Flora 224 (2016) 172–182

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Down to future: Transplanted mountain meadows react with increasing phytomass or shifting species composition

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ARTICLE INFO

Article history:
Received 27 November 2015
Received in revised form 29 June 2016
Accepted 20 July 2016
Edited by Hermann Heilmeier
Available online 22 July 2016

Keywords:
Climate change
Biodiversity
Plant traits
Elevation gradient
Multidimensional scaling
Mesocosm

ABSTRACT

Manipulative approaches under natural conditions are fundamental for understanding impacts of climate warming on grassland (agro-) ecosystems. In this paper we present 3 years of data from two simultaneously conducted transplantation experiments, where meadow monoliths were transplanted downwards along an elevation gradient from the subalpine to the montane belt (2000 m to 1500 m a.s.l.), and in parallel from the montane belt to the foothill zone (1500 m to 1000 m a.s.l.) respectively. Each downward transplantation simulated a temperature increase of 2.8 K. Control and downward transplanted mesocosms were compared regarding aboveground phytomass, phytodiversity, and species composition. Downward transplanted mesocosms from the upper transplantation reacted significantly to warming in terms of aboveground phytomass (legumes +213.6%, herbs +128.2%, graminoids +51.7%, total aboveground phytomass +66.2%), but not with regard to species composition. The lower transplantation, however, induced the complete opposite effect, while average species number and species evenness remained unaffected on all treatments. Further analysis based on five plant traits indicated that the observed shifts were both a consequence of warming and methodological artifacts. Interestingly, the relative importance of warming, artifacts and unaffected species changed with elevation: At the higher transplantation 81.2% of the species remained stable in their abundance, 17.5% were affected by the transplantation, and almost no warming effect could be detected. At the lower transplantation percentage of artifact- and warming-affected species increased consistently (37.5% respectively 44.3%). The results showed that transplantation experiments along elevation transects are an appropriate approach to detect warming impact on agriculturally used grassland at different elevations. Nevertheless, the increasing influence of method-caused side effects became more and more evident over time and with decreasing elevation, underlining the importance of quantifying artifacts in in vivo experiments.

1. Introduction

Climate scenarios predict an increase in global mean temperature of 1.5–4.8 K by the end of the 21st century due to rising atmospheric greenhouse gas concentrations (IPCC, 2013). This trend has initiated numerous studies aimed at detecting, quantifying and predicting ecological impacts on grassland ecosystems (for reviews see Dieleman et al., 2012; Izaurralde et al., 2011; Reyer et al., 2013; Rustad et al., 2001). The observed responses vary widely depending on the scale of observation, type of biome and climate region (Elmendorf et al., 2012; Shaver Gr Canadell et al., 2000). Thus, rising temperatures affect the N and C budget of grassland ecosystems by causing higher photosynthesis and mineralization rates (Körner and Larcher, 1988), elongated growing seasons (Myneni et al., 1997) and increased nutrient uptake (Bassirirad, 2000) in areas where nutrients are not limited. On the other hand, in water-limited areas warming can lead to drought effects in terms of reduced transpiration and decreased above- and belowground productivity (Hoeppner and Dukes, 2012; Xu et al., 2004). Climatic extreme events are expected to have even more severe consequences (Fuhrer et al., 2006), hence a detailed knowledge of impacts, thresholds and trade-offs of rising temperatures is fundamental in order to fit agriculture for a warmer future.

Field experiments are an effective and common way of studying potential impacts on grassland productivity and species composition (Rustad, 2008). While techniques for precipitation and CO_2

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http://dx.doi.org/10.1016/j.flora.2016.07.013

manipulation are relatively uniform (using Free Air Carbon Dioxide Enrichment and rainout shelters; Rustad, 2008; Weltzin et al., 2003; Wu et al., 2011) temperature manipulation experiments differ widely regarding their set up, effort and validity. Shaver Gr Canadell et al. (2000) and Aronson and McNulty (2009) discussed the strengths and weaknesses of the most frequently used techniques, including field chambers, passive night-time warming, overhead infrared heating or active soil warming using heat resistance cables. However, all manipulative experiments lead to an unintended manipulation of the microclimate (Dunne et al., 2004).

Interestingly, space for time substitutions in the form of transplantation experiments are relatively rare in the context of climate change (CC) issues (De Frenne et al., 2011; Sebastià et al., 2008). Shaver Gr Canadell et al. (2000) list two main limitations for transplantation experiments:

1) Multiple environment changes impede a clear deduction from a specific treatment to an observed response.

To solve this problem an ideal transect/gradient is needed, where site conditions such as exposure, inclination, soil properties and type of management are uniform. Furthermore, meteorological conditions must be comparable except for the intended temperature/precipitation gradient (Körner, 2007). This refers in particular to the timing of precipitation, which is a determining factor for grassland productivity especially in water limited areas (Robertson et al., 2009).

2) In vivo transplanting activities lead to (unwanted) disturbance effects.

