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外来入侵植物对土壤氮转化主要过程及相关微生物的影响

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摘 要 外来入侵植物不仅影响植物群落组成、生物多样性以及生态系统的结构和功能, 而且显著影响土壤氮(N)的转化过程。外来入侵植物对N循环影响的研究已成为入侵生态学的研究热点。N循环与凋落物的分解和养分释放有关, 外来入侵植物能够改变凋落物的组成与结构, 进而影响土壤的N转化过程。另外, 外来入侵植物的化感作用也会影响土壤N转化过程, 这些作用与土壤微生物的结构与功能变化密不可分。该文主要从凋落物分解与养分释放及外来入侵植物化感作用两个方面综述了外来入侵植物对土壤N转化的影响, 总结了外来入侵植物对土壤N转化相关土壤微生物(尤其是氨氧化细菌与氨氧化古菌)的影响, 探讨了土壤N转化对外来植物入侵的反馈, 并探讨了丛植菌根真菌与外来入侵植物的互相影响。

关键词 生物入侵; 化感; 凋落物; 硝化; 氨氧化微生物; 丛枝菌根真菌

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Effects of plant invasion on soil nitrogen transformation processes and its associated microbes

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Abstract

Invasive alien plants not only influence plant community composition, biodiversity and ecosystem structure and function, but also have severe impacts on soil nitrogen transformation processes. The effects of invasive alien plants on nitrogen (N) cycling have been one of the hot topics in invasion ecology. Litter decomposition and its nutrient release play an important role in nutrient cycling. In addition, invasive alien plants have the potential to influence soil N transformation through allelopathy. All these processes are tightly related to soil microbes. Therefore, this review mainly focuses on litter decomposition and its nutrient release, and allelopathy to understand the effects of plant invasion on soil N transformation. Changes in soil N transformation and soil microbes (esp. Ammonia oxidizing bacteria and Ammonia oxidizing archaea) due to plant invasion, as well as the feedbacks of these changes to further invasion of alien plants were discussed. Finally, the interactions between arbuscular mycorrhizal fungi and plant invasion were reviewed.

Key words biological invasion; allelopathy; litter; nitrification; ammonia oxidizer; arbuscular mycorrhizal fungi

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生物入侵已经成为影响全球生态环境和经济的重大问题。外来入侵植物对生物多样性及生态系统的结构与功能具有显著影响(D’Antonio & Vitousek, 1992; Mack *et al*., 2001; Vilà *et al*., 2011; Pyšek *et al*., 2012; D’Antonio & Flory, 2017)。氮(N)循环作为生态系统物质循环的重要组成部分, 其主要过程极易受到生态系统结构与物种组成改变的影响, 外来入侵植物对N循环的影响已成为入侵生态学的研究热点

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之一(Evans *et al*., 2001; Knops *et al*., 2002; Ehrenfeld, 2003; Liao *et al*., 2008; Castro-Díez *et al*., 2012; Wang *et al*., 2015a; McLeod *et al*., 2016; Jo *et al*., 2017)。

N循环过程主要包括: 植物对N的吸收利用、枯枝落叶对土壤N的输入、土壤微生物对N的固定、土壤不同形态N之间的转换、N释放等过程。目前, 外来入侵植物影响土壤N循环的研究主要是通过比较外来植物与本地植物对土壤的总N含量、无机N含量、矿化速率、硝化速率和反硝化速率影响的差异, 以及对比研究外来入侵植物与本地植物的凋落物分解与养分释放的差异, 进而阐述外来入侵植物对土壤N转化过程的影响(Kourtev *et al*., 1999; Mack *et al*., 2001; Mack & D'Antonio, 2003; Windham & Ehrenfeld, 2003; Hawkes *et al*., 2005; Liao *et al*., 2008; Chen *et al*., 2009b; Stark & Norton, 2015; McLeod *et al*., 2016)。

