



陆地生态系统过程对气候变暖的响应与适应

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摘 要 陆地生态系统包含一系列时空连续、尺度多元且互相联系的生态学过程。由于大部分生态学过程都受到温度调控, 因此气候变暖会对全球陆地生态系统产生深远的影响。近年来, 全球变化生态学的基本科学问题之一是陆地生态系统的关键过程如何响应与适应全球气候变暖。围绕该问题, 该文梳理了近年来的研究进展, 重点关注植物生理生态过程、物候期、群落动态、生产力及其分配、凋落物与土壤有机质分解、养分循环等过程对温度升高的响应与适应机理。通过定量分析近20年来发表于主流期刊的相关论文, 展望了该领域的前沿方向, 包括物种性状对生态系统过程的预测能力, 生物地球化学循环的耦合过程, 极端高温与低温事件的响应与适应机理, 不对称气候变暖的影响机理和基于过程的生态系统模拟预测等。基于这些研究进展, 该文建议进一步研究陆地生态系统如何适应气候变暖, 更多关注我国的特色生态系统类型, 并整合实验、观测或模型等研究手段开展跨尺度的合作研究。

关键词 气候变暖; 生态过程; 碳循环; 氮循环; 生产力; 极端气候事件

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Response and adaptation of terrestrial ecosystem processes to climate warming

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Abstract

Terrestrial ecosystems are characterized by a series of spatiotemporally continuous, multiple scaled, and mutually connected processes. Since most of these ecological processes are regulated by temperature, climate warming will profoundly impact terrestrial ecosystems at global scale. Recently, how key processes in terrestrial ecosystems respond and/or adapt to climate warming has become a fundamental question in global change ecology. Here, we reviewed the recent research progress related to such question. This review focuses on key ecosystem processes, such as plant ecophysiological processes, phenology, community dynamics, productivity and carbon allocation, decomposition of litter and soil organic carbon, nutrient cycling, and carbon-nitrogen coupling. Based on a literature review, we propose perspectives for future research to tackle fundamental questions, such as the predictability of plant traits on ecosystem processes, coupling between biogeochemical cycles, mechanisms driving ecosystem responses to extreme climate and asymmetric warming, and ecological forecasting with models. We finally suggest more research efforts on warming adaptation rather than response on China's specific ecosystems, and on the integration of experiments, observations, and models for coordinating studies across scales.

Key words climate warming; ecosystem processes; carbon cycle; nitrogen cycle; productivity; extreme climate

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关于陆地生态系统响应与适应气候变化方面的研究, 最早可以追溯到公元前3世纪。古希腊哲学家提奥夫拉斯图斯(Theophrastus)通过植物移栽实验, 发现植物的落叶与常绿特征随着气候条件的变化会

发生规律性改变(Morton, 1981)。自18世纪以来, 植被分布格局与气候条件之间的关系逐渐成为生态学研究的热点领域。大量的研究结果表明, 温度与降水条件的结合可以解释陆地植被类型及其关键功能

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在全球空间尺度的分布格局。例如, Holdridge (1947) 基于温度与水分条件将全球划分为38个生命区系, 并被Emanuel等(1985)应用于全球植被响应未来气候变化的预测。Lieth (1975) 基于温度与降水条件推算生态系统初级生产力的全球分布, 并将该方法命名为迈阿密模型。自工业革命以来, 地球表面温度的增加幅度约为 $0.87\text{ }^{\circ}\text{C}$, 预计在2030–2052年间达到 $1.5\text{ }^{\circ}\text{C}$ (IPCC, 2018)。全球气候变暖及其伴随产生的降水格局改变、冰川和冻土消融、海平面上升等气候与环境变化对陆地生态系统的结构与功能产生了深远的影响。因此, 陆地生态系统如何响应与适应全球温度的迅速升高在近年来成为了生态学领域的热点和难点问题。

自20世纪60年代以来, 国际科学联合会(ICSU)陆续启动了国际生物学计划(IBP)与国际地圈生物圈计划(IGBP), 极大地推动了陆地生态系统响应气候变化的研究。1988年成立的政府间气候变化委员会(IPCC), 陆续出版了多种形式的气候变化评估报告。其中, 第三次IPCC报告(IPCC, 2001)首次将碳循环作为重要评估对象, 从而推动了近年来陆地生态系统过程响应与适应气候变化相关研究的蓬勃发展。这些研究逐渐呈现出多时空尺度、多学科交叉和多种研究方法融合等特点, 并且关注的生态学过程也日趋丰富。这些生态学过程不仅发生于有机体的不同组织层次, 并且涵盖了各种时间尺度。例如, 近来颇受关注的陆地生态系统过程包括分秒尺度的植物酶活性和电子传递速率, 小时与日尺度的植物光合作用及土壤呼吸过程, 季节尺度的植物物候过程(包括展叶、开花、结果与落叶等), 季节与年尺度的植物群落动态和生态系统生产力变异, 年际或年代际尺度的植物物种分布与迁移, 更长时间尺度的土壤有机质稳定与分解过程等方面。因此, 针对国际上研究进展较快的生态系统过程, 开展综述性研究, 有助于梳理该领域近期的重要进展与存在的主要问题。

针对陆地生态系统响应与适应气候变暖这一新兴领域, 近年来国内已有多个研究团队进行了综述研究(傅伯杰等, 2005; 徐小峰等, 2007; 方精云等, 2018; 朴世龙等, 2019)。本文在这些综述研究的基础上, 重点关注陆地生态系统的核心过程如何响应与适应全球温度升高, 并总结该领域近年来的研究

进展。同时, 本文系统地调研了自2000年以来发表于*Science*、*Nature*、*PNAS*与*Global Change Biology* 4本优秀期刊的所有相关论文, 定量分析了该领域的发展动态, 并以此展望未来的研究方向。因篇幅所限, 本文主要围绕图1所示的关键生态系统过程展开综述, 以期激发国内相关领域的进一步讨论与研究。

