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氮磷供应量及比例对灰绿藜种子性状的影响

田大栓*

中国科学院地理科学与资源研究所生态系统网络观测与模拟重点实验室, 北京 100101

摘 要 全球氮沉降不仅改变土壤氮和磷的有效性, 同时也改变氮磷比例。氮磷供应量、比例及其交互作用可能会影响植物种子性状。该研究在内蒙古草原基于沙培盆栽实验种植灰绿藜(*Chenopodium glaucum*), 设置3个氮磷供应量水平和3个氮磷比例的正交实验来探究氮磷供应量、比例及其交互作用对灰绿藜种子性状的影响。结果发现氮磷供应量对种子氮浓度、磷浓度和萌发率影响的相对贡献(15%–24%)大于氮磷比例(3%–7%), 而种子大小只受氮磷比例的影响。同时氮磷供应量和比例之间的交互作用显著影响种子氮浓度和磷浓度。同等氮磷比例情况下, 低量养分供应提高种子氮浓度、磷浓度和萌发率。氮磷比例只有在养分匮乏的环境中才会对种子大小和萌发率产生显著影响。总之, 灰绿藜种子不同性状对氮或磷限制的敏感性不同, 同时种子性状也对养分限制表现出适应性和被动响应。

关键词 种子性状; 氮供应水平; 磷供应水平; 氮磷比例; 沙培盆栽实验; 适应性响应

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Effects of the supply levels and ratios of nitrogen and phosphorus on seed traits of *Chenopodium glaucum*

TIAN Da-Shuan*

Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China

Abstract

Aims Global nitrogen (N) deposition not only alters soil N and phosphorus (P) availability, but also changes their ratio. The levels and ratios of N and P supply and their interaction may simultaneously influence plant seed traits. However, so far there has been no experiments to distinguish these complex impacts on plant seed traits in the field.

Methods A pot experiment with a factorial design of three levels and ratios of N and P supply was conducted in the Nei Mongol grassland to explore the effects of levels and ratios of N and P supply and their interaction on seed traits of *Chenopodium glaucum*.

Important findings We found that the relative contribution (15%–24%) of N and P supply levels in affecting the N concentrations, P concentrations and germination rates of seeds was larger than that (3%–7%) of N:P supply ratios, whereas seed size was only significantly influenced by N:P. Simultaneously, seed N and P concentrations were impacted by the interaction of N and P supply levels and ratios. At the same N:P, decrease in nutrient supply levels increased seed N concentrations, P concentrations and germination rates. N:P supply ratios only had a significant effect on seed size and germination rates under low nutrient levels. Overall, these results indicate that different seed traits of *C. glaucum* show different sensitivities to N or P limitations, leading to adaptive and passive responses under different nutrient limitations. This study presents the the first field experiment to distinguish the effects of nutrient supply levels, ratios and their interactions on plant seed traits, which provides a new case study on the influences of global N deposition on future dynamics of plant population and community.

Key words seed trait; nutrient supply level; phosphorus supply level; N:P; sand cultured pot experiment; adaptive response

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* E-mail: tiands@igsnrr.ac.cn

自工业革命100多年来，伴随着愈演愈烈的人类工业和农业活动，氮沉降已经成为一个严重的全球性环境问题(Liu *et al*., 2013; Peñuelas *et al*., 2013)。氮富集正威胁着生物多样性(Stevens *et al*., 2004; Bobbink *et al*., 2010)、深刻影响生态系统结构和功能(Bai *et al*., 2010; Liu & Greaver, 2010; Lu *et al*., 2011)。氮沉降在增加土壤氮有效性的同时，也加剧陆地生态系统磷限制(Li *et al*., 2016)。这暗含着氮沉降背景下土壤氮磷供应水平改变的同时，它们之间的比例也在改变。但是，目前考虑解析氮磷供应量、比例及其交互作用对自然生态系统影响的实验还比较少，主要集中在对植物生长和营养性状的研究(Gusewell, 2005a; Luo *et al*., 2016; Zhang *et al*., 2017)，而对野外植物种子性状影响的研究还很少。

