LETTER

Warming-induced shift towards forbs and grasses and its relation to the carbon sequestration in an alpine meadow

Fei Peng1,2,4, Xian Xue1,2,4, Manhou Xu3, Quangang You1, Guo Jian1 and Shaoxiu Ma1

1 Key Laboratory of Desert and Desertification, Northwest Institute of Eco-Environment and Resource, Chinese Academy of Sciences, Lanzhou, 730000, People’s Republic of China
2 Department of Microbiology and Plant Biology, University of Oklahoma, Norman, 73019, United States of America
3 Taiyuan Normal University, Jinzhong, 030619, People’s Republic of China
4 Author to whom any correspondence should be addressed. E-mail: pengfei@lzb.ac.cn and xianxue@lzb.ac.cn

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Abstract

Global warming is often associated with changes in abiotic factors and the community composition across alpine ecosystems. However, the way that an altered community dynamics affects the ecosystem carbon (C) balance remains unclear. A warming experiment was initiated in 2010 to assess the potential impacts of warming-induced changes in the community composition and how these changes affect the C balance in mountain meadows located in the permafrost region of the Qinghai–Tibet Plateau (China).

Under warming conditions, we found an increased importance value (IV) of forbs and grasses of 4.9%, in contrast to the IV of sedges, which decreased by 4.4%. For forbs and grasses, the IV showed positive exponential relationships with gross ecosystem production and ecosystem respiration, while negative correlations were found for sedges. These results indicate that a slight change in the IVs of sedges, grasses and forbs favors C sequestration. Moreover, the warming treatment significantly increased the mean height of sedges, grasses and forbs, and the net ecosystem exchange increase was positively correlated with the increase in the mean height of grasses and forbs. In summary, the warming-induced shift toward forb and grass species and the increase in plant height strengthen the C uptake capacity of alpine meadow ecosystems.

Introduction

Biodiversity and community composition play essential roles in sustaining terrestrial ecosystem processes (Klein et al 2004). They impact ecosystem functions (De Boeck et al 2007, Luo 2007) such as gross ecosystem production (GEP), ecosystem respiration (ER), net ecosystem exchange (NEE), nutrient cycling and aggregate stability (Eviner and Chapin 2003). Moreover, functional characteristics, such as size, photosynthesis rate and stomatal conductance of community individuals are considered to be the primary factors that affect ecosystem carbon (C) fluxes beyond the number of individuals or species (Tilman 1988, Tilman et al 1997, De Boeck et al 2007). Thus, the change in functional and compositional patterns of plant diversity might affect the ecosystem C balance (Johnson et al 2008, Ward et al 2009, Metcalfe et al 2011). For instance, in northern England (United Kingdom), the removal of shrubs increased soil respiration rate and photosynthesis by >200% compared to undisturbed control (Ward et al 2009). Soil respiration was also observed to be smaller in plots with four species belonging to the same functional group than in a mixture of four species belonging to different functional groups (Johnson et al 2008).

The global mean temperature has increased by 0.74 °C since 1850 and is expected to rise by an additional 1.8 °C–4.0 °C by the end of the 21st century (IPCC 2007), which would greatly change species diversity and community composition at an unprecedented rate (Sala et al 2000). Diverse responses of plant species diversity and community composition to a warmer climate have been documented for various ecosystems (Klein et al 2004, Elmendorf et al 2012, Zhang et al 2015). In particular, a decline in species diversity, with dominance patterns shifting towards shrubs and grasses (even in short times) has been
observed in a wide variety of tundra and alpine meadows (Harte and Shaw 1995, Walker et al. 2006, Elmendorf et al. 2012, Alatalo et al. 2016). In a climate manipulation experiment in the Swedish subarctic (Callaghan et al. 2013), shrub expansion was observed only where the ambient temperature was relatively high, while grass expansion occurred primarily in the coldest site (Elmendorf et al. 2012, Alatalo et al. 2016). As a matter of fact, the mean annual temperature, soil moisture, and nitrogen availability regulate the different responses of species richness and community composition to warming conditions among sites (Dormann and Woodin 2002, Klein et al. 2004).

