



Phenology and seed setting success of snowbed plant species in contrasting snowmelt regimes in the Central Pyrenees

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ABSTRACT

Plant growth and performance in snowbed communities are strongly influenced by the length of the growing period remaining after the snowmelt date. Under the scenario of climate change, studying the phenological responses of snowbed species to variations in snowmelt date might be crucial to understand their ability to adapt and survive under changing conditions. We studied 13 plant species from contrasting biological and ecological groups (i.e. 'snowbed specialists', 'preferential species' and 'generalist species') growing in four snowbed plots with siliceous substrates in the Central Pyrenees. These species were monitored for two consecutive years and in two different microsites, namely the central part and the peripheral part of each snowbed plot. We characterised their phenological cycle and length and their success in seed setting, measured as the number of individuals succeeding in dispersing their seeds.

Phenology and cycle length did not differ greatly between locations for any of the species, but their success in setting seeds was variable. We did not find substantial differences in species' cycle length under varying snowmelt regimes (neither between years nor between microsites); this lack of differences was more evident for snowbed specialists. Moreover, this group showed shorter cycles and less ability to modify their phenology with varying snowmelt regimes than generalist species and some of the preferential species. These two latter groups showed a trend towards reduced success in setting seeds with retarded snowmelt, but the plant community structure exerted a complementary effect on seed setting which in some cases was even greater than snowmelt date. The ability to produce and disperse seeds seems to be a less conservative feature than cycle length in snowbed plants. Thus, their adaptation to future climate changes might take place as a result of variations in their reproductive performance rather than in the modification of their phenological cycle. In addition, shifts in plant community composition as a result of environmental changes might be of special importance in the behaviour of these species.

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Introduction

In alpine landscapes snowbeds represent a singular habitat, mainly characterised by a short growing season determined by the snowmelt date, which has a strong influence on plant growth and phenology (Bell and Bliss, 1979; Billings and Bliss, 1959; Bliss, 1971; Holway and Ward, 1965; Kudo et al., 1999; Kudo, 1991; Totland and Alatalo, 2002). Species inhabiting snowbeds are thus adapted to short summers and other environmental constraints such as poorly developed soils, but they are also favoured by other factors such as the protection afforded by snow against winter frost or by the absence of water shortage (Bell and Bliss, 1979; Billings and Bliss, 1959; Gjørevoll, 1956; Kudo and Hirao, 2006; Ostler et al., 1982; Retzer, 1956).

Many species (mainly boreo-alpine taxa), encounter their southern distribution limits in mid-latitude mountain ranges like the Pyrenees; thus, the snowbed ecosystem in this region is particularly singular and vulnerable. Due to the environmental particularities of snowbeds, the number of taxa inhabiting them is quite low and some of the species and communities are markedly restricted to these habitats (Braun-Blanquet, 1948; Dullinger et al., 2000; Illa et al., 2006; Keller et al., 2005; Ninot et al., 2013). These restrictive species, or 'snowbed specialists', co-occur in the snowbeds with 'preferential' and 'generalist' species, according to studies dealing with vegetation structure (Braun-Blanquet, 1948; Lluent, 2007).

Snowbed specialist taxa are very diverse in terms of functionality. Some species have been described to have a remarkable ability to grow at the start of the growing season, whereas others stay green under the snow during winter (Bell, 1974), present permanent seed banks (Onipchenko et al., 1998; Lluent, 2007) or have enhanced diaspore wind dispersal (McGraw and Antonovics, 1983; Ninot et al., 2013). Although snowbed species are poorly competitive in conditions of average snowmelt calendar (Hülber et al.,

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2011; Wijk, 1986), they predominate where snow accumulates and stays very long on the ground, thanks to their ability to cope with the particular environmental conditions found in this harsh habitat (Schöb et al., 2009). Nevertheless, because of the sharp environmental gradient between those areas where snow melts in the early summer and the snowbed cores, grassland species and species typical of rocky patches may also establish in snowbed communities (Carbognani et al., 2012; Galen and Stanton, 1995; Heegaard and Vandvik, 2004), whilst some snowbed species may occur in cleared patches within grasslands (Evans et al., 1989; Heegaard, 2002).

Since high mountain temperatures are predicted to increase in mid latitudes (ACIA, 2005; Esteban et al., 2010; IPCC, 2007) and snow is predicted to melt earlier in the future (Beniston et al., 2003), snowbed plants might experience phenological changes which might, in turn, cause distributional changes in the snowbed communities. Snowbed specialist taxa are especially vulnerable in this context of climate change (Björk and Molau, 2007; Hülber et al., 2011; Schöb et al., 2008, 2009), since the climate shifts will also enhance changes in the role of transitional species and non-chionophilous ones. Some studies have emphasised the threat that warming represents for snowbed specialists through the increased competitiveness of species from less snow covered areas and grasslands (Dullinger et al., 2012; Grabherr, 2003; Hülber et al., 2011; Schöb et al., 2009).

The study of the performance of snowbed species in relation to variations in the snowmelt date and different snowmelt regimes is crucial to better predict and understand possible future changes in plant species performance and shifts in community structure. Although some of these species have been widely studied in terms of adaptive traits and reproductive biology (Baptist et al., 2010; Galen and Stanton, 1995; Huelber et al., 2006; Inouye, 2008; Kawai and Kudo, 2011; Kudo, 1991, 1992; Wijk, 1986), the specific features of the reproductive cycle of chionophilous plants still remain poorly understood. Moreover, little is known about how the inter-annual variations in the snow cover regime cause changes in the performance of the species by means of primary productivity, flowering success and seed setting or dispersal, amongst other aspects. The relationship between the life cycle of snowbed plants and environmental variables, and the extent to which these variables contribute to explaining the dominance of strict chionophilous plants in snowbeds, require further research in order to understand and predict the vegetation response to a changing climate (Björk and Molau, 2007).

The aim of this study was to analyse the response to different snowmelt regimes of several silicicolous snowbed species (from strictly chionophilous to generalist taxa) with regard to their main reproductive traits, namely flowering, fruiting and seed dispersal. The snow regimes were distinguished by a) two distinct scenarios of snow persistence over winter as a consequence of different meteorological conditions in two consecutive years, and by b) spatial variability in snowmelt caused by the heterogeneity of communities' distribution at a small scale (i.e. central vs. peripheral areas of the snowbed). For each species, several populations under the combination of these different snow cover regimes were considered.

Our primary hypotheses were that (i) specialist species will present faster reproductive cycles (from flowering to seed dispersal) and (ii) a longer snow cover period will favour the success in seed setting of snowbed specialists with respect to non-chionophilous plants.

Materials and methods

Study area

The study was conducted during 2004 and 2005 at four snowbed plots with siliceous substrate located in the Central Pyrenees, along

the main range and between Val d'Aran (Catalonia) and Andorra. The four plots were: Lac Redon (UTM ED50, 31T CH18212307; 2260 m a.s.l.), Port de Ratera (31T CH32951887; 2520 m a.s.l.), Coll de Creussans (31T CH74702165; 2615 m a.s.l.) and Estany de Juclar (31T CH94401746; 2240 m a.s.l.), here referred as Redon, Ratera, Creussans and Juclar, respectively. Despite the noticeable differences in altitude between plots, their main climatic parameters do not differ greatly. A detailed environmental characterisation of three of the snowbed plots (Redon, Ratera and Creussans) is given in Lluent (2007) and partially in Illa et al. (2011). Environmental data, including soil temperature and moisture, air temperature, radiation, and pluviometry were exhaustively recorded over the study period by means of micrometeorological stations covering the snowmelting gradient. The winter snow depth in the study plots was variable according to topography, but in most cases it reached from 3 to 7 m in their central parts. During the snow cover period, temperatures on the ground layer remained near zero, and ranged between 10 °C and 15 °C for most of the summer (and from 5 °C to 25 °C as frequent minima and maxima, respectively). Summer rainfall (July, August and September) mostly ranged between 170 and 270 mm (140–334 as extreme values). Since rain events were fairly evenly distributed, the soil remained from moist to very humid throughout the growing period in the plots studied. Very rarely, the water potential was lower than field capacity (–33 kPa) and only on very few occasions did it reach values between –120 kPa and –200 kPa.

