Trends in Flowering Phenology of Herbaceous Plants and Its Response to Precipitation and Snow Cover on the Qinghai—Tibetan Plateau from 1983 to 2017

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Abstract: Based on limited controlled experiments, both advanced and delayed shifts in flowering phenology induced by precipitation and snow cover have been reported on the Qinghai–Tibetan Plateau (QTP). To clarify the impact of precipitation and snow cover on flowering phenology, we conducted a comprehensive statistical analysis of the temporal change in flowering phenology and its responses to precipitation and snow cover changes using regression models built on the largest collection of ground phenological observation data on the QTP. We found that first flowering date (FFD) for the early-flowering time series significantly advanced at the rate of \(-0.371 \pm 0.149\) days/year (\(p < 0.001\)), whereas FFD mid-to-late-flowering time series showed no trend at the rate of \(0.158 \pm 0.193\) days/year (\(p = 0.108\)). Cumulative pre-season precipitation regressed with FFD positively for early-flowering time series, with the explained variation ranging from 11.7 to 49.4% over different pre-season periods. The negative impact of precipitation on flowering phenology is unexpected, because an increase in precipitation should not hamper plant growth in the semi-arid and arid environments on the QTP. However, precipitation was found to be inversely correlated with temperature. Thus, it is likely that temperature, and not precipitation, regulated flowering phenology over the study period. No relationship was found between FFD and snow-cover melt date or duration. This result indicated that snow cover may not affect flowering phenology significantly, which may be because plant flowering time was much later than the snow-cover melt date on the QTP. These findings contrast the results of controlled experiments on the QTP, which showed that precipitation regulated flowering phenology, and with other studies that showed that snow-cover melting time determined flowering dates of early-flowering species in high latitude and Arctic zones in Europe and North America, where the low-temperature environment is similar to the QTP. These findings can improve flowering phenology models, assist in the prediction of phenological responses of herbaceous plants to climate change, and forecast changes in the structure and function of the grassland ecosystem on the QTP.

Keywords: flowering phenology shift; functional groups; precipitation; snow cover; Qinghai–Tibetan Plateau
1. Introduction

The Qinghai–Tibetan Plateau (QTP) has experienced striking impacts from global changes [1–5], and distinct shifts in plant phenology in the area have been observed [1, 4–14]. Flowering is the beginning of the reproductive phase of the plant life cycle [15–17]. Changes in flowering time may alter species’ competitive abilities for water, nutrients, and light [18–20], affecting the phenological patterns and species composition of alpine ecosystems [14]. Understanding the trends in flowering times of herbaceous plants and the mechanisms of phenological change is essential to devise appropriate countermeasures to cope with changes in the grassland ecosystem’s structure and function on the QTP [21–23].

Precipitation is the primary source of soil water and determines water availability for plant growth [24, 25], and moisture limitation can play an important role in structuring plant phenology [26, 27]. However, studies on the QTP have indicated divergent impacts of precipitation on flowering time. A precipitation enhancement experiment on the QTP showed that more precipitation advanced the first flowering date (FFD) of early-flowering species but not of mid-to-late-flowering species [28]. A snow addition experiment significantly advanced the flowering time of *Kobresia pygmaea* but had no significant effect on the reproductive phenology of *Astragalus rigidulus* and *Potentilla fruticosa*, and the flowering of *Potentilla saundersiana* was significantly delayed by snow addition [23]. However, the relationship between precipitation and flowering time was weak for both *Plantago asiatica* and *Taraxacum mongolicum* based on continuous and long-term ground-observed phenology records on the QTP [13]. The rate and magnitude of the enhanced precipitation from the controlled experiment were much higher than those under natural conditions. The number of controlled experiments was limited, and their durations were short. All these factors may introduce uncertainty to what is known of the response of phenology to precipitation on the QTP. Although the shifts in the flowering time were reported using observational data from 16 stations from 2000 to 2012 [13], the studied species were only two non-dominant forbs on the QTP. Long-term observations from more species and more sites are required to explore the response of the flowering phenology of herbaceous plants to precipitation on the QTP.

Snow cover can affect flowering phenology in alpine and Arctic regions [29, 30]. The thickness and duration of snow cover can influence the timing and duration of phenological events [31], and the observed flowering time of early-flowering species is closely associated with the melting date of snow cover [32, 33]. However, the snow cover on the QTP may be different from that of the alpine and Arctic regions in Europe and North America because snowfall is quite limited, and the average multiyear mean snow cover days are less than one month on the QTP [34]. The mechanism of impact of snow cover on flowering phenology may differ from that in the alpine and Arctic regions of Europe and North America [35, 36]. However, to our knowledge, no studies of the effect of snow cover on flowering phenology have ever been conducted on the QTP; thus, this study provides important long-term observation data for multiple sites on the QTP.

To accurately detect the changes in flowering phenology and assess the effects of precipitation and snow cover on the shifts in flowering phenology, we conducted comprehensive statistical analyses using long-term, ground-observed data, which included the FFD records from 27 phenological stations from 1983 to 2017, precipitation records from 21 stations from 1980 to 2017, and snow depth data from 102 stations from 1961 to 2013. We investigated the following: (1) How did the flowering phenology of the QTP herbaceous plants change from 1983 to 2017? (2) How did the flowering phenology of herbaceous plants respond to precipitation? (3) How did snow cover affect the flowering phenology of herbaceous plants on the QTP? Because the observation data used in this study were conducted by multiple technicians, this may introduce increased variation into the data. Therefore, we do not confirm that the analysis based on a species at a site was reliable enough, but we believe that a study based on a large number of long-term observations from many sites and many species should be more reliable than one based on a small number of observations of site and species. Thus, we mainly analyzed flowering
phenological trends and their responses to precipitation and snow cover changes based on different functional groups of early-flowering and mid-to-late-flowering species at regional scale and not based on a species at a site.

