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ENVIRONMENTAL INFLUENCES ON THE PHENOLOGY AND ABUNDANCE OF FLOWERING BY *ANDROSACE SEPTENTRIONALIS* (PRIMULACEAE)[1]

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We studied the timing and abundance of flowering by *Androsace septentrionalis* L. (Primulaceae), an indeterminate winter annual or short-lived perennial, in 2 × 2 m plots at the Rocky Mountain Biological Laboratory in Colorado, USA, from 1982 to 2000. Flowers were counted every other day for most or all of the growing season in seven plots in a rocky meadow habitat and nine plots in a wet meadow habitat. The phenology and abundance of flowering were both highly variable, with mean dates of first flowering ranging from 16 May to 12 July and maximum daily counts of flowers ranging from 1 to 1187. Snowmelt date was the primary determinant of timing of flowering. For rocky meadow plots, the previous year's summer precipitation and the current year's average minimum temperature in May had significant effects on maximum number of flowers produced, but no environmental variable we considered was significantly correlated with flower abundance in the wet meadow plots. Length of flowering in individual plots ranged from 2 to 85 d, and many plot-years had both primary (about 1 mo) and secondary (about 10–12 d) flowering periods. The predicted increase in variability of precipitation accompanying climate change will affect negatively the long-term abundance and persistence of this species at our study site.

Key words: *Androsace septentrionalis*; climate change; flowering; phenology; precipitation; Primulaceae; snowmelt.

Flowering phenology is a critical reproductive trait of plants because it determines the number of potential mates and can provide a mechanism for reproductive isolation or speciation over time (Rathcke, 1983; Bronstein et al., 1990). Flowers also provide important food resources for pollinators and other visitors, giving the study of flowering phenology both ecological and evolutionary significance. From an ecological perspective, current topics of interest include (a) potential competition for pollinators if one species overlaps in flowering time with another, (b) the consequences for an individual flowering at the beginning, middle, or end of a population's flowering period, and (c) the consequences of phenological differences for seed production or herbivory (e.g., Mosquin, 1971; Augspurger, 1980; Ågren, 1987; Totland, 1993, 1994; Domínguez and Dirzo, 1995). From an evolutionary perspective, current discussions related to phenology include questions about the sequence of flowering in communities (e.g., Kochmer and Handel, 1986) and reproductive isolation of potentially interfertile species or races (e.g., Stace and Fripp, 1977).

Flowering phenology can also be viewed from an ecophysiological perspective. Researchers have sought to identify environmental factors that correlate with phenological events such as the initiation of flowering, the synchronization of flowering, the length of flowering, and variation in flower abundance (Opler et al., 1980; Borchert, 1983; Inouye and McGuire, 1991; Milton, 1992; Beaubien and Johnson, 1994; Domínguez and Dirzo, 1995; Inouye et al., 2002). Environmental cues that initiate onset of flowering include photoperiod, temperature, and precipitation (Rathcke and Lacey, 1985). Thus, the same abiotic cues that delimit the flowering season in some environments, such as rains in the desert and snowmelt in the alpine, may also serve as cues to trigger flowering (e.g., Borchert, 1980; Inouye and McGuire, 1991; Suaybaguio and Odtojan, 1992).

Once flowering has been initiated, the amount of precipitation over the growing season may affect the number of flowers and the duration of flowering for a given species (Firmage and Cole, 1988; Gerlach, 1992; Friedel et al., 1993; Struck, 1994). Global climate change could affect both the cues used by plants to begin flowering and the number of flowers produced. Climate change models predict an overall increase in precipitation, although some areas are expected to become wetter and other areas drier (IPCC, 2001). Long-term studies have shown that mean precipitation has not increased in the last century in some areas, while fluctuations about the mean have increased significantly (Tsonis, 1996). This type of climate change may affect the composition of plant communities by affecting the establishment, growth, flowering, and local extinction of plant species. Many past efforts conducted to predict the effects of climate change have focused on trees (e.g., Shugart, 1990), but there have been few studies on herbaceous plant communities (but see Fitter et al., 1995; Dunne et al., 2003). Predicting the effects of climate change on herbaceous plant species may provide insights into the impact of future climate change on both flowering plants and important pollinators. Such predictions are possible by assessing the relationships between weather patterns and flowering phenology in long-term studies.

