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A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia, Silene acaulis* and *Ranunculus nivalis*

Marianne Philipp, Jens Böcher, Ole Mattsson and Stanley R. J. Woodell

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Gert Steen Mogensen, Botanical Museum, Gothersgade 130, DK-1123 Copenhagen K. Telephone +4533 11 17 44.

Scientific editor – Zoology

G. Høpner Petersen, Zoological Museum, Universitetsparken 15, DK-2100 Copenhagen Ø. Telephone +4531 35 41 11.

This volume edited by Gert Steen Mogensen.

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This work is dedicated to the memory of Professor T.W. Böcher who initiated the project and took part in the field work in 1976. We feel very much indebted to his inspiring enthusiasm and immense knowledge of the Greenlandic flora which he loved so much.

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A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia, Silene acaulis* and *Ranunculus nivalis*

MARIANNE PHILIPP, JENS BÖCHER, OLE MATTSSON and STANLEY R. J. WOODELL

Philipp, M., Böcher, J., Mattsson, O. & Woodell, 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*. – Meddr Grønland, Biosci. 34, 60 pp. Copenhagen 1990-11-8.

The population ecology of three species in northwest Greenland (*Dryas integrifolia, Silene acaulis* and *Ranunculus nivalis*) was studied in two consecutive seasons. Flowering phenology, population structure, flowering biology (including numbers of pollen grains per anther, germinated pollen grains per stigma, ovules per gynoecium, seeds per fruit), pollination and insect activity were the main features investigated. They were related to the micro- and macroclimatic conditions.

The results can be summarized as follows:

1. The unpredictability of the quality and length of the growing season makes the success of the reproductive cycle (i.e. production of mature seeds) very uncertain.
2. There are seedlings at the studied sites of the three species.
3. Most of the seedlings disappear.
4. Population structure results indicate that seedlings become established in at least some years, but input of new individuals is episodic.
5. Of the three species studied, *R. nivalis* allocates most resources to reproduction.
6. Percentage normal pollen varies mostly between plants, less between days and sites (*D. integrifolia*).
7. All three species are self-compatible.
8. Full seed set is obtained only after insect visits.
9. In *S. acaulis* seed set may be limited by the number of pollen grains reaching the stigmas.
10. The flowers provide food (pollen and nectar) for the insects. They also provide shelter, warmth, and a mating place for them.
11. There are sufficient insect visits per flower to ensure seed set, except possibly in *S. acaulis*.
12. About 1% of total pollen grain production is found as germinated pollen grains on stigmas.
13. The utilization of pollen and stigmas varies between the three species. *R. nivalis* is the most efficient, whereas *D. integrifolia* is the most extravagant.
14. A cold and rainy summer in 1976 resulted in conspicuously lower seed set in 1977 in spite of the latter summer being comparatively dry and warm.
15. A 'reproductive budget' quantifying the various steps in the reproductive cycle is presented.

Marianne Philipp, Institute of Plant Ecology, University of Copenhagen, Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark, Jens Böcher, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark, Ole Mattsson, Institute of Plant Physiology, University of Copenhagen, Øster Farimagsgade 2A, DK-1353 Copenhagen K, Denmark, Stanley R. J. Woodell, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford, OX1 3RA, England.

Introduction

The ability of arctic plants to survive and reproduce in what appears to be a highly unfavourable environment has attracted the attention of botanists for many decades. Though the arctic environment is harsh, arctic floras are not necessarily depauperate. Greenland, for instance, has over 500 species of higher plants. Their survival must depend on successful reproduction.

Early workers, e.g. Warming (1886, 1920), Jessen (1911) made valuable general observations. They all stressed the importance of vegetative reproduction. Self-pollination has also been reported in some species (Hagerup 1950, 1951), and T. W. Böcher (1972) has discussed the importance of apomixis. In more recent works the general view has been expressed that vegetative propagation is more important than sexual reproduction (Billings & Mooney 1968, Bliss 1971). Bliss states: "Though many tundra plants produce fruits and seeds, many others set little seed, especially in more severe habitats." Billings (1974) pointed out that the number of viable seeds may be low even in a relatively "good" year (a point to which we shall refer later). He noted that many arctic and alpine plants do produce seeds rather regularly and in apparent abundance. Chapin & Shaver (1985) commented that successful reproduction by seed is infrequent in the Arctic, but went on to point out that there is considerable allocation of resources to sexual reproduction, and that if one considers the time scale of many centuries sexual establishment is probably as important in the Arctic as it is elsewhere. Callaghan & Emanuelsson (1985) have also agreed that sexual reproduction may be important for tundra plants. More recently Bliss (1988) has also acknowledged the importance of sexual reproduction in the Arctic.

Other recent work has been concerned with pollination (Hocking 1968, Kevan e.g. 1970 et seq.), seed dormancy and germination (Amen 1965, 1966, 1968), and with seedling establishment (Chapin & Shaver 1985).

While all these and other studies have greatly enhanced our knowledge of the reproductive biology of arctic plants, there is still a need for an integrated study of the life histories of individual species. Our project was aimed at providing this. The study area chosen was around the Arctic Station of the University of Copenhagen at Qeqertarsuak/Godhavn, on Disko Island, West Greenland. Here the flora and fauna are well known as the result of many years of visits and study by a succession of biologists.

