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草地生态系统生物量在不同气候及多时间尺度上对氮添加和增雨处理的响应

刁励玮[1,2*] 李 平[2,3*] 刘卫星[2] 徐 姗[4] 乔春连[5] 曾 辉[1,6] 刘玲莉[2,3**]

[1]北京大学深圳研究生院, 城市规划与设计学院, 广东深圳 518055; [2]中国科学院植物研究所, 植被与环境变化国家重点实验室, 北京 100093; [3]中国科学院大学, 北京 100049; [4]中国科学院华南植物园, 广州 510650; [5]信阳师范学院大别山生物农业资源开发与利用研究院, 河南信阳 464000; [6]北京大学城市与环境学院, 北京 100084

摘 要 生产力是草地生态系统重要的服务功能, 而生物量作为生态系统生产力的主要组成部分, 往往同时受到氮和水分两个因素的限制。在全球变化背景下, 研究草地生态系统生物量对氮沉降增加和降水变化的响应具有重要意义, 但现有研究缺乏对其在大区域空间尺度以及长时间尺度上响应的综合评估和量化。本研究搜集了1990–2017年间发表论文的有关模拟氮沉降及降水变化研究的相关数据, 进行整合分析, 探讨草地生态系统生物量对氮沉降和降水量两个因素的变化在空间和时间尺度上的响应。结果表明: (1)氮添加、增雨处理以及同时增氮增雨处理都能够显著地提高草地生态系统的地上生物量(37%, 41%, 104%)、总生物量(32%, 23%, 60%)和地上地下生物量比(29%, 25%, 46%)。单独增雨显著提高地下生物量(10%), 单独施氮对地下生物量影响不显著, 但同时增雨则能显著提高地下生物量(43%); (2)氮添加和增雨处理对草地生态系统生物量的影响存在明显的空间变异。在温暖性气候区和海洋性气候区的草地生态系统中, 氮添加对地上、总生物量及地上地下生物量比的促进作用更强, 而在寒冷性气候区和温带大陆性气候区的草地生态系统中, 则增雨处理对地下、总生物量的促进作用更强; (3)草地生态系统生物量对氮添加和增雨处理的响应也存在时间格局上的变化, 地下生物量随着氮添加年限的增加有降低的趋势, 地上、总生物量及地上地下生物量比则有增加的趋势。增雨年限的增加对总生物量没有明显的影响, 但持续促进地上生物量和地下生物量, 增加地上地下生物量比, 可见长期增氮、长期增雨对地上生物量的促进作用更明显。

关键词 草地生物量; 氮添加; 增雨; 响应比; 整合回归; 气候条件; 时间尺度

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Response of plant biomass to nitrogen addition and precipitation increasing under different climate conditions and time scales in grassland

DIAO Li-Wei[1,2*], LI Ping[2,3*], LIU Wei-Xing[2], XU Shan[4], QIAO Chun-Lian[5], ZENG Hui[1,6], and LIU Ling-Li[2,3**]

[1] School of Urban Plan and Design, Shenzhen Graduate School, Peking University, Shenzhen, Guangdong 518055, China; [2]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China; [3]University of Chinese Academy of Sciences, Beijing 100049, China; [4]South China Botanical Garden, Chinese Academy of Science, Guangzhou 510650, China; [5]Institute for Conservation and Utilization of Agro-bioresources in the Dabie Mountains, Xinyang Normal University, Xinyang, Henan 464000, China; and [6]College of Urban and Environmental Sciences, Peking University, Beijing 100084, China

Abstract

Aims Plant biomass accounts for the main part of grassland productivity. The productivity of grassland regarded as one of important ecosystem function is always co-limited by nitrogen and water availability, therefore, how grasslands respond to atmosphic nitrogen (N) addition and precipitation increasing need to be systematically and quantitatively evaluated at different climate conditions and temporal scales.

Methods To investigate the impact of nitrogen addition and precipitation increasing on grassland biomass over climate conditions and temproal scales, a meta-analysis was conducted based on 46 papers that were published during 1990–2017 involving 1 350 observations.

Important findings Results showed that: (1) N addtion, precipitation increasing and the combinations of these two treatments significantly increased the aboveground biomass (37%, 41%, 104%), total biomass (32%, 23%,

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* 同等贡献Contributed equally to this work.

** 通信作者Corresponding author (Lingli.liu@ibcas.ac.cn)

60%) and the ratio of aboveground biomass to belowground biomass (29%, 25%, 46%) in grassland ecosystem. Belowground biomass showed no response to single N addtion, but could be significantly enhanced together with increaseing precipitation; (2) The response of grassland biomass under these N addtion and the increasing of precipitation showed obvious spatial pattern under different climate conditions. The N addition tended to increase more aboveground biomass, total biomass and the ratio of aboveground biomass to belowground biomass under high sites with high mean annual air temperature (MAT) and mean annual precipitation (MAP) while precipitation increasing tended to simulate more belowground biomass and total biomass under low MAT and MAP sites; (3) In addition, the response of grassland biomass under these two global change index showed obvious temporal pattern. With the increase of duration of N addition, the belowgound biomass tended to decrease, while the aboveground biomass, total biomass and the ratio of aboveground biomass to belowground biomass tended to increase under N addition. With the increase of duration of precipitation manipulation, the total biomass showed no response to precipitation increasing, while aboveground biomass, belowground biomass and the ratio of aboveground biomass to belowground biomass tended to be enhanced. The results indicated that aboveground biomass was more likely to be enhanced than belowground biomass under N addition or precipitation increasing in the long term.

Key words grassland biomass; nitrogen addition; precipitation increasing; response ratio; meta-regression; climate condition; temporal scale

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草地生态系统作为陆地生态系统重要的组成部分, 其生产力约占陆地总初级生产力的1/3 (Hoekstra *et al*., 2005), 具有重要的生态系统服务功能(Wrage *et al*., 2011)。氮和水分是草地生态系统生产力的两个重要限制性因素(Hooper & Johnson, 1999; Yahdjian *et al*., 2011)。氮进入生态系统后对光合作用和植物生长的影响存在差异, 进而导致植物生产力的不同响应(Ren *et al*., 2017)。同时, 干旱和湿润的草地生态系统生产力对降水变异所产生的响应也存在差异(Wu *et al*., 2011)。生物量是构成生态系统生产力的重要组分, 在许多研究中生物量常被近似等同于生态系统生产力(Waring *et al*., 1998; DeLucia *et al*., 2007; Goulden *et al*., 2011)。因此, 在前所未有的全球变化的大背景下, 理解草地生态系统生物量对氮沉降和降水的时空响应显得十分重要。

研究发现, 在低氮条件下, 植物为了获取氮, 会增加向地下分配的光合产物(Dingkuhn *et al*., 2007; Grechi *et al*., 2007); 随着外源氮的添加, 草地生态系统地上生物量显著增加(Lee *et al*., 2010), 分配到地下的生物量减少, 草地群落生产力提高(Bai *et al*., 2001)。然而, 不同植物种生物量的变化幅度存在差异(Pan *et al*., 2011), 随着处理年限的增加, 群落物种组成发生变化, 适应环境的植物物种生物量显著提高, 成为优势种(Bai *et al*., 2010)。在环境较为干旱时, 养分的迁移和传输均受到限制(Rouphael *et al*., 2012; He & Dijkstra, 2014), 添加的氮不易被植物快速吸收。随着降水量的增加(Hayes & Seastedt, 1987), 养分的可利用性增强(Tilman & Wedin, 1991), 增加的生物量更多地被分配到地上, 导致地上生物量与地下生物量的比值增加(Li *et al*., 2011)。目前, 地下生物量对增雨的响应尚没有完全统一的结论, 呈增加(Sala *et al*., 1988; Lauenroth & Sala, 1992; Wang *et al*., 2012; Kang *et al*., 2013)、减少(Knapp *et al*., 2001; Li *et al*., 2011)或不变的趋势(Fay *et al*., 2000; Weltzin *et al*., 2003; Zhou *et al*., 2009)。

