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模拟增温对土壤呼吸影响机制的研究进展与展望

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摘 要 土壤呼吸是土壤碳库向大气碳库输入的主要途径，而温度升高会影响土壤呼吸从而改变全球碳平衡.据预测在21世纪末，全球平均地表温度将升高0.3~4.8 ℃，因此野外自然条件下的模拟增温试验对土壤呼吸的影响是全球变化研究的热点之一.本文综述了不同时空格局下土壤呼吸对模拟增温的响应特征，指出短期增温能提高土壤呼吸，而长期增温下无统一规律，并且不同生态系统之间也存在差异; 重点讨论了模拟增温对土壤呼吸的影响机制，指出增温能直接影响土壤呼吸，同时增温也能通过影响土壤水分、盐分、土壤理化性质等环境因子以及光合作用、凋落物等生物因子对土壤呼吸产生间接影响; 另外，分析了土壤呼吸对增温产生适应性的形成机制，主要包括微生物、根、酶的温度适应性、水分限制、氮素过量以及呼吸底物限制.在此基础上对今后的研究方向加以展望: 加强根际微生态系统的研究; 重点研究不对称增温下土壤呼吸的特征及机制; 关注典型物候期和不同季节典型天气土壤呼吸的测定; 构建土壤呼吸响应模拟增温试验的研究网络，进行联网试验.

关键词 模拟增温; 土壤呼吸; 适应性

Research and prospects for response mechanisms of soil respiration to experimental warming. SUN Bao-yu[1,2], HAN Guang-xuan[1*] ([1]*Key Laboratory of Coastal Environmental Processes and Ecological Remediation, Chinese Academy of Sciences, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai* 264003, *Shandong, China*; [2]*University of Chinese Academy of Sciences, Beijing* 100049, *China*).

Abstract: Soil respiration (R_s) is the main efflux of carbon pool from soil to atmosphere. Increasing R_s caused by rising temperature can result in significant change in the global carbon balance. Global mean land-surface temperature is predicted to rise by 0.3-4.8 ℃ by the end of 21 century. Therefore, how R_s responds to simulated experimental warming in the natural field is one of the critical issues in global change research. Here, we reviewed the response characteristics of R_s to simulated warming under different temporal and spatial patterns. Experimental warming can increase R_s at the short time scale, but there was no uniform law in the long-term warming experiments, and there were differences among different ecosystems. This paper also reviewed the mechanism underlying the simulated warming response of R_s. Warming can directly affect R_s, and warming can also affect R_s indirectly by affecting the environmental factors (*e.g.*, soil water, soil salt, soil physical and chemical properties), and the regulation of biological factors (*e.g.*, photosynthesis, litter decomposition). Furthermore, we synthesized the formation mechanism of adaptability of R_s to warming, including adaptability of microbes, roots and enzymes to warming, water restriction, and regulation by excessive nitrogen and the substrate supply. Finally, the future research directions were proposed. The study of micro-ecosystem of rhizosphere, characteristics and mechanism of R_s under asymmetric warming should be strengthened. Also, more attention should be paid to the measurement of R_s in typical phenological periods and typical weather in different seasons. The research network of R_s response to simulated warming should be constructed for networking test.

Key words: experimental warming; soil respiration; adaptability.

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土壤呼吸作用是土壤碳库向大气层碳库输入的主要途径[1],主要包括来自植物根系的自养呼吸作用和土壤微生物异养呼吸作用.土壤是地球表面最大的碳库($2.2\times10^3\sim3\times10^3$ Pg),为植被碳库的 2~3 倍、全球大气碳库的 2 倍[2].因此,土壤呼吸速率相对微小的改变都会显著改变大气中 CO_2 的浓度和土壤碳的累积速率,从而加剧或减缓全球气候变暖[3].截止到 20 世纪末,全球地表平均温度上升了约 1.5~2.0 ℃[4].同时,模型预测表明,2016—2035 年全球平均地表温度将升高 0.3~0.7 ℃,2018—2100 年将升高 0.3~4.8 ℃[4],并且北半球高纬度和高海拔地区温度升幅更大[5].温度升高会促进土壤呼吸[6-8],进而使大气 CO_2 浓度增加,在陆地生态系统与大气之间产生一个强烈的正反馈作用[9],从而使全球变暖的情况更加恶化[10].因此,研究全球变暖下的土壤呼吸作用已成为当今热点问题.

