Agricultural and Forest Meteorology 287 (2020) 107943

Contents lists available at ScienceDirect

Agricultural and Forest Meteorology

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

Warming and precipitation addition interact to affect plant spring phenology in alpine meadows on the central Qinghai-Tibetan Plateau

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ARTICLE INFO

Keywords:
Green up
Flowering
Functional group
Spring precipitation
Temperature
Grassland

ABSTRACT

Temperature and precipitation are primary regulators of plant phenology. However, our knowledge of how these factors might interact to affect plant phenology is incomplete. The Qinghai-Tibetan Plateau, a cold and high region, has experienced no consistent changes in spring phenology, despite a significant warming trend. We conducted a manipulative experiment of warming and precipitation addition in an alpine meadow on the Qinghai-Tibetan Plateau in 2015 (cold and wet), 2016 (warm and dry) and 2017 (mild and very wet). We found that warming increased annual variability of plant spring phenology. Warming delayed green up of all monitored species in 2016, advanced green up of early flowering species in 2015, and did not alter green up in 2017. For example, green up of the shallow rooted *Kobresia pygmaea* advanced 8 (± 2) days in 2015 and was delayed by 23 (± 3) days in a dry year (2016) under warming compared with control. Early spring precipitation addition can offset the delaying effects of warming in a dry year on the Qinghai-Tibetan Plateau. Under warming plus precipitation addition, community average green up advanced compared to control plots in 2015 and 2016, and community average flowering advanced for all three years. In 2016, flowering of *K. pygmaea* (an early flowering species) advanced under warming plus precipitation addition compared to control while flowering of other species did not change. Our results highlight that annual variation of soil moisture condition plays a critical role in determining the magnitude and direction of spring phenology response to warming. We provide insights in how plant spring phenology might change in a warmer future in the presence or absence of precipitation increase.

1. Introduction

Phenology is the sequence of life cycle events across the year. In addition to being useful for understanding the life cycle of individual species and populations, phenology can provide insight into higher-level dynamics. For example, for plants, the timing of phenological events predict season-long ecosystem productivity, nutrient cycling, carbon budget, and species interactions in terrestrial ecosystems (Yang and Rudolf, 2010; Estiarte and Peñuelas, 2015; Zhou et al., 2016). The timing of spring plant growth and flowering is an important predictor of seasonal biomass production and annual plant fitness and has been shown to be sensitive to climatic variability (Li et al., 2016).

Climate change has been shown to alter spring plant phenology (Fu et al., 2014; Ge et al., 2015), and these changes could possibly impact ecosystem structure and function (Shen et al., 2015; Meng et al., 2017). Predicting responses of plant phenology to climate change has become a globally active research topic in terrestrial ecosystems (Wolkovich et al., 2012; Xia and Wan, 2013; Meng et al., 2017). Warming has advanced plant spring phenology across biomes worldwide, including forests and grasslands in temperate and cold regions (Ahas et al., 2010; Xia and Wan, 2013; Fu et al., 2015; Rice et al., 2018). For example, observational studies show that leaf unfolding advanced by 0.9, 4.2 and 4.7 days per decade on average for the period 1982–2011 in USA, China and Europe, respectively (Piao et al., 2019). However, plant phenology is not consistently advanced by warming. For example, vegetation green up delayed in the southwest region of Qinghai-Tibetan Plateau while it advanced in the other areas of the same region between 2000 and 2011 (Shen et al., 2014). The phenology of a number of species has been delayed under warming conditions in grasslands across the world (Bokhorst et al., 2011; Dorji et al., 2013;

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https://doi.org/10.1016/j.agrformet.2020.107943
Received 7 August 2019; Received in revised form 12 February 2020; Accepted 15 February 2020
Available online 21 February 2020

Whittington et al., 2015). These delays may be driven by factors other than temperature (Cleland et al., 2006).

In cold grassland ecosystems, soil moisture, snow melt and nitrogen deposition have significant effects on plant phenology (Huelber et al., 2006; Bloor et al., 2010; Smith et al., 2012). In arid environments, water can have significant effects on vegetation phenology (Cleverly et al., 2016). Pre-growing season snowfall and timing of snowmelt are closely related to soil water availability in cold regions. In the Qinghai-Tibetan Plateau, Dorji et al. (2013) found that warming delayed flowering phenology while snow addition offset the negative effects of warming. In alpine tundra, forbs responded to warming by flowering earlier and responded to increase snowpack and nitrogen addition by flowering later, but interactions of warming, snowpack and nitrogen addition advanced flowering (Smith et al., 2012). Commonly, in sub-arid grasslands, interannual variation in precipitation controls the direction of warming effects (delay or advance) on plant phenology (Zelikova et al., 2015).

