

# Asymmetric sensitivity of first flowering date to warming and cooling in alpine plants

S. P. WANG,<sup>1,13</sup> F. D. MENG,<sup>1,2</sup> J. C. DUAN,<sup>3,4</sup> Y. F. WANG,<sup>2</sup> X. Y. CUI,<sup>2</sup> S. L. PIAO,<sup>1</sup> H. S. NIU,<sup>2</sup> G. P. XU,<sup>5</sup> C. Y. LUO,<sup>3</sup> Z. H. ZHANG,<sup>3</sup> X. X. ZHU,<sup>2,3</sup> M. G. SHEN,<sup>1</sup> Y. N. LI,<sup>2</sup> M. Y. DU,<sup>6</sup> Y. H. TANG,<sup>7</sup> X. Q. ZHAO,<sup>3</sup> P. CIAIS,<sup>8</sup> B. KIMBALL,<sup>9</sup> J. PEÑUELAS,<sup>10,11</sup> I. A. JANSSENS,<sup>12</sup> S. J. CUI,<sup>2,3</sup> L. ZHAO,<sup>3</sup> AND F. W. ZHANG<sup>3</sup>

<sup>1</sup>Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101 China

<sup>2</sup>Chinese Academy of Sciences, Beijing 100049 China

<sup>3</sup>Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008 China

<sup>4</sup>Binhai Research Institute in Tianjin, Tianjin 300457 China

<sup>5</sup>Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guangxi 541006 China

<sup>6</sup>National Institute for Agro-Environment Sciences, Tsukuba 305 8604 Japan

<sup>7</sup>National Institute of Environmental Studies, Tsukuba 305 8506 Japan

<sup>8</sup>Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, 91191 Gif sur Yvette, France

<sup>9</sup>U.S. Arid-Land Agricultural Research Center, USDA, Agricultural Research Service, 21881 North Cardon Lane, Maricopa, Arizona 85138 USA

<sup>10</sup>Centre de Recerca Ecològica i Aplicacions Forestals (CREAF), Cerdanyola del Valles, Barcelona 08193 Catalonia, Spain

<sup>11</sup>Consejo Superior de Investigaciones (CSIC), Global Ecology Unit CREAF-CEAB-CSIC-UAB, Cerdanyola del Vallès, Barcelona 08193 Catalonia, Spain

<sup>12</sup>Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium

**Abstract.** Understanding how flowering phenology responds to warming and cooling (i.e., symmetric or asymmetric response) is needed to predict the response of flowering phenology to future climate change that will happen with the occurrence of warm and cold years superimposed upon a long-term trend. A three-year reciprocal translocation experiment was performed along an elevation gradient from 3200 m to 3800 m in the Tibetan Plateau for six alpine plants. Transplanting to lower elevation (warming) advanced the first flowering date (FFD) and transplanting to higher elevation (cooling) had the opposite effect. The FFD of early spring flowering plants (ESF) was four times less sensitive to warming than to cooling (by  $-2.1$  d/°C and  $8.4$  d/°C, respectively), while midsummer flowering plants (MSF) were about twice as sensitive to warming than to cooling ( $-8.0$  d/°C and  $4.9$  d/°C, respectively). Compared with pooled warming and cooling data, warming alone significantly underpredicted  $3.1$  d/°C for ESF and overestimated  $1.7$  d/°C for MSF. These results suggest that future empirical and experimental studies should consider nonlinear temperature responses that can cause such warming-cooling asymmetries as well as differing life strategies (ESF vs. MSF) among plant species.

**Key words:** early spring flowering; first flowering date; global warming; midsummer flowering; temperature sensitivity; Tibetan Plateau; warming and cooling.

## INTRODUCTION

In higher latitude and altitude ecosystems where temperature limits the length of the growing season, phenology is strongly influenced by warming (Walker et al. 2006, Dorji et al. 2013). Studies exist on the response of phenology to warming in Arctic regions (Walker et al. 2006), but as the third pole of the earth, there are few data for the Tibetan Plateau (Dorji et al. 2013). Historical climate records show that the Tibetan Plateau has experienced substantial warming (i.e.,  $0.32^{\circ}\text{C}$  per decade; Liu and Chen 2000), and it likely will continue

in the future. Accurate understanding of how climate changes influence phenology in the Tibetan Plateau is critical for predicting future evolution of local terrestrial ecosystems, and thus, for a sustainable ecological development of this region.

Although earlier flowering is found in both long-term observations and short-term warming experiments (Peñuelas and Filella 2001, Sherry et al. 2007, Amano et al. 2010, Cook et al. 2012, Wolkovich et al. 2012), a recent study suggested that the results from controlled warming experiments could not match the observational data in sign or magnitude (Wolkovich et al. 2012). Long-term phenological observations show that plant phenology may depend on the balance between warming and cooling effects during the observational period (Rutishauser et al. 2008, Schleip et al. 2008, Menzel et al.

Manuscript received 15 January 2014; revised 28 May 2014; accepted 30 May 2014. Corresponding Editor: G. A. Fox.

<sup>13</sup> E-mail: wangsp@itpcas.ac.cn

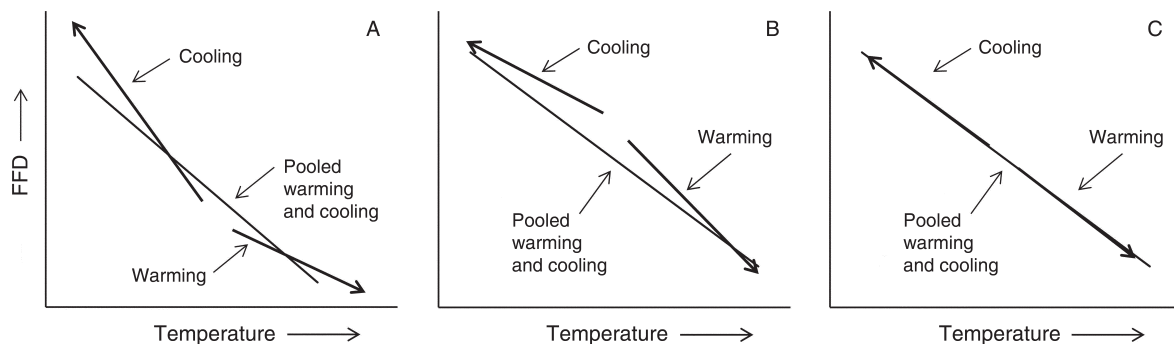


FIG. 1. Conceptual diagram of the response of first flowering date (FFD; day of year) to temperature. Temperature sensitivity of FFD ( $d/^\circ C^{-1}$ ) is (A) higher, (B) lower, and (C) equal for pooled warming and cooling data compared with warming alone, which depends on difference of temperature sensitivity of FFD to warming and cooling alone (i.e., asymmetry or symmetry), respectively.

2011, Wolkovich et al. 2012) because trends in time series are often analyzed using simple linear regression where phenological dates are plotted against temperature variability (i.e., warming and cooling spells) and changes (Rutishauser et al. 2008, Amano et al. 2010, Hülber et al. 2010, Menzel et al. 2011, Wolkovich et al. 2012). However, for inherently nonlinear processes (Sparks et al. 2000, 2009, Schleip et al. 2008, Primack et al. 2009, Ishizuka and Goto 2012, Iler et al. 2013), it is difficult to find a linear model that fits the data well as the range of the data increases (Schleip et al. 2008, Iler et al. 2013). For manipulative warming experiments, the temperature sensitivity of plant phenology is calculated from the observed phenological and temperature changes between warmed and control plots (Sherry et al. 2007, Wolkovich et al. 2012), and this calculation does not consider the cooling effects. Fig. 1 illustrates three possible kinds of responses of first flowering date (FFD) to a particular temperature range. Starting at mid-range temperature, when FFD temperature sensitivity to warming is lower or higher than to cooling (i.e., asymmetry or nonlinear response), pooled warming and cooling data may overestimate (Fig. 1A) or underestimate (Fig. 1B) FFD temperature sensitivity than that by warming data alone. FFD temperature sensitivity is the same for pooled warming and cooling data and warming data alone only when they are symmetric and have the same linear response to warming and cooling (Fig. 1C). Therefore, understanding how flowering phenology responds to warming and cooling (i.e., symmetric or asymmetric response) is warranted to predict the response of flowering phenology to future climate change that will happen with the occurrence of warm and cold years, superimposed upon a long-term trend.

