Site-specific factors influence the richness and phenology of snowbed plants in the Pyrenees

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Abstract
Although the timing of snowmelt and growth temperatures appear to be the main factors that influence the species richness and phenology of snowbed plants, site-specific characteristics may also play a role in modifying the effects of the timing of snowmelt and temperature. In this study, the effects of site-specific factors (microtopography and snow origin) on species richness and plant phenology were evaluated in 72 plots in two snowbeds in the Andorran Pyrenees. Snowmelt patterns influenced the spatial distribution of species richness and abundance. Site-specific factors had significant effects on the responses of species (shortening or lengthening the duration of the phenophase) and on the extent to which the timing of snowmelt influenced leaf expansion and flowering. Notably, the highest rates of leaf expansion occurred on late snowmelt isoclines, where, nevertheless, the time taken to reach peak flowering was significantly longer than on the early snowmelt isoclines. The results of this study highlight the fact that, in addition to the effects of interannual variability in climate, site-specific factors have a significant effect on the phenology and reproductive success of the commonest plants in the snowbed communities of the Pyrenees.

Keywords: Phenology, Pyrenees, richness, site-specific, snowbed

Introduction
Climate change is a threat to alpine plants (Theurillat & Guisan 2001; Grabherr 2003; Hülber et al. 2006; Dávila et al. 2012; Fernández Calzano et al. 2012) and, above all, to those such as snowbed plants that depend on snow cover for protection against harsh weather (Nagy 2006; Björk & Molau 2007; Schöb et al. 2009). Global circulation models forecast an increase in temperatures of 1.4–5.8°C (IPCC 2007) during the twenty-first century, and in the Pyrenees, the mean annual temperature is expected to increase by 2.5–5°C (AEMET 2008). Ambient temperature has a significant effect on the timing of snowmelt, and most studies report reductions in or the disappearance of snow cover in alpine habitats (Walker et al. 1993; Stanton et al. 1994; Beniston et al. 2003; EEA 2004; Muñoz et al. 2007). This highlights the vulnerability of the flora and vegetation of snowbeds to climate change (Lluent 2007; Schöb et al. 2009; Surina Modric & Surina 2010).

Numerous studies link the influence of the timing of snowmelt and temperature with plant cover and species richness in snowbeds (Totland & Alatalo 2002; Lluent 2007; Hülber et al. 2011) and in the snowpack (Chen et al. 2011). The effects of climate change (e.g., the timing of snowmelt and temperature) will probably modify the current physical conditions of snowbed habitats, thereby affecting species richness and plant cover.

Numerous studies have demonstrated for alpine snowbeds the influence during the growing season of snowmelt date (Galen & Stanton 1995; Totland & Alatalo 2002; Körner 2003; Hülber et al. 2006, 2010) and temperature (Körner 2003; Molau et al. 2005; Hülber et al. 2006; Kudo & Hirao 2006) on plant development and phenology, as well as on species richness and plant cover (Lluent 2007; Schöb et al. 2009; Surina Modric & Surina 2010).
Hülber et al. 2011), which thus indicates the susceptibility of snowbed communities to climate change effects. Although those factors appear to be the major drivers of the development of snowbed plants, site-specific factors might modify (exacerbate or diminish) the overall effects of the timing of snowmelt and temperature. However, few studies to date have examined the influence of site-specific factors such as microtopography and snow origin on the phenology of alpine plants (Kudo & Hirao 2006; Lluent 2007; Hülber et al. 2010).

To gain a more comprehensive understanding of the impacts of climate change on the cover, richness, and phenology of alpine plants in snowbed communities, it is important to know whether changes in phenologies and variations in patterns of species richness can be attributed to site-specific factors. These issues are particularly important on the Iberian side of the Pyrenees, where global warming is predicted to have an especially significant effect (Lluent 2007), and where snowbeds are being reduced in size – or even disappearing altogether – as the cryo-Mediterranean belt moves upward in altitude (Tomaselli 1991). Furthermore, the Pyrenees represent the southern limit of most alpine snowbed plants; therefore, the snowbed habitat of these mountains is particularly vulnerable to the effects of climate change.

In this study, we addressed the following specific questions: How do site-specific factors influence plant cover and species richness in snowbeds? Do site-specific factors influence the date of snowmelt and the microclimate in snowbeds? Do the effects of snowmelt on plant phenology (leaf expansion and flowering) differ between early and late snowmelt sites? Do the phenologies of snowbed plant species differ in their responses to the timing of snowmelt?