1 陆地生态系统关键过程对气候变暖的响应与适应

1.1 植物生理生态过程

在植物响应与适应温度变化的生理生态学方向, 光合与呼吸作用一直是研究的重点内容。总体而言, 植物光合速率与呼吸速率随着温度的变化呈现出不同的响应曲线。植物的光合速率在最适温度区间($20\text{--}30\text{ }^{\circ}\text{C}$)达到最大值, 而在过高的温度区间迅速下降(Berry & Björkman, 1980; Yamori *et al.*, 2014)。近年来, 许多文献报道了高温对光合作用的限制作用, 并提出了不同的假说。第一个假说认为高温使Rubisco活化酶的热稳定性下降, 并伴随大量失活现象, 从而导致叶片光合速率下降(Crafts-Brandner & Salvucci, 2000; Yamori & von Caemmerer, 2009; Busch & Sage, 2017)。第二个假说认为高温限制了电子传递速率, 从而降低Rubisco活化酶的活性与光合速率(Sharkey, 2005; Sage & Kubien, 2007)。呼吸速率随着温度的上升总体上呈现指数增高的趋势(Hofstra & Hesketh, 1969; Clark & Menary, 1980; Hesketh *et al.*, 2016)。因此, 温度升高对植物叶片水平碳收支的影响取决于光合与呼吸作用二者对温度变化的响应差异。

植物光合与呼吸作用对温度升高都存在短期顺应(acclimation)与长期适应(adaptation)机制。该现象早期发现于植物的光合作用中, 即高温条件促使光合最适温度升高(Berry & Björkman, 1980; Sage & Kubien, 2007; Smith & Dukes, 2013; Way & Yamori, 2014)。其程度在不同植物物种之间存在明显差异(Way & Yamori, 2014; Smith & Dukes, 2017)。近年来, 光合最适温度随温度升高而上移的现象也在生态系统水平得到证实(Niu *et al.*, 2012)。最新的大尺度分析研究表明全球生态系统尺度总初级生产力的最适温度大约为 $(23 \pm 6)\text{ }^{\circ}\text{C}$ (Huang *et al.*, 2019)。

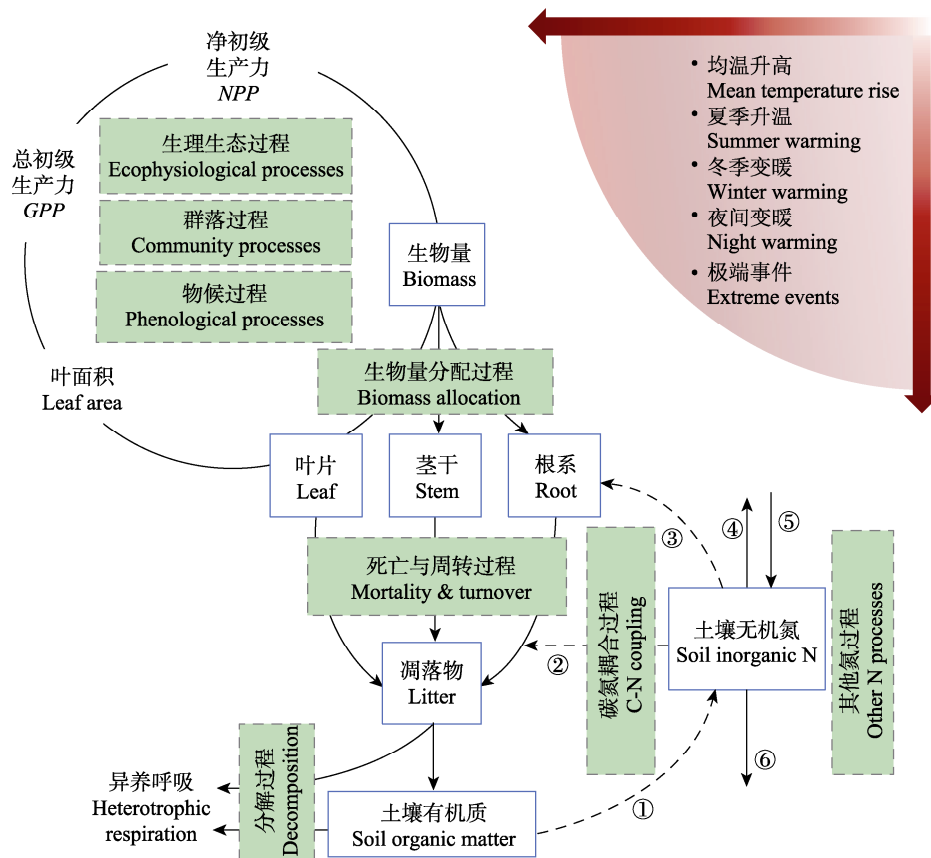


图1 气候变暖对陆地生态系统关键过程的影响。①氮矿化过程；②氮固持过程；③氮吸收过程；④反硝化过程；⑤固氮过程；⑥氮淋溶与径流过程。绿色虚线方框代表各关键过程，蓝色方框代表各碳氮储存库，虚线箭头表示碳氮耦合过程。

Fig. 1 Impact of climate warming on key processes in terrestrial ecosystems. ① N mineralization; ② N immobilization; ③ N uptake; ④ N denitrification; ⑤ N fixation; ⑥ N leaching and running off. GPP, gross primary productivity; NPP, net primary productivity. Green dashed boxes indicate key processes, blue boxes show C and N storage pools, and dashed arrows represent the carbon-nitrogen coupling processes.

