



凋落物输入变化和氮添加对半干旱草原群落生产力及功能群组成的影响

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摘 要 不同的草原利用方式(围封、放牧和割草等)随着大气氮沉降的不断加剧, 改变了凋落物输入量。凋落物作为连接地上-地下碳循环过程的关键环节, 对草原生态系统生产力和碳循环过程影响显著。氮是草原生产力的主要限制因子, 凋落物输入量的变化对草原生态系统结构和功能的影响仍缺乏长期实验证据支持。该研究在内蒙古半干旱典型草原建立一个凋落物输入变化和氮添加控制实验平台, 通过连续6年对群落生产力和功能群组成的监测, 研究了凋落物添加与去除和氮添加对半干旱草原群落生产力和功能群组成的影响。研究发现: 1)凋落物输入量增加和氮添加均显著提高了群落生产力, 在对照和氮添加处理下, 凋落物去除处理导致生产力分别降低了8.4%和7.6%, 而凋落物添加处理使生产力分别提高了10.7%和6.3%; 2)不同植物功能群对凋落物输入变化和氮添加的响应存在差异, 导致群落功能群结构发生变化。随着凋落物输入量增加和氮添加, 群落优势功能群多年生禾草(包括多年生丛生禾草和多年生根茎禾草)的生物量显著提高, 对群落生产力的贡献增加, 在群落中的优势地位增强; 而另一优势功能群多年生杂类草生物量对凋落物和氮添加处理均无显著响应, 进而导致在氮添加处理下其对群落生物量的贡献比例显著降低; 3)凋落物输入主要改善土壤水分状况, 而氮添加则主要通过提高土壤养分含量, 促进群落生产力, 并通过影响主要功能群生物量, 导致群落结构发生变化。以上结果表明, 适当的草原管理方式如围封禁牧和降低放牧强度等都能通过增加凋落物的输入来提高草原生产力, 维持生态系统稳定性。而适量的氮等养分添加管理也有助于提高草原生产力, 促进其恢复。

关键词 地上净初级生产力; 植物功能群; 凋落物输入变化; 氮添加; 半干旱草原

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Effect of altered litter input and nitrogen addition on ecosystem aboveground primary productivity and plant functional group composition in a semiarid grassland

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Abstract

Aims Litter is the major input source of soil organic carbon and nutrients in natural ecosystems and considered as a key link between above- and belowground carbon cycles. Changes in litter input amount have been proven to exert significant impacts on plant productivity, community structure, and therefore ecosystem function. In Nei Mongol semiarid grasslands, different grassland management practices such as grazing, clipping, and fencing have caused dramatic changes in litter production and input. In addition, as a nitrogen-limited ecosystem, Nei Mongol semiarid grasslands also experienced increasing nitrogen deposition. However, how do changes in litter input and nitrogen addition impact the community productivity and composition of plant functional groups are still unclear in the semiarid grasslands. In this study, our objectives are: 1) to investigate the effects of altered litter

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input and nitrogen addition on community productivity; 2) to study the changes in aboveground biomass of different plant functional groups and their contribution to community productivity under different litter input and N addition treatments.

Methods We established a manipulative experiment with altered litter input and nitrogen addition treatments in a semiarid typical grassland in West Ujimqin Banner, Nei Mongol. A randomized block split-plot design was applied with five blocks. Three litter input treatments, including litter removal (C0), control (C1) and litter addition (C2), were assigned randomly in each block. Each plot (6 m × 7 m) of litter input treatment was separated into two subplots. One of the subplots was assigned as the N addition treatment (N1) and another subplot was considered as the control treatment without N addition (N0). In N addition treatment, 15 g N·m⁻²·a⁻¹ N fertilizer (as NH₄NO₃) was applied every year since 2013. Aboveground net primary productivity (ANPP) in community and plant functional group levels of each treatment were determined during the peak season from 2013 to 2018.

Important findings Based on 6-year measurements, we found the following results. 1) Litter input increase and nitrogen addition increased community ANPP. Compared with the control, litter removal treatment significantly decreased ANPP by 8.4% and 7.6% in plots without and with N addition, respectively. Litter addition increased ANPP by 10.7% and 6.3% in plots without and with N addition, respectively. 2) Different responses of plant functional groups to altered litter input and N addition led to a change in plant functional group composition. The biomass of perennial bunch grass (PB) and perennial rhizome grass (PR) increased significantly with the increment of litter and nitrogen, which enhanced their dominant status in the community. 3) Improved soil water condition by litter input and nutrient supply by N addition are the major pathways that enhanced ANPP and changed the functional group composition. These results show that proper management, such as grazing exclusion and reducing grazing intensity, can promote productivity by increasing inputs of litter in semiarid grasslands, which leads to the maintenance of ecosystem stability. Suitable nutrients management, like nitrogen addition, is also helpful for productivity improvement and the recovery of degraded grasslands.

Key words aboveground net primary productivity (ANPP); plant functional group; altered litter input; nitrogen addition; semiarid grassland

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凋落物是陆地生态系统重要碳库之一, 其分解过程作为重要养分释放的途径, 连接着地上地下碳循环过程(Facelli & Pickett, 1991b; Sayer *et al.*, 2011; Wang *et al.*, 2011)。人类活动和土地利用方式的改变正在显著影响着凋落物的产生及其向土壤的输入(Xu *et al.*, 2013a; Fang *et al.*, 2018)。凋落物数量及其分解速度会直接影响植物和土壤微生物吸收利用养分的过程, 并进一步调控生态系统结构和功能(Wardle *et al.*, 2004; Zhang *et al.*, 2018a)。目前有关凋落物输入变化对群落生产力影响的研究已有很多(Lamb, 2008; Ruprecht *et al.*, 2010), 并得到了普遍的共识, 即凋落物输入量增加能够提高植被生产力(Patrick *et al.*, 2008; Deutsch *et al.*, 2010b; Wang *et al.*, 2011; Kelemen *et al.*, 2013), 而去除凋落物会导致群落生产力的下降(Wikeem *et al.*, 1989; Xu *et al.*, 2013b)。凋落物输入量变化主要通过以下途径影响群落生产力: 首先, 作为土壤养分的重要来源, 凋

落物输入量的变化会改变土壤养分的可利用性, 并直接影响植物的生长。如凋落物输入量增加会显著提高土壤可溶性碳氮含量(Brearley *et al.*, 2003; Bansal *et al.*, 2014; Wang *et al.*, 2017a), 但对土壤有机碳库的影响通常是不显著的(Varga *et al.*, 2008)。第二, 凋落物输入量变化通过改变底物供给状况影响土壤微生物活性和群落组成, 从而影响凋落物分解和养分释放速率(Yarwood *et al.*, 2013; Kohmann *et al.*, 2019)。第三, 作为植被和大气间的缓冲层, 覆盖地表的凋落物层会造成地表光、热和水等资源的重新分配, 影响土壤和植物群落微环境, 如凋落物层通过减少地表日间接收到的光辐射和夜间的热量散失来维持土壤相对稳定的温度状态(Facelli & Pickett, 1991a), 也可以通过减少蒸发来提高土壤含水量(Deutsch *et al.*, 2010b), 进而间接影响植物生长和群落结构(Facelli & Pickett, 1991a, 1991b; Jensen & Gutschkunst, 2003)。

近年来,凋落物输入变化对生态系统结构功能的影响更多聚焦在植被生产力、土壤微生物介导的养分循环过程和土壤碳库稳定性的变化上(Xu *et al.*, 2013a),而对于凋落物输入变化对群落结构影响的报道比较有限(王静, 2011; 蒋红志, 2018)。凋落物对群落结构的影响则主要通过其对不同植物功能群的影响差异来实现,如Facelli和Pickett (1991b)发现凋落物输入增加会抑制草本植物的生长,其中既发现对外来种生长建群的抑制(Patrick *et al.*, 2008),也有对原生种生长的抑制,这主要与凋落物类型有关(Facelli & Pickett, 1991b; Foster & Gross, 1998; Amatangelo *et al.*, 2008; Letts *et al.*, 2015)。此外,凋落物的累积能通过防止种子进入土壤层而对种子补充过程形成抑制,也会通过化感作用抑制种子萌发,累积的凋落物也能通过降低物种丰富度和均匀度来改变群落的物种组成(Foster & Gross, 1998; Amatangelo *et al.*, 2008; Letts *et al.*, 2015)。

在大多数陆地生态系统中,氮是植物生长的主要限制因子(Vitousek & Howarth, 1991; LeBauer & Treseder, 2008; Xia & Wan, 2008; Lu *et al.*, 2011; Ågren *et al.*, 2012; Gao *et al.*, 2019)。大量研究表明氮添加会提高植物群落生产力,但群落植物物种多样性却显著降低(Stevens *et al.*, 2004; Suding *et al.*, 2005; Clark & Tilman, 2008; Isbell *et al.*, 2013)。由于植物对氮、磷等养分元素的重吸收作用,凋落物中的碳氮比相对较高(Deng *et al.*, 2018)。日益加剧的大气氮沉降,会提高环境中活性氮的含量(Gruber & Galloway, 2008)。这一方面降低了凋落物中碳氮比,另一方面缓解了微生物的营养限制,促进微生物活性,进而加速凋落物的分解(Austin & Vivanco, 2006; Yue *et al.*, 2016; Wang *et al.*, 2017b),改善了环境中的养分状况(Manning *et al.*, 2008; Zhang *et al.*, 2018a)。那么,凋落物和氮两者共同作用会对生态系统生产力和群落结构产生怎样的影响呢?目前还缺乏长期的实验研究。

我国天然草地面积约4亿 hm^2 ,是我国面积最大的陆地植被类型,其中北方温带草原所占比例最大(陈佐忠和汪诗平, 2000; Piao *et al.*, 2009; Fang *et al.*, 2010)。由于不合理的开发利用和气候变化,全国90%的天然草地存在不同程度的退化(白永飞等, 2016)。为了治理草原退化,国家从2003年开始通过

一系列管理措施,改善了草原生态环境(张英俊等, 2013)。与放牧和打草等传统草原利用方式相比,围封禁牧可以使退化草原植被得到迅速恢复,因而作为最经济有效的草地恢复方式得到推广(Wu *et al.*, 2009; Jing *et al.*, 2013)。但也有研究发现长期围封所造成的凋落物大量累积反而会抑制生产力(Rice & Parenti, 1978; Knapp & Seastedt, 1986)。

