Enhanced spring temperature sensitivity of carbon emission links to earlier phenology

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HIGHLIGHTS

- Variation of onset of phenophases determines the duration of phenophases on the Tibetan Plateau.
- Reproductive stage has a higher temperature sensitivity of ecosystem respiration.
- Advanced early phenophases enhanced spring temperature sensitivity of carbon emission.

GRAPHICAL ABSTRACT

+ and − denote positive and negative relationships between two variables; onset, duration and Re indicate onset of phenology, duration of phenology and ecosystem respiration. Re is significantly affected by abiotic factors (temperature and moisture) and biotic factor (phenology). Effects of phenology on Re are mainly achieved by lengthening plant activity time and increasing growth rate.

ARTICLE INFO

Article history:
Received 18 May 2020
Received in revised form 9 July 2020
Accepted 13 July 2020
Available online 18 July 2020
Editor: G. Darrel Jenerette

Keywords:
Phenological sequences
Climate warming
Temperature sensitivity

ABSTRACT

Phenology has a great effect on the carbon cycle. Significant relationships have been well demonstrated between phenology and photosynthesis. However, few studies have been undertaken to characterize relationships between phenology and ecosystem respiration (Re). We conducted a reciprocal transplant experiment among three elevations for two-years to measure Re over six phenological sequences throughout the growing seasons. Our results showed that changes in phenological duration were mainly determined by the onset of phenology, as one day advance of phenological onset could lengthen 0.13 days of phenological duration. Advances in early spring phenophases (i.e., first leaf-out, first bud/boot-set and first flowering) under warming strengthened the temperature sensitivity of Re. However, the late phenophases (i.e., first seeding-set, first post-fruiting vegetation and first leaf-coloring) had non-significant relationships with Re. In total, after pooling all the data, one day advance of phenophases would increase Re by 2.23% under warming. In particular, Re would increase by 29.12% with an advance of phenophases by 8.46 days under a 1.5 °C warming scenario. Our analysis of the coupling...
1. Introduction

Ecosystem respiration (hereafter “Re”) by all organisms in the ecosystem converts organic carbon to inorganic carbon (i.e., carbon dioxide) (Yvon-Durocher et al., 2012), and plants are the leading contributor among all organisms (Boone et al., 1998; Wan and Luo, 2003; Schmitt et al., 2013). Re is mainly affected by climate and biological factors (Hu et al., 2016; Niu et al., 2017; Zhao et al., 2018), among which climate change is considered as the main driving force. However, the biological mechanisms affecting Re are still less well researched (Niu et al., 2017). Transitions in plant phenology have large effects on ecosystem processes by altering plant activity periods (Richardson et al., 2013), because plant phenology greatly affects plant development and metabolism (Barr et al., 2009). Plant phenology has a particularly strong relationship with climate change (Richardson et al., 2013; Richardson et al., 2018). Therefore, climate change exerts a strong influence on terrestrial carbon balances mediated through plant phenology (Barr et al., 2009; Richardson et al., 2010). Most studies pay attention to relationships between phenology and photosynthesis or carbon sink (Richardson et al., 2010; Keenan et al., 2014), while few studies have focused on the relationships between phenology and Re. Plant photosynthetic activity could be enhanced by earlier phenology, and may also increase Re based on dynamic equilibrium relationships between them (Odum, 1969; Keenan and Williams, 2018). Some studies have found remarkable relationships between soil respiration and plant photosynthesis (Fu et al., 2002; Curiel yuste et al., 2004; DeForest et al., 2006), because soil respiration largely relies on recent photosynthetic products transferred from aboveground plants (Högberg et al., 2001; Ryan and Law, 2005; Tang et al., 2005; Huang et al., 2012). Thus, Re may also have close relationships with plant phenology, because it is composed of soil respiration and aboveground plants’ autotrophic respiration. A better understanding of the relationships between carbon emission and plant phenology may improve predictions of the terrestrial carbon budget under climate change.

