Variation in life history traits of *Gentiana nivalis* (Gentianaceae) in alpine and sub-alpine habitats in the Norwegian mountains and its implications for biodiversity in relation to environmental change

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The alpine gentian, *Gentiana nivalis*, is an obligate annual. Because of its complete population turnover every year, it is likely to be more responsive to environmental shifts than are perennials, and also likely to undergo more rapid genetic change in response to selection pressure. The detected morphological differentiation between habitats was related to different proportions of spring- and autumn-germinating individuals with a larger proportion of winter annuals in the subalpine habitats. The spring-germinating annuals that have shorter time for development and have a shorter stature can still develop at the alpine sites where competition is weaker. The subalpine habitats are all semi-natural, shaped by livestock grazing and human activities related to summer farming. Declining human impact is leading to successional changes in the mountain landscape. The future of *G. nivalis* in the light of current trends in landscape development and climate change is discussed.

Introduction

In mountain environments, plants are subjected to contrasting selection pressures at low and high altitudes due to the very different environmental conditions (Körner 1999, Zhigang *et al*. 2006, Haggerty & Galloway 2011). Between subalpine and alpine habitats, that is, below and above tree limit, respectively, the environment of a plant differs, i.e., in terms of local climate with a longer growth season, higher monthly mean temperature, calmer winds, as well as the microclimate with higher and more even soil temperature and soil moisture, and comparatively less light influx due to shading from trees and shrubs at subalpine sites than at alpine sites. However, species composition and abundance of organisms that the plant interacts with (competitors,

herbivores and pollinators) vary along climatic (and edaphic) clines, as do the abiotic conditions (Totland & Eide 1999) and they all may have great impact on the plants' survival and reproduction, particularly in arctic and alpine environments (Molau 1993).

Grazing by vertebrate herbivores has been a significant ecological factor in the Scandinavian mountains since prehistory, although the populations of wild reindeer in northern Scandinavia have been heavily decimated by human hunting (Bevanger & Jordhøy 2004). This long-term grazing pressure has been evident in shaping the biodiversity patterns of mountain plant communities (Austrheim & Eriksson 2001) and contributing to landscape diversity by maintaining grassland habitats (Honnay *et al.* 2006, Mack *et al.* 2013). Grazing by ungulates, including domestic livestock of cattle, sheep and goats, reduces the thickness of litter layer, creates 'safe sites' for establishment of herb species, and decreases the dominance of grasses and sedges, thus increasing biological diversity. This was demonstrated by field experiments in the Scottish mountains by Miller *et al.* (1999) and Miller and Geddes (2004). Long-term livestock grazing in combination with human activities in the context of summer farming has created semi-natural grasslands, open habitats devoid of trees and shrubs in the subalpine region in the Norwegian mountains (Olsson *et al.* 2000). Influence of grazing in the Norwegian mountains is today much weaker than before and is exerted by semi-domestic reindeer and domestic livestock, mainly sheep (Austrheim & Eriksson 2001).

In alpine as well as subalpine habitats most plant species are perennials reproducing by vegetative spread and, more rarely, by seeds (Molau 1993, Karlsson & Callaghan 1996, Körner 1999). However, the importance of sexual reproduction in mountain plants might be equally important as vegetative reproduction for maintaining local vegetation dynamics but closely responding to environmental variation by feedback in seed germination (Weppler *et al.* 2006).

There are a few annual or biennial plants in the arctic and alpine flora, and they merit particular consideration as they do not have life histories typical of tundra plants. In his review on tundra plant reproductive strategies, Molau (1993) considered late-flowering and especially annual plants as "seed riskers" relying mainly on selfing for seed set and risking losing the entire seed crop due to high variability in local climate.