Tundra and alpine ecosystems store a large amount of C and are very sensitive to warming (Schuur et al. 2008, Yang et al. 2008, Tarnocai et al. 2009). The net effect of the expected future warming on such a big C stock depends on whether the increase in C uptake in the form of primary production can offset warming-induced increases in soil heterotrophic respiration (Euskirchen et al. 2006). In alpine meadows, the plant community is mainly composed of sedges, grasses and forbs (Zhao and Zhou 1999). Each plant group affects ecosystem C fluxes with its own functional traits, though these groups share similarities because of their long adaptation to harsh environments (Tolvanen et al. 2004, Johnson et al. 2008, Phoenix et al. 2008, Rudgers et al. 2014). As a consequence, assessing how altered patterns in species richness and community composition impact on the C balance (inputs and outputs) of alpine meadow ecosystems is of great relevance for understanding possible future changes in permafrost C storage (Ward et al. 2009). The influence of species richness on ecosystem C has been extensively examined (De Boeck et al. 2007, De Deyn et al. 2009, Delgado-Balbuena et al. 2013). However, the impact of warming-induced changes in community composition on ecosystem C fluxes has hardly been explored, especially in the alpine area of the Qinghai–Tibet Plateau (QTP) of China.

In a warmer climate, the rate of loss of plant species is greater in sites with lower water availability (Klein et al. 2004) and grass species expand their distribution into relatively cooler areas (Elmendorf et al. 2012). In the permafrost area of central QTP, the mean air temperature is relatively low and the water supply is not limiting to plants in the growing season because of the relatively high rainfall in the area, which contrasts to the dry site studies of Klein et al. (2004). With a focus on a permafrost area of the central QTP, we tested in this study the hypothesis that there is a relatively slow or insignificant change in species richness and grass expansion in response to a warming experiment. Another objective was to investigate the relationship between warming-induced changes in community composition and ecosystem C fluxes.

### Materials and methods

#### Site description and experimental design

The study site is located in the source region of the Yangtze River, in central QTP (92° 56' E, 34° 49' N). The mean altitude is 4635 m a.s.l. and the climate is typically alpine. Detailed information about climate background can be found in a previous paper (Xue et al. 2015). The study site is a winter-grazed range with mean plant height of about 5 cm. The plant species in the study site are categorized into three major plant functional groups: sedges, grasses and forbs (table 1). The dominant species are *Kobresia capillitfolia*, *K. pygmaea*, and *Carex moorcroftii*. Plant roots are mainly in the 0–20 cm upper soil layer and the average soil organic C content is about 1.5% (based on the upper 0–30 cm). The soil development is weak. It belongs to alpine meadow soil (Chinese soil taxonomy), classified as a Cryosol according to World Reference Base for Soil Resources (2006), with a Mattic Epipedon (approximately 0–10 cm depth), and an organic-rich layer in the upper 0–30 cm (Wang et al. 2007). The soil parent material is of fluvisol-glacial origin where sand content is 99%. The permafrost thickness observed near the experimental site is 30–70 m, and the active layer is 1.5–3.5 m (Wu and Liu 2004). The thickness of the active layer has been increasing at a rate of 3.1 cm y⁻¹ since 1995 in response to atmospheric warming (Wu and Liu 2004).

A paired experimental design was used where ten 2 m × 2 m plots were divided into five pairs of control (unwarmed) and warmed plots. In each warmed plot, one 165 cm × 15 cm infrared heater (MR-2420, Kalglo Electronics Inc., Utah, USA) was suspended in the middle of the plot at a height of 1.5 m above the ground with a radiation output of 150 Watts m⁻². The heating

