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土壤线虫对气候变化响应的研究进展

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摘要:全球变化对陆地生态系统功能具有重要而深远的影响。陆地生态系统地下部分具有重要的生态功能,其组成及结构对气候变化的响应将进一步减缓或加剧全球化进程。土壤线虫在各类生态系统中分布十分广泛,是地下食物网的重要组分,在维持土壤生物多样性及营养物质循环过程中发挥重要作用,其组成及结构对不同气候变化驱动因子的响应机制与模式不尽相同。增温及降水格局变化主要是通过改变线虫生境而直接影响其种群密度与结构,两者通常表现为正效应且作用效果随处理时间的延长而增强。CO_2与大气氮沉降主要是通过影响地上植被,凋落物质量,土壤理化性质等间接过程影响土壤线虫。同时,不同的全球变化因子之间存在着复杂的交互作用,深入理解这些因子之间交互作用对线虫群落的影响模式与机制对于探讨未来气候变化情景下生态统生物多样性及养分循环过程具有重要的理论指导意义。
关键词:气候变暖; 降水格局变化; 大气 CO_2浓度升高; 氮沉降;;线虫群落

Response of soil nematodes to climate change:A review

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Abstract: Global climate change constitutes an important influence on terrestrial ecosystem functions. Soil nematodes exist widely in diverse ecological systems. As an important component of the soil food web, the soil nematode is crucial in maintaining biodiversity and regulating soil nutrient cycling. The various factors driving global change affect the soil nematode community via diverse mechanisms. Changes in temperature and precipitation directly affect soil nematode populations by changing the habitat. In addition, the positive effects would increase with time. CO_2 enrichment and atmospheric nitrogen deposition can indirectly affect soil nematode communities via changes in vegetation, litter quality, and soil physiochemical properties (e. g., soil moisture, pH, ammonium concentration). At the same time, a better understanding of the complex interactions among the drivers of global change, and of how these interactions influence soil nematode communities, is required to predict how terrestrial ecosystems will respond to future climate changes.

Key Words: climate warming; precipitation pattern change; elevated CO_2 concentration; nitrogen deposition; soil nematode community

工业革命以来,伴随着化石燃料的燃烧及土地利用方式的转变,地球生态系统的物质循环也在不断加速。以大气二氧化碳浓度升高,气候变暖,降水格局变化及大气氮沉降为主要特征的全球变化正在对我们赖以生存的陆地生态系统产生重要而深远的影响,如物种灭绝,多样性丧失及由此引发的生态系统功能的改变[1-3]。

陆地生态系统由地上、地下两部分组成,两者相互依存,不可分割。一方面,地上植物通过凋落物及根际

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分泌等方式为地下生物提供碳源,另一方面,地下生物通过矿化作用将储存于有机质中的养分释放,用于植物生长。然而,由于研究方法等因素限制,过去对于全球变化对陆地生态系统影响的研究主要集中于地上部分,而对于地下生态系统研究相对较少[4-5]。土壤中含有植物根系、凋落物、微生物及土壤动物等众多组分,其中土壤动物通过对凋落物进行破碎及取食微生物等方式影响土壤有机质的矿化过程[6-7]。对维持陆地生态系统的生物地球化学循环和生态系统功能至关重要。

线虫是土壤动物的主要功能类群之一,分布广泛,数量巨大,种类繁多[8-9],结构简单,易于鉴定,处于食物网的多个营养级。同时,线虫对环境变化十分敏感,是土壤营养元素循环过程的重要参与者与执行者[10-11],其群落组成及结构的变化将对生态系统服务及功能产生重要影响,进而减缓或加剧气候变化进程[12-14]。土壤线虫群落动态主要受资源有效性(resources availability)及所处生境微环境(microenvironment)变化的调控[15-16]。然而,不同全球变化驱动因子对土壤养分及环境影响的机制及幅度不同[17-19]。同时,线虫的不同营养类群及种属对气候变化的敏感性也不尽相同[18,20-22](根据线虫食物来源的不同,可分为食细菌性线虫、食真菌线虫、植物寄生线虫、杂食性线虫及捕食性线虫)。线虫群落动态调控因子的复杂性及其不同类群间的差异性导致目前对于土壤线虫群落对不同气候变化因子的响应模式与机制依然缺乏规律性认识。

本文通过归纳总结近年发表的土壤线虫对气候变化响应的研究结果,论述了土壤线虫在群落水平、营养类群水平及种属水平上对不同气候变化驱动因子及其交互作用的响应。进一步综合探讨了这些响应模式在时间尺度及空间尺度上的差异,旨在加深全球变化对线虫群落结构及功能影响的理解和认识,为未来全球变化情景下,土壤生物多样性保护及土壤碳动态研究提供参考。

1 二氧化碳浓度升高对土壤线虫的影响

1.1 二氧化碳浓度升高在群落水平上对土壤线虫的影响

2011 年,大气中 CO_2浓度达到 391 ppm,比工业化前的 1750 年高了 40%[1]。二氧化碳浓度升高可以通过改善地下资源有效性及微环境进而对土壤线虫种群密度产生有利影响[23-29],例如,Yeates 通过在一个放牧草地进行大气 CO_2富集实验(FACE),发现大气 CO_2浓度增加能显著提高表层土壤中线虫数量[]30]。究其原因,一方面,CO_2浓度升高可以促进植物的光合作用,提高植物净初级生产力(NPP)并增加光合产物向地下的分配[31],促进细根生长,提高根际周转速率并增加根际分泌[32-33]。这些可利用资源的增加将促进土壤微生物的生长与繁殖[34-35],并进一步通过上行效应(bottom-up)影响土壤线虫的种群密度[36]。另一方面, CO_2浓度升高将降低植物气孔导度,减少蒸腾作用,从而增加土壤湿度[37-39],对线虫产生有利影响。

1.2 二氧化碳浓度升在高营养类群及种属水平对土壤线虫的影响

线虫群落中,不同的营养类群对 CO_2浓度升高的响应不同。Eisenhauer 在美国明尼苏达 Cedar Creek 草地的研究发现,13 年的 FACE 实验显著增加了食真菌线虫的数量,但降低了杂捕类线虫的数量[40];而Hoeksema[27]及 Neher[41]在森林 FACE 实验中却得出了完全相反的结论。土壤有机质含量的差异可能是造成线虫群落结构在草地及森林生态系统中对二氧化碳浓度升高出现不一致响应的重要原因[35,42]。

