

SUN-TRACKING FLOWER MOVEMENT AND SEED PRODUCTION
OF MOUNTAIN AVENS, *DRYAS OCTOPETALA* L.
IN THE HIGH ARCTIC, NY-ÅLESUND, SVALBARD

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Abstract: I observed the sun-tracking behavior, temperature increment within flowers, and seed production of mountain avens, *Dryas octopetala* L., occurring near Brøgger glacier in Ny-Ålesund (78°55'N, 11°56'E), Svalbard in Norway. The flowers showed sun-tracking movement on sunny days, but the movement was mostly found around noon and was not so active throughout a sunny day. The temperature increment of the gynoecium in flowers facing the sun was *ca.* 2°C higher than in flowers with their back to the sun. Petal removal resulted in considerable reduction of the gynoecium temperature. Insects (mostly mosquitoes) visiting flowers were very infrequent, suggesting that a severe pollinator limitation restricted the cross-pollination. During the experiments, flowers of *Dryas octopetala* did not produce any developed seeds under natural condition (0% seed-set). Cross-pollinated flowers showed 8% seed-set, while flowers which were artificially warmed by small greenhouses during the flowering period showed 60% seed-set, indicating that the reproduction of *D. octopetala* is strongly restricted by low temperature during the flowering period, rather than by pollinator limitation, in the population of Ny-Ålesund, Svalbard. These results suggest that the sun-tracking behavior and parabola-shaped flower structure with large petals are important for seed-setting success by increasing the gynoecium temperature.

key words: artificial warming, cross pollination, flower heliotropism, High Arctic, seed production

Introduction

Arctic environments are primarily characterized by low solar radiation, *ca.* 420–450 MJ/m²/year (KELLEY and WEAVER, 1969; SAKAI, 1995). Such harsh environments restrict many arctic plants in producing carbohydrate by photosynthesis, and then reduce the carbon resources available for seed production in the short and cold summer (BELL and BLISS, 1980). Cool temperature during the flowering periods may restrict 1) the gene flow throughout pollinator activities (TOTLAND, 1994), and 2) pollen germination and its tube elongation to ovules (CORBET, 1990; WILLIAMS and ROUSE, 1990; KUDO, 1995), which result in low seed production.

Sun-tracking behavior of flowers (flower heliotropism), which is mediated by changes in cell turgor pressure (VOGELMANN, 1984), is considered to be one of the

adaptations to low temperature (KEVAN, 1972a, 1975) in order to increase reproductive success not only through female function by producing seeds but also through male function by pollen transported to other flowers by insects (*e.g.* STANTON and GALEN, 1989). So far, species showing flower heliotropism are known at least in four families: Compositae (*Matricaria ambigua* and *Senecio congestus*), Papaveraceae (*Papaver radicum*), Ranunculaceae (*Ranunculus adoneus*, *R. acris*, and *Adonis ramosa*) and Rosaceae (*Dryas integrifolia*) (KEVAN, 1972a; STANTON and GALEN, 1989; KUDO, 1995; TOTLAND, 1996), mostly inhabiting arctic and alpine environments (KNUTSON, 1981). These plants commonly have large petals and parabola-shaped flowers to focus solar radiation and then increase gynoeceum temperature on sunny days (KEVAN, 1975; KJELLBERG *et al.*, 1982; STANTON and GALEN, 1989; KUDO, 1995; TOTLAND, 1996), resulting in producing heavier seeds (KJELLBERG *et al.*, 1982; STANTON and GALEN, 1989; KRANNITZ, 1996) and more insect visitation (STANTON and GALEN, 1989; KUDO, 1995; KRANNITZ, 1996).

Mountain avens, *Dryas octopetala* L. is one of the species which show flower heliotropism (KJELLBERG *et al.*, 1982). I observed the sun-tracking behavior, temperature increment within flowers, and seed production of *Dryas octopetala* in a population near a glacier in the high arctic, in Ny-Ålesund, Svalbard, where climatic conditions are extremely severe for plant reproduction. I also examined the effects of cross-pollination and artificial warming during a short period on seed production, to clarify which factors limit the reproduction of *D. octopetala* in this population.