**Methods**

**Study site**

The study was conducted in two snowbeds in the northwest of the alpine region of Andorra: Cataperdis (1° 28’ 48.1079"; 42° 37’ 1.7774") at an elevation of 2525 m a.s.l. and Arbella (1° 29’ 24.1448; 42° 39’ 3.2380") at an elevation of 2475 m a.s.l. (Figure 1).
Acidic soils have developed on the gneiss, granodiorite, and granite bedrocks of both snowbeds. However, the origin of the snow is different: in Cataperdis, snow accumulates primarily because of the topography, whereas in Arbella, the snowbed is fed by snow from avalanches. These snowbeds have slope aspects of 15–22° and 20–30°, respectively, and continuous snowmelt gradients varying from concave forms to moderately exposed slopes. The area has a cold continental climate with Mediterranean influences. In the Central Pyrenees (Andorra), 2009 was warm and dry, 2010 was cold and wet, and 2011 was warm and wet (Servei Meteorològic de Catalunya 2013).

**Data collection**

In 2009, we established 36 permanent plots (50 cm × 50 cm) in both of the two snowbeds, 12 each on the late-snowmelt (LSM), intermediate-snowmelt (ISM), and early-snowmelt (ESM) isoclines. The 12 plots on one isocline were located within a 20 m² area. To monitor snowmelt patterns, the snowbeds were observed in June–August in 2009, 2010, and 2011 at weekly intervals. We defined the growing season as the period between permanent snow release in spring and permanent snowfall in autumn.

Six temperature data loggers (Temperature logger i-button – Maxim Integrated Products, Sunnyvale, CA, USA, range −40° to +85°) were placed on each of the three isoclines in each snowbed. From June 2010 to October 2011, soil surface temperatures were recorded at 3-h intervals.

**Species and plant cover**

During the growing season (early July–early October), the number of species and the plant cover of all vascular plants and bryophytes in each plot were recorded at weekly intervals (14 times per year). The main phenological sequences of each plant species were recorded weekly during the growing season, which included the two following phenophases: cessation of leaf expansion and peak flower opening. We gauged that for the plot, main peak flower opening had occurred when more than 70% of the species of the permanent plots (50 cm × 50 cm) had entered the flowering phenophase, and for species, it occurred when more than 70% of individuals of each species of the plots had entered the flowering phenophase. In addition, we documented the abundance of the four most common species in both of the snowbeds, *Sedum alpestre*, *Mucizonia sedoides*, *Gnaphalium supinum*, and *Poa alpina*. Plant identification and nomenclature follow Bolós et al. (2005).

**Data analysis**

The factors affecting the timing of snowmelt (days elapsed since the end of the snowmelt) and accumulated temperature during the growth period (°C) were evaluated separately using a general linear model, with year (2010 and 2011), site (Cataperdis and Arbella snowbeds), and the snowmelt isoclines (LSM, ISM, and ESM) as the explanatory variables. To test for normality, data were subjected to a Kolmogorov–Smirnov test, whereas to estimate the independent explanatory power of each predictor variable, hierarchical partitioning (Chevan & Sutherland 1991) was used to obtain a measure of the independent contribution of each variable as a proportion (%) of the total explained variance (Mac Nally & Walsh 2005). The statistical significance of the amount of variance explained by each variable was tested using a randomization test based on 100 randomizations of each of the independent variables. To test for significant differences in the timing of snowmelt and accumulated temperature between the different levels of the environmental factors, Tukey-HSD tests were performed, whereas to assess the collinearity between the timing of snowmelt and accumulated temperature, a Pearson Chi-squared test was performed.

Furthermore, species richness and total plant cover were subjected to an analysis of variance (ANOVA) that included the following explanatory factors: snowmelt isocline (LSM, ISM, and ESM), site (Cataperdis and Arbella snowbeds), year (2010 and 2011), and the plot nested within the isocline in a general linear model. To test for normality, data were subjected to a Kolmogorov–Smirnov test, whereas a Tukey’s post hoc multiple comparisons test was used to test for significant differences in species richness and plant cover.