Snow fall and accumulation were greater in 2004 than in 2005, and thus the vegetation remained covered by snow for a longer period during the first year. Thus, in 2004 the plant populations studied started their growing period between the end of June and mid August (depending on the melting gradient), and between the end of May and early August in 2005.

The four plots lie in typical, mostly rugged alpine landscapes and contain high plant diversity, due to physiographic and microclimatic heterogeneity. This diversity is evidenced by the presence of various plant communities, such as dwarf heaths, mesoxerophilous open grasslands, mesophilous grasslands and snowbed carpets. Regarding the snowmelt gradient, the plant communities found in the four plots could be characterised through the amount of degree-days (the sum of the positive centigrade degrees measured over total number of days; Bliss and Gold, 1999) they experienced over the study period. According to data given by Lluent (2007) they can be sorted as follows: Hieracio-Festucetum supinae Br.-Bl. 1948 (mesoxerophilous open grassland; 1250–1500 degree-days) > Leontodo-Caricetum curvulae Br.-Bl. 1948 ~ *Festuca nigrescens* grassland ~ Nardion strictae Br.-Bl. 1926 (mesophilous grasslands; 1000–1300 degree-days) > Anthelio-Salicetum herbaceae Br.-Bl. 1948 (snowbed carpet with *Salix herbacea*; 900–1000 degree-days) > Gnaphalio-Sedetum candollei Br.-Bl. 1948 (snowbed carpet with *Sedum candollei*; 800–900 degree-days).

Sampling strategy

We evaluated the vegetation occurring in each snowbed plot and selected a pool of species to monitor their phenology. This set consisted of all the species occurring along the snowmelting gradient in at least three out of the four snowbed plots, as well as *Plantago alpina* and *Salix herbacea*, which were only found in two of them but which showed a high cover in both. Moreover, they are both typical species of Pyrenean snowbeds (Braun-Blanquet, 1948; Carrillo and Ninot, 1992). This resulted in the selection of 13 species, namely *Cardamine bellidifolia* L. ssp. *alpina* (Willd.) B.M.G. Jones (hereafter shortened as *Cardamine alpina*), *Carex pyrenaica* Wahlenb., *Cerastium cerastoides* (L.) Britton, *Epilobium anagallidifolium* Lam., *Euphrasia minima* Jacq. ex DC., *Gnaphalium supinum* L.,

Table 1
Biological and ecological characteristics of the species studied: family, life form (Th, therophyte; Hng, non-graminoid hemicryptophyte; Hg, graminoid hemicryptophyte; Chr, creeping chamaephyte), plant height (of upper leaves), lateral expansion (1, none; 2, few resprouts to short distance; 3, many to short distance), prevailing regeneration strategy (asp, annual seed production; psb, permanent soil seed bank; wwd, wide wind dispersal; ve, vegetative expansion), life strategy (C, competitive; S, stress-tolerant; R, ruderal), ecological preference (Spec., snowbed specialist; Pref., snowbed preferential; Gen., generalists more frequently found in grasslands, grsl, or in rocky sites, rck).

Species	Family	Life form	Plant height (mm)	Lateral expansion	Regeneration strategy	Life strategy	Ecological preference
<i>Cardamine alpina</i>	Brassicaceae	Hng	15	2	psb	CSR	Spec.
<i>Carex pyrenaica</i>	Cyperaceae	Hg	55	3	asp, ve	S/CSR	Pref.
<i>Cerastium cerastoides</i>	Caryophyllaceae	Chr	29	2	psb	SC	Pref.
<i>Epilobium anagallidifolium</i>	Oenotheraceae	Hng	36	2	wwd	S/CSR	Pref.
<i>Euphrasia minima</i>	Orobanchaceae	Th	24	1	asp	SR	Gen. (grsl)
<i>Gnaphalium supinum</i>	Asteraceae	Hng	13	2	wwd, psb, ve	R/CSR	Pref.
<i>Murbeckiella pinnatifida</i>	Brassicaceae	Hng	39	2	psb	S	Gen. (rck)
<i>Nardus stricta</i>	Poaceae	Hg	61	3	asp, ve	SC	Gen. (grsl)
<i>Plantago alpina</i>	Plantaginaceae	Hng	32	2	asp	S	Gen. (grsl)
<i>Salix herbacea</i>	Salicaceae	Chr	22	2	wwd, ve	CSR/SC	Spec.
<i>Sedum candollei</i>	Crassulaceae	Th ^a	14	1	psb	SR	Spec.
<i>Sibbaldia procumbens</i>	Rosaceae	Hng	21	2	psb	SC	Spec.
<i>Veronica alpina</i>	Orobanchaceae	Hng	33	2	psb	S	Spec.

^a Although classified as a therophyte in standard floras, this study shows that *Sedum candollei* behaves as a semelparous paucennial species.

Murbeckiella pinnatifida (Lam.) Rothm., *Nardus stricta* L., *Plantago alpina* L., *Salix herbacea* L., *Sedum candollei* Raym.-Hamet, *Sibbaldia procumbens* L., and *Veronica alpina* L.

This group of species included a variety of types in terms of biological traits and ecological preferences, as synthesised in Table 1. Some of the traits listed in this table come from standard floras (family, life form; Bolòs et al., 2005) or from more specific literature (lateral expansion; Ninot et al., 2013), whereas others have been directly determined. Plant height was obtained from direct measuring of the height reached by the upper leaves in a number (12–15) of field or herbarium samples; regenerative strategy was attributed from data on alpine soil seed banks (Cerberolini et al.,

2003; Marcante et al., 2009; Ninot et al., 2013; Semenova, 2004) and from direct observations of space dispersal attributes, according to Grime (2001); and life strategy was obtained from the application of the criteria set by Grime (2001), considering the mentioned plant traits and other related biological aspects. Ecological preference reflects the characterisation given in former floristic and phytosociological works (Bolòs et al., 2005; Carrillo and Ninot, 1992; Illa et al., 2006; Lluent et al., 2004) and was refined by taking into account the phytosociological information from the BDBC data bank (Font, 2011). Namely, we sorted the 13 species studied according to their relative occurrence in snowbeds from a pool of 1600 relevés taken in the alpine belt of the Catalan Pyrenees; five species had at least

Table 2
Number of individuals analysed for each species, and plant communities where they occurred, in each of the four plots, in their peripheral (P) and central (C) parts. Plant communities are: G-S, snowbed carpet with *Sedum candollei* (Gnaphalio-Sedetum); A-S, snowbed carpet of *Salix herbacea* (Anthelio-Salicetum); L-C, *Carex curvula* grassland (Leontodo-Caricetum); Na, *Nardus stricta* grassland (Nardion); Fn, *Festuca nigrescens* grassland; H-F, *Festuca airoides* grassland (Hieracio-Festucetum).