Materials and Methods

Study site

The study site is located *ca.* 1.5 km distant from Brøgger glacier, and *ca.* 0.5 km from Kingsfjorden, in Ny-Ålesund (78°55'N, 11°56'E), Svalbard in Norway (Fig. 1). The monthly average temperatures of June, July, and August in 1996 were 1.9°C, 3.8°C, and 3.5°C, respectively, slightly lower than the respective average monthly temperatures from 1992 to 1995 (Fig. 2, data from Norsk Polarinstittutt). The vegetation of this site

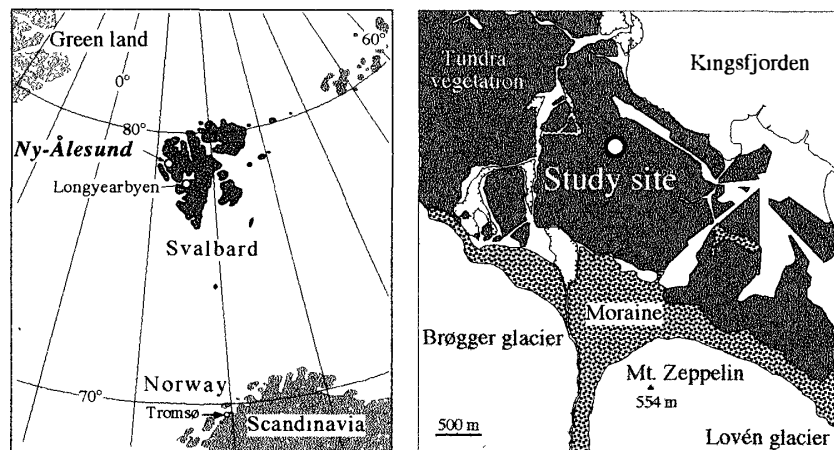


Fig. 1. Study area (Ny-Ålesund; 78°55'N, 11°56'E: left figure) and study site located *ca.* 1.5 km distant from Brøgger glacier (right figure).

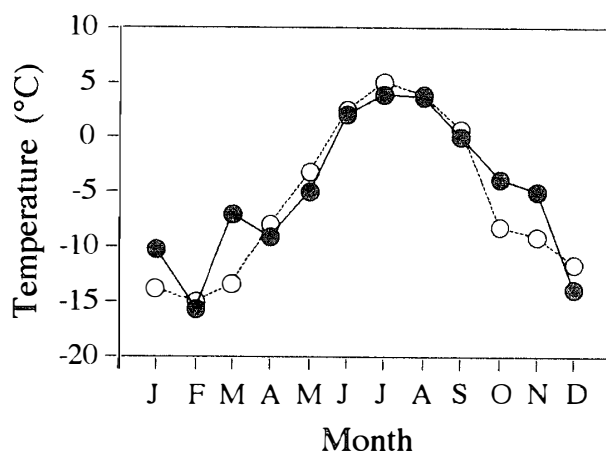


Fig. 2. Monthly average temperature in Ny-Ålesund. Solid circle and line, in 1996, open circle and broken line, average temperature from 1992 to 1995 (data from Norsk Polarinstitutt)

is almost in the climax stage (MINAMI and KANDA, 1995; MINAMI *et al.*, 1996), mostly dominated by *Dryas octopetala*, and partly composed of *Salix polaris*, *Saxifraga oppositifolia*, *Silene acaulis*, *Oxyria digyna*, *Polygonum viviparum*, and many bryophytes.

Sun-tracking behavior and temperature increment within flowers of *Dryas octopetala*

Dryas octopetala usually had hermaphrodite flowers, but sometimes male flowers (WADA, unpublished data). In this study, all observations and field experiments were conducted by using hermaphrodite flowers. I arbitrarily selected and tagged fifty flowers of *D. octopetala* by plastic plates (*ca.* 5 cm × 1 cm) in a *Dryas* dominant population on a sunny day, 28 July 1996. At noon (12 o'clock), evening (18 o'clock) and midnight (24 o'clock), I recorded the flower direction and deviation from the sun of each flower by using a clinometer (Showa Sokki Co., Tokyo, Japan). However, ten flowers were apparently grazed by reindeer during the night. The next morning, due to fog and cloud, I could not observe the sun-tracking behavior of the remaining forty flowers.

