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陆生植物生物量分配对模拟氮沉降响应的 Meta 分析

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摘要: 分析了陆生植物地上、地下各组织中生物量分配对氮沉降的响应, 为研究大气氮沉降背景下陆地生态系统的碳、氮循环过程及植物生物量分配、立木收获、定向培育等相关研究和实践提供参考依据。共收集整理了国内外 63 篇论文的原始数据资料进行 Meta 分析 (Meta-analysis), 用以定量评估氮沉降对植物生物量分配的影响, 并通过亚组分析进一步探讨了不同生态系统类型、植物种类、氮肥形式、施氮水平和持续时间对生物量分配的影响。结果表明, 总体来看施氮会显著促进植物地上部分生物量分配, 植物叶生物量和茎生物量在施氮条件下均显著增加; 然而地下生物量所受促进作用要低于地上部分, 表现为植物细根生物量和粗根生物量在氮输入下并没有显著变化; 植物根冠比在氮沉降下显著降低; 叶重比、茎重比和根重比在氮沉降下没有显著变化。此外, 亚组分析结果表明生态系统类型和植物类型会显著影响植物总生物量和根冠比对氮沉降的响应, 草本植物在氮沉降下的生物量累积明显优于木本, 这说明短期氮沉降可能会增加草本的覆盖面积; 施肥形式对根冠比的影响存在明显差异, 相比于尿素, 硝酸铵对植物根冠比的作用更显著; 不同施氮水平显著影响地上生物量分配, 中氮水平 (本研究为 60—120 kg hm⁻² a⁻¹) 促进作用最大, 高氮水平 (本研究为 ≥120 kg hm⁻² a⁻¹) 促进作用明显减弱, 这与总生物量的变化一致, 表明过高的氮沉降量将抑制植物生长; 氮沉降处理时间长短对植物地上生物量的影响也存在显著差异, 当施氮时间高于 3 年, 氮沉降对地上生物量的促进作用几乎消失。总之, 短期氮沉降会使植物分配更多生物量给地上部分, 且氮沉降对草本植物生物量的累积作用明显优于木本, 这些发现可为未来大气氮沉降背景下植物地上、地下部分碳存储、植物群落结构、植被动态等相关研究提供科学依据。

关键词: 陆生植物; meta 分析; 氮沉降; 植物生物量分配; 根冠比; 根重比

A meta-analysis of the response of terrestrial plant biomass allocation to simulated N deposition

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Abstract: This study aimed to reveal terrestrial plant biomass allocation between aboveground and belowground tissues under nitrogen (N) deposition and to provide a foundation for studying carbon (C) and N cycles, stand harvests, direct cultivation in different ecosystems, and relevant research and practices regarding plant biomass allocation. Through synthesizing data from 63 peer-reviewed publications, we quantified the response of plant biomass allocation to N deposition by meta-analysis and assessed the influences on plant biomass allocation of different ecosystem types, plant species, and N forms and levels. This study found that N deposition significantly increased the aboveground biomass of plants, with plant leaf biomass and stem biomass showing an increasing trend under N application. However, although underground biomass

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increased under N deposition, the increase was less than that of the aboveground biomass. Fine root biomass and coarse root biomass did not change significantly under N deposition. The root:shoot ratio decreased significantly under N application. Leaf weight ratio, stem weight ratio, and root weight ratio did not change significantly under N deposition. In addition, subgroup analysis showed that there were differences in the response of the root:shoot ratio and total biomass to N deposition for both ecosystem type and plant species. Herbaceous plant biomass accumulation increased significantly more than that of woody plants, which meant N deposition could increase the coverage of herbaceous plants. Nitrogen forms significantly affected the response of the root:shoot ratio to N application, with ammonium nitrate having a more significant effect on the root:shoot ratio than urea. The response of aboveground biomass to N application was significantly affected by the level of N application. Aboveground biomass was promoted the most at a medium N level ($60\text{--}120\text{ kg hm}^{-2}\text{a}^{-1}$) and at a high N level ($\geq 120\text{ kg hm}^{-2}\text{a}^{-1}$), there was less of an effect, which was consistent with the change in total biomass. This result indicates that excessive N deposition inhibits plant growth. In addition, there were temporal differences in the effects of N application on the aboveground biomass of plants. In this study, when the N application time was longer than 3 years, the effect of N application on aboveground biomass was negligible. In conclusion, short term N application will allow most terrestrial plants to allocate more biomass to aboveground parts and the biomass accumulation of herbaceous plants is better than that of woody plants. These conclusions will provide a reasonable scientific basis for future correlative studies on plant carbon storage, community structure, tree species diversity, and vegetation dynamics under N deposition.