在同时考虑凋落物输入变化与氮添加对草原生态系统生产力和组成影响的研究中,大部分只考虑凋落物移除或者添加,缺乏凋落物同时添加剔除并添加氮的长期控制实验研究,从而限制了我们对于氮沉降背景下不同草原管理方式对草原生产力、群落结构方面影响的理解。鉴于此,本研究在内蒙古半干旱典型草原建立了一个凋落物输入变化和氮添加控制实验平台,通过连续6年对群落生产力和组成的连续监测,研究了凋落物添加和去除以及氮添加对半干旱草原群落生产力和功能群组成的影响。

1 材料和方法

1.1 研究区概况

本研究区域位于内蒙古自治区锡林郭勒盟西乌珠穆沁旗, 117.58° E, 44.37° N, 海拔1 148 m, 属典型温带半干旱大陆性气候(陈佐忠和汪诗平, 2000)。根据当地气象站长期气象数据(1955–2011年),本区域年平均气温为1.5 °C,年降水量333 mm,大部分降水(超过87%)发生在生长季(5–9月)。降水量年际间波动剧烈,年降水量最多和最少分别能达到508和118 mm。本区域典型植被类型为温带半干旱草原,以多年生禾草和多年生杂类草为优势植物,放牧和打草是本区域最普遍的草原利用方式。土壤类型为栗钙土,表层土壤(0–10 cm)有机碳含量(14.2 ± 0.4) $\text{g} \cdot \text{kg}^{-1}$,氮含量(1.8 ± 0.1) $\text{g} \cdot \text{kg}^{-1}$, pH为 7.7 ± 0.5 (王珊珊, 2016; Zhang *et al.*, 2017)。

1.2 凋落物输入变化实验平台的建立与处理设置

本研究选择该区域的典型温带半干旱草原作为研究样地,主要优势物种包括大针茅(*Stipa grandis*)、羊草(*Leymus chinensis*)和知母(*Anemarrhena asphodeloides*)等。为减少干扰,自2011年起对样地(100 m \times 100 m)进行围封。围封前,该样地主要作为打草场,每年8月初打草一次。实验平台设立了3个凋落物输入变化处理(包括凋落物去除(C0)、对照

(C1)和凋落物添加(C2))和2个氮添加处理(包括氮添加(N1)和无氮添加(N0)), 共计6个实验处理(C0N0、C0N1、C1N0、C1N1、C2N0和C2N1)。采取随机区组裂区实验设计, 设置5个区组(即5个重复), 每个区组设置3个小区, 小区大小为6 m × 7 m, 3个凋落物处理(C0、C1和C2)为主因素随机分布在每个区组内。将每个凋落物处理小区一分为二, 中间设置0.4 m的过道间隔, 分别进行两种氮处理(N0和N1)。其中N1的氮添加量为15 g·m⁻²·a⁻¹, 以NH₄NO₃的形式每年分两次(5–7月)均匀加入处理小区中。

实验平台建立于2012年, 并于当年进行了凋落物处理。凋落物处理在每年植物完全枯黄(10月底)后进行, 具体处理方法如下: C0采用刈割法(留茬5 cm)将小区内的植物剪除并移出; C2是将同一区组内凋落物去除小区(包括氮添加和无氮添加处理)中所收集的凋落物均匀添加到相应的小区中; 为排除刈割影响, C1小区中的全部植物也同时进行刈割, 并保留在原地。处理后至次年4月, 每个小区用孔径大小为5 cm的尼龙网覆盖, 以防凋落物被吹走。根据当年植物生物量的差异, 每年添加的凋落物量是不同的。2012–2017年凋落物添加处理小区中的凋落物量添加范围是101–433 g·m⁻², 除了2012年外, 与无氮添加的凋落物倍增处理相比, 氮添加处理样方中添加的凋落物增加了25.6%–66.7% (表1)。

1.3 样品采集与指标测定

1.3.1 环境指标测定

实验期间, 实验样地的降水量和大气温度等气象指标由设置在样地附近的自动气象站进行观测。

2013–2018年生长季, 测定每个处理小区表层(0–10 cm)土壤温度和土壤含水量, 每2周测定1次。土壤温度和土壤含水量分别使用LI-8100土壤呼吸测量系统配备的土壤热电偶探头(LI-COR, Lincoln, USA)和便携式TDR-300土壤水分仪(Spectrum Technologies, Plainfield, USA)进行测定。

表1 2013–2018年凋落物添加处理中每年的凋落物添加量(g·m⁻²)
Table 1 Annual litter addition amount of litter addition treatment in 2013–2018 (g·m⁻²)

处理 Treatment	2013	2014	2015	2016	2017	2018
N0	433 ± 13	199 ± 24	203 ± 26	135 ± 38	101 ± 8	129 ± 16
N1	433 ± 13	250 ± 23	291 ± 50	225 ± 47	158 ± 10	190 ± 17

表中数据为平均值±标准误差(n = 5)。N0, 无氮添加对照; N1, 氮添加处理。

Data in the table are mean ± SE (n = 5). N0, nitrogen-free control; N1, nitrogen addition.

2015、2017和2018年8月, 在每个处理小区内用土钻采集0–10 cm新鲜土壤样品, 过2 mm筛后, 取10 g土样, 加50 mL纯净水振荡1 h, 静置过滤后的滤液冷冻保存用于土壤可溶性碳氮含量的测定(Jones & Willett, 2006)。土壤可溶性有机碳(DOC)含量和可溶性有机氮(DON)含量使用N/C 3100 TOC/TN分析仪(Aanalytik Jena AG, Jena, Germany)进行测定。

1.3.2 植被物种组成和地上净初级生产力

2013–2018年, 每年8月初, 采用样方法在每个处理小区内设置一个0.2 m × 1.0 m的样方, 记录样方内所有物种, 按物种剪取样方内植物地上部分, 并区分活体和往年凋落物。全部样品在烘箱内65 °C烘干48 h后称质量, 其中活体植物的干质量即为当年地上净初级生产力(ANPP)。

1.3.3 功能群划分

为了更好地研究物种组成的变化, 本研究按照物种的生活型将植物划分为5个不同功能群, 包括多年生丛生禾草(PB)、多年生根茎禾草(PR)、多年生杂类草(PF)、灌木与半灌木(SS)和一二年生植物(AB)(Bai *et al.*, 2004)。

1.4 数据分析

土壤的温度和含水量的季节平均值通过当年所有观测值的平均值计算表示。采用重复测量方差分析(RANOVA)检验凋落物输入变化、氮添加及其交互作用对所有响应变量(包括土壤环境、群落生产力和功能群生物量等)影响的显著性, 其中区组和年份作为随机因子。然后通过单因素方差分析和邓肯(Duncan)检验比较实验处理对变量影响的差异显著性。除ANPP与生长季降水间相关分析采用二次回归方程拟合外, 群落ANPP和功能群生物量与环境因子之间的相关分析采用线性混合效应模型(LMM), 为了消除处理年份的潜在影响, 在LMM相关分析时将年份作为随机因子进行考虑。使用结构方程模型(SEM)分析凋落物输入变化和氮添加影响ANPP和功能群组成的可能途径, 土壤可溶性有机物(DOM)含量由DOC和DON含量的第一主成分表示(解释度达0.88), 由于这个指标仅有3年数据, 所以模型使用数据也仅包含2015、2017和2018这3年。RANOVA分析在SPSS 24.0中进行, 其他数据分析均在R 3.6.2 (stats, lme4, piecewiseSEM)中实现。

2 结果

2.1 降水量与土壤微环境变化

除了实验处理开始当年(2012年)降水量达到406.3 mm, 为长期平均降水量的140%以上, 其余年份(2013–2018年)均接近或低于长期降水量平均值, 特别是2016和2017年, 其生长季降水量仅为224.1和226.1 mm, 相当于多年平均值的77%和78%, 是较为干旱的年份(图1)。

2013–2018年生长季土壤温度和土壤含水量表现出显著的年际变化(表2)。实验6年间土壤月平均温度逐渐升高, 土壤月含水量随降水量变化波动显著(图2A、2C)。多年平均值的统计分析表明, 无论

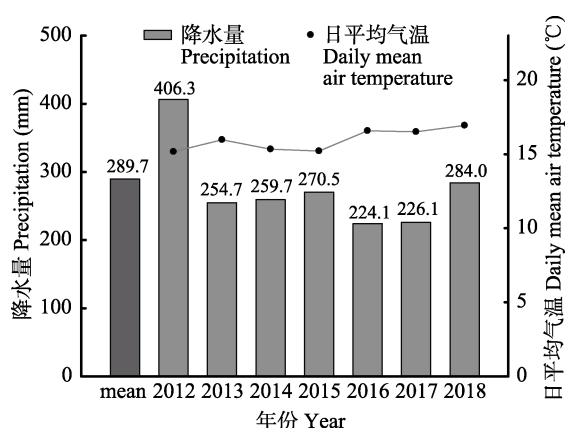


图1 长期平均(1955–2011年)和实验年份(2012–2018年)生长季(5–9月)降水量及日平均气温。

Fig. 1 Changes in growing season precipitation and daily mean air temperature during the studied period (2012–2018) and the longterm mean growing season precipitation during 1955–2011.

表2 凋落物输入变化(C)和氮添加(N)对土壤微环境影响的重复测量方差分析(RANOVA)结果

Table 2 Effects of altered litter input (C) and nitrogen addition (N) on soil microenvironment evaluated using repeated measures analysis of variance (RANOVA)

	df	DOC含量 DOC content	DON含量 DON content	df	Ts	SWC
区组 Block	4	0.86	0.39	4	15.61***	3.99*
凋落物管理 C	2	0.76	0.77	2	14.44***	10.49***
氮添加 N	1	28.13***	61.81***	1	10.52**	0.12
年 Year (Y)	2	20.14***	15.33***	5	780.49***	302.17***
C × N	2	0.06	0.36	2	0.09	0.52
C × Y	4	1.19	4.08**	10	1.89#	11.12***
N × Y	2	8.41**	5.18*	5	2.20#	8.42***
C × N × Y	4	0.48	3.18*	10	0.32	4.27***

#, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. DOC, 土壤可溶性有机碳; DON, 土壤可溶性有机氮; SWC, 土壤含水量; Ts, 土壤温度。

#, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. DOC, soil soluble organic carbon; DON, soil soluble organic nitrogen; SWC, soil water content; Ts, soil temperature.