I selected and measured temperatures on the gynoecia of twenty flowers and ambient temperature of each flower by a digital thermometer (SK-2000MC, Sato Keiryoki MFG. Co., Ltd., Japan) at 1700 on a sunny day, 25 July, when the temperature near the ground was more than 10°C. Of these, ten flowers faced the sun, and the other ten flowers were back to the sun. After the measurements of intact flower temperature, I immediately removed all petals of the twenty flowers and measured gynoecium temperatures as mentioned above.

Observation of insect visitors

I observed insects visiting in flowers of *Dryas octopetala* from early to late July. I tagged 122 flower buds arbitrarily on 11 July, and recorded the number of insects visited in each flower once every day from the onset to the end of flowering (defined as half or more of eight petals withered or dropped). The visitation rate of insects was calculated in each flowering shoot as the number of observed insects per census.

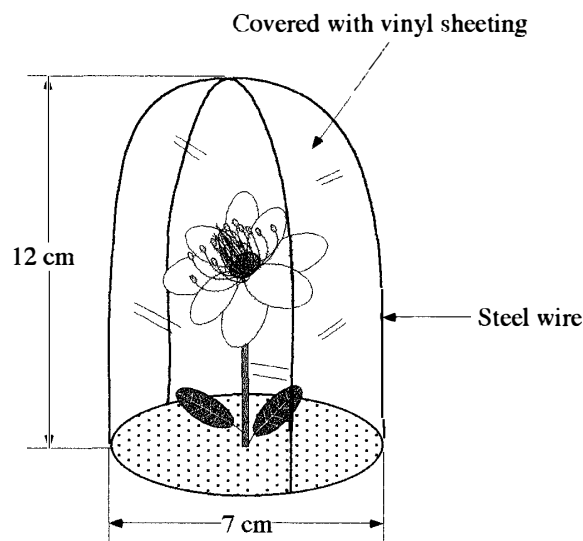


Fig. 3. A small greenhouse used for the artificial warming experiment.

Effects of cross-pollination and artificial warming on seed production

To determine whether seed production is restricted by pollen limitation or by low temperature, 1) I supplied the gynoecia of twenty-five flowers with pollen collected from the other five flowers and 2) artificially increased temperatures of fifteen *Dryas* flowering shoots by using small greenhouses made of steel wire and vinyl sheeting (Fig. 3). This greenhouse increased temperature about $2.8 \pm 0.8^\circ\text{C}$ (mean \pm sd, $n = 20$; range 1.7 – 4.4°C) on a sunny day (25 July), and $1.6 \pm 0.9^\circ\text{C}$ ($n = 20$; range 0.5 – 2.9°C) on a cloudy day (29 July). Because the greenhouse was wholly covered with the vinyl sheeting, insect pollinators were completely excluded. Therefore, this treatment also tested the self-compatibility of flowers of *Dryas octopetala*.

I covered fifteen flowering shoots soon after the opening of petals with the fifteen greenhouses on 18 July (warming treatment). On 4 August, all greenhouses were removed when all petals of the flowers completely dropped (17 days). I emasculated twenty-five *Dryas* flower buds, and conducted cross-pollination when those petals opened in late July (cross-pollination treatment). I tagged twenty-five flower buds occurring near the greenhouses as control, in addition to 122 tagged flowers (as mentioned in “Observation of insect visitors”). On 20 August, I collected these shoots and compared the seed-set per flowering shoot among the cross-pollinated shoots, the artificially warmed shoots and the control ones. According to WOOKEY *et al.* (1993), I defined “seed-setting” as the number of fruiting shoots that had one or more mature seeds with well developed feathery styles beyond the extent of the sepals, divided by the number of flowering shoots.