In this paper, we use data from a long-term study of flow-

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ering phenology of *Androsace septentrionalis* L. (Primulaceae), a subalpine herbaceous plant species, to determine the relationship between the current and previous season's weather conditions and variation in timing and abundance of flowering. *Androsace septentrionalis* is shallowly rooted and likely to be sensitive to fluctuations in precipitation. This species is also short lived, and therefore an individual plant's fitness is hypothesized to be strongly influenced by its performance during its one or two growing seasons. Consequently, *A. septentrionalis* is an ideal species to study the effect of weather on flowering.

MATERIALS AND METHODS

Study site and system—*Androsace septentrionalis* L. (rock jasmine), an herbaceous subalpine and alpine wildflower, is described in floras as an annual (e.g., Weber and Wittmann, 2001), but at our study site it appears to be an indeterminate winter annual or short-lived perennial. An indeterminate winter annual is defined as a species that germinates before winter, overwinters, and continues to develop and flower through the next the growing season before dying (Harper, 1977). It is one of very few short-lived species found in the plant communities we studied. Germination occurs in late summer or early fall, with small rosettes (up to 15 mm in diameter) produced with up to 25 leaves. By late October or early November, these rosettes are usually covered by snow. They remain under snow (up to 2–3 m deep) until the following spring (April–June, depending on depth of the winter snowpack). After the snow has melted, the basal rosette continues to grow before producing a spindly and sometimes spreading inflorescence up to 10–20 cm in height. Individual plants can bear from one to 90 open flowers on a given date. The white flowers are only a few millimeters in diameter, and the only insects we have seen visiting the flowers are single individuals of a small syrphid fly and a small solitary bee. Because *A. septentrionalis* plants are shallowly rooted, flowering continues only until the top few centimeters of soil dries out, at which point the plants may die. In wet summers, flowering may continue until close to snowfall in the fall (September–October), and the rosettes may survive to flower the next summer.

Our study sites are located in montane meadows near the Rocky Mountain Biological Laboratory (RMBL), located in the West Elk Mountains of Colorado, USA. Plants were followed in 2 × 2 m plots in two different habitats: seven ''Rocky Meadow'' (RM) plots with shallow soil and relatively sparse vegetation and nine ''Wet Meadow'' (WM) plots with deep soil and relatively dense herbaceous vegetation. The seven RM plots (all in the same small meadow) ranged in altitude from 2941 to 2988 m (latitude 38°57.745–605′ N, longitude 106°59.135–213′ W) and the nine WM plots (all in the same large meadow) were all at about 2886 m (latitude 38°57.336–770′ N, longitude 106°59.212–276′ W). The RM plots, some of which are on south-facing exposures, melt out earlier in the spring and dry out earlier in the summer than the WM plots, which are all on level ground.

Weather data—We obtained climatic information for Crested Butte, Colorado, from 1982 through 2000 (NOAA, National Climatic Data Center, Asheville, North Carolina, USA, and The Colorado Climate Center, Colorado State University, Fort Collins, Colorado, USA). Crested Butte is located approximately 10 km from RMBL and is lower in elevation (approximately 2708 m). While the localized nature of summer thunderstorms means that precipitation differs somewhat between the two sites, these differences are probably not significant for this study. Data on winter accumulation of snowfall were collected by Billy Barr at RMBL, starting in 1975 from a site within 0.9 km of the phenology plots.

Data collection—The phenology and abundance of flowering by *A. septentrionalis* were tracked for most years between 1982 and 2000 (except 1989, 1990, 1992) in the 16 2 × 2 m plots. The total number of flowers per plot and/or the number of flowers per rosette were recorded from these plots every 2 d during most or all of the growing season (typically late May to mid-September). Flowers were counted as open if the floral parts were expanded enough for potential pollinators to visit the flowers for nectar and pollen, and if they had not begun to lose petals, or dry. Length of flowering period was determined from this information. In eight plot-years in the RM plots, we missed the beginning of flowering, and in one plot-year in the WM plots, we missed the end of flowering. These missing data were not used in the analyses described next.