野外自然条件下的模拟增温试验是研究全球变化重要的信息来源[11],是研究全球变暖与陆地生态系统相互关系的主要方法之一[3,12-13],不仅能够获取气候变暖对生态系统影响的直接证据,还可以解释陆地生态系统对气候变化响应的内在机制[13].目前,模拟增温的方法主要包括主动增温和被动增温,并且根据其特点应用于各种生态系统类型中,在增温对土壤呼吸影响的特征及机制方面取得了重要进展.但是,在有关研究的广度和深度方面仍存在大量不足[14].因此,本文综述了此领域近十几年来的主要研究工作,总结了模拟增温的方法、对土壤呼吸的影响及其机制,并指出以往研究中存在的主要问题以及未来研究的主要方向.

1　增温方法与装置

试验装置的发展是模拟增温试验的重要推动力.目前,有关全球变暖对陆地生态系统影响的增温装置主要分为被动增温和主动增温两类.被动增温包括开顶式生长箱、温室和红外反射器;而人工气候生长箱、土壤加热管道和电缆[15]、红外线辐射器[16]等则为主动加热装置.其中,温室或开顶箱作为最早最简单且最普遍的增温装置[17]被广泛应用在草地生态系统中[18-20],包括北极和南极冻原亚高山草地青藏高原和温带草原,在高海拔和高纬度地区的增温试验主要通过温室设施实现[3].而在 20 世纪 70 年代,有研究者利用发电厂的废热水埋管道增温,以此为启示出现了土壤加热电缆增温方式[21].红外线发射器作为能够模拟夜间增温的试验装置被开发出来,它的原理和设计比较简单[22-24],在生态系统控制试验中逐渐得到应用[25].

尽管不同类型的增温装置有着不同的增温效果,但是作为全球变化生态学研究的主要手段之一,生态系统增温试验在研究陆地生态系统对全球变暖的响应和适应机理方面有不可替代的作用[3].被动加热装置较为省钱和省力,但对自然环境的干扰较大,装置本身产生的干扰效应有时会大于增温处理的效应,而且增温的幅度和时间不能很好地控制[26];主动加热装置对自然环境干扰较小,可控性强,但配置和维护费用高,且受电力等能源供应条件的限制[12-13,25,27].不同增温装置的设计、技术和增温机制差异可能导致研究结果大相径庭.因此,选择能够真实地模拟气候变暖机制且对环境干扰最少的增温装置显得尤为重要.

气候变暖主要是由于温室气体反射的具有热效应的长波辐射(主要是红外线)增强导致的,这种增强的向下红外辐射主要通过 3 种能量方式(显热、潜热和土壤热通量)影响气候变化[28],从而导致空气和土壤温度升高[6].红外辐射技术恰好能模拟这种增强的向下红外辐射,能同时改变显热、潜热和土壤热通量[3,29],对土壤无物理干扰,同时不改变小气候状况,能更真实有效地模拟全球变暖的增温机制,是现有的模拟增温的理想方法,近年来被广泛应用于森林、草地、苔原等生态系统[3].

2　模拟增温对土壤呼吸速率的影响

基于以上方法,国内外众多学者布置了大量试验,研究区纬度跨度大,在 45.4° S—78.9° N,但是主要集中在北半球,包含多种生态系统类型,如森林、草地、苔原、湿地、农田等.研究区年平均温度为 -18.1~19.6 ℃,年平均降水量为 150~1741 mm.研究持续时间从一两年到十几年不等,其中,有 7 个生态系统的持续增温时间在 6 年以上[6,30-35],其余试验研究期均在 4 年以内.