The phenological responses to warming of different plant species depend on plant functional type (Shen et al., 2011; Richardson et al., 2019). Many studies have demonstrated that plant spring phenology has advanced under warming with interspecific differences (Dunne et al., 2003; Meng et al., 2017; Cui et al., 2017; Suonan et al., 2017). For example, in a low arctic site, warming did not change the timing of green up of forbs while it advanced the greening and flowering of shrubs (Post et al., 2008). In the Qinghai-Tibetan Plateau, mid and late flowering species appear to be more sensitive to warming than early flowering species as warming delayed the completion of cold exposure for early flowering plants (Suonan et al., 2017). However, others note that some shallow-rooted early flowering species are more sensitive to warming where spring phenology is delayed under warming-induced drought in the Qinghai-Tibetan Plateau (Dorji et al., 2013; Zhu et al., 2016). In alpine grasslands, heat waves can have a negative impact on plant growth (De Boeck et al., 2016) and forbs can be more sensitive to a heat wave compared to grasses (Cremonese et al., 2017).

In cold ecosystems, warming has a pronounced effect on plant phenology (Kug et al., 2015; Pepin et al., 2015; Bjorkman et al., 2016) and these regions have frequently experienced larger than average warming (Stocker et al., 2013; Pepin et al., 2015). The Qinghai-Tibetan Plateau, as a high and cold region, would therefore be expected to show strong patterns of advanced phenology across species. However, the evidence from this region is mixed. In the Qinghai-Tibetan Plateau, both temperature and moisture are limiting factors for spring phenology because plants begin the growing season in a very dry state with soil water content increasing only with the onset of the summer monsoon (Shen et al., 2011; Ganjurjav et al., 2016a). As a result, these types of systems are useful for addressing questions about complex interactions between temperature and precipitation on plant phenology. In this region, many studies correlated spring phenology with temperature and precipitation (Ram et al., 1988; Shen et al., 2011; Wang et al., 2015). Most of these studies used remotely sensed data to explore climate change impacts on spring phenology. However, remotely sensed data cannot explore responses of specific functional groups and have also not documented consistent changing trends. Some researchers have found advanced spring phenology (Zhang et al., 2013; Zheng et al., 2016), while others found spring phenology to be delayed with warming (Yu et al., 2010). The different sources of remotely sensed data may contribute to these divergent results. In this region, the phenological response of different functional groups to temperature and precipitation interactions is unclear and needs to be investigated with manipulative experiments in alpine grasslands on the Qinghai-Tibetan Plateau.

In an alpine meadow in the central Qinghai-Tibetan Plateau. we performed a warming experiment based on year-round fixed open top chambers combined with the addition of different levels of spring precipitation over 3 years to answer the question: how do warming and precipitation addition affect plant phenology at both the species and the community level? We hypothesized that the direction and magnitude of the effect of warming on plant phenology will depend on soil water content and the response of spring phenology to warming and water addition will be different among functional groups.

2. Methods

2.1. Site description

We conducted a manipulative climate experiment in an alpine meadow ecosystem of Nagqu county (31.441°N, 92.017°E; 4460 m elevation) in the Tibet Autonomous Region, China, which is known as "the third pole" or "the roof of the world" (Qiu, 2008; Chen et al., 2015). The experimental site is characterized as a cold alpine region, with a short plant growing season (from May to September). Over the past thirty years (1980–2013), the mean annual air temperature was −1.2 °C and the mean annual total precipitation was 431.7 mm (data were obtained from the China Meteorological Data Sharing Service System of the China Meteorological Administration). Due to a continental monsoon climate, more than 90% of the annual total precipitation falls in the growing season. Snowfall is low in the experimental area and snow pack begins to melt in March.

Grassland is the dominant system type on the Qinghai-Tibetan Plateau, and these landscapes are the focus of human activity and grazing. Alpine meadow, mainly located in the eastern part of the plateau, are a fragile ecosystem and is very sensitive to environmental change. Since the 1960s, the Qinghai-Tibetan Plateau has experienced significant year-around warming at a rate of 0.2 °C per decade and increasing spring precipitation at a rate of about 0.5 mm per year (Li et al., 2010). The alpine meadow at our experimental site is dominated by sedges including *Carex capillifolia, Carex moorcroftii, Kobresia humilis* and *Kobresia pygmaea*, and grasses including *Poa pratensis*, and forbs including *Lancea tibetica, Potentilla multifida* and *Potentilla saundersiana*. In general, the vegetation begins greening in early to mid-May. Our experimental site was grazed by yak every summer before the experiment and was fenced in 2010 to exclude grazing.

