



Title	Dynamics of flowering phenology of alpine plant communities in response to temperature and snowmelt time: Analysis of a nine-year phenological record collected by citizen volunteers
Author(s)	Kudo, Gaku
Citation	Environmental and Experimental Botany, 170, 103843 <a href="https://doi.org/10.1016/j.envexpbot.2019.103843">https://doi.org/10.1016/j.envexpbot.2019.103843</a>
Issue Date	2020-02
Doc URL	<a href="http://hdl.handle.net/2115/83984">http://hdl.handle.net/2115/83984</a>
Rights	© 2020. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <a href="http://creativecommons.org/licenses/by-nc-nd/4.0/">http://creativecommons.org/licenses/by-nc-nd/4.0/</a>
Rights(URL)	<a href="http://creativecommons.org/licenses/by-nc-nd/4.0/">http://creativecommons.org/licenses/by-nc-nd/4.0/</a>
Type	article (author version)
File Information	KudoEEB2019.103843pdf.pdf



[Instructions for use](#)

Environmental and Experimental Botany 170: 2019.103843

**Dynamics of flowering phenology of alpine plant communities in response to temperature and snowmelt time: Analysis of a nine-year phenological record collected by citizen volunteers**

Gaku Kudo

*Faculty of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan*

E-mail address: [gaku@ees.hokudai.ac.jp](mailto:gaku@ees.hokudai.ac.jp)

Short title: Impacts of climate change on alpine plant phenology

## Abstract

Phenological modification is one of the most serious effects of global warming on ecosystems with clear seasonality, such as alpine ecosystems in mid- to high latitudes. Changes in flowering time and duration in plant communities are likely to influence plant-pollinator interactions. However, the effects of global warming on community-scale phenology have scarcely been studied in alpine ecosystems. I analyzed the flowering records of fellfield and snowbed communities collected over a nine-year period in the Taisetsu Mountains of northern Japan. The flowering structure of alpine communities is composed of a flowering sequence of early-blooming fellfield species (FE), late-blooming fellfield species (FL), and snowbed species. Flowering initiation in FE showed small interannual variation, while peak flowering time was accelerated according to warmer temperature. Both the initiation and peak flowering time of FL depended on heat sum during early summer. The flowering period of fellfield communities was shortened under warmer conditions, and 1 °C warming thought to shorten the major flowering period by 3.8 days. The flowering initiation of snowbed plants strongly depended on snowmelt time, and the peak flowering time further advanced in warmer summers. However, the major flowering period of snowbed communities was independent of snowmelt time and thermal conditions because many snowbed species shifted flowering onset days with little changes in flowering period. As a result, the total flowering period of alpine plant communities was largely determined by snowmelt time, independent of thermal conditions. It is predicted that a 10-day earlier snowmelt will shorten the total flowering season by 4.8 days and a 10-day later snowmelt will extend the total flowering season by 5.8 days. Therefore, snowmelt regime is a major determinant factor of the flowering structure of alpine ecosystems. Clarification of snowmelt dynamics is crucial to predict the global warming impacts on the phenology of alpine ecosystems.

**Keywords:** Alpine plants; Climate change; Flowering phenology; Pollination; Snowbed; Snowmelt time; Temperature.

## 1. Introduction

Phenological modification is one of the most serious impacts of global warming on natural ecosystems, especially those at high latitudes and altitudes (Parmesan, 2006, 2007; Høye et al., 2007; Ovaskainen et al., 2013). Phenological changes may influence not only the fitness of individual species but also population dynamics, migration or local extinction of individual species, and interspecific interactions, resulting in the transformation of community structures (Elzinga et al., 2007). Therefore, not only phenological changes within individual species but also the dynamics of community-scale phenology are important to understand the impacts of global warming on the whole ecosystem. Alpine plant communities are most sensitive to climate change, and there are several studies reporting interannual variations in the flowering phenology of individual species in response to climatic conditions (Molau et al., 2005; Studer et al., 2005; Hoffmann et al., 2010; Hülber et al., 2010). However, little is known about how the phenological structures of whole communities at high latitudes and altitudes respond to climate change (Aldridge et al., 2011; Høye et al., 2013; CaraDonna et al., 2014).

The flowering phenology of alpine plants is largely determined by snowmelt regimes and temperature sum (Inouye and Wielgolaski, 2003; Molau et al., 2005; Iler et al., 2013). Although spring snowmelt is generally accelerated with global warming (IPCC, 2013), there are large year-to-year variations in snowmelt time in alpine regions (Kudo and Hirao, 2006). Therefore, it is important to separate the effects of temperature and snowmelt time to understand the mechanisms of phenological dynamics at the community scale (Iler et al., 2013; Petraglia et al., 2014). Flowering sequences in exposed habitats with little snow cover are mainly regulated by seasonal accumulation of heat sum, while flowering patterns in snowy habitats are strongly determined by snowmelt time (Molau, 1993; Molau et al., 2005; Kudo and Hirao, 2006; Carbognani et al., 2016). Because the factors determining flowering phenology and the sensitivity to each factor vary between species and growing habitats (Hülber et al., 2010), phenological responses to climate change at the community scale may vary depending on species composition and habitat type.

Alpine ecosystems in mid- to high latitudes are composed of exposed fellfield habitat with little snow cover during the winter and snowbed habitat with late snowmelt.

Spatiotemporal patterns of flowering sequences at the regional scale is characterized by a combination of fellfield communities and snowbed communities (Kudo and Hirao, 2006; Hülber et al., 2010). Thus, the whole flowering structure at the regional scale is regulated by the interplay between temperature and snowmelt regimes. Flowering initiation of fellfield communities occurs early in the season, while flowering of snowbed communities often starts in mid-summer due to late snowmelt (Kudo and Hirao, 2006; Kudo, 2016). Because foraging activity of flower visitors is often maximized in the middle of the season, snowbed plants provide major floral resources for pollinators, such as bumblebees and syrphid flies (Kudo, 2016; Mizunaga and Kudo, 2017). A previous study reported that the flowering of snowbed species progressed rapidly in one unusually warm summer in which the snow melted early, resulting in the completion of the flowering season before the peak season of flower visitors (Kudo, 2014). This highlights the increasing risk of phenological mismatch between alpine flowers and pollinators as a result of climate change. Furthermore, if climate change results in earlier flowering, flowers might become more susceptible to frost damage (Inouye, 2008; Rixen et al., 2012). This may result in lower seed-set success and disrupt plant–pollinator mutualism (Inouye, 2000). However, it is not clear how flowering patterns of alpine communities change in response to climatic variation.

In the present study, I analyzed interannual variations in flowering phenology at community scale with reference to temperature and snowmelt time using nine-year flowering phenology records from Daisetsuzan National Park (Taisetsu Mountains), Hokkaido, northern Japan. The long-term monitoring sites were established by the Biodiversity Center of Japan, Ministry of the Environment in 2010 with the aim of monitoring the impacts of global warming on alpine ecosystems. At these sites, flowering phenology was recorded by citizen volunteers. This governmental project, called “Monitoring Sites 1000” ([http://www.biodic.go.jp/index\\_e.html](http://www.biodic.go.jp/index_e.html)), is expected to result in the accumulation of long-term records of flowering phenology. There are two monitoring sites in Daisetsuzan National Park, and each site is composed of a fellfield plot and a snowbed plot (Fig. S1). During the growing season (late May to mid-September), the flowering phenology of all insect-pollinated species in these plots was recorded at 2–3 day

intervals by volunteer researchers. This is the first report analyzing the monitoring records from the past nine years. In this study, only insect-pollinated flowers were targeted because identification of wind-pollinated species, especially grasses and sedges, is difficult for many of citizen volunteers. Thus, this paper reports dynamics of flowering phenology of insect-pollinated alpine plants.

