物-土壤系统中的分配比例。植物地上、地下生物量都是盐沼湿地碳汇的重要组成部分(韩广轩, 2017; Hayes *et al.*, 2017)。首先, 植物地上部分能够拦截海水中的泥沙及颗粒有机质, 帮助盐沼湿地快速抬升高程, 增大其有机碳的储存空间; 同时, 植物地上部分是植物作为初级生产者固定光合碳的器官, 其生物量大小对滨海盐沼湿地的初级生产力具有直接影响。植物地下部分一方面能够分泌根际沉积物, 是土壤可溶性有机碳等易分解碳的重要来源; 另一方面, 植物地下根系能够锚定沉积物, 防止潮汐作用对有机质的侵蚀等(Kirwan & Patrick Megonigal, 2013; Mao *et al.*, 2018)。因此, 植物生物量的空间分配能够反映近期光合同化的新碳向根系和土壤碳库的转移规律, 是土壤碳输入和碳埋藏的重要参考指标, 深刻影响着土壤碳库的变化(Bolinder *et al.*, 2012)。通常情况下, 植物光合固定的碳即时分配大小为茎叶>根>土壤, 大部分光合固定碳都留在地上部分, 氮增加则会更加提高植物同化碳向植物地上部分的流动, 同时显著增加根际土壤中碳的累积与回收率, 而降低植物根系中的光合碳分配(王婷婷等, 2017)。随着同位素技术的发展和运用, 通过测定土壤或植物中的碳同位素自然丰度值可以量化光合碳在植物-土壤系统中的动态变化、周转规律及其对环境变化的响应(Wang *et al.*, 2019; Xiao *et al.*, 2019)。例如,  $^{13}\text{C}$ 脉冲标记实验表明, 适量氮输入显著提高即时光合碳分配给根系的比例(Wang *et al.*, 2019)。氮输入通常刺激植物生长早期同化碳向土壤方向迁移, 但生长后期可能降低, 这种由生长阶段造成的差异使得光合碳在根系中的分配模式对氮输入的响应具有一定的不确定性(王婷婷等, 2017; Xiao *et al.*, 2019)。

周期性潮汐作用下, 氮输入影响盐沼湿地植物地上/地下生物量分配, 主要受时间尺度(Smith *et al.*, 2015; Armitage & Fourqurean, 2016)和氮输入水平(Bubier *et al.*, 2007; Liu *et al.*, 2016)的影响。最优分配假说认为, 在氮限制生态系统中, 氮输入提高土壤中氮利用率, 植物更易获取养分, 导致植物地上部分增量通常高于地下部分, 即氮输入引起植物根冠比降低(Wang *et al.*, 2019)。潮汐盐沼湿地通常受到氮限制, 土壤中无机氮含量升高能通过提高植物氮利用效率, 短期内显著提高植物地上及地下生物量, 进而加快土壤有机质积累速率(Deegan *et al.*,

2012; Alongi, 2014); 此外, 植物地上部分生物量增加还能捕获更多潮水中的有机碳, 同时减少土壤有机质的侵蚀(Gacia *et al.*, 2002)。从长时间尺度来看, 土壤中氮利用率升高意味着植物更易获取养分。因此长期、过量的氮输入导致盐沼湿地植物根系生长受到抑制, 地下生物量降低, 甚至还能显著提高根系的死亡率(Majdi & Öhrvik, 2004); 最终造成潮沟崩塌, 盐沼湿地退化成光滩, 反而对盐沼湿地土壤碳汇产生消极的影响(Deegan *et al.*, 2012; Pennings, 2012; Graham & Mendelsohn, 2016)。可见, 盐沼湿地碳积累过程对氮输入的响应并非简单的线性变化(Vivanco *et al.*, 2015)。异速生长理论认为, 氮输入条件下, 群落中植株不同器官随植株整体生物量变化发生非线性(异速)变化, 这种分配主要受到植物固有的异速性决定, 也受到环境因素的影响(Shipley & Meziane, 2002)。Meta分析表明, 氮输入造成不同类型植物的根冠比降低或无影响, 但从全球尺度上看, 氮输入通常降低植物根冠比(Li *et al.*, 2020)。

### 3 氮输入对盐沼湿地土壤有机碳分解的影响及微生物机制

氮输入可通过影响植物生长、根系活动、凋落物分解、微生物特性等, 进而影响土壤有机碳分解。盐沼湿地作为一个巨大的蓝色碳汇, 其碳存储主要以土壤有机碳的形式存在(Macreadie *et al.*, 2019)。氮输入影响植物生长和碳分配, 光合作用产物由叶片输送到细根, 影响细根生长及土壤呼吸。我们前期的研究发现, 盐沼湿地植物冠层光合作用在日尺度上对土壤呼吸动态变化具有明显的调节作用(Han *et al.*, 2014)。同时, 土壤微生物过程直接或间接受到氮输入的影响(图2)。氮输入通过改变土壤氮有效性, 调节土壤微生物生长、活性、群落组成/多样性及酶活性, 进而对土壤有机碳分解产生影响(Zhou *et al.*, 2017; Yang *et al.*, 2018; Xiao *et al.*, 2019; Qu *et al.*, 2020)。一方面, 氮输入可以通过提高土壤中碳、氮的含量从而改变土壤微生物生物量和微生物活性, 导致土壤有机质组分分解的变化。当底物中的氮含量较高时, 施氮更容易使微生物大量聚集, 形成较为稳定的土壤有机质; 当底物中氮含量较低时, 施氮通常促进土壤呼吸作用, 土壤中的碳不容易留存下来(Manzoni *et al.*, 2012; Cotrufo *et al.*, 2013; Xu *et al.*, 2014)。另一方面, 氮输入可能会降低土壤pH,



**图2** 氮(N)输入对盐沼湿地土壤有机碳分解的影响(参考 Hester *et al.*, 2018)。微生物过程直接或间接受到氮输入的影响。植物主要吸收铵态氮, 它刺激植物生产力和根际有机质的沉积, 从而刺激根际物质循环, 有利于根际微生物代谢。植物源性碳输入和更高的氮利用性联合刺激微生物异养呼吸, 进而刺激有氧状态下CO<sub>2</sub>的产生和排放; 而在厌氧状态下, 过量的硝态氮转化为铵态氮, 增加的铵态氮将抑制CH<sub>4</sub>氧化。

**Fig. 2** Effect of nitrogen (N) input on decomposition of soil organic carbon in a salt marsh (adapted from Hester *et al.*, 2018). Microbial processes are directly or indirectly affected by N input. Plants mainly absorb NH<sub>4</sub><sup>+</sup>-N, which stimulates plant productivity and the deposition of organic matter from the rhizosphere, thus stimulating the material circulation of rhizosphere and the metabolism of rhizosphere microorganisms. Plant derived carbon input and higher N utilization jointly stimulate microbial heterotrophic respiration, and then stimulate the production and emission of CO<sub>2</sub> in aerobic condition. In anaerobic condition, excessive NO<sub>3</sub><sup>-</sup>-N is converted into NH<sub>4</sub><sup>+</sup>-N, which will inhibit CH<sub>4</sub> oxidation.