2.2. Experimental design

Our experiment included two temperature treatments (ambient and warming) and four levels of precipitation treatment (0%, 33%, 67% and 100% increase of historical precipitation averages). Our experiment included four replicates of each of the following six treatments: control (no warming and no precipitation addition), warming (W), low precipitation addition (33%; LP), medium precipitation addition (67%; MP), high precipitation addition (100%; HP) and warming plus high precipitation addition (WHP). We have no interactive treatments of low or medium level of precipitation and warming (Table 1). There were twenty-four 2 *m* × 2 m plots randomly located at our site and the spacing between plots was 2 m. To simulate warming we used an open top chamber (OTC, transparent plastic column height: 0.45 m, base diameter: 1.20 m, top diameter: 0.65 m, see in the Fig. S1). OTCs were

Table 1
Experimental design. C: control, W: warming, LP: low precipitation addition, MP: medium precipitation addition, HP: high precipitation addition, WHP: warming plus high precipitation addition. "√" indicates the treatments include warming.

Treatments	C	W	LP	MP	HP	WHP
Warming	–	√	–	–	–	√
Precipitation addition level (mm)	–	–	20	40	60	60
Precipitation addition rate in 2015 (%)	–	–	50	100	150	150
Precipitation addition rate in 2016 (%)	–	–	67	133	200	200
Precipitation addition rate in 2017 (%)	–	–	27	53	80	80

placed in the middle of the warming plots to impose warming throughout the year.

Precipitation treatments were deployed during late March and late April to manipulate the amount of precipitation (both from rain and snow) in the system before spring onset or at the end of the non-growing season period (from October to April). We established precipitation addition levels of 20 mm (LP), 40 mm (MP) and 60 mm (HP and WHP), reflecting 33%, 67% and 100% increases of historical mean (from 1980 to 2013) non-growing season precipitation. During 2015 to 2017, the non-growing season precipitation reached 41.1 mm, 29.5 mm and 75 mm. Hence, our increase of precipitation ranged from 27% to 200% (Table 1). We used a watering can to add water from a river near the site on each precipitation addition plot (area of 2 × 2 m^2) once every three days from late March to late April for a total of ten times per year, adding 2 mm, 4 mm, 6 mm and 6 mm per watering instance in LP, MP, HP and WHP plots, respectively. The inorganic nitrogen contents reached 0.27 mg L^{-1} in the adding water and it was equal to 0.05, 0.11 and 0.16 kg N ha^{-1} yr^{-1} nitrogen wet deposition in low, medium and high precipitation addition level, respectively, which were significantly lower than local average nitrogen wet deposition (0.92 kg N ha^{-1} yr^{-1}; Liu et al., 2015). We watered the plots early in the morning, about 6:00 ∼ 7:00 in local time, to reduce evaporative losses.

2.3. Data collection

2.3.1. Environmental data

We measured soil temperature and soil water content at 5 cm depth (the primary root zone) automatically every 30 min during the experiment using an EM 50 Data Collection System (Decagon Devices, Inc., NE, USA).

2.3.2. Phenology measurements

We selected five common plant species that sum to 80.5% of total cover of all plots to measure phenological change under warming and spring precipitation addition (Table 2). The monitored species were classified into sedge, grass and forb based on their growth form. They were also classified by flowering functional group (e.g. early flowering species (flower before June) and mid flowering species (flower after June)) and rooting depth (shallow rooted species (at 10 cm depth) and deep rooted species (at 20 cm depth)). We monitored plant phenology at 5 day intervals from April to September in 2015, 2016 and 2017. Five individuals or stems for each species were randomly labeled and monitored for spring phenology in each plot. For each individual, we defined green up (or flowering) as the date when the first leaf (or flower) emerged. We did not monitor the flowering of *C. moorcroftii* due to its low flowering rate. We averaged phenological days of five individuals of each species to represent the green up and first flowering in each plot.

2.4. Data analysis

We used repeated-measures analysis of variance (RMANOVA) to examine the separate and interactive effects of year, species, warming and precipitation addition on plant green up and first flowering. Bonferroni tests were used to conduct pairwise comparisons of differences of green up and flowering between control and warming, control and high precipitation addition, warming and warming plus high precipitation addition, and high precipitation addition and warming plus high precipitation addition for each species. Three-way ANOVA was used to test the main and interactive effects of species, warming and precipitation addition on green up and flowering in each year. We used two-way ANOVA to test the main and interactive effects of warming and precipitation addition on soil temperature and soil moisture in each year. LP and MP treatments were not included in these models because we have no interactive treatments of low or medium level of precipitation and warming. Bonferroni tests were used to conduct pairwise comparisons of differences of community green up and flowering between control and warming, warming and warming plus high precipitation addition, and high precipitation addition and warming plus high precipitation addition. Bonferroni tests were also used to conduct multiple comparisons of differences of community green up and flowering among different level of precipitation treatments. We log-transformed the data to achieve normality and homogeneity. All analyses were conducted in IBM SPSS version 22.