土壤的硝化作用与反硝化作用是两个伴随发生的动态过程。许多研究表明外来植物入侵提高了土壤的无机N含量与硝化速率(Liao *et al*., 2008; 刘小文等, 2016), 但也有部分研究发现外来植物入侵区域的土壤N矿化速率低于本地植物生长区域(Evans *et al*., 2001)。外来入侵植物除了影响硝化过程, 也会因增加反硝化微生物碳源的供给而促进反硝化作用(Rooth *et al*., 2003; Ehrenfeld, 2010)。由于反硝化作用常发生在厌氧环境, 所以外来入侵植物对湿地生态系统的反硝化作用影响尤为明显。李家兵等(2017)在闽江口鳝鱼滩湿地研究外来入侵植物互花米草(*Spartina alterniflora*)对N转化的影响, 发现不同季节互花米草入侵对沉积物反硝化速率的影响不同, 在夏季互花米草入侵显著提高了沉积物反硝化速率, 沉积物-水界面N_2O交换通量明显升高。然而, 近期Roley等(2018)采用推挽式同位素配对技术(push-pull isotope pairing technique)对比研究了入侵澳大利亚的外来植物芦苇(*Phragmites australis*)与本地植物长苞香蒲(*Typha domingensis*)单优群落沉积物的反硝化作用, 发现反硝化作用变化较大, 外来植物芦苇的入侵对反硝化作用的影响并不显著(Roley *et al*., 2018)。

赵同谦等(2011)综述了外来植物对陆地生态系统N循环的影响途径, 这些影响途径主要包括: 植物的固N作用(Maron & Connors, 1996; Haubensak & D'Antonio, 2011), 植物的N吸收、分配及再利用, 凋落物的分解(Kaproth *et al*., 2013; 黄成成等, 2018), 土壤生物群落(Dawson & Schrama, 2016)与土壤微环境的改变等。凋落物的分解与养分释放是土壤N转化的主要环节(Ehrenfeld, 2003; Allison & Vitousek, 2004; Hättenschwiler *et al*., 2005; Jo *et al*., 2017), 土壤微生物(包括氨氧化微生物)在这些过程中起关键作用(Hawkes *et al*., 2005; Shannon-Firestone *et al*., 2015)。外来入侵植物对土壤微生物具有显著的影响(Callaway *et al*., 2004b; Hawkes *et al*., 2006; van der Putten *et al*., 2007), 可见入侵植物通过改变土壤微生物进而影响凋落物的分解与土壤N转化过程。另外, 外来入侵植物往往具有较强的化感作用(Callaway & Aschehoug, 2000; Bais *et al*., 2003; Hierro & Callaway, 2003; Callaway & Ridenour, 2004), 它们释放的化感物质对N循环过程影响显著(Ridenour & Callaway, 2001; Chen *et al*., 2009b; Inderjit *et al*., 2011a, 2011b)。已有许多针对外来植物入侵过程中凋落物的分解和养分释放, 以及入侵植物的化感作用对土壤N转化过程开展的研究。因此, 本文在阐述外来入侵植物对土壤N转化影响的基础上, 重点从外来入侵植物的化感作用与凋落物分解两个方面综述入侵植物对土壤N转化的影响, 并从土壤微生物的角度对入侵植物影响土壤N转化的机制进行了初步探讨。

1 外来入侵植物凋落物与土壤氮转化

凋落物分解与养分释放是生态系统养分循环中的重要过程(Vogt *et al*., 1991), 它控制着植物养分的再循环以及土壤养分的可利用性(Parker *et al*., 1984; Koukoura, 1998)。入侵植物通过影响凋落物分解与养分释放过程改变土壤N循环。大多数研究表明, 入侵植物凋落物的分解速率比本地植物凋落物的分解速率快, 导致外来植物入侵会加快系统的养分循环速率, 这主要与入侵植物凋落物的化学组成有关(Allison & Vitousek, 2004; Rothstein *et al*., 2004; 陈宝明等, 2008; Meisner *et al*., 2012)。入侵植物凋落物含N量往往比本地种的高, 含N量高的凋落物分解更快, 所以入侵植物的凋落物分解相对更快(Allison & Vitousek, 2004)。Liao等(2008)采用meta分析发现外来入侵植物可以加速被入侵生态系统的凋落物的分解速率, 这会使植物体的N含量上升

