CHAPTER 3

NO EVIDENCE FOR ADAPTATION OF TWO POLYGONUM VIVIPARUM GENOTYPES TO LENGTH OF GROWING SEASON: ABUNDANCE, BIOMASS AND GERMINATION[1]

Abstract The high degree of habitat heterogeneity and fragmentation in arctic ecosystems may support a high genotypic and ecotypic variability. This may buffer the survival of plant species threatened by global climate change, in particular in the Arctic where temperature increases are expected to be greatest. Here, we assessed if two genotypes of *Polygonum viviparum* (characterised by different colours of their bulbils), i) differ in their abundance along a snowmelt gradient, ii) if their biomass allocation pattern are influenced differentially by environmental variables, and iii) if the temperature dependency of bulbil germination differs between genotypes. We found slight differences in the effect of timing of snowmelt on abundance of the genotypes, which seem to have little ecological relevance. Total plant biomass and biomass allocation to the different plant compartments was similar for both genotypes and was negatively correlated with soil water content. Bulbil germination was assessed over a temperature range from 2 to 25°C and results indicate an earlier (maximum of five days) germination of one genotype, but final germination (> 80%) and germination rate were similar for both types. Germination was weakly temperature dependent, with faster germination at higher temperatures. *Polygonum viviparum* bulbils clearly did not germinate as would be expected by the constant thermal time concept for agricultural seeds, as they were able to compensate for low temperatures. Overall our results could provide no convincing evidence for genotypic variability in *Polygonum vivipa-*

[1] together with Sarah J. Woodin and Steve D. Albon (submitted to Ecography)

rum being of ecological relevance with respect to anticipated climate change in the Arctic.

INTRODUCTION

The observed rate of global warming has been greatest in the Arctic (Serreze *et al.* 2000) and the general circulation models predict this will continue (IPCC 1990, 1998; Maxwell 1992). The potential consequences for plants and vegetation are immense, and the question of whether the changes anticipated will lead to the extinction of plants characteristic to this severe environment has caused some concern (Chapin & Körner 1994). It has been argued, however, that spatial heterogeniety at a very small scale (proximity of very different habitats within a metre), a natural feature of arctic vegetation, has given rise to high ecotypic variation within species, each ecotype being adapted to slightly different set of environmental conditions (Crawford *et al.* 1993; Crawford 1997a, b). This might allow plant species to survive vegetational change by changes in the relative abundance of these ecotypes.

So far, evidence for differences in important ecological properties within a arctic species is circumstantial: higher maximum photosynthesis seems to compensate for a shorter growing season in *Saxifraga oppositifolia* (Crawford *et al.* 1995), and along a gradient of season length some species (*Polygonum viviparum*, *Saxifraga oppositifolia*) differ in their morphology (Crawford *et al.* 1993; Crawford & Smith 1997). *Dryas octopetala* significantly reduces its allocation to the gynoecium in sites with a shorter growing season (Wada 1999). On the other hand, it has recently been shown that seeds from different altitudes in the Andes differ in their stratification requirements, as well as their percentage of maximum germination (Cavieres & Arroyo 2000).

Polygonum viviparum is a widespread arctic-alpine species, common to periglacial regions of the northern hemisphere. Vegetative reproduction, a feature of many arctic plants (Billings 1987), occurs via bulbils, i.e. seed-analogue structures produced on the flowering stalk (Law *et al.* 1983). In the Arctic, production of mature fruits is a very rare event (Law *et al.* 1983; Söyrinki 1989), and for populations in the Alps it was shown that there is a trade-off between the production of flowers and bulbils (Law *et al.* 1983), which shifts with increasing altitude in favour of bulbils (Bauert 1993). The bulbils are pre-formed as long as four years before emergence (Diggle 1997). They ripen over the summer and usually become dispersed in late summer or early

autumn. Occasionally, bulbils germinate on the flowering stalk ("vivipary"), but this has been observed only very sporadically in the population investigated here (CFD, personal observation). Germination apparently takes place in the next spring, growth in the first year relies mainly on stored starch, as by late August only the cotyledons have emerged (personal observation). Around 10% of the bulbils germinate successfully (range 0 - 63%; CFD, unpublished data), especially in very moist places.

Individuals of *Polygonum viviparum* differ in the colour of the bulbils. It can range from light to dark red, pale yellow to dark brown and even green and purple bulbils have been reported (Bauert 1993; Crawford & Smith 1997). Bulbil colour is a genetically determined trait (Bauert 1996), which means that differences in success and distribution of bulbil colours has direct implications for the genetic structure and diversity of the *Polygonum viviparum* population at a given site. It has been suggested (Crawford & Smith 1997) that the genotypes represented by different bulbil colours are adapted to differences in season length, with individual with red bulbils being more abundant on short-season low-shore sites, while brown ones dominate in long-season ridge sites.

