Changes in soil or air temperature lead to dynamics of alpine plant biomass associated with phenological or growth patterns

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Abstract

Understanding the effects of climate change on plant phenological dynamics and growth patterns is critical for predicting climatic changes on the Qinghai-Tibetan Plateau (QTP). We used data over 21 years (1997 to 2017) for four dominant species on the QTP, namely Astragalus laxmannii (legume), Artemisia scoparia (forb), Kobresia humilis (sedge), Stipa purpurea (grass), and examined the relationships among climatic changes, plant phenology, growth pattern, and biomass. Most phenological periods in Stipa purpurea and Artemisia scoparia were delayed, whereas in Astragalus laxmannii, they were advanced. Soil temperature and maximum air temperature were the most important drivers. There were trade-offs between reproductive phenology and vegetative phenology, as well as between the length of the rapid growth period and the intrinsic growth rate. The impacts of the phenological or growth processes were species-specific. Our findings provide evidence of long-term changes and are of great significance for improving the accuracy of models.

Introduction

Plant biomass, the amount of carbon captured by photosynthesis (Potter*et al.* 1999), is an important ecosystem property and an indicator of climatic changes (Wang *et al.* 2007; Swemmer *et al.*2007; Ma *et al.* 2010). In the past decades, significant climate changes (Ma *et al.* 2010; IPCC 2013; Hansen *et al.* 2006) have altered plant biomass, especially in the arctic and alpine regions (Walker *et al.* 1995; Jonas *et al.* 2018; Kardol *et al.* 2010; Zhang *et al.* 2018; Wang *et al.* 2020). While some studies suggest that plant phenology is a bridge between climate change and plant biomass (Zhang *et al.* 2018; Walther *et al.* 2002; Albert *et al.* 2019), others show that alpine plants will accumulate biomass by accelerating growth rates (Rammig *et al.* 2019; Wingler *et al.* 2016) to compensate for limited growing seasons and low temperatures (Suonan *et al.* 2019).

In the last decades, there has been an increased interest in the impacts of climate change drivers on plant phenology; however, the relationship between climatic changes and plant phenology is still largely unclear (Zhang *et al.* 2018; Suonan *et al.* 2019; Shen *et al.*2015; Reed *et al.* 2019). For example, *in-situ* observations and satellite observations show that temperature is the main determinant of phenology, and increased warming in spring can result in advanced spring phenology (Zhang *et al.* 2018; Wang *et al.* 2020; Shen *et al.* 2015; Piao *et al.* 2011; Fu *et al.*2014). Conversely, some studies have shown that climate change-related warming reduced temperature sensitivity (Shen *et al.* 2015; Yu*et al.* 2010; Fu *et al.* 2015; Piao *et al.* 2019) of plants. In contrast to overall warming, daytime warming and night warming are asynchronous processes (Yang *et*

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al. 2016; Zhou et al. 2019) and may have different effects on plant phenology (Shen et al. 2015; Piao et al. 2015). We speculate that the effects of air temperature, rather than soil temperature, on plant phenology are more important (Cleland et al. 2012) especially in spring. According to previous studies, precipitation or soil moisture can affect the plant phenology independently or jointly with increasing temperatures (Zhang et al. 2018; Duparc et al. 2013). In addition to temperature and precipitation, relative air humidity (Sparks et al. 2002) and photoperiod (Zhang et al. 2018; Shen et al. 2015; Ernakovich et al. 2014; Fu et al. 2019) may also affect plant phenology. However, the impacts of multiple climate factors on plant phenology in alpine regions have rarely been evaluated.

