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GENDER VARIATION OF *DRYAS OCTOPETALA* ALONG SNOWMELT AND LATITUDINAL GRADIENTS IN THE SUBARCTIC AND THE HIGH ARCTIC

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Abstract: We describe variations of floral traits of *Dryas octopetala* L. along a snowmelt gradient within and among three sites: 1) the Subarctic Latnjajaure in northernmost Sweden, 2) the High Arctic Longyearbyen and 3) Ny-Ålesund, Svalbard in Norway, also High Arctic. *Dryas octopetala* had two types of flowers, hermaphrodite flowers and male flowers, lacking any gynoeceum. The frequency of male flowers was higher in late snow-melt habitats (*i.e.* late flowering populations) both at Latnjajaure and Ny-Ålesund. Male flowers were significantly lighter in dry weight than hermaphrodite flowers; the difference was larger in the High Arctic than in the Subarctic, suggesting a higher resource limitation in male flowers in the High Arctic. Flower weight also varied among the three sites, and showed a significant difference along the latitudinal gradient both in hermaphrodite and male flowers. In the hermaphrodite flowers, the gynoeceum dry weight differed among the three sites, being significantly heavier at Latnjajaure than at Longyearbyen and Ny-Ålesund. As a result, the “femaleness” (gynoeceum weight/androecium + gynoeceum weight) showed significantly higher values at Latnjajaure than at Longyearbyen and Ny-Ålesund. Thus, the floral allocation to female function in *D. octopetala* decreases with an increase in latitude from the Subarctic to the High Arctic. Gender variation of flowers is a size-dependent phenomenon; a positive correlation between flower size and femaleness was observed within each site.

key words: Arctic, *Dryas octopetala*, femaleness, sex allocation, snowmelt

Introduction

In Arctic and alpine environments, low temperature, cloudy or foggy weather, and short growing season considerably restrict the photosynthetic carbon gain of plants (KELLEY and WEAVER, 1969; BELL and BLISS, 1980). These factors often act as depressive effects on reproduction of arctic and alpine plants. It is known that some plants show significant variations of reproductive success and floral traits along altitudinal gradients (BAUERT, 1993; ALATALO and MOLAU, 1995). For instance, *Polygonum viviparum*

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(Polygonaceae), which reproduces sexually by seeds and vegetatively by bulbils, decreases the resource allocation to reproductive organs and increases the ratio of bulbil to number of flowers with increase in altitude (BAUERT, 1993). This result suggests that sexual reproduction is restricted under stressful conditions.

In addition to the large-scale environmental changes along altitudinal or latitudinal gradients, small-scale environmental variations may also act as selective pressures on reproductive traits of plants. For example, topographic undulations cause variations of time of snowmelt and snow-free duration within a year (= growing season length), resulting in phenological and functional changes in reproductive traits and outputs of alpine plants (KUDO, 1991, 1992, 1997). In the Taisetsu Mountains of Hokkaido, northern Japan, KUDO (1992) found that the numbers of flowers in *Veronica stelleri* var. *longistryla* (Scrophulariaceae) and *Solidago virga-aurea* var. *leiocarpa* (Compositae) decreased in a shorter snow-free duration, while those in *Peucedanum multivittatum* (Umbelliferae), *Primula cuneifolia* (Primulaceae) and *Potentilla matsumurae* (Rosaceae) were relatively constant along the snowmelt gradient. This suggests that sensitivities of reproductive outputs (e.g. the number of flowers) against the shortened growing season length may vary among species, depending on species-specific growth and reproductive performances. Several studies have examined variations of the number of flowers, seeds or fruits in relation to onset of flowering (e.g. SPIRA and POLLACK, 1986; MOLAU, 1991; TOTLAND, 1994, 1997) or timing of snow-melting (e.g. KUDO, 1992, 1993a), but only a few studies focus on variations of flower size, gender expression (MOLAU, 1991; KUDO, 1997) and sex allocation along environmental gradients. Because reproduction through female function, producing seeds and fruits, is costly compared to that through male function, we predict that reproductive investment to a female organ (= gynoecium weight) or reproductive allocation to female function in the flowering stage will decrease under more resource-limited environments, with an increase in latitude and/or with a decrease in the growing season length.

In the summers of 1996 and 1997, we found that a circumpolar plant, *Dryas octopetala* (Rosaceae), had two types of flowers, hermaphrodite and male flowers (Fig. 1), both in the Subarctic (Latnjajaure in northernmost Sweden) and the High Arctic regions (Longyearbyen and Ny-Ålesund in Svalbard). In the present study, we describe phenological differences between hermaphrodite and male flowers along snowmelt gradients, and size differences between them within each population of *D. octopetala* along a latitudinal gradient. Moreover, we compare the dry-weight allocation to androecium and gynoecium within the hermaphrodite flowers along a latitudinal gradient. Thus, aims of this study are to address the following questions: 1) How does the ratio of numbers of male to hermaphroditic flowers vary along the snowmelt gradient both in the Subarctic and the High Arctic? 2) Does the ratio of numbers of male to hermaphroditic flowers differ between the Subarctic and the High Arctic? 3) How do flower size, gender expression and dry-weight allocation to each reproductive organ within a hermaphrodite flower vary along the latitudinal gradient?

Material and Methods

We selected two study sites in the High Arctic, Ny-Ålesund (78°55'N, 11°56'E) and Longyearbyen (78°15'N, 15°30'E) in Svalbard, Norway, and one Subarctic alpine site,



Fig. 1. A photograph of hermaphrodite flowering shoots (two larger shoots, *left side*) and male shoots (two smaller shoots, *right side*) of *Dryas octopetala* at Longyearbyen.