植物功能性状紧密关联生态系统功能(Lavorel & Garnier, 2002; Violle *et al*., 2007; Cornwell *et al*., 2008)。尽管前人已经检验了氮磷供应水平、比例及其交互作用对植物生长(Gusewell & Bollens, 2003; Fujita *et al*., 2010)、资源分配(Luo *et al*., 2016)、植物营养(Gusewell, 2005b)以及养分回收等(Gusewell, 2005a)的影响。但是，却忽略了氮磷养分对植物生殖性状的作用。植物营养性状变化只关系到当下生态系统功能的变化，而生殖性状(如种子)变化会影响到未来植物群落乃至生态系统的动态变化(Leishman, 2001; Walck *et al*., 2011)。例如，种子大小和氮浓度可以很好地预测幼苗存活和生长，它们关系到种群和群落的更新，特别是在不利的环境中(Milberg & Lamont, 1997; Walters & Reich, 2000; 刘志民等, 2004a; Moles & Westoby, 2004; Naegle *et al*., 2005)。相比于氮浓度，种子磷浓度可能对幼苗的生长发育更为重要(Gusewell, 2004; Balestri *et al*., 2009)，这在农业研究中已经得到广泛证实(Zhang *et al*., 1990; Grant *et al*., 2001; Zhu & Smith, 2001; Nadeem *et al*., 2011)。并且，萌发快的种子(特别是一年生植物)产生的幼苗在存活、生长和竞争方面都更具有优势(Aarssen & Burton, 1990; Schmid & Dolt, 1994; Verdu & Traveset, 2005)。种子萌发率也可以反映种子质量，因为营养缺乏的种子通常不能萌发(Howard & Goldberg, 2001; Navarro & Guitian, 2003; 刘志民等, 2004b)。

前人研究表明土壤氮含量增加会显著影响种子大小(增加或降低)、氮浓度(增加)、磷浓度(降低)、萌发率(降低)和萌发速度(降低)(Fortunel *et al*., 2009; Manning *et al*., 2009; Hrdlickova *et al*., 2011; Hejcman *et al*., 2012; 胡星云等, 2017; Li *et al*., 2017)。同时，土壤磷富集也显著改变种子大小(增加或降低)、磷浓度(增加)、氮浓度(增加)和种子萌发率(降低) (Hrdlickova *et al*., 2011; Hejcman *et al*., 2012; 刘庆艳等, 2013; Li *et al*., 2017)。但是，目前还很少有研究分析氮磷供应比例对野外植物种子性状的影响(孙志高等, 2017)。因此，全面解析氮磷供应量、比例及其交互作用对植物种子性状的影响显得尤为必要。

灰绿藜(*Chenopodium glaucum*)广泛分布在全球温带区域，同时也是内蒙古草原的一年生先锋物种和资源利用型草本植物(Bai *et al*., 2010)。采用灰绿藜作为本实验研究对象，并利用野外沙培盆栽实验，我们设置3个氮磷供应总量和3个供应比例的正交实验，旨在区分氮磷供应量、比例及其交互作用对灰绿藜种子性状的影响。拟解决的科学问题如下：1)氮磷供应量和比例对灰绿藜种子性状影响的相对重要性？2)氮磷供应量和比例对种子性状的影响是否存在交互作用？3)在不同的氮磷供应比例或供应量情况下，种子性状对氮磷供应量或比例的响应有何不同?

1 材料和方法

1.1 沙培盆栽实验

本实验在内蒙古草原生态系统定位研究站实施。实验台站位于内蒙古自治区锡林河流域，具体地理位置为43.63° N, 116.70° E。实验区域年平均气温0.3 ℃，月平均气温1月份最低(–21.6 ℃)，7月份最高(19 ℃)。年降水量346.1 mm，生长季降水(5–8月)占到全年降水量的60%–80%。该区域的植被类型为典型草原，灰绿藜为实验区域的一年生先锋物种和资源利用型草本植物(Bai *et al*., 2010)。

沙培盆栽实验进行时间为2010年6月18日至9月4日。实验包括9个处理，采用3个氮磷供应量水平和3个氮磷供应比例的完全正交设计(表1; Gusewell & Bollens, 2003; Gusewell, 2005a)，每个处理20个重复。氮磷供应量通过灰绿藜植物个体生命周期所需要的氮量(44.5 mg)和磷量(3.1 mg)的几何平均数计算得出，选用几何平均数是基于氮和磷对植物生长影响的乘法效应(multiplicative effect)(Gusewell &

Bollens, 2003; Gusewell, 2005a)。所以, 我们选取的氮磷供应量为3.93 mg (低量供应), 11.80 mg (中量供应)和35.40 mg (高量供应)。氮磷供应比例基于野外灰绿藜不同器官(叶片、根系、种子和茎)的N:P范围(4.9至46.2), 因而选取N:P为5、15和45。具体的氮磷供应量和比例见表1。