2. Materials and Methods

2.1. Study Area

The QTP is located in western China. It extends from 23°00′ N to 39°47′ N and from 73°26′ E to 104°23′ E, comprising a total area of $2.58 \times 10^6$ km$^2$ (Figure 1). On the QTP, the altitude is predominantly higher than 4000 m above sea level, and the terrain inclines from the northwest to the southeast. The climate of the QTP is characterized by a thermal/moisture gradient from southeast to northwest, influenced by monsoonal winds from the Indian Ocean and the terrain. The annual mean precipitation decreases from 1764 mm in the southeast to 16 mm in the northwest, while the annual mean air temperature decreases from 15.5 °C in the southeast to −5.0 °C in the northwest, based on data from 1981 to 2011 [1,3,4,37]. Grassland, including steppe and meadow, is the dominant vegetation type and accounts for almost 63.6% of the plateau area. Plants on the QTP usually flower from March to August, with a peak flowering period in June and July.

![Figure 1. Location of the Qinghai-Tibetan Plateau and the spatial distribution of observation stations used in this study. PM stations present both phenological and meteorological data; P stations present only phenological data; M stations present only meteorological data.](image-url)

2.2. Phenological and Meteorological Data

Ground-observed first flowering dates (FFD) recorded at observation stations on the QTP during 1983–2017 were derived from the annual reports of phenological records for natural plants (PRNP) and growth records for forages (GRF). The observation stations belong to the China Meteorological Administration (CMA) phenology network, and data have been recorded since 1983. Phenological observations were conducted every two days at fixed field sites following the CMA criteria [38]. The first flowering date (FFD), peak flowering date (PFD), and last flowering date (LFD) from PRNP and FFD and PFD from GRF observations are recorded. The FFD was taken as the index of flowering phenology in this study because of the incompleteness of the records for peak flowering date and last flowering date.

For PRNP observations, the FFD is defined as the date when several individual plants of a species fully bloom; the PFD, the date when more than half of the individual plants of a species fully bloom; and the LFD, the date when few individual plants of a species fully bloom [38]. For GRF observations, the observation plot is a minimum of 50 m $\times$ 50 m...
and is divided into four areas in which the plants are observed every year. The selected areas were further divided into four cells. For herbaceous species, 10 individual plants were selected as fixed observation objects for each of the four cells. The species’ FFD was determined when 10% of the 40 individual plants in the four cells were in full bloom. The species’ PFD was determined when 50% of the 40 individual plants in the four cells were in full bloom [38].

A total of 1646 effective phenological records were collected from 21 herbaceous plant species at 27 stations on the QTP (Table 1). These records were further categorized into 78 observed FFD time series for plant species at a station. Two types of flowering mechanisms on the QTP can be commonly observed: preformation and vernalization-induced flower organ growth. Early-flowering species mainly undergo flower preformation, and more mid-to-late-flowering species experience vernalization-induced floral organ growth. The flower buds of early-flowering species form in the preceding autumn of the concurrent flowering year [39]; floral primordium differentiation in mid-to-late-flowering species is synchronized with vegetative growth in spring, before flowering, with flower buds forming in the spring [9]. Thus, the trends in flowering phenology and responses to climatic change should be different for early-flowering and mid-to-late-flowering species.

### Table 1. Geographical coordinates, elevation, and observed species at the 27 phenological stations on the Qinghai–Tibetan Plateau. a: stations presenting both phenological and meteorological data; b: stations presenting only phenological data.

| Station No. | Station     | Province | Latitude (°) | Longitude (°) | Altitude (m) | Observed Species                                           |
|-------------|-------------|----------|--------------|---------------|--------------|------------------------------------------------------------|
| 1           | Datong      | Qinghai  | 36.95        | 101.68        | 2450.00      | Iris lactea Pall., Taraxacum mongolicum, Plantago asiatica, |
| 2           | Menyuan     | Qinghai  | 37.38        | 101.62        | 2850.00      | Taraxacum mongolicum, Iris lactea Pall.                   |
| 3           | Huzhu       | Qinghai  | 36.82        | 101.95        | 2480.00      | Agropyron cristatum, Plantago asiatica                    |
| 4           | Huangyuan   | Qinghai  | 36.68        | 101.23        | 2634.00      | Plantago asiatica, Iris lactea Pall.                      |
| 5           | Huangzhong  | Qinghai  | 36.52        | 101.57        | 2668.00      | Iris lactea Pall., Taraxacum mongolicum, Stipa krylovii,   |
|             |             |          |              |               |              | Koeleria macrantha, Poa crymophila, Kobresia humilis,     |
|             |             |          |              |               |              | Plantago asiatica, Taraxacum mongolicum, Iris lactea Pall,|
|             |             |          |              |               |              | Artemisia scoparia                                         |
| 6           | Haibei      | Qinghai  | 36.97        | 100.90        | 3115.00      | Elymus nutans, Taraxacum mongolicum, Plantago asiatica,   |
|             |             |          |              |               |              | Iris lactea Pall., Puccinellia tenuiflora, Kobresia pygmaea,|
|             |             |          |              |               |              | Scirpus distigmaticus, Plantago asiatica                  |
| 7           | Shiqu       | Sichuan  | 32.98        | 98.10         | 4200.00      | Elymus nutans, Taraxacum mongolicum, Plantago asiatica,   |
| 8           | Hainanzhou  | Qinghai  | 36.27        | 100.62        | 2835.00      | Taraxacum mongolicum, Agropyron cristatum, Plantago asiatica|
| 9           | Guide       | Qinghai  | 36.03        | 101.43        | 2237.10      | Iris lactea Pall., Elymus nutans, Puccinellia tenuiflora,  |
| 10          | Guinan      | Qinghai  | 35.58        | 100.75        | 3120.00      | Kobresia humilis, Elymus nutans, Taraxacum mongolicum,     |
|             |             |          |              |               |              | Iris lactea Pall., Elymus nutans, Poa crymophila,          |
|             |             |          |              |               |              | Kobresia humilis                                         |
| 11          | Tongde      | Qinghai  | 35.27        | 100.65        | 3269.00      | Elymus nutans, Taraxacum mongolicum, Plantago asiatica    |
| 12          | Henan       | Qinghai  | 34.73        | 101.60        | 3500.00      | Elymus nutans, Puccinellia tenuiflora, Kobresia pygmaea,  |
| 13          | Maqu        | Gansu    | 34.00        | 102.05        | 3471.4       | Elymus nutans, Taraxacum mongolicum, Scirpus distigmaticus,|
| 14          | Nomhon      | Qinghai  | 36.43        | 96.42         | 2790.40      | Puccinellia tenuiflora, Kobresia pygmaea, Carices montana,  |
| 15          | Qumarleb    | Qinghai  | 34.13        | 95.78         | 4175.00      | Plantago asiatica, Taraxacum mongolicum                   |
Table 1. Cont.