In the present study, I aim to clarify the factors affecting the flowering phenology of alpine plants at the species and community levels, and to predict how flowering patterns are altered by climate change. In this paper, the flowering structure of the plant community is defined as the seasonal transition in the number of species flowering at a given time. Questions of the species-level analysis were as follows: (1) How do flowering traits (onset time and flowering period) vary from year to year among species, reflecting flowering schedule (early and late bloomer) and growing habitat (fellfield and snowbed)? (2) Do the determinant factors of flowering phenology differ among species, reflecting flowering schedule and growing habitat? It is expected that the flowering time of fellfield species depends on temperature, while that of snowbed species is determined primarily by snowmelt time. If earlier flowering increases the risk of frost damage (e.g., Inouye, 2008), conservative flowering phenology against fluctuating weather conditions may be adaptive for early bloomers in fellfield communities in comparison with late bloomers and snowbed plants. Questions of the community-level analysis were as follows: (1) Do flowering patterns in fellfield and snowbed communities vary synchronously or independently between years? (2) How is the landscape phenology of the alpine ecosystem modified by the interplay between warming and snowmelt dynamics? It is expected that flowering in fellfield communities will be accelerated by warming, while the flowering season in snowbed communities will shift directly in response to the dynamics of snowmelt regimes (Kudo and Hirao, 2006).

## 2. Materials and methods

### 2.1. Study sites

Flowering phenology was monitored at two sites: Mt. Aka (43°40' N, 142°56' E) and Mt. Kuro (43°41' N, 142°54' E) in the Taisetsu Mts., Hokkaido. The sites are 5.5 km apart

(Fig. S1). At each site, two monitoring plots, 20 m × 10 m in size, were established to include typical vegetation of both fellfield and snowbed habitat. The fellfield plots are located at 1830 m and 1960 m elevation and the snowbed plots are located at 1970 m and 1890 m elevation at the Mt. Aka site and the Mt. Kuro site, respectively. The timberline in this area is located at around 1500–1600 m elevation. The fellfield plots are exposed, with little snow cover during the winter, while the snowbed plots are covered with thick snow from mid-October to the middle of summer. Air temperature (1.5 m above the ground) was recorded at one-hour intervals throughout the year in the fellfield plot at the Mt. Aka site. The annual mean temperature at 1830 m elevation was  $-2.9^{\circ}\text{C}$ , ranging from  $-17.8^{\circ}\text{C}$  (January) to  $12.5^{\circ}\text{C}$  (July). Snowmelt occurred from early July to early August in the snowbeds of Mt. Aka, and mid-June to mid-July in the snowbeds of Mt. Kuro.

## 2.2. Methods

Throughout growing seasons (late May to mid-September) from 2010 to 2018, the flowering condition of every entomophilous species within the plots was recorded repeatedly. Flowering conditions were recorded by registered citizen volunteers, who were trained to identify flowering species and flowering stage. Because many of the volunteers were not professional researchers, simple and easy-to-use monitoring protocols were crucial for long-term monitoring. Therefore, observations were based on qualitative grading of phenological stage to minimize observation efforts and simplify classification. First, all blooming species in each plot were listed and their flowering situation was visually classified into four stages as follows:

*Stage A*: early flowering stage with many floral buds

*Stage B*: middle flowering stage with few floral buds remaining

*Stage C*: late flowering stage with many withered flowers

*Stage D*: terminal stage with only a few occasional flowers

Furthermore, the amount of flowers of each species within a plot was based on frequency and density as follows:

*Low*: isolated small flowering patches at low density (rare bloomer)

*Medium*: scattered flowering patches at moderate density (medium bloomer)

*High*: large or dense flowering patches (dominant bloomer)

Submitted data records were carefully checked, apparently incorrect records were revised if possible or removed, and overlapping records of same days were combined. After checking all records, there were 35–48 records per year for the Mt. Aka site and 29–44 records per year for the Mt. Kuro site remaining, corresponding to 2.3–3.4 day observation intervals during the growing seasons for each year and site.

The day of flowering onset and end for each species was defined as the first record of *stage A* and the last record of *stage C*, respectively. The flowering period for each species corresponds to the duration from flowering onset day to end day. Although a small amount of sporadic flowering sometimes occurred (recorded as *stage D*) after *stage C*, this stage was not considered part of the flowering period. Data of rare species indicating small amounts of sporadic flowering (class *Low*) were also excluded from the analyses to reduce a bias caused by low frequency. Fellfield species were divided into early bloomers and late bloomers based on the frequency of flowering across the communities over observation years; the anthesis of the former group usually began in June, while that of the latter group usually began in July or August (see results). This distinction was made due to the possibility that the flowering phenology of early bloomers and late bloomers might be affected by different factors. Therefore, species at each site were classified into three groups: fellfield early bloomer (FE), fellfield late bloomer (FL), and snowbed bloomer (S). Furthermore, pollination mode of individual species was classified into three types based on Mizunaga and Kudo (2017) and field observation as follows: bee-pollinated type (bee), fly-pollinated type (fly), and mixed type (bee+fly).

### 2.3. Analysis

#### 2.3.1. Species-level analysis

The thermal requirement of individual species for flowering onset was assessed by comparing the relationship between onset day and degree days (DD), which is the summation of daily mean temperature during a specific period. I calculated both of thawing degree days (TDD) in which a threshold temperature is 0 °C and growing degree days (GDD) in which a threshold temperature is 5 °C (Molau, 1996) for the analyses of flowering events. I constructed generalized linear models (GLMs) with gamma error distribution and log-link function for individual species for which flowering onset day was a response variable, and the degree days (TDD or GDD) for specific months and sites (Mt. Aka or Mt. Kuro) were included as explanatory variables. Similarly, I analyzed the relationships between flowering period, degree days (TDD or GDD), and site for individual species using GLMs. For snowbed species, snowmelt time (deviation from mean snowmelt day at each site) was also included as an explanatory variable. The period of thermal conditions conducive to flowering should be different among species depending on flowering schedule and growing habitat. Thus, I applied degree days for different time periods for FE, FL, and S species. For FE species, the degree days for May and June separately or in combination (May to June) were applied in the GLMs. For FL species, the degree days for separate months (May, June, July) or months in combination (May to July, May to June, June to July) were applied in the GLMs. For S species, the degree days for July and August separately or in combination (July to August) or the degree days for one month after snowmelt were applied in the GLMs. The most effective explanatory variables (including the selection of TDD or GDD) were selected based on AIC (Akaike's information criterion); the model with the lowest AIC values ( $\Delta\text{AIC} > 2$ ) was selected. Using the selected GLMs, I evaluated the phenological sensitivity of individual species to the changes in temperature (1 °C warming) and snowmelt time (10-day earlier or later). Yearly deviations of summer monthly temperature (each of June, July and August) from the mean value across the observation period (2010–2018) ranged from -1.5 °C to +1.9 °C, and those of snowmelt time ranged from -13.2 days to +16.8 days in Mt. Aka and from -16.5 days to +10.5 days in Mt. Kuro. Therefore, the 1 °C warming and the 10-day fluctuation of snowmelt time are realistic climate change in future.