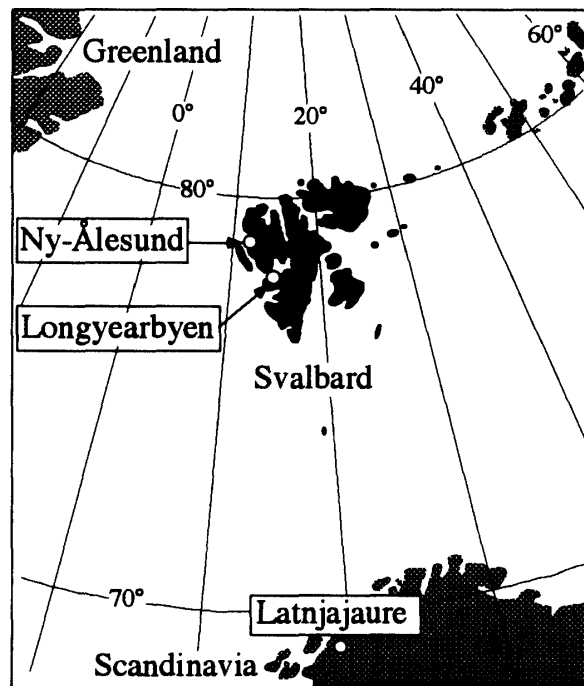


Fig. 2. Study sites: Ny-Ålesund (78°55'N, 11°56'E), Longyearbyen (78°15'N, 15°30'E), and Latnjajaure (68°22'N, 18°29'E).

Latnjajaure (68°22'N, 18°29'E) in northernmost Sweden (Fig. 2). In 1996, we mainly studied at Ny-Ålesund and Latnjajaure; additional data were collected at Longyearbyen in 1997. The study site at Ny-Ålesund is located *ca.* 1.5 km from the Brøgger Glacier. The vegetation is mainly composed of *Dryas octopetala*, *Oxyria digyna* (Polygonaceae), *Polygonum viviparum*, *Salix polaris* (Salicaceae), *Saxifraga oppositifolia* (Saxifragaceae), *Silene acaulis* (Caryophyllaceae), and bryophytes and lichens. Latnjajaure (1000 m a.s.l.)

is located 13 km west of Abisko. The vegetation is composed of *Betula nana* (Betulaceae), *Cassiope tetragona* (Ericaceae), *Dryas octopetala*, *Empetrum hermaphroditum* (Empetraceae), *Loiseleuria procumbens* (Ericaceae), *Oxyria digyna*, *Polygonum viviparum*, *Potentilla crantzii* (Rosaceae), *Ranunculus nivalis* (Ranunculaceae), *Salix herbacea* (Salicaceae), *S. polaris*, *Vaccinium uliginosum* (Ericaceae), and many other arctic and alpine plants.

The climatic conditions of Ny-Ålesund and Latnjajaure during the summer season are shown in Table 1. The High Arctic Ny-Ålesund is characterized by lower temperature, solar radiation, and precipitation as compared to the Subarctic Latnjajaure, indicating a harsher environment for plant growth and reproduction in Svalbard.

Dryas octopetala L. is widely distributed in the Low Arctic in Alaska (MCGRAW, 1985) and Scandinavia, and in the High Arctic in Svalbard, Greenland, and Russia (HULTÉN, 1959; RØNNING, 1969). According to MOLAU (1993), *D. octopetala* has been recognized as a typical gynodioecious plant species, composed of a mixture of hermaphrodite and purely female flowering shoots at the Subarctic Latnjajaure. In Greenland, PHILIPP *et al.* (1990) reported that *Dryas integrifolia* (Rosaceae) has male flowers and hermaphrodite ones. We did not find purely female flowering shoots in this study, but frequently observed male flowering shoots in addition to perfect hermaphrodite flowering shoots both at the Subarctic Latnjajaure and the High Arctic Longyearbyen and Ny-Ålesund. Therefore, we defined *D. octopetala* as an andromonoecious plant species in this study.

Dryas octopetala forms a cushion on the ground; the cushion is sometimes unclear and it is difficult to determine individual plants. *D. octopetala* has one flower per terminal shoot. This species is considered an exclusive outbreeder, and the level of autodeposition and subsequent self-compatibility are low at the Subarctic Latnjajaure (MOLAU, 1993). The bowl-shaped flowers show sun-tracking behavior, resulting in high temperature in the gynoeceum as compared to ambient temperature (KJELLBERG *et al.*, 1982; WADA, 1998). The most frequent pollinators are small flies (WELKER *et al.*, 1997), and seed-setting success of this species primarily depends on temperature during a flowering period rather than pollinator activity, at the High Arctic Ny-Ålesund (WADA, 1998).

In the summer of 1996, we observed three *Dryas* populations at Ny-Ålesund and four populations at Latnjajaure along snowmelt gradients. In each population, we recorded

Table 1. Monthly mean air temperature, global solar radiation, and precipitation during the summer season in the Subarctic (Latnjajaure) and the High Arctic (Ny-Ålesund). Mean values are shown with standard deviations in parentheses during 1992–1996. Data from AOKI *et al.* (1996a, b) and the Norsk Polarinstitt (unpublished data) for Ny-Ålesund, and U. MOLAU (personal communication) for Latnjajaure.

