

# 增温和增/减水及氮沉降对中国草地植物多样性影响的研究进展

夏露<sup>1</sup>,张苏人<sup>2,3</sup>,刘培培<sup>2,3</sup>,吕汪汪<sup>2,3</sup>,洪欢<sup>2,3</sup>,周阳<sup>2,3</sup>,李博文<sup>2,3</sup>,王奇<sup>2,3</sup>,阿旺<sup>2,3</sup>,  
姜丽丽<sup>2</sup>,斯确多吉<sup>2</sup>,汪诗平<sup>2</sup>,张立荣<sup>1,2,3,4</sup>

(1. 西藏大学理学院,西藏 拉萨 850000;2. 中国科学院青藏高原研究所高寒生态重点实验室,北京 100101;3. 中国科学院大学,北京 10049;4. 河北民族师范学院,河北 承德 067600)

**摘要:**植物是生态系统的第一营养级,植物多样性在生物多样性中占主要地位。回顾了国内外学者近年来关于我国草地生态系统的研究,综述了气候变化和氮沉降增加对草地植物多样性的影响。温度增加没有显著改变高寒草甸和温性草地的物种丰富度,但降低了高寒草原和荒漠草原的物种丰富度,但是增温的影响与增温方式、增温年限有关。增水增加了物种丰富度,减水则相反。氮添加显著降低草地植物物种丰富度。增温和水分耦合以及氮添加和水分耦合对物种多样性的作用是可加的,总效应可能取决于相对效应大小:降水增加减缓了温度增加对物种丰富度的降低效应,降水增加和氮添加耦合作用降低了物种丰富度。未来需要加强长期监测温度增加对草地植物多样性的影响、更加关注物种组成的动态变化、加强降水格局变化的模拟试验和多因子耦合试验对草地植物多样性的影响的研究。

**关键词:**增温;增/减水;氮沉降;物种丰富度;物种组成

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全球环境变化正在加剧,尤以气候变暖、降水格局的改变和大气氮沉降的增加最为明显。自工业革命以来,全球平均温度呈显著的上升趋势,1901~2012年全球气温上升了 $0.89\text{ }^{\circ}\text{C}$ <sup>[1]</sup>,尤其以高海拔和高纬度地区气候变暖更迅速<sup>[2-3]</sup>。气候变暖的同时降水格局正发生剧烈的变化<sup>[4]</sup>。根据预测,到21世纪末全球中

纬度湿润地区的降水减少,高纬度地区和赤道太平洋地区的年平均降水量增加,许多中纬度和亚热带干旱地区,平均降水量减少,呈现“干者越干,湿者越湿,区域和季节降水的变化突出,区域极端降水事件增加”的趋势<sup>[1]</sup>。由于人类活动的影响,全球大气中的活性氮含量增加了数倍导致全球氮沉降增加,现今全球氮沉降值为 $125\sim 132\text{ Tg/a}$ <sup>[5]</sup>。中国活性氮排放更为突出,1910~2010年由920万t增加到5600万t<sup>[6]</sup>,而且未来氮沉降将持续上升<sup>[7-8]</sup>。

中国草地面积 $4\times 10^8\text{ hm}^2$ ,占国土面积的41.7%,是我国陆地最大的生态系统。草地生态系统不仅支撑着我国的畜牧业发展和牧民的生产生活,而且是我国重要的生态屏障,尤其在生物多样性维持中也扮演着重要角色。气候变暖、降水格局变化以及氮沉降,不仅影响生物多样性保护政策的制定,而且进一步影响生态系统功能和稳定性<sup>[9]</sup>。植物多样性是生物多样性最主要的方面,本文将围绕气候变暖、降水格局变

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**作者简介:**夏露(1998-),女,河南信阳人,硕士研究生。

E-mail:1243933816@qq.com

张立荣为通信作者。

E-mail:zhanglir09@163.com

化以及氮沉降的影响,回顾国内外学者近年来关于我国草地生态系统的研究,系统总结气候变化及氮沉降对草地植物多样性影响等方面的最新研究成果,为深入推动我国草地植物多样性变化的研究提供一定理论价值。

## 1 增温对草地植物多样性的影响

### 1.1 不同草地类型及增温幅度

增温对物种丰富度的影响因草地类型不同而不同。一般认为,低温是影响高寒草地生态系统的主要限制因子,相比于其他草地类型,高寒草地植物多样性对增温的响应可能更强烈。然而,根据12个增温试验发现,增温后高寒草甸丰富度的变化并不显著,但是高寒草原的丰富度降低<sup>[10]</sup>。在部分研究中,增温显著降低了高寒草甸物种丰富度<sup>[11-15]</sup>,这与同样受低温影响的苔原表现一致<sup>[16]</sup>。对温性草原<sup>[17-18]</sup>和温性草甸<sup>[19]</sup>来讲,丰富度的变化同样不显著,但增温使荒漠草原丰富度降低<sup>[20]</sup>。