Most relevant to our investigation is the account of the flora of Disko Island and the adjacent part of the mainland, in a little known paper by Porsild (1920). Indeed had his work been more widely known, the misleading view of sexual reproduction in the Arctic, which was prevalent until recently, might not have held way. Porsild made notes on the phytogeographical and ecological relations of the species and on their flowering and fruiting. Some of his observations are summarized in Table 1. He found that 71.9% of the species seeded regularly and 12.3% did so occasionally. An analysis of his information on geographical affinities and snow cover in winter shows that those plants with more "northern" affinities are more likely to set seed if uncovered by snow in winter than those of southern distributions (38% as compared with 3%). Nonetheless, 46% of all the species seen to set seed by Porsild were of "southern" or "temperate" range. However, of the southern element 28, or 10.4% were not seen to set seed, whereas only 2, or 0.7% of the "northern" element failed to do so.

Porsild's results might lead one to the conclusion that the climate of Disko is unusually favourable, but a study by Sørensen (1941) on Eskimonæs in NE Greenland supports Porsild's data. Of the 138 species tested by Sørensen, 99 had ripe seeds. The species included *Dryas integrifolia, Silene acaulis, Chamaenerion latifolium* and three species of *Pedicularis*, all of which are common on Disko. He recorded germination in 62, or 44% of the species. This is reinforced by the observations of Aleksandrova (1988) in the Soviet Arctic, more specifically on the island of Zemlya Aleksandra, at over 80° N. Here of 22 species in the 1959 season, she recorded three as setting seed in the same year, 12 setting seed in the second year and only 7 failing to set seed.

Our study extended over two seasons, 1976 and 1977. The selection of species was made with the object of obtaining a spread of flowering throughout the season and to sample a range of habitats. The species chosen are common and widespread on Disko and have a wide range in Greenland; indeed some of them are widespread in the Arctic generally. Some important families and genera were not included, because of limitations of time and personnel. We feel that the family Ericaceae, which is very well represented in the area, merits attention in the future.

The species chosen were *Silene acaulis, Papaver radicatum, Dryas integrifolia, Chamaenerion latifolium,*

Table 1. Seed set in plant species of the Disko Island region (data from Porsild 1920).

Distribution type	High arctic	Northern	Wide range	Southern	Non-arctic
Setting seeds or spores	4	40	84	72	30
Not seen to set seed	–	–	4	9	21

Ranunculus nivalis, Bartsia alpina, Potentilla vahliana and four species of *Pedicularis (P. lanata, P. hirsuta, P. lapponica* and *P. flammea)*. In this paper we deal with *Dryas integrifolia, Silene acaulis* and *Ranunculus nivalis*. In subsequent papers we shall consider *Chamaenerion latifolium* and *Pedicularis* spp.

Our aim was to ask a series of questions about these species' sexual reproduction, bearing in mind the fact that any answers we might obtain are applicable only to a rather limited range of populations in a small area. Nevertheless, we hoped that we would be taking a further step toward understanding the reproduction and population dynamics of arctic plants.

The questions were:

1. To what extent do these species reproduce sexually?
2. If they reproduce sexually are the seeds the result of inbreeding or outbreeding or both?
3. Are there adequate numbers of pollinators or are they scarce enough to limit seed production?
4. What are the quantitative relations between pollen, ovules, fertilized ovules, mature seeds, seedlings, young plants and flowering plants?
5. What influences do the climate and other environmental factors have upon reproduction of the species?

Site descriptions

The sites chosen were all within 2 km of the Arctic Station. The choice was based on the presence of a sufficiently large population of one or more of the species to be studied.

Site 3 (Fig. 1):
A very gentle (3°) slope in the Lyngmarken, an extensive valley sheltered to the north, west and east by steep slopes, altitude c. 20 m. The soil is peaty, up to about 20 cm deep, over a coarse gravelly substrate which is exposed in places. Large polygons are apparent and in the exposed gravel small ones also. The vegetation of these open areas indicates that some of them are the products of recent erosion whereas others are being recolonized. The vegetation elsewhere is heath, dominated by *Empetrum nigrum, Betula nana, Vaccinium uliginosum* and

