Relatively stable response of fruiting stage to warming and cooling relative to other

phenological events

Short title: Stable fruit set under warming and cooling

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Abstract The timing of the fruit-set stage (i.e. start and end of fruit set) is crucial in a plant's life cycle, but its response to temperature change is still unclear. We investigated the timing of seven phenological events, including fruit-set dates during 3 years for six alpine plants transplanted to warmer (+ ~3.5 °C in soils) and cooler (- ~3.5 °C in soils) locations along an altitudinal gradient in the Tibetan area. We found that fruit-set dates remained relatively stable under both warming and cooling during the 3-years transplant experiment. Three earlier phenological events (emergence of first leaf, first bud set, and first flowering) and two later phenological events (first leaf coloring and complete leaf coloring) were earlier by 4.8-8.2 days °C^{-1} and later by 3.2-7.1 days °C^{-1} in response to warming. Conversely, cooling delayed the three earlier events by 3.8-6.9 days °C^{-1} and advanced the two later events by 3.2-8.1 days °C^{-1} for all plant species. The timing of the first and/or last fruit-set dates, however, did not change significantly compared to earlier and later phenological events. Statistical analyses also showed that the dates of fruit set were not significantly correlated or had lower correlations with changes of soil temperature relative to the earlier and later phenological events. Alpine plants may thus acclimate to changes in temperature for their fruiting function by maintaining relatively stable timings of fruit set compared with other phenological events to maximize the success of seed maturation and dispersal in response to short-term warming or cooling.

Keywords: phenological sequence; seed-production stage; alpine plants; early-spring flowering plants; mid-summer flowering plants; temperature change; Tibetan plateau

Introduction

Most studies of the response of phenological events to temperature have been based on the analysis of events early or late in the season such as leaf onset, first flowering, and senescence (Walker et al. 2006, Amano et al. 2010, Yu et al. 2010; Shen et al. 2011; Piao et al. 2011; Cook et al. 2012; Wolkovich et al. 2012; Wang et al. 2014a). Plants may face trade-offs between the adjustment of one phenological event to temperature and the timing of subsequent events during the growing season (Post et al. 2008; Sherry et al. 2007, 2011; Haggerty and Galloway 2011; Dorji et al., 2013; CaraDonna et al. 2014; Wang et al. 2014b). This is illustrated by Fig. 1. Changes of flowering dates may alter the timing of fruit maturation, whereas fruit phenology in turn determines seed maturation and dispersal, which further feeds back on the diversity of species in an ecosystem (Primack 1987). The response of timing of fruiting to warming relative to other phenological events is still unclear because of inconsistent results from different plant species (Post et al. 2008; Haggerty and Galloway 2011; Sherry et al. 2007) and because few studies have analyzed the effects from both warming and cooling at the same location.

The timing of fruit set is closely related to production of offspring, survival and reproductive success (Primack 1987; Miller-Rushing and Primack 2008). The response of timing of fruit set to changes in temperature in alpine grassland communities has received little attention, either from direct observations or manipulative experiments (Dorji et al. 2013; Wang et al. 2014b). Temperate regions have a fruiting period that generally occurs in late summer or in autumn (Ting et al. 2008). For alpine communities where the growing season is short, we hypothesize that the fruiting stage does not change in response to short-term warming or

cooling. Fruit set should indeed occur during a narrow period of the warmer days of the year

due to large diurnal variations of temperature early and late in the growing season in

mountainous regions (Li et al. 2004), which causes a risk of reproduction failure for species

setting seeds too early or too late. This area of research has provided scant data. We thus

tested the hypothesis that alpine plants maintain a relatively stable fruit-set date because they

will be more exposed to reproduction failure if they immediately adjust the timing of their

fruit production to a short-term temperature change. We tested this hypothesis in a

high-altitude meadow on the Tibetan plateau. The plateau has warmed considerably over the

last 40 years but also has years cooler than usual (Li et al. 2004) and is thus a suitable

location for obtaining an understanding of how fruiting responds to temperature changes for

projecting future plant diversity and ecosystemic productivity. Short-term warming and

cooling occur on decadal and inter-annual time scales as part of natural climatic variability.

