第78卷 第9期
2023年9月

地 理 学 报
ACTA GEOGRAPHICA SINICA

Vol.78, No.9
September, 2023

植被物候对极端气候响应及机制

张 晶[1],郝芳华[2],吴兆飞[1],李明蔚[1],张 璇[1],付永硕[1]
(1. 北京师范大学水科学研究院,北京 100875; 2. 华中师范大学城市与环境科学学院,武汉 430079)

摘要: 人类活动引起的气候变化导致极端气候事件频发,改变植物的生理过程,影响陆地生态系统碳、水循环和能量平衡。植被物候是气候变化最敏感的生物学指示指标,近年来植被物候对气候变化的响应研究主要关注气候平均态,植被物候如何响应极端气候事件研究相对较少,响应机制仍不清楚。本文梳理了植被春季和秋季物候对各类极端气候事件的响应及其机制,发现北半球中高纬度地区,季前极端低温与极端降水直接导致植被返青期推迟、枯黄期提前,而极端高温和极端干旱导致植物气孔关闭,抑制光合和蒸腾作用,间接导致枯黄期提前。目前植被物候响应极端气候事件研究缺乏对复合极端气候事件的关注,而且植被物候对极端气候响应的滞后效应以及极端气候事件发生后植被的恢复过程研究较少。未来气候变化情景下,需构建考虑极端气候事件影响的植被物候模型,并与动态植被模型耦合,以提高陆地生态系统碳循环的模拟精度。

关键词: 植被物候;极端气候事件;响应机制;复合极端事件;滞后效应
DOI: 10.11821/dlxb202309008

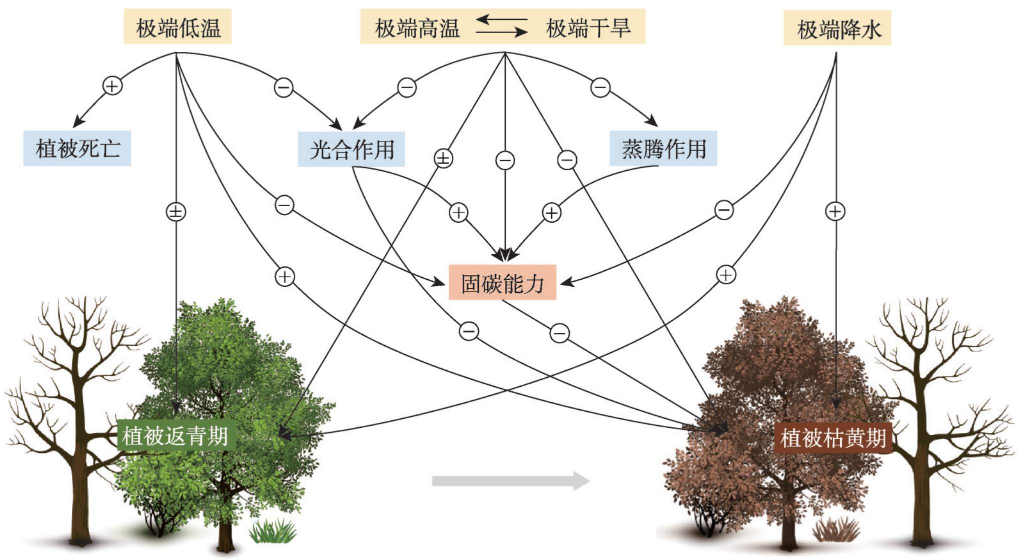
1 引言

气候变化导致全球极端气候事件频发,生态系统面临的风险日益增加[1-2]。IPCC第六次工作报告指出,未来持续增温会引起愈加频繁和强烈的极端温度、降水和干旱事件[3-4]。目前关于极端气候事件的定义不尽相同,IPCC报告将极端气候事件定义为天气或气候变量的值高于或低于某个阈值[5],气候变化检测与极端气候事件指标专家组(ETCCDI)推荐了27个极端气候核心指标,并被广泛用于极端气候变化研究[4, 6-7]。高温热浪、极端干旱、暴雨洪涝和寒潮等极端气候事件具有突发性强、破坏性大和难以预测等特征,当植物不能适应气候异常变化时会抑制植物光合作用,导致生产力降低,影响陆地生态系统结构和功能[8-11]。因此,认识植被动态对极端气候事件的响应及其机制,对于深刻理解陆地生态系统对气候变化与极端气候的响应具有重要意义。

植被物候是植被对气候变化响应最敏感的生物学指标之一,中国著名地理学家竺可桢曾依据物候绘制了中国近五千年来的温度变化曲线[12]。植被物候变化对陆地生态系统碳水循环和能量平衡具有重要的控制作用[13]。温度是影响植被物候的重要因素[14-17],之前的研究主要关注植被物候对平均温度的响应,如日均温升高导致植被返青期提前、枯

收稿日期: 2023-06-30; **修订日期:** 2023-08-20
基金项目: 国家自然科学基金杰出青年科学基金项目(42025101); 国家自然科学基金国际合作研究项目(42261144755) **[Foundation:** National Science Fund for Distinguished Young Scholars, No.42025101; International Cooperation and Exchanges of NSFC, No.42261144755]
作者简介: 张晶(1994-), 女, 黑龙江绥化人, 博士生, 研究方向为植被物候学。E-mail: zhangj1127@mail.bnu.edu.cn
通讯作者: 付永硕(1979-), 男, 山东济宁人, 教授, 博士生导师, 中国地理学会会员(S110017319M), 主要从事全球变化生态学、生态水文和植被物候学研究。E-mail: yfu@bnu.edu.cn

黄期推迟[18-24]。除温度外，降水对植被物候也有很强的控制作用，生长季开始前1~3个月降水不仅可以直接影响植被物候[25-27]，还可以通过调节辐射和热量需求间接影响植被物候，在干旱半干旱地区尤为显著。近年来，一些学者研究了植被生长与植被物候对极端气候事件的响应[28]，发现春季极端高温导致植被返青期提前、极端复合干旱减缓地球变绿[29]，生长季极端干旱和高热胁迫导致植被枯黄期提前[6]。与气候平均态相比，极端气候事件对植被物候的影响更加明显[19, 30-36]，如极端干旱发生年份植被返青期与多年平均返青期相比延迟了6~34 d，枯黄期提前了约12 d，远远超过气候平均态的影响[37-39]。但是目前植被物候对极端气候事件响应研究依旧较少，响应机制仍不清楚。因此，本文从气候冷热干湿性质出发，以极端温度（高温和低温）、极端干旱、极端降水等常见极端气候事件为例，系统梳理植被物候对极端气候事件的响应及其潜在机制（图1），并针对目前研究的不足对未来研究方向提出展望。



注：在表示植被物候对极端气候事件的响应时，“+”代表植被返青期、枯黄期推迟，“-”代表植被返青期、枯黄期提前。在表示极端气候事件对植被死亡、光合作用、蒸腾作用和固碳能力影响时，“+”代表促进作用，“-”代表抑制作用。

图1 植被物候对极端气候事件响应示意图

Fig. 1 Schematic diagram of response of vegetation phenology to extreme climatic events

2 植被物候对极端温度的响应及机制

温度是影响植被物候的关键因素[18, 40-42]，植物生长存在最适温度范围，温度过高或过低超出适宜植物生长的温度阈值，会影响植物正常的生理代谢，改变植被返青期和枯黄期。以往研究关于极端高温和极端低温的定义大多采用固定阈值法（如日最高气温超过35 ℃）与百分位阈值法[43-44]，或者根据ETCCDI推荐的极端气候指数进行计算[45-46]，极端高温指数如暖昼日数、冷昼日数、年最大（小）日最高气温以及持续暖日日数等指标，极端低温指数如冷昼日数、冷夜日数、年最大（小）日最低气温以及持续冷日日数等指标。

