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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 (micro-topography 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 inter-annual 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 and Guisan 2001, Grabherr 2003, Hülber et al. 2006) and, above all, to those such as snowbed plants that depend on snow cover for protection against harsh weather (Schöb et al. 2009, Björk and Molau 2007, Nagy 2006). Global circulation models forecast an increase in temperatures of 1.4–5.8ºC (IPCC 2007) during the twenty-first century and in the Pyrenees the mean annual temperature is expected to increase by 2.5–5ºC (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 (EEA 2004, Stanton et al 1994, Walker et al. 1993, Beniston et al. 2003, 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 et al. 2010).

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

The timing of snowmelt (Galen and Stanton 1995, Körner 2003, Hülber et al. 2010, Hülber et al. 2006, Totland and Alatalo 2002) and the temperature during the growing season (Kudo and Hirao 2006, Molau et al. 2005, Hülber et al. 2006, Körner 2003) have a significant effect on plant development and phenology in alpine snowbeds. Numerous studies have demonstrated the influence of the timing of snowmelt and temperature on species richness and plant cover in snowbeds (Lluent 2007, Hülber et al. 2011) and have indicated 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 micro-topography and snow origin on the phenology of alpine plants (Kudo and Hirao 2006, Hülber et al. 2010, Lluent 2007).

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 and 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 (1º 28' 48.1079''; 42º 37' 1.7774'') at an elevation of 2,525 m a.s.l. and Arbella (1º 29' 24.1448''; 42º 39' 3.2380'') at an elevation of 2,475 m. a.s.l. (Fig. 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, while in Arbella the snowbed is fed by snow from avalanches. These snowbeds have slope aspects of 15-22º and 20-30º, 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, 2012).

Data collection

In 2009, we established 36 permanent plots (50x50 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-m^2 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, USA, range -40º to +85º) were placed on each of the three isoclines in each snowbed. From June 2010 to October 2011, soil surface temperatures were recorded at 3-hour 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 determined the main peak flower opening to have occurred when more than 70% of the species had entered the flowering phenophase or when more than 70% of individuals of each species were in the flowering phenophase. In addition, we documented the abundance of the four most common species in both of the snowbeds; viz., *Sedum alpestre*, *Mucizonia sedoides*, *Gnaphalium supinum* and *Poa alpina*. Plant identification and nomenclature follows Bolòs 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 (ºC) 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. To estimate the independent explanatory power of each predictor variable, we used hierarchical partitioning (Chevan and Sutherland 1991), specifically, the “hier.part” procedure of the “hier.part” package (Mac Nally and Walsh 2005) in R, to obtain a measure of the independent contribution of each variable as a proportion (%) of the total explained variance (Mac Nally and 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, while to assess the co-linearity between the timing of snowmelt and accumulated temperature, a Pearson Chi-squared Test was performed.

Species richness and total plant cover were subjected to an analysis of variance 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, the data were subjected to a Kolmogorov-Smirnov Test. To test for significant differences in species richness and plant cover, we used Tukey's Post-hoc Multiple Comparisons Test.

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 Kruskall-Wallis Test (non-parametric 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 Word Team, 2010).

RESULTS

Timing of snowmelt and accumulated temperature

The earliest snowmelt on ESM isoclines occurred at Cataperdis on 6 July 2010, while the latest on LSM isoclines began at Arbella on 24 August 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 d, ISM sites = 61.75 d and LSM sites = 47.75 d). 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 188ºC (desv=3.77ºC) at an LSM site to 1150 ºC (desv=7.01ºC) at an LSM site (Table 2), but did not vary significantly between years (F= 1.10; p=0.330) or snowbeds (F= 0.62; p=0.460); 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 timing of the snowmelt, while the snowmelt isocline explained a substantial amount of the variance in accumulated temperature over the growing season (Table II).

Species richness and plant cover

Thirty-four 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%±38.72) and were lowest on the LSM isocline (mean richness per plot=4.77±1.70 species, mean plant cover per plot=57.59%±28.12).

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 ISM 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=12.16; p<0.002), between years (Chi= 29.38; p<0.001) and between sites (Chi=4.19; p=0.040). This period was significantly shorter on LSM isoclines than on either ESM (4.87 d) or ISM isoclines (6.64 d). In 2010, this period lasted 6.34 d longer than in 2011 and, on average, was 2.49 d longer at Cataperdis than at Arbella.