Several cooling events occurred during the Holocene (Mayle and Cwynar 1995) and the last

century, e.g. after volcanic eruptions (Sirocko et al. 2012), but the phenological responses to

cooling remain unclear (Wang et al. 2014a) because most experiments that manipulate

ecosystems have focused on warming rather than cooling. In previous study, we already

showed that looking at warming alone over- or under-estimated the sensitivity of flowering

date to temperature change if one does not compare the response from warming experiment

to the one of independent cooling experiments (Wang et al. 2014a). We thus conducted a

reciprocal transplantation experiment to expose grassland communities to both warming and

cooling. The transplanted blocks were monitored from 2008 to 2010 (Wang et al. 2014b) to

evaluate the response of phenological events (Fig. 1) to warming and cooling. The aims of

the study were to determine the changes in the dates of the first fruit set (FFS) and the last

fruit set (LFS) in response to warming and cooling and to compare these changes to temporal

shifts in early-season (the emergence of first leaf (EFL), first budding-set (FBS), and first

flowering (FF)) and late-season (the first leaf coloring (FLC) and complete leaf coloring

(CLC)) phenological events.

Materials and methods

Experimental site and data collection

Details of the experimental site and design and the monitoring of the soil temperature, soil

moisture, and phenological events are reported by Wang et al. (2014a, b). In brief, the

experiment was conducted at the Haibei Alpine Meadow Ecosystem Research Station of the

Chinese Academy of Sciences in Qinghai China (37°37′N, 101°12′E) along a 3200-3800 m

altitudinal gradient (3200, 3400, 3600, and 3800 m). Four plant communities within 9 km of

each other were selected for study. Twelve intact soil blocks (100×100 cm and 30-40 cm deep)

(i.e. 30 cm depth at 3800 m due to the shallower soil layer) with attached vegetation from

each altitude were reciprocally transplanted across the altitudinal gradient after the soils

started to thaw in early May 2007 (Wang et al. 2014b). Three replicates were transplanted

from each altitude, and these intact soil blocks were fully randomized throughout the study

site.

Measurements of soil temperature, soil moisture, and phenological events

HOBO weather stations (Onset Computer Corporation, Cape Cod, USA) were established at

the center of each site to monitor soil temperature (ST) at 5-cm depths with 1-minute

intervals, and the data were stored in a data logger. Annual average soil temperatures at 5-cm

soil depths for 2008-2010 were 3.9, 2.5, 2.0, and 0.4 °C at 3200, 3400, 3600, and 3800 m,

respectively (Wang et al. 2014a).

Six common plant species from these blocks were monitored for all phenological events at

each elevation during the growing seasons of 2008-2010. Events were monitored for six

representative species at each elevation at intervals of 4-5 days from early April to

mid-November in each year. The six species were two early-season flowering sedges

Kobresia humilis (Kh) and *Carex scabrirostris* (Cs), two mid-season flowering forbs

Potentilla anserine (Pa) and *P. nivea* (Pn), and two mid-season flowering grasses *Poa*

pratensis (Pp) and *Stipa aliena* (Sa). Ten individuals of each forb and ten stems of each

graminoid in each plot along the gradient were marked during the previous autumn so that

phenological events affecting individual plants could be accurately monitored throughout the

growing season. Data were collected at intervals of 4-5, The onset dates of seven

phenological events were recorded (Wang et al. 2014b). No data were obtained at 3600 m in

2010 because mice destroyed the plots.

Data analysis

An analysis of variance (ANOVA) and multi-comparisons were conducted with SPSS version

22.0 (SPSS Inc., Chicago, USA), and the data were fitted with three types of functions using

R version 3.1.0. Linear mixed models with repeated measurements were used for the ANOVA.

Type III sum of squares was adopted for the changes in the start date compared to the donor

site due to the missing data at 3600 m in 2010. For the warming and cooling due to the

transplantings, a plot (i.e. a soil block) was a subject, the original (i.e. donor) and

transplantation (i.e. receptor) sites were between-subject factors, and species and year were within-subject factors. The changes of start date under warming and cooling were analyzed by one-way ANOVAs, and multi-comparisons of all variables were conducted using least significant difference (LSD) tests. Simple linear regression was performed between the average start date of each phenological event and the pooled data for the changes of soil temperatures at the receptor and donor sites due to warming and cooling to test the responses of the start date to the temperature change. Simple correlations were performed between the start date of each phenological event. The correlations were not corrected, and a *p*-value was added to each Pearson correlation coefficient. Significant differences are reported in the text at *p*<0.05.