大量研究发现,对于短期增温来说,土壤呼吸速率随着土壤温度的升高而增加[6,29,32,36].如 Schindlbacher 等[35]对挪威云杉(*Picea asperata*)成熟林进行增温试验(土壤温度提高 4 ℃),使得土壤呼吸分别在第 1、2 年提高了 39%、45%;在美国俄亥俄州西部森林 2 年的增温试验中,当温度升高 2.5 ℃,土壤呼吸速率增加 26%[36];在为期 3 年的日本广岛常绿阔叶林中,当温度升高 1.4 ℃,土壤呼吸速率增加 13.9%[37];内蒙古多伦多草原增温 3 年间,当温度升

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高 0.47 ℃,土壤呼吸速率增加 3.2%[6];在北美高草草原的控制加热对比试验中也得到了类似结论[29,32];Wang 等[7] 通过 Meta 分析总结了 50 个陆地生态系统增温对土壤呼吸速率的影响,得到土壤温度平均增加 2 ℃,土壤呼吸速率提高 12%.

对于长期增温的试验,土壤呼吸对增温的响应则无统一规律.例如,在美国 Harward 森林两个长期变暖的试验中,1991 年开始的试验表明,前 6 年温度升高使 CO_2通量平均增加了 28%,后 4 年,温度升高对土壤呼吸的影响明显降低[30];而 2003—2009 年的试验中,土壤呼吸随增温持续升高[31].在一个草原长期增温的试验中,在试验开始的前两年,土壤呼吸对增温无明显变化[25],而在接下来的 5 年中,增温使得土壤呼吸速率提高[32].

增温对土壤呼吸的作用在空间格局上也表现出很大差异[33].增温引起土壤呼吸的改变也会因植被类型、土壤结构及背景气候特征的差别而异.例如,在苔原生态系统中,平均土壤温度升高 1.73 ℃时,土壤呼吸速率提高 28%;在北方针叶林中,平均土壤温度升高 3.42 ℃,土壤呼吸速率提高 10%;在温带森林中,平均土壤温度升高 3.72 ℃,土壤呼吸速率提高 12%;在草地生态系统中,土壤温度升高 2.02 ℃,土壤呼吸速率提高 6%;在农田生态系统中,土壤温度升高 2.63 ℃时,土壤呼吸速率提高 6%[7].

3 模拟增温对土壤呼吸的影响机制

3.1 增温对土壤呼吸的直接影响

增温可对根呼吸和微生物呼吸产生直接影响.首先,当温度较低时,呼吸速率主要受生化反应限制,根呼吸随着温度升高呈指数增加[39].温度较高时,那些主要依赖扩散运输代谢和代谢产物成限制因子,并且超过 35 ℃时,原生质体开始降解,从而使根呼吸对温度的响应变弱[40].其次,增温也能够通过改变土壤微生物的量、微生物的群落结构及微生物的活性[17]从而影响土壤 CO_2的释放速率.一方面,增温可以增加土壤微生物量[41],也可能降低土壤微生物量[42],而微生物量的改变直接影响微生物的呼吸.另一方面,增温后土壤微生物总量可能没有显著变化,但温度升高能够增强真菌优势[42],增加其丰富度[43],从而改变微生物群落结构[44],影响微生物活性,最终导致微生物呼吸的改变[43].此外,微生物呼吸和根系呼吸都需要酶的参与,土壤酶活性在土壤呼吸过程中发挥着重要作用.增温对其的影响一般表现为促进作用,但是由于增温引起的土壤物理状况、养分差异也可能导致土壤酶活性受增温的影响很小甚至不明显[45].

