GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 17 (2016) 388–395
Basic and Applied Ecology
www.elsevier.com/locate/baae

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

Ying Wang[a], Lei Li[b], Dao-wei Zhou[c,*], Jacob Weiner[d]

[a]*Key Laboratory of Songliao Aquatic Environment, Ministry of Education, Jilin Jianzhu University, Changchun 130118, China*
[b]*Center for Watershed Ecology, Institute of Life Science, Nanchang University, Nanchang 330031, China*
[c]*Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130012, China*
[d]*Department of Plant and Environmental Sciences, University of Copenhagen, DK-1871 Frederiksberg, Denmark*

Received 28 January 2015; received in revised form 21 January 2016; accepted 27 January 2016
Available online 4 February 2016

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

*Corresponding author. Tel.: +86 0431 85542231.
E-mail address: zhoudaowei@iga.ac.cn (D.-w. Zhou).

http://dx.doi.org/10.1016/j.baae.2016.01.004

Stickstoffgabe, ging bei der höchsten Dosis (20 g N/m^2) aber zurück. Die reproduktive Leistung (Masse der produzierten Samen) war bei einer Stickstoffgabe von 2.5 g N/m^2 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.

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.