Onset and duration are two key characteristics of phenology (Post et al., 2008; Haggerty and Galloway, 2011; Wang et al., 2014). A prolonged growing season is generally considered as an indicator of photosynthetic activity (Wu et al., 2012; Richardson et al., 2013; Xia et al., 2015). However, few studies have focused on the effects of the onset of phenology and variation in different phenophases on the carbon cycle. First, phenological duration is determined by the balance between changes in the onset and offset of a given phenophase, and some studies show that the onset of specific phenophases has a greater temperature response than phenological duration (Price and Waser, 1998; Post et al., 2008; Haggerty and Galloway, 2011; CaraDonna et al., 2014; Wang et al., 2014). Therefore, phenological onset may be a better indicator of the carbon cycle than its duration due to possible uniform advance in phenological onset and non-uniform variation in phenological offset in response to warming. One reason is that the advanced onset of phenology could lengthen plant activity time. Another is that advanced onset of phenology may lead to a higher growth rate of height or biomass in the community (Sun and Frelich, 2011). Better separation of these two phenological components is needed. We therefore hypothesize that phenological onset rather than its duration exerts a stronger effect on Re. Second, plant respiration varies between phenophases (Fu et al., 2002; Balogh et al., 2019). This may be attributed to different phenophases having divergent nutrient-consuming and metabolic strategies (Körner, 2003; Wang et al., 2014). For example, a higher rhizosphere respiration rate has been observed at flowering stage at the species-level (Fu et al., 2002). The reproductive stage has a higher temperature sensitivity due to it being dominated by the growing season under warming (Li et al., 2016). We therefore hypothesize that Re in the early reproductive stages may have a higher temperature sensitivity than during other phenophases at the community level.

To investigate the effects of phenological variation on Re, we conducted a reciprocal transplant experiment on the Tibetan Plateau over two years (i.e., 2008 and 2009). We applied reciprocal transplanting along three elevational gradients (i.e., 3200 m, 3400 m and 3800 m), because it is an important method involving space-for-time substitution to examine the effects of global changes on plants (Körner, 2003). Firstly, the reciprocal transplant experiment included warming (downward transplant) and cooling (upward transplant) treatments, as global warming is not in a trend of continuous warming but consists of warming and cooling spells (Menzel et al., 2011; Li et al., 2016). Secondly, most current warming experiments are designed with less than two or three gradients (e.g., warming or elevational gradients), which may lead to erroneous conclusions because one single gradient is insufficient to describe future phenological trends (Wolkovich et al., 2012; Kreyling et al., 2018). We therefore simulated six temperature change gradients by reciprocal transplant of plants downhill and uphill among three elevations. We then continuously observed community phenological sequences (i.e., six phenophases from leaf-out to leaf-coloration) and monitored Re across the whole growing season in each year. The objective of our study was to address how the transitions in the onset and duration of phenological sequences control Re, especially under a scenario of 1.5 °C warming.

2. Materials and methods

2.1. Experimental design

In early May 2007, we conducted a reciprocal transplant experiment along three elevations near Haibei Station on the Tibetan Plateau, China (3200 m in 37°62′N, 101°31′E, 3400 m in 37°67′N, 101°33′E and 3800 m in 37°70′N, 101°37′E). The research area has a typical continental climate. The long-term average annual temperature is −1.7 °C. Annual precipitation is from 420 to 860 mm. In general, the growing season lasts from May to September. All sites at each of the three elevations were fenced since 2007 to avoid grazing by yak and goats. The dominant species at 3200 m are Elymus nutans, Stipa aliena, Poa pratensis, Thalictrum alpinum, Medicago ruthenica, Gentiana straminea and Kobresia humilis, the total coverages of which account for ~70% in the community (Meng et al., 2016). At 3400 m, the dominant species are Carex scabrirostris and Anemone cathayensis, the reproductive stage has a higher temperature sensitivity due to it being dominated by the growing season under warming (Li et al., 2016). We therefore hypothesize that Re in the early reproductive stages may have a higher temperature sensitivity than during other phenophases at the community level.