表1　所有处理的氮磷供应量
Table 1　Levels and ratios of nitrogen and phosphorus supply in each treatment

N:P	氮/磷供应量 N/P supply amount (mg·pot^{-1})		
	低量 Low	中量 Middle	高量 High
5	8.80/1.76	26.55/5.28	79.15/15.83
15	15.15/1.01	45.75/3.05	137.11/9.14
45	26.55/0.59	79.15/1.76	237.62/5.28

氮肥采用KNO_3, 磷肥采用KH_2PO_4。基于Hoagland营养液配方供应足够并且等量的其他植物所需的必需元素。用KCl来平衡溶液中的K^+离子。用稀释的KOH溶液来调整pH值到7左右。每周营养液的供应量通过氮磷供应总量除以灰绿藜生活周期的时间来计算。

灰绿藜种子播种在装有洗干净的沙子的盆里(直径20 cm, 高度25 cm), 每盆10粒种子。每个处理20盆, 9个处理共180盆。种子萌发日期为6月18日, 到植物长到3至5片叶时, 每盆只保留一植株, 挑选标准为3片叶的植物个体, 以尽量减少个体间差异所带来的影响。每周用针管将营养液注入, 每盆100 mL。采用塑料布遮掉自然降雨以保证处理效果, 同时每盆供应充足并且等量的水分以排除水分限制效应。

1.2　种子性状测定

当灰绿藜种子成熟时(9月4日), 对所有植物个体都进行取样。在实验室里把种子从植物个体里分离出来, 并在空气中风干。每株随机选取20粒种子称质量, 用来估算种子大小。种子萌发实验在正常室温下进行(18–20 ℃), 同时接受自然光照(Tripathi & Khan, 1990; Wulff *et al*., 1999; Defalco *et al*., 2003)。每株随机选取30粒种子用于测定种子萌发率。种子萌发采用直径12 cm的玻璃培养皿, 里面放2层滤纸, 经常喷蒸馏水以保证种子萌发所需的充足水分。每隔6 h对萌发的种子数目进行记录, 标准是胚根伸出。萌发实验持续7天。萌发速度通过Horak和Wax (1991)的方程计算得出。种子氮浓度采用凯氏定氮法测定。种子先用过硫酸盐氧化, 再用钼酸铵分光光度法测定磷浓度(Liu *et al*., 2016), 并与已知的参考物质进行比对校正。

1.3　数据分析

采用两因素方差分析来比较氮磷供应量、比例以及它们之间的交互作用对种子性状的影响。种子磷浓度数据在方差分析之前进行对数转化以保证数据的正态分布。然后, 采用Duncan多重比较分析相同氮磷供应水平下不同氮磷供应比例对种子性状的影响, 同样也分析相同氮磷供应比例情况下不同氮磷供应量对种子性状的影响。所有的统计分析采用SPSS 22.0软件完成, 所有的图形使用SigmaPlot 12.5软件制作。

2　结果和分析

总体来说, 氮磷供应量对种子性状影响的相对贡献(15.13%–23.58%)普遍大于氮磷供应比例(4.41%–7.07%)(表2)。氮磷供应量与比例之间的交互作用显著影响种子氮浓度和磷浓度。

对于形态性状来说, 氮磷供应比例可以解释种子大小变异的4.41%, 而氮磷供应量及它们之间的交互作用影响不显著(表2)。只有在低养分水平下, 随着氮磷比例的提高, 种子显著变小(图1)。

对于养分性状来说, 氮磷供应量分别解释种子氮浓度和磷浓度变异的23.58%和23.21%, 氮磷比例只显著影响种子磷浓度, 它们之间的交互作用分别解释氮浓度和磷浓度变异的13.77%和17.45% (表2)。种子氮浓度在氮磷比例为15或45时, 高量养分供应显著降低种子氮浓度, 而在氮磷比例为5时, 养分供应量没有显著影响(图2)。种子磷浓度在低养分

表2　氮磷供应量、比例及其交互作用对种子大小、氮浓度、磷浓度、萌发率和萌发速度的影响
Table 2　Effects of nitrogen (N) and phosphorus (P) supply levels, ratios and their interactions on the size, N concentrations, P concentrations, germination rates and germination speed of seeds