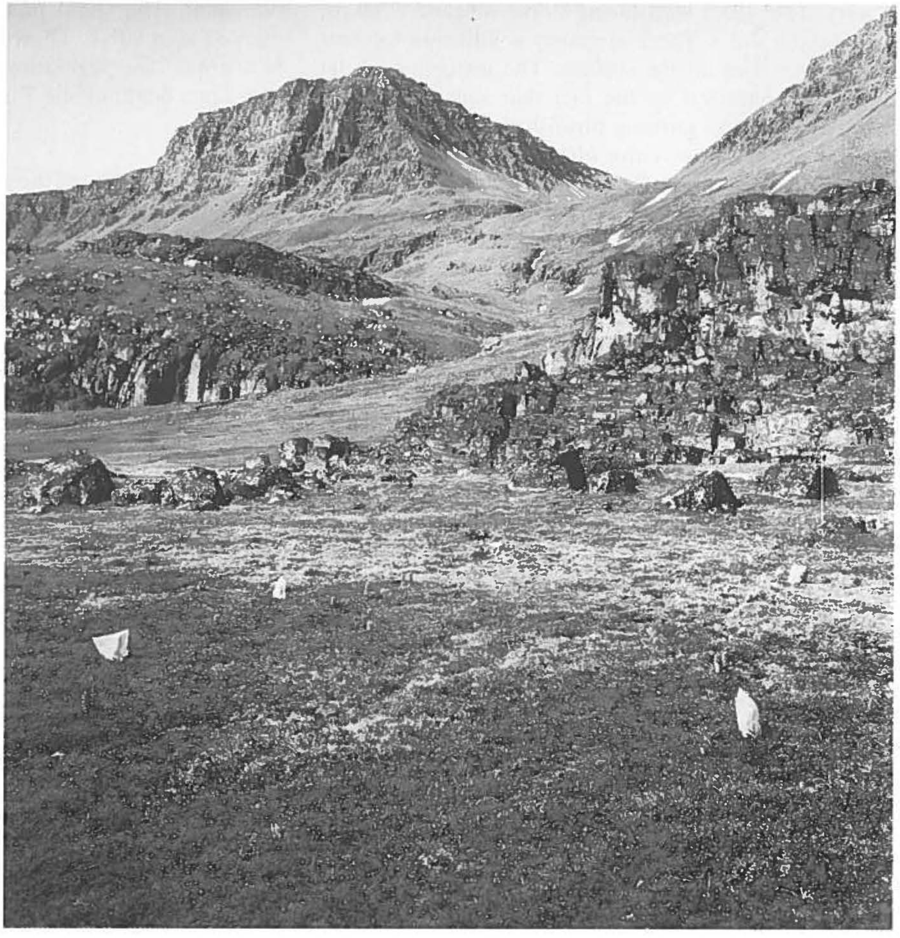


Fig. 1. Site 3, looking NNW. The polyamid bags exclude insects from flowering *Silene acaulis*. In the background Apostelfjeld.

in places *Salix glauca.* Other abundant species are *Polygonum viviparum, Carex rupestris, Dryas integrifolia* and *Silene acaulis,* and *Pedicularis lanata, P. hirsuta, P. flammea* and *P. lapponica.*

Site 4 (Fig. 2):
A series of little hollows and hummocks on level ground at the southeast end of a small lake, altitude 50 m. The hummocks are densely clothed with *Salix glauca,* hollows between them are dominated by *Carex* spp. and bryophytes. The substratum is very soft and peaty. *Ranunculus nivalis* grows mainly on the steep sides of the hummocks, with its flowers partly protected by and partly protruding through the willow branches.

Site 5 (Fig. 2):
At the western end of the same lake. Water drains from the lake through a series of pools, from the lowest of which flows a small stream. *Ranunculus nivalis* is on the steep, almost vertical banks of these pools, mainly on the west-facing banks. These banks are clothed with *Salix glauca,* beneath which is a dense bryophyte cover. The whole area is constantly wet.

Site 6:
A very steep (25°) west-facing slope, altitude c. 80 m, overlooking site 3. There are many solifluction terraces and loose stones on the surface. The instability of the slope is emphasized by the fact that some plants are dying upslope and growing downslope. The vegetation is dominated by *Vaccinium uliginosum, Empetrum nigrum, Betula nana* and *Dryas integrifolia,* with frequent plants of *Rhododendron lapponicum.* Total cover is about 70%, and *E. nigrum* is more abundant on the upper slope with *D. integrifolia* being more prominent on the lower slopes.

Site 7:
A highly exposed SW slope (8–10°) below the lower slopes of the Lyngmarksfjeld, altitude 165 m, and open to the sea from SW to NW. The soil surface is gravelly with prominent narrow downslope stripes. Beneath the surface the soil is silty and compact, and bare rock is exposed over about 15% of the area. Vegetation cover is also about 15%, and it forms small patches consisting of mosaics of *Salix glauca, Dryas integrifolia,* some *Cassiope tetragona* and *Vaccinium uliginosum,* with many bryophytes and lichens. The bryophytes are especially associated with the willow. Lichens grow abundantly over the bryophytes and especially over the cushions of *D. integrifolia.* The roots of the plants are exposed upslope and young shoots grow downslope. The whole area is being actively eroded. Within some of the vegetation patches are areas of bare or almost bare peaty soil, with obvious plant remains in them. In these areas young plants and seedlings of *D. integrifolia* and *Silene acaulis* are occasionally found. *D. integrifolia* is most prominent in the smaller patches, where it is often the only angiosperm. It is much less abundant in the larger, more vigorous patches. Older plants of *D. integrifolia* are undergoing disintegration. *S. acaulis* is scattered, almost exclusively in the larger patches of heath.

Site 8 (Fig. 2):
This comprises the banks of a small rivulet running SW within the larger, steep-sided valley of the stream which it feeds. The rivulet is fed partly by a constantly warm (9°C) stream. At an altitude of 105 m, it is really a series of shallow pools linked by little waterfalls, or mossy slopes through which the water trickles. *Ranunculus nivalis* grows on the steep banks and the mossy slopes in a narrow band along the stream. The most common associated species are *Alchemilla glomerulans, Chamaenerion latifolium* and *Gnaphalium norvegicum,* and on both sides there is heath dominated by *Empetrum nigrum.*

Site 9 (Fig. 3):
Above site 7, altitude 185 m. A gentle (5°) slope facing SSW. Open heath dominated by *Cassiope tetragona,* with about 40% vegetation cover. *Dryas integrifolia,* with about 10% cover is a major component of the vegetation and *Vaccinium uliginosum* is the other main dominant. The slight downslope movement is not so marked as at site 7. There are narrow soil stripes in the bare areas. The vegetation is intermediate between the very open heath of site 7 and the closed heath of site 3.

Site 12:
A V-shaped hollow in the rocks above the coast, sloping at about 8–10°. It is sheltered by a small cliff. Much water drains through the area making bare channels. There is a series of stripes of bare silty soil alternating with vegetation dominated by *Salix arctophila* with *Carex rupestris, Silene acaulis* and abundant mosses. A small amount of *Salix herbaceae* indicates late snow lie. Three species of *Pedicularis* are abundant: *P. flammea, P. hirsuta* and *P. lapponica.*

Site 13 (Fig. 4):
A gentle (8°) slope facing NNW, altitude 170 m. *Cassiope tetragona* heath developed on prominent solifluction lobes with plenty of bare ground on the lobes

Table 2. List of sites where the three species were studied.