一般而言, 添加氮和增雨交互作用能显著提高群落地上生物量和总生物量(Gao *et al*., 2011), 然而也可能导致植物群落组成单一化, 进而降低植物多样性(Harpole *et al*., 2007; 陆婷婷等, 2014)。同时有研究表明, 不同植被类型的生物量对于氮水交互作用的响应存在差异, 呈增加、减少或先增加后减少的趋势(李文娇等, 2015; Ren *et al*., 2017), 但尚未得到统一的结论。因此, 整合分析草地生态系统生物量如何响应氮添加和增雨及其交互作用非常有必要。

模型预测的结果表明, 未来草地生态系统仍将受到氮沉降加剧(Liu *et al*., 2013)和降水增加(Cholaw *et al*., 2003)的影响。据估计, 全球氮沉降水平在未来25年内还会加倍(Neff *et al*., 2002)。全球大气环流改变引起的降水格局发生显著变化(Sugiyama *et al*., 2010), 未来高纬度地区的降水量将增加, 大部

分地区的单次强降水事件也将增加(Easterling *et al.*, 2000; IPCC, 2012)。目前, 大多数关于草地生态系统生物量的野外控制实验的研究存在很大的局限性: 仅研究单一站点生物量变化及其影响因素; 仅研究氮或降水单一因素对生物量变化的影响; 仅研究生物量在短时间尺度上的变化及其影响因素(Vitousek & Howarth, 1991; Bai *et al*., 2008; LeBauer & Treseder, 2008; Fay *et al*., 2015)。

综合以上因素, 在全球尺度上探讨草地生态系统生物量在空间和时间尺度上对氮添加和增雨处理的响应, 有助于更好地应对未来氮沉降加剧和极端降水频发的全球变化, 为草地管理提供科学指导。针对上述现有问题, 本研究从46篇已发表的文献中, 收集全球41个野外实验站点时间跨度约为30年的1 350条独立数据, 进行整合响应比与回归分析, 用以研究草地生态系统生物量对氮增加和增雨两个独立因素及其交互作用的影响, 并进一步探讨生物量随氮添加梯度、增雨处理梯度的变化, 以及在空间格局和时间尺度上的响应。

1 材料和方法

1.1 数据来源

本文数据均提取自Web of Science™和Google Scholar数据库中近30年间(即1990–2017年)有关氮添加和增雨处理对草地生态系统生物量影响的相关文献。通过对相关研究的数据及其来源的空间、时间信息进行收集, 建立数据库, 从而开展本文草地生态系统生物量在空间、时间尺度上对氮添加、增雨处理响应的整合研究。本研究共整合文献46篇, 独立数据1 350条, 整个数据库实验站点经度跨度247.16° (123.61° W–123.51° E), 纬度跨度82.18° (25.75° S–56.43° N), 集中分布在北半球中低纬度地区。实验年限涵盖1–10年, 年平均气温涵盖0.3–24.5 ℃, 年降水量涵盖159–1 400 mm (图1)。

实验数据的筛选标准为: (1)实验设置位点需是野外原位草地生态系统, 非室内控制实验; (2)野外控制实验结果以图或表的形式说明实验组(如: 氮添加)和对照组的处理结果 $\bar{X}_T$ 和 $\bar{X}_C$; 重复次数 N_T 和 N_C; 标准误 SE_T 和 SE_C; 标准偏差 SD_T 和 SD_C; (3)单一实验处理至少包含两个处理梯度; (4)增雨处理仅包含雨量的变化, 不含降雨格局的变化; (5)在不同实验处理(如氮添加、增雨处理和同时增氮增雨处理)中, 测定相应变化指标, 主要包括草地生态系统地上、地下、总生物量及地上、地下生物量比。同时, 本研究收集包括野外实验站点经纬度、年平均气温(MAT)、年降水量(MAP)等辅助信息。对于缺失MAT、MAP信息的文献, 本研究通过R软件程序包, 利用Climatic Research Unit Climatology version 2.0 dataset (CRUCL 2.0, New *et al*., 2002)根据站点的经纬度信息提取相应的MAT和MAP数据(附录I)。

其次, 为保证数据的相对独立性, 发表在不同文献中的同一站点的同一实验数据被剔除, 不同期刊中同一控制实验的不同实验处理, 如氮添加

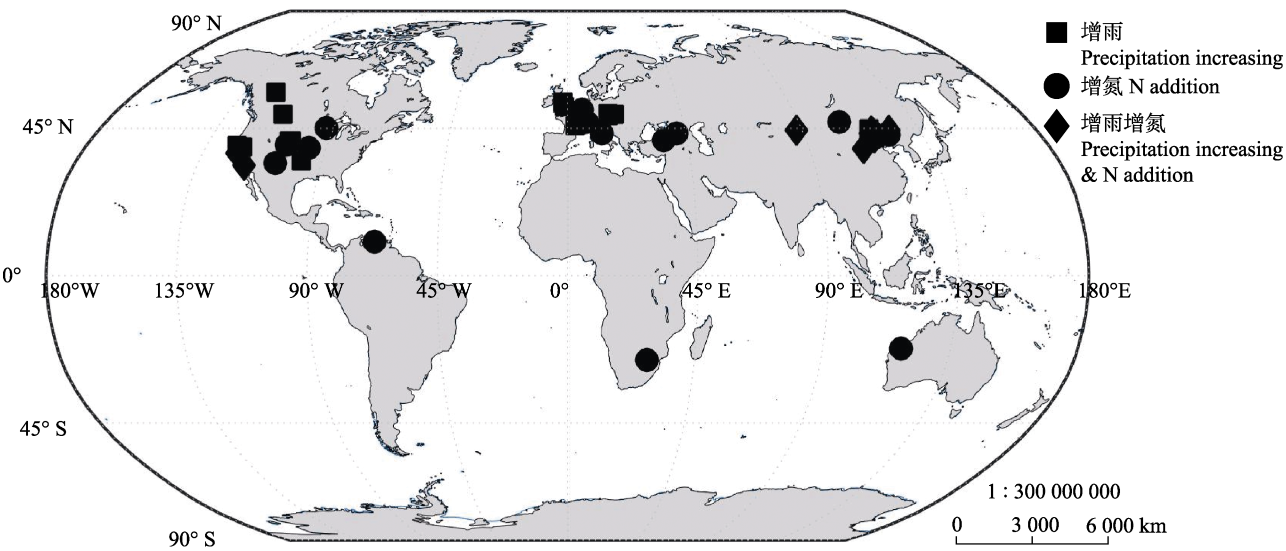

图1 整合分析站点分布图。
Fig. 1 The map of distribution of all the field experiments in this meta-analysis.

浓度、氮添加形式，或同一实验处理的不同实验年份视为一条独立数据。数据的提取方法包括从表格中的数据直接摘录和从图中间接提取，使用Engauge Digitizer (Free Software Foundation, Boston, USA)软件数字化图以提取量化的数据，并尽量按照统一标准减少人工处理误差，生物量单位统一为$g \cdot m^{-2} \cdot a^{-1}$。

为探讨氮添加、增雨处理下，草地生态系统生物量在不同气候条件和不同时间尺度上的响应，我们将收集的数据分为两类：第一类，不同站点同一实验处理的年均结果，用来探究不同气候条件上的响应；第二类，不同站点同一实验研究的逐年结果，用来研究时间格局上的响应(表1)。

1.2　分析方法

本研究通过数据整合(meta-analysis, Hedges *et al*., 1999)的方法对表1所列的数据进行分析。利用响应比(response ratio, *RR*)以及对数响应比(log response ratio, *LRR*)量化各个参数(草地生态系统地上、地下、总生物量及地上地下生物量比)对氮添加、增雨处理以及同时增氮增雨处理的效应，即：

$$RR = \frac{\bar{X}_T}{\bar{X}_C} \quad (1)$$

$$lnRR = log\frac{\bar{X}_T}{\bar{X}_C} \quad (2)$$

变异系数v的计算公式为：

$$v = \frac{(S_T)^2}{N_T(\bar{X}_T)^2} + \frac{(S_C)^2}{N_C(\bar{X}_C)^2} \quad (3)$$