The alpine gentian, *Gentiana nivalis*, is unusual by reproducing annually by seeds alone. Because of its complete population turnover every year, this species is likely to undergo more rapid genetic change in response to selection pressure and to be more responsive to environmental shifts, including livestock grazing pattern, than are perennials. A conspicuous feature of *G. nivalis* is its morphological variability with a mixture of tall- and short-statured individuals as well as uni- and multi-branched plants in both alpine and subalpine habitats. Since each branch is terminated by a flower bud, the number of flowers is directly correlated with the number of branches and thus the reproductive output is highly variable and dependent on the number of branches. Based on those observations in the Norwegian mountain landscapes undergoing successional changes, we formulated the following research questions: (1) Is there a consistent pattern of variation in morphological and reproductive traits of populations of *G. nivalis* in relation to alpine *versus* subalpine habitats? (2) If so, how is the pattern related to life history? (3) What are the possible implications for this species of the ongoing land use and climatic change?

Material and methods

Plant biology and distribution

Gentiana nivalis (Gentianaceae) has an amphi-Atlantic distribution pattern and occurs in the mountains of Scandinavia, Greenland, Iceland, and has very restricted and scattered populations in Britain, the Alps, the Carpathian mountains and along the west coast of Labrador, North America (Hultén & Fries 1986). The plant is a diploid (2n = 14; Hämmerli 2007), annual herb with a height range of 1–20 cm and with erect, often branched stems (Mossberg & Stenberg 2003, Lid & Lid 2005). Leaves are ovate, elliptical, pair-wise on the stem, the basal ones forming a rosette. Flowers have a deep blue corolla,

with five calyx teeth, and the corolla opens only in bright sunshine. All species within *Gentiana* have been documented as facultative hosts for arbuscular mycorrhizae (Harley & Harley 1987, Demuth *et al.* 1989).

Study sites

Eight populations of *G. nivalis* were studied in eastern parts of the Jotunheimen mountain range, mid-Norway (61°37′N, 8°57′E). The current treeline (at 1100–1200 m a.s.l.), which is a result of climatic and human-cultural influences (Wehn *et al.* 2012), is used as distinction between alpine and subalpine sites. The climate in the Jotunheimen mountain region is slightly continental (Odland & Moen 1998) with a low annual mean precipitation of 540 mm (means over the period 1961–1990, Det Norske Meterologiske Institutt unpubl. data), and an annual mean temperature of 1.1 °C (means over the period 1995–2003, Det Norske Meterologiske Institutt unpubl. data). The soils in this region are derived from bedrock composed of archaic gneisses mixed with younger phyllites, sandstones and gabbros, and with intrusions of lime (Siedlecka *et al.* 1987, Lutro & Tveten 1996). The alpine sites often have shallow soil layers (< 20 cm), while the soil generally is deeper (> 50 cm) in the subalpine sites. The soil pH of the study sites ranges from 5.3 to 5.9 (pers. obs.).

The eight study sites are located in four mountain valleys; in each valley one subalpine (SA) and one alpine (A) site was selected (*see* Table 1 for description of the study sites). The subalpine sites are located at the altitudes of 920–1050 m a.s.l., and the alpine at 1290–1330 m a.s.l., respectively. All the subalpine sites are former enclosures of mountain summer farms, and have been used for haymaking and as livestock pastures. There was no fertiliser (inorganic chemicals) application although before 1950 some manuring (dung) occurred during the haymaking period (O. Sandbu, Vågå, pers. comm.). The alpine sites are all unfertilised and have never been manured. Today all sites are grazed by sheep and to some extent by reindeer (Table 1). However, some sites also experience grazing pressure from cattle, horses or goats

Table 1. Characteristics of the study sites. STU = Stuttgongi, SMÅ = Smådalen, PRI = Prinsehytta, DYR = Dyrtjørnbekken, BES = Besstrondfjellet, SMØ = Smørli, FAL = Fallet, TJØ = Tjørnosdalen.