种子性状 Seed trait	氮磷供应水平 N and P supply level	氮磷供应比例 N:P supply ratio	交互作用 Their interaction
自由度 *d.f.*	2	2	4
种子大小 Seed size	0.74%^{ns}	4.41%*	5.38%^{ns}
氮浓度 N concentration	23.58%***	2.90%^{ns}	13.77%**
磷浓度 P concentration	23.21%***	7.07%**	17.45%***
萌发率 Germination rate	15.13%***	5.86%**	2.79%^{ns}
萌发速度 Germination speed	0.20%^{ns}	2.00%^{ns}	4.07%^{ns}

表中结果为两因素方差分析得到的各处理的方差解释率(%)和显著性水平。***, **, *, ns分别表示$p < 0.001$, $p < 0.01$, $p < 0.05$和$p > 0.05$.
Results in the table show the variance percentage explained by different treatments and the significance level from two-way ANOVA. ***, **, * and ns represent $p < 0.001$, $p < 0.01$, $p < 0.0$ and $p > 0.05$, respectively.

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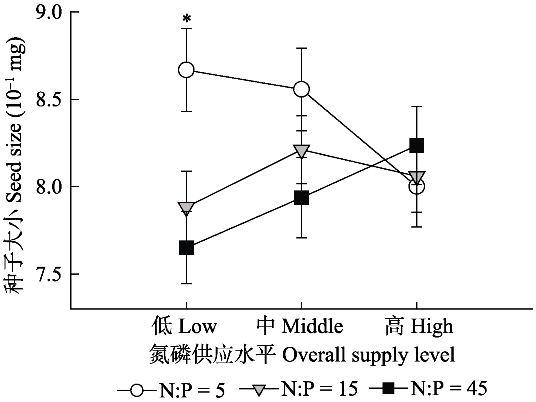

图1 氮磷供应量或比例对灰绿藜种子大小的影响(平均值±标准误差, *n* = 20)。*表示相同氮磷供应水平下不同氮磷比例的效应是显著的。

Fig. 1 Effects of N and P supply levels or ratios on seed size of *Chenopodium glaucum* (mean ± *SE*, *n* = 20). * represents a significant impact of N:P at the same nutrient supply level.

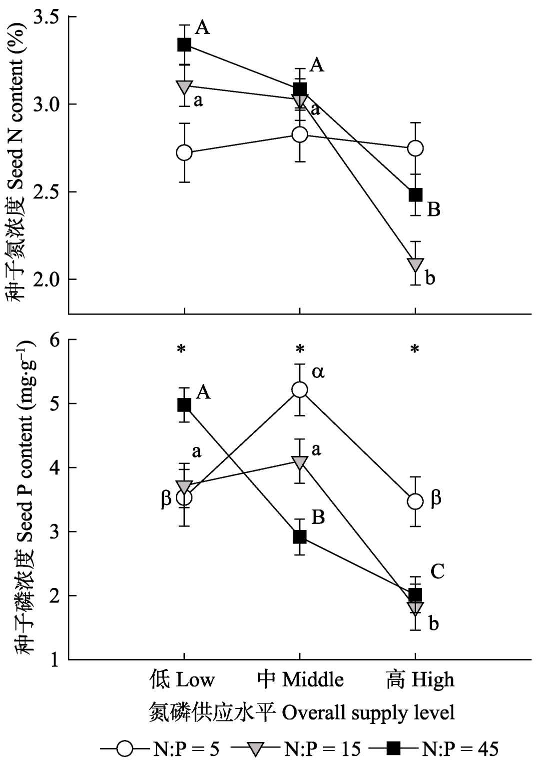

图2 氮磷供应量或比例对灰绿藜种子氮浓度和磷浓度的影响(平均值±标准误差, *n* = 20)。*表示相同氮磷供应水平下不同氮磷比例的影响是显著的。不同字母表示相同氮磷供应比例情况下不同氮磷量的效应是显著的。

Fig. 2 Effects of nitrogen (N) and phosphorus (P) supply levels or ratios on seed N and P contents of *Chenopodium glaucum* (mean ± *SE*, *n* = 20). * represents a significant effect of N:P at the same nutrient supply level. Different letters indicate a significant effect of nutrient supply level at the same N:P.

