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Phenological Responses of Snowbed Species to Snow Removal Dates in the Central Alps: Implications for Climate Warming

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Abstract

Low temperatures and the short growing season in high altitude snow patches in temperate mountains constrain life cycles and reproduction of snowbed species. This leads to a highly adapted timing of sexual reproduction. Winter precipitation and temperature, the main factors determining growing season length, are predicted to change with global warming. To understand their impacts on plant phenology, we studied the responses of seven alpine vascular plant species during 2001.

Temperature had a clear impact on phenological patterns. The start of the reproductive development was not directly linked with the date of snowmelt, but rather with the cumulative energy input. In addition, photoperiodism may also contribute to the control of plant development through an increasing temporal adjustment of phenology until flowering.

Introduction

The anticipated increases of greenhouse gases, especially carbon dioxide, in the atmosphere are predicted to raise temperatures by about 2.1 to 5.0°C globally within the next 100 years (Wigley and Raper, 1992; IPCC, 2001). Global warming will therefore affect ecosystems (Grabherr et al., 1994; Theurillat and Guisan, 2001) in many respects including changes in the timing of growth and development of plants (Beniston, 1996; Körner, 1999). For snowbeds, time for growth can be viewed as a limited resource (Galen and Stanton, 1991; Inouye and McGuire, 1991) causing convergence of phenological rhythms (Schemske et al., 1978; Arroyo et al., 1981). In most areas, duration of snow cover will be reduced as a consequence of global warming (Baumgartner and Apfl, 1994; Brown et al., 1994; Groisman et al., 1994; IPCC, 2001) with strong impacts on the timing of sexual reproduction of plants (Galen and Stanton, 1995; Price and Waser, 1998). Even if species composition does not change substantially over short time periods as earlier found in late-melting snowbeds (Sandvik et al., 2004), influences on reproductive characteristics are possible (Turkington and Aarssen, 1984; Díaz et al., 1994).

Temperature (e.g., Hegg, 1977; Rathcke and Lacey, 1985; Alatalo and Totland, 1997; Welker et al., 1997; Sandvik and Totland, 2000; Blionis et al., 2001), date of snowmelt (Billings and Bliss, 1959; Holway and Ward, 1963, 1965; Ratcliffe and Turkington, 1989; Kudo, 1991; Galen and Stanton, 1993, 1995; Walker et al., 1995; Henry and Molau, 1997; Price and Waser, 1998), and photoperiod (Heide, 1992; Keller and Körner, 2003) emerge as the most important environmental factors synchronizing the generative reproduction of arctic and alpine vascular plants. Molau (1993) and Körner (1994) emphasized the strong species-specific differences in the dependence of phenology on environmental factors. Körner (1994) pointed out that the degree of impact of a climatic factor on a species can vary strongly among phenological phases.

This study aims to assess potential impacts of climate warming on flowering phenology of selected snowbed species at the alpine/nival ecotone of the Alps. In particular, the following questions were addressed: (1) Is the flowering phenology of snowbed species triggered by the date of snowmelt, temperature, or photoperiod? (2) Does the degree of impact of these environmental factors vary among phenological phases of the studied species?

Methods

STUDY AREA

The study was conducted on the lateral moraine of the Schwarzenberger-Seespitze glacier (Stubaier Alpen, Tyrol, Austria; 47°03′N, 11°06′E). The study sites were situated on a northwestern slope of the moraine at an altitude between 2630 and 2680 m a. s. l. The area is characterized by a cold temperate, continental climate (Walter and Lieth, 1960–1967) with –4.0 to –2.8°C average annual temperatures and annual precipitation of almost 2000 mm (Pitschmann et al., 1970) at the alpine belt.

Siliceous bedrock is predominating in the surrounding mountains, hence the substrate of the moraine consists of unsorted, siliceous debris with a high proportion of small-sized gravel. There is no organic soil layer developed.

The exposition and unstable substrate provides appropriate conditions for a very scattered vegetation of Sieversio-Oxyrietum digynae (Grabherr and Mucina, 1993), typical for the alpine/nival ecotone. Zonal vegetation at this altitude is composed of closed swards of Caricion curvulae communities (Pauli et al., 1999).

SAMPLING DESIGN

Vegetation

Three study sites, each representing an area of about 30–50 m^2 with homogenous vegetation, were selected along a snow-melt gradient on the moraine slope. On each site, ten individuals of seven high-alpine

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TABLE 1

Basic climatic description of study sites for phenological observations. Data derived from StowAway Tidbit dataloggers. Snowfree period was calculated by interpreting the daily soil temperature amplitudes. Growing period was defined as all times with measurements above 5°C. Temperature sums were calculated by summarizing all temperature values exceeding 5°C.

