1 **Changes in phenological sequences of alpine communities across a natural**
2 **elevation gradient**

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Abstract

Change in individual species phenology is often unsuitable for predicting change in community phenology because of different responses of different species to temperature change. However, few studies have observed community phenological sequences in the field. Here we explore the changes in timing and duration of the community phenological sequence (i.e. onset of leaf-out (OLO), first flower bud (FB), first flowering (FF), first fruiting-set (FFS), post-fruiting vegetation (OPFV), first leaf-coloring (FLC) and complete leaf-coloring (CLC)) along an elevation gradient from 3200 to 3800 m in an alpine meadow on the Tibetan plateau. Our results indicate that OLO and FFS significantly advanced and other timings of phenological events significantly delayed at 3200 m compared with higher elevations (3600 and 3800 m). The flowering duration of the community was shortest and other phenological durations (except budding stage and post-fruiting vegetation stage) were longest at 3200 m. The duration of the growing season decreased as elevation increased, and the ratio of the durations of the reproductive period and growing season was smallest at 3200 m. There were negative correlations between the proportion of early-spring flowering functional group plants and FB, and the durations of leafing and post-fruiting vegetation of the community. Positive correlations were found between the proportion of mid-summer flowering functional group plants in the community and these variables. There were significant negative correlations between flowering duration of the community and annual mean air temperature and soil moisture.

48 Therefore, our results suggest that different community compositions might respond
49 differently to climate change.

50 **Keywords:** Timing and duration, Community phenology, Alpine meadow, Climate
51 change, Tibetan plateau

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1. Introduction

Phenology is the recurring life of plants, which is one of most sensitive bio-indicators of climate change. Many studies have indicated that temperature change alters the timing and duration of phenological events of individual plant species (Sherry et al., 2011; CaraDonna et al., 2014; Wang et al., 2014a; Wang et al., 2014b). However, a lack of observation of the response of community phenology to temperature change limits our ability to predict because different species in the community show different responses to temperature change (Sherry et al., 2007; Steltzer and Post, 2009; Crimmins et al., 2010; Wang et al., 2014a; Wang et al., 2014b). Remote sensing has been widely used to monitor community phenology in the Tibetan Plateau, but inconsistent and even contrary results have been reported about the response of phenology to climate change during the past 30-years (Piao et al., 2006; Yu et al., 2010; Shen et al., 2011; Shen et al., 2013; Zhang et al., 2013). In particular, although remote sensing has the strength of enabling analysis at large scale of long-term sequences, typically only the beginning and end of the growing season is monitored in grasslands, and results are affected by cloud, aerosol and sensor condition (Zhang et al., 2013). Thus, field observations are needed to validate remote sensing data, especially on the Tibetan plateau.

Climate change is deemed to have serious impacts on plant phenology in arctic and alpine ecosystems (Walker et al. 2006; Dorji et al., 2013). Grassland plant communities usually include different seasonal flowering plant species (i.e., early,

middle and late flowering plants), and their phenology or phenological sequences have different responses to temperature change (Sherry et al., 2007; Crimmins et al., 2010; Wang et al., 2014a; Wang et al., 2014b). Early flowering plants are more sensitive to temperature change than middle and late flowering plants (Sherry et al., 2007; Castro Marin et al., 2011; Pau et al., 2011; Wolkovich et al., 2012; Richardson et al., 2013). Moreover, our previous results have shown that responses of phenological events to climate change are species-specific and vary with flowering functional group (i.e. early-spring and mid-summer flowering plants) (Wang et al., 2014b). Therefore, we hypothesized that changes in the timing and duration of community phenological sequences along the elevation gradient could be determined by the combination of the relative proportion of the flowering functional groups in the community and climate change. Our objective was to investigate (1) how the timings and durations of phenological sequences of alpine communities change at the community-level across the natural elevation gradient, and (2) the biotic (i.e. flowering functional group) and abiotic (temperature and soil moisture) effects on phenological sequences during three years in an alpine meadow on the Tibetan plateau.