有无氮添加处理, 凋落物输入变化均显著影响土壤温度, 表现出土壤温度随凋落物的添加而降低的结果(与对照相比, C2N0和C2N1分别降低3.3%和3.8%)(图2B)。同时, 凋落物去除降低了土壤含水量(C0N0降低7.9%), 而凋落物添加提高了土壤含水量(C2N1提高9.3%)(图2D)。并且发现氮添加显著降低了土壤温度, 对土壤含水量却没有显著影响(图2B、2D)。

表层土壤(0–10 cm) DOC和DON含量仅在2015、2017和2018年进行测定, 均表现出明显的年际变异(表2)。凋落物输入变化对DOC和DON含量没有显著影响, 而氮添加显著提高了表层土壤DOC和DON含量(图2E、2F、2G、2H)。没有发现凋落物输入变化和氮添加的交互作用对土壤环境条件的显著影响。

2.2 凋落物输入变化和氮添加对群落地上净初级生产力的影响

在进行实验处理的6年间, 群落ANPP表现出明显的年际波动, 特别是在2016和2017两个干旱年份, ANPP显著降低(图3)。对照样地(C1N0)的平均ANPP为 $183.3 \text{ g} \cdot \text{m}^{-2}$, 年际变化范围为 $113.6\text{--}231.4 \text{ g} \cdot \text{m}^{-2}$ 。单一年份的方差分析表明, 在2013年($p < 0.1$)和2016年($p < 0.05$)凋落物处理对ANPP有显著影响, 其余年份凋落物输入变化对群落ANPP没有显著影响($p > 0.1$, 图3A)。但综合6年结果的方差分析表明, 凋落物输入变化对ANPP有较显著影响, 表现为随着凋落物的添加, 群落ANPP随之提高(图3B)。在无氮添加和氮添加处理中, 与对照相比, 凋落物去除处理导致ANPP分别降低了8.4%和7.6%; 而凋落物添加处理使ANPP分别提高了10.7%和6.3%。

无论是单个年份还是多年总体分析结果均表明, 氮添加显著提高了ANPP (图3A、3B)。在凋落物去除、对照和凋落物添加处理下, 氮添加分别使群落ANPP提高了54.4%、53.1%和47.0%。凋落物输入变化与年份和氮添加处理间没有显著的交互作用, 而氮添加处理和年份之间的交互作用明显(表3)。

2.3 凋落物输入变化和氮添加对不同植物功能群地上生物量的影响

本研究样地植被是以多年生丛生禾草、多年生根茎禾草和多年生杂类草为主要功能群。以对照样地为例, 多年生丛生禾草、多年生根茎禾草和多年生杂类草分别贡献了群落地上生物量的32.1%、

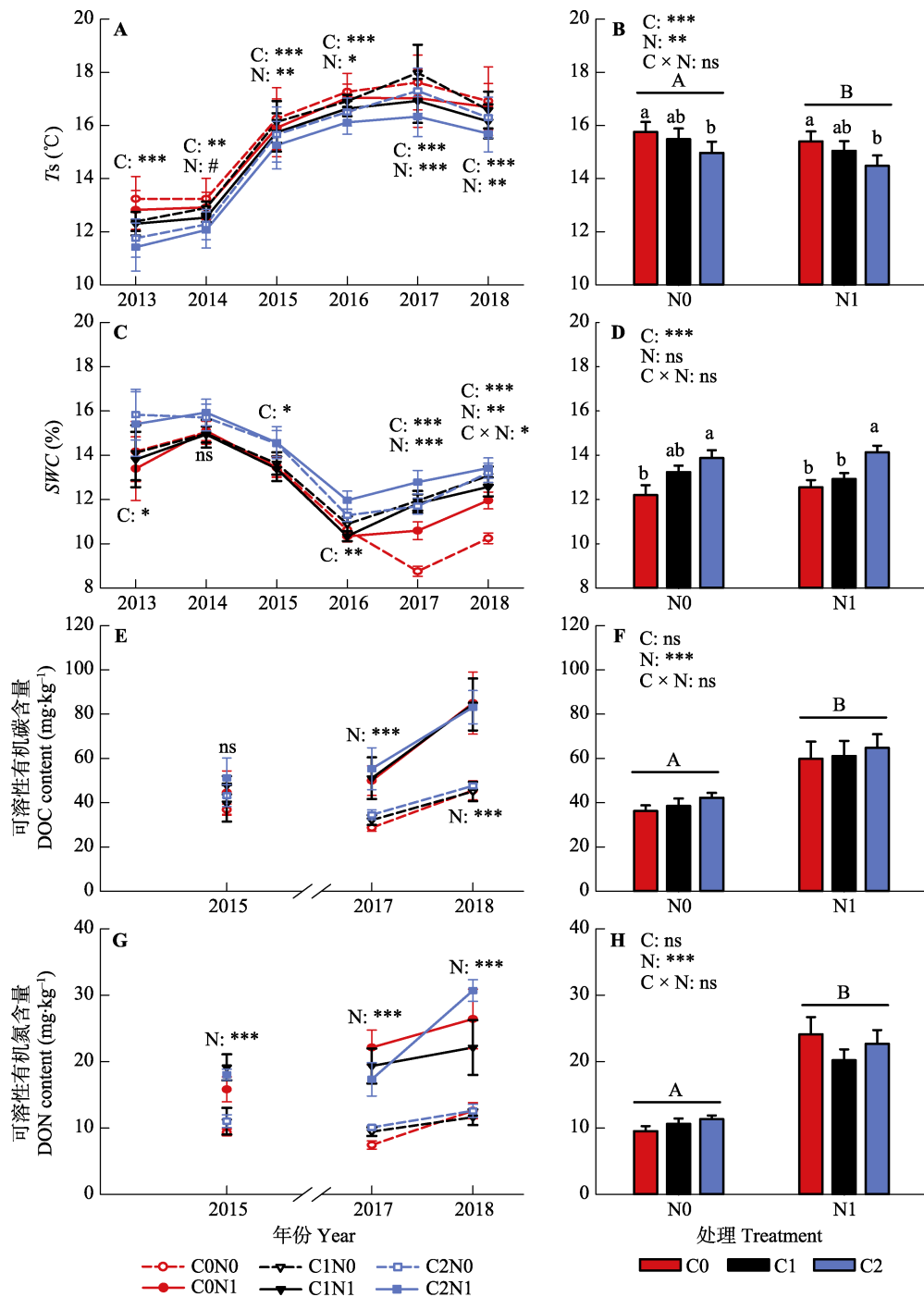


图2 2013–2018年不同凋落物输入变化和氮添加处理下, 表层(0–10 cm)土壤温度(T_s)、土壤含水量(SWC)和土壤可溶性有机碳氮(DOC和DON)含量的年际变异(A、C、E、G)和6年平均值(B、D、F、H)(平均值 \pm 标准误差)。图中给出了凋落物输入变化(C)和氮添加(N)对生产力影响的差异显著性分析结果(ns, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。柱状图中的字母表示不同凋落物输入变化和氮添加处理间各指标的多重比较结果, 不同小写字母表示不同凋落物输入变化处理间的差异显著($p < 0.05$), 不同大写字母代表不同氮添加处理间的差异显著($p < 0.05$)。C0, 凋落物去除; C1, 凋落物对照; C2, 凋落物添加; N0, 无氮添加; N1, 氮添加。

Fig. 2 Inter-annual variations (A, C, E, G) and the 6-year average (B, D, F, H) of soil temperature (T_s), soil water content (SWC), dissolved organic carbon (DOC) and nitrogen (DON) content in surface soil layer (0–10 cm) in different litter input and nitrogen addition treatments during 2013–2018 (mean \pm SE). Significance levels were presented to show the effects of altered litter input (C) and nitrogen addition (N) treatments and their interaction (C \times N) on these parameters (ns, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). The letters in the bar graph indicate the results of multiple comparisons among different litter input and nitrogen addition treatments. Different lowercase letters indicate significant difference among three altered litter input treatments ($p < 0.05$), and uppercase letters indicate the significant difference between two nitrogen treatments ($p < 0.05$). C0, litter removal; C1, control; C2, litter addition; N0, without nitrogen addition; N1, nitrogen addition.

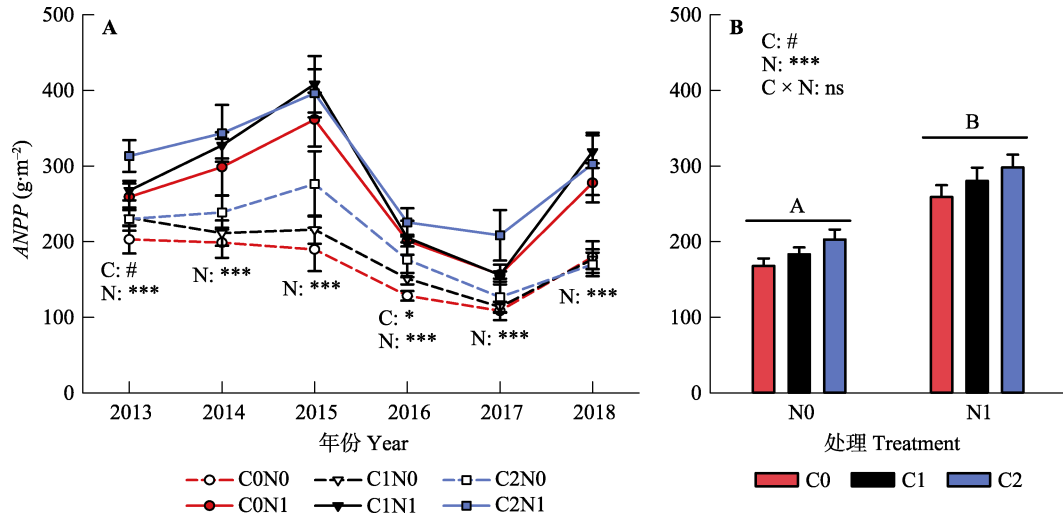


图3 2013–2018年不同凋落物输入变化和氮添加处理下, 群落地上净初级生产力(ANPP)的年际变异(A)和6年平均值(B)。图中数据均为平均值±标准误差。图中给出了凋落物输入变化(C)和氮添加(N)对生产力影响的差异显著性分析结果(ns, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。图中不同大写字母表示氮添加对生产力影响的差异显著($p < 0.05$)。C0, 凋落物去除; C1, 凋落物对照; C2, 凋落物添加; N0, 无氮添加; N1, 氮添加。

Fig. 3 Inter-annual variation (A) and the 6-year average (B) of aboveground net primary productivity (ANPP) in different litter input and nitrogen addition treatments during 2013–2018. The data in the figure are mean ± SE. Significance levels were presented to show the effects of altered litter input (C) and nitrogen addition (N) on ANPP (ns, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). Different uppercase letters in the bar graph indicate significant difference results of multiple comparisons between two nitrogen treatments ($p < 0.05$). C0, litter removal; C1, control; C2, litter addition; N0, without nitrogen addition; N1, nitrogen addition.

