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No evidence for adaptation of two *Polygonum viviparum* morphotypes of different bulbil characteristics to length of growing season: abundance, biomass and germination

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Abstract. The high degree of habitat heterogeneity and habitat 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, which affects the Arctic more strongly than other ecosystems. Here, we assessed if two morphotypes of *Polygonum viviparum* (characterised by different colours of their bulbils) differ in their abundance along a snowmelt gradient, if their biomass allocation patterns are influenced differentially by environmental variables, and if the temperature dependency of bulbil germination differs between morphotypes. We found slight differences in the effect of timing of snowmelt on abundance of the morphotypes, which seem to have little ecological relevance. Total biomass and biomass allocation were similar between morphotypes and were negatively correlated with soil-water content. Bulbil germination (the onset of growth of the bulbil) was assessed over a temperature range from 2 to 25°C and results indicate an earlier (maximum of 5 days) "germination" of one morphotype, but final bulbil germination (>80%) and bulbil-germination rate were similar for both types. Bulbil germination was weakly temperature dependent, with faster emergence at higher temperatures. Overall, our results could provide no convincing evidence for differences between the two examined morphotypes that could be of ecological relevance with respect to anticipated climate change in the Arctic.

Introduction

The terrestrial high Arctic will experience the strongest relative changes in climate world wide, as predicted by General Circulation Models (IPCC *1990*, *1998*; Maxwell *1992*) and observed over the last decades (Serreze et al. *2000*). The potential consequences for individual plants and vegetation are immense, and the question of whether the changes anticipated will lead to the extinction of plant species characteristic to this severe environment has caused some concern (Chapin and Körner *1994*). It has been argued, however, that the high degree of spatial heterogeneity ("habitat fragility", Crawford *1997b*), a natural feature of arctic vegetation, has given rise to high ecotypic variation within species, each ecotype being adapted to a 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 an 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*, *S. oppositifolia*) differ in their morphology (Crawford et al. *1993*; Crawford and Smith *1997*). *Dryas octopetala* significantly reduces its allocation to the gynoecium in sites with a shorter growing season (Wada *1999*). However, 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 and Arroyo *2000*).

P. 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 1 year 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 (which led to its name’s epithet), but this has been observed only very sporadically in the population investigated here. Bulbil germination apparently takes place in the next spring; growth in the 1st year relies mainly on stored starch, as by late August only the first leaf pair has emerged (personal observation). Around 10% of the bulbils germinate successfully (range 0-63%; C.F. Dormann, unpublished data), especially in very moist places.

Individuals of *P. 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 and Smith *1997*). Bulbil colour is a genetically determined trait (Bauert *1996*), which means that differences in success and distribution of bulbil morphotypes has direct implications for the genetic structure and diversity of the *P. viviparum* population at a given site. It has been suggested (Crawford and Smith *1997*) that the genotypes represented by different bulbil colours are adapted to differences in season length, with individuals 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 morphotypes of *P. viviparum* differ in their distribution with respect to environmental variables, and (2) whether temperature dependency of bulbil germination (i.e. the beginning of growth of the bulbils) correlates with the distribution of the morphotypes.

Materials and methods

Site and species description

Fieldwork was carried out in Semmeldalen, Svalbard (78°N 15°E). This inner-fjord 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 waterlogged *Eriophorum scheuchzeri*-swamps (Rønning *1967*, *1996*).

P. 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 square metre. Most individuals of *P. viviparum* at this site produce red bulbils (ca. 85%), but brown (ca. 15%), pale-yellow and purple bulbils (each <1%) are also encountered.

Survey

In August 1999, 40 permanent plots (1 m^2) were established in Semeldalen, 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 plot on 26 July 2000. Season length was estimated on a five-point scale based on the duration of snowlie. Aspect and slope were measured with a compass and inclinometer, respectively. Exposure was estimated on a five-point scale, from raised above the surrounding area (5) to troph position (1). This was applied both at the scale of 4 m^2 and 100 m^2. From each plot, a pair of *P. viviparum* plants was excavated, one with red and one with brown bulbils. As both red and brown plants did not always occur at each plot, sample sizes are less than 40. Plants were sorted into rhizome, bulbils and leaves plus flower stalk, and pre-dried at 40°C for 1 week. After transport back to the laboratory, samples were re-dried at 70°C for 24 h 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 data).

