The Impact of Climate on Flowering in the High Arctic—The Case of Dryas in a Hybrid Zone

Authors: Høye, Toke Thomas, Mølgaard Ellebjerg, Susanne, and Philipp, Marianne

Source: Arctic, Antarctic, and Alpine Research, 39(3) : 412-421

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(06-018)[HOYE]2.0.CO;2

Arctic, Antarctic and Alpine Research, Vol. 39, No. 3, 2007, pp. 412–421

The Impact of Climate on Flowering in the High Arctic—The Case of *Dryas* in a Hybrid Zone

*Toke Thomas Høye**†§*
Susanne Mølgaard Ellebjerg†‡*
*and Marianne Philipp**

*Department of Population Biology, Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark.
†Department of Arctic Environment, National Environmental Research Institute, University of Aarhus, Frederiksborgvej 399, PO Box 358, DK-4000 Roskilde, Denmark.
‡Department of Terrestrial Ecology, Institute of Biology, University of Copenhagen, Øster Farimagsgade 2D, DK-1353 Copenhagen, Denmark.
§Corresponding author.
toh@dmu.dk

Abstract

The extreme seasonality of the High Arctic creates very different flowering conditions for plants in areas of early and late snowmelt. Therefore, future reproductive responses to climate change may be dependent on the timing of snowmelt. We combined genetic, morphological, and long-term monitoring data on *Dryas* from a High Arctic hybrid zone of *D. integrifolia* and *D. octopetala* to assess whether climate variation influenced flowering differently in areas of early and late snowmelt, and whether this could have a genetic origin. We found a non-linear relationship between timing of snowmelt and flowering. The duration of the period between snowmelt and the onset of flowering (pre-floration interval) varied with the date of snowmelt. Shorter pre-floration intervals were associated with warmer average temperature during the pre-floration intervals in both early and late melting plots. However, the pre-floration interval was much shorter in early than in late plots at the same average temperature. Likewise, the interannual variation in flower abundance differed between early and late melting plots. Flower abundance was negatively influenced by frost after snowmelt in the year of flowering in early plots. In late plots, flower abundance was positively influenced by the length of the previous growing season. We identified two morpho-types in the study area, but their distribution and genetic differentiation was not related to the snowmelt gradient. We conclude that the different flowering responses found along the snowmelt gradient are a result of environmental variation. Based on our results and projected climatic change for the study area, we predict that the onset of flowering will advance and flower abundance will increase in areas of early snowmelt. In areas of late snowmelt, the onset of flowering will remain unchanged or be delayed and flower abundance will decrease.

DOI: 10.1657/1523-0430(06-018)[HOYE]2.0.CO;2

Introduction

Environmental constraints on sexual reproduction in plants may be common at high latitudes (Callaghan et al., 1992; Molau, 1993). Indeed, experimental warming resulted in increased reproductive effort in a number of plant species in the High Arctic (Arft et al., 1999). At the same time, the most dramatic climatic changes are seen at high northern latitudes (Serreze et al., 2000). Therefore, the trade-off between sexual reproduction and vegetative proliferation in High Arctic plants may shift in response to climatic change, and this could affect vegetation dynamics and lead to the colonization of un-vegetated ground (Wookey et al., 1995). Sexual reproductive success may, however, also be under genetic control. In some plant species, different morpho-types inhabit abrasion plateaus and snowbeds and these morpho-types may be genetically distinct (McGraw, 1995; Max et al., 1999; Hirao and Kudo, 2004). Locally, reproductive responses to climatic variation have been found to differ between such morpho-types (McGraw and Antonovics, 1983) and may therefore be under genetic control. To predict future changes in plant reproductive success, we need to know whether intra-seasonal variation in sexual reproductive responses to climate is mainly under environmental or genetic control (Sørensen, 1941; Aydelotte and Diggle, 1997; Stinson, 2004).

The timing of flowering has documented effects on pollination success (Gugerli, 1998), gene flow among populations (McGraw and Antonovics, 1983), seed number (Wookey et al., 1995), seed size (Galen and Stanton, 1991), and the likelihood of seed predation (Brody, 1997) in Arctic and alpine plants. As such, the timing of flowering is an important component of reproductive success in these areas (Molau, 1993). It is well known from alpine and Low Arctic regions that timing of flowering is influenced by snowmelt (Thórhallsdóttir, 1998; Price and Waser, 1998; Inouye et al., 2002; Dunne et al., 2003; Molau et al., 2005). In the High Arctic, the seasonal gradients in temperature and day length are strong compared to lower latitudes, and this creates very different conditions for flowering in areas of early and late snowmelt. Therefore, individuals in areas of early and late snowmelt could be constrained by different aspects of the abiotic environment in the High Arctic. For instance, the development period from snowmelt to onset of flowering (pre-floration interval) may be prolonged by low temperatures early in the season but not later when it is warmer.

Flower abundance is also an important component of reproduction and may vary across a snowmelt gradient. Because the formation of flower primordia takes place during the previous growing season in many Arctic plants species, including *Dryas*, the maximal flower production is defined prior to snowmelt (Sørensen, 1941; Lloyd et al., 1980; Lloyd, 1980; Stephenson, 1981). Thus, an abbreviated growing season may result in low flower abundance in the following year (Johnstone and Henry, 1997), and frost events prior to anthesis in the year of flowering may cause

1523-0430/07 $7.00

flower abortion (Shaver and Kummerow, 1992). Individuals inhabiting areas of early snowmelt experience the longest growing seasons but are more prone to frost events. The longer growing season in areas of early snowmelt may lead to more flowers, but occasional late frost in some years may increase the interannual variation in flower abundance compared to areas of late snowmelt (Inouye et al., 2002; Bechtold et al., 2002). Due to differences in growing conditions, individuals in areas of early and late snowmelt may respond differently to future climatic change, but these hypotheses need further empirical support.

Here we analyze the role of environmental (snowmelt and temperature) and genetic (hybrid status) factors in the onset of flowering and flower abundance. We use spatially and temporally replicated long-term data on the widespread Arctic plant *Dryas* in a hybrid zone between the two species *D. integrifolia* and *D. octopetala* in High Arctic North-East Greenland (Philipp and Siegismund, 2003).

We specifically asked the following questions: 1) how is onset of flowering related to snowmelt and temperature, 2) is flower abundance in areas of early and late snowmelt affected differently by the duration of the growing season in the previous year and frost in the pre-floration interval in the current year, 3) does hybridization influence timing and abundance of flowering, and 4) given the results, how will future changes in temperature and snowmelt affect the pre-floration interval and flower abundance of individuals inhabiting areas of early and late snowmelt.