We conducted a field experiment with a reciprocal translocation of vegetation-intact grassland soil blocks along an elevation gradient spanning from 3200 m to 3800 m (Appendix B: Fig. B) between 2008 and 2010. The objectives of the study were to investigate how first flowering date (FFD) of six alpine plant species with different life history strategies changes along a natural

elevation gradient (i.e., nontransplanted plants); and how, over the short term, their FFD respond to warming (i.e., downward translocation) and cooling (i.e., upward translocation).

## MATERIALS AND METHODS

### Experimental design

The experiment was conducted at Haibei Alpine Meadow Ecosystem Research Station (HBAMERS) of the Chinese Academy of Sciences, located at latitude  $37^\circ 37' N$ , and longitude  $101^\circ 12' E$  along a 3200–3800 m elevational gradient on the south slope of the Qilian Mountains in Qinghai, China. Four 20 m long  $\times$  8 m wide plots were fenced at 3200 m ( $37^\circ 36' 42.3'' N$ ,  $101^\circ 18' 47.9'' E$ ), 3400 m ( $37^\circ 39' 55.1'' N$ ,  $101^\circ 19' 52.7'' E$ ), 3600 m ( $37^\circ 41' 46.0'' N$ ,  $101^\circ 21' 33.4'' E$ ), and 3800 m ( $37^\circ 42' 17.7'' N$ ,  $101^\circ 22' 09.2'' E$ ) in 2006 (as seen in Appendix B: Fig. B1). These four sites included four different plant communities within 9 km of one another (Li et al. 2011). At 3200 m, the vegetation is dominated by *Kobresia humilis*, *Elymus nutans*, *Poa* spp., *Carex* spp., *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontopodium odiumnanum*, and *Potentilla nivea*. At 3400 m, the vegetation is dominated by alpine shrub *Potentilla fruticosa*, and jointly by *Kobresia capillifolia*, *K. humilis*, *Saussurea superba*. At 3600 m, the vegetation is dominated by *K. humilis*, *Saussurea katochaete Maxim*, *P. nivea*, *Thalictrum alpinum*, *Carex* spp., *Poa* spp., and *P. fruticosa*. At 3800 m, the vegetation is dominated by *K. humilis*, *L. odiumnanum*, *Poa* spp. Any differences in day length and photoperiod can be ignored due to the close proximity of the sites.

Twelve intact soil blocks (100  $cm^2$  wide  $\times$  30–40 cm deep; i.e., 30 cm depth at 3800 m due to shallower soil layer) with attached vegetation from each altitude were reciprocally transferred across the altitudinal gradient after the soils started to thaw in early May 2007 (as seen in Appendix B: Fig. B1). The translocation of the intact soil depth caused only minimal damage to the plant roots because 85% of the total root biomass within a 40 cm soil depth was distributed above 10 cm

(Wang and Shi 1999). Among the transferred intact soil blocks, three blocks from each altitude were also removed and then reinstated at the same site to produce experimental control blocks that had been handled as similarly as possible as those blocks moved to other elevations. Thus, there were three replicate transfers from each altitude, and these intact soil blocks that were fully randomized throughout the study site. Six common plant species from these intact soil blocks were chosen for monitoring of their flowering phenology at each altitude through the growing seasons of 2008–2010.

*Air and soil temperatures and soil moisture along the elevation gradient*

At the center of each site, HOBO weather stations (Onset Computer Corporation, Cape Cod, Massachusetts, USA) were used to monitor air temperature and relative humidity (RH) at 150 cm above the soil surface and soil temperature (ST) at 5 cm depth and soil moisture (SM) at 20 cm soil depth. Model S-THB-M002 air temperature/RH smart sensors (Onset Computer, Bourne, Massachusetts, USA;  $\pm 0.2^\circ\text{C}$ ;  $\pm 2.5\%$  RH) with model RS3 louvered, naturally ventilated solar radiation shields (Onset Computer, Bourne, Massachusetts, USA) were used to ensure high accuracy measurements. Model S-TMB-M002 temperature sensors and model S-SMC-M005  $\text{ECH}_2\text{O}$  soil moisture smart sensors (Onset Computer, Bourne, Massachusetts, USA;  $\pm 3\%$ ) were installed horizontally into undisturbed soil by digging a hole and pushing the probes into the side of the hole. Data were sampled at one-minute intervals, and then 30-minute averages were stored in the data logger.

*Measurement of first flowering date (FFD)*

We selected two common early spring-flowering species (ESF; *Kobresia humilis* and *Carex scabrivostris*) that flower before May and four midsummer flowering species (MSF; two grasses, *Poa pratensis* and *Stipa aliena*, and two forbs, *Potentilla anserina* and *P. nivea*) that flower between the end of June and end of July (Zhou et al. 2002). During the previous autumn, 10 individuals for forbs and 10 stems for graminoids for each plant species in each plot along the elevation gradient were marked so that individual plants could be followed throughout the growing season. Their FFD was monitored at an interval of three or four days per week between April and October each year. For each individual, FFD is defined as the day of the year at which  $>10\%$  flowering in inflorescence was observed (i.e., forbs, first flowers open; graminoids, first anthers visible). We chose similar size plant nearby to replace them if individuals for forbs and stems for graminoids died for each plant species. No data were obtained at 3600 m in 2010 because mice destroyed most of the transferred plots.

*Data calculation*

The FFDs for each species were averaged across the 10 individuals from each intact soil block and the three replicate intact soil blocks for each elevation and warming/cooling transfers. Linear regressions between FFD differences and temperature change between control sites and transferred sites for the reciprocally transplanted plants (i.e., downward/warming and upward/cooling, respectively) were used to test the effects of temperature changes on FFD for each species. The slopes of these linear regression models were used as sensitivities of FFD (i.e.,  $\text{d}/^\circ\text{C}$ ). Thus, negative and positive values in sensitivities of FFD signify advance and delay days per degree soil temperature change, respectively.

*Theoretical estimations of FFD*

In order to reveal the direct potential effects of temperature change on FFD, theoretical estimations of FFD were performed. We assumed that required cumulative soil temperature (RCST) at 5 cm depth prior to flowering with a threshold of  $0^\circ\text{C}$  did not change with altitude change for these alpine plants when they were reciprocally transferred. Thus, their FFD change may be thought to be driven by temperature change alone. First, we calculated RCST before flowering each year for each plant species based on the measured data of their FFD at the original sites. RCST is the sum of soil temperatures exceeding  $0^\circ\text{C}$  at 5 cm depth between the first time that soil temperature remained above  $0^\circ\text{C}$  during five days and the date of flowering of each plant species. The relationships were linear between change in soil temperature at 5 cm depth (as seen in Appendix C: Fig. C1) and days of more than  $0^\circ\text{C}$ . Thus, average change rates of soil temperature at 5 cm depth (as seen in Appendix A: Table A1) per 100-m altitude change were calculated each year over the three-year periods based on the slopes of the regression equations in Appendix C. Therefore, theoretically, the days required to reach their RCST prior to flowering for each plant species were estimated through the equation  $\text{CRT} \times (1 + 2 + 3 + 4 + \dots + n) = \text{CRT} \times n(n+1)/2 = \text{RCST}$ , where CRT stands for change rate of soil temperature at 5 cm depth since first day when soil temperature is more than  $0^\circ\text{C}$  under different altitudes;  $n$  = days reached to RCST for each species under different altitudes; and RCST stands for required cumulative soil temperature (i.e., daily degree days) at 5 cm depth prior to flowering for each plant species under different altitudes, respectively. Finally, theoretically estimated FFD each species under different altitudes is the sum of  $n$  and the days when soil temperature at 5 cm depth is  $\geq 0^\circ\text{C}$  after 1 January of each year.

