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Effects of Heliotropic Movements of Flowers of *Dryas octopetala* L. on Gynoecium Temperature and Seed Development

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Abstract. Dryas octopetala has heliotropic flowers, whose petals reflect the light on the pistils, thus warming them up. The effects of this reflection on seed formation and development were studied by measuring the pistil temperature of intact flowers, of flowers with petals removed, of shaded flowers, and of flowers constrained in such a way as always to be directed towards the zenith. In August, the seeds of these flowers were collected, counted and weighed. The temperature differences between the differently treated flowers were greatest about noon, the flowers ranking as follows in ascending order of temperature: shaded flowers, flowers without petals, constrained flowers and intact flowers. The mean temperature differences between the gynoecia and the air, in degrees Celsius, were: 1.1, 1.8, 2.5 and 3.2, respectively. The same ranking was obtained for the different treatments, when arranged in order of ascending weight per seed, except that the positions of the shaded flowers and the flowers without petals were interchanged. The mean values of the weight per seed in milligrams were: 0.42, 0.48, 0.53 and 0.61 for the groups flowers without petals, shaded flowers, constrained flowers and intact flowers, respectively.

Introduction

The leaves and flowers of many species show heliotropic movements, which regulate the amount of radiation absorbed. The ecological aspects of heliotropic movements of leaves have been discussed in a number of papers (eg., Wainwright 1977; Mooney and Ehleringer 1978; Forseth and Ehleriger 1980). Less attention has been paid to the movements of flowers, however, heliotropism in Helianthus annuus has been found to reduce flower temperature (Lang and Beggs 1979), while in two arctic species – Dryas integrifolia and Papaver radicatum – it has been found to increase it (Hocking 1968; Kevan 1975). These arctic flowers were studied in connection with insect studies. In these studies, the Papaver flowers were found to be turned towards the sun 24 h a day, while most Dryas flowers faced the sun from 8 a.m. to 3 p.m. Flower temperatures exceeding that of the surrounding air by 10° C were measured. It was found that the increased temperature in the flowers attracted insects, which enhanced pollination.

Another possible effect of an increased temperature is faster seed development, which should be of importance, especially in alpine and arctic environments. The hypothesis behind this study is, that in an alpine subarctic environment, seed development in Dryas octopetala L. is influenced by the heliotropic movement of the flowers, which causes an increased temperature in the gynoecium. A field experiment was carried out in the summer of 1980 to test this hypothesis.

Investigation Site and Methods

The measurements were carried out on Mount Njulla, in Abisko National Park, northern Sweden (68°22′N, 18°42′E), 900 metres above sea-level. The site has an area of approximately 73 m^2. It is more or less flat and is covered with vegetation dominated by Dryas octopetala. The area was selected because it offered maximum exposure to the sun. However, between 7 p.m. and midnight it lies in the shadow of a peak.

At the beginning of the experiment in the end of June, the soil was wet owing to snowmelt and the weather was unstable, with periods of rain and fog. From 1 July the weather turned warm and sunny, though with some afternoon cloud. The soil dried out during this period. The air temperature recorded on a thermohydrograph standing on the ground varied between 5° C and 20° C during the flowering period, 26 June–5 July. During this 10-day period, a heliograph at the Abisko Scientific Research Station, in the valley 500 metres below, recorded 74 hours of sunshine, whereof 43.5 hours during daytime (7 a.m.–7 p.m., solar time).

The summer of 1980 was relatively dry and warm in the area. The mean June and July temperatures at the Abisko Scientific Research Station were 10.7° C and 13.3° C, respectively, as compared with the long term means (1930–1960) of 8.1° C and 12.3° C. Precipitation during June and July 1980 amounted to 58.3 mm and 28.1 mm, the mean being 30 and 45 mm, respectively.

Sixty shoots of Dryas octopetala with flower buds were selected in the investigation site and divided into four groups. The groups consisted of:

1. Intact Flowers. This group was left undisturbed. The gynoecia received direct radiation as well as radiation reflected by the petals.