86%–112%, 植物N含量的增加会进一步提高(+38%)生态系统凋落物的N含量, 进而加快入侵地的凋落物分解与养分的释放。然而, 也有研究表明外来入侵植物的凋落物分解比本地植物的慢。例如, 外来入侵植物*Phragmites australis*地上部分凋落物的分解速率比本地植物*Spartina patens*的慢(Windham & Ehrenfeld, 2003); 外来入侵草本植物*Aegilops triuncialis*使入侵系统的凋落物分解变慢, 进而减缓了入侵系统的养分循环(Rodgers *et al*., 2008), 入侵植物凋落物分解速率慢可能与外来入侵植物凋落物的木质素含量和多酚含量高有关(Godoy *et al*., 2010)。

外来入侵植物对N循环的影响除了与其凋落物累积量和凋落物分解速率有关, 还与被入侵生态系统本地植物的凋落物分解与养分释放有关。许多研究表明凋落物分解速率与凋落物的N含量、碳氮比(C:N)、单宁与N的比值(lignin:N)、木质素与氮(cellulose:N)的比值呈负相关关系, 与凋落物的N含量呈正相关关系(Taylor *et al*., 1989; Conn & Dighton, 2000), 这说明N含量高的凋落物往往分解较快。当外来入侵植物进入本地群落之后, 外来入侵植物的凋落物会与本地植物的凋落物混合, 通常入侵植物的凋落物N含量较高, 它们与本地植物的凋落物(N含量较低)混合后会加快被入侵生态系统凋落物的分解与养分释放, 这主要与凋落物混合分解的协同效应有关, 也就是说入侵植物与本地植物凋落物混合会产生正的“非加和”效应(Scherer-Lorenzen, 2008; Chapman *et al*., 2013; Chen *et al*., 2013; Finerty *et al*., 2016)。Hättenschwiler等(2005)在其综述中将混合凋落物分解与单一物种凋落物分解的差异归结于以下四个方面: 1)养分含量高的凋落物通常拥有更快的分解速率, 从而会加快混合凋落物中较难分解的凋落物的分解速率; 2)不同凋落物中含有其特异性的化合物(如多酚类物质), 这些化合物可能促进或者抑制凋落物的分解; 3)多个物种的凋落物混合能增加微环境的异质性, 微环境的改变会影响凋落物的分解, 从而导致混合凋落物不同于单一物种凋落物的分解; 4)混合凋落物为土壤动物提供了更丰富的栖息地与食物来源, 同时也能改变土壤动物的行为和取食偏好, 因此土壤动物的改变会影响混合凋落物的分解。

可见, 外来入侵植物的凋落物通常具有较高的N含量, 其凋落物分解速率较快, 这会加快凋落物中N的释放进而提高土壤N的可利用性, 有利于其进一步入侵(Ehrenfeld, 2003; Liao *et al*., 2008; Rodgers *et al*., 2008; Sharma & Raghubanshi, 2009; Chen *et al*., 2013; Jo *et al*., 2017), 同时土壤N的可利用性的提高也会促进植物体N含量及凋落物N含量的增加, 会加快入侵地植物的凋落物分解与养分释放, 从而形成“外来入侵植物-加快凋落物分解与养分释放-提高土壤N可利用性-加剧入侵”的正反馈循环效应。

2 外来入侵植物的化感作用对土壤N转化及微生物的影响

许多研究证实外来入侵植物的化感作用会抑制本地植物的生长, 化感作用被认为是其成功入侵的“新奇武器” (Bais *et al*., 2003; Callaway & Ridenour, 2004; 于兴军等, 2004; Thorpe *et al*., 2009; 万欢欢等, 2011; Uddin *et al*., 2017; Warren *et al*., 2017; Becerra *et al*., 2018)。外来入侵植物释放的化感物质对土壤N转化过程具有显著影响(Chen *et al*., 2009b; Thorpe & Callaway, 2011)。例如, 入侵加拿大北部森林的外来植物*Kalmia angustifolia*凋落物中的单宁显著抑制了微生物酶活性, 减缓了凋落物的分解速度, 进而影响了土壤的N转化速率(Bradley *et al*., 2000; Joanisse *et al*., 2007)。有研究发现, 外来入侵植物薇甘菊(*Mikania micrantha*)水提液显著提高了土壤铵态氮(NH_4^+)、硝态氮(NO_3^-)含量和硝化速率(Chen *et al*., 2009b)。为了进一步阐述改变土壤N转化的化感物质类别是什么, 针对外来入侵植物的特定化感物质进行了相关研究。有研究发现, 入侵北美的外来植物矢车菊(*Centaurea stobe*)的根系分泌物儿茶素(-catechin)显著降低了土壤的硝化速率(Thorpe & Callaway, 2011); 入侵北美的外来植物虎杖(*Polygonum cuspidatum*)凋落物中的单宁显著抑制了土壤的N矿化作用(Tharayil *et al*., 2013)。