另外,由于线虫种类繁多,不同种属线虫在繁殖策略、生活史周期及体型大小方面存在诸多差异,传统的按营养类群进行功能分类的方法往往会掩盖线虫个体生物学特征对环境变化的响应。Yeates 对草地 CO_2富集实验的研究发现,CO_2浓度升高显著增加了 *Longidorus elongatus* 线虫的种群密度[30],而 Neher 在北方森林的研究结果表明,在 CO_2升高处理下,*Aphelenchoides* 线虫种群密度明显下降,而 *Filenchus* 线虫种群密度明显增加。线虫种属水平上对 CO_2浓度升高响应的差异将改变群落竞争关系,并引起线虫群落结构的变化,进而影响其生态功能[18]。

1.3 不同时空尺度下,线虫群落对二氧化碳浓度升高响应的差异

土壤线虫对 CO_2浓度升高的响应与生态系统类型无关,且 CO_2浓度升高的正效应随处理时间的延长而减弱。Sonnemann[28]通过研究温带草原地下食物网对二氧化碳浓度升高的响应发现,土壤线虫种群密度在实验

处理第一年显著增加,然而,实验处理第三年时线虫种群密度重新回归到处理前水平。这一结果与 Blankinship 利用整合分析方法得出的结论相一致[43]。究其原因,一方面可能是由于长期[CO_2]升高导致诸如氮元素更多流向植物体内和土壤有机质中,而通过凋落物分解返还到土壤中的氮素减少,以及固氮作用的下降[44]等,结果最终导致地下生态系统由最初的碳限制转变为氮限制[45],这种“渐进性氮限制”(progressive nitrogen limitation)通过改变土壤微生物群落组成及结构进而影响土壤线虫群落构成。另一方面,长期[CO_2]升高还会导致土壤离子流失及土壤酸化[46]并进一步影响土壤线虫的数量及取食活性[47]。

2　全球变暖对土壤线虫的影响

1880—2012 年全球平均温度已升温 0.85℃。温度是调节陆地生态系统生物地球化学过程的重要环境因子。碳循环的关键过程如植物光合作用、凋落物分解、土壤呼吸、微生物及土壤动物活性等都受环境温度的调控[47-50],是线虫群落结构变化的重要驱动因子[15,51]。

2.1　全球变暖在群落水平上对土壤线虫的影响

诸多研究发现,温度升高处理下,土壤线虫的种群密度显著降低而种群多样性及匀均度显著增加,Simmons 等[52]研究发现,在南极州干谷,增温通过直接或间接改变土壤微环境显著降低了线虫的种群密度。而 Matute[47]对位于美国阿肯色州一处农场研究也发现,土壤线虫表现出明显的畏热性(thermophobic)。虽然有研究认为,增温促进了植物特别是细根的生长,增加了异养呼吸的底物供应[53], 有利于线虫种群密度的扩增,然而,另一方面,温度升高可导致蒸腾作用增强,加重土壤水分流失[54-55]及热应激[17,56],从而影响土壤线虫群落。Dong 对农田生态系统土壤线虫对温度升高响应的研究发现,线虫群落物种多样性与温度呈正相关关系[57], Bakonyi 对半干旱草原的研究也得出了相似结论[15]。

2.2　全球变暖在营养类群及种属水平上对土壤线虫的影响

土壤线虫群落中不同营养类群及种属对增温的响应不尽相同。Ruess 等[51]认为,食细菌类线虫及食真菌类线虫的种群密度与土壤温度呈负相关而植食性线虫的种群密度则不受温度变化的影响。而 Stevnbak[58]的研究结果表明,温度升高 1℃后,线虫种群密度显著下降,特别是植食性线虫,降低幅度达 50%,并且群落构成上以世代周期较长的种属占优势。Bakonyi 及 Papatheodorou 等[15,21]发现在属的水平上,小杆属线虫(*Rhabditida*)及滑刃属线虫(*Tylenchida*)对低温敏感;丽突(*Acrobeles*)、拟丽突(*Acrobeloides*),绕线(*plectus*)属线虫与温度呈正相关,而头叶属线虫(*Cephalobus*)与温度呈负相关。Bakonyi 等[15]的研究结果则显示出拟丽突属线虫(*Acrobeloide*)与温度呈负相关。Anderson[59]发现拟丽突 *Acrobeloides* 具有很宽的生态幅(12-35℃),这似乎可以解释以上实验结果的差异。Sohlenius 等[20]同样也发现了不同属线虫对温度变化的响应不同的现象,但他认为这一结论的前提是所有种属共同出现。然而,由于复杂的种间关系的存在,我们无法判断某一特定属线虫对温度变化的响应,同时,也很难将温度变化的直接影响与其间接影响区分开来。

2.3　不同时空尺度下,线虫群落对温度升高响应的差异

土壤线虫对气温升高的响应与当地具体的气候类型密切相关。Ruess 通过极地土壤增温实验发现,土壤线虫与温度之间存在显著的正相关关系[51],而 Simmons 对南极州干谷的研究却得出了相反的结论[52]。同时,一些对北方森林、农田及沙漠土壤的研究则显示,增温对土壤线虫的群落组成及结构无显著影响[60-61]。这些矛盾的结果说明,线虫对增温的响应受不同的生态系统类型及地区气候条件的控制。Blankinship 等[43]采用整合分析的方法对不同生态系统类型下土壤动物对气温升高响应研究发现,土壤动物对增温处理的响应与类群、体型及生态系统类型无关,主要受年均温度与年均降水量的影响,在气温较低及降水较少区域,增温显著降低了土壤线虫的数量,在年降水量超过 626mm 时,增温对土壤动物的数量表现为正效应。同时,土壤动物对增温的响应与增温幅度无关,而与增温的持续时间成负相关,其原因主要是由于增温减少了土壤可利用水分含量,限制了土壤生物的生长和繁殖[62]。