Species	Creussans		Juclar		Ratera		Redon	
	P	C	P	C	P	C	P	C
<i>Cardamine alpina</i>	15 Na	15 G-S	30 Fn	30 G-S	30 A-S	30 G-S	30 Na	30 G-S
<i>Carex pyrenaica</i>	– –	– –	30 Fn	30 G-S	30 A-S	30 G-S	30 Na	12 G-S
<i>Cerastium cerastoides</i>	15 G-S	30 G-S	30 G-S	30 G-S	30 A-S	30 G-S	– –	– –
<i>Epilobium anagallidifolium</i>	– –	– –	30 G-S	30 G-S	30 A-S	25 G-S	15 Na	30 G-S
<i>Euphrasia minima</i>	30 H-F	19 G-S	– –	– –	30 L-C	24 A-S	30 Na	– –
<i>Gnaphalium supinum</i>	30 Na	30 G-S	30 Fn	30 G-S	30 L-C	30 G-S	30 Na	30 G-S
<i>Murbeckiella pinnatifida</i>	30 Na	30 G-S	30 Fn	30 G-S	– –	– –	30 G-S	30 G-S
<i>Nardus stricta</i>	30 Na	30 G-S	– –	– –	30 L-C	30 A-S	30 Na	15 G-S
<i>Plantago alpina</i>	– –	– –	– –	– –	30 L-C	30 A-S	30 Na	30 G-S
<i>Salix herbacea</i>	30 H-F	30 A-S	– –	– –	30 G-S	30 A-S	– –	– –
<i>Sedum candollei</i>	15 G-S	30 G-S	30 G-S	– –	30 G-S	24 G-S	15 Fn	– –
<i>Sibbaldia procumbens</i>	15 A-S	30 G-S	– –	– –	17 A-S	2 G-S	30 Na	30 G-S
<i>Veronica alpina</i>	– –	– –	30 G-S	30 G-S	30 A-S	30 G-S	30 G-S	30 G-S

Table 3

Phenological phases used in the field data collection (left column) and for data elaboration (right column). Phases in bold are those used in our analyses to characterise phenology and to study cycle length and seed setting.

(0) Without new shoots, only remnant parts of the previous year	Sterile
(1) Growth start. First buds appearance	
(2) Vegetative individual, still sterile	
(3) Flower buds	Flower buds
(4) Flowering start, with open flowers and flower buds	Flowering
(5) Flowering maximum. All or almost all flowers opened	
(6) Fruiting start. First fruits appear but the individual still has flowers or undeveloped fruits	Fruit ripening
(7) Fruiting. All fruits are formed but still immature	
(8) Opened fruits or diaspores disseminated	Seed dispersal
(9) Senescence	Senescence

66% of their occurrences in relevés of the class Salicetea herbaceae (i.e. more than 64 occurrences over 96 relevés), and thus may be taken as snowbed specialists; four species showed clearly lower occurrence percentages (27–47%) to the same class – but still far lower percentages to other classes – and were taken as plants which preferentially grow in snowbeds (preferentials); and the remaining four species had a much lower frequency in this class (3–16%), being more frequently found in grassland or in rocky sites, and we thus considered them generalists.

For each snowbed plot and species we labelled 30 individuals in the central part of the snowbed and 30 in the peripheral part, and we considered these two groups as subpopulations in two different microsites, within the same whole population corresponding to each snowbed plot. Where it was impossible to find 30 individuals, we labelled and monitored the maximum number possible, generally more than 15 (Table 2). The two subpopulations in each plot generally occurred in distinct plant communities, related to variations in the snowmelt date, and these also differed among plots (Table 2).

The labelling was carried out in 2004 during the snowmelt, and we monitored the same individuals during the snow-free periods in 2004 and 2005 except where a labelled individual died. We visited the sites every 2 weeks to record the phenological status of each individual. We divided the cycle into ten phases similar to those defined by Price and Waser (1998), and tried to accurately record the phenological phase of each individual at each sampling date. When plants were found to present two phases simultaneously, we recorded the most advanced. We assumed a lineal succession between these ten phases to interpolate the start of flowering, fruiting or seed dispersal when they occurred between our sampling dates. Then, we simplified the ten phase division into a six phase system, to facilitate comparison and elaboration of data (Table 3). Finally, we defined the three main phases on which most of the study would be based: flowering, fruit ripening and seed dispersal, the latter corresponding to cycle completion.

Data analysis

We analysed the reproductive phenology, cycle length and success in seed setting of each species comparing both sampling years (2004 or 2005) and microsites (centre or periphery), and taking the snowbed plots as replicates. To characterise the phenology we used the percentage of individuals reaching each phase. In all cases we considered the main three phenological phases (flowering, fruiting and seed dispersal) separately to observe any possible trends in succeeding more in one phase than another or in completing them faster or slower. We considered cycle length as the number of days needed to reach the last phenological phase for those individuals

that completed the cycle, and we calculated this by pooling the data of all the individuals studied in all the snowbed plots, separating microsite and year of study. We calculated the success in seed setting as the percentage of individuals completing the cycle, so we already had one value per snowbed plot, and then, we obtained the mean values. In addition, we used degree-days to conduct comparative analyses of cycle length, since these provide a better evaluation of the energy needed.

Although all the species studied were characterised phenologically during the recording period, ultimately it was not possible to use *Euphrasia minima*, *Plantago alpina*, *Salix herbacea* and *Sedum candollei* for the statistical analyses of cycle length and success in seed setting when pooling all the localities together. We excluded *Plantago alpina* and *Salix herbacea* because they only occurred in two snowbeds and thus we only had two replicates for these species. Similarly, since *Euphrasia minima* presented minimal reproduction at Redon, only two snowbed plots with data remained. Finally, we excluded *Sedum candollei* because of its low seed setting, which rendered our data too poor to perform any analysis.

We analysed cycle length and success in setting seeds data for the effects of a longer snow cover by means of a 2-way ANOVA with Type III Sum of Squares, using microsite and year as binary fixed factors. We analysed whether the two response variables – cycle length and success in seed setting – differed between both microsites and between both years, and we tested for interactions between these factors. The response variables were transformed when necessary by square root or log 10 transformations to reach normality and homogeneity of variance.

The relationships between cycle length or seed setting and snowmelt date were tested with linear regression analyses.

Analyses were performed using PASW STATISTICS 17.0 (SPSS Inc., 2009).

Results

Snowmelt regimes were consistent between microsites (centre and periphery) for the studied plant populations and showed

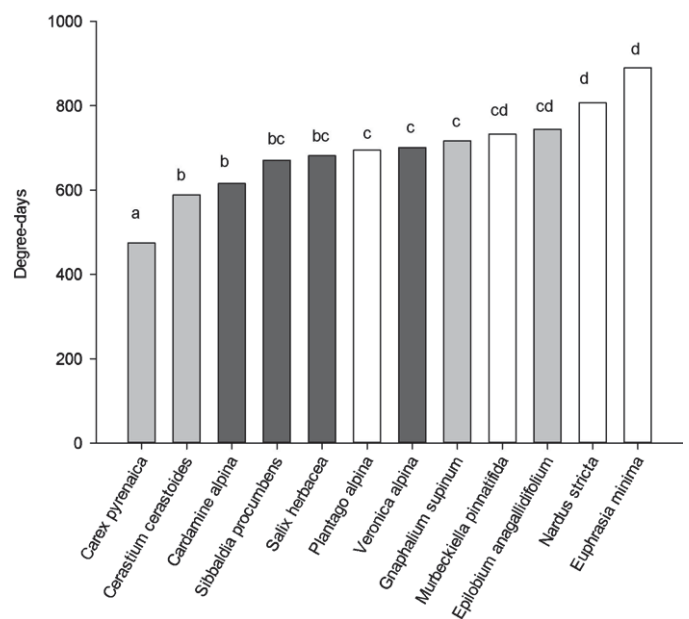


Fig. 1. Cycle length of the species studied, measured as degree-days, pooling together data for the different localities, microsites and years. Different letters indicate significant differences in the mean values, and bar shading identifies the three ecological preferences considered (see Table 1). Dark grey, snowbed specialists; light grey, snowbed preferentials; white, generalist taxa.

no remarkable differences between the four replicates. Pooling together data for both years for each subpopulation, snowmelt occurred $19.5 (\pm 11.2)$ days sooner in 2005 than in 2004, and $21 (\pm 9)$ days sooner in the peripheral subpopulations than in the central ones.