The present study assesses 1.) whether different genotypes of *Polygonum viviparum* show differences in their distribution with respect to environmental variables, and 2.) whether temperature dependency of germination correlates with the distribution of the genotypes.

METHODS

Site and species description

Field work was carried out in Semmeldalen, Svalbard (78ºN 15ºE). This innerfjord valley harbours a variety of vegetation types, from dry, unvegetated schist humps, over a dry peat *Salix polaris*-heath, to wet, graminoid rich communities and water-logged *Eriophorum scheuchzeri*-swamps (for details see Rønning 1996, 1967).

Polygonum viviparum occurs in almost all of these communities, except for the extremely wet and extremely dry ones. Its cover rarely exceeds 1%, but occasionally one can find over 100 individuals per m^2. Most individuals of *Polygonum viviparum* at this site produce red bulbils (c. 85%), but brown (c. 15%), pale-yellow and purple bulbils (each < 1%) can also be encountered.

Survey

In August 1999 40 permanent plots were established in Semmeldalen, representing points on various environmental gradients (soil water content, season length, slope, exposure, aspect). Volumetric soil water content was measured with a soil conductivity insertion probe (SCIP, CEH Wallingford, UK) at four subsamples per site on 26 July 2000. Season length was estimated on a five point scale based on the duration of snowlie. Slope and aspect were measured with a compass and inclinometer, respectively. Exposure was estimated on a five point scale from raised above the surrounding area (5) to trough position (1). This was applied both at the scale of 4 m^2 and 100 m^2 (small scale relevant to individual, larger scale relevant to plant community structure). At each site two *Polygonum viviparum* plants was excavated, one with red and one with brown bulbils. As both red and brown plants did not always occur at each site, sample sizes are less than 40. Plants were sorted into rhizome, seeds and leaves plus flower stalk, and pre-dried at 40°C for one week. After transport back to the lab, samples were re-dried at 70°C for 24 hours and weighed to the nearest 0.1 mg.

Snowmelt transect

A 520 m long transect was established in May 1999, to assess patterns of snowmelt and hydrological conditions over a range of vegetation types and topographic positions. The transect consisted of three parallel lines, 40 m apart, with an aluminium pole every 40 m. During spring 2000, the transect was monitored every other day to assess when poles became snowfree. Subsequently volumetric soil water content was measured with the SCIP at four points around the pole at least biweekly throughout the summer, until mid August 2000. For each of the 45 poles the date when it became snowfree and soil water content data for the summer are available (S.D. Albon, unpublished results).

On the 25 July 2000 *Polygonum viviparum* individuals with red and brown were counted in a 4 m^2 circle around each pole. Some (< 5%) *Polygonum viviparum* inflorescences were infested by a fungus and the colour of their bulbils could not be determined.

Germination test

Bulbils of *Polygonum viviparum* were collected in a dry *Salix polaris*-heath in Semmeldalen, Svalbard, in the first week of August 1999. They were manually stripped

from plants with either brown or red bulbils, stored in plastic bags and kept frozen (-12°C) until the start of the germination experiment.

The germination test was carried out using a temperature gradient plate (Grant Instruments Inc., U.K.). This was set to a temperature range from 1 to 26°C, with 14 temperature steps of approximately 2°C. The aluminium gradient plate was cleaned with bleach (20%) prior to the experiment. Two layers of paper kitchen towel were placed on the plate and sprinkled with distilled water until saturated. Onto this, a plastic grid of 14 by 14 cells was placed to reduce airflow and to compartmentalise the bulbils. Above the plate, two greenhouse lights provided continuous illumination (c. 250 μmol m^{-2} s^{-1}). The exact temperature in the germination cells was measured with a Squirrel temperature data logger (Skye Instruments, UK). These deviated from the set temperature by +1°C at the low end to -1°C at the high end. The realised temperature range thus was 2 to 25°C.

On 1 May 2000 (the beginning of the growing season), 25 randomly picked bulbils were put into each of the cells across the whole temperature gradient, in the middle six rows of the grid, with alternating rows of brown and red bulbils. This resulted in three replicates per temperature and colour. Another set of 25 bulbils of each colour was weighed wet, dried and re-weighed to assess possible size differences between the colours. The results indicate that there was no difference in dry or fresh weight between red and brown bulbils, but red bulbils had significantly higher water content than brown ones (Table 1). Germination seemed to be independent of bulbil size (personal observation, Gugerli 1997).