调动土壤中的铝, 从而抑制微生物活性。氮输入可以降低真菌和细菌的比例(F:B), 同时也会引起土壤酸化(提高F:B)(Rousk *et al.*, 2010; Chen *et al.*, 2015a)。另外, 土壤酶的功能通常分为氧化或者水解, 氧化酶降解木质素等难降解的化合物, 而水解酶降解纤维素等简单的化合物(Sinsabaugh & Moorhead, 1994)。较高的矿质氮输入可以促进纤维素的分解, 但也会抑制难降解的木质素有机物的分解, 从而延缓惰性有机质分解。

氮输入对盐沼湿地土壤有机碳分解存在不确定性, 或促进、或抑制或不显著。研究发现, 氮输入可以促进湿地土壤CO<sub>2</sub>和CH<sub>4</sub>排放(Fang *et al.*, 2017; Herbert *et al.*, 2020), 但是在氮输入量很高的情况下, 土壤CO<sub>2</sub>排放量会逐渐趋向饱和, 甚至受到抑制(Xiao *et al.*, 2019)。氮输入可以促进土壤CO<sub>2</sub>排放,

这是由于氮可能促进土壤酶活性, 降低氮对生物代谢的胁迫和限制, 同时改善凋落物质量(Bragazza *et al.*, 2006; Song *et al.*, 2013; Fang *et al.*, 2017)。但是, 土壤微生物也会受到氮、磷等变化范围的限制。在施氮量较高的情况下, 土壤CO<sub>2</sub>排放量会呈现饱和和趋势(Bragazza *et al.*, 2006)。也有研究发现, 氮输入对土壤有机碳分解和土壤CO<sub>2</sub>排放的影响可能是中性的(Chen *et al.*, 2017), 这可能是由于碳对土壤微生物的限制作用(Song *et al.*, 2010), 也可能是因为氮输入后会刺激植被的自养呼吸, 但却通过抑制有机质分解降低其异养呼吸(Högberg *et al.*, 2010; Wang *et al.*, 2014)。值得注意的是, 由于土壤肥力的差异, 光合碳输入对根际土壤的“激发效应”产生或正或负的影响, 从而调节土壤有机碳分解和碳埋藏过程(Pausch & Kuzyakov, 2018)。另外, 氮输入通过影响微生物群落结构和功能进而影响CH<sub>4</sub>产生(Sinsabaugh *et al.*, 2015)。CH<sub>4</sub>由产甲烷古菌生成(Angel *et al.*, 2012), 探究产甲烷古菌的反应可能是了解土壤CH<sub>4</sub>排放对氮输入响应的关键(Xiao *et al.*, 2017)。铵态氮和硝态氮由于生物化学性质的差异, 它们对有机碳矿化的影响也不同(Chen *et al.*, 2017, 2018)。目前大量研究揭示了氮输入量和土壤有机碳分解的关系, 但是有关氮类型对土壤有机碳稳定性的影响研究较少。例如, 相对NO<sub>3</sub><sup>-</sup>, *Juncus acutiflorus* 湿地优先选择NH<sub>4</sub><sup>+</sup>作为氮源, 导致根际中NO<sub>3</sub><sup>-</sup>过剩, 改变了根际氮循环动态, 从而有利于提高微生物的种类和数量(Hester *et al.*, 2018)。当氮输入量较高时, 土壤微生物可能会优先选择能耗更低的铵态氮; 添加NH<sub>4</sub><sup>+</sup>和硝酸铵会减少CO<sub>2</sub>排放, 但也有研究发现添加NO<sub>3</sub><sup>-</sup>对土壤CO<sub>2</sub>排放影响不大(Min *et al.*, 2011)。过量的NO<sub>3</sub><sup>-</sup>会促进厌氧呼吸, 过量的NH<sub>4</sub><sup>+</sup>会抑制CH<sub>4</sub>氧化, 可能会导致CH<sub>4</sub>排放不稳定(Hester *et al.*, 2018)。我们前期在黄河三角洲4年的野外控制实验发现, 铵态氮在全年均提高了CH<sub>4</sub>排放; 硝态氮虽然在淹水期对CH<sub>4</sub>排放具有促进作用, 但影响较小(Xiao *et al.*, 2017)。另外, 我们还发现, 铵态氮对土壤呼吸有显著促进作用, 但是硝态氮施加对年平均土壤呼吸速率没有显著影响(Qu *et al.*, 2020)。铵态氮和硝态氮对土壤有机碳分解的影响不同, 这种差异也可能是土壤pH和酶活性的响应不同导致的(Min *et al.*, 2011)。

#### 4 氮输入对盐沼湿地土壤可溶性有机碳释放的影响

外源氮输入影响盐沼湿地土壤DOC的产生和累积,进而影响盐沼湿地横向碳流失。盐沼湿地土壤中的碳流失主要有2种方式,一种是以CO<sub>2</sub>和CH<sub>4</sub>等气体形式排放,另一种是以DOC形式流失。尽管DOC仅占土壤总有机碳的0.04%–0.22%,但它却是有机碳库中最活跃和不容忽视的组成部分(Bauer *et al.*, 2013)。例如,由于受到充沛降雨和周期性的潮汐作用,横向碳输出量大约占温带滨海湿地总碳输出量的40%(Majidzadeh *et al.*, 2017)。毫无疑问,外源氮输入对盐沼湿地土壤DOC的产生和释放具有显著影响(图3)。首先,外源氮输入能促进盐沼植被生长和生物量增加,而植物凋落物和根系分泌物增加能促进土壤DOC的形成和释放。但是长期氮富集可能导致盐沼湿地退化,根际激发效应促进了分解,从而降低了DOC含量(Deegan *et al.*, 2012)。其次,氮输入通过影响土壤pH间接影响土壤有机质中DOC释放,同时氮类型也会改变DOC对氮输入的响应(Chang *et al.*, 2018)。铵态氮增加通常能降低土壤pH,抑制土壤中DOC淋溶,从而减少土壤有机碳的横向流失;但硝态氮增加则通过提高土壤pH,从而促进DOC释放(Chang *et al.*, 2018; Preston *et al.*, 2020)。再次,氮输入增加了土壤微生物生物量,加快了微生物新陈代谢活动,从而加速了土壤DOC分

解(Fellman *et al.*, 2017)。然而目前研究多集中在氮输入对盐沼湿地垂直方向碳流失(CO<sub>2</sub>和CH<sub>4</sub>)的影响,忽视了近岸水体富营养化背景下以DOC为主要形式的陆海横向碳交换,制约着对滨海盐沼湿地碳循环过程的整体理解以及对其碳收支的准确评估。

#### 5 氮输入对盐沼湿地土壤碳库的影响

滨海湿地土壤碳库功能是滨海湿地一种重要的生态系统服务功能,并在全球陆地生态系统碳循环中起着关键作用,滨海湿地碳储量是其他陆地生态系统碳储量的50多倍(Ma *et al.*, 2019)。结合实际观测和生态模型预测发现,盐沼湿地中的土壤碳累积速率为(218 ± 24) g·m<sup>-2</sup>·a<sup>-1</sup> (Chmura *et al.*, 2003; Duarte *et al.*, 2005),相比之下,温带、热带森林和北方森林的土壤碳累积速率仅为0.7–13.1 g·m<sup>-2</sup>·a<sup>-1</sup> (McLeod *et al.*, 2011)。据估算,全球盐沼湿地的年际碳储量约为(87.2 ± 9.6) Tg·a<sup>-1</sup> (Chmura *et al.*, 2003; Duarte *et al.*, 2005),其碳存储密度远高于具有高植被覆盖度和地上生物量的森林生态系统。与森林生态系统的植被光合固碳不同,滨海湿地的固碳主要是由于沉积物的累积和土壤有机质的难分解性。研究发现,滨海湿地常年有大量沉积物的累积,且沉积物中有机碳的固存率高,植物产生的大量有机物质难以分解,并以土壤有机质的形式存在于地下,因而滨海湿地生态系统具有很高的土壤固碳潜力(McLeod *et al.*, 2011)。氮作为陆地生态系统最重