植物释放的化感物质会影响凋落物的分解与养分释放, 这主要与化感物质影响土壤生物(微生物、小动物)活性有关(Chomel *et al*., 2014, 2016)。我们前期的研究发现, 外来入侵植物薇甘菊释放的化感物质显著改变了本地植物的凋落物分解速率与养分释放量, 进而影响了入侵生态系统的N循环过程(Chen *et al*., 2007, 2009a)。近期研究发现入侵植物凤仙花(*Impatiens glandulifera*)造成入侵群落凋落物的分解

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速率变慢，这可能与化感物质对分解者(如真菌群落)的影响有关(Helsen *et al*., 2018)。

探讨入侵植物化感作用对土壤微生物结构与功能的影响能够更好地认识外来入侵植物的化感作用对土壤N转化的影响机制。许多研究表明：入侵植物释放的化感物质能够影响土壤微生物群落结构与功能(Ni *et al*., 2006; Watkins *et al*., 2009; Inderdjit & Putten, 2010; Cipollini *et al*., 2012; Lorenzo *et al*., 2013; Zhu *et al*., 2017; Czaban *et al*., 2018)。入侵北美的斑点矢车菊(*Centaurea maculosa*)根部分泌的儿茶酚不仅影响土壤中可培养的细菌数量和特定微生物类群，而且对根部的病原菌具有抑制作用(Bais *et al*., 2003)；加拿大一枝黄花(*Solidago canadensis*)的根系分泌物会抑制土壤中的病原菌，进而有利于其入侵扩张(Zhang *et al*., 2009)；铺散矢车菊(*Centaurea diffusa*)根系分泌的化感物8-羟基喹啉有较强的抗菌能力，尤其对根际病原微生物产生较大影响(Vivanco *et al*., 2004; Watkins *et al*., 2009)。植物释放的化感物质会影响氨氧化微生物的结构与活性，这是因为土壤微生物利用酚类物质作为碳源，微生物吸收的酚类物质能够刺激氨氧化细菌(AOB)的活性，影响氨氧化微生物的结构与活性(Souto *et al*., 2000)，进而影响土壤的N转化过程(Souto *et al*., 2000; Ley & Schmidt, 2002)。尽管外来入侵植物的化感作用明显改变了土壤N转化过程(Bradley *et al*., 2000; Joanisse *et al*., 2007; Chen *et al*., 2009a, 2009b; Uddin *et al*., 2017)与土壤微生物的结构与功能(Inderdjit & Putten, 2010; Lorenzo *et al*., 2013; Zhu *et al*., 2017)，但有关外来入侵植物化感作用对氨氧化微生物数量、组成结构与功能的研究还很少，今后要加强从氨氧化微生物的角度揭示入侵植物的化感作用对N循环影响的机制。

除了认识外来入侵植物的化感作用对土壤微生物的影响(Hierro & Callaway, 2003; Inderjit *et al*., 2011b; Zubek *et al*., 2016)，了解土壤微生物对入侵植物化感作用的影响也非常必要。Li等(2017)研究了能够降解紫茎泽兰(*Ageratina adenophora*)化感物质的微生物的功能，发现紫茎泽兰入侵的土壤中能够降解化感物质的微生物活性较高，对化感作用的缓解速度也快于未被入侵的土壤；并在紫茎泽兰入侵地的土壤微生物中分离出能够降解化感物质的菌株*Arthrobacter* sp. ZS。说明遭受入侵的土壤在外来植物入侵过程中能够累积降解化感物质的微生物，进而降低入侵植物的化感作用。未来应加强对降解化感物质微生物的研究，筛选分离出降解化感物质的菌株，有望通过它们来降解有害的化感物质，将有利于入侵植物的防控与入侵地的生态恢复。