Site	*D. integrifolia*	*S. acaulis*	*R. nivalis*
2			x
3		x	
4			x
5			x
6	x		
7	x	x	
8			x
9	x		
12	x		
13		x	

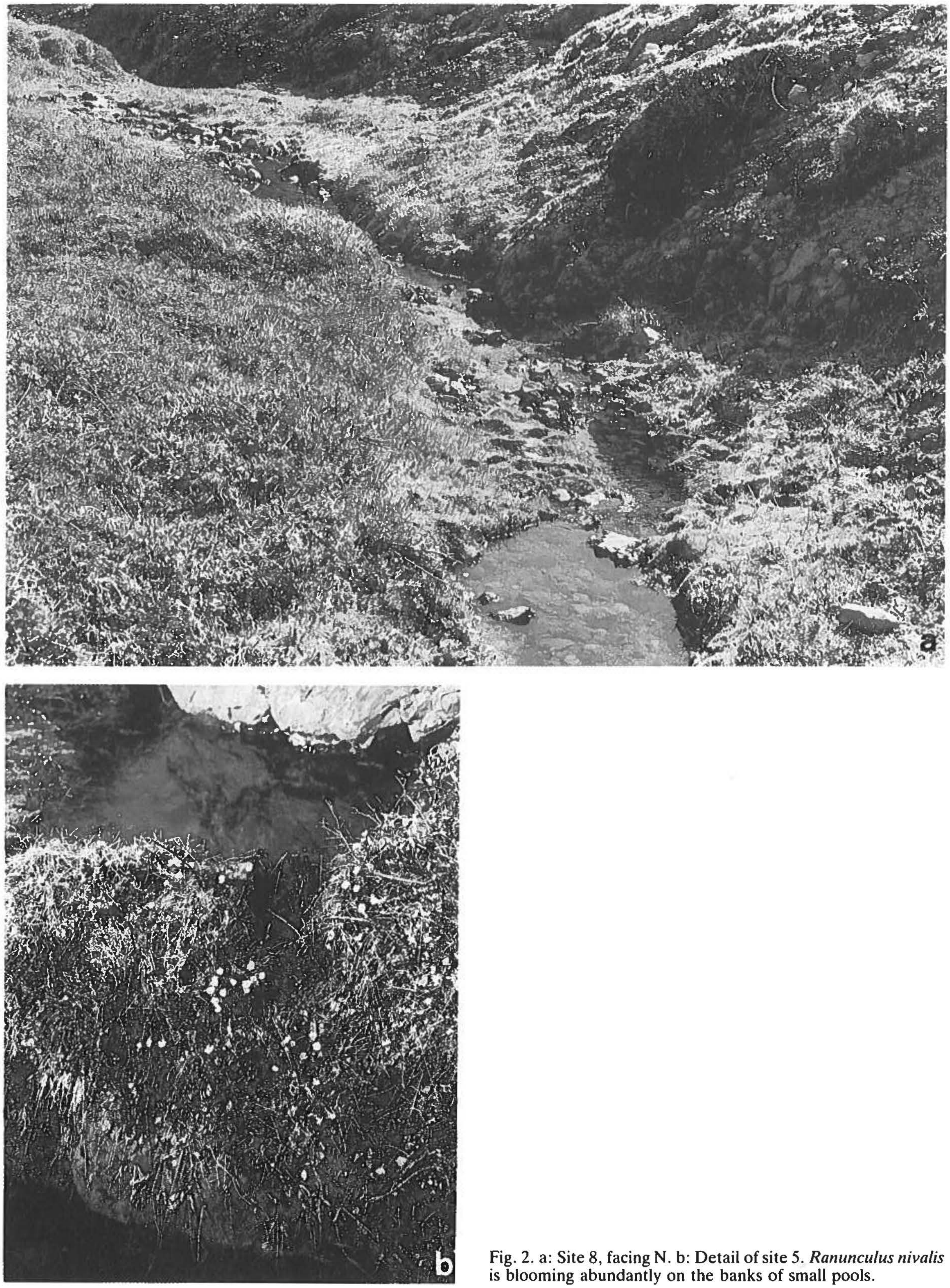


Fig. 2. a: Site 8, facing N. b: Detail of site 5. *Ranunculus nivalis* is blooming abundantly on the banks of small pools.