Key Words: terrestrial plant; meta-analysis; N deposition; plant biomass allocation; root:shoot ratio; root weight ratio

自工业革命以来,由于化石燃料的燃烧及化肥的使用,大气氮沉降明显加重,预计全球平均氮沉降量到 21 世纪中期将达到 200 Tg N a^{-1} ,约为现在氮沉降量的二倍左右^[1],氮沉降会对陆地生态系统产生严重影响^[2-3],有关氮沉降的模拟研究已经成为全球气候变化的热点领域。氮沉降增加会提高氮的可利用性,进而改变土壤的养分状况,影响植物各组织中光合作用产物的数量和分配^[4-5]。有研究表明在养分贫瘠的生境中,植物会分配更多的生物量给根部,而当养分充足时地上生物量更大,这符合功能平衡假说^[6]。植物会通过改变生物量分配模式来适应外界环境的变化^[7-9],目前虽然有大量氮沉降背景下植物生物量分配的相关研究^[10-11],但氮沉降对生物量在植物各组织中具体分配的影响尚不清楚,需要加强该领域研究。

根、茎、叶等器官在植物生活史中均发挥至关重要的作用,它们共同调节植物的生存、生长和繁殖^[12]。资源分配在调节植物生长、发育、繁殖和抗性等方面起着重要作用,同时也是陆地生态系统碳、氮循环的重要影响因素。陆生植物生物量在地上和地下的分配策略是为适应不同环境所采取的重要措施,植物根冠间生物量的分配模式是长期适应自然选择的结果,根冠比在一定程度上可反应某种植物在陆地环境中生殖隔离的进化史^[13-14],定量了解植物的生物量分配模式对生态学研究具有重要意义。近年来有大量研究探索植物地上、地下生物量和根冠比对环境变化的响应^[15-18],但是不同研究所得出的结论不尽相同,因此,试图得出植物生物量分配的一般性规律,有必要对全球范围内相关研究的试验数据进行整合分析。

本研究收集了国内外有关大气氮沉降对植物生物量分配影响的野外模拟试验观测数据,通过 Meta 分析定量评估了氮沉降处理对植物生物量分配的影响,并通过亚组分析阐明了不同生态系统类型、植物种类、氮肥形式、施氮水平及持续时间影响下的植物地上、地下生物量、根冠比和总生物量 4 个指标对外源氮输入的影响,探索了氮沉降对植物生物量分配的影响规律,为未来大气氮沉降加重情景下植物生物量分配的相关研究提供参考依据。

1 材料与方法

1.1 数据的收集及纳入标准

通过对 Web of Science 和 China National Knowledge Infrastructure(CNKI)等数据库的检索,本文利用关键

词“氮沉降、氮添加、氮肥和生物量分配等”共收集到 63 篇同行发表的论文(见附录),共 562 个观测值用于 Meta 分析。所收集的论文必须符合以下标准:(1)所选论文中必须包含至少一个用于分析植物生物量分配所选定的指标,而且文章中对试验持续时间、施氮量、种类以及试验地的气候类型、生态系统类型均有明确说明;(2)为考虑施氮条件下气候条件和生态系统类型对生物量分配的影响,仅仅野外模拟氮沉降的试验被考虑在内,室内试验被排除;(3)各独立研究中试验区 and 对照区要处于同样的气候条件下;(4)各指标的均值、方差或标准差均在文章中有说明或可通过软件 Engauge Digitizer (Free Software Foundation, Inc., Boston, MA, USA) 从各研究的图表中进行提取或可通过计算得出;(5)对于交互作用的研究,仅提取模拟氮沉降的实验组和对照组数据。为了避免发表偏倚,本文通过 Stata12(Stata Corp., College Station, TX, USA)的 Egger 直线回归法对各数据进行检验使数据来源更可靠。