3 外来入侵植物对土壤微生物的影响

外来入侵植物影响土壤真菌、细菌和病原菌的群落结构(Kourtev *et al*., 2002, 2003)，也能改变氨氧化微生物(与N循环密切相关)的结构与功能(Hawkes *et al*., 2005; McLeod *et al*., 2016)，还会影响微生物共生体，进而影响生态系统的N循环过程(Rodríguez-Echeverría *et al*., 2009; 柏艳芳等, 2011; Dawson & Schrama, 2016)。

3.1 外来入侵植物对固氮细菌的影响与反馈作用

外来植物成功入侵之后，能够提高固N微生物的固N能力与土壤N水平，这有利于其进一步入侵。章振亚等(2012)研究了崇明东滩湿地入侵植物互花米草与本地植物芦苇、海三棱藨草(*Scirpus × mariqueter*)根际固N微生物的多样性，发现固N菌主要分布在互花米草根际，而本地植物根际较少；由于固N微生物能促进入侵植物的土壤养分吸收利用，所以互花米草根际固N微生物的固N作用对其成功入侵具有重要作用。李会娜等(2009)研究发现外来植物紫茎泽兰入侵提高了土壤自生固N菌、氨氧化细菌和真菌的数量，提高了土壤养分含量及相关酶活性。说明紫茎泽兰改变了入侵地土壤微生物群落的结构和功能，这种因微生物的改变引起的土壤酶活性的提高有利于其入侵扩张。另外，固N的外来植物入侵会显著提高土壤N含量和N的可利用性(Hellmann *et al*., 2011)，这会进一步加剧外来植物的入侵(Maron & Connors, 1996; Ehrenfeld, 2003; Yelenik *et al*., 2004)。

3.2 外来入侵植物对氨氧化微生物的影响与反馈

土壤微生物是生态系统N循环的关键驱动因素，氨氧化微生物是影响土壤硝化作用的限速因子(Kowalchuk & Stephen, 2001; Hawkes *et al*., 2005)。隶属变形菌纲的AOB一直被认为是土壤中参与氨氧化作用的唯一微生物类群。然而，基于宏基因组学发现海洋古菌基因组中含有类似AOB的氨单加氧酶基因(Venter *et al*., 2004; Treusch *et al*., 2005)。随后，研究者从海水中分离培养出氨氧化古菌

(ammonia oxidizing archaea, AOA), 证实了氨氧化古菌具有氨氧化作用(Könneke *et al*., 2005)。AOA广泛存在于森林(Isobe *et al*., 2012)、草地(Di *et al*., 2009)、农田(Leininger *et al*., 2006)等多种陆地生态系统土壤中, 且数量远高于AOB (Leininger *et al*., 2006)。