Methods

STUDY SPECIES

The genus *Dryas* (Rosaceae) has a circumpolar distribution in Arctic and alpine regions and is often a dominant component of heath vegetation (Welker et al., 1997; Wahren et al., 2005). The species are wintergreen dwarf shrubs (chamaephytes) forming matted cushions. Their leaves are leathery, and the flowers are lateral and solitary, about 2 cm in diameter, and are comprised of creamy white petals (typically eight petals per flower). The flowers are insect pollinated and the fruits are achenes, which are wind-dispersed by means of a persistent, elongated, and feathery style. In North-East Greenland, two species (*D. octopetala* and *D. integrifolia*) are found (Philipp and Siegismund, 2003). The species *D. octopetala* has brown, branched hairs on the lower side of leaves (octopetala scales *sensu* Hultén, 1959) and indentations on the leaf margins. The species *D. integrifolia* lack these two characters.

STUDY AREA AND DATA

The study took place at Zackenberg, North-East Greenland (74°28′N, 20°34′W). The climate is High Arctic, with a mean (June through August) summer temperature of 4.2°C and the date of 50% snow cover varying more than a month between 5 June and 9 July over the last 17 years (Hinkler, 2005). The vegetation is dominated by moist dwarf shrub heaths mixed with *Salix arctica* snowbeds, grasslands, and fens (Bay, 1998).

Dryas was studied in eight plots (labeled A–H), each divided into four equally sized subplots, as part of the Zackenberg Basic monitoring program (Meltofte and Berg, 2004). Every week from 1 June to 1 September during the years 1995 to 2004, the percentage of snow cover was estimated from visual inspection, and the proportion of buds relative to open or senescent flowers was estimated from counts of 50 randomly chosen flowers in each subplot (Meltofte and Berg, 2004). Although this procedure meant that the same individuals were not necessarily recorded at every visit, phenology within each subplot was found to be very synchronous (T. T. Høye, personal observation). A flower was defined as *bud* until insect pollination was possible and *open* until petals fall off and *senescent* thereafter. All flowers in each subplot were counted once a year at peak flowering. In 1995 and 1996, data from the subplots were not separated. For two plots (B and F) weekly observations of snowmelt and phenology were only made in the years 1998 and 1999. Therefore, we restricted analyses of phenology to the six remaining plots. The vegetation in the plots ranged from dry, windswept fellfields to moist snowbeds (Bay, 1998). Grasses and sedges along with *Dryas* were dominant where snowmelt was early. Snowbeds were dominated by *Salix arctica* and *Cassiope tetragona*, whereas *Dryas* was sparse. The plots varied in size from 2 to 91 m^2 to ensure that at least 50 flowers could be recorded in each of the four subplots. Three plots were enlarged in 1997 for the same reason (Table 1).

TABLE 1

The relative cover of *Dryas*, frequency of hybrids, and size of the eight study plots. Three plots were enlarged in 1997. In 1995 and 1996, plots A and C were 3 m^2 and plot E was 4 m^2.

Plot	*Dryas* cover (in % of total area)	Hybrid frequency (in %)	Size (m^2)
A	65.4	92	4
B	26.7	93	12
C	44.2	96	6
D	64.4	97	2
E	42.7	72	6
F	55.2	89	12
G	1.8	81	91
H	3.2	72	60

A climate station, operated as part of the monitoring program, provided data on air temperature, incoming shortwave radiation (SWR), and photosynthetically active radiation (PAR) in the wave band 400–700 nm (Meltofte and Thing, 1996). Air temperature and SWR data used in this study were measured continuously two meters above the ground every hour from 17 August 1995 to 31 August 2004, whereas PAR was measured from 13 June 2002 to 31 August 2004 (Rasch and Caning, 2004). The end of the growing season was defined as the last day before mean temperature drops below −2°C, as an estimate of the first date of frozen soil in winter. In years where PAR was not measured, it was predicted using a linear regression model with SWR as predictor for the months May through August (PAR [unit: μmol m^{-2} s^{-1}] = 7.414 + 2.033 × SWR [units: W m^{-2}]; $R^2 = 0.978$).

SNOW COVER

During the snowmelt period, the snow cover in each plot decreased from 100% to 0% within 2–3 weeks. Since snow cover was only recorded weekly, any sigmoid relation between date and proportion of snow cover was difficult to detect and model. However, the relation would be approximately linear at intermediate proportions, and we described timing of snowmelt by the date of 50% snow cover (hereafter termed snowmelt). This was estimated by linear interpolation between the latest weekly observation in which snow cover was above 50% and the earliest weekly observation in which snow cover was below 50%. In some cases snowmelt in some plots occurred prior to arrival at Zackenberg; in these cases, the plot-specific date of snowmelt was estimated as the date at which ground daily mean temperature rose above one degree Celsius (Price and Waser, 1998). Ground

temperature was logged by a Tiny Tag data logger (Gemini Data Loggers, Chichester, UK) installed in each plot on the soil surface covered by the vegetation. This date was highly correlated to the observed date of snowmelt (Pearson correlation; $R^2 = 0.98$; $P < 0.0001$). The Tiny Tag logger data were missing for a few of the years and for some plots due to malfunctioning and removal by arctic fox (*Alopex lagopus*), and no other data on snowmelt exists. We used the data logger time series solely to estimate date of snowmelt because of the large number of missing values. Since the spatial pattern of snowmelt is relatively consistent across years (Hinkler, 2005), we predicted missing values of snowmelt statistically by using a general linear mixed model. The response variable was the observed date of snowmelt, and the model included year as the random factor and plot and subplot nested within plot as fixed factors. Model reduction was based on likelihood ratio tests (correlation of observed vs. predicted $R^2 = 0.998$; $P < 0.0001$). We ran all subsequent analyses involving date of snowmelt with and without values predicted by the linear mixed model.

PHENOLOGY AND FLOWER ABUNDANCE

The phenological development of flowers was recorded as weekly estimates of the proportion of buds relative to open and senescent flowers. The date when 50% of the flower buds had opened (hereafter termed onset of flowering) was estimated by linear interpolation between the latest weekly observation in which less than 50% of the flower buds had opened and the earliest weekly observation in which more than 50% of the flower buds had opened. By definition, this date is later than first flowering dates used in some other studies, but it should be less sensitive to annual variation in flower abundance. We excluded estimates of the onset of flowering in subplots based on less than 20 individuals.

To make estimates of the flower abundance comparable across subplots and plots, the number of flowers in each subplot was divided by the total area (see next section) covered by *Dryas* in the subplot. We characterized flowering conditions by two measures. First, the length (in terms of possibility for resource accumulation to flower production) of the previous growing season was estimated using the number of hours between snowmelt in spring and frozen ground in autumn, where both PAR (in $\mu mol\ m^{-2}\ s^{-1}$) and temperature (in degrees Celsius) were above zero. Second, the risk of flower frost damage during the pre-floration interval in the year of flowering was estimated using the number of hours in the pre-floration interval during which temperatures were below zero degrees Celsius (Inouye et al., 2002).