Linear regressions with data from theoretically estimated FFD differences and temperature changes between original sites and transferred sites for the reciprocally transplanted plants (i.e., downward and upward, respectively) were conducted to test the effects

of temperature changes on FFD for each species using theoretically estimated values, respectively. The regression coefficients (i.e., slopes) of these linear regression models were used as sensitivities of FFD (i.e.,  $d/^\circ\text{C}$ ).

#### *Data analysis*

Linear mixed models with repeated measurements was used for analysis of variance with SPSS version 22.0. Type III SS was adopted since missing data at 3600 m in 2010. For the undisturbed sites vs. altitude, individual plant was taken as the subject that nested within a combination of (elevations-species-year), and year was taken as within-subject factor. The elevation means the site where ambient plants were sampled. For the transfer-caused warming and cooling, plot (i.e., soil block) was taken as subject, original site (i.e., home site) and transferred site (i.e., away site) were between-subject factors, species and year were within-subject factors. One-way ANOVAs in FFD sensitivity were analyzed for ESF vs. MSF and warming vs. cooling data alone or vs. pooled warming and cooling data. ANOVAs were performed using the average FFDs each plant species, and simple linear regressions were performed using all of data per individual at each intact soil block. Differences are considered to be significant at  $P < 0.05$ .

The response of FFD to the change in soil temperature was fitted with three types of model: linear, exponential, and piecewise linear regression. The form of the exponential function is  $y = \exp(a \times x) + b$ , where  $a$  and  $b$  were the coefficients to be estimated based on observations. The `nls()` function in R 3.1.0 (R Development Core Team 2013) was used to estimate the coefficients. The piecewise linear regression was implemented with R package `segmented` 0.3-1.0. The `segmented()` function of the package was used to estimate the position of the breakpoint. The fitness of the models was compared based on Akaike's information criterion (AIC). R 3.1.0 was used in the procedures of model fitting and estimation.

To test the slope heterogeneity (i.e., between cooling and warming scenarios), two methods were used. The first one was an ANCOVA method. A linear model (`lm`) with the form of `lm(FFD ~ ST × grp)` was implemented in R-3.1.0, in which `ST` denoted soil temperature and `grp` was a categorical variable to separate data into two groups, i.e., the cooling group and the warming one. The significant interaction effect could be taken as an evidence of presence slope heterogeneity, or put another way, the slopes changing with groups. The second method adopted was implemented with `SMATR` 3.4-3, an R package that has been widely used in published research papers (Warton et al. 2012). The primary function of `SMATR` 3.4-3 was to test whether a common slope exists among groups of samples. Function `SMA()` in `SMATR` was used in this analysis, in which  $H_0$  was that there exists a common slope.

## RESULTS

### *Air and soil temperatures and soil moisture along the altitude*

Fig. 2 shows the average monthly air temperatures, soil temperatures at 5 cm depth, and soil moistures at 20 cm depth for each site. Annual average air temperatures ( $T_a$ ) over three years were  $-0.9^\circ\text{C}$ ,  $-1.2^\circ\text{C}$ ,  $-0.9^\circ\text{C}$ , and  $-1.8^\circ\text{C}$  at 3200 m, 3400 m, 3600 m, and 3800 m, respectively. They were  $6.6^\circ\text{C}$ ,  $5.9^\circ\text{C}$ ,  $5.5^\circ\text{C}$ , and  $4.5^\circ\text{C}$  during the growing seasons from May to October; and  $-8.4^\circ\text{C}$ ,  $-8.4^\circ\text{C}$ ,  $-7.3^\circ\text{C}$ , and  $-8.0^\circ\text{C}$  during the non-growing seasons from November to April. The annual average soil temperatures ( $T_s$ ) at 5 cm soil depth were  $3.9^\circ\text{C}$ ,  $2.5^\circ\text{C}$ ,  $2.0^\circ\text{C}$ , and  $0.4^\circ\text{C}$  at 3200 m, 3400 m, 3600 m, and 3800 m, respectively. They were  $10.1^\circ\text{C}$ ,  $8.1^\circ\text{C}$ ,  $7.3^\circ\text{C}$ , and  $5.9^\circ\text{C}$  during the growing seasons from May to October; and  $-2.3^\circ\text{C}$ ,  $-3.0^\circ\text{C}$ ,  $-3.3^\circ\text{C}$ , and  $-5.0^\circ\text{C}$  during the nongrowing seasons from November to April, respectively. The average  $T_s$  elevation gradient was  $0.56^\circ\text{C}$  per 100 m in spring, and  $0.72^\circ\text{C}$  per 100 m in summer. The average range of  $T_s$  change experienced by transplanted plants thus spans  $4.0^\circ\text{C}$  in spring and  $4.3^\circ\text{C}$  in summer. The annual average soil moistures at 20 cm depth were 11.8%, 11.3%, 12.7%, and 10.2% at 3200 m, 3400 m, 3600 m, and 3800 m, respectively (15.8%, 16.0%, 19.1%, and 18.3% during growing seasons and 7.9%, 6.7%, 6.4%, and 2.1% during nongrowing seasons).

### *Ambient differences in first flower date (FFD) at undisturbed sites vs. altitude*

Variation in FFD and especially in the required cumulative soil temperature (RCST) at 5 cm depth of nontransplanted plants prior to flowering with a threshold of  $0^\circ\text{C}$  with elevation is an indication of evolutionary adaptation of flowering phenology to climate change in the long-term. FFDs of the six plant species were controlled by year, species, elevation, and their interactions (Table 1). The FFD of nontransplanted plants decreased (i.e., occurred later in spring) with increasing elevation for ESF, but not for MSF for which the FFD was only different at 3600 m (Fig. 3A), highlighting that FFD for MSF plants did not seem to vary consistently with increasing elevation. The RCST associated with flowering was found to decrease with elevation for both ESF and MSF plants (Fig. 3B), consistent with adaptation mechanisms by which plants living in colder conditions need less cumulative soil warming to start flowering.