3.2 增温改变其他环境因子从而间接影响土壤呼吸

温度升高会影响土壤水分含量,而土壤水分含量对土壤呼吸有重要影响,尤其在干旱或半干旱地区,土壤水分可能取代温度而成为土壤呼吸的主要控制因子[46].首先,土壤水分直接参与生物的生理过程,土壤水分在过低或过高都会限制根呼吸作用[47].其次,土壤水分主要通过影响酶和基质的扩散、氧气在土壤中的传输来影响土壤呼吸[48].模拟增温一方面促进了冻土层的凝结水转化成有效水,另一方面模拟增温又会通过增加蒸发和蒸腾形成暖干的趋势[38].在草地生态系统中,水分作为其主导因子,增温加速了蒸发使土壤水分含量降低,而水分含量过低会降低胞外酶和呼吸底物的扩散以及微生物的移动,从而降低了微生物与呼吸底物的接触机会[48],最终降低土壤呼吸[46].但在苔原、泰加林、高寒草甸等生态系统中,由于冻土层的存在,增温加速了冻土层的凝结水转化为有效水,从而增加了土壤水分含量[7],进而提高土壤呼吸[7,37,49].在热带雨林、季雨林生态系统中,水分含量过高,虽然酶和可利用基质的含量充足,但土壤孔隙被水填充,限制了土壤呼吸所需氧气的传输,并且这种通气性较差和厌氧的环境能够降低微生物呼吸以及根呼吸[48].因此,增温加速了土壤变干的过程,从而缓解了由于水分过量而导致的土壤呼吸降低[29,48-52].此外,增温引起的土壤水分变化也将影响叶片水势(Ψ)和相对含水量(RWC),进而影响气孔的开闭、碳的固定和植物的生存,从而使根系的生长和活性受到影响,最终导致土壤呼吸的改变[53].

在滨海湿地生态系统中,当土壤温度升高时,土壤水分的蒸发加速,从而促进了地下咸水向土壤表面的输送[54],导致土壤表层盐分含量升高.盐分含量的升高将导致土壤呼吸降低[55-56].首先,盐分抑制土壤微生物活性,使得土壤呼吸随盐度的升高而降低[57-59];其次,高的含盐量会降低微生物数量[60-62]以及微生物群落的多样性[52];同时,高盐度能使微生物生理形态发生明显变化,从而使其分解有机质的能力受到强烈影响[63];此外,多数土壤水解酶与氧化还原酶类活性均随盐渍化的水平升高而明显下降[64-66],低盐分对酶的活性有促进作用而高盐分条件下其活性反而下降[66].因此,盐分含量的

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高低影响土壤呼吸.

此外,温度升高会促进氮的矿化作用,增加土壤可利用氮素含量[67-70].土壤中氮的变化,一方面能够影响微生物的活性[71-72],微生物活性的变化将会影响其呼吸,最终影响土壤 CO_2 的排放;另一方面能够通过影响细根的生物量来影响根呼吸[73-74].同时,氮素含量增加使得 C/N 降低,植物获取氮素相对容易,植物向地下分配光合产物的比例便会相应减小.一方面,这直接导致了植物根系呼吸的降低,另一方面,植物根系分泌物的减少不仅限制了根际微生物进行呼吸作用的基质来源,而且根系分泌物对土壤有机碳分解的激发作用也会有所降低[75].另外,受光合产物分配比例的影响,根系的伸长活动受到一定程度的抑制,其对土壤团聚体的机械破坏也相应减少,不利于受物理保护的土壤有机碳的释放[76],从而影响土壤呼吸.

3.3　增温影响生物要素从而间接影响土壤呼吸

增温能够影响生物量进而影响土壤中凋落物和碎屑的数量从而导致微生物的生长和活性发生改变,最终改变土壤呼吸[77].首先,增温能够改变植物的生长速率,进而提高植被的净第一生产力和碳固定能力,从而进一步提高凋落物的产生量和质量[78].而凋落物层的微生物控制着土壤中的主要生物化学过程,其更容易受到分解物和根系分泌物的影响[78].其次,凋落物作为土壤有机质输入的主要来源,是真菌或微生物进行生命活动的物质基础,且对土壤的温度、湿度也会产生影响,进而影响到土壤呼吸[79].