We used structural equation modeling (SEM, using IBM SPSS AMOS 24) to explore whether changes in soil temperature and soil moisture affected flowering through changing plant green up at the species and community level. Firstly, we provided an *a priori* conceptual model based on our hypothesis (Fig. S2). Then, we selected the fitted model with the lowest Akaike information criterion (AIC) (Table S1, Fig. S3). The data used in the SEM were collected from each plot in each year and we ran models separately for each species and the community as a whole. We used a weighted average of relative cover of each monitored species to represent community level phenology in this study.

3. Results

3.1. Changes of environmental factors

In spring (during late March and late April), soil temperature and soil moisture varied across the three years of the experiment (Table S2, Fig. S4). The average spring soil temperature was 3.6 °C, 6.5 °C and 4.6 °C in 2015, 2016 and 2017, respectively under ambient conditions. The average spring soil water content was 15.3%, 9.8%, and 14.2% in 2015, 2016 and 2017, respectively under ambient conditions. Specifically, 2016 was characterized by a warm and dry spring compared to 2015 and 2017.

Our experimental warming treatments, increased spring soil temperature by 0.7 °C, 2.8 °C and 0.7 °C in 2015, 2016 and 2017 compared to controls (Fig. S4). Soil water content in experimentally warmed plots decreased significantly in 2016 (8.9% compared to 9.8%, $p < 0.05$) and 2017 (11.8% compared to 14.2%, $p < 0.05$) while no change relative to control was observed in 2015 (Fig. S4).

3.2. Effects of warming and precipitation addition on community spring phenology

We observed significant interactive effects of year, warming and water addition on plant green up and flowering (Table 3). In control plots, plant green up in 2015 and 2017 was 15 (± 0) and 22 (± 4) days earlier than in 2016. Plant flowered at 145 (± 2), 161 (± 2) and 147 (± 3) DOY (day of year), respectively, in 2015, 2016 and 2017 in

Table 2
Monitored species.

Species	Growth form	Flowering functional group	Root depth	Relative cover (%)
Kobresia pygmaea	Sedge	Early	Shallow	59.4
Carex moorcroftii	Sedge	Early	Deep	12.6
Poa pratensis	Grass	Mid	Shallow	1.7
Potentilla saundersiana	Forb	Mid	Shallow	4.1
Potentilla multifida	Forb	Mid	Shallow	2.7

Table 3
Result of repeated measured analysis of variance (RMANOVA) for main and interactive effects of year (Y), species (S), warming (W) and precipitation addition (P) on plant green-up and flowering. The *p* values lower than 0.05 are bolded.

Factors	Green up date			Flowering date		
	df	F	p	df	F	p
S	4	19.50	< **0.001**	3	206.23	< **0.001**
W	1	18.14	< **0.001**	1	4.46	**0.040**
P	1	74.35	< **0.001**	3	31.42	< **0.001**
S* × *W	4	2.88	**0.030**	3	4.01	**0.013**
S* × *P	4	2.60	0.045	9	16.81	< **0.001**
W* × *P	1	21.74	< **0.001**	1	3.43	0.070
S* × *W* × *P	4	0.98	0.428	3	5.44	**0.003**
Y	2	540.99	< **0.001**	2	154.02	< **0.001**
Y* × *S	8	4.69	< **0.001**	6	4.41	**0.001**
Y* × *W	2	54.10	< **0.001**	2	51.18	< **0.001**
Y* × *P	2	81.77	< **0.001**	2	18.91	< **0.001**
Y* × *S* × *W	8	1.92	0.064	6	3.08	**0.008**
Y* × *S* × *P	8	2.62	**0.011**	6	4.53	< **0.001**
Y* × *W* × *P	2	39.74	< **0.001**	2	16.78	< **0.001**
Y* × *S* × *W* × *P	8	1.83	0.078	6	1.74	0.121

control plots. Warming and precipitation addition effects differed among years (Table 3, Table S3). For example, community average green up and flowering advanced significantly under each precipitation addition treatment compared with control plots in 2016, while precipitation addition caused no change in 2015 and 2017 ($p < 0.05$; Fig. 1a, b). In the warm and dry year (2016), community average green up was delayed 23 (± 6) days by warming treatments while it was advanced 6 (± 4) days by warming in the cool and wet year (2015) ($p < 0.05$; Fig. 1c). Warming delayed community average flowering by 22 (± 5) days compared to control in 2016, while it caused no change in 2015 and 2017 ($p < 0.05$; Fig. 1c). In WHP plots, community average green up advanced compared to control plots in both wet (2015) and dry (2016) years, while community average flowering advanced in all three years ($p < 0.05$; Fig. 1c, d). In WHP plots, community average green up and flowering advanced compared to the W plots in 2016, while they did not change in 2015 and 2017 (Fig. 1c, d). However, compared to the HP plots, community average green up and flowering advanced in 2015 in the WHP treatment while they did not change in 2016 and 2017 (Fig. 1c, d).