The dynamics of spring phenology of alpine plants against the background of a changing climate have been widely examined (Zhang et al. 2018; Shen et al. 2015; Piao et al. 2015; Dong et al. 2013), whereas other while the other phenological processes (i.e., flowering, fruiting, and withering) remain poorly studied (Fridley 2012; Gallinat et al. 2015; Xie et al. 2015). However, plant reproductive phenology of flowering and fruiting of plants (Sherry et al. 2007; Munson et al. 2017) is as important as plant vegetative phenology (Xie et al. 2015), and the trade-off between vegetative and reproductive phenology under climate change (Wang et al. 2014) can affect plant biomass (Millerrushing et al. 2008). Most studies have only focused on the phenology of plant leaves, flowers, and fruits (e.g., green-up, flowering, and fruiting period), whereas little is known about the growth patterns in grasslands (Sun & Frelich 2011).

We assume that there is a trade-off between the length of the fast-growing phase and the intrinsic growth (Brienen et al. 2020), especially in areas with a limited growing seasons and low temperatures (Wingler & Hennessy 2019; Suonan et al. 2019; Brienen et al. 2020). The trade-offs in plant phenology or growth patterns with climatic changes can be attributed to the responses of functional groups (Wang et al. 2020; Vitasse et al. 2009; Suonan et al. 2017).

On the Qinghai Tibetan Plateau, alpine grassland is the largest ecosystem, providing key ecological services for a variety of livestock for humans (Li et al. 2019; Dong et al. 2020). As one of the regions which is most sensitive to climatic changes (5), the QTP has experienced overall warming and increased precipitation from 1961 to 2010 (Chen et al. 2013). Using data from 21 years (1997 to 2017), with 2-day intervals for phenology dynamics and 10-day intervals for growth patterns, using annual biomass data of four key species in an alpine meadow on the QTP, we conducted this study to address the following questions: (1) How do the phenology and growth patterns of different functional groups of plant species in alpine grassland on the QTP change over time? (2) Can climate change affect the biomass of different functional groups of alpine plant species through altered growth patterns or phenology dynamics? (3) Which environmental factors most significantly affect the key growth and phenological events of different functional groups of alpine plant species?

Materials and Methods

This study was conducted in the town of Xihai, Haiyan County (100°57'N, 36deg56'E, 3100 m ASL), Qinghai Province, China, at the eastern edge of Qinghai Lake (Fig. S1). Mean annual temperature is 1.4degC, mean annual precipitation is 330–370 mm, and mean annual potential evaporation is approximately 1,400 mm. The typical vegetation is alpine meadow, dominated by sedges and grasses. The soil type is loam, and the vertical profile is 0–30 cm for clay loam and 30–50 cm for silty loam.

Four key species in the alpine meadow on the QTP, i.e., *Stipa purpurea* (grass), *Kobresia humilis* (sedge), *Artemisia scoparia* (non-legume forb), and *Astragalus laxmannii* (legume) have been monitored from 1997 to 2017 (with one observation for each of the four species in 2000; for 2006, data for *Astragalus laxmannii* were missing) (Figs. S1 to S5). A randomly selected area of 100 x 100-m was equally divided into four 50 x 50-m blocks; each block was divided into four 25 x 25-m cells and marked permanently, and each cell was further separated into three sections. The first section was used for monitoring phenological time periods (e.g., green-up, flowering, fruiting, and withering), using 10 individuals of each species in each cell. Plant phenology was recorded every 2 days after the green-up period. The second section was used for monitoring plant height, using 10 individuals of each species in each cell. Plant height was recorded every 10 days

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after the green-up period. The last section was used for monitoring plant biomass, for which each plant in a randomly selected 1 x 1-m quadrant was harvested after the withering period, and the selected cell was rotated clockwise every 4 years in each block (Fig. S1). After harvesting, each plant was oven-dried at 65degC to constant weight. Soil moisture at a depth of 0–30 cm was determined via oven-drying of soil samples at 105 to constant weight every 10 days from March to the end of September. The climatic data were obtained from the Haiyan meteorological station (nearby the study site), recording daily average temperature, daily maximum temperature, daily minimum temperature, daily average soil temperature (0–30 cm), daily precipitation, daily relative humidity, and daily sunshine length (note: data of daily sunshine length were missing in the second half of 2017).