The response of FFD to the change in soil temperature was fitted with three types of models: linear, exponential, and piecewise linear (segmented) regression (Wang et al. 2014a; Iler et al. 2013). The fit of the models was compared based on Akaike's information criterion (AIC) (Iler et al. 2013). AIC values were used to determine whether a linear or nonlinear model was a better fit to the dates of phenological events. Only models with ΔAIC >2 were considered to be different (i.e. asymmetric, unequal responses to warming vs. cooling), whereas models with ΔAIC <2 were considered to have equal fits to the data (i.e. symmetric, equal responses to warming vs. cooling) (Wang et al. 2014a; Iler et al. 2013).

Results

The statistical power of the transplant experiment was evaluated by fitting the data to a full linear model (Appendix S1: Table S1). Various sources of error exist, but most items of the

full model were significant at $p<0.001$, with the exception of the year factor and the 5-way interaction (Appendix S1: Table S1). The response of phenological events to warming and cooling were not always the same in direction or magnitude (Fig. 2). The similarity or a difference in the shift of a given phenological event to temperature change was evaluated based on shift direction and magnitude. First, if shift directions were the same, then we compared shift magnitude. Finding the same shift magnitude of different phenological events cannot tease apart whether

these events were dependent or independent on each other. Different shift directions lead us to assume that events were independent of each other.

Our results indicated that shifts for early-season phenological events under warming and cooling were of the same magnitude for the same species. For example, warming significantly advanced the average date of the three early-season events by the same magnitudes for the same species (average advances of 4.8-8.2 day $°C^{-1}$) and delayed the date of the two late-season events (average delays of 3.2-7.1 days $°C^{-1}$) (Fig. 2). In contrast, cooling delayed the three early-season events by an average of 3.8-6.9 day $°C^{-1}$ and advanced the two late-season events by an average of 3.2-7.1 days $°C^{-1}$ (Fig. 2).

By contrast, we found that the responses of FFS under warming and of LFS under cooling were relatively stable relative to the early- and late-season phenological events. The small change of the average FFS was even significantly smaller for the mid-season flowering plants (i.e. Pa, Pn, Pp, and Sa) under warming and for Pa and Pn under cooling relative to the early- and late-season phenological events, suggesting that the change of FFS was independent of the early- and late-season phenological events (Fig. 2). The magnitude of the delay for FFS,

however, remained approximately the same for the early-flowering plants (i.e. Kh and Cs) relative to the late-season phenological events under warming (Fig. 2). This suggests that FFS was only independent of the early-season events but not of the late-season events. The change of LFS was significantly smaller for all plant species under cooling relative to the early- and late-season phenological events (Fig. 2).

We observed asymmetric responses for the phenological events to warming and cooling in most situations. Most of phenological events for all species responded asymmetrically to warming and cooling, as indicated by the difference of Akaike's information criterion (ΔAIC) between the three fitted models, because ΔAIC was <2 for the three models in most situations (Table 1).

Correlations were determined between dates of phenological events and changes in soil temperature by pooling warming and cooling data together (Fig. 3). The three early-season events, namely the emergence of the first leaf (EFL), first bud set (FBS), and first flowering (FF), were negatively correlated for all species with the difference in soil temperature between the receptor and donor sites (ΔT) (Fig. 3 and Appendix S2: Table S1). Leaf senescence late-season events, namely the dates of first leaf coloring (FLC) and complete leaf coloring (CLC), were on the other hand positively correlated with ΔT (Fig. 3 and Appendix S2: Table S1). These correlations indicated that warming lengthened the growing season both by advancing onset and delaying senescence. Neither FFS nor LFS, however, were significantly correlated with ΔT for either the early-flowering (Kh and Cs) or the mid-season flowering forbs (Pa and Pn) (Fig. 3A-3D and Appendix S2: Table S1). FFS and LFS were significantly correlated with ΔT for the two other mid-season flowering grasses (i.e. Pp and

Sa) (Fig. 3 and Appendix S2: Table S1), but the slopes of the regression lines were 2-5 fold

smaller than those obtained for the early and late-season events (Appendix S2: Table S1). In

sum, the timing of fruiting events remained relatively stable during three years of warming

and cooling.