相比于光合作用，植物的呼吸作用具有更高的最适温度区间。然而，呼吸作用也会对持续的温度上升产生顺应性或适应性(Atkin & Tjoelker, 2003; Atkin *et al.*, 2005)，并产生温度敏感性下降的现象(Atkin & Tjoelker, 2003; Slot & Kitajima, 2015)。目前关于植物呼吸作用对升温产生顺应或适应性的原因仍存在争议，包括叶片氮含量降低(Tjoelker *et al.*, 1999; Crous *et al.*, 2017)，线粒体的密度或结构发生改变(Armstrong *et al.*, 2006)与呼吸底物和腺苷酸的限制(Atkin & Tjoelker, 2003)等。需要指出的是，目前该方向的许多研究论文在报道结果时未严格定义顺应性与适应性，因此难以梳理二者在已有研究结果中的异同。

虽然植物的光合与呼吸作用对增温的响应存在较大差异，但是二者的比例(即呼吸速率/净光合速率)在一定温度范围内可以达到稳态(Dusenge *et al.*, 2019)。具体而言，随着温度逐渐升高，不断累积的

光合产物为呼吸作用的升高提供了底物；当光合速率由于高温胁迫开始下降时，植物的呼吸速率由于底物不足无法继续上升甚至开始下降，最终使二者达到平衡(Slot & Kitajima, 2015; Dusenge *et al.*, 2019)。因此，植物光合与呼吸作用如何协同地响应气温升高是探究陆地生态系统对气候变化反馈作用的关键问题。

1.2 植物物候

植物的展叶、落叶、开花与结果等物候事件对温度变化极为敏感。目前，中高纬度地区的春季和秋季物候对气候变暖的响应受到了学者的广泛关注。大量的地面和遥感观测数据表明气候变暖促使春季物候提前(Fitter & Fitter, 2002; Zheng *et al.*, 2002; Menzel, 2003; Piao *et al.*, 2015)。然而，随着气温持续升高，近年来的一些研究发现春季物候对温度响应的敏感性逐渐降低(Fu *et al.*, 2015)，甚至发生逆转导致春季物候推迟(Fu *et al.*, 2014)。另一方面，

春季物候的温度响应在空间变异上也出现一些新现象, 例如欧洲阿尔卑斯山脉的植物春季物候在海拔梯度上呈现出趋同的规律(Vitasse *et al.*, 2018)。这些新发现挑战了生态学中的一些经典规律, 例如“霍普金斯法则”(Hopkins bioclimatic law)(Hopkins, 1920)认为植物春季物候随纬度与海拔上升呈现稳步推迟的变化规律。相比于春季物候, 温度升高对秋季物候的延迟作用不明显, 并且其驱动因子仍不十分清楚(Menzel *et al.*, 2006; Liu *et al.*, 2016)。基于大尺度资料的研究发现增温对春季和秋季物候的影响最终都导致了植物生长季的延长(Parmesan, 2007; Piao *et al.*, 2007), 但是对个体物种的观测却发现许多物种应对气候变暖时缩短了生命周期(Cleland *et al.*, 2006; Sherry *et al.*, 2007)或保持不变(Xia & Wan, 2013)。因此, 为了全面地理解植物个体与群落水平的物候响应差异, 未来的研究需要基于不同时空尺度水平的物候观测资料进行整合研究(Steltzer & Post, 2009)。

近年来, 许多研究开始关注植物与动物物候对气候变暖的响应差异(While & Uller, 2014; Ge *et al.*, 2015; Thackeray *et al.*, 2016)。有研究认为, 鸟类和昆虫等的物候过程主要受到短期温度变化的影响, 而植物物候的变化则更多受到长期气候变暖的驱动(Ovaskainen *et al.*, 2013)。此外, 动物物候对气温升高的响应受到系统发育和个体体型的影响(Cohen *et al.*, 2018)。近几十年来, 植物与动物之间物候同步性已经发生了变化(Kharouba *et al.*, 2018)。然而, 目前我们对动植物物候过程对气候变暖的差异化响应及其对生态系统其他过程的影响仍然缺乏深入的认识。

1.3 植物群落动态

生态学领域通常基于大尺度的观测以及小尺度的控制实验来探究气候变暖在植物群落尺度的生态学效应。大尺度的观测结果显示, 气候变暖正在推动世界范围内物种分布向高纬度和高海拔地区迁移(Parmesan & Yohe, 2003; Pauli *et al.*, 2012; Steinbauer *et al.*, 2018), 从而导致新的物种组合(Wing *et al.*, 2005; Bertrand *et al.*, 2011)。例如, 气候变暖导致全球树线位置向更高的海拔和纬度推进(Harsch *et al.*, 2009)。小尺度的控制实验数据能够排除其他因素的干扰, 因而为评估气候变化对群落的影响提供必要的机理解释。近年来的许多实验都发现增温能够显

著改变群落的物种组成。例如, 在北美高草草原, 实验增温处理对C₃和C₄物种的生长产生了不同影响, 并使植物群落朝C₄植物占优势的方向变化(Luo *et al.*, 2009)。需要注意的是, 增温对该草地群落结构的改变在极湿润的年份最为显著(Shi *et al.*, 2015)。在北半球苔原地区11个站点的增温实验发现, 温度上升增加了落叶灌木和禾本科植物的高度和盖度, 降低了苔藓和地衣的盖度和物种多样性, 从而迅速改变了植物群落结构(Walker *et al.*, 2006)。在明尼苏达州北部沼泽进行的增温实验则发现, 酸性沼泽中灌木比禾本科物种更占优势, 而在碱性沼泽中禾本科物种比非禾本科草本植物更占优势(Weltzin *et al.*, 2000)。实验增温虽然未改变我国青藏高原高山草甸生态系统的生产力, 但是显著地降低了植物物种之间的时间非同步性, 从而降低了生产力的稳定性(Ma *et al.*, 2017)。以上研究结论的差异证明植物群落动态对气候变暖的响应与适应具有很高的复杂性。Smith等(2009)提出了一个“层级响应框架”(hierarchical-response framework)试图解释植物群落响应气候变化的统一性机理。然而, 该框架主要关注草原生态系统模拟降水实验中出现的现象, 因此至今尚未得到普遍关注和应用。

虽然目前已有大量的观测与实验证据说明气候变暖能改变陆地植物群落的结构, 但是对于其生态学机理仍缺乏统一认识。这主要是由于气候变暖不仅通过温度升高直接影响物种的生理生态过程, 还可以通过改变土壤水分条件与养分利用效率等调控植物群落的种内和种间关系, 从而间接影响群落结构的动态。例如, 北半球苔原的湿润区比干燥区具有更高的物种多样性(Walker *et al.*, 2006); 内蒙古半干旱草原通过土壤水分和种间相互作用来调节植物群落结构和组成对增温的响应(Yang *et al.*, 2011)。在北方森林生态系统, 温度升高对树木生长的影响也显著依赖于土壤水分条件(Reich *et al.*, 2018b)。气候变暖对土壤氮循环也存在显著影响, 尤其是普遍促进了氮矿化速率(Bai *et al.*, 2013), 且该现象大多伴随着植物群落物种组成的改变(Wu *et al.*, 2012)。由于氮对植物的增产效应存在显著的种间差异(Xia & Wan, 2008; Midolo *et al.*, 2019), 因此可以推断氮循环的改变是调控植物群落响应气候变暖的重要机理。然而, 目前探讨该机理的实验性研究仍然较少(An *et al.*, 2005), 大多只关注氮添加与增温处理对

