



Does an extreme drought event alter the response of grassland communities to a changing climate?

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ARTICLE INFO

Article history:

Received 5 November 2009

Received in revised form 19 August 2010

Accepted 29 August 2010

Keywords:

Soil water stress

Climate warming

Elevated CO₂

Net CO₂ assimilation rate

Productivity

ABSTRACT

Global temperatures and atmospheric CO₂ concentrations are expected to both increase, but their combined effect on plant communities has been far less investigated than the single factors of global change. Moreover, drought events are expected to become more frequent and intense in the near future what might alter plant responses to the changing climate.

In this study synthesised grassland communities in a current or future climate were subjected to several drought levels (0, 15, 22 and 35 days of drought). The grassland communities were grown in six sunlit, climate-controlled chambers. Three of the chambers were exposed to ambient temperature and CO₂ (current climate), while the other three were continuously warmed 3 °C above ambient temperature at 620 ppm of CO₂ (future climate).

The aim of this study was to investigate the effect of drought on the response of grassland communities to a future climate. Therefore, the response to future climate was observed (1) in the absence of drought and (2) in the occurrence of an extreme drought event, both early and late in the growing season.

- (1) In the absence of drought, plant productivity was positively affected by future climate early in the growing season. Later in the growing season this effect tended to turn negative, resulting in a disappearance of the overall effect of climate at the end of the growing season.
- (2) During drought there was a stronger decrease in net CO₂ assimilation rate (A_{sat}) in future than in current climate due to stronger stomatal closure. Consistently, the beneficial biomass response to future climate stagnated during drought. At the end of the season, after a period of recovery, there was no effect of climate on plant productivity. As in the absence of drought, plant productivity was not affected by climate at the end of the growing season. Hence, the occurrence of an extreme drought event during the growing season did not alter the overall response of plant productivity to a future climate.

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1. Introduction

Most experimental research on responses of plant communities to climate change has focused on single factors, like the effects of increasing CO₂ concentration or elevated temperature. The two fundamental responses of plants to rising atmospheric CO₂ are increased photosynthesis and reduced stomatal conductance (g_s). All other effects of elevated CO₂ on plants and ecosystems are derived from these changes (Long et al., 2004). In the absence of photosynthetic acclimation, elevated temperature increases rates of photosynthesis as long as the plant's optimal temperature is not

exceeded (Berry and Björkman, 1980). However, elevated temperature may reduce g_s , CO₂ uptake and carbon fixation through its effect on soil moisture and leaf water relations (Loik et al., 2000).

Single factor studies provide a functional understanding of the impact of various climatic changes, but obtaining a functional understanding of the responses to simultaneously changing factors from these reports alone remains difficult (Beier, 2004). The few examples of studies on the combination of elevated atmospheric CO₂ concentration and increased temperature point out that the responses to these simultaneously occurring factors of climate change are not necessarily an addition of the responses to the individual factors (Shaw et al., 2002).

The magnitude of plant responses to a changing climate depends on the availability of potentially limiting resources (Campbell et al., 1997). Nitrogen is very often limiting plant productivity and

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its response to elevated CO₂ (Vitousek and Howarth, 1991; Oren et al., 2001), but low water availability is considered a more important growth limiting factor in the vast majority of terrestrial ecosystems (Schulze et al., 1987). Low soil water availability limits the above-ground production rates mainly through decreases in stomatal conductivity, down-regulation of the photosynthetic machinery and increased allocation to the roots (Chaves et al., 2002). In the future, drought occurrences will be more frequent and more intense, and will progressively affect an increasing land surface (Chaves et al., 2002). Hence, there is a need for studies on the combined effects of elevated CO₂ and temperature that incorporate the impact of drought. To date, experiments that have addressed plant responses to a changing climate during a period of drought are rare. The single and interactive effects of elevated CO₂, warming and drought were investigated for *Brassica napus* and *Lotus corniculatus* (Carter et al., 1997; Qaderi et al., 2006). In the experiment on *B. napus*, half of the plants were kept at field capacity and half at wilting point for each single or combined CO₂ and temperature treatment. Thus, this experimental design did not account for possible differences in soil water content caused by the environmental treatments. In both mentioned experiments, plants were grown individually in trays or in monocultures under laboratory conditions with artificial light and fixed temperature treatments. As higher complementarity and selection of water-efficient species lead to more efficient water use in multi-species communities as compared to monocultures (De Boeck et al., 2006), experiments on climate change need to include more realistic plant communities.

In the present study realistically assembled grassland communities were subjected to a range of drought periods under current and future climate conditions. The main objective was to improve our knowledge of the ecophysiological and biomass responses of grassland communities to a future climate that also incorporated an extreme drought event. More specifically, the following research questions were addressed: (1) What is the effect of a future climate (i.e. elevated temperature and increased CO₂ concentration) on plant photosynthesis and community biomass in the beginning and at the end of the growing season? (2) Is this response to future climate altered during an extreme drought event? (3) Does this drought event alter the community biomass response to a future climate at the end of the growing season?