2. Materials and methods

2.1. Experimental design

The experimental platform was previously described by Wang et al. (2014b). It is

located at the southern slope of the Qilian Mountains in Qinghai, China. Four 20-m length $\times$ 8-m width plots were fenced at 3200, 3400, 3600 and 3800 m in 2006. Three 1 m $\times$ 1 m quadrats at each elevation were chosen to measure the community phenological events. At 3200 m, the vegetation is dominated by *Kobresia humilis*, *Elymus nutans*, *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontopodium nanum*, *Potentilla nivea*, *Carex* spp and *Poa* spp. At 3400 m, the vegetation is dominated by alpine shrub *Potentilla fruticosa* (shrub), accompanied by *K. capillifolia*, *K. humilis*, *Saussurea superba*, *Poa* spp. and *Carex* spp. At 3600 m, the vegetation is dominated by *K. humilis*, *S. katochaete* Maxim, *P. nivea*, *Thalictrum alpinum*, *P. fruticose*, *Carex* spp. and *Poa* spp.. At 3800m, the vegetation is dominated by *K. humilis*, *L. odiumnanum* and *Poa* spp. (Wang et al., 2014b).

2.2. Air temperature and soil moisture

The dynamics of air temperature and soil moisture were reported by Wang *et al.* (2014b) along the elevation gradient from 2006 to 2008. Mean annual air temperatures (MAT) were -0.92, -1.23, -0.89 and -1.76 °C across the increasing elevation during the three year period, and the annual mean soil moisture at 20 cm was 26%, 21%, 30% and 8% at each elevation, respectively (Wang et al., 2014a; Wang et al., 2014b).

2.3. Measurement of plant coverage and community phenology

Each 1 m $\times$ 1 m quadrat was divided into 100 grid cells (10 cm $\times$ 10 cm grid). Observations were made at an interval of three or four days from early April to the

116 end of October from 2008 to 2010. Coverage was monitored for all species, for each
117 functional group of seasonal flowering species and at the community level. Maximum
118 coverage of different species during the growing season period was calculated as its
119 coverage in squares with species presence divided by 100 grid cells in each plot.
120 Similarly, maximum vegetation coverage during the growing season period was
121 calculated as vegetation coverage in squares with any species presence divided by 100
122 grid cells in each plot. All species were classified into three functional groups based
123 on their life history as early, middle and late flowering plants (Liu, 1999; Wang et al.,
124 2014a) (Table S1). The relative coverage of different functional groups was calculated
125 as the total relative coverage of species in each functional group divided by the total
126 coverage of all species in the squares in each plot. The 7 phenological events
127 monitored included onset of leaf-out (OLO), first bud/boot-set (FB), first flowering
128 (FF), first fruit-set for forbs or seeding-set for graminoids (FFS), onset of post-fruiting
129 vegetation (OPFV), first leaf-coloring (FLC) and the date of complete leaf-coloring
130 (CLC). The starting date of each phenological event of the community was the day
131 when 15% of the total touched plant individuals at cross points of the quadrat
132 exhibited the phenological event. The end date of senescence was the day when 95%
133 of total touched plant individuals at cross points of the quadrat had completely
134 colored. The duration of the growing season for all phenological events was
135 calculated as the difference between the ending and onset dates of the phenological
136 events. The reproductive period was calculated as the sum of the duration of budding,

flowering and fruiting.

2.4. Data analysis

Variance analysis of the phenological events was performed using the univariate general linear model in SPSS version 20. The fixed factors were year and elevation, and the dependent factors were the timing and duration of community phenology. If there was no interaction between two factors, one-way ANOVA was used to study the response of phenological events to elevation. If interactions were identified, we proceeded to analyze using pairwise comparisons of estimated marginal means (EEMANS) in the GLM. Least significant difference (LSD) was used to analyze the significance of difference for each phenological event, and relative coverages of plant species, functional group and at the community level at different elevations. Simple correlation analyses were performed between the timing and duration of the phenological events and air temperature, soil moisture and relative coverages of plant species, functional group and at the community level. Significant differences and correlations are reported at the 0.05 level unless otherwise noted.