Next, I analyzed how flowering onset time and flowering period of individual species vary between years with reference to the phenological group (FE, FL, S) and the pollination type (bee, fly, bee+fly) by generalized linear mixed models (GLMMs) with gamma error distribution and log-link function. In the GLMM of flowering onset variation, absolute value of the onset time deviation from the mean value in each species in each year was a response variable, phenological group, pollination type and site were explanatory variables, and species nested in each year was included as a random factor. Same explanatory variables and random factors were used for the GLMM of flowering period. Explanatory variables of best fit models were selected based on AIC.

### *2.3.2. Community-level analysis*

Community-scale flowering phenology was quantified by the seasonal transition in the number of flowering species in each phenological group (FE, FL, S), habitat (fellfield, snowbed), and whole site (combination of fellfield and snowbed plots at the Mt. Aka and Mt. Kuro sites). Based on the data records, I plotted the number of flowering species in the three groups on each observation day throughout the season in each year and fitted an exponential function of time with a quadratic term as follows:

$$y = \exp(ax^2 + bx + c)$$

in which  $y$  is the number of species at flowering,  $x$  is the day number from May 1, and  $a$ – $c$  are coefficients. Using the obtained equation, I estimated the beginning of the major flowering season, flowering peak time, and the major flowering period of individual groups (Fig. 1). The beginning (or ending) of the major flowering season was defined as the day of the year on which the cumulative number of species at flowering (or post-flowering) reached 50% of all species flowering in that year. The period from the beginning of FE group flowering to the end of FL group flowering was defined as the major flowering period of the fellfield community, while the period from the beginning to the end of S group flowering was defined as the major flowering period of the snowbed community. The total flowering period at each site was expressed as the period from the

beginning of FE group flowering to the end of S group flowering. I used the 50% threshold mentioned above to mark the beginning and end of the flowering season in order to exclude the effects of the earliest and/or latest flowering species.

Relationships between flowering phenology (beginning, peak, and total period) and climatic conditions (TDD or GDD and snowmelt time) were analyzed for each group using GLMs with gamma error distribution and log-link function, in which each phenological event was a response variable and climatic factors and site were explanatory variables. For the GLMs, the degree days (TDD or GDD) term for each phenological group or each habitat type was the same as for the species-level analyses. A best-fit model was selected based on AIC values. Based on the selected GLMs, I evaluated how the flowering pattern of alpine plant communities is affected by global warming (1 °C warming) and fluctuations in snowmelt time (10-day earlier or later). All statistical analyses were conducted using R ver. 3.4.4 (R Development Core Team, 2017).

### 3. Results

#### 3.1. Site conditions

The major growing season was from late May to the middle of September. Air temperature increased at the rate of 5 °C per month from May to July, remained around 11–14 °C during July and August, and decreased rapidly in September (Table S1). Monthly mean temperatures fluctuated by 3–4 °C between years. The timing of snowmelt in the snowbed plots varied greatly between years. It started in late June to late July at Mt. Aka, and in mid-June to early July in Mt. Kuro. The period from the start to the end of snowmelt within plots was 19–27 days at Mt. Aka, while it took only 6–13 days at Mt. Kuro. This difference reflects the topographic features of individual plots; the snowbed plot at Mt. Aka was located on a steep slope, while that at Mt. Kuro was located on a gentle slope.

Snowmelt time at each site was negatively correlated with April temperature with marginal significance ( $r = -0.63, p = 0.068$  at Mt. Aka;  $r = -0.66, p = 0.052$  at Mt. Kuro). However, there was no significant correlation in snowmelt time between Mt. Aka and Mt. Kuro over the nine-year study period ( $r = 0.32, p > 0.10$ ), indicating that there was no

synchronization in snowmelt patterns between the snowbeds although observation years were limited ( $n = 9$ ).

### 3.2. Species responses

During the monitoring period (2010–2018), the flowering of 35 species was recorded throughout the plots, and four species occurred in both the fellfield and snowbed plots (Table 1). At Mt. Aka, 15 species were recorded in the fellfield plot and 16 species in the snowbed plot. At Mt. Kuro, 16 species were recorded in the fellfield plot and 13 species in the snowbed plot.

In the fellfield plots, the flowering of early bloomers started in the beginning of June and the flowering other species occurred continuously until late July (Fig. 2A). The latest bloomer in the fellfield plot (*Gentiana algida*) flowered in early August at Mt. Aka. Among 19 fellfield species, eight were classified as FE, and 11 were classified as FL (Table 1). In the snowbed plots, the flowering of individual species started between mid-July and mid-August at Mt. Aka, and between early July and mid-August at Mt. Kuro (Fig. 2A). Year-to-year variation in flowering onset time was smallest in FE species and largest in S species (Appendix Table S2), indicating that the flowering onset time of early bloomers was relatively stable. There was no difference in the variation in flowering onset time among pollination types.

The flowering period within plots varied greatly among species (ranging from 9 to 41 days; Fig. 2B). There was no significant difference in flowering period between FE, FL, and S species, but the flowering period of S species at Mt. Kuro was significantly shorter than that at Mt. Aka (Appendix Table S3). This is because the slower progress of snowmelt within the plot of the Mt. Aka site extended the flowering period of S species relative to that of the Mt. Kuro site. Among pollination types, fly-pollinated species showed longer flowering periods than bee-pollinated species.

The GLM analyses revealed that the flowering onset time of six of eight FE species was negatively affected by a heat sum of May or June temperatures, and that the flowering periods of five FE species were negatively affected by June or July temperatures (Appendix Table S4). Also, for FL plants, the flowering onset times of eight of ten species

were negatively affected by a heat sum of June temperatures, while the effects of temperature on flowering period were less clear, i.e., two species were negatively but two species were positively influenced by TDD or GDD (Appendix Table S4). These results indicate that the flowering onset of many (but not all) fellfield plants might be accelerated under warm conditions, although this change in flowering period was not consistent. Largely, the flowering period of early bloomers tended to shorten under warm conditions, but there was no clear trend among late bloomers.

As for snowbed species, the flowering onset time of 16 of 17 species responded positively to snowmelt time, while GDD after snowmelt influenced the onset time of only five species (Table S4). Thus, the flowering onset of snowbed plants was mainly determined by snowmelt regimes. In contrast, the response of the flowering period varied greatly: the flowering period of eight species shortened under warm conditions, that of three species shortened due to earlier snowmelt, and that of one species extended due to earlier snowmelt.