2.1 植被物候对极端高温的响应及机制

随着全球变暖，极端高温天气的发生频率、强度和空间范围大幅增加[3]。研究表明，春季极端高温显著影响北半球温带和寒带森林的冠层发育[47]，导致欧洲和北美洲温带森

林返青期提前了3~40 d[48-49]，实验研究也发现了相似的结果[50]。但是，一些研究得到了相反的结果，例如冬季多重极端变暖事件导致亚北极欧石楠地优势矮灌木返青期推迟了一周[11]。与植被返青期相比，植被枯黄期对极端高温的响应更为复杂。秋季极端高温（如暖昼日数、中热胁迫和暖夜日数）导致北半球高纬度植被枯黄期延迟[7]，比如极端高温导致欧洲高纬度地区常绿针叶林、落叶阔叶林和针阔混交林的枯黄期延迟了5~15 d[51]。同时，极端气温暖极值（年最大日最低气温、年最大日最高气温、暖昼日数和暖夜日数等）升高也广泛推迟了中国温带草地枯黄期[34, 52]。但是，生长季极端高温也会缩短植被生长季长度，如极端高温导致中国高寒草原、新英格兰温带落叶林、阿尔卑斯山草地枯黄期提前[53-55]，进而导致生长季变短。不同区域植被枯黄期对极端高温指数的响应存在差异，如内蒙古植被枯黄期主要受到春夏暖昼日数和暖夜日数影响[56]，而中亚植被枯黄期除了受到暖昼日数的影响外，还受到冷昼日数和年均日最高气温的影响[57]。

极端高温可能导致植被返青期和枯黄期提前或者推迟，植被物候对极端高温的响应机制在不同区域不同植被类型存在较大差异。在较寒冷或较湿润地区，早春极端高温可以提高植物酶的活性，加快植被生长，导致植被返青期提前[58-60]。但由于热需求、冷激、降水以及光周期对植被返青期存在复杂相互作用[25, 61-63]，冬季极端高温也可能导致植物因无法满足解除休眠的低温刺激而推迟植被返青期。植被返青期对极端高温事件的响应因植被类型而异，如祁连山草地返青期比森林和灌木对极端高温的响应更敏感[37]，这可能与区域干旱严重程度和海拔高度有关。对于植被枯黄期，高热胁迫能够催化植物蛋白质降解，进而促使植被提前枯黄[64-65]，但是发生在较寒冷地区的极端高温事件却能够促进光合作用，维持植物的生理活动，延缓植被枯黄期。不同类型植被枯黄期对极端高温事件的响应也存在差异。以内蒙古草地为例，荒漠草原、森林草原和典型草原西部的枯黄期主要受春夏季暖昼日数的影响，而森林和典型草原东部枯黄期主要受春夏季暖夜日数的影响[56]，且不同类型草地枯黄期受到极端高温的影响程度存在差异[34, 52, 55]，这可能与区域干旱程度有关。

2.2 植被物候对极端低温的响应及机制

除极端高温事件，极端低温事件对植被物候也具有重要影响。春季极端低温导致植被返青期延迟，如2007年春季霜冻导致大部分美国温带落叶林树种返青延迟16~34 d[66]。植被返青期对不同强度的极端温度事件的响应存在差异，如季前的年最大日最高气温与年最小日最高气温，以及年最小日最低气温均与中国温带植被返青期之前存在显著负相关关系，但季前的年最大日最低气温却与返青期存在显著正相关关系[67]。不同类型植被返青期对极端低温事件的响应程度也不相同，如在中国温带植被区域，草地和植被稀疏区域的返青期与季前霜冻日数的显著相关系数明显大于混交林[67]。对于植被枯黄期，秋季霜冻通常导致植被枯黄期提前，如霜冻日数、冷夜日数和冷昼日数等低温胁迫导致北半球中高纬度植被枯黄期平均每年提前0.02~0.59 d，且随纬度降低极端低温对植被枯黄期的提前效应减弱[7]。此外，中国内蒙古沙地和草原沙漠的植被枯黄期主要受到春夏季冷夜日数和冷昼日数的影响[56]。

与极端高温类似，植被物候对极端低温的响应机制也较为复杂，极端低温可能导致植被返青期推迟、枯黄期发生提前或者推迟现象。气候变暖导致植被返青提前，增加花叶暴露在极端低温环境中的可能性[68-71]，研究发现，晚春霜冻使温带树种生长速度减慢[72]，导致植物叶片脱落、冠层发育迟缓甚至死亡，严重影响生态系统生产力[73]。总的来说，极端低温推迟植被返青期主要有两方面原因：一是当极端低温发生在早春时，极端寒冷会减缓季前热量的积累，会延迟植被返青期；二是当极端低温发生在晚春时，霜冻可能

使植被叶芽受损，需要植物重新发芽展叶，导致植被返青期延迟。对于植被枯黄期，由于晚秋霜冻时间发生频率较高，植物通过自身的进化机制，为了避免遭受霜冻损害提前枯黄期。当生长季霜冻导致植被叶片受损时[70, 74-75]，植物会通过推迟秋季衰老补偿生长亏损[76]，这可能是极端低温导致植被枯黄期推迟的主要原因。此外，不同类型植被枯黄期对极端低温事件的响应不同，如高寒草原、高寒草甸、典型草原和荒漠草原与极端低温之间以负相关为主，而草甸草原与极端低温之间则以正相关为主[55]，这可能与植被所在区域干旱严重程度有关，草甸草原所在区域较为干旱。

2.3 植被物候对其它极端温度事件的响应及机制

除了极端高温和极端低温事件，昼夜不对称增温也会影响植被物候，而且存在明显的区域差异。白天升温导致北半球中高纬度植被返青期提前，其效应大于夜晚升温和日均温升高[41]。而对于青藏高原和中国东部样带，植被返青期对夜晚升温的响应大于白天升温，这可能与低温约束有关，春季夜晚升温加快了植被返青所需热量累积进而提前返青[77-78]。植被返青期对昼夜不对称增温的响应还存在季节性差异，中国温带草原返青期在冬季主要受白天升温影响、在春季主要受夜晚升温影响[79]。昼夜增温对植被返青期还会出现相反作用[80]，冬季白天升温促进热量积累提前植被返青期，而冬季夜晚升温减少冷激延迟植被返青期[81]。植被枯黄期对昼夜不对称增温的响应与水分胁迫有关[82]，白天和夜晚升温分别导致湿润地区植被枯黄期推迟和提前、干旱地区植被枯黄期提前和推迟。除昼夜不对称增温外，北半球中高纬度植被返青期也对温度日较差响应敏感，但在温度季节性较强的地区，植被返青期对季前温度日较差的敏感性较小，这可能与植被热耐受性增强有关[83]。

3 植被物候对极端降水的响应及机制

植被物候对极端降水的响应比对极端温度的响应更为复杂。极端降水事件的定义也常采用固定阈值法（如日降水量超过1 mm）与百分位阈值法[84-85]，或者使用ETCCDI推荐的极端气候指数进行计算[86]，如极端大雨日数、持续湿润日数、1 d最大降水量、连续5 d最大降雨量以及极端强降水总量等指标。已有研究表明春季极端降水对植被返青期存在推迟作用，如频繁的极端降雨减慢了美国大陆春季植被返青的速度[87]，1 d最大降雨量和连续5 d最大降雨量减少导致中亚中西部植被返青期推迟[57]，连续5 d最大降雨量增加导致中国西南地区植被返青期推迟[88]。然而干旱半干旱区的极端降水事件导致植被返青期提前[26, 89]，如降雨频率的减少提前了北方生态系统植被返青期[90]。也有研究表明，植被返青期还会受到降水持续时间和降水强度的影响[91]，如在1982—2015年中国温带植被返青期与生长季前强降水总量、1 d最大降雨量之间呈显著正相关，与极端强降水总量、连续5 d最大降雨量之间则呈显著负相关[67]。植被枯黄期对极端降水事件的响应与极端降水的发生强度和研究区域有关。尽管不同强度的生长季极端降水都提前了北半球高纬度植被枯黄期[7, 54]，但是植被枯黄期对低强度降水和高强度降水响应的主要时间段为季前1~2个月，而中等强度降水为季前2~3个月[7]。