### Table 1. Plant species of sedges, grasses and forbs in the study area.

| Sedges                  | Grasses                  | Forbs                   |
|-------------------------|--------------------------|-------------------------|
| *Kobresia humilis*      | *Elymus nutans*          | *Saussurea stella*     |
| *K. pygmaea*            | *Poa orinosa*            | *S. superba*            |
| *K. tibetica*           | *Stipa aliena*           | *S. kokonensis*         |
| *K. capillifolia*       | *Festuca ovina*          | *Taraxacum mongolicum*  |
| *Blysums sinocompressus*| *Koeleria koeleria*      | *T. lecanthum*          |
| *Carex arrofusca*       |                          | *Aster flaccidum*       |
| *C. kansuensis*         |                          | *Leontopodium nanum*    |
|                         |                          | *Thalictrum alpinum*    |

Due to the limitation of space, some plant species are not listed. The plant species in the study area are categorized into three major plant functional groups: sedges, grasses and forbs (table 1). The dominant species are *Kobresia capillitfolia*, *K. pygmaea*, and *Carex moorcroftii*. Plant roots are mainly in the 0–20 cm upper soil layer and the average soil organic C content is about 1.5% (based on the upper 0–30 cm). The soil development is weak. It belongs to alpine meadow soil (Chinese soil taxonomy), classified as a Cryosol according to World Reference Base for Soil Resources (2006), with a Mattic Epipedon (approximately 0–10 cm depth), and an organic-rich layer in the upper 0–30 cm (Wang et al. 2007). The soil parent material is of fluvisol-glacial origin where sand content is 99%. The permafrost thickness observed near the experimental site is 30–70 m, and the active layer is 1.5–3.5 m (Wu and Liu 2004). The thickness of the active layer has been increasing at a rate of 3.1 cm y⁻¹ since 1995 in response to atmospheric warming (Wu and Liu 2004).
was operated year-round from 1 July, 2010 and continued till now. To simulate the shading effect of heaters, one ‘dummy’ heater made of metal sheet with the same shape and size as the heater was also installed in the control plots.

**Measurement protocol**

The soil temperature was monitored using a thermoprobe (Model 109, Campbell Scientific, Inc, Utah, USA) installed at 5.0 cm depth in the center of each plot. The volumetric soil water content (v/v, %) was measured by frequency domain reflectometry (FDR, EnviroSmart sensor, Sentek Pty Ltd., Stepney, Australia) at 0–10 cm depth. The daily average soil temperature and moisture were recorded in a CR 1000 data logger (Campbell Scientific, Inc, Utah, USA) with a 10 min interval. The 10 min recorded data were then averaged into daily data. The warming effect on soil temperature and soil moisture was analyzed based on the daily data.

A 0.5 × 0.5 m metal frame was set up in each plot. The NEE was measured using a transparent chamber (0.5 × 0.5 × 0.5 m) attached to an infrared gas analyzer (IRGA; LI-6400, Li-Cor, Lincoln, NE, USA) on the frame in each plot. During measurements, the chamber was tightly sealed with the base surface of the frame, with a small fan running to mix the air inside the chamber. Nine consecutive recordings of CO₂ concentration were taken at 10 s intervals during a 90 s period. The NEE was determined from the time-course of the CO₂ concentration, air temperature, volume of the chamber and air pressure (Steduto et al 2002, Niu et al 2008). The procedure for measuring ER was similar but the chamber was covered with a piece of light-proof cover during ER measurements. Measurements were conducted between 10 am and 4 pm on bright and clear days.

Measurements of NEE and ER were taken once a month from May to September in 2012 and 2013 (10 measurements in total). The net photosynthesis rate ($P_n$) of one sedge species (Carex atrofusca) and two forb species (Saussurea superba, Polygonum viviparum) was measured on 7 July, 28 August and 29 August 2011, and on 26 July 2012, by examining fully-developed mature leaves with a Li-Cor 6400 xt (Li-Cor, Lincoln, NE, USA). The measuring days were bright and clear with no wind. As the stabilization status indicator reached one, the photosynthesis rate was recorded five times in 90 s. For each species, measurements were replicated on five leaves. GEP was calculated as the difference between NEE and ER. We used negative NEE values to indicate C uptake by the vegetation. Community above ground biomass (AGB) was obtained from a step-wise linear regression with AGB as the dependent variable, and coverage and plant height as independent variables (Peng et al 2014, Xu et al 2015). Coverage of each plot was measured using a 27 cm × 27 cm frame in four diagonally divided subplots replicated eight times in each plot. Root biomass was sampled by using a soil corer with an internal diameter of 7 cm. One core was extracted every 10 cm between 0 and 50 cm depth in the center of each experimental plot during the growing seasons in 2012 and 2013. Root and soil samples were immediately placed in a cooler and transported to the laboratory by train. In the laboratory, soil samples were air-dried and crumbled by hand to pass through a 2 mm diameter sieve to remove large particles from the finer soil. Then, the fine living roots were hand-picked based on their color and consistency in a distilled water bath (Yang et al 2009) and the separated roots were dried at 75°C for 48 h.