Valley no. and site	Subalpine habitats				Alpine habitats			
	1. STU	2. SMÅ	3. PRI	4. DYR	1. BES	2. SMØ	3. FAL	4. TJØ
Altitude (m)	920	1150	1010	1010	1330	1320	1280	1290
Aspect	SW	SE	S	SSE	SE	SE	S	SE
Species richness[1]	27	21	21.5	26	27	16	27	34
Grazing regime[2]	reindeer, sheep	reindeer, (sheep), cattle	reindeer, (sheep), horses	reindeer, (sheep), goats	**reindeer, sheep**	**reindeer, sheep**	reindeer, sheep, horses	**reindeer, sheep**
UTM coordinates[3]	N6830070, E498610	N6843145, E485820	N6815645, E502320	N6824081, E503253	N6821880, E490730	N6846910, E492620	N6815645, E502320	N6825835, E503160

[1] Mean of vascular plant species per 0.25 m².
[2] Major herbivores are in boldface, and those exerting minor grazing impact are in parentheses.
[3] Map coordinate system: WGS84, UTM zone 32.

(Table 1). Mountain voles (*Lemmus lemmus*) are frequent in both the alpine and subalpine habitats over the year. The variation in plant species richness among the sites (Table 1) might partly be related to different effects of lime-rich bedrock and partly to other factors such as previous land use and local climate. At the sub-alpine sites, the vegetation is generally characterised by species-rich, open grassland communities with a high proportion of graminoids. The vegetation of the alpine sites is a mosaic of dwarf shrubs, grassy vegetation with lichens and bryophytes, and patches with exposed rock and mineral soil.

Population variables

Morphological data from four populations in two valleys were recorded in July 1996 and 1997 (valleys 1 and 2) and in three valleys in 1997 (valleys 1–3, *see* Table 1). Forty individuals from each population were randomly sampled. For each individual the following variables were recorded in the field in late July–early August 1996 and 1997: plant height, number of flowers, number of branches, number of rosette leaves, total number of leaves, width and length of upper leaf, width and length of largest rosette leaf. Seed capsules (top capsule, or rarely, if it was already open, the next below it) were collected in August/early September, and the number of seeds, number of ovules and defective seeds, and seed weight (per 100 seeds) were determined in laboratory.

For an assessment of life cycle (seedlings germinated in spring or autumn, respectively), 30 individuals per population were randomly selected from six populations in the two types of habitat, alpine (A) and subalpine (SA), in early August 1997 and 1999, from valley 1: Sjodalen with the sites Stuttgongi SA, Besstrond A; valley 2: Smådalen with the sites Smådalen SA, Smørli A, and, only 1999, valley 4: Griningsdalen with the sites Dyrtjørnbekken SA, Tjørnungsdalen A (Table 1). Criteria indicating autumn germination and over-wintering from previous year were (i) remains of old, basal rosette leaves present in August at field sampling, and (ii) branches > 1 and height > 3 cm (cf. Batty *et al.* 1984, Miller & Geddes 2004).

Seedlings in the rosette stage were observed in both types of habitats, in early June during snow melting, and in August.

To collect information on seed set related to the mating system of *G. nivalis*, a pilot experimental pollination study was performed in valley 1, Stuttgongi (STU, subalpine site) during late July–late August 1997, in one population, with 25 individuals per treatment. The treatments were: C = control, open pollination; MSP = manual self pollination and bagged; NT = control, bagged; MCP = manual cross pollination, emasculated and bagged; E = emasculated and bagged. MCP was performed between individuals > 10 m apart. Bagging was done by covering the plant with a thin, light-permeable, elastic nylon net stretched over plastic pins. Seed capsules were collected just before onset of opening in late August.