2. Flowers Without Petals. The petals of the flowers in this group were removed at a late bud phase. This treatment eliminated the radiation reflected by the petals on the gynoecium.

3. Constrained Flowers. A thin wire ring was placed under the flower head in contact with the sepals to prevent heliotropic movement of the flowers. The ring was then attached to pegs in three different directions. The gynoecia received radiation directly from the sun and, to some extent, radiation reflected from the petals.

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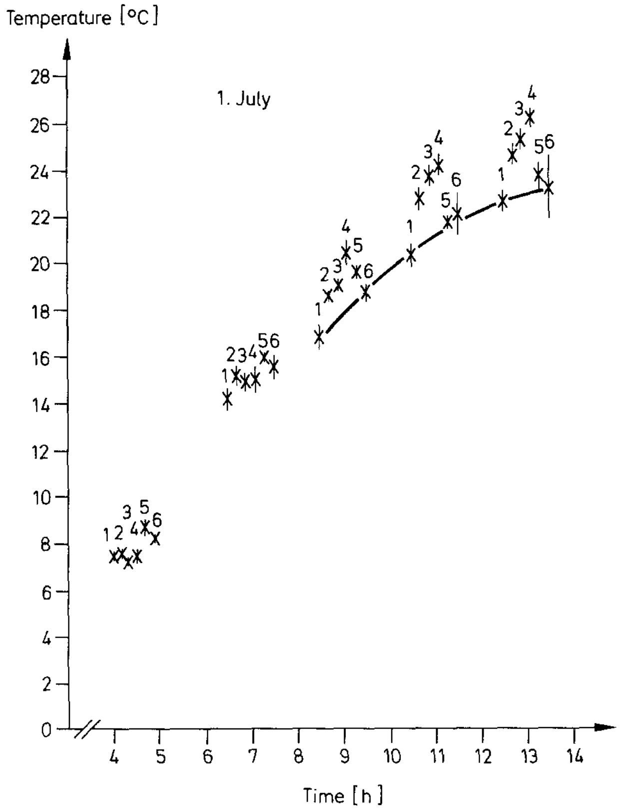

Fig. 1. Gynoecium and air temperature in the various measurement series (mean and standard error)
1=ambient air (sensor exposed to the sun), *2*=flowers without petals, *3*=constrained flowers, *4*=intact flowers, *5*=shaded flowers, *6*=air in the shaded area

4. Shaded Flowers. Shading was effected by setting up a fence made of a piece of sacking, 60 cm high, around an area 50 × 50 cm in size. The incoming radiation was reduced by approximately 50% by the sacking. However, about noon the flowers occasionally received sunlight. The 15 shaded flowers were dispersed over two such enclosures.

The flowers from the other groups were distributed over the rest of the area. After five days, 10 extra flowers were chosen – 5 "intact" and 5 "constrained" – to replace the withered flowers. The seeds of the extra 5 constrained flowers were not taken into account.

The temperature measurements were made with thermocouples composed of a copper wire and a constantan wire soldered together each wire having a diameter of 0.008 mm. A thermocouple was mounted on each flower and 15 were additionally spread out at flower height for measuring the ambient air temperature – 13 in the unshaded area and 3 in the shaded area. The temperature was measured on the southern aspect of the pistil. When a flower had less than seven petals, it was considered withered, and was excluded from the measurements; and when a flower from the group "shaded flowers" stood in the sunshine, it was also excluded. The electric current from the thermocouple was amplified by an Omega Thermocouple D.C. Millivolt Amplifier and measured with a millivoltmeter. The calibration of the measuring equipment gave a linear relationship between millivolt output and temperature: temp. (°C) = mV + 2.15, with a regression correlation coefficient of 1.0.

Measurements of wind speed were made with a Flügelradanemometer at ground level near the flowers. The wind speed up to a level of 10 cm above the ground was thus obtained.

The measuring periods were distributed throughout the days concerned, under varying weather conditions. Measurements were made on 26, 28, 29, and 30 June and on 1 and 2 July. Measurements interrupted by rain were not taken into consideration and nor were measurements made about midnight and in the fog, since the instruments were unable to record the temperatures.