在数据库中通过地上生物量(AGB)、地下生物量(BGB)、根冠比(R/S)、总生物量(TB)、叶生物量(LB)、茎生物量(SB)、细根生物量(FRB)、粗根生物量(CRB)、茎重比(SWR)、根重比(RWR)和叶重比(LWR)这 11 个指标(表 1)来说明氮沉降条件下植物生物量的分配情况,并将地上、地下生物量、根冠比和总生物量分成了不同亚组用于进一步探讨不同因素对氮沉降引起生物量分配变化的相对影响。具体分组情况如下:氮处理水平分为高氮(HN) $\geq 120 \text{ kg hm}^{-2} \text{ a}^{-1}$,中氮(MN) $60\text{—}120 \text{ kg hm}^{-2} \text{ a}^{-1}$ 和低氮(LN) $\leq 60 \text{ kg hm}^{-2} \text{ a}^{-1}$;氮添加形式分为硝酸铵(NH_4NO_3)、尿素(urea)和其他;生态系统类型分为森林(forest)、草原(grassland)和其他;植物种类分为草本(grass)、阔叶树(broadleaf)、针叶树(conifer)、灌木(shrub)和其他;研究持续时间分为不超过1年、1—3年和3年及以上3个阶段。

表 1 文中各指标的缩写、定义和单位

Table 1 Abbreviation used in this article, together with a definition and the units applied here

缩写 Abbreviation	英文全拼 English full name	指标 Variables	定义 Definition	单位 Unit
AGB	Aboveground biomass	地上生物量	植物叶和茎的干重	g
BGB	Belowground biomass	地下生物量	植物根的干重	g
R/S	Root/shoot ratio	根冠比	根干重/叶干重+茎干重	g/g
TB	Total biomass	总生物量	根、茎和叶的总干重	g
LB	Leaf biomass	叶生物量	叶干重	g
SB	Stem biomass	茎生物量	茎干重	g
FRB	Fine root biomass	细根生物量	$\leq 2\text{mm}$ 根的干重	g
CRB	Coarse root biomass	粗根生物量	2mm 以上根的干重	g
SWR	Stem weight ratio	茎重比	茎干重/根茎叶的总干重	g/g
RWR	Root weight ratio	根重比	根干重/根茎叶的总干重	g/g
LWR	Leaf weight ratio	叶重比	叶干重/根茎叶的总干重	g/g

1.2 Meta 分析

Meta 分析通过 METAWIN 2.1 (Sinauer Associates Inc., Sunderland, MA, USA) 和 Stata 12 (Stata Corp., College Station, TX, USA) 实现,通过响应比(RR)的自然对数作为效应量(effect size)来衡量氮沉降对植物生物量分配的影响,公式如下:

$$RR = X_t / X_c \quad (1)$$

式中 $\bar{X}_t$ 和 $\bar{X}_c$ 分别表示试验组和对照组的均值。

$$\ln RR = \ln(X_t / X_c) \quad (2)$$

方差为:

$$v = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (3)$$

式中, S_i 和 S_c 分别代表试验组和对照组的标准差, n_i 和 n_c 分别代表试验组和对照组的样本量。

权重 w 由公式(4)计算得出。由于某些研究中的观测值个数要大于 1, 因此将权重调整为每个研究中的观测值总数, 通过总权重 w' (公式(5)) 来估计总效应量 (RR_{++} , 公式(6、7))。

$$w = \frac{1}{v \hat{\sigma}_\lambda^2} \quad (4)$$

$$w' = \frac{w}{n} \quad (5)$$

$$\ln RR' = w' \times \ln RR \quad (6)$$

$$RR_{++} = \frac{\sum_k \ln RR'_k}{\sum_k w'_k} \quad (7)$$

式中, n 是每项研究中观测值的总个数, w'_k 和 $\ln RR'_k$ 是第 k 个观测值所对应的 w' 和 $\ln RR'$ 。

本研究采取随机效应模型进行 Meta 分析, 当某一指标平均效应量的 95% 置信区间和“0”没有交叉时, 表示氮沉降对该指标有显著影响, 即认为氮沉降对该指标的影响具有统计学意义, 当效应量大于 0 时表示氮沉降对指标产生正效应, 相反则表示产生负效应。