Data analysis

To investigate whether life history, vegetative, and reproductive traits differed between subalpine and alpine *G. nivalis* populations we used mixed-models analysis. In all models, habitat was treated as a fixed factor. Year, valley, and the interaction of habitat and valley were treated as random factors. Specifically we tested whether germination time (a life-history trait), number of leaves, leaf size and plant height (vegetative traits), and number of flowers and seed production per capsule, and mean seed weight (reproductive traits) differed between alpine and subalpine populations. We also investigated whether some of the vegetative and reproductive traits were affected by habitat directly or through the life history trait by comparing the likelihood statistics of several nested models (*see* below). The analyses were performed using the procedures MIXED and GLIMMIX of the SAS package, ver. X (Littell *et al.* 1996). Before analysis, some of the variables were log- or square-root- transformed to achieve normality. This was done because mixed models analysis of variance and the MIXED procedure presumes normal distribution of the residuals. In the case of the categorical response variable 'germination time', we used the procedure GLIMMIX with a binomial

error distribution. We also used the procedure GLIMMIX for the Poisson-distributed rosette-leaf number and flower (branch) number linking a log function and allowing for dispersion. The method to solve the MIXED models equations was REML (Restricted Maximum Likelihood). The statistical significances of the fixed parameters were determined using a standard type-3 test (F-statistics). We used a likelihood-ratio test to determine the statistical significance of the random factor by calculating the difference in –2 residual log-likelihood between the full model and a model that did not include the random factor. The p value for this statistic can be determined by a one-tailed χ^2 test with 1 df (Littell *et al.* 1996). Analyses of seed set in the pollination experiment were performed using one-way ANOVA (Underwood 1997).

Results

Pollination study

The pollination study yielded the highest seed set in the control (untreated individuals) allowing possible self fertilization and possible crosspollination (Fig. 1). The seed set data from the pollination experiment were highly skewed towards the outskirts of the spectrum, mainly due to a large number of zero scores in the emasculated (E) treatment and high seed set in the control, open (C), manual self pollination (MSP), and bagged (NT) treatments. No transformation to reach normality was possible, hence the pairwise comparisons among treatments were performed by non-parametric statistics (Mann-Whitney U-test; *see* Fig. 1). Treatments were however significantly different from one another in all cases except one, (MSP *vs.* NT, p = 0.0864), even with this robust method. The significant difference between C and MSP (p = 0.0215) is due to the low variance in seed set within the two categories. Cross pollination can occur (Fig. 1, MCP) although the significantly lower seed set for the treatment 'manual crosspollination with emasculation' is interpreted as an injury effect of the experimental treatment when handling the very small flower organs. Apomixis is probably non-existent; the small number of seeds pro-
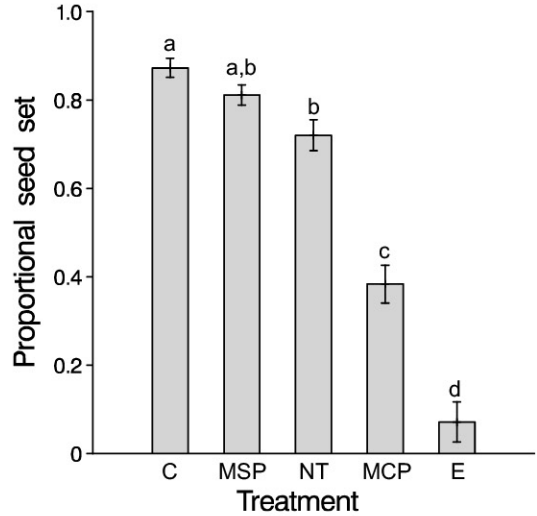
Fig. 1. Proportional seed sets (S/[S + O + D]; S = seeds; O = ovules; D = defect seed) for different pollination treatments (given are means with their standard errors); n = 25 for each treatment. C = control, open pollination; MSP = manual self pollination and bagged; NT = control bagged; MCP = manual cross pollination, emasculated and bagged; E = emasculated and bagged. Different letters indicate significant differences between treatments (Mann-Whitney U-test) at p < 0.0001 (p = 0.0215 for C *vs.* MSP, and p = 0.0864 for MSP *vs.* NT) (*see* text for details).

duced after emasculation and bagging (Fig. 1) is probably an artefact of pollen contamination. However, the outcrossing rate and effect of inbreeding in terms of genetic structure and inbreeding depression has never been studied. Individuals of the insect genus *Zygaena* (Lepidoptera), and families Syrphidae, Muscidae and Scathophagidae (Diptera) were observed visiting the plants and are possible pollinators.