### *Model fitting of the response of FFD to soil temperature change*

In situ soil temperature measured at 5 cm depth ( $T_s$ ) is used as a predictor of the FFD rather than air temperature (as seen in Appendix D: Fig. D1). Growing degree days of air temperature (daily degree days, calculated as the sum of all daily mean  $T_s > 0^\circ\text{C}$  following continuous 5 days in March to FFD) prior to



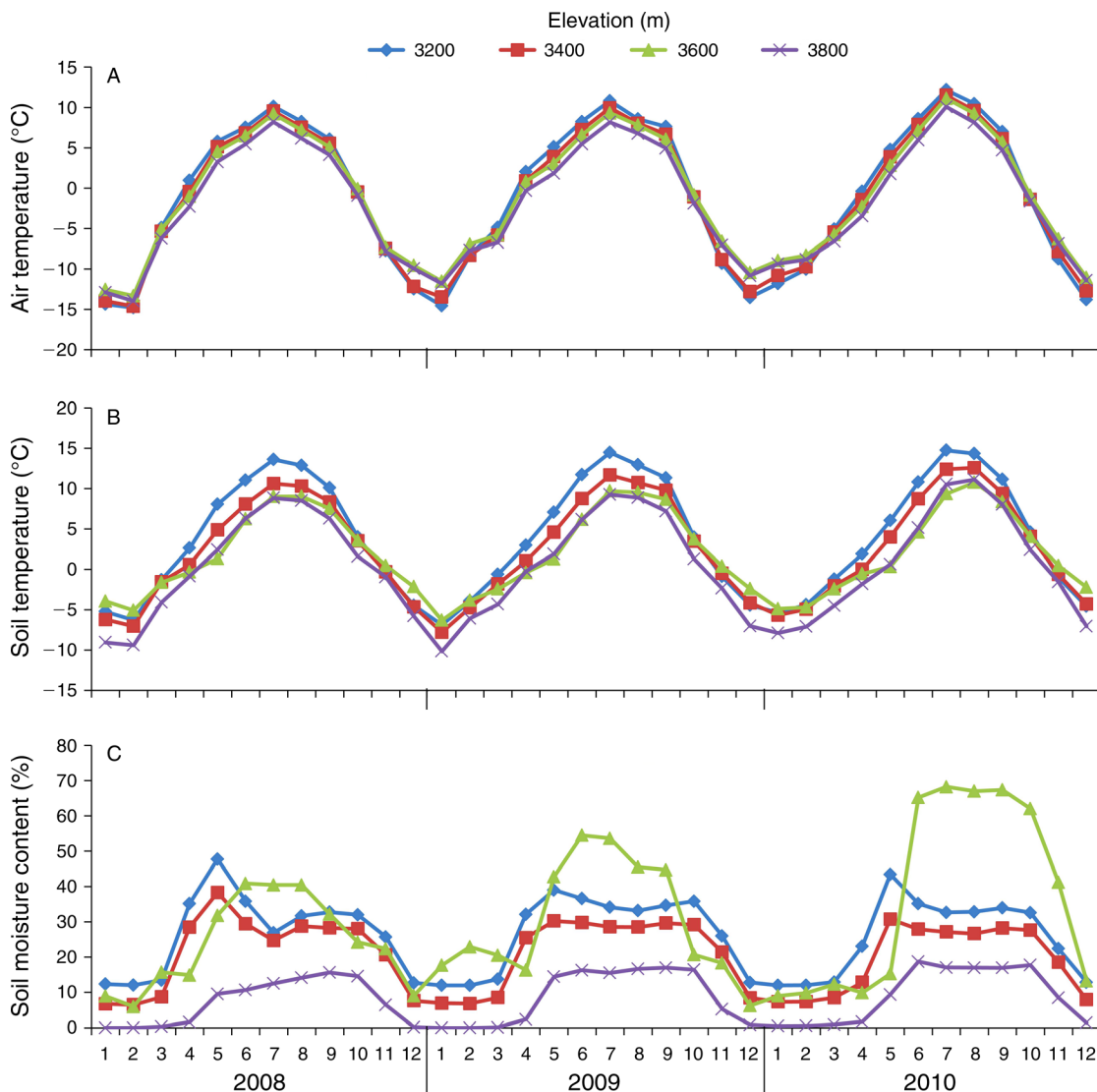


FIG. 2. (A) Air temperature (°C), (B) soil temperature at 5 cm depth (°C), and (C) soil moisture (%) at 20 cm for each month (where 1 is January) under different elevations.

FFD (as seen in Appendix E: Fig. E1) was not as effective as RCST (as seen in Appendix F: Fig. F1) for predicting the timing of FFD.

Three models used to fit the response of FFD to soil temperature change were linear, exponential, and piecewise linear regression. Although the *P* value of linear regression was very low (*P* < 0.001) for all six species, the residual diagnostic suggested that linear regressions failed to fit the six species. An apparent curve pattern was presented in residual plots for five species except Pa (as seen in Appendices G–L). However, the quantile-quantile (Q-Q) plot for Pa suggested that prerequisite of normal distribution was violated (as seen in Appendices G–L).

The exponential curves, which took the form  $y = \exp(a \times x) + b$ , neatly crossed the origin for four species

(Table 2), i.e., the coefficients *b* were very close to  $-1$ . Since the effects of cooling and warming on FFD are opposite each other, it was rational to expect that they met at the origin point, and thus, a well-fitted model

TABLE 1. Type III test of fixed effects on first flowering date of ambient plants as a summary of repeated-measures analysis.

Source	Numerator df	Denominator df	F	P
Intercept	1	3.856	543071.335	<0.001
Elevation (E)	3	12.356	25.542	<0.001
Species (S)	5	59.124	14062.677	<0.001
Year (Y)	2	94.050	1284.696	<0.001
E × S	15	48.338	63.443	<0.001
E × Y	5	98.142	79.498	<0.001
S × Y	10	107.158	34.464	<0.001
E × S × Y	25	105.267	48.214	<0.001

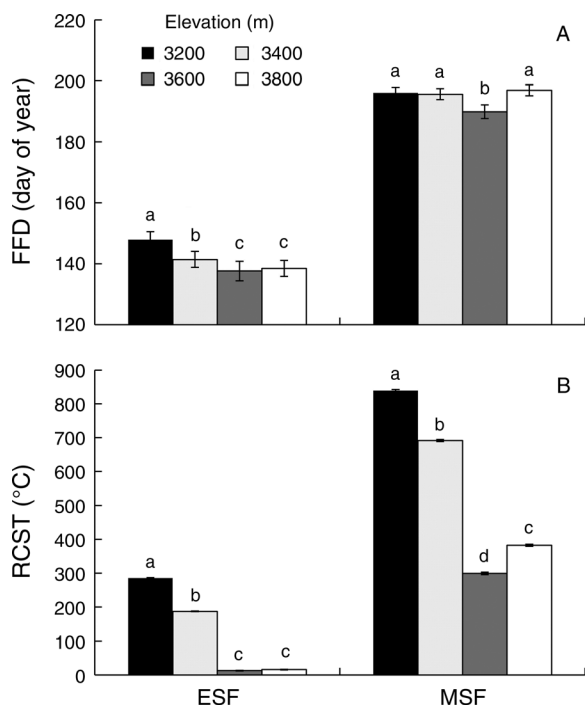


FIG. 3. (A) First flowering date (FFD) for early spring flowering plants (ESF;  $F_{3,44} = 218.099$ ,  $P < 0.001$ ) and for midsummer flowering plants (MSF;  $F_{3,88} = 47.989$ ,  $P < 0.001$ ) and (B) required cumulative soil temperature (RCST) at 5 cm depth prior to flowering with increasing elevation for the ambient plants (for ESF,  $F_{3,44} = 19086.350$ ,  $P < 0.001$  and for MSF,  $F_{3,88} = 5532.778$ ,  $P < 0.001$ ) on the original sites. Different letters above bars indicate significant difference at  $P > 0.05$  level. Mean  $\pm$  SE are shown in the figures.

could also cross the point. The linear regression lines do not cross origin (Table 2). The breakpoints of the piecewise regression, estimated for the six species, were all far from the origin. Based on AIC, the segmented linear regression was the best fitted model for all six species (Table 3), while the exponential regression fit as well as it (i.e.,  $\Delta AIC < 2$ ) in four species.

*Response of first flowering date (FFD) to transfer-caused warming and cooling*

After being transplanted, we monitored how FFD of the plants changed over a three-year period. The

TABLE 2. Coefficients of linear, exponential, and piecewise linear regression estimated with observations.