Linear mixed effect models with plot and subplot nested within plot as random factors were used to account for uncontrolled variation among plots and subplots. Choice of error distribution was dictated by the scale of the response variable (normal or binomial). Full models included all interactions among fixed factors, which, for models of flower abundance, included measures of both flowering conditions and flower abundance in the previous year. Parameter estimation in mixed models was based on the residual maximum likelihood method (Venables and Ripley, 2002), model reduction was based on Akaike Information Criteria (AIC) (Anderson et al., 2000), and models were built on datasets where all variables were available for all observations. Parameter estimation and model reduction in models without random effects was based on the least squares estimation method. Whenever response variables were arcsine or $\log_e$ transformed to stabilize variances, it is given in the text.

ISOZYMES, MORPHOLOGY, AND SIZE OF INDIVIDUALS

In 2003 a sketch of the form and exact location of all cushions was made for each plot in the field and leaves were sampled for morphological and isozyme analyses. Subsequently, starch gel electrophoresis was performed and analyzed on six isozymes systems following the methods of Philipp and Siegismund (2003). The sketches of the cushions and the multilocus genotypes were used to identify genets (hereafter referred to as individuals). If two neighboring cushions had the same alleles in all six isozyme systems, they were regarded as one individual. Genetic diversity was quantified by gene diversity (expected heterozygosity) H_e. The phylogenetic relationships among populations, based on Nei's genetic distances (Nei, 1972), were estimated using the program FITCH (PHYLIP, Felsenstein, 1993).

From each of the genets, identified by isozymes, seven morphological characters were measured on five leaves: leaf length, middle width of leaves after unfolding, depth of indentations of the most central indentation and number of indentations, the number of octopetala scales, and the presence of glands on the dorsal and ventral side of the leaves (Philipp and Siegismund, 2003). For the two largest plots G and H, only 73.5% and 76.4% of the plot was sampled, respectively, and only data on two of the subplots were used in subsequent statistical analyses involving morphological and isozyme data. The clustering of morphological data was investigated using principal component analysis (PCA) (Quinn and Keough, 2002). We based calculations on the correlation matrix instead of the covariation matrix, as the characters were measured on different scales. We also combined the genetic and morphological data (see Philipp and Siegismund, 2003).

The area covered by each cushion was estimated by a circle, with the diameter equal to the mean of two perpendicular axes across the cushion. One of them was aligned along the longest axis through the cushion and the other was perpendicular and crossing the midpoint of the first axis. For each subplot the proportion of the plot covered by *Dryas* was calculated from these data. In analyses involving the size of individuals, areas were square-root transformed to make values proportional to diameters and age under the assumption of linear growth. The mean size of individuals in each subplot was the average size of all individuals in the subplot weighted by the proportion of the individual being inside the plot.

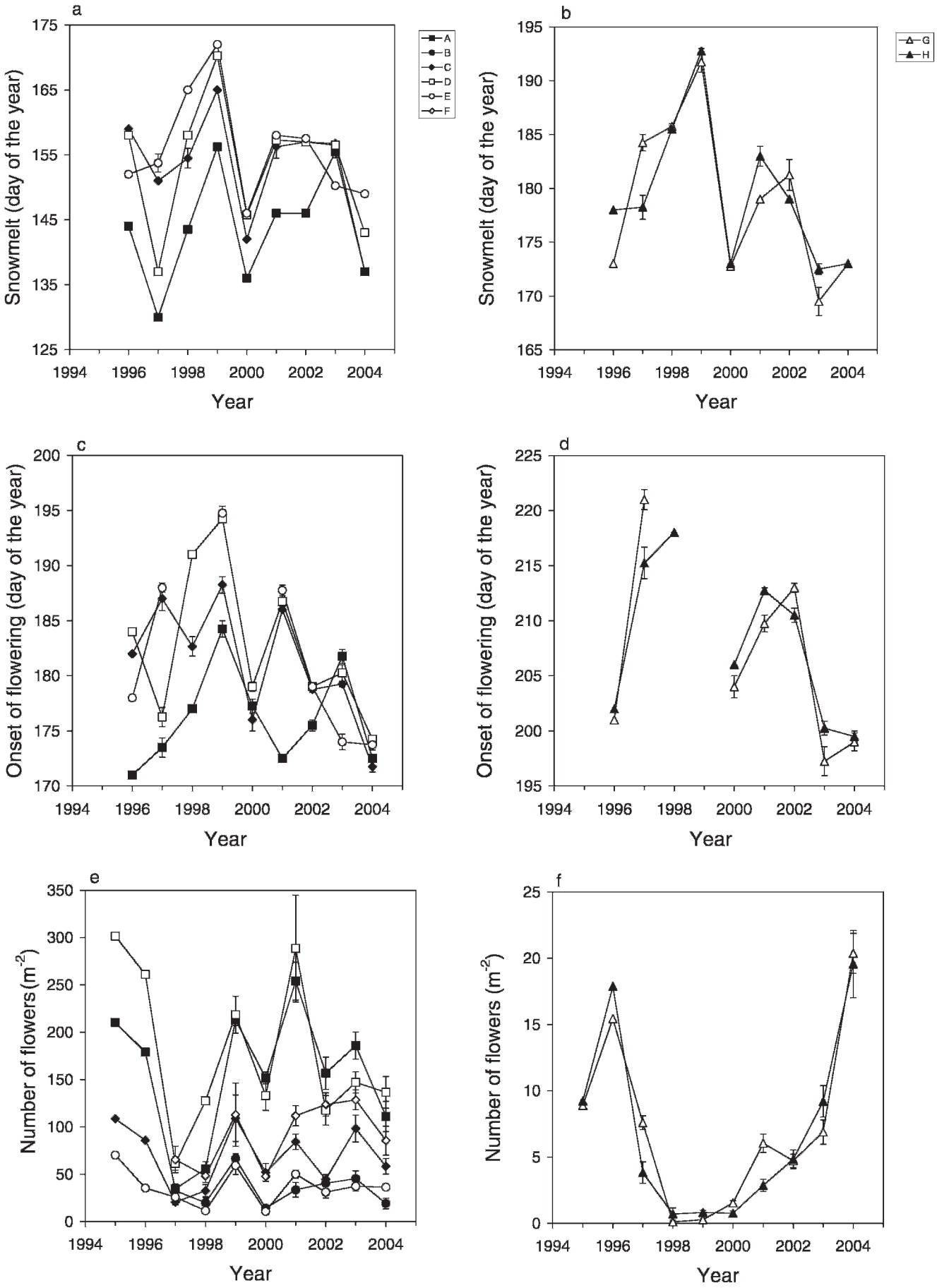
Results

PHENOLOGY AND FLOWER ABUNDANCE

The dates of snowmelt fell within a two-month span across years and plots, between day 130 of 1997 (10 May) for plot A and day 193 (12 July) of 1999 for plot H, and about a one-month span within plots (Figs. 1a and 1b). Average date of snowmelt differed