本研究将总异质性 Q_T 分为各亚组的组间异质性 Q_B 和组内异质性 Q_W , 通过组间异质性 (Q_B) 来检验同一指标的效应量在不同亚组 (生态系统类型、植物种类、施氮形式、施氮水平和持续时间) 之间的差异, 具体计算过程见公式(8)^[19]。

$$Q_B = \sum_m w'_{i++} RR_{i++}^2 - \frac{\left(\sum_m w'_{i++} RR_{i++} \right)^2}{\sum_m w'_{i++}} \quad (8)$$

式中, m 代表某一分组的组数, i 代表第 i 个亚组, RR_{i++} 代表第 i 个亚组的总效应量。

当某指标的 95% 置信区间和“0”没有交叉且显著性在 0.05 水平时, 则表明该效应量具有显著差异。上述计算过程通过 METAWIN 软件实现。

2 结果与分析

2.1 氮沉降对生物量分配的影响

总体而言, 外源施氮能有效促进植物生物量的累积, 植物总生物量在施氮条件下明显增加 (平均效应量 = 0.266; 95% CI: 0.155—0.378; 图 1)。在 11 个选定指标中, 地上生物量、地下生物量、根冠比、总生物量、叶生物量、茎生物量 6 个指标对外源施氮响应明显。外源施氮会显著提高植物地上生物量的分配 (图 1), 而对地下生物量的促进作用要低于地上部分。这就导致植物的根冠比在施氮条件下明显降低 (平均效应量 = -0.055; 95% CI: -0.106—-0.004; 图 1), 说明植物地上部分对氮沉降更敏感。对于植物的地上部分, 茎生物量和叶生物量在施氮条件下都显著增加, 相反的, 施氮对植物地下部分的细根和粗根生物量虽然均有促进作用, 但并不显著。根重比在施氮条件下有降低趋势 (平均效应量 = -0.186; 95% CI: -0.426—-0.054; 图 1), 茎重比 (平均效应量 = 0.060; 95% CI: -0.036—0.155; 图 1) 和叶重比 (平均效应量 = 0.024; 95% CI: -0.070—0.119; 图 1) 表现为增加趋势, 但并不显著。

2.2 不同生态系统类型植物生物量分配对模拟氮沉降的响应

本研究将生态系统类型分为森林、草原和其他三类, 不同生态系统植物的根冠比对模拟氮沉降的响应差异极显著 (表 2)。施氮会显著降低森林生态系统中植物的根冠比 (图 2c)。然而在草原中, 氮输入对植物根冠比不存在显著影响。植物总生物量在不同生态系统中对模拟氮沉降的响应差异极显著, 总的来看, 氮沉降在各生态系统中均有利于植物生物量的累积, 其中草原 (平均效应量 = 0.354; 95% CI: 0.161—0.547; 图 2d) 以及其他 (平均效应量 = 0.553; 95% CI: 0.303—0.802; 图 2c) 均表现为显著增加。与根冠比和总生物量不同, 不

同生态系统类型和氮沉降对植物地上及地下生物量分配影响的关联性很弱,即生态系统类型对植物地上和地下生物量的影响差异不显著(表 2)。

2.3 不同植物种类的生物量分配对氮沉降的响应

本文将植物分为草本、灌木、针叶、阔叶和其他五类,不同植物的根冠比对模拟氮沉降的响应差异极显著(表 2)。阔叶树种的根冠比在氮输入条件下显著降低(平均效应量 = -0.155 ; 95% CI: -0.223 — -0.086 ; 图 2c),但针叶树种、灌木和草本植物的根冠比在氮输入下并无显著变化。不同植物的总生物量对氮沉降的响应差异极显著(表 2),其中草本植物(平均效应量 = 0.371 ; 95% CI: 0.186 — 0.556 ; 图 2d)和阔叶树种(平均效应量 = 0.265 ; 95% CI: 0.098 — 0.433 ; 图 2d)的总生物量在氮沉降影响下均明显增加,氮沉降对针叶树种总生物量影响不显著。不同植物类型的地上生物量和地下生物量差异不显著(表 2)。

2.4 不同氮肥形式下植物生物量分配对模拟氮沉降的响应

现有的大量氮沉降模拟研究以硝酸铵(NH_4NO_3)和尿素($\text{CO}(\text{NH}_2)_2$)为主,本研究中将氮肥形式分为硝酸铵、尿素和其他三种。氮肥形式对植物根冠比的影响差异显著,硝酸铵作用下植物根冠比明显降低(平均效应量 = -0.102 ; 95% CI: -0.162 — -0.041 ; 图 2c),尿素和其他氮肥对植物根冠比的影响不明显。氮肥种类对植物地上、地下和总生物量影响的差异不显著(表 2)。