Analysis—We used repeated measures for analyses (within plot over time) of date of first flower, length of flowering period, and maximum number of flowers. In some years, there was a second, shorter, flowering period. Because this occurred irregularly, the length of the first flowering period was used in the analysis. We used year as the repeated measure to test the effect of year on the response variables and to determine which weather variables could best explain them. For this analysis, we included as covariates the following variables: total precipitation from the previous summer (May–August); May, June, and July precipitation of the present summer; mean temperature of the previous summer (mean of mean temperatures for May–August); average minimum temperatures of May, June, and July the current summer; total snowfall two winters ago; and first date of bare ground at the study site (numbered using 1 May as day one). We used the same covariates for all response variables with the exception of first date of flower. In the analysis of first date of flower, we did not include July's temperature and precipitation because they were not logical biological explanations. We used the SP(POW) (spatial power law) covariance matrix to model the correlation among years within the same plot, because it does not assume equal distance between repeated measures (SAS, 1996). We used the option DDFM = KENWARD-ROGER to estimate degrees of freedom (SAS, 1999).

Assumptions for analysis of variance (normality and homogeneity of the variance) were checked. (1) *Date of first flower:* The data were square-root transformed before analysis in both sites. We could not correct the lack of normality for the wet-meadow site, but we still used the square-root transformation to facilitate comparisons between sites. (2) *Length of flowering period:* There was no need to transform the data before analysis in either of the two sites. (3) *Maximum number of flowers:* Data were log transformed before analysis for both sites.

RESULTS

Rocky Meadow plots (RM)—*Date of first flower*—The average date of first flowering for *A. septentrionalis* between 1982 and 2000 was 8 June (SD = 11.02, range of annual means = 16 May–8 July, $N = 80$ plot-years). Repeated measures analyses indicated that the first date of bare ground at the snow measurement station was the best explanatory variable for the date of the first flower at this study site ($P < 0.0001$) (Table 1). *Androsace septentrionalis* flowers earlier when the snow melts earlier ($r = 0.857$, $P < 0.0001$, Fig. 1a).

Length of flowering period—For the RM plots, the length of the first (main) flowering period ranged from 3 to 87 d (mean = 27.92, SD =15.81, $N = 79$ plot-years; this is a slight underestimate as flowering was already in progress when the annual counts began in eight plot-years). Repeated measures analyses indicated that year, by itself, did not affect length of the main flowering period ($P > 0.05$). The first date of bare ground was the only covariate that has a significant effect on the length of flowering ($P = 0.0438$) (Table 2). However, length of flowering was not significantly correlated with first date of bare ground ($r = 0.017$, $P = 0.883$).

In some years there were two or more flowering periods with a gap between them; we used a minimum gap of 8 d to define different flowering periods. For the RM plots, 19 of 95 plot-years (for this analysis we included data for 1992) had secondary flowering periods with a mean length of 9.8 d (SD = 10.8, range = 2–46 d) and a mean gap length between

TABLE 1. Repeated measures analysis of the effect of year and of different weather variables on the date of first flower of *Androsace septentrionalis*, Rocky Meadow plots (80 observations), near the Rocky Mountain Biological Laboratory, Colorado, USA.

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	19	1.73	0.2035
L-Temp	F	1	58.3	0.33	0.5655
L-Prec	F	1	44.9	1.91	0.1733
L-Snow	F	1	69.2	1.72	0.1937
Brgmay	**F**	**1**	**67.4**	**73.66**	**<0.0001**
Temp-May	F	1	52.1	0.55	0.4627
Temp-Jun	F	1	43.1	2.21	0.1443
Prec-May	F	1	40.9	0.67	0.4185
Prec-Jun	F	1	37.6	3.51	0.0688
Error	R	70			

Notes: LSdf = least squares degrees of freedom; Ddf = denominator degree of freedom; F = fixed effect; R = random effect. Weather variables were used as the covariates. Significant effects are shown in boldface type. L-Temp = mean temperature of previous summer; L-Prec = total precipitation from the previous summer; L-Snow = total snowfall from the previous winter; Brgmay = first day of bare ground using 1 May as day one; Temp-May and Temp-Jun = May and June average minimum temperature of present summer; and Prec-May and Prec-Jun = May and June precipitation of present summer.

flowering periods of 24.0 d (SD = 14.0, range = 8–49 d; N = 26). Four plots had two secondary flowering periods in one summer and one had three. Including both the main and secondary flowering periods increased the mean length of flowering to 37.4 d (SD = 24.1, range = 3–100), which is significantly longer than the first flowering period alone ($P = 0.002$, t test). Repeated measures analysis indicated (data not shown) that neither year nor any of the covariates used had a significant effect on the total length of flowering (first plus second flowering period).