其中，$\bar{X}_C$、S_C和N_C分别为对照处理下相应指标的平均值、标准偏差和样本量，$\bar{X}_T$ S_T和N_T分别为实验处理水平下相应指标的平均值、标准偏差和样本量。

指标的累积效应($\bar{E}$)通过求权重的方式进行计算，即：

$$\bar{E} = \frac{\sum_{i=1}^{n} w_i(logRR)_i}{w_i} \quad (4)$$

其中，n为所有实验的总数，W_i为第i个实验的权重，计算方法为其变异系数的倒数，即：

$$W_i = \frac{1}{v_i} \quad (5)$$

每个指标*RR*的计算是通过对$\bar{E}$进行反对数转换以降低偏倚，使样本近似成正态分布(Hedegs *et al*., 1999; Koricheva *et al*., 2013; Lu *et al*., 2013)。为了在数据样本相对较小时更加精确地计算整合分析数值，我们采用9 999次重复迭代的方法计算95%的置信区间来作为*RR*的异质性(Adams *et al*., 1997)。如果95%置信区间(95%CI)与1没有重叠表明变量有显著的正效应或负效应，反之则认为变量间不存在显著效应。*RR*取对数后*LRR*的95%置信区间则与0比较是否存在显著差异。

将*LRR*进行标准化以排除处理浓度的影响，即将单个实验处理水平以数据库平均值进行标准化，以氮添加对地上生物量影响的标准化为例：数据库平均施氮浓度为8.4 $g \cdot m^{-2} \cdot a^{-1}$，即：

$$\bar{X}_{NT} = \bar{X}_T + \frac{\bar{X}_T - \bar{X}_C}{N} \times (\sim 8.4) \quad (6)$$

其中，$\bar{X}_{NT}$是标准化后的施氮响应值，效应值$\bar{X}_T$、$\bar{X}_C$分别为原始实验处理和对照数值，标准化*LRR*

表1　数据库结构及参数
Table 1　Database structure and parameters

氮添加 Nitrogen addition				
实验数量 Study numbers	地上生物量 AGB	地下生物量 BGB	总生物量 TB	地上地下生物量比 AGB/BGB
年均 Annual mean	109	56	59	42
年际 Inter-annual	169	79	74	37
增雨处理 Precipitation increasing				
实验数量 Study numbers	地上生物量 AGB	地下生物量 BGB	总生物量 TB	地上地下生物量比 AGB/BGB
年均 Annual mean	77	82	71	51
年际 Inter-annual	62	90	98	32
增氮增雨处理 Nitrogen addition and precipitation increasing				
实验数量 Study numbers	地上生物量 AGB	地下生物量 BGB	总生物量 TB	地上地下生物量比 AGB/BGB
年均 Annual mean	19	21	17	14
年际 Inter-annual	21	32	27	11

数字表示独立实验个数。
Values are the number of independent measurements. AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass; AGB/BGB, the ratio of AGB to BGB.

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(normalized *LRR*) = $\log \frac{\overline{X}_{NT}}{\overline{X}_{C}}$ (Liu *et al*., 2016)。其他指标标准化过程同理。

以上所有整合分析及整合回归计算由R软件里的metafor软件包实现(Viechtbauer, 2010)。同时, 使用填补法检验偏爱性对研究结果的影响, 结果表明整合分析仅在氮添加处理下低估了总生物量增加的程度, 其余研究结果均不受影响(附录II–V)。

2　结果

2.1　草地生态系统生物量对氮添加和增雨处理及增氮增雨处理的响应

氮添加显著增加草地生态系统的地上生物量和总生物量(37%, 32%, 图2A、2C), 增加生物量的地上部分分配比例(29%, 图2D)。增雨处理显著增加地上、地下和总生物量(41%, 10%, 23%, 图2A–2C), 同时显著增加地上部分的分配比例(25%, 图2D)。地下生物量对单独氮添加处理的响应不显著(图2B), 而同时进行增雨处理时, 地下生物量则显著增加(42%, 图2B), 且其促进作用显著高于增雨处理(10%, 图2B)。

增氮增雨处理对地上、地下、总生物量(104%, 42%, 60%, 图2A–2C)均有显著的促进作用, 其中对地上生物量的促进作用显著高于地下生物量(104%, 42%, 图2A、2B), 从而显著增加地上地下生物量的比例(46%, 图2D)。

2.2　草地生态系统生物量对氮添加和增雨处理沿处理梯度的变化

氮添加和增雨处理对地上生物量的促进作用沿着氮添加处理水平($p < 0.01$, 图3A)、增雨处理梯度($p < 0.001$, 图3E)增加而增加, 但地下生物量、总生物量及地上地下生物量比的响应与处理水平并无显著相关性(图3B–3D, 3F–3H)。

2.3　草地生态系统生物量对氮添加和增雨处理的响应随不同气候条件的变化

随着年均温升高, 氮添加对年均温较高的草地生态系统的地上生物量、总生物量及生物量向地上分配的促进作用显著增强($p < 0.001$; $p < 0.001$; $p < 0.01$, 图4A、4C、4D)。随着年降水量增加, 氮添加对降水量较高的草地生态系统的地上生物量、总生物量及生物量向地上分配的促进作用增强($p < 0.001$; $p < 0.001$; $p < 0.01$, 图5A、5C、5D)。

在年平均气温较高的草地生态系统中, 增雨处理对地下生物量、总生物量的促进作用显著低于年

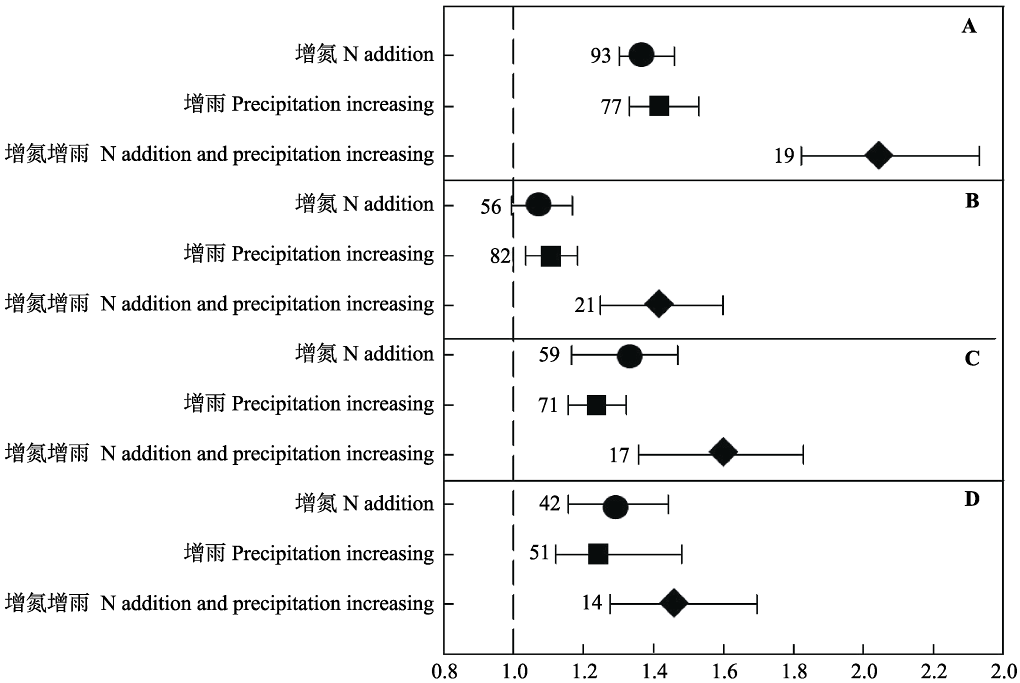

图2　氮添加处理(圆圈)、增雨处理(正方形)及同时增氮增雨处理(菱形)对地上生物量(AGB)(**A**)、地下生物量(BGB)(**B**)、总生物量(TB)(**C**)及地上地下生物量比(AGB/BGB)(**D**)的影响(平均值± 95%*CI*)。图中数字代表独立研究数量。

Fig. 2　Effects of N addition (in circle), precipitation increasing (in square) and N addition plus precipitation increasing (in rhombus) on aboveground biomass (AGB)(**A**), belowground biomass (BGB)(**B**), total biomass (TB)(**C**) and the ratio of aboveground biomass to belowground biomass (AGB/BGB)(**D**) (mean ± 95%*CI*). Numbers in the parentheses represent study number.