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

Bulbil emergence test

Bulbils of *P. viviparum* were collected in Semmeldalen, Svalbard, in the 1st week of August 1999 from all along the transect. 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 bulbil-germination experiment.

The bulbil-germination test was carried out using a temperature gradient plate (Grant Instruments). 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 (each ca. 5 cm × 5 cm) was placed to reduce airflow and to

compartmentalise the bulbils. Above the plate, two greenhouse lights provided continuous illumination (ca. 250 mmol m^{-2} s^{-1}). The exact temperature in the germination cells was measured with a Squirrel temperature data logger (Skye Instruments) at the end of the experiment. These deviated from the set temperature by +1°C at the low end to -1°C at the high end. The realised temperature range was therefore 2-25°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 6 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 for 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). Bulbil germination seemed to be independent of bulbil size (personal observation, Gugerli *1997*).

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

All bulbils were checked for signs of emergence every morning for 1 month. The bulbils are cone-shaped, and the rootlet generally emerges at the bottom end, being visible even before emergence as a white dot at the bottom of the bulbils. Emergence of the roots was scored as successful "germination" and the germinated bulbil was removed from the plate. The red bulbils deviated from this pattern: in about half of them the root emerged through the side of the bulbil, rather than through the bottom. 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 *1989*). As the best-fitting regression model for the effect of soil-water content on total biomass of *P. viviparum* along the survey sites was an exponential function, both biomass and soil-water content data were ln-transformed.

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

Weighted germination coefficients (using 1/*coefficient of variance* as the weighing variable) for each cell were then compared for red and brown bulbils using a Generalised Linear Model (GLM) 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 that 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.

Results

Survey: biomass allocation and environmental gradients

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

Table 2. Comparison of dry weights of *Polygonum viviparum* with brown (N=33) and red (N=36) bulbils. Data given are means, 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 and 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
Bulbil weight (mg)	29.3±3.59	27.8±2.88	0.01	0.923
Number of bulbils	23.0±1.63	23.1±1.93	0.20	0.652

Of the parameters assessed at the survey sites (slope, aspect, soil-water content, exposure, season length), only soil-water content was significantly related to the weight of *P. viviparum* ($F_{1,29}=5.38$, $P<0.05$; 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 ($F_{1,29}=0.25$, $P=0.62$).

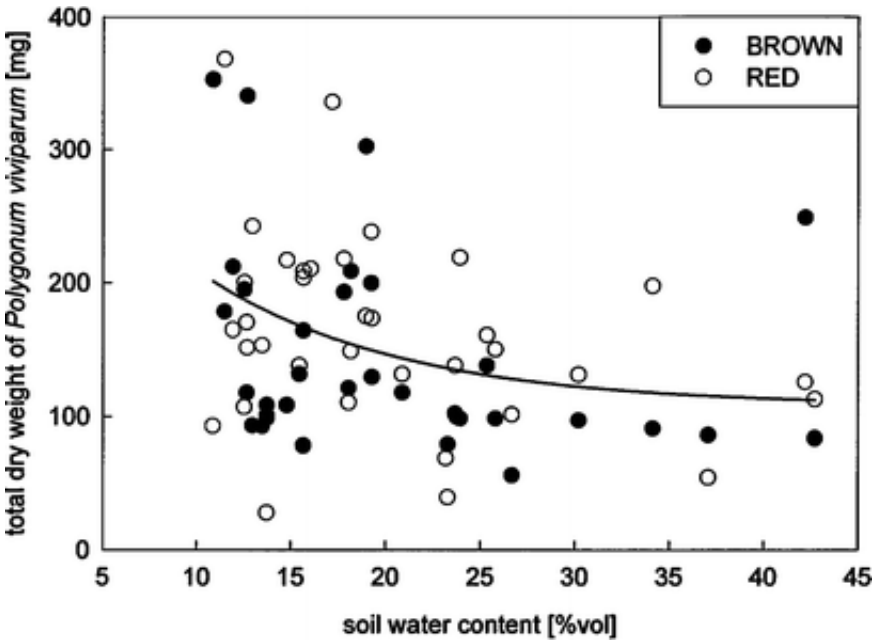

Fig. 1. Total biomass of *Polygonum viviparum* as a function of soil-water content. Dry weights of brown and red *P. viviparum* did not differ; the regression line (biomass $107.8 + 260.6\ e^{-0.094 \cdot \text{soil water content}}$; $F_{1,31}=5.38$, $P<0.05$, $R^2=0.177$) represents both bulbil colours