量水平下随着氮磷供应比例的增加而增加，而在中或高量水平下，磷浓度对氮磷比例的响应正好相反。氮磷比例为15或45时，高量养分供应显著降低种子磷浓度，而在氮磷比例为5时，磷浓度随着养分供应量没有明显趋势。

对于萌发性状来说，氮磷供应量和比例分别解释种子萌发率变异的15.13%和5.86% (表2)。在低量水平，种子萌发率随着氮磷比例的增加而显著增加(图3)，但是在中量或高量水平下，氮磷供应比例对萌发率没有显著影响。在氮磷供应比例为5、15或45的情况下，高量养分供应均显著降低萌发率。种子萌发速度不受任何处理的影响。

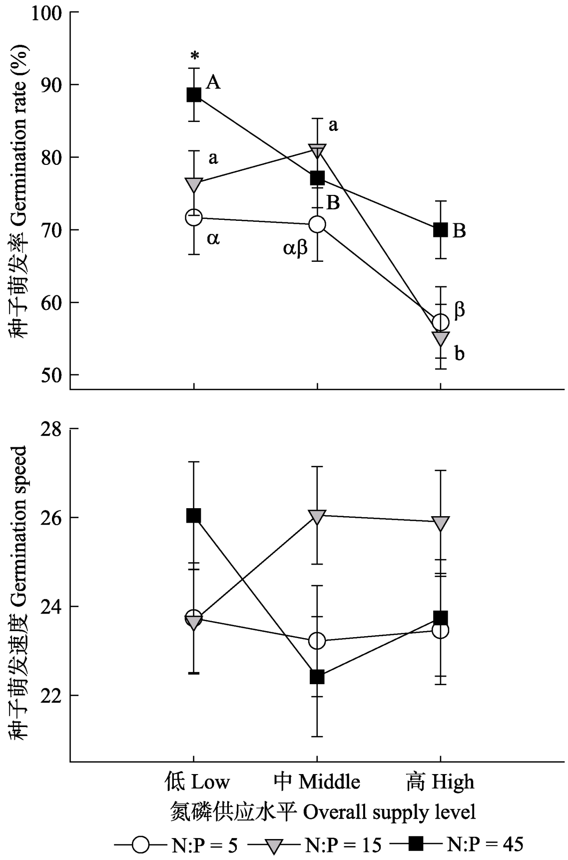

图3 氮磷供应量或比例对灰绿藜种子萌发率和萌发速度的影响(平均值±标准误差, *n* = 20)。*表示相同氮磷供应水平下不同氮磷比例的影响是显著的。不同字母表示相同氮磷供应比例情况下不同氮磷供应量的效应是显著的。

Fig. 3 Effects of nitrogen (N) and phosphorus (P) supply levels or ratios on seed germination rate and speed of *Chenopodium glaucum* (mean ± *SE*, *n* = 20). * indicates a significant effect of N:P at the same nutrient supply level. Different letters indicate a significant effect of nutrient supply level at the same N:P.

3 讨论

本研究的主要创新性在于系统区分和揭示了氮磷供应量、比例及其交互作用对植物种子性状影响的相对贡献。前人研究主要集中在氮或磷添加水平

对种子的影响, 并发现氮或磷供应量显著改变种子性状(Tungate *et al*., 2006; Breen & Richards, 2008; Fortunel *et al*., 2009; Hrdlickova *et al*., 2011; Hejcman *et al*., 2012)。与以往实验结果类似, 我们也发现氮磷供应量主要影响种子氮浓度、磷浓度和萌发率。但是, 我们发现种子磷浓度和萌发率同时也受到氮磷供应比例的影响, 而种子大小只受氮磷比例的影响, 说明未来土壤氮磷比例变化也会影响种子性状。这在以往相关研究中很少被揭示, 也经常被忽略掉。而且, 我们还发现种子氮浓度和磷浓度受氮磷供应量和比例之间交互作用的影响。这说明即使相同的养分供应水平, 对种子性状的影响效应也会随着氮磷比例的不同而发生变化。或者相同的氮磷供应比例的影响效应也会随不同的养分水平而发生变化。这些研究结果说明全球氮富集背景下自然生态系统中土壤氮磷变化对植物种子性状的影响是复杂的, 不仅仅是土壤氮或磷有效性变化的影响, 同时还掺杂着氮磷比例及其与氮磷供应量之间的交互作用。同时, 种子性状变化紧密关联未来植物种群和群落变化(Galloway, 2001; Leishman, 2001; Naegle *et al*., 2005; Li *et al*., 2017), 因此本实验也为我们认识全球养分富集对种群乃至群落的未来动态变化提供新的视角。