Study site	Air temperature (°C)			Global radiation (MJ/m ²)			Precipitation (mm)		
	June	July	Aug.	June	July	Aug.	June	July	Aug.
Latnjajaure	3.5 (1.6)	7.0 (1.3)	7.0 (1.9)	582 (74)	481 (26)	328 (43)	51 (26)	76 (35)	73 (40)
Ny-Ålesund	2.4 (0.4)	4.5 (0.9)	3.5 (1.2)	568 (67)	375 (75)	253 (30)	11 (2)	38 (36)	39 (40)

the times of snow disappearance and flowering, and counted the numbers of hermaphrodite and male flowers. Male flowers did not have any gynoecium, so we could easily distinguish male flowers from hermaphrodite ones. Then, we compared the frequency of hermaphrodite and male flowers among populations along the snowmelt gradients, and between the Subarctic and the High Arctic.

We collected 24 hermaphrodite flowers and 20 male flowers in late July 1996 at Ny-Ålesund, 10 hermaphrodite flowers and 10 male flowers in early August 1997 at Longyearbyen, and 11 hermaphrodite flowers and eight male flowers in early August 1996 at Latnjajaure. In each flower, we measured the length (L) and width (W) of four petals per flower, and calculated individual petal area (PA) according to the following formula:

$$PA = (L \times W) \times \pi \times 0.25,$$

where petal area was assumed to be elliptic. After that, we dissected each flower into petals, androecium, gynoecium (of hermaphrodite flowers) and calyx+receptacle, and dried them for 48 hours at 80°C. This species has superior ovary, and the receptacle closely adheres to the calyx. We measured the dry weights of these parts, and compared them between hermaphrodite and male flowers within and among the three sites.

To clarify the variation of sex allocation based on dry weight in hermaphrodite flowers along the latitudinal gradient, we calculated the “femaleness”, defined by the following formula:

$$\text{Femaleness} = GW / (GW + AW),$$

where GW is the dry weight of gynoecium and AW is that of androecium. This formula closely links with Lloyd's usage of relative gender, *e.g.* relative femaleness in co-sexual plants (LLOYD, 1980; MOLAU, 1991). In this study, we used the “femaleness” as an indicator of the reproductive effort (phenotypic gender) of female function, and it was compared among the three sites.

Results

Proportion of male and hermaphrodite flowers along the snowmelt and the latitudinal gradients

Flowering occurred in early to mid July at locations having early snowmelt, and late July to mid August at locations having late snowmelt, both at Latnjajaure and Ny-Ålesund. The frequency of hermaphrodite and male flowers along the snowmelt gradients is shown in Table 2. The proportion of male flowers was high in the later snow-melt populations both at Latnjajaure and Ny-Ålesund.

When we compared the ratio of numbers of male to hermaphroditic flowers among the populations having similar flowering timing between Latnjajaure (Population 3+4) and Ny-Ålesund (Population 2+3), there were no remarkable differences between them; 0.42 in Latnjajaure ($n=431$ flowers) and 0.47 in Ny-Ålesund ($n=361$ flowers). Thus, we found that the ratio of numbers of male to hermaphroditic flowers did not largely differ between the Subarctic and the High Arctic, but slightly differed within the same sites along the snowmelt gradients.

Table 2. Flowering season and the frequency (%) of hermaphrodite (HF) and male flowers (MF) along the snowmelt gradients in the Subarctic (Latnjajaure; A) and the High Arctic (Ny-Ålesund, Svalbard; B).

(A) Latnjajaure

	Snow melt	Flowering season	HF	MF	Sample size
Population 1	late May	early to mid July	84%	16%	242
Population 2	late June	late July to early August	70%	30%	219
Population 3	late June	late July to early August	77%	23%	179
Population 4	early July	late July to mid August	64%	36%	252

(B) Ny-Ålesund

	Snow melt	Flowering season	HF	MF	Sample size
Population 1	before late June	early to mid July	77%	23%	192
Population 2	late June	late July to early August	68%	32%	166
Population 3	early July	late July to mid August	68%	32%	195

Comparisons of flower size and floral allocation along the latitudinal gradient

At each site, male flowers were significantly lighter in dry weight than hermaphrodite flowers ($P < 0.05$ at Latnjajaure, $P < 0.001$ at Longyearbyen, $P < 0.001$ at Ny-Ålesund; analyzed by Student's *t*-test), and the difference was larger in the High Arctic than in the Subarctic. The ratios of dry weight of male flowers to that of hermaphrodite flowers at Latnjajaure, Longyearbyen, and Ny-Ålesund were 0.69, 0.60, and 0.57, respectively, showing smaller investments in male flower production in the High Arctic than in the Subarctic. Flower weight also varied among the three sites (Fig. 3), and showed a significant difference along the latitudinal gradient both in male ($P = 0.0003$, by Kruskal-Wallis test) and hermaphrodite flowers ($P = 0.0013$, by Kruskal-Wallis test).

We compared individual petal area, total petal weight per flower, and androecium weight between hermaphrodite and male flowers at each site (Fig. 4). Individual petal area and total petal weight per flower were significantly smaller and lighter in male flowers than in hermaphrodite flowers at Ny-Ålesund and Longyearbyen, while there were no significant differences between them at Latnjajaure. The dry weight of the androecium showed a significant difference between male and hermaphrodite flowers only at Ny-Ålesund (Fig. 4). In male flowers, the petal area and petal weight decreased significantly from Latnjajaure to Ny-Ålesund ($P = 0.008$, by Kruskal-Wallis test for petal area; $F = 14.97$, $df = 2, 35$, $P < 0.0001$, by one-way ANOVA for petal weight, Table 3A). The androecium weight also varied significantly among the three sites ($F = 11.82$, $df = 2, 35$, $P = 0.0001$, by one-way ANOVA); higher values at Latnjajaure and Longyearbyen than at Ny-Ålesund. These tendencies were also found in hermaphrodite flowers in the petal area ($F = 6.58$, $df = 2, 42$, $P = 0.003$, by one-way ANOVA, Table 3B) and in the androecium weight ($F = 8.17$, $df = 2, 42$, $P = 0.010$, by one-way ANOVA), but not in the petal weight ($P = 0.215$, by Kruskal-Wallis test).