Variation in morphological traits and reproductive success

Number of *G. nivalis* rosette leaves, rosette-leaf size and plant height did not differ significantly among the alpine and subalpine populations, although the significant interactions indicate that there were differences in the effects of habitat among valleys (Tables 2 and 3). Plant height was the only trait that differed significantly between the two study years.

Number of flowers produced per plant differed among habitats, as did number of seeds per capsule and reproductive capacity (Tables 2–4). Seed weight did not differ among habitats (results not shown). Reproductive capacity (the product of number of flowers and seed number) was almost four times greater in the subalpine habitats (Table 4). However, among the repro-

ductive characters there are significant variations among the sampled populations irrespective of populations (Table 2). The mixed models analysis indicates that there are significant interactions between 'habitat' and 'valley' for the three vegetative traits (number of rosette leaves, rosette leaf size and plant height), which might indicate a site effect (Table 3).

Table 2. Means ± SDs and number of observations (n) of four morphological traits in three subalpine and three alpine *Gentiana nivalis* populations from three valleys (*see* Table 1) in Norway. *See* Table 4 for statistical tests.

Trait	Year	Valley	Subalpine		Alpine	
			Mean ± SD	n	Mean ± SD	n
Number of rosette leaves	1996	1	4.41 ± 2.53	29	4.29 ± 1.05	57
		2	6.16 ± 2.20	38	3.67 ± 1.18	68
	1997	1	3.83 ± 1.34	40	4.23 ± 1.14	80
		2	4.70 ± 1.60	40	4.10 ± 1.01	80
		3	6.20 ± 2.04	40	5.00 ± 1.48	80
Rosette-leaf size* (mm²)	1996	1	20.5 ± 14.3	29	15.8 ± 8.4	28
		2	26.4 ± 14.5	38	9.0 ± 5.7	30
	1997	1	15.7 ± 10.7	40	14.0 ± 9.0	40
		2	22.6 ± 12.7	40	9.2 ± 4.4	40
		3	27.1 ± 14.7	40	14.0 ± 9.0	40
Plant height (mm)	1996	1	56.0 ± 21.8	29	49.0 ± 15.4	28
		2	55.2 ± 19.2	38	39.1 ± 15.8	30
	1997	1	74.8 ± 26.6	40	59.1 ± 19.9	40
		2	70.4 ± 22.0	40	33.5 ± 15.1	40
		3	53.6 ± 17.8	40	46.9 ± 17.5	40
Number of flowers	1996	1	2.79 ± 2.47	29	1.61 ± 1.03	28
		2	4.34 ± 2.85	38	1.77 ± 1.04	30
	1997	1	4.08 ± 3.21	40	1.33 ± 0.73	40
		2	4.25 ± 3.05	40	1.48 ± 0.78	40
		3	5.10 ± 3.08	40	1.93 ± 1.40	40

* Calculated as leaf length × leaf width.

Table 3. Mixed models analyses on four plant traits testing for differences among habitats and years. Habitat (alpine and subalpine) was treated as a fixed effect whereas year, valley and habitat × valley were treated as random effects. Number of rosette leaves and number of flowers were fitted with a log function (Poisson distribution). The significance of the fixed effect was tested using a standard F-test (the denominator's df was estimated using the Satterthwaite method), while the significance of the random effects was tested using a log-likelihood ratio test (*see* Material and methods).* $p < 0.05$, *** $p < 0.0001$.

