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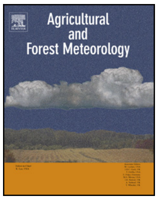

Differential response of alpine steppe and alpine meadow to climate warming in the central Qinghai–Tibetan Plateau

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ABSTRACT

Recently, the Qinghai–Tibetan Plateau has experienced significant warming. Climate warming is expected to have profound effects on plant community productivity and composition, which can drive ecosystem structure and function. To explore effects of warming on plant community productivity and composition, we conducted a warming experiment using open top chambers (OTCs) from 2012 to 2014 in alpine meadow and alpine steppe habitat on the central Qinghai–Tibetan Plateau. We measured aboveground net primary productivity (ANPP), community composition and species diversity under ambient and two levels of artificially warmed conditions across three years. Our results showed that warming significantly stimulated plant growth in the alpine meadow, but reduced growth on the alpine steppe. The increase of ANPP in alpine meadow was a result of an increase of plant height under warming. Warming-induced drought conditions were primarily responsible for the observed decrease of ANPP in an alpine steppe. Plant community composition and species diversity were not influenced by warming in alpine meadow. Alternatively, in alpine steppe, cover of graminoids and forbs significantly declined while legumes substantially increased under warming, subsequently resulting in rapid species losses. Changes in soil moisture were responsible for observed changes in graminoids and legumes in the alpine steppe. Overall, experimental results demonstrated that warming had a positive impact on plant community structure and function in alpine meadow and had a negative impact on these characteristics in an alpine steppe. This work highlights the important role of soil moisture for regulating plant productivity and community composition response to warming in the alpine steppe. In particular, the deep-rooted, drought resistant plants may increase in a warmer future in the central Qinghai–Tibetan Plateau. These changes may reduce habitat quality for the local community of grazers because many of the species that increased are also unpalatable to grazers.

1. Introduction

Recently, as a result of increase of greenhouse gases emissions, global temperature has been rapidly increasing (IPCC, 2014). Climate change has been shown to invoke dramatic impact on the structure and function of terrestrial ecosystems (Grimm et al., 2013). Because grasslands occupy a considerable portion of the global terrestrial ecosystem (Saugier et al., 2001), subsequently providing enormous economic and ecological value, many studies have investigated the effects of warming on plant communities in these systems (Walker et al., 2006; Klein et al., 2008; Hudson et al., 2011).

Alpine grasslands, mainly distributed in high altitude regions, are particularly sensitive to the effects of global change. The cold climate in these areas is responsible for soil temperature, soil moisture and soil properties which directly regulate plant growth (Hudson et al., 2011). Climate warming can thaw frozen soil, which is expected to enhance nutrient cycling and increase plant productiv-

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ity (Klady et al., 2011). In grasslands, warming may actually induce water stress because of increased evapotranspiration and result in decreased ecosystem productivity (Peñuelas et al., 2007). This is supported by a *meta*-analysis by Wu et al. (2011) that summarized warming effects on terrestrial ecosystems on the global scale. The authors found that in cases where warming had a negative effect on ecosystems, productivity can be enhanced when warming and precipitation increase occur simultaneously (Wu et al., 2011). Clearly, conditions of ecosystem water supply are important for understanding the directional effect of warming on grassland ecosystems (Mowll et al., 2015).

Climate change can have a significant effect on plant community structure and composition, which will have feedbacks on ecosystem productivity (Polley et al., 2014). This is because species interactions are driven by many factors that are affected by warming, such as microclimates, ecosystem water level and nutrient availability (Mccluney et al., 2012). Climate change effects on community structure and composition is dependent on species identity, the number of functional groups and community types, and geographical distributions (Sheldon et al., 2011; Yang et al., 2011; Frenette-Dussault et al., 2013). In regions with small seed banks and low invisibility, like arctic and alpine regions, climate change effects at community level can be considerable. In alpine tundra, for example, warming can induce an increase in the coverage of deciduous shrub and graminoids, and a decrease in the proportions of moss and lichens, resulting in an overall decrease in species diversity (Walker et al., 2006). Also, in alpine grasslands, researchers have found that warming induced sharp decreases of low stature forbs, bryophytes and lichens (Klanderud, 2008).

The Qinghai–Tibetan Plateau, a 2.5 million sq. km region dominated by alpine grassland ecosystems (Gao et al., 2014), is known as the ‘third pole’ on the world because of its high altitude and low temperature (Qiu, 2008) and has experienced continuous warming since the 1960s (Chen et al., 2013; Gao et al., 2013). The region supports domestic grazing by yak and Qinghai–Tibetan sheep as well as natural grazing by endangered ungulates, such as the Qinghai–Tibetan antelope and wild yak. Many studies have been conducted in this region to explore effects of warming on alpine grassland productivity and community structure, but results differ in the identification of a mechanism driving plant community response. Some studies have documented increased productivity under warming in Qinghai–Tibetan Plateau (Li et al., 2011; Peng et al., 2014; Wang et al., 2014). For example, Xu et al. (2009) found that warming stimulated shoot and leaf growth on the eastern plateau. But in northeastern Qinghai–Tibetan Plateau, warming has been found to significantly decrease alpine grassland productivity (Klein et al., 2008). The warming induced heat effects were responsible for decrease of plant productivity and proportion of palatable grasses (Klein et al., 2008). Therefore, it is also unclear how alpine grasslands should be expected to respond to warming in Qinghai–Tibetan Plateau.