2.5 不同施氮水平下植物生物量分配对模拟氮沉降的响应

本研究中包含 3 个施氮水平,高氮(HN, $\geq 120 \text{ kg hm}^{-2} \text{ a}^{-1}$)、中氮(MN, $60\text{—}120 \text{ kg hm}^{-2} \text{ a}^{-1}$)和低氮(LN, $\leq 60 \text{ kg hm}^{-2} \text{ a}^{-1}$)。不同施氮水平对植物地上生物量和总生物量的影响差异显著,地上生物量和总生物量在不同施氮水平下均明显增加,其中中氮水平($60\text{—}120 \text{ kg hm}^{-2} \text{ a}^{-1}$)增加最多,分别为(平均效应量 = 0.334 ; 95% CI: 0.225 — 0.443 ; 图 2a)和(平均效应量 = 0.475 ; 95% CI: 0.270 — 0.680 ; 图 2d)。高氮水平和低氮水平植物地上生物量增加相接近,分别为(平均效应量 = 0.176 ; 95% CI: 0.058 — 0.294 ; 图 2a)和(平均效应量 = 0.155 ; 95% CI: 0.085 — 0.225 ; 图 2d)。高氮水平的总生物量增加量低于低氮水平,分别为(平均效应量 = 0.163 ; 95% CI: 0.022 — 0.304 ; 图 2d)和(平均效应量 = 0.230 ; 95% CI: 0.055 — 0.405 ; 图 2d)。不同施氮水平对植物地下生物量和总生物量的影响差异不显著(表 2)。

2.6 不同施氮持续时间下植物生物量分配对模拟氮沉降的响应

本研究将施氮持续时间分为 3 个阶段,不同持续时间对植物地上和地下生物量的影响差异极显著,施氮短于 1 年及 1—3 年会明显提高植物地上生物量分配,当施氮 3 年及以上时这种促进作用变得不明显(图 2a)。施氮短于 1 年时,植物地下生物量分配明显提高(平均效应量 = 0.337 ; 95% CI: 0.176 — 0.498 ; 图 2b),继续延长施氮时间,植物地下生物量分配变化不再明显(图 2b)。植物根冠比在不同施氮持续时间普遍降低,总生物量普遍增加,但施氮持续时间对根冠比和总生物量的影响差异并不显著(表 2)。

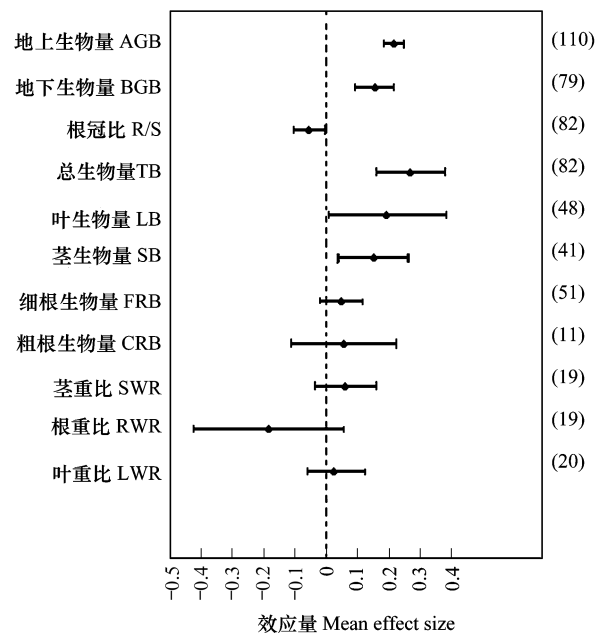


图 1 外源氮输入对植物生物量分配各指标的影响

Fig. 1 Impacts of elevated nitrogen on biomass allocation variables of plant

AGB: 地上生物量, aboveground biomass; BGB: 地下生物量, belowground biomass; R/S: 根冠比, Root/shoot; TB: 总生物量, total biomass; LB: 叶生物量, leaf biomass; SB: 茎生物量, stem biomass; FRB: 细根生物量, fine root biomass; CRB: 粗根生物量, coarse root biomass; SWR: 茎重比, stem weight ratio; RWR: 根重比, root weight ratio; LWR: 叶重比, leaf weight ratio; 效应量 = (平均值 $\pm$ 95% 置信区间); 图右括号内的数值代表观测值个数