Discussion

The reciprocal transplants may have experienced changes in soil moisture along the

elevational gradient, but previous studies have indicated that alpine-plant phenology is

primarily affected by changes in temperature, not moisture (Wang et al. 2014a, b). We

monitored only six species, but our results suggested that their fruit-set events in the

community did not change in response to warming and cooling but that the other

phenological events late and early in the season were relatively responsive to temperature

change. Fruiting was found to advance more than budding and flowering events during

warming experiments performed in temperate grasslands (Post et al., 2008; Haggerty and

Galloway, 2011). Sherry et al. (2007) reported that changes in fruiting under warming were

species-specific, depending on their specific flowering dates. These results, compared with

ours for the alpine meadow of Tibet led us to conclude that fruiting may not respond

uniformly to climate change across different grassland ecosystems, given plant phylogenetics

and the biotic interactions within communities (Cortés-Flores et al. 2013). Fruiting time may

depend on trade-offs between resource availability, the presence of pollinators, the abundance

of herbivores, suitable conditions for seed production, and phylogenetic constraints (Murali

and Sukumar 1994; Wright and Calderón 1995; Sherry et al. 2007; Nakajima et al. 2012).

The relatively stable fruiting date in response to short-term changes in soil temperature for the Tibetan meadows in this study can be attributed to three potential mechanisms. Firstly, similar to first flowering events studied in a previous report (Wang et al. 2014a), the response of fruiting to warming and cooling differed in direction and magnitude (Fig. 2), implying that short term cooling (e.g. occurrence of cold years) could modify the effective magnitude of long-term warming on fruiting because of the asymmetric annual response to warming and cooling (Table 1). For example, for the early-flowering plants (i.e. Kh and Cs), the change of FFS was correlated negatively with ΔT under cooling but positively with ΔT under warming (Fig. S1), which could explain the lack of significant correlation between ΔFFS and ΔT when pooled warming and cooling data together (Fig. 3 and Appendix S2: Table S1). The asymmetric response of LFS to warming and cooling for the early-flowering plants may have a similar explanation. In contrast, the changes of FFS and LFS were not correlated with ΔT under warming for the mid-season flowering grasses (i.e. Pp and Sa), but FFS and LFS were correlated with ΔT when separating the warming and cooling data (Fig. 3, Appendix S2: Table S1, Appendix S4: Fig. S1, and Appendix S5: Fig. S1). Similar to first flowering (Wang et al. 2014a), warming experiments alone may thus over- or underestimate the response of fruit set, depending on species, relative to warming and cooling experiments. The effect of cooler years which can occur as part of the natural climate variability at each site should thus be measured when evaluating the effects of warming on phenology, because the alternation of cool and warm years during a decade with a warming trend will not cause the same response as a continuous warming trend.

Secondly, each life-history stage of a plant is to some extent dependent on or constrained by the preceding and succeeding stages (Sherry et al. 2007; Post et al. 2008; Wang et al. 2014b). Plant phylogenetic constraints in the fruit-set stage severely limit adaptive potential (Bradshaw 1984). Previous studies have shown that the temporal patterns of fruiting can depend on flowering phenology (Primack 1987). We, however, found that the changes of flowering and fruiting dates were poorly correlated for warming (r^2=0.16) and warming+cooling (r^2=0.19), even though their relationships were significant (Appendix S3, Table S1), and well correlated only for cooling alone (r^2=0.60) (Appendix S3, Table S1). The change of FF was not correlated with the change of LFS under warming, and the correlations were low under cooling (r^2=0.21) and under warming+cooling (r^2=0.04) (Appendix S3, Table S1). These results suggest that the adaptive adjustment of fruiting time may be independent on flowering phenology (Thompson and Willson 1979; Stiles 1980, Eriksson and Ehrlén 1991). Moreover, fruiting patterns were the same for the two plant species of each family (i.e. Kh and Cs of the Cyperaceae family, Pa and Pn of the Asteraceae family, and Pp and Sa of the Gramineae family). Flowering usually simply occurs when a plant reaches a critical size or developmental stage or accumulated degree days (Diekmann 1996; Wang et al. 2014a), whereas the phenology of fruit set is governed by different constraints (Jordano 1992). Fruiting time, by definition, equals flowering time plus the developmental time from flower to fruit. One likely constraint on this developmental time is seed size, which is significantly correlated with developmental time (Eriksson and Ehrlén 1991), although fruit production is largely controlled by the accumulation of photosynthates (French 1992). A relatively stable or delayed timing of fruit set could thus be associated with the formation of larger seeds

(Primack 1987; Sherry et al. 2007; Menzel et al. 2011), which could improve seedling

establishment and growth (Wang et al. 2012), and not limit the period of seed maturation,

especially for the early-flowering plants in the warming environments. Late-flowering

individuals, however, may not have enough time for fruit maturation (Helenurm and Barrett

1987; Rathcke 1988; Kudo 1993; Wang et al. 2014b), which would be an important constraint.