Snowmelt transect

The abundance of *P. viviparum* of the two bulbil colours 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 and their distribution was, hence, spread out more evenly across the gradient (Fig. 2; Table 3). *P. viviparum* individuals with red bulbils decreased from ca. 150 ind. m^{-2} at places with very early snowmelt in late May (Julian date of ca. 145) to 0 at a snowmelt date of early July (Julian date of ca. 185). *P. viviparum* with brown bulbils did not occur in areas of late snowmelt either, even though they shared no overall correlation with snowmelt data. The percentage red decreased significantly with Julian day from 99% to 56% (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 morphotype compared to the other is influenced by the timing of snowmelt.

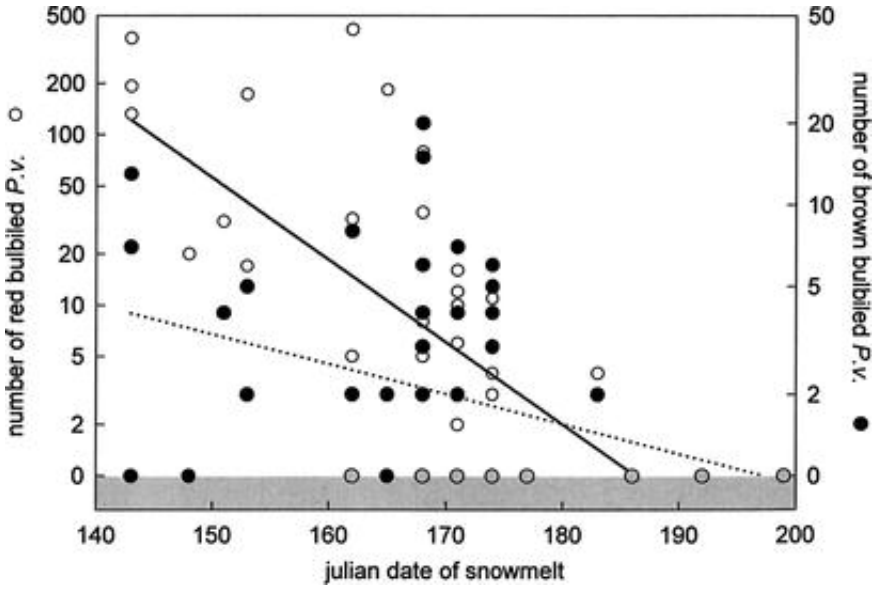

Fig. 2. Number of *Polygonum viviparum* of the two colour varieties per m^2 along a snowmelt gradient. Julian day on *x*-axis refers to time when plot became snowfree. Note difference in scaling. Regression line for red (*unbroken line*): y=742.2-4.17 x ($F_{1,43}$=17.25, P<0.001) and for brown (*broken line*): y=18.17-0.094 x ($F_{1,43}$=3.43, P=0.071). *Grey* data points contain *white* and *black* dots

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Table 3. Summary of statistical test of differences in the number of *Polygonum viviparum* occurring along a snowmelt gradient. *Colour* refers to differences between *P. 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		

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). Therefore, there was no relationship between density and soil-water content for either colour and no significant interaction between colour and soil-water content.

Bulbil-emergence test

P. viviparum showed surprisingly little sensitivity to environmental temperature: bulbils emerged at all temperatures (2-25°C). Bulbil germination was rapid and almost complete for both bulbil colours (>90%; Fig. 3). The onset of emergence was faster and (as germination rate was the same for both bulbil varieties) the time-span to half-maximal germination was significantly lower for brown bulbils than for red (Fig. 4; Table 4). The greatest difference occurred at temperatures of 12-22°C and was

minimal at both low and high temperatures (Figs. 3, 4). Maximum bulbil germination was slightly lower at low temperatures, but still very high (90% at 2°C; Figs. 3, 4). Once emergence commenced, rates (*b*) were similar for both bulbil colours, but again dependent on temperature (Fig. 4; Table 4). Increasing temperature from 2°C to 10°C accelerates the onset of emergence and increases the maximum bulbil germination with little impact on germination rate (Figs. 3, 4). From 12°C to 25°C, x_0 decreases slowly and maximum bulbil germination remains constant, while the germination rate fluctuates inconsistently. As the error bars in Fig. 4 indicate, time at half-maximum germination (x_0) and maximum bulbil germination vary more between replicates at low than at higher temperatures. No such pattern is apparent for *b*.