The effects of snowmelt isocline, site, year, and plot on the number of days before each phenophase was reached were evaluated collectively for all of the species and individually for *Mucizonia sedoides*, *Sedum alpestre*, *Gnaphalium supinum*, and *Poa alpina*. To quantify the explanatory power of each variable (site, year, and snowmelt isocline) on the response variables (the timing of snowmelt and accumulated temperature), we used hierarchical partitioning.

The effects of the time taken to reach each phenophase on the three snowmelt isoclines in the two snowbeds were performed using the non-parametric Kruskal–Wallis test (nonparametric one-way ANOVA).

All of the analyses were performed using the SAS statistical package (SAS 9.0, SAS Institute 2003) and the R (version 2.12.1, R Development Core Team 2010).
Table I. Timing of snowmelt (Julian date), and accumulated temperature (°C) on three snowmelt isoclines (LSM, ISM, and ESM) in two snowbeds in the Andorran Pyrenees.

| Site      | Year | Snowmelt isocline | Timing of snowmelt (day of year) | Accumulated temperature (°C) |
|-----------|------|-------------------|----------------------------------|-----------------------------|
| Cataperdis | 2010 | LSM               | 188                              | 1150                        |
| Cataperdis | 2010 | ISM               | 200                              | 572                         |
| Cataperdis | 2010 | ESM               | 230                              | 184                         |
| Cataperdis | 2011 | LSM               | 195                              | 978                         |
| Cataperdis | 2011 | ISM               | 202                              | 668                         |
| Cataperdis | 2011 | ESM               | 209                              | 336                         |
| Arbella   | 2010 | LSM               | 209                              | 941                         |
| Arbella   | 2010 | ISM               | 230                              | 513                         |
| Arbella   | 2010 | ESM               | 237                              | 212                         |
| Arbella   | 2011 | LSM               | 202                              | 923                         |
| Arbella   | 2011 | ISM               | 223                              | 744                         |
| Arbella   | 2011 | ESM               | 237                              | 284                         |

Results

Timing of snowmelt and accumulated temperature

The earliest snowmelt on ESM isoclines occurred at Cataperdis on July 6, 2010, while the latest on LSM isoclines began at Arbella on August 24, 2010; thus, the difference between the extreme dates for snowmelt was substantial (49 days) (Table I). The mean length of the growing season differed significantly between the snowmelt isoclines (ESM sites = 77.5 days, ISM sites = 61.75 days, and LSM sites = 47.75 days). The timing of snowmelt did not vary significantly between years ($F = 2.59; p = 0.15$); however, the timing differed significantly between snowbeds ($F = 23.28; p = 0.002$) and snowmelt isoclines ($F = 22.66; p < 0.001$). Snowmelt occurred 18 days later at Arbella than at Cataperdis. On average, the snow melted 30 days later on LSM isoclines than on ESM isoclines; on the other hand, the timing of snowmelt did not differ significantly between the ISM and the LSM sites.

Accumulated temperature ranged from 188°C (desv ± 3.77°C) at an LSM site to 1150°C (desv = 7.01°C) at an LSM site (Table II), but did not vary significantly between years ($F = 1.10; p = 0.33$) or snowbeds ($F = 0.62; p = 0.46$); however, the accumulated temperatures of the snowmelt isoclines did differ significantly ($F = 56.18; p < 0.0001$).

The timing of snowmelt and accumulated temperature during the growing period were significantly correlated ($r = 0.965; p < 0.001$). Snowmelt isocline and site explained much of the variance in the snowmelt date; snowmelt isocline also explained a substantial amount of the variance in the accumulated temperature during the growing season (Table II).

Species richness and plant cover

A total of 34 plant species were found in the two snowbeds (28 species at Cataperdis and 33 at Arbella) (Table III). The species richness of vascular plants (mainly forbs) was much higher than the richness of bryophytes (Table IV). Overall, mean plant cover was 87.54%, ranging from 14% at the LSM site at Arbella to 100% at the ESM site at Cataperdis. Plant cover varied significantly between years ($F = 16.12; p < 0.001$), sites ($F = 39.11; p < 0.001$), and snowmelt isoclines ($F = 22.59; p < 0.001$), but did not vary significantly within plots ($F = 0.14; p < 0.867$). Species richness varied significantly between years ($F = 18.13; p < 0.001$), sites ($F = 111.46; p < 0.001$), and snowmelt isoclines ($F = 80.84; p < 0.001$), but not within plots ($F = 0.51; p < 0.581$). Plant cover and species richness were highest on the ESM isocline (mean richness per plot = 9.64 ± 2.06 species, mean plant cover per plot = 84.04%) and were lowest on the

