



The allometry of reproductive allocation in a *Chloris virgata* population in response to simulated atmospheric nitrogen deposition

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Abstract

The quantitative relationship between the size of a plant and its reproductive output is a central aspect of its reproductive strategy. Resource availability influences plant size and the allocation of biomass to different structures. Here we investigate how variation in nitrogen (N) addition affects the allocation of biomass to vegetative and reproductive structures in a population of *Chloris virgata*. We used four levels of N addition to simulate atmospheric N deposition in the field, and evaluated size-dependent and size-independent effects on reproductive allocation. Total biomass of *C. virgata* increased with increasing N levels but decreased at the highest level (20 g m⁻² N). Reproductive output (mass of seeds produced) was higher when plants were fertilized with 2.5 g m⁻² N than in the control treatment (no N addition), but further increases in N did not result in a significant further increase in seed production. The relationship between size and reproduction in *C. virgata* in response to different N levels was largely allometric (size dependent), but there were also size-independent effects. *C. virgata* allocated absolutely more, but proportionally less, biomass to reproduction in response to increased N availability, except at the very highest level of N addition, where biomass production was lower. *C. virgata* is adapted to low nutrient levels, and this limits its ability to utilize high N levels to produce more offspring.

Zusammenfassung

Die quantitative Beziehung zwischen der Größe einer Pflanze und ihrer reproduktiven Leistung ist ein zentraler Aspekt ihrer Reproduktionsstrategie. Die Ressourcenverfügbarkeit beeinflusst die Größe der Pflanze und die Verteilung der Biomasse auf unterschiedliche Strukturen. Wir untersuchen hier an einer Population von *Chloris virgata*, wie die Veränderung der Stickstoffgabe (N) die Allokation der Biomasse auf vegetative und reproduktive Strukturen beeinflusst. Wir stellten vier Stufen der Stickstoffgabe her, um den atmosphärischen N-Eintrag im Freiland zu simulieren, und werteten größenabhängige und größenunabhängige Effekte auf die reproduktive Allokation aus. Die Gesamtbiomasse von *C. virgata* stieg mit zunehmender

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Stickstoffgabe, ging bei der höchsten Dosis (20 g N/m²) aber zurück. Die reproduktive Leistung (Masse der produzierten Samen) war bei einer Stickstoffgabe von 2.5 g N/m² höher als bei der Kontrolle ohne Stickstoffgabe, aber weitere Erhöhungen der Dosis erbrachten keine zusätzliche Steigerung der Samenproduktion. Die Beziehung zwischen Größe und Reproduktion als Reaktion auf unterschiedliche Stickstoffgaben war bei *C. virgata* weitgehend allometrisch, also größenabhängig, es gab aber auch größenunabhängige Effekte. *C. virgata* investierte als Antwort auf erhöhte Stickstoffgaben absolut mehr, aber proportional weniger, Biomasse in die Reproduktion, außer bei der höchsten N-Dosis, bei der die Biomasseproduktion geringer war. *C. virgata* ist adaptiert an ein geringes Nährstoffangebot, und dieser Umstand begrenzt ihre Fähigkeit, hohe Stickstoffgehalte für eine höhere Produktion von Nachkommen auszunutzen.

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Keywords: Allometric analysis; Reproductive allocation; Reproductive strategy

Introduction

Growth and reproduction are the most fundamental activities of plants, but there is often a tradeoff between these because allocation to one function often comes at a cost to other functions (Reekie & Bazzaz 2005). The pattern of reproductive allocation (RA) is a core component of a plant's life history strategy, which is the result of natural selection. Plants evolve different patterns of RA in response to different selection pressures. RA plays a critical role for plant adaptation by maximizing the overall fitness of plants growing in different environments (Bazzaz, Chiarello, Coley, & Pitelka 1987). Studies of RA are therefore useful in understanding the adaptation of plants to their natural environments.