On 28 June the flowers were pollinated artificially with a soft paint brush.

On 5 July, when all the flowers had lost their petals, the sacking and wire rings were taken away.

On 31 July the seeds were harvested, each flower head being placed in a separate bag. The seeds were killed in a microwave oven to avoid respiration losses.

The significance of the differences between the groups was tested by means of the "Student's" *t*-test (Bailey 1959).

Results

On clear sunny mornings, the gynoecium temperature rose progressively between each of the measuring series, as did the light intensity (Fig. 1). Early in the morning, the flower temperatures were about the same as the air temperature in all cases, but about midday differences between the groups were noticeable. Since the heliotropic movement was most pronounced about noon, the measurements were divided into three groups depending on when the measurements were made: (1) before 9 a.m.

Table 1. Deviations in gynoecium and air temperature in the shaded area from the mean of the ambient air temperature during the period 1 a.m.–9 a.m. on two sunny days

Group	Temperature differences (°C)		Number of measurements	Prob. of the groups beeing diff.				
	$\bar{x}$	S.E.		I	W	A	Sa	a
Sf	1.6	0.19	81	<0.90	<0.90	<0.90	0.95	0.999
I	1.5	0.24	82		<0.90	<0.90	0.95	0.999
W	1.3	0.17	90			<0.90	<0.90	0.999
A	1.1	0.18	86				<0.90	0.999
Sa	0.9	0.26	18					0.99
a	0.0	0.15	72					

Groups: I = intact flowers, A = constrained flowers, W = flowers without petals, Sf = shaded flowers, Sa = air in the shade, a = ambient air, $\bar{x}$ = mean, S.E. = standard error

Table 2. Deviations in gynoecium and air temperature in the shaded area from the mean of the ambient air temperature during the time 9 a.m.–1 p.m. on two sunny days. Abbreviations as in Table 1

Group	Temperature differences (°C)		Number of measurements	Prob. of the groups beeing diff.				
	$\bar{x}$	S.E.		A	W	Sf	Sa	a
I	3.2	0.26	54	<0.90	0.999	0.999	0.999	0.999
A	2.5	0.29	52		<0.90	0.999	0.99	0.999
W	1.8	0.22	60			0.95	0.95	0.999
Sf	1.1	0.27	39				<0.90	0.99
Sa	0.6	0.52	12					<0.90
a	0.0	0.22	48					

Table 3. Results of seed production. Abbreviations as in Table 1

Group	Number of flower heads	Number of seeds per flower head		Seed weight per flower head, mg		Weight per seed, mg		Prob. of the groups beeing diff.		
		$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.	A	Sf	W
I	17	51	3	32.3	3.3	0.61	0.03	0.99	0.999	0.999
A	11	63	3	33.2	2.7	0.53	0.03		<0.90	0.95
Sf	6	58	4	28.2	4.6	0.48	0.05			<0.90
W	10	59	5	24.9	2.9	0.42	0.03			

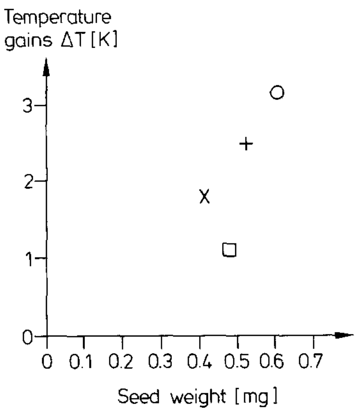

Fig. 2. Comparition between seed weight and the mean gynoecium temperature about midday ○ = intact flowers, + = constrained flowers, × = flowers without petals, □ = shaded flowers

and cloudy days, (2) on days with broken cloudiness, and (3) between 9 a.m. and 1 p.m. on clear days. The gynoecium temperature was related to the air temperature. Only small temperature gains were detected before 9 a.m. The mean temperature gains for the treatments were (Table 1): shaded flowers, 1.6° C, intact flowers, 1.5° C; flowers without petals, 1.3° C, and constrained flowers, 1.1° C, there was no significant difference between the treatments. About noon on clear days (group 3) the gynoecia of the different groups showed varying temperature gains were (Table 2): intact flowers, 3.2° C, constrained flowers, 2.5° C, flowers without petals, 1.8° C, shaded flowers, 1.1° C. Group 2 showed intermediary results.