→

FIGURE 1. Time series of date of snowmelt (a and b), date of onset of flowering (c and d), and flower abundance per square meter (e and f) for early (a, c, and e) and late (b, d, and f) plots. Values are averaged across subplots and error bars indicate one standard error. No error bars are given in the years 1995 and 1996, since observations were not made separately for each subplot in these years. In other cases, missing error bars are due to lack of intra-plot variation or because only information from one subplot was available.



across plots. We defined plots A–F as early melting (or merely early) and G–H as late. Accordingly, flowering was considerably earlier in early melting plots than in late melting plots (Figs. 1c and 1d). Flower abundance also varied considerably from year to year (Figs. 1e and 1f). The interannual dynamics of flower abundance was similar within early and late plots but differed between early and late plots. Pearson correlation coefficients of flower abundances ($\log_e$ transformed) in pairs of either early or late plots ranged between 0.35 and 0.96 (10 of 16 significant), but in pairs of one early and one late plot the range was between −0.29 and 0.22 (0 of 12 significant).

There was a clearly nonlinear relationship between the onset of flowering and the date of snowmelt across plots (Fig. 2a). A second-order polynomial model explained the relation significantly better than a linear model ($R^2_{linear} = 0.857$; $R^2_{second\text{-}order} = 0.932$; t-test of second order term: $t = 13.57$, d.f. = 1, $P < 0.0001$). Therefore, the length of the pre-floration interval varied with date of snowmelt (Fig. 2b). We found a significant negative relationship between the duration of the pre-floration interval and the average temperature in the pre-floration interval in both early and late plots ($\text{slope}_{early} = -4.733$, $F_{1,111} = 82.73$, $p < 0.0001$; $\text{slope}_{late} = -2.926$, $F_{1,43} = 36.42$, $p < 0.0001$) (Fig. 2c). There was no significant difference between plots in either early or late plots. Running statistical analyses without the predicted dates of snowmelt did not qualitatively change the results.

The factors explaining variation in flower abundance varied between early and late plots. For early plots the final model included the number of frost hours between snowmelt and flowering as the only fixed predictor (slope = −0.00239; $F_{1,111} = 49.96$; $P < 0.0001$). For late plots only the number of hours with positive values of both PAR and temperature during the previous growing season were present in the final model (slope = 0.006226; $F_{1,26} = 47.86$; $P < 0.0001$). Thus, in early plots, the flower abundance was negatively related to frost in the pre-floration interval, whereas for late plots it was positively related to the conditions for resource accumulation in the summer preceding flowering. Flower abundance in each year was not related to flower abundance in the previous year in either early or late plots. There was a significant within and across plot variation in early plots but not in late plots (excluding plot and subplot nested within plot increased AIC in the final model from 261.4 to 350.8 for early plots but did not increase AIC in the final model for late plots).

ISOZYMES, MORPHOLOGY, AND SIZE OF INDIVIDUALS

A total of 309 putative individuals were identified in the field, as judged by the color and size of the leaves. Among these individuals, the analysis of multi-locus genotypes identified 275 genetically distinct individuals. The allele frequencies varied significantly among plots (G-test, $P < 0.01$) (Appendix 1) and an unrooted maximum likelihood tree (not shown) showed that the two most geographically distant plots (B and F) are, genetically, the most different populations. The PCA analyses of the isozyme data alone, or combined with the morphological data, did not reveal any clustering in groups, and the first two principal component axes explained only 27.67% and 28.88% of the variation, respectively. However, PCA analysis of the morphological data alone revealed two groups of *Dryas* within the study area, and the first two principal component axes explained 67.91% of the variation (40.19% by the first axis and 27.72% by the second axis) (Fig. 3). The main characters separating the two groups were octopetala scales and glands ventrally and dorsally on the leaf. The correlation coefficients for the first and second PCA axes were of opposite signs in these characters, whereas both were positive in other characters. Since one group resembled previous descriptions of *D. octopetala* (Hultén, 1959) and the other group was intermediate to *D. octopetala* and *D. integrifolia*, we denote them *D. octopetala* morpho-type and hybrid morpho-type, respectively. All characters, except the presence of dorsal glands, varied significantly among plots (Appendix 2). Comparing the individuals in the two morpho-types revealed no genetic differentiation among the two groups ($P = 0.22$, Genepop, version 3.4). Hence, the genetic data were discarded in further analyses of hybrid status.

The frequency of the hybrid morpho-type varied among plots (GLM with binomial errors: Wald statistic = 18.18; $P = 0.0112$), but the proportion of the hybrid morpho-type (arcsine-transformed) in subplots was not significantly different between early and late plots (One-way ANOVA: $\text{Mean}_{early} = 0.940$; $\text{Mean}_{late} = 0.784$; $F_{1,26} = 2.98$; $P = 0.097$). The size distribution varied among plots (Appendix 3), and individuals were consistently larger in early plots than in late plots (One-way ANOVA: $\text{Mean}_{early} = 762.6\ \text{cm}^2$; $\text{Mean}_{late} = 308.8\ \text{cm}^2$; $F_{2,273} = 385.59$; $P < 0.0001$). The size of individuals did not vary between the two morpho-types (linear mixed model with plot and subplot nested within plot as random factors. Test of difference between morpho-types: $F_{1,247} = 0.84$; $P = 0.360$).

Discussion

Our results indicate that timing of flowering in *Dryas* is closely related to date of snowmelt. Interestingly, the relation between the onset of flowering and the plot-specific timing of snowmelt is nonlinear and, hence, the duration of the pre-floration interval varies through the season. This has several implications. First, it indicates that the timing of flowering is related to both the date of snowmelt and the environmental conditions during the pre-floration interval. Second, it indicates that snowmelt is more important to the timing of flowering in areas of late snowmelt than in areas of early snowmelt. Finally, it suggests that conditions during the pre-floration interval may be more important in areas of early snowmelt than in areas of late snowmelt. Experimental warming led to shorter pre-floration intervals in a previous study of *Dryas octopetala* from a subarctic locality (Welker et al., 1997), but not in the herb *Ranunculus glacialis* from an alpine locality (Totland and Alatalo, 2002). We found that pre-floration intervals were shorter when the average temperature during the pre-floration interval was high and vice versa, but the exact relation differed between early and late plots. The effect of temperature was stronger in early plots than in late plots. We had expected that pre-floration intervals would be shorter in late melting plots because the temperature generally increases during summer. Instead, we found that pre-floration intervals were longer in late rather than in early plots at similar average temperatures. The soil moisture content is generally higher in areas of late snowmelt due to increased accumulation of meltwater. This is likely to have a chilling effect on plants in areas of late snowmelt and may explain why the relation between the duration of the pre-floration interval and average temperature differs between early and late plots.