Traditionally, allocation has been conceptualized as “partitioning” and reproductive effort (RE = [reproductive biomass]/[total biomass]) has been the measure of RA in many studies (e.g. Cheplick 2005). However, the partitioning approach is not consistent with the observation that RA is allometric in the broad sense, i.e. it changes with size. Most patterns of RA that have been investigated are size-dependent (Guo et al. 2012; McConnaughay & Coleman 1999; Weiner 2004). Therefore any factor that influences plant size will also affect RA (Weiner 2004), and individuals in a population can vary enormously in size due to a variety of factors, including size-asymmetric competition. Consequently, allometric analysis provides an effective method for distinguishing size-dependent from size-independent effects on variation in RA (Bonser & Aarssen 2009). This means analyzing the relationship between reproductive (R, y-axis) and vegetative (V, x-axis) biomass among individuals within a population. Analyzing size-dependent allocation is a principal step in understanding plant RA, but more information is needed before we can predict patterns of RA in response to different environmental conditions.

Atmospheric N deposition is an important component in the global N cycle (Phoenix et al. 2006) and has profound impacts on plant community structure and biodiversity in the terrestrial biosphere (Drenovsky & Richards 2005; Vourlitis & Pasquini 2009). By 2050, large areas of the planet will experience N deposition rates over twice those observed in the

1990s (Galloway et al. 2004). China is currently experiencing intense air pollution, much of which is a result of emissions of reactive N (Liu et al. 2013; Richter, Burrows, Nüß, Granier, & Niemeier 2005). Excess N deposition has negative effects on ecosystem performance and services: eutrophication results in N saturation (Aber et al. 1998) and a reduction in biodiversity (Hautier, Niklaus, & Hector 2009). Changes in the N cycle and in the soil quality resulting from N deposition affect plant growth and reproduction (Liu et al. 2011; Nadelhoffer et al. 1999). N addition not only affects plant biomass, it can also affect allocation to different plant structures (Pan, Bai, Han, & Yang 2005; Zhang et al. 2010). Atmospheric N deposition profoundly influences the structure and function of grassland ecosystems (Stevens, Dise, & Mountford 2004). Consequently, investigating species-level responses in RA is important for our understanding of the causes for community-level changes under global change in degenerated grasslands. To date, many studies have focused on RA in different environments (Hulshof, Stegen, Swenson, Enquist, & Enquist 2012; Sadras, Bange, & Milroy 1997), but there is limited information on how atmospheric N deposition affects the RA of plants.

Grassland degradation has been extensive in Songnen plain in northern China, with most areas experiencing soil salinity and alkalinity problems, which result in ionic imbalance and hyperosmotic stress in plants. Not only is productivity low, there are bare patches from the salt and alkaline conditions. *Chloris virgata* Sw. is a widely distributed annual grass with a high protein content, which makes it a high quality forage plant widely grown for hay, green forage, silage or grain. *C. virgata* is drought and alkaline tolerant and it can colonize bare alkaline patches, forming a relatively stable and productive community dominated by this single species (Zheng & Li 1999). *C. virgata* is therefore an important species for restoration of such degraded semi-arid grasslands. More information about the reproductive ecology of this species should be useful for utilizing its potential for grassland restoration. The objective of this study was to evaluate the effects of simulated atmospheric N deposition on reproductive allocation in this important species of degraded grasslands in China.

Materials and methods

Plant material

Like other grasses, *C. virgata* individuals consist of roots, vegetative tillers and reproductive tillers. Reproductive tillers of *C. virgata* have a spike above the vegetative organs. The spike can be divided into seeds (actually fruits) with glumes and reproductive support structures. The reproductive investment of *C. virgata* can be described in terms of the allocation of biomass to seeds or spikes.

Experimental design

The experiment was carried out at Northeast Normal University, Jilin Province, China in 2012. *C. virgata* seeds were collected from the Ecological Research Station for Grassland Farming, Chinese Academy of Sciences, in Changling, China (44°33' N, 123°31' E) in 2011. Fifty 20 cm diameter plastic pots were filled with local nutrient-poor sandy aeolian soil on 1 June 2012. Twenty seeds were sown in each pot, and 10 days later the germinated seedlings were thinned to five individuals. There were 5 treatments, corresponding to 0, 2.5, 5.0, 10.0, 20.0 g m⁻² N, which were created by adding NH₄NO₃ (CN = 35%) to the pots 30 d after seeding emergence to simulate atmospheric N deposition. The N addition levels were chosen based on the current atmospheric N deposition level and its predicted change in the next 50 years, based on existing experiments in semi-arid temperate steppe of China, where *C. virgata* is widely distributed (Jia et al. 2015; Pan et al., 2005). The average annual bulk deposition of N in China increased by approximately 7 kg N/ha from the 1980s (13.2 kg N/ha) to the 2000s (20.1 kg N/ha; Liu et al. 2013). Atmospheric N deposition in Jilin province in 2007 was 13.79 kg ha⁻¹ yr⁻¹ (Lü & Tian 2007). Initially, there were 10 replicates of each level and 10 control pots to which no NH₄NO₃ was added. Some pots were damaged by locusts during the course of the experiment and were excluded from the analyses. The final number of pots were 6, 8, 7, 8 and 7 for the 5 N levels, respectively, giving 30, 40, 35, 40 and 35 individuals. Pots were arranged in a randomized block design outdoors under a rain shelter made from transparent 200-μm polyethylene sheeting on 1 June 2012.