Minor shifts to the end of fruit set under cooling (Fig. 2) could thus mainly provide plants

under cooling in alpine regions with enough time for seed maturation due to a shorter

vegetative stage after fruit set (Kudo 1997).

Thirdly, biotic interactions could also be important drivers in determining the fruiting stage.

Herbivores exert a strong selection pressure on plants in grasslands. For example,

earlier-flowering plants (e.g. Kh and Cs) (Fig. 2) are grazed by animals such as sheep, yaks,

mice, and caterpillars (Zhao 2009; Cao et al. 2015). A possible strategy of plants in a

community for reducing herbivorous pressure is a short period of synchronous production of

leaves, buds, and flowers, thereby satiating the herbivores (Aide 1991; Fenner 1998).

Early-flowering plants complete their floral primordia the previous autumn and winter

(Körner 2003), and limited accumulation of photosynthates can support their reproductive

development. Their later FFS under warming and cooling (Fig. 2), however, may reduce the

loss of seeds, because breeding birds need the number of highly nutritious seeds to peak

during the early spring. The seeds would benefit from 'temporal dispersal' with a persistent

seed bank because of the lower expected flight distances of birds during the breeding season.

The differentiation of floral primordia in mid-season-flowering plants is synchronized with

vegetative growth before flowering (Körner 2003), and vegetative growth before budding is

slow (Zhou 2001). In particular, mid-season-flowering forbs (i.e. Pa and Pn) with large

yellow flowers are under the vegetative canopy of insect-pollinated plants. Simultaneous

phenological sequences (Fig. 2), especially joint floral display, may thus increase visitation

rates, leading to enhanced seed set for one or both species (Thompson 1978, 1981, 1982;

Schemske 1981), because synchronous blooming would attract proportionally more

pollinators than asynchronous blooming (Rathcke 1983). Moreover, earlier flowering but a

stable fruiting date (i.e. longer period of flowering) under warming should increase pollinator

activity in a situation when plants and pollinators respond to warming differently (Kudo and

Suzuki 2002) to avoid pollination deficits due to phenological mismatches between plants

and pollinators (Kudo et al. 2004; Memmott et al. 2007; Williams and Jackson 2007). Neither

warming nor cooling altered or reduced shifts in the fruit-set stage in the taller

mid-season-flowering grasses in the community (Pp and Sa), probably because most

bird-dispersed plants ripen their fruit during the peak of bird abundance, usually in early fall

(Stiles 1980), to escape pathogens and non-disperser frugivores (Thompson and Willson

1979). Many temperate regions receive massive annual influxes of migratory frugivorous

birds (Herrera 1998; Teller'a and Pérez-Tris 2003, 2007). Their abundance thus varies

seasonally, peaking in autumn during migration to winter quarters, which may facilitate the

spread of seeds over larger distances (Snow 1971; Thompson and Willson 1979; Herrera

1984).

Conclusions

Our finding of a relatively stable fruiting stage is analogous to the earlier arrival of migratory birds at their breeding grounds with warming (Root et al. 2003) but with a comparatively minor shift in egg-laying (Both and Visser 2005). Changes in the commencement of flowering are likely to lead to changes in fruit maturation and seed dispersal under warming and cooling periods in alpine regions. Fruit production is the central function of flowering, and seed dissemination is the major function of the fruit, so we should expect relatively stable fruiting phenology to be influenced by selective pressures that would favor successful seed maturation and dispersal. Information for fruiting phenology is of central importance for the conservation of community diversity and is especially valuable for alpine regions that support a diversity of fruit-dependent species.

Acknowledgements

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Table 1 Akaike's information criterion of the three fitted models for various phenological

events.