表3 凋落物输入变化(C)和氮添加(N)对群落地上净初级生产力(ANPP)及各功能群绝对和相对生物量影响的重复测量方差分析(RANOVA)结果

Table 3 Effects of altered litter input (C) and nitrogen addition (N) on community above-ground net primary productivity (ANPP) and absolute and relative biomass of each functional group evaluated using repeated measures analysis of variance (RANOVA)

	df	地上净初级生产力 ANPP	绝对生物量 Absolute biomass					相对生物量 Relative biomass				
			PB	PR	PF	SS	AB	PB%	PR%	PF%	SS%	AB%
区组Block	4	1.72	1.60	0.66	1.17	1.39	1.16	0.87	0.31	1.11	1.94	0.42
C	2	3.20 [#]	0.77	3.30 [#]	0.01	0.66	3.13 [#]	0.18	1.65	0.36	0.70	3.70 [*]
N	1	62.87 ^{***}	31.22 ^{***}	7.60 [*]	1.45	0.17	42.97 ^{***}	9.04 ^{**}	0.24	12.50 ^{**}	2.81	37.54 ^{***}
年Year (Y)	5	57.28 ^{***}	15.66 ^{***}	22.04 ^{***}	17.54 ^{***}	1.51	4.32 ^{**}	4.87 ^{***}	8.73 ^{***}	6.41 ^{***}	1.50	4.32 ^{**}
C × N	2	0.02	0.02	0.02	0.08	1.33	2.65 [#]	0.08	0.18	0.23	1.21	2.96 [#]
C × Y	10	0.59	1.31	6.36 ^{***}	0.76	0.68	1.85 [#]	2.78 ^{**}	5.03 ^{***}	0.86	0.44	1.78 [#]
N × Y	5	7.64 ^{***}	8.05 ^{***}	2.63 [*]	5.27 ^{***}	2.46 [*]	3.91 ^{**}	8.59 ^{***}	0.30	10.38 ^{***}	2.72 [*]	3.67 ^{**}
C × N × Y	10	0.84	0.95	1.63	1.22	0.65	1.81 [#]	0.39	2.26 [*]	1.46	0.84	1.70 [#]

#, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. AB, 一二年生植物; PB, 多年生丛生禾草; PF, 多年生杂类草; PR, 多年生根茎禾草; SS, 灌木与半灌木。
#, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. AB, perennial plants; PB, perennial bunchgrass; PF, perennial forbs; PR, perennial rhizome grass; SS, shrubs, and semi-shrubs.

22.5%和41.3%; 此外, 还伴生有灌木与半灌木和一二年生植物功能群, 分别占群落生物量的4.0%和0.1% (图4)。实验期间, 除灌木与半灌木外, 其他各功能群地上生物量均表现出显著的年际间波动 (表3)。

凋落物输入变化显著影响了多年生根茎禾草和一二年生植物的地上生物量($p < 0.1$), 而对其他功

能群生物量没有明显影响($p > 0.1$, 表3)。多年生根茎禾草的地上生物量随着凋落物的添加而增加, 凋落物移除处理造成多年生根茎禾草生物量在N0和N1条件下分别降低了35.1%与17.7%; 而凋落物添加处理使多年生根茎禾草的地上生物量提高了23.8% (N0)与21.6% (N1)。凋落物添加处理造成一二年生植物地上生物量显著降低。

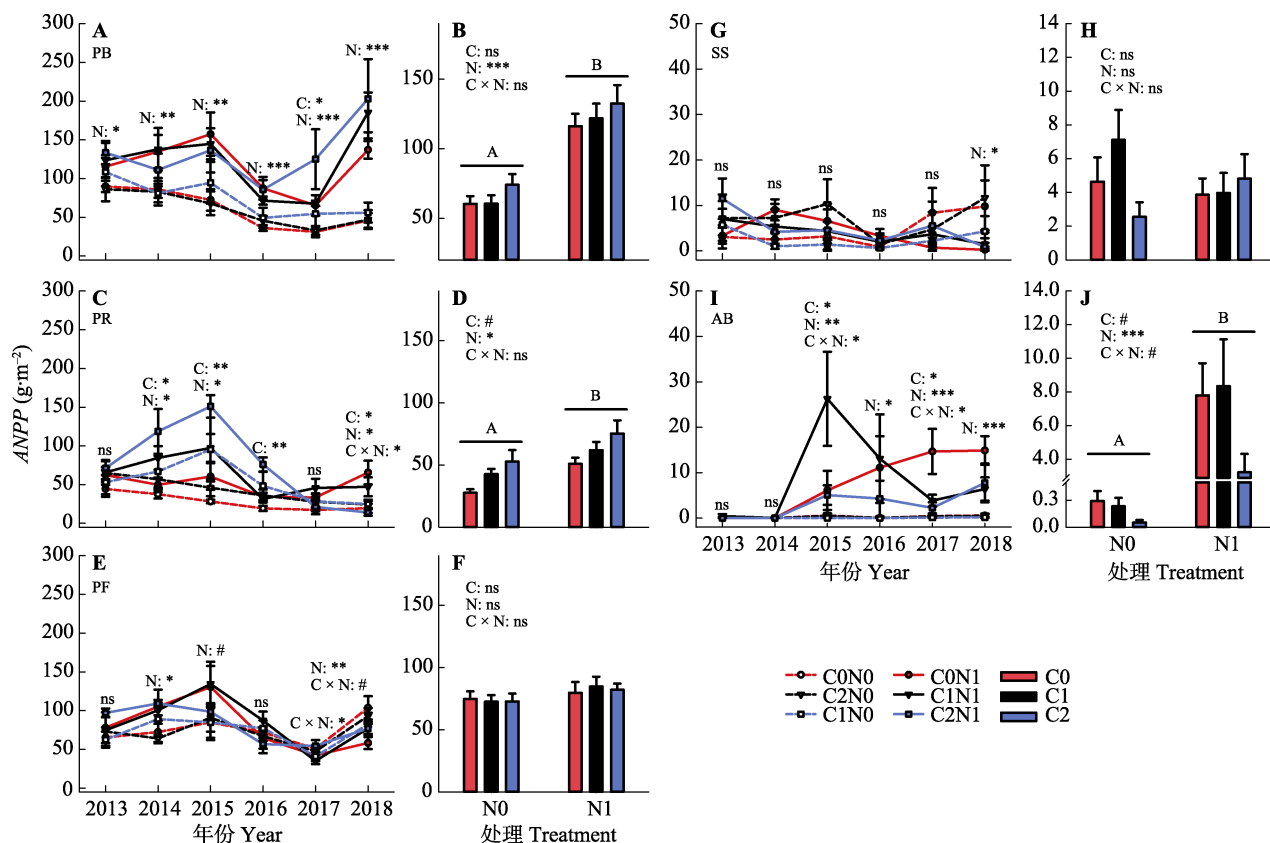


图4 2013–2018年不同凋落物输入变化和氮添加处理下,各功能群地上净初级生产力(*ANPP*)年际变异(**A、C、E、G、I**)和6年平均值(**B、D、F、H、J**)。图中数据均为平均值±标准误差。图中给出了每个年份以及多年平均凋落物输入变化(*C*)氮添加(*N*)及其交互作用(*C* × *N*)对各功能群地上净初级生产力影响的差异显著性分析结果(*ns*, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。不同大写字母表示不同氮添加处理(*N*)对各功能群地上净初级生产力影响的多重比较结果差异显著($p < 0.05$)。C0, 凋落物去除; C1, 凋落物对照; C2, 凋落物添加; N0, 无氮添加; N1, 氮添加。AB, 一二年生植物; PB, 多年生丛生禾草; PF, 多年生杂类草; PR, 多年生根茎禾草; SS, 灌木与半灌木。

Fig. 4 Inter-annual variations (**A, C, E, G, I**) and 6-year average (**B, D, F, H, J**) of aboveground net primary productivity (*ANPP*) of five functional groups in different litter input and nitrogen addition treatments during 2013–2018. The data in the figure are mean ± *SE*. Significance levels were presented to show the effects of altered litter input (*C*) and nitrogen addition (*N*) treatments and their interaction (*C* × *N*) on *ANPP* of each functional group (*ns*, $p > 0.1$; #, $p < 0.1$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). C0, litter removal; C1, control; C2, litter addition; N0, without nitrogen addition; N1, nitrogen addition. Different uppercase letters in the bar graph indicate significant difference of multiple comparisons between two nitrogen addition treatments. AB, annual and biannual plants; PB, perennial bunch grasses; PF, perennial forbs; PR, perennial rhizome grasses; SS, shrubs and semi-shrubs.

氮添加处理显著提高了多年生丛生禾草、多年生根茎禾草和一二年生植物三个功能群的地上生物量($p < 0.05$),而对多年生杂类草和灌木与半灌木地上生物量没有显著影响($p > 0.05$)(表3)。在凋落物去除条件下,氮添加使多年生丛生禾草、多年生根茎禾草和一二年生植物的生物量分别增加了92.6%、84.1%和2 586.7%;在凋落物输入对照条件下,氮添加使多年生丛生禾草、多年生根茎禾草和一二年生植物的生物量分别增加了101.3%、45.2%和3 490.2%;而在凋落物添加条件下,氮添加使多年生丛生禾草、多年生根茎禾草和一二年生植物的生物量分别增加了78.9%、42.7%和6 078.2%。除一二年生植物功能群外,凋落物输入变化和氮添加处理对各功能

群生物量的影响没有显著的交互作用(表3)。

从各功能群在群落中*ANPP*所占的比例来看,除一二年生植物功能群外,凋落物处理并未显著影响其他功能群的相对生物量($p > 0.05$)(表3;图5)。氮添加显著提高了多年生丛生禾草和一二年生植物在群落*ANPP*所占的比例,显著降低了多年生杂类草所占比例,而并没有改变多年生根茎禾草和灌木与半灌木所占比例(表3;图5)。

2.4 群落*ANPP*与凋落物添加量、降水量以及土壤环境条件之间的关系

在对照和氮添加条件下,随着凋落物添加量的增加,*ANPP*显著增加($p < 0.05$,图6A)。随着凋落物添加量的增加,土壤温度显著下降($p < 0.05$,图6B),