Sampling procedure and data collection

On 20 September 2012, when all *C. virgata* individuals were fully mature and senescing, the number of non-reproductive and reproductive tillers of *C. virgata* were recorded for each individual in each pot. The plants were then harvested at soil level. Each plant was harvested above ground and separated into vegetative and reproductive tillers. Reproductive tillers were further divided into vegetative structures, reproductive support structures and seeds. All the separated components of the samples were put into individual paper

bags, dried at 65 °C for 48 h in the laboratory and then weighed. Below, we use the following terms for the separated biomass components.

Seed mass: mass of seeds produced by a plant;

Non-seed biomass: total above-ground biomass excluding seed mass;

Reproductive biomass: all structures above the last joint on the spike, including seeds;

Vegetative biomass: total above-ground biomass minus reproductive biomass;

Reproductive support structure biomass: reproductive biomass minus seed mass.

Data analysis

One-way ANOVA was used to analyze reproductive tiller number, non-reproductive tiller number, non-reproductive tiller biomass, reproductive tiller biomass, seed mass, total above-ground biomass and the allocation to different components under different N levels. Differences between different N levels were tested using the Least Significant Difference (LSD) test, with significance level of $P \leq 0.05$. All analyses were performed with SPSS statistical software (version 17.0, SPSS Inc., Chicago IL, USA).

To analyze allocation patterns allometrically and to homogenize variance, biomass values were log transformed. Allometric relationships among individuals were analyzed by the log transformed version of the classical “allometric” model: $\log Y = a \log X + b$, where a is the allometric slope and b (intercept) is the log of the allometric coefficient. Standardized Major Axis (SMA) regression was used to determine the slopes and intercepts using the software package SMATR (Standardized Major Axis Tests and Routines; Warton, Wright, Falster, & Westoby 2006). The slopes were first tested to determine whether they were significantly different from 1 for each allometric relationship. We then compared the difference in allometric slopes among N levels. If the slopes were not significantly different, the intercepts were tested.

Results

Reproductive and non-reproductive tiller growth

Growth and reproduction in our *C. virgata* population responded differently to simulated atmospheric N deposition. Reproductive and non-reproductive tiller number responded strongly to N addition (Fig. 1A). The reproductive tiller number was significantly higher in the 2.5 g m⁻² N treatment than the control, but remained unchanged above 2.5 g m⁻² N. The number of non-reproductive tillers increased significantly from 0 to 2.5 g m⁻² N, was similar at 2.5–10.0 g m⁻² N, and was lower at 20.0 g m⁻² N than at 10.0 g m⁻² N. The