根呼吸作用的物质基础来源于植物光合作用[77],增温使得光合作用增强[80],从而使光合产物向地下部分分配增加[26],而根系呼吸作用主要依赖于植物地上部分光合产物对地下部分的分配[81],其中,分配到根系中的光合产物约 75% 被呼吸消耗掉,只有 25% 用于树木生长[82],因此,增温能间接驱动根呼吸[82]使得地下的呼吸作用也旺盛[38].同时,根系分泌物是根际微生物的主要碳源[75],增温引起的植被碳素的向下分配加速了根系分泌物以及死根和活根的分解[83],从而提高了根际微生物的呼吸作用.此外,增温能够直接影响植物根系的特征,或者通过影响种间关系对群落结构和物种多样性产生影响[37]进而影响根系生长,而根呼吸与根系的主要特性之间具有强烈的相关性[84].因此,增温能够通过影响根系的发展从而影响土壤呼吸.

4　土壤呼吸对模拟增温的适应性

众多研究表明,随着温度的升高或增温时间的延长,土壤呼吸速率的增长幅度往往下降甚至停止,其对温度变化的敏感程度降低,表现出所谓的温度适应性[85].关于土壤呼吸对温度适应性的机制,目前尚未达成共识,其原因可能包括以下几个方面:

1) 微生物的温度适应性.这种适应性极可能是单一种群对较大温度区间的适应[86];也可能是种群通过结构调整来适应温度的变化,即随着温度的变化,优势种群发生改变[48].造成的结果是,增温对微生物呼吸的影响减小.

2) 酶的温度适应性.驱动有机质与氧气反应产生 CO_2 的酶(由微生物分泌)具有较强的温度适应性,随着温度的升高,酶的最优温度变大[87],继续驱动较复杂有机质的转化,从而对微生物呼吸的影响变弱.

3) 根生长的温度适应性.根生长具有一个最适温度,超过最适温度后开始下降[40],因为氧通过细胞膜的扩散可能限制呼吸,特别在长时间的热胁迫下,对呼吸产物需求的减少会造成呼吸的进一步降低.因此,短期增温尽管可以刺激根系自养呼吸,从而使土壤呼吸产生大量的 CO_2,但增温并不能使根呼吸持续增加,即随增温时间的延长,根呼吸对温度变化表现出一定的适应和驯化现象,从而降低和缓解土壤呼吸对增温的正反馈效应[25,30].

4) 水分限制.增温能够促进植物蒸腾与土壤水分的蒸发,从而造成过高或过低的水分状况[88].而这种水分状况能够限制温度对土壤呼吸的作用,土壤水分的变化自然会影响到土壤呼吸对温度升高响应的敏感程度,并在一定条件下导致土壤呼吸对温度升高的适应.

5) 氮素过量.温度的升高势必导致土壤氮素矿化速率的增加和土壤可利用氮素的增加,从而导致植物 C/N 降低,植物体向土壤中分泌的有机物减少,进而限制土壤呼吸的进行[30].

6) 呼吸底物的限制.温度可以通过影响底物供应对土壤呼吸产生影响.在温度升高的初期,土壤微生物呼吸因为温度升高的刺激而耗竭大量活性较大的碳(labile C)[89-90],一旦土壤中这些易于分解的活性较大的碳被分解掉,随着温度的进一步升高或升温时间的延长,土壤微生物获取基质困难,从而可能出现土壤呼吸对温度升高响应迟钝的情况[71].同时,温度升高促进活性碳库向钝性或缓性(保护性)

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碳库转移[91-92]，使得土壤微生物可利用的活性碳源也会相应减少[93]，进而导致土壤呼吸的温度敏感性降低.因此，短期上，增温使得土壤异养呼吸增强，但是随着温度的进一步升高或较高温度持续时间的延长，呼吸底物的有效性降低[81]，从而降低了土壤呼吸温度敏感性，进而减缓土壤呼吸随温度升高而增加的量[25,30,71,83,85].