All bulbils were checked for signs of germination every morning for one month. The bulbils are cone-shaped, and the radicle generally emerges at the bottom end, being visible even before emergence as a white dot in the aperture of the bulbils. Emergence of the radicle was scored as successful germination and the germinated bulbil was removed from the plate. The red bulbils deviated from this germination pattern: in about half of them the radicle emerged through the side of the bulbil, rather than through

Table 1 Initial fresh and dry weights (mg) and water content (in % fresh weight) of *Polygonum viviparum* bulbils, with standard errors and one-way ANOVA statistics. N=25 per colour.

	red	brown	F	*P*
fresh	3.00 ± 0.25	3.34 ± 0.25	0.91	0.344
dry	1.15 ± 0.10	1.38 ± 0.11	2.30	0.136
% H_2O	62.4 ± 0.66	58.8 ± 0.49	13.45	0.001

Table 2 Comparison of *Polygonum viviparum* with brown (N = 33) and red (N = 36) bulbils. Data given are means for dry weight, standard error and Kruskal-Wallis statistics.

	brown	red	H	*P*
total weight [mg]	146.5 ± 13.2	161.0 ± 12.0	2.50	0.114
leaves & stalks [mg]	31.5 ± 3.11	33.9 ± 2.79	0.41	0.475
rhizome [mg]	85.7 ± 8.23	99.3 ± 8.07	3.08	0.079
seed weight [mg]	29.3 ± 3.59	27.8 ± 2.88	0.01	0.923
number of seeds	23.0 ± 1.63	23.1 ± 1.93	0.20	0.652

the bottom aperture. This was hardly ever observed in the brown bulbils.

Statistical analysis

Survey data were analysed using Generalised Linear Mixed Models, with bulbil colour nested within site and site as a random factor (SAS Institute Inc. 1989). As the best fitting regression model for the effect of soil water content on total biomass of *Polygonum viviparum* along the survey sites was an exponential function, both biomass and soil water content data were ln-transformed.

Cumulative germination was calculated for each cell separately and regressed against the non-linear logistic function ($y = a / (1 + (x/x_0)^b)$), using the SigmaPlot (Jandel Scientific Software, San Rafael, California) regression module. The maximum germination coefficient a was constrained to be equal or less than 100%. x_0 represents time to half-maximal germination, and $-b$ is the slope in x_0.

Weighed germination coefficients (using 1/*coefficient of variance* as weight) for each cell were than compared for red and brown bulbils using a Generalised Linear Mixed Model with bulbil colour as fixed effect, temperature as covariate, and block (pairing adjacent rows with red and brown bulbils together) as random factor. The initial model also contained the temperature × colour interaction, and was simplified by excluding all terms which were not significant at $P < 0.1$ (Crawley 1993). For all tests the response variables showed no significant divergence from either a normal distribution or homogeneity of variance.

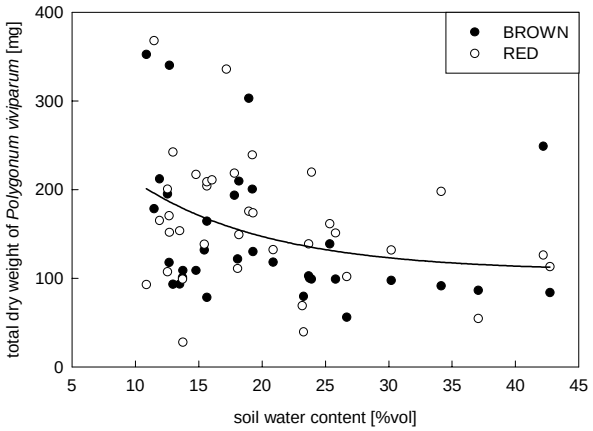

Fig. 1 Total biomass of *Polygonum viviparum* as a function of soil water content. Dry weights of brown and red *Polygonum viviparum* did not differ, the regression line (biomass = $107.8 + 260.6 \cdot e^{-0.094 \cdot x}$; $F_{1, 31} = 5.38$, $P < 0.05$, $R^2 = 0.177$) represents both bulbil colours.

Thermal time (in degree-days) was calculated as cell temperature·x_0, as neither optimal nor maximal germination temperature were reached, and the calculation according to Garcia-Huidobro *et al.* (1982) were therefore not applicable.