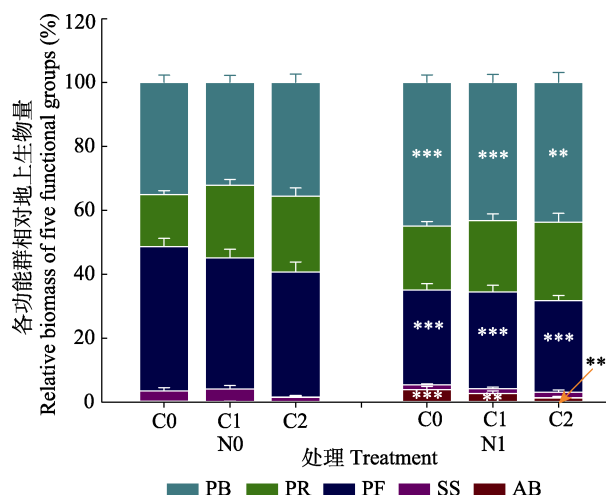


图5 不同凋落物输入变化和氮添加处理下, 各功能群相对生物量多年平均值的变化。图中数据均为平均值 \pm 标准误差。星号表示不同氮处理间的差异显著(**, $p < 0.01$; ***, $p < 0.001$)。C0, 凋落物移除; C1, 对照; C2, 凋落物添加; N0, 无氮添加; N1, 氮添加。AB, 一二年生植物; PB, 多年生丛生禾草; PF, 多年生杂类草; PR, 多年生根茎禾草; SS, 灌木与半灌木。

Fig. 5 Variations in the relative biomass of the five functional groups in different litter input and nitrogen addition treatments. The data in the figure are mean \pm SE. Asterisk indicated significant difference between different nitrogen treatments (**, $p < 0.01$; ***, $p < 0.001$). C0, litter removal; C1, control; and C2, litter addition; N0, nitrogen-free control; N1, nitrogen addition. AB, annual and biennial plants; PB, perennial bunch grasses; PF, perennial forbs; PR, perennial rhizome grasses; SS, shrubs, and semi-shrubs.

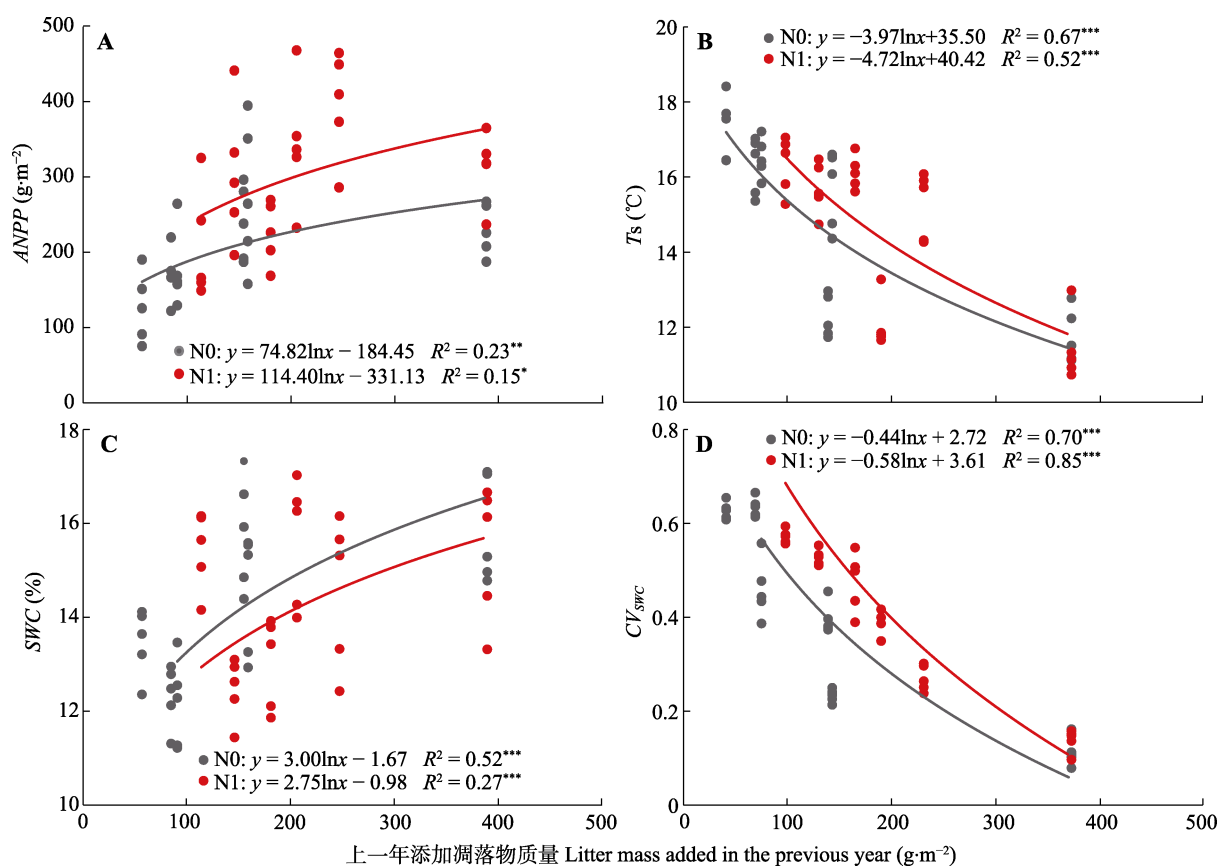


图6 不同氮处理条件下, 地上净初级生产力(ANPP)、土壤温度(T_s)、土壤含水量(SWC)及其季节变异(CV_{SWC})与上一年添加的凋落物质量间的相关关系。图中标出相关系数(R^2)和差异显著性分析结果(*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。N0, 无氮添加; N1, 氮添加。

Fig. 6 Correlation analysis of aboveground net primary productivity (ANPP), soil temperature (T_s), soil water content (SWC) and its variation (CV_{SWC}) with litter biomass added in the previous year under each nitrogen treatment. The correlation coefficient (R^2) and significance levels are presented in the figure (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). N0, nitrogen-free control; N1, nitrogen addition.

土壤含水量显著提高($p < 0.05$, 图6C), 而土壤含水量的季节变异显著降低($p < 0.001$, 图6D)。

各处理中群落ANPP与生长季降水量表现出显著的二次曲线关系($p < 0.05$, 图7A), 即随着降水量

增加, 群落ANPP显著提高至饱和阈值而后出现降低趋势。氮添加显著提高了ANPP对降水响应的敏感性, 其降水量饱和阈值从无氮添加条件下的260 mm提高至氮添加条件下的271 mm。除C0N1、C1N1处

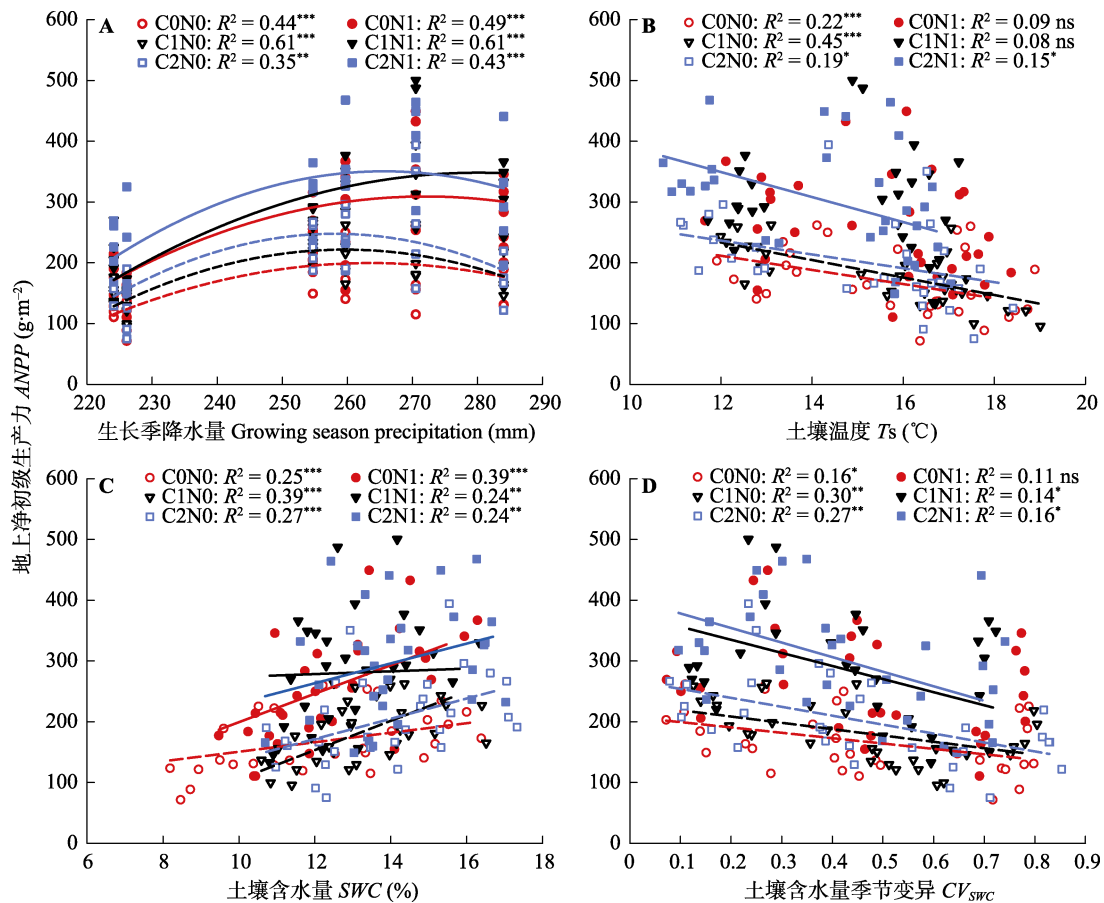


图7 群落地上净初级生产力与生长季降水量(A)、土壤温度(B)、土壤含水量(C)和土壤含水量季节变异(D)之间的关系。图中标出相关系数(R^2)和差异显著性分析结果(ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$)。C0, 凋落物去除; C1, 凋落物对照; C2, 凋落物添加; N0, 无氮添加; N1, 氮添加。

Fig. 7 Correlation analysis between aboveground net primary productivity (ANPP) and precipitation (A), soil temperature (T_s) (B), soil water content (SWC) (C), and seasonal variation of soil water content (CV_{SWC}) (D) during the growing season. The correlation coefficient (R^2) and the significance levels are presented in the figure (ns, $p > 0.05$; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$). C0, litter removal; C1, control; C2, litter addition; N0, without nitrogen addition; N1, nitrogen addition.