The height and frequency of each species were measured in a 20 cm × 20 cm small sub-plot of each plot. A frame with 100 small quadrats (1 × 1 cm) was used to measure the frequency. The height of each species was assessed based on the number of individuals for each species. If the number of individuals of a given species was less than 20, then the height of each individual was taken, otherwise the height of that species was derived by 20 measurements with a ruler. The measured heights were then averaged for each species. The importance value (IV) of each species was derived by average values of relative frequency and relative height. The relative height of a species is the ratio of the average height of that species to the summed height of all the species in the plot. The IV of each plant functional group was the sum of the IVs of any species belonging to that group.

To examine changes in species diversity under warming treatment, diversity-related indices, namely the Shannon–Wiener Index ($H$), Simpson’s Index ($D_s$) and evenness ($E$) were calculated in each plot, as follows (Xu et al 2015):

$$P_i = \frac{IV_i}{IV_{total}}$$

$$H = -\sum_{i=1}^{S} P_i \ln(P_i)$$

$$D_s = 1 - \sum_{i=1}^{S} P_i^2$$

$$E = \frac{H}{\ln(S)}$$

where $IV_i$ is the IV of a specific species, $IV_{total}$ is the sum of the $IV_i$ values of all the species. $S$ is the total number of species.

**Data analysis**

Two-way ANOVA was used to test warming, year and their interaction on species richness, diversity-related indices, ER, NEE, and GEP, and it was also used to test warming, plant functional type and their interaction with average species number, height, relative frequency, and IV. In the analysis, height, relative frequency, and IV of sedges, grasses and forbs...
were the mean of height, relative frequency, and IV of species belonging to the specific plant functional type in each plot. ER, NEE, and GEP were the averages of five replicates in each measurement. Warming treatment, year and plant functional type are fixed factors. One-way ANOVA was used to test the statistical significance of warming on species-specific $P_{n}$ and aboveground and root biomass. The exponential model ($y = a \times e^{bx}$) was used to fit the relationship between C fluxes and the IV of different plant functional types. All the above-mentioned statistical analyses were conducted using SPSS 17.0 for Windows (SPSS, Inc., Chicago, IL, USA). Additionally, confirmatory analysis of structural equation modeling (SEM) was applied to explore the abiotic and biotic impacts on NEE. In the SEM analysis, only abiotic and biotic factors with significant change were included in the model. Data were fitted to the model using the maximum likelihood estimation method. SEM analysis was performed using lavaan packages in R v 3.3.1 (R Core Team 2016).

Results

The change in microclimate

Although the warming experiment started from 2010, the species composition was only investigated in 2012 and 2013, thus the warming impact on soil temperature and soil moisture was reported based on data in 2012 and 2013. The warming treatment significantly increased the soil temperature by 1.77 °C ($p < 0.01$) at a depth of 5 cm but decreased the soil moisture by 12.4% ($p < 0.01$) at 0–10 cm. There was a noticeable variation of annual precipitation (420.1 and 238.8 mm in 2012 and 2013, respectively).