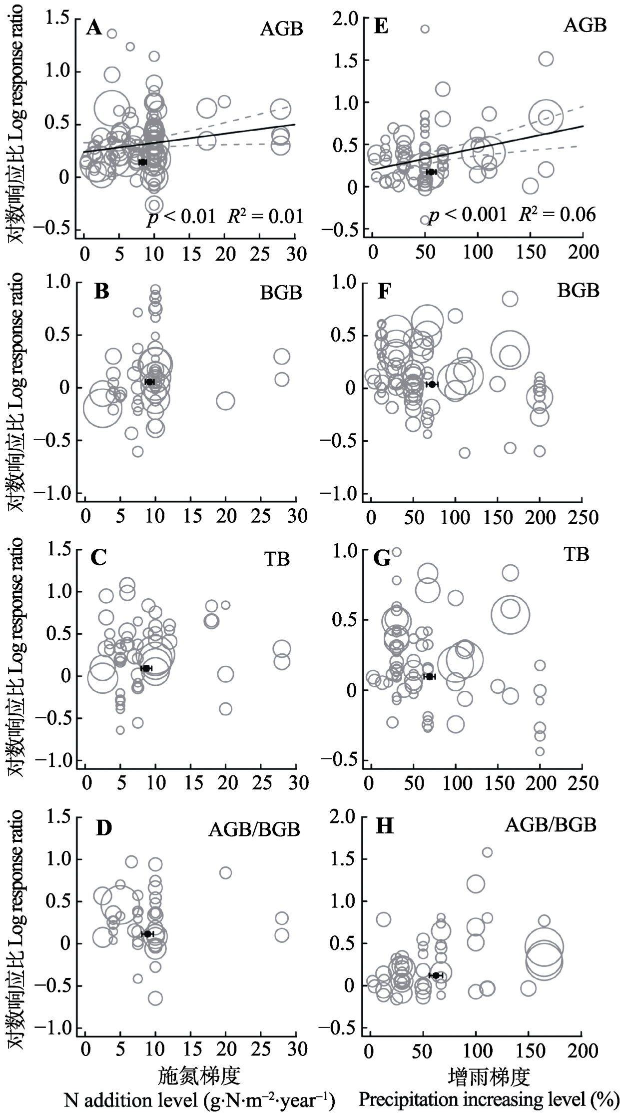

图3　整合回归结果显示地上生物量(AGB)(**A, E**)、地下生物量(BGB)(**B, F**)、总生物量(TB)(**C, G**)和地上地下生物量比(AGB/BGB)(**D, H**)沿处理梯度的变化。**A**–**D**代表氮添加, **E**–**H**代表增雨处理, 圆圈的大小代表响应比在随机效应meta回归中的权重。圆圈越大, 权重越大, 贡献度越高。黑色圆点纵坐标为响应比平均值±标准误差, 横坐标为处理梯度平均值±标准误差。

Fig. 3　Bubble plots of the meta-regression results between the response of aboveground biomass (AGB)(**A, E**), belowground biomass (BGB)(**B, F**), total biomass(TB)(**C, G**) and the ratio of aboveground biomass to belowground biomass (AGB/BGB)(**D, H**) to the treatment level of N addition and precipitation increasing. **A**–**D** represent the N addition treatment; **E**–**H** represent the precipitation increasing treatment. The size of the bubble is the relative weight of the effect size (response ratio, RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contribute a great overall weight in meta-regression. The *y*-direction error bars of the black dots represent the standard error of the means of response ratio; the *x*-direction error bars represent the standard error of treatment level under N addition and precipitation increasing.

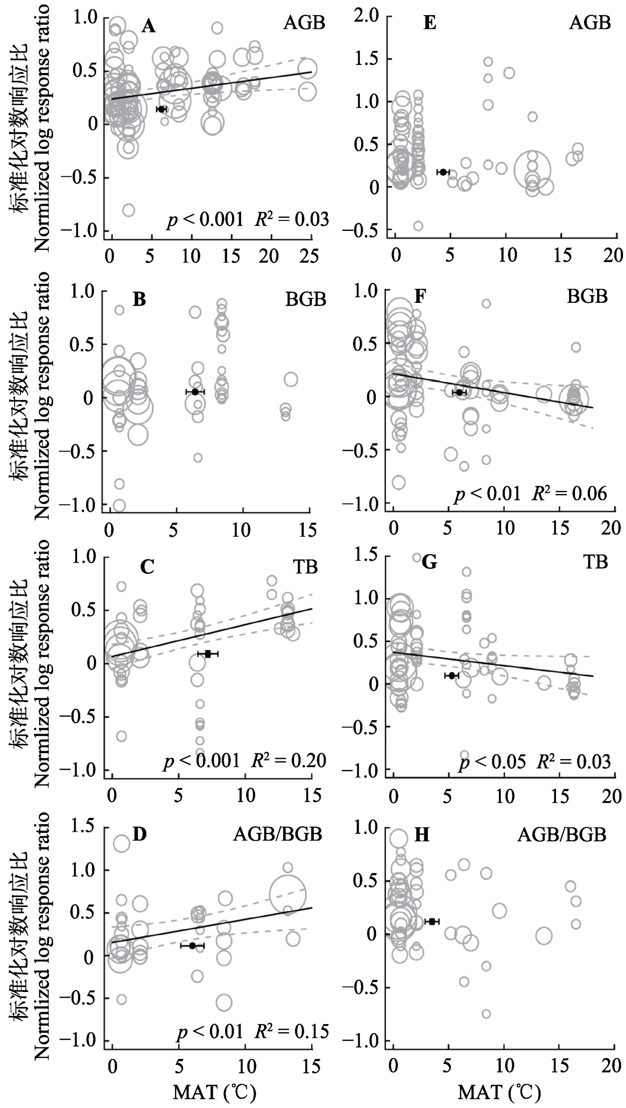

图4　整合回归结果显示随着实验站点年平均气温(MAT)升高, 地上生物量(AGB)(**A, E**)、地下生物量(BGB)(**B, F**)、总生物量(TB)(**C, G**)和地上地下生物量比(AGB/BGB)(**D, H**)在不同处理下的变化。**A**–**D**代表氮添加, **E**–**H**代表增雨处理, 圆圈的大小代表响应比在随机效应meta回归中的权重。圆圈越大, 权重越大, 贡献度越高。黑色圆点纵坐标为响应比平均值±标准误差, 横坐标为处理梯度平均值±标准误差。

Fig. 4　Bubble plots of the meta-regression results between the response of aboveground biomass (AGB)(**A, E**), belowground biomass (BGB)(**B, F**), total biomass (TB)(**C, G**) and the ratio of aboveground biomass to belowground biomass (AGB/BGB)(**D, H**) to the mean annual temperature (MAT) in the study sites. **A**–**D** represent the N addition treatment; **E**–**H** represent the precipitation increasing treatment. The size of the bubble is the relative weight of the effect size (response ratio, RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contribute a great overall weight in meta-regression. The *y*-direction error bars of the black dots represent the standard error of the means of response ratio; the *x*-direction error bars represent the standard error of the means of mean annual temperature (MAT).