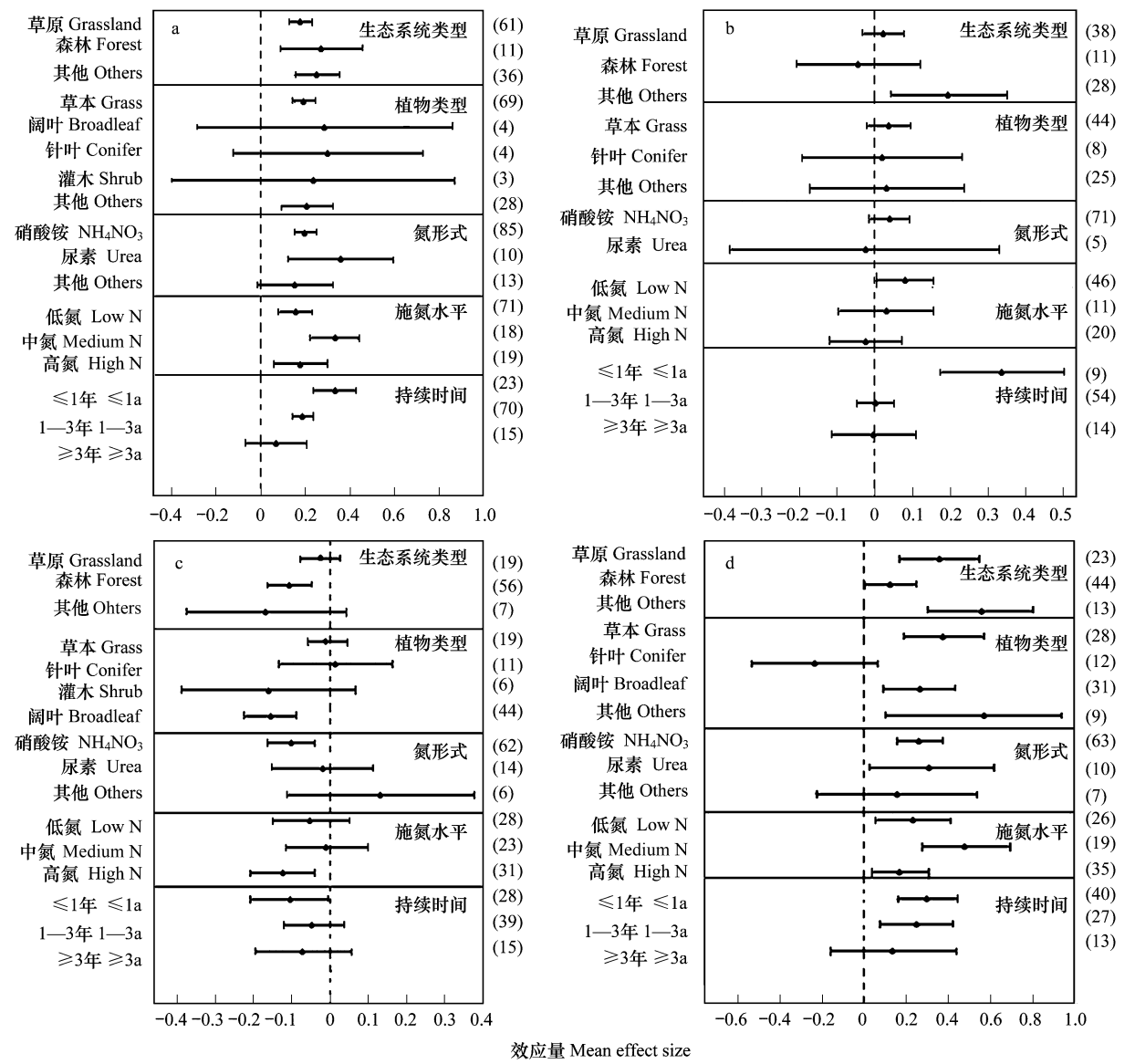


图2 不同生态系统类型、植物类型、氮形式、施氮水平和施氮持续时间对植物生物量分配的影响

Fig.2 Effect of elevated nitrogen on biomass allocation with different ecological type, vegetation type, N form, N level and duration
a;地上生物量,aboveground biomass;b;地下生物量,belowground biomass;c;根冠比,Root/shoot;d;总生物量,total biomass;图右括号内的数值代表观测值个数