For realistic conditions entire natural communities (mesocosms) should be transplanted to minimize root damage and keep the natural community structure (Gross et al., 2009). The monoliths should be reinserted safely in their new environment, ideally with direct contact to the surrounding area in order to ensure soil water fluxes and bioturbation processes to remain undisturbed. This in turn provokes a high probability of generative and vegetative species invasion from the surrounding area (Bruelheide, 2003; De Frenne et al., 2011). Although preventing, individuating or quantifying an artificially caused species turnover is fundamental for a correct interpretation of the results, many transplantation studies lack of a species monitoring.

Otherwise, if a clean temperature gradient can be found and such methodological artifacts can be excluded or at least quantified, there are strong arguments which favor transplant experiments in comparison to other warming methods. The intended elevated temperature affects aboveground and belowground processes evenly without creating any unnatural temperature gradients (Harte and Shaw, 1995). Furthermore, realistic climatic conditions are ensured as differences between day and night or sunny and cloudy days are better considered. The greatest advantage of the method is a realistic simulation of future vegetation period length, a factor which is crucial especially for productivity in mountain grassland ecosystems (Jonas et al., 2008). Not surprisingly, current large scale projects such as the TERENO project in Germany (Zacharias et al., 2011) take advantage of these positive aspects of the transplantation approach and necessitate to understand the effective driving forces for the species turnover in such experiments.

Here we present results from a parallel transplantation experiment along an elevation gradient in the Central Alps, where meadow monoliths were transplanted 500 m downwards exposing them for three years to 2.8 K higher temperatures, which is in line with regional climate models for the end of the 21st century (IPCC A2 scenario; Beniston, 2006). Two particularities characterize this approach. At first, a homogeneous elevation transect along one mountain slope from the subalpine belt (2000 m) to the foothill zone (1000 m a.s.l.), which ensures comparable site and weather conditions apart from the temperature lapse rate. Second, two identical transplantation steps were conducted in parallel on top of each other, which allows an elevation-resolved interpretation of the results. This is essentially important as CC impacts on grassland are known to vary highly within space and time, and therefore require integrated approaches combining plot-scale experiments with transect observations (De Frenne et al., 2011; Dunne et al., 2004; Rustad, 2008). Thus, we hypothesized that 1) transplanted grassland mesocosms react positively to warming in terms of aboveground phytomass and phytodiversity, and 2) the effects differ significantly along the altitudinal gradient. Finally the aim of this study was to quantify method-caused effects on species composition and to test whether transplantations can be reasonably used to study CC impacts on agriculturally used grassland ecosystems.

2. Methods

2.1. Site description

The study was conducted along a homogeneous elevation transect in the LTER-site Matsch/Mazia-Valley in the Autonomous Province of Bozen/Bolzano (Central Alps, Italy), where three southwest inclined hay meadows areas are located below each other (4.2 km linear distance from the highest to the lowest site). In respect to their elevation they are labeled in this study as B2000, B1500 and B1000 (Fig. 1). Microclimate stations were installed directly at the sites, sampling the following parameters on a quarter-hourly scale: air temperature and humidity, wind speed and direction, soil moisture at 5 and 20 cm depth, global shortwave radiation, photosynthetic active radiation above the grassland vegetation canopy and at the soil surface within the canopy, precipitation, and snow height. Mean annual temperature (year 2010–2012) ranged from 9.0 °C on the foothill zone (B1000) to 3.4 °C in the subalpine belt (B2000, Table 1). Mean temperature difference during the growing season (April 1–October 31) between both donor and receiving sites was 2.8 K, Mean annual precipitation (2010–2012) reached 568 mm at B1000 and increased with 12.2 mm per 100 m elevation. As precipitation scenarios do not predict substantial changes for the Central Alps (Beniston, 2006), we compensated the natural lapse rate with artificial irrigation (see Table 1).

Management of the sites followed traditional land-use at the respective elevation ranging from two cuts at the B2000 site to four cuts at the B1000 site. All three sites were fertilized once a year with 3 kg cow dung per m^2, corresponding ca. to 15 $g\,m^{-2}$ N_{tot}, 12 $g\,m^{-2}$ P_2O_5 and 22 $g\,m^{-2}$ K_2O. Soil type on all three sites was determined as loamy-sandy (dystric) cambisols, pH value decreased slightly with elevation; however, as all three sites were fertilized, none of the main nutrients was assessed to be limiting (Lair et al., in preparation).

2.2. Treatments

Two parallel transplantations were conducted from B2000 to B1500 and from B1500 to B1000. Control monoliths were also transplanted locally and labeled with “co” after the elevation label, whilst downward transplanted monoliths were given the suffix “tp” (Fig. 1). The grassland monoliths have been chosen randomly in the area at the respective site and had a dimension of 0.7 m × 0.7 m, which is in line with other transplantation experiments (Kiehl et al., 2010). Measurements took place within a 0.5 m × 0.5 m core area