The period from the cessation of leaf expansion to peak flowering differed significantly between snowmelt isoclines (Chi= 8.03; p<0.010) and between years (Chi= 15.64; p<0.001), but not between sites (Chi= 0.77; p=0.370). This period was significantly longer on LSM isoclines than on either ESM (8.82 d) or ISM isoclines (6.84 d), and was 4.37 d longer in 2011 than in 2010.

The period from the end of snowmelt to peak flowering differed significantly between sites (Chi=5.43; p<0.010) but not between years (Chi=1.49; p=0.220) or snowmelt isoclines (Chi=1.85; p=0.390), and was significantly shorter (4.06 d) in the plots at Arbella than at Cataperdis.

The mean accumulated temperature at the cessation of leaf expansion in ESM plots (131 ºC) was significantly (F = 4.55; p<0.010) higher than in LSM plots (85ºC). The mean accumulated temperature at peak flowering in the plots on ESM isoclines (212 ºC) was significantly higher than on ISM isoclines (148 ºC), 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 (Fig. 2) and the number of flowering species was greater on ESM than on LSM isoclines. The flowering period was, respectively, 17.5 d and 38 d 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 d) and *S. alpestre* and *M. sedoides* (14 d and 21 d, 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, micro-topography 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 d later in 2010 than in 2011; consequently, the accumulated temperature was higher in 2011. At the ESM site at Cataperdis, snowmelt occurred 7 d later in 2011 than in 2010, and so the accumulated temperature was higher. 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 mid-summer, the effective accumulated temperature increases at a constant rate, initially, but then decreases (Kudo and 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 and Hirao 2006).

Species richness and plant cover

In the snowbeds in the Andorran Pyrenees, the diversity of vascular plants and the amount of plant cover were correlated with the snowmelt isocline gradient; specifically, diversity and plant cover decreased between early and late snowmelt isoclines, a finding that has been observed elsewhere (Totland and Alatalo 2002, Lluent 2007). Abiotic factors such as water content, nutrient fixation capacity and the C/N ratio differ between snowmelt isoclines (Retzer 1956, Billings and 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 the present study, overall plant diversity was highest at ESM sites at both snowbeds. However, the relatively low diversity 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 micro-variations) influence and help maintain the floral diversity of snowbeds. We found that the diversity 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 diversity 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 and 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 (Wipf 2010, Hülber et al. 2006, Galen and Stanton 1995) 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. Furthermore, Kudo and Hirao (2006) have demonstrated the importance of the minimum temperature for the onset of flowering, which might explain why only 50% of the plots at LSM sites in these two Andorran snowbeds reached the flowering phenophase.

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 (Bliss 1960, Lluent 2007) and 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.

As already commented, in these two Pyrenean snowbeds the timing of snowmelt differed between snowmelt isoclines (ESM sites *vs.* LSM sites), which affected the number of species that flowered and the timing of the peak flowering period. Despite this, there were differences between the two snowbeds: the temperature and the timing of snowmelt had a significant influence on phenologies and site-specific factors (probably, the micro-topography and snow origin) were important due to their influence on the timing of snowmelt and accumulated temperature.

Species-specific phenology responses

We found that *Poa alpine* – 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, Hülber et al. 2006, Peñuelas and Filella 2001, Peñuelas et al. 2002) and, typically, such phenological responses are highly species-specific, even among closely related taxa (Miller-Rushing and 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 inter-annual variation in climate has a significant effect on the phenology of these plants. Domènech et al. (submitted) 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. Inter-annual 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 (Johnson and Billings 1962, Scott and Billings 1964, Tieszen 1975, Evans and Fonda 1990, Auerbach and 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 (micro-topography 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 inter-annual 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 micro-variations. Thus, these environmental micro-variations could act as a source of survival possibilities for plant snowbeds in the future.

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Tables

Table I. Timing of snowmelt (Julian date) and accumulated temperature (ºC) on three snowmelt isoclines [late snowmelt (LSM), intermediate snowmelt (ISM) and early snowmelt (ESM)] in two snowbeds in the Andorran Pyrenees.

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

Table II. Hierarchical partioning analysis of the factors considered (year, site and snowmelt isocline explaining the variance (%) in snowmelt date and accumulated temperature in two snowbeds in the Andorran Pyrenees. Values represent a measure of importance that adds up to 100. Significant factors (p<0.05) are given in bold.