3.3. Different species responses to treatments

We observed different responses to warming and precipitation addition treatments among the dominant focal species in our plots (Table 3). The three year mean green up of all species demonstrated no significant change under precipitation addition compared to control while flowering of *K. pygmaea* was advanced in MP and HP treatments compared to control (Fig. 2a, b). However, low and medium precipitation addition delayed green up of *P. pratensis* in 2015 while medium and high precipitation addition advanced the green up of *K. pygmaea* and *P. pratensis* in 2016 (Fig. 3). Under warming treatment, the three year mean green up of *P. saundersiana* and *P. multifida* was delayed compared to control (Fig. 2c). Moreover, warming increased the annual variability of green up and flowering in all monitored species. For example, green up of *K. pygmaea* advanced 8 (± 2) days in 2015 and delayed 23 (± 3) days in 2016 under warming compared to control (Fig. 3), resulting in green up occurred at 125 (± 5) to 170 (± 3) in the day of the year. Compared to control, warming plus precipitation addition significantly advanced the three year mean flowering date of *K. pygmaea* and *P. multifida* (Figs. 2d, 3). Specifically, the flowering of *K. pygmaea* in WHP plots advanced significantly compared with the control in all three years, but had no changes in other species in 2016 (Fig. 3). In WHP plots, the three year mean green up of *K. pygmaea, P. saundersiana* and *P. multifida*, and the flowering of *K. pygmaea* and *P. multifida* significantly advanced compared to warming (Fig. 2c, d). However, the three year mean green up and flowering of all monitored species demonstrated no differences between HP and WHP treatments (Fig. 2c, d).

3.4. Correlations of spring phenology with environmental factors

Spring soil temperature and soil water content were significantly correlated with community average green up (Fig. 4) with warmer soil temperatures and drier soil water content associated with later green up. These results, however, are strongly driven by observations from the warming treatment in 2016. The SEM results showed that path coefficients of soil temperature and soil water content to green up were 0.44 and −0.32 and soil temperature and soil water content accounted for 50% of the variation in the community average plant green up date. Soil temperature also had a positive effect on plant flowering while soil water content had no direct effects on flowering date. However, soil moisture had significant indirect effects on community average flowering date by influencing green up date (Fig. 4, Table 4). At the species level, all of the monitored species (except for *C. moorcroftii*, due to no

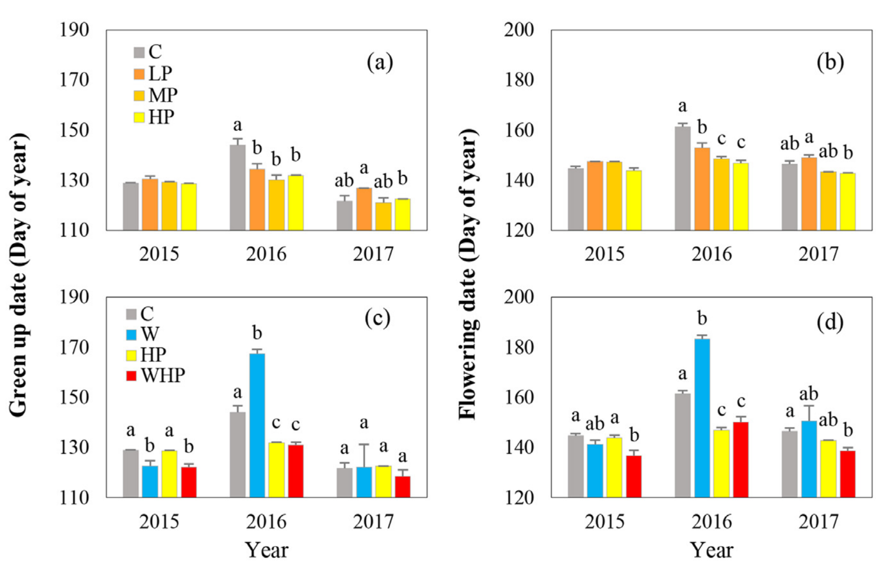

Fig. 1. Effects of warming and precipitation addition on community average green up and flowering. The error bars indicate standard error ($n = 4$). C: control, W: warming, LP: low precipitation addition, MP: medium precipitation addition, HP: high precipitation addition, WHP: warming plus high precipitation addition. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