3. Results

3.1. Plant species composition and coverage

The species richness was 17.17 ± 0.17 , 23 ± 0.37 , 18.33 ± 0.42 and 15.33 ± 0.76 at 3200, 3400, 3600 and 3800m, respectively (Fig. 1). There was a significant difference in species richness, with a decreasing trend as elevation increased, except at 3200 m

(Fig. 1). The relative coverage of early-spring flowering functional group plants increased with elevation increase, except at 3400 m, which was the highest (i.e. 38%) (Fig. 1). Mid-summer flowering functional group plants had the highest relative coverage at 3200 (i.e. 70%) and 3600 m (i.e. 69%), and its relative coverage was larger at 3800 m than at 3400 m. The relative coverage of late-flowering functional group plants was the smallest at 3400 m (e.g., 1%), and there were no significant differences at 3200, 3600 and 3800 m (Fig. 1).

3.2. Timing of community phenological events

The first day of community phenological events was significantly affected by year, elevation and their interaction (Table S2). OLO at 3200 m and FB at 3400 m significantly advanced compared with these variables at 3600 and 3800 m, respectively (Fig. 2). However, FFS at 3400 m was significantly delayed compared with other three elevations (Fig. 2). FF, OPFV, FLC and CLC were significantly advanced at 3800 and 3600m compared with 3200 and 3400 m (Fig. 2).

3.3. Duration of community phenological events

The duration of community phenological events was significantly influenced by year, elevation and their interaction (Table S3). VS and FS at 3200 m were significantly longer or shorter compared with other elevations (Fig. 3). BS was significantly longer at lower elevations (i.e., 3200 and 3400 m) than at higher elevations (i.e., 3600 and 3800 m) (Fig. 3). FSS and CS were significantly shorter at higher elevations (Fig. 3). However, PFVS was significantly longer at 3200 and 3600

m compared with other elevations (Fig. 3).

3.4. Durations of the entire reproductive stage and growing season

The duration of the growing season of the community was the longest at 3200 m (i.e., 174.44 ± 4.50 days), followed by 3400 m (i.e., 160.56 ± 3.24 days), and there was no significant difference between duration at 3600 m (i.e., 144.33 ± 4.03 days) and 3800 m (i.e., 135.89 ± 1.93 days) (Fig.4A). However, the duration of the reproductive period of the community was the longest at 3400 m and there were no significant differences at 3200, 3600 and 3800 m (Fig. 4B). The ratio between the duration of the reproductive period and growing season was the lowest at 3200 m and there were no significant differences at 3400, 3600 and 3800 m (Fig.4C).

3.5. Biotic factors affecting the timing and duration of phenological events

There were significant negative correlations between FB, VS and PFVS and the ratio of coverage of the early-spring flowering functional group to total coverage of the community (RCEF), and positive correlations between these variables and the ratio of coverage of the mid-summer flowering functional group to total coverage of the community (RCMF) (Table 1). The FFS and FS had significant positive and negative correlations with RCEF and RCMF, respectively (Table 1).

3.6. Abiotic factors affecting the timing and duration of phenological events

There were positive correlations between the timings of FF, FLC, CLC and/or OPFV and annual mean air temperature (MAT), and negative correlations between these variables and monthly air temperature in November and December of the

previous year (Table S5). The FB, FF, OPFV and CLC had positive correlations with air temperature from July to August, June to September, May to August and March to September, respectively (Table S5).

