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Contrasting effects of precipitation and fertilization on seed viability and production of *Stipa krylovii* in Mongolia

Katrin Ronnenberg[a,b,*], Isabell Hensen[a], Karsten Wesche[b]

[a]*Institute of Biology, Dept. of Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, 06099 Halle, Germany*
[b]*Senckenberg Museum of Natural History Görlitz, PO Box 300 154, 02806 Görlitz, Germany*

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Abstract

In drylands, primary production is predominantly limited by water availability; however, there is evidence for co-limitation by nutrients. We tested whether improved water and nutrient availability facilitate reproduction of dominant steppe species, and studied the effects of increased moisture and fertilization on seed production of the steppe grass *Stipa krylovii*.

Effects of water availability on seed production and seed viability were investigated in a large-scale study on three sites with decreasing precipitation in Mongolia, over three to five consecutive years. In dry southern Mongolia, we additionally conducted an *in situ* irrigation and fertilization experiment to clarify the role of environmentally induced effects on seed production.

Seed viability of *S. krylovii* was negatively correlated with annual precipitation over five years at the driest study site. The relation between annual precipitation and seed viability in the large-scale study was not as clear, however, in the two moister regions there was a trend of lower seed viability. Experimental irrigation also significantly decreased seed viability and seed mass. Seed production per hectare was not affected by irrigation, while fertilization resulted in a more than fivefold increase in both seed weight and number of viable seeds. The underlying mechanisms for these unexpected results were not investigated. However, a switch from cleistogamous pollination under dry conditions to less effective cross-pollination in moist years may be an explanation. Our data indicate that plant reproduction may show complex and unexpected reactions, and that nutrient limitation must be considered in global change scenarios even for dry regions.

Zusammenfassung

In Trockengebieten ist die Primärproduktion vor allem durch Wasserverfügbarkeit limitiert, es gibt jedoch auch Hinweise auf eine Ko-Limitierung durch Nährstoffe. Wir haben getestet, ob sich Wasser- und Nährstoffverfügbarkeit auf die Reproduktion eines dominanten Steppengrases auswirken. Dazu untersuchten wir die Auswirkung unterschiedlicher Bewässerung und Düngung auf die Samenproduktion und–qualität der Federgrasart *Stipa krylovii*. Den Effekt der Wasserverfügbarkeit testeten wir in einem großräumigen Vergleich abnehmender Niederschläge in der Mongolei; die Messungen liefen über drei bis fünf aufeinanderfolgende Jahre. Darüber hinaus führten wir in der südlichen Mongolei, im trockensten der drei Untersuchungsgebiete, ein *in situ* Experiment mit Beregnung und Düngung durch, um die Rolle von umweltinduzierten Effekten auf die Samenproduktion zu analysieren.

*Corresponding author at: Institute of Biology–Dept. of Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, 06099 Halle, Germany. Tel.: +49 0581 4760; fax: +49 3581 4760 5102.
E-mail address: katrin.ronnenberg@botanik.uni-halle.de (K. Ronnenberg).

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Die Samenlebensfähigkeit im trockensten Untersuchungsgebiet korrelierte signifikant negativ mit dem jährlichen Niederschlag. Das Verhältnis zwischen jährlichem Niederschlag und Samenlebensfähigkeit in der großräumigen Studie verhielt sich weniger eindeutig; die Lebensfähigkeit in den feuchteren Regionen war jedoch tendenziell niedriger. Experimentelle Bewässerung reduzierte sowohl die Samenlebensfähigkeit als auch das Samengewicht. Die Gesamtproduktion von Samen pro Hektar wurde durch die Bewässerung nicht beeinflusst; Düngung hingegen führte zu einer mehr als fünffachen Zunahme von Gesamt-Samengewicht und Anzahl lebensfähiger Samen.

Die Ursachen für diese unerwarteten Ergebnisse wurden von uns nicht untersucht, jedoch könnte ein Wechsel von kleistogamer Bestäubung bei trockenen Bedingungen zu weniger effektiver Fremdbestäubung in feuchteren Jahren unsere Ergebnisse erklären. Unsere Daten zeigen, dass die Reproduktion von Pflanzen komplexe und unerwartete Reaktionen auf den Klimawandel zeigen könnte, und dass Nährstoffmangel in entsprechenden Zukunftszenarien selbst für sehr trockene Gebiete einbezogen werden sollte.