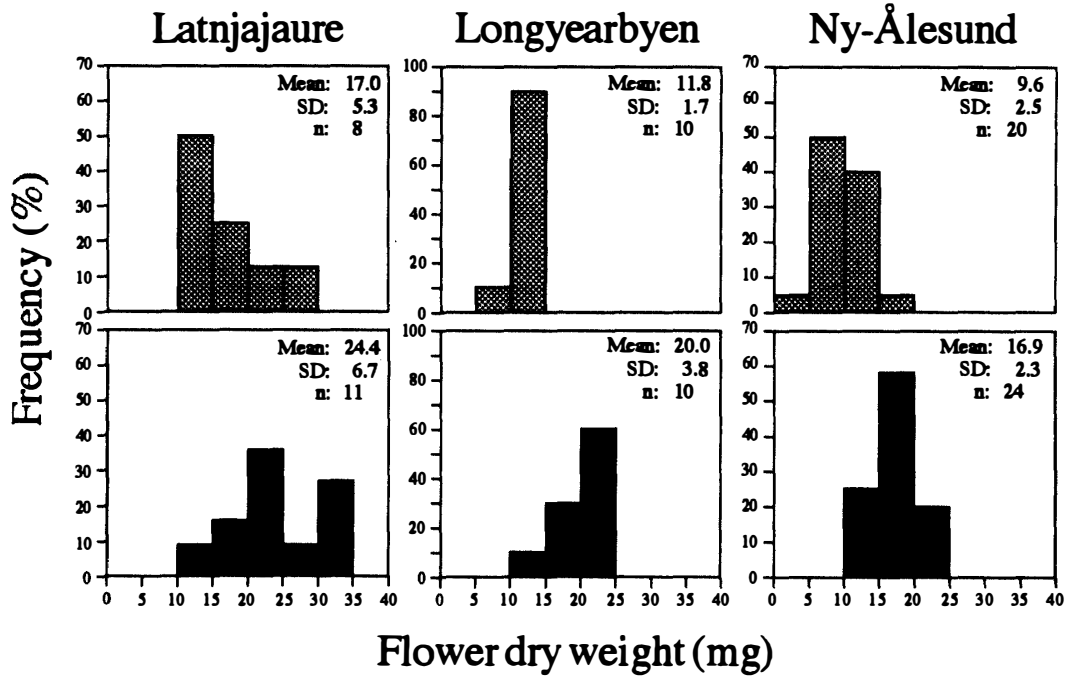


Fig. 3. Size (dry weight) distributions of male flowers (top figures, light-gray shaded) and hermaphrodite flowers (bottom figures, dark-gray shaded) at the Subarctic Latnjajaure and the High Arctic Longyearbyen and Ny-Ålesund.

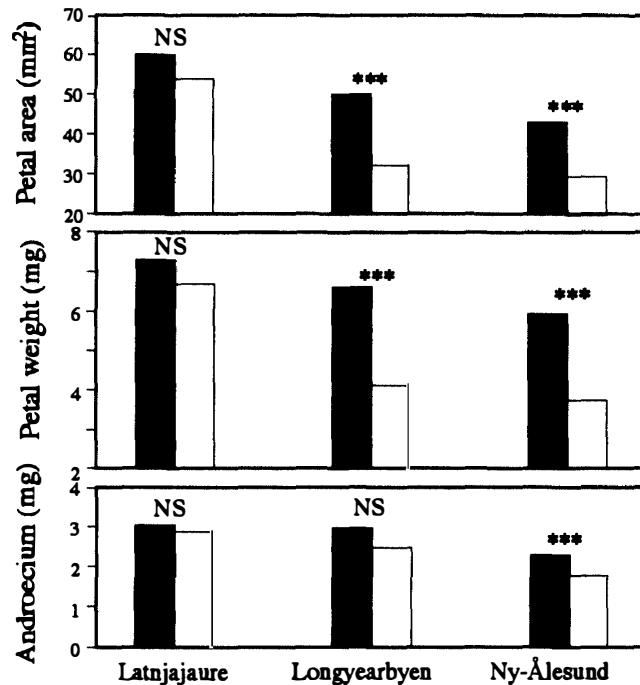


Fig. 4. Mean values of floral traits (petal area, petal weight and androecium weight) in hermaphrodite flowers (gray-shaded bars) and male flowers (unshaded bars) within each population; Latnjajaure, Longyearbyen, and Ny-Ålesund. ***, $P < 0.001$; NS, non-significant at $P > 0.05$ level, analyzed by Student's t test.

Table 3. Variations of individual petal area, petal weight per flower, androecium weight, and gynoecium weight (only hermaphrodite flower) among the three sites, Latnjajaure, Longyearbyen, and Ny-Ålesund, in male flowers (A) and hermaphrodite flowers (B). Mean values with standard deviations are shown; different letters on the numerals indicate a statistically significant difference ($P < 0.05$).