	Date of snowmelt	Snowfree period (days)	Growing period (h d^{-1})	Temperature sum (cumulative °C)
Site 1	30–31 May 2001	84	1432/60	4968
Site 2	27 June–1 July 2001	65	1227/51	4661
Site 3	10–12 July 2001	53	1075/48	4441

species (*Agrostis rupestris*, *Gnaphalium supinum*, *Leucanthemopsis alpina*, *Oxyria digyna*, *Poa laxa*, *Sedum alpestre*, and *Veronica alpina*) closest to the site centre were selected to ensure very similar microclimatic conditions within a site. During summer 2001, nine observations were made at approximately weekly intervals. Generative shoots with their phenological phase (unopened buds, open flowers, expanding fruits, and mature fruits) were recorded for each plant. Discrimination of consecutive stages was based on species-specific differences.

Temperature

For soil temperature measurements, two StowAway Tidbit dataloggers (four on the larger Site 3) were buried at central positions on each site in 5 cm soil depth, the layer of the most compact rooting (compare Kudo, 1991). From August 2000 to October 2001, measurements were taken at intervals of 90 min (i.e., 16 measurements per day and logger).

DATA ANALYSIS

Beside temperature two other parameters can be derived from that temperature data set. Closed snow cover reduces the daily temperature fluctuations and generates nearly uniform temperature measurements. By moving a time window of three days over the data series, the daily temperature amplitudes within this window were analyzed. We defined temperature levels of about 0°C combined with low amplitudes as data derived from loggers below a snowpack and computed for every day and logger the presence/absence of snow cover.

Temperature sums are frequently used as indices to describe phenological processes (Jackson, 1966; Sparks and Carey, 1995; Thórhallsdóttir, 1998). At 5°C, high alpine plants have at least 50% of their maximal CO_2 fixation rate (Larcher, 1983). Hence, temperature sums were calculated by adding all values above 5°C (e.g., a temperature of 8°C contributes a value of 3 to the sum) for each day from 1 April until the end of the growing season 2001. Times with temperatures above that threshold value can be regarded as the growing season. Table 1 illustrates climatic conditions of the three study sites inferred from temperature measurements.

All plants independent from their species were assigned to the nearest datalogger and included in the analysis with the presence/absence data of snow cover and temperature sums of this logger.

To analyze the effects of temperature and length of the snow-free period on phenology of the selected species, four phenological stages were distinguished: first bud, main bud, first blossom, and main blossom. The time of first bud or blossom is defined as the day where the respective stage was observed at least on one flower on the respective individual. Main bud and blossom characterize the day, where an individual has the highest number of flowers in that phenological stage.

Time to reach consecutive stages was compared among sites with Kruskal Wallis test. Proportion of species and individuals with mature seeds were compared among sites with Fisher's Exact test and Pearson's chi-squared test. All statistical analyses were performed with S-Plus 2000.

Results

Effects of different microclimatic conditions on study sites (Table 1) on timing of blossom and fruiting are shown in Table 2. Time span from snow release to main blossom depended on the time of snowmelt for all species observed. Plants of Site 3 required only 60% to 80% of the time than did plants on Site 1. Of the individuals, 50% for each species reached blossom within 48 to 69 days on Site 1, within 17 to 53 days on Site 2, and 19 to 42 days on Site 3 (*Agrostis rupestris* was excluded from this calculation because less than 50% of individuals reached blossom on Site 2 and 3). Such a trend could not be detected for the cumulative energy input (temperature sums). Differences among sites do mostly not exceed intrasite variation. As an exception, temperature sums show a clear decline from Sites 1 to 3 in *Poa laxa*.

TABLE 2

Temperature sum in cumulative °C and time span from snowmelt to main blossom and fruit in number of days (mean ± SD). Early flowering: *Oxyria digyna* (OD), *Veronica alpina* (VA); intermediate flowering: *Sedum alpestre* (SA), *Leucanthemopsis alpina* (LA), *Gnaphalium supinum* (GS); late flowering: *Agrostis rupestris* (AR), *Poa laxa* (PL). Sample sizes in parentheses.