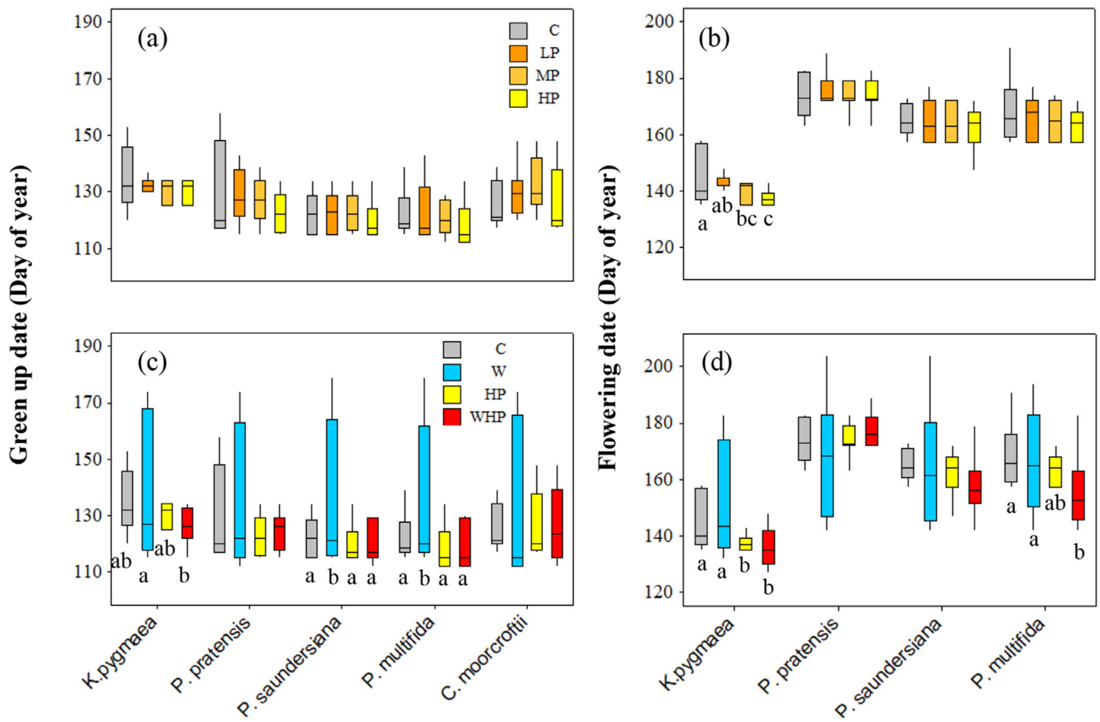

Fig. 2. Effects of warming and precipitation addition on three year mean green up and flowering of each monitored species. C: control, W: warming, LP: low precipitation addition, MP: medium precipitation addition, HP: high precipitation addition, WHP: warming plus high precipitation addition. Different lowercase letters indicate significant differences among treatments ($p < 0.05$).

Fig. 3. Changes of green up and flowering of each monitored species in each year. W: warming, LP: low precipitation addition, MP: medium precipitation addition, HP: high precipitation addition, WHP: warming plus high precipitation addition. "*" indicates significant differences from zero ($p < 0.05$).

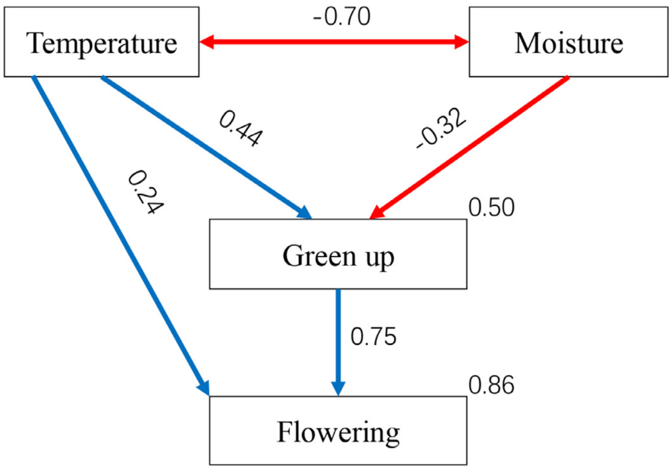

Fig. 4. Effects of spring soil temperature and spring soil moisture on community average green up and flowering in an alpine meadow. $\chi^2 = 1.282$, $p = 0.258$, $AIC = 27.282$. The red lines indicate negative correlations; the blue lines indicate positive correlations. The data shown here include all data collected across the treatments and years. More details of the SEM model are shown in Table S1. In our experiment, both temperature and moisture are controlling factors and they have a significant negative correlation. We cannot conclude that temperature changes result in moisture changes and vice versa. Therefore, the line between temperature and moisture is bidirectional.