The expected changes in the flowering phenology of individual species based on the GLM results are shown in Figure 3, presuming +1 °C of warming and a 10-day earlier snowmelt time. Of 18 fellfield species, the flowering onset of 13 species was accelerated by 0.4–7.1 days due to the 1 °C of warming. The responses of early bloomers and very late bloomers to the warming were small, while mid-season bloomers were most sensitive to the warming. In contrast, none of 17 snowbed species accelerated the flowering onset and five species was delayed under warm conditions if snowmelt time did not change. When early snowmelt was combined with warming, however, the flowering onset of all snowbed species but one species was accelerated by 2.2–10.8 days. The flowering period of seven fellfield species was shortened by 2.4–7.1 days and that of four species was extended by 1.0–2.7 days due to the 1 °C of warming. Among the snowbed species, the flowering period of five species was shortened by 0.4–6.4 days due to the warming without changes in snowmelt time. When early snowmelt was combined with warming, the flowering periods of five species were shortened by 1.6–11.5 days. In summary, the flowering onset time of many fellfield species depended on the heat sum of a specific period, while that of

snowbed species strictly depended on snowmelt time. The flowering periods of about one-third of all studied species decreased as a result of warming.

### *3.3. Community responses*

Year-to-year fluctuations of the flowering patterns, i.e., temporal dynamics of the number of flowering species, of species groups (FE, FL, S) are shown in Figure 4.

Interannual variation in the flowering patterns was the smallest in FE type and the largest in S type. The peak flowering day was June 27 ( $\pm 3.5$  SD days) in FE, July 26 ( $\pm 5.4$  days) in FL, and August 15 ( $\pm 8.7$  days) in S at the Mt. Aka site, and June 21 ( $\pm 3.7$  days) in FE, July 23 ( $\pm 5.2$  days) in FL, and August 2 ( $\pm 7.7$  days) at the Mt. Kuro site. Because of the earlier snowmelt, flowering of snowbed community started about 10 days earlier at Mt. Kuro than at Mt. Aka. Total major flowering period from the beginning in FE type to the ending in S type was  $110 \pm 8.2$  days at Mt. Aka, and  $95 \pm 7.3$  days at Mt. Kuro.

The GLMs conducted for FE type revealed that the beginning of major flowering was marginally related to TDD of May ( $t = -1.76, P = 0.098$ ) and June ( $t = -1.81, P = 0.090$ ), while the peak flowering period was accelerated with increasing TDD of May–June ( $t = -4.05, P = 0.001$ ; Appendix Table S5). The beginning of major flowering in FL type was accelerated with increasing TDD of June ( $t = -8.90, P < 0.0001$ ), and the peak flowering period was accelerated with increasing TDD of May ( $t = -2.16, P = 0.048$ ) and June ( $t = -8.05, P < 0.0001$ ; Appendix Table S5). The beginning of major flowering in the snowbed community positively depended on snowmelt time ( $t = 11.75, P < 0.0001$ ) but it was independent of TDD after snowmelt. The peak flowering period also positively depended on snowmelt time ( $t = 13.14, P < 0.0001$ ) and negatively related to TDD of August ( $t = -3.08, P = 0.008$ ; Appendix Table S5).

The major flowering period of the fellfield community was negatively related to TDD of May–June ( $t = -2.64, P = 0.018$ ), while that of the snowbed community was independent of both snowmelt time and heat sum (Appendix Table S5). Total major flowering period across the fellfield and snowbed communities within a site depended on snowmelt time ( $t = 2.40, P = 0.030$ ; Appendix Table S5).

Based on the GLMs results, it was estimated that the 1 °C warming might shorten the major flowering period of fellfield community (present period = 65.8 days) by 3.8 days, while the major flowering period of snowbed community (present period = 35.9 days) did not change (Fig. 5). Major flowering season across the fellfield and snowbed communities within a site (present period = 87.4 days) was independent of heat sum, but it was shortened by 4.8 days when snowmelt time was accelerated by 10 days. In contrast, the 10-day later snowmelt extended the total flowering season by 5.8 days. The overlapping period of major flowering season between the fellfield and snowbed communities (present period = 18.1 days) was slightly increased under the 1 °C warming combined with a 10-day earlier snowmelt (+1.0 day), while highly decreased under the 1 °C warming combined with a 10-day later snowmelt (-9.6 days).

## 4. Discussion

### 4.1. Species responses

This study demonstrated that phenological responses and determinant factors of flowering pattern of individual species varies between the phenological groups. Flowering time of fellfield species was largely determined by heat sum, while that of snowbed species was strongly determined by snowmelt time. However, flowering of some fellfield species was independent of temperature, i.e., *Arctous alpina*, *Arcterica nana*, *Loiseleuria procumbens*, and *Potentilla matsumure* showed small interannual variation in flowering onset time. The daily minimum temperature early in the season (late May to early June) often falls below zero. Because cold tolerance of flowers and young leaves is usually lower than that of mature leaves and buds (Ladinig et al., 2013; Neuner, 2014), too early flowering increases the risk of frost damage (Inouye, 2000, 2008; Rixen et al., 2012). Early-blooming species in high latitudes and altitudes have commonly preformed floral buds (in the former season), and it enables to open flowers as soon as weather conditions permit during the next season (Bliss, 1971). A conservative flowering habit independent of spring temperature may be adaptive for early bloomers to reduce frost damage. A similar trend was reported in a subarctic plant community in Canada in which early-blooming

species tended to show smaller variation in onset time than late-blooming species (Lessard-Therrien, 2014).

Mid-season bloomers of fellfield plants, flowering in late June to mid-July, were most sensitive to June temperature. A 1 °C warming caused the flowering onset of these species to advance by 4–5 days. This prediction is comparable to the previous report in high arctic (3.9 days/degree) and mid-latitude subalpine plants (6.6 days/degree; Iler et al., 2013).

During the nine-year observation period, June temperatures fluctuated between 6.1 and 10.8 °C. These large interannual variations strongly affect the flowering phenology of these species. In a warm summer, the flowering periods of many species were shortened. In contrast, a few late bloomers (*Saussurea yanagisawae* and *Gentiana algida*, which flower after late July) showed little response to heat sum. Flowering onset of these species might be determined by photoperiod (Keller and Körner, 2003; Hülber et al., 2010).

Flowering onset time of almost all snowbed species was simply determined by snowmelt time and thermal conditions after snowmelt did not affect the pre-flowering periods. In contrast to this study, Petraglia et al. (2014) reported that pre-flowering periods after snowmelt were extended when snowmelt was earlier in the Rhaetian Alps, indicating that flowering progress of snowbed species depended on temperature. This discrepancy might be because snowmelt in my snowbed plots occurred in the middle of summer (July and August), when temperature increased high enough (Table S1), resulting in no temperature limitation for development. Therefore, ecological impacts of snowmelt time on plant fitness should vary within a growing season (Wipe et al., 2006).

In contrast to the flowering onset time, responses of flowering period to warming and earlier snowmelt varied among species. Because the analysis of this study was based on the rank data of phenological stage, the year-to-year fluctuation of floral density within plots might influence the variation in flowering period, i.e., population size effect on phenology (Miller-Rushing et al., 2008). Nevertheless, about one-third of species were expected to decrease the flowering period under warm conditions and several snowbed species were expected to decrease the flowering period by earlier snowmelt. It means that the rapid snowmelt under warm conditions tend to shorten the flowering period of some, but not all species.