Results and Discussion

Flower heliotropism

Table 1 shows the results of flower movement of *Dryas octopetala*. At noon, most flowers faced the sun, and the flower direction was $181^\circ \pm 40^\circ$ (mean \pm sd). In the evening and at midnight, the direction of flowers slightly increased toward the sun (Table 1,

Fig. 4), but these movements were not significantly different among the observation times ($F_{2, 137} = 2.695$, $P = 0.071$, by one-way ANOVA). Therefore, the flower deviation from the sun significantly increased from noon to midnight ($F_{2, 137} = 123.641$, $P = 0.0001$, by one-way ANOVA). From noon to evening, flowers moved $13.3^\circ \pm 13.7^\circ$ (mean \pm sd) toward the sun, but only $5.3^\circ \pm 21.7^\circ$ from evening to midnight. These flower movements were significantly different ($\chi^2 = 11.52$, $P = 0.006$, by Kolmogorov-Smirnov test). Although flowers of *Dryas octopetala* actually showed sun-tracking behavior, these movements were not so active throughout the day, and most flowers faced south on a sunny day (Fig. 4). Similar tendencies were observed by KEVAN (1972b) in *Dryas integrifolia* and by KJELLBERG *et al.* (1982) in *D. octopetala*, in which flowers showed

Table 1 Flower direction and deviation from the sun (mean \pm sd) of *Dryas octopetala* at noon, evening and midnight on a sunny day (July 28, 1996, n = 50 at noon and evening, and n = 40 at midnight) The direction is shown as 0° for the north (compass direction)

	Noon	Evening	Midnight
Sun direction	180°	270°	360°
Flower direction	$181^\circ \pm 40^\circ$	$194^\circ \pm 37^\circ$	$201^\circ \pm 51^\circ$
Deviation from the sun*	$33^\circ \pm 22^{2a}$	$76^\circ \pm 37^{ob}$	$136^\circ \pm 33^{oc}$

* Scheffe's F test Different letters on the numerals (a, b, and c) show a statistically significant difference at $P < 0.05$ level

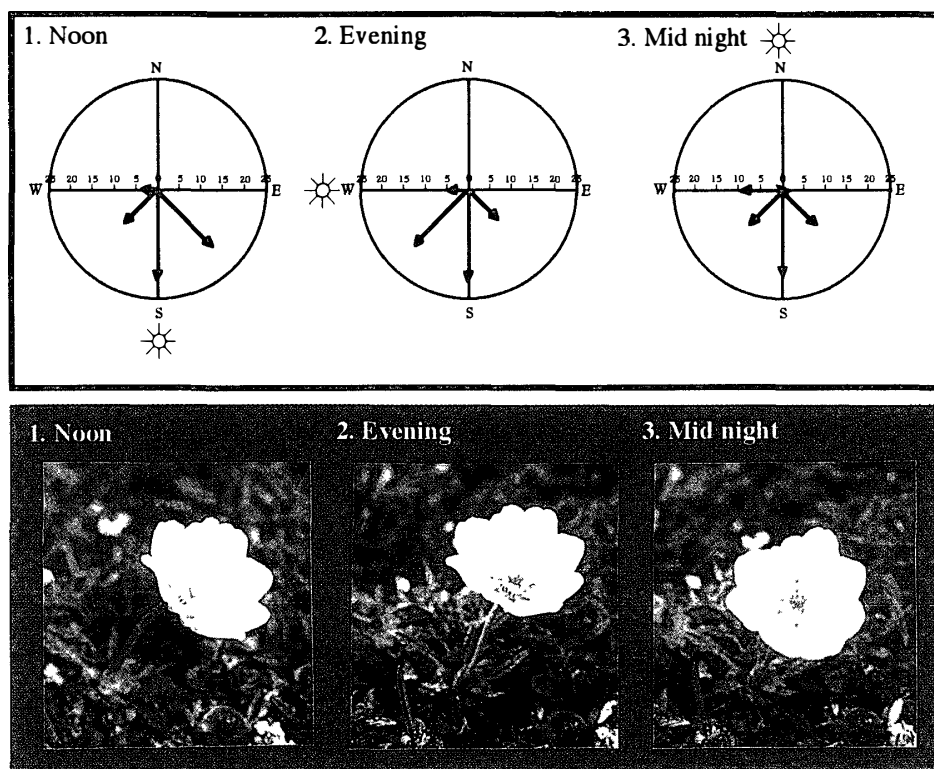


Fig. 4 Flower movements of *Dryas octopetala*. Top, flower compass direction in 8 degrees is shown with arrows. The length of arrows shows the number of flowers. Bottom, flower movement of a *Dryas* flower from noon to midnight