生态系统过程的交互效应(Xia *et al.*, 2009, 2013; Wu *et al.*, 2012; Xiong *et al.*, 2018)。近来的许多研究表明, 菌根真菌有利于增强寄主植物对气候变暖的适应性, 因此在调控植物群落响应气候变暖的过程中扮演了重要的角色(Cowden *et al.*, 2019)。总之, 植物群落结构与物种组成对气候变暖的响应是多个复杂过程综合作用的结果, 也是未来预测气候变化背景下植物群落动态的重要挑战。

1.4 生态系统生产力及其分配过程

气候变暖对生态系统生产力的影响有明显的水热依赖性, 即在湿润寒冷的生态系统表现为正效应, 但在干旱高温生态系统存在负作用(Quan *et al.*, 2019)。在气候变暖下, 北半球中高纬度地区和青藏高原地区的植被呈现出光合作用增强和生长季延长的变化趋势, 进而促进生态系统生产力显著升高(Keeling *et al.*, 1996; Myneni *et al.*, 1997; Nemani *et al.*, 2003; Xu *et al.*, 2013; Zhu *et al.*, 2016)。例如, 温度升高显著促进了北寒带地区(阿拉斯加西部, 北魁北克北部和西伯利亚东北部等)木本植物的生长(McManus *et al.*, 2012)。全球变暖引发的北高纬度地区积雪和冻土融化加速了灌木在苔原地区的扩张(Myers-Smith *et al.*, 2011)。与此同时, 中高纬度地区植被生长活动与温度的敏感性强度在近30年中呈现出明显下降趋势(Piao *et al.*, 2014)。持续增温可能会对热带植被的生长产生负面影响。例如, 有研究表明温度升高会抑制叶片气体交换从而降低热带森林的植被生产力和生长速率(Clark *et al.*, 2003)。另一方面, 温度持续升高所引发的干旱和热浪事件会显著抑制植被生长, 甚至导致全球大范围的树木死亡(Allen *et al.*, 2010, 2015)。例如, 2003年欧洲高温热浪抑制陆地植被对大气CO₂的吸收(Ciais *et al.*, 2005)。干旱胁迫甚至可以通过破坏热带雨林的植物水分吸收运输机制从而导致树木的死亡(Rowland *et al.*, 2015; McDowell *et al.*, 2018)。在气候变暖导致干旱和热浪事件剧增的背景下, 植被生长对于极端事件的响应和恢复是未来需要重点关注的方向。

生态系统生产力分配方面的首要问题是陆地生态系统净初级生产力与总初级生产力之间的比例(*NPP/GPP*)是否随气候变化发生改变。最近, Collalti 和 Prentice (2019)对*NPP/GPP*进行了系统地综述, 并认为该比值对温度变化的响应较小。这个结论也

得到一项基于整树同位素标记实验(Drake *et al.*, 2019)的支持。虽然大多数陆地生态系统模型中的*NPP/GPP*内部变异极小, 但是模型之间的数值差异很大(Xia *et al.*, 2017)。此外, 生态系统净初级生产力分配到根系、茎干与叶片等组织器官的过程将对生态系统的结构与功能产生重要影响。总体而言, 温度升高在寒冷生态系统中会促进植物更多地向地上生长分配(Lin *et al.*, 2010; Way & Oren, 2010)。然而需要指出的是, 自然生态系统中的净初级生产力分配过程难以被直接测定, 所以文献中大多报道的是生物量的分配比例。近年来, 许多关于生产力分配的研究开始关注非结构性碳水化合物的动态, 这是由于大量实验证据发现碳水化合物在调节植物适应极端气候变化方面具有重要意义(Doughty *et al.*, 2015; Malhi *et al.*, 2017; Du *et al.*, 2020)。

1.5 凋落物与土壤有机质分解过程

植物凋落物在生态系统的物质循环过程中具有重要作用(图1)。长期以来, 气候条件被认为是植物凋落物分解速率的主要调控因子(Meentemeyer, 1978; Wall *et al.*, 2008; Zhang *et al.*, 2008; Gregorich *et al.*, 2017), 因此气候变暖被认为将加速凋落物的分解过程。近年来, 有大量的野外生态学研究发现凋落物的功能性状或微生物群落是控制凋落物分解速率的首要因子(Bradford *et al.*, 2014; Ward *et al.*, 2015; Parker *et al.*, 2018), 因此气候变暖不能从根本上改变植物凋落物的分解速率。事实上, Tenney和Waksman (1929)最早提出的假说认为凋落物分解速率受温度、湿度与凋落物质量三者共同调控。最近在美国黄石国家公园的一项研究表明, 除了气候与凋落物质量之外, 大型食草动物也是凋落物分解速率的重要影响因子(Penner & Frank, 2019)。因此, 生物与气候因子在不同生态系统中的相对重要性及其转换机制是目前该方向上比较重要的问题。

土壤有机碳是陆地有机碳库的重要组成部分, 也是陆地生态系统反馈未来气候变化的主要不确定性来源(Knorr *et al.*, 2005; Bond-Lamberty *et al.*, 2018)。例如, Crowther等(2016)整合分析了49个野外增温实验中土壤有机碳库的变化, 发现土壤有机碳储量更大的生态系统丢失更多有机碳, 因此认为气候变暖将加剧大气CO₂浓度上升。然而, 该研究结果随后受到了van Gestel等(2018)的挑战, 该研究整合