Although the variation in flowering onset time across years was independent on pollination type, flowering period was significantly longer in fly-pollinated species in comparison with bee-pollinated species. Longer flowering period in fly-pollinated species was reported also in our previous studies (Kudo, 2016; Mizunaga and Kudo, 2017) reflecting longer active season of dipteran pollinators in comparison with bees. Therefore, pollination type can be a significant factor affecting flowering phenology of alpine plants.

#### *4.2. Community responses*

Reflecting the flowering patterns of individual species, flowering patterns at community scale varied differently between the fellfield and snowbed communities. In the fellfield community, the starting point of flowering season was relatively stable, but the subsequent flowering sequence was accelerated with increasing temperature, resulting in shorter flowering period at community scale. This pattern was different from the subalpine community in the Rocky Mountains, where early bloomers tended to advance the flowering time more than late bloomers under warm conditions, resulting in longer flowering period of the community (CaraDonna et al., 2014). As mentioned before, conservative flowering in the early bloomers of fellfield species may reflect a strategy to avoid the risk of frost damage. On the other hand, flowering dynamics of snowbed communities was determined by snowmelt regime in which flowering initiation strongly depended on snowmelt time, while major flowering period was stable irrespective of snowmelt time and thermal conditions after snowmelt. It means that flowering pattern of snowbed communities shift uniformly responding to snowmelt time.

Because the flowering onset time of the fellfield community is stable and the ending time of the snowbed community was determined by snowmelt time, total length of flowering season is governed by snowmelt regime in the alpine ecosystem. However, the component of co-flowering species within the flowering season varies depending on the interplay between thermal condition and snowmelt pattern. When warm climate advances snowmelt time, the flowering overlap between fellfield community and snowbed community increases, resulting in a shorter flowering season with high flowering overlap among species. Advanced and shorter flowering season may influence the abundance and

diversity of flower visitors due to the limitation of floral availability (Memmott et al., 2007; Hegland et al., 2009; Høye et al., 2013). Bumblebees are the most important pollinators in the alpine ecosystems, and the activity of worker bees is maximized in the middle of summer from late July to August (Mizunaga and Kudo, 2017). Because major floral resources of worker bees are snowbed flowers, advanced and shortened flowering season of snowbed communities cause negative effects on bumblebees. Actually, advanced flowering phenology of snowbed communities in an unusually warm summer (2012) caused a serious phenological mismatch between alpine flowers and bumblebees in which major flowering season had finished when the foraging activity of worker bees was highest (Kudo, 2014). On the other hand, when warm summer accompanies late snowmelt, the flowering overlap between fellfield community and snowbed community decreases. This may cause a bimodal flowering pattern with a low number of flowering species in the middle of summer (Aldridge et al., 2011). This situation causes the temporal shortage of floral resources for many flower visitors.

#### *4.3. Future perspectives*

In summary, the interplay between heat sum and snowmelt dynamics is a key issue for the prediction of the impacts of global warming on the phenological structure of alpine ecosystems. Long-term climate records from the Taisetsu Mountains revealed that the summer temperature (June–August) has increased at a rate of 0.32 °C/decade over the last 38 years (1980–2018), and the snowmelt time at a snowbed located 13 km south of Mt. Aka has become earlier at a rate of 2.8 day/decade over the last 30 years (G. Kudo, unpublished data). Similar warming and snowmelt trends have been reported in the Rocky Mountains (CaraDonna et al., 2014) and the Swiss Alps (Rixen et al., 2012). Thus, warmer climate and earlier snowmelt are common trends in mid-latitude mountain ecosystems in the Northern Hemisphere. Although global warming generally tends to accelerate snowmelt time in alpine and arctic regions (Iler et al., 2013), actual snowmelt time is highly variable from year to year. Also in the present study, there was a large difference in snowmelt days during the observation years (about 30 days). Furthermore, the interannual patterns of snowmelt did not synchronize between snowbed sites within a local area. Thus,

it is difficult to predict a consistent relationship between temperature and snowmelt dynamics in the alpine ecosystems. It is predicted that global warming will increase not only mean temperature but also the interannual variability of temperature and precipitation (IPCC, 2013), which may accelerate the interannual fluctuation of phenological structure.

Finally, the present study demonstrated that the accumulation of phenology records by volunteer activity is enough for the assessment of phenological change in local alpine ecosystem. Diversity of alpine vegetation reflects local variations in topographic, geographic, and climatic factors in addition to the local species composition including a lot of endemic species. Therefore, the sensitivity of phenological structure to climate change must be strongly specific to the locality. The protocol of phenological survey in the Monitoring Sites 1000 project is based on the simple and easy-to-use method, and it is applicable to other alpine sites and regions. The establishment of a phenological network is very useful for a comparative assessment of climate change impacts on alpine ecosystems.

### Acknowledgments

I would like to thank K. Yokosuka, H. Sumiyoshi, T. Imoto, and all volunteer members for their great efforts and cooperation for field survey and aggregation of data. This study was conducted using the Monitoring Sites 1000 Alpine Zone database of Biodiversity Center of Japan, and supported by funding from JSPS KAKENHI (15H02641, 17K07551).

## References

- Aldridge, G., Inouye, D.W., Forrest, J.R.K., Barr, W.A., Miller-Rushing, A.J., 2011. Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climatic change. *J. Ecol.* 99, 905–913.
- Bliss, L. C., 1971. Arctic and alpine plant life cycles. *Annu. Rev. Ecol. Syst.* 2, 405–438.
- CaraDonna, P.J., Iler, A.M., Inouye, D.W., 2014. Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl. Acad. Sci. U. S. A.* 111, 4916–4921.
- Carbognani, M., Bernareggi, G., Perucco, F., Tomaselli, M., Petraglia, A., 2016. Micro-climatic controls and warming effects on flowering time in alpine snowbeds. *Oecologia* 182, 573–585.
- Elzinga, J.A., Atlan, A., Biere, A., Gigord, L., Weis, A.E., Bernasconi, G., 2007. Time after time: flowering phenology and biotic interactions. *Trends. Ecol. Evol.* 22, 432–439.
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjerknes, A.-L., Totland, Ø., 2009. How does climate warming affect plant–pollinator interactions? *Ecol. Lett.* 12, 184–195.
- Hoffmann, A.A., Camac, J.S., Williams, R.J., Papst, W., Jarrad, F.C., Wahren, C.H., 2010. Phenological changes in six Australian subalpine plants in response to experimental warming and year-to-year variation. *J. Ecol.* 98, 927–937.
- Høye, T.T., Post, E., Meltofte, H., Schmidt, N.M., Forchhammer, M.C. 2007. Rapid advancement of spring in the High Arctic. *Curr. Biol.* 17: R449–R451.
- Høye, T.T., Post, E., Schmidt, N.M., Trøjelsgaard, K., Forchhammer M.C., 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nat. Clim. Change* 3, 759–763.
- Hülber, K., Winkler, M., Grabherr, G., 2010. Intraseasonal climate and habitat-specific variability controls the flowering phenology of high alpine plant species. *Funct. Ecol.* 24, 245–252.
- Iler, A.M., Høye, T.T., Inouye, D.W., Schmidt, N.M., 2013. Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Phil. Trans. R. Soc. B* 368, 20120489.