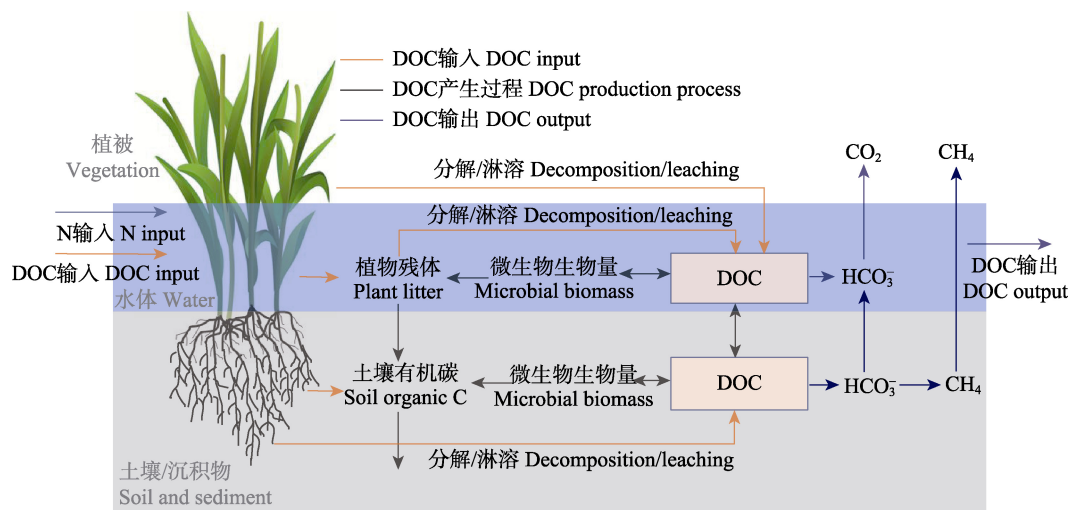


图3 氮(N)输入对盐沼湿地可溶性有机碳(DOC)产生和释放的影响。外源氮输入通常伴随着DOC输入,影响到植被生长,通过植物残体和微生物生物量改变了土壤和水体中DOC的含量,从而也会干扰CO<sub>2</sub>和CH<sub>4</sub>的排放以及DOC输出。

Fig. 3 Effect of nitrogen (N) input on production and release of dissolved organic carbon (DOC) in a salt marsh. N input is generally accompanied by DOC input, which affects vegetation growth. It alters DOC content in soil and water through plant litter and microbial biomass, thus also interfering with CO<sub>2</sub> and CH<sub>4</sub> emissions and DOC output.

要的养分, 氮的有效性对滨海湿地土壤碳收支也有着重要的影响(Mitsch & Gosselink, 2011)。为明确外源氮输入对盐沼湿地及其他湿地类型土壤碳库的影响, 许多研究通过原位控制实验、模型模拟以及meta分析等手段对氮输入背景下的湿地土壤碳储量进行了整体评估(表1)。评估结果不尽相同, 究其原因, 土壤碳库存是由碳输入和碳输出之间的平衡所决定的。已有的研究表明, 土壤呼吸作为湿地主要的碳输出途径, 对氮输入响应也是不同的, 如中国高寒湿地中,  $\text{NO}_3\text{-N}$ 的添加降低了土壤的呼吸速率(Chen *et al.*, 2017), 然而在加拿大高寒湿地以及中国滨海湿地中, 氮添加反而促进了土壤呼吸, 从而加快了土壤的碳输出(Juutinen *et al.*, 2010, Tao *et al.*, 2018)。同样, 氮添加也可以促进植被的生长并吸收更多 $\text{CO}_2$ , 提高湿地土壤地上和地下生物量, 从而提高土壤的碳输入。如在美国和加拿大的湿地碳循环研究中发现, 氮添加会通过提高生物量进而提高土壤的碳储存(Wendel *et al.*, 2011, Pastore *et al.*, 2017)。准确测量或估算湿地生态系统碳储存变化对外源氮输入的响应对研究湿地对全球生态系统碳平衡的贡献具有重要意义。

在氮有效性较高、分解率低的潮汐盐沼湿地, 氮输入一方面可能会促进植被根系生长, 提高土壤有机质输入, 加快有机质积累, 从而短期内大量氮输入可能会提高湿地的碳汇量(Hayes *et al.*, 2017)。对于森林生态系统而言, 新碳的加入能激发促进土壤老碳的更新循环。氮输入驱动下增加的碳大部分都是新的植物生物量, 而非土壤碳。因此, 氮输入对这类生态系统长期土壤碳汇反而具有消极的影响(Tipping *et al.*, 2012; Mills *et al.*, 2014)。因此, 相比之下, 由于沼泽、泥炭地等生态系统土壤有机质分解受到高湿度和富含难分解化合物的限制, 新输入的植物凋落物等有机质被封存和隔离, 甚至能够在土壤中埋藏成百上千年(Dise, 2009)。有研究表明, 在滨海湿地生态系统中, 氮输入促进芦苇(*Phragmites australis*)生长、提高芦苇生物量, 增加了土壤中的碳含量(Qu *et al.*, 2020)。另一方面, 氮输入通过影响植被的地下生物量分配进而影响土壤碳库。已有研究表明, 盐沼湿地在氮有效性较高时, 总生物量会增加, 但当氮有效性较低时, 地下部分的生物量分配会相对提高(Clough, 1992; Sherman *et al.*, 2003)。生态系统氮饱和假说认为, 向氮饱和

的生态系统中继续加氮会导致土壤功能的丧失, 例如养分循环和氮固持功能等减弱, 进而对植物生长产生影响(Aber *et al.*, 1998)。

同时, 潮汐盐沼湿地的氮有效性也会影响土壤有机质分解(Romero *et al.*, 2005; Huxham *et al.*, 2010), 并对促进微生物分解植物碎屑很重要(Romero *et al.*, 2005), 但过高的氮输入也会抑制植物根系及土壤的碳分解。因此, 氮添加充足时, 氮输入抑制了有机质分解, 同时考虑到植被生产力的提高, 从而可能会提高潮汐盐沼湿地土壤碳汇能力(Janssens *et al.*, 2010; Keuskamp *et al.*, 2015)。因而, 评估氮输入对盐沼湿地碳汇功能时应当区分氮限制生态系统和富氮生态系统(Chen *et al.*, 2015b), 目前大多数潮汐盐沼湿地都是贫氮生态系统(Mou *et al.*, 2011)。对于贫氮生态系统, 氮输入能刺激植被生长固碳, 改善土壤养分、生化特性和代谢活性, 使其更适合于微生物生境(Zhou *et al.*, 2017; Yao *et al.*, 2021), 增加土壤有机碳含量, 提高有机碳分解速率。例如, 位于美国马萨诸塞州东北部的一个长达9年的研究通过野外控制实验发现近岸水体富营养化导致的长期大量氮输入可能造成生态系统氮饱和, 从而制约潮汐盐沼湿地土壤的“蓝碳”功能(Deegan *et al.*, 2012)。