表 2 氮沉降对植物生物量分配影响因子的异质性分析

Table 2 Between-group heterogeneity (Q_B) for N deposition effect size across different categorical variables of biomass allocation								
变量 Variables	地上生物量(AGB)		地下生物量(BGB)		根冠比(R/S)		总生物量(TB)	
	Q_B	P	Q_B	P	Q_B	P	Q_B	P
生态系统类型 Ecosystem type	2.499	0.287	5.846	0.054	13.730	0.001 **	12.460	0.002 **
植物类型 Vegetation type	0.932	0.919	0.039	0.980	19.730	<0.001 **	18.924	<0.001 **
氮形式 N-form	2.692	0.260	0.232	0.630	6.380	0.041 *	0.591	0.744
氮水平 N-addition level	8.179	0.017 *	3.073	0.215	3.050	0.218	6.915	0.032 *
持续时间 Duration	11.683	0.003 **	20.952	<0.001 **	0.870	0.646	1.173	0.556

Q_B : 组间异质性, between-group heterogeneity. 表中星号代表在 $P<0.05$ 处差异显著, 两个星号代表差异极显著

3 讨论与结论

3.1 讨论

Fu 等^[20]的 Meta 分析研究表明,氮沉降对植物地上生物量有明显的促进作用,与本研究结果一致,植物地上生物量在氮沉降下明显增加可能是因为氮沉降增加了土壤有效氮,土壤养分充足使植物分配更多生物量给地上组织造成的^[21-22]。本研究发现,茎生物量在氮输入条件下表现为明显增加趋势,这和 Lu^[23]等的 Meta 分析结果一致,可能原因是氮沉降使植物养分运输能力加强,进而表现为茎部的显著增加。除上述结论外,本研究还发现随施氮时间延长(本研究中为 ≥ 3 年),氮处理对植物地上生物量的促进作用逐渐消失,由此可见氮沉降对植物生长的促进作用存在时间差异。因此,如果大气氮沉降在未来得不到有效控制,其对植物生长所产生的抑制作用会随时间推移而慢慢显现出来。施氮水平的高低也会显著影响植物地上生物量,陆生植物地上生物量在中氮水平所受促进作用最大,更高的施氮水平反而会减弱促进作用,大量研究也发现了同样的结论^[24-25]。造成这一现象的可能原因是长期高浓度施氮会使土壤酸化^[26-27]或养分失衡^[28-29]进而抑制植物生长。由于 Metawin 只能用于分析单因素因子对效应值的影响,而植物生物量分配对氮沉降的响应受多因子控制,如氮沉降量、沉降时间等,因此在进行植物生物量分配对氮沉降响应的亚组分析时,可能存在一定的局限性。

根冠比在研究陆地生态系统中碳、氮分配和储存时起着重要的指示作用,预测植物在应对全球气候变化情景时是如何进行地上、地下生物量分配具有重要意义。大量有关氮沉降模拟试验的 Meta 分析结果表明外源施氮会显著降低植物的根冠比^[23,30-31],与本研究的结果一致。植物地上生物量对氮沉降的敏感性要显著高于地下^[32],根冠比降低可能和地上生物量对氮沉降响应更敏感有关。本研究发现生态系统类型会显著影响植物的地上、地下生物量分配对氮沉降的响应,与 Wang 等^[33]的结果一致。相比于森林生态系统,草地生态系统中植物根冠比在氮沉降下减小并不明显,可能原因是在氮输入时植物的光合作用会显著加强,植物对水分和养分的需求也会随之增强,进而使更多的有机物和能源分配给根系用以维持土壤和根系之间的水分运输和养分获取,而这种现象草地比森林更明显^[34-35],本研究中草地植物的地下生物量在外源氮输入时有增加趋势,也进一步验证了上述解释。植物种类的差异会显著影响植物根冠比对模拟氮沉降的响应^[36-37],本研究证实了上述结论,除阔叶树外,其他植物根冠比对氮沉降的响应与未分类前存在差异,可能原因是样本量太小。与本研究不同的是 Fu 等^[20]的 Meta 分析发现氮沉降对根冠比的影响不显著,可能是因为 Fu 等的 Meta 分析只研究了高山植物根冠比在氮沉降下的变化。