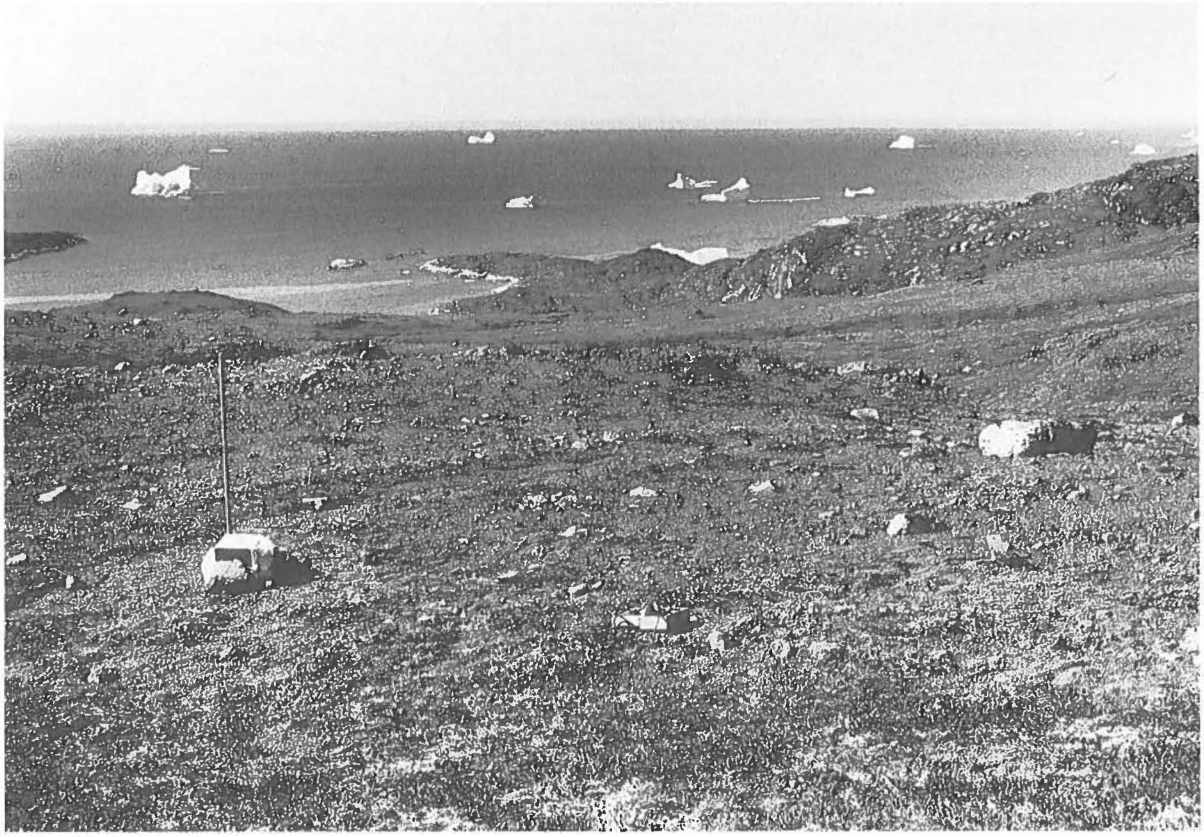


Fig. 3. Site 9, looking SSW. A microclimate station in front, left.

themselves. These are surrounded by *C. tetragona* and *Salix glauca*. *Silene acaulis* is mainly on the bare or nearly bare soil, which consists of a poorly drained peaty silt over a gravel substrate, up to 40 cm deep. Rocks protrude through the surface all over the site.

Table 2 gives a survey of which species are studied at which sites.

General climate

Godhavn has a low arctic climate with an annual mean temperature of -3.2°C, an annual mean precipitation of 381 mm and a July mean temperature of 8.0°C (Fristrup 1981). Because of the benign influence of the West Greenland Current in combination with the southerly exposure of the Godhavn area, the local climate is quite favourable and the flora is relatively rich. It includes many species with a southern distribution in Greenland together with real arctic species (Porsild 1920), and both oceanic and continental floral elements are found (T. W. Böcher 1963). On the other hand the weather at Godhavn varies greatly from year to year (J. Böcher 1976).

The weather was indeed different during the two summers (Table 3). In 1976 June was dry and sunny, while July and August had highly changeable weather with little sunshine and periods of heavy precipitation. In 1977 the reverse was the case, with rain in June and dry and sunny weather during July and August. July 1977 had more than three times the amount of sunshine of July 1976 and a mean temperature of 10.0°C as compared with 6.3°C in 1976. Godhavn is an exposed place, but the mean wind speed was not significantly different between the two summers.

We attempted to express the possibility of insect pollination occurring on a particular date by a single value. On the basis of initial observations of insect behaviour in relation to climatic factors (see below) we considered that there was a positive correlation between the amount of sunshine and insect activity, but also that maximum temperatures above a certain value, say 10°C, must have a positive effect. On the contrary, wind and rain have a negative effect. Therefore, for the periods during which pollination was observed, daily "weather

Fig. 4. Site 13, looking E.

indicators" (WI) were calculated using a simple formula:

$$WI = Hsun + Tmax\ (>10°C) - W - P$$

where Hsun is the number of hours of sunshine, Tmax is maximum temperature, W is mean wind speed in m/sec (approximately, converted from the Beaufort Scale) and P is precipitation in mm. The weather indicators are shown as histograms in Figs 13 and 18.

Subsequent observations proved that the weather indicators and insect activity were well correlated.

Methods

Reproductive data

Number of flowers per individual:
The number of flowers was counted at regular intervals throughout the flowering period, either on marked plants or as total flowers in marked areas within each site.

Number of anthers and carpels/ovules per flower:
Counts of numbers of anthers and carpels/ovules per flower were made using flower buds fixed in 50% ethanol (see below). Additional counts of ovules and of

Table 3. Summary of weather conditions in Godhavn, comparing the summers of 1976 and 1977. (Annual means of temperature and precipitation in June, July and August: 5.1°C, 8.0°C, 7.2°C, and 33 mm, 47 mm, 45 mm).

	1976			1977		
	June	July	August	June	July	August
Temperature (mean, °C)	4.7	6.3	4.5	3.6	10.0	7.9
Sunshine (total hours)	256	202	116	143	658	258
Precipitation (mm)	5.1	57.8	75.8	87.7	9.9	3.7
Wind-speed (mean, m/sec.)	3.4	3.5	3.8	3.1	4.0	4.1

fertilized ovules/carpels were carried out on opened and withered flowers.