Species	Intcpt	<i>a</i>	<i>b</i>	BrkPnt
Kh	0.21	-0.29	-1.18	-1.50
Cs	0.55	-0.34	-1.23	-1.47
Pa	-1.21	0.12	-1.01	2.98
Pn	-1.61	0.12	-1.00	3.05
Pp	-1.91	0.13	-1.00	1.57
Sa	-1.75	0.17	-1.01	-0.49

Note: Intcpt is the intercept of linear regression; *a* and *b* are coefficients in the exponential function  $y = \exp(a \times x) = b$ ; BrkPnt is the breakpoint in piecewise regression.

TABLE 3. Comparison of three fitted models showing Akaike's information criterion (AIC).

Species	Linear	Segmented	Exponential
Kh	599	578.7	582.9
Cs	607	582	580.7
Pa	674.1	675	674.8
Pn	569.8	563.1	566.1
Pp	588.9	583.9	584.1
Sa	544.8	531.1	529.9

Notes: Values are considered to be the same if the difference in AIC values ( $\Delta AIC$ )  $< 2$ .

observed FFD responses were found to be controlled by year, species, native site (homesite), transplant site (awaysite), and their interactions (Table 4). For all species, warming (species displaced to lower altitude) advanced the FFD and cooling (species moved upwards) had the opposite effect (Fig. 4). The most important result was that the FFD responses to warming and cooling were not symmetrical except in Pa (Fig. 5). In the ANCOVA test, the interaction effect (between temperature change and grouping variable) is an indicator of the heterogeneity in slopes of different groups, and in the SMATR test, the  $H_0$  is that a common slope is followed by the groups. Slope heterogeneity was observed in five species except Pa, with two different tests (Table 5).

The average FFD sensitivity to cooling was of 8.4 d/ $^{\circ}$ C (Ts) for the ESF against 4.9 d/ $^{\circ}$ C for the MSF (positive values indicate delay flowering for cooling condition), and the average FFD sensitivity to warming was of -2.1 d/ $^{\circ}$ C and -8.0 d/ $^{\circ}$ C (Ts), respectively for ESF and MSF (Fig. 6A; negative values indicate an advance flowering for warming conditions). We found that RCST decreased by 24.9 $^{\circ}$ C per 100 m elevation increase (i.e., cooling) and increased by 54.3 $^{\circ}$ C per 100 m elevation decrease (i.e., warming) for MSF, whereas it decreased by 25.6 $^{\circ}$ C per 100 m elevation increase and increased by 28.8 $^{\circ}$ C per 100 m elevation decrease for ESF (Fig. 6B).

We modeled FFD to reveal the direct potential effects of temperature change on FFD. The model is based on the assumption that the RCST requirement remains unaltered by the transplanting (i.e., plants did not acclimate or adapt to the new climate within three years) and allowed us to theoretically calculate the expected FFD changes and their temperature sensitivities for transplanted plants based on the imposed temperature change (Appendix A, C). This assumed that the observed FFD change was controlled by temperature changes alone. We found that the theoretical FFD sensitivities to cooling and warming were 11.3 d/ $^{\circ}$ C vs. 13.4 d/ $^{\circ}$ C ( $F_{1,2} = 619$ ,  $P = 0.002$ ) for ESF and 12.4 d/ $^{\circ}$ C vs. 14.7 d/ $^{\circ}$ C for MSF ( $F_{1,6} = 161$ ,  $P < 0.001$ ; Fig. 7A). These values (Fig. 7B) are different from the observed temperature sensitivities (Fig. 6A).

TABLE 4. Summary of the analysis of variance of first flowering date in transplanted plants for three years.

Source	Numerator df	Denominator df	F	P
Intercept	1	160.537	5 650 459.190	<0.001
Homesite (H)	3	113.373	5 215.591	<0.001
Awaysite (A)	3	138.736	5 202.750	<0.001
Species (S)	5	396.699	62 017.211	<0.001
Year (Y)	2	209.431	1 625.130	<0.001
H × A	9	112.353	39.156	<0.001
H × S	15	396.698	99.794	<0.001
H × Y	6	162.196	1.242	0.288
A × S	15	396.536	171.037	<0.001
A × Y	6	183.594	96.321	<0.001
S × Y	10	382.464	135.654	<0.001
H × A × S	45	396.534	44.442	<0.001
H × A × Y	15	164.718	1.223	0.259
H × S × Y	30	382.460	2.543	<0.001
A × S × Y	25	383.273	171.849	<0.001
H × A × S × Y	75	383.335	2.206	<0.001

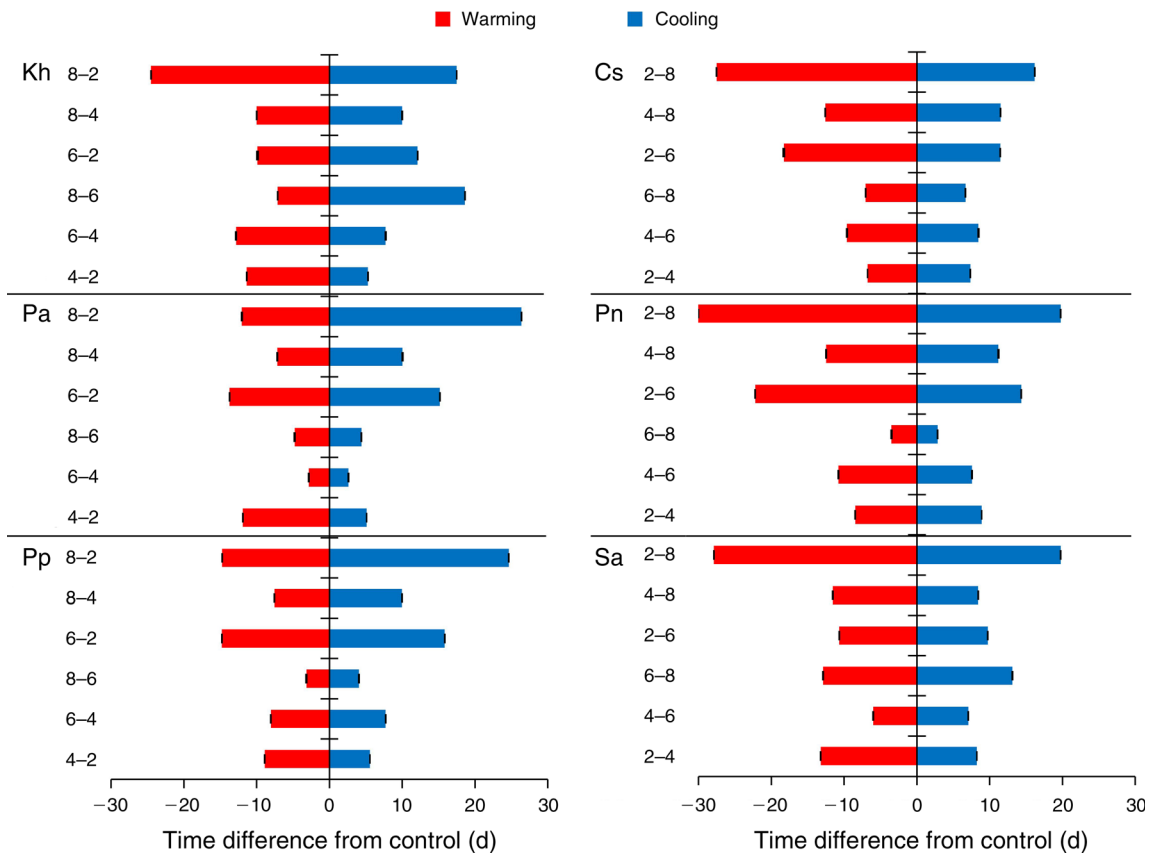


FIG. 4. First flowering date (FFD) varying with altitude change (i.e., warming and cooling). The ranges 8–2, 8–4, and 8–6 mean transferred from 3800 m to 3200 m, 3400 m, and 3600 m; 6–2 and 6–4 mean transferred from 3600 m to 3200 m and 3400 m; 4–2 means transferred from 3400 m to 3200 m; 2–8, 2–6, and 2–4 mean transferred from 3200 m to 3800 m, 3600 m, and 3200 m; 4–8 and 4–6 mean transferred from 3400 m to 3800 m and 3600 m; 6–8 means transferred from 3600 m to 3800 m. Positive and negative values are to delay/advance days in FFD. Mean and SE are shown. Kh stands for *Kobresia humilis*; Cs for *Carex scabrostris*; Pa for *Potentilla anserine*; Pn for *P. nivea*; Pp for *Poa pratensis*; and Sa for *Stipa aliena*.

