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Timing and duration of phenological sequences of alpine plants along an elevation gradient on the Tibetan plateau

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A B S T R A C T

Previous studies have focused on the effects of increased temperatures on a single green-up and/or flowering event, but less is known about how acceleration of spring phenology may change subsequent phenological events. We present results of a field experiment to test the hypotheses that (1) the timing of phenological events does not necessarily delay as elevation increases; (2) changes in the timing of a sequence of phenological events will be consistent for all phenological events along the elevation gradient; and thus (3) change in the timing of phenological events does not affect the duration of the entire reproductive stage in the alpine region. The experiment was conducted along an elevation gradient from 3200 to 3800 m using two early-spring flowering (ESF) sedges and four mid-summer flowering (MSF) plants (two forbs and two grasses). Generally, our results only supported the first hypothesis. Lower elevation delayed the starting dates of all phenological events for ESF plants at 3200 m compared with other elevations, whereas the opposite trend was observed for MSF-grasses. MSF-forbs had the earliest leaf-out at 3200 m and the earliest first flowering at 3600 m, and onset of fruit-set advanced with increasing elevation. The entire reproductive duration was shortened with increasing elevation for MSF-forbs, whereas it was the shortest for ESF at 3600 m and for MSF-grasses at 3200 and/or 3800 m. Individual reproductive stages had independent responses to climate change. The duration of the entire growing season for ESF plants decreased as elevation increased. For MSF-forbs, it was longest at 3200 m and shortest at 3400 m, while for MSF-grasses it was shortest at 3200 m and at 3800 m. Reproduction was compressed into shorter time periods only for MSF-forbs at 3600 and 3800 m. Therefore, reproduction is not tightly integrated across the life cycle, and earlier reproductive development induced by warmer spring temperatures did not consistently advance flowering and fruiting times and their durations for the alpine plants studied. The effects of climate change on the timing and duration of phenological events were species-specific. Selection for changes in the timing and duration of individual phenological stages in response to climate change due to evolutionary adaptation should be taken into account.

1. Introduction

Previous phenological studies have focused on the effects of increased temperatures on a single phenological event such as flowering through observational studies (Miller-Rushing and Primack, 2008; Dunnell and Travers, 2011; Wolkovich et al., 2012) and climate manipulation experiments (Arft et al., 1999; Dunne et al., 2003; Walker et al., 2006; Sherry et al., 2007, 2011), and by interpreting the onset and end of the growing season through remote sensing (Yu et al., 2010; Shen et al., 2011; Piao et al., 2011). Less is known about how accelerating green-up and/or flowering may change subsequent phenological events (Post et al., 2008). Recently, the effects of climate change on seasonal phenological events (i.e., leaf unfolding, flowering, fruit and coloring) for one species relative to those of an interacting species have become increasingly apparent (Durant et al., 2005; Visser and Both, 2005; Post et al., 2008; Yang and Rudolf, 2010). Therefore, it is important to understand how sequences of phenological events respond to climate change. In particular, understanding both the timing

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and duration of each phenological event will give a more informative picture of where the greatest or least flexibility in life history response to warming occurs in the life cycle of organisms (Post et al., 2008; Sherry et al., 2011).

Alpine ecosystems on the Tibetan plateau are very sensitive to climate change (IPCC, 2007). In order to better predict climate change impacts on those ecosystems, scientists have been assessing how climate change is affecting – and will affect in the future – plant phenology at the regional scale using remote sensing and/or model derived information as proxies for measurement of vegetation green-up (Yu et al., 2010; Shen et al., 2011; Piao et al., 2011). Few manipulative experiments have been performed in the region (Dorji et al., 2013). Moreover, almost no data is available on the effects of sequences of phenological events on the response of alpine plants to climate change. Here we intend to fill this gap using a 3-year field experiment along an elevation gradient involving sites at 3200, 3400, 3600 and 3800 m on the Tibetan plateau.

Although elevation drives phenological phases mainly by means of a temperature decrease of about 0.6 °C every 100 m (Barry, 1981), the cumulative heat requirement (i.e., growing degree-days) of phenological events also decreases as altitude increases (Shen et al., 2011). Organisms may experience trade-offs between adjustment of one phenological event to climatic change and the timing of subsequent phenological events. Such trade-offs may determine the manner in which both the timing and duration of successive phenological events respond to climate change (Post et al., 2008). Some studies show that the effects of climate change on the timing of reproduction is greater than on the duration of reproduction, and that responses are species-specific (Price and Waser, 1998; Post et al., 2008). We test three hypotheses in our study, namely that (1) the timing of phenological events does not necessarily delay as elevation increases, because this depends on the balance of the magnitudes of changes in temperature and heat requirements for phenological events; (2) changes in the timing of a sequence of phenological events will be consistent (i.e., earlier–earlier or later–later) for all phenological events along the elevation gradient; and thus (3) change in the timing of phenological events does not affect the duration of the entire reproductive stage in the alpine region.