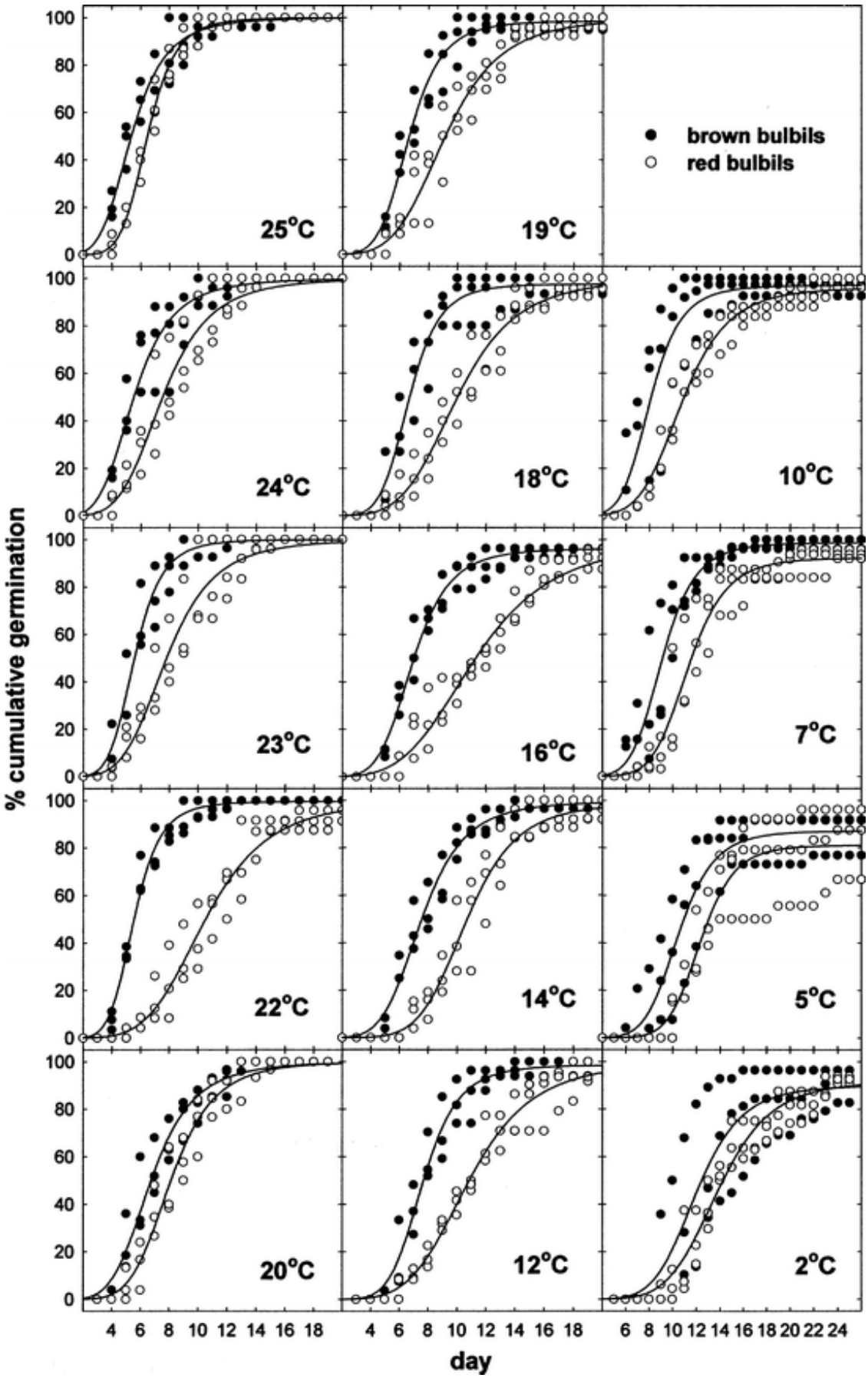
% cumulative germination
day
brown bulbils
red bulbils
25°C
19°C
24°C
18°C
10°C
23°C
16°C
7°C
22°C
14°C
5°C
20°C
12°C
2°C