3 大气氮沉降对土壤线虫的影响

工业革命以来,由于化石燃料的燃烧及土地利用方式的改变,大气氮(N)沉降现象日趋严重,成为目前人类面临的重要全球变化因子[63-64]。大气氮沉降通过影响植物生长[42,65],改变种间竞争关系[66-67];影响土壤理化性质[68-69],减少根系分泌及抑制微生物胞外酶活性[70-71]等方式影响土壤线虫的资源有效性及栖息地微环境。然而,目前只有少数通过氮素添加模拟大气氮沉降的野外控制实验用以研究大气氮沉降对土壤线虫群落组成及结构的影响[19,72-74]。而这些研究的结果还存在诸多不确定性。

3.1 群落水平线虫对大气氮沉降的响应

大气氮沉降对土壤线虫群落表现出明显的负效应,降低了种群密度及物种多样性,使群落结构趋于简单化。虽然 Sjursen[75]等认为,低水平的氮素添加因减缓了生态系统的氮限制,促进了植物生长,增加了地下生物量,从而提高了土壤线虫的种群密度。然而,诸多森林、草地、农田实验研究中,氮素的添加显著降低了线虫的种群数量及物种多样性[76]。Liang 研究中国北方地区长期氮素添加对土壤线虫的影响发现,氮素添加显著降低了线虫种群密度及物种丰富度[77],Eisenhauer[40]在明尼苏达州草原生态系统的研究也得到了相似的结论,究其原因,一方面,长期较高浓度的 N 沉降能造成土壤酸化[14], 而 pH 值是土壤线虫分布的重要限制性因素, 大多数土壤线虫适宜在微酸和中性条件下生活, 因而土壤 pH 值的变化将影响土壤线虫的种群密度[78-79]。另一方面,氮添加导致土壤中铵盐浓度增高,产生的铵毒性对线虫种群特别是根食性线虫具有较强的抑制作用。直接接触这些铵毒性物质可以引起土壤线虫机体衰弱, 成长速度减缓、繁殖能力减退,数量减少,甚至导致其死亡[19]。氮添加还可通过降低根际分泌,减少植物光合产物向地下的分配[74],改变植物群落构成进而间接影响土壤线虫群落。土壤线虫通过植物根系及凋落物获得碳源[80-81],因此,植物物种构成及多样性的改变将导致其碳输入数量及质量的变化,并间接影响土壤线虫的群落结构和功能[82]。

3.2 营养类群及种属水平土壤线虫对氮素添加的响应。

不同线虫营养类群及种属对氮素添加的响应方向与程度不尽相同。Sun[83]对森林生态系统研究发现,氮素添加显著降低了群落中食真菌性线虫、根食性线虫及杂食-捕食类线虫的种群密度。这种变化主要是由于氮添加对土壤真菌的抑制作用导致了食真菌性线虫种群密度的降低。杂-捕类线虫多为 r 策略线虫,更易受氮添加引起的环境搅动影响[19,84]。Gruber[85]及 Papanikolaou[86]等研究表明,根食性线虫,特别是 *Geocenamus arcticus* 属线虫及食真菌线虫丰度与土壤中铵态氮及硝态浓度呈显著负相关,表明了施氮对土壤线虫的直接影响。

3.3 不同时空尺度下,线虫群落对氮沉降响应的差异

氮素添加的效应与生态系统类型无关。Sun[83]对森林生态系统研究发现,土壤线虫群落对氮素添加的响应模式受降水的影响。氮循环的诸多过程如凋落物分解,有机氮矿化及有效氮淋溶等都与降水条件密切相关[87],另外 Liang[77]研究发现,线虫群落对氮素添加的响应随处理持续时间的不同而不同,表现为处理初期,根食性线虫种群密度显著降低,而随着处理时间的延长,其种群密度逐渐恢复。因此,在研究氮素添加对土壤线虫生态效应时应充分考虑不同地区的降水格局及实验处理持续时间的影响。

4 降水格局变化对土壤线虫的响应

据联合国政府间气候变化专门委员会第一工作组第五次评估报告(IPCC 2013)预测,到 21 世纪末,高纬度地区和热带太平洋区域的年降水量将会增加;许多中纬度的潮湿地区,平均降水也将增加。但在中纬度干燥地区、副热带的干燥地区平均降水将减少。在全球持续变暖的趋势下,到 21 本世纪末,中纬度大部分陆地区域与热带区域的湿区,极端降水事件将很可能更剧烈并更频繁[1]。线虫生活在土壤孔隙水中,降水格局的变化将对土壤线虫产生重要影响。

4.1 群落水平土壤线虫对降水格局变化的响应

大多数实验研究表明,在一定湿度范围内,土壤线虫种群密度与土壤湿度呈显著的正相关关系。Ruan 对

中国北方半干旱草原土壤线虫研究发现,增加降水显著增了线虫的种群密度[88]。Landesman 对美国新泽西州森林土壤线虫的研究也得出了相似的结论[87]。水分对土壤线虫种群密度的正效应一方面是增加降水有利于线虫的摄食、运动、生长及繁殖[55]。另一方面,降水的增加促进植物生长,增加植物净初级生长力[89],促进氮矿化,提高土壤有效氮含量[90],增加微生物量进而提高土壤线虫的种群密度。

4.2　营养类群及种属水平土壤线虫对降水格局变化的响应

不同营养类群及种属线虫对增加降水及干旱的响应不同。湿润环境利于食细菌性线虫的生长繁殖而干燥环境更利于食真菌线虫种群扩增。Ruan 对内蒙草原的研究发现,增加降水处理,增加了植食性线虫数量而降低了细菌性及杂捕类线虫的数量[88]。Landesman 的研究发现,所有营养类群线虫均对干旱敏感,食细菌性线种表现最为明显,特别是 *plectidae* 的数量在干旱处理下显著降低,然而,对于同样属于食细菌性线虫的 *Cephalobidae* 和 *qudsianematidae* 则对干旱处理无响应[87]。Sohlenius[91]通过实验室培养实验发现拟丽突线虫 *Acrobeloides* 与水分呈正相关,滑刃属线虫 *Tylenchida* 与水分呈负相关。他认为这是由于两种线虫间的竞争关系导致的。然而,由于这两种线虫的食性不同,因此这种差异也可能是由于资源有效性所导致的。Bakonyi[15]认为丽突(*Acrobeles*)与拟丽突(*Acrobeloides*)属线虫种群密度与水分条件无关,而 Griffiths 等发现拟丽突属线虫(*Acrobeloides*)更适合于干燥环境。另一项田间实验与证明了绕线属线虫(*Plectus*)在干燥环境中密度增加[92]。植食性线虫中不同种属对土壤水分条件变化的响应也不尽相同[15,93-96],Griffin 研究发现矮化属线虫(*Tylenchorhynchus acutoides*)及剑属线虫(*Xiphinema americanum*)对湿度变化比短针属线虫(*Pratylenchus neglectus*)更敏感。对于杂捕类线虫,Porazinska 等通过农田灌溉实验发现除孔咽属线虫(*Aporcelaimellus*)和真矛属线虫(*Eudorylaimus*)与灌溉呈正相关外,其它种属线虫的种群密度不受土壤水分条件的影响[97]。线虫种属水平上对降水格局变化的响应不同导致其群落组成及结构的变化,并影响其生态功能。