- Inouye, D.W., 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecol. Lett.* 3, 457–463.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89, 353–362.
- Inouye, D.W., Wielgolaski, F.E., 2003. Phenology of high-altitude climates, in: Schwartz, M.D. (Ed.), *Phenology: An integrative environmental science*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp.195–214.
- IPCC, 2013. *Climate change 2013: The Physical Science Basis; Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. New York, Cambridge University Press. 1535 pp.
- Keller, F., Körner, C., 2003. The role of photoperiodism in alpine plant development. *Arct. Antarct. Alp. Res.* 35, 361–368.
- Kudo, G., 2014. Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecol. Res.* 29, 571–581.
- Kudo, G., 2016. Landscape structure of flowering phenology in alpine ecosystems: significance of plant–pollinator interactions and evolutionary aspects, in: Kudo, G. (Ed.), *Structure and Function of Mountain Ecosystems in Japan*. Springer Japan, Tokyo, pp.41–62.
- Kudo, G., Hirao, A.S., 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Population Ecol.* 48, 49–58.
- Ladinig, U., Hacker, J., Neuner, G., Wagner, J., 2013. How endangered is sexual reproduction of high-mountain plants by summer frost? Frost resistance, frequency of frost events and risk assessment. *Oecologia* 171, 743–760.
- Lessard-Therrien, M., Bolmgren, K., Davies, T.J., 2014. Predicting flowering phenology in a subarctic plant community. *Botany* 92, 749–756.
- Memmott, J., Craze, P., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10, 710–717.

- Miller-Rushing, A.J., Inouye, D.W., Primack, R.B., 2008. How well do first flowering dates measure plant responses to climate change? The effects of population size and sampling frequency. *J. Ecol.* 96, 1289–1296.
- Mizunaga, Y., Kudo, G., 2017. A linkage between flowering phenology and fruit-set success of alpine plant communities with reference to the seasonality and pollination effectiveness of bees and flies. *Oecologia* 185, 453–464.
- Molau, U., 1993. Relationships between flowering phenology and life history strategies in tundra plants. *Arct. Alp. Res.* 25, 391–402.
- Molau, U., 1996. ITEX climate stations, in: Molau, U. and Mølgaard, P. (eds.), ITEX manual, 2nd ed., Danish Polar Center, Copenhagen, Denmark, pp.6–10.
- Molau, U., Nordenhäll, U., Eriksen, B., 2005. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *Am. J. Bot.* 92, 422–431.
- Neuner, G., 2014. Frost resistance in alpine woody plants. *Front. Plant Sci.* 5, Article 654.
- Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., del Mar Delgado, M., 2013. Community-level phenological response to climate change. *Proc. Natl. Acad. Sci. U. S. A.* 110, 13434–13439.
- Parmesan, C., 2006. Ecological and evolutionary response to recent climate change. *Annu. Rev. Ecol. Syst.* 37, 637–669.
- Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* 13, 1860–1872.
- Petraglia, A., Tomaselli, M., Bon, M.P., Delnevo, N., Chiari, G., Carbognani, M., 2014. Responses of flowering phenology of snowbed plants to an experimentally imposed extreme advanced snowmelt. *Plant Ecol.* 215, 759–768.
- R Development Core Team, 2017. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna.
- Rixen, C., Dawes, M.D., Wipf, S., Hagedorn, F., 2012. Evidence of enhanced freezing damage in treeline plants during six years of CO<sub>2</sub> enrichment and soil warming. *Oikos* 121, 1532–1543.

- Studer, S., Appenzeller, C., Defila, C., 2005. Inter-annual variability and decadal trends in alpine spring phenology: a multivariate analysis approach. *Climatic Change* 73, 395–414.
- Wipf, S., Rixen, C., Mulder, C. P., 2006. Advanced snowmelt causes shift towards positive neighbour interactions in a subarctic tundra community. *Glob. Change Biol.* 12, 1496–1506.

### Figure caption

**Fig. 1.** (A) An example of flowering patterns at the Mt. Aka site (in 2017), composed of a fellfield plot and a snowbed plot. Species are classified into three types: fellfield early bloomer (FE), fellfield late bloomer (FL), and snowbed plants (S). Refer to Table 1 for species code. (B) Seasonal patterns in the number of flowering species of individual groups (FE, FL, S) fitted to the exponential model. Filled circles indicate the beginning of major flowering season and open circles indicate the peak flowering time of each group.

**Fig. 2.** (A) Sequences of flowering onset time and (B) flowering period of individual species in the fellfield plot (FE, FL) and the snowbed plot (S) at each site (Mt. Aka, Mt. Kuro). Mean  $\pm$  SD of the nine-year record. Refer to Table 1 for species code.

**Fig. 3.** Predicted responses of (A) flowering onset time and (B) flowering period of major species to a 1 °C warming (circles and solid lines) and a 10-day earlier snowmelt time (squares and broken lines) in the fellfield (upper) and snowbed habitat (lower). Species in each habitat are arranged in order of flowering occurrence. Black circles: early bloomer of fellfield plants, gray circles: late bloomer of fellfield plants. Refer to Table 1 for species code.

**Fig. 4.** Year-to-year variations in community-scale flowering phenology of fellfield early bloomer (FE, black lines), fellfield late bloomer (FL, gray lines), and snowbed plants (S, broken lines) during the nine-year observation. The length of major flowering period and peak flowering day of each group are indicated (mean  $\pm$  SD).

**Fig. 5.** Prediction of the changes in flowering phenology of fellfield early bloomer (FE, black lines), fellfield late bloomer (FL, gray lines), and snowbed plants (S, broken lines) based on the three climate change scenarios: (A) 1 °C warming with no change in snowmelt time, (B) 1 °C warming and a 10-day earlier snowmelt, and (C) 1 °C warming and a 10-day later snowmelt. Thin lines indicate average situations during the nine-year monitoring. The length of the major flowering period of fellfield community, snowbed community, and whole community is indicated (mean  $\pm$  SD) with a changing value under each climate change scenario in the parenthesis.

**Table 1.** List of flowering species observed in the plots. Every species is classified into three phenological groups; FE: early bloomers of fellfield species, FL: late bloomers of fellfield species, S: snowbed species. Species code is arranged in order of flowering occurrence in each of the fellfield and snowbed habitats. Pollination type of individual species is classified into bee-pollinated plants (bee), fly-pollinated plants (fly), and mixture of bee- and fly-pollinated plants (bee+fly).