We first dug out 9 cubic soil blocks (i.e., 1 m² [base area] × 0.3/0.4 m [depth]), with a shallower depth at 3800 m due to the shallower soil layer) at each elevation with minimum damage to belowground roots. We then randomly chose 6 cubic soil blocks at each elevation, and reciprocally transplanted them to two other elevations, leaving 3 cubic soil blocks in situ. For example, 9 blocks from 3200 m were placed at

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3200 m, 3400 m and 3800 m (i.e., 3 blocks per elevation), and 3200 m also received 6 blocks from 3400 m and 3800 m. Therefore, the site at 3200 m had 9 blocks, including 3 blocks from 3200 m, 3 blocks from 3400 m and 3 blocks from 3800 m. To insulate each block against the effects of soil fertility and soil moisture from nearby soil, the four vertical sides of each block were sealed by plastic. We started our field observations and measurements in 2008 to eliminate to the extent possible the effects of disturbance caused by transplanting.

2.2. Soil temperature and soil moisture

Soil temperature and soil moisture at 20 cm depth were continuously monitored at a frequency of 1 min by HOBO (Onset Computer Corporation, Bourne, Massachusetts, USA) weather stations at each site, and the logger automatically calculated and stored data on the half-hour average. Averaging across the two experimental years, annual mean soil temperature at 20-cm depth was 3.44 ± 1.27 °C, 2.17 ± 1.14 °C and 0.18 ± 1.19 °C at 3200 m, 3400 m and 3800 m, respectively, and annual mean soil moisture at 20-cm depth was 27 ± 2%, 21 ± 2% and 8 ± 1% at each elevation (Fig. S1).

2.3. Community phenological observations and calculations

In 2008 and 2009, community phenological sequences were observed every 3–5 days across the whole growing season. We used a quadrate method (1 m × 1 m) with 100 cross points (10 cm × 10 cm) to monitor phenological variation from April to October. The state of plant growth was observed under each cross point. Onset and duration of phenological sequences were calculated based on field observations of individuals at each of the 100 cross points, with the onset of the community phenophase defined as emergence of 15% of individuals at each given phenophase, and the end of the community phenophase defined as achievement by 95% individuals of the given phenophase (Meng et al., 2016; Meng et al., 2017). Therefore, the duration of the community phenophase was defined as the difference between the date of the end and the date of the onset of the community phenophase. Onset of phenological sequences included first leaf-out (FL), first bud/fruiting vegetation (FP), first flowering (FF), first seedling-set (FS), first post-fructifying vegetation (PP), first leaf-coloring (FC). The corresponding duration of phenological sequences included duration of leaf-out (DL), duration of bud/fruiting vegetation (DB), duration of flowering (DF), duration of seedling-set for graminoids or fruit-set for forbs (DS), duration of post-fructifying vegetation (DP) and duration of leaf-coloring (DC). The temperature sensitivity of the onset and duration of community phenophases (°C·°C−1) was calculated as the difference in a given phenophase between the transferred elevation and the original elevation divided by annual soil temperature change (°C) at 20-cm depth.

2.4. Re measurements and calculations

In 2008 and 2009, Re was measured at each elevation every 7–10 days depending on weather conditions during the whole growing season from early May to late September. A static chamber with dimensions of 40 cm × 40 cm × 40 cm was chosen to monitor Re. Chambers were not opened until the end of each 30 min measurement event. Four 100 ml plastic syringes were used to extract air from the closed static chamber at an interval of 10 min (i.e., 0, 10, 20 and 30 min) at each plot. Each measurement event was finished on the same day between 9 a.m. and 11 a.m. All gas samples were protected from exposure to light. The CO2 concentration was analyzed by gas chromatography (HP Series 4890D, Hewlett Packard, USA), which was completed within 24 h after sampling. The coefficient of variation of CO2 concentration was less than 1% for four repeats. More details are given in Hu et al. (Hu et al., 2016).

The temperature sensitivity of Re (°C·°C−1) was defined as the percentage change in Re divided by current soil temperature change (°C) at a 20-cm depth between the transferred elevation and the original elevation. The percentage change in Re was calculated as the increase or decrease in Re between the transferred elevation and the original elevation divided by Re at the original elevation.