近年来, 基于AOA与AOB探究外来植物入侵引起土壤N转化改变的微生物机制已成为入侵生态学的研究热点。野外调查研究发现, 外来植物入侵显著改变土壤氨氧化微生物群落结构, 进而影响N循环过程(Zhang *et al*., 2011; Piper *et al*., 2015; McLeod *et al*., 2016)。Zhang等(2011)调查研究了福建九龙江口红树林自然保护区外来植物互花米草入侵对土壤N转化与氨氧化微生物的影响, 结果表明互花米草入侵不仅改变了AOB群落多样性, 而且显著提高了土壤潜在硝化速率, 这与AOB的数量及其转录表达活性的提高密切相关(Wang *et al*., 2015b)。Piper等(2015)采用^{15}N同位素分析方法, 研究了加拿大萨斯卡通(Saskatoon)草原外来入侵植物无芒雀麦(*Bromus inermis*)对入侵地N转化的影响, 发现入侵不仅改变了AOB的丰度, 也改变了AOA的丰度。McLeod等(2016)研究了美国蒙大拿西部草原入侵区域与非入侵区域土壤氨氧化微生物与土壤N的可利用性, 结果表明所有4种入侵植物生长区域的土壤AOB丰度明显比邻近本地植物生长区域的高, 其中3种入侵植物生长区域的硝态氮与潜在硝化速率明显比本地植物生长区域的高。外来入侵草本植物雀麦(*Bromus hordeaceus*)和燕麦(*Avena barbata*)总的硝化速率是本地植物的两倍, 入侵导致土壤AOB丰度的增加和组成的改变是其硝化速率增加的原因之一, 说明AOB可能驱动入侵系统土壤的硝化作用, 进而提高土壤NO_3^-量(Hawkes *et al*., 2005)。此外, 研究发现外来植物入侵对土壤AOA的影响也较显著, 这种影响随着入侵植物的消退也会减弱。入侵植物柔枝莠竹(*Microstegium vimineum*)能够改变AOA的群落组成和丰度, 这种影响能够持续2–3年; 进一步分析发现柔枝莠竹入侵对N循环的影响主要与AOA的丰度和群落结构变化有关, 这种影响会随着柔枝莠竹的退化或消失而减弱(Shannon-Firestone *et al*., 2015)。李科利等(2017)研究了天津市静海县黄顶菊(*Flaveria bidentis*)入侵重发区土壤与非入侵区土壤AOA的多样性, 发现黄顶菊入侵增加了入侵地根际土AOA的多样性, 这主要与入侵地氨氧化菌群种类的增加有关。

3.3 外来入侵植物对反硝化细菌的影响及其反馈

反硝化作用是在反硝化细菌的作用下将土壤中的硝酸盐还原成N_2和N_2O的过程。外来植物入侵能够改变反硝化细菌的群落结构与功能(Hawkes *et al*., 2005; Souza-Alonso *et al*., 2014), Dassonville等(2011)发现外来入侵植物*Fallopia* spp.能够降低土壤水分含量与土壤反硝化细菌的密度, 进而降低了土壤反硝化酶的活性与反硝化作用, 这种影响能减少被入侵生态系统的N损失(硝态N的淋失与氮氧化物的逸失)。外来植物香蒲(*Typha* × *glauca*)的入侵显著提高了土壤无机N含量, 同时也提高了土壤细菌的丰富度和反硝化群落的丰富度(基于*nirS*基因的测定结果)(Angeloni *et al*., 2006)。李会娜等(2009)发现, 反硝化细菌数量随着紫茎泽兰入侵程度的加重呈下降趋势。沈荔花等(2007)研究了入侵植物加拿大一枝黄花和本地植物一枝黄花(*Solidago decurrens*)根际微生物区系, 结果表明加拿大一枝黄花根部土壤中的真菌、细菌和放线菌的数量均高于一枝黄花, 且一枝黄花对根际土壤微生物的生长均表现出抑制效应, 一枝黄花对土壤的反硝化细菌生长的抑制率明显高于加拿大一枝黄花。

4 丛枝菌根真菌与外来入侵植物的互相影响

丛枝菌根真菌(AMF)在自然界分布广泛, 它能够与大部分高等植物的根系形成共生关系(Jansa *et al*., 2008)。AMF能够影响N的吸收同化、有机N矿化、生物固N、硝化、反硝化等过程, 在N循环中发挥着重要的作用(Veresoglou *et al*., 2012a, 2012b; 陈永亮等, 2014)。Nuccio等(2013)研究发现AMF *Glomus hoi*改变了大约10%的细菌群落, 进而加速了凋落物的分解与N的释放。另外, AMF能够通过增强细菌对无机N源的利用, 加速有机N的降解(Johansen *et al*., 1992)。

外来入侵植物, 尤其是入侵草本植物具有较高的菌根侵染率(Walling & Zabinski, 2006; Nijjer *et al*., 2008)。在土壤有效N低的情况下, AMF显著促进外来入侵植物豚草(*Ambrosia artemisiifolia*)对N的吸收, 这有利于豚草适应低N生境, 进而促进其成功入侵(黄栋等, 2010)。可见, AMF作为参与N循环的重要微生物, 在外来植物入侵过程中能够改变土壤环境与