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均温较低地区的草地生态系统(p < 0. 01; p < 0.05, 图4F、4G)。在年降水量较低的草地生态系统中, 增雨处理促进草地生态系统的地上、地下和总生物量。然而, 随着年降水量的增加, 增雨处理对生物量的促进作用逐渐减弱, 而抑制作用则逐渐增强, 且随年降水量越高抑制作用越强(p < 0.01; p < 0.01; p < 0.001, 图5E–5G)。

2.4 草地生态系统生物量对氮添加和增雨处理的响应随时间尺度的变化

随着处理年限的增加, 氮添加和增雨对地上生物量以及地上地下生物量分配比例的促进作用显著增强(p < 0.001; p < 0.001; p < 0.001; p < 0.05, 图6A、6E、6D、6H)。总生物量的增加仅在氮添加处理下有显著的增强趋势(p < 0.001, 图6C), 在增雨处理下没有明显的变化。早期施氮可以促进地下生物量, 但随施氮年限的增加, 地下生物量显著下降(p < 0.001, 图6B)。增雨处理下, 地下生物量随着处理年限的增加显著增加(p < 0.001, 图6H)。

3 讨论

3.1 氮添加和增雨处理及两者交互作用对草地生态系统生物量的影响

氮添加对草地生态系统生产力的促进作用存在阈值(Fang *et al*., 2012)。植物生长发育受到氮限制时, 一定量的氮添加能够促进植物叶片的抗衰老过程(韩炳宏等, 2016), 提高光合速率、增加植被高度和叶面积指数(韩会阁等, 2015); 而当氮冗余时, 可能引起土壤酸化、NH_4^+和Al^{3+}浓度增加, 对植物的生长产生毒害作用(Bobbink *et al*., 1998; Stevens *et al*., 2010), 抑制植物的生长发育, 从而降低植物生产力(Mack *et al*., 2004)。本研究结果中氮添加浓度达到30 g·m^{-2}·a^{-1}、增雨处理水平达到200%时, 地上生物量的促进作用仍有显著的增加趋势(图3A、3E), 说明草地生态系统的植物群落组成可能发生改变, 向着适应高氮高降雨的环境方向发展。因此, 生物量在高氮高降雨下仍有响应, 尚未达到阈值。

随氮添加浓度提高, 草地地下、总生物量及地上地下分配比例没有明显的增加趋势(图3B–3D)。一般而言, 氮添加会增加地上生物量, 导致群落透光率降低, 植物对养分的竞争转变为对光的竞争, 加剧物种间的竞争排斥效应, 容易造成低矮植被的丢失(Tilman, 1985; Gough *et al*., 2000)。植被的改变会进一步影响地上和地下生物量的分配, 从而表现为其生产力增加趋势不明显。此外, 沿增雨处理梯度的提高, 地下、总生物量及地上地下分配比例也

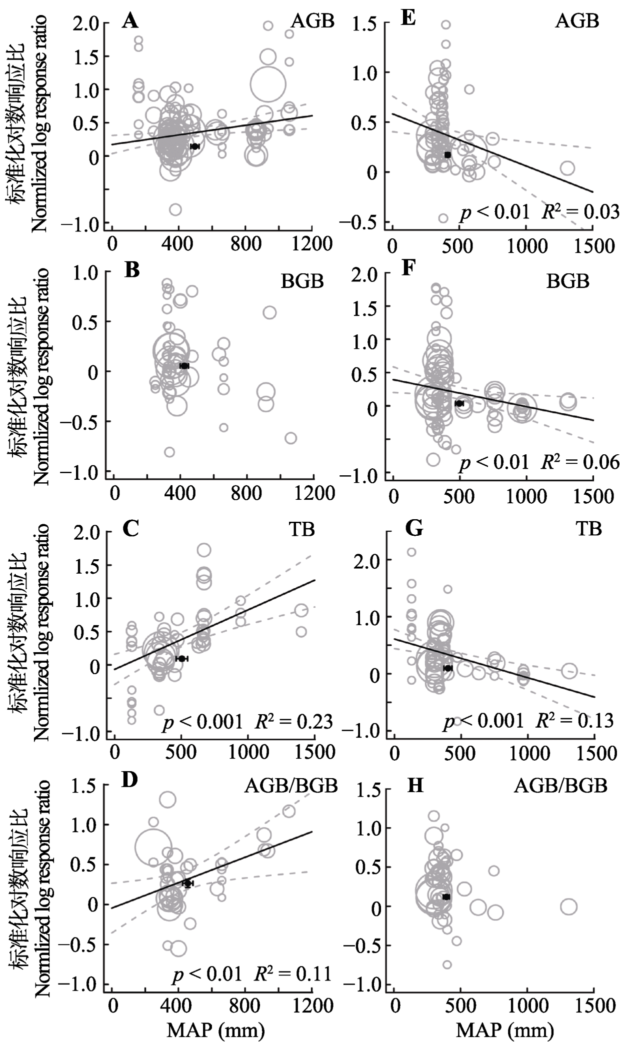

图5 整合回归结果显示随着实验站点年降水量(MAP)增加, 地上生物量(AGB)(**A, E**)、地下生物量(BGB)(**B, F**)、总生物量(TB)(**C, G**)和地上地下生物量比(AGB/BGB)(**D, H**)在不同处理下的变化。**A**–**D**代表氮添加, **E**–**H**代表增雨处理, 圆圈的大小代表响应比在随机效应meta回归中的权重。圆圈越大, 权重越大, 贡献度越高。黑色圆点纵坐标为响应比平均值±标准误差, 横坐标为处理梯度平均值±标准误差。

Fig. 5 Bubble plots of the meta-regression results between the response of aboveground biomass (AGB)(**A, E**), belowground biomass (BGB)(**B, F**), total biomass(TB)(**C, G**) and the ratio of aboveground biomass to belowground biomass (AGB/BGB)(**D, H**) to the mean annual precipitation (MAP) in the study sites. **A**–**D** represent the N addition treatment; **E**–**H** represent the precipitation increasing treatment. The size of the bubble is the relative weight of the effect size (response ratio, RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contribute a great overall weight in meta-regression. The *y*-direction error bars of the black dots represent the standard error of the means of response ratio; the *x*-direction error bars represent the standard error of the means of mean annual precipitation (MAP).

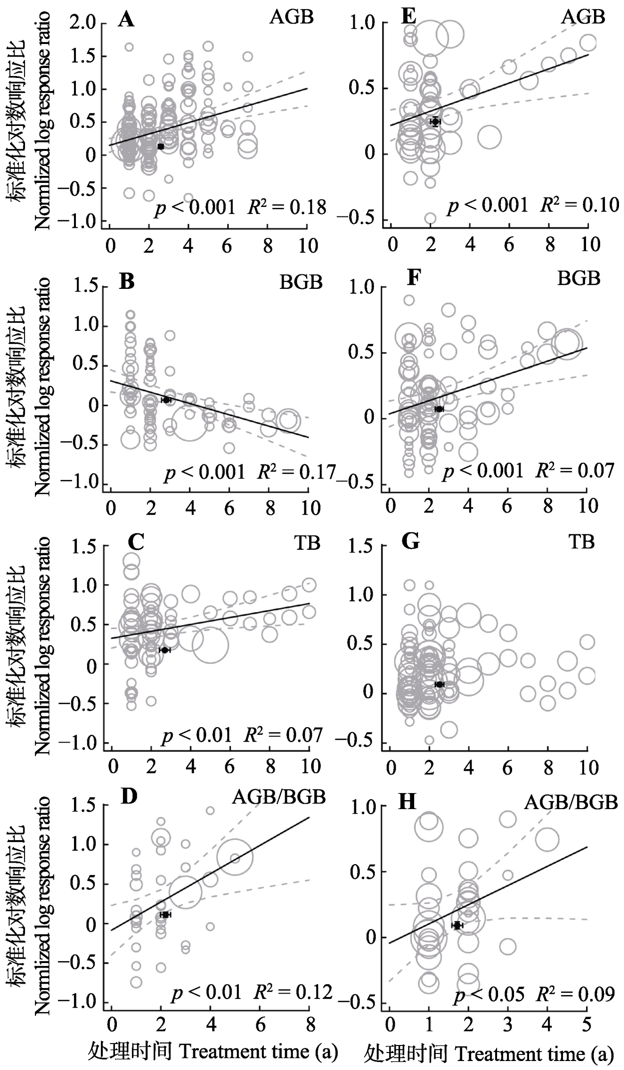

图6　整合回归结果显示随处理年限增加, 地上生物量(AGB)(**A, E**)、地下生物量(BGB)(**B, F**)、总生物量(TB)(**C, G**)和地上地下生物量比(AGB/BGB)(**D, H**)在不同处理下的变化。**A**–**D**代表氮添加, **E**–**H**代表增雨处理, 圆圈的大小代表响应比在随机效应meta回归中的权重。圆圈越大, 权重越大, 贡献度高。黑色圆点纵坐标为响应比平均值±标准误差, 横坐标为处理梯度平均值±标准误差。

Fig. 6　Bubble plots of the meta-regression results between the response of aboveground biomass (AGB)(**A, E**), belowground biomass (BGB)(**B, F**), total biomass(TB)(**C, G**)and the ratio of aboveground biomass to belowground biomass (AGB/BGB)(**D, H**) to the study year. **A**–**D** represent the N addition treatment; **E**–**H** represent the precipitation increase treatment. The size of the bubble is the relative weight of the effect size (response ratio, RR) in the random-effects meta- regression. Larger bubbles indicate study outcomes that contribute a great overall weight in meta-regression. The *y*-direction error bars of the black dots represent the standard error of the means of response ratio; the *x*-direction error bars represent the standard error of the means of treatment time (a).