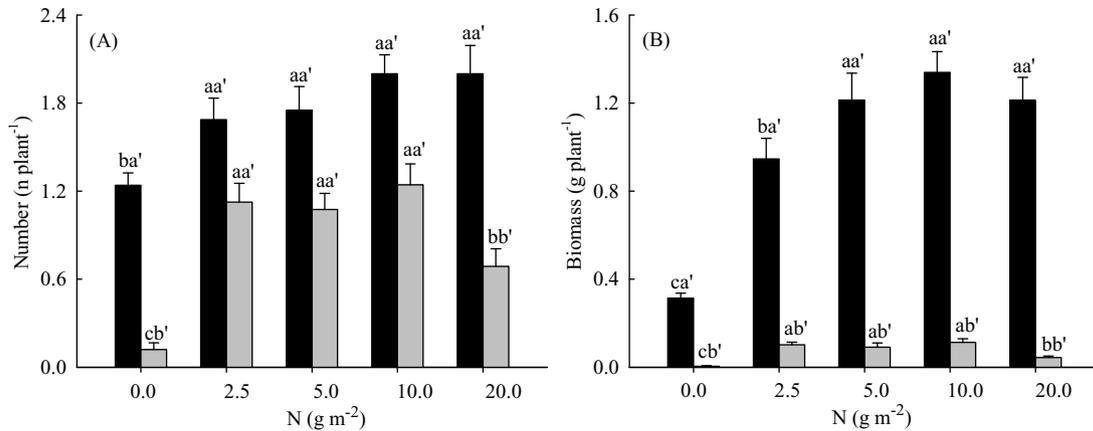


Fig. 1. Effects of N fertilization level on (A) number and (B) biomass of reproductive and non-reproductive tillers of *C. virgata*. ■ : reproductive tillers; ■ : non-reproductive tillers. Error bars indicate SEs. Means with different letters attached to them are significantly different at $P < 0.05$; letters a, b, and c are used for comparisons between treatments, while a', b' and c' are used for comparisons within N treatments.

number of reproductive tillers was higher than that of non-reproductive tillers in the control and 20.0 g m⁻² N treatments, while there were no significant differences between reproductive number and non-reproductive number from 2.5 to 10.0 g m⁻² N.

Nitrogen markedly increased reproductive tiller biomass from 0 to 5.0 g m⁻² N, above which there was no further change (Fig. 1B). The non-reproductive tiller biomass increased significantly from 0 to 2.5 g m⁻² N, was similar at 2.5–10.0 g m⁻² N, and was lower at 20.0 g m⁻² N than at 10.0 g m⁻² N. The highest reproductive and non-reproductive tiller biomass occurred at 10.0 g m⁻² N, the highest values being 1.34 and 0.11 g, respectively. The lowest reproductive and non-reproductive tiller biomass occurred in the control pots, 0.31 and 0.004 g, respectively. The reproductive tiller biomass was significantly higher than that of non-reproductive tiller at all N levels.

Biomass allocation

The total biomass of *C. virgata* increased sharply from 0 to 5.0 g m⁻² N, but did not significantly change with further addition of N (Fig. 2A). The highest total biomass, 1.47 g, was observed at 10.0 g m⁻² N. There was no difference in the seed mass of *C. virgata* when N levels increased from 2.5 to 20.0 g m⁻² N, but seed mass was significantly higher than in the control treatment in all added N treatments (Fig. 2A).

Changes in the N level did not affect the percent allocation to reproductive support structure biomass (Fig. 2B), but allocation to seed mass and vegetative biomass varied significantly among treatments (Fig. 2B). Allocation to seed mass was lowest at 5.0 and 10.0 g m⁻² N, and the highest at control. The allocation to vegetative biomass was lowest in the control treatments, increased from 0 to 5.0 g m⁻² N and then decreased at 20.0 g m⁻² N.