Phenological event	Model	Kh	Cs	Pa	Pn	Pp	Sa
EFL	Linear	526.9	518.6	492.9	541.1	509.4	507.5
	Seg.	**521.4**	**513.7**	**473.2**	**527.4**	**507.8**	**506.9**
	Exp.	527.8	519.3	482.7	535.1	508.6	**506.9**
FBS	Linear	594.7	588.1	659.6	583.7	**620.0**	**568.0**
	Seg.	**582.7**	**565.1**	**659.6**	**576.3**	622.9	569.5
	Exp.	584.4	566.6	659.9	579.2	621.4	569.0

		Kh	Cs	Pa	Pn	Pp	Sa
FFS	Linear	609.8	645.5	607.1	606.5	595.2	505.6
	Seg.	**543.5**	**609.8**	NA	**605.4**	594.7	502.0
	Exp.	614.3	639.1	609.0	608.4	**594.3**	**501.9**
LFS	Linear	619.2	667.5	619.4	647.9	581.4	718.5
	Seg.	**572.1**	**634.6**	**608.8**	**639.1**	**580.9**	**714.9**
	Exp.	606.2	653.1	620.5	NA	581.9	717.7
FLC	Linear	570.5	676.9	612.9	629.7	684.4	681.5
	Seg.	NA	**676.1**	**581.3**	**601.5**	**682.5**	**680.2**
	Exp.	572.3	678.3	587.6	608.3	686.4	683.3
CLC	Linear	514.1	530.7	614.6	644.8	595.1	586.5
	Seg.	**512.1**	**517.1**	**592.8**	**633.6**	**591.9**	**583.9**
	Exp.	515.0	523.1	603.9	639.3	597.0	588.5

Notes: Kh, *Kobresia humilis*; Cs, *Carex scabrirostris*; Pa, *Potentilla anserine*; Pn, *P. nivea*; Pp, *Poa pratensis*; Sa, *Stipa aliena*; EFL, emergence of first leaf; FBS, first budding/booting set; FFS, first fruit set for forbs or seed set for graminoids; VAFS, vegetative stage after fruit/seed set; FLC, first leaf coloring; CLC, complete leaf coloring; Linear, linear regression; Seg., segmented regression; Exp., exponential regression; and NA, not available. Values are considered to be the same if the difference in Akaike's information criterion (AIC) is <2. The results of first flowering were reported by Wang et al. (2014a). The lowest AIC values are bolded.

Fig. 1 Conceptual diagram illustrating the changes of phenological sequence with changes of soil temperature during the growing season. The black line represents no temperature change (i.e. donor site), The red line represents warming (i.e. downward translocation), and the blue line represents cooling (i.e. upward translocation). EFL, emergence of first leaf; FBS, first bud/boot set; FF, first flowering; FFS, first fruit set for forbs or seed set for graminoids; LFS, last fruit/seed set; FLC, first leaf coloring; and CLC, complete leaf coloring. We hypothesize that the seed-production (shaded area) is a relative stable under a short-term warming and cooling.

Fig. 2 Comparison of changes of start or end date of phenological events under warming or cooling. EFL, emergence of first leaf; FBS, first bud/boot set; FF, first flowering; FFS, first fruit set for forbs or seed set for graminoids; LFS, last fruit/seed set; FLC, first leaf coloring; and CLC, complete leaf coloring. Early-season phenological events include EFL, FBS, and FF. Late-season phenological events include FLC and CLC. Early-season phenological events are above the solid line. Late-season phenological events are below the dashed line. Fruit events are between the solid and dashed lines. ∆days is the difference between transplantation site (i.e. receptor site) and original site (i.e. donor site). Positive and negative values are delays and advances, respectively, of phenological events when transplanted compared to the donor site. Kh, *Kobresia humilis*; Cs, *Carex scabrirostris*; Pa, *Potentilla anserine*; Pn, *P. nivea*; Pp, *Poa pratensis*; and Sa, *Stipa aliena*. The data are means ± SE. Different letters indicate significant differences at the 0.05 level.

Fig. 3 Linear regressions between the first day of different phenological events and differences in soil temperature at a depth of 5 cm from receptor and donor sites. A, B, C, D, E, and F are *Kobresia humilis* (Kh), *Carex scabrirostris* (Cs), *Potentilla anserine* (Pa), *P. nivea* (Pn), *Poa pratensis* (Pp), and *Stipa aliena* (Sa), respectively. EFL, emergence of first leaf; FBS, first bud/boot set; FF, first flowering; FFS, first fruit set for forbs or seed-set for graminoids; LFS, last fruit/seed set; FLC, first leaf coloring; and CLC, complete leaf coloring. Early-season phenological events include EFL, FBS, and FF. Late-season phenological events include FLC and CLC. Differences in soil temperature on the x-axis are for a depth of 5 cm between receptor and donor sites (°C).