没有明显的增加趋势(图3F–3H)。尽管生长季后期降水量减少、土壤含水量下降, 多年生植物通过利用土壤深层水累积地上、地下生物量, 减少次年春季一年生植物可利用的水分(Corbin & D’Antonio, 2004)。但5 mm的有效降水量就能满足一年生植物基本完成生活史, 且一年生小禾草类植物能够根据降水量变化及时调整物候长短以适应生长(闫建成等, 2013)。因此, 有研究表明增雨能通过增强一年生植物的光竞争能力, 减少多年生植物的生物量(毛伟等, 2014)。此外, 降雨量增加能够提高土壤有效水分, 促进光合作用(Thomey *et al*., 2011), 但也会影响土壤中的其他因素, 如促进土壤氮矿化, 从而提高土壤无机氮含量(Burke *et al*., 1997)。土壤无机氮含量的增加会减少植被对地下生物量的分配(陈骥等, 2013), 同时, 水分增加还会限制根系呼吸, 从而抑制根系的生长, 导致地下生物量降低(Dukes *et al*., 2005)。

氮添加的同时进行增雨处理显著增加地下生物量, 而且效果显著高于单独增雨(42%, 10%, 图 2B), 说明水分和土壤氮含量对草地生态系统生产力的影响存在交互作用(Bell *et al*., 2008; Brueck *et al*., 2010; Li *et al*., 2011)。在环境较为干旱时, 养分的迁移和传输均受到限制, 随着降雨量的增加, 土壤中养分限制得以解除, 从而提高养分的可利用性, 促进植物对养分的吸收利用, 最终提高生态系统生产力(Li *et al*., 2011), 因此氮水的交互作用往往呈协同效应(Niu *et al*., 2009)。

3.2　草地生态系统生物量对氮添加和增雨处理的响应在不同气候变化尺度下的格局

较大区域尺度上, 温度、降水等环境因子是影响植物生产力的关键气候因素(Fang *et al*., 2001; Swemmer & Knapp, 2008; Yang *et al*., 2008)。在氮添加处理下, 温暖性气候区的草地生态系统的地上生物量、总生物量及生物量向地上分配的促进作用较高(图4A、4C、4D), 这可能是由于从温暖性气候区到寒冷性气候区, 年均温逐渐降低, 植被生长季明显缩短(陈智等, 2014), 导致生产力受到的促进作用降低。除了温度的调控作用之外, 不同气候区的陆地生态系统也同时受到水分状况的影响, 无论是热带、亚热带还是温带区域内, 在其相对湿润的气候区具有更高的生产力(陈智等, 2014)。本研究的整合结果也支持该观点, 即在海洋性气候区的草地生态系统中, 施氮处理对地上生物量、总生物量及生物量向地上分配的促进作用显著高于温带大陆性气候

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区的草地生态系统(图5A、5C、5D)。

在增雨处理下, 寒冷性气候区的草地生态系统的地下生物量、总生物量受到的促进作用显著高于温暖性气候区的草地生态系统(图4F、4G)。一般而言, 低温条件下, 草地生态系统土壤碳矿化速率较低(黄文华等, 2014)、微生物活性较弱, 会受到更多的氮限制(Fay *et al*., 2015)。增雨使土壤中可利用性氮增加(Burke *et al*., 1997), 从而缓解草地生态系统由低温引发的氮限制, 且研究发现寒冷性气候区的植物生物量比温暖性气候区的植物生物量对氮添加的响应更为敏感(Xia & Wan, 2008)。因此, 相比于荒漠草地、典型草地和温带湿润草地, 冻原和高山草地等受温度限制的草地生态系统增雨后生物量增加更为明显。未来在高纬度、赤道太平洋附近及中纬度的湿润气候区中年降水量呈增加趋势, 而大部分中纬度和亚热带干旱气候区的年降水量将进一步减少(Stocker *et al*., 2013), 这种区域性的降水量改变将使优势物种的分布区域向高海拔偏移(Kelly & Goulden, 2008), 可能进一步促进寒冷性气候区草地生态系统生产力。

3.3 草地生态系统生物量对氮添加和增雨处理的响应在时间尺度上的格局

长期氮添加处理对地下生物量的促进作用在处理后期转为抑制作用(图6B), 这表明草地生态系统可能发生物种组成的改变(Clark & Tilman, 2008), 植被由深根系向浅根系物种发生转变。长期增雨处理下地上、地下生产量的促进作用都有增加的趋势(图6E、6F), 可能是在水分条件充足时, 植物个体生长得到促进, 地上生物量持续累积, 根系生物量随着个体植株的增大也得到促进(Li *et al*., 2011)。一般认为, 降水变化对植物地上初级生产力的影响具有累积效应, 群落地上初级生产力与年降水量在空间尺度上呈线性相关关系, 在时间尺度上呈二次曲线关系(王玉辉和周广胜, 2004)。然而, 总生物量的促进作用(图6G)在长期增雨处理下没有显著变化, 说明长期的水分添加可能引起淋溶(Zhu *et al*., 2016), 使得土壤中氮流失。因此, 生产力长期持续的增加需要外源营养元素添加(Ren *et al*., 2017)。长期氮、水分的添加有利于改善草地生态系统的养分条件, 促进植物迅速生长, 加快养分周转, 进而有利于竞争得到更多的养分。但是在养分贫瘠时, 植物生长较慢, 滞留吸收养分的能力较强, 反而可以防止养分损失或被其他竞争性植物吸收利用(Yuan *et al*., 2006)。

长期氮添加、增雨及同时增氮增雨三种处理下, 地上地下生物量比都显著增加, 生物量更多地向地上分配(29%、25%、46%, 图2D), 且随着处理年限的增加, 比值也呈现逐渐增加的趋势(图6D、6H)。在短期时间尺度上, 地上生物量的持续增加有利于在农牧业活动中收获更多作物; 在长时间尺度上, 若缺乏相应合理的草地生态系统管理措施, 则可能因过度放牧、割草等活动打破其系统平衡, 对草地生态系统生物量造成负面影响。

参考文献

Adams DC, Gurevitch J, Rosenberg MS (1997). Resampling tests for meta-analysis of ecological data. *Ecology,* 78, 1277–1283.

Bai YF, Li LH, Huang JH, Chen ZZ (2001). The influence of plant diversity and functional composition on ecosystem stability of four *Stipa* communities in the Inner Mongolia Plateau. *Acta Botanica Sinica,* 43, 280–287.

Bai YF, Wu JG, Clark CM, Naeem S, Pan QM, Huang JH, Zhang LX, Han XG (2010). Tradeoffs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: Evidence from inner Mongolia grasslands. *Global Change Biology*, 16, 358–372.

Bai YF, Wu JG, Xing Q, Pan QM, Huang JH, Yang DL, Han XG (2008). Primary production and rain use efficiency across a precipitation gradient on the Mongolia Plateau. *Ecology*, 89, 2140–2153.