2.5. Data analysis

The time series of Re were classified by the duration of each phenophase across the growing season and Re observations were distributed to six intervals corresponding to the duration of phenological sequences (i.e., DL, DB, DF, DS, DP and DC). LSD of one-way ANOVAs and t-tests were performed to make multiple comparisons among the temperature sensitivities of Re in different phenophases. The analysis was conducted in SPSS v.23. Simple linear regressions were used to analyze relationships between phenological onset and duration, and between abiotic (i.e., soil temperature and soil moisture) or biotic factors (onset and duration of phenological sequences) and ecological respiration. Structural equation modeling (SEM) was used to determine how different pathways of abiotic and biotic factors affected Re. We first specified all possible linkages as a saturated SEM model (Figs. S2 and S3). Although this was not necessarily a bad model, the statistical results did not report goodness-of-fit statistics. We then sequentially deleted non-significant paths in the saturated model and obtained the final model with better goodness-of-fit statistics. We used the chi-square value ($\chi^2$) and the root mean square error of approximation (RMSEA) together with their $P$ value to evaluate the fit of the model to the data. The $\chi^2$ test is used to perform a test of perfect fitness of the model. The null hypothesis of perfect fitness of the model is rejected (i.e., $P < 0.001$). RMSEA is an index of the goodness-of-fit of a model, whereby a smaller RMSEA is considered acceptable. However, if some pathway coefficients are greater than 1, this may either signify a strong relationship (Grace et al., 2016) or multicollinearity. To further verify the robustness of the SEM results, we also used partial correlation analysis to analyze relationships between Re and abiotic/biotic factors. For example, we executed partial correlations between Re and soil temperature, setting soil moisture, onset and duration of phenophases as the control variables.

We used phenological sequences as an indicator of plant activity time. We used leaf area index (hereafter “LAI”), defined as the total green leaf area on one side per unit ground surface area, i.e., $LAI = \text{leaf area} / \text{ground area} \left( \text{m}^2 \cdot \text{m}^{-2} \right)$, as an indicator of community plant growth rate, due to a high relationship between LAI and vegetation primary biomass (Prince, 1991; Zhu et al., 2016). The duration between the date of peak LAI and the date of the end of leaf-coloring was considered as the leaf growth stage, with a shorter duration indicating a faster growth rate. The duration between the date of peak LAI and the date of the end of leaf-coloring was considered as the leaf aging stage. Because we lacked directly measured LAI data, we modeled daily LAI dynamics to examine whether warming increased the community growth rate in early phenological stages and the lengthened leaf coloring stage across the entire growing season. We used empirical formulas (Eqs. (1) and (2)) fitted based on measured LAI data at a nearby site to simulate LAI at three elevations for two years (Sun et al., 2010). We then extracted the maximum LAI values as the peak LAI in the growing season (Fig. S6). To validate the reliability of this method, we used community first flowering date (FFD) to see whether the peak time of LAI had a similar trend with FFD. Results showed they had similar trends with different magnitudes (Fig. S7).

$$\text{LAI} = 1.055 + 0.019 \cdot \text{GDD} - 5.09 \times 10^{-5} \cdot \text{GDD}^2 + 3.451 \times 10^{-8} \cdot \text{GDD}^3$$

$$\text{GDD} = \sum_{i=1}^{\text{FFD}} | T_i - T_{\text{base}} |. \text{If } T_i > T_{\text{base}}$$

where GDD is growing degree days (°C·d), which sums daily air temperature exceeding the base air temperature ($T_{\text{base}}$) of 3 °C.
3. Results

3.1. Relationship between temperature sensitivity of onset and duration of community phenological sequences

The temperature sensitivities of the onset and duration of community phenological sequences were significantly affected by the transfer treatments when all data was pooled (Linear mixed model: P < 0.001 and P = 0.02; Table S1). All temperature sensitivities of the onset and duration of phenophases had significant linear responses to temperature change (P < 0.05, Fig. S4) across the two years. There were significant relationships between the onset and duration of phenological sequences, except for FB and FF (Fig. 1 and Table S2). Meanwhile, all absolute values of the slope were smaller than 1, except for FC (from −0.33 to −0.15, Fig. 1 and Table S2).