2. Materials and methods

2.1. Site description

The study was performed on artificially assembled but representative grassland communities at the Drie Eiken Campus, University of Antwerp, Wilrijk, Belgium (51°09'N, 04°24'E, 10 m elevation). Average annual precipitation at this location is 776 mm, average annual air temperature varies around 9.6°C. The experimental set-up consisted of six sunlit, climate-controlled chambers, facing south. The interior surface area was 150 cm × 150 cm, the height at the north side 150 cm and at the south side 120 cm. The top of the chambers consisted of a colorless polycarbonate plate (4 mm thick), whereas the sides were made of polyethylene film (200 mm thick), both UV transparent. Three of the chambers were exposed to ambient T_{air} and CO₂ (current climate), while the others were continuously warmed 3°C above fluctuating ambient air temperature and exposed to 620 ppm of CO₂ (future climate). Each chamber under future climate had its individual CO₂ concentration control group, where CO₂ concentration was measured every 8 s with a CO₂ analyzer (WMA-4, PPSsystems, Hitchin, UK) and adjusted to a target of 620 ppm. In the current climate chambers the CO₂ concentration was 375 ± 17 ppm (SD) and in the future climate chambers it was within 10% and 20% of the target of 620 ppm

during 84.4% and 95.6% of the time, respectively. Inside each chamber, relative humidity and air temperature were monitored with a humidity–temperature sensor (Siemens, type QFA66, Germany) and photosynthetically active radiation was measured with a quantum sensor (SDEC, type JYP1000, France). All microclimate parameters inside and outside each chamber were automatically logged every 30 min. During the experiment (May 7–October 4, 2007), monthly average T_{air} was 14.5, 17.6, 17.4, 17.4 and 14.6°C in May, June, July, August and September, respectively. In the current climate chambers T_{air} was on average 0.3 ± 1.6°C (SD) higher than outside and the future climate chambers were 3.3 ± 2.1°C (SD) warmer than outside. The average daily PAR sum inside the chambers was 26.9 mol m⁻² d⁻¹ and differed very little between the two climates (2.1 ± 0.6 mol m⁻² d⁻¹ (SD)). Outside the chambers the average daily PAR sum was 34.9 mol m⁻² d⁻¹. Average vapour pressure deficit (VPD) was 0.28 ± 0.31 and 0.66 ± 0.41 kPa (SD) in the current and future climate, respectively.

2.2. Plant communities

This research was part of a larger experimental platform that consisted of 30 grassland communities per chamber, randomly placed to account for possible position effects. The experiment in the present study used a subset of 8 communities per chamber. Species were selected from three functional groups, which were equally represented: two grass species (*Poa pratensis* L. and *Lolium perenne* L.), two N-fixing dicots (*Medicago lupulina* L. and *L. corniculatus* L.), and two non-N-fixing dicots (*Rumex acetosa* L. and *Plantago lanceolata* L.). Each community contained 18 individuals (three individuals per species) planted in a hexagonal grid with a 4.5 cm interspace between plants, with interspecific interactions maximized by avoiding clumping. Communities were established early May 2007 (DOY 127–130) by transplanting 5-week-old seedlings to PVC containers (tubes, 24 cm inner diameter and 40 cm height, closed with a lid at the bottom) filled with a soil mixture (93.23% sand, 4.59% silt, 2.19% clay; pH 6.0; 1.8% total C, 42 mg N and 11 mg P per 100 g of air dry soil; CEC = 3.9; field capacity 0.13 m³ m⁻³). The containers were buried into the soil to avoid unrealistic soil temperatures. All communities were fertilized with 15 g N m⁻² NH₄NO₃, 7.5 g m⁻² P₂O₅, 15 g m⁻² K₂O and micro-elements (Fe, Mn, Zn, Cu, B, Mo). The fertilizer was given dissolved in water (assuring no percolation), in four equal amounts evenly spread over the growing season. Weeding was done manually and when necessary plants were sprayed with commercially available products to control leaf fungal infections and insect damage. Irrigation was based on the 10 year average monthly precipitation recorded in the nearby meteorological station of Deurne, Antwerp, Belgium (51°12'N, 04°28'E, 14 m elevation) and was corrected for differences in evapotranspiration (ET) inside and outside the chambers. To this end, ET inside the current climate chambers was calculated from changes in soil water content (SWC) and the amount of administered water (De Boeck et al., 2006), and the outside ET with Hamon's equation (Haith and Shoemaker, 1987) based on day length, vapour pressure and T_{air}. Total monthly irrigation matched 61.5, 64.4, 85.1, 80.2, 80.9 and 69.7 mm in May, June, July, August, September and October, respectively. Communities were watered three times a week with a drip irrigation system. The future climate chambers received the same amount of water as the current climate chambers, so that any enhanced consumption would result in aggravated soil drought. Water could freely drain from the containers while capillary rise was prevented by a drainage system below the chambers.

2.3. Imposed drought

In each chamber six grassland communities were subjected to drought by withholding water for a period (drought duration) of

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