与此同时,并没有发现增温幅度对植物多样性的显著影响<sup>[21]</sup>。尽管物种多样性变化不显著,但是增温显著改变了所有草地的物种组成:增温显著提高了高寒草甸禾草盖度<sup>[22]</sup>和温性草原C<sub>4</sub>禾草盖度<sup>[20]</sup>。物种多样性的变化主要物种丢失速率和物种迁入速率决定<sup>[23]</sup>。增温直接使土壤湿度降低<sup>[18,22]</sup>和物种间竞争作用加强<sup>[24]</sup>,这些均会造成物种丢失速率的增加。比如,对青藏高原高寒草甸来说,适应干旱条件的禾草比例上升,莎草和杂类草比例降低<sup>[15,25]</sup>。增温增加了植物的生物量和植物高度,降低了群落下层的光照强度,使得矮小、不耐荫物种在竞争中处于劣势,同时凋落物的增多抑制种子萌发<sup>[26]</sup>等,从而降低了物种丰富度<sup>[27-29]</sup>。与此同时,温度上升直接导致热适应物种组成比例增加<sup>[16,30]</sup>,这可能提高物种多样性。

### 1.2 增温年限

增温年限同样影响物种多样性。比如,对青藏高原高寒草甸的研究发现,短期增温使物种丰富度降低40%<sup>[13,31]</sup>,但由于物种优势度变化及迁入物种增加,在增温18年后物种数迅速恢复<sup>[32]</sup>。短期增温试验只能反映植物的胁迫变化,很难揭示植物的适应性结果。因此我们需要关注不同增温时间对草地植物多样性

的影响。

### 1.3 增温方式

不同增温方式影响温度上升,造成物种丰富度变化不同。Yang等<sup>[33]</sup>在横断山脉同一地点利用移栽、开顶式气室(OTC)和梯度格局3种方法模拟温度上升发现,3种方法得到的结果并不一致:通过OTC和梯度格局模拟增温后,温度上升使物种丰富度降低,符合自然梯度上高寒草甸和高寒草原物种丰富度均与温度成负相关的结果<sup>[29]</sup>。对长期原地观测的结果显示,在高海拔地区植被物种丰富度有明显增加的趋势<sup>[34]</sup>,这与青藏高原高寒草甸的山体垂直带移栽试验结果相同<sup>[23]</sup>。但是,温性草原的长期定位观测试验发现增温使丰富度降低<sup>[35-36]</sup>。植物物种分布范围变迁的假说认为,气候的持续变化可能会迫使物种适应当地的环境条件,也可能会促使物种迁移到适宜其生长、发育和繁殖的环境<sup>[37-38]</sup>,即物种发生了明显的向高海拔和高纬度地区上移<sup>[39,40]</sup>。当物种的迁入的数量超过了物种的丢失数量时,物种丰富度将增加<sup>[23,41-43]</sup>,这可能解释了高海拔地区物种丰富度上升的原因。但是,现今对物种迁移的研究仍比较缺乏。

常见的模拟增温方式OTC和红外增温法可能也造成不同结果。OTC增温试验表明,增温会导致物种丰富度的快速下降<sup>[13,31]</sup>,而红外增温试验往往不改变群落的物种丰富度<sup>[24,44]</sup>或者物种丰富度下降幅度较小<sup>[15]</sup>。可能是因为开顶箱法物理阻隔而抑制物种的入侵和种子扩散<sup>[23]</sup>,同时降低了风速,改变了光照,并不能真实模拟气候变暖的情境<sup>[33]</sup>。

## 2 增/减水对草地植物多样性的影响

无论是在高寒草地或是温性草地,在自然梯度下,降水量与草地物种丰富度成正相关<sup>[45-47]</sup>。因此,在人为控制试验中,不难发现降水增加物种丰富度,减少则降低了物种丰富度<sup>[18,48-53]</sup>。但是,与温性草地相比,高寒草地物种丰富度对降水增加不敏感<sup>[54]</sup>甚至使丰富度降低<sup>[25]</sup>。在高寒草地生态系统中,在水分变化相同的条件下,高寒草原物种丰富度对降水增加的反应更敏感,而高寒草甸对降水减少更敏感。由于高寒荒漠本身物种丰富度降低,其对降水增加和减少的反应均不敏感<sup>[55]</sup>。温带草原植物物种对降水减少比