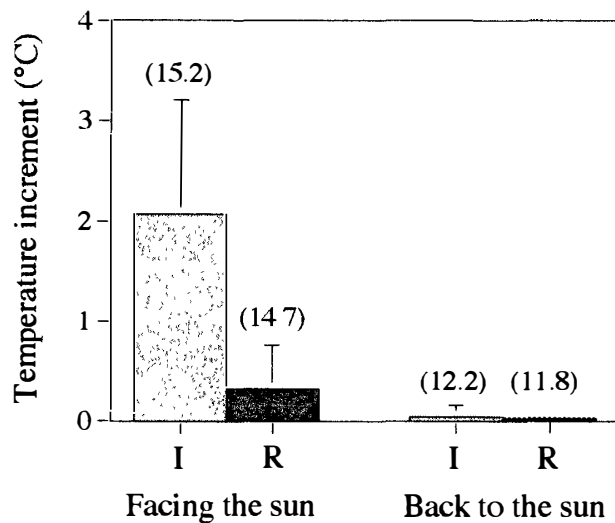


Fig. 5. Temperature increment on gynoecium of *Dryas octopetala* against ambient temperature ($n=10$). I, intact flowers (gray bar); R, petal removed flowers (black bar). Vertical lines on each bar show standard deviations. Numerals in parentheses show mean ambient temperatures ($n=10$).

heliotropic behavior only for several hours around noon.

I compared temperature increments on gynoecia between sun-facing flowers and those with their backs to the sun (Fig. 5). The gynoecium temperature was 2.1°C higher than ambient temperature in sun-facing flowers, whereas it was only 0.04°C higher in flowers with back to the sun, and the warming effects were significantly different between the flowers ($P=0.0001$, by Mann-Whiney U test). Petal removal experiments showed significant reduction of the warming effect from *ca.* 2°C to *ca.* 0.3°C in sun-facing flowers ($P=0.0003$, by Mann-Whiney U test). Thus, sun-tracking behavior and flower structure with large petals may be very important to increase the temperature of the gynoecium, suggesting significant impact on the reproduction of *Dryas octopetala* as reported by KJELLBERG *et al.* (1982): individual seed size (mg) was heavier in heliotropic flowers than in flowers with artificially constrained heliotropic movements, or that had their petals removed.

Flower visitors

A flowering period of *D. octopetala* was *ca.* 9 days (mean \pm sd, 8.8 ± 1.6 days; $n=122$). The total number of flower visitors during the flowering period was only 0.2 per flower (mean \pm sd, 0.2 ± 0.6 ; $n=122$), and the visitation rate was 0.02 per census (mean \pm sd, 0.023 ± 0.056 ; $n=122$). Most of the visitors were mosquitoes. As shown in Fig. 6, I observed that 84% (102) of the 122 flowers were not visited by any insects during a flowering period, suggesting a severe pollinator limitation and a rarity of cross-pollination under natural conditions.

Effects of cross-pollination and artificial warming on seed production

There were no shoots that produced fruits with mature seeds in 147 control flowers (0% seed-set). The achenes of these shoots had immature white and short styles with