(A) Male flower

Flower traits	Latnjajaure ($n=8$)	Longyearbyen ($n=10$)	Ny-Ålesund ($n=20$)
Petal area (mm ²)*	53.9 ± 23.4 ^a	32.3 ± 8.0 ^b	29.7 ± 11.1 ^b
Petal weight (mg)†	6.7 ± 2.1 ^a	4.1 ± 1.0 ^b	3.7 ± 1.2 ^b
Androecium weight (mg)†	2.9 ± 0.8 ^a	2.5 ± 0.5 ^a	1.8 ± 0.6 ^b

(B) Hermaphrodite flower

Flower traits	Latnjajaure ($n=11$)	Longyearbyen ($n=10$)	Ny-Ålesund ($n=24$)
Petal area (mm ²)†	59.7 ± 17.5 ^a	50.1 ± 12.1 ^{ab}	43.2 ± 9.9 ^b
Petal weight (mg)*	7.2 ± 2.6 ^a	6.6 ± 1.2 ^a	5.9 ± 1.6 ^a
Androecium weight (mg)†	3.1 ± 0.8 ^a	3.0 ± 0.5 ^a	2.3 ± 0.5 ^b
Gynoecium weight (mg)†	6.5 ± 2.4 ^a	3.7 ± 1.3 ^b	2.6 ± 0.9 ^b

*Kruskal-Wallis test and Mann-Whitney U -test; †One-way ANOVA and Scheffe's F test.

Gender variations of hermaphrodite flowers along the latitudinal gradient

Gynoecium dry weight of hermaphrodite flowers differed among the three sites ($F = 25.12$, $df = 2, 42$, $P < 0.0001$, by one-way ANOVA); it was significantly heavier at Latnjajaure (mean ± SD: 6.5 ± 2.4 mg, $n = 11$) than at Longyearbyen (3.7 ± 1.3 mg, $n = 10$) and Ny-Ålesund (2.6 ± 0.9 mg, $n = 24$; Table 3B). Femaleness also varied among the sites ($F = 8.89$, $df = 2, 42$, $P = 0.0006$, by one-way ANOVA), and showed a significantly higher value at Latnjajaure (mean ± SD: 0.67 ± 0.08, $n = 11$) than at Longyearbyen (0.53 ± 0.11, $n = 10$) and at Ny-Ålesund (0.51 ± 0.17, $n = 24$; Fig. 5). When the relationship between total flower weight and femaleness was compared within each site, there was a positive correlation between them (Fig. 6). This indicates that the variation of floral gender is size-dependent and the allocation to female function increases with an increase in flower size.

Dry weight allocation to the androecium in hermaphrodite flowers did not differ significantly among the three sites ($F = 1.33$, $df = 2, 42$, $P = 0.275$, by one-way ANOVA, Fig. 7), but the allocation to the gynoecium varied significantly among the sites ($F = 24.65$, $df = 2, 42$, $P < 0.0001$, by one-way ANOVA); a higher proportion at Latnjajaure (25.9%) than at Longyearbyen (17.7%) and Ny-Ålesund (15.3%; Scheffe's F test, $P < 0.01$). In contrast, the allocation to petals significantly increased from the Subarctic to the High Arctic ($F = 5.49$, $df = 2, 42$, $P = 0.0077$, by one-way ANOVA): a lower proportion at Latnjajaure (29.0%) than at Ny-Ålesund (35.0%; Scheffe's F test, $P < 0.01$). Thus, the reproductive allocation to female function in *Dryas octopetala* decreased with an increase in the latitude from the Subarctic to the High Arctic.

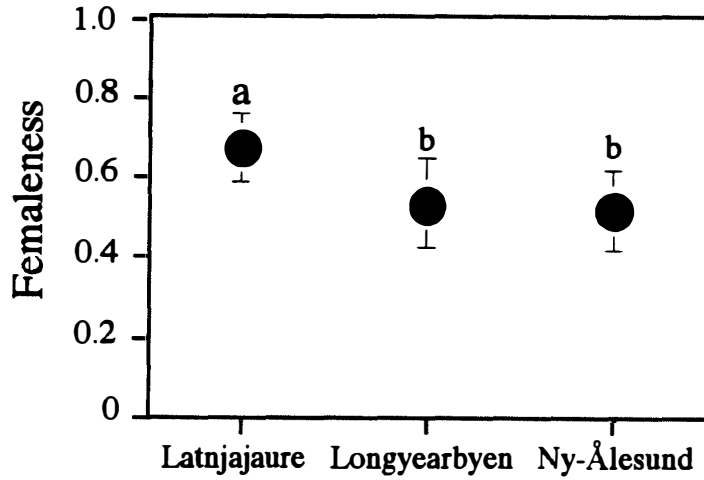


Fig. 5. Mean values (solid circles) with standard deviations (lines) of "Femaleness" in hermaphrodite flowers at Latnjajaure ($n=11$), Longyearbyen ($n=10$), and Ny-Ålesund ($n=24$). The different letters on the SD lines show statistically significant differences at the $P < 0.05$ level (Scheffe's F test).