Subsequently, we characterised the reproductive phenology of the species studied, taking snowmelt as the starting point. In the following sections we analyse the cycle length and success in seed setting of each species for each year and microsite and the variations in this success related to variations in the snowmelt date.

Reproductive phenology and cycle length

The performance of each species was very similar between the different localities. In addition, the length of each phenological phase, as well as the overall cycle length, did not differ between microsites (centre or periphery) or between years in almost any of the species (Table 4), although there was a tendency to extend the reproductive cycle with a longer growing season, and in the peripheral areas of the snowbed in some plots.

According to the cycle length values, the species can be distributed into four significantly different groups, which are only partially related to the ecological groups considered (Fig. 1). Whereas generalist taxa showed long cycles, except for *Plantago alpina*, which showed an intermediate cycle length, snowbed specialists were moderately fast and snowbed preferentials showed a high heterogeneity, including relatively slow species as well as the two fastest ones.

A general overview of the phenological patterns of the species studied is given by the calendar distribution of the number of individuals reaching each phase (flowering, fruit ripening and seed dispersal), as shown in Fig. 2.

Cardamine alpina was one of the fastest species monitored, which might be due to the overwintering of some of its leaves. The fruiting maximum was achieved 25–30 days after the snowmelt by individuals in the centre of the snowbed plots, and by 40 days after the snowmelt by those on the periphery. In 2005, individuals in the centre took about 3 days longer to complete this phase. Nevertheless, the length of each phenological phase did not differ significantly between microsites or years (Table 4).

Of all the species studied, *Carex pyrenaica*, which also has overwintering leaves, was the one with the shortest cycle, which lasted 39–44 days (Table 4). Some individuals presented the earliest flowering start within all the species studied (5 days after snowmelt), and flowering and fruit maturation were short phases in this species. The fruiting period was longer in 2004 than in 2005, but the overall cycle length was not significantly different between both years. However, this species showed quite remarkable differences between years or plots. For instance, seeds in Juclar were dispersed 31 days after the snowmelt in 2004 but 47 days after in 2005.

Cerastium cerastoides also had a short cycle. Flowering was longer than in *Carex pyrenaica*, lasting 24–28 days (Table 4). Fruit maturation started approximately 40 days after the snowmelt and capsules only took 10 days to open. The whole cycle lasted 52–55 days and it was not affected either by the microsite or by the year.

Epilobium anagallidifolium had a relatively long cycle. Since it did not start flowering until the whole vegetative part was generated, this phase occurred quite late (mean values around 30 days after the snowmelt). However, some individuals started flowering much earlier (around 10 days).

Euphrasia minima presented the longest cycle of all the species studied, reaching 150 days in the peripheral part of Creussans in 2005. Flowering maximum took place at 40–47 days after the snowmelt at the centre and between 50 and 60 days after on the periphery. Capsule ripening was quite fast (12–16 days). Due to the late blossom, the entire cycle lasted more than 2 months, from an

average of 68 days in the central part in 2004 to an average of 93 days in the outer part in 2005.

Gnaphalium supinum flowering was slightly faster in 2004 than in 2005. Maximum fruiting was earlier in 2004 (around 45 days after snowmelt) than in 2005 (around 53 days), and lasted longer in the latter (12 days in 2004 and 23 days in 2005). Individuals growing in the central part in 2004 presented the fastest cycle (55 days), whereas individuals in the same location in 2005 were the slowest ones (68 days). In 2005, the cycle was longer in the central parts, but shorter considering degree-days (727 degree days in the centre, 750 on the periphery). However, we did not find significant differences, either between microsites or between years (Table 4).

Murbeckiella pinnatifida was an early flowering species (some individuals started flowering 5–10 days after the snowmelt). First fruits appeared around 30 days after the snowmelt. Reaching seed dispersal was quite slow, which is the reason why the cycle lasted about 60 days in the central parts and 63–67 on the periphery.

Nardus stricta presented a long flowering phase. The fruit maturation period lasted around 20 days. The overall cycle took 66–76 days to be completed, which is quite long. Individuals at the centre were a bit faster than those on the periphery, but these differences were not significant.

Plantago alpina started flowering when the first leaves appeared, which took place 5 days after the snowmelt in the centre and 10 days after the snowmelt on the periphery. In 2004, flowering lasted less time than in 2005 (10 days and 18–20 days, respectively). Fruit maturation maximum occurred slightly later on the periphery and, whereas in 2005 fruit maturation lasted 23 days, in 2004 it lasted 28 and 38 days (centre and periphery, respectively). The cycle was longer in 2004 (64 days) than in 2005 (58 days), but none of these differences were significant.

We studied *Salix herbacea* by means of ramets, since we could not distinguish individuals in this clonal species. Flowering length was very variable and it was always shorter at the centre. Fruit maturation started 20 days after the snowmelt in the centre and 35 days on the periphery. However, the peripheral subpopulations only included a few female individuals, so data were poorly representative. Fruit maturation lasted 23 days (2005) and 34 days (2004) in the centre, although the same amount of degree-days was needed. On the periphery, only one out of the two individuals studied completed the cycle. The cycle lasted 60 days (2004) and 53 days (2005) in the centre of the snowbed.

Sedum candollei showed an unexpected response. Although considered an annual species in standard floras (e.g. Bolòs et al., 2005), the data obtained in this study revealed that it behaves as a semelparous perennial, since the same individuals studied in 2004 were present in 2005, and basal rosettes were already present 1 or 2 days after the snowmelt. In addition, the proportion of individuals that flowered and fruited was extremely low or even zero. In 2004 none of the individuals located in the central part of the snowbed plots flowered, and only a couple of those growing on the periphery did so. In 2005 some individuals flowered in the central parts of Creussans and Ratera (those with less snow) but none flowered in Redon and Juclar. At the outer parts, some individuals flowered in every snowbed plot. Only nine individuals completed the cycle during the study period, and it was very long, lasting more than 100 days.

Sibbaldia procumbens showed variable flowering patterns. Flowering maximum took place around 20 days after the snowmelt in the centre but around 30 days outside. The maximum number of individuals bearing fruits occurred at 45–50 days in 2004 and at 35–40 days in 2005. Nevertheless, fruit maturation was slightly faster in 2004 than in 2005. Cycle length did not present any trend between microsites or years.

Veronica alpina flowering length was longer on the periphery than in the centre (Table 4). Flowering started around 22 days after

Table 4

Time required (in days after snowmelt) for reaching each phenological phase, and success (in percentage of individuals) achieving the same phases in the species studied, in each microsite (C, centre; P, periphery) and year, expressed as mean values and standard error. M* indicates significant differences for microsite, and Y* for year, at $p < 0.05$.