Table 4
Standardized total, direct and indirect effects of spring soil temperature and spring soil moisture on community average green up and flowering shown in the SEM model in Fig. 4. .

Environmental factors	Spring phenology	Total effects	Direct effects	Indirect effects
Temperature	Green up	0.44	0.44	0
	Flowering	0.57	0.24	0.33
Soil moisture	Green up	−0.32	−0.32	0
	Flowering	−0.24	0	−0.24

flowering data) showed the same directions of relationships among spring phenology and soil environmental factors, although the path coefficients were different for each species (Fig. S5–S8).

4. Discussion

Our results explained how warming and spring precipitation addition interact to affect timing of plant green up and flowering in an alpine meadow on the Qinghai-Tibetan Plateau. Warming delayed plant green up and flowering in a warm and dry spring, while warming advanced plant green up in a cold and wet spring. Flowering of *K. pygmaea,* a shallow rooted and early flowering species, was more likely to advance under warming plus precipitation addition than other species in a warm and dry year. Our study highlights the important role of annual variation of spring temperature and soil water content in dictating plant green up and flowering in alpine meadows on the Qinghai–Tibetan Plateau. Furthermore, our results suggest that both community and species level responses of plant phenology to change of temperature and water should be considered when assessing climate change impacts.

4.1. Responses of community level spring phenology to warming and precipitation addition

Plants need a certain amount of cumulative temperature to green up (Ram et al., 1988). Therefore, warming is expected to advance plant green up in the cold Qinghai-Tibetan Plateau (Li et al., 2016; Meng et al., 2017; Suonan et al., 2017). However, warming can also increase drought stress, which can delay plant growth (Dorji et al., 2013). In OTCs warming manipulative experiments, a decrease in soil moisture can occurred due to a well-known unintentional rain-sheltering effect (Hudson et al., 2011; Dorji et al., 2013; Zhu et al., 2016). In the Qinghai-Tibetan Plateau, remote sensing studies have shown that warming advanced spring green up in wet regions while it delayed green up in dry regions (Shen et al., 2015). Hence, preseason water availability is an important factor regulating the warming effects on plant phenology. In the USA, field experiment has showed that seasonal variation in the timing and amount of precipitation governs grassland green up of great plain ecosystems (Zelikova et al., 2015). After conducting three years of year-round warming and spring precipitation addition experiment, we found that warming delayed plant green up and flowering in a warm and dry year (2016) while advanced plant green up in a cold and wet year (2015). Our results also showed that augmenting spring precipitation significantly advanced spring phenology in 2016 but caused no change in 2015 and 2017. In other words, warming tends to advance plant phenology in wet conditions while water addition tends to advance phenology in dry conditions. Based on a remote sensing study, Shen et al. (2011) confirmed that increasing preseason temperature tended to advance green-up in relatively moist areas while increased preseason precipitation tended to advance green-up in drier areas on the Qinghai-Tibetan Plateau.

The interaction of temperature and precipitation is the main factor dictating spring phenology on the Qinghai-Tibetan Plateau (Shen et al., 2011). In the central Qinghai-Tibetan Plateau, drought induced by manipulative warming appears to be the dominant regulator for plant flowering in a dry spring (Zhu et al., 2016) and snow addition could offset the negative effects of warming (Dorji et al., 2013). However, in the northeastern Qinghai-Tibetan Plateau, a wetter region compared with the central part of the plateau, plant phenology was strongly advanced by warming, was slightly advanced by precipitation addition, but did not appear to respond to interactive effects of temperature and precipitation (Suonan et al., 2019). Our results showed that interactive effects of warming and water addition on plant phenology were year dependent (Fig. 1, Table 3). For example, the advancing effect of warming on plant green up was not influenced by water addition in 2015 while the delaying effect of warming on plant green up was offset by water addition in 2016. This suggests that temperature alone does not explain phenological variation of plants and plant spring phenology is controlled by both temperature and precipitation in the Qinghai-Tibetan Plateau (Chen et al., 2015).