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

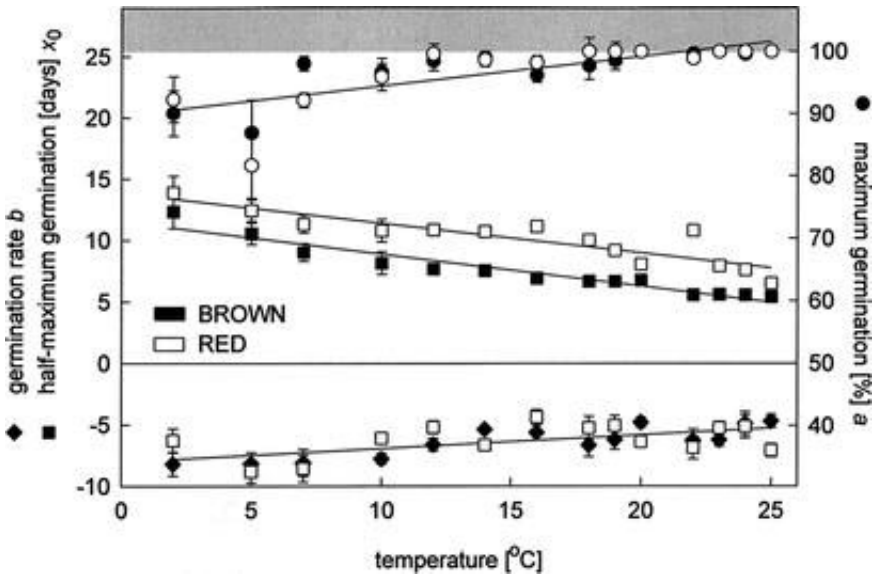

Fig. 4. Regression parameters for the different temperatures. Data from red and brown bulbils were indistinguishable for maximum germination (*a*) and germination rate (-*b*), but differed significantly for time to half-maximum germination (x_0). Regressions depicted are: a=89.94+0.436 temperature; b=-7.29+0.083 temperature; x_0(brown)=10.79-0.24 temperature and x_0(red)=13.80-0.27 temperature. *Error bars* depict ±1 standard error. See Table 4 for statistical analysis of parameters.

Table 4. Statistical results from the analysis of "germination" regression coefficients (Fig. 4) for red and brown bulbils

Parameter	Effect	*df*	MS	*F*	R^2
Final bulbil germination (*a*)	Block	2	4.295	5.98**	0.08
	Temperature	1	47.800	66.54***	0.42
	Error	80	0.718		
Slope (*b*)	Block	2	1.0807	2.73 †	0.08
	Temperature	1	6.0946	15.42***	0.15
	Error	80	0.3953		
Time to half-maximal germination (x_0)	Block	2	87.91	24.15***	0.08
	Temperature	1	1123.82	308.74***	0.52
	Colour	1	569.65	156.49***	0.26
	Error	80	3.64		

†, ** 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

Discussion

Ecotypes adapted to different season lengths?

Overall, we found no convincing evidence for the adaptation of different morphotypes of *P. viviparum* to differences in season length as hypothesised by Crawford and Smith (*1997*). In our study area, the red-bulbil type of *P. viviparum* was always 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 morphotype is not based on any of the parameters we measured, but might be related, for example, to differential susceptibility to rust (as shown for interspecific differences in *Rumex* by Hatcher et al. *1994*).

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

Emergence characteristics of the two bulbil colours are consistent with the field findings, in as much as slight differences between morphotypes could be detected, but their ecological relevance in the field is doubtful. Roots emerged a few days earlier from brown than from red bulbils, but total bulbil germination (*a*) and germination rate - once it started - (*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 morphotype more successful than the brown one. One possible reason is that the genes coding for bulbil colour are not coupled to those providing ecological benefits. Alternatively, the high genetic diversity of *P. 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, are very high, we found no support for the idea of Crawford and Smith (*1997*) that *P. viviparum* bulbil colours reflect this ecological potential.