Species	Flowering				Fruiting				Seed dispersal				
	Days after snowmelt		% individuals		Days after snowmelt		% individuals		Days after snowmelt		% individuals		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
<i>Cardamine alpina</i>													
2004	C	14.67	2.04	89	11	29.50	1.33	80	10	55.19	1.35	42	15
	P	16.84	1.30	63	17	29.84	1.97	56	13	52.59	2.95	45	15
2005	C	18.91	3.31	68	14	31.32	4.18	58	17	53.63	0.93	26	13
	P	19.66	2.72	61	10	34.38	4.02	54	13	52.42	3.51	43	14
<i>Carex pyrenaica</i>													
2004	C	13.98	2.72	89	5	28.08	1.48	89	05	39.10	1.64	81	9
	P	22.34	4.09	47	25	33.59	1.97	40	20	44.70	1.23	36	16
2005	C	11.02	2.45	93	2	22.74	2.66	89	3	40.56	3.51	74	5
	P	14.94	1.67	46	21	27.17	2.41	42	21	39.07	4.41	41	20
				M*		Y*		M*				M*	
<i>Cerastium cerastoides</i>													
2004	C	24.79	0.87	80	8	44.20	1.88	60	20	53.45	1.12	33	20
	P	25.83	1.18	68	17	43.87	0.94	39	11	52.54	0.91	37	13
2005	C	28.18	3.22	71	11	44.29	3.63	52	13	55.65	5.37	43	19
	P	27.12	1.18	51	22	42.75	1.03	38	25	53.35	2.43	37	25
<i>Epilobium anagallidifolium</i>													
2004	C	27.86	4.35	60	25	42.63	2.69	50	23	55.90	0.00	11	11
	P	32.78	3.64	59	16	45.66	1.72	53	15	63.90	4.28	23	5
2005	C	27.76	3.08	82	13	44.11	4.06	69	23	67.80	1.11	44	25
	P	29.92	2.54	70	16	45.45	1.15	63	19	70.45	2.49	32	22
<i>Gnaphalium supinum</i>													
2004	C	26.77	0.74	32	9	43.47	1.40	31	8	54.60	1.10	13	8
	P	27.65	2.49	14	4	41.29	1.78	12	3	60.38	3.83	11	3
2005	C	30.70	4.19	44	6	47.20	4.26	33	9	67.31	3.74	23	9
	P	30.21	2.70	36	7	45.45	3.24	33	5	64.37	4.18	28	5
				Y*									
<i>Murbeckiella pinnatifida</i>													
2004	C	19.74	5.06	61	4	32.54	3.32	56	5	60.01	3.68	18	7
	P	15.38	0.91	64	14	28.43	2.20	63	13	67.02	6.52	47	20
2005	C	19.30	3.41	68	6	31.07	3.82	66	7	60.81	6.15	32	10
	P	18.44	2.68	62	14	33.44	3.32	57	15	63.09	5.46	47	20
<i>Nardus stricta</i>													
2004	C	34.44	3.84	60	15	55.65	5.27	53	12	66.61	4.82	38	22
	P	38.87	2.50	67	13	60.14	3.64	61	13	76.19	3.39	48	9
2005	C	33.55	4.00	77	10	57.28	3.07	64	8	72.93	0.83	57	7
	P	33.96	1.47	72	5	53.70	4.80	69	4	74.03	4.40	62	1
<i>Sibbaldia procumbens</i>													
2004	C	19.27	1.92	61	7	32.84	2.47	60	7	56.78	1.43	50	0
	P	26.98	3.73	32	12	39.53	2.73	32	12	63.38	4.23	30	12
2005	C	17.95	0.93	81	9	29.64	3.49	80	11	61.75	3.72	79	12
	P	19.17	1.78	44	11	31.86	1.61	43	12	57.64	1.60	43	16
				M*				M*				M*	
<i>Veronica alpina</i>													
2004	C	22.97	1.07	63	13	42.56	1.01	49	20	57.27	1.27	14	11
	P	30.38	3.29	56	6	45.48	2.73	49	7	63.57	4.70	41	6
2005	C	23.04	3.39	78	9	43.06	4.11	48	3	63.16	4.93	22	11
	P	26.08	1.21	71	6	39.65	2.23	56	6	65.10	4.45	34	3
		M*											

the snowmelt in the central parts and around 30 days outside. Fruit maturation length was also very variable, between 13 and 20 days. Cycle length took 57–65 days.

At the species level, the time required to complete the reproductive cycle was observed to be shorter after later snowmelt dates in

most of the species. When plotting values for different microsites and years together, the correlation between snowmelt date and cycle length varied between species (Table 5) although it showed negative values for most of them. *Epilobium anagallidifolium* was found to have a significantly negative correlation ($R^2 = -0.76$),

followed by *Veronica alpina* ($R^2 = -0.62$). *Nardus stricta*, *Gnaphalium supinum* and *Murbeckiella pinnatifida* also presented a negative correlation, although not particularly strong ($R^2 = -0.39, -0.25, -0.14$, respectively). *Sibbaldia procumbens* showed no correlation between snowmelt date and cycle length and *Cardamine alpina* and *Carex pyrenaica* gave very low values. *Cerastium cerastoides* also presented a poor relationship, although in this case it was positive ($R^2 = 0.07$).

Seed setting

Success in seed setting varied greatly between species, from the lowest values in *Sedum candollei* to the highest in *Carex pyrenaica*, but was relatively low in all the species studied (Table 4). In general, earlier snowmelting promoted a higher seed setting success, since values were lower in 2004, when 35% of all the individuals dispersed seeds, than in 2005, when 42% reached this phase

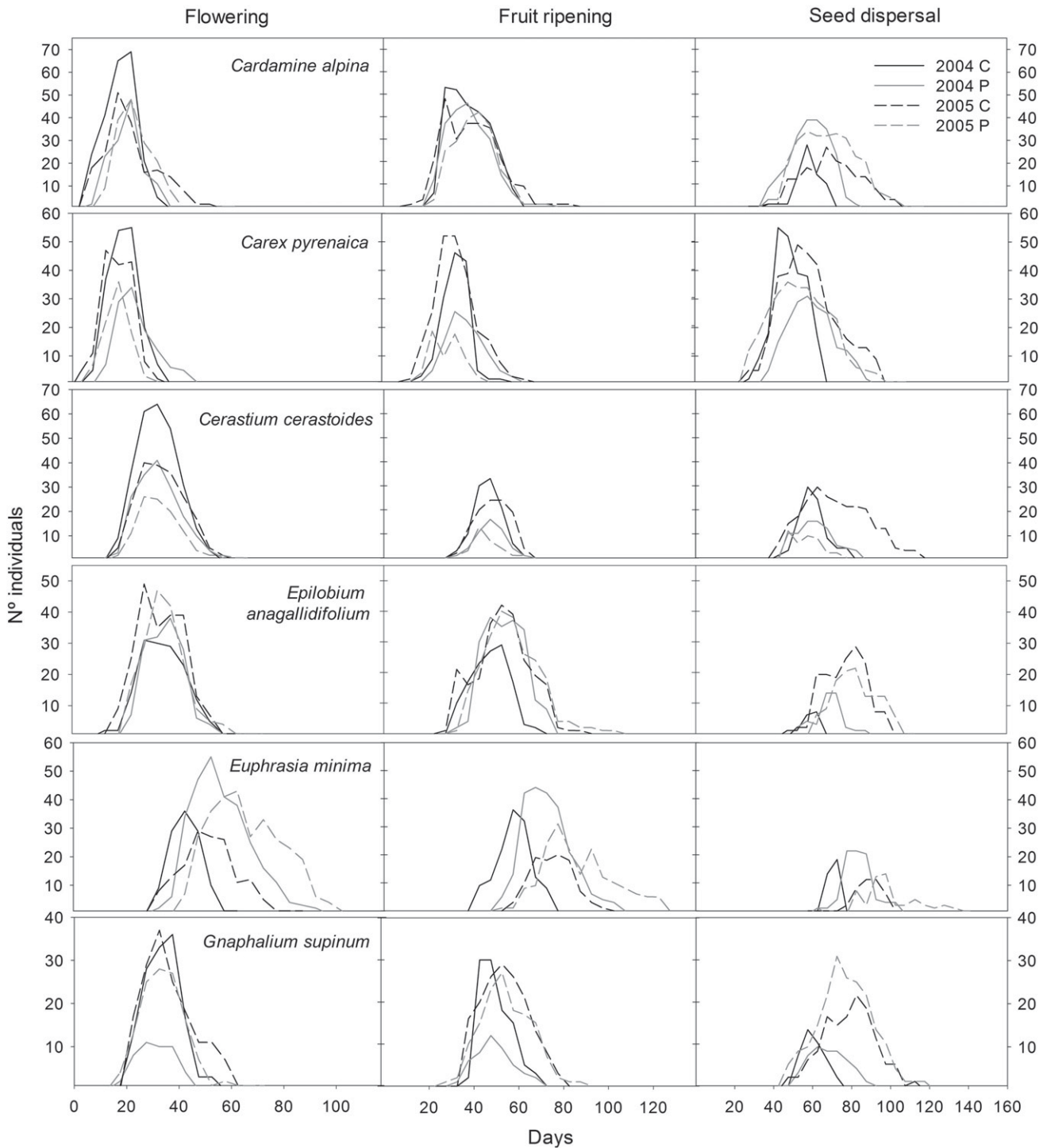


Fig. 2. Development through the growing period (in days after snowmelt) of the main three phenological phases (flowering; fruit ripening; seed dispersal) in the species recorded (except for *Sedum candollei*, due to its poor results), evaluated as total number of individuals over the plots studied, under the four conditions considered (2004 and 2005 years, central and peripheral locations – C and P).