There were significant negative correlations between the durations of FS and CS and MAT, and positive correlations between these variables and MAT (Table S6). Significant negative correlations were found with the monthly air temperature in November and December of the previous year and the durations of VS, BS, FSS and CS, but there were positive correlations between the monthly air temperature of most months from March to September and the durations of VS, BS, FSS and CS (Table S6). By contrast, there were positive correlations with monthly air temperature in November and December of the previous year for FS, while negative correlation was observed for FS with monthly air temperature from March to September (Table S6).

There were significant positive correlations between mean annual soil moisture at 20 cm depth and FB and FF, and negative correlations between soil moisture and FFS (Table S7). The monthly soil moisture at 20 cm depth in November and December of the previous year had significant positive correlations with FF, OPFV, FFL and CLC (Table S7). Positive correlations were observed with monthly soil moisture from August to October for FB, and in April and/or May for OPFV, FFL and CLC, but there were negative correlations with monthly soil moisture in January and April for FFS and in July and August for OPFV (Table S7).

There was a negative correlation between FS and mean annual soil moisture at

20 cm depth, and a positive correlation between CS and mean annual soil moisture (Table S7). The durations of VS, BS, FSS, and CS were significantly positively correlated with monthly soil moisture in November and December of the previous year, but FS was negatively correlated with monthly soil moisture in all months except July (Table S7). Meanwhile, the monthly soil moisture in April and May or from January to May were positively correlated with the durations of FSS and CS (Table S7).

4. Discussion

Our results indicate that relative coverage of mid-summer flowering plants was about two times that of early-spring flowering plants in the community, while late-autumn flowering plants was only 1% of coverage along the elevation gradient. The responses of the timings and durations of community phenological events were significantly different across the elevation gradient. On the whole, OLO and FFS at 3200 m were significantly advanced while timings of other phenological events at 3200 m were significant delayed compared with higher elevations (i.e., 3600 and 3800 m). Almost all durations of phenological events were significantly longer at lower elevations (i.e., 3200 and/or 3400 m), but the flowering duration at 3200 m was the shortest. The relative proportion of different seasonal flowering functional group plants in the community had a significant influence on the response of community

phenological events to temperature change. These results could be attributed to two reasons.

First, we found that trends along the elevation gradient in the timing and duration of community phenological sequences (Fig. 2 and 3) were different from our previous report on individual species or plant functional groups (Wang et al. 2014b), probably because differences within the communities in the direction and magnitude of phenological variance offset many of the previously reported effects at species and functional group levels (Abu-Asab et al., 2001; Fitter and Fitter, 2002; Cleland et al., 2006; Cleland et al., 2007; Wang et al., 2014b). This is especially so for the spring phenological events (Menzel, 2000). For example, onsets of leaf-out delayed with elevation increase for early-spring flowering plants, but advanced with elevation increase for mid-summer flowering plants (Wang et al., 2014b), which could cause leaf-out timing to be significantly delayed with increasing elevation, except at 3600 m (Fig. 2). First budding and flowering of the community were latest at 3200 m (Fig. 2), which was consistent with early-spring but inconsistent with mid-summer flowering plants (Wang et al., 2014b), probably because plants at the lower elevation site had a higher growing–degree days requirement for flowering (Wang et al., 2014b) and mid-summer flowering was more sensitive to warming than to cooling (Wang et al., 2014a). The leaf coloring of the community was latest at 3200 m, which is consistent with early-spring flowering plants and mid-summer flowering forbs but inconsistent with mid-summer flowering grasses (Wang et al., 2014b). In our results, early-spring

and mid-summer flowering species had significantly higher and lower relative coverage at 3400 m, respectively. Negative correlations between FB and RCEF and between FFS and RCMF (Table 1) suggested that the higher RCEF had earlier FB in the community, and higher RCMF had earlier FFS in the community along the elevation gradient. Similarly, higher RCEF had longer flowering duration and shorter durations of leafing and post-fruiting vegetation along the elevation gradient, while the opposite results were found for RCMF (Table 1). Previous studies indicated that warming caused coverage changes of grasses and forbs in the community (Walker et al. 2006; Wang et al. 2012). Therefore, our results suggest that changes in the relative proportion of different seasonal flowering functional group plants in the community could determine the response of community phenological sequences to climate change.