4.2. Specific responses of plant species to warming and precipitation addition

Plant species have different interactions with environmental factors based on growth form or functional type (Rollinson and Kaye, 2012; Bråthen and Ravolainen, 2015). As such, phenological responses to environmental change often depend on functional group (Rollinson and Kaye, 2012; Zhu et al., 2016). In this study, we found that warming increased annual variability of plant green up of all functional groups, especially early flowering species including *K. pygmaea* and *C. moorcroftii*, which, under warming, advanced green up in 2015 and delayed it in 2016. Studies have shown that shallow-rooted species are more sensitive to soil moisture changes than other species (Derner et al., 2008; Dorji et al., 2013). Our results showed that in a warm and dry year (2016), precipitation addition had no effects on *C. moorcroftii*, a deep rooted species, while shallow rooted graminoids like *K. pygmaea* and *P. pratensis* had benefit from an increase of precipitation during the preseason (Fig. 3). Our previous study found that cover of graminoids was positively correlated with soil water content on the Qinghai-Tibetan Plateau (Ganjurjav et al., 2016b). Likewise, Yang et al. (2011) showed that cover of graminoids tends to increase under precipitation addition and decrease under warming in a temperate steppe. However, in a wet and cold year (2015), precipitation addition delayed green up of *C. moorcroftii* and *P. pratensis* and had no effects on *K. pygmaea* (Fig. 3). This suggests that the positive or neutral effects of precipitation addition on plant growth may diminish or even reverse when the soils are supported by adequate moisture.

Environmental cues are main regulators for flowering time of plants (McKeown et al., 2017). Plants alter their flowering time under environmental change to maximize reproductive success (Greenup et al., 2009). Our results showed that in wet years (2015 and 2017), warming plus precipitation addition advanced flowering of *K pygmaea, P saundersiana* and *P multifida*. However, in a warm and dry year (2016), warming plus precipitation addition advanced flowering of *K pygmaea*, an early flowering species, but had no effects on mid flowering species (Fig. 3). Early flowering species are expected to be more sensitive to environmental change (Xia and Wan, 2013; Zhu et al., 2016; Meng et al., 2017) due to their low drought resistance and high exposure to spring drought (Zhu et al., 2016; Cui et al., 2017). Generally, the mid flowering species flowered after the summer monsoon arrived, when they had adequate moisture to offset drought effects of warming (Dorji et al., 2013). Overall, we found that life history traits are critical for driving different responses of early and mid-flowering species to warming and precipitation addition.

4.3. Future projection and implications

In our experiment, warming advanced spring phenology in 2015, delayed it in 2016, and did not change it in 2017. Historical data showed that in our experimental region, climate conditions in 2015 were similar to the long-term mean, while 2016 was an extremely dry year. Hence, we need to consider future spring precipitation change when predicting warming impacts on plant phenology on the Qinghai-Tibetan Plateau. In the future, based on observational data and climate models, the temperature of the Qinghai-Tibetan Plateau is expected to continuously increase (Liu et al., 2009; Ji and Kang, 2013). Moreover, the projection of regional climate models suggests that, in addition to warming, precipitation will increase in the future (Gao et al., 2012). However, the projections of precipitation shown high uncertainties and overestimation in the Qinghai-Tibetan Plateau (Ji and Kang, 2013; Gao et al., 2012). That's why experiments as ours with different levels of precipitation addition are needed.

5. Conclusion

We found that warming increases annual variability of plant spring phenology. Warming delayed green up of all monitored species in a warm and dry year, but advanced spring onset of early flowering species in a cold and wet year. Early spring precipitation addition can offset the delaying effects of warming in a dry year on the Qinghai-Tibetan Plateau. Further, the interactions of warming and precipitation addition appear to impact flowering of the dominant sedge *K. pygmaea* more than other species in a dry condition in the ecosystem, suggesting that following the response of one dominant species in a system is not indicative of how most of the species in the community might respond. Precipitation plays a very important role in plant phenology in many grassland ecosystems but it is understudied relative to the effects of temperature. Early spring precipitation shows high yearly variations and there are great uncertainties in prediction regarding the future of spring precipitation on the Qinghai-Tibetan Plateau. Here, we provide evidence that soil moisture condition plays a critical role in determining the magnitude and direction of spring phenology response to warming.

CRediT authorship contribution statement

Hasbagan Ganjurjav: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Elise S. Gornish:** Writing - original draft. **Guozheng Hu:** Methodology. **Mark W. Schwartz:** Conceptualization, Writing - original draft. **Yunfan Wan:** Methodology. **Yue Li:** Methodology. **Qingzhu Gao:** Conceptualization, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We gratefully acknowledge the financial support from the National Natural Science Foundation of China (31901142, 31570484) and Young Elite Scientists Sponsorship Program by CAST (2019-2021QNRC001). We thank for the constructive suggestions and comments of editors and anonymous reviewers.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.107943.

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