4.3　不同时空尺度下,线虫群落对降水格局变化响应的差异

森林生态系统土壤线虫更易受降水格局变化影响,增加降水的正效应随处理时间的延长而增强,土壤线虫群落对干旱的响应强于增加降水的响应。Eisenhauer 对美国明尼苏达州草原土壤研究发现,线虫群落对夏季干旱无响应。Landesman[82]等在森林生态系统得出的结论与这一结果相反。由于土壤生物对环境具有一定的适应能力,因此,相对于干旱,碳源是土壤线虫更重要的限制因子。在美国新泽西州森林进行的为期一年的降水控制实验结果表明,干旱对线虫群落的影响强于增加降水[98],这可能是与干旱对凋落物层及矿质土层影响程度不同有关[99],另外,水分不足情况下,由于植被与土壤动物之间对于水分的竞争能力亦不相同[100],因此导致了土壤线虫对干旱的响应强于增加降水。

根据不同全球变化驱动因子对线虫群落影响机制与模式绘制模式图如下。

5　多因子交互作用对土壤线虫群落的影响

全球变化是以大气 CO_2浓度上升,气候变暖,大气氮沉降及降水格局变化为主要特征的多个驱动因子共同作用的结果,各个驱动因子之间存在复杂的交互作用。如气候变暖,可通过改变土壤呼吸速率及大气环流而影响大气 CO_2浓度及降水格局,并进一步影响植物群落及土壤微环境,并从资源与环境两方面影响土壤线虫群落。因此,前期的单因子控制实验结果无法准确模拟未来气候变化情境下土壤线虫群落的真实响应[101-102],近年来,关于不同全球变化因子间的交互作用对地下生态系统结构与功能影响的野外控制实验陆续开展[88,103-104],Kardol[105]发现自然 CO_2浓度下增温和干旱表现出对线虫群落的负效应,而在增高 CO_2的处理中,增温及干旱对线虫群落无影响。Chung[106]认为土壤动物群落的组成及结构受植物多样性、CO_2浓度及氮素水平的共同影响;Hoeksema[27]及 Li [107] 的实验结果表明,土壤线虫的种群密度及多样性受 CO_2和氮素添加间交互作用的影响。Fu2 功能团线虫对 CO_2及氮肥的交互作用响应最显著[108]。总之,各种全球变化因子通过复杂的交互作用共同调节地上植物群落及土壤微环境,进而改变土壤线虫食物资源有效性及生境稳定性,

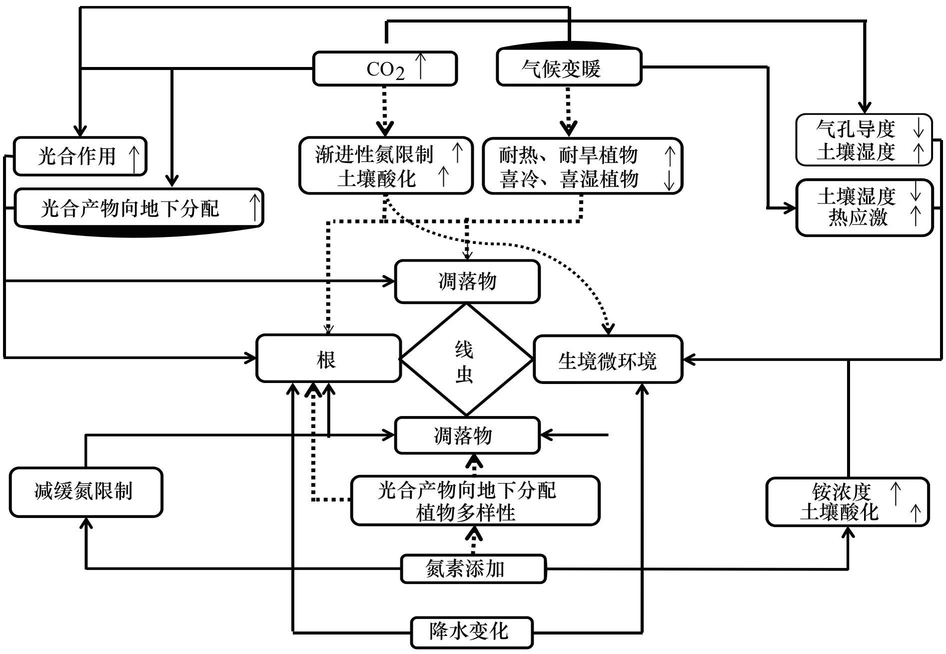

图1 土壤线虫对不同气候变化驱动因子(二氧化碳浓度升高;气候变暖;大气氮沉降;降水格局变化)的响应

Fig.1 The responses of soil nematode to global change (elevated CO_2; warming; nitrogen deposition; changing precipitation)

虚线表示长期效应。"↑"表示增高,"↓"表示降低

触发养分介导的"上行效应"及种间关系介导的"下行效应",共同改变土壤线虫群落的组成及结构。作为地下食物网的重要组分,线虫群落的变化将引起整个地下食物网结构与功能的变化,进而改变土壤养分循环过程,对陆地生态系统结构与功能造成广泛而深远的影响[109]。