RESULTS

Survey: biomass allocation and environmental gradients

Polygonum viviparum plants with brown bulbils did not differ significantly in their biomass, or its allocation, from those with red bulbils (Table 2). Rhizomes made up c. 60% of the total biomass of bulbil-bearing plants, with the other 40% being evenly split between leaves and bulbils.

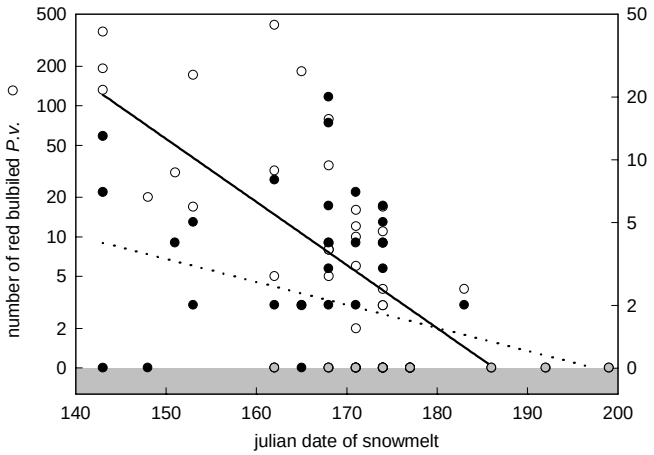

Fig. 2 Number of *Polygonum viviparum* of the two colour varieties per m^2 (log-scale) along a snowmelt gradient. Julian day on x-axis refers to time when plot became snowfree. Note difference in scaling. Regression of log(x+1)-transformed data for red: y = 8.970 – 0.048 x ($F_{1, 43} = 42.41$, $P < 0.001$, $R^2 = 0.49$) and for brown: y = 2.181 – 0.011 x ($F_{1, 43} = 5.28$, $P < 0.05$, $R^2 = 0.09$).

Of the parameters assessed at the survey sites (slope, aspect, soil water content, exposure, season length), the weight of *Polygonum viviparum* was significantly related only to soil water content ($F_{1, 29} = 5.38$, $P < 0.05$; Fig. 1). However, no difference between bulbil colours could be detected ($F_{1, 29} = 0.15$, $P = 0.69$), nor was there an interaction between bulbil colour and soil water content ($F_{1, 29} = 0.25$, $P = 0.62$).

Table 3 Summary of statistical test of differences in the number of *Polygonum viviparum* occurring along a snowmelt gradient. Colour refers to differences between *Polygonum viviparum* with red and brown bulbils. Data were $\log_{10}$-transformed prior to analysis.

Effect	df	F	*P*
Snowmelt	1	32.55	0.0001
Colour	1	33.05	0.0001
Interaction	1	28.75	0.0001
Residual	42		

Snowmelt transect

The abundance of the two bulbil colours of *Polygonum viviparum* differed significantly with respect to timing of snowmelt. Plants with red bulbils showed a strong negative correlation with Julian date of snowmelt, while that for brown bulbils was rather weak (Figure 2; Table 3). *Polygonum viviparum* individuals with red bulbils decrease from c. 150 ind. m^{-2} at very early snowmelt (Julian Date of c. 145) to 0 at a snowmelt date of early July (Julian date of c. 185). *Polygonum viviparum* with brown bulbils did not occur in areas of late snowmelt either. The percentage red decreased significantly with Julian day from c. 96% to 59% (arcsine-square root-transformed data: $F_{1, 31} = 4.25$, $P < 0.05$, $R^2 = 0.092$; regression equation for untransformed data: %red = 248 - 1.05·Julian day), indicating that the *relative* abundance of one genotype compared to the other is influenced by the timing of snowmelt. However, red *Polygonum viviparum* were always c. 20 times more abundant than brown ones, thus no shift in *dominance* was observed.

The density of the two colour varieties showed no significant difference in relation to soil water content on these sites (soil water content: $F_{1, 43} = 0.75$, $P = 0.391$; soil water content × colour $F_{1, 43} = 2.85$, $P = 0.099$), although soil water content and snowmelt were weakly correlated ($F_{1, 44} = 3.56$, $P = 0.066$, $r = 0.276$). That is to say that there was no relationship between density and soil water content for either colour and no significant interaction between colour and soil water content. Moreover, no relationship between percentage red and soil water content was detected ($P > 0.29$).