植物地下生物量是全球陆地生态系统碳储量的重要组成部分,在全球生态系统碳循环中起重要作用。本研究中植物细根和粗根生物量在模拟氮沉降条件下并没有显著变化(图 1),但总的地下生物量却显著增加,与 Liu 等^[38]的 Meta 分析结果一致,这表明当前植物生长仍处于氮限制状态。细根生物量在氮输入时并不会增加,但细根周转率和呼吸却会显著提高,植物主要靠细根吸收养分,细根周转率提高会促进植物对养分的吸收^[30],此外,根系呼吸和根系中的氮含量成正比^[39],因此,即使细根生物量没有显著增加,但植物在氮沉降下依然可以加强对土壤有效氮的吸收。氮沉降对植物地下生物量的促进作用只在短时间内表现,当沉降持续时间过长,促进作用消失,可能是长期持续性供氮使土壤处于氮饱和状态,进而限制了地下部分的生长。

目前有关氮输入对植物生物量累积作用较为一致的结论是:氮输入能有效促进氮缺乏生态系统植物生物量累积,但在氮饱和生态系统中却有相反结论^[40-41]。本研究发现尽管植物生物量累积对氮输入的响应较一致,但生态系统类型、植物类型和施氮水平等不同均会显著影响植物生物量累积对模拟氮沉降的响应。目前所进行的氮沉降模拟研究在不同陆地生态系统均有开展,草原约覆盖了陆地表面的 25%,通常处于氮限制状态^[42-43],本研究中氮沉降对草原生物量的促进作用要明显高于森林,Xia 等^[44]的 Meta 分析结果也表明氮输入对草本生物量的促进作用要显著大于木本。其原因可能是氮沉降会缓解草原的氮限制状态,使草本植物得以旺盛生长;而对于森林,尽管温带森林处于氮限制状态,但热带森林一般处于氮饱和状态^[45](本研究中森林的

试验样地以热带、亚热带居多,见附录),这也就很好的诠释了为何草原中植物生物量受氮沉降的促进作用要明显高于森林,这一变化对未来群落演替和植被动态具有重要意义。植物生物量累积在中氮水平(本研究为 $60-120 \text{ kg hm}^{-2} \text{ a}^{-1}$) 达到最大,这和地上生物量的变化一致,也进一步说明植物生物量在模拟氮沉降研究中的累积主要是由地上生物量增加引起的。

3.2 结论

(1) 氮沉降会对植物的地上生物量产生显著影响。具体表现为:地上生物量在外源氮输入时显著增加,叶生物量和茎生物量在氮输入时均表现出明显增加趋势,这可能和氮输入条件下植物加强光合作用和养分运输有关,植物地上部分所受的促进作用表明植物冠层结构有可能在氮沉降下扩大。

(2) 植物地下生物量在外源氮输入时所受促进作用不及地上部分,氮输入对细根和粗根生物量均表现出促进作用,但并不显著。植物地上和地下生物量对氮输入响应的差异导致根冠比在氮输入时显著降低,这说明相比于根部,植物的地上部分对氮输入更加敏感,即地上部分更有可能从短期氮沉降中获利。

(3) 生态系统类型和植物种类会显著影响植物根冠比和总生物量对氮输入的响应。氮沉降对草地(草本)的促进作用要优于森林(木本),这说明氮沉降有可能会对未来的植被动态及群落演替产生影响。此外,根冠比对氮沉降的响应会显著受到施氮形式影响,相比于尿素,硝酸铵对根冠比的作用更明显,这说明在氮沉降对植物生物量影响的模拟试验中,施氮形式有可能是造成各独立研究结果差异的一个重要原因。

(4) 短期内氮沉降将有利于植物生物量累积,随着时间延长促进作用逐渐消失。这暗示着未来氮沉降背景下植物生长可能受限,这为提前应对氮沉降对植物生长可能产生的消极影响起到了很好的警示作用,也可对未来植被和生态系统管理提供理论指导和科学依据。

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附录:用于提取数据的 63 篇参考文献清单

A list of 63 papers from which the data were extracted for this meta-analysis

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