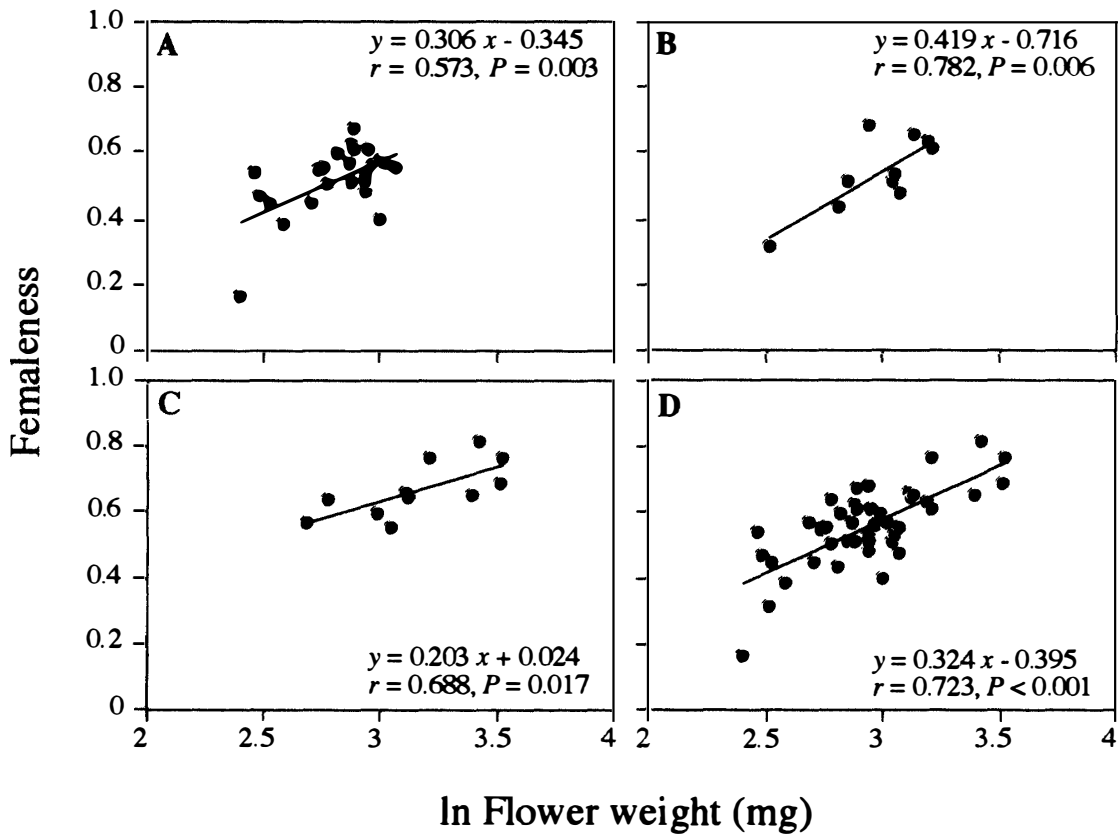


Fig. 6. Relationship between flower size (ln flower weight) and the femaleness in *Dryas octopetala*. A, Ny-Ålesund; B, Longyearbyen; C, Latnjajaure; D, total.

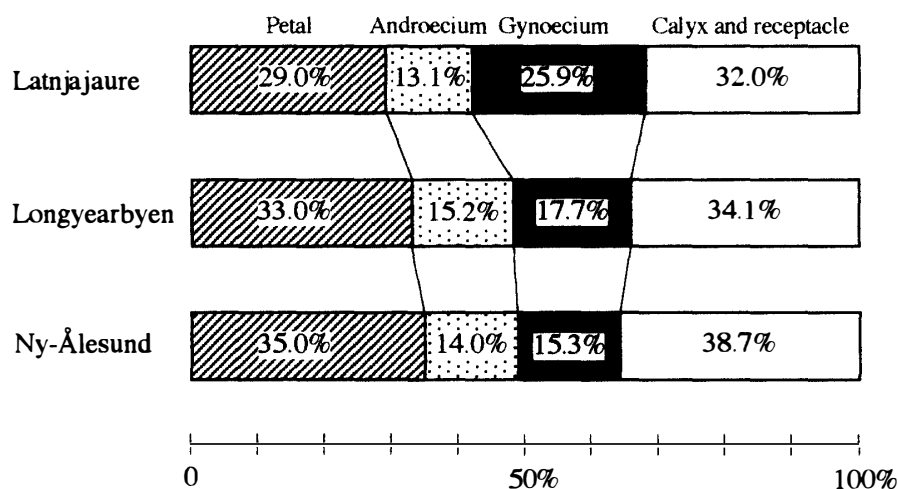


Fig. 7. Dry weight allocation patterns in hermaphrodite flowers at Latnjajaure ($n=11$), Longyearbyen ($n=10$), and Ny-Ålesund ($n=24$).

Discussion

Why does the proportion of male flowers increased at locations having later snowmelt ?

We found that the proportion of male flowers increased in later snowmelt populations both in the Subarctic and the High Arctic. For arctic and alpine plants, timing of the onset of flowering is one of the critical factors affecting completion of seed maturation during the limited growing season; late-flowering plants often produce fewer seeds (SPIRA and POLLACK, 1986; KUDO, 1991, 1993a, 1997; TOTLAND, 1994, 1997) or lighter seeds (GALEN and STANTON, 1991, 1993; TOTLAND, 1997) than early-flowering plants. Plants growing at locations having late snowmelt may experience less accumulation of effective temperature and solar radiation (Table 1) which strongly affects the seed-setting success (WOOKEY *et al.*, 1993; TOTLAND, 1997; WADA, 1998). In general, plants tend to allocate relatively more resources to male function than to female function under the conditions of low resource availability for reproduction (LOVETT DOUST and LOVETT DOUST, 1988; KLINKHAMER and DE JONG, 1993; KUDO, 1993b). Thus, the higher occurrence of male flowers at locations having late snowmelt where flowering occurs later in the summer may reflect the fact that production of female function within flowers is restricted by resource limitation due to the short photosynthetic period. Size-dependent variations of femaleness observed within each site seems to support the resource limitation hypothesis. Such environmental pressures may increase the frequencies of male flowers in late flowering populations along the snowmelt gradients.