Germination test

Polygonum viviparum showed surprisingly little sensitivity to environmental temperature: bulbils germinated at all temperatures (2-25ºC). Germination was rapid and almost complete for both bulbil colours (Fig. 3). The onset of germination was faster and (as germination rate was the same for both bulbil varieties) x_0-values was signifi-

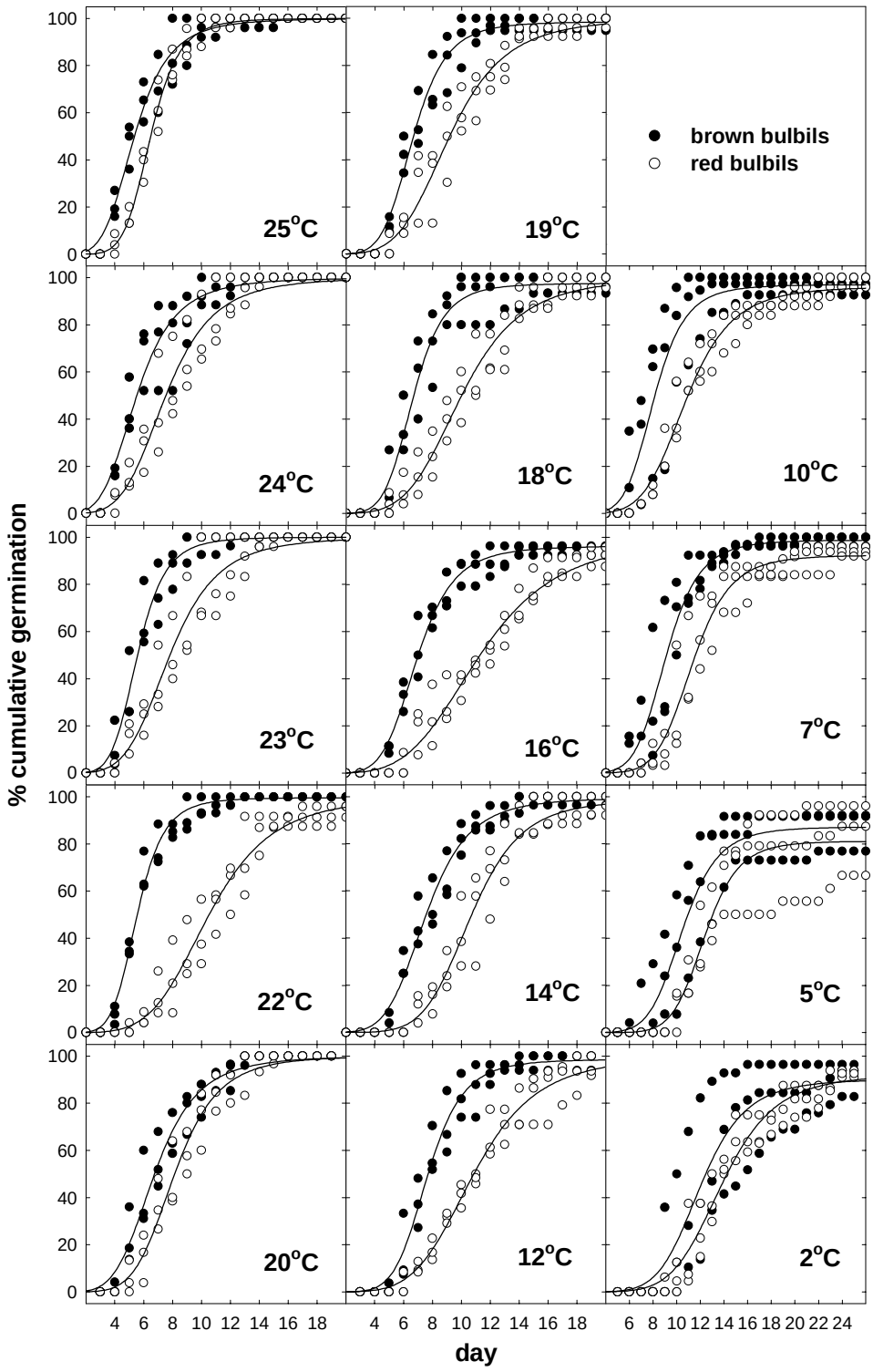

Fig. 3 Cumulative germination of red and brown bulbils at different temperature. A logistic regression function was fitted to the data of each experimental plot: germination=$a/(1+(\text{day}/x_0)^b)$. For regression coefficients see Fig. 4.

