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Research Paper

Grassland experiments under climatic extremes: Reproductive fitness versus biomass

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ABSTRACT

Too little is known about changes in plant reproduction caused by modified regimes of extreme weather events. While it is important to understand how climatic extremes affect physiological processes in leaves or roots, on a long scale, it is successful reproduction, which ultimately matters. In an experimental grassland, we investigated the vegetative response and reproductive fitness of the grasses *Holcus lanatus* and *Arrhenatherum elatius* to drought and heavy rainfall. We perform a quantitative analysis of biomass, number of flowers per inflorescences, seed weight, germination rate and establishment. Target species were sampled from three grassland assemblages (two species-communities, four-species communities with and without a legume).

H. lanatus reacted with a reduced number of flowers per inflorescences and a reduced germinability to climatic extremes. Nevertheless, *H. lanatus* reacted with an increased seedling establishment in face of extreme weather events. However, the two investigated grass species responded differently in the same experimental communities. *A. elatius* reached a higher number of flowers per inflorescences, higher germination rate, and higher establishment when exposed to drought compared to control.

Yet, heavy rainfall and respective water-saturated soil conditions influenced both grasses more negatively, i.e., leading to a lower number of flowers per inflorescences, germination rate and reproductive biomass, than extreme drought.

This study illustrates that the impact on reproduction during short periods needs consideration when long-term responses of grassland ecosystems to climate change are assessed.

1. Introduction

Reproduction is crucial for the survival and evolution of non-clonal plant species' populations. The reproductive phase is comparatively short at the scale of plant life cycles. However, this phase is particularly sensitive to negative impacts. Despite its potential importance, however, reproductive fitness is rarely studied in global change experiments.

Besides temporal trends in long-term average conditions, climate change is associated with changes in climatic variability and extreme events (Min et al., 2011; IPCC 2012). Evidently, an increasing frequency and magnitude of climatic events modifies probabilities of occurrence and even reduces statistical extremeness of particular events (Hegerl et al., 2011). Nevertheless, an increasing stress to plant life is expected dependent on the timing of extreme weather events and plant life stages (Walter et al., 2012; Orsenigo et al., 2014; Kazan and Lyons, 2016; Zeiter et al., 2016). Short events during sensitive periods can be expected to have stronger impacts on plants and plant communities than changes in average conditions (Easterling et al., 2000; Jentsch et al., 2007; Smith 2011).

Gutschick and BassiriRad (2003) point out that selection is the strongest on an evolutionary timescale during extreme events. Notably, the authors focus on extreme events where the extreme relates specifically to the investigated organisms. Understandably, disadvantageous conditions during the critical stage of reproduction are relevant (Kazan and Lyons, 2016). Extreme events can hamper reproduction of individual species with consequences for dominance patterns and community composition.

Research on the reproduction of grass species under extreme climatic events such as drought or heavy rain is scarce (e.g. Zeiter et al.,

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2016). Obviously, most studies and meta-analyses on effects of extreme events in grassland focus on biomass (e.g. Isbell et al., 2015), which is also the common currency at the global scale in grassland biodiversity research (Fraser et al., 2015).

Zeiter et al. (2016) found that drought reduces reproductive output of grasses, which was related to the reproductive shoot and to seed rain. Single-plant pot experiments and monocultures are difficult to compare with old-growth stands due to juvenile plants, the lack of competition, reduced species richness and functional diversity, and immature biotic interactions with soil biota, pollinators, and herbivores (Grime et al., 2000; Beierkuhnlein and Neßhöver, 2006; Hector et al., 2007; Gellesch et al., 2015; Zeiter et al., 2016).

Meta-analyses hint that extreme drought reduces biomass production across grasslands while extreme wet periods tend to increase biomass production (Isbell et al., 2015). Vegetative plant tissue was found to respond differently to drought in metabolic products above- and below-ground (Gargallo-Garriga et al., 2015; Kreyling et al., 2008). Comparably, conclusions on the reproductive fitness cannot been drawn from observations on the vegetative fitness (Gellesch et al., 2015).

The expected changes in the variability of precipitation include a higher likelihood of heavy rainfall. However, due to the even shorter duration and high natural stochasticity of heavy precipitation, there is a lack of studies on ecological effects of heavy rainfall, which also applies to the reproductive output of grasses (Zeiter et al., 2016). In a previous study, we found hints that precipitation variation shifts the reproductive success, i.e. the number of seeds multiplied by the germination rate of plants (Gellesch et al., 2015). For example, a shift in the carbon uptake of grasslands is reported by several authors (Fay et al., 2008; Prevéy and Seastedt 2015).