分析了143个实验数据,发现Crowther等(2016)报道的规律在更大的数据样本中没有出现。因此,从生态学机理方面理解土壤有机碳分解的温度敏感性对预测生态系统对气候变暖的响应至关重要(Smith *et al.*, 2008; Paustian *et al.*, 2016)。已有的研究结果已经证实土壤底物质量和微生物活性是影响土壤有机碳温度敏感性的关键限制因素(Karhu *et al.*, 2014; Moinet *et al.*, 2018)。然而,全球变暖背景下土壤底物质量如何变化,以及微生物活性是否存在顺应或适应现象仍不清楚(Luo *et al.*, 2001; Frey *et al.*, 2013; Allison *et al.*, 2018)。近年来,分布于全球不同区域的野外模拟增温实验报道了一些新现象。例如,Melillo等(2017)在26年增温实验中观测到美国哈佛森林的土壤有机质分解速率对温度升高出现周期性响应节律,并可被分为四个阶段。这些阶段包括土壤表层易分解有机质大量丢失、微生物群落重组、难分解有机质成为微生物主要碳基质与微生物群落再重组,最终使难分解有机质在增温条件下加速分解。然而,由于其他增温实验大多运行时间较短(Song *et al.*, 2019),因此该研究揭示的生态学机理仍有待于进一步验证。

1.6 元素循环及其耦合过程

气候变暖深刻地影响了陆地生态系统中碳、氮、磷与水等物质的循环过程及其相互之间的耦合关系。如图1所示,陆地生态系统的碳氮循环存在紧密的耦合关系(Thornton *et al.*, 2009; Niu *et al.*, 2016)。碳通过植物光合作用进入陆地碳循环,并通过植物呼吸、凋落物分解与土壤有机质分解过程返回大气,从而形成一个循环系统。相比于碳循环,陆地氮循环更加开放,且多个氮输入(沉降、生物固氮、矿化作用等)与输出(植物吸收、淋溶、反硝化、固持等)过程同时影响土壤无机氮库的动态。Lu等(2013)与Bai等(2013)分别利用元分析方法估算了全球增温实验中陆地碳、氮循环过程的响应。目前比较明确的结论是气候变暖显著提高了土壤氮矿化速率,从而增加土壤中氮的有效性。对碳循环而言,当前的全球尺度碳循环模型普遍地预测气候变暖将削弱陆地生态系统的碳汇能力(Cox *et al.*, 2000; Friedlingstein *et al.*, 2006)。然而,需要注意的是,目前用于IPCC评估报告的模型预测结果大多未考虑养分循环对碳循环的调控作用。

相对于碳、氮之间的紧密耦合性而言,气候变

化可能导致磷循环与二者发生解耦合的趋势(Peñuelas *et al.*, 2013; Yuan & Chen, 2015; Mooshammer *et al.*, 2017)。由于磷循环没有显著的气体通量过程,且其转化过程具有速率低、时间长与跨空间等特点(Schlesinger & Bernhardt, 2012),因此难以借助野外增温实验的手段开展机理性研究。目前已有的研究发现气候变暖在一定程度上会增强土壤中微生物的酶活性(Xue *et al.*, 2016; Melillo *et al.*, 2017),加速土壤有机质的分解(Bai *et al.*, 2013),促进有效氮、有效磷的释放和植物对养分的吸收(Shaver *et al.*, 2000; Melillo *et al.*, 2011)。此外,气候变暖也能够通过改变土壤湿度从而间接调控生态系统氮磷循环(Dijkstra *et al.*, 2012; Greaver *et al.*, 2016),如通过提高土壤湿度从而增大磷的溶解率,进而促进植物和微生物对磷的吸收(Lambers *et al.*, 2006)。在增温引起干旱的生态系统中,有机质矿化速率、磷的扩散速率降低,植物和微生物对养分的吸收将受到水分胁迫(Greaver *et al.*, 2016)。目前,更多的研究主要关注增温对植物和微生物体内碳氮磷计量关系的影响(Dijkstra *et al.*, 2012)。然而需要指出的是,生物体内的碳氮磷计量关系对生物地球化学过程的耦合关系虽然具有重要指示作用,但并不等同于该耦合关系。因此,未来的研究仍需探明增温改变生态系统碳氮磷计量关系的生态学机理,以及分析该关系的变化如何从不同时空尺度影响生态系统的服务功能。

围绕以上生态系统关键过程,我们通过梳理已发表的文献资料,进一步评估了其中10个受关注度较高过程响应气候变暖的置信度(图2)。目前置信度最高的现象是春季物候提前现象,不仅证据量充足而且一致性较高。然而,仍然需要指出的是,近期的一些研究发现春季植物物候对温度的敏感性呈下降趋势(Fu *et al.*, 2015),因此可能使未来研究之间的一致性降低。对土壤有机质加速分解与土壤矿化速率加快等现象而言,虽然研究的数量较少,但是结论高度一致。光合作用的过补偿效应(Wan *et al.*, 2009)虽然已提出十余年,但是不同生态系统报道的结果存在较大差异,因此仍需要更多的研究揭示调控该现象的生物学机理。此外,呼吸作用的热适应性现象在植物叶片中一致性非常高,但是对土壤而言则置信度较低。因此,我们建议未来的研究进一步关注证据量少且一致性低的关键生态系统过程,以期发现其背后的普适性生态学机制。

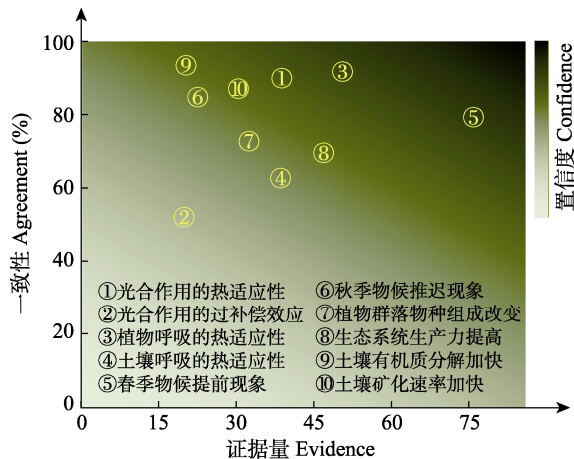


图2 生态系统部分关键过程响应气候变暖的证据量、一致性及置信度。证据量是指报道该生态系统过程的研究文献数量，一致性是指所有文献中支持该响应现象的百分比。置信度由证据量与一致性的乘积表示。该方法参考了第五次IPCC报告(IPCC, 2013)中的置信度概念，并沿用了Xia等(2014)一文中的表达方法。本图中涉及的具体发表文献请见附录1。