极端降水可能导致植被返青期和枯黄期发生提前或者推迟现象。植被物候对极端降水的响应机制随研究区域和植被类型而异。在暴雨、洪涝等极端降水发生时，土壤水分急剧增加，降低植物的水分和养分吸收效率，严重者破坏植物根系，导致植物生长受阻、萎蔫甚至死亡[92-93]，这就会导致植被返青期推迟，特别是在水资源丰富的区域该影响更加明显。但是，发生在干旱半干旱区的极端降水事件，可以对水资源亏缺区域进行一

定的补给，进而产生更适宜植被生长的环境，有利于植被提前返青。此外，不同植被类型返青期对极端降水的响应存在一定的差异，如祁连山地区灌丛和森林返青期对极端降水事件响应大于草地，并以低灌木为主的亚高山地区影响最大，造成这种格局的原因可能是以高寒草甸为主的高海拔地区气候寒冷潮湿，而以森林和灌木为主的低海拔地区气候相对温暖干燥[37]。对于植被枯黄期，由于极端降水会造成植被根系产生厌氧环境，从而会加速枯黄期的到来[94]。但是在干旱半干旱区，极端降水可以缓解土壤水分胁迫，进而推迟植被枯黄期[34, 95]。对于不同植被类型，极端降水导致中国荒漠草原枯黄期提前，却导致高寒草甸枯黄期推迟，这主要是因为极端降水有效补充了荒漠草原的土壤含水量[55]。也有研究表明极端降水减少对水分限制区域植被枯黄期的趋势变化没有显著影响，这可能是因为中亚地区植被已经适应了干旱环境[57]。

4 植被物候对极端干旱的响应及机制

随着气候变暖，极端干旱的发生频率和强度显著增加[96-97]，当干旱发生强度超过植物对干旱的耐受阈值时，轻则抑制植被生长，重则使植被损伤甚至死亡[9, 98-100]（表1）。极端干旱事件的定义除表1所述外，ETCCDI推荐的极端气候指数中的持续干旱指数也可以用于表征极端干旱[55]。极端干旱对植被物候也产生了重要影响[101-102]。研究表明，春季干旱导致欧洲西南部和中国北方干旱半干旱区植被返青期延迟了7~40 d[37, 103-107]。但是，春冬季干旱导致北美洲、欧亚边界以及亚洲东北部植被返青期提前[107]，控制实验中也发现一致结果[108]。植被枯黄期对干旱的响应因地理位置和干旱发生时间而异。季前干旱胁迫导致中国温带草地干旱区域、北方半干旱区草地和稀疏植被以及青藏高原等干旱区和半干旱区植被枯黄期平均每10 a提前约2 d[6, 103, 109]。但是极端干旱导致欧洲和中国云贵高原植被枯黄期延迟[110-111]。植被枯黄期对干旱不同发生时间也可能产生相反的响应，例如夏季前的干旱导致云贵高原植被枯黄期延迟，夏季干旱导致云贵高原植被枯黄期提前[110]。

表1　干旱等级划分

Tab. 1　Classification of drought

分类	SPEI或SPI	PDSI	危害程度
基本正常	−0.49~0.49	−0.99~0.99	无危害
轻旱	−0.99~−0.50	−1.99~−1.00	轻微危害
中旱	−1.49~−1.00	−2.99~−2.00	中等危害
重旱	−1.99~−1.50	−3.99~−3.00	严重危害
特旱	≤−2.00	≤−4.00	特重危害

注：干旱事件识别一般采用固定阈值法与百分位阈值法，前者如表中使用的标准化降水蒸散指数（SPEI）[112]、帕尔默干旱强度指数（PDSI）[113]、标准化降水指数（SPI）[114]等常见干旱指标的阈值划分干旱等级；后者定义干旱阈值为多年升序排列数据分布的十百分位[107, 115]。

极端干旱可能通过不同的机制导致植被返青期和枯黄期发生提前或者推迟现象，其差异可能在于区域水分盈亏程度。植被对干旱胁迫的生理响应机制发挥重要作用，植被通过增加根系吸水能力、关闭部分气孔以及调节组织渗透性以积极维持生理水分平衡[116]，例如干旱区和湿润区植被能够快速响应干旱，前者更能迅速适应干旱胁迫，后者则适应性较差，而半干旱区和半湿润区植被对水分亏缺的承受能力较强、对干旱的反应时间更长[117]。极端干旱导致植被返青期提前的响应机制可能有两个主要解释，一是气候变暖对

植被返青期的提前作用大于干旱胁迫的抑制作用，二是气候变暖导致的冰雪或冻土融化可以补充土壤水分，进而缓解了干旱胁迫。但是，极端干旱也会导致植被返青期推迟，这主要是由于季前干旱能够降低土壤含水量，进一步加剧水分胁迫，进而导致植被返青期推迟，特别是在干旱区和半干旱区。对于植被枯黄期，干旱促使植物关闭气孔降低蒸散和光合速率，同时维持更高呼吸速率加速碳分解，导致植被枯黄期提前。但是在湿润区和半湿润区，干旱胁迫对植被枯黄期的影响可能不会抵消气候变暖对植被枯黄期的延迟作用，最终导致枯黄期推迟。此外，不同类型植被物候对极端干旱的响应存在明显差异，如在祁连山与澳大利亚的中等海拔灌木的返青期对干旱的响应大于更缺水的低海拔森林或草原[37, 39]；持续干旱指数与高寒草原枯黄期之间以正相关为主，却与荒漠草原枯黄期之间主要存在负相关关系[55]，这都可能与区域干旱程度与海拔高度有关。

5 植被物候对其他极端气候事件的响应及机制

除了极端温度、降水和干旱事件，植被物候对复合极端气候事件、野火等其他极端气候事件也存在响应。复合极端气候事件是指多个极端气候事件同时发生、并发影响植被生长动态，比单个极端气候事件对生态系统的影响更加剧烈[118]，如在极端温暖和极端湿润年份祁连山植被返青期分别提前6.4 d、5.1 d，但在极端暖湿年份其返青期提前了13.2 d[37]，这可能是因为极端变暖与极端降水的综合影响是通过某种更为复杂的优化协同机制来调控植被物候变化[37]。复合冷干事件对北半球植被生产力的抑制作用也超过单一冷干事件[119]。近年来，复合高温干旱频发[120]，比单一极端气候事件对植被造成的影响更为严重。控制实验表明，极端干旱和高温复合事件导致大量叶片死亡、提前植被衰老，其影响远远超过了单独的极端干旱或高温事件[121]。例如，复合高温干旱胁迫导致鹅耳枥和樱桃树枯黄期比多年平均枯黄期分别提前了5 d和16 d[122]。这主要是由于频繁的高温天气加快土壤水分蒸发，进一步加重干旱程度，从而加剧了对植被物候的影响。

随着高温干旱复合事件增多，森林火灾更加频繁，进而影响植被物候。科罗拉多州海曼森林大火使植被返青期由延迟趋势转变为提前趋势，火烧痕迹区比缓冲区的植被返青期更早，并在漫长恢复期内对植被返青期产生持续影响[123]。旱季和雨季的交替时间异常也会影响叶片脱落与生长时间[124]。此外，异常风速也会对植被物候产生影响，如春季大风导致北方生态系统植被返青期延迟[125]，秋季风速减弱推迟了北半球高纬度区域的植被枯黄期，且植被枯黄期对风的响应高于温度和降水[126]。关于植被物候对其他极端气候事件的响应研究相对较少，且这些极端气候事件发生原因更为复杂，目前尚无较为统一的响应机制来解释它们对植被物候的影响。

6 植被物候响应极端气候研究展望

综上所述，全球极端气候频发对植被物候产生了深刻影响。本文基于当前植被物候对极端气候事件响应机制研究进展，概述了当前研究中存在的问题并对未来可能的研究方向提出了展望，主要包括3个方面：① 植被物候对（复合）极端气候事件的响应与反馈机制仍存在较大的不确定性；② 缺乏多时间尺度下植被物候对极端气候变化响应的滞后效应研究；③ 耦合极端气候事件到植被物候模型的研究不够全面。