Keywords: Central Asia; Drylands; Irrigation; Nitrogen deposition; Nutrient limitation; Poaceae; Reproduction; Seed ecology; Steppes; Water availability

Introduction

In arid environments water is regarded as the driving force limiting plant productivity and performance (Noy-Meir 1973). Water availability is thus the main topic of discussions on potential climate change effects on the vast drylands of Central Asia (Christensen, Coughenour, Ellis, & Zuo 2004; Zheng, Xie, Robert, Jiang, & Shimizu 2006). Recent climate change scenarios predict an increase in precipitation for the Gobi and the deserts of north-western China (Gao, Zhao, & Giorgi 2002; Christensen et al. 2007). Following more favourable water conditions, nutrient availability may become increasingly important (Hooper and Johnson 1999; LeBauer and Treseder 2008). Nitrogen depositions are also predicted to increase in Central Asia (Galloway et al. 2004), however, experimental tests on water and/or nutrient limitation on plant growth are scarcely available for the region.

Precipitation is known to have pronounced effects on plant vigour, including reproductive parameters (Wang and Gao 2004; Wesche, Ronnenberg, Retzer, & Miehe 2010). Considerable differences in seed numbers and/or seed quality have been reported between habitats occupied by a given species (Renison, Hensen, & Cingolani 2004; Loha, Tigabu, Teketay, Lundkvist, & Fries 2006), and also between years (Houle and Filion 1993). Some populations, especially in harsh environments, produce few viable seeds and almost exclusively depend on prolonged clonal growth for long-term persistence (Liang, Michalk, & Millar 2002; Honnay and Bossyut 2005; Wesche, Ronnenberg, & Hensen 2005). These differences in reproductive strategies can either be genetically determined (e.g. Bischoff, Vonlanthen, Steinger, & Müller-Schärer 2006) or they are the result of phenotypic plasticity as a response to different maternal environments. Nutrients are also known to affect reproductive activity in plants (especially P-limitation, Marschner 1995), corroborated by evidence for co-limitation of nutrient and water availability affecting seed number and quality in the Californian desert shrub *Sarcobatus vermiculatus* (Breen and Richards 2008). Recent evidence also indicates that nutrient limitation may constrain plant performance in arid northern hemisphere grasslands, including the arid steppes of southern Mongolia (Slemnev, Sanjid, Khongor, & Tsooj 2004; Harpole, Potts, & Suding 2007; Wesche, Nadrowski, & Retzer 2007).

The genus *Stipa* is widespread and dominant in large parts of the zonal grasslands of the northern hemisphere (Lavrenko and Karamysheva 1993). Our study species *S. krylovii* is widespread and important as a fodder plant in Central Asia, where it is typical of the dry southern Mongolian mountain steppes and semi-deserts (Wesche, Miehe, & Miehe 2005).

Over the course of 3–5 years, we investigated the main indicators of seed production and seed quality of *S. krylovii* in three study sites of decreasing precipitation in Mongolia. Additionally, a factorial field experiment combining the factors water and nutrients was conducted at our driest study site.

The following hypotheses were tested: (1) Water availability positively affects seed production, seed mass and seed viability of *S. krylovii*. (2) Measures of seed production are thus higher in moister regions and increase in moist years in a given region (3) Fertilization enhances seed-production, mass and viability.

To our knowledge, this is the first time that reproductive traits of one of the most important grass species of the Central Asian steppes have been studied comparing several sites and years in a large-scale study.

Materials and methods

Study sites

The main study site for seed (*sensu stricto*: caryopses) collection and field experiments was situated at an altitude of 2300 m asl. (N 43°36.76′; E 103°46.36′) in the Dund Saykhan mountain range in Gobi Gurvan Saykhan National Park, southern Mongolia (Fig. 1). This region receives an estimated 180 mm mean annual precipitation (Hijmans, Susan, Cameron, Parra, & Jones 2005, Table 1). The two other