Source	Number of rosette leaves	Rosette leaf size[a]	Plant height[b]	Number of flowers	Number of seeds per capsule[a]	Reproductive capacity[a]
Habitat	$F_{1,2.0} = 2.3$	$F_{1,4.0} = 6.1$	$F_{1,2.0} = 5.3$	$F_{1,361} = 137$***	$F_{1,4.3} = 8.7$*	$F_{1,2.1} = 39.3$*
Year	$\chi^2_1 = 5.6$*	$\chi^2_1 = 1.1$	$\chi^2_1 = 8.8$**	$\chi^2_1 = 0$	–	–
Valley	$\chi^2_1 = 0.91$	$\chi^2_1 = 0$	$\chi^2_1 = 0.10$	$\chi^2_1 = 1.9$	$\chi^2_1 = 0$	$\chi^2_1 = 0$
Habitat × valley	$\chi^2_1 = 8.4$**	$\chi^2_1 = 16.8$***	$\chi^2_1 = 15.7$***	$\chi^2_1 = 0$	$\chi^2_1 = 2.6$	$\chi^2_1 = 1.2$

[a] log-transformed, [b] square-root-transformed.

Variation in life history and the effect on morphology

Gentiana nivalis populations are composed of a mixture of individuals which germinate either during autumn or spring. Germination time varied significantly among habitats but not among valleys and years, and germination occurred more often in the autumn at the subalpine as compared with that at the alpine sites (Fig. 2). The life history had a direct effect on plant morphology: plants with spring germination were shorter and produced fewer flowers than plants that germinated in the autumn (Table 5). In addition to this direct effect of life history (that differs among habitats), habitat had a significant main effect on plant height, but not on number of flowers produced per plant.

Discussion

Influence of grazing on establishment, morphology and population dynamics of *G. nivalis*

Herbivory is generally an important disturbance factor in the alpine and subalpine ecosystems (Oksanen & Ranta 1992, Virtanen 1996). Grazing by domestic livestock is known to have shaped both landscapes and vegetation in alpine regions (Aronsson 1991, Miller *et al*. 1999, Olsson *et al*. 2000, Evju 2000, Endresen 2001)
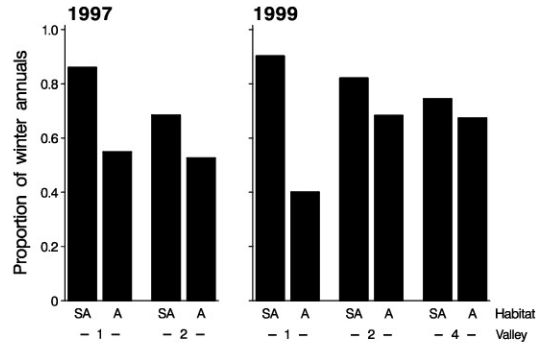
Fig. 2. Proportion of winter annuals in three subalpine (SA) and three alpine (A) populations from three geographical areas (valleys 1, 2, and 4; *see* Table 1) during two flowering seasons (1997 and 1999). Generalized mixed analysis of the impact of habitat on the binary life history trait germination time (autumn or spring) revealed significant effect of habitat ($F_{1,3.95}$ = 7.74, p = 0.05; df estimation method Satterthwaite). There was no effect of year, valley, or site nested within valley (included as random factors in the analyses) as indicated by a log-likelihood ratio test (not shown, *see* Material and methods).

and, interacting with local climatic factors, it contributes to the maintenance of patches of alpine grasslands, e.g., in snow patches. In the subalpine zone below the tree line and above the upper limit of the forest cover (Körner 1999), grazing by large herbivores and tree felling linked to the summer-farming activities contributed to create the semi-natural grasslands that were colonised by several alpine species, including *G. nivalis* (Geddes & Miller 2010). The

Table 4. Reproductive success in three subalpine and three alpine *Gentiana nivalis* populations during 1997. *See* Table 4 for statistical tests.