Table III. Species recorded in the two snowbeds studied in the Andorran Pyrenees in 2010 and 2011.

| Species                        | Notes                              |
|--------------------------------|------------------------------------|
| Agrostis rupestris             |                                    |
| Arabis alpina                  |                                    |
| Armeria maritima               |                                    |
| Androsace carnea               |                                    |
| Alnus viridis germarii          |                                    |
| Anthisja juratzkana            |                                    |
| Cardamine bellifolia           |                                    |
| Carex pyrenaica                |                                    |
| Cerastium cerastoides          |                                    |
| Cryptograma crispa             | A                                  |
| Epilobium anagallifolium       |                                    |
| Festuca glacialis              | C                                  |
| Gnaphalium supinum             |                                    |
| Hieracium gr. pilosella        |                                    |
| Leucanthemopsis alpina         |                                    |
| Luzula alpiniflora             | A                                  |

Note: The species present only in the Cataperdis or Arbella snowbeds are indicated by a superscript C and A, respectively.
Table IV. Species richness (mean richness and standard deviation per plot of all species, vascular plants (except grasses), bryophytes, and grasses) at Cataperdis, at Arbella, and at both snowbeds in the Andorran Pyrenees.

|                     | Both snowbeds | Cataperdis | Arbella |
|---------------------|---------------|------------|---------|
| All species        | 7.19 ± 3.25   | 8.83 ± 2.97| 5.52 ± 2.64|
| Vascular plants    | 5.34 ± 3.09   | 6.56 ± 2.61| 4.12 ± 3.08|
| Bryophytes         | 1.85 ± 1.03   | 2.33 ± 0.95| 1.37 ± 0.87|
| Grasses            | 1.43 ± 1.28   | 1.81 ± 0.93| 1.06 ± 1.48|

LSM isocline (mean richness per plot = 4.77 ± 1.70 species, mean plant cover per plot = 57.59%).

The species richness of vascular plants, especially grasses (e.g., Poa alpina, Agrostis rupestris, and Nardus stricta), was significantly higher on ESM isoclines (mean richness per plot = 2.10; desv ± 1.10) than on LSM isoclines (mean richness per plot = 0.37; desv ± 0.60); nonetheless, bryophytes species richness was significantly higher on LSM isoclines than on the other isoclines.

On average, at Cataperdis, there were significantly higher plant richness per plot (8.83 species) and greater plant cover (94.29%) than at Arbella (5.52 species, 66.80% plant cover). Mean richness per plot and mean plant cover were significantly higher in 2010 (7.84 species, 86% plant cover) than in 2011 (6.51 species and 64.22% plant cover).

Growth and flowering phenology

All the plots on ESM isoclines reached the cessation of leaf expansion and flowering phenophases. On LSM isoclines, plants in 96% and 85% of the plots reached the cessation of leaf expansion phenophase and the flowering phenophase, respectively; however, the corresponding figures for the LSM isoclines were only 68% and 50% of plots, respectively.

The period from the end of snowmelt to the cessation of leaf expansion differed significantly between snowmelt isoclines ($\chi^2 = 12.16; p < 0.002$), between years ($\chi^2 = 29.38; p < 0.001$), and between sites ($\chi^2 = 4.19; p = 0.04$). This period was significantly shorter on LSM isoclines than on either ESM (4.87 days) or ISM isoclines (6.64 days). In 2010, this period lasted 6.34 days longer than in 2011 and, on average, was 2.49 days longer at Cataperdis than at Arbella.

The period from the cessation of leaf expansion to peak flowering differed significantly between snowmelt isoclines ($\chi^2 = 8.03; p < 0.01$) and between years ($\chi^2 = 15.64; p < 0.001$), but not between sites ($\chi^2 = 0.77; p = 0.37$). This period was significantly longer on LSM isoclines than on either ESM (8.82 days) or ISM isoclines (6.84 days), and was 4.37 days longer in 2011 than in 2010.

The period from the end of snowmelt to peak flowering differed significantly between sites ($\chi^2 = 5.43; p < 0.01$) but not between years ($\chi^2 = 1.49; p = 0.22$) or snowmelt isoclines ($\chi^2 = 1.85; p = 0.39$), and was significantly shorter (4.06 days) in the plots at Arbella than at Cataperdis.