Total number of pollen grains and number of morphologically normal pollen grains:

Undehisced anthers were sampled at three or six day intervals at the different sites. Three buds from each of ten plants were chosen on each sampling day and fixed in 50% ethanol. The low strength of the ethanol was chosen in order to reduce the rate of dehydration and the chance of dehiscence of the immature anthers. Assessments of the number of morphologically normal pollen grains and abnormal pollen grains were made using carmine-glycerol preparations according to a standard procedure. Three or more anthers from some of the sampled buds were used. A single anther was dissected into fine pieces in a standard drop of carmine-glycerol saturated with sucrose in a dissecting microscope. The material was then carefully mixed, spread out on an approximately 15 x 15 mm square field and covered by a 20 x 20 mm coverslip put down vertically, allowing some time for the material to sediment. Fifty fields in a predetermined pattern, corresponding to 30.066% of the coverslip area, were analyzed in the microscope, and the number of grains per anther of the two categories were calculated. Total number of grains were obtained by summation. In preparations where the total was below 200 an additional fifty fields or the whole preparation were counted.

Number of germinated pollen grains per stigma:

At approximately three day intervals stigmas from three open flowers from each of ten individuals were fixed in ethanol-acetic acid (3:1). Some of the fixed stigmas were treated with 8N NaOH (3 – 6 hours at 40°C) and stained in leuco-aniline blue. The whole stigmas were mounted in leuco-aniline blue with 10% glycerol added, and the number of germinated pollen grains was assessed using a fluorescence and/or phase contrast microscope.

Number of fruits/seeds per flower:

At the end of the season fruits or seeds were collected from all the species and the number of non-fruiting flowers was noted where possible. The fruits were dried or fixed in 50% ethanol and later counted in the laboratory.

Isolation experiments:

These were carried out by covering unopened flowers with bags of polyamid net (mesh width 200 µm). Some of the isolated plants received no further treatment. Others were emasculated before isolation and not handled again. Yet other plants were actively self-pollinated or cross-pollinated following isolation and sometimes emasculation. A number of marked non-treated plants with ripe seeds was collected as references for comparison.

Development of the flowers:

The development of flowers was studied from bud to fruiting stage. The time of anther dehiscence and stigma receptivity, the positions of anthers in relation to stigmas, the number of days during which the flower was open, and the time from start of flowering to fruiting were noted.

Climatic data

These were obtained from the Meteorological Institute, Copenhagen.

Microclimatic observations

Measurements of temperature were carried out in the chosen sites or in similar situations nearby in fine weather when differences in the climate near the ground were conspicuous. In some cases temperature measurements were combined with measurements of wind speed 2 m above ground, light and relative humidity close to the ground. Temperature was measured with a Grant miniature temperature recorder. In most cases "normal" thermistor probes were used (thermistors confined in reflective stainless steel tubing, 3 mm wide), but for flower temperatures a thinner 1 mm wide needle-shaped probe was used in 1976. In 1977 it was replaced by a flexible, thread-like probe which could follow the natural movements of the flowers (Fig. 5). In exposed situations the probes were not artificially shaded. It was considered that the effect of shading the micro-sites might disturb the natural situation more than letting the sun heat the steel tubing. The consequent temperature rise amounted to no more than a couple of degrees as compared to a shaded probe. Relative humidity was measured with simple hair-hygrometers (Lambrecht) placed on the ground. Light and wind speed were measured by means of a luxmeter and a cup-anemometer.

Entomological observations

Two methods were used to obtain quantitative data. 1) The insects observed in flowers along a fixed route were recorded at regular intervals, mostly one or two hours. 2) The insect visits to a small and easily observed group of flowers were recorded during time intervals (usually 10 or 15 minutes each hour). In the last case all landings of insects in flowers were counted, even when performed repeatedly by the same individual in the same flower.

Population observations

Population structure was investigated by selecting quadrats, usually 4 x 4 m, using random number tables. Within each quadrat the largest and smallest diameter of each plant was measured, and the whole area was

Fig. 5. a: *Potentilla vahliana* at site 7. A thread-like thermistor probe is placed in the centre of a flower. b: *Spilogona* sp. in flower of *P. vahliana.*

searched for small plants and seedlings. In small localities quadrats of 1 x 1 m were placed in rows across the area. Harvesting of plants for dry weight measurements was carried out by careful excavation of each plant using a trowel. Any soil remaining on the plants was carefully washed over a sieve to retain root fragments. The plants were then divided into their components, dried in an oven at 85°C to steady weight, and weighed.

Results

Dryas integrifolia

Morphology

D. integrifolia is a dwarf shrub (chamaephyte) forming prostrate cushions. The leaves are c. 1 cm long, leathery, with revolute margins.The flowers are lateral, solitary, on c. 5 cm long pedicels and c. 2 cm in diameter (range 1.5 – 2.6). They have 8 – 11 creamy white petals. The average numbers of various flower parts are seen in

Table 4. Mean numbers of various parts of flowers of *Dryas integrifolia* at different sites (number of samples in brackets).

Site	Stamens/flower	Pollen/anther	Carpels/flower	Pollen/flower	P/O-ratio	% normal pollen
6	91.7 (18)	2123 (17)	72.2 (160)	194641	2694	80.7
7	75.0 (3)	2621 (10)	52.0 (3)	196575	3773	79.4
9	86.7 (19)	2080 (23)	70.0 (33)	185278	2647	80.9

Table 4. There is a correlation between the number of stamens and number of carpels ($y = 1.04 + 0.71x$; $r = 0.76$). Each flower has a ring-shaped nectary around the gynoecium. The achenes have elongated, persistent styles with long lateral hairs which are an aid to wind dispersal. The species has no means of vegetative propagation.