We conducted a three-year warming experiment in alpine meadow and alpine steppe on the central Qinghai–Tibetan Plateau, by using open top chambers (OTCs). We collected data describing abiotic soil conditions (including moisture, temperature, organic carbon and nitrogen) and biotic aboveground conditions (such as aboveground net primary productivity (ANPP), composition, cover, and height of each species). We hypothesized that (1) warming would impact ANPP and that this effect may be contingent upon water availability and hence differ between meadows and steppe; (2) warming induced change of ANPP will be distributed differentially among species and alter the competition of species, resulting in changes of plant community structure and species diversity in alpine meadow and alpine steppe.

2. Materials and methods

2.1. Site description and experimental design

We conducted the warming experiment in Nagqu County (31.441°N, 92.017°E; 4460 m above sea level) and Baingoin County (31.389°N, 90.028°E; 4725 m above sea level), Nagqu Prefecture, Tibet Autonomous Region, China. The experimental site located in Nagqu County is characterized by alpine meadow habitat and the site in Baingoin County is characterized by alpine steppe habitat. The mean annual temperature is −1.2 °C and −0.4 °C in Nagqu County and Baingoin County, respectively. The annual precipitation is 431.7 mm in Nagqu County and 334.1 mm in Baingoin County. The dominant graminoids in the meadow site were *Kobresia pygmaea*, *Carex moorcroftii*, *Poa pratensis*; the dominant forbs were *Potentilla acaulis* and *Lancea tibetica*. The graminoids at the steppe site were *Stipa purpurea*, *Koeleria argentea*, *Festuca ovina*; the dominant forb was *Leontopodium nanum*; and the dominant legume was *Oxytropis microphylla*. The experimental area was grazed by yak before the experiment and fenced in 2010. The site was not grazed or mowed during the experimental period.

The open top chambers (OTCs) were deployed to simulate warming for the entire duration of the year. The OTCs were made of solar transmitting plastic and were cylindrical, with the height of 0.45 m, the diameter of 1.20 m at ground height, and the diameter of 0.65 m at the maximum height (Ganjurjav et al., 2015). Dominant vegetation averaged less than 10 cm in height providing air space above the plant canopy inside chambers. Two types of OTCs were used in this study. One is the typical type, as described above. A second modified type, which includes a fan to reduce the heating effect, was also used. We initiated the warming experiment in July 2011 with four replicates of each of three treatment types: control plots (control), low warming plots (LW, modified OTCs) and High warming plots (HW, use of general type of OTCs) for a 12 plots in both sites, with a total of 24 plots for the whole study.

2.2. Soil measurements

We used the EM50 Data Collection System (Decagon Devices, Inc., NE, USA) for microclimate measurements. We measured the soil temperature and soil water content at 5 cm, 15 cm and 30 cm depth because the roots were mainly distributed at 0–30 cm depth. Because there were no differences among the plots (Control, LW and HW) in soil temperature and moisture at 15 cm (12.4 °C and 11.2% cm^3/cm^3 in meadow; 13.0 °C and 8.8% cm^3/cm^3 in steppe) and 30 cm (11.3 °C and 10.9% cm^3/cm^3 in meadow; 12.3 °C and 8.3% cm^3/cm^3 in steppe), we only present the soil microclimates collected at 5 cm depth in this paper. The data were collected at 30 min intervals from June to August.

The total organic carbon (TOC), total nitrogen (TN) and available nitrogen were determined by standard methods (Soon and Hendershot, 2007). The availability of ammonium nitrogen (NH_4^+–N) and nitrate nitrogen (NO_3^-–N) were measured by ion exchange resin membrane (IERM) as a plant root simulator. First, the IERM (area of 5 × 2.5 cm) was inserted into the soil and laid at 0–5 cm soil depth in each plot in early June in 2014. After one month, we replaced the previous one. In total, we collected three (June–August) IERM per plot in 2014. The IERM were immersed in a KCl solution (2 mol l^{-1}) and then the NH_4^+–N and NO_3^-–N content were measured with an autoanalyzer (BRAN + LUEBBE, AA3, Germany). The availability of NH_4^+–N and NO_3^-–N were represented by absorption of NH_4^+–N and NO_3^-–N per area per day ($\mu g\ cm^{-2}\ d^{-1}$) by IERM.