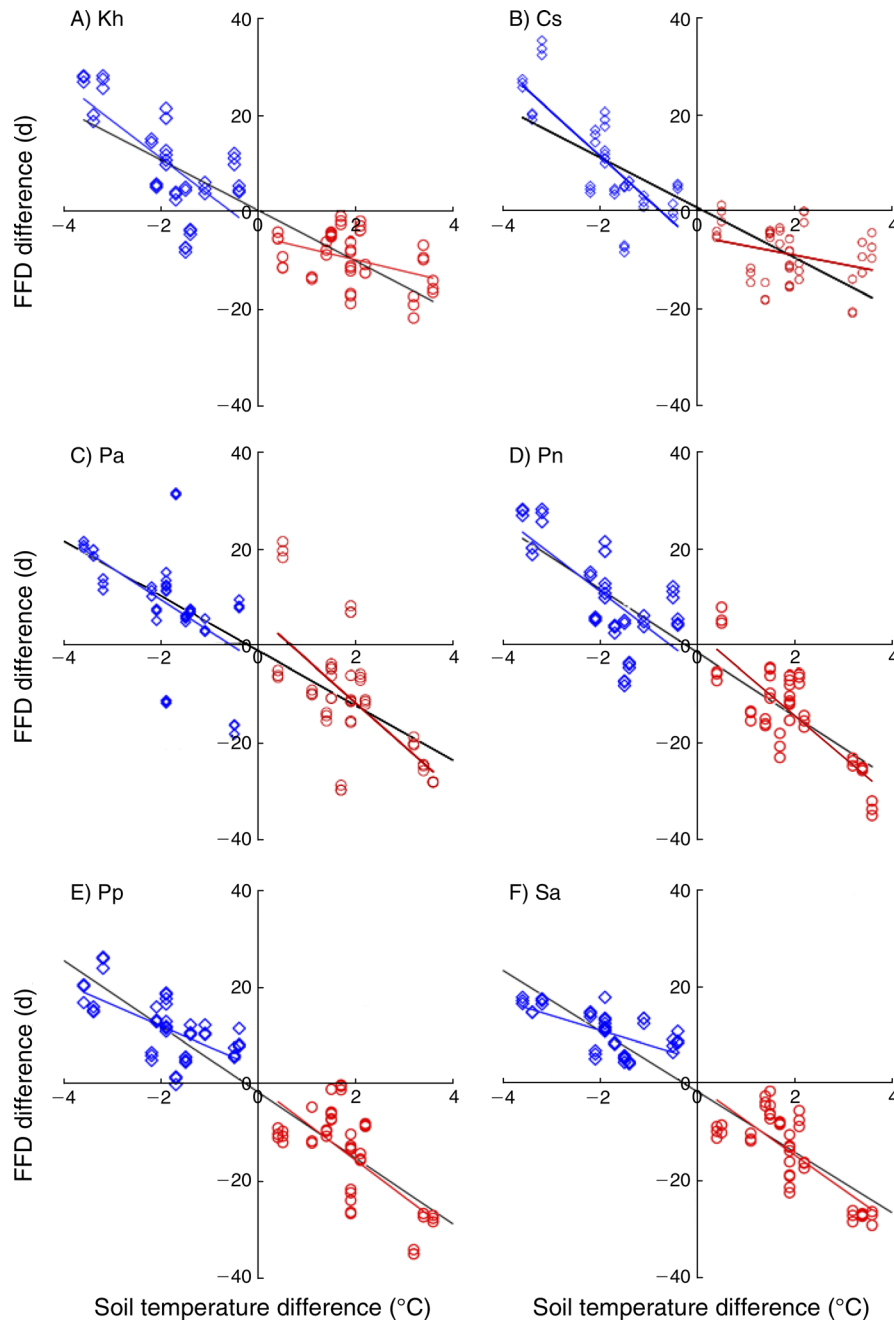


FIG. 5. Relationships of the difference of FFD between transferred and original sites (i.e., control site) and altitude increase (blue lines signify cooling) and decrease (red lines signify warming) for different plant species. The FFD values are measured in the field. Black lines are regression equations between FFD difference and altitude increase when pooled with cooling and warming data. The slopes of these regression equations are FFD sensitivities to elevation variation. See Fig. 4 for definitions of abbreviations. (A) Cooling,  $y = -7.65x - 4.321$ ,  $R^2 = 0.493$ ,  $P < 0.001$ ; warming,  $y = -2.376x - 5.220$ ,  $R^2 = 0.41$ ,  $P = 0.006$ ; pooled,  $y = -5.21x + 0.211$ ,  $R^2 = 0.74$ ,  $P < 0.001$ . (B) Cooling,  $y = -9.0856x - 6.9793$ ,  $R^2 = 0.62$ ,  $P < 0.001$ ; warming,  $y = -1.927x - 5.426$ ,  $R^2 = 0.10$ ,  $P = 0.041$ ; pooled,  $y = -5.173x + 0.550$ ,  $R^2 = 0.72$ ,  $P < 0.001$ . (C) Cooling,  $y = -6.517x - 3.782$ ,  $R^2 = 0.27$ ,  $P < 0.001$ ; warming,  $y = -8.902x - 5.867$ ,  $R^2 = 0.42$ ,  $P < 0.001$ ; pooled,  $y = -5.645x - 1.208$ ,  $R^2 = 0.59$ ,  $P < 0.001$ . (D) Cooling,  $y = -6.543x - 1.606$ ,  $R^2 = 0.86$ ,  $P < 0.001$ ; warming,  $y = -8.842x + 2.293$ ,  $R^2 = 0.66$ ,  $P < 0.001$ ; pooled,  $y = -5.706x - 0.267$ ,  $R^2 = 0.50$ ,  $P < 0.001$ . (E) Cooling,  $y = -4.357x + 3.038$ ,  $R^2 = 0.40$ ,  $P < 0.001$ ; warming,  $y = -7.553x - 0.832$ ,  $R^2 = 0.50$ ,  $P < 0.001$ ; pooled,  $y = -6.787x - 1.912$ ,  $R^2 = 0.84$ ,  $P < 0.001$ . (F) Cooling,  $y = -3.040x + 4.811$ ,  $R^2 = 0.40$ ,  $P < 0.001$ ; warming,  $y = -7.097x - 0.653$ ,  $R^2 = 0.62$ ,  $P < 0.001$ ; pooled,  $y = -6.243x - 1.748$ ,  $R^2 = 0.66$ ,  $P < 0.001$ .



TABLE 5. The *P* values of the two tests of slope heterogeneity.