6 问题与展望

土壤线虫是地下食物网的重要组成部分,在维持生态系统生物多样性及营养元素循环过程中发挥重要作用,是研究未来气候变化情景下地下生态系统结构、功能变化的重要指示性生物。然而,目前,在研究线虫群落组成及结构对全球变化响应方面还存在诸多不足,主要表现在:

(1)对于线虫的生态学功能认识不足。以往研究,特别是在传统农牧业管理措施中,线虫往往被作为害虫加以防控,直到近年来,线虫在土壤质量评估、生境稳定性检测,环境污染、人为及自然干扰强度及物质循环等过程中的作用才逐渐引起人们的重视。

(2)研究方法落后,研究尺度较窄。目前对土壤线虫的研究主要沿习传统的形态学鉴定方法,这一方法虽然具有简便,准确等优点,但鉴定速度较慢,不适用于大尺度、大样本量研究。同时,形态学鉴定只能反映线虫群落的组成及结构变化,无法反应不同营养级间的物质及能量流通情况。分子生物学及同位素示踪技术可有效弥补形态学鉴定方法的不足,在未来,现代生物学技术与传统方法相结合成为必然的趋势。

(3)关于土壤线虫在全球变化领域中的作用研究有等进一步深入和细化。目前,在全球变化研究领域,土壤线虫的作用越来越受到生态学家的重视,然而,其研究内容往往主要集中于土壤线虫种群密度、营养类群组成的变化等方面。土壤线虫类群极其丰富,简单地按食性进行功能群划分往往会掩盖不同属线虫的个体生物学差异,因此,有必要对不同属线虫的繁殖策略,生境选择,对干扰的抵抗力与恢复力,种间竞争关系等问题进行深入细致的研究。

(4)全球变化是由诸多驱动因子共同作用的结果,各个驱动因子之间存在复杂的交互作用。因此,前期的单因子控制实验结果无法准确模拟未来气候变化情景下地下食物网的真实响应,然而,受经费及人力等因

素制约,目前包括以上四种变化因子的大型、长期野外控制实验平台还十分有限。

(5)目前关于全球变化对土壤线虫群落影响的研究多限于 2—3 年的短期实验,而气候变化所导致的如植被构成、土壤理化性质的变化是一个长期的渐变过程,因此迫切需要建立长期野外控制实验以揭示土壤线虫对气候变化的真实响应。

参考文献(References):

[1] Intergovernmental Panel on Climate Change (IPCC). 2013. Working group I contribution to the IPCC fifth assessment report, climate change 2013: the physical science basis.

[2] Cox P M, Betts R A, Jones C D, Spall S A, Totterdell L J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature, 2000, 408(6809):184-187.

[3] Frank D C, Esper J, Raible C C, Büntgen U, Trouet V, Stocker B, Joos F. Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. Nature, 2010, 463(7280):527-530.

[4] Xia J Y, Wan S Q. Independent effects of warming and nitrogen addition on plant phenology in the Inner Mongolian steppe. Annals of Botany, 2013, 111(6):1207-1217.

[5] Liang J Y, Xia J Y, Liu L L, Wan S Q. Global patterns of the responses of leaf-level photosynthesis and respiration in terrestrial plants to experimental warming. Journal of Plant Ecology, 2013, 6(6):437-447.

[6] Wardle D A, Bardgett RD, Klironomos J N, Setälä H, van der Putten W H, Wall D H. Ecological linkages between aboveground and belowground biota. Science, 2004, 304(5677):1629-1633.

[7] Kostenko O, van de Voorde T F J, Mulder P P J, van der Putten W H, Martijn Bezemer T. Legacy effects of aboveground-belowground interactions. Ecology Letters, 2012, 15(8):813-821.

[8] Wu T H, Ayres E, Bardgett R D, Wall D H, Garey J R. Molecular study of worldwide distribution and diversity of soil animals. The Proceedings of the National Academy of Sciences of the United States of America, 2011, 108(43):17720-17725.

[9] Yeates G W. Nematodes as soil indicators: functional and biodiversity aspects. Biology and Fertility of Soils, 2003, 37(4):199-210.

[10] Freckman D W, Caswell E P. The ecology of nematodes in agroecosystems. Annual Review of Phytopathology, 1985, 23:275-296.

[11] Bardgett R. The Biology of Soil: A Community and Ecosystem Approach. Oxford: Oxford University Press, 2005.

[12] Bushby H V A, Marshall K C. Some factors affecting the survival of root-nodule bacteria on desiccation. Soil Biology and Biochemistry, 1997, 9(3):143-147.

[13] Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal O W, Dhillion S. Soil function in a changing world: the role of invertebrate ecosystem engineers. European Journal of Soil Biology, 1997, 33(4):159-193.

[14] Bradford M A, Tordoff G M, Eggers T, Jones T H, Newington J E. *Microbiota*, fauna, and mesh size interactions in litter decomposition. Oikos, 2002, 99(2):317-323.

[15] Bakonyi G, Nagy P. Temperature- and moisture-induced changes in the structure of the nematode fauna of a semiarid grassland- patterns and mechanisms. Global Change Biology, 2000, 6(6):697-707.

[16] Keith A M, Brooker R W, Osler G H R, Chapman S J, Burslem D F R P, van der Wal R. Strong impacts of belowground tree inputs on soil nematode trophic composition. Soil Biology and Biochemistry, 2009, 41(6):1060-1065.

[17] Briones M J I, Ostle N J, Mcnamara N P, Poskitt J. Functional shifts of grassland soil communities in response to soil warming. Soil Biology and Biochemistry, 2009, 41(2):315-322.

[18] Neher D A, Weicht T R. Nematode genera in forest soil respond differentially to elevated CO_2. Journal of Nematology, 2013, 45(3):214-222.

[19] Wei C Z, Zheng H F, LI Q, Lü X T, Yu Q, Zhang H Y, Chen Q S, He N P, Kardol P, Liang W J, Han X G. Nitrogen addition regulates soil nematode community composition through ammonium suppression. PloS ONE, 2012, 7(8):e43384.

[20] Sohlenius B, Boström S. Effects of climate change on soil factors and metazoan microfauna (nematodes, tardigrades and rotifers) in a Swedish tundra soil-a soil transplantation experiment. Applied Soil Ecology, 1999, 12(2):113-128.