With the possible consequences of extreme events on plant reproduction in mind, we study two common and widespread model species: *Arrhenaterum elatius* (L.) P. Beauv. ex J. Presl & C. Presl and *Holcus lanatus* (L.). The study was conducted in the EVENT experiment in Bayreuth, where the temperate climate of Central Europe was artificially manipulated towards more extreme conditions. In this experiment, numerous plant traits of these species had been investigated, e.g. ANPP and tissue die-back (Kreyling et al., 2008), leaf protein content, leaf nitrogen isotope signal (Jentsch et al., 2011), leaf water potential, leaf gas exchange, biomass (Otieno et al., 2012), interaction strength (Grant et al., 2014), and legume facilitation (Arfin Khan et al., 2014). Most of these studies investigated vegetative parameters only; however, considering these parameters can give a deeper understanding of the reproductive fitness.Here, we assessed parameters for reproductive fitness (reproductive biomass, number of flowers per inflorescences, seed weight, germination rate, and establishment) under drought and heavy rainfall.

We hypothesize that (i) reproductive fitness will decrease under drought stress and (ii) reproductive fitness should also be diminished after a heavy rainfall event.

2. Materials

2.1. Experimental design and plant community composition

The EVENT experiment (Jentsch et al., 2007) was established in the Ecological Botanical Garden of the University of Bayreuth, Germany (49°55′19″N, 11°34′55″E, 365 m above sea level), by planting grassland species in the year 2005. The mean annual temperature of the site is 8.2 °C and the mean annual precipitation is 724 mm (1971–2000). The experiment has been carried out with two fully-crossed factors. The factors were climate treatments (three levels: drought, heavy rainfall, and control) and community composition (three richness levels: four-species, i.e., grasses *Arrhenaterum elatius* and *Holcus lanatus* and the herb *Plantago lanceolata* with the legume *Lotus corniculatus* abbreviated "GL", or four-species with the non-legume *Geranium pretense* abbreviated "G4", or two- grass species abbreviated "G2"; see Table 1 for more details). The experimental design consisted of 45 plots (three weather treatments × three community compositions × five replications). Plots were 2m × 2 m in size. The data acquisition was carried out in the central square meter of each plot in order to avoid edge effects. Experimental plant communities (G2, G4, and GL) were blocked and randomly assigned within each of the five replications of each climate manipulation (drought, heavy rainfall, and control; see also supplement 1). 100 plant individuals per plot were planted in a defined quantitative composition in a systematic hexagonal grid with 20 cm distance between individuals in April 2005. The original species composition was maintained by weeding three times per year. The experimental site was built-up artificially (about 80 cm in depth) with homogenized sandy subsoil from a nearby quarry. Underlain drainage facilities were installed to avoid soil related heterogeneity. The upper layer (20 cm depth) consisted of homogenized topsoil of the quarry containing high amounts of organic material. The texture of the soil body was loamy sand (82% sand, 13% silt, 5% clay) with a pH(KCl) of 4.5 and 0.07% total N in the upper layer, and with a pH(KCl) of 6.2 and 0.01% total N in the lower soil layer.

Table 1
Experimental plant communities of the present study.

Community	Description	Species
G2	two species, one functional group (grass)	*Arrhenatherum elatius, Holcus lanatus*
G4	four species, two functional groups (grass, herb)	*Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata, Geranium pratense*
GL	four species, three functional groups (grass, herb, legume herb)	*Arrhenatherum elatius, Holcus lanatus, Plantago lanceolata, Lotus corniculatus*

2.2. Climate manipulations

The climate treatments involved either annually-recurrent pulsed drought or heavy rainfall events in early summer and ambient conditions for control. The intensity of the climate manipulations was based on the local 100-year extreme event in 2005–2007 and subsequently intensified to the local 1000-year extreme event during the year 2008. We determined the extremeness of weather treatments by statistical extremity with respect to a historical reference period (extreme value theory) independent of its effects on vegetation (Jentsch, 2006). We used the growing seasons (March–September) of 1961–2000 as a reference period (data: German Weather Service). Gumbel I distributions were fitted to the annual extremes, and 100 or 1000-year recurrent events were calculated. We defined drought as the number of consecutive days without effective precipitation (< 1 mm/day) during the growing season.

The control plots remained without climate manipulation throughout the entire period. We maintained drought plots under rain-out shelters during climate manipulations. These were constructed with a steel frame (Hochtunnel, E & R Stolte GmbH, Germany), and covered with a transparent plastic sheet (material: 0.2 mm polyethylene, SPR 5, Hermann Meyer KG, Germany). Rain-out shelters permitted nearly 90% penetration of photosynthetically active radiation. A total of 32 days of drought in 2005–2007 and of 42 days of drought in 2008 was applied in the experiment during the peak growing season in June. Maximum values in the historical data set were 33 days without rain during June and July 1976. We removed the rain-out shelter after the experimental drought period. Greenhouse effects due to rain-out shelters were minimized by having an 80 cm clearance between the roof and the ground, allowing for near-surface air exchange.

We applied heavy rainfall using portable irrigation systems with Veejet 80100 nozzles. The drop size and rainfall intensity resembled