	Main blossom						Fruit	
	Temperature sum			Time span			Temp. sum	Duration
	Site 1	Site 2	Site 3	Site 1	Site 2	Site 3	Site 1	Site 1
Early flowering								
OD	2527 ± 744 (9)	1891 ± 691 (8)	2199 ± 525 (10)	45.5 ± 9.5 (9)	27.4 ± 8.2 (8)	27.5 ± 5.5 (10)	4736 ± 364 (6)	75.1 ± 5.1 (6)
VA	2554 ± 413 (9)	2895 ± 506 (9)	2229 ± 359 (9)	48.5 ± 8.9 (9)	39.4 ± 6 (9)	29.1 ± 4 (9)	4970 ± 2 (6)	80 ± 3.8 (6)
Intermediate flowering								
LA	3391 ± 25 (9)	2564 ± 465 (8)	3012 ± 740 (6)	59.4 ± 3.9 (9)	39.3 ± 5.2 (8)	36.8 ± 7 (6)	4971 ± 1 (2)	78.4 ± 0 (2)
SA	3233 ± 356 (6)	3061 ± 526 (5)	3507 ± 163 (5)	55.5 ± 4.8 (6)	44.4 ± 5.5 (5)	42.1 ± 1 (5)	4830 ± 315 (5)	76.4 ± 4.4 (5)
GS	3379 ± 0 (8)	3790 ± 366 (7)	3579 ± 189 (10)	57.5 ± 0 (8)	52.1 ± 4.8 (7)	42.6 ± 1.2 (10)	4971 ± 0 (10)	78.4 ± 0 (10)
Late flowering								
PL	4237 ± 523 (10)	3899 ± 114 (9)	3510 ± 142 (6)	70 ± 6.4 (10)	54.3 ± 1.8 (9)	42.7 ± 1 (6)	4971 ± 1 (2)	78.5 ± 0 (2)
AR	4764 ± 330 (10)	4510 ± 1 (3)	4524 ± 332 (2)	80 ± 4.1 (10)	66.6 ± 0 (3)	54 ± 0.5 (2)	4964 ± 1 (5)	88.5 ± 0 (5)

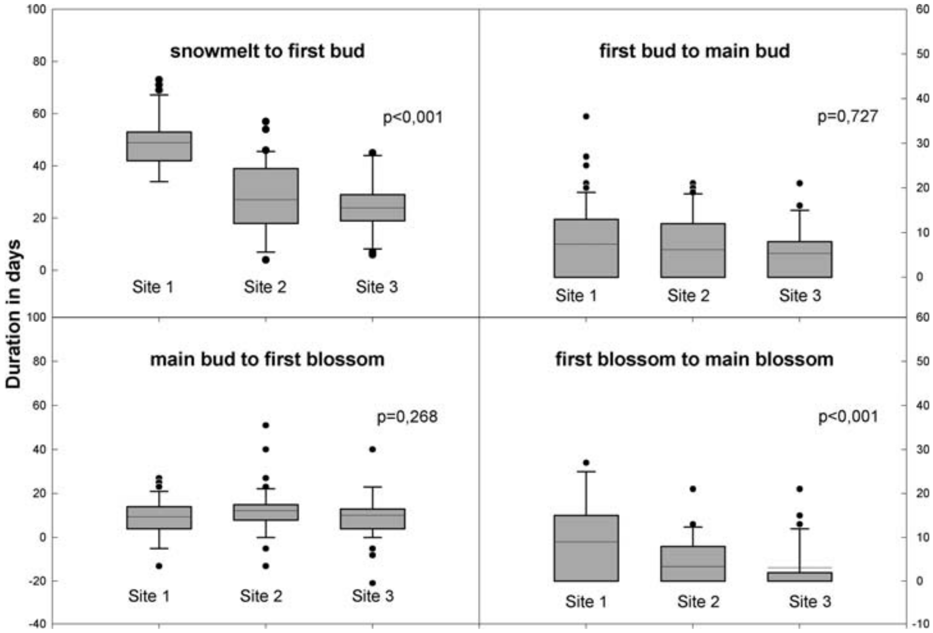

FIGURE 1. Duration in days to reach the phenological phases first bud, main bud, first blossom, and main blossom from their preceding stage are illustrated as mean, 1st/3rd quartile (boxes), and 10th/90th quantile (whiskers) with all outliers. Data pooled for all species.

At Site 1, duration and temperature sums necessary to mature fruits are—unlike sums necessary to reach blossom—very similar for all species. Required energy input ranges from about 4700 to 5000 accumulative °C—a little less for *Oxyria digyna*. These values were not attained at Sites 2 and 3. Hence, fruit phenology cannot be compared between sites, because plants at Sites 2 and 3 (except for a few individuals of *Oxyria digyna*) failed to produce ripe fruits in 2001. Accordingly, the following analyses were restricted to buds and flowers.

Plants can be grouped into early, intermediate, and late flowering species (Table 2). Phenological development until main blossom was analyzed in more detail in Figure 1. The time spans between snowmelt and first bud, and between first blossom and main blossom, decreased significantly from Site 1 to Site 3; i.e., the later a site became snow-free, the shorter were these time spans (Fig. 1). In contrast, duration of development from first bud to first blossom did not differ among sites. Negative values for duration occurred because some plants bore the first flower before the main part of their inflorescences reached bud stage.

The number of individuals ($P < 0.0001$; Pearson's chi-squared test) as well as the number of species developing mature seeds in 2001 ($P = 0.0073$; Fisher's Exact test) differed significantly among sites (Fig. 2). At Site 1, more than 50% of individuals representing all species produced mature seeds, whereas only one species and 2.9% of individuals matured seeds on at Site 3.