## 6 问题和展望

综上所述, 近岸水体富营养化背景下, 大量氮输入对盐沼湿地植物光合碳输入、植物-土壤碳分配和土壤碳输出等碳循环关键过程产生深刻影响, 进而影响其碳汇功能的准确评估。首先, 氮输入对湿地植物光合固碳的影响存在阈值效应(Vivanco *et al.*, 2015; Peng *et al.*, 2019)。低水平氮输入可以增强植物光合固碳能力, 但是达到一定阈值后, 继续加氮可能抑制这种正效应(Peng *et al.*, 2019)。其次, 氮输入影响植物光合产物在植物-土壤系统中的分配比例。光合固定碳向根系和土壤碳库的分配和转移规律, 深刻影响着土壤碳库的走向(Xu *et al.*, 2020)。再次, 氮输入会影响土壤有机碳的分解, 但是影响结果与氮输入类型和水平、土壤初始碳氮含量、施氮时间尺度等有很大的关系, 研究结论甚至截然相反(Chen *et al.*, 2017; Zhou *et al.*, 2017)。另外, 氮输入对盐沼湿地土壤DOC的产生和累积有显著影响(Deegan *et al.*, 2012; Chang *et al.*, 2018), 进而影响

表1 氮(N)输入对盐沼湿地及其他湿地类型土壤碳库的影响  
Table 1 Effect of nitrogen (N) input on carbon sink function of wetland ecosystems

| 湿地类型<br>Wetland type              | 国家/地区<br>Country/<br>Region | 气候类型<br>Climate type                                        | 植被类型<br>Vegetation type                                                                                                                        | 氮输入处理<br>N input treatment                                                                                                                                                                                                                                            | 氮储量现状<br>N stock<br>condition | 碳储量变化<br>Change of<br>carbon stock | 控制机理<br>Control mechanism                                                                                       | 参考文献<br>Reference                |
|-----------------------------------|-----------------------------|-------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|------------------------------------|-----------------------------------------------------------------------------------------------------------------|----------------------------------|
| 盐沼湿地<br>Salt marsh                | 美国<br>America               | 温带大陆性气候<br>Temperate continental<br>climate                 | 互花米草<br><i>Spartina alterniflora</i>                                                                                                           | NH <sub>4</sub> NO <sub>3</sub>                                                                                                                                                                                                                                       | 贫氮<br>N-limited               | 无显著影响<br>No significant<br>effect  | 提高了碳流失, 但可以在其他过程中得<br>到补偿<br>Increase gross carbon loss, but that this is<br>compensated for by other processes | Anisfeld &<br>Hill, 2011         |
|                                   | 美国<br>America               | 温带大陆性气候<br>Temperate continental<br>climate                 | <i>Schoenoplectus americanus</i> , <i>Spartina pat-</i><br><i>ens</i> , <i>Distichlis et al.</i>                                               | NH <sub>4</sub> Cl (5 g N·m <sup>-2</sup> )(5-9月, 每月加5<br>次氮)<br>NH <sub>4</sub> Cl (5 g N·m <sup>-2</sup> )(5 times monthly<br>from May to September)                                                                                                                | 未提及<br>Not given              | 增加<br>Increase                     | 提高土壤生物量, 促进碳分解<br>Increase soil biomass and stimulate de-<br>composition                                        | Pastore <i>et al.</i> ,<br>2017  |
|                                   | 中国<br>China                 | 暖温带大陆性季风气候<br>Warm temperate continental<br>monsoon climate | 芦苇、柽柳、盐地碱蓬<br><i>Phragmites australis</i> , <i>Tamaris chinensis</i> ,<br>and <i>Suaeda salsa</i>                                              | NH <sub>4</sub> NO <sub>3</sub> (100 mg N·kg <sup>-1</sup> )                                                                                                                                                                                                          | 贫氮<br>N-limited               | 减少<br>Decrease                     | 提高土壤呼吸速率<br>Increase soil respiration rate                                                                      | Tao <i>et al.</i> , 2018         |
|                                   | 韩国<br>Korea                 | 温带季风气候<br>Temperate monsoon<br>climate                      | 糙叶苔藓草、盐地碱蓬、芦苇<br><i>Carex scabrifolia</i> , <i>Phragmites australis</i> ,<br><i>Suaeda salsa</i>                                               | NH <sub>4</sub> NO <sub>3</sub> (0, 5, 25 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                      | 贫氮<br>N-limited               | 减少<br>Decrease                     | 促进甲烷排放<br>Increase methane emission                                                                             | Kim <i>et al.</i> ,<br>2020      |
|                                   | 韩国<br>Korea                 | 亚热带季风气候<br>Subtropical monsoon<br>climate                   | 茭白、芦苇<br><i>Zizania latifolia</i> , <i>Phragmites australis</i>                                                                                | NH <sub>4</sub> NO <sub>3</sub> = 4:1;<br>NH <sub>4</sub> NO <sub>3</sub> = 1:1;<br>NH <sub>4</sub> NO <sub>3</sub> = 1:4                                                                                                                                             | 贫氮<br>N-limited               | 增加<br>Increase                     | 降低土壤酶活性和 pH<br>Decreases in the microbial enzyme activities<br>and soil pH                                      | Min <i>et al.</i> ,<br>2011      |
|                                   | 荷兰<br>Netherlands           | 温带海洋性气候<br>Temperate marine climate                         | <i>Spergularia media</i> , <i>Limonium vulgare</i> ,<br><i>Festuca rubra</i> , <i>Artemisia maritima</i>                                       | NH <sub>4</sub> NO <sub>3</sub> (0, 5, 25 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                      | 贫氮<br>N-limited               | 增加<br>Increase                     | 促进植被生长<br>Stimulate plant growth                                                                                | van Wijnen &<br>Bakker, 1999     |
| 淡水湿地<br>Freshwater<br>wetland     | 苏格兰<br>Scotland             | 温带海洋性气候<br>Temperate marine climate                         | 帚石楠、白毛羊胡子草<br><i>Calluna vulgaris</i> , <i>Eriophorum vaginatum</i>                                                                            | NH <sub>4</sub> Cl, NaNO <sub>3</sub> (0, 8, 24, 56 kg<br>N·hm <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                       | 贫氮<br>N-limited               | 减少<br>Decrease                     | 提高土壤呼吸速率<br>Increase soil respiration rate                                                                      | Kivimäki <i>et al.</i> ,<br>2013 |
|                                   | 中国<br>China                 | 温带大陆性气候<br>Temperate continental cli-<br>mate               | 小叶草<br><i>Calamagrostis angustifolia</i>                                                                                                       | NH <sub>4</sub> Cl (0, 1, 3, 5 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                                 | 贫氮<br>N-limited               | 增加<br>Increase                     | 提高生物量和碳输入<br>Increase total biomass and carbon uptake                                                           | Wang <i>et al.</i> ,<br>2014     |
|                                   | 中国<br>China                 | 温带大陆性气候<br>Temperate continental<br>climate                 | 小叶草<br><i>Calamagrostis angustifolia</i>                                                                                                       | NH <sub>4</sub> NO <sub>3</sub> (24 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                            | 贫氮<br>N-limited               | 减少<br>Decrease                     | 提高微生物活性, 加速凋落物分解<br>Enhance microbial activity and increase<br>litter decomposition                             | Song <i>et al.</i> ,<br>2011     |
|                                   | 加拿大<br>Canada               | 寒温带大陆性气候<br>Cold temperate continental<br>monsoon climate   | <i>Ericaceous</i> shrubs, <i>Chamaedaphne<br/>calyculata</i> , <i>Rhododendron groenlandicum</i> ,<br><i>Kalmia angustifolia et al.</i>        | 周边环境夏季大气湿氮沉降量的 5<br>倍(1.6 g N·m <sup>-2</sup> ), 10 倍(3.2 g N·m <sup>-2</sup> ),<br>20 倍(6.4 g N·m <sup>-2</sup> )<br>5 (1.6 g N·m <sup>-2</sup> ), 10 (3.2 g N·m <sup>-2</sup> ),<br>and 20 times (6.4 g N·m <sup>-2</sup> ) ambient<br>summer time wet N deposition | 贫氮<br>N-limited               | 减少<br>Decrease                     | 提高生态系统呼吸速率<br>Increase ecosystem respiration rate                                                               | Larmola <i>et al.</i> ,<br>2013  |
| 高寒湿地<br>Alpine<br>swamp<br>meadow | 加拿大<br>Canada               | 大陆性气候<br>Continental climate                                | 泥炭藓、金发藓<br><i>Sphagnum palustre</i> , <i>Polytrichum commune</i> ,                                                                             | NH <sub>4</sub> NO <sub>3</sub> (0, 3.2, 6.4 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                   | 贫氮<br>N-limited               | 减少<br>Decrease                     | 提高土壤呼吸速率<br>Increase soil respiration rate                                                                      | Juutinen <i>et al.</i> ,<br>2010 |
|                                   | 加拿大<br>Canada               | 大陆性气候<br>Continental climate                                | <i>Sphagnum magellanicum</i> , <i>Sphagnum<br/>capillifolium</i> , <i>Polytrichum strictum et al.</i>                                          | NH <sub>4</sub> NO <sub>3</sub> (0, 5, 10, 20 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                  | 贫氮<br>N-limited               | 增加<br>Increase                     | 提高植被生物量, 降低土壤呼吸速率<br>Increase plant biomass, decrease soil res-<br>piration rate                                | Wendel <i>et al.</i> ,<br>2011   |
|                                   | 中国<br>China                 | 大陆性季风气候<br>Continental monsoon<br>climate                   | 帕米尔藓草、黑褐藓草、杉叶藻、水<br>麦冬等<br><i>Carex panirensis</i> , <i>Carex atrofusca</i> , <i>Hippuris<br/>vulgaris</i> , <i>Triglochin palustre et al.</i> | NH <sub>4</sub> NO <sub>3</sub> (0, 30 kg N·hm <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                       | 贫氮<br>N-limited               | 增加<br>Increase                     | 提高净 CO <sub>2</sub> 吸收<br>Increase net CO <sub>2</sub> uptake                                                   | Wang <i>et al.</i> ,<br>2017     |
|                                   | 中国<br>China                 | 高原气候<br>Plateau climate                                     | 西藏蒿草、异针茅<br><i>Kobresiatibetica Maximowicz</i> , <i>Stipaalienu<br/>Keng</i>                                                                   | NH <sub>4</sub> NO <sub>3</sub> (4 g N·m <sup>-2</sup> ·a <sup>-1</sup> )                                                                                                                                                                                             | 贫氮<br>N-limited               | 增加<br>Increase                     | 降低土壤呼吸速率<br>Decrease soil respiration rate                                                                      | Chen <i>et al.</i> ,<br>2017     |