We found strikingly different year-to-year fluctuations of flower abundance in areas of early and late snowmelt. Previous studies from an alpine site have shown that flower abundance is related to timing of snowmelt and that the effect is probably mediated through increased frost damage when snowmelt is early

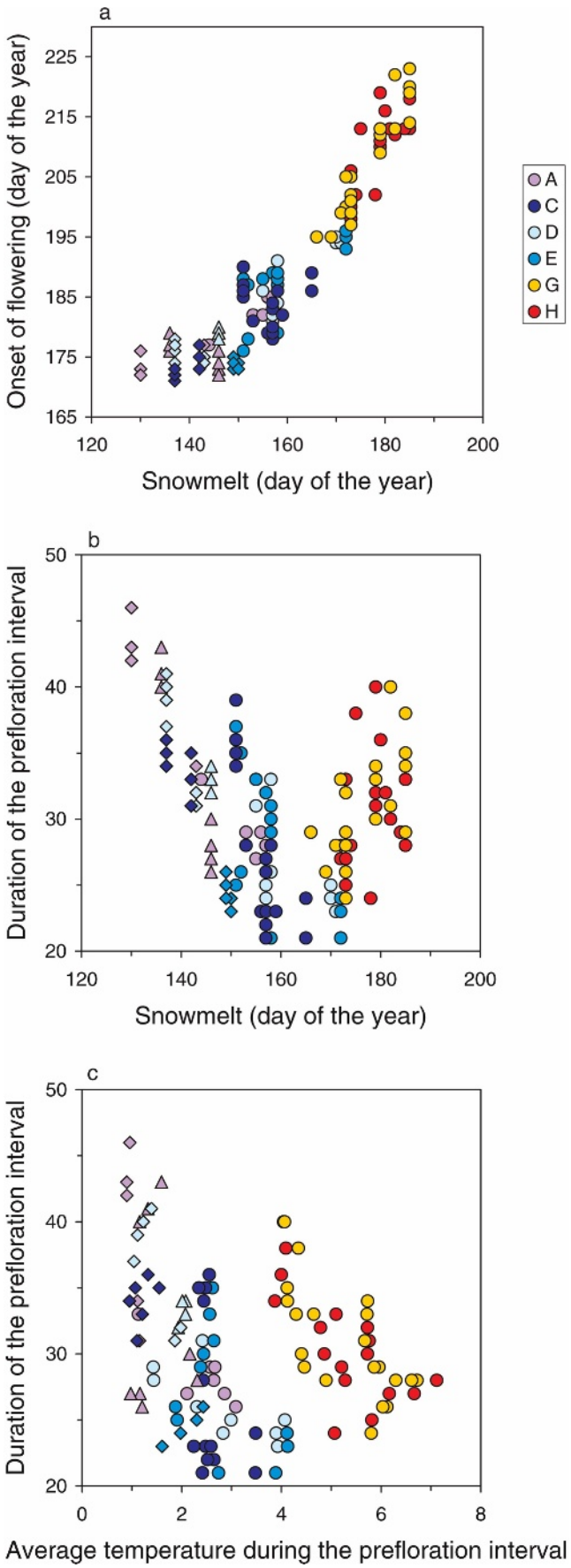


FIGURE 2. The relation between a) onset of flowering and date of snowmelt, b) the duration of the pre-floration interval in days and date of snowmelt, and c) the duration of the pre-floration interval in days and average temperature in Celsius during the pre-floration interval. Dots indicate that date of snowmelt was based on direct observation, diamonds are observations where snowmelt was estimated from temperature data loggers installed in each plot, and triangles are statistically predicted values.

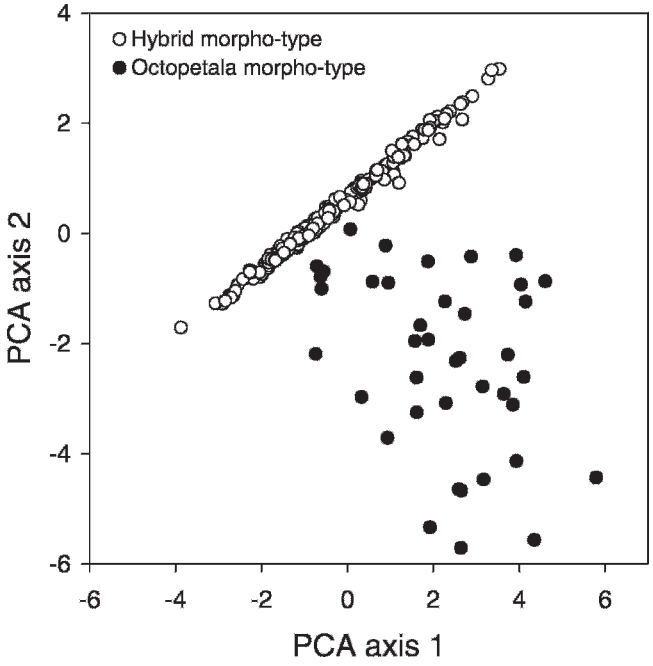


FIGURE 3. Scatter plot of the first two principal component axes describing 40.19% and 27.72% of the variation in seven morphological characters based on the correlation matrix, respectively. The grouping of individuals in black and white is based on clustering along the two axes.

(Inouye and McGuire, 1991; Inouye et al., 2002). Arctic studies have attributed variation in flower abundance to the length or quality of the previous growing season (Johnstone and Henry, 1997; Bliss and Gold, 1999). Our results suggest that both frost after snowmelt and variation in the length of the previous growing season can affect flower abundance in *Dryas*, and this could be related to the seasonal change in temperature and day length. The significant relationship between flower abundance and frost in the pre-floration interval in early plots indicates that over-wintering buds are prone to frost damage in our study area. For instance, two early plots (A and D) experienced earlier snowmelt, more hours of frost, and had lower flower abundance in 1997 than in any other year. In contrast, frost during the pre-floration interval is rare in areas of late snowmelt. Therefore, the over-wintering buds are less prone to frost damage in these areas. The shorter growing season in areas of late snowmelt may, on the other hand, restrict the accumulation of resources for flower bud production (Johnstone and Henry, 1997). Our results indicate that flower abundance is affected by the length of the previous growing season where snowmelt is late but not where it is early.