Fig. 2 Evidence, agreement and thus confidence of key ecosystem processes in response to climate warming. “Evidence” shows the number of studies that report on ecosystem processes. “Agreement” indicates the percentage of evidence supporting the specific warming response. Confidence is the product of “Evidence” and “Agreement” and is based on the confidence concept in the fifth IPCC report (IPCC, 2013). The figure was adapted from Xia *et al.* (2014). Data was obtained by a comprehensive literature search (Supplement I). ① photosynthetic acclimation; ② photosynthetic overcompensation; ③ acclimation of plant respiration; ④ acclimation of soil respiration; ⑤ earlier spring phenology; ⑥ delayed autumn phenology; ⑦ changed species composition of plant community; ⑧ enhanced ecosystem productivity; ⑨ faster decomposition of soil organic matter; ⑩ faster soil nutrient mineralization.

2 前沿方向展望

本研究调研了2000年以来发表于*Science*、*Nature*、*PNAS*与*Global Change Biology* 4本优秀期刊的相关论文，得出了以下几个比较明显的趋势。首先，最近十年中，国内第一单位发表的论文数量呈现上升趋势(图3A)；其次，*Science*与*PNAS*主要发表以观测数据为基础的研究论文，而*Nature*与*Global Change Biology*则发表更多实验性研究论文(图3B)；此外，过去发表的论文大多包含生理生态学过程与植物群落动态，而且不同期刊对不同生态系统过程的发表比例有差异(图3C)。通过仔细研究近期的相关学术论文，可以得出若干陆地生态系统与气候变暖相关的前沿方向。以下列举五方面内容，谨供国内相关领域参考。

2.1 物种性状与生态系统功能

植物功能性状是与植物生长、生存、竞争和繁殖紧密相关的一系列功能属性(Wright *et al.*, 2004; Kunstler *et al.*, 2016)，常见的功能性状有表征植物资源利用能力的比叶面积、叶氮含量、胞间和大气CO₂浓度比、边材和叶面积之比等；表征植物光合能力的最大羧化速率和最大电子传递速率等(Reich *et al.*, 1997; Reich, 2014)。植物功能性状既取决于遗传因素，又受到外界环境的修饰作用(van Bodegom *et al.*, 2012)。全球变暖可以直接影响植物的功能性状(Cui *et al.*, 2020)，进而影响生态系统结构和功能(Atkin *et al.*, 2008; Meng *et al.*, 2015; Doughty *et al.*,

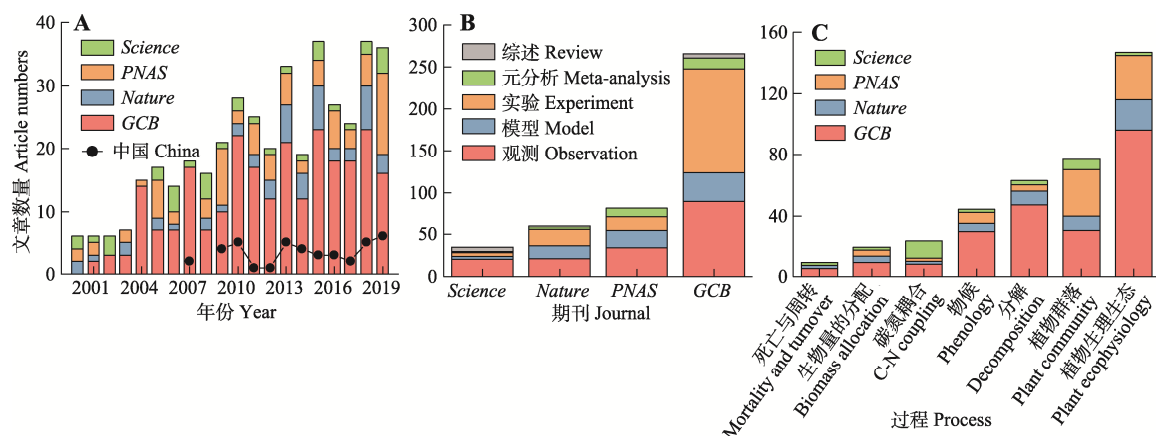


图3 4份主流期刊(*Science*、*Nature*、*PNAS*与*Global Change Biology* (GCB))在2000–2019年间的发表文章数量(A)及其在研究方法(B)与生态学过程(C)方面的分布情况。论文检索结果来源于各期刊网站，首先采用关键词“warming”进行搜索。然后，再逐篇筛查是否包含陆地生态系统过程。中国地区的文章即第一作者单位为中国境内的研究机构。

Fig. 3 Publications of four high-impact journals (*Science*, *Nature*, *PNAS* and *Global Change Biology* (GCB)) (2000–2019), including the total number of papers (A) and their distribution in different methods (B) and ecological processes (C). Literature was first searched by the keyword “warming” from the homepage of each journal, then manually screened for whether it includes terrestrial ecosystem processes. The black line for “China” represents the published papers with the first affiliated address located in China.