6.1 植被物候对极端气候的响应与反馈机制

目前，植被物候对极端气候事件的响应机制不够清楚，这主要是因为不同频率、强

度、空间区域的极端气候事件对植被物候存在复杂影响。极端高温、低温、降水与干旱事件均可能导致植被物候提前或推迟，且响应机制并不一致，这可能与研究区域（包括不同水热条件、气候特征等）、研究对象、研究方法（控制实验、遥感、再分析等手段）、以及极端气候指标选择（极端气候事件发生频率以及严重程度）等方面有关。不同生态系统植被物候对各极端气候事件的响应不同[34, 56, 106, 127]，例如在中亚不同生态分区，大多为草地覆盖的生态区枯黄期主要受到暖昼日数的影响，而在以裸地或稀疏植被为主的生态区植被枯黄期主要受到冷昼日数的影响[57]。而且，植被物候对极端温度和极端降水的响应程度也存在不同，例如在生长阶段极端降水对青藏高原干旱半干旱区草地枯黄期的影响远大于极端温度[34]。不同树种对极端气候的抵抗力和恢复力也存在差别[128]。此外，随着高温热浪与干旱并发事件增加[120]，热胁迫和干旱复合胁迫影响了植被物候的各个阶段[129]。为深刻理解植被物候对极端气候事件，特别是复合极端气候事件的响应机制，需要加强基于野外观测、控制实验、遥感反演及模型模拟等多源数据、多尺度、多方法、多过程的集成耦合研究。植被物候不仅会响应气候变化与极端气候事件，植被物候还通过改变陆气系统的碳水循环、能量交换等生物物理化学过程对气候系统产生影响[130-131]。因此，关注极端气候条件下植被物候变化对气候系统的反馈效应，需要综合观测、模拟和实验等方法，从不同的尺度和层面开展研究，以便更好地理解和应对气候变化。

6.2 植被物候对极端气候响应的滞后效应

植被生长和物候变化对气候变化与极端气候变化存在显著滞后和积累效应，并存在明显的空间异质性[107, 132-136]，在气候变化—植被生长模型中考虑气候因子的累积作用显著提高了植被生长的拟合效果[137]。植被物候与其生长相似，不仅对极端气候事件产生萎蔫甚至死亡等即时响应，也存在明显的滞后效应和累积效应，这对于植被物候对极端气候的响应过程与机制的理解增加了难度。不同植被物候期对极端气候事件响应最敏感的滞后时间也不同[106, 127]。以干旱事件为例，干旱胁迫对全球地表物候具有显著的累积和滞后效应[107, 135]，在中国东北过渡带的西北部区域，植被返青期对1~3个月时间尺度干旱的响应最敏感[106]。北半球植被枯黄期对季前干旱响应的主要时间尺度为累积1~4个月、滞后2~6个月，且干旱对草地、稀树草原和灌木的影响超过森林[127]。植被在干旱发生后需要一段时间修复受损根系以恢复到正常生长状态，恢复时间长短取决于生长环境和植被类型[127, 137]，同时植被动态也会通过直接或间接生物物理反馈影响旱后恢复[138]。以往研究多探讨植被物候对月、季或年尺度干旱等极端气候变化的响应[139]，植被物候对多时间尺度极端气候变化的时滞和累积效应的综合研究亟待增加。因此，未来的研究可以通过综合运用生态学、气象学、植物学等多学科的知识和方法，深入探究植被物候对极端气候事件响应的滞后效应及其在植被恢复过程中的调控作用，以此提高极端气候对生态系统功能和恢复力影响的预测能力。

6.3 耦合极端气候事件的植被物候模型

在极端气候下，植被物候模型将面临更大的挑战，其模拟结果准确性有待进一步提高。目前常用的植被物候模型包括积温模型、冷度日模型、温度与光周期模型等[140-141]，随着植被物候对极端气候响应研究的开展，其响应机制在植被物候模型构建中也被考虑。例如，对于北半球植被枯黄期，耦合干旱的秋季物候模型模拟精度平均提升了约12%[142]；对于青藏高原，引入多个极端气候指数模拟植被物候的精度明显提升[6]；耦合温度日较差到冷度日模型模拟的欧洲植被枯黄期具有更高的预测精度[143]。植被物候对极端气候事件的响应机制探究仍然有限，多驱动因子相互作用与极端气候事件的偶然发生使

植被物候模型模拟与预测难度加大。随着新技术的进步，可以考虑在机器学习等算法中耦合极端气候事件来预测植被物候[140]。因此，综合考虑不同极端气候事件对植被物候的影响及其差异，有利于准确模拟历史和未来植被物候的演变特征，为气候变化下生态系统经营与管理以及脆弱性评价提供科学参考。

7 结论

综上所述，极端气候事件对植被生长干扰更剧烈，对植被物候影响更大。植被物候对极端气候事件的响应及其机制与平均气候相比更加复杂，且存在明显的空间异质性和不确定性，并随植被类型差异具有较大的差异。同时，极端气候事件的表征指标在各研究中不尽相同，在探究植被物候对极端气候的响应时应予以注意。随着气候变暖，复合极端气候事件的发生频率和强度增加，其影响程度和范围往往更大，虽然植被物候对极端气候事件响应机制的研究在逐步增多，但植被物候对复合极端气候事件响应的认识依旧受到限制，缺乏对其机制的综合理解。因此，亟需加强植被物候对各极端气候事件响应机制的认识，并从水热条件、气候分区、植被类型与季节阶段等多角度深入剖析其复杂性，同时推进耦合极端气候事件的植被物候模型研究，为全球动态植被模型提供更可靠的理论和技术支撑。

参考文献(References)

[1] Zhou Guiyao, Zhou Lingyan, Shao Junjiong, et al. Effects of extreme drought on terrestrial ecosystems: Review and prospects. Chinese Journal of Plant Ecology, 2020, 44(5): 515-525. [周贵尧, 周灵燕, 邵钧炯, 等. 极端干旱对陆地生态系统的影响: 进展与展望. 植物生态学报, 2020, 44(5): 515-525.]

[2] Piao Shilong, Zhang Xinping, Chen Anping, et al. The impacts of climate extremes on the terrestrial carbon cycle: A review. Science China: Terrae, 2019, 49(9): 1321-1334. [朴世龙, 张新平, 陈安平, 等. 极端气候事件对陆地生态系统碳循环的影响. 中国科学: 地球科学, 2019, 49(9): 1321-1334.]

[3] IPCC AR6. Climate Change 2021: The Physical Science Basis. Cambridge and New York: Cambridge University Press, 2021.

[4] Sillmann J, Roeckner E. Indices for extreme events in projections of anthropogenic climate change. Climatic Change, 2008, 86(1): 83-104.

[5] IPCC. Global Warming of 1.5°C: IPCC Special Report on Impacts of Global Warming of 1.5°C above Pre-industrial Levels in Context of Strengthening Response to Climate Change, Sustainable Development, and Efforts to Eradicate Poverty. Cambridge and New York: Cambridge University Press, 2018.

[6] Li P, Liu Z L, Zhou X L, et al. Combined control of multiple extreme climate stressors on autumn vegetation phenology on the Tibetan Plateau under past and future climate change. Agricultural and Forest Meteorology, 2021, 308-309: 108571. DOI: 10.1016/j.agrformet.2021.108571.

[7] Wang M, Li P, Peng C H, et al. Divergent responses of autumn vegetation phenology to climate extremes over northern middle and high latitudes. Global Ecology and Biogeography, 2022, 31: 2281-2296.

[8] Easterling D R, Meehl G A, Parmesan C, et al. Climate extremes: Observations, modeling, and impacts. Science, 2000, 289(5487): 2068-2074.

[9] Ciais P, Reichstein M, Viovy N, et al. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature, 2005, 437(7058): 529-533.

[10] Rammig A, Mahecha M D. Ecosystem responses to climate extremes. Nature, 2015, 527(7578): 315-316.

[11] Xu C G, McDowell N G, Fisher R A, et al. Increasing impacts of extreme droughts on vegetation productivity under climate change. Nature Climate Change, 2019, 9(12): 948-953.