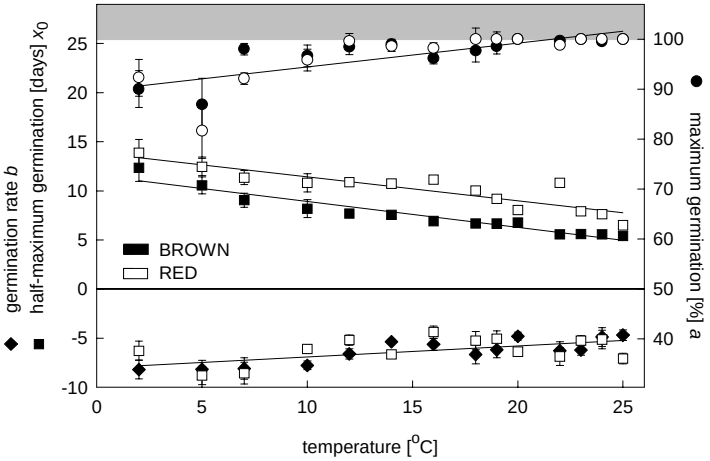

Fig. 4 Regression parameters for the different temperatures. Data from red and brown bulbils were indistinguishable for maximum germination (*a*) and germination rate (*–b*), but differed significantly for time to half-maximum germination (x_0). Regressions depicted are: $a = 89.94 + 0.436 \cdot$ temperature; $b = -7.29 + 0.083 \cdot$ temperature; x_0(brown) $= 10.79 - 0.24 \cdot$ temperature and x_0(red) $= 13.80 - 0.27 \cdot$ temperature. See Table 4 for statistical analysis of parameters.

cantly lower for brown bulbils than for red (Fig. 4; Table 5). The maximal difference of c. 5 days occurred at temperatures of 12 to 19°C and was minimal at both low and high temperatures (Fig. 3 & 4).

Maximum germination of red and brown bulbils alike was slightly lower at low temperatures, but still very high (90% at 2°C; Figures 3 & 4). Once germination started, rates (*b*) were similar for both bulbil colours, but again dependent on temperature (Figure 4; Table 4). Increasing temperature from 2°C to 10°C accelerates the onset of germination and increases the maximum germination with little impact on germination rate (Figs. 3 & 4). From 12°C to 25°C x_0 decreases more slowly and

Table 4 Statistical results from the analysis of germination regression coefficients (Fig. 4) for red and brown bulbils. †, ** and *** refer to $P < 0.1$, 0.01 and 0.001, respectively. Effects not given and interaction of colour and temperature were not significant at $P > 0.1$ and hence removed from the model.

parameter	Effect	df	MS	F	R^2
	Block	2	4.295	5.98**	0.08
final germination (*a*)	temperature	1	47.800	66.54***	0.42
	error	80	0.718		
	block	2	1.0807	2.73 †	0.08
slope (*b*)	temperature	1	6.0946	15.42***	0.15
	error	80	0.3953		
	block	2	87.91	24.15***	0.08
time to half-maximal	temperature	1	1123.82	308.74***	0.52
germination (x_0)	colour	1	569.65	156.49***	0.26
	Error	80	3.64		

maximum germination remains constant, while the germination rate fluctuates inconsistently. As the error bars in Fig. 4 indicate, time half-maximum germination (x_0) and maximum germination varies more between replicates at low than at higher temperatures. No such pattern is apparent for *b*.

DISCUSSION

With respect to germination requirements, arctic-alpine plants are exceptionally tolerant to low temperature (Söyrinki 1941). However, even these plants hardly germinate below 5°C (Mooney & Billings 1961; Sayers & Ward 1966), and out of 12 high arctic species tested by Bell and Bliss (1980) only three ruderals (*Oxyria digyna*, *Phippsia algida* and *Saxifraga cernua*) germinated below 5°C. As the microclimate in the shelter of the vegetation deviates from the ambient air temperature, this low germination ability at very low temperature might not be limiting recruitment, however. With respect to maximal germination, arctic-alpine plants seem to fall into one of two categories: either they germinated most fully, or hardly at all (Bliss 1958). Interestingly, *Polygonum viviparum* was described as a poorly germinating species (4-10%, Bliss 1958), in contrast to our findings, although it is unclear if this study was performed on bulbils or the very rare seeds. Our study indicates that germination can occur at temperatures close to freezing, and that maximum germination is very high and decreases little with temperature (Fig. 4). Indeed the temperature dependency of all germination parameters, but especially for x_0, is very low: increasing temperature by a factor of 12 only halves the time to half-maximum germination (Fig. 4). This clearly demonstrates the adaptation of *Polygonum viviparum* bulbils to low germination temperatures in its arctic-alpine habitat.

Ecotypes adapted to different season lengths?