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自身的结构与数量, 进而对外来植物进一步入侵产生反馈作用(Callaway *et al*., 2004a; 柏艳芳等, 2011)。

外来入侵植物有时能增加有利于自身生长的AMF种类, 降低本地植物通过菌根吸收养分(特别是N)的能力, 从而使其在与本地植物的竞争中占据优势, 这说明AMF对入侵植物具有正反馈效应。近期研究发现3种外来入侵植物虎杖(*Reynoutria japonica*)(非AMF共生植物), 金光菊(*Rudbeckia laciniate*)(与AMF共生)和*Solidago gigantean* (与AMF共生)都明显降低了AMF的丰度, 这种影响取决于入侵植物与AMF的共生关系。与本地植物相比, 非AMF共生的入侵植物虎杖对AMF丰度的影响明显大于其他两种与AMF共生的入侵植物金光菊和*Solidago gigantean*。另外, 入侵植物的化感作用也会影响植物与AMF的共生关系, Pinzone等(2018)选择AMF型和外生菌根(ECM)型乔木, 研究了外来入侵植物虎杖和欧洲鼠李(*Rhamnus cathartica*)的化感作用对植物-真菌共生关系的影响, 结果表明入侵植物的化感作用不仅能够直接抑制本地植物种子萌发, 还能够通过减弱本地植物与真菌的共生关系间接地抑制本地植物的生长。此外, 一些具有固N能力的入侵植物在新生境能与当地非特异性固N菌形成共生关系, 与原产地相比这种新的共生关系更能促进外来入侵植物的生长, 进而对入侵产生正反馈效应(Rodríguez-Echeverría *et al*., 2009; 柏艳芳等, 2011; Callaway *et al*., 2011)。

5 研究展望

综上所述, 外来植物入侵明显改变了土壤的硝化、矿化过程以及土壤的N水平, 同时也改变了土壤微生物结构与功能, 这些改变对其进一步入侵产生反馈。然而, 更深入的研究还有待进行, 主要包括以下三个方面。

(1) 近年来, 从土壤氨氧化微生物(AOA, AOB)角度探讨外来植物入侵对土壤N转化的影响机制已成为研究热点(Shannon-Firestone *et al*., 2015; Byrnes *et al*., 2017)。今后要加强对外来植对物成功入侵后AOA与AOB参与土壤N转化过程的差异的研究, 并探究由外来植物入侵引起的非生物环境的改变(如: 土壤pH值、化感物质、其他营养元素)对AOA和AOB的影响及其机制(Xiao *et al*., 2017)。另外, 应该加强外来植物入侵引起的温室效应气体氮氧化物(NO_x)的释放及其机制(Byrnes *et al*., 2017), 这些研究能够更深入地了解外来植物入侵对生态系统结构与功能的影响。

(2) AMF能够与大部分入侵植物, 尤其是草本入侵植物的根系形成共生关系(Nijjer *et al*., 2008), 而AMF能够影响N的吸收同化、有机N矿化、生物固N、硝化、反硝化等过程(Veresoglou *et al*., 2012a)。未来应加强对AMF和氨氧化微生物之间的相互作用的研究, 以期进一步阐述入侵植物对N循环的影响机制。这有助于人们更好地认识土壤N转化过程的机制, 以及对外来植物入侵的反馈作用, 为今后通过养分资源及土壤微生物的调控开展外来植物入侵的防控提供更加充分的科学依据。

(3) 全球变化(如CO_2浓度升高、增温、N沉降等)会影响外来入侵植物的能量利用效率、资源分配、化感物质合成等诸多特性(Bradley *et al*., 2010; Song *et al*., 2010a, 2010b; Wang *et al*., 2010; Dukes *et al*., 2011; Sheppard *et al*., 2016; Chen *et al*., 2017; Liu *et al*., 2018), 外来入侵植物这些生物特性的改变会影响N循环过程, 今后要加强全球变化背景下外来入侵植物对土壤N转化影响的研究, 为评估未来全球变化背景下外来入侵植物的扩散与入侵风险提供依据。

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