[12] Zhu Kezhen. A preliminary study on the climatic fluctuations during the last 5000 years in China. Scientia Sinica, 1973, 3(2): 226-256. [竺可桢. 中国近五千年来气候变迁的初步研究. 中国科学, 1973, 3(2): 226-256.]

[13] Piao S L, Liu Q, Chen A P, et al. Plant phenology and global climate change: Current progresses and challenges. Global

Change Biology, 2019, 25(6): 1922-1940.

[14] Zhang Fuchun. Effects of global warming on plant phenological events in China. Acta Geographica Sinica, 1995, 50(5): 402-410. [张福春. 气候变化对中国木本植物物候的可能影响. 地理学报, 1995, 50(5): 402-410.]

[15] Deng Chenhui, Bai Hongying, Gao Shan, et al. Comprehensive effect of climatic factors on plant phenology in Qinling Mountains region during 1964-2015. Acta Geographica Sinica, 2018, 73(5): 917-931. [邓晨晖, 白红英, 高山, 等. 1964—2015年气候因子对秦岭地区植物物候的综合影响效应. 地理学报, 2018, 73(5): 917-931.]

[16] Zhuo Li, Zhang Ziyan, Lei Xiaoyu, et al. Monte Carlo survival analysis on the influencing factors of forest phenology in Northeast China. Acta Geographica Sinica, 2019, 74(3): 490-503. [卓莉, 张子彦, 雷小雨, 等. 基于蒙特卡洛生存分析探究东北森林物候的影响因素. 地理学报, 2019, 74(3): 490-503.]

[17] Wang S X, Wu Z F, Gong Y F, et al. Larger responses of trees' leaf senescence to cooling than warming: Results from a climate manipulation experiment. Agricultural and Forest Meteorology, 2023, 339: 109568. DOI: 10.1016/j.agrformet.2023.109568.

[18] Menzel A, Fabian P. Growing season extended in Europe. Nature, 1999, 397: 659. DOI: 10.1038/17709.

[19] Piao S L, Fang J Y, Zhou L M, et al. Variations in satellite-derived phenology in China's temperate vegetation. Global Change Biology, 2006, 12(4): 672-685.

[20] Chen X Q, Xu L. Temperature controls on the spatial pattern of tree phenology in China's temperate zone. Agricultural and Forest Meteorology, 2012, 154-155: 195-202.

[21] Fu Y H, Piao S L, Delpierre N, et al. Larger temperature response of autumn leaf senescence than spring leaf-out phenology. Global Change Biology, 2018, 24(5): 2159-2168.

[22] Fu Yongshuo, Zhang Jing, Wu Zhaofei, et al. Vegetation phenology response to climate change in China. Journal of Beijing Normal University: Natural Science, 2022, 58(3): 424-433. [付永硕, 张晶, 吴兆飞, 等. 中国植被物候研究进展及展望. 北京师范大学学报: 自然科学版, 2022, 58(3): 424-433.]

[23] Kong Dongdong, Zhang Qiang, Huang Wenlin, et al. Vegetation phenology change in Tibetan Plateau from 1982 to 2013 and its related meteorological factors. Acta Geographica Sinica, 2017, 72(1): 39-52. [孔冬冬, 张强, 黄文琳, 等. 1982—2013年青藏高原植被物候变化及气象因素影响. 地理学报, 2017, 72(1): 39-52.]

[24] Ding M J, Li L H, Zhang Y L, et al. Start of vegetation growing season on the Tibetan Plateau inferred from multiple methods based on GIMMS and SPOT NDVI data. Journal of Geographical Sciences, 2015, 25(2): 131-148.

[25] Fu Y H, Piao S L, Zhao H F, et al. Unexpected role of winter precipitation in determining heat requirement for spring vegetation green-up at northern middle and high latitudes. Global Change Biology, 2014, 20(12): 3743-3755.

[26] Li X X, Fu Y H, Chen S Z, et al. Increasing importance of precipitation in spring phenology with decreasing latitudes in subtropical forest area in China. Agricultural and Forest Meteorology, 2021, 304-305: 108427. DOI: 10.1016/j.agrformet.2021.108427.

[27] Liu Q, Fu Y H, Zeng Z Z, et al. Temperature, precipitation, and insolation effects on autumn vegetation phenology in temperate China. Global Change Biology, 2016, 22(2): 644-655.

[28] Nagy L, Kreyling J, Gellesch E, et al. Recurring weather extremes alter the flowering phenology of two common temperate shrubs. International Journal of Biometeorology, 2013, 57(4): 579-588.

[29] Liu X F, Sun G P, Fu Z, et al. Compound droughts slow down the greening of the Earth. Global Change Biology, 2023, 29: 3072-3084.

[30] Jentsch A, Kreyling J, Boettcher-Treschkow J, et al. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology, 2009, 15(4): 837-849.

[31] Lobell D B, Sibley A, Ivan Ortiz-Monasterio J. Extreme heat effects on wheat senescence in India. Nature Climate Change, 2012, 2(3): 186-189.

[32] Liu Q, Fu Y H, Zhu Z C, et al. Delayed autumn phenology in the Northern Hemisphere is related to change in both climate and spring phenology. Global Change Biology, 2016, 22(11): 3702-3711.

[33] Fu Y H, Zhou X C, Li X X, et al. Decreasing control of precipitation on grassland spring phenology in temperate China. Global Ecology and Biogeography, 2021, 30(2): 490-499.

[34] Qin G X, Adu B, Li C B, et al. Diverse responses of phenology in multi-grassland to environmental factors on Qinghai-Tibetan Plateau in China. Theoretical and Applied Climatology, 2022, 148(3): 931-942.

[35] Shen M G, Wang S P, Jiang N, et al. Plant phenology changes and drivers on the Qinghai-Tibetan Plateau. Nature Reviews Earth & Environment, 2022, 3(10): 633-651.

[36] Zhang J, Chen S Z, Wu Z F, et al. Review of vegetation phenology trends in China in a changing climate. Progress in

Physical Geography: Earth and Environment, 2022, 46(6): 829-845.

[37] He Z B, Du J, Chen L F, et al. Impacts of recent climate extremes on spring phenology in arid-mountain ecosystems in China. Agricultural and Forest Meteorology, 2018, 260-261: 31-40.

[38] Javed T, Li Y, Feng K, et al. Monitoring responses of vegetation phenology and productivity to extreme climatic conditions using remote sensing across different sub-regions of China. Environmental Science and Pollution Research, 2021, 28(3): 3644-3659.

[39] Ma X L, Huete A, Moran S S, et al. Abrupt shifts in phenology and vegetation productivity under climate extremes. Journal of Geophysical Research: Biogeosciences, 2015, 120(10): 2036-2052.

[40] Körner C, Basler D. Phenology under global warming. Science, 2010, 327(5972): 1461-1462.

[41] Piao S L, Tan J G, Chen A P, et al. Leaf onset in the Northern Hemisphere triggered by daytime temperature. Nature Communications, 2015, 6: 6911. DOI: 10.1038/ncomms7911.

[42] Zhao J J, Wang Y Y, Zhang Z X, et al. The variations of land surface phenology in Northeast China and its responses to climate change from 1982 to 2013. Remote Sensing, 2016, 8(5): 400. DOI: 10.3390/rs8050400.

[43] Xue Y T, Chen Q L, Zhang J Y, et al. Trends in extreme high temperature at different altitudes of Southwest China during 1961-2014. Atmospheric and Oceanic Science Letters, 2020, 13(5): 417-425.

[44] Zhang Y X, Wang G F. Assessment of the hazard of extreme low-temperature events over China in 2021. Advances in Climate Change Research, 2022, 13(6): 811-818.

[45] Zhang Y X, Liu Y J, Ding Y H. Identification of winter long-lasting regional extreme low-temperature events in Eurasia and their variation during 1948-2017. Advances in Climate Change Research, 2021, 12(3): 353-362.