2. Materials and methods

2.1. Experimental design

The experiment was conducted at Haibei Alpine Meadow Ecosystem Research station (HBAMERS) of the Chinese Academy of Sciences, located at latitude 37°37′ N, and longitude 101°12′ E. A southern slope of the Qilian Mountains from 3200 to 3800 m in elevation was selected for the elevation gradient (Fig. 1) and four 20 m long × 10 m wide sites were fenced at 3200, 3400, 3600 and 3800 m in 2006 Three plots of 1 m × 1 m were identified, and six

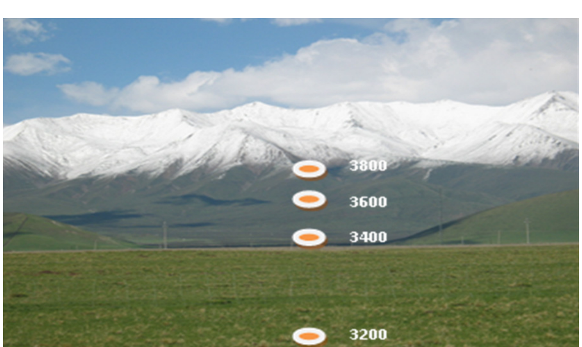

Fig. 1. Diagram of the landscape and experimental sites. ( ) Experimental sites.

common plant species from these plots were chosen for monitoring of all phenological events at each elevation during the growing seasons of 2008–2010. The plant species observed were two early-spring flowering (ESF) species (i.e., *Kobresia humilis* (Kh) and *Carex scabrirostris* (Cs)) which flower before May, and four mid-summer flowering (MSF) species (i.e., two grasses, *Poa pratensis* (Pp) and *Stipa aliena* (Sa), and two forbs, *Potentilla anserine* (Pa) and *Potentilla nivea* (Pn)), which flower between late June and July.

2.2. Air temperature and soil moisture

At the center of each site, HOBO weather stations (Onset Computer Corporation, Cape Cod, Massachusetts, USA) were used to monitor air temperature and soil moisture (SM) at 20 cm soil depth. Model S-THB-M002 air temperature/RH smart sensors (±0.2 °C; ±25% RH) with Model RS3 louvered naturally ventilated solar radiation shields were used to ensure high accuracy measurements. Model S-SMC-M005 ECH$_2$O soil moisture smart sensors (±3%) were installed horizontally into undisturbed soil by digging a hole and pushing the probes into the side of the hole. Data were sampled at 1-min intervals, and 30-min averages were stored in the data logger.

2.3. Measurement of phenological events

Observations were made at an interval of three or four days from early April to the end of October in each year and recordings were made of the onset dates of seven phenological events, including emergence of first leaf (EFL), bud/boot-set (BS); first flowering (FF), first fruit-set for forbs or seeding-set for graminoids (FFS), vegetative stage after fruit/seeding (VAFS), first leaf-coloring (FFL) and the date of complete leaf-coloring (ELC) (Table 1). Ten individuals for forbs and ten stems for graminoids of each plant species in each plot along the elevation gradient were marked during the previous autumn so individual plants could be followed throughout the growing season. The first date of each phenological event present on each marked plant was noted and an unweighted average calculated for each species, i.e., the first day of each phenological event was calculated as the day of the year on which phenological characteristics were visible for 10% of individuals or 10% of marked stems of a species. The end date of leaf-coloring was calculated as the day of the year on which 90% of leaves were colored on the marked individuals or stems. If a marked plant died or was grazed during observations, another nearby stem was marked to replace it, when available. The duration of each phenological event was calculated as the average number of days between successive phenological events for all individuals or stems in a species. The entire reproductive stage included three observed developmental phenological events (i.e., a bud event, a flowering event, and a fruiting event), but excluded the event of seed ripeness because this was difficult to monitor in the field. No data were obtained at 3600 m in 2010 because mice destroyed the plots.

2.4. Data analysis

A univariate general linear model (GLM) was applied for analysis of variance using SPSS 160 version. Fixed factors were year, plant species and elevation, and the dependent variables were the timing and duration of all phenological events measured. One-way ANOVA on timing and duration of each phenological event was analyzed along the elevation gradient. Multi-comparison of least significant difference (LSD) was conducted for all measured variables. Simple correlation analysis was performed between the timing and duration of all phenological events and to test the possible dependency of the timing and duration of all phenological events on annual/monthly air temperature and soil moisture. Significant difference is shown at 0.05 level in the text.