降水增加更敏感<sup>[49]</sup>。水分是影响植物生长的关键因素,水分增加可以提高土壤水分有效性,有效缓解水分亏缺对植物生长的抑制作用<sup>[52]</sup>,尤其在植物生长早期<sup>[56]</sup>,对浅根植物<sup>[50]</sup>的缓解作用更明显,从而会提高物种迁入速率,降低物种丧失速率<sup>[57]</sup>,提高物种多样性。降水减少则导致物种向耐旱物种转变<sup>[49,58]</sup>,降低需水量较高的功能群数量和物种个体数量<sup>[58]</sup>,从而降低物种丰富度。

### 3 氮沉降变化对草地植物多样性的影响

研究发现向草地施用氮肥可显著降低物种丰富度和多样性指数<sup>[59-60]</sup>。主要原因为:(1)当土壤养分充足时,资源利用较高的植物迅速生长而增加植被盖度和密度,降低了群落下层的光照强度,使矮小、不耐荫和返青较晚的物种在光的竞争中处于劣势<sup>[61]</sup>;(2)氮添加导致土壤中锰离子释放,而杂草吸收大量的锰离子,从而降低了杂草的光合速率,抑制其生长,同时土壤酸化直接影响了不耐酸的植物物种生长<sup>[62-63]</sup>;(3)凋落物的增多抑制了种子萌发<sup>[26]</sup>。这些原因导致物种面临逐渐减少或消失的风险<sup>[61,64]</sup>。但是,另外一些研究发现,在干旱条件下,氮添加不会引起干旱草原群落植物物种多样性的显著变化<sup>[65-66]</sup>。

氮沉降造成的多样性变化伴随着群落组成的变化。适当的氮素增加会改善植物组成结构,但是过量的氮素添加或氮沉降可能会加快一些物种的减少甚至消失,对草地生态系统产生负面影响<sup>[60,67-68]</sup>。有研究表明<sup>[60]</sup>,在草原上氮添加量为 $9\sim 19\text{ g/m}^2$ ,Pielou均匀度指数有增加趋势,超过 $19\text{ g/m}^2$ 时则表现下降趋势。在15年氮( $12\text{ g/m}^2$ )添加试验发现<sup>[69]</sup>,苔藓常见种已经消失,禾草物种的个体数和莎草的盖度显著增加。表明植物物种的氮利用策略和氮需求量的不同导致草地植物多样性变化<sup>[70-71]</sup>。但是,在长期试验发现,氮添加没有造成常见物种消失,也没有改变优势种<sup>[69]</sup>。Gotelli等<sup>[67]</sup>模拟试验发现,若每年氮沉降增加1%,到100年后有些常见种将面临灭绝风险。因此氮添加对物种的周转可能存在累积效应<sup>[67]</sup>。未来氮沉降加剧下,不仅那些不适应高氮环境下的罕见和稀少草地植物物种面临比例减少和灭绝、替换,而且常见

物种也可能面临同样的情况。

## 4 增温、水分和氮元素耦合对草地植物多样性的影响

### 4.1 温度和水分耦合对植物多样性的影响

多数研究发现增温和水分变化对植物多样性的作用是可加的<sup>[20,54,72]</sup>。Luo等<sup>[73]</sup>研究发现,在沙质草地干旱地区,增温降低了物种丰富度、植物总密度和生长速度,但增加降水能够改善植物群落结构。此外,Yang等<sup>[18]</sup>对半干旱温带地区的草地生态系统研究表明,增水与增温耦合对物种丰富度没有显著影响,但改变了植物物种组成和均匀度。增温显著降低了高寒草甸的物种丰富度,而增水缓解了下降速度<sup>[54]</sup>。增温提高了植物呼吸和蒸散,而增加了植物对水分的需求,因而增水可能会缓解这种负面影响<sup>[25,73]</sup>,减水的作用则相反。由于增温和水分的影响的可加性,增温和增水/减水的作用取决于两者的相互作用大小。

### 4.2 水分和氮元素耦合对草地植物多样性的影响

全球尺度上大部分研究发现,增水增加了物种丰富度,氮添加降低了物种丰富度,增水、氮添加交互作用降低了物种丰富度<sup>[74]</sup>和均匀度,因为氮添加和增水交互作用能增加群落盖度,抑制底层植物,使其受到光限制,改变植物对养分的利用效率<sup>[61,66,75]</sup>,导致物种丰富度下降。但在不同的草地生态系统类型中表现有所差异。如在半干旱地区,增水、氮添加耦合下可能存在抵消作用,增水增加了物种丰富度,但增水和氮添加交互作用下,物种丰富度没有显著变化<sup>[76]</sup>。

## 5 未来研究建议

综上所述,建议未来研究应该更加关注以下4个问题:

### 5.1 需要长期监测增温对草地植物多样性的影响

目前有关增温试验时间较短,多数只有3~5年的结果,只能反映短期增温对一些植物的胁迫变化,很难揭示植物的适应性结果。有研究表明<sup>[13]</sup>,开始增温可能导致草地植物丰富度下降,但长期增温对草地物种丰富度的影响不显著<sup>[22,24,44]</sup>。特别是不同增温方式、气候背景和草地类型的响应方向和程度也有所不同。因此,需要开展不同增温方法和草地类型的长期增温试验的比较研究。

## 5.2 更加关注物种组成的动态变化

目前多数研究结果只报道了物种丰富度的变化,事实上某一时间段内物种丰富度的变化是物种获得与消失数量的净结果,当获得的物种数大于消失的物种数时,则表现为物种丰富度的增加,反之则降低或不变<sup>[23]</sup>。然而,这些过程中物种组成却发生了显著变化,包括优势物种和次优势物种在群落比例及空间结构的变化<sup>[24]</sup>,而这些变化可能比揭示单纯的物种丰富度的变化更重要。特别是物种丰富度的变化往往是由那些稀少物种的年际动态变化造成的<sup>[15]</sup>,而这些物种可能对气候变化更敏感,但目前这方面的信息很少。

## 5.3 需要加强降水格局变化的模拟试验

不同水分梯度试验处理能够预测区域降水增加或减少对草地植物多样性的影响。但是,这种试验结果无法预测草地植物多样性对季节降水变化和极端降水事件的响应,如冰雹的增多通过对植物花瓣的破坏,影响草地植物的繁殖从而改变植物多样性。持续 1 天或多天的累计大降水事件;年平均降水量虽然增加,但是生长季节降水减少也可能会引起物种多样性变化。极端降水事件增多和季节降水变化可能对植物多样性影响存在更大的作用。因此,未来需要加强季节降水变化和极端降水事件对草地植物多样性影响的模拟试验,从而提高降水格局变化对草地植物多样性影响的更深入理解。

## 5.4 加强多因子耦合试验研究

Rillig 等<sup>[77]</sup>对文献进行了综述发现,目前发表的有关全球变化对土壤功能和微生物多样性的影响的研究中,对单一全球变化因子的模拟占 80%,对双因子的模拟占 19%,而对多因子的控制试验只占不到 2%。然而,全球变化往往表现为多因子耦合发生,比如温度在增加,降水格局也在变化。气候变化因子的相互作用共同影响着草地植物多样性,仅仅依靠单因子试验结果不能全面反映气候变化对草地植物多样性的真实影响方向和程度,甚至会得出相反的结果。目前多因子耦合模拟试验较少,不同气候变化因子对草地植物多样性变化的贡献率或比例仍不清楚。因此,近年来多因子耦合试验研究是全球研究的热点和难点。

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# Effects of climate change and N deposition on plant diversity in grassland in China

XIA LU<sup>1</sup>, ZHNAG Su-ren<sup>2,3</sup>, LIU Pei-pei<sup>2,3</sup>, LV Wang-wang<sup>2,3</sup>, HONG Huan<sup>2,3</sup>,  
ZHOU Yang<sup>2,3</sup>, LI Bo-wen<sup>2,3</sup>, WANG Qi<sup>2,3</sup>, A Wang<sup>2,3</sup>, JIANG Li-li<sup>2</sup>, TSECHOE  
Dor-ji<sup>2</sup>, WANG Shi-ping<sup>2</sup>, ZHANG Li-rong<sup>1,2,3,4</sup>

(1. *College of Science, Tibet University, Lhasa 850000, China*; 2. *Key Laboratory of Alpine Ecology, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China*; 3. *University of the Chinese Academy of Sciences, Beijing 100494, China*; 4. *Department of Resources and Environment, Hebei Normal University for Nationalities, Chengde 067600, China*)

**Abstract:** Plants make up the first trophic level in ecosystems. Plant diversity plays a leading role in biodiversity and reflects bio-community characteristics. Changes in plant diversity not only influence diversity conservation but also induces changes in ecosystem functions. Here, the paper reviews the effects of climate change and nitrogen deposition on plant diversity in grassland in China. Warming did not significantly change species richness in alpine meadows and temperate grasslands but reduced species richness in alpine steppe and desert grasslands. However, the influences of warming on plant diversity varied with heating methods and experiment duration. Increased water precipitation yielded an increase in species richness, but decreasing in precipitation reduced species richness. Nitrogen addition significantly reduced grassland species richness. The interactions between warming and precipitation were additive and their coupling effects were determined by their relative effect. Increased precipitation would alleviate the decrease in plant species richness through warming. Interactive effects of multi-factors, such as interaction of warming, precipitation pattern and nitrogen deposition, on plant composition and diversity need to be addressed further in the future.

**Key words:** climate warming; change in precipitation pattern; nitrogen deposition; species richness; community composition