Plant traits and community composition change

The relative frequency and IV of sedge was about 0.6 suggesting the dominance of sedge in the study site (figures 1(c) and (d)). The species number, $H$, $D_{s}$ and $E$ did not significantly change under warming in a plot scale (table 2). The species number and relative frequency of grasses (figures 1(a) and (c)), and summed IV of grasses and forbs (figure 1(d)) were significantly increased while the IV of sedge was significantly reduced in the warmed plots (figure 1(d)). The warming-induced changes in plant height were significantly different among plant functional types (figure 1(b)) with the highest increase in grasses (51%, $p < 0.01$), followed by forbs (45%, $p < 0.05$) and sedges (22%, $p < 0.05$).

The $P_{n}$ was much higher in $S. superb$ and $P. viviparum$ than in $C. atrofusca$, which was almost double or three times higher for forbs than for the species. Warming had no significant effect on $P_{n}$ and light use efficiency (LUE) in all three species ($p > 0.05$).

Ecosystem carbon fluxes and biomass

Ecosystem C fluxes demonstrated yearly variation with higher values in 2012 than in 2013. Warming
significantly stimulated the mean GEP and ER in 2012 and 2013 (figure 2(a), table 2), and the higher increment in GEP (1.48 \(\mu\) mol m\(^{-2}\) s\(^{-1}\)) than in ER (0.74 \(\mu\) mol m\(^{-2}\) s\(^{-1}\)) resulted in an increase in average NEE. The interaction of warming treatment in two years had no significant effect on the C fluxes (table 2). Warming had no significant effect on the AGB but significantly increased the root biomass in 0–50 cm by 16.9%. The effect of warming on root biomass was opposite between surface and deep layers, which non-significantly decreased in 0–10 cm but significantly increased in 10–50 cm (figure 2(b)).

**Discussion**

**Community composition response to warming**

No significant change in species number (figure 1(a)) is similar to that of an open-top chamber (OTC) warming experiment 30 km from our study site (Li et al 2011) but inconsistent with the sharp decline of species richness observed in a sub-alpine meadow in QTP (Klein et al 2004). The initial conditions regarding abiotic background, plant community structure, and nutrient availability might underpin the different responses. In general, drier sites are more responsive to warming (Grime et al 2000, Klein et al 2004). Higher soil moisture in our study site (annual mean: about 6.5% in warmed plots) compared with the sub-alpine sites (rainy season mean in OTCs <3%, Klein et al study) therefore could contribute to the non-significant change in species number. Although the nitrogen content is low, increased net mineralization rate resulting from warming (Peng et al 2016) might loosen the constraints associated with the insufficient availability of nitrogen, thus dampening the loss of species richness in our site. The reason for the non-significant changes in species number might be a divergent response of the different plant functional types (figure 1). This is somewhat analogous to the result that increases in grass abundance are at the expense of a decrease in other species in a sub-alpine meadow (Zhang and Welker 1996). The long-lived nature of plants in alpine regions helps them to buffer against climate change (Morris et al 2008). However, in previous studies the observed reduction of species richness in two (Zhang and Welker 1996, Walker et al 2006) and four years (Klein...
et al 2004) of warming demonstrates the fast changes in community composition of alpine meadows as a result of warming. This change in IV observed in the current study after three to four years of warming is consistent with the results of such previous studies. The increase in relative frequency of grasses together with decrease in that of forbs (figure 1(c)), and the increase in the IV of forbs and grasses together with a decrease in that of sedge (figure 1(d)) are consistent with previous studies (Klanderud and Totland 2005, Elmendorf et al 2012). However, these results differ from the evidence provided by Rudgers et al (2014) about the increase in abundance of sedges and the decline in that of grasses in a sub-alpine meadow of the Rocky Mountains. The low mean air temperature (−3.8 °C) might be responsible for the increase in the IV of grasses and forbs in the current study as cross-site synthesis shows that graminoids increased primarily in the coldest study sites (Elmendorf et al 2012). The abundance of sedges positively correlates with the soil moisture in the alpine meadow (Dorji et al 2014). Arbuscular mycorrhizal fungi, associated with grasses more than with sedges (Rudgers et al 2014), can enhance the water uptake capacity of grasses when soils are dried by experimental warming, which probably explains the decrease in the IV of sedge. In nutrient poor sites such as alpine, sub-alpine meadows and tundra ecosystems, the expected increase in nutrient levels could bring about an increase in the abundance of grasses and forbs (Jägerbrand et al 2009). The arbuscular mycorrhizal fungi in grasses allowed grasses and forbs to outcompete sedges in using increased available nitrogen (Klanderud 2008, Jägerbrand et al 2009, Zhang et al 2015). As a consequence, the increased nitrogen mineralization in the study site (Peng et al 2016) could support the increase in the IV of