Trait	Valley	Subalpine		Alpine	
		Mean ± SD	*n*	Mean ± SD	*n*
Number of seeds per capsule	1	308 ± 145	28	151 ± 82	33
	2	249 ± 131	17	193 ± 113	33
	3	229 ± 93	31	214 ± 126	37
Seed set (%)	1	85.3 ± 15.3	28	74.7 ± 20.4	33
	2	80.1 ± 18.3	17	80.9 ± 12.2	32
	3	69.4 ± 16.8	31	72.9 ± 17.5	37
Reproductive capacity*	1	1693 ± 1617	27	272 ± 316	33
	2	1029 ± 839	17	315 ± 272	32
	3	1421 ± 1033	31	523 ± 126	37

* Estimated number of seeds per plant.

occurrence of gentians in those habitats is related to the ongoing grazing and trampling, continuously creating a mosaic of patches suitable for germination.

After the decline of long-term grazing and other types of human impact in mountains, a decrease in landscape diversity occurred (Olsson *et al.* 2000). According to the first author's own observations, the number of vascular species in the grazed semi-natural sub-alpine grasslands was five times higher in comparison with ungrazed *Pinus–Betula* woodland that is the natural vegetation there. Without grazing by large mammals that maintain the semi-natural and non-forested habitats, the survival of short-statured plants, such as alpine *G. nivalis*, would not be possible in the sub-alpine habitats except in patches with little or no vegetation cover due to some kind of disturbance, e.g. along foot paths or watercourses. The hypothesis regarding the importance of human impact by livestock grazing for the maintenance of biological diversity in European woodlands (Pykälä 2000) was supported by our results from the Jotunheimen mountains.

For the developing *G. nivalis* seedlings in the subalpine habitats there is strong competition for light due to higher vegetation than in alpine sites. This favors tall *G. nivalis* individuals, which

Table 5. Effect of life history and habitat on two plant traits. Habitat (alpine and subalpine) and life history, i.e. winter or spring germination, were treated as fixed effects whereas year and valley were treated as random effects. Number of flowers was fitted with a log function (poisson distribution). The significance of the fixed effects was tested using a standard *F*-test (the denominator degrees of freedom was estimated using the Satterthwaite method), while the significance of the random effects was tested using log-likelihood ratio tests (*see* Material and methods). ** $p < 0.01$, *** $p < 0.001$.

Source	Plant height[#]	Number of flowers
Habitat	$F_{1,400} = 8.1^*$	$F_{1,403} = 3.8$
Germination time	$F_{1,400} = 18.3^{***}$	$F_{1,401} = 85.5^{***}$
Germination time × habitat	$F_{1,401} = 10.7^{**}$	$F_{1,402} = 7.33^{**}$
Year	$\chi^2_1 = 99.7^{***}$	$\chi^2_1 = 0$
Valley	$\chi^2_1 = 5.5^*$	$\chi^2_1 = 0.86$
Habitat × valley	$\chi^2_1 = 0$	$\chi^2_1 = 0$

[#] square-root-transformed;

often are winter annuals, as shown in this study (Tables 2 and 3; Fig. 2). Grazing by large herbivores occurs in the alpine and subalpine habitats (Table 1) although grazing as a factor creating suitable germination patches for the gentians is less critical in the alpine habitats due to the interaction of the climatic factors. Wind, snow and low temperature are influential in the creation of open patches of bare soil, thus reducing the competition. Very few of the *G. nivalis* individuals themselves had signs of mammal herbivory in either habitat. The same observation of lack of herbivory on *G. nivalis* individuals was made in northern Norway (Vesterbukt 2003).