[46] Guo D L, Zhang Y, Gao X J, et al. Evaluation and ensemble projection of extreme high and low temperature events in China from four dynamical downscaling simulations. International Journal of Climatology, 2021, 41(Suppl.1): E1252-E1269.

[47] Park H, Jeong S J, Ho C H, et al. Nonlinear response of vegetation green-up to local temperature variations in temperate and boreal forests in the Northern Hemisphere. Remote Sensing of Environment, 2015, 165: 100-108.

[48] Bórnez K, Verger A, Descals A, et al. Monitoring the responses of deciduous forest phenology to 2000-2018 climatic anomalies in the Northern Hemisphere. Remote Sensing, 2021, 13(14): 2806. DOI: 10.3390/rs13142806.

[49] Zheng C, Tang X G, Gu Q, et al. Climatic anomaly and its impact on vegetation phenology, carbon sequestration and water-use efficiency at a humid temperate forest. Journal of Hydrology, 2018, 565: 150-159.

[50] Ladwig L M, Chandler J L, Guiden P W, et al. Extreme winter warm event causes exceptionally early bud break for many woody species. Ecosphere, 2019, 10(1): e02542. DOI: 10.1002/ecs2.2542.

[51] Crabbe R A, Dash J, Rodriguez-Galiano V F, et al. Extreme warm temperatures alter forest phenology and productivity in Europe. Science of the Total Environment, 2016, 563/564: 486-495.

[52] Yuan Moxi, Zhao Lin, Li Xinxin, et al. Diverse responses of end of growing season to extreme climate events in different grasslands in temperate China during 1982-2015. Acta Ecologica Sinica, 2023, 43(14): 6015-6032. [袁沫汐, 赵林, 李鑫鑫, 等. 1982—2015年中国温带不同草地植被枯黄期对极端气候事件的响应. 生态学报, 2023, 43(14): 6015-6032.]

[53] Cremonese E, Filippa G, Galvagno M, et al. Heat wave hinders green wave: The impact of climate extreme on the phenology of a mountain grassland. Agricultural and Forest Meteorology, 2017, 247: 320-330.

[54] Xie Y Y, Wang X J, Silander J A. Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts. PNAS, 2015, 112(44): 13585-13590.

[55] Zhao Z H, Wang X Y, Li R J, et al. Impacts of climate extremes on autumn phenology in contrasting temperate and alpine grasslands in China. Agricultural and Forest Meteorology, 2023, 336: 109495. DOI: 10.1016/j.agrformet.2023.109495.

[56] Ying H, Zhang H Y, Zhao J J, et al. Effects of spring and summer extreme climate events on the autumn phenology of different vegetation types of Inner Mongolia, China, from 1982 to 2015. Ecological Indicators, 2020, 111: 105974. DOI: 10.1016/j.ecolind.2019.105974.

[57] Wu L Z, Zhao C Y, Li J Y, et al. Impact of extreme climates on land surface phenology in Central Asia. Ecological Indicators, 2023, 146: 109832. DOI: 10.1016/j.ecolind.2022.109832.

[58] Jeong S J, Ho C H, Gim H J, et al. Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982-2008. Global Change Biology, 2011, 17(7): 2385-2399.

[59] Zhang J, Zhao J J, Wang Y Q, et al. Comparison of land surface phenology in the Northern Hemisphere based on

AVHRR GIMMS3g and MODIS datasets. ISPRS Journal of Photogrammetry and Remote Sensing, 2020, 169: 1-16.
[60] Zhao J J, Zhang H Y, Zhang Z X, et al. Spatial and temporal changes in vegetation phenology at middle and high latitudes of the Northern Hemisphere over the past three decades. Remote Sensing, 2015, 7(8): 10973-10995.
[61] Wang S X, Wu Z F, Gong Y F, et al. Climate warming shifts the time interval between flowering and leaf unfolding depending on the warming period. Science China Life Sciences, 2022, 65(11): 2316-2324.
[62] Wu Z F, Lin C F, Wang S X, et al. The sensitivity of ginkgo leaf unfolding to the temperature and photoperiod decreases with increasing elevation. Agricultural and Forest Meteorology, 2022, 315: 108840. DOI: 10.1016/j.agrformet.2022.108840.
[63] Gong Yufeng, Wu Zhaofei, Fu Yongshuo, et al. Effects of climate change on spring budburst of typical tree species in Beijing based on manipulative experiments. Acta Ecologica Sinica., 2023, 43(5): 1948-1958. [龚玉凤, 吴兆飞, 付永硕, 等. 气候变化对北京常见树种春季萌芽的影响: 基于控制实验研究. 生态学报, 2023, 43(5): 1948-1958.]
[64] Gulen H, Eris A. Effect of heat stress on peroxidase activity and total protein content in strawberry plants. Plant Science, 2004, 166(3): 739-744.
[65] He Y L, Liu X Z, Huang B R. Changes in protein content, protease activity, and amino acid content associated with heat injury in creeping bentgrass. Journal of the American Society for Horticultural Science, 2005, 130(6): 842-847.
[66] Augspurger C K. Spring 2007 warmth and frost: Phenology, damage and refoliation in a temperate deciduous forest. Functional Ecology, 2009, 23(6): 1031-1039.
[67] Mo Y H, Zhang X, Liu Z C, et al. Effects of climate extremes on spring phenology of temperate vegetation in China. Remote Sensing, 2023, 15(3): 686. DOI: 10.3390/rs15030686.
[68] Cannell M G R, Smith R I. Climatic warming, spring budburst and forest damage on trees. Journal of Applied Ecology, 1986, 23(1): 177. DOI: 10.2307/2403090.
[69] Gu L H, Hanson P J, Post W M, et al. The 2007 Eastern US Spring Freeze: Increased cold damage in a warming world? BioScience, 2008, 58(3): 253-262.
[70] Liu Q, Piao S L, Janssens I A, et al. Extension of the growing season increases vegetation exposure to frost. Nature Communications, 2018, 9: 426. DOI: 10.1038/s41467-017-02690-y.
[71] Zohner C M, Mo L D, Sebald V, et al. Leaf-out in northern ecotypes of wide-ranging trees requires less spring warming, enhancing the risk of spring frost damage at cold range limits. Global Ecology and Biogeography, 2020, 29(6): 1065-1072.
[72] Lamichhane J R. Rising risks of late-spring frosts in a changing climate. Nature Climate Change, 2021, 11(7): 554-555.
[73] Hufkens K, Friedl M A, Keenan T F, et al. Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology, 2012, 18(7): 2365-2377.
[74] Bennie J, Kubin E, Wiltshire A, et al. Predicting spatial and temporal patterns of bud-burst and spring frost risk in north-west Europe: The implications of local adaptation to climate. Global Change Biology, 2010, 16(5): 1503-1514.
[75] Vitasse Y, Lenz A, Körner C. The interaction between freezing tolerance and phenology in temperate deciduous trees. Frontiers in Plant Science, 2014, 5: 541. DOI: 10.3389/fpls.2014.00541.
[76] Zohner C M, Rockinger A, Renner S S. Increased autumn productivity permits temperate trees to compensate for spring frost damage. New Phytologist, 2019, 221(2): 789-795.
[77] Shen M G, Piao S L, Chen X Q, et al. Strong impacts of daily minimum temperature on the green-up date and summer greenness of the Tibetan Plateau. Global Change Biology, 2016, 22(9): 3057-3066.
[78] Wang X, Gao Q, Wang C, et al. Spatiotemporal patterns of vegetation phenology change and relationships with climate in the two transects of East China. Global Ecology and Conservation, 2017, 10: 206-219.
[79] Shen X J, Liu B H, Henderson M, et al. Asymmetric effects of daytime and nighttime warming on spring phenology in the temperate grasslands of China. Agricultural and Forest Meteorology, 2018, 259: 240-249.
[80] Meng L, Zhou Y Y, Li X C, et al. Divergent responses of spring phenology to daytime and nighttime warming. Agricultural and Forest Meteorology, 2020, 281: 107832. DOI: 10.1016/j.agrformet.2019.107832.
[81] Meng F D, Zhang L R, Zhang Z H, et al. Opposite effects of winter day and night temperature changes on early phenophases. Ecology, 2019, 100(9): e02775. DOI: 10.1002/ecy.2775.
[82] Wu C Y, Wang X Y, Wang H J, et al. Contrasting responses of autumn-leaf senescence to daytime and night-time warming. Nature Climate Change, 2018, 8(12): 1092-1096.
[83] Huang Y, Jiang N, Shen M G, et al. Effect of preseason diurnal temperature range on the start of vegetation growing season in the Northern Hemisphere. Ecological Indicators, 2020, 112: 106161. DOI: 10.1016/j.ecolind.2020.106161.