Figure 3. Exponential model fitting of ER and GEP with the IV of sedges and the summed IV of grasses and forbs. Data used in the plotting for each measurement was the mean of five replicates.

Figure 4. Indirect or direct paths of soil temperature and biotic factors (plant height and importance value, root biomass) to ecosystem C fluxes. Solid and dashed arrows represent significant (p < 0.05) and non-significant (p > 0.05) paths in a fitted structural equation model depicting the impact of variables on C fluxes.
grasses. Tall species may expand at the expense of low stature species in the alpine region if temperature and soil nutrient increase (Klanderud 2008), thus higher plant height in grass species and in some forbs species (figure 1(b)) might contribute to the increase in relative frequency of grasses and the increase in IV of grasses and forbs, which supports the hypothesis that the competitive ability of plants primarily depends on size (Bengtsson et al 1994).

**Biomass**

Although the increase in temperature could stimulate plant growth, the associated soil moisture decline might cause a negative effect on plant production. The coupled change in soil temperature and moisture thus could explain the non-significant change in AGB (De Boeck et al 2008). Moreover, the response of individual species to warming may vary greatly, and the production by the whole vegetation might be unchanged (Hollister and Flaherty 2010) because of the compensatory growth among different species (Harte and Shaw 1995, Perfors et al 2003). For instance, experimental warming in Swedish tussock tundra doubled the biomass of evergreen shrubs relative to control plots, but reduced the biomass of the dominant sedge species (Molau 2010). The increase in the IV of grasses and forbs (figure 1(d)) and the high \( P_n \) of forbs imply stimulation of ecosystem productivity, supported by an increase in GEP under warming (table 2). By contrast, a non-significant change in AGB but an increase in RB in the 0–50 cm layer (figure 2) indicate that the more fixed C mostly goes to the below ground compartment (to increase root biomass) through changing shoot/root ratio (Hollister and Flaherty 2010, Li et al 2011), as forbs and grasses allocate more biomass to roots than sedge species (Wu et al 2013). The negative relationship of the mean height of sedge species with the root biomass in the 0–50 cm layer, and the positive relationship of the mean height of grasses and forbs with the root biomass observed in the path analysis, (figure 4) are explained by the shallow root of sedges and the deep root of grasses and forbs. The reduction in the IV of sedges but the increase in the IV of forbs and grasses correspond to root biomass reduction in the 0–10 cm layer but an increase in root biomass in the 10–50 cm layer.

**Implications for the ecosystem carbon balance**

Our analysis revealed that the increase in NEE was positively correlated with the warming-induced change in the mean height of forbs and grasses (figure 5(b)) but had no relationship with the warming-induced change in the height of sedges (figure 5(a)). This indicates the importance of community composition, and the associated change in plant growth, in regulating the response of net ecosystem C balance to warming.