[21] Papatheodorou E M, Argyropoulou M D, Stamou G P. The effects of large- and small-scale differences in soil temperature and moisture on bacterial functional diversity and the community of bacterivorous nematodes. Applied Soil Ecology, 2004, 25(1):37-49.

[22] Bakonyi G, Nagy P, Edit K L, Kovács E, Barabás S, Répási V, Seres A. Soil nematode community structure as affected by temperature and moisture in a temperate semiarid shrubland. Applied Soil Ecology, 2007, 37(1):31-40.

[23] Newton P C D, Clark H, Bell C C, Glasgow E M, Tate K R, Ross D J, Yeates G W, Saggar S. Plant growth and soil processes in temperate grassland communities at elevated CO_2. Journal of Biogeography, 1995, 22(2/3):235-240.

[24] Klironomos J N, Rillig M C, Allen M F. Below-ground microbial and microfaunal responses to Artemisia tridentate grown under elevated atmospheric CO_2. Functional Ecology, 1996, 10(4):527-534.

[25] Yeates G W, Tate K R, Newton P C D. Response of the fauna of a grassland soil to doubling of atmospheric carbon dioxide concentration. Biology and Fertility of Soils, 1997, 25(3):307-315.

[26] Jones T H, Thompson L J, Lawton J H, Bezemer T M, Bardgett R D, Blackburn T M, Bruce K D, Cannon P F, Hall G S, Hartley S E, Howson G, Jones C G, Kampichler C, Kandeler E, Ritchie D A. Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. Science, 1998, 280(5362):441-443.

[27] Hoeksema J D, Lussenhop J, Teeri J A. Soil nematodes indicate food web responses to elevated atmospheric CO_2. Pedobiologia, 2000, 44(6): 725-735.

[28] Sonnemann I, Wolters V. The microfood web of grassland soils responds to a moderate increase in atmospheric CO_2. Global Change Biology, 2005, 11(7):1148-1155.

[29] Eisenhauer N, Cesarz S, Koller R, Worm K, Rich P B. Global change belowground: impacts of elevated CO_2, nitrogen, and summer drought on soil food webs and biodiversity. Global Change Biology, 2011, 18(2):435-447.

[30] Yeates G W, Newton P C D. Long-term changes in topsoil nematode populations in grazed pasture under elevated atmospheric carbon dioxide. Biology and Fertility of Soils, 2009, 45(8):799-808.

[31] Norby R J, Luo Y Q. Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multi-factor world. New Phytologist, 2004, 162(2):281-293.

[32] Rogers H H, Runion G B, Krupa S V. Plant response to atmospheric CO_2 with emphasis on roots and the rhizosphere. Environmental Pollution, 1994, 83(1/2):155-189.

[33] Körner C. Biosphere responses to CO_2 enrichment. Ecological Applications, 2000, 10(6):1590-1619.

[34] Blagodatskaya E, Blagodatsky S, Dorodnikov M, Kuzyakov Y. Elevated atmospheric CO_2 increases microbial growth rates in soil: results of three CO_2 enrichment experiments. Global Change Biology, 2010, 16(2):836-848.

[35] Drigo B, Pijl A S, Duyts H, Kielaka A M, Gampera H A, Houtekamerd M J, Boschkerd H T S, Bodeliere P L E, Whiteleyf A S, van Veena J A, Kowalchuka G A. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. The Proceedings of the National Academy of Sciences of the United States of America, 2010, 107(24):10938-10942.

[36] Gregor W, Yeates, Paul C D. Newton Long-term changes in topsoil nematode populations in grazed pasture under elevated atmospheric carbon dioxide. Biology and Fertility of Soils, 2009, 45(8):799-808.

[37] Lee T D, Barrott S H, Reich P B. Photosynthetic responses of 13 grassland species across 11 years of free-air CO_2 enrichment is modest, consistent and independent of N supply. Global Change Biology, 2011, 17(9):2893-2904.

[38] Reich P B. Elevated CO_2 reduces losses of plant diversity caused by nitrogen deposition. Science, 2009, 326(5958):1399-1402.

[39] Adair E C, Reich P B, Hobbie S E, Knops J M H. Interactive effects of time, CO_2, N and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. Ecosystems, 2009, 12(6):1037-1052.

[40] Eisenhauer N, DobiesT, Cesarz S. Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. The Proceedings of the National Academy of Sciences of the United States of America, 2013, 110(17):6889-6894.

[41] Neher D A, Weicht T R, Moorhead D L, Sinsabaugh R L. Elevated CO_2 alters functional attributes of nematode communities in forest soils. Functional Ecology, 2004, 18(4):584-591.

[42] Reich P B, Knops J, Tilman D, Craine J, Ellsworth D, Tjoelker M, Lee T, Wedin D, Naeem S, Bahauddin D, Hendrey G, Jose S, Wrage K, Goth J, Bengston W. Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature, 2001, 410(6830):809-812.

[43] Blankinship J C, Niklaus P A, Hungate B A. A meta-analysis of responses of soil biota to global change. Oecologia, 2011, 165(3):553-565.

[44] Hungate B A, Stiling P D, Dijkstra P, Johnson D W, Ketterer M E, Hymus G J, Hinkle C R, Drake B G. CO_2 elicits long-term decline in nitrogen fixation. Science, 2004, 304:1291-1291.

[45] Luo Y Q. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. BioScience, 2004, 54(8):731-739.

[46] Cheng L, Zhu L, Chen G, Zheng X, Oh N H, Rufty T W, Richter D de B, Hu S. Atmospheric CO_2 enrichment facilitates cation release from soil. Ecology Letters, 2010, 13(3):284-291.

[47] Matute M M. Soil nematodes of Brassica rapa: influence of temperature and pH. Advances in Natural Science, 2013, 6(4):20-26.

[48] Weltzin J F, Bridgham S D, Pastor J, Chen J Q, Harth C. Potential effects of warming and drying on peatland plant community composition. Global Change Biology, 2003, 9(2):141-151.

[49] Schuur E A G, Crummer K G, Vogel J G, Mack M C. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. Ecosystems, 2007, 10(2):280-292.

[50] Bai W M, Wan S Q, Niu S L, Liu W X, Chen Q S, Wang Q B, Zhang W H, Han X G, Li L H. Increased temperature and precipitation interact to affect root production, mortality and turnover in a temperate steppe: implications for ecosystem C cycling. Global Change Biology, 2009, 16(4): 1306-1316.