| Station No. | Station   | Province | Latitude (°) | Longitude (°) | Altitude (m) | Observed Species |
|-------------|-----------|----------|--------------|--------------|--------------|------------------|
| 16          | Xinghai a | Qinghai  | 35.58        | 99.98        | 3323.20      | *Agropyron cristatum*, *Leymus secalinus*, *Stipa krylovii*, *Plantago asiatica*, *Taraxacum mongolicum*, *Iris lactea Pall.*, *Poa crymophila*, *Artemisia scoparia* |
| 17          | Tiebujia b | Qinghai  | 37.08        | 99.58        | 3269.00      | *Poa crymophila*, *Artemisia scoparia* |
| 18          | Delingha a | Qinghai  | 37.37        | 97.37        | 2981.50      | *Agropyron cristatum*, *Medicago sativa* |
| 19          | Gade a    | Qinghai  | 33.97        | 99.90        | 4050.00      | *Koeleria macrantha*, *Elymus nutans*, *Festuca ovina*, *Kobresia humilis*, *Plantago asiatica*, *Taraxacum mongolicum*, *Gentiana algida* |
| 20          | Garz a    | Sichuan  | 31.62        | 100.00       | 3393.50      | *Taraxacum mongolicum*, *Phragmites australis* |
| 21          | Golmud a  | Qinghai  | 36.42        | 94.90        | 2807.60      | *Plantago asiatica*, *Taraxacum mongolicum* |
| 22          | Daocheng a| Sichuan  | 29.05        | 100.30       | 3727.70      | *Platynotus laetissimus*, *Plantago asiatica*, *Taraxacum mongolicum* |
| 23          | Lhasa a   | Tibet    | 29.67        | 91.13        | 3648.70      | *Plantago asiatica*, *Taraxacum mongolicum* |
| 24          | Nyingchi a| Tibet    | 29.67        | 94.33        | 2991.80      | *Platynotus laetissimus*, *Plantago asiatica*, *Taraxacum mongolicum* |
| 25          | Shigatse a| Tibet    | 29.30        | 88.88        | 3836.15      | *Platynotus laetissimus*, *Plantago asiatica*, *Taraxacum mongolicum* |
| 26          | Zoige a   | Sichuan  | 33.58        | 102.97       | 3439.60      | *Platynotus laetissimus*, *Plantago asiatica*, *Taraxacum mongolicum* |
| 27          | Lhoka a   | Tibet    | 29.25        | 91.77        | 3551.70      | *Platynotus laetissimus*, *Plantago asiatica*, *Taraxacum mongolicum* |

Therefore, the FFD time series was further grouped into 47 early-flowering and 31 mid-to-late-flowering groups. The early-flowering time series were defined as those whose FFD occurred before July, and the mid-to-late-flowering time series were defined as those in or after July [40]. Hereafter, the corresponding FFD time series are referred to as early-flowering and mid-to-late-flowering time series, respectively. The 27 phenological stations were primarily located in Qinghai Province and the Tibet Autonomous Region, Sichuan Province, and Gansu Province. The elevation of the stations ranged from 2237 m in Guide to 4200 m in Shiqu.

Daily precipitation data from 1980 to 2017 for 19 stations were derived from the China Meteorological Data Sharing Service System of the CMA (http://data.cma.cn/, accessed on 11 May 2018), and data for two stations (Gade and Haibei) were obtained from the Qinghai Province Meteorological Bureau of China. The distance from meteorological observation field to phenological observation field is generally less than two kilometers, and the elevations of the two fields are similar. Daily snow depth (SD) data from 1961 to 2013 at 102 stations were also acquired from the National Tibetan Plateau Data Center (http://westdc.westgis.ac.cn, accessed on 20 April 2019). Based on the observation guidelines of the China Meteorological Administration [41], if at least half of the observation fetch of the station is covered by snow, the SD is measured by a ruler and then rounded to the nearest integer in centimeters, and any SD ≤ 0.4 cm is recorded as zero to avoid the impact of thin snow.