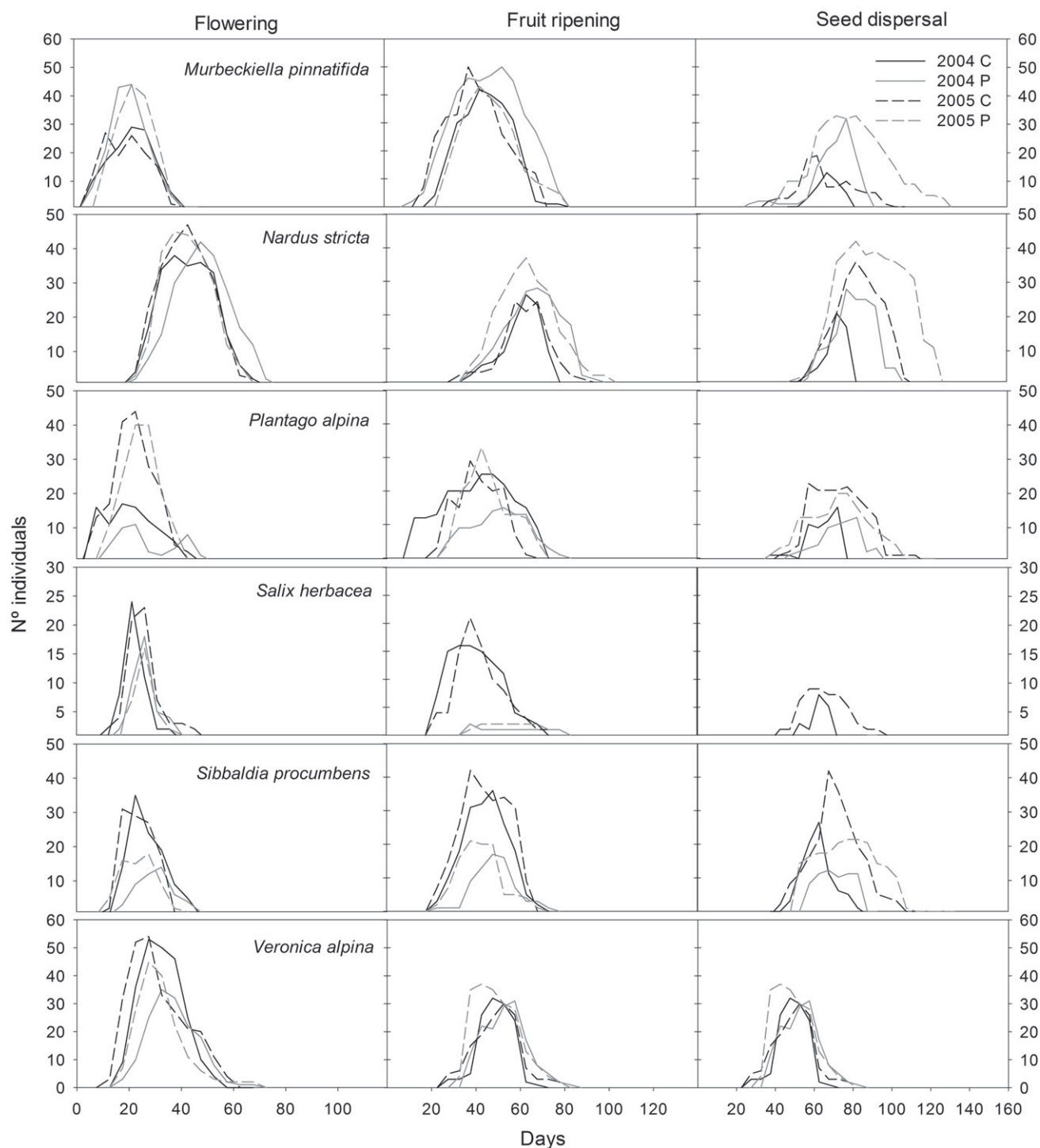


Fig. 2. (Continued).

(see also Table 5). 22% of individuals completed the cycle both years, which was a significantly higher proportion than would be expected (about 14%) if there were independence in the probability of reaching maturity for each individual between years.

Despite this tendency towards increased success in setting seeds with an earlier snowmelt, in general species showed little statistical difference in their success between either microsites or years when plotting all localities together (Table 4). Indeed, the only species showing a significant difference between microsites, *Carex pyrenaica* and *Sibbaldia procumbens*, presented precisely the opposite behaviour, increasing their seed setting success in the central parts

of the snowbed. *Gnaphalium supinum* was the only species that showed a greater number of individuals flowering in 2005 than in 2004. However, these differences were not maintained in the subsequent phenological phases, and seed setting success was similar for both years and microsites.

When plotting values for each microsite and year together for each species, the success in setting seeds was found to be negatively correlated with the snowmelt date in most of the species (Table 5). *Cerastium cerastoides* showed the lowest R^2 value ($R^2 = -0.51$), followed by *Epilobium anagallidifolium* and *Gnaphalium supinum*. *Carex pyrenaica* was the only species that seemed to be favoured by a

Table 5
Responses (R^2 values after linear regression) of cycle length and seed setting to snowmelt date for the species statistically analysed; and comments on their success in seed setting related to microsite (P, periphery; C, centre) and to vegetation structure (with the plant communities abbreviated as in Table 2).

Species	Cycle length	Seed setting	Effects of microsite or vegetation structure
<i>Cardamine alpina</i>	−0.03	−0.19	Contrasting preference for C or P depending on plots, and no clear effect of the vegetation structure
<i>Carex pyrenaica</i>	−0.07	0.47	Always higher success in C than in P, coinciding with contrasting vegetation structure (open G-S vs. denser N, A-S or Fn)
<i>Cerastium cerastoides</i>	0.07	−0.51	Variable response to microsite, and no clear effect of the vegetation structure
<i>Epilobium anagallidifolium</i>	−0.76	−0.43	Higher success in P than in C, but in Ratera site the trend was the opposite; probably favoured by vegetation structure (open G-S vs. dense A-S)
<i>Gnaphalium supinum</i>	−0.25	−0.42	Higher success in C than in P, probably related to contrasting vegetation structure (open G-S vs. denser N or Fn)
<i>Murbeckiella pinnatifida</i>	−0.14	−0.22	Variable response to microsite depending on plots, and no clear effect of the vegetation structure
<i>Nardus stricta</i>	−0.39	−0.19	Variable response to microsite and vegetation structure
<i>Sibbaldia procumbens</i>	0.00	−0.05	Generally higher success in C than in P, coinciding with contrasting vegetation structure (open G-S vs. denser A-S or N)
<i>Veronica alpina</i>	−0.62	−0.39	Variable response to microsite depending on plots, and no clear effect of the vegetation structure

late snowmelt, since it presented a positive correlation between snowmelt date and seed setting success ($R^2 = 0.47$, Table 5). On the other hand, *Sibbaldia procumbens* did not show a significant correlation between snowmelt date and seed setting success, although from Table 4 we might have expected a similar behaviour as in *Carex pyrenaica*. This is explained by the variation in the data when pooling microsite and year together, and it does not account for the real events (see next paragraph).