		Hierarchical partitioning		
	Variance explained (%)	**Year**	**Site**	**Snowmelt isocline**
Snowmelt date	**15.2**	6.0	**36.3**	**57.7**
Accumulated temperature	**16.6**	1.5	2.5	**96.0**

Table III. Species recorded in the two snowbeds studied in the Andorran Pyrenees in 2010 and 2011. The species present only in the Cataperdis or Arbella snowbeds are indicated by a superscript C and A, respectively.

Species	
Agrostis rupestris	*Mucizonia sedoides*
Arabis alpina	*Murbeckiella pinnatifida*
Armeria maritima	*Nardus stricta*
Androsace carnea	*Polytrichum sexangulare*
Alopecurus gerardii^{A}	*Polytrichum piliferum*
Anthelia juratzkana	*Pohlia drumondi*
Cardamine bellidifolia	*Kiaeria starkei*^{A}
Carex pyrenaica	*Oreochloa disticha*^{A}
Cerastium cerastoides	*Poa alpina*
Cryptogama crispa^{A}	*Polytrichum piliferum*
Epilobium anagalifolium	*Polytrichum sexangulare*
Festuca glacialis^{C}	*Sedum alpestre*
Gnaphalium supinum	*Sagina saginoides*
Hieracium gr. pilosella	*Saxifraga stellaris*^{A}
Leucanthemopsis alpina	*Sibbaldia procumbens*
Luzula alpinopilosa^{A}	*Veronica alpina*
Minuartia recurva	*Veronica nummularia*

Table IV. Species richness (mean richness and standard deviation per plot of all species, vascular plants, 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

Table V. Hierarchical partioning analyisis 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 Significant terms (p<0.05) are given in bold.

				Hierarchical partitioning			
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	38	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

Table VI. Non-parametric one-way ANOVA of the time taken to reach each phenophase on three snowmelt isoclines in two snowbeds in the Andorran Pyrenees. P-values for significant terms are indicated in bold. SA *Sedum alpestre*; MS *Mucizonia sedoides*; GS *Gnaphalium supinum* and PA *Poa alpina*.

Species	**Phenology (days)**	**n**	**Chi^2 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

Figure captions

Figure 1. Location of the two snowbeds in the Andorran Pyrenees (black dots).

Figure 2. Peak flowering at early (ESM isoclines) and late (LSM isoclines) snowmelt plots in two snowbeds (Cataperdis and Arbella) in the Andorran Pyrenees in 2010 and 2011. Flowering duration at Cataperdis in 2010 and at ESM sites was 7 weeks, 4 in 2011. Flowering duration at Cataperdis in 2010 and at LSM sites was 2 weeks, 3 in 2011. Flowering duration at Arbella in 2010 and at ESM sites was 7 weeks, 7 in 2011. Flowering duration at Arbella in 2010 and at LSM sites was 3 weeks, 2 in 2011.

Figure 1.