	Kh	Cs	Pa	Pn	Pp	Sa
ANCOVA	0.000415	0.00000249	0.298	0.0320	0.0256	0.000144
SMATR	0.000557	0.000633	0.616	0.0625	0.00842	0.0000596

Note: The *P* value in the ANCOVA method is the *P* of the interaction effect in the test of linear model  $FFD \sim ST \times grp$ , where FFD is the first flowering data, ST is soil temperature change, and grp is a categorical variable separating the data into cooling and warming groups.

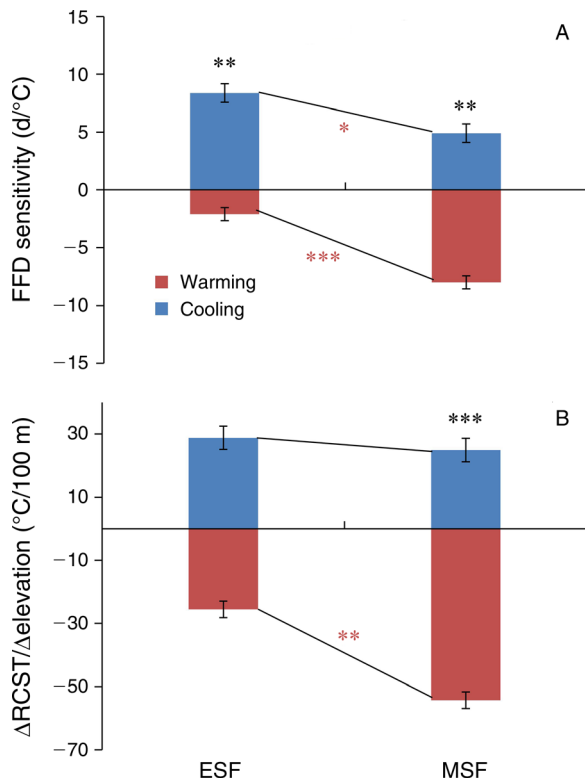


FIG. 6. (A) FFD sensitivity to soil temperature change and (B) differences of ratios between RCST change and elevation change ( $\Delta$ ) for alpine plants. Black double asterisks mean there is a significant difference between warming and cooling at  $P < 0.01$  level (for ESF,  $F_{1,2} = 94.445$ ,  $P = 0.010$  and, for MSF,  $F_{1,6} = 15.240$ ,  $P = 0.008$ ) and red single and triple asterisks mean significant differences of FFD sensitivity to cooling and warming at  $P < 0.05$  and  $P < 0.001$  levels, respectively, between ESF and MSF plants (for warming,  $F_{1,4} = 88.352$ ,  $P = 0.001$  and for cooling,  $F_{1,4} = 7.925$ ,  $P = 0.048$ ). Positive and negative values are to delay/advance days per  $^{\circ}\text{C}$  in FFD. In panel (B), black triple asterisks mean significant differences between warming and cooling at  $P < 0.001$  level (Fig. 6B, for ESF,  $F_{1,3} = 0.325$ ,  $P = 0.624$  and, for MSF,  $F_{1,7} = 52.426$ ,  $P < 0.001$ ). Red double asterisks mean significant differences of ratios between RCST change and elevation change at  $P < 0.01$  level (for cooling,  $F_{1,5} = 47.323$ ,  $P = 0.002$ ) between ESF and MSF plants. Positive and negative values are to increase/decrease RCST per 100-m increase/decrease of elevation. Mean  $\pm$  SE are shown in the figures. See Fig. 3 for definitions of abbreviations.

*Difference between bidirectional temperature changes and unidirectional temperature increases*

The average FFD sensitivity was 5.2 d/ $^{\circ}\text{C}$  for the ESF and 6.3 d/ $^{\circ}\text{C}$  for the MSF when pooling warming and cooling data (Ts; i.e., temperature variability; see Fig. 8A). Comparing them, warming alone significantly underpredicted 3.1 d/ $^{\circ}\text{C}$  for ESF and overestimated 1.7 d/ $^{\circ}\text{C}$  for MSF, respectively (Fig. 8A). Similarly, there were significant differences in the ratio of FFD change and the RCST change for MSF and ESF. For example, when average RCST prior to flowering increases 100 $^{\circ}\text{C}$  induced by warming or by warming and cooling spells, warming and warming with cooling spells advance 6.1

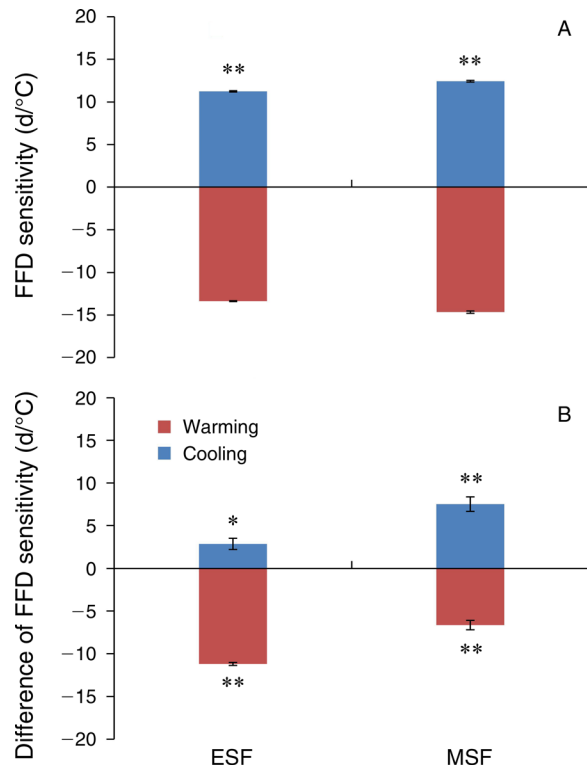


FIG. 7. (A) Theoretical sensitivity of FFD for ESF and MSF plants to soil temperature change and (B) its difference between theoretically estimated and measured values in FFD sensitivity under warming and cooling. Mean  $\pm$  SE are shown in the figures. In panel (A), double asterisks indicates significant difference between warming and cooling at  $P < 0.01$ . In panel (B), single and double asterisks indicate significant differences between theoretically estimated and measured values in FFD sensitivity under warming and cooling at  $P < 0.05$  and  $P < 0.01$ , respectively.

and 9.9 d for ESF, and 11.2 and 7.2 d for MSF, respectively (Fig. 8B).

#### DISCUSSION

Several climate variables affect plant phenology (Ranjitkar et al. 2012), such as temperature, sunshine duration, humidity (precipitation and soil moisture), and winter chilling (Kalbarczyk 2009, Seghieri et al. 2009, Körner and Basler 2010, Robbirt et al. 2010). There are also biotic factors such as plant life history (Körner 2003) and acclimation and/or evolutionary adaptation (Frank et al. 2007, Steven et al. 2007).

##### *Direct effects of temperature*

Temperature is typically considered the most critical driver of the FFD (Sherry et al. 2007, Miller-Rushing and Primack 2008, Marin et al. 2011, Pau et al. 2011, Wolkovich et al. 2012, Richardson et al. 2013). Our results indicated that the differences between the theoretical and observed FFD sensitivities to cooling for ESF and to warming for MSF were small (Fig. 7B), suggesting the FFD sensitivities to cooling for ESF and to warming for MSF may potentially be explained by the direct soil temperature effect. However, the observed FFD response to temperature manipulation is much less than theoretically estimated from the assumption of constant RCST (Fig. 7B), implying that other mechanisms may control FFD change when warming and cooling occur. For example, Dorji et al. (2013) find that there is interactive effect of warming and snow addition on FFD, because snow addition mitigates the negative effects of warming on flowering phenology and reproductive effort of *K. pygmaea* in the alpine meadow. Some research shows that in the Tibetan Plateau, where snow does not cover the landscape during the whole dormant season, the timing of soil thaw and subsequent soil water availability, rather than snow melt timing, are the main environmental cues for plant phenology (e.g., Dorji et al. 2013). In an alpine meadow, warming can also cause water stress, particularly in the early, premonsoon growing season, which in turn can affect the phenology of plants with different life history traits (early vs. late flowering; Dorji et al. 2013).