[51] Ruess L, Michelsen A, Schmidt I K, Jonasson S. Simulated climate change affecting microorganisms, nematode density and biodiversity in subarctic soils. Plant and Soil, 1999, 212(1): 63-73.

[52] Simmons B L, Wall D H, Adams B J, Ayres E, Barrett J E, Virginia R A. Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. Soil Biology and Biochemistry, 2009, 41(10): 2052-2060.

[53] Briones M J I, Ineson P, Sleep D. Use of ^{13}C to determine food selection in collembolan species. Soil Biology and Biochemistry, 1999, 31(6): 937-940.

[54] Hodkinson I D, Healey V, Coulson S. Moisture relationships of the high arctic collembolan Onychiurus arcticus. Physiological Entomology, 1994, 19(2): 109-114.

[55] Kardol P, Nicholas Reynolds W, Norby R J, Classen A T. Climate change effects on soil microarthropod abundance and community structure. Applied Soil Ecology, 2011, 47(1): 37-44.

[56] Bokhorst S, Huikes A, Convey P, van Bodegom P M, Aerts R. Climate change effects on soil arthropod communities from the Falkland Islands and the Maritime Antarctic. Soil Biology & Biochemistry, 2008, 40(7): 1547-1556.

[57] Dong Z K, Hou R X, Chen Q Y, Ouyang Z, Ge F. Response of soil nematodes to elevated temperature in conventional and no-tillage cropland systems. Plant and Soil, 2013, 373(1/2): 907-918.

[58] Stevnbak K S, Maraldo K, Georgieva S, Strandmark L B, Beier C, Schmidt I K, Christensen S. Suppression of soil decomposers and promotion of long-lived, root herbivorous nematodes by climate change. European Journal of Soil Biology, 2012, 52: 1-7.

[59] Anderson R V, Coleman D C. Nematode temperature responses: a niche dimension in population of bacterial-feeding nematodes. Journal of Nematology, 1982, 14(1): 69-76.

[60] Haimi J, Laamanen J, Penttinen R, Mika R, Seppo K, Seppo K. Impacts of elevated CO_2 and temperature on the soil fauna in boreal forests. Applied Soil Ecology, 2005, 30(2) 104-112.

[61] Darby B J, Neher D A, Housman D C, Belnap J. Few apparent short-term effects of elevated soil temperature and increased frequency of summer precipitation on the abundance and taxonomic diversity of desert soil micro- and meso-fauna. Soil Biology and Biochemistry, 2011, 43(7): 1474-1481.

[62] Aerts R. The freezer defrosting: global warming and litter decomposition rates in cold biomes. Journal of Ecology, 2006, 94(4): 713-724.

[63] Reay D S, Dentener F, Smith P, Grace1 J, Feely R A. Global nitrogen deposition and carbon sinks. Nature Geoscience, 2008, 1(7): 430-437.

[64] Vitousek P M, Aber J D, Howarth RW, Likens G E, Matson P A, Schindler D W, Schlesinger W G, Tilman D G. Human alteration of the global nitrogen cycle: Sources and consequences. Ecological Applications, 1997, 7(3): 737-750

[65] Reich P B, Hobbie S E, Lee T, Ellsworth D S, West J B, Tilman D, Knops J M H, Naeem S, Trost J. Nitrogen limitation constrains sustainability of ecosystem response to CO_2. Nature, 2006. 440: 922-925.

[66] Yang H, Jiang L, Li L, Li A, Wu M, Wan S. Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. Ecology Letters, 2012, 15(6): 619-626.

[67] Yang H J, Li Y, Wu M Y, Zhang Z, Li L H, Wan S Q. Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species' traits. Global Change Biology, 2011, 17(9): 2936-2944.

[68] Niu S L, Wu M Y, Han Y, Xia J Y, Zhang Z, Yang H J, Wan S Q. Nitrogen effects on net ecosystem carbon exchange in a temperate steppe. Global Change Biology, 2010, 16(1): 144-155.

[69] Contosta A R, Frey S D, Cooper A B. Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. Ecosphere, 2011, 2(3): 1-21.

[70] Dijkstra F A, Hobbie S E, Reich P B, Knops J M H. Divergent effects of elevated CO_2, N fertilization, and plant diversity on soil C and N dynamics in a grassland field experiment. Plant and Soil, 2005, 272(1/2): 41-52.

[71] DeForest J L, Zak D R, Pregitzer K S, Burton A J. Atmospheric nitrate deposition, microbial community composition, and enzyme activity in northern hardwood forests. Soil Science Society of America Journal, 2004, 68(1): 132-138.

[72] Sarathchandra S U, Ghani A, Yeates G W, Burch G, Cox N R. Effect of nitrogen and phosphate fertilisers on microbial and nematode diversity in pasture soils. Soil Biology and Biochemistry, 2001, 33(7): 953-964.

[73] Qi L, Yong J, Wen J L, Yi L L, Zhang E P, Liang C H. Long-term effect of fertility management on the soil nematode community in vegetable production under greenhouse conditions. Applied Soil Ecology, 2010, 46(1): 111-118.

[74] Hogberg M N, Maria J, Briones I, Keel S G, Metcalfe D B. 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, 2010, 187(2):485-493.

[75] Sjursen H, Michelsen A, Jonasson S. Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. Applied Soil Ecology, 2005, 30(3):148-161.

[76] Berg M P, Verhoef H A. Ecological characteristics of a nitrogen saturated coniferous forest in The Netherlands. Biology and Fertility of Soils, 1998, 26(4):258-267.

[77] Liang W J, LouY L, Li Q, Zhong S, Zhang X K, Wang J K. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in northeast China. Soil Biology and Biochemistry, 2009, 41(5):883-890.

[78] 钱复生, 王宗英. 水东枣园土壤动物与土壤环境的关系. 应用生态学报, 1995, 6(1):44-50.

[79] 殷秀琴, 李健东. 羊草草原土壤动物群落多样性的研究. 应用生态学报, 1998, 9(2):186-188.

[80] Eissfeller V, Beyer F, Valtanen K, Hertel D, Maraun M, Polle A, Scheu S. Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash. Soil Biology and Biochemistry, 2013, 62:76-81.