The clear differences between flowering phenology and flower abundance of the same species in areas of early and late snowmelt could be caused by genetic differentiation. The morphological variation in *Dryas* leaves enabled us to assign individuals to one morpho-type that was very similar to *D. octopetala* and one that was intermediate to *D. octopetala* and *D. integrifolia*. However, we

found no support for a spatial organization of the two morpho-types along the snowmelt gradient as reported for Alaskan subspecies (Max et al., 1999). The present dominance of the hybrid morpho-type relative to the *D. octopetala* morpho-type and their almost even distribution across plots prevented us from detailed studies of the differences in flowering response between the two morpho-types. However, the higher proportion of the *D. octopetala* morpho-type in plot E and H did not translate into a different length of the pre-floration interval and abundance of flowers. Hence, we conclude that the frequency of hybrids in the plots does not affect the flowering phenology and flower abundance. We did find a difference in allele frequency across plots, but it was largely explained by geographic distance and not related to the snowmelt gradient. Also, we found no genetic differentiation among the two morpho-types. Thus, we found no support for genetic or morphological differentiation being a result of the timing of snowmelt in the plots. Individuals were smaller in late plots, but ascribing the qualitatively different flowering dynamics to the differences in the size of individuals is not warranted by the difference in size distribution between plots (Appendix 3). The absence of studies of Arctic plant phenology and reproduction that have documented different flowering responses of the same species in areas of early and late snowmelt could also be related to the bias towards Low Arctic studies (Arft et al., 1999). The seasonal gradients in temperature and day length are less pronounced and the difference in environmental conditions experienced by plants in areas of early and late snowmelt may consequently be smaller in the Low Arctic.

Individuals in areas of early and late snowmelt respond differently to temperature and snowmelt in terms of the timing of flowering and flower abundance. Hence, any change in either temperature or snowmelt regime may also have different effects on early and late melting areas. Actually, individuals in areas of early snowmelt may not respond to even earlier snowmelt by flowering earlier if summer temperatures do not exhibit a parallel increase. The climate predictions for North-East Greenland are increased temperature and unchanged snowmelt in most areas, with later snowmelt possible in areas of late snowmelt due to increased snow precipitation during winter (Hinkler, 2005). If temperatures increase with no associated change in date of snowmelt, the onset of flowering will occur earlier and flower abundance will increase in all areas, according to our results. Furthermore, the interannual variation in flower abundance in areas of early snowmelt will decrease due to a lower risk of frost damage to flower buds (Bannister et al., 2005). If snowmelt will occur later in areas of late snowmelt, the onset of flowering may be unchanged or delayed depending on the relative role of snowmelt and temperature in these areas. The flower abundance may decrease even further because of the shorter growing season. In fact, considering the difference in cover of *Dryas* between areas of early and late snowmelt, a further reduction of the growing season in snowbeds may cause *Dryas* to disappear completely in these areas. Since the distribution of vegetation types is linked to the distribution of the snowpack, changing snow regimes may, in the long term, have repercussions on population dynamics and community structure. Therefore, the predictions of changes in flower abundance are partially dependent on the competitive ability of *Dryas* relative to other species.

Acknowledgments

We acknowledge the Zackenberg Basic monitoring program for providing access to ecosystem monitoring data and the Danish Polar Center for logistical support at the research station at Zackenberg. We thank Niels M. Schmidt for inspiration and stimulating discussions, and Mads C. Forchhammer, Lotte Illeris, Hans Meltofte, Anders Michelsen, Greg H. R. Henry, and two anonymous referees for helpful comments on a previous draft. Ruth Bruus Jakobsen contributed valuable technical help.

References Cited

Anderson, D. R., Burnham, K. P., and Thompson, W. L., 2000: Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, 64: 912–923.

Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Diemer, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jónsdottir, I. S., Laine, K., Lévesque, E., Marion, G. M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., and Wookey, P. A., 1999: Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.

Aydelotte, A. R., and Diggle, P. K., 1997: Analysis of developmental preformation in the alpine herb *Caltha leptosepala* (Ranunculaceae). *American Journal of Botany*, 84: 1646–1657.

Bannister, P., Maegli, T., Dickinson, K. J. M., Halloy, S. R. P., Knight, A., Lord, J. M., Mark, A. F., and Spencer, K. L., 2005: Will loss of snow cover during climatic warming expose New Zealand alpine plants to increased frost damage? *Oecologia*, 144: 245–256.

Bay, C., 1998: *Vegetation mapping of Zackenberg valley, North-East Greenland*. Copenhagen: Danish Polar Center and Botanical Museum, University of Copenhagen, 29 pp.

Bechtold, H. A., Forbis, T. A., Bowman, W. D., and Diggle, P. J., 2002: Lack of reproductive plasticity in alpine *Saxifraga rhomboidea* (Saxifragaceae). *Nordic Journal of Botany*, 22: 361–368.

Bliss, L. C., and Gold, W. G., 1999: Vascular plant reproduction, establishment, and growth, and the effects of cryptogamic crusts within a polar desert ecosystem, Devon Island, N.W.T., Canada. *Canadian Journal of Botany*, 77: 623–636.

Brody, A. K., 1997: Effects of pollinators, herbivores, and seed predators on flowering phenology. *Ecology*, 78: 1624–1631.

Callaghan, T. V., Carlsson, B. Å., Jónsdóttir, I. S., Svensson, B. M., and Jonasson, S., 1992: Clonal plants and environmental change: introduction to the proceedings and summary. *Oikos*, 63: 341–347.

Dunne, J. A., Harte, J., and Taylor, K. J., 2003: Subalpine meadow flowering phenology responses to climate change: integrating experimental and gradient methods. *Ecological Monographs*, 73: 69–86.

Felsenstein, J., 1993: PHYLIP (Phylogeny Inference Package). Seattle, WA: Department of Genetics, University of Washington.

Galen, C., and Stanton, M. L., 1991: Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). *American Journal of Botany*, 78: 978–988.

Gugerli, F., 1998: Effect of elevation on sexual reproduction in alpine populations of *Saxifraga oppositifolia* (Saxifragaceae). *Oecologia*, 114: 60–66.

Hinkler, J., 2005: *From digital cameras to large-scale sea-ice dynamics: A snow-ecosystem perspective*. Ph.D. thesis. Copenhagen, University of Copenhagen, 184 pp.

Hirao, A. S., and Kudo, G., 2004: Landscape genetics of alpine-snowbed plants: comparisons along geographic and snowmelt gradients. *Heredity*, 93: 290–298.

Hultén, E., 1959: Studies in the genus *Dryas*. *Svensk Botanisk Tidsskrift*, 53: 507–541.