We defined the date when the phenomenon occurred (Julian day) in more than 50% of the marked plants as the time of the phenological period (e.g., green-up, flowering, fruiting, and withering) and the duration (number of days) from flowering to fruiting as the length of the generative growth period. We used the duration (number of days) from green-up to withering minus the length of the generative growth period as the length of the vegetative growth period.

To describe the growth dynamics across growing seasons with the height measured every 10 days (Figs. S2 to S5), we used a three-parameter logistic function (Paine *et al.* 2012). We also calculated the annual peak height, the timing of maximum growth (Julian day), and the intrinsic growth rate. To determine the start and end growth for each species, we consulted previous studies (Richardson *et al.* 2013) and set the time to reach 21% of the maximum height as the time for the start of the rapid growth phase (Julian day) and to reach 79% of the maximum height as the time for the end of the rapid growth phase (Julian day). We defined the duration (number of days) from the beginning of rapid growth to the end of rapid growth as the length of the rapid growth phase.

To determine phenology dynamics, growth patterns, and annual biomass in different plants, we used variance analysis (Table S1) and employed a linear model to show the trends at the start of the rapid growth phase, the timing of maximum growth, the end of the rapid growth phase, green-up time, flowering time, fruiting time, withering time, annual peak height, intrinsic rate of plant growth, and biomass of key plant species (Figs. 1 to 3). We used linear regression to explore the relationships among plant biomass, intrinsic growth rate, length of the rapid growth phase, length of the vegetative growth period, and length of the generative growth period over time (Table S2).

To identify optimal length thresholds (i.e., how many days) and the factors determining the growth and phenological events which are significantly associated with plant biomass, we also used linear models to evaluate the effects of average temperature, maximum temperature, minimum temperature, average soil temperature, precipitation, relative humidity, soil moisture, and sunshine length on plant growth (start of the rapid growth phase, the timing of maximum growth, and the end of the rapid growth phase) and phenological events (green-up, flowering, fruiting, and withering) during the growing season. To determine which days affected the key growth and phenological events, we compared the fit of each factor to each growth and phenological event with a step length of 2 to 60 (30 models in total), in which precipitation and sunshine length were the sums of multi-day values. However, other factors (average temperature, maximum temperature, minimum temperature, average soil temperature, relative humidity, and soil moisture) were represented by the average of multi-day values, and we used the measured values to indicate the value of 5 days before and after the measurement since the soil moisture was measured once every 10 days. There was collinearity between average and maximum temperature (Pearson's correlation coefficient = 0.85), average temperature and minimum temperature (Pearson's correlation coefficient = 0.85), average temperature and average soil temperature (Pearson's correlation coefficient = 0.90), as well as maximum temperature and average soil temperature (Pearson's correlation coefficient = 0.86) (Fig. S6). Three parallel models were constructed to remove collinearity, i.e., average temperature + precipitation + relative humidity+ soil moisture + sunshine length; maximum temperature+ minimum temperature + precipitation + relative humidity+ soil moisture + sunshine length; minimum temperature + soil temperature+ precipitation + relative humidity+ soil moisture + sunshine length, resulting in a total of 90 models (30 * 3 parallel models). Finally, we produced

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candidate models based on a cut-off of ΔAIC < 5 and subsequently selected the model with the shortest number of days as the best model among the candidate models. We calculated the average of the factors in multiple parallel models to select the best model, i.e., the multiple parallel models within the same day (Tables S3 and S4).

The 'stats' and 'deSolve' packages were employed for the logistic function, the 'multcomp' and 'agricolae' packages to perform variance analysis, and the 'basicTrendline' package for the linear model. We used the 'PerformanceAnalytics' package for correlation analysis and the 'stats' package for multiple regression analysis in R v. 3.5.1 (R Development Core Team).