Changes in plant community composition have long-term effects on the ecosystem C balance (Luo 2007). The shift from more productive forbs to less productive shrubs (Harte and Shaw 1995) may underpin the reduction of ecosystem CO2 uptake in a mountain meadow (Saleska et al 2002). The increase in the summed IV of grasses and forbs (figure 1(d)) with high \( P_n \) in forbs species thus could be responsible for the increase in GEP. GEP negatively correlated with the IV of sedges (figure 3(c)) and positively with the IV of grasses and forbs (figure 3(d)), thus changes in the IVs of sedges, grasses and forbs (figure 1(d)) could contribute to the GEP increase in our study. The negative exponential relationships between the IV of sedges with GEP and ER (figures 3(b) and (d)) suggest a threshold percentage of sedge IV on ecosystem C
sequestration and emissions. Beyond this threshold, the increase in IV of sedges will have no effect on the ecosystem C balance. The significant increase in ER could only be the result of the increase in soil respiration (Peng et al. 2015) given that above-ground plant respiration did not significantly change due to the unchanged AGB. However, soil respiration would be suppressed as decomposability of litter declines as shrubs take more coverage in the community (Saleska et al. 2002, Duan et al. 2013). The readily decomposable litter of forbs compared to sedges (Hobbie 1996) might explain the negative relationship between the IV of sedges and ER (figure 3(a)). The net effect of community composition on C balance depends on the direction of responses of uptake and emissions to warming-induced plant community change. Ecosystem C uptake is globally more sensitive than C emissions to the percentage loss of species richness (Hooper et al. 2012). Sharper fitting slopes of IVs with GEP than with ER (figure 3) indicate that the ecosystem C uptake is more sensitive than emissions to the warming-induced composition change. The community composition change in the form of a decrease in sedges and an increase in forbs and grasses would intensify the C sequestration capacity of alpine meadows in the QTP permafrost region.

Ecosystem C fluxes showed yearly variations but, with warming, these variations were not significant. Previous studies carried out in European alpine and tundra ecosystems showed divergent vegetative growth responses to heat waves in high and low elevations (Jolly et al. 2005). Alpine grasslands, in particular, are affected by heat waves only in combination with drought (De Boeck et al. 2016). The average air temperature was elevated by 6.7 °C and soil temperature was increased by 2 °C–3 °C in the study of De Boeck et al. 2008 which is a higher temperature change than in our study. Comparing the daily rainfall data of the two years, major differences were observed in July. One large rainfall event (43 mm) observed in July 2012 mainly contributed to the difference in precipitation totals between the two years. This may explain the non-significant ecosystem C fluxes in the two years because plants could not use the excess water made available by the torrential event of July 2012.

As warming induces an alteration in the growing season, the associated rates of terrestrial productivity influence the ability of these ecosystems to sequester atmospheric CO2 (Euskirchen et al. 2006). Field and modeling studies estimate that for each additional day of the growing season, the net ecosystem C uptake increases from 1 to 6 g C m–2 (Aurela et al. 2004, Euskirchen et al. 2006). The observed longer periods of non-frozen active layer indicate a longer growing season in the study site (Peng et al. 2014). Warming could accelerate the leaf bud burst of alpine plants, with woody plants showing a greater advancement of leaf bud burst than herbaceous plants. However, Arft et al. (1999) showed no difference in the response of the timing of leaf bud burst to warmth among narrow functional types, such as the herbaceous species of our study. In addition, the warming effects on plant phenology are yearly specific, e.g. woody plants exhibited accelerated bud burst in the first two-year warming treatment, but it was not until the fourth year that herbaceous plants exhibited an acceleration of leaf bud burst (Arft et al. 1999). Thus, the effect of warming induced phenological alteration of different functional groups, whose effects on ecosystem C fluxes should be further studied in the future. However, over a long time scale, new plant functional groups with larger biomass and C storage potential may become dominant, as observed in our study, with an IV increase in forbs and grasses species.

Conclusion

While species richness was maintained in a warmer climate, the IV of forbs and grasses increased and the IV of sedges decreased in the alpine meadow ecosystem studied here, located in the permafrost area of the QTP. Divergent responses alter the community composition through a shift in community composition towards forbs and grasses. The increasing IV and height of forbs and grasses result in the stimulation of C uptake in alpine meadows as forbs have higher net photosynthesis. Soil moisture reduction in the top layer and an increase in the deep layer, and different C allocation strategies to the above- and below-ground biomass of each plant functional type, lead to intensified below-ground C storage. We conclude that alpine ecosystems with low temperature and relatively high soil moisture tend to absorb more C in a warmer climate. This is done by a shift in dominance towards more productive species while maintaining species diversity.

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