The mean accumulated temperature at the cessation of leaf expansion in ESM plots (131°C) was significantly ($F = 4.55; p < 0.01$) higher than in LSM plots (85°C). The mean accumulated temperature at peak flowering in the plots on ESM isoclines (212°C) was significantly higher than on ISM isoclines (148°C), but did not differ significantly from the plots on LSM isoclines, possibly because only 50% of plots on LSM isoclines reached the flowering phenophase.

Peak flowering occurred earlier (Figure 2), and the number of flowering species was greater on ESM than on LSM isoclines. The flowering period was, respectively, 17.5 days and 38 days shorter at the LSM sites than at ESM sites, which left very little time for the later phenophases including fructification. Peak flowering always occurred later at Arbella than at Cataperdis.

Species-specific phenological responses

The amount of variance in the time needed to reach the two phenophases explained by site-specific factors was very high (>36.9%) for all species in the flowering phenophase except Mucizonia sedoides (18.7%) and Gnaphalium supinum (20%) (Table V). Snowmelt isoclines and year had the greatest effect on the phenologies of most of the snowbed species; however, the cessation of the leaf expansion phenophase in Sedum alpestre was much more influenced by site than by year. As was expected, the proportion of plots in which all species reached the flowering phase was lower than the proportion of the plots in which the plants reached the cessation of leaf expansion.

In Sedum alpestre, Mucizonia sedoides, and Gnaphalium supinum, but not Poa alpina, the time needed to reach the flowering phenophase differed significantly between snowmelt isoclines (Table VI). G. supinum (mean = 11 days) and S. alpestre and M. sedoides (14 days and 21 days, respectively) required more time from the end of snowmelt to reach the flowering phase on ESM than on LSM isoclines.

Discussion

Timing of snowmelt and accumulated temperature

In the two studied snowbeds in the Andorran Pyrenees, the timing of snowmelt, but not accumulated temperature, differed significantly, which
suggests that site-specific factors may have had a significant effect on accumulated temperature through their localized effects on the microclimate of the snowbeds. At the Arbella snowbed, avalanches are the main source of accumulated snow, whereas at Cataperdis, microtopography is responsible for the accumulated snow. Consequently, the volume of accumulated snow is greater, and snowmelt occurs later in the former than in the latter. At the ESM site at Arbella, snowmelt occurred 7 days later in 2010 than in 2011, and so, the accumulated temperature was higher in 2011. On the other hand, at the ESM site at Cataperdis, snowmelt occurred 7 days later in 2011 than in 2010, and the accumulated temperature was higher in 2010. When snowmelt occurs early in the summer, the effective accumulated temperature increases gradually, initially, but the rate of increase accelerates quickly. However, when the snow cover on a snowbed is removed after midsummer, initially the effective accumulated temperature increases at a constant rate, and then decreases (Kudo & Hirao 2006). At LSM sites in the Andorran Pyrenees, accumulated temperatures were similar between sites and years, even when there were differences in the date of snowmelt. Thus, at ESM sites, the snowmelt date might have had a greater effect on phenologies than on accumulated temperature (see also Kudo & Hirao 2006).

Species richness and plant cover

In the snowbeds in the Andorran Pyrenees, the richness of vascular plants and the amount of plant cover were correlated with the snowmelt isocline gradient; specifically, richness and plant cover decreased between early and late snowmelt isoclines, a finding that has been observed elsewhere (Totland & Alatalo 2002; Luuent 2007). Abiotic factors such as water content, nutrient fixation capacity, and the C/N ratio differ between snowmelt isoclines (Retzer 1956; Billings & Bliss 1959; Hülber et al. 2011), and Galen and Stanton (1995), for example, reported strong correlations between the timing of snowmelt, soil quality, and structure, and the productivity of alpine plants.

In this study, overall plant richness was highest at ESM sites at both snowbeds. However, the relatively low richness at LSM sites, where bryophytes predominated, was associated with snowbed specialists, and in these sites, we failed to find many of the species that occur in adjacent habitats and at ESM sites (mainly grasses) (see also Stanton et al. 1994; Schöb et al. 2009). Thus, snowmelt isoclines (i.e., the gradient of microvariations) influence and help maintain the floral richness of snowbeds. We found that the richness per plot was higher at Cataperdis than at Arbella, probably because, at the former, the snow melted earlier and plants had a longer growing season. Even so, the total number of species (Table III) shows higher global richness in the Arbella snowbed.