理外, ANPP与 T_s 均表现出显著的负相关关系($p < 0.05$, 图7B)。各处理ANPP与SWC间表现出显著的线性正相关关系($p < 0.05$, 图7C), 而与土壤含水量的变异(CV_{SWC} , C0N1除外)之间呈现显著的负相关关系($p < 0.05$, 图7D)。

2.5 凋落物输入变化和氮添加通过土壤环境影响功能群组成及生产力

凋落物输入变化除了对多年生丛生禾草和多年生根茎禾草的直接促进外, 主要通过提高土壤含水量提高了多年生丛生禾草和一二年生植物的生物量, 通过降低土壤温度直接提高群落ANPP; 氮添加则除了直接提高一二年生植物生物量外, 主要通过提高土壤可利用态氮含量促进多年生丛生禾草、多年生根茎禾草的生长。各功能群之间则发现多年生杂类草主要受到多年生根茎禾草的抑制, 而与环境因

素无直接关联。各功能群植物共同构成ANPP, 其中多年生丛生禾草、多年生根茎禾草和多年生杂类草对ANPP具有明显的决定作用(图8)。

3 讨论

3.1 凋落物输入变化和氮添加对ANPP的影响

连续6年的实验处理结果表明, 凋落物输入量的增加显著提高了群落ANPP, 而凋落物去除则降低了ANPP (图3B)。相关分析表明随着凋落物添加量的增加, 群落ANPP显著提高(图6A)。已有研究表明凋落物对ANPP的影响主要分为两个方面, 一方面是通过凋落物自身分解直接增加生态系统碳输入, 提高土壤养分可利用性来促进ANPP (Brearley *et al.*, 2003; Bansal *et al.*, 2014); 另一方面是通过对微环境条件(如土壤温度、水分状况等)的调控来间接影

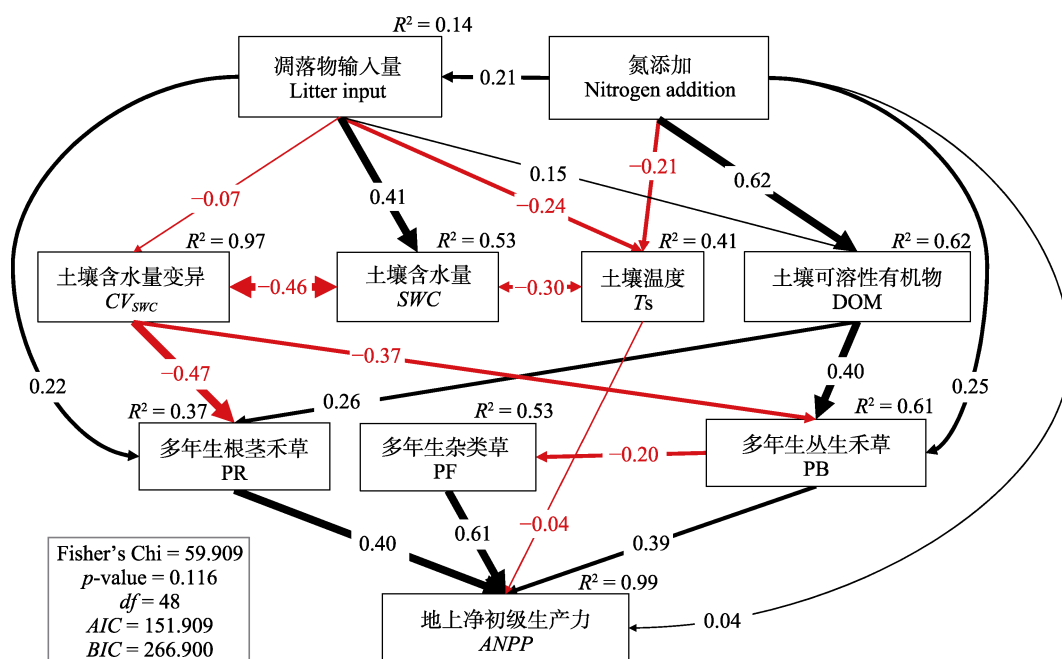


图8 凋落物输入变化和氮添加通过土壤环境影响群落功能群组成及地上净初级生产力(ANPP)的结构方程模型。AIC, 赤池信息量; BIC, 贝叶斯信息量; Fisher's Chi, 费舍尔精确检验值。

Fig. 8 Structural equation model (SEM) on how litter manipulation and nitrogen addition affect the community functional group composition and aboveground net primary productivity (ANPP) through soil environment. CV_{SWC} , variance of soil water content; DOM, soil dissolved organic matter (the first principal component of DOC and DON, which explained 0.88 of them); PB, perennial bunch grasses; PF, perennial forbs; PR, perennial rhizome grasses; SWC, soil water content; T_s , soil temperature. AIC, Akaike Information Criterion; BIC, Bayesian Information Criterion; Fisher's Chi, result of Fisher exact test.

响ANPP (Booth *et al.*, 2005; Deutsch *et al.*, 2010a)。在本研究中, 凋落物输入变化并没有显著改变DOC和DON等土壤养分含量, 而是显著改善了土壤水分和温度等土壤环境条件间接影响植被生产力。ANPP与降水量以及土壤含水量的关系表明, 水分是限制群落生产力的主要限制因子, 凋落物添加通过降低土温, 减少水分蒸发, 提高表层土壤水分可利用性, 降低土壤水分的季节变异, 从而降低了植物遭受干旱胁迫风险, 进而促进植物生长, 提高群落ANPP。Xu等(2013a)在关于生态系统中凋落物作用的meta分析中发现, 在草原生态系统的研究中, 凋落物添加会增加土壤微生物碳以及总碳含量, 并降低土壤温度、增加土壤含水量。我们的研究虽然在统计上尚未检测到凋落物输入变化对土壤DOC和DON含量的显著影响, 但还是发现随着凋落物的增加, DOC含量呈现出增加的趋势。这表明凋落物输入变化对土壤DOC等养分可利用性的影响可能需要更长期的实验研究结果来检验(Wang *et al.*, 2017a)。尤其在干旱半干旱生态系统中, 因为受到水分条件的限制, 凋落物分解速率相对更慢(Zhang & Wang, 2015)。

以往的研究表明, 氮添加会显著提高半干旱草原生态系统生产力(潘庆民等, 2005; 沈月, 2016; Yue *et al.*, 2016; Wang *et al.*, 2019; Zhao *et al.*, 2019)。本研究也发现, 氮添加显著提高了土壤DOC和DON含量, 促进植物生长, 显著提高了群落生产力。内蒙古半干旱草原作为一个水氮共同限制的生态系统(Heisler-White *et al.*, 2008; Li *et al.*, 2011; Ren *et al.*, 2017)。氮对草原生产力的影响强度甚至方向都是依赖于生态系统的水分状况的(Yan *et al.*, 2010; Shen *et al.*, 2016)。在本研究中, 氮添加对生产力的促进作用在降水量较高的湿润年份表现得更为明显, 而在较为干旱的年份(2016和2017年), 氮添加对ANPP的促进作用明显减弱(图3A)。ANPP与降水量之间的关系也表明, 氮添加显著提高了ANPP-降水量关系的阈值, 随着降水量增加, ANPP增加的趋势更加明显, 这也进一步证实了氮添加处理对水分条件的依赖性(Yang *et al.*, 2011; Zong *et al.*, 2019)。此外, 氮添加显著降低了土壤温度, 这主要是由于氮添加促进植物生长, 提高植被盖度, 同时导致第二年凋落物输入量的进一步增多, 对土壤温度调节表现出显著的负反馈作用, 这也有助于缓解干旱年份

的水分胁迫作用(Li *et al.*, 2011; Zhao *et al.*, 2019)。我们的研究还发现氮添加并未改变凋落物输入变化对群落ANPP的影响,二者没有显著的交互作用。与Shen等(2016)在本区域进行氮和凋落物添加实验的结果相同。这可能与半干旱草原降水量和生产力剧烈的年际变异有关,要想进一步探讨这两者之间的交互作用是否会对系统生产力形成影响,还需要更长期的实验数据积累减弱或去除数据分析过程中年份等其他因素的影响。

3.2 凋落物输入变化和氮添加对植物功能群生物量及其组成的影响

不同草原管理方式不仅会影响群落生产力,同时还可以通过改变物种和功能群间的相互作用和竞争关系,影响群落结构和生产力稳定性。我们的研究发现凋落物输入量的变化对不同植物功能群的影响程度存在显著差异,随着凋落物输入量的增加,多年生根茎禾草的生物量表现出显著增加的趋势,而一二年生植物的生物量明显降低(图4)。在本研究区域中,多年生根茎禾草仅包括羊草一个物种,与其他功能群植物相比,羊草在水分和养分资源丰富的生境中具有更高的光合同化速率,更具竞争优势(潘庆民等, 2005; 万宏伟等, 2008; 沈月, 2016)。在本研究中,凋落物输入改善土壤物理环境,促进了多年生禾草的生长。凋落物层的覆盖会抑制其他以种子繁殖的功能群的建成,这样会提高以根茎分蘖为主要繁殖方式的羊草在群落中的优势地位,影响植物群落结构(Bosy & Reader, 1995; Carlyle *et al.*, 2014)。此外,本研究还发现凋落物输入变化对多年生根茎禾草生物量的影响与年份间存在显著的交互作用,表明凋落物对多年生根茎禾草的调控作用依赖于年际间降水的变化,多年生根茎禾草生物量的年际波动表明,在接近长期平均降水量的前3个正常年份(2013–2015年),凋落物添加显著增加了多年生根茎禾草的生物量;在经历过干旱年份(2016年)后,由于水分胁迫导致多年生根茎禾草生物量骤然下降,并造成其在后3年里生物量处于较低的水平。而对于干旱胁迫适应性更强的多年生丛生禾草在较为干旱的后3年中生物量继续显著提高。凋落物输入变化对本研究中另一个主要功能群多年生杂类草的生物量并没有产生显著影响。