Second, many studies have documented that temperature and moisture are two important factors affecting plant phenology (Penuelas et al., 2004; Xia and Wan, 2013), and that temperature variation may act as a long-lasting controller on surface vegetation (Wolkovich et al., 2012) because warming may alter the water balance affecting plant development (Crimmins et al., 2011). Previous studies have suggested that winter warming delayed green-up (Yu et al., 2010; Polgar et al., 2014) while spring warming advanced it (Wolkovich et al., 2012). However, we found that there were no significant correlations between the winter temperature of the previous year and OLO or FB, but that there were negative correlations between these variables in

February and April of the present year (Table S5). These results suggest that spring warming rather than winter warming could have a greater effect on OLO and FB across the natural elevation gradient. In particular, although FF was positively correlated with annual mean temperature, negative correlations were found between FF and mean temperature in November and December of the previous year, suggesting that the chilling requirement for flowering of the community may not be limited, which is inconsistent with previous reports (Yu et al., 2010). Consistent with previous studies (Sherry et al., 2007; Morin et al., 2010), our results showed no significant correlation between soil moisture and OLO, whereas there was a significant positive correlation between soil moisture and FF (Table S5). This may be attributed to effects of upper and deeper soil moisture on shallow-rooted and deep-rooted species (Xu et al., 2009; Dorji et al., 2013), where higher temperature with higher soil moisture could promote vegetative growth of the community.

The OPFV and leaf coloring (i.e. FLC and CLC) of the community advanced at higher elevations (Fig. 2). Many studies have indicated that the photoperiod rather than temperature controls the senescence date in arctic regions (Arft et al., 1999; Marchand et al., 2004), but some studies have found that warming retarded autumn senescence in arctic tundra and alpine species (Arft et al., 1999; Wolkovich et al., 2012; Wang et al., 2014b). Our results indicate that annual mean air temperature had a positive correlation with leaf coloring (Table S5), but there was no significant correlation between annual mean soil moisture and leaf coloring (Table S6). However,

there were significant positive correlations between these variables in November and December of the previous year and before May in the present year (Table S6). Thus, our results suggest that higher temperature with higher soil moisture could cause a delay in leaf coloring.

Low temperature restricts the length of the growing season in alpine areas, so phenology may be more sensitive to climate warming (Walker et al., 2006; Dorji et al., 2013). The prolonged duration of the growing season at lower elevations in the alpine meadow primarily derived from advanced leaf out and delayed leaf coloring (Fig. 2 and 3). However, a previous study has shown that warming may accelerate plant growth, leading to a shorter growing season (Halevy, 1985). In particular, there is a trade-off between the reproductive and vegetative period, because variations in these periods determine the evolutionary direction and process (Miller-Rushing and Primack, 2008; Wang et al., 2014b). Most studies have suggested that warming prolongs reproductive duration and growing season (Price and Waser, 1998; Dunne et al., 2003; Post et al., 2008; Sherry et al., 2011; Wang et al., 2014b). However, a previous study in alpine areas found that plants exposed to continued warming invest more resources in the vegetative period rather than the reproductive period (Arft et al., 1999). In our study we found that the reproductive duration at 3400 m was significantly longer than other elevations. A previous report showed that low moisture content could shorten the duration of budding and fruiting stages (Galen, 1999). However, the soil moisture at 20 cm was highest during the growing season at 3600 m,