Maximum number of flowers—The peak number of flowers open in a plot on a single day (excluding years without flowers) ranged from 1 to 1187 flowers (mean = 117.30, SD = 187.22, N = 88 plot-years) between 1982 and 2000. Repeated measures analyses indicated that the previous year's total precipitation and the average minimum temperature in May had a significant effect on maximum number of flowers (Table 3). More rainfall in the previous summer tended to be positively correlated with *A. septentrionalis* flower number in the next summer ($P < 0.0001$), while the effect of temperature in May was negative ($P = 0.01$).

In summary, date of first flowering in the Rocky Meadow site was correlated positively with the date of first bare ground at the snow measurement station. Date of first bare ground was also the only significant covariate that explained the length of flowering at this site. Maximum flower number was best explained by the previous year's total summer precipitation.

Wet Meadow plots (WM)—*Date of first flower*—The average date of first flowering for *A. septentrionalis* between 1982 and 2000 was 13 June (SD = 9.77, range of annual means = 24 May–12 July, N = 89 plot-years). Repeated measures analyses indicated that the first date of bare ground is the best predictor of the date of the first flower ($P < 0.0001$, Table 4). Earlier snowmelt led to earlier flowering by *A. septentrionalis* ($r = 0.86$, $P < 0.0001$, Fig. 1b). Repeated measures analyses also indicated that total precipitation and average minimum

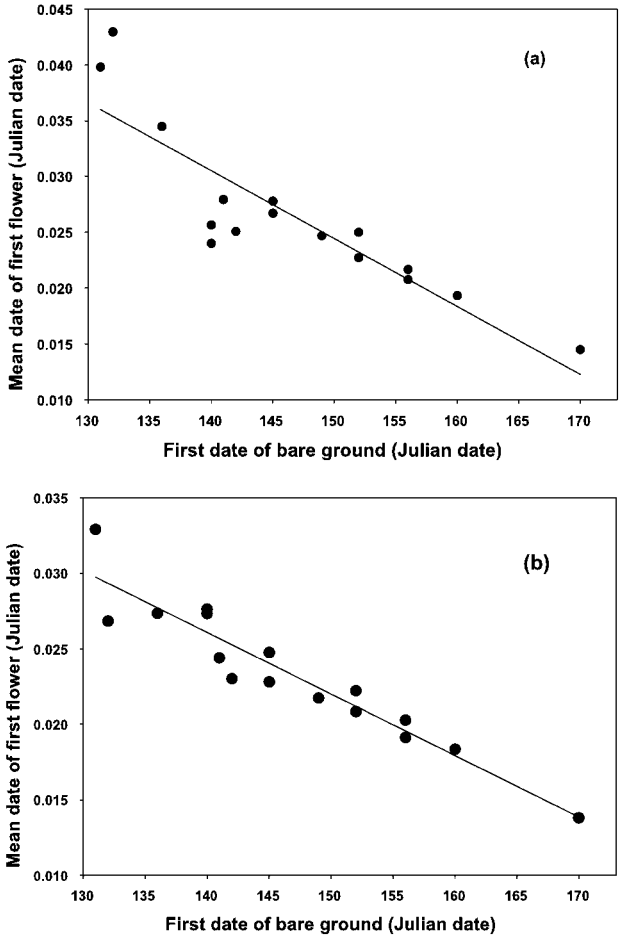

Fig. 1. The relationship between the first date of bare ground in the spring at the snow measurement station near the Rocky Mountain Biological Laboratory, Colorado, USA, and the mean first date of flowering of *Androsace septentrionalis* for the seven Rocky Meadow plots (N = 16 yr; date of first flowering transformed as $1/x$; $y = 0.1157 - 0.0006082x$, $r^2 = 0.783$, $P < 0.0001$) and (b) data for the nine Wet Meadow plots ($y = 0.0831 - 0.000407x$, $r^2 = 0.898$, $P < 0.0001$).

TABLE 2. Repeated measures analysis of the effect of year and of different weather variables on the length of flowering period of *Androsace septentrionalis*, Rocky Meadow plots (79 observations).