Results

Long-term changes in plant phenology, growth, and biomass

Over the 21 years, all phenological periods (green-up, flowering, fruiting, and withering periods) of *Stipa purpurea* and *Artemisia scoparia*, except the flowering time of *Stipa purpurea*, were significantly ($p < 0.05$) delayed. In contrast, all phenological periods of *Astragalus laxmannii* were significantly ($p < 0.05$) advanced. The green-up and fruiting periods of *Kobresia humilis* were significantly ($p < 0.05$) delayed, whilst the withering period was significantly ($p < 0.05$) advanced. The flowering and withering periods of *Kobresia humilis* were not significantly changed (Fig. 1).

From 1997 to 2017, only the start of the rapid growth phase (Fig. 2a) and the growth peak (Fig. 2b) of *Kobresia humilis* were significantly ($p < 0.05$) advanced. Annual peak height, intrinsic rate, and aboveground biomass of *Kobresia humilis* and *Astragalus laxmanni* were significantly ($p < 0.05$) increased (Fig. 2). Aboveground biomass of *Artemisia scoparia* (Fig. 3i) was significantly ($p < 0.05$) decreased, but that of *Stipa purpurea* (Fig. 3l) was not significantly ($p > 0.05$) changed.

Effects of the length of plant growth and phenological phases on plant biomass

The length of the rapid growth phase was significantly ($p < 0.05$) negatively correlated with the intrinsic growth rate in four species (Fig. S7). The length of the vegetative growth period was significantly negatively correlated with the length of the generative growth period in four plant species (Fig. S7).

The plant biomass of *Kobresia humilis* was significantly negatively correlated with the length of the vegetative growth period but positively correlated with the length of the generative growth period. The plant biomass of *Astragalus laxmannii* was significantly negatively correlated with the length of the rapid growth period and positively correlated with the intrinsic growth rate. The plant biomass of *Stipa purpurea* and *Artemisia scoparia* was only significantly correlated with the length of the vegetative growth period (Table S2).

Effects of climate change on plant growth and phenology

For *Kobresia humilis*, soil temperature was the most important factor impacting the green-up period (significantly delayed), the flowering period (significantly delayed), and the withering period (significantly advanced), and the optimum thresholds were 38, 54, and 54 days. Maximum air temperature was the most important factor for the fruiting period (significantly delayed), with an optimum threshold of more than 60 days (Tables S2 and S3, Fig. 4a).

For *Astragalus laxmannii*, soil temperature was the most important factor impacting the start of the rapid growth phase (significantly delayed), with an optimum threshold of 58 days. Air temperature was the most important factor impacting maximum growth (significantly delayed), with an optimum threshold of 48 days. Maximum air temperature was the most important factor determining the end of the rapid growth phase (significantly delayed), and the optimum threshold was more than 60 days (Tables S2 and S3, Fig. 4b).

For *Stipa purpurea* and *Artemisia scoparia*, soil temperature was the most important factor impacting the green-up period (significantly delayed), with an optimum threshold of 58 days (*Artemisia scoparia*) and 56 days (*Stipa purpurea*). Soil temperature was also the most important factor impacting the withering period (significantly advanced) of *Artemisia scoparia* (optimum threshold of 48 days), whereas for *Stipa purpurea*,

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temperature was the most important factor, with an optimum threshold of 40 days (Tables S2 and S3, Fig. 4c and 4d).

Fig. 1 Trends of green-up, flowering, fruiting, and withering periods for *Kobresia humilis* , *Astragalus laxmannii* ,*Artemisia scoparia* , and *Stipa purpurea* over time. Dots indicate the Julian day, the line indicates the trend of the Julian day by the linear model, grey areas represent the 95% confidence intervals. The solid line indicates p -values < 0.05, the dashed line indicates p -values > 0.05. The blue line represents significant positive correlations, and the red line represents significant negative correlations.