whereas the durations of these stages were shorter at 3600 m than at 3200 and 3400 m (Fig. 3), probably due to lower temperature (Wang et al., 2014b). Many previous studies have reported that drought shortened the duration of the flowering stage (Dickinson and Dodd, 1976; Alizoti et al., 2010; Penuelas et al., 2004). However, we found that there were significant negative correlations between flowering duration of the community and annual mean air temperature and soil moisture, suggesting that higher temperature with higher soil moisture could promote flower development and shorten flowering duration of the community in the alpine region. This implies that the flowering of different plants may greatly overlap, which will result in greater competition of plants for resources because plant demand for resources is usually higher during the reproduction period compared with the vegetative period (Kliber and Eckert, 2004). In particular, shortened flowering duration of the community may increase the potential for phenological mismatch between interdependent species of plants and pollinators (Memmott et al. 2007; Hegland et al., 2009).

5. Conclusions

We found that the timings of leaf-out and fruit-set significantly advanced, but other timings of phenological events were significantly delayed at 3200 m compared with 3600 and 3800 m. The prolonged duration of the community growing season at lower elevations primarily derived from advanced leaf out and delayed leaf coloring in the alpine meadow. The higher the proportion of early-spring flowering plants in

the community, the earlier the first flower bud and the longer the durations of leafing and post-fruiting vegetation stages. Contrary relationships were observed between the duration of these stages and the proportion of mid-summer flowering plants. Therefore, our results suggest that flowering functional groups should be taken into account when models are used to simulate the response of community phenology to climate change.

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Fig.1. Ratio of total relative coverage of seasonal flowering functional group plants to total coverage of the community across the elevation gradient. Inset is the species richness in each plot along the elevation gradient. ESF represents early-spring flowering functional group plants; MSF represents mid-summer flowering functional group plants; LAF represent late-autumn flowering functional group plants.

Fig.2. Timing of community phenological events at different elevations. OLO: onset of leaf-out; FB: first bud/boot-set; FF: first flowering; FFS: first fruit-set for forbs or seeding-set for graminoids; OPFV: onset of post-fruiting vegetation; FLC: first leaf coloring; CLC: the date of complete leaf-coloring.

Fig.3. Duration of community phenological events at different elevations. VS: vegetation stage; BS: budding stage; FS: flowering stage; FSS: fruiting-set stage; PFVS: post-fruiting vegetation stage; CS: coloring stage.

Fig.4. DGS (duration of growing season) (A) and DRP (duration of reproductive period) (B), and their ratios (C) at different elevations.

Table 1 Correlations between the timing and duration of phenological events and the ratio of relative coverage of flowering functional group to total coverage of the community at four elevation gradients.

Phenophase	RCEF	RCMF	RCLF
OLO	0.522	-0.54	-0.094
FB	-0.863**	0.790**	0.427
FF	-0.243	0.278	-0.027
FFS	0.918**	-0.911**	-0.267
OPFV	0.518	-0.38	-0.505
FLC	0.126	0.043	-0.481
CLC	-0.103	0.215	-0.268
VS	-0.751**	0.720**	0.288
BS	0.382	-0.28	-0.373
FS	0.651*	-0.668*	-0.133
FSS	-0.013	0.142	-0.337
PFVS	-0.863**	0.898**	0.141
CS	-0.187	0.273	-0.177

Note: RCEF is the ratio of relative coverage of early-spring flowering functional group plants to total coverage of the community; RCMF is the ratio of relative coverage of mid-summer flowering functional group plants to total coverage of the community; RCLF is the ratio of relative coverage of late flowering functional group plants to total coverage of the community. OLO: onset of leaf-out; FB: first bud/boot-set; FF: first flowering; FFS: first fruit-set for forbs or seeding-set for graminoids; OPFV: onset of post-fruiting vegetation; FLC: first leaf coloring; CLC: the date of complete leaf-coloring. VS: vegetation stage; BS: budding stage; FS: flowering stage; FSS: fruiting-set stage; PFVS: post-fruiting vegetation stage; CS: coloring stage.

533 Fig. 1

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539 Fig. 2

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Fig. 3

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