[84] Myhre G, Alterskjær K, Stjern C W, et al. Frequency of extreme precipitation increases extensively with event rareness under global warming. Scientific Reports, 2019, 9(1): 16063. DOI: 10.1038/s41598-019-52277-4.

[85] Tang Y, Huang A N, Wu P L, et al. Drivers of summer extreme precipitation events over East China. Geophysical Research Letters, 2021, 48(11): e2021GL093670. DOI: 10.1029/2021GL093670.

[86] Gimeno L, Sorí R, Vázquez M, et al. Extreme precipitation events. WIREs Water, 2022, 9(6): e1611. DOI: 10.1002/wat2.1611.

[87] Qiu T, Song C H, Clark J S, et al. Understanding the continuous phenological development at daily time step with a Bayesian hierarchical space-time model: Impacts of climate change and extreme weather events. Remote Sensing of Environment, 2020, 247: 111956. DOI: 10.1016/j.rse.2020.111956.

[88] Adu B, Qin G X, Li C B, et al. Grassland phenology's sensitivity to extreme climate indices in the Sichuan province, western China. Atmosphere, 2021, 12(12): 1650. DOI: 10.3390/atmos12121650.

[89] Zhang L H, Shen M G, Jiang N, et al. Spatial variations in the response of spring onset of photosynthesis of evergreen vegetation to climate factors across the Tibetan Plateau: The roles of interactions between temperature, precipitation, and solar radiation. Agricultural and Forest Meteorology, 2023, 335: 109440. DOI: 10.1016/j.agrformet.2023.109440.

[90] Wang J, Liu D S, Ciais P, et al. Decreasing rainfall frequency contributes to earlier leaf onset in northern ecosystems. Nature Climate Change, 2022, 12(4): 386-392.

[91] Cong N, Wang T, Nan H J, et al. Changes in satellite-derived spring vegetation green-up date and its linkage to climate in China from 1982 to 2010: A multimethod analysis. Global Change Biology, 2013, 19(3): 881-891.

[92] Heisler-White J L, Blair J M, Kelly E F, et al. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Global Change Biology, 2009, 15(12): 2894-2904.

[93] Zhang Bin, Zhu Jianjun, Liu Huamin, et al. Effects of extreme rainfall and drought events on grassland ecosystems. Chinese Journal of Plant Ecology, 2014, 38(9): 1008-1018. [张彬, 朱建军, 刘华民, 等. 极端降水和极端干旱事件对草原生态系统的影响. 植物生态学报, 2014, 38(9): 1008-1018.]

[94] Haugaasen T, Peres C A. Tree phenology in adjacent Amazonian flooded and unflooded forests. Biotropica, 2005, 37(4): 620-630.

[95] Pei T T, Ji Z X, Chen Y, et al. The sensitivity of vegetation phenology to extreme climate indices in the Loess Plateau, China. Sustainability, 2021, 13(14): 7623. DOI: 10.3390/su13147623.

[96] Dai A G. Increasing drought under global warming in observations and models. Nature Climate Change, 2013, 3(1): 52-58.

[97] Trenberth K E, Dai A G, van der Schrier G, et al. Global warming and changes in drought. Nature Climate Change, 2014, 4(1): 17-22.

[98] Choat B, Brodribb T J, Brodersen C R, et al. Triggers of tree mortality under drought. Nature, 2018, 558(7711): 531-539.

[99] Gitlin A R, Sthultz C M, Bowker M A, et al. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. Conservation Biology, 2006, 20(5): 1477-1486.

[100] Li X Y, Piao S L, Huntingford C, et al. Global variations in critical drought thresholds that impact vegetation. National Science Review, 2023, 10(5): nwad049. DOI: 10.1093/nsr/nwad049.

[101] Rivero R M, Kojima M, Gepstein A, et al. Delayed leaf senescence induces extreme drought tolerance in a flowering plant. PNAS, 2007, 104(49): 19631-19636.

[102] Bernal M, Estiarte M, Peñuelas J. Drought advances spring growth phenology of the Mediterranean shrub *Erica multiflora*. Plant Biology, 2011, 13(2): 252-257.

[103] Kang W P, Wang T, Liu S L. The response of vegetation phenology and productivity to drought in semi-arid regions of northern China. Remote Sensing, 2018, 10(5): 727. DOI: 10.3390/rs10050727.

[104] Wu R H, Zhao J J, Zhang H Y, et al. Preseason drought controls on patterns of spring phenology in grasslands of the Mongolian Plateau. Science of the Total Environment, 2022, 838: 156018. DOI: 10.1016/j.scitotenv.2022.156018.

[105] Tao F, Yokozawa M, Zhang Z, et al. Land surface phenology dynamics and climate variations in the North East China Transect (NECT), 1982-2000. International Journal of Remote Sensing, 2008, 29(19): 5461-5478.

[106] Yuan M X, Zhao L, Lin A W, et al. Impacts of preseason drought on vegetation spring phenology across the Northeast China Transect. Science of the Total Environment, 2020, 738: 140297. DOI: 10.1016/j.scitotenv.2020.140297.

[107] Zeng Z Q, Wu W X, Ge Q S, et al. Legacy effects of spring phenology on vegetation growth under Preseason meteorological drought in the Northern Hemisphere. Agricultural and Forest Meteorology, 2021, 310: 108630. DOI: 10.1016/j.agrformet.2021.108630.

[108] Mou Chengxiang, Sun Geng, Luo Peng, et al. Flowering responses of alpine meadow plant in the Qinghai-Tibetan Plateau to lowering responses of alpine meadow plant in the Qinghai-Tibetan Plateau to extreme drought imposed in different periods. Chinese Journal of Applied & Environmental Biology, 2013, 19(2): 272-279. [牟成香, 孙庚, 罗鹏, 等. 青藏高原高寒草甸植物开花物候对极端干旱的响应. 应用与环境生物学报, 2013, 19(2): 272-279.]

[109] Yuan Z H, Tong S Q, Bao G, et al. Spatiotemporal variation of autumn phenology responses to preseason drought and temperature in alpine and temperate grasslands in China. Science of the Total Environment, 2023, 859: 160373. DOI: 10.1016/j.scitotenv.2022.160373.

[110] Ge W Y, Han J Q, Zhang D J, et al. Divergent impacts of droughts on vegetation phenology and productivity in the Yungui Plateau, southwest China. Ecological Indicators, 2021, 127: 107743. DOI: 10.1016/j.ecolind.2021.107743.

[111] Arend M, Sever K, Pflug E, et al. Seasonal photosynthetic response of European beech to severe summer drought: Limitation, recovery and post-drought stimulation. Agricultural and Forest Meteorology, 2016, 220: 83-89.

[112] Hui-Mean F, Yusop Z, Yusof F. Drought analysis and water resource availability using standardised precipitation evapotranspiration index. Atmospheric Research, 2018, 201: 102-115.

[113] Wells N, Goddard S, Hayes M J. A self-calibrating Palmer drought severity index. Journal of Climate, 2004, 17(12): 2335-2351.

[114] Mckee T B, Doesken N J, Kleist J. The relationship of drought frequency and duration to time scales//American Meteorological Society. Proceedings of the 8th Conference on Applied Climatology. Boston, 1993: 17-22.

[115] Li X Y, Piao S L, Wang K, et al. Temporal trade-off between gymnosperm resistance and resilience increases forest sensitivity to extreme drought. Nature Ecology & Evolution, 2020, 4(8): 1075-1083.