Fig. 2 Trends of the start of the rapid growth phase, the timing of maximum growth and the end of the rapid growth phase for *Kobresia humilis* , *Astragalus laxmannii* , *Artemisia scoparia* , and *Stipa purpurea* over time. Dots indicate the Julian day, the line indicates the trend of the Julian day by the linear model, grey areas represent 95% confidence intervals. The solid line indicates p -values < 0.05, the dashed line indicates p -values > 0.05. The blue line represents the significant positive correlations, and the red line represents the significant negative correlations.

Fig. 3 Trends of annual peak height, intrinsic growth rate, and biomass of *Kobresia humilis* , *Astragalus laxmannii* ,*Artemisia scoparia* , and *Stipa purpurea* over time. Dots indicate annual peak height, intrinsic growth rate, and biomass. The lines indicate the trends of annual peak height, intrinsic growth rate, and biomass by the linear model, grey areas represent 95% confidence intervals. The solid line indicates p -values < 0.05, the dashed line indicates p -values > 0.05. The blue line represents the significant positive correlations, and the red line represents the significant negative correlations.
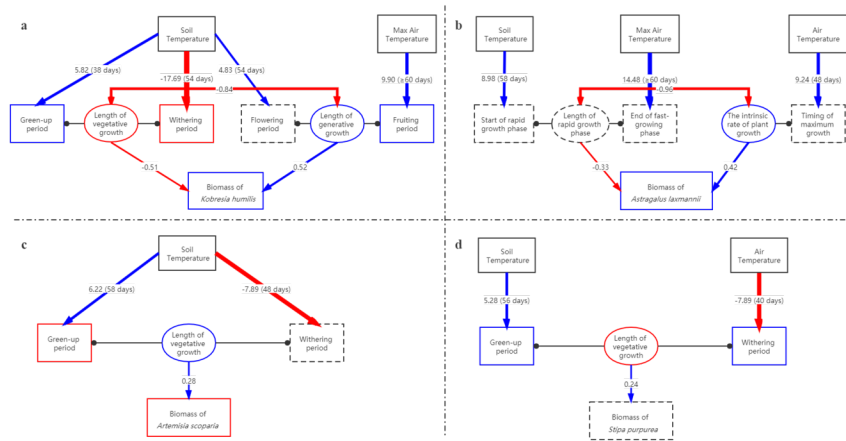

Fig. 4 Relationships among plant biomass, plant growth, and phenology. Blue lines represent the significant positive correlations, red lines represent the significant negative correlations, blue boxes represent significantly increased trends over time, red lines represent significantly decreased trends over time, the dashed line represents non-significant correlations, the dashed boxes represent non-significant trends over time. The number in the middle of the line represents Pearson's correlation coefficient and optimal daylength threshold.

Discussion

Although previous studies have largely examined the impacts of climate warming on plant phenology in alpine meadows on the QTP by using either manipulative experiments (Dorji *et al.* 2013; Wang *et al.* 2014; Shi*et al.* 2014) or remote sensing data (Zhang *et al.* 2018; Wang *et al.* 2020; Shen *et al.* 2015; Yu *et al.* 2010; Dong *et al.* 2013), only few studies (Chen *et al.* 2015) have documented the impacts of natural climate variations on plant phenology in alpine meadows in the long term. Therefore, using data from a period of 21 years, we investigated the impacts of climatic variation on phenological dynamics (green-up,

flowering, fruiting, and withering periods) and growth patterns (heights) of different alpine plants from various functional groups.