2.3. Temporal Trend Analysis of FFD and Precipitation Time Series

Precipitation over a period before flowering (pre-season) was found to play an important role in plant phenology on the QTP [42,43]. In this study, we assumed that flowering phenology is also driven by cumulative pre-season precipitation (CPP). The trend of an FFD time series or its corresponding pre-season precipitation was determined by ordinary linear least-squares regression over the observation periods. The slope of the regression line represents the FFD or precipitation trend over time and is expressed in days/year or mm/year. The fitted slopes were analyzed using the F-test, with a significance level of 0.05. A negative value for the FFD or precipitation indicated a temporal advance in phenological
events or precipitation, whereas a positive value represented a delay or decrease. The overall trend in FFDs or precipitation of all the time series, or those of early-flowering or mid-to-late-flowering series, and a species was computed using a weighted least-squares (WLS) meta-analysis method based on the detected trends for each individual FFD or precipitation time series [4,12,44,45]. For each time series, the weight was the reciprocal of the regression slope standard error, and t values for slope tests. The formulas used were as follows:

$$\bar{\beta} = \frac{\sum_{j=1}^{k} \omega_j \beta_j}{\sum_{j=1}^{k} \omega_j}$$  \hspace{1cm} (1)$$

$$\omega_j = \frac{1}{SE_j}, \quad \beta_j = \frac{\sum_{i=1}^{n} X_i Y_i - n \bar{X}_j \bar{Y}_j}{\sum_{i=1}^{n} X_i^2 - n \bar{X}_j^2}$$  \hspace{1cm} (2)$$

where $\bar{\beta}$ is the overall FFD or precipitation trend of all the time series or the time series of a functional group or a species; $\omega_j$ and $\beta_j$ are the weight and trend of the $j$th FFD or precipitation time series, respectively; $SE_j$ is the standard error of the regression slope for the $j$th FFD or precipitation time series; $k$ is the total number of individual FFD or precipitation time series; $X_j$ is the $j$th year of the $j$th FFD or precipitation time series; $Y_j$ is the FFD or precipitation of the $i$th year of the $j$th FFD or precipitation time series; $n$ is the total number of FFD or precipitation records for the $j$th FFD or precipitation time series; and $\bar{X}_j$ and $\bar{Y}_j$ are the mean number of years and mean FFD or precipitation for the $j$th FFD or precipitation time series.

2.4. FFD Response to Precipitation and Snow Cover Change

FFD responses to precipitation and snow cover changes were tested for early-flowering and mid-to-late-flowering time series. Regressions between FFD and CPP were conducted to test the impact of precipitation on flowering phenology. The length of the pre-season period may vary among different site species, but it usually ends the day before FFD [25,36]. Thus, we tested all the regressions at 10-day intervals, and the minimum and maximum lengths of the pre-season period were set as 10 and 90 days, respectively.

The snow-cover duration (SCD) and snow-cover melt date (SCMD) can influence the timing of flowering phenology in alpine and Arctic regions [31–33]. These two snow-cover indices were also used to study the impact of snow cover on the flowering phenology of the QTP. First, the SCD and SCMD were calculated based on the daily SD data for each hydrological year (September 1 to August 31 of the following year) from 1961 to 2013 [46]. The SCD was calculated using the following equation:

$$SCD = \sum_{i=1}^{n} S_i$$  \hspace{1cm} (3)$$

$$S_i = \begin{cases} 1, & \text{snow} \\ 0, & \text{no snow} \end{cases}$$  \hspace{1cm} (4)$$

where SCD stands for snow-cover duration, $n$ is the total number of days within the snow-cover duration, and $S_i$ is the occurrence of snow cover, with values of 1 for snow and 0 for no snow. The start date of snow-cover duration was defined as the first five consecutive days when snow occurred, and SCMD was defined as the start date of the last five consecutive days to avoid the impact of ephemeral snow during each hydrological year [47,48].

As with the day of the year (DOY), FFD and SCDM were also converted into the day of the hydrological year (DoHY) based on the corresponding calendar format “Month
Day” [34]. Finally, FFD was regressed with SCD and SCMD to test the impact of snow cover on flowering phenology during the period when the FFD was observed from 1983 to 2013. The DoHY of FFD was input as a dependent variable, and the DoHYs of SCD and SCMD were independent variables.

Since the flowering phenology related to precipitation and snow cover may vary among different sites, a two-way ANOVA was used to examine the effects of site and precipitation (snow cover), and the interactions between site and precipitation, as random factors. This allowed us to understand the impact of precipitation and snow cover on flowering phenology more thoroughly.

3. Results
3.1. Trends of Temporal Changes in FFD and Precipitation

The overall FFD trend for all FFD time series on the QTP significantly advanced at a rate of $-0.159 \pm 0.126$ days/year ($p < 0.05$). However, divergent trends were observed between the two functional groups of plants. The overall trends of FFD of the early-flowering time series advanced significantly, and the calculated trends were $-0.371 \pm 0.149$ days/year ($p < 0.001$), whereas those of the mid-to-late-flowering time series showed no trend at the rate of $0.158 \pm 0.193$ days/year ($p = 0.108$).

Divergent trends of each individual FFD time series between the two plant functional groups were also observed. Among the 47 early-flowering time series, 31.9% showed a significantly advanced trend in FFD ($p < 0.05$), whereas 4.3% showed a significantly delayed trend in FFD ($p < 0.05$). In contrast, 22.6% of the mid-to-late-flowering time series showed a significantly delayed trend in FFD ($p < 0.05$), and only 3.2% of those showed a significantly advanced trend in FFD ($p < 0.05$) (Figure 2).