Most of the species responded to a retarded snowmelt date with decreased success between years of study, but some species presented heterogeneous responses and some variability between localities (Fig. 3). Plant species assemblage at small scale differed between localities and microsites and thus, the behaviour of the species might also be affected by their neighbour plant species and not only by the snowmelt date.

Discussion

Reproductive success

Although the success in setting seeds was very high in some subpopulations for some species (*Cardamine*, *Carex*, *Cerastium*, *Epilobium*, *Murbeckiella*, *Sibbaldia*), the mean percentages of most species was rather low. Except for *Sedum candollei* (with very low success) and *Carex pyrenaica* (the most successful species), the mean percentage of individuals which dispersed seeds ranged between 18% and 50%. Thus, in the best case, only half of the investigated individuals (i.e. selected as well-established adults) completed their reproductive cycle, but this percentage was generally much lower. Similar reproductive values have also been found for snowbed species in previous studies (Huelber et al., 2006; Kudo and Hirao, 2006).

Sexual reproduction may remain as relatively secondary in the dynamics of alpine perennial species, for which strong vegetative persistence and expansion is an important way to maintain populations (Bell and Bliss, 1980; Bliss, 1971; Molau, 1993). However, seed production and dispersal would be crucial in short-lived species, and are also important in the rest of species for an enhanced intraspecific variability and for the eventual colonisation of new habitats (Klady et al., 2011; Steltzer et al., 2008; Stöcklin et al., 2009). Therefore, the role of seeds may have a particular relevance for snowbed specialists in relation to the variations in distribution and extension presented by snowbeds over time following climate changes (Stehlik, 2003). In fact, snowbed specialists would take advantage of permanent soil seed banks (Ninot et al., 2013), which prevail as the main regeneration strategy for the majority of the specialists monitored in this study. In contrast, reproductive

success in the snowbed habitat might not be so relevant for generalist and preferential species, since their snowbed subpopulations may regenerate by seed immigration from larger neighbouring non-snowbed populations (Dullinger et al., 2011; Shimono et al., 2009).

Therefore, yearly seed production represents one of the snowbed species' sexual strategies, but even for the specialists this is only one part of their overall adaptive strategy. Some specialists (e.g. *Salix herbacea*) seem to largely depend on strong persistence and longevity in combination with clonal growth, whereas other specialists regenerate mostly from dense persistent seed banks, which may vary irregularly between years, depending on environmental conditions. The most extreme case was that of *Sedum candollei*, which showed very low seed production during the years recorded in all the different snow conditions, but maintained a dense viable soil seed bank (Lluent, 2007).

Thus, the final success of the species and populations studied in a given plot may be considered as only partly dependent on their reproductive phenology and success. This might help to explain why the results obtained do not give clear patterns (e.g. discrimination between specialists and non-specialists). In addition, since most of the species studied are perennials, some of them long-lived, the seed set in a given year is partly determined by the life history of each individual rather than by current year's events (Rose et al., 1998; Watkinson and White, 1986). The relevance of the individual life cycle would be also the reason of the lower differences in seed setting success that was generally found in the same subpopulation between the two study years, than those found between neighbouring central and peripheral subpopulations, although the differences in melting date within each couple were similar.

According to the data obtained in 2004 and 2005, the species studied seem to produce seeds yearly at population level, since no clear shifts were recorded between years or between plots. Probably, the few short-lived species present amongst the studied species (mainly *Euphrasia minima* and *Sedum candollei*) produce high amounts of seeds in particularly favourable years. This would be in accordance with the low success achieved in the study years (locally in *Euphrasia minima*, which showed a strongly variable response; generalised in *Sedum candollei*) and the high concentration of viable seeds of these species found in the soil at the same plots (Lluent, 2007).

Seed setting success of snowbed species has been described as highly variable, depending on the actual fine-scale conditions experienced by each individual (Kameyama and Kudo, 2009; Kudo and Hirao, 2006). This was also evidenced in our study by strong heterogeneity between individuals throughout the 2 years monitored. Competition with other plants and specific snowmelting

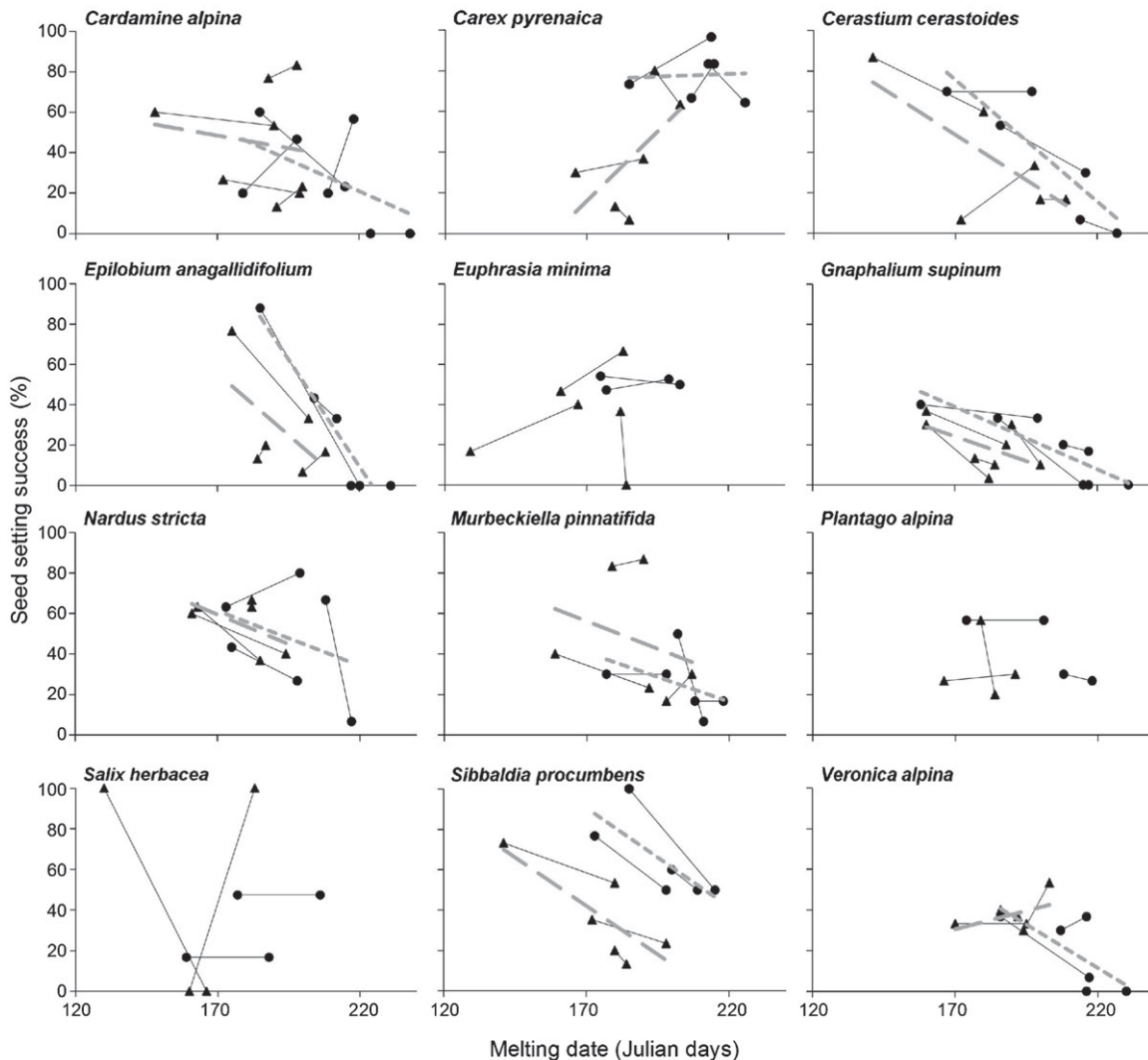


Fig. 3. Relationship between melting date (Julian day) and reproductive success (percentage of individuals reaching seed setting) in each year and in the two subpopulations (central or peripheral) for the species recorded in all the plots studied. Each solid line corresponds to one subpopulation, and connects the data corresponding to the 2 years considered (in which 2004 experienced retarded melting dates compared to 2005); and dotted lines draw general tendencies in central and peripheral subpopulations through plots. Triangles and short-dashed lines correspond to peripheral subpopulations whereas circles and long-dashed lines correspond to central subpopulations.