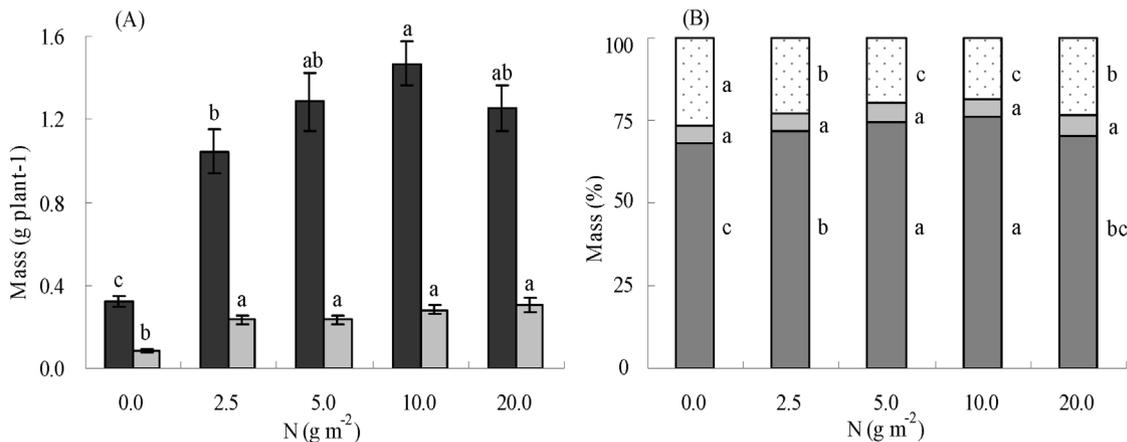


Fig. 2. Effects of N fertilization level on (A) total biomass (black bars) and seed mass (gray bars) and allocation to the different fractions of *Chloris virgata* biomass (vegetative, dark gray; reproductive support structures, light gray; seeds, white). Error bars indicate SEs. Treatments with the same letter (a, b, c) are not significantly different at $P < 0.05$.

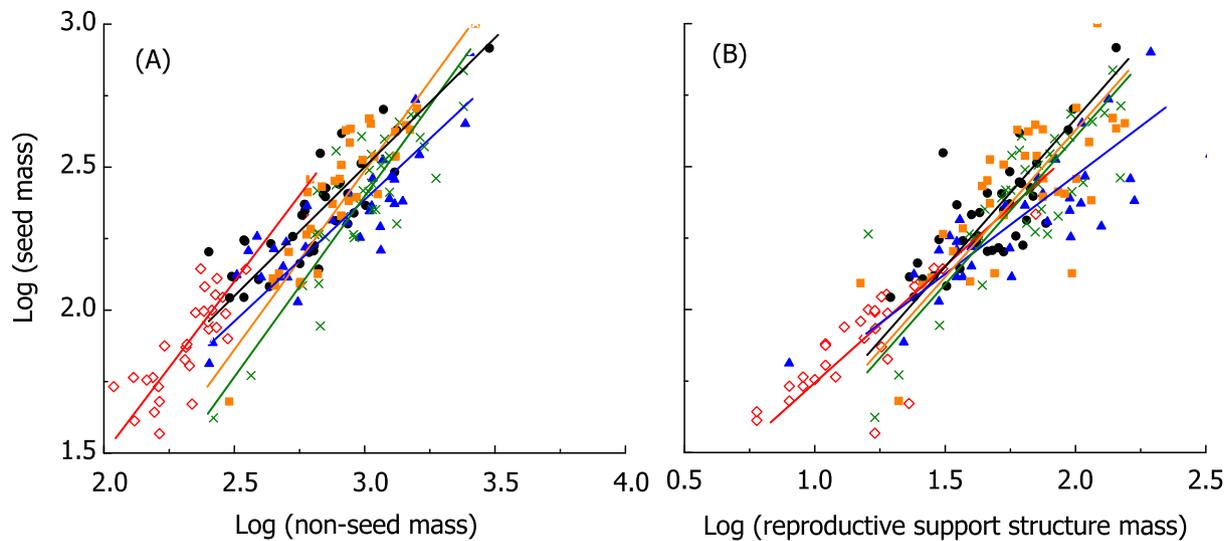


Fig. 3. Allometric relationships between seed mass vs. non-seed mass (A) and seed mass vs. reproductive support structure mass (B) of *Chloris virgata* grown at N addition levels 0 (\diamond), 2.5 (\bullet), 5.0 (\blacktriangle), 10.0 (\times) and 20.0 (\blacksquare) g m^{-2} N.

Reproductive allometric relationships

The allometric relationships between seed mass and reproductive support structure biomass, and between seed mass and non-seed biomass, differed among the treatments (Fig. 3 and Table 1). The slopes of the SMA regression decreased at intermediate (5.0 g m^{-2} N) levels of added N and then increased again (Table 1). The slope of the relationship between seed mass and non-seed biomass at 5.0 g m^{-2} N level was significantly lower than 1 (lower and upper 95% CIs = 0.71 and 0.99, respectively; Table 1). In addition, the slopes of seed mass vs. non-seed biomass were significantly higher than 1 at 10.0 and 20.0 g m^{-2} N treatments (Fig. 3A, Table 1).

The allometric relationship between reproductive biomass and vegetative biomass was also affected by the N level as indicated by different slopes (Fig. 4 and Table 1). The slopes of the SMA regression were lower at 2.5 and 5.0 g m^{-2} N levels than at lower and higher N levels (Table 1), where the slopes were significantly higher than 1 (Fig. 4 and Table 1).