盐沼湿地横向碳流失(韩广轩, 2017)。最后, 氮输入在提高植被固碳潜力的同时, 也会促进土壤, 尤其是深层土壤中有机碳分解(Mack *et al.*, 2004)。因此, 氮输入对盐沼湿地碳循环过程的影响存在不确定性, 无疑将在很大程度上制约着对盐沼湿地碳循环和碳汇功能的整体理解以及水体富营养化背景下盐沼湿地“蓝碳”吸存能力的评估和预测。

未来外源氮输入对盐沼湿地碳循环与碳收支的影响还需要在以下研究方向深入探究。

(1)氮输入对盐沼湿地植物光合固碳及碳分配过程的影响。植物光合固碳是盐沼湿地碳循环过程的一个重要环节, 但是氮输入对植物光合固碳的影响过程和机制还存在一定的局限性和不确定性。同时, 氮输入对光合碳分配的影响仍有待深入研究。利用稳定碳同位素测定技术和分子生物学技术, 阐明氮对盐沼湿地植物光合生理指标、物质代谢等生理活动和光合固碳的影响, 以及氮输入影响下光合产物在土壤-植物体系中的流动、分配和运转特征。

(2)氮输入对盐沼湿地土壤有机碳分解的微生物机制。氮输入直接影响土壤微生物多样性、代谢模式、酶活性等, 改变土壤微生物碳代谢过程以及土壤微生物群落储存、利用碳的方式, 最终影响盐沼湿地土壤有机碳的分解。综合应用高通量测序、核酸分析、同位素技术等新兴技术手段, 分析微生物底物利用效率以及控制氮转化的关键微生物功能基因, 进一步明确氮输入对盐沼湿地土壤有机碳分解的微生物机制。

(3)氮输入对盐沼湿地土壤DOC产生和横向流动的影响。盐沼湿地碳与近海水体之间的横向碳交换通量对于滨海湿地碳库动态变化有着重要贡献。外源氮输入影响盐沼湿地土壤DOC的产生和释放, 进而影响盐沼湿地横向碳流失。但是关于潮汐作用下外源氮输入对滨海盐沼湿地土壤DOC产生和输出影响的研究较为薄弱。

(4)氮类型对盐沼湿地土壤碳库的影响。随着全球NO<sub>x</sub>排放的有效控制, 硝态氮输入持续下降, 而铵态氮输入呈上升趋势。目前大量研究揭示了氮输入量和碳循环过程之间的关系, 但是有关氮类型对盐沼湿地碳汇功能的影响研究较少。因此, 需要综合研究不同氮类型对盐沼湿地植物光合碳输入、植物-土壤碳分配和土壤碳输出等碳循环关键过程的影响, 深入了解氮类型对盐沼湿地生态系统土壤碳

库的影响。

## 参考文献

- Aber J, McDowell W, Nadelhoffer K, Magill A, Berntson G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I (1998). Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. *BioScience*, 48, 921-934.
- Alongi DM (2014). Carbon cycling and storage in mangrove forests. *Annual Review of Marine Science*, 6, 195-219.
- Angel R, Claus P, Conrad R (2012). Methanogenic archaea are globally ubiquitous in aerated soils and become active under wet anoxic conditions. *The ISME Journal*, 6, 847-862.
- Anisfeld SC, Hill TD (2012). Fertilization effects on elevation change and belowground carbon balance in a long island sound tidal marsh. *Estuaries and Coasts*, 35, 201-211.
- Armitage AR, Fourqurean JW (2016). Carbon storage in sea-grass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences*, 13, 313-321.
- Bauer JE, Cai WJ, Raymond PA, Bianchi TS, Hopkinson CS, Regnier PAG (2013). The changing carbon cycle of the coastal ocean. *Nature*, 504, 61-70.
- Bolinder MA, Kätterer T, Andrén O, Parent LE (2012). Estimating carbon inputs to soil in forage-based crop rotations and modeling the effects on soil carbon dynamics in a Swedish long-term field experiment. *Canadian Journal of Soil Science*, 92, 821-833.
- Bragazza L, Freeman C, Jones T, Rydin H, Limpens J, Fenner N, Ellis T, Gerdol R, Hájek M, Hájek T, Iacumin P, Kutnar L, Tahvanainen T, Toberman H (2006). Atmospheric nitrogen deposition promotes carbon loss from peat bogs. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 19386-19389.
- Breitbart D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ, Garçon V, Gilbert D, Gutiérrez D, Isensee K, Jacinto GS, Limburg KE, Montes I, Naqvi SWA, Pitcher GC, *et al.* (2018). Declining oxygen in the global ocean and coastal waters. *Science*, 359, eaam7240. DOI: 10.1126/science.aam7240.
- Bubier JL, Moore TR, Bledzki LA (2007). Effects of nutrient addition on vegetation and carbon cycling in an ombrotrophic bog. *Global Change Biology*, 13, 1168-1186.
- Chang RY, Li N, Sun XY, Hu ZY, Bai XS, Wang GX (2018). Nitrogen addition reduces dissolved organic carbon leaching in a montane forest. *Soil Biology & Biochemistry*, 127, 31-38.
- Chapin III FS, Matson PA, Mooney HA (2011). Carbon input to terrestrial ecosystems//Chapin III FS, Matson PA, Mooney HA. *Principles of Terrestrial Ecosystem Ecology*. Springer, New York.
- Chen DM, Lan ZC, Hu SJ, Bai YF (2015a). Effects of nitrogen