Species	Family	Sp. code	Pheno. group	Polli. type	Site
<b>Fellfield species</b>					
<i>Arctous alpina</i>	Ericaceae	F01	FE	bee	Aka, Kuro
<i>Arcterica nana</i>	Ericaceae	F02	FE	bee	Kuro
<i>Loiseleuria procumbens</i>	Ericaceae	F03	FE	bee+fly	Aka, Kuro
<i>Potentilla matsumurae</i>	Rosaceae	F04	FE	fly	Aka, Kuro
<i>Diapensia lapponica</i> ssp. <i>ovovata</i>	Diapensiaceae	F05	FE	bee+fly	Aka, Kuro
<i>Potentilla miyabei</i>	Rosaceae	F06	FE	fly	Aka, Kuro
<i>Vaccinium uliginosum</i> var. <i>alpinum</i>	Ericaceae	F07	FE	bee	Aka, Kuro
<i>Dicentra peregrina</i>	Papaveraceae	F08	FE	bee	Aka, Kuro*
<i>Patrinia sibirica</i>	Valerianaceae	F09	FL	bee+fly	Aka, Kuro
<i>Pedicularis oederi</i> var. <i>heteroglossa</i>	Orobanchaceae	F10	FL	bee	Aka
<i>Spiraea betulifolia</i> var. <i>aemiliana</i>	Rosaceae	F11	FL	bee+fly	Aka, Kuro
<i>Therorhodion camtschaticum</i>	Ericaceae	F12	FL	bee+fly	Kuro
<i>Pennellianthus frutescens</i>	Plantaginaceae	F13	FL	bee+fly	Kuro
<i>Tilingia ajanensis</i>	Apiaceae	F14	FL	fly	Aka, Kuro
<i>Bryanthus gmelinii</i>	Ericaceae	F15	FL	bee+fly	Aka, Kuro
<i>Bistorta vivipara</i>	Polygonaceae	F16	FL	fly	Aka*
<i>Campanula lasiocarpa</i>	Campanulaceae	F17	FL	bee+fly	Kuro
<i>Saussurea yanagisawae</i>	Asteraceae	F18	FL	bee+fly	Aka, Kuro*
<i>Gentiana algida</i>	Gentianaceae	F19	FL	bee	Aka
<b>Snowbed species</b>					
<i>Harrimanella stelleriana</i>	Ericaceae	S01	S	fly	Aka, Kuro
<i>Loiseleuria procumbens</i>	Ericaceae	S02	S	bee+fly	Kuro
<i>Primula cuneifolia</i>	Primulaceae	S03	S	bee	Aka, Kuro
<i>Potentilla matsumurae</i>	Rosaceae	S04	S	fly	Aka, Kuro
<i>Rhododendron aureum</i>	Ericaceae	S05	S	bee+fly	Aka, Kuro
<i>Sieversia pentapetala</i>	Rosaceae	S06	S	bee+fly	Aka, Kuro
<i>Phyllodoce caerulea</i> var. <i>yezoensis</i>	Ericaceae	S07	S	bee	Aka, Kuro
<i>Veronica stelleri</i> var. <i>longistyla</i>	Plantaginaceae	S08	S	bee+fly	Aka
<i>Pedicularis chamissonis</i> var. <i>japonica</i>	Orobanchaceae	S09	S	bee	Aka, Kuro
<i>Cassiope lycopodioides</i>	Ericaceae	S10	S	bee	Kuro*
<i>Peucedanum multivittatum</i>	Apiaceae	S11	S	fly	Aka
<i>Phyllodoce aleutica</i>	Ericaceae	S12	S	bee	Aka
<i>Tilingia ajanensis</i>	Apiaceae	S13	S	fly	Kuro
<i>Gentiana nipponica</i>	Gentianaceae	S14	S	bee+fly	Aka, Kuro
<i>Cirsium kamtschaticum</i>	Asteraceae	S15	S	bee	Aka
<i>Solidago virgaurea</i> ssp. <i>leiocarpa</i>	Asteraceae	S16	S	fly	Aka, Kuro
<i>Sanguisorba stipulata</i>	Rosaceae	S17	S	bee+fly	Aka
<i>Campanula lasiocarpa</i>	Campanulaceae	S18	S	bee+fly	Kuro
<i>Saxifraga merkii</i>	Saxifragaceae	S19	S	fly	Aka*
<i>Parnassia palustris</i>	Celastraceae	S20	S	bee+fly	Aka*

\* Rare species in the plots that are excluded from the analyses.

Figure 1 (Kudo)

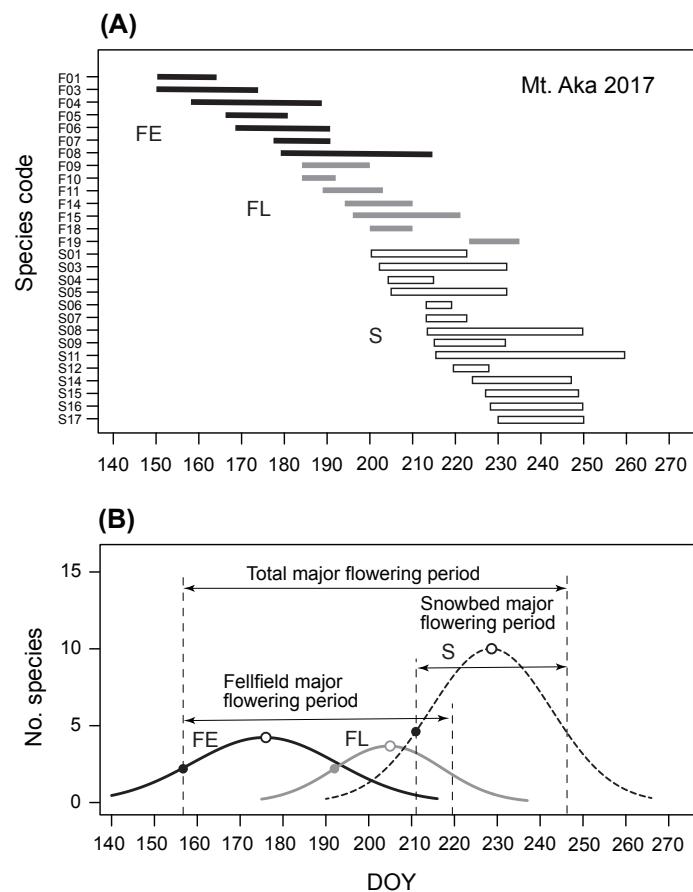


Figure 2 (Kudo)