2018)。植物功能性状对气候变暖的响应, 在预测植被分布、反映植被对气候变化的响应和评估生态系统服务功能等方面发挥着重要的作用。尽管已有成果有力地推动了全球变化生态学的发展, 但仍存在很多值得发展和探索的空白区域: (1)目前功能性状的研究与理论发展主要基于个体水平的观测。不同植物个体对气候变暖的响应模式不同, 根据个体反应难以预测群落或生态系统的整体响应模式, 未来应该加强群落或生态系统水平性状的观测研究(He *et al.*, 2019)。(2)功能性状的研究主要集中于地上性状, 地下性状对于植物生长发育、养分循环等同样至关重要(Ma *et al.*, 2018)。(3)缺乏增温梯度控制实验研究, 以往的实验模拟研究大多没有增温梯度, 难以深入探究功能性状对于气候变暖的敏感性及其适应性。(4)基于植被功能性状及其环境变异性对动态植被模型进行改进(Verheijen *et al.*, 2015; Ma *et al.*, 2017), 发展我国自主知识产权的动态植被模型。

土壤微生物作为土壤中活的有机体系, 是生态系统养分循环和能量流动的重要纽带(Wieder *et al.*, 2015)。全球变暖可能会改变土壤微生物结构和功能组成, 从而影响植物与土壤微生物之间的相互作用与反馈(Xue *et al.*, 2016)。然而, 目前学术界对土壤微生物群落如何响应气候变暖等问题认识不足, 且缺乏相关实验证据, 成为了限制陆地生态系统气候反馈预测的重要因素(Li *et al.*, 2014; Abramoff *et al.*, 2018)。因此, 未来需要借助新兴技术手段及方法加强对微生物关键过程和机理的研究, 如利用高通量测序手段对微生物群落进行全面而准确地分析; 借助稳定同位素标记进行代谢途径、养分分配等机理研究。

2.2 生物地球化学循环的耦合过程

生物地球化学循环各个过程相互关联且紧密耦合, 因此气候变暖可以通过改变陆地水、氮、磷循环间接调控碳循环和陆地-大气系统之间的反馈作用(Heimann & Reichstein, 2008; Arneeth *et al.*, 2010)。然而, 目前对于各个元素循环间耦合机制的理解十分有限, 且生物地球化学循环对气候变暖的响应可能存在长期多相性, 即各个过程的短期响应在长期可能发生逆转(Melillo *et al.*, 2002, 2017; Reich *et al.*, 2018a)。同时, 由于对相关机理的理解尚不成熟, 及相关过程观测数据的欠缺, 导致模型模拟的结果存在很大的不确定性。在未来, 一方面需要借助更多

的长期控制实验深入研究关键过程的变化机理, 另一方面则需要将实验研究结果与过程模型相结合以优化模型各个过程的模拟。

目前, 我们对深层土壤(例如30 cm以下)物质循环过程的理解较浅, 例如仅了解深层土壤物质具有更长的碳滞留时间(Rumpel & Kögel-Knabner, 2011)。但是, 深层土壤的碳含量占整个土壤碳库的一半以上, 而且其C:N的变化和丰富的化学物质成分表明深层土壤物质循环具有强烈的生化反应过程, 这些过程给土壤碳循环的研究带来很大的不确定性(Salome *et al.*, 2010; Rumpel & Kögel-Knabner, 2011)。例如, 在深层土壤碳循环过程中, 新的土壤有机碳输入会激发深层土壤有机碳的分解(Rumpel & Kögel-Knabner, 2011)。而且, 在对气候变化的响应方面, 深层土壤有机碳的机理和浅层土壤有很大的区别, 例如深层土壤面对扰动更加容易矿化(Salome *et al.*, 2010)。近年来, 在美国明尼苏达州的云杉林-泥炭地生态系统(Wilson *et al.*, 2016; Hanson *et al.*, 2017; Richardson *et al.*, 2018)与加利福尼亚州的针叶林生态系统(Pries *et al.*, 2017)都开展了全土壤坡面的增温实验。开展这些实验的一个重要科学假设是地球系统模式往往预测气候变暖提高了全土壤坡面的温度。然而需要注意的是, 当前地球系统模式中的陆面模式大多没有考虑土壤的深度分层, 因此其预测的土壤温度变化仍需更多的观测资料进行验证。尽管如此, 在气候变暖的情境下准确预测土壤碳循环的变化趋势, 仍需更加注重对深层土壤的研究(Chaopricha & Marin-Spiotta, 2014)。

冻土区贮存了约1 700 Gt土壤碳, 约为大气碳库的2倍, 其微小扰动都会对全球碳循环产生重要影响(Schuur *et al.*, 2009; Koven *et al.*, 2011)。一方面温度上升会加速冻土融化, 刺激微生物分解, 增加土壤有机碳释放, 从而对全球气候变化起到正反馈作用并加速全球变暖(Tarnocai *et al.*, 2009; Koven *et al.*, 2011; Schuur *et al.*, 2015)。另一方面, 气候变暖会加速土壤氮磷矿化, 刺激冻土区植被生长, 进而增加生态系统碳固定(Ding *et al.*, 2017; Zhu *et al.*, 2017)。由于缺乏长期观测资料, 已有的研究结果对于气候变暖下植被生长碳累积是否能抵消冻土融化造成的碳损失仍存在较大争议。同时, 由于冻土区土壤碳循环过程的复杂性, 当前全球陆地碳循环模型对冻土区生产力的模拟和预测存在2-3倍的差异

(Xia *et al.*, 2017)。因此, 未来冻土区的研究应该加强探索气候变暖对生态系统碳氮磷交互作用的生态学机理(Li *et al.*, 2017)。

2.3 生态系统对极端低温与高温事件的响应与适应机理

随着全球增温趋势的不断加剧, 极端低温和高温事件呈现出破坏性大、突发性强、难以预测等特点(Fischer & Knutti, 2015; Dong *et al.*, 2017)。极端低温和高温对陆地生态系统的结构和功能以及碳循环过程造成了严重的破坏(Cavanaugh *et al.*, 2014; Perkins, 2015)。其中极端低温事件会影响生物学温度阈值, 导致生物多样性降低(Taylor *et al.*, 2006; Miller & Barry, 2009), 生态系统生产力下降(Doran *et al.*, 2002; Marchand *et al.*, 2006), 同时也会使入侵物种减少(Walther *et al.*, 2002; Firth *et al.* 2011), 抑制虫害爆发(Jentsch & Beierkuhnlein, 2008)。极端高温事件既能直接影响动植物的生理过程(Smith, 2011; Teskey *et al.*, 2015; Harris *et al.*, 2018), 也会通过改变土壤水分状况间接作用于植物光合作用和呼吸作用(Anderegg *et al.*, 2012; Choat *et al.*, 2012)。极端高温胁迫的滞后影响包括火灾、病原体和虫害暴发风险等都会进一步对陆地植被生长与生态系统生产力造成损害(van Mantgem *et al.*, 2009; Gaylord *et al.*, 2013)。