Discussion

Reproductive and non-reproductive tiller growth

Different biotic and abiotic environments select for different reproductive strategies (Sugiyama & Bazzaz 1998; Wang & Wang 2015). The reproductive strategy selected in a given environment should maximize fitness. Offspring are the currency of natural selection, but plants must first accumulate resources to build up the reproductive machinery (Weiner, Campbell, Pino, & Echarte 2009). A plant's morphology, e.g.

the numbers meristems that can develop into branches, can limit reproduction. In *C. virgata*, reproductive tiller number was one of the major factors influencing reproductive output, and our results show a trade-off between reproductive and non-reproductive tiller numbers. Once a bud of *C. virgata* develops into a tiller, the plant makes a decision whether this tiller will become reproductive or remain non-reproductive. This decision is based to some degree on environmental conditions. Since the plant cannot always predict the future accurately, such a decision is not always optimal, especially when the conditions are different from those in the recent evolutionary history of the population.

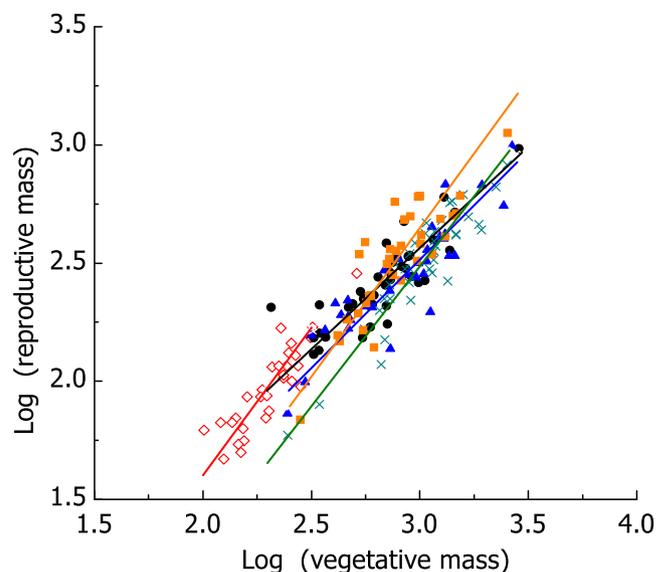


Fig. 4. Allometric relationships between reproductive mass and vegetative mass of *Chloris virgata* grown at N fertilization levels 0 (\diamond), 2.5 (\bullet), 5.0 (\blacktriangle), 10.0 (\times) and 20.0 g m^{-2} N.

Table 1. Effects of N level on the slopes and intercepts of allometric relationships between log (total seed mass) and log (non-seed biomass), log (reproductive biomass) and log (vegetative biomass), log (seed mass) and log (reproductive support biomass) of *Chloris virgata* grown at 5 levels of N addition, using Standardized Major Axis. Values with different letters are significantly different at $P < 0.05$.

	N addition (g m^{-2})				
	0	2.5	5.0	10.0	20.0
Log (total seed mass) vs. log (non-seed biomass)					
Slope	1.18 ^a	0.90 ^b	0.84 ^b	1.24 ^a	1.33 ^a
Intercept	-0.87	-0.25	-0.16	-1.36	-1.48
R^2	0.75	0.72	0.79	0.82	0.81
CI of slope	0.98–1.432	0.75–1.08	0.71–0.99	1.07–1.43	1.33–1.14
log (reproductive biomass) vs. log (vegetative biomass)					
Slope	1.20 ^a	0.85 ^b	0.91 ^b	1.18 ^a	1.25 ^a
Intercept	-0.80	0.021	-0.22	-1.07	-1.11
R^2	0.79	0.72	0.81	0.85	0.74
CI of slope	1.01–1.43	0.71–1.01	0.78–1.07	1.04–1.35	1.05–1.50
Log (total seed mass) vs. log (reproductive support structure mass)					
Slope	0.81 ^{a,b}	1.02 ^a	0.69 ^b	1.03 ^a	1.03 ^a
Intercept	0.94	0.62	1.09	0.55	0.57
R^2	0.63	0.63	0.67	0.63	0.52
CI of slope	0.64–1.02	0.83–1.25	0.56–0.85	0.83–1.267	0.78–1.36