Species richness and plant cover were greater in 2010, a colder and more humid year, than in 2011; however, this was probably a carry-over effect from 2009, warmer and drier, and with an earlier snowmelt than in 2010. Presumably, the flowering
season in 2009 influenced seed success and phenology in 2010 (Kudo & Hirao 2006) and, consequently, may well have increased species richness and plant cover in 2010.

Plant growth and flowering phenology

As expected, in the Andorran snowbeds, accumulated temperatures were lower at LSM sites than at ESM sites, even though the highest rates of leaf expansion were found at LSM sites. The contrary occurred with the flowering phenophases: the time taken to reach peak flowering was significantly longer on LSM than on ESM isoclines. Other studies have noted this (Galen & Stanton 1995; Hüüber et al. 2006; Wipf 2010) and, for example, Wipf (2010) reported that early season phenophases are more affected by the timing of snowmelt than by temperature. Nevertheless, in later phenophases, temperature has a stronger effect on both Alpine and Andorran snowbeds.

The time between snowmelt and peak flowering did not differ significantly between the snowmelt isoclines in the studied snowbeds, although the time elapsed between the cessation of leaf expansion and flowering was longer at LSM than ESM sites. Plants at LSM sites flowered in late summer when the air temperatures were decreasing and accumulated temperatures were lower than at ESM sites. It is likely that the low input of thermal energy at LSM sites was responsible for this delay in the flowering phenophases, which negatively affected the success of sexual reproduction, because fructification and fruit dispersal occurred just before the new snowfall (onset of winter). Thus, it appears that the onset of winter (a stochastic event) dictates the sexual reproductive success of plants at LSM sites.

Given that the growing season was longer at ESM than at LSM sites, it is plausible that increases in global temperatures – thereby causing an earlier retreat of the snow – led to a lengthening of the growing season at LSM sites and therefore greater sexual reproductive success. Nevertheless, in most alpine species, reproduction is generally clonal rather than sexual.

Table V. Hierarchical partitioning analysis of the factors considered (year, site, snowmelt isocline, and plot) explaining the variance (%) in the time required to reach phenophases (cessation of leaf expansion and flowering) in the four commonest species (Gnaphalium supinum, Mucizonia sedoides, Poa alpina and Sedum alpestre) occurring in two snowbeds in the Andorran Pyrenees.

| Species  | Phenophase               | n  | Variance explained (in %) | Year | Site | Snowmelt isocline | Plot |
|----------|--------------------------|----|---------------------------|------|------|------------------|------|
| Gnaphalium supinum | Cessation of leaf expansion | 80 | 37.1                      | 42.1 | 9.7 | 47.6             | 0.6  |
|          | Flowering                | 57 | 20.0                      | 43.0 | 7.9 | 47.0             | 2.1  |
| Mucizonia sedoides | Cessation of leaf expansion | 72 | 71.0                      | 66.2 | 7.0 | 26.7             | 0.1  |
|          | Flowering                | 52 | 18.7                      | 59.6 | 22.4| 9.7              | 8.3  |
| Poa alpina | Cessation of leaf expansion | 42 | 40.1                      | 27.4 | 27.4| 44.4             | 0.8  |
|          | Flowering                | 52 | 36.9                      | 46.6 | 28.5| 27.1             | 2.8  |
| Sedum alpestre | Cessation of leaf expansion | 91 | 92.7                      | 12.9 | 48.0| 38.9             | 0.2  |
|          | Flowering                | 46 | 58.2                      | 56.0 | 26.8| 16.7             | 0.5  |

Note: Significant terms (p < 0.05) are given in bold.