Inouye, D. W., and McGuire, A. D., 1991: Effects of snowpack on timing and abundance of flowering in *Delphinium nelsonii*

(Ranunculaceae): implications for climate change. *American Journal of Botany*, 78: 997–1001.
Inouye, D. W., Morales, M. A., and Dodge, G. J., 2002: Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia*, 130: 543–550.
Johnstone, J. F., and Henry, G. H. R., 1997: Retrospective analysis of growth and reproduction in *Cassiope tetragona* and relations to climate in the Canadian High Arctic. *Arctic and Alpine Research*, 29: 459–469.
Lloyd, D. G., 1980: Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. *New Phytologist*, 86: 69–79.
Lloyd, D. G., Webb, C. J., and Primack, R. B., 1980: Sexual strategies in plants. II. Data on the temporal regulation of maternal investment. *New Phytologist*, 86: 81–92.
Max, K. N., Mouchaty, S. K., and Schwaegerle, K. E., 1999: Allozyme and morphological variation in two subspecies of *Dryas octopetala* (Rosaceae) in Alaska. *American Journal of Botany*, 86: 1637–1644.
McGraw, J. B., 1995: Patterns and causes of genetic diversity in arctic plants. *In* Chapin III, F. S., and Körner, C. (eds.), *Arctic and alpine biodiversity: patterns, causes, and ecosystem consequences*. New York, Berlin: Springer Verlag, 33–43.
McGraw, J. B., and Antonovics, J., 1983: Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentation and life cycle stages of selection. *Journal of Ecology*, 71: 879–897.
Meltofte, H., and Berg, T. B., 2004: *BioBasis—Conceptual design and sampling procedures of the biological programme of Zackenberg Basic*. Seventh edition. Denmark: National Environmental Research Institute, 69 pp.
Meltofte, H., and Thing, H., 1996: *Zackenberg Ecological Research Operations*. First Annual Report, 1995. Meltofte, H., and Thing, H. (eds.), Copenhagen: Danish Polar Center, Ministry of Research and Technology, 64 pp.
Molau, U., 1993: Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research*, 25: 391–402.
Molau, U., Nordenhäll, U., and Eriksen, B., 2005: Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany*, 92: 422–431.
Nei, M., 1972: Genetic distance between populations. *American Naturalist*, 106: 283–292.
Philipp, M., and Siegismund, H. R., 2003: What can morphology and isozymes tell us about the history of the *Dryas integrifolia-octopetala* complex? *Molecular Ecology*, 12: 2231–2242.
Price, M. V., and Waser, N. M., 1998: Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology*, 79: 1261–1271.
Quinn, G. P., and Keough, M. J., 2002: *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press, 537 pp.
Rasch, M., and Caning, K., 2004: *Zackenberg Ecological Research Operations*. Ninth Annual Report, 2003. Rasch, M., and Caning, K. (eds.), Copenhagen: Danish Polar Center, Ministry of Science, Technology and Innovation.
Serreze, M. C., Walsh, J. E., Chapin III, F. S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., and Barry, R. G., 2000: Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, 46: 159–207.
Shaver, G. R., and Kummerow, J., 1992: Phenology, resource allocation and growth of arctic vascular plants. *In* Chapin III, F. S., Jefferies, R. L., Reynolds, J. F., Shaver, G. R., and Svoboda, J. (eds.), *Arctic ecosystems in a changing climate. An ecophysiological perspective*. New York, London, San Diego: Academic Press, 193–211.
Sørensen, T., 1941: Temperature relations and phenology of North-East Greenland flowering plants. *Meddelelser om Grønland*, 125: 1–305.
Stephenson, A. G., 1981: Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, 12: 253–279.
Stinson, K. A., 2004: Natural selection favors rapid reproductive phenology in *Potentilla pulcherrima* (Rosaceae) at opposite ends of a subalpine snowmelt gradient. *American Journal of Botany*, 91: 531–539.
Thórhallsdóttir, T. E., 1998: Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia*, 114: 43–49.
Totland, Ø., and Alatalo, J. M., 2002: Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia*, 133: 168–175.
Venables, W. N., and Ripley, B. D., 2002: *Modern applied statistics with S*. Fourth edition. New York, Berlin: Springer Verlag, 495 pp.
Wahren, C. H. A., Walker, M. D., and Bret-Harte, M. S., 2005: Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, 11: 537–552.
Welker, J. M., Molau, U., Parsons, A. N., Robinson, C. H., and Wookey, P. A., 1997: Responses of *Dryas octopetala* to ITEX environmental manipulations: a synthesis with circumpolar comparisons. *Global Change Biology*, 3(Suppl. 1): 61–73.
Wookey, P. A., Robinson, C. H., Parsons, A. N., Welker, J. M., Press, M. C., Callaghan, T. V., and Lee, J. A., 1995: Environmental constraints on the growth, photosynthesis, and reproductive development of *Dryas octopetala* at a High Arctic polar semidesert, Svalbard. *Oecologia*, 102: 478–489.

Ms accepted September 2006

APPENDIX 1

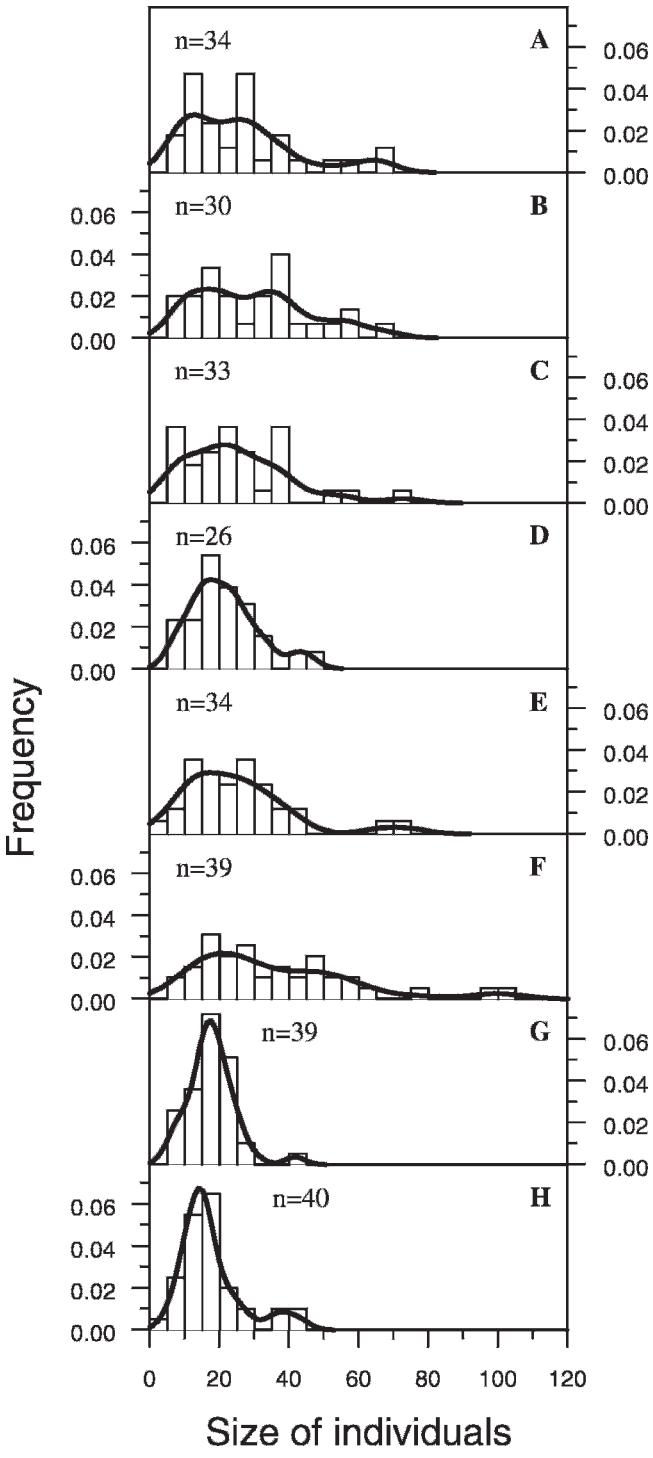
Allele frequencies in the six enzyme systems found in individuals from the *Dryas* plots. The enzymes were ACO (aconitase, E.C. 4.2.1.3), GPI (glucosephosphate isomerase, E.C. 5.3.1.9), PGD (6-phosphogluconate dehydrogenase, E.C. 1.1.1.44), SKD (shikimate dehydrogenase, E.C. 1.1.1.25), TPI (triosephosphate isomerase, E.C. 5.3.1.1), and UGPP (UDP glucose pyrophosphorylase, E.C. 2.7.7.9). Asterisks indicate that frequencies were based on less than 20 observations. Mobilities are relative to the most common allele, which was arbitrarily set to 100.