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	49.8	1.57	0.2164
L-Temp	F	1	66.5	0.01	0.9306
L-Prec	F	1	64.7	2.92	0.0921
L-Snow	F	1	65.3	2.28	0.1357
Brgmay	**F**	**1**	**65.9**	**4.22**	**0.0438**
Temp-May	F	1	66.5	1.83	0.1801
Temp-Jun	F	1	61.9	2.78	0.1006
Temp-Jul	F	1	64	1.97	0.1656
Prec-May	F	1	65.4	1.88	0.1754
Prec-Jun	F	1	63.5	2.52	0.1172
Prec-Jul	F	1	62.7	1.64	0.2052
Error	R	67			

Note: See Table 1 for meanings of abbreviations. Temp-Jul = July average minimum temperature of present summer. Prec-Jul = July precipitation of present summer.

TABLE 3. Repeated measures analysis of the effect of year and of different weather variables on the maximum number of flowers of *Androsace septentrionalis* open on a single day, Rocky Meadow plots (88 observations).

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	27	0.37	0.5468
L-Temp	F	1	72.3	2.47	0.1203
L-Prec	**F**	**1**	**72.1**	**18.77**	**<0.0001**
L-Snow	F	1	73.6	3.34	0.0718
Brgmay	F	1	75	1.53	0.2199
Temp-May	**F**	**1**	**76**	**6.28**	**0.0144**
Temp-Jun	F	1	62.8	3.65	0.0606
Temp-Jul	F	1	72	3.79	0.0553
Prec-May	F	1	62	2.11	0.1512
Prec-Jun	F	1	53.6	1.71	0.1971
Prec-Jul	F	1	48.8	0.83	0.3655
Error	R	76			

Note: See Tables 1 and 2 for meanings of abbreviations.

temperature in June affect date of first flower significantly (Table 4). The less it rained or snowed during the month of June the earlier *A. septentrionalis* flowered ($r = 0.262$, $P = 0.011$), but the correlation between temperature and flowering date was not quite significant ($r = 0.178$, $P = 0.09$).

Length of flowering period—For the WM plots, the length of the first (main) flowering period ranged from 2 to 85 d (mean = 32.88, SD = 15.57, $N = 90$ plot-years; this is a slight underestimate as we missed the end of flowering in one plot-year). Repeated measures analyses indicated that none of the covariates used affect length of the first flowering period ($P > 0.05$) (Table 5). There is no significant correlation between length of the main flowering period and any of the covariates used in the analysis.

For the WM plots, 25 of 96 plot-years (for this analysis we included data for 1992) had secondary flowering periods with a mean length of 12.0 d (SD = 12.6, range = 2–48 d) and a mean gap length between flowering periods of 18.9 d (SD = 9.3, range = 7–39 d; $N = 31$). Four plots had two secondary flowering periods, and one had four. Figure 2 shows the timing and abundance of flowers for a typical plot (WM plot #5 in 1997) with two flowering periods. Including all flowering periods increases the mean length of flowering for these plots to 41.3 d (SD = 23.4, range = 2–111; this analysis included one datum of 76 d that is a minimum estimate as there were flowers on the last census date of the year), which is significantly

TABLE 4. Repeated measures analysis of the effect of year and of different weather variables on the date of first flower of *Androsace septentrionalis*, Wet Meadow plots (89 observations), near the Rocky Mountain Biological Laboratory, Colorado, USA.

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	33.6	0.02	0.8890
L-Temp	F	1	78.7	0.02	0.8915
L-Prec	F	1	70.6	2.18	0.1442
L-Snow	F	1	79	1.57	0.2138
Brgmay	**F**	**1**	**76.3**	**117.96**	**<0.0001**
Temp-May	F	1	70.5	0.02	0.8954
Temp-Jun	**F**	**1**	**57.7**	**4.91**	**0.0306**
Prec-May	F	1	64	2.08	0.1543
Prec-Jun	**F**	**1**	**55.3**	**17.50**	**0.0001**
Error	R	79			

Note: See Table 1 for meanings of abbreviations.

TABLE 5. Repeated measures analysis of the effect of year and of different weather variables on the length of flowering period of *Androsace septentrionalis*, Wet Meadow plots (90 observations).

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	23.7	0.59	0.4495
L-Temp	F	1	76.4	0.17	0.6847
L-Prec	F	1	77.2	0.14	0.7138
L-Snow	F	1	73.5	0.93	0.3377
Brgmay	F	1	77.1	0.08	0.7752
Temp-May	F	1	76.8	0.09	0.7666
Temp-Jun	F	1	60.6	0.48	0.4900
Temp-Jul	F	1	54.2	0.49	0.4866
Prec-May	F	1	75.6	0.26	0.6133
Prec-Jun	F	1	62	0.13	0.7190
Prec-Jul	F	1	65.3	3.02	0.0868
Error	R	78			

Note: See Tables 1 and 2 for meanings of abbreviations.

longer than the first flowering period alone ($P = 0.002$, *t* test). As for the analysis of the first flowering period, repeated measures analyses (data not shown) indicated that none of the covariates used had a significant effect on the total length of flowering (first plus second flowering period).