- enrichment on belowground communities in grassland: relative role of soil nitrogen availability vs. soil acidification. *Soil Biology & Biochemistry*, 89, 99-108.
- Chen H, Li D, Gurmessa GA, Yu G, Li L, Zhang W, Fang H, Mo J (2015b). Effects of nitrogen deposition on carbon cycle in terrestrial ecosystems of China: a meta-analysis. *Environmental Pollution*, 206, 352-360.
- Chen XP, Wang GX, Zhang T, Mao TX, Wei D, Song CL, Hu ZY, Huang KW (2017). Effects of warming and nitrogen fertilization on GHG flux in an alpine swamp meadow of a permafrost region. *Science of the Total Environment*, 601-602, 1389-1399.
- Chen ZM, Xu YL, He YJ, Zhou XH, Fan JL, Yu HY, Ding WX (2018). Nitrogen fertilization stimulated soil heterotrophic but not autotrophic respiration in cropland soils: a greater role of organic over inorganic fertilizer. *Soil Biology & Biochemistry*, 116, 253-264.
- Chmura GL, Anisfeld SC, Cahoon DR, Lynch JC (2003). Global carbon sequestration in tidal, saline wetland soils. *Global Biogeochemical Cycles*, 17, 1111. DOI: 10.1029/2002GB001917.
- Choi Y, Wang Y (2004). Dynamics of carbon sequestration in a coastal wetland using radiocarbon measurements. *Global Biogeochemical Cycles*, 18, GB4016. DOI: 10.1029/2004GB002261.
- Clough BF (1992). Primary productivity and growth of mangrove forests//Robertson AI, Alongi DM. *Tropical Mangrove Ecosystems*. The American Geophysical Union, Washington D.C. 225-249.
- Cotrufo MF, Wallenstein MD, Boot CM, Deneff K, Paul E (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? *Global Change Biology*, 19, 988-995.
- Deegan LA, Johnson DS, Warren RS, Peterson BJ, Fleeger JW, Fagherazzi S, Wollheim WM (2012). Coastal eutrophication as a driver of salt marsh loss. *Nature*, 490, 388-392.
- Dise NB (2009). Peatland response to global change. *Science*, 326, 810-811.
- Du E, Terrer C, Pellegrini AFA, Ahlström A, van Lissa CJ, Zhao X, Xia N, Wu X, Jackson RB (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, 13, 221-226.
- Duarte CM, Middelburg JJ, Caraco N (2005). Major role of marine vegetation on the oceanic carbon cycle. *Biogeochemistry*, 2, 1-8.
- Fang C, Ye JS, Gong Y, Pei J, Yuan Z, Xie C, Zhu Y, Yu Y (2017). Seasonal responses of soil respiration to warming and nitrogen addition in a semi-arid alfalfa-pasture of the Loess Plateau, China. *Science of the Total Environment*, 590-591, 729-738.
- Fellman JB, D'Amore DV, Hood E, Cunningham P (2017). Vulnerability of wetland soil carbon stocks to climate warming in the perhumid coastal temperate rainforest. *Biogeochemistry*, 133, 165-179.
- Fernández-Martínez M, Vicca S, Janssens IA, Sardans J, Luysaert S, Campioli M, Chapin III FS, Ciais P, Malhi Y, Obersteiner M, Papale D, Piao SL, Reichstein M, Rodà F, Peñuelas J (2014). Nutrient availability as the key regulator of global forest carbon balance. *Nature Climate Change*, 4, 471-476.
- Gacia E, Duarte CM, Middelburg JJ (2002). Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnology and Oceanography*, 47, 23-32.
- Graham SA, Mendelsohn IA (2016). Contrasting effects of nutrient enrichment on below-ground biomass in coastal wetlands. *Journal of Ecology*, 104, 249-260.
- Guerrieri R, Mencuccini M, Sheppard LJ, Saurer M, Perks MP, Levy P, Sutton MA, Borghetti M, Grace J (2011). The legacy of enhanced N and S deposition as revealed by the combined analysis of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$  and  $\delta^{15}\text{N}$  in tree rings. *Global Change Biology*, 17, 1946-1962.
- Han G, Xing Q, Yu J, Luo Y, Li D, Yang L, Wang G, Mao P, Xie B, Mickle N (2014). Agricultural reclamation effects on ecosystem  $\text{CO}_2$  exchange of a coastal wetland in the Yellow River Delta. *Agriculture Ecosystems & Environment*, 196, 187-198.
- Han GX (2017). Effect of tidal action and drying-wetting cycles on carbon exchange in a salt marsh: progress and prospects. *Acta Ecologica Sinica*, 37, 8170-8178. [韩广轩 (2017). 潮汐作用和干湿交替对盐沼湿地碳交换的影响机制研究进展. *生态学报*, 37, 8170-8178.]
- Harpole WS, Sullivan LL, Lind EM, Firn J, Adler PB, Borer ET, Chase J, Fay PA, Hautier Y, Hillebrand H, MacDougall AS, Seabloom EW, Williams R, Bakker JD, Cadotte MW, et al. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537, 93-96.
- Hayes MA, Jesse A, Tabet B, Reef R, Keuskamp JA, Lovelock CE (2017). The contrasting effects of nutrient enrichment on growth, biomass allocation and decomposition of plant tissue in coastal wetlands. *Plant and Soil*, 416, 193-204.
- Herbert ER, Schubauer-Berigan JP, Craft CB (2020). Effects of 10 yr of nitrogen and phosphorus fertilization on carbon and nutrient cycling in a tidal freshwater marsh. *Limnology and Oceanography*, 65, 1669-1687.
- Hester ER, Harpenslager SF, van Diggelen JMH, Lamers LL, Jetten MSM, Lüke C, Lückner S, Welte CU (2018). Linking nitrogen load to the structure and function of wetland soil and rhizosphere microbial communities. *mSystems*, 3, e00214-17. DOI: 10.1128/mSystems.00214-17.
- Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm