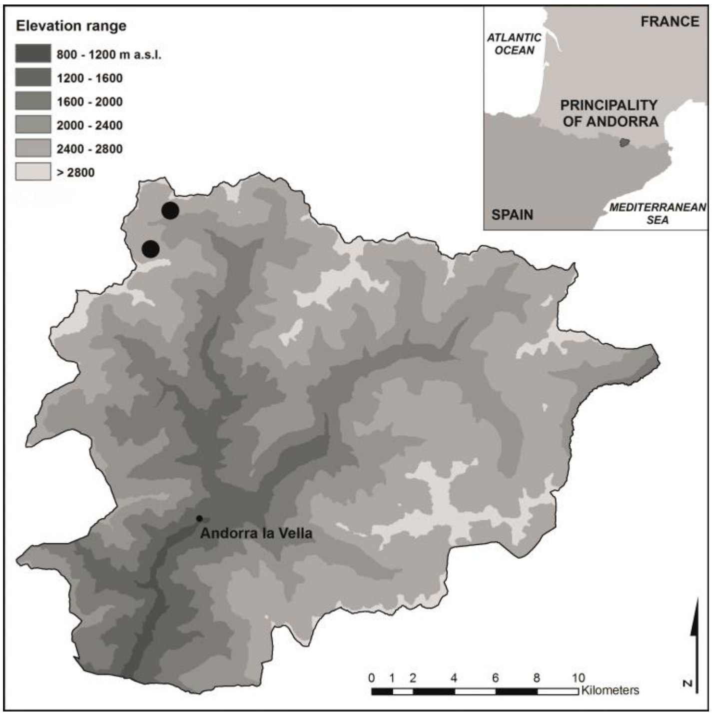
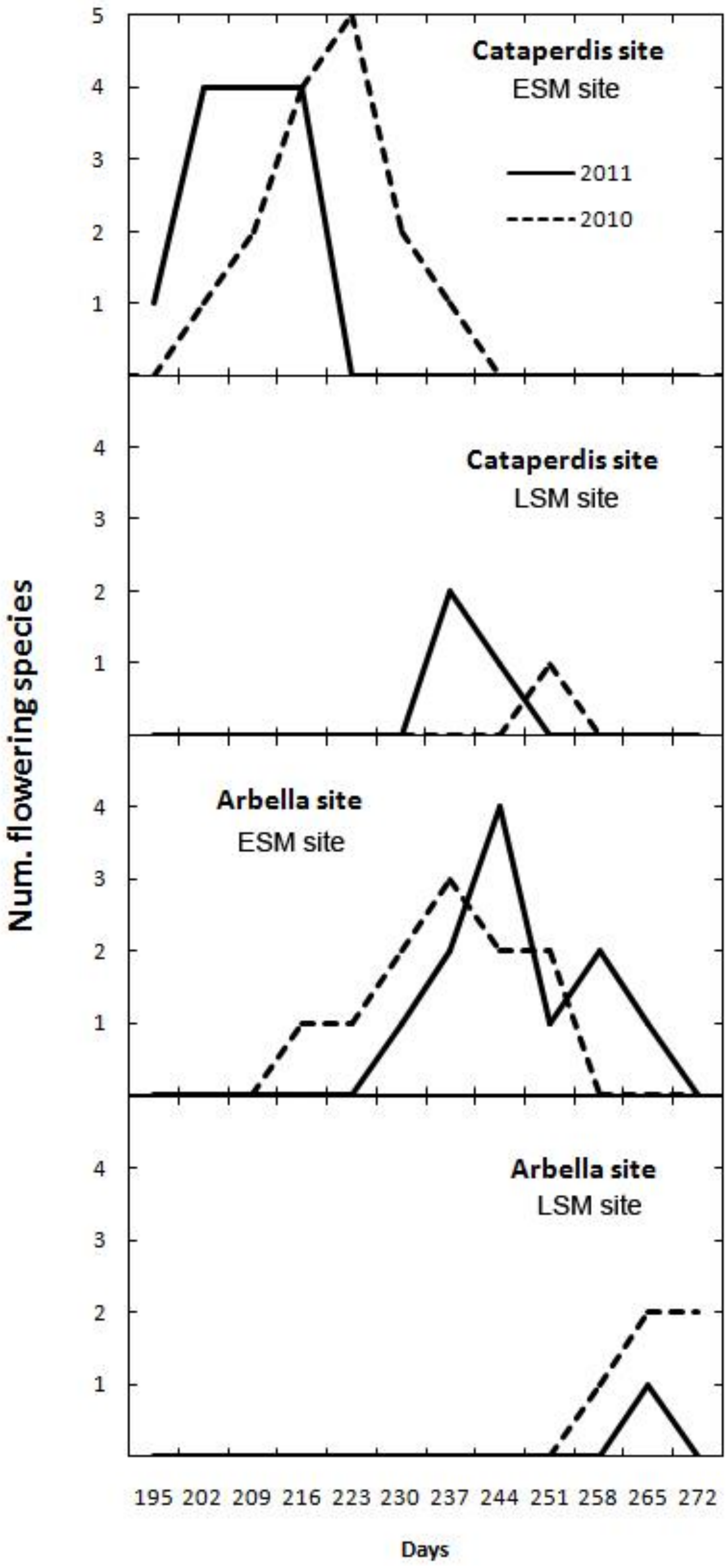

Elevation range
800 - 1200 m a.s.l.
1200 - 1600
1600 - 2000
2000 - 2400
2400 - 2800
> 2800
FRANCE
ATLANTIC OCEAN
PRINCIPALITY OF ANDORRA
SPAIN
MEDITERRANEAN SEA
Andorra la Vella
0 1 2 4 6 8 10
Kilometers
N

Figure 2.


Cataperdis site
ESM site
2011
2010
Cataperdis site
LSM site
Arbella site
ESM site
Arbella site
LSM site
Num. flowering species
5
4
3
2
1
195 202 209 216 223 230 237 244 251 258 265 272
Days

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