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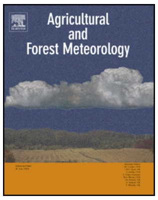

Changes in phenological sequences of alpine communities across a natural elevation gradient

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

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,b). 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,b). 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.,

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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,b). 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 × 8-m width plots were fenced at 3200, 3400, 3600 and 3800 m in 2006. Three 1 m × 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 3800 m, 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,b).

2.3. Measurement of plant coverage and community phenology

Each 1 m × 1 m quadrat was divided into 100 gird cells (10 cm × 10 cm grid). Observations were made at an interval of three or four days from early April to the end of October from 2008 to 2010. Coverage was monitored for all species, for each functional group of seasonal flowering species and at the community level. Maximum coverage of different species during the growing season period was calculated as its coverage in squares with species presence divided by 100 grid cells in each plot. Similarly, maximum vegetation coverage during the growing season period was calculated as vegetation coverage in squares with any species presence divided by 100 grid cells in each plot. All species were classified into three functional groups based on their life history as early, middle and late flowering plants (Liu, 1999; Wang et al., 2014a) (Table S1). The relative coverage of different functional groups was calculated as the total relative coverage of species in each functional group divided by the total coverage of all species in the squares in each plot. The 7 phenological events monitored included onset of leaf-out (OLO), first bud/boot-set (FB), first flowering (FF), first fruit-set for forbs or seeding-set for graminoids (FFS), onset of post-fruiting vegetation (OPFV), first leaf-coloring (FLC) and the date of complete leaf-coloring (CLC). The starting date of each phenological event of the community was the day when 15% of the total touched plant individuals at cross points of the quadrat exhibited the phenological event. The end date of senescence was the day when 95% of total touched plant individuals at cross points of the quadrat had completely colored. The duration of the growing season for all phenological events was calculated as the difference between the ending and onset dates of the phenological 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 (EEMEANS) 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).