It has not been clear in this study whether the ratio of numbers of male to hermaphrodite flowers is genetically determined in each population, and whether *Dryas octopetala* is functionally androdioecy or andromonoecy, because strict determination of individuality of each patch was sometimes difficult due to the indistinct cushion forms at our study sites. If gender variations observed in this study reflect genetic differences among populations, consideration from the viewpoint of sex allocation theory (CHARNOV, 1982; SPALIK, 1991) is important to understand the gender variations along the snowmelt gradient. When fitness gain through female function is highly costly, the sex allocation theory predicts more

investment in male function until the reproductive cost for male function is almost equal to the cost for female function within a population. As the growing season length becomes shorter with lateness of snowmelt, the cost of reproduction for female function of hermaphrodite flowers may increase, which may result in the higher ratio of male to hermaphrodite flowers. For further interpretation of gender variation in *Dryas octopetala* along the snowmelt gradient, detailed information about plasticity of sex expression, genetic differences, and the degree of self-compatibility among populations is needed (e.g. DIGGLE, 1993).

Flower size variation along the latitudinal gradient

Flower size (dry weight) decreased at higher latitude sites both in male and hermaphrodite flowers. This may partly reflect severe climatic conditions and/or low availability of soil nutrient in the High Arctic. Since the decreases in temperature and global radiation in the late growing season (August) are smaller at the Subarctic Latnjajaure than at the High Arctic Ny-Ålesund (Table 1), plants growing in the High Arctic will suffer more from resource limitation for reproductive output than plants in the Subarctic. However, there are many other factors affecting variations of flower size, e.g. pollinator attraction (BELL, 1985), pollinator matching floral morphology (STEBBINS, 1971; INOUE *et al.*, 1996) and water availability (GALEN, 1998). According to GALEN (1998), plants with large flowers require high rates of water supply during the flower bud expansion and anthesis compared to plants with smaller flowers; therefore, the greater cost of large flowers is likely to occur in dry environments. In our study, precipitation in June and July (when flower buds develop and flowers bloom) was 49 mm at the High Arctic Ny-Ålesund and 127 mm at the Subarctic Latnjajaure (Table 1), suggesting a water-limited environment for a *Dryas* population of Ny-Ålesund as compared to that for a population of Latnjajaure. This environmental factor, in part, may cause flowers to be smaller at Ny-Ålesund than at Latnjajaure, in addition to poor fauna and density of insect pollinators at Ny-Ålesund (unidentified flies: WADA, personal observation) than at Latnjajaure (bumblebees, flies, and butterflies: STENSTRÖM and MOLAU, 1992; MOLAU, 1996).

Sex allocation pattern along a latitudinal gradient

In hermaphrodite flowers, both the dry weight and the allocation to the gynoecium decreased from the Subarctic to the High Arctic, while allocation to the androecium was almost constant. As a consequence, the femaleness decreased significantly from the Subarctic to the High Arctic. These results indicate that plants decrease investment in female organs at first, then investment in petals within flowers as the resource for reproduction decreases.

Although the proportion of male flowers was not remarkably different between the Subarctic and the High Arctic populations when populations with similar snowmelt conditions were compared, androecium dry weight of male flowers decreased significantly from the Subarctic to the High Arctic. This indicates that pollen production by male flowers decreases in the High Arctic populations. A decrease in femaleness of hermaphrodite flowers along the latitudinal gradient seems to be a reasonable response to maintain the pollen/ovule ratio within a population from a viewpoint of sex allocation theory (CHARNOV, 1982). Such high variations of gender expression and floral sex allocation may

enable *D. octopetala* to grow across wide range of climatic and snowmelt conditions.

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References

- ALATALO, J.M. and MOLAU, U. (1995): Effect of altitude on the sex ratio in populations of *Silene acaulis*. Nord. J. Bot., **15**, 251–256.
- AOKI, S., NAKANISHI, Y., WADA, M. and YAMANOUCHI, T. (1996a): Meteorological data at Japanese Ny-Ålesund Observatory, Svalbard in 1992 and 1993. NIPR Arct. Data Rep., **1**, 111 p.
- AOKI, S., NAKANISHI, Y., WADA, M. and YAMANOUCHI, T. (1996b): Meteorological data at Japanese Ny-Ålesund Observatory, Svalbard in 1994 and 1995. NIPR Arct. Data Rep., **2**, 179 p.
- BAUERT, M.R. (1993): Vivipary in *Polygonum viviparum*: an adaptation to cold climate? Nord. J. Bot., **13**, 473–480.
- BELL, G. (1985): On the function of flowers. Proc. R. Soc. London B, **224**, 223–265.
- BELL, K.L. and BLISS, L.C. (1980): Plant reproduction in an arctic environment. Arc. Alp. Res., **12**, 1–10.
- CHARNOV, E.L. (1982): Theory of Sex Allocation. Princeton, Princeton University Press.
- DIGGLE, P.K. (1993): Developmental plasticity, genetic variation, and the evolution of andromonoecy in *Solanum hirtum* (Solanaceae). Am. J. Bot., **80**, 967–973.
- GALEN, C. (1998): Why do April showers bring May flowers? Physiological costs of flower size in the alpine wildflower, *Polemonium viscosum*. Program with abstracts of papers, posters, special lectures, and symposia. Am. J. Bot., **85**, 33.
- GALEN, C. and STANTON, M.L. (1991): Consequences of emergence phenology for reproductive success in *Ranunculus adoneus* (Ranunculaceae). Am. J. Bot., **78**, 978–988.
- GALEN, C. and STANTON, M.L. (1993): Short-term responses of alpine buttercups to experimental manipulations of growing season length. Ecology, **74**, 1052–1058.
- HULTÉN, E. (1959): Studies on the genus *Dryas*. Sven. Bot. Tidskr., **53**, 507–547.
- INOUE, K., MAKI, M. and MASUDA, M. (1996): Evolution of *Campanula* flowers in relation to insect pollinators on Islands. Floral Biology. Studies on Floral Evolution in Animal-Pollinated Plants, ed. by D.G. LLOYD and S.C.H. BARRETT. New York, Chapman & Hall, 377–400.
- KELLEY, J.J. and WEAVER, D.F. (1969): Physical processes at the surface of the Arctic tundra. Arctic, **22**, 425–437.
- KJELLBERG, B., KARLSSON, S. and KERSTENSSON, I. (1982): Effects of heliotropic movements of flowers of *Dryas octopetala* L. on gynoecium temperature and seed development. Oecologia, **54**, 10–13.
- KLINKHAMER, P.G.L. and DE JONG, T.J. (1993): Phenotypic gender in plants: Effects of plant size and environment on allocation to seeds and flowers in *Cynoglossum officinale*. Oikos, **67**, 81–86.
- KUDO, G. (1991): Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. Arc. Alp. Res., **23**, 436–443.
- KUDO, G. (1992): Performance and phenology of alpine herbs along a snow-melting gradient. Ecol. Res., **7**, 297–304.
- KUDO, G. (1993a): Relationship between flowering time and fruit set of the entomophilous alpine shrub, *Rhododendron aureum* (Ericaceae), inhabiting snow patches. Am. J. Bot., **80**, 1300–