3.2. Divergent temperature sensitivities of Re at different phenological stages

The temperature sensitivity of Re was significantly affected by transfer treatments when all data was pooled (Linear mixed model: P = .10 and t-test: P = 0.001; Fig. 2 and Table S1). All temperature sensitivities of Re were significantly increased by warming in each phenophase (Figs. 2 and S5). The temperature sensitivity of Re at DB was higher than at other phenological stages, but there were no significant differences among the other phenological stages (Figs. 2 and S5).

3.3. Relationships between abiotic/biotic effects and Re

Based on simple linear regressions, the temperature sensitivity of Re had significant relationships with soil temperature ($R^2 = 0.34$, $P < 0.001$) and soil moisture ($R^2 = 0.47$, $P < 0.001$), and with the temperature sensitivity of the onset of community phenological sequences ($R^2 = 0.41$, $P < 0.001$, Fig. 3a–c and Table S3). Although the duration of community phenological sequences significantly affected Re ($P < 0.001$), its coefficient of determination was very small ($R^2 = 0.03$, Fig. 3d and Table S3). In particular, the temperature sensitivity of Re was 29.12 °C⁻¹ with a phenological temperature sensitivity of −8.46 d °C⁻¹ under a 1.5 °C scenario (Fig. 3c).

The SEM showed that the temperature sensitivity of Re could be mainly explained by soil temperature and moisture together with the onset of community phenological sequences (Fig. 4). In general, soil temperature and moisture had direct positive relationships with Re, while the advanced onset of community phenological sequences caused by warming had a direct negative relationship with the temperature sensitivity of Re (Fig. 4). For separate phenophases, only the onset of early phenophases had direct negative effects on Re, while the duration of phenophases had non-significant effects on Re, except for DP (Fig. 5).

4. Discussion

4.1. Effects of phenological transitions on Re under temperature changes

The effects of warming have been well demonstrated by many studies (Rustad et al., 2001). Similar to previous studies in the same area (Hu et al., 2016; Zhao et al., 2018), we also found that soil temperature and soil moisture significantly affected Re, as soil temperature and soil moisture generally had significant positive relationships with Re when all data was merged (Fig. 4). However, for biotic factors, our results partially supported our aforementioned hypothesis, as we found that Re was significantly enhanced by advanced onset of community phenophases in spring (i.e., FL, FB and FF). This finding is similar to that of previous studies (Fu et al., 2002; Keenan et al., 2014). However, the onset of other phenophases and the duration of nearly all phenophases had non–significant influences on Re. The following mechanisms may explain these divergent effects of phenological changes on Re.

Effects of phenology on Re may be mainly achieved through photosynthesis. Because autotrophic respiration (leaf, root and mycorrhiza) directly depends on carbohydrates transported from aboveground photosynthesis, as directly evidenced by large-scale forest girdling experiments (Högberg et al., 2001). It may be more so for grassland, as a large percentage of photosynthetic product is allocated to roots (Kuzyakov and Domanski, 2000; Robinson, 2007). Belowground heterotrophic respiration largely relies on carbohydrate transported from dead organic matter, and dead organic materials may be indirectly related to phenology over one or several years (Kuzyakov and Sun et al., 2010): DOY is the day of the year; and $T_t$ is daily mean air temperature (°C).
Fig. 3. Linear relationships between abiotic/biotic factors and temperature responses of Re (n = 601, a–d). Dashed and solid lines indicate non-significance and significance at 0.05 level. Black lines indicate linear regressions of all merged data. Colored lines indicate linear regressions of grouped variables. Details of regression parameters are given in Table S3. The onset of phenology includes FL: first leaf-out; FB: first bud/boot-set; FF: first flowering; FS: first seeding-set for graminoids or fruit-set for forbs; FP: first post-fruiting vegetation; and FC: first leaf-coloring. The duration of phenology includes DL: duration of leaf-out; DB: duration of bud/boot-set; DF: duration of flowering; DS: duration of seeding-set for graminoids or fruit-set for forbs; DP: duration of post-fruiting vegetation; and DC: duration of leaf-coloring. The vertical dashed line represents the temperature scenario under 1.5 °C warming in (c). (d) Shares the same legend with (c).