We observed a significant delay in the green-up period for *Kobresia humilis* , *Stipa purpurea* , and *Artemisia scoparia* , which is consistent with the findings of Yu *et al.*(2010), Chen *et al.* (2015), and Zhu *et al.* (2019), but in contrast to the observations made by Wang *et al.* (2020) using remote sensing modelling. Although our study sites were close to those of Wang *et al.* (2020) (about 80 km away), and both sites had a similar vegetation type (alpine meadow), we believe that the different results can be attributed to two major reasons. First, we observed warming and wetting trends in our research site (Zhou *et al.*2019), whilst Wang et al. (2020) observed warming and drying trends. This leads us to infer that different climate change patterns, associated with geometric and geographical factors, may result in different responses of plant phenology in neighboring sites, which suggests that long-time observations across different sites can provide a scientific basis for the study of alpine plants on the QTP under a changing climate. Second, we believe that different phenological observation methods have led to different findings. In our study, we used field observation, whereas Wang et al. (2020) applied remote sensing data. Additionally, the advance green-up period of *Astragalus laxmannii* is consistent with the findings of Chen et al. (2015). Hence, we speculate that the green-up period of legumes on the QTP may be advanced under a warmer and wetter climate, which means that the response of spring phenology to climate change depends, among other factors, on the functional plant group.

For the withering period, *Kobresia humilis* , *Stipa purpurea* , and *Artemisia scoparia* showed delays, whereas*Kobresia humilis* showed an advanced withering period, this supports the findings of previous studies, where the responses of autumn phenology were more complex (Chen *et al.* 2020) than those of spring phenology. Previous studies have also shown that reproductive phenology, in contrast to other phenological periods, is relatively stable in its response to climate change on the QTP (Jiang *et al.*2016). The trends of green-up and fruiting periods were consistent, which means that the functional groups and community scales show a consistently delayed fruiting period, which agrees with Zhang et al. (2011) and Yang et al. (2014).

The growth patterns of *Kobresia humilis* and *Astragalus laxmannii* were more sensitive to climate change than those of*Stipa purpurea* and *Artemisia scoparia* , which is inconsistent with Wang et al. (2020). This could be attributed to the measurement of growth patterns; i.e., we used changes in height, whereas Wang et al. (2020) used changes in biomass over time. The trends of plant biomass found in our study are not consistent with those observed by Liu et al. (2018) finding, i.e., the biomass of the sedge*Kobresia humilis* increased significantly, whereas there was no significant increase in the biomass of *Stipa purpurea* and*Artemisia scoparia* . We believe that these different responses may be due to the "root effect" (2018); *Stipa purpurea* with deeper roots can endure more severe droughts than *Kobresia humilis* with shallower roots. In our study area, *Kobresia humilis* may therefore benefit more significantly from wetting. However, the trends of the two forbs *Artemisia scoparia* and *Astragalus laxmannii* showed different responses, which may be related to the "functional group (legume and non-legume forb) effect".

The responses of plant phenology and growth to climate change generally show a lag effect (Fu *et al.* 2019; Dong *et al.* 2013; Ahas*et al.* 2000; Li *et al.* 2016). For example, plants must undergo endodormancy before entering the green-up periods (Chuine*et al.* 2016); the spore cells begin to grow during the period of ecological dormancy, and the plant gradually recovers from dormancy and starts a new growth cycle before reaching the threshold of a certain temperature, water, or photoperiod (Fu *et al.* 2019). In our study, the optimum thresholds for all phenological phases and height growth patterns of most species were more than 30 days, which agrees with the results of previous studies. For example, 30–60 days of climate factors are related to the green-up period on the QTP (Dong*et al.* 2013), and climate factors with a 6-week delay can best fit the flowering phenology of alpine plants on the QTP (Li *et al.* 2016).

There is evidence that the air temperature under a warming climate is the most important environmental factor affecting spring phenology, especially on the QTP (Zhang *et al.* 2018; Wang *et al.*2020; Yu *et al.* 2010; Wang *et al.* 2014; Shi *et al.*2014). However, in our study, it was soil temperature rather than air temperature that determined the spring phenology or the start of the rapid growth phase of our four species, confirming

our hypothesis that soil temperature is the primary driver of plant growth. However, our results show that increased soil temperature may delay spring phenology or the start of the rapid growth phase because of an insufficient chilling period under a warmer climate (Yu *et al.* 2010; Ernakovich *et al.* 2014).