![Figure 2. Trends in first flower date (FFD) for early-flowering time series and mid-to-late-flowering time series in the 78 FFD time series of herbaceous plant species on the Qinghai–Tibetan Plateau. The fitted slopes were analyzed using the F-test. Error bars indicate the 95% confidence interval. The pink (dashed) line shows the 181st day of the year, and before and after it are the early-flowering and mid-to-late-flowering time series, respectively.](image-url)
Most FFD trends in two widely observed perennial herbs, *Plantago asiatica* and *Taraxacum mongolicum*, showed no distinct trend \((p < 0.05)\). Eight of sixteen (50.0%) FFD time series for *Plantago asiatica* and 3 of 18 (16.7%) for *Taraxacum mongolicum* showed significant changes \((p < 0.05)\). No spatial patterns of FFD trends were clearly observed for either *Plantago asiatica* or *Taraxacum mongolicum* (Figure 3).

![Figure 3](image-url) The spatial distribution of the trends in first flowering date of *Plantago asiatica* and *Taraxacum mongolicum* at the observation stations. Green solid circles indicate stations with significant advanced trends in first flowering date over the study period \((p < 0.05)\), blue solid circles indicate those with significant delayed trends \((p < 0.05)\), and hollow circles indicate those with no significant change trend \((p \geq 0.05)\).

Five of eight (62.5%) early-flowering species, including *Scirpus distigmaticus*, *Medicago sativa*, *Kobresia humilis*, *Iris lactea Pall.*, and *Taraxacum mongolicum*, indicated significantly advanced FFD, whereas 3 of 13 mid-to-late-flowering species, including *Gentiana algida*, *Poa annua*, and *Stipa krylovii*, showed significantly delayed FFD and no species advanced significantly \((p < 0.05)\). However, only one in eight early-flowering species precipitation time series indicated significant advance, and the others showed no trend. In contrast, 4 of 13 precipitation time series for mid-to-late-flowering species showed a significant increase, while others indicated no trend \((p < 0.05)\). Only 2 (*Scirpus distigmaticus* and *Stipa krylovii*) among the 21 species showed significant changes in both FFD and precipitation. For these two species, FFD was inversely correlated with precipitation (Figure 4).

### 3.2. Response of FFD to Variation in CPP

The two functional groups of early-flowering and mid-to-late-flowering FFD time series showed different responses to precipitation. For the early-flowering time series, it was evident that more precipitation delayed FFD. Regressions between FFD and CPP were significantly positive during all the different pre-season periods, and the cumulative precipitation explained 19.7–48.0% of the variation in FFD. The higher explained variation in FFD occurred during the pre-season periods with a length of more than 30 days (Figure 5A).
Figure 4. The overall trends in first flowering date and CPP, which are computed using a weighted least-squares meta-analysis method. P_n is the length (days) of the pre-season period of precipitation. Error bars indicate the 95% confidence interval of the overall trends in first flower date and precipitation. ***: p < 0.001; **: p < 0.01.
However, for the mid-to-late-flowering time series, regressions between FFD and CPP indicated no close relationship during most pre-season periods, and the $R^2$ value was relatively low and varied from 0.8 to 2.3%. Thus, it seems that precipitation had a less pronounced impact on the FFD of the mid-to-late-flowering time series than on the early-flowering time series (Figure 5B).

Based on two-way ANOVA analysis, the main effects of site ($p < 0.001$), precipitation ($p < 0.05$), and the interactions of site × precipitation ($p < 0.001$) on FFD were all statistically significant for early-flowering species. For mid-to-late-flowering species, site significantly
affected FFD when pre-season periods were 10 days and 30–50 days ($p < 0.05$); however, precipitation did not have a significant effect on FFD. Site $\times$ precipitation significantly affected FFD when the pre-season period was 10 days and 30–90 days ($p < 0.05$). Thus, precipitation may affect FFD for early-flowering species rather than mid-to-late-flowering species, which is similar to the relationship between FFD and precipitation from the regression analysis (Table 2).

**Table 2.** The two-way ANOVA results for the effects of site, precipitation, and their interactions on first flower date. ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$. d.f. is degree of freedom, and $F$ is the value of the $F$-test.

| Groups         | Pre-Season Period Length | Site $d.f.$ | Precipitation $d.f.$ | Site $\times$ Precipitation $d.f.$ |
|----------------|--------------------------|-------------|----------------------|-------------------------------------|
|                |                           |             |                      |                                     |
| Early-flowering| 10                       | 21.414 ***  | 367                  | 1.228 *                             |
|                | 20                       | 11.204 ***  | 478                  | 1.348 **                            |
|                | 30                       | 12.528 ***  | 511                  | 1.845 ***                           |
|                | 40                       | 10.601 ***  | 552                  | 1.634 ***                           |
|                | 50                       | 9.489 ***   | 549                  | 1.851 ***                           |
|                | 60                       | 10.513 ***  | 557                  | 1.974 ***                           |
|                | 70                       | 9.621 ***   | 566                  | 1.632 **                            |
|                | 80                       | 7.725 ***   | 576                  | 1.661 **                            |
|                | 90                       | 6.846 ***   | 577                  | 1.705 **                            |
| Mid-to-late-flowering | 10          | 2.510 *     | 320                  | 1.145                               |
|                | 20                       | 1.959       | 381                  | 1.055                               |
|                | 30                       | 2.495 *     | 389                  | 1.314                               |
|                | 40                       | 2.564 *     | 400                  | 0.906                               |
|                | 50                       | 3.870 **    | 407                  | 1.012                               |
|                | 60                       | 1.149       | 392                  | 0.757                               |
|                | 70                       | 2.319       | 420                  | 0.895                               |
|                | 80                       | 0.938       | 412                  | 0.689                               |
|                | 90                       | 1.481       | 400                  | 1.156                               |

3.3. Relationship between Precipitation and Temperature

More precipitation was accompanied by more clouds and low solar radiation. Low solar radiation can further induce low temperatures. We analyzed the regression between monthly average temperature and total monthly precipitation from January to June, when precipitation can affect flowering phenology for early-flowering time series on the QTP (Figure 6). Precipitation showed a significantly negative regression with average temperature, which indicated that periods of higher precipitation were associated with lower temperatures ($p < 0.001$). Higher elevation sites experienced heavier rainfall than low elevation sites (Figure 7). The relationship between rainfall and temperature may indicate that a positive relationship between flowering dates and rainfall may reflect elevation differences.