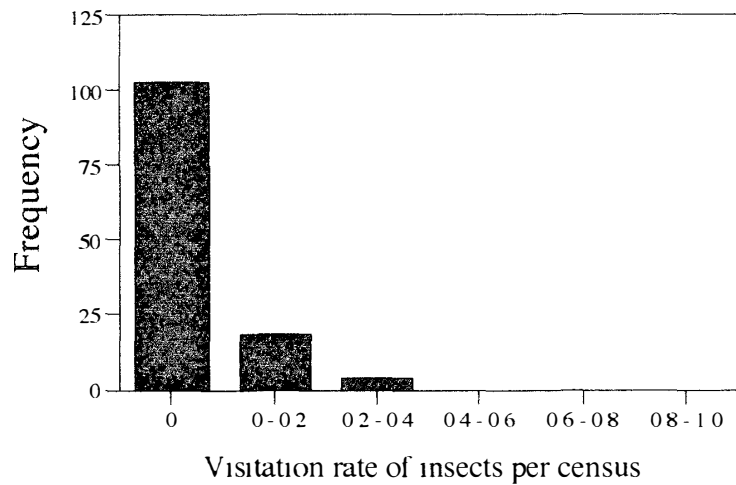


Fig. 6 Insect visitation on *Dryas* flowers during the flowering periods

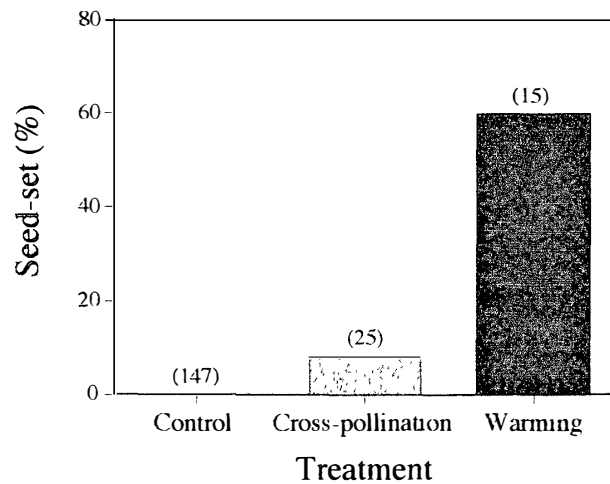


Fig. 7. Effects of cross-pollination and artificial warming on seed production. Seed-set per flowering shoot is shown in control shoots, cross-pollinated shoots, and artificially warmed shoots during the flowering periods. Numerals in parentheses show the number of samples

no developed seeds. Cross-pollination treatment showed an 8% seed-set, but *ca.* 90% shoots could not produce any mature fruits, the same as the control shoots. In contrast, 60% of shoots had developed fruits and seeds with long styles by artificial warming treatment (Fig. 7). The results clearly indicated that 1) flowers of *Dryas octopetala* inhabiting the area near the Brøgger glacier in Ny-Ålesund are self-compatible, but 2) the seed or fruit production is strongly restricted by low temperature and a short growing season, rather than by few pollinator visitations. The results mostly support WOOKEY *et al.*'s study (1993) in Ny-Ålesund; *D. octopetala* showed *ca.* 60% seed-set by an artificial warming treatment by using polythene tents, while there was no seed-set in the control. A high seed-set in the short-term artificial warmed shoots suggests that the temperature-dependent physiological process such as pollen germination and/or its tube elongation may be restricted in a natural population in Ny-Ålesund. It is necessary to examine the pollen activity under various temperature conditions to elucidate the

temperature-dependent traits.

Concluding Remarks

Although flowers of mountain avens, *Dryas octopetala*, track the sun mostly around noon, temperature increments throughout the heliotropic movement were insufficient for the plant to produce the fruits and seeds in 1996. As shown in Fig. 7, however, the seed production of *Dryas octopetala* is very sensitive, and quickly responds to the modification of temperature. The results in this study suggest that most flowers will produce mature fruits and seeds in unpredictable good weather conditions.

In the present study, I could not find a relationship between insect visitation and increase of temperature on the gynoecium by sun-tracking flower movements, because very few pollinators were observed in this season. KEVAN (1972b) demonstrated the importance of insect pollination on seed production of *Dryas integrifolia*. In cold environments, heliotropic flowers provide warmer habitats for insect pollinators (e.g. KUDO, 1995), resulting in frequent pollinator visitation, high opportunity for cross-pollination, and also high efficiency of pollen dispersal to other flowers through pollinator activities, as compared to non-heliotropic flowers. These may affect the reproductive success of the male function in hermaphrodite flowers (STANTON and GALEN, 1989).

To understand the reproductive activities of *D. octopetala* in Ny-Ålesund, in the second step, it is necessary to examine how seed viability, germination, and seedling establishment are affected by biotic and abiotic factors; interaction of insect cross-pollination and warming treatment, nutrient availability, precipitation, and temperature in summer. Further long-term experimental studies are needed in the field.

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