Flower phenology (Fig. 6)

The buds develop the autumn before the flowering season (Jessen 1913, Sørensen 1941). At the sites each flower was on average open from 7 to 9.5 days (Table 5). Following the opening of the bud which takes one day, a few anthers start to open. By the third day approximately 20 anthers will have opened. The remaining anthers open during the following two days during which they bend towards the petals. We found protandrous flowers only, although Warming (1886) mentions that protogynous flowers can be found. After the petals have withered the sepals move to an upright position and cover the gynoecium.

In 1976 the flowering period for each population was about three weeks (Table 5). Sørensen (1941) recorded a flowering period of 23 days in NE Greenland. As described by Warming (1886), hermaphrodite and male flowers may be found on the same plant. In 1976 the number of open flowers was counted within marked areas on different dates (Fig. 7). At site 6 the male flowers appeared later than the hermaphrodite flowers, but this did not seem to be true of sites 7 and 9 (Fig. 8). On July 4 1976 a sample of 20 plants from site 6 had 15% male flowers (Table 6). At sites 7 and 9 the percentage of male flowers varied throughout the season, but it was consistently higher at site 9 than at site 7 except at the very end of the season. In 1976 the flowers were heavily predated by caterpillars which usually ate both gynoecium and stamens (Fig. 9). This damage occurred in 68% of the flowers at site 7 and 71% in site 9 in the first week of July, but during the flowering season the infestation declined (Fig. 8). In 1977 there was no predation – not a single caterpillar could be found! M. Ahola, (Koski, Finland) identified the larvae as *Sympistis labradoris* (Staudinger), which has not been recorded from Greenland before, but according to Ahola (in litt.) it may be regarded as a subspecies of *S. zetterstedtii* (Staudinger), which is common in the Godhavn area.

Table 6. Sex of flowers on *Dryas integrifolia* plants at site 6, July 4 1976 (herm. = hermaphrodite).

Sex of plant	No. of plants	Total no. of flowers	% flowers herm.	% flowers male
herm. + male	9	103	78	22
herm.	10	90	100	0
male	1	7	0	100

Table 5. Length of flowering period and anthesis of *Dryas integrifolia* at three sites in 1976 (number of observed flowers in brackets).

Site	Flowering period	No. of days	Length of anthesis
6	19/6–13/7	24	7 days (10)
7	27/6–17/7	20	9 - (10)
9	3/7–24/7	21	9.5 - (10)

Pollen production

Pollen counts are summarized in Fig. 10. A general feature shown by the histograms is that of a pronounced variation in all parameters and sites, and there is no clear-cut difference between the sites. In order to study the components of variation an analysis of variance at four levels with three items in each was carried out on those counts which fulfil the requirements of the statistical model. Table 7 shows the estimates obtained of the various components. It appears that the variance due to variation between anthers and plants is much larger than that due to sites and days. Thus, the ecological differences between sites and the climatic changes between periods of sampling seem to be minor factors in creating variability in comparison with local genetic and developmental factors. In this study it has not been possible to specify the relative importance of genetic and environmental factors.

The relation between the mean percentage of normal pollen in anthers from the same bud and the corresponding coefficient of variation (CV = sample standard deviation expressed as a percentage of the sample mean) may give a little information on the question

Fig. 6. Flower phenology of *Dryas integrifolia*. a: Male flowers. b: Various stages of hermaphrodite flowers.