Population differentiation in the two types of habitats

The detected differences between habitats in morphological and reproductive features are directly related to the different proportions of spring- and autumn-germinating individuals, where the proportion of winter annuals is greater in the subalpine habitats (Fig. 2). The alpine sites are located at 200–300 m higher altitudes (Table 1), which is likely to give those sites a harsher local climate implying a poorer survival of winter annuals. Another factor making the competition situation different between the two habitats are the vegetation communities. The subalpine habitats are all former, enclosed meadows used for haymaking and grazing close to the summer farm settlements. Those meadows were manured to increase fodder production and the vegetation is a closed grass-dominated sward. In contrast, in the alpine habitats the vegetation is not closed, small patches of exposed mineral soil and gravel are existing, although the species richness is similar (Table 1). The combination of climatic factors and vegetation differences gives a different competition situation that favors survival of taller *G. nivalis* individuals in the subalpine sites, and tall individuals are likely to be winter annuals which are dominating in those sites (Tables 2 and 5). The spring-germinating annuals that have shorter time for growth and development and have a shorter stature, can still develop at the alpine sites where the competition is weaker.

Shimono *et al.* (2009) found significant morphological differences among populations of *Potentilla matsumurae* growing in different alpine habitats (fellfields and snowbeds). This differentiation was maintained under uniform growing conditions in greenhouse, indicating a genetic component. Another study, of the alpine annual *Koenigia islandica* (Wagner & Simons 2009), revealed significant morphological differentiation between populations from different habitats also when grown in growth chambers. This differentiation was inferred as genetic among populations, evidencing local adaptation. A study of the genetic variation within and between two populations of *G. nivalis* in the Oriental Carpathians of Romania employing RAPD markers clearly showed a larger genetic diversity between populations rather than within (Raica *et al.* 2006).

Our study showed that *G. nivalis* produces seeds, mainly by self-pollination, although cross-pollination occurs with unknown frequency. It is likely that cross-pollination is rare and the plant relies mostly on self-fertilization as many alpine and arctic plants do (Molau 1993, Mu *et al.* 2010). Different selective forces are operating in the alpine and subalpine habitats used for the present study. Whether the recorded differences in life-cycles among populations of *G. nivalis* in the two types of habitats can be related to genetic differentiation needs further studies by molecular data or in a common garden experiment. If such differentiation occurs it would have implications for adaptation of this species to the ongoing environmental changes.

Future of *G. nivalis* in the light of current trends of landscape development and climate change

The current trend in mountain land use in Europe including Norway is agricultural abandonment with decreasing livestock grazing (Olsson *et al.* 2011). The effect of this is a noticeable forest invasion on former open semi-natural mountain grasslands and heathlands and a rise of the anthropogenic tree-limit (Bryn 2008, Wehn *et al.* 2012). Domestic livestock and semi-domestic reindeer have been grazing in those mountains

for a millennium and thus have had a significant effect on the shaping of the mountain landscape and the distribution of mountain habitats (Wehn *et al.* 2012). The current density of reindeer cannot substitute the decreasing or absent livestock herds and the abandoned summer-farming (Olsson *et al.* 2011). The process of forest regrowth and shrinking of semi-open habitats interacts with the effects of climate warming, when many species change their altitudinal distribution uphill (Lenoir *et al.* 2008, Pauli *et al.* 2012) and thus facilitate the process of tree colonisation of open subalpine habitats and rising of tree and forest lines. The implication of this process is that suitable habitats for *G. nivalis* will be restricted to the alpine habitats.

Our study shows that populations of *G. nivalis* have different life cycles in the two types of habitats with a greater number of winter annuals in the subalpine habitats. We also show that selfing is occurring as a reproduction strategy for *G. nivalis*. If the plant will be restricted to the alpine habitats only where insect pollination — and thus cross-pollination — generally is rare, it is possible that the result will be increasing homozygosity and decreased genetic variability. This might lead to weaker possibilities for *G. nivalis* to cope with environmental variability and weather unpredictability resulting from climate change.

The alpine plant communities and the landscape dynamics in those mountains have evolved under pressure of grazing of large herbivores, of which domestic livestock have been dominating since prehistoric times. This era now has come to an end and (changing) climate will become the major evolutionary factor shaping the landscapes and biological communities.

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