在我国半干旱草原,持续大量的氮添加会降低

群落生物多样性是已经被大量的实验证实的结论(Stevens *et al.*, 2004; Clark & Tilman, 2010; Zhang *et al.*, 2016; Liu *et al.*, 2018),但与以往研究不同的是,本研究经过6年的氮添加处理,并没有发现物种和功能群多样性发生显著变化,这可能是与本实验的氮添加量有关。在本研究区域已开展的长期氮添加梯度实验中,草原生产力和多样性均与氮添加量表现出非线性关系,呈现先增加后降低的趋势,而拐点为 $10\text{--}15\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$,过量的氮添加会因为土壤酸化和有害离子的富集而导致群落生产力和多样性的降低(Stevens *et al.*, 2004; Tian *et al.*, 2016; Gao *et al.*, 2019)。本研究的施氮量为 $15\text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$,对该区域草原生态系统是一个比较适宜的氮添加水平,因此本实验中的氮添加处理对物种和功能群多样性并没有显著的影响。我们发现,氮添加提高土壤养分含量,显著促进多年生丛生禾草、多年生根茎禾草和一二年生植物的生长,增大其对群落ANPP的贡献。而另一个优势功能群多年生杂类草的生物量主要与多年生根茎禾草此消彼长,由于多年生根茎禾草的增加,最终造成多年生杂类草在群落ANPP相对贡献的显著下降;并且还发现灌木与半灌木的生物量因多年生禾草的增加而减少。Bai等(2004)通过分析本区域草原生产力的长期动态,提出多年生丛生禾草和多年生根茎禾草两个主要功能群之间的补偿作用是维持半干旱草原生产力稳定性的重要机制。与多年生根茎禾草相比,多年生丛生禾草(以大针茅、冰草(*Agropyron cristatum*)等丛生禾草为主)更能忍耐干旱和贫瘠的生境,又因其生长速率较慢,因此在较为干旱的年份可以保持相对稳定的生长;而在较为湿润的年份,多年生根茎禾草则可以迅速利用水分和养分资源,实现快速生长。在本研究中,我们也发现了类似的补偿现象,实验前3年(2013–2015)雨水较为充足,特别是在氮添加处理下,多年生根茎禾草的生物量持续增加;但在2016年后,由于降水减少,多年生根茎禾草的生物量迅速下降,而多年生丛生禾草仍然维持了较高的生物量。近年来的研究也证实物种间的非同步性是维持草原群落生产力稳定性的重要途径(Yang *et al.*, 2012; Xu *et al.*, 2015; Zhang *et al.*, 2016; Wilcox *et al.*, 2017; Zhang *et al.*, 2018b; Sasaki *et al.*, 2019; Wu & Wang, 2019)。

4 结论

通过6年的凋落物输入变化和氮添加野外控制实验研究,我们发现:1)凋落物输入量增加和氮添加均显著提高了群落生产力;2)不同植物功能群对凋落物管理和氮添加的响应存在差异,导致群落功能群结构发生变化。随着凋落物输入量增加和氮添加,群落优势功能群多年生禾草(包括多年生根茎禾草和多年生丛生禾草)的生物量显著提高,对群落生产力的贡献增加,在群落中的优势地位增强;3)凋落物输入主要改善土壤物理环境而氮添加则通过提高土壤养分可利用性,对各功能群生物量产生影响,进而决定群落生产力及其稳定性。

以上结果表明,适当的草原管理方式如围封禁牧和降低放牧强度等都能通过增加凋落物的输入来提高草原生产力,维持生态系统稳定性。而适量的氮等养分添加管理也有助于提高草原生产力,促进其恢复。我们的研究还表明,群落结构变化和生态系统功能变化需要长期控制实验的研究,特别是对存在剧烈年际波动的干旱半干旱生态系统,长期监测数据的支持是非常重要的。

参考文献

- Ågren GI, Wetterstedt JÅM, Billberger MFK (2012). Nutrient limitation on terrestrial plant growth-modeling the interaction between nitrogen and phosphorus. *New Phytologist*, 194, 953–960.
- Amatangelo KL, Dukes JS, Field CB (2008). Responses of a California annual grassland to litter manipulation. *Journal of Vegetation Science*, 19, 605–612.
- Austin AT, Vivanco L (2006). Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature*, 442, 555–558.
- Bai YF, Han XG, Wu JG, Chen ZZ, Li LH (2004). Ecosystem stability and compensatory effects in the Inner Mongolia grassland. *Nature*, 431, 181–184.
- Bai YF, Pan QM, Xing Q (2016). Fundamental theories and technologies for optimizing the production functions and ecological functions in grassland ecosystems. *Chinese Science Bulletin*, 61, 201–212. [白永飞, 潘庆民, 邢旗 (2016). 草地生产与生态功能合理配置的理论基础与关键技术. 科学通报, 61, 201–212.]
- Bansal S, Sheley RL, Blank B, Vasquez EA (2014). Plant litter effects on soil nutrient availability and vegetation dynamics: changes that occur when annual grasses invade shrub-steppe communities. *Plant Ecology*, 215, 367–378.
- Booth MS, Stark JM, Rastetter E (2005). Controls on nitrogen cycling in terrestrial ecosystems: a synthetic analysis of literature data. *Ecological Monographs*, 75, 139–157.
- Bosy JL, Reader RJ (1995). Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. *Functional Ecology*, 9, 635–639.
- Brearely FQ, Press MC, Scholes JD (2003). Nutrients obtained from leaf litter can improve the growth of dipterocarp seedlings. *New Phytologist*, 160, 101–110.
- Carlyle CN, Fraser LH, Turkington R (2014). Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. *Oecologia*, 174, 1065–1073.
- Chen ZZ, Wang SP (2000). *Typical Chinese Grassland Ecosystem*. Science Press, Beijing. [陈佐忠, 汪诗平 (2000). 中国典型草原生态系统. 科学出版社, 北京.]
- Clark CM, Tilman D (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 451, 712–715.
- Clark CM, Tilman D (2010). Recovery of plant diversity following N cessation: effects of recruitment, litter, and elevated N cycling. *Ecology*, 91, 3620–3630.
- Deng MF, Liu LL, Jiang L, Liu WX, Wang X, Li SP, Yang S, Wang B (2018). Ecosystem scale trade-off in nitrogen acquisition pathways. *Nature Ecology & Evolution*, 2, 1724–1734.
- Deutsch ES, Bork EW, Willms WD (2010a). Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics. *Plant Ecology*, 209, 135–145.
- Deutsch ES, Bork EW, Willms WD (2010b). Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. *Agriculture Ecosystems & Environment*, 135, 1–9.
- Facelli JM, Pickett STA (1991a). Plant litter: light interception and effects on an old-field plant community. *Ecology*, 72, 1024–1031.
- Facelli JM, Pickett STA (1991b). Plant litter: its dynamics and effects on plant community structure. *The Botanical Review*, 57, 1–32.
- Fang JY, Yang YH, Ma WH, Mohammad A, Shen HH (2010). Ecosystem carbon stocks and their changes in China's grasslands. *Science China Life Sciences*, 53, 757–765.
- Fang JY, Yu GR, Liu LL, Hu SJ, Chapin III FS (2018). Climate change, human impacts, and carbon sequestration in China. *Proceedings of the National Academy of Sciences of the United States of America*, 115, 4015–4020.
- Foster BL, Gross KL (1998). Species richness in a successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, 79, 2593–2602.
- Gao Y, Sun SN, Xing F, Mu XM, Bai YG (2019). Nitrogen addition interacted with salinity-alkalinity to modify plant diversity, microbial PLFAs and soil coupled elements: a 5-year experiment. *Applied Soil Ecology*, 137, 78–86.
- Gruber N, Galloway JN (2008). An Earth-system perspective of the global nitrogen cycle. *Nature*, 451, 293–296.
- Heisler-White JL, Knapp AK, Kelly EF (2008). Increasing

- precipitation event size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia*, 158, 129–140.
- Isbell F, Reich PB, Tilman D, Hobbie SE, Polasky S, Binder S (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 11911–11916.
- Jensen K, Gutschkunst K (2003). Effects of litter on establishment of grassland plant species: the role of seed size and successional status. *Basic and Applied Ecology*, 4, 579–587.
- Jiang HZ (2018). *Effects of Litter Removal and Litter Addition on Community Structure and Ecosystem Function of Stepper Ecosystem*. Master degree dissertation, University of Chinese Academy of Sciences, Beijing. [蒋红志 (2018). 凋落物移除与添加对草原生态系统群落结构和生态系统的影响. 硕士学位论文, 中国科学院大学, 北京.]
- Jing ZB, Cheng JM, Chen A (2013). Assessment of vegetative ecological characteristics and the succession process during three decades of grazing exclusion in a continental steppe grassland. *Ecological Engineering*, 57, 162–169.
- Jones DL, Willett VB (2006). Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC) in soil. *Soil Biology & Biochemistry*, 38, 991–999.
- Kelemen A, Török P, Valkó O, Migléc T, Tóthmérész B (2013). Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science*, 24, 1195–1203.
- Knapp AK, Seastedt TR (1986). Detritus accumulation limits productivity of tallgrass prairie. *BioScience*, 36, 662–668.
- Kohmann MM, Sollenberger LE, Dubeux Jr JCB, Silveira ML, Moreno LSB (2019). Legume proportion in grassland litter affects decomposition dynamics and nutrient mineralization. *Agronomy Journal*, 111, 1079–1089.
- Lamb EG (2008). Direct and indirect control of grassland community structure by litter, resources, and biomass. *Ecology*, 89, 216–225.
- LeBauer DS, Treseder KK (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, 89, 371–379.
- Letts B, Lamb EG, Mischkolz JM, Romo JT (2015). Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. *Plant Ecology*, 216, 357–370.
- 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.
- Liu JS, Cui Y, Li XF, Wilsey BJ, Isbell F, Wan SQ, Wang L, Wang DL (2018). Reversal of nitrogen-induced species diversity declines mediated by change in dominant grass and litter. *Oecologia*, 188, 921–929.
- Lu M, Zhou XH, Luo YQ, Yang YH, Fang CM, Chen JK, Li B (2011). Minor stimulation of soil carbon storage by nitrogen addition: a meta-analysis. *Agriculture, Ecosystems & Environment*, 140, 234–244.
- Manning P, Saunders M, Bardgett RD, Bonkowski M, Bradford MA, Ellis RJ, Kandeler E, Marhan S, Tscherko D (2008). Direct and indirect effects of nitrogen deposition on litter decomposition. *Soil Biology & Biochemistry*, 40, 688–698.
- Pan QM, Bai YF, Han XG, Yang JC (2005). Effects of nitrogen additions on a *Leymus chinensis* population in typical steppe of Inner Mongolia. *Acta Phytoecologica Sinica*, 29, 311–317. [潘庆民, 白永飞, 韩兴国, 杨景成 (2005). 氮素对内蒙古典型草原羊草种群的影响. 植物生态学报, 29, 311–317.]
- Patrick LB, Fraser LH, Kershner MW (2008). Large-scale manipulation of plant litter and fertilizer in a managed successional temperate grassland. *Plant Ecology*, 197, 183–195.
- Piao S, Fang J, Ciais P, Peylin P, Huang Y, Sitch S, Wang T (2009). The carbon balance of terrestrial ecosystems in China. *Nature*, 458, 1009–1013.
- 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.
- Rice EL, Parenti RL (1978). Causes of decreases in productivity in undisturbed tall grass prairie. *American Journal of Botany*, 65, 1091–1097.
- Ruprecht E, Enyedi MZ, Eckstein RL, Donath TW (2010). Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biological Conservation*, 143, 449–456.
- Sasaki T, Lu X, Hirota M, Bai Y (2019). Species asynchrony and response diversity determine multifunctional stability of natural grasslands. *Journal of Ecology*, 107, 1862–1875.
- Sayer EJ, Heard MS, Grant HK, Marthews TR, Tanner EVJ (2011). Soil carbon release enhanced by increased tropical forest litterfall. *Nature Climate Change*, 1, 304–307.
- Shen Y (2016). *Effects of Water and Nitrogen and Litter Addition on Leymus chinensis Grassland*. PhD dissertation, China Agricultural University, Beijing. [沈月 (2016). 水和氮及凋落物添加对羊草草地的影响机制. 博士学位论文, 中国农业大学, 北京.]
- Shen Y, Chen WQ, Yang GW, Yang X, Liu N, Sun X, Chen JS, Zhang YJ (2016). Can litter addition mediate plant productivity responses to increased precipitation and nitrogen deposition in a typical steppe? *Ecological Research*, 31, 579–587.
- Stevens CJ, Dise NB, Mountford JO, Gowing DJ (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876–1879.
- Suding KN, Collins SL, Gough L, Clark C, Cleland EE, Gross KL, Milchunas DG, Pennings S (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 4387–4392.