- T, Högberg P (2010). Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist*, 187, 485-493.
- Hu Y, Wang L, Fu X, Yan J, Wu J, Tsang Y, Le Y, Sun Y (2016). Salinity and nutrient contents of tidal water affects soil respiration and carbon sequestration of high and low tidal flats of Jiuduansha wetlands in different ways. *Science of the Total Environment*, 565, 637-648.
- Huxham M, Langat J, Tamooh F, Kennedy H, Mencuccini M, Skov MW, Kairo J (2010). Decomposition of mangrove roots: effects of location, nutrients, species identity and mix in a Kenyan forest. *Estuarine Coastal and Shelf Science*, 88, 135-142.
- Iversen CM, Bridgman SD, Kellogg LE (2010). Scaling plant nitrogen use and uptake efficiencies in response to nutrient addition in peatlands. *Ecology*, 91, 693-707.
- Janssens IA, Dieleman W, Luysaert S, Subke JA, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G, Papale D, Piao SL, Schulze ED, Tang J, Law BE (2010). Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, 3, 315-322.
- Jones DL, Kielland K (2012). Amino acid, peptide and protein mineralization dynamics in a taiga forest soil. *Soil Biology & Biochemistry*, 55, 60-69.
- Juutinen S, Bubier JL, Moore TR (2010). Responses of vegetation and ecosystem CO<sub>2</sub> exchange to 9 years of nutrient addition at Mer Bleue bog. *Ecosystems*, 13, 874-887.
- Keuskamp JA, Feller IC, Laanbroek HJ, Verhoeven JTA, Hefting MM (2015). Short- and long-term effects of nutrient enrichment on microbial exoenzyme activity in mangrove peat. *Soil Biology & Biochemistry*, 81, 38-47.
- Kiba T, Krapp A (2016). Plant nitrogen acquisition under low availability: regulation of uptake and root architecture. *Plant and Cell Physiology*, 57, 707-714.
- Kim J, Chaudhary DR, Kang H (2020). Nitrogen addition differently alters GHGs production and soil microbial community of tidal salt marsh soil depending on the types of halophyte. *Applied Soil Ecology*, 150, 103440. DOI: 10.1016/j.apsoil.2019.103440.
- Kirwan ML, Patrick Megonigal J (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, 504, 53-60.
- Kivimäki SK, Sheppard LJ, Leith ID, Grace J (2013). Long-term enhanced nitrogen deposition increases ecosystem respiration and carbon loss from a *Sphagnum* bog in the Scottish Borders. *Environmental and Experimental Botany*, 90, 53-61.
- Larmola T, Bubier JL, Kobylyanec C, Basiliko N, Juutinen S, Humphreys E, Preston M, Moore TR (2013). Vegetation feedbacks of nutrient addition lead to a weaker carbon sink in an ombrotrophic bog. *Global Change Biology*, 19, 3729-3739.
- Li W, Zhang H, Huang G, Liu R, Zhao C, McDowell NG (2020). Effects of nitrogen enrichment on tree carbon allocation: a global synthesis. *Global Ecology and Biogeography*, 29, 573-589.
- Liu J, Wu N, Wang H, Sun J, Peng B, Jiang P, Bai E (2016). Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. *Ecology*, 97, 1796-1806.
- Ma TT, Li XW, Bai JH, Ding SY, Zhou FW, Cui BS (2019). Four decades' dynamics of coastal blue carbon storage driven by land use/land cover transformation under natural and anthropogenic processes in the Yellow River Delta, China. *Science of the Total Environment*, 655, 741-750.
- Mack MC, Schuur EAG, Sydonia Bret-Harte M, Shaver GR, Chapin III FS (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, 431, 440-443.
- Macreadie PI, Anton A, Raven JA, Beaumont N, Connolly RM, Friess DA, Kelleway JJ, Kennedy H, Kuwae T, Lavery PS, Lovelock CE, Smale DA, Apostolaki ET, Atwood TB, Baldock J, et al. (2019). The future of Blue Carbon science. *Nature Communications*, 10, 3998. DOI: 10.1038/s41467-019-11693-w.
- Majdi H, Öhrvik J (2004). Interactive effects of soil warming and fertilization on root production, mortality, and longevity in a Norway spruce stand in Northern Sweden. *Global Change Biology*, 10, 182-188.
- Majidzadeh H, Uzun H, Ruecker A, Miller D, Vernon J, Zhang HY, Bao SW, Tsui MTK, Karanfil T, Chow AT (2017). Extreme flooding mobilized dissolved organic matter from coastal forested wetlands. *Biogeochemistry*, 136, 293-309.
- 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.
- Mao Q, Lu X, Mo H, Gundersen P, Mo J (2018). Effects of simulated N deposition on foliar nutrient status, N metabolism and photosynthetic capacity of three dominant understory plant species in a mature tropical forest. *Science of the Total Environment*, 610-611, 555-562.
- McLeod E, Chmura GL, Bouillon S, Salm R, Björk M, Duarte CM, Lovelock CE, Schlesinger WH, Silliman BR (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Frontiers in Ecology and the Environment*, 9, 552-560.
- Mills RTE, Tipping E, Bryant CL, Emmett BA (2014). Long-term organic carbon turnover rates in natural and semi-natural topsoils. *Biogeochemistry*, 118, 257-272.
- 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.
- Mitsch WJ, Gosselink JG (2011). *Wetlands*. 4th ed. John Wiley & Sons, Hoboken, USA.
- Mou XJ, Sun ZG, Wang LL, Wang CY (2011). Nitrogen cycle of a typical *Suaeda salsa* marsh ecosystem in the Yellow River estuary. *Journal of Environmental Sciences*, 23, 958-967.
- Pardo LH, Fenn ME, Goodale CL, Geiser LH, Driscoll CT, Allen EB, Baron JS, Bobbink R, Bowman WD, Clark CM, Emmett B, Gilliam FS, Greaver TL, Hall SJ, Lilleskov EA, et al. (2011). Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications*, 21, 3049-3082.
- Pastore MA, Megonigal JP, Langley JA (2017). Elevated CO<sub>2</sub> and nitrogen addition accelerate net carbon gain in a brackish marsh. *Biogeochemistry*, 133, 73-87.
- Pausch J, Kuzyakov Y (2018). Carbon input by roots into the soil: quantification of rhizodeposition from root to ecosystem scale. *Global Change Biology*, 24, 1-12.
- Peng Y, Peng Z, Zeng X, Hou X, JH (2019). Effects of nitrogen-phosphorus imbalance on plant biomass production: a global perspective. *Plant and Soil*, 436, 245-252.
- Pennings SC (2012). Ecology: the big picture of marsh loss. *Nature*, 490, 352-353.
- Preston DL, Sokol ER, Hell K, McKnight DM, Johnson PTJ (2020). Experimental effects of elevated temperature and nitrogen deposition on high-elevation aquatic communities. *Aquatic Sciences*, 82, 7. DOI: 10.1007/s00027-019-0678-4.
- Qu W, Han G, Eller F, Xie B, Wang J, Wu H, Li J, Zhao M (2020). Nitrogen input in different chemical forms and levels stimulates soil organic carbon decomposition in a coastal wetland. *Catena*, 194, 104672. DOI: 10.1016/j.catena.2020.104672.
- Radabaugh KR, Moyer RP, Chappel AR, Powell CE, Bociu I, Clark BC, Smoak JM (2018). Coastal blue carbon assessment of mangroves, salt marshes, and salt barrens in Tampa Bay, Florida, USA. *Estuaries and Coasts*, 41, 1496-1510.
- Romero LM, Smith III TJ, Fourqurean JW (2005). Changes in mass and nutrient content of wood during decomposition in a South Florida mangrove forest. *Journal of Ecology*, 93, 618-631.
- Rousk J, Brookes PC, Bååth E (2010). Investigating the mechanisms for the opposing pH relationships of fungal and bacterial growth in soil. *Soil Biology & Biochemistry*, 42, 926-934.
- Shen H, Dong S, Li S, Xiao J, Han Y, Yang M, Zhang J, Gao X, Xu Y, Li Y, Zhi Y, Liu S, Dong Q, Zhou H, Yeomans JC (2019). Effects of simulated N deposition on photosynthesis and productivity of key plants from different functional groups of alpine meadow on Qinghai-Tibetan Plateau. *Environmental Pollution*, 251, 731-737.
- Sherman RE, Fahey TJ, Martinez P (2003). Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. *Ecosystems*, 6, 384-398.
- Shipley B, Meziane D (2002). The balanced-growth hypothesis and the allometry of leaf and root biomass allocation. *Functional Ecology*, 16, 326-331.
- Sinsabaugh RL, Belnap J, Rudgers J, Kuske CR, Martinez N, Sandquist D (2015). Soil microbial responses to nitrogen addition in arid ecosystems. *Frontiers in Microbiology*, 6, 819. DOI: 10.3389/fmicb.2015.00819.
- Sinsabaugh RL, Moorhead DL (1994). Resource allocation to extracellular enzyme production: a model for nitrogen and phosphorus control of litter decomposition. *Soil Biology & Biochemistry*, 26, 1305-1311.
- Smith MD, La Pierre KJ, Collins SL, Knapp AK, Gross KL, Barrett JE, Frey SD, Gough L, Miller RJ, Morris JT, Rustad LE, Yarie J (2015). Global environmental change and the nature of aboveground net primary productivity responses: insights from long-term experiments. *Oecologia*, 177, 935-947.
- Song CC, Liu DY, Yang GS, Song YY, Mao R (2011). Effect of nitrogen addition on decomposition of *Calamagrostis angustifolia* litters from freshwater marshes of Northeast China. *Ecological Engineering*, 37, 1578-1582.
- Song CC, Wang LL, Tian HQ, Liu DY, Lu CQ, Xu XF, Zhang LH, Yang GS, Wan ZM (2013). Effect of continued nitrogen enrichment on greenhouse gas emissions from a wetland ecosystem in the Sanjiang Plain, Northeast China: a 5 year nitrogen addition experiment. *Journal of Geophysical Research*, 118, 741-751.
- Song MH, Jiang J, Cao GM, Xu XL (2010). Effects of temperature, glucose and inorganic nitrogen inputs on carbon mineralization in a Tibetan alpine meadow soil. *European Journal of Soil Biology*, 46, 375-380.
- Strokal M, Yang H, Zhang Y, Kroeze C, Li L, Luan S, Wang H, Yang S, Zhang Y (2014). Increasing eutrophication in the coastal seas of China from 1970 to 2050. *Marine Pollution Bulletin*, 85, 123-140.
- Tao BX, Liu CY, Zhang BH, Dong J (2018). Effects of inorganic and organic nitrogen additions on CO<sub>2</sub> emissions in the coastal wetlands of the Yellow River Delta, China. *Atmospheric Environment*, 185, 159-167.
- Tipping E, Rowe EC, Evans CD, Mills RTE, Emmett BA, Chaplow JS, Hall JR (2012). N<sup>14</sup>C: a plant-soil nitrogen and carbon cycling model to simulate terrestrial ecosystem responses to atmospheric nitrogen deposition. *Ecological Modelling*, 247, 11-26.
- van Wijnen HJ, Bakker JP (1999). Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. *Journal of Ecology*, 87,