Maximum number of flowers—The peak number of flowers open in a plot (excluding years without flowers) ranged from 1 to 536 flowers (mean = 75.07, SD = 115.40, $N = 90$ plot-years) between 1982 and 2000. Repeated measures analyses indicated that none of the covariates used had a significant effect on the maximum number of flowers at this site ($P > 0.05$, Table 6).

In summary, this site matched the RM site in that date of first flowering was correlated with first date of bare ground. The mean first date of flowering was 5 d earlier in the RM plots, which typically melt earlier than the WM plots. Length of flowering and maximum number of flowers at this site could not be explained by any of the variables used in the analyses.

DISCUSSION

The temporal pattern of flowering in a given species may reflect selection from a variety of factors, including competi-

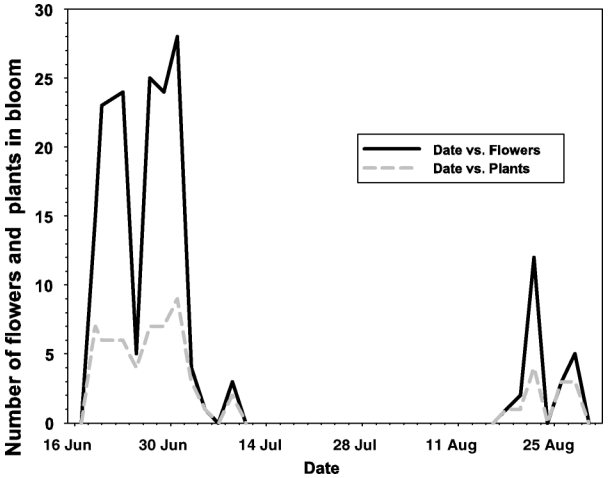

Fig. 2. The temporal pattern of flowering of *Androsace septentrionalis* for Wet Meadow plot #5 near the Rocky Mountain Biological Laboratory, Colorado, USA, in 1997 showing both the total number of flowers and the number of plants in bloom.

TABLE 6. Repeated measures analysis of the effect of year and of different weather variables on the maximum number of flowers of *Androsace septentrionalis* open on a single day, Wet Meadow plots (90 observations).

Source	Effect	LSdf	Ddf	*F*	*P*
Year	F	1	26.3	0.11	0.7483
L-Temp	F	1	77.6	0.00	0.9918
L-Prec	F	1	78	0.01	0.9289
L-Snow	F	1	77.9	0.03	0.8735
Brgmay	F	1	77.2	0.37	0.5473
Temp-May	F	1	76.6	0.86	0.3574
Temp-Jun	F	1	76.8	0.23	0.6347
Temp-Jul	F	1	76.1	0.74	0.3914
Prec-May	F	1	69.9	0.69	0.4086
Prec-Jun	F	1	67.5	2.83	0.0971
Prec-Jul	F	1	61.9	0.63	0.4296
Error	R	78			

Note: See Tables 1 and 2 for meanings of abbreviations.

tion for pollinators, avoidance of herbivores, adaptation to a limited growing season, or adaptation to the amount and seasonality of precipitation. Long-term data on flowering phenology can provide insights into the temporal and quantitative variation of resource availability for pollinators and, in conjunction with weather data, into the environmental factors that may be responsible for this variation. Several studies (e.g., Pitt and Heady, 1978; Augspurger, 1979; Kemp, 1983; Prins and Loth, 1988; Suaybaguio and Odtojan, 1992; Petit, 2001) have shown that rainfall patterns significantly affect plant phenology.

Flowering by *A. septentrionalis* is highly variable in its start date, length, and abundance, and environmental factors were correlated with this variation. Shortly after snowmelt, *A. septentrionalis* rosettes grow and begin to flower. The first flowers in WM plots have been seen as early as 14 May (and the plants were already in bloom when we made the first census that year) and, for an individual plot, as late as 22 July. Much of this variation in date of first flowering, however, can be explained by the environmental event of snowmelt (Fig. 1). This relationship makes sense as the growing season cannot begin until the winter snowpack has disappeared, and it also explains why flowering tends to be earlier in the RM plots (which melt first) compared to the WM plots (mean of 2.2–11.8 d earlier; data for 1997–1998 and 2000–2001). Other species in the plots also show this close relationship between snowmelt and timing of flowering (e.g., Inouye and McGuire, 1991; Inouye et al., 2002).