- Tian QY, Liu NN, Bai WM, Li LH, Chen JQ, Reich PB, Yu Q, Guo DL, Smith MD, Knapp AK, Cheng WX, Lu P, Gao Y, Yang A, Wang TZ, Li X, Wang ZW, Ma YB, Han XG, Zhang WH (2016). A novel soil manganese mechanism drives plant species loss with increased nitrogen deposition in a temperate steppe. *Ecology*, 97, 65–74.
- Varga C, Fekete I, Kotrocó Z, Krakomperger Z, Vincze G (2008). The effect of litter on soil organic matter (SOM) turnover in Sikfökt site. *Cereal Research Communications*, 36, 547–550.
- Vitousek PM, Howarth RW (1991). Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry*, 13, 87–115.
- Wan HW, Yang Y, Bai SQ, Xu YH, Bai YH (2008). Variation in leaf functional traits of six species along a nitrogen addition gradient in *Leymus chinensis* steppe in Inner Mongolia. *Journal of Plant Ecology (Chinese Version)*, 32, 611–621. [万宏伟, 杨阳, 白世勤, 徐云虎, 白永飞 (2008). 羊草草原群落6种植物叶片功能特性对氮素添加的响应. 植物生态学报, 32, 611–621.]
- Wang J (2011). *The Effect of Litter on Vegetation and Soil Moisture in Typical Grassland*. PhD dissertation, Inner Mongolia Agricultural University, Hohhot. [王静 (2011). 凋落物对典型草原植被及土壤水分的影响. 博士学位论文, 内蒙古农业大学, 呼和浩特.]
- Wang J, Gao YZ, Zhang YH, Yang JJ, Smith MD, Knapp AK, Eissenstat DM, Han XG (2019). Asymmetry in above- and belowground productivity responses to N addition in a semi-arid temperate steppe. *Global Change Biology*, 25, 2958–2969.
- Wang J, Zhao ML, Willms WD, Han GD, Wang ZW, Bai YF (2011). Can plant litter affect net primary production of a typical steppe in Inner Mongolia? *Journal of Vegetation Science*, 22, 367–376.
- Wang J-J, Pisani O, Lin LH, Lun OY, Bowden RD, Lajtha K, Simpson AJ, Simpson MJ (2017a). Long-term litter manipulation alters soil organic matter turnover in a temperate deciduous forest. *Science of the Total Environment*, 607–608, 865–875.
- Wang SS (2016). *Effects of Altered Litter Input on Productivity and Carbon Fluxes of a Semiarid Grassland, Inner Mongolia*. Master degree dissertation, University of Chinese Academy of Sciences, Beijing. [王珊珊 (2016). 凋落物输入变化对半干旱草原生产力和碳通量的影响. 硕士学位论文, 中国科学院大学, 北京.]
- Wang X, Xu Z, Lü X, Wang R, Cai J, Yang S, Li M-H, Jiang Y (2017b). Responses of litter decomposition and nutrient release rate to water and nitrogen addition differed among three plant species dominated in a semi-arid grassland. *Plant and Soil*, 418, 241–253.
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004). Ecological linkages between aboveground and belowground biota. *Science*, 304, 1629–1633.
- Wikeem BM, Newman RF, Ryswyk AL (1989). Effect of fertilization date and litter removal on grassland forage production. *Journal of Range Management*, 42, 412–415.
- Wilcox KR, Tredennick AT, Koerner SE, Grman E, Hallett LM, Avolio ML, La Pierre KJ, Houseman GR, Isbell F, Johnson DS, Alatalo JM, Baldwin AH, Bork EW, Boughton EH, Bowman WD, Britton AJ, Cahill Jr JF, Collins SL, Du GZ, Eskelinen A, Gough L, Jentsch A, Kern C, Klanderud K, Knapp AK, Kreyling J, Luo YQ, McLaren JR, Megonigal P, Onipchenko V, Prev  y J, Price JN, Robinson CH, Sala OE, Smith MD, Soudzilovskaia NA, Souza L, Tilman D, White SR, Xu ZW, Yahdjian L, Yu Q, Zhang PF, Zhang YH (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters*, 20, 1534–1545.
- Wu GL, Du GZ, Liu ZH, Thirgood S (2009). Effect of fencing and grazing on a *Kobresia*-dominated meadow in the Qinghai-Tibetan Plateau. *Plant and Soil*, 319, 115–126.
- Wu JB, Wang XD (2019). Temporal stability of aboveground net primary production in northern Tibet alpine steppe in response to nitrogen addition. *Journal of Mountain Science*, 16, 2679–2686.
- Xia JY, Wan SQ (2008). Global response patterns of terrestrial plant species to nitrogen addition. *New Phytologist*, 179, 428–439.
- Xu S, Liu L, Sayer EJ (2013a). Variability of above-ground litter inputs alters soil physicochemical and biological processes: a meta-analysis of litterfall-manipulation experiments. *Biogeosciences*, 10, 7423–7433.
- Xu X, Sherry RA, Niu S, Li D, Luo Y (2013b). Net primary productivity and rain-use efficiency as affected by warming, altered precipitation, and clipping in a mixed-grass prairie. *Global Change Biology*, 19, 2753–2764.
- Xu ZW, Ren HY, Li MH, van Ruijven J, Han XG, Wan SQ, Li H, Yu Q, Jiang Y, Jiang L (2015). Environmental changes drive the temporal stability of semi-arid natural grasslands through altering species asynchrony. *Journal of Ecology*, 103, 1308–1316.
- Yan LM, Chen SP, Huang JH, Lin GH (2010). Differential responses of auto- and heterotrophic soil respiration to water and nitrogen addition in a semiarid temperate steppe. *Global Change Biology*, 16, 2345–2357.
- Yang H, Jiang L, Li L, Li A, Wu MY, Wan SQ (2012). Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. *Ecology Letters*, 15, 619–626.
- Yang H, Li Y, Wu MY, Zhang Z, Li L, Wan SQ (2011). Plant community responses to nitrogen addition and increased precipitation: the importance of water availability and species traits. *Global Change Biology*, 17, 2936–2944.
- Yarwood S, Brewer E, Yarwood R, Lajtha K, Myrold D (2013). Soil microbe active community composition and capability of responding to litter addition after 12 years of no inputs. *Applied and Environmental Microbiology*, 79, 1385–1392.
- Yue K, Peng Y, Peng CH, Yang WQ, Peng X, Wu FZ (2016). Stimulation of terrestrial ecosystem carbon storage by

- nitrogen addition: a meta-analysis. *Scientific Reports*, 6, 19895. DOI: 10.1038/srep19895.
- Zhang BW, Tan XR, Wang SS, Chen ML, Chen SP, Ren TT, Xia JY, Bai YF, Huang JH, Han XG (2017). Asymmetric sensitivity of ecosystem carbon and water processes in response to precipitation change in a semi-arid steppe. *Functional Ecology*, 31, 1301–1311.
- Zhang TA, Luo Y, Chen HYH, Ruan H (2018a). Responses of litter decomposition and nutrient release to N addition: a meta-analysis of terrestrial ecosystems. *Applied Soil Ecology*, 128, 35–42.
- Zhang XY, Wang W (2015). Control of climate and litter quality on leaf litter decomposition in different climatic zones. *Journal of Plant Research*, 128, 791–802.
- Zhang Y, Loreau M, Lü X, He N, Zhang G, Han X (2016). Nitrogen enrichment weakens ecosystem stability through decreased species asynchrony and population stability in a temperate grassland. *Global Change Biology*, 22, 1445–1455.
- Zhang YH, He NP, Loreau M, Pan QM, Han XG (2018b). Scale dependence of the diversity-stability relationship in a temperate grassland. *Journal of Ecology*, 106, 1277–1285.
- Zhang YJ, Yang GW, Liu N, Chang SJ, Wang XY (2013). Review of grassland management practices for carbon sequestration. *Acta Prataculturae Sinica*, 22, 290–299. [张英俊, 杨高文, 刘楠, 常书娟, 王晓亚 (2013). 草原碳汇管理对策. 草业学报, 22, 290–299.]
- Zhao YN, Yang B, Li MX, Xiao RQ, Rao KY, Wang JQ, Zhang T, Guo JX (2019). Community composition, structure and productivity in response to nitrogen and phosphorus additions in a temperate meadow. *Science of the Total Environment*, 654, 863–871.
- Zong N, Zhao GS, Shi PL (2019). Different sensitivity and threshold in response to nitrogen addition in four alpine grasslands along a precipitation transect on the Northern Tibetan Plateau. *Ecology and Evolution*, 9, 9782–9793.

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