Previous studies have shown that the daytime temperature in summer exceeded the physiological threshold of alpine plants (Sherry al. 2007; Aldridge al. 2011) and delayed reproductive phenology. However, here, it was soil temperature rather than air temperature that delayed the flowering of *Kobresia humilis* . This may be explained by the fact that the flowering period of this species was earlier (in late spring) and it reached a lower height (less than 10 cm). Besides, we found that the maximum air temperature delayed the fruiting of *Kobresia humilis* , confirming previous hypotheses (Sherry *et al.* 2007; Aldridge *et al.* 2011).

The withering periods of *Kobresia humilis* , *Stipa purpurea* , and *Artemisia scoparia* were advanced under a warming climate. However, these results do not support the hypothesis that autumn warming will prolong the growing season, which has been stated by several authors (Zhang *et al.* 2018; Liu *et al.* 2016). This may be related to the adaptability of these species: an earlier ending of the growth period and an advanced dormancy can help to avoid unfavorable conditions and transfer more resources to the roots for later years (Xie*et al.* 2015).

Regarding the period of maximum growth, air temperature rather than other factors was the most impacting important for *Astragalus laxmannii* . This is consistent with the findings of a previous studies (Gonsamo *et al.* 2018), emphasizing that the average air temperature is always lower than the optimum air temperature for plant growth, especially in alpine regions. Wang et al. (2020) speculated that the moisture in the soil limited the end of the rapid growth period, but this could not be confirmed in our study. The different responses may be due to the different climatic conditions in the two sites (Shen *et al.* 2015) and the different calculation methods for growth patterns (Wang *et al.* 2020).

Although some studies have investigated the effects of manipulative warming on reproductive phenology on the QTP (Dorji *et al.* 2013; Wang *et al.* 2014; Zhu *et al.* 2016), the trade-off relationships between reproductive phenology and vegetative phenology and its impact on the ecosystem in the context of climate change have been largely neglected. We confirm the hypothesis that there are significant negative correlations between reproductive and vegetative phenology (Millerrushing *et al.* 2008; Wang *et al.* 2014; Arft *et al.* 1999) in the four functional groups. Besides, there was a similar trade-off in the growth pattern, and significant negative correlations were also found between the length of the rapid growth phase and the intrinsic growth rate in all four functional groups, confirming the hypothesis that there is a trade-off between the length of the rapid growth phase and the intrinsic growth rate (Brienen*et al.* 2020) in alpine plants. However, only one of the trade-offs played a key role in regulating aboveground biomass, and the impacts of the phenological or growth processes on alpine plant biomass are species-specific: soil temperature and average air temperature affect *Stipa purpurea* (significantly negative) and*Artemisia scoparia* (significantly positive) biomass by impacting vegetative reproduction; soil temperature and maximum air temperature affect *Kobresia humilis* biomass by affecting reproductive and vegetative phenology, which is inconsistent with previous findings (Ma*et al.* 2017; Xu *et al.* 2018). Also, soil temperature and average/ maximum air temperature affect *Astragalus laxmannii*biomass by affecting the length of the rapid growth phase and the intrinsic growth rate, which does not support the hypothesis of Suonan et al. (2019).

In summary, our findings highlight the trade-offs between phenological dynamics and plant growth patterns of key species in the alpine grassland of the QTP against the background of a changing climate. We explored the role of air and soil temperature in driving observation models, which is of great significance for understanding the feedbacks of alpine plants to climate change. The functional groups cannot be ignored in examining the responses of alpine plants to climate change. Although the predicted warming of the climate may have significant positive effects on the biomass of sedges and legumes, in non-legume forbs, the growth patterns of phenological dynamics may be affected. Our findings have profound implications for the adaptation of livestock feeding systems and the sustainable delivery of key ecosystem services on the Qinghai-Tibetan Plateau.

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