Bell C, McIntyre N, Cox S, Tissue D, Zak J (2008). Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert grassland. *Microbial Ecology*, 56, 153–167.

Bobbink R, Hornung M, Roelofs JG (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology,* 86, 717–738.

Brueck H, Erdle K, Gao Y, Giese M, Zhao Y, Peth S, Lin S (2010). Effects of N and water supply on water use-efficiency of a semiarid grassland in Inner Mongolia. *Plant and Soil*, 328, 495–505.

Burke IC, Lauenroth WK, Parton WJ (1997). Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology,* 78, 1330–1340.

Chen J, Cao JJ, Liu Y, Zhang BC, Wei YL, Ma ZT, Zhu BW (2013). Research progress and prospect of nitrogen fertilization on soil respiration. *Grassland and Turf,* 33(6), 87–93. [陈骥, 曹军骥, 刘玉, 张宝成, 魏永林, 马宗泰, 朱宝文 (2013). 氮添加对土壤呼吸影响的研究进展. 草原与草坪, 33(6), 87–93.]

Chen Z, Yu GR, Zhu XJ, Wang QF (2014). Spatial pattern and regional characteristics of terrestrial ecosystem carbon fluxes in the northern hemisphere. *Quaternary Sciences*, 34, 710–722. [陈智, 于贵瑞, 朱先进, 王秋凤 (2014). 北半球陆地生态系统碳交换通量的空间格局及其区域特征. 第四纪研究, 34, 710–722.]

Cholaw B, Cubasch U, Yonghui L, Liren J (2003). The change of North China climate in transient simulations using the IPCC SRES A2 and B2 scenarios with a coupled atmosphere-ocean general circulation model. *Advances in Atmospheric Sciences*, 20, 755–766.

Clark CM, Tilman D (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 451, 712–715.

Corbin JD, D'Antonio CM (2004). Competition between native perennial and exotic annual grasses: Implications for an historical invasion. *Ecology*, 85, 1273–1283.

DeLucia EV, Drake JE, Thomas RB, Gonzaiez MI (2007). Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? *Global Change Biology*, 13, 1157–1167.

Dingkuhn M, Luquet D, Clément-Vidal A, Tambour L, Kim HK, Song YH (2007). Is plant growth driven by sink regulation? Implications for crop models, phenotyping approaches and ideotypes. *Frontis*, 155–168.

Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, Thayer S, Field CB (2005). Responses of grassland production to single and multiple global environmental changes. *PLOS Biology*, 3, e319. DOI: 10.1371/journal.pbio.0030319.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000). Climate extremes: Observations, modeling, and impacts. *Science*, 289, 2068–2074.

Fang JY, Yu SY, Wu PC, Huang YB, Tsai YH (2001). *In vitro* skin permeation of estradiol from various proniosome formulations. *International Journal of Pharmaceutics*, 215, 91–99.

Fang Y, Xun F, Bai WM, Zhang WH, Li LH (2012). Long-term nitrogen addition leads to loss of species richness due to litter accumulation and soil acidification in a temperate steppe. *PLOS ONE*, 7, e47369. DOI: 10.1371/journal.pone.0047369.

Fay PA, Carlisle JD, Knapp AK, Blair JM, Collins SL (2000). Altering rainfall timing and quantity in a mesic grassland ecosystem: Design and performance of rainfall manipulation shelters. *Ecosystems*, 3, 308–319.

Fay PA, Prober SM, Harpole WS, Knops JM, Bakker JD, Borer ET, Adler PB (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, 1, 15080. DOI: 10.1038/nplants.2015.80.

Gao YZ, Chen Q, Lin S, Giese M, Brueck H (2011). Resource manipulation effects on net primary production, biomass allocation and rain-use efficiency of two semiarid grassland sites in Inner Mongolia, China. *Oecologia*, 165, 855–864.

Gough L, Shaver GR, Carroll J, Royer DL, Laundre JA (2000). Vascular plant species richness in Alaskan arctic tundra: The importance of soil pH. *Journal of Ecology*, 88, 54–66.

Goulden ML, McMillan AM, Winston GC, Rocha AV, Manies KL, Harden JW, Bond-Lamberty BP (2011). Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*, 17, 855–871.

Grechi I, Vivin PH, Hilbert G, Milin S, Robert T, Gaudillere JP (2007). Effect of light and nitrogen supply on internal C:N balance and control of root-to-shoot biomass allocation in grapevine. *Environmental and Experimental Botany*, 59, 139–149.

Han BH, Shang ZY, Yuan XB, An Z, Wen HY, Li JB, Fu H, Niu DC (2016). Effects of N addition on photosynthetic characteristic and leaf senescence in *Stipa bungeana* of steppe grasslands in the Loess Plateau. *Pratacultural Science*, 33, 1070–1076. [韩炳宏, 尚振艳, 袁晓波, 安卓, 文海燕, 李金博, 傅华, 牛得草 (2016). 氮添加对黄土高原典型草原长芒草光合特性的影响. 草业科学, 33, 1070–1076.]

Han HG, Shang ZY, Niu DC, Fu H (2015). Effect of nitrogen addition on the specific leaf area and important value of dominant species in the typical steppe of the Loess Plateau, China. *Acta Agrestia Sinica*, 23, 69–74. [韩会阁, 尚振艳, 牛得草, 傅华 (2015). 氮添加对黄土高原典型草原植物比叶面积及其重要值的影响. 草地学报, 23, 69–74.]

Harpole WS, Potts DL, Suding KN (2007). Ecosystem responses to water and nitrogen amendment in a California grassland. *Global Change Biology*, 13, 2341–2348.

Hayes DC, Seastedt TR (1987). Root dynamics of tallgrass prairie in wet and dry years. *Canadian Journal of Botany*, 65, 787–791.

He M, Dijkstra FA (2014). Drought effect on plant nitrogen and phosphorus: A meta-analysis. *New Phytologist*, 204, 924–931.

Hedges LV, Gurevitch J, Curtis PS (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005). Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters*, 8, 23–29.

Hooper DU, Johnson L (1999). Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry*, 46, 247–293.

Huang WH, Wang SY, Han B, Jiao ZJ, Han GD (2014). The research of grassland ecosystem response to simulated atmospheric warming. *Pratacultural Science*, 31, 2069–2076. [黄文华, 王树彦, 韩冰, 焦志军, 韩国栋 (2014). 草地生态系统对模拟大气增温的响应. 草业科学, 31, 2069–2076.]

DOI: 10.17521/cjpe.2018.0056

IPCC (2012). *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation. A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, UK. 582.

Kang MY, Dai C, Ji WY, Jiang Y, Yuan ZY, Chen HY (2013). Biomass and its allocation in relation to temperature, precipitation, and soil nutrients in Inner Mongolia grasslands, China. *PLOS ONE,* 8, e69561. DOI: 10.1371/journal.pone.0069561.

Kelly AE, Goulden ML (2008). Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America,* 105, 11823–11826.

Knapp AK, Briggs JM, Koelliker JK (2001). Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems,* 4, 19–28.

Koricheva J, Gurevitch J, Mengersen K (2013). *Handbook of Meta-analysis in Ecology and Evolution.* Princeton University Press, Princeton, USA.

Lauenroth WK, Sala OE (1992). Long-term forage production of North American shortgrass steppe. *Ecological Applications,* 2, 397–403.

LeBauer DS, Treseder KK (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology,* 89, 371–379.

Lee M, Manning P, Rist J, Power SA, Marsh C (2010). A global comparison of grassland biomass responses to CO_2 and nitrogen enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 365, 2047–2056.

Li JZ, Lin S, Taube F, Pan QM, Dittert K (2011). Above and belowground net primary productivity of grassland influenced by supplemental water and nitrogen in Inner Mongolia. *Plant and Soil,* 340, 253–264.