##### *Acclimation and vernalization*

We propose two other mechanisms that may explain the observed asymmetric sensitivity of FFD to temperature change besides direct temperature effects and constant RCST. First, acclimation (Frank et al. 2007, Steven et al. 2007), as evidenced by the FFD of nontransplanted plants along the altitude gradient (see Fig. 3), is a rapid process that can occur soon after the transplant, thereby modifying the RCST, and thus, the temperature sensitivity of FFD. Under this mechanism, our results should be interpreted as evidence for a rapid acclimation in flowering phenology after a change of

temperature. Yet, acclimation appears to be different for ESF and MSF to warming and cooling. For example, the RCST inferred to match our data was found to change more with cooling than with warming for MSF (Fig. 6B) under this mechanism of an acclimation caused change of RCST. Therefore, although increases or decreases of  $T_s$  synchronized with increases or decreases of RCST when those plants were transferred downwards or upwards, the magnitudes were different for the increased or decreased differences between  $T_s$  and RCST. Compared with warming, the difference between  $T_s$  decreases and RCST decreases with cooling was smaller, which may explain the smaller temperature sensitivity of FFD with cooling (Fig. 6A). Similarly, the difference between ESF and MSF plants in the temperature sensitivity of RCST under cooling (Fig. 6B) might explain partially their different FFD sensitivity to cooling (Fig. 6A).

A second alternative mechanism is that different vernalization requirements between ESF and MSF species may interact with the direct effect of soil warming. Typically, ESF plants complete their floral primordia in the former autumn and winter, whereas in MSF plants, the floral primordium differentiation is synchronized with vegetative growth before flowering (Körner 2003). Thus, the vernalization effect on FFD may be greater for the ESF plants than for the MSF plants. Warmer winter temperatures at lower altitude may cause a delay in the completion of vernalization (Cook et al. 2012), thereby delaying the flowering initiation for ESF plants transplanted downward.

##### *Implications*

We acknowledge up front that this study is based on only six alpine grasses and forbs, including only two early flowering species, which limits the scope of any generalizations. However, our study showed that, at least for these six species on the Tibetan Plateau, ESF plants were not more sensitive to warming than MSF plants, which is inconsistent with other studies (Sherry et al. 2007, Marin et al. 2011, Pau et al. 2011, Wolkovich et al. 2012, Richardson et al. 2013). These different temperature responses of flowering phenology for ESF and MSF plants could alter the relative timing of species interactions and influence how their ontogenetic stages interact with each other under future climate change (Pau et al. 2011). For instance, for ESF plants subject to warming, the costs of earlier flowering could be higher because flowering that is excessively early could lead to death or extensive tissue loss due to frost damage (Thórhallsdóttir 1998). Conversely, in MSF plants, flowering that is excessively late may result in the failure of seed maturation owing to the shortness of the growth period (Menzel et al. 2011).

Wolkovich et al. (2012) report that warming experiments underpredict advances in the timing of flowering due to complex interactions among multiple drivers in the observational data or due to remediable artifacts in

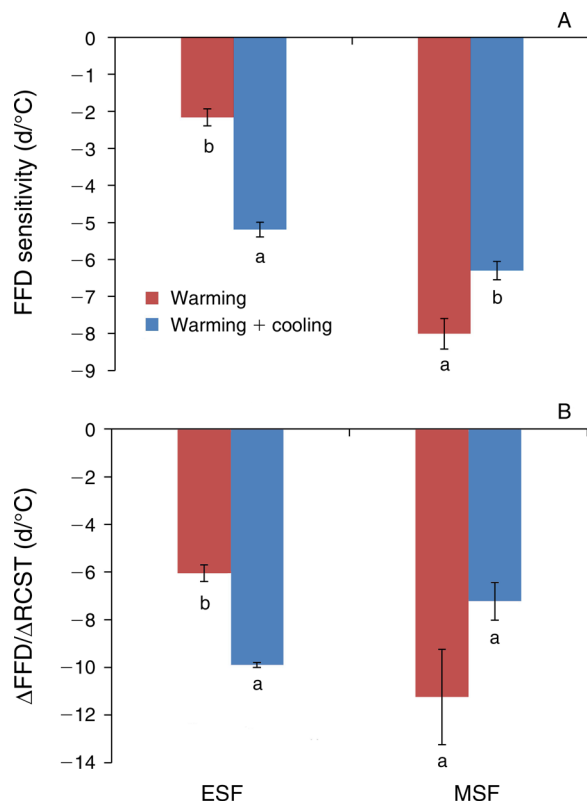


FIG. 8. Differences of bidirectional temperature changes and unidirectional temperature increases. (A) Differences of the sensitivities of FFD to soil temperature change (for ESF,  $F_{1,3} = 182.133$ ,  $P = 0.005$  and, for MSF,  $F_{1,7} = 11.994$ ,  $P = 0.013$ ) and (B) the ratio of change in FFD to change in RCST between native sites and transferred sites (for ESF,  $F_{1,3} = 5.194$ ,  $P = 0.009$  and for MSF,  $F_{1,7} = 3.484$ ,  $P = 0.111$ ) for the alpine plants between warming alone and pooled warming and cooling data. Warming means warming alone; warming and cooling means pooled warming and cooling data; see Fig. 4 for definitions of other abbreviations. Different letters indicate significant differences between warming alone and pooled warming and cooling data in FFD sensitivity at  $P < 0.05$  level for ESF and MSF, respectively. Mean  $\pm$  SE are shown.

the experiments that result in lower irradiance and drier soils, thus dampening the phenological responses to manipulated warming. However, our results indicate that the differences of FFD sensitivity to  $T_s$  change between warming and warming-cooling vary with species (i.e., ESF vs. MSF), suggesting that the mismatch of the observation and warming experiment could at least be partially caused by asymmetric response of FFD to warming and cooling and be species-specific because of different offsets of cooling to warming effects for ESF and MSF species. Therefore, our results (Fig. 5) confirmed our conceptual diagram (Fig. 1), suggesting that a linear model may contribute to the mismatch because of nonlinear responses of FFD to temperature (Sparks et al. 2000, 2009, Schleip et al. 2008, Primack et al. 2009, Ishizuka and Goto 2012, Iler et al. 2013).

## CONCLUSIONS

Responses of flowering phenology were different and asymmetric for plants moved upward (cooled) or downward (warmed) along an elevation gradient. Opposite asymmetric responses were observed for early spring- and midsummer-flowering species. Although this study was based on only six alpine grasses and forbs, the different asymmetric responses may explain in part different sensitivities identified between long-term trend observations and manipulative warming experiments. The differences of first flowering date sensitivity to soil temperature change between warming and warming vs. cooling in empirical and experimental studies could be species-specific because of different offsets of cooling to warming effects for early spring- and midsummer-flowering species.

## ACKNOWLEDGMENTS

This work was supported by programs from Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB03030403), National Basic Research Programs (2013CB956000), and National Science Foundation of China (41230750 and 31272488).

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#### SUPPLEMENTAL MATERIAL

##### Ecological Archives

Appendices A–L are available online: <http://dx.doi.org/10.1890/13-2235.1.sm>