Overall, we found no convincing evidence for the adaptation of different genotypes of *Polygonum viviparum* to differences in season length as hypothesised by Crawford and Smith (1997). In our study area the red type of *Polygonum viviparum* always was far more abundant than the brown type, yet a decrease in its dominance along the snowmelt gradient could be detected. The dominance of the red over the brown genotype is not based on any of the parameter we measured, but might be e.g. related to differential susceptibility to rust (as shown for interspecific differences in the Polygonaceae by Hatcher *et al.* 1994).

The biomass performance of both genotypes of *Polygonum viviparum* was similar, weakly related to soil water content, with a preference shown by both types to drier sites. However, we did detect a difference in response to a gradient in snowmelt, i.e. differences in season length, which indicates less tolerance of shorter seasons in *Polygonum viviparum* with red bulbils. However, beyond a threshold date of snowmelt (Julian date 185; i.e. 4 July) no *Polygonum viviparum* of either bulbil colour could be found. Thus, both genotypes have the same minimum season length requirements, and, beyond this, the different dependencies on season length has no impact on the total weight, but only on the abundance of *Polygonum viviparum* generally.

Along an environmental gradient, there was no difference in biomass allocation between *Polygonum viviparum* with red and brown bulbils. We thus have to conclude that the ecological difference with respect to snowmelt cannot be corroborated by the survey data.

Germination characteristics of the two bulbil colours are consistent with the field findings, in as much as slight differences between genotypes could be detected, but their ecological relevance in the field is doubtful. Brown bulbils emerged a few days earlier than the red, but total germination (*a*) and germination rate (*b*) were identical (Fig. 4). This leaves the problem of the very different abundances of the two bulbil colours. Red dominates brown by an order of magnitude (Fig. 2). However, we could detect no characteristic that made this genotype more successful than the brown one. One obvious reason is that the genes coding for bulbil colour are not coupled to those providing ecological benefits. Alternatively, the high genetic diversity of *Polygonum viviparum* in the Arctic (Bauert 1996) and in alpine areas (Diggle *et al.* 1998) is not adequately represented by bulbil colour. While we cannot reject the idea that environmental change will have limited effects in the High Arctic because ecotypic variation, and thus adaptational potential, is very high, we found no support for the idea of Crawford and Smith (1993) that *Polygonum viviparum* bulbil colours reflect this ecological preadaptation.

The base temperature and thermal time problem

In plants adapted to cold climate it is of particular interest to know the minimum temperature requirements for germination (base temperature T_b) and the temperature·time required for, say, 50% germination (thermal time 50% Tt_{50}). The concept of thermal time assumes that a constant temperature sum is needed for seeds to germinate, thus temperature·time to germination = constant. How useful is this concept for the bulbil germination of *Polygonum viviparum*?

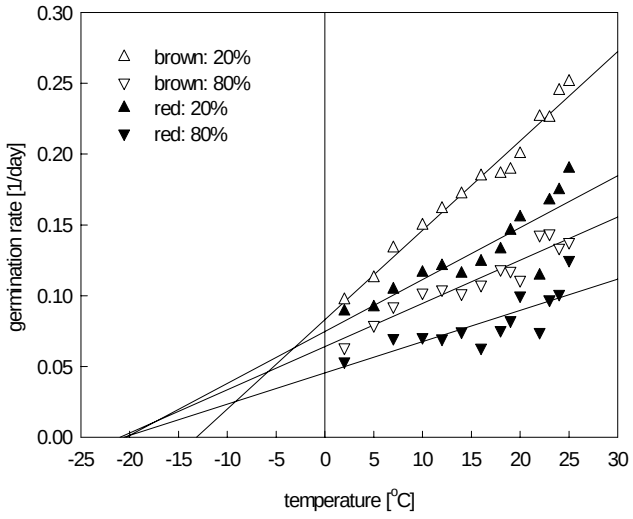

Fig. 5 Germination rate as a function of temperature. Only 20th and 80th germination percentile rates are depicted (average of three replicates). Brown and red bulbils differed significantly in slope (see Table 4 for analysis of 50th percentile). Linear regression is extended to x-axis to estimate base temperature.

The common approach to determining base temperature (T_b) is to regress germination rate (= 1/time required for x% of the seeds to germinate) against temperature (Angus *et al.* 1981; Garcia-Huidobro *et al.* 1982). Doing this for various percentiles of germination all regressions should share the same x-axis intercept, the base temperature (e.g. Pritchard & Manger 1990). With our data set, this approach yielded no satisfactory result: data points did not lie on a straight line (Fig. 5; Table 5). More importantly, however, the base temperature extrapolated from this approach was about -20°C, which is obviously unrealistic. The approach should be carried out on a "clean" data set, from which low or high temperatures, at which germination times deviate from the assumed relation, are deleted (Angus *et al.* 1981; Moot *et al.* 2000). However, there is no apparent break in the data for *Polygonum viviparum*, either at high or low temperatures (Fig. 5).