[116] Gupta A, Rico-Medina A, Caño-Delgado A I. The physiology of plant responses to drought. Science, 2020, 368(6488): 266-269.

[117] Vicente-Serrano S M, Gouveia C, Camarero J J, et al. Response of vegetation to drought time-scales across global land biomes. PNAS, 2013, 110(1): 52-57.

[118] Hao Z C. Compound events and associated impacts in China. iScience. 2022, 25(8): 104689. DOI: 10.1016/j.isci.2022.104689.

[119] Li J, Bevacqua E, Chen C, et al. Regional asymmetry in the response of global vegetation growth to springtime compound climate events. Communications Earth & Environment, 2022, 3: 123. DOI: 10.1038/s43247-022-00455-0.

[120] Mazdiyasni O, AghaKouchak A. Substantial increase in concurrent droughts and heatwaves in the United States. PNAS, 2015, 112(37): 11484-11489.

[121] Dreesen F E, De Boeck H J, Janssens I A, et al. Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages. Biogeosciences, 2014, 11(1): 109-121.

[122] Škvareninová J, Babálová D, Valach J, et al. Impact of temperature and wetness of summer months on autumn vegetative phenological phases of selected species in Fageto-Quercetum in the years 2011-2015. Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis, 2017, 65(3): 939-946.

[123] Wang J M, Zhang X Y. Impacts of wildfires on interannual trends in land surface phenology: An investigation of the Hayman Fire. Environmental Research Letters, 2017, 12(5): 054008. DOI: 10.1088/1748-9326/aa6ad9.

[124] Borchert R, Rivera G, Hagnauer W. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. Biotropica, 2002, 34(1): 27-39.

[125] Dong L W, Wu C Y, Wang X Y, et al. Satellite observed delaying effects of increased winds on spring green-up dates. Remote Sensing of Environment, 2023, 284: 113363. DOI: 10.1016/j.rse.2022.113363.

[126] Wu C Y, Wang J, Ciais P, et al. Widespread decline in winds delayed autumn foliar senescence over high latitudes. PNAS, 2021, 118(16): e2015821118. DOI: 10.1073/pnas.2015821118.

[127] Peng J, Wu C Y, Zhang X Y, et al. Satellite detection of cumulative and lagged effects of drought on autumn leaf senescence over the Northern Hemisphere. Global Change Biology, 2019, 25(6): 2174-2188.

[128] Vitasse Y, Bottero A, Cailleret M, et al. Contrasting resistance and resilience to extreme drought and late spring frost in five major European tree species. Global Change Biology, 2019, 25(11): 3781-3792.

[129] Choukri H, Hejjaoui K, El-Baouchi A, et al. Heat and drought stress impact on phenology, grain yield, and nutritional quality of lentil (*Lens culinaris Medikus*). Frontiers in Nutrition, 2020, 7: 596307. DOI: 10.3389/fnut.2020.596307.

[130] Peñuelas J, Rutishauser T, Filella I. Phenology feedbacks on climate change. Science, 2009, 324(5929): 887-888.

[131] Liu Fengshan, Chen Ying, Shi Wenjiao, et al. Influences of agricultural phenology dynamics on land surface biophysical processes and climate feedback: A review. Acta Geographica Sinica, 2017, 72(7): 1139-1150. [刘凤山, 陈

莹, 史文娇, 等. 农业物候动态对地表生物物理过程及气候的反馈研究进展. 地理学报, 2017, 72(7): 1139-1150.]

[132] Li C L, Wang J, Hu R C, et al. Relationship between vegetation change and extreme climate indices on the Inner Mongolia Plateau, China, from 1982 to 2013. Ecological Indicators, 2018, 89: 101-109.

[133] Ding Y X, Li Z, Peng S Z. Global analysis of time-lag and -accumulation effects of climate on vegetation growth. International Journal of Applied Earth Observation and Geoinformation, 2020, 92: 102179. DOI: 10.1016/j.jag.2020.102179.

[134] Zhao A Z, Yu Q Y, Feng L L, et al. Evaluating the cumulative and time-lag effects of drought on grassland vegetation: A case study in the Chinese Loess Plateau. Journal of Environmental Management, 2020, 261: 110214. DOI: 10.1016/j.jenvman.2020.110214.

[135] Zhou R L, Liu Y Y, Cui M Y, et al. Global assessment of cumulative and time-lag effects of drought on land surface phenology. GIScience & Remote Sensing, 2022, 59(1): 1918-1937.

[136] Huang Wenlin, Zhang Qiang, Kong Dongdong, et al. Response of vegetation phenology to drought in Inner Mongolia from 1982 to 2013. Acta Ecologica Sinica, 2019, 39(13): 4953-4965. [黄文琳, 张强, 孔冬冬, 等. 1982—2013年内蒙古地区植被物候对干旱变化的响应. 生态学报, 2019, 39(13): 4953-4965.]

[137] Wen Y Y, Liu X P, Xin Q C, et al. Cumulative effects of climatic factors on terrestrial vegetation growth. Journal of Geophysical Research: Biogeosciences, 2019, 124(4): 789-806.

[138] Wang L X. Spring phenology alters vegetation drought recovery. Nature Climate Change, 2023, 13: 123-124.

[139] Ge C H, Sun S, Yao R, et al. Long-term vegetation phenology changes and response to multi-scale meteorological drought on the Loess Plateau, China. Journal of Hydrology, 2022, 614: 128605. DOI: 10.1016/j.jhydrol.2022.128605.

[140] Fu Y S, Li X X, Zhou X C, et al. Progress in plant phenology modeling under global climate change. Science China Earth Sciences, 2020, 63(9): 1237-1247.

[141] Zhou Guangsheng, Song Xingyang, Zhou Mengzi, et al. Advances in influencing mechanism and model of total climatic production factors of plant phenology change. Scientia Sinica Vitae, 2023, 53(3): 380-389. [周广胜, 宋兴阳, 周梦子, 等. 植物物候变化的全气候生产要素影响机制与模型研究. 中国科学: 生命科学, 2023, 53(3): 380-389.]

[142] Wu C Y, Peng J, Ciais P, et al. Increased drought effects on the phenology of autumn leaf senescence. Nature Climate Change, 2022, 12: 943-949.

[143] Wang J, Liu D S. Larger diurnal temperature range undermined later autumn leaf senescence with warming in Europe. Global Ecology and Biogeography, 2023, 32(5): 734-746.

Response of vegetation phenology to extreme climate and its mechanism

ZHANG Jing[1], HAO Fanghua[2], WU Zhaofei[1],
LI Mingwei[1], ZHANG Xuan[1], FU Yongshuo[1]
(1. College of Water Sciences, Beijing Normal University, Beijing 100875, China;
2. College of Urban and Environmental Sciences, Central China Normal University, Wuhan 430079, China)

Abstract: Global climate change caused by human activities results in frequent extreme climate events, and shifts the physiological processes of plants, and the carbon, water cycle and energy balance of terrestrial ecosystems. Vegetation phenology is the most sensitive biological indicator to climate change. In recent years, the responses of vegetation phenology to climate change mainly focus on the mean state of the climate, while the response mechanisms of vegetation phenology to extreme climate are still unclear. In this paper, the response of vegetation spring and autumn phenology to various extreme climatic events and their mechanisms were reviewed. We found that extreme low temperature and extreme precipitation directly delayed the vegetation green-up date and advanced the leaf senescence, while extreme high temperature and extreme drought led to stomatal closure, inhibited photosynthesis and transpiration, and thus advanced leaf senescence at middle and high latitudes of the Northern Hemisphere. Currently, the studies on the response of vegetation phenology to extreme climate events pay less attention to compound extreme climate events, and there are only few studies on the lag effect of vegetation phenology response to extreme climate events and the recovery process of vegetation after the occurrence of extreme events. Under future climate change scenarios, it is necessary to modify the vegetation phenological models by considering the impact of extreme climate events and couple it into the dynamic global vegetation models to improve the simulation accuracy of the carbon cycle in terrestrial ecosystems.

Keywords: vegetation phenology; extreme climatic events; response mechanism; compound extreme events; lagged effect