conditions seem to strongly determine seed setting (Huelber et al., 2006; Kudo, 1991). In our study, late snowmelt led to lower seed production in the populations of a great number of the species through a decrease in the individuals' seed setting and the shortening of their reproductive period. This, in turn, resulted in lower seed production. Only some chionophilous species with a short cycle (clearly *Cardamine alpina* and *Carex pyrenaica* in some localities) seemed to be generally unaffected by a shortened growing period, and even favoured by a retarded snowmelt (*Cardamine alpina* in Redon). These results do not support our second hypothesis that a late snow cover would indirectly enhance the seed setting of snowbed specialists by means of negatively affecting the performance of generalist species, since the results were not significant in most cases. On the other hand, the competition exerted by neighbouring species in denser or taller plant cover microsites explained the lower success in seed setting of some subpopulations, and this effect was proved to be stronger than snowmelt date in some cases (e.g. *Carex pyrenaica* or *Cardamine alpina* and *Cerastium cerastoides* in Ratera). Whereas the *Gnaphalio-Sedetum* seems to be a more suitable habitat for the studied species, denser communities such as the *Anthelio-Salicetum* or *Nardion* grasslands apparently are less favourable for seed setting. The low canopy

and moderate ability for lateral expansion of most specialists and preferentials provides little competitive ability against grassland species (e.g. *Nardus stricta*). Even the dense carpets of *Salix herbacea* seem to hamper the success of other snowbed plants.

The response at the species level was rather variable between subpopulations, which might partly be the result of these microscale effects (the effect of neighbouring plants or the microtopographic differences in snowmelt). In addition, mesoscale effects may influence the subpopulation structures of some generalist species, because these might be maintained by strong immigration from non-snowbed populations, being unsustainable at the subpopulation level (Kudo, 1991).

Cycle length

Thermal conditions vary at micro- and mesoscale, modifying the cycle length over the period that remains after snowmelt. Warmer patches related to microtopographic factors lead to shorter cycles in the species occurring in snowbeds, compared to colder patches, as cycle length is based on a species-specific accumulative threshold of degree-days during the growing period (Illa et al., 2011; Lluent, 2007).

Snowbed specialists showed a shorter cycle length compared to the generalists, as stated in our first hypothesis. Preferentials showed a short or a rather long cycle length depending on the species. Snowmelting in mid-August as the latest is the limit for reaching maturity in at least one individual per subpopulation in all the species studied. *Carex pyrenaica* was the only species that reached some success when the snow melted later than August 4. In fact, this sedge has been shown to be a very plastic species, since some greenhouse-germinated seeds were able to develop into mature individuals setting seeds within the same growing period (unpublished data). With a shorter growing period, most of the species shortened their life cycle at subpopulation level, although this was more evident in those with a longer cycle. This shortening is due to two factors: (i) the days at mid-summer – those occurring after late snowmelting – are warmer than in early summer. As a result, the number of days needed for maturation is lower (Lluent, 2007), and (ii) only the fastest individuals in each subpopulation were considered, since only these could reach maturity. Thus, the species found to be prone to shorten their cycle following late snowmelting actually corresponded to those with more phenological heterogeneity at population level. Therefore, the species with shorter cycles (*Cardamine alpina*, *Carex pyrenaica*, *Cerastium cerastoides*, *Sibbaldia procumbens*) showed lower heterogeneity in this aspect at the subpopulation level, and were less dependent on the length of the growing period. On the other hand, species with a longer cycle (*Nardus stricta*, *Epilobium anagallidifolium*, *Murbeckiella pinnatifida*, *Gnaphalium supinum*) were able to shorten the cycle at the subpopulation level through higher heterogeneity, the slower individuals remaining sterile.

Concluding remarks

The snowbed plant species studied formed a heterogeneous assembly of plants which did not constitute a true functional group, nor showed a coincident phenological strategy. Some of them (*Cardamine alpina*, *Cerastium cerastoides*, *Sibbaldia procumbens*, *Murbeckiella pinnatifida*, *Gnaphalium supinum*) showed an opportunistic trend, denoted by a better seed production in good years and in less dense plant cover at small scale, i.e. taking advantage of space and time windows to strongly regenerate their permanent soil seed bank. *Carex pyrenaica*, *Veronica alpina*, *Sedum candollei* and *Cardamine alpina* were particularly tolerant to the stressful environment of the snowbeds due to their short cycle or other adaptive traits. This was most evident in *Sedum candollei*, which behaved as a semelparous pauciennial, since it is known to form a strong soil seed bank despite its very low success in seed setting per individual and year. In contrast, other snowbed plants (*Salix herbacea*, *Plantago alpina*) may be considered competitive due to their longevity and strong persistence, their seed production being less relevant. On the other hand, the generalist species (*Nardus stricta*, *Euphrasia minima*, *Murbeckiella pinnatifida*) form an even more heterogeneous group concerning reproductive and vegetative strategies. Seed production does not drive their role in snowbeds at larger scale, since these marginal subpopulations are maintained by seed immigration from the neighbouring habitats.

The only general trend found in the chionophilous plants (the specialists and some of the preferentials) seems to be a marked uniformity of cycle length at population scale, generally short or very short, as an adaptive response to the snowbed conditions. These species are not very plastic in terms of extending or shortening their cycle length, and do not substantially respond to interannual variations in snowmelt date or to interspatial snowmelt conditions. This low plasticity could imply that these plants might face difficulties in adapting their life cycle to future changes in snowmelt date (Baptist et al., 2010; Björk and Molau, 2007; Schöb et al., 2009).

Seed setting seems to be a less conservative characteristic than reproductive phenology and cycle length in these species, and it might be a key factor for future adaptations in a changing climate. The effects of plant community structure on species' reproductive success found in this study suggest that future shifts in snowbed habitat composition (Björk and Molau, 2007) might have strong effects on snowbed species' behaviour and success. Therefore, further studies should be carried out in this direction to determine the extent of plant responses to environmental and community changes.

On the other hand, the snowbed habitat has most probably selected for other adaptive traits not considered in this study, such as particular leaf phenology or nutrient dynamics and uptake (Billings and Bliss, 1959; Galen and Stanton, 1995; Mullen et al., 1998; Onipchenko et al., 2009). For instance, the insulation properties of the snow cover promotes the retention of leaves over winter in *Cardamine alpina* and *Sedum candollei*, which is crucial for a quick start of growth just after snow melts, whilst recycling reserves from relatively massive roots or twigs may have a similar effect in *Salix herbacea* and *Plantago alpina*. Thus, reproductive phenology is one of the aspects in which plants may have adapted to particular snowbed habitats, together with other life history traits and population dynamics.

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