Biomass allocation

The results clearly indicate that an increased allocation to vegetative biomass relative to the control treatment due to increased N levels does not necessarily affect seed production: seed mass produced did not differ from 2.5 to 20.0 g m^{-2} N. The proportional allocation of biomass to seeds was highest in the control treatment (Fig. 2B). The higher percent allocation to seeds in the control treatment may be due to nutrition limitation. Low resource levels can induce flowering or result in higher allocation to reproduction as plants have been selected to reproduce as much as possible when prospects for further growth or survival are limited. Similarly, plants sometimes postpone reproduction when they have access to high resource levels, presumably because chances are good that the plant can increase its size and potential reproduction later (Weiner et al. 2009). Surprisingly, the biomass of seeds produced was the same for all N levels except the lowest (control treatment). Most studies show increased seed production at higher N availability (Galloway 2001; Sultan 2001), which is why N fertilization usually increases yield, but some studies on wild species show little or no effect on seed production in response to increased N supply (Luzuriaga, Escudero, & Pérez-García 2006; Silvertown, Franco, & Harper 1997; Weiner, Martinez, Müller-Schärer, Stoll, & Schmid 1997). In our study total above-ground biomass was unchanged from 5.0 to 20.0 g m^{-2} N (Fig. 3A), consistent with previous results (Neff et al. 2002; Tian et al. 2012). Similarly, the overall productivity of the Horqin Sand Land vegetation, including *C. virgata*, remained stable under simulated N deposition of 5.0 and 10.0 g m^{-2} N (Jiang et al. 2011). We conclude that the ability of this species to utilize very high N levels (20.0 g m^{-2} N) may be limited. This may

be due to the evolutionary history of *C. virgata* in NE China. It is adapted to very low N levels (Wang, Seki Katsutoshi Miyazaki, & Ishihama 2009), so it cannot use high levels of N efficiently (Jia, Li, & Xiao 2005). It is even possible that high N levels could have toxic effects, but there was no evidence of this and we could find no information on potential N toxicity in this species.

Reproductive allometric relationships

Species performance depends on their ecological strategies, revealed by suites of traits, conferring different relative ecological advantages in different environments (Fortunel et al. 2009). According to optimal allocation theory, plants should allocate all resources to growth for most of their lives, and then switch at a certain time to investing all resources into reproductive to maximize seed production. This strategy has evolved in monocarpic species (Ellner 1987). *C. virgata* does not show an extreme example of a monocarpic or a polycarpic strategy. Rather *C. virgata* invests more resources to reproductive organs when the environment becomes less favorable.

Allometric analyses can be useful in understanding many plant behaviors (Weiner 2004). The relationship between seed mass and reproductive support structure biomass, seed mass and non-seed biomass, as well as reproductive biomass and vegetative biomass followed plastic allometric trajectories (Figs. 3 and 4; Table 1), implying that size-dependent effects are important for reproductive allocation of *C. virgata* in response to N availability, but there are also size-independent effects. High reproductive allocation under poor conditions could be adaptive for *C. virgata*, which

often faces nutrition deficiency in Songnen grasslands (Wang, Mu, Yu, & Li 2008). Size-independent changes in reproductive allocation can buffer plant populations from the effects of environmental variation (Ghalambor, Mckay, Carroll, & Reznick 2007; Niu, Choler, Pino, & Echarte 2009). Therefore, the ability to reproduce under such conditions is crucial for this annual species.

The slopes of seed mass vs. reproductive support structure biomass were not significantly different from 1, which means that the increase in seed mass was proportional to the increase in reproductive support structure biomass. This makes intuitive sense because both these variables reflect reproductive output, and this result is consistent with previous studies (Echarte & Andrade 2003; Schmid & Weiner 1993). In contrast, two out of five slopes of seed mass vs. non-seed mass were significantly higher than 1, which means that larger plants allocated proportionally more biomass to seeds than to other structures. This also indicates that once a bud of *C. virgata* has developed into a reproductive tiller it will maximize its reproductive output, i.e. its fitness.

In conclusion, our results suggest that *C. virgata* will benefit from some N deposition, but its adaptation to low N conditions will limit its ability to benefit greatly at high N levels. In areas with very high N input, it is likely that other species will do better at the expense of *C. virgata*.

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