- 265-272.
- Vitousek PM, Hättenschwiler S, Olander L, Allison S (2002). Nitrogen and nature. *AMBIO: A Journal of the Human Environment*, 31, 97-101.
- Vivanco L, Irvine IC, Martiny JBH (2015). Nonlinear responses in salt marsh functioning to increased nitrogen addition. *Ecology*, 96, 936-947.
- Wang B, Xin M, Wei Q, Xie L (2018). A historical overview of coastal eutrophication in the China Seas. *Marine Pollution Bulletin*, 136, 394-400.
- Wang H, Yu L, Zhang Z, Liu W, Chen L, Cao G, Yue H, Zhou J, Yang Y, Tang Y, He J (2017). Molecular mechanisms of water table lowering and nitrogen deposition in affecting greenhouse gas emissions from a Tibetan alpine wetland. *Global Change Biology*, 23, 815-829.
- Wang J, Gao Y, Zhang Y, Yang J, Smith MD, Knapp AK, Eisenstat DM, Han X (2019). Asymmetry in above- and belowground productivity responses to N addition in a semi-arid temperate steppe. *Global Change Biology*, 25, 2958-2969.
- Wang Q, Wang S, He T, Liu L, Wu J (2014). Response of organic carbon mineralization and microbial community to leaf litter and nutrient additions in subtropical forest soils. *Soil Biology & Biochemistry*, 71, 13-20.
- Wang TT, Zhu ZK, Zhu HH, Tang ZZ, Pang J, Li BZ, Su YR, Ge TD, Wu JS (2017). Input and distribution of photosynthesized carbon in soil-rice system affected by water management and nitrogen fertilization. *Environmental Science*, 38, 1227-1234. [王婷婷, 祝贞科, 朱捍华, 汤珍珠, 庞静, 李宝珍, 苏以荣, 葛体达, 吴金水 (2017). 施氮和水分管理对光合碳在土壤-水稻系统间分配的量化研究. *环境科学*, 38, 1227-1234.]
- Wei C, Yu Q, Bai E, Lü X, Li Q, Xia J, Kardol P, Liang W, Wang Z, Han X (2013). Nitrogen deposition weakens plant-microbe interactions in grassland ecosystems. *Global Change Biology*, 19, 3688-3697.
- Wendel S, Moore T, Bubier J, Blodau C (2011). Experimental nitrogen, phosphorus, and potassium deposition decreases summer soil temperatures, water contents, and soil CO<sub>2</sub> concentrations in a northern bog. *Biogeosciences*, 8, 585-595.
- Wu Y, Blodau C, Moore TR, Bubier J, Juutinen S, Larmola T (2015). Effects of experimental nitrogen deposition on peatland carbon pools and fluxes: a modelling analysis. *Biogeosciences*, 12, 79-101.
- Xiao LL, Xie BH, Liu JC, Zhang HX, Han GX, Wang OM, Liu FH (2017). Stimulation of long-term ammonium nitrogen deposition on methanogenesis by Methanocellaceae in a coastal wetland. *Science of the Total Environment*, 595, 337-343.
- Xiao ML, Zang HD, Liu SL, Ye RZ, Zhu ZK, Su YR, Wu JS, Ge TD (2019). Nitrogen fertilization alters the distribution and fates of photosynthesized carbon in rice-soil systems: a <sup>13</sup>C-CO<sub>2</sub> pulse labeling study. *Plant and Soil*, 445, 101-112.
- Xu X, Liu H, Liu YZ, Zhou CH, Pan LH, Fang CM, Nie M, Li B (2020). Human eutrophication drives biogeographic salt marsh productivity patterns in China. *Ecological Applications*, 30, e02045. DOI: 10.1002/eap.2045.
- Xu X, Schimel JP, Thornton PE, Song X, Yuan F, Goswami S (2014). Substrate and environmental controls on microbial assimilation of soil organic carbon: a framework for Earth system models. *Ecology Letters*, 17, 547-555.
- Yang K, Zhu JJ, Gu JC, Xu S, Yu LZ, Wang ZQ (2018). Effects of continuous nitrogen addition on microbial properties and soil organic matter in a *Larix gmelinii* plantation in China. *Journal of Forestry Research*, 29, 85-92.
- Yao RJ, Yang JS, Wang XP, Xie WP, Zheng FL, Li HQ, Tang C, Zhu H (2021). Response of soil characteristics and bacterial communities to nitrogen fertilization gradients in a coastal salt-affected agroecosystem. *Land Degradation & Development*, 32, 338-353.
- Zhou ZH, Wang CK, Zheng MH, Jiang LF, Luo YQ (2017). Patterns and mechanisms of responses by soil microbial communities to nitrogen addition. *Soil Biology & Biochemistry*, 115, 433-441.

责任编辑: 阎恩荣 编辑: 赵航