Table VI. Nonparametric one-way ANOVA of the time taken to reach each phenophase on three snowmelt isoclines in two snowbeds in the Andorran Pyrenees.

| Species | Phenology (days)                      | n  | χ² value | P-value |
|---------|--------------------------------------|----|----------|---------|
| SA      | Snowmelt to the cessation of leaf expansion | 94 | 36.42    | 0.001   |
|         | Leaf expansion to flowering           | 48 | 3.55     | 0.168   |
|         | Snowmelt to flowering                 | 48 | 8.78     | 0.012   |
| MS      | Snowmelt to the cessation of leaf expansion | 69 | 5.89     | 0.052   |
|         | Leaf expansion to flowering           | 54 | 12.79    | 0.001   |
|         | Snowmelt to flowering                 | 54 | 14.63    | 0.001   |
| GS      | Snowmelt to the cessation of leaf expansion | 79 | 1.22     | 0.542   |
|         | Leaf expansion to flowering           | 61 | 1.47     | 0.478   |
|         | Snowmelt to flowering                 | 61 | 10.62    | 0.004   |
| PA      | Snowmelt to the cessation of leaf expansion | 48 | 0.16     | 0.923   |
|         | Leaf expansion to flowering           | 39 | 5.83     | 0.054   |
|         | Snowmelt to flowering                 | 39 | 2.63     | 0.268   |

Notes: P-values for significant terms are indicated in bold. SA, Sedum alpestre; MS, Mucizonia sedoides; GS, Gnaphalium supinum; PA, Poa alpina.
than sexual (Bliss 1960; Lluent 2007); therefore, vegetative growth phenophases may be more important than flowering phenophases (Wipf 2010).

In our study, the differences in the durations of the phenophases (cessation of leaf expansion and flowering) between the three snowmelt isoclines were probably the product of the phenotypic plasticity of the plants and their adaptive responses to environmental variability (Post et al. 2008). At LSM sites, species have to adapt to having relatively less time to reach leaf expansion but cannot reduce the amount of time needed to reach flowering because of the fall in temperatures in late summer.

Species-specific phenology responses

We found that Poa alpina – but not Mucizonia sedoides, Sedum alpestre, or Gnaphalium supinum – was highly conservative in its phenological responses to differences in snowmelt isoclines in these snowbeds. Probably, these three other species are better adapted to variations in the timing of snowmelt than this grass. Many studies have demonstrated the strong phenotypic responses of plant species to changes in their environment (Arft et al. 1999; Peñuelas & Filella 2001; Peñuelas et al. 2002; Hülber et al. 2006), and, typically, such phenological responses are highly species-specific, even among closely related taxa (Miller-Rushing & Primack 2008).

In two of the snowbed species (Mucizonia sedoides and Sedum alpestre), the flowering period was shortest at LSM sites, which enabled them to maximize the period for seed maturation and conferred an advantage on the sites where snowmelt occurs later in the season. Thus, site-specific factors such as the effects of isocline or climate in a given year on the timing of snowmelt can influence the competitive advantage of some species.

In our study, the year had a significant effect on the phenologies of all of the snowbed plants evaluated and on the duration of the growing season, which indicates that interannual variation in climate has a significant effect on the phenology of these plants. Domènech (2012) found a close relationship between annual climate and the number and extent of snowbeds in the Pyrenees and suggested that changes in climate will have a strong influence in the future on Pyrenean snowbeds. Interaural variation in climate is common in the Pyrenees (López Moreno et al. 2009) and in many other mountainous areas such as the Alps (Hülber et al. 2011) and will probably increase in the near future. Changes in climate (above all, temperature and precipitation) will affect the snowpack (Scott & Billings 1964; Tieszen 1975; Evans & Fonda 1990; Auerbach & Halfpenny 1991; Cess et al. 1991; Walker et al. 1993; Stanton et al. 1994) and the rate of snowmelt (affected by air temperature), which, in turn, will modify the timing of snowmelt and, consequently, the nature of the growing season.

Conclusions

In two snowbeds in the Andorran Pyrenees, (1) site-specific factors (microtopography and snow origin) had significant effects on the timing of snowmelt, (2) the timing of snowmelt had a greater effect on plant phenologies than accumulated temperature at early snowmelting sites, (3) the timing of snowmelt had a significant effect on leaf expansion and flowering schedules, (4) species richness and abundance were greater at early snowmelt isoclines, and (5) species differed in their reactions (shortening or lengthening the duration of the phenophases) to differences in the timing of snowmelt, probably, because of differences in their phenotypic responses.

In summary, this study showed that, in addition to the effects of interannual variation in climate, site-specific factors had a significant effect on snowbed plant diversity and on the phenology and reproduction of the commonest plants in snowbed communities in the Pyrenees. Hence, site-specific factors may influence – and accentuate – the effects of climate change on alpine plants given that they encourage a diversity of environmental microvariations. Thus, these environmental microvariations could act as a source of survival possibilities for plantation snowbeds in the future.

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