从种子形态性状来看, 在氮磷比例为5、15或45的情况下, 氮磷供应量对种子大小没有显著影响(图1)。这与前人的一项实验结果类似——Fortunel等(2009)基于地中海生态系统不同演替阶段的18个物种, 利用盆栽实验发现植物种子大小几乎不受养分添加的影响。但是, 我们发现在低量养分水平下, 高氮磷比例显著降低种子大小。这说明灰绿藜植物在贫瘠的环境中, 可能主要是土壤磷的有效性限制其种子大小(Vergeer *et al*., 2003)。然而, 该显著效应会随着养分供应水平的提高而消失, 指示出氮磷比例只有在养分匮乏的环境中才会对种子大小产生显著作用, 而在养分丰富的环境中对种子的影响不大。

从种子养分性状来看, 在氮磷比例为15或45的情况下, 低量养分供应显著提高种子氮浓度, 尽管在氮磷比例为5的情况下养分供应量的效应不显著。这与以往低养分条件对种子氮浓度影响的实验结果(降低或不影响)(Hrdlickova *et al*., 2011; Hejcman *et al*., 2012)不一致。具体原因可能如下: 1)高氮磷供应比例(15和45)比低氮磷比例(5)意味着更少的磷供应, 再随着氮磷供应量的减少就会出现更少的磷输入; 2)在低磷的环境中, 植物可能会主动增加种子氮浓度以增强后代应对不利环境的能力(Violle *et al*., 2009)。类似地, 氮磷比例为15或45的情况下, 低量养分输入增加种子磷浓度, 而在比例为5的情况下没有明显的增加趋势。这可能也是因为在磷非常匮乏的条件下, 植物主动在种子中累积更多的磷, 来补偿不利环境对植物及其后代的负面影响(Vergeer *et al*., 2003)。氮磷供应比例对种子氮浓度没有显著影响, 表明灰绿藜种子氮浓度对土壤氮磷有效性之间的相对变化不敏感。有意思的是, 在养分中等或高量水平下, 灰绿藜种子磷浓度随着氮磷供应比例的增加而降低, 说明种子磷浓度可能对土壤磷限制很敏感。但是在养分低量水平下, 种子磷浓度却随着氮磷供应比例的增加而增加, 进一步印证灰绿藜种子主动累积磷养分以应对严重磷缺乏环境这一结论。同样, 前人实验结果也显示种子磷浓度会随着土壤磷有效性的降低而表现出降低(Grant *et al*., 2001; Ma *et al*., 2002)或升高(Groom & Lamont, 2010)的响应, 并且相关研究表明同一植物种子的不同性状会对养分添加同时表现出适应性响应(adaptive response)和被动响应(passive response)(Sultan, 1996; Violle *et al*., 2009)。而我们的实验发现, 即使同一植物的同一种子性状(磷浓度)也会同时表现出对土壤氮磷相对有效性的适应性和被动响应。

从种子萌发性状来看, 我们发现在不同的氮磷比例情况下, 低的氮磷供应量均增加种子萌发率。这与以往实验发现低养分条件促进种子萌发率的结果(Hejcman *et al*., 2012; Li *et al*., 2017)一致, 而我们并没有发现氮磷供应量对种子萌发速度的影响(Hrdlickova *et al*., 2011; Li *et al*., 2017)。在低养分水平下, 高氮磷比例显著提高种子萌发率, 表明植物在土壤养分匮乏的情况下可能主要是氮有效性限制种子萌发率(Breen & Richards, 2008)。但是, 这些影响效应在养分丰富的环境中不存在, 指示出氮磷比例只有养分匮乏时才会对种子的萌发率产生影响。而灰绿藜种子的萌发速度对氮磷相对有效性不敏感。

总之, 本研究系统阐述氮磷供应量、比例及其交互作用对灰绿藜种子性状影响的相对重要性, 并发现不同种子性状对氮磷绝对有效性和相对有效性的响应不同。不同种子性状受到的氮或磷限制不同,

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种子性状同时也对氮或磷限制表现出适应性响应和被动响应。这些实验结果指示出氮或磷富集对植物性状影响的复杂性，这些复杂效应增加了在内蒙古草原养分富集背景下预测资源利用型草本种群乃至群落未来动态的不确定性。因此，未来需要更多的氮磷供应量和比例的正交实验来全面解析这些复杂效应。

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