[81] Elfstrand S, Lagerlo J, Hedlund K, Mårtensson A. Carbon routes from decomposing plant residues and living roots into soil food webs assessed with ^{13}C labeling. Soil Biology and Biochemistry, 2008, 40(10):2530-2539.

[82] Eisenhauer N, Migunova V D, Ackermann M, Ruess L, Scheu S. Changes in plant species richness induce functional shifts in soil nematode communities in experimental grassland. PLoS ONE, 2011, 6(9):e24087..

[83] Sun X, Zhang X K, Zhang S X, Dai G H, Han S J, Liang W J. Soil nematode responses to increases in nitrogen deposition and precipitation in a Temperate Forest. PLoS ONE, 2013, 8(12):e82468.

[84] Hu C H, Zheng L Z. The effect of acid deposition on soil fauna. Hubei Forest Technology, 1999, 2:41.

[85] Gruber N, Galloway J N. An earth-system perspective of the global nitrogen cycle. Nature, 2008, 451(7176):293-296.

[86] Papanikolaou N, Britton A J, Helliwell R C, Johnson D. Nitrogen deposition, vegetation burning and climate warming act independently on microbial community structure and enzyme activity associated with decomposing litter in low-alpine heath. Global Change Biology, 2010, 16(11):3120-3132.

[87] Landesman W J, Treonis A M, Dighton J. Effects of a one-year rainfall manipulation on soil nematode abundances and community composition. Pedobiologia, 2011, 54(2):87-91.

[88] Ruan W B, Yuan S, Chen Q. The response of soil nematode community to nitrogen, water, and grazing history in the Inner Mongolian Steppe, China. Ecosystems, 2012, 15(7):1121-1133.

[89] Bai Y F, Wu J G, Xing Q, Pan Q M, Huang J H, Yang D L, Han X G. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. Ecology, 2008, 89(8):2140-2153.

[90] Wang C H, Wan S Q, Xing X R, Zhang L, Han X G. Temperature and soil moisture interactively affected soil net N mineralization in temperate grassland in Northern China. Soil Biology and Biochemistry, 2006, 38(5):1101-1110.

[91] Sohlenius B. Influence of climatic conditions on nematode coexistence: a laboratory experiment with a coniferous forest soil. Oikos, 1985, 44(3):430-438.

[92] Griffiths B S, Neilson R, Bengough A G. Soil factors determined nematode community composition in a 2 year pot experiment. Nematology, 2003, 5(6):889-897.

[93] Horton W H. Factors affecting population trends of plant-parasitic nematodes on rangeland grasses. Nematology, 1996, 28(1):107-114.

[94] Verschoor B C, de Goede R G M, de Vries F W, Brussaard L. Changes in the composition of the plant-feeding nematode community in grasslands after cessation of fertiliser application. Appl. Applied Soil Ecology, 2001, 17(1):1-17.

[95] Todd T C, Blair J M, Milliken G A. Effects of altered soil-water availability on a tallgrass prairie nematode community. Applied Soil Ecology, 1999, 13(1):45-55.

[96] Smolik J D, Dodd J L. Effect of water and nitrogen, and grazing on nematodes in a shortgrass prairie. Journal of Range Management, 1983, 36(6):744-748.

[97] Porazinska D L, McSorley R, Duncan L W, Graham J H, Wheaton T A, Parsons L R. Nematode community composition under various irrigation schemes in a citrus soil ecosystem. Nematology, 1998, 30(2):170-178.

[98] Landesman W J, Dighton J. Response of soil microbial communities and the production of plant-available nitrogen to a two-year rainfall manipulation in the New Jersey Pinelands. Soil Biology and Biochemistry, 2010, 42(10):1751-1758.

[99] Keith D M, Johnson E A, Valeo C. Moisture cycles of the forest floor organic layer (F and H layers) during drying. Water Resources Research, 2010, 46(7):W07529, doi:10.1029/2009WR007984.

[100] Odhiambo H O, Ong C K, Deans J D, Wilson J, Khan A A H, Sprent J I. Roots, soil water and crop yield: tree crop interactions in a semi-arid agroforestry system in Kenya. Plant and Soil, 2001, 235(2):221-233.

[101] Luo Y Q, Gerten D, le Maire G, Parton W J, Weng E S, Zhou Z H, Keough C, Beier C, Ciais P, Cramer W, Dukes J S, Emmett B, Hanson P J, Knapp A, Linder S, Nepstad D, Rustad L. Modeled interactive effects of precipitation, temperature, and CO_2 on ecosystem carbon and water dynamics in different climatic zones. Global Change Biology, 2008, 14(9):1986-1999.

[102] Butenschoen O, Scheu S, Eisenhauer N. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. Soil Biology and Biochemistry, 2011, 43(9):1902-1907.

[103] Emmerson M, Bezemer M, Hunter M D, Jones T H. Global change alters the stability of food webs. Global Change Biology, 2005, 11(3):490-501.

[104] Nielsen, Wall U N, Diana H. The future of soil invertebrate communities in polar regions:different climate change responses in the Arctic and Antarctic? Ecology Letters, 2013, 16(3):409-413.

[105] Kardol P, Cregger M A, Campany C E, Classen A T. Soil ecosystem functioning under climate change:plant species and community effects. Ecology, 2010, 91(3):767-781.

[106] Chung H, Zak D, Reich P B, Ellsworth D S. Plant species richness, elevated CO_2, and atmospheric N deposition alter soil microbial community composition and function. Global Change Biology, 2007, 13(5):980-989.

[107] Li Q, Liang W J, Jiang Y, Neher D A. Effects of elevated CO_2 and N fertilization on soil nematode abundance and diversity in a wheat field. Applied Soil Ecology, 2007, 36(1):63-69.

[108] 鲍雪莲, 李琪, 梁文举, 朱建国. 大气 CO_2浓度升高和氮肥管理对稻麦轮作系统土壤线虫群落组成的影响. 中国农业科学, 2011, 44(22):4627-4635.

[109] Bardgett R D, Wardle D A. Aboveground-Belowground Linkages:Biotic Interactions, Ecosystem Processes, and Global Change. Oxford Series in Ecology and Evolution). New York:Oxford University Press, 2010.