Li WJ, Liu HM, Zhao JN, Xiu WM, Zhang GL, Huangfu CH, Yang DL (2015). Effects of nitrogen and water addition on plant species diversity and biomass of common species in the *Stipa baicalensis* steppe, Inner Mongolia, China. *Acta Ecologica Sinica,* 35, 6460–6469. [李文娇, 刘红梅, 赵建宁, 修伟明, 张贵龙, 皇甫超河, 杨殿林 (2015). 氮和水分添加对贝加尔针茅草原植物多样性及生物量的影响. 生态学报, 35, 6460–6469.]

Liu LL, Wang X, Lajeunesse MJ, Miao G, Piao SL, Wan SQ, Deng MF (2016). A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. *Global Change Biology,* 22, 1394–1405.

Liu XJ, Zhang Y, Han WX, Tang AH, Shen JL, Cui ZL, Vitousek P, Erisman JW, Goulding K, Christie P, Fangmeier A, Zhang FS (2013). Enhanced nitrogen deposition over China. *Nature,* 494, 459–462.

Lu M, Zhou X, Yang Q, Li H, Luo YQ, Fang CM, Chen JK, Yang X, Li B (2013). Response of ecosystem carbon cycle to experimental warming: A meta-analysis. *Ecology,* 94, 726–738.

Lu TT, Zhai XJ, Liu XJ, Wang CJ (2014). Influence of short-term enclosure on characteristics of community and species diversity on meadow steppe. *Chinese Journal of Grassland,* 36(3), 57–60. [陆婷婷, 翟夏杰, 刘晓娟, 王成杰 (2014). 施肥, 灌溉及火烧对荒漠草原土壤养分和植物群落特征的影响. 中国草地学报, 36(3), 57–60.]

Mack MC, Schuur EA, Bret-Harte MS, Shaver GR, Chapin III FS (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature,* 431, 440–443.

Mao W, Li YL, Cui D, Zhao XY, Zhang TH, Li YQ (2014). Biomass allocation response of species with different life history strategies to nitrogen and water addition in sandy grassland in Inner Mongolia. *Chinese Journal of Plant Ecology,* 38, 125–133. [毛伟, 李玉霖, 崔夺, 赵学勇, 张铜会, 李玉强 (2014). 沙质草地不同生活史植物的生物量分配对氮和水分添加的响应. 植物生态学报, 38, 125–133.]

Neff JC, Townsend AR, Gleixner G, Lehman SJ, Turnbull J, Bowman WD (2002). Variable effects of nitrogen additions on the stability and turnover of soil carbon. *Nature,* 419, 915–917.

New M, Lister D, Hulme M, Makin I (2002). A high-resolution data set of surface climate over global land areas. *Climate Research,* 21, 1–25.

Niu SL, Yang HJ, Zhang Z, Wu MY, Lu Q, Li LH, Wan SQ (2009). Non-additive effects of water and nitrogen addition on ecosystem carbon exchange in a temperate steppe. *Ecosystems,* 12, 915–926.

Pan QM, Bai YF, Wu JG, Han XG (2011). Hierarchical plant responses and diversity loss after nitrogen addition: Testing three functionally-based hypotheses in the Inner Mongolia grassland. *PLOS ONE,* 6, e20078. DOI: 10.1371/journal.pone.0020078.

Ren HY, Xu ZW, Isbell F, Huang JH, Han XG, Wan SQ, Chen SP, Wang RZ, Zeng DH, Jiang Y, Fang YT (2017). Exacerbated nitrogen limitation ends transient stimulation of grassland productivity by increased precipitation. *Ecological Monographs,* 87, 457–469.

Rouphael Y, Cardarelli M, Schwarz D, Franken P, Colla G (2012). Effects of drought on nutrient uptake and assimilation in vegetable crops. In: Aroca R ed. *Plant Responses to Drought Stress.* Springer, Berlin. 171–195.

Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988). Primary production of the central grassland region of the United States. *Ecology,* 69, 40–45.

Stevens CJ, Thompson K, Grime JP, Long CJ, Gowing DJ (2010). Contribution of acidification and eutrophication to declines in species richness of calcifuge grasslands along a gradient of atmospheric nitrogen deposition. *Functional*

Ecology, 24, 478–484.

Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Midgley PM (2013). *Climate Change 2013: The Physical Science Basis.* Intergovernmental Panel on Climate Change, Working Group I Contribution to the IPCC Fifth Assessment Report (AR5). New York.

Sugiyama M, Shiogama H, Emori S (2010). Precipitation extreme changes exceeding moisture content increases in MIROC and IPCC climate models. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 571–575.

Swemmer AM, Knapp AK (2008). Defoliation synchronizes aboveground growth of co-occurring C_4 grass species. *Ecology*, 89, 2860–2867.

Thomey ML, Collins SL, Vargas R, Johnson JE, Brown RF, Natvig DO, Friggens MT (2011). Effect of precipitation variability on net primary production and soil respiration in a Chihuahuan Desert grassland. *Global Change Biology*, 17, 1505–1515.

Tilman D (1985). The resource-ratio hypothesis of plant succession. *The American Naturalist*, 125, 827–852.

Tilman D, Wedin D (1991). Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, 72, 685–700.

Viechtbauer W (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistic Software*, 36, 1–48.

Vitousek PM, Howarth RW (1991). Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, 13, 87–115.

Wang J, Liu LL, Wang X, Chen YW (2015). The interaction between abiotic photodegradation and microbial decomposition under ultraviolet radiation. *Global Change Biology*, 21, 2095–2104.

Wang KB, Li JP, Shangguan ZP (2012). Biomass components and environmental controls in Ningxia grasslands. *Journal of Integrative Agriculture*, 11, 2079–2087.

Wang YH, Zhou GS (2004). Response of temporal dynamics of aboveground net primary productivity of *Leymus chinensis* community to precipitation fluctuation in Inner Mongolia. *Acta Ecologica Sinica*, 24, 1140–1145. [王玉辉, 周广胜 (2004). 内蒙古羊草草原植物群落地上初级生产力时间动态对降水变化的响应. 生态学报, 24, 1140–1145.]

Waring RH, Landsberg JJ, Williams M (1998). Net primary production of forests: A constant fraction of gross primary production? *Tree Physiology*, 18, 129–134.

Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Pockman WT (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *AIBS Bulletin*, 53, 941–952.

Wrage N, Strodthoff J, Cuchillo HM, Isselstein J, Kayser M (2011). Phytodiversity of temperate permanent grasslands: Ecosystem services for agriculture and livestock management for diversity conservation. *Biodiversity and Conservation*, 20, 3317–3339.

Wu Z, Dijkstra P, Koch GW, Penuelas J, Hungate BA (2011). Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, 17, 927–942.

Xia JY, Wan SQ (2008). Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, 179, 428–439.

Yahdjian L, Gherardi L, Sala OE (2011). Nitrogen limitation in arid-subhumid ecosystems: A meta-analysis of fertilization studies. *Journal of Arid Environments*, 75, 675–680.

Yan JC, Liang CZ, Fu XY, Wang W, Wang LX, Jia CZ (2013). The responses of annual plant traits to rainfall variation in steppe and desert regions. *Pratacultural Science*, 22(1), 68–76. [闫建成, 梁存柱, 付晓瀌, 王炜, 王立新, 贾成朕 (2013). 草原与荒漠一年生植物性状对降水变化的响应. 草业学报, 22(1), 68–76.]

Yang YH, Fang JY, Ma WH, Wang W (2008). Relationship between variability in aboveground net primary production and precipitation in global grasslands. *Geophysical Research Letters*, 35(23), 46–63.

Yuan ZY, Li LH, Han XG, Chen SP, Wang ZW, Chen QS, Bai WM (2006). Nitrogen response efficiency increased monotonically with decreasing soil resource availability: A case study from a semiarid grassland in northern China. *Oecologia*, 148, 564–572.

Zhou X, Talley M, Luo YQ (2009). Biomass, litter, and soil respiration along a precipitation gradient in southern Great Plains, USA. *Ecosystems*, 12, 1369–1380.

Zhu K, Chiariello NR, Tobeck T, Fukami T, Field CB (2016). Nonlinear, interacting responses to climate limit grassland production under global change. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 10589–10594.

责任编委: 吕晓涛　责任编辑: 李　敏

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