陆地植被对于长期温度变化具有一定的适应性, 可在一定程度上减少极端事件的破坏性(Niu *et al.*, 2012)。生态系统对极端温度事件的抵抗力以及灾害发生后的恢复情况也是目前研究的热点和难点问题(Ruthrof *et al.*, 2018)。未来的研究需要量化分析极端温度事件的正负效应, 生态系统抵抗和恢复机制及其驱动因素, 并建立完善的观测体系记录极端温度事件与生态系统间的联系(Flach *et al.*, 2018)。

2.4 不对称性增温对生态系统的特异性影响

IPCC第五次评估报告指出, 全球气温的升高在昼夜间和季节间均呈现出明显的不对称性, 即平均夜间增温幅度大于白天增温幅度(Easterling *et al.*, 1997; Hartman *et al.*, 2013), 而中高纬度地区冬季和春季的增温速度比夏季快(Xu *et al.*, 2013)。昼夜和季节的不对称增温对植物的生理、物候及生态系统功能都存在重要影响(Xia *et al.*, 2014)。

昼夜的不对称增温会对生态系统产生不同影响, 即白天增温能够在光合最适温度范围内提高植物的

碳吸收能力(Peng *et al.*, 2013), 夜间增温则刺激植物呼吸作用导致CO₂的释放(Turnbull *et al.*, 2002; Peng *et al.*, 2004)。近年来的一些研究报道了夜间增温对生态系统碳循环的重要影响。例如, 温室和野外实验发现在干旱和半干旱区域夜间增温对光合作用的过补偿现象(Wan *et al.*, 2009), 并促进干旱区的植物生长与生态系统生产力(Peng *et al.*, 2013; Xia *et al.*, 2014), 基于大尺度的遥感观测数据却发现夜间增温对全球热带生态系统的碳汇能力表现为负作用(Anderegg *et al.*, 2015)。截至目前, 关于陆地生态系统如何响应昼夜不对称增温的实验研究仍然局限于草地生态系统(Xia *et al.*, 2014), 因此需要在更多的生态系统进行验证和研究。最近, Gaston (2019)甚至提出“夜间生态学”(Nighttime Ecology)的概念, 呼吁生态学领域加强对夜间生态学过程的关注。季节性不对称的增温主要体现在冬春季相对增温明显。冬春季变暖一方面促使植物的生长季提前(Wolkovich *et al.*, 2012), 另一方面减少了雪被覆盖厚度从而对地下生态学过程产生复杂影响(Fitzhugh *et al.*, 2001)。此外, 不同季节的增温可能会通过“滞后”(Xia *et al.*, 2014)或“补偿”作用(Buermann *et al.*, 2018)互相影响。因此, 未来的研究难点在于如何在昼夜与季节尺度整合不同生态系统过程, 并使观测数据能覆盖夜间与冬季等易被忽视的时期。

2.5 生态系统的模拟与预测

生态系统的可持续性发展包含生态系统及其服务在未来会如何变化, 人类的行为决策将如何影响生态系统的发展轨迹等核心问题。回答或解决这些问题需要生态系统的关键过程具有较高的可模拟和可预测能力(Clark *et al.*, 2001; Dietze *et al.*, 2018)。然而, 目前生态系统过程模型存在巨大的不确定性(Luo *et al.*, 2009; Xia *et al.*, 2017)。为了提高生态系统模型模拟和预测的准确性, 需要在分析和降低模型的不确定性, 观测数据和模型的融合, 以及生态系统对气候变化的反馈作用等领域进一步加强研究。如图3所示, 自2000年以来*Science*、*Nature*、*PNAS*与*Global Change Biology* 4个期刊发表了大量关于陆地生态系统响应与适应气候变暖的学术论文。除了实验与观测以外, 模型模拟在近年来也成为了主流的研究手段。随着对全球变化响应机理的深入研究, 生态系统模型的结构越来越复杂, 因此进一步增加了不同模型间的差异(Xia *et al.*, 2013; Shi *et al.*,

2016; Liang *et al.*, 2018; Du *et al.*, 2020)。所以, 在未来生态系统模型的发展中, 需要更加深入地研究生态系统对气候变化的反馈机理以及合适的模型化手段, 以提高模型模拟和预测的能力。

3 总结

在过去几十年中, 国内外生态学界在“陆地生态系统响应与适应气候变暖”这一领域取得了一系列重要成果。基于以上文献综述, 可以获得以下可信度较高的结论: (1)植物光合作用与呼吸作用对温度升高的响应与适应过程存在差异, 使气候变暖对生态系统净碳平衡的影响呈现出显著的时空变异; (2)植物的春季物候对气候变暖十分敏感, 但近年来呈现出温度敏感性下降的趋势; (3)气候变暖伴随着土壤干旱化增大了全球森林的死亡风险; (4)生物地球化学循环对长期升温的响应可能存在周期性的变化。

除此之外, 其他进展较快的方向包括冻土区碳循环、深层土壤碳循环、植物群落结构变化、土壤微生物结构与功能等。然而, 这些研究依然存在一些共性不足, 主要体现在: (1)过去的研究设计更多针对气候变暖如何“影响”陆地生态系统, 但对陆地生态系统如何“适应”气候变暖研究相对较少; (2)大多关注森林与草地生态系统, 对湿地与荒漠等生态系统等研究较少; (3)实验设计多采用平均温升高或长期增温, 对极端温度事件的响应与适应机理缺乏野外实验研究; (4)主要关注碳循环本身, 而忽略了水、氮、磷等循环对碳循环的调控作用; (5)大多采用实验、观测或模型为研究手段, 极少有研究能够同时整合多种研究方法。这些方面还需要在未来的研究中逐步加强。

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附录I 图2中涉及的参考文献列表

Supplement I List of references involved in Fig. 2

<http://www.plant-ecology.com/fileup/1005-264X/PDF/cjpe.2019.0323-S1.pdf>