Fig. 4. Structural equation model for the effects of different abiotic (soil temperature, soil moisture) and biotic (onset and duration of community phenological sequences) factors on Re. Red and black arrows indicate positive and negative direction of causation, respectively. Dashed arrows signify non-significant relationships. The numbers adjacent to arrows are standardized path coefficients, which reflect the effect size of the relationship. The R^2 given in each box is the proportion of variance explained for each response variable. Goodness-of-fit statistics for SEM are shown below the model. *P < .05, **P < .001. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
Therefore, aboveground and soil respiration are driven by phenology which has strong relationships with photosynthesis (Richardson et al., 2010; Keenan et al., 2014). We found that all temperature sensitivities of the onset and duration of community phenophases were significantly advanced and lengthened under warming (Fig. 1). The length of community phenological duration was mainly determined by phenological onset, because their absolute slopes were less than 1, except for FC (lengthening 0.13 d per day advance, Fig. 1), which is similar to previous studies (CaraDonna et al., 2014; Wang et al., 2014). Therefore, onset of community phenophases determined changes in Re. However, our results showed that only early onset of community phenophases (i.e., FL, FB and FF) affected Re.

Onset of early phenophases has a large effect on Re, primarily through lengthening plant activity time and improving growth rates (Sun and Frelich, 2011). Warming decreases the low temperature limit of alpine plants, lengthening the greening period of leaf phenology. Therefore, longer growing seasons also have a longer growth respiration period. Similar to a previous study (Zhang et al., 2013), our results also demonstrated that advanced onset of early phenophases led to a longer duration (Fig. 3), and LAI reached maximum values quickly with warming in early phenophases (Fig. S6). This indicates that warming induced a fast growth rate or photosynthesis rate. Plants, therefore, could have a higher biomass and generate more recent photosynthates for higher maintenance and growth respiration during the early phenophases (Molau, 1993; Körner, 2003; Ernakovich et al., 2014; Collalti et al., 2020), such as the flowering stage (Körner, 2003). Our result also supports our hypothesis that Re in the reproductive stage (i.e., DB) would have a higher temperature sensitivity than at other stages (Fig. 2). This may indicate that plants consume more nutrients in the reproductive stage, which could be attributed to the need to maintain population stability in the harsh environment of the Tibetan Plateau (Jiang et al., 2016).

Changes in late phenophases had non-significant effects on Re. This may be caused by precocious plants in the early phenophases, as full leaf cover is generally completed in about one month in early spring (Fatichi et al., 2019). Our results also showed a similar trend in LAI, which

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**Fig. 5.** Structural equation model for the effects of different abiotic (soil temperature, soil moisture) and biotic (onset and duration of community phenological sequences) factors on Re at different phenophases. Red and black arrows indicate positive and negative direction of causation, respectively. Dashed arrows signify non-significant relationships. The numbers adjacent to arrows are standardized path coefficients, which reflect the effect size of the relationship. The R² given in each box is the proportion of variance explained for each response variable. Goodness-of-fit statistics for the SEM are shown below the model. *P < 0.05, **P < 0.01, ***P < 0.001. Onset of phenology includes: FL: first leaf-out; FB: first bud/boot-set; FF: first flowering; FS: first seeding-set for graminoids or fruit-set for forbs; FP: first post-fruiting vegetation; and FC: first leaf-coloring. Duration of phenology includes: DL: duration of leaf-out; DB: duration of bud/boot-set; DF: duration of flowering; DS: duration of seeding-set for graminoids or fruit-set for forbs; DP: duration of post-fruiting vegetation; and DC: duration of leaf-coloring. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
quickly reached maximum values after less than two months, while the duration of leaf aging was longer (Fig. S6). This may indicate that warming not only advances early phenophases but also advances leaf coloration (Archetti et al., 2013; Fu et al., 2014; Li et al., 2016). Autotrophic respiration therefore decreases for recycling nutrients, and heterotrophic respiration may be the predominant contributor compared to autotrophic respiration in the late growing season (Savage et al., 2013). Another reason may be that coverage increases in the community and higher plant height could overshadow shorter plants (Körner, 2003), or it may be due to change in day length (Bauerle et al., 2012), which may also alleviate increased Re in the late growing season. Therefore, in the late season, changes in soil temperature and soil moisture mainly affect Re, not phenology. Non-significant relationships between nearly all durations and Re may be because the onset of phenology has a legacy effect on late phenophases (Fu et al., 2014; Li et al., 2016) and concurrently accelerates the ending of plant development (Halevy, 1985; Qiang et al., 2016). The duration of phenophases therefore may have a non-uniform trend compared with trend in the onset of phenology (Fig. S4). Hence, early onset of phenophases, not phenological duration, determines Re.