- 1304.
- KUDO, G. (1993b): Size-dependent resource allocation pattern and gender variation of *Anemone debilis* Fisch. *Pl. Sp. Biol.*, **8**, 29–34.
- KUDO, G. (1997): Sex expression and fruit set of an andromonoecious herb, *Peucedanum multivittatum* (Umbelliferae) along a snowmelt gradient. *Opera Bot.*, **32**, 121–128.
- LLOYD, D.G. (1980): Sexual strategies in plants. III. A quantitative method for describing the gender in plants. *N. Z. J. Bot.*, **18**, 103–108.
- LOVETT DOUST, J. and LOVETT DOUST, L. (1988): Sociobiology of plants: An emerging synthesis. *Plant Reproductive Ecology*, ed. by J. LOVETT DOUST and L. LOVETT DOUST. New York, Oxford University Press, 5–29.
- MCGRAW, J.B. (1985): Experimental ecology of *Dryas octopetala* ecotypes. III. Environmental factors and plant growth. *Arc. Alp. Res.*, **17**, 229–239.
- MOLAU, U. (1991): Gender variation in *Bartsia alpina* (Scrophulariaceae), a subarctic perennial hermaphrodite. *Am. J. Bot.*, **78**, 326–339.
- MOLAU, U. (1993): Relationships between flowering phenology and life history strategies in tundra plants. *Arc. Alp. Res.*, **25**, 391–402.
- MOLAU, U. (1996): Phenology and reproductive success in arctic plants: susceptibility to climate change. *Global Change and Arctic Terrestrial Ecosystems. Ecological Studies 124*, ed. by W.C. OECHEL *et al.* New York, Springer, 153–170.
- PHILIPP, M., BÖCHER, J., MATSSON, O. and WOODSELL, S.R.J. (1990): A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia*, *Silene acaulis* and *Ranunculus nivalis*. *Medd. Grønland, Biosci.*, **34**, 1–60.
- RØNNING, O.I. (1969): Features of the ecology of some Spitzbergen plant communities. *Arc. Alp. Res.*, **1**, 29–44.
- SPALIK, K. (1991): On evolution of andromonoecy and 'overproduction' of flowers: a resource allocation model. *Biol. J. Linn. Soc.*, **42**, 325–336.
- SPIRA, T.P. and POLLACK, O.D. (1986): Comparative reproductive biology of alpine biennial and perennial gentians (*Gentiana*: Gentianaceae) in California. *Am. J. Bot.*, **73**, 39–47.
- STEBBINS, G.L. (1971): Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. *Ann. Rev. Ecol. Syst.*, **1**, 307–326.
- STENSTRÖM, M. and MOLAU, U. (1992): Reproductive ecology of *Saxifraga oppositifolia*: Phenology, mating system, and reproductive success. *Arc. Alp. Res.*, **24**, 337–343.
- TOTLAND, Ø. (1994): Intraseasonal variation in pollination intensity and seed set in an alpine population of *Ranunculus acris* in southwestern Norway. *Ecography*, **17**, 159–165.
- TOTLAND, Ø. (1997): Effects of flowering time and temperature on growth and reproduction in *Leontodon autumnalis* var. *taraxaci*, A late-flowering alpine plant. *Arc. Alp. Res.*, **29**, 285–290.
- WADA, N. (1998): Sun-tracking flower movement and seed production of mountain avens, *Dryas octopetala* L. in the High Arctic, Ny-Ålesund, Svalbard. *Proc. NIPR Symp. Polar Biol.*, **11**, 133–141.
- 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 Biol.*, **3**, 61–73.
- WOOKEY, P.A., PARSONS, A.N., WELKER, J.M., POTTER, J.A., CALLAGHAN, T.V., LEE, J.A. and PRESS, M.C. (1993): Comparative responses of phenology and reproductive development to simulated environmental change in Subarctic and high arctic plants. *Oikos*, **67**, 490–502.

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