5 研究展望

由于野外增温模拟试验需要昂贵的资金支持和长期的管理维护，因此，尽管增温模拟试验对揭示全球陆地生态系统对气候变暖的响应规律有重要参考和指导意义，并且方法和理论已经相当成熟，但是国内迄今为止相关试验开展较少.而且增温对土壤呼吸的影响是一个复杂和长期的生态过程，目前尽管模拟增温对土壤呼吸的影响及反馈机制取得了大量研究成果，但是由增温引起的植被生长、光合作用变化，土壤水分和养分供应变化以及其他环境因子的变化也将对土壤呼吸产生影响，而该领域目前仍然还有一些问题和不足.同时可以预见，在未来数年乃至数十年间，气候变暖必将对土壤呼吸产生巨大影响，这对于本领域的研究工作既是机遇也是挑战，在未来数年间需要在以下几方面加强研究:

1) 加强全球变暖条件下根际微生态系统的研究.根呼吸与微生物呼吸的区分是土壤呼吸研究的一个重点和难点.气候变暖通过直接或间接影响根系生产力、根系周转、根系呼吸、菌根生长、根系分泌物的产量与质量，进而影响各组分碳通量变化及其对森林地下碳分配的贡献，并且由于根际微生态系统的复杂性和对环境因子的敏感性，加之缺乏有效的研究手段和方法，目前有关根际微生态系统碳循环对全球气候变暖的响应系统性研究很少，从而导致地下碳库预算存在一定损失.根际微生态系统是土壤呼吸研究中最不确定的区域，还需进一步研究.

2) 重点研究不对称增温下土壤呼吸的特征及机制.由于地理要素的复杂性和气候因子的相互作用，全球变暖还存在明显的不对称性[94]，即北方增温大于南方、冬春季增温大于夏秋季、夜温增幅高于白天[5].目前，土壤呼吸的研究多集中在生长季，有关土壤呼吸冬季特征的报道很少，尤其是高纬度地区受冬季温度大幅降低和试验条件的限制.另外，研究发现冬季积雪能够防止土壤冻结、维持微生物活力、显著影响生态系统的碳平衡[46]，因此，研究冬季温度的升高以及积雪覆盖的减少对于土壤呼吸的影响，对深刻认识生态系统碳循环和碳平衡以及预测全球变暖对陆地生态系统碳汇/碳源有重要意义.同时，关于增温时间段目前多侧重于全天平均温度的升高效应，关于夜间增温影响的研究很少[94].一天之中增温幅度并不一致，夜间最低温度的增温幅度比白天最高温度的增温幅度平均高 1 倍，这种昼夜增温幅度的不均匀性深刻地影响着陆地生态系统碳循环对全球气候变化的响应和反馈.

3) 关注典型物候期和不同季节典型天气土壤呼吸的测定.由于影响土壤呼吸的影响因素十分复杂，植物本身的发育期、生理代谢活动强度、气温与土壤表层地温、湿度等均不同程度影响呼吸的大小，某些情况下还会成为决定呼吸通量的主要环境因子，并且在群落不同的物候期以及同一物候期的不同观测日，其影响因子也不同，由此使相关研究更加复杂化.应该把典型天气、典型物候期以及不同季节与土壤呼吸结合起来加强研究，以增强测量的权威性和测定的可靠性.

4) 构建全球模拟增温试验的研究网络，在生态系统联合的观测基础上，进行增温对土壤呼吸影响的研究.目前，全球有关模拟增温研究的站点有很多，包含多种生态系统类型，积累了大量数据资料，取得了一定进展，但是由于生态系统的差异性和环境过程的复杂性，单个站点的研究已不能满足未来发展的需要.因此，加强联网观测与试验，利用多尺度、多要素、多过程、多途径的综合集成分析等手段，开展联合观测势在必得.土壤呼吸是一个复杂的生态系统过程，受到多种因素的制约，其对气候变暖的响应与适应机制是未来气候变化研究的重要组成部分.未来应在生态系统联合的观测基础上，进行增温对土壤呼吸的联网研究.

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