			Plot							
Enzyme system	Allele	Mobility	A	B	C	D	E	F	G	H
ACO	**1**	109	0.14	0.68	0.50	0.35	0.60	0.57	0.39	0.47
	2	100	0.86	0.32	0.50	0.65	0.40	0.43	0.61	0.53
GPI	**1**	213	0.24	0.09	0	0.10	0.10	0.12	0.10	0.08
	2	100	0.44	0.41	0.59	0.40	0.50	0.56	0.44	0.46
	3	−59	0.08	0.19	0.05	0.13	0.07	0.06	0.24	0.14
	4	−116	0.20	0.09	0.27	0.37	0.16	0.19	0.14	0.23
	5	−154	0.05	0.22	0.09	0	0.16	0.06	0.08	0.10
PGD	**1**	100	0.65	0.73	0.67	0.44	0.57	0.68	0.46	0.59
	2	63	0.35	0.27	0.33	0.56	0.43	0.32	0.54	0.41
SKD	**1**	110	0.21	0*	0.15	0.29*	0.08	0	0.06	0.11
	2	100	0.79	0.58*	0.83	0.43*	0.78	0.59	0.61	0.57
	3	93	0	0.42*	0.02	0.29*	0.14	0.41	0.33	0.33
TPI	**1**	108	0.20	0.53	0.58	0.46	0.26	0.51	0.47	0.47
	2	100	0.80	0.47	0.42	0.54	0.74	0.49	0.53	0.53
UGP	**1**	115	0.16	0.18	0.17	0.21	0.10	0.13	0.18	0.10
	2	100	0.31	0.30	0.23	0.37	0.25	0.26	0.31	0.31
	3	93	0.19	0.02	0.12	0.08	0.29	0.18	0.28	0.17
	4	73	0.28	0.45	0.35	0.15	0.24	0.19	0.16	0.38
	5	57	0.06	0.05	0.14	0.19	0.12	0.24	0.07	0.05

APPENDIX 2

Averages ±1 SE of seven morphological traits (see text for definitions) measured on five leaves from all individuals in the eight study plots except for plot G and H, where only a proportion of the plot was sampled (see text for details). For each character, different letters denote significant differences among plots (Tukey HSD post hoc test, $\alpha = 0.05$).

						Proportion of individuals with glands	
Plot	Length of leaf (mm)	Width of leaf (mm)	Depth of indentations (mm)	No. of indentations	No. of octopetala scales	dorsally	ventrally
A	$8.55^{a} \pm 0.239$	$4.54^{a,b,c} \pm 0.111$	$0.98^{a,b} \pm 0.025$	$6.41^{b,c} \pm 0.153$	$2.51^{a,b} \pm 1.209$	0^{a}	$0.088^{a,b} \pm 0.049$
B	$8.36^{a} \pm 0.223$	$4.32^{a,b} \pm 0.116$	$1.00^{b} \pm 0.025$	$6.64^{c} \pm 0.166$	$1.60^{a} \pm 1.012$	$0.053^{a} \pm 0.038$	$0.067^{a,b} \pm 0.046$
C	$8.21^{a} \pm 0.203$	$4.24^{a,b} \pm 0.106$	$0.87^{a} \pm 0.024$	$5.93^{a,b} \pm 0.184$	$0.27^{a} \pm 0.159$	0^{a}	$0.006^{a} \pm 0.006$
D	$8.39^{a} \pm 0.187$	$4.13^{a,b} \pm 0.111$	$1.00^{b} \pm 0.026$	$6.64^{c} \pm 0.165$	$1.81^{a,b} \pm 1.182$	$0.015^{a} \pm 0.015$	$0.077^{a,b} \pm 0.053$
E	$8.74^{a} \pm 0.226$	$4.29^{a,b} \pm 0.100$	$1.01^{b} \pm 0.024$	$6.71^{c} \pm 0.129$	$6.83^{b} \pm 1.911$	$0.088^{a} \pm 0.049$	$0.232^{b} \pm 0.065$
F	$8.23^{a} \pm 0.170$	$4.14^{a} \pm 0.074$	$0.95^{a,b} \pm 0.023$	$6.34^{b,c} \pm 0.145$	$1.78^{a} \pm 1.000$	0^{a}	$0.067^{a,b} \pm 0.038$
G	$9.77^{b} \pm 0.267$	$4.97^{c} \pm 0.105$	$1.03^{b} \pm 0.028$	$5.58^{a} \pm 0.129$	$2.21^{a} \pm 0.727$	$0.046^{a} \pm 0.030$	$0.128^{a,b} \pm 0.049$
H	$8.53^{a} \pm 0.213$	$4.59^{b,c} \pm 0.108$	$1.03^{b} \pm 0.029$	$5.43^{a} \pm 0.133$	$2.72^{a,b} \pm 0.899$	$0.020^{a} \pm 0.020$	$0.185^{a,b} \pm 0.058$



APPENDIX 3. Size distribution of individuals in the eight study plots. Sizes of individuals are square-root transformed areas in cm^2. The black line is the probability density line.