Temperature dependency of emergence

With respect to germination requirements, arctic-alpine plants are exceptionally tolerant to low temperature (Söyrinki *1941*; Baskin and Baskin *1998*). However, even these plants hardly germinate below 5°C (Mooney and Billings *1961*; Sayers and Ward *1966*), and out of 12 high-arctic species tested by Bell and Bliss (*1980*) only 3 ruderals (*Oxyria digyna*, *Phippsia algida*, *Saxifraga cernua*) germinated below 5°C. With respect to maximal germination, arctic-alpine plants seem to fall into one of two categories: either their germination success was very high, or virtually absent (Bliss *1958*). Interestingly, *P. viviparum* was described as a poorly germinating species (4-10%, Bliss *1958*), in contrast to our findings, although it is unclear if the cited study was performed on bulbils or the very rare seeds.

Our study indicates that bulbil germination can occur at temperatures close to freezing, and that bulbil germination is very high and decreases little with temperature (Fig. 4). As pointed out by Baskin and Baskin (*1998*), bulbils are usually non-dormant and start to grow as soon as they come in contact with

moist soil. Temperature dependency of all "germination" parameters, but especially for x_0 (time to half-maximum germination), is very low: increasing temperature from 2°C to 25°C, i.e. by a factor of 12, only halves the time to half-maximum germination (Fig. 4). This demonstrates the preadaptation of *P. viviparum* bulbils to low germination temperatures in its arctic-alpine habitat. The same tendency was reported by Harmer and Lee (*1978*) for plantlets of *Festuca vivipara*, with a somewhat lower growth rate at 3°C.

P. viviparum seems to be able to compensate for the lack of warmth at low temperatures (Fig. 5). This hints at the adaptation of the enzymes involved in emergence (e.g. α -amylase to break down the starch) to very low temperatures, being little influenced by the cold in this experiment. The onset of emergence is almost immediate and temperature-insensitive. As these bulbils are purely vegetative, lacking the anatomical structures of true seeds (Diggle *1997*), the bulbils' *growth* is temperature-insensitive, rather than the clues that initiate "germination". Nevertheless, the results for bulbils support the evidence provided for seeds of *Koenigia islandica* by Heide and Gauslaa (*1999*) of almost temperature-independent germination below a threshold temperature of ca. 20°C.

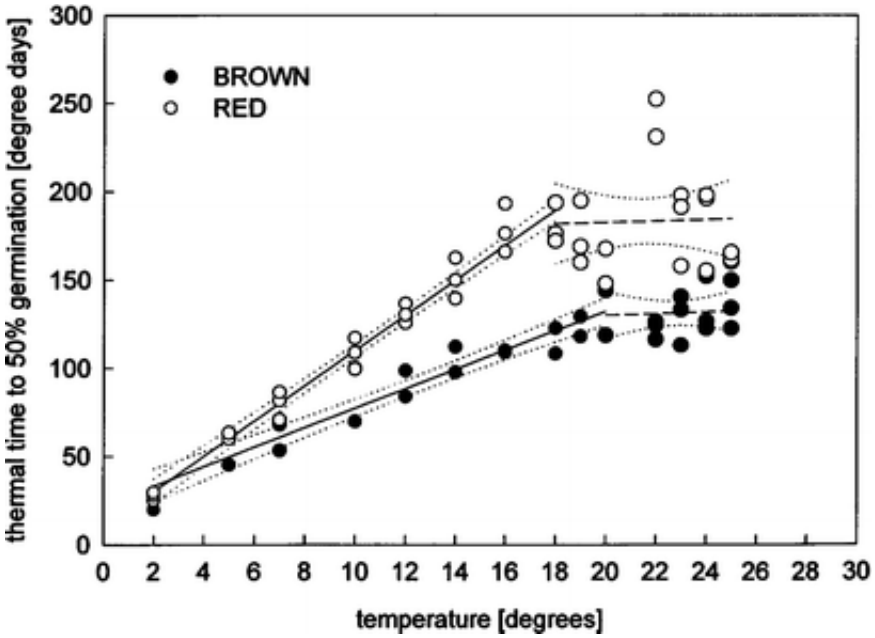

Fig. 5. Thermal time accumulated until 50% "germination", comparing red and brown bulbils. Fitting a continuous function to the data always led to unacceptably high deviation from the obviously linear relation in the temperature range from 2 to 18°C (or 20°C for the brown bulbils). For regression parameters, see Table 4. *Dotted lines* are 95% confidence limits. *Dashed lines* are not significant ($P>0.8$).

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