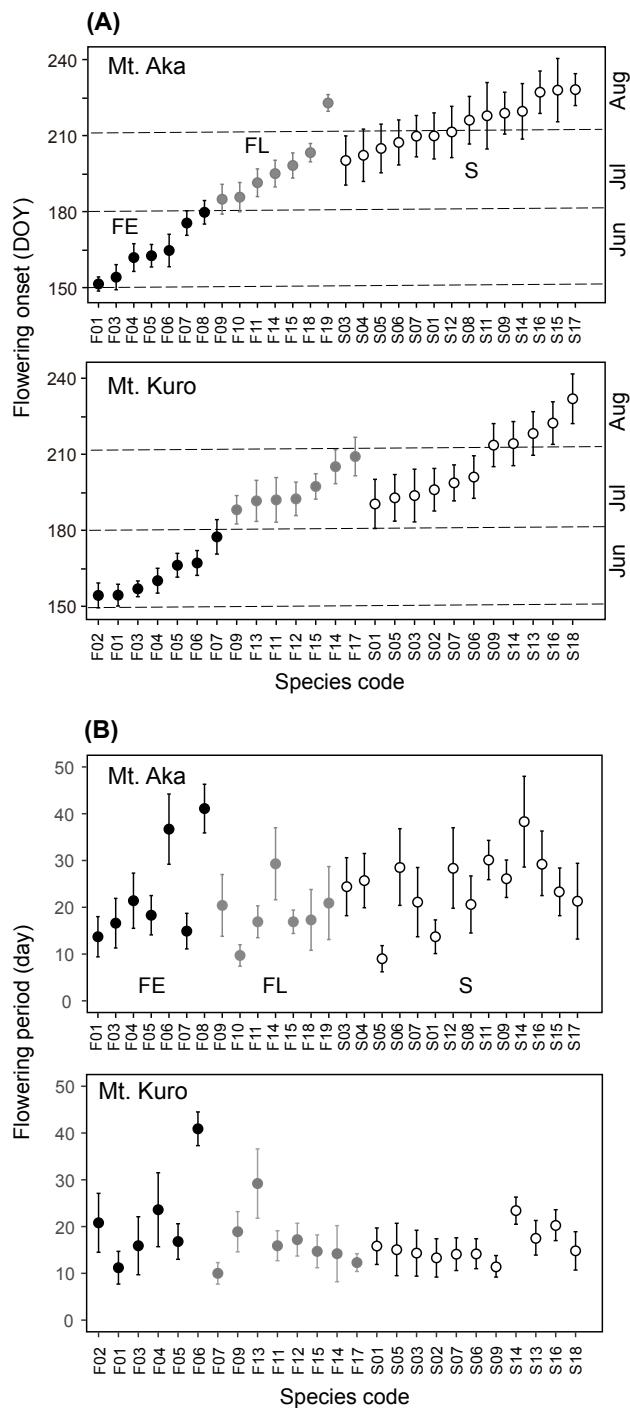


Figure 3 (Kudo)

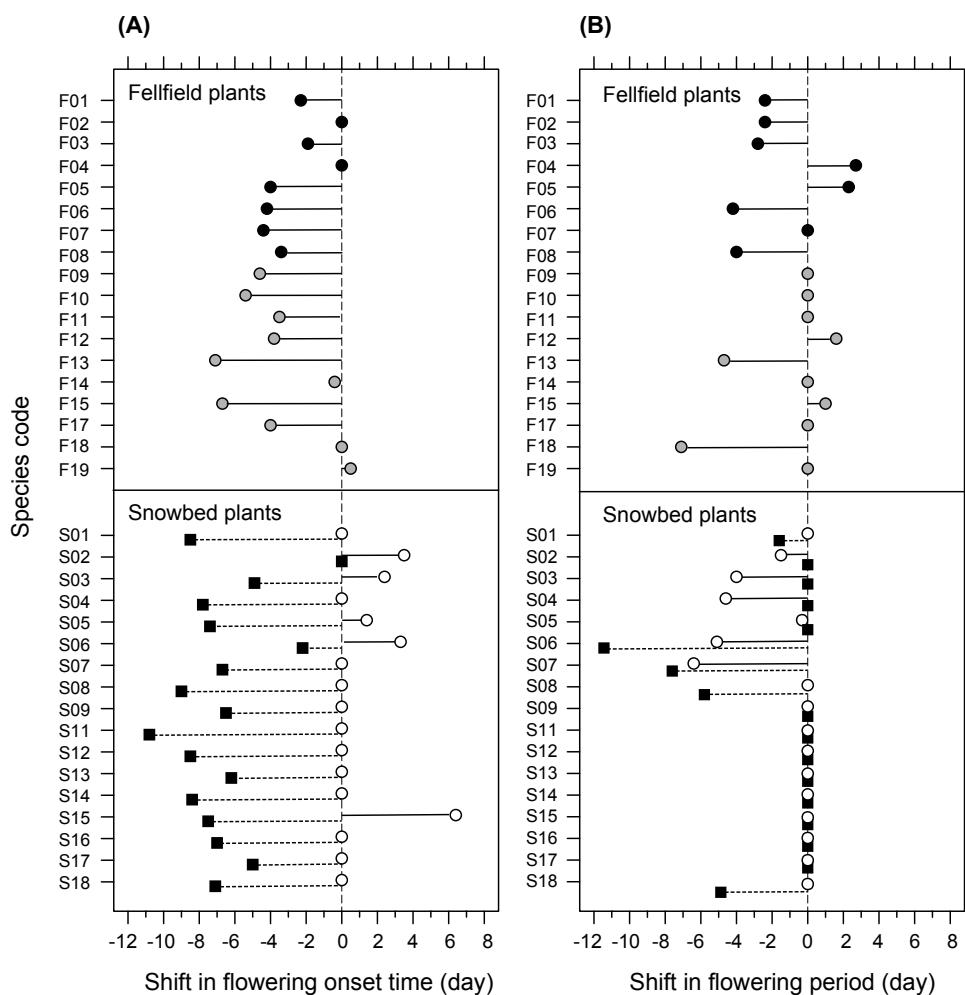


Figure 4 (Kudo)

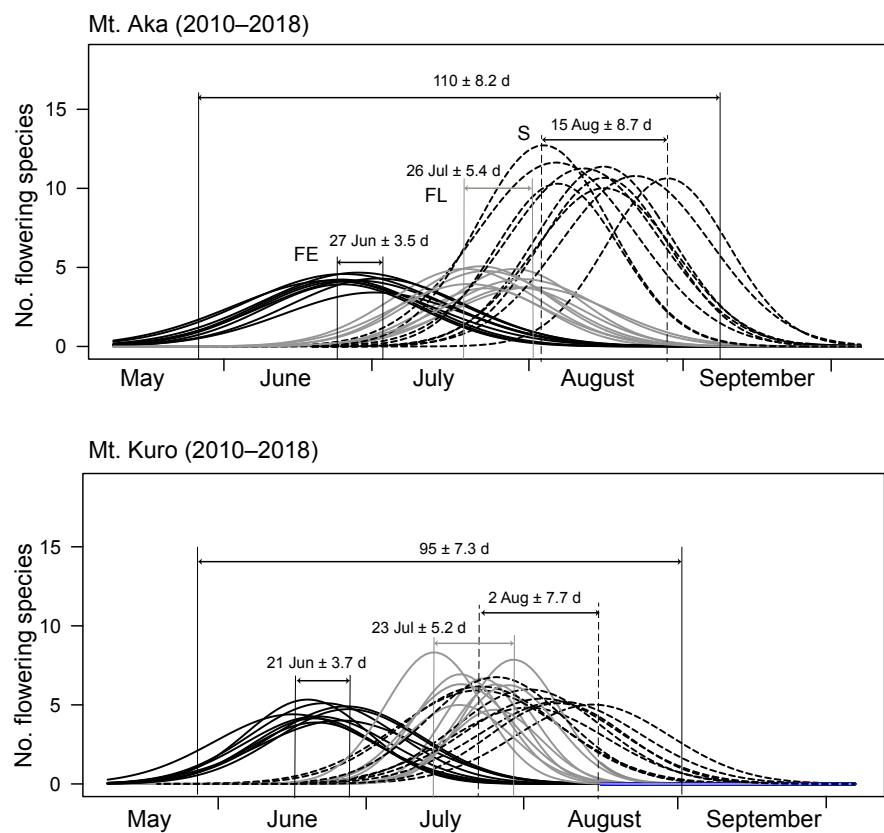


Figure 5 (Kudo)