Discussion

Cumulative energy input to reach a certain phenological phase was about equal for all phases on all sites. Thus, energy required for generative development of study species does not depend on date of snowmelt.

In contrast, remarkable differences in timing of reproductive development among study sites were detected in all observed plant species. Starting from very different dates of snowmelt, an increasing temporal adjustment of budding and especially flowering was observed. On the contrary, out of the four developmental phases from snowmelt to main blossom, only duration of the first and the last phase appeared to depend on snowmelt date (compare Walker et al., 1995). The earlier a plant became snow-free, the longer the time until the first bud was visible, whereas main blossom occurred nearly at the same time.

After snow release, climatic conditions differed widely among sites. Site 1 became snow-free at the end of May and the subsequent time was characterized by repeated snowfalls and low temperatures, whereas Site 3 was free of snow in mid-July under high summer conditions. Thus, differences in developmental speed of the early phases can be explained by thermal requirements. In contrast, differences in speed of development shortly before main blossom cannot be explained by differences in the temperature regime of study sites alone, because this part of development takes place in the most favorable time of year with high temperature levels on all sites. In fact, a possible photoperiodic influence on developmental processes was suppressed by a strong control of the dynamics of early phenological phases (buds) by temperature or snow regimes. Later in the year the temporal relationship between the beginning of the development and a phenological phase (flower) was less strong.

Despite the fact that the main blossom stage is reached at approximately the same time on all sites, the length of growing season had severe impacts on the time of seed maturity and therefore on

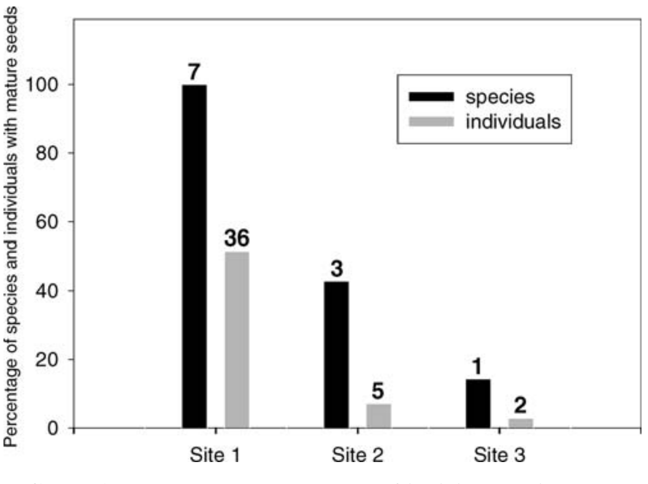

FIGURE 2. Percentage and number of individuals with mature seeds and species with at least one plant that has completed its reproductive cycle in 2001.

reproductive success. The percentage of species and individuals that were able to finish their reproductive cycle decreased dramatically with decreasing duration of growing season.

This apparent contradiction could be due to a pollen-centered reproduction strategy of plants with late release from snowpack. Very late snowmelt strongly reduces the probability of successful seed maturation. As a response, plants could disproportionately invest in the first stages of generative reproduction to achieve a synchronization of anthesis with individuals located at more favorable sites for cross pollination (see Heide, 1985). Thus, at least gene flow via pollen dispersal could be ensured, when reproduction via seeds will most probably be inhibited by climate conditions. This could explain observations of nearly simultaneous main blossom but major differences in seed maturation at study sites. In this case, flowering is likely to be triggered mainly by day length (i.e., photoperiod). Another reason for the synchronization of flowering could be a high seasonality of pollinators restricted to that short time period.

Our data provides clear evidence of a strong impact of temperature on plant phenology, but due to the convergence of the timing of phenological stages from snowmelt to main blossom, an impact of photoperiod can neither be proved nor ruled out. Such an impact can be expected to be most pronounced for blossom, whereas early phenological stages seem to be only slightly related to day length. Sensitivity of phenological patterns to climatic changes will be indirectly correlated with the degree of the photoperiodic synchronization.

Heide (1992) understood temperature and photoperiodism as the main factors controlling flowering phenology. Kudo (1991) considered time to flowering as largely constant and hardly adaptable to site conditions. On the contrary, Keller and Körner (2003) observed a remarkable reduction of prefloral time at advanced temperature for *Poa laxa*, *Sedum alpestre*, *Leucanthemopsis alpina*, and *Gnaphalium supinum*, but only under long-day conditions (16 h daylight). Accordingly, time shifts due to global warming would have a twofold effect, because the majority of plants observed in this study flower after the longest day of the year: time span for reproduction will be longer and temperature sensitivity can be expected to be enhanced by global warming.

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