Precipitation not only has an inverse relationship to air temperature but also dramatically reduces the temperature of the plant itself. Temperature is the most important factor affecting flowering phenology [49–51]. Thus, an increase in temperature generally leads to earlier flowering phenology. Since precipitation was negatively correlated with temperature, significantly advanced FFD for early-flowering time series on the QTP may be related to temperature increase rather than precipitation variation.
3.4. Impact of Snow Cover Changes on FFD

Among the 102 observations, 47 stations indicated zero years with at least one month of continuous snow cover over the whole hydrological year from 1961 to 2013. At the other 55 stations, the median percentage of years with at least one month of continuous snow cover for all observed years was only 11.2%. At least one month of continuous snow cover was observed at only four stations (3.9%) (Figure 8). These results mean that the snow cover affected the flowering phenology in a limited manner on the QTP. In addition, the trend analysis of snow-cover indices was not explored because most stations showed fewer than 10 years in which there had been continuous snow cover for at least one month.
The observed flowering dates were much later than those of the SCMDs. The flowering dates were 120 days and 143 days later on average than SCMD for early-flowering and mid-to-late-flowering time series, respectively (Figure 9A,B). The SCD varied from 10 to 123 days, with an average of 37 days on QTP (Figure 9C). The ratio of snow-free days to the total number of days during snow-cover duration ranged from 1.3 to 90.6%, with an average of 50.0% (Figure 9D).

Even in the years when continuous snow cover existed, for both early-flowering and mid-to-late-flowering time series, their regressions associating FFD with SCMD and
SCD showed similar responses and indicated no close relationship in general. SCMD can only explain 0.8% and 0.1% of the FFD variation, and SCD can explain 0.8% and 0.0%, for early-flowering and mid-to-late-flowering time series, respectively (Figure 10). These results indicated that continuous snow cover did not affect FFD for early-flowering or mid-to-late-flowering FFD time series.

Figure 10. Regressions associating first flower date with snow cover duration and snow cover melt date for early-flowering (A, B) and mid-to-late-flowering (C, D) species.

Based on the two-way ANOVA analysis for the early-flowering species, site affected FFD significantly ($p < 0.001$); SCD and SCMD did not have a significant effect on FFD, and the interactive effects of site $\times$ SCD and site $\times$ SCMD were not found. For mid-to-late-flowering species, site ($p < 0.001$) and SCD ($p < 0.01$) affected FFD significantly, and no interactive effects of site $\times$ SCD and site $\times$ SCMD were found (Table 3).

Table 3. Two-way ANOVA for the effects of site, snow cover, and their interactions on first flower date. SCD: snow cover duration; SCMD: snow cover melt date. ***: $p < 0.001$; **: $p < 0.01$. d.f. is degree of freedom, and $F$ is the value of $F$-test.

| Functional Group          | Site       | SCD         | Site $\times$ SCD |
|---------------------------|------------|-------------|-------------------|
| Early-flowering           | d.f.       | $F$         | d.f.              | $F$         | d.f. | $F$         |
|                           | 11         | 26.776 ***  | 55                | 1.905       | 47   | 0.419       |
| Mid-to-late-flowering     | 9          | 7.688 ***   | 57                | 2.603 **    | 41   | 0.715       |

| Functional Group          | Site       | SCMD        | Site $\times$ SCMD |
|---------------------------|------------|-------------|---------------------|
| Early-flowering           | d.f.       | $F$         | d.f.              | $F$         | d.f. | $F$         |
|                           | 11         | 13.794 ***  | 91                | 2.054       | 34   | 0.384       |
| Mid-to-late-flowering     | 9          | 6.074 ***   | 92                | 3.302       | 26   | 0.536       |

4. Discussion

4.1. Positive Regression between Flowering Phenology and Precipitation for Early-Flowering Time Series

This study showed that precipitation was positively correlated with FFD, especially in the early-flowering time series. This finding suggests that more precipitation may delay flowering time on the QTP. Because precipitation is the primary source of soil moisture and determines water availability for plant growth [24,25], many previous studies indicated
that more precipitation advanced the onset of flowering [26,52–54], and moisture deficiency usually slowed down phenological events [25,52]. The findings of this study contradict those of previous studies. The QTP is characterized as a semi-arid or arid region [55], and most herbaceous plants existing there are xerophytes, mesophytes, or their transitional types [48]. Therefore, it is unlikely that plant growth and reproduction are stunted by increasing precipitation. Because plant development is governed by thermal time, we hypothesized that the periods of precipitation were accompanied by more clouds and low solar radiation, resulting in lower temperatures that delayed plant development. We analyzed the regression between flowering phenology and precipitation. The significantly positive regression between flowering phenology and precipitation for the early-flowering time series may be statistically significant because increased precipitation is often accompanied by a reduction in temperature.