The primary flowering period for this species lasted for approximately 1 mo in both sites, and there may be a secondary flowering period (as was also reported by Holway and Ward, 1965) of 10–12 d. From our study, the length of the main flowering period for *A. septentrionalis* appears to be dependent mostly on the timing of the beginning of flowering (in the Rocky Meadow plots) and marginally ($P = 0.09$) on July precipitation (in the Wet Meadow plots). This latter result likely reflects the fact that these small plants are shallowly rooted and so are very dependent on surface moisture fluctuations; if flowering starts early, it may last longer before the soil dries out (RM) or continue if there is rain in July (WM). By July the soil moisture is typically quite low, and only if it rains will the plants survive and start flowering again.

The incidence of second flowering events did not differ much between the two sites, but the length of the total flowering period was a few days longer in the WM plots (mean = 41.3 vs. 36.2 d, but $P > 0.10$, *t* test). There was no significant difference ($P > 0.10$, *t* test) between RM and WM plots in the length of the gaps between first and secondary flowering periods. We found no significant correlation between summer precipitation (July, August, or both) and the number of plots that had secondary flowering periods, but our impression is that these events tend to occur in years when a dry period in the middle of the summer (which shuts down flowering) is followed by significant precipitation later in the summer.

For both the first and second flowering periods, plants in the RM site had a shorter flowering period. The deeper soil and taller and denser vegetation in the WM plots probably help to protect *Androsace* plants from the desiccation that more commonly affects the RM plots. After August, most plants have finished flowering for the season, although in unusual years flowering can continue into October. After flowering, the plants must still set seed and the seeds must either germinate before the end of the growing season and the onset of snowfall or become part of a seed bank. It is not clear whether late-blooming flowers can actually produce seeds before snowfall. Therefore, reproduction of this species is most likely constrained by the brevity of the growing season in subalpine habitats.

The abundance of flowering is also highly variable, but maximum number of flowers per plant is higher in the RM plots. Vegetative cover is much less dense in the RM plots, and there is no canopy over *Androsace* plants, as there often is in the WM plots. This may explain why, in 13 of 16 yr, plants in the RM plots had a higher ratio of open flowers to flowering plants than did WM plots. The significant correlation between the previous summer's precipitation and flower abundance in the RM plots may be explained by an increased survival of rosettes from one summer to the next resulting from summer rains, but we have not carried out the demographic studies required to test this hypothesis.

The importance of long-term studies of flowering lies in part in providing information on the variation among years in time, length, and abundance of flowering. Comparisons with environmental variables may then help to elucidate the reasons for this variation. From this study, the flowering period for *A. septentrionalis* is dependent on precipitation in the form of winter snowpack as well as summer rainfall. In our study sites, snow covers the ground from late October or early November to mid-April or early June. Because this short-lived species is constrained to a limited growing season, there is likely to be strong selective pressure to begin flowering soon after the first day of bare ground. The melting snowpack from the previous winter provides ample moisture for the inflorescence to initiate growth once the ground is bare, and then the plants typically have a month or two before the soil gets dry enough to kill plants or at least signal an end to the main flowering period. The constraints of this short growing season might explain the scarcity of subalpine annuals.

Climate change models predict that a doubling of CO_2 and other greenhouse gases should trigger an average temperature increase of 1°–6°C in the next century and also should affect precipitation patterns, soil moisture, and snow and ice cover. Predictions about precipitation are less certain (IPCC, 2001). However, long-term studies have shown that mean precipitation has not increased in the last century, while fluctuations about the mean have increased significantly (Tsonis, 1996). In other words the probability of drought events has increased.

Because the reproduction and long-term persistence of this herbaceous species are dependent on one, or sometimes two, short episodes of reproduction, we expect that an increase in variability of precipitation will affect negatively the long-term abundance and persistence of this species at our study site. Changes in snowfall and temperature will influence the phenology of flowering through effects on the date of snowmelt, and changes in summer precipitation and temperature will affect the abundance of flowering in at least the Rocky Meadow habitat.

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