The number of seeds produced per flower showed great variations, which did not show any correlation with the treatments, whereas the weight per seed could be correlated to the different groups (Table 3): the group "intact flowers" had the heaviest seeds, next came the groups "constrained flowers", "shaded flowers" and "flowers without petals".

A comparition made between the seed weights and the temperature gains of the gynoecia about noon showed a linear relatioship except for the group "shaded flowers" (Fig. 2).

A correlation was tested for the gynoecium temperatures and the wind speed, but at shifting wind speeds the temperature varied very little except that it showed a tendency to rise when no wind was recorded. However, the material from which this correlation was made was very restricted.

Discussion

In this study no systematic measurements were made of the heliotropic movements of the flowers of Dryas octopetala, but the observations made agree with Kevan's (1975) results for Dryas integrifolia. The proportion of flowers following the sun rose rapidly from 5 a.m. to 9 a.m., reaching a maximum of nearly 100% between 9 a.m. and 1 p.m., and then decreasing during the afternoon. The effect of heliotropism in Dryas should hence be most pronounced between 9 a.m. and 1 p.m. This was recorded in the temperature measurements, between 1 a.m. and 9 a.m. The mean gynoecium temperatures were 1.1–1.6° C above the ambient air temperature, with no significant differences between the different treatment groups. Between 9 a.m. and 1 p.m. the temperature in the intact flowers had increased to 3.2° C above the ambient air temperature, being significantly higher than for the other treatments. The next highest temperature was shown by flowers whose heliotropic movements had been prevented – 2.5° C above air temperature; then followed the flowers without petals – 1.8° C above air temperature; and the lowest temperature was found in the shaded flowers – 1.1° C above air temperature. The gynoecium temperature was hence raised 0.7° C by the petals and another 0.7° C by the heliotropic movements. The temperature gain in Kevan's study was: $Tf = 0.3\, Ta + 2.56$, where Tf is the temperature gain in the Dryas flower and Ta is the air temperature. If this formula is applied to our data, a temperature gain of the order of 8 to 9° C is predicted, which is a three times greater than the increase which our results showed. However, there are several important factors influencing flower temperature that are not included in Kevan's formula, such as radiation intensity, wind speed, and shape and behaviour of the flower.

The effect of the treatment on seed weight shows a close relationship with the temperature gain about noon, the flowers with the highest temperature having the heaviest seeds, with the exception of the group of shaded flowers, where the seed weight was found to be higher than that suggested by the temperature measurements. This could, however, be explained by the fact that these flowers were occasionally sunlit (temperature measurements taken when the shaded flowers were sunlit were excluded from the calculations of the mean temperatures). Also, the outgoing radiation was perhaps reduced by the sacking at night, when these flowers showed the highest temperatures. This treatment also altered light climate for the leaves, but since the photosynthetic light saturation is low (Mayo et al. 1977), we assume that the treatment did not have any important effect on the photosynthesis.

Since the seed weight in this study was calculated by weighing all the seeds from one flower head together and dividing the weight obtained by the number of seeds, it was not shown whether the differences between the treatments were caused by differences in the proportion of empty seeds or by differences in the actual seed weight. In the former case our results would indicate a difference in the number of fully developed seeds. In the latter case, if the average seed weight differs, it would seem that a heavier seed would give the seedling a better start, the embryo being more developed or the endosperm being more plentiful. Work has been done on Pinus sylvestris which shows that germination is influenced favourably by a higher seed weight obtained by weighing 1,000 seeds together (Andersson 1965; Kardell 1973).

The results of this study indicate that heliotropic movement has a favourable effect on seed production, thus probably increasing the possibilities of Dryas octopetala to propagate by seeds.

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