4.2. Impact of Precipitation on Flowering Phenology on the QTP

As discussed in Section 4.1, the relationship between flowering phenology and precipitation may indicate that higher precipitation is only statistically associated with delayed FFD on the QTP and is not a causal link. These results are consistent with the findings of a weak relationship between precipitation and FFD for both Plantago asiatica and Taraxacum mongolicum [13]. The results were also similar to those found in the alpine mountains and Arctic regions of Europe and North America, where soil moisture plays a less decisive role in flowering phenology [40,56,57]. Although the climatic environment is mainly semi-arid and arid on the QTP, the soil moisture deficiency is not severe because soil moisture can be kept in the frozen soil in winter in a low-temperature environment on the QTP, and available soil moisture can be partly provided by the thawing of the soil in spring and summer [58]. Thus, precipitation might have a weak impact on flowering phenology on the QTP.

Our results differ from those of the controlled experiments on the QTP. Precipitation enhancement advanced the FFD of early-flowering species such as Kobresia pygmaea and Kobresia humilis, but not for mid-to-late-flowering species such as Potentilla bifurca and Lagotis brachystachya [28]. Snow addition advanced the flowering phenology of early-flowering species Kobresia pygmaea, but not of Astragalus rigidulus and Potentilla fruticosa [23]. This inconsistency may be caused by different precipitation magnitudes between the controlled experiments and observational data under natural conditions [59]. Although the soil moisture deficiency is not severe on the QTP, shallow-rooted and early-flowering species are sensitive to soil water stress because of their weak ability to absorb deep soil water [14]. Enhanced precipitation in the controlled experiment was much greater than that under natural conditions over the study period. Thus, it is likely that the addition of water in the controlled experiment removed moisture stress that had inhibited development, thereby advancing the FFD of shallow-rooted species such as Kobresia pygmaea and Kobresia humilis [23,28].

4.3. Impact of Snow Cover on Flowering Phenology on the QTP

The QTP is characterized as an extremely cold region because of its high elevation. However, most of the QTP interior has infrequent snowfall, even in winter, at elevations above 4000 m due to rain shadow and leeward-side orientation caused by large-scale shielding by the Himalaya and Karakoram mountains [60]. Monthly snowfall data in winter (December to February) from 55 weather stations on the QTP from 1971 to 2011 showed that the multi-year average winter snowfall was usually less than 30 mm [61], which is much lower than that in the high-latitude and Arctic regions of Europe and North America, where the low-temperature environment is similar to the QTP [62–64]. Lower and less frequent snowfall leads to a very thin snow cover, and strong winds in winter also hamper snow-cover preservation [34,65,66]. Among the 102 observations, 47 stations indicated no continuous snow cover of one-month duration over the entire hydrological year (Figure 6). Therefore, continuous snow cover, common in tundra ecosystems in high-
latitude and Arctic regions of Europe and North America, is much rarer on the QTP. Due to the absence of snow-cover protection (i.e., provision of a favorable subnivean microclimate for plants), FFD on the QTP may not be influenced greatly by snow cover even in the early-flowering time series.

Even in the years when continuous snow cover existed, SCMD and SCD did not significantly affect FFD, either for early-flowering or mid-to-late-flowering FFD time series on the QTP (Figure 9). This finding may be because the observed flowering dates were much later than the SCMDs (Figure 9A,B). Thus, the SCMD affecting flowering phenology cannot occur on the QTP as it does in the high-latitude and Arctic regions of Europe and North America. In the years when snow cover existed, the SCD was quite short. This is because, with limited winter snowfall of less than 30 mm [61], there can be intermittent snow-free conditions during the snow-cover period on the QTP [34,65,66]. The SCD varied from 10 to 123 days, and the percent of snow-free days during the period of snow cover duration ranged from 1.3 to 90.6% (Figure 9C). Thus, the protection of snow cover on flower reproductive organs was quite limited during the period of snow cover duration and had little impact on flowering phenology on the QTP. In this study, we considered a snow depth of 0.4 cm as the threshold for snow cover. The impact of snow cover may be overestimated on flower phenology because the protection function of snow at 0.4 cm depth is limited. However, even under the condition of an overestimated impact of snow cover on flower phenology, the snow cover did not appear to affect flower phenology.

4.4. Possible Causes of Divergent Flowering Phenology

As discussed above, precipitation may not be a major phenological driver of flowering phenology on the QTP. This suggests that other factors control the divergent flowering phenology of QTP. Dispersive shifting trends have also been reported for flowering phenology in previous studies, explained by other mechanisms associated with photoperiod [67,68], temperature increase in summer [40], and functional traits [69–71].

Sun et al. (2020) showed that the spring green-up date of herbaceous plants on the QTP showed no trend from 1981 to 2017. This observation means that the start time of photoperiod induction for plants on the QTP was stable over the past 30 years. Thus, photoperiod should not affect the primary induction of plant flowering and the corresponding flowering dates on the QTP [1].

Sherry et al. (2007) indicated that delayed FFD of mid-to-late-flowering species might be caused by a temperature increase in summer, which may exceed optimal ranges for reproductive tissues and slow or completely suspend development in these species [40]. However, in alpine environments, plants show strong adaptability to temperature variation, and the range of optimal temperatures for plant development is quite broad at low temperatures [56]. The limited temperature increase of about 1 °C during the period of this study may have little influence on the development of reproductive tissues and corresponding flowering dates on the QTP.

Differences in FFD trends may also be explained by the traits of different functional groups [23,72]. Plant species with a higher specific leaf area (SLA) tend to show a positive relationship with photosynthetic rate and leaf nitrogen concentration, and fast-growing plant species generally consume substantial resources and tend to show a lower leaf dry matter content (LDMC) [73]. The FFD of such species is more sensitive to warming [74]. However, in the present study, this phenomenon was not observed. Grasses with higher SLA and lower LDMC showed delayed FFD, whereas sedges with lower SLA and higher LDMC showed advanced FFD.