4.2. Limitations and implications of this study

In our reciprocal transplant experiments, continuously observing temporal variations in community phenological sequences and Re allowed us to explore their relationships across the growing season. However, there are some limitations that may be improved by future studies. Firstly, although a previous study using girdling experiments demonstrated that aboveground processes directly affect soil respiration, roots still have stored carbohydrates which may continue to be used for some time (Bhupinderpal-Singh et al., 2003). However, other studies consider that soil respiration may strongly depend on newly retrieved carbohydrates (Wertin and Teskey, 2008) or LAI dynamics (Bond-Lamberty and Thomson, 2010). Therefore, whether root carbohydrate stocks affect soil respiration, or how long they will affect soil respiration, still needs further investigation. This may be important because nutrient supply and environmental perception are controlled by roots due to dieback of aboveground leaves of herbs in winter or early spring. Secondly, changes in photosynthesis among different phenophases should also be studied. The balance between photosynthesis and Re determines the carbon sink or carbon source of an ecosystem (Piao et al., 2008), and they may also have interactions with each other (Zhao et al., 2018).

Phenological transitions, including coordinated variation of climate information, may alter Re by affecting other biotic factors, because advanced phenology is always accompanied by increased plant height, leaf area index, tiller and biomass (Dahlgren et al., 2006; Kolb et al., 2006; Richardson et al., 2013; Meng et al., 2017). In particular, biomass is considered to be an important indicator of ecosystem respiration (Hu et al., 2016; Zhao et al., 2018). However, biomass may non-uniformly change with Re, because carbon budgets are determined by two contrasting processes: carbon uptake through photosynthesis and carbon release through Re. These two processes are generally increased at the same time under warming, so changes in biomass depend on their relative difference. Mismatch of co-enhancement between photosynthesis and Re may not lead to increased biomass, such as when autumn warming leads to carbon losses due to increasing mismatch (Piao et al., 2008).

5. Conclusions

Our results showed that the temperature sensitivity of phenological onset mainly determined phenological duration due to a mutual offsetting effect between onset and offset of phenophases. Furthermore, advanced early phenophases significantly enhanced the temperature sensitivity of Re under warming in spring, but not the onset of late phenophases or the duration of nearly all phenophases. In a context of accelerated global warming to 1.5 °C (Hoegh-Guldberg et al., 2018), the generality of our study findings should be tested in alpine or arctic grasslands on a regional scale.

CRediT authorship contribution statement


Declaration of competing interest

There is no conflict of Interest Statement.

Acknowledgements

This work was supported by projects from the National Science Foundation of China (41731175, 31672470 and 41988101), the Strategic Priority Research Program A of the Chinese Academy of Sciences (XDA20050101), the China Postdoctoral Science Foundation (2017LH033 and 2018M640187), the National Natural Science Foundation for the Youth of China (31702162) and the State Scholarship Fund of the China Scholarship Council (201804910175). The authors declare no conflicts of interest in this work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.140999.

References


Formal analysis.

Writing - review & editing.

Investigation.

Formal analysis.

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