As Figure 6 shows, thermal time is proportional to temperature (at least up to c. 18°C), indicating that less thermal time is required for germination at low temperatures. This assumes an 0 °C as base temperature, which is ecologically sound. Using

Table 5 Comparison of two alternative ways to calculate base temperature (lowest temperature where germination could occur). 1. Regression of germination rate (until 50%: $1/Tt_{50}$) against temperature (see Fig. 5) and 2. thermal time (until 50% germination (Tt_{50}) against germination (see Fig. 6). The table shows regression parameters for the two approaches as well as the derived base temperature (T_b) and thermal time for 50% germination (Tt_{50}). *** indicates a significance level of $P < 0.001$. Assuming temperature independent germination would yield a slope of 7.47 ± 0.33 (SE) for brown and 10.19 ± 0.32 for red bulbils (calculated as grand mean of x_0 for all temperatures; N = 42). Notice how marginally the regression for red bulbils deviates from this null model, indicating extremely weak temperature dependence of x_0.

		regression parameters					derived	
	colour	**intercept**	**slope**	**df**	**F**	**R^2**	**Tb [°C]**	**Tt50 [°Cd]**
1/Tt50%	brown	0.0765	0.0043	40	195.1***	0.830	-17.79	232.55
	red	0.0634	0.0026	40	67.0***	0.626	-24.38	384.61
Tt50%	brown	21.19	5.71	28[1]	413.4***	0.937	-1.04	-[3]
	red	10.37	9.93	21[2]	791.9***	0.973	-3.71	-[3]

[1] only data < 20°C used

[2] only data < 18°C used

[3] temperature dependent, see regression parameters

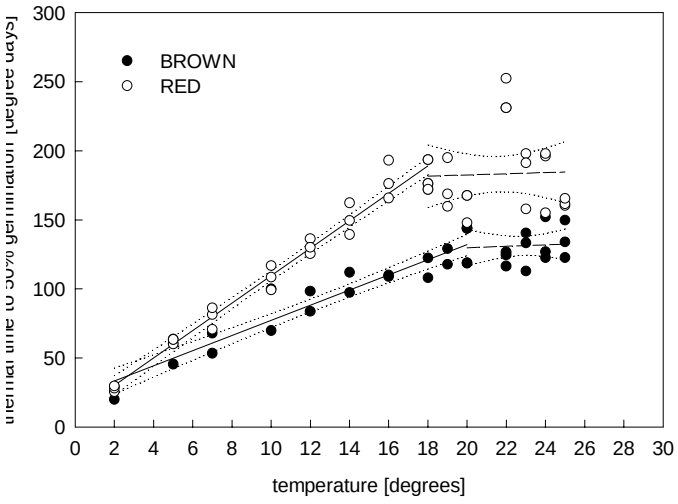

Fig. 6 Thermal time accumulated until 50% germination, comparing red and brown bulbils. Fitting a continuous function to the data always led to unacceptably high deviation from the obviously linear relation in the temperature range from 2 to 18°C (or 20°C for the brown bulbils). For regression parameters see Table 4. Dotted lines are 95% confidence limits. Dashed lines are not significant ($P > 0.8$).

the unrealistic –20 °C from the method described previously, thermal time would indeed be almost constant, but the base temperature would not relate to reality. Extrapolating the lines in Fig. 6 to the x-axis yields a base temperature of c. -2°C (Table 5), which is much more reasonable.

It can thus be concluded that the thermal time concept can not be readily applied to plants growing in very cold climates, as they seem to be able to compensate for the lack of warmth at low

temperatures (see also Heide 1992). This hints at the adaptation of the enzymes involved in germination (e.g. α-amylase to break down the starch) to very low temperatures, being little influenced by the low temperatures of this experiment (notice shallow slopes in Fig. 4). The linear relationship between thermal time and germination temperature (Fig. 6) would then be a consequence of the greater variability of temperature (varies 12-fold) compared to x_0 (varies 2-fold). The results thus support the evidence provided by Heide (1992) of almost temperature independent germination below a threshold temperature of c. 20°C.

ACKNOWLEDGEMENTS

Many thanks to Audun Stien for help with the survey, to David Burslem for allowing us to use his temperature gradient plate and to Robert Crawford and Matt Daws for useful comments on an earlier draft.