Various studies have indicated that warming alters the reproductive phenology of alpine and Arctic plants [13,75,76]. Delayed flowering phenology may be caused by the different impacts of warming temperatures on endodormancy and ecodormancy (wherein warming delays dormancy break with unfulfilled chilling requirements and accelerates bud cell growth) [77]. However, we believe that differences in flowering mechanisms of
different species induced divergence in flowering phenology under global warming on the QTP.

Two types of flowering mechanisms on the QTP can be commonly observed: preformation and vernalization-induced growth of flower organs. Early-flowering species undergo flower preformation in the preceding autumn of the concurrent flowering year or earlier, and thus flowering phenology can start early [56]. Vernalization induces or hastens the development of flowering capacity, taking several weeks of exposure at low temperatures from 0 to about 10 °C [78]; the flower organ only forms in the concurrent flowering year, and the species tend to be mid-to-late-flowering ones. The FFD of preformation-induced early-flowering species on the QTP was mainly controlled by forcing temperature in spring; a reduced number of chilling days was also beneficial for the development and fitness of preformed floral organs, and thus, temperature increase significantly advanced FFD. Retarded vernalization completion under global warming may be responsible for the stable flowering phenology of mid-to-late-flowering species [79].

4.5. Uncertainties and Implications of This Study

This study determined flowering phenological changes based on observation data from the phenology network established by the CMA, not based on controlled experiments. The observations were conducted by multiple technicians, which introduces increased variation into the data, thereby adding an error term to the statistical model. As shown in Figure 2, among the 47 early-flowering time series, 72.3% showed a trend for advance in FFD, but only 31.9% were significant; 71.0% of the mid-late-flowering time series showed a trend for delayed FFD, but only 4.3% of these trends were significant (p < 0.05). All these insignificant trends in FFD may be related to the quality of the observation data to some degree. In addition, the database represents 27 phenological stations that often have incomparably differentiated ecological conditions. However, not a single botanical species connects all 27 phenological stations. Therefore, we do not confirm that the analysis based on a species at a site was reliable enough, but it might be better than small-scale (controlled) studies and should be more reliable than analysis based on a small number of samples. Thus, we analyzed flowering phenological trends and their responses to precipitation based on different functional groups of early-flowering and mid-to-late-flowering species and not on a species at a site.

Species that show advanced flowering in response to climate change may be more competitive in the community because they avoid warmer temperatures and drought later in the growing season [56,80,81], and species that show weak phenological responses are more prone to population decline [81,82]. Thus, the divergent FFD trends in early-flowering and mid-to-late-flowering species may change the species composition and ecosystem services of alpine ecosystems on the QTP. Our results suggest that precipitation, including rainfall and snow cover, was not the major factor affecting flowering phenology in the QTP. These findings can improve the flowering phenology model and help predict the phenological responses of herbaceous plants to climate change in this area. It is important to forecast the changes in the structure and function of the grassland ecosystem on the QTP.

Temperature, rather than precipitation and snow cover, may be the major driver of flowering phenology. Because the rate of warming due to climate change on the QTP is advancing at twice the global average [83,84], the impact of global warming on flowering phenology should be more evident than in other regions. The divergent FFD trends in early-flowering and mid-to-late-flowering species may change the species composition and ecosystem services of alpine ecosystems on the QTP, as discussed above. Field observations of changes in plant species’ population have been conducted in the Three-River Headwater Region on the QTP since the implementation of an ecological conservation and restoration project in 2005. Based on observation data from 2005 to 2018, rapid increases in forbs and decreases in sedges and grasses have been observed after a reduction in human disturbance. Additional observations and experiments are needed to confirm whether the changes in species composition are related to phenological shifts, such as flowering phenology.
Although soil moisture deficiency is not severe on the QTP because available water is also provided by the thawing of the frozen soil in spring and summer [58], dramatic increases in soil temperature continue to lower the active layer of permafrost; thus, soil water infiltration will be enhanced [85], and evapotranspiration will also increase [86] concurrently with warming on the QTP. In the future, precipitation may also become a limiting factor affecting flowering phenology. Thus, it will be crucial to continuously observe and study the relationship between precipitation and flowering phenology on the QTP in the future.

5. Conclusions

Based on ground-observed phenology data from 27 phenological stations from 1983 to 2017, precipitation records at 21 stations from 1980 to 2017, and snow-depth data from 102 stations from 1961 to 2013 on the QTP, this study conducted a comprehensive statistical analysis of the temporal change in flowering phenology and its responses to precipitation and snow cover changes through regression models. We found that the early-flowering FFD time series showed an overall trend for a significant advance in FFD, whereas the mid-to-late-flowering time series indicated no trend. Regressions between FFD and CPP showed a significantly positive relationship with the early-flowering time series. However, because temperature and precipitation are correlated on the QTP, and an increase in precipitation should not hamper plant growth in the semi-arid and arid environment of the QTP, it is likely that the reduced temperature, not the increased precipitation, resulted in the delayed flowering phenology observed in early-flowering time series. Regressions were correlated with FFD together with SCMD and SCD and showed no close relationship. These results indicate that snow cover may not affect flowering phenology, which may be because the plant flowering date is much later than that of snow-cover melting on the QTP. These findings contrast reports that precipitation advanced or delayed flowering phenology based on controlled experiments on the QTP and that snow-cover melting time determined flowering dates of early-flowering species in high latitude and Arctic regions in Europe and North America where the low-temperature environment is similar to the QTP. These findings can improve flowering phenology models, help predict phenological responses of herbaceous plants to climate change, and forecast changes in the structure and function of the grassland ecosystem on the QTP.

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