a
b

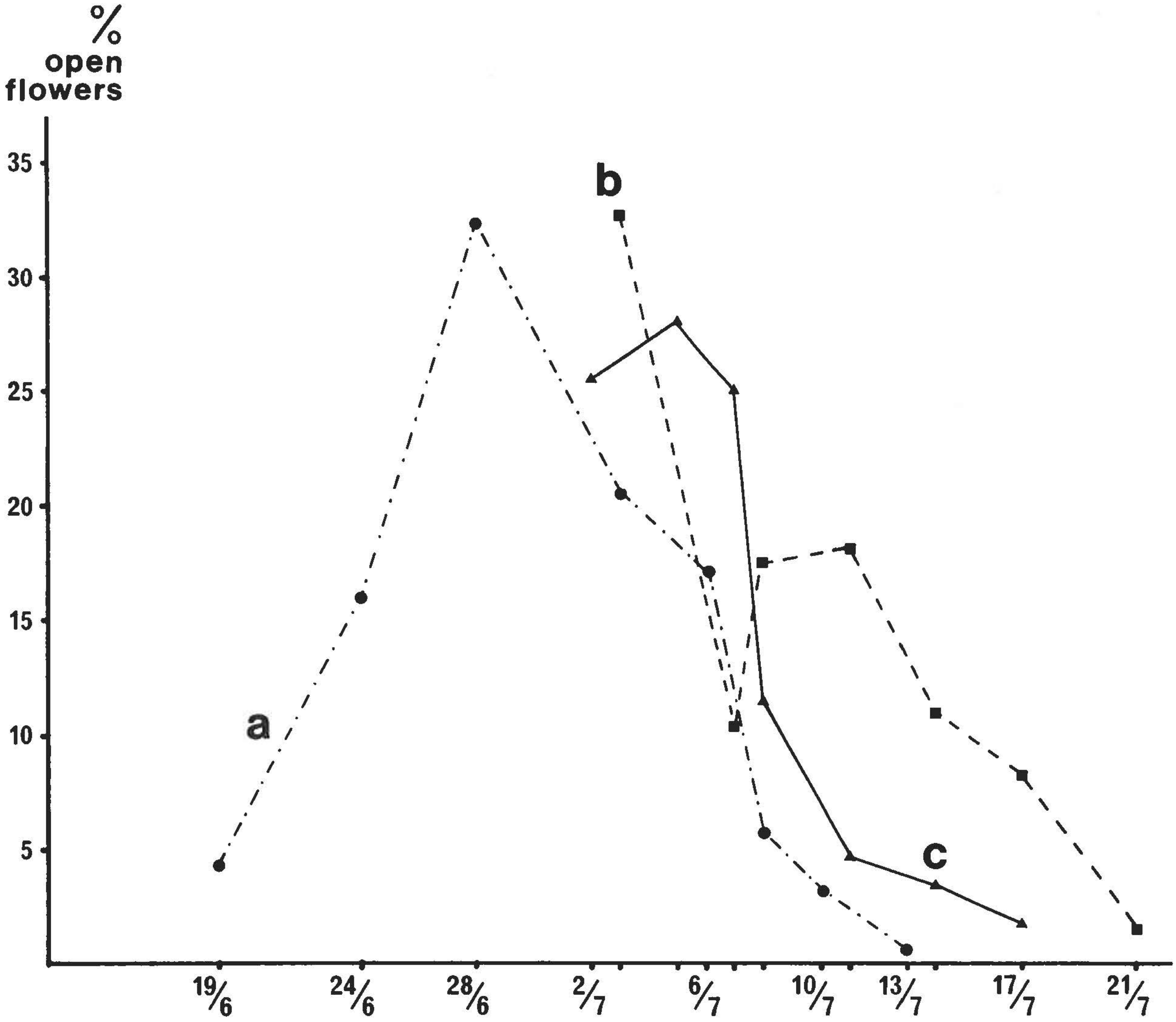


Fig. 7. Flower phenology of populations of *Dryas integrifolia*. a: Site 6. b: Site 7. c: Site 9.

based on the following considerations. In many cases where a reduction in pollen fertility is known to be due to structural hybridity all anthers from plants with that particular genotype will produce the same proportion of sterile pollen grains. This proportion will often be relatively unaffected by environmental changes, and any variation in the fertility percentage is expected to be due to statistical fluctuations, and not to show any correlation with the CV. A different picture is expected in cases where a reduced fertility is caused mainly by ad-

Table 7. Pollen production and fertility in *Dryas integrifolia*. Analysis of variance at four hierarchical levels with three items in each.

	Estimate of variance components		
	Total no. of pollen grains	No. of normal pollen grains	% normal pollen grains
Between sites	$F(1.6)_{p=0.28}=1.57$	$F(1.6)_{p=0.60}=0.55$	$F(1.6)_{p=0.70}=0.37$
Between days	$(\sim 0)^2$	$(148)^2$	$(\sim 0)^2$
Between buds from one plant*	$(580)^2$	$(584)^2$	$(0.11)^2$
Between anthers from one plant	$(421)^2$	$(456)^2$	$(0.12)^2$

*) Variance components significant at $p < 0.001$.

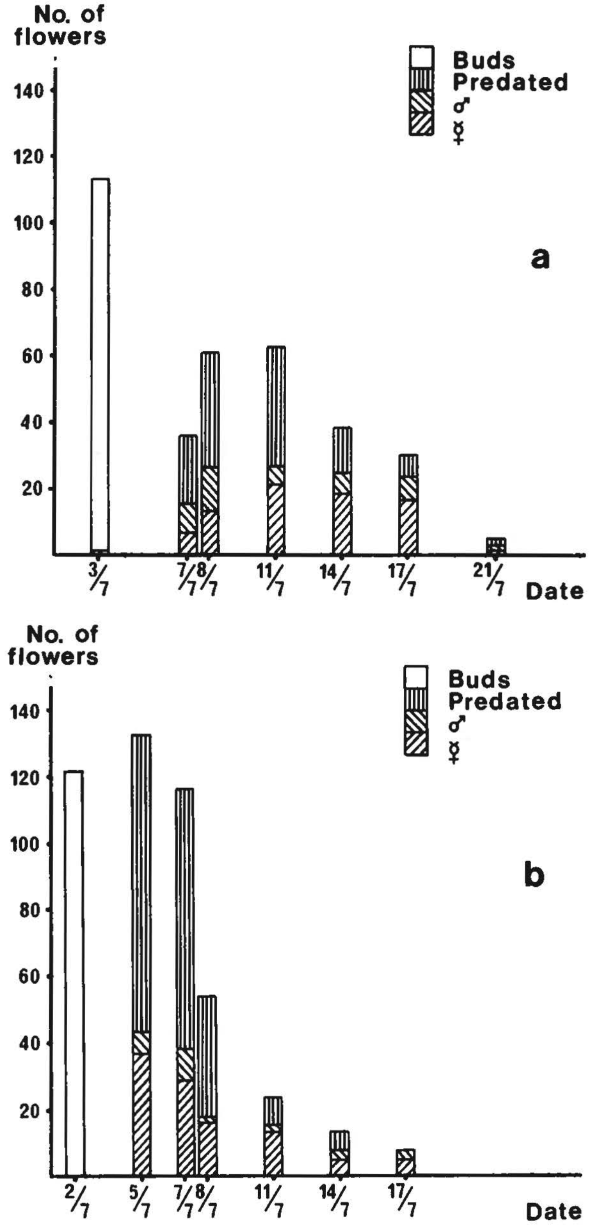


Fig. 8. Predation on flowers of *Dryas integrifolia*. a: Site 7. b: Site 9.

verse environmental conditions. The fertility percentage will most likely vary from anther to anther and from bud to bud, and some correlation between the mean and the corresponding CV is expected. These reflections do not permit any rigorous distinction between genetic and environmental factors. A number of sterility genes have been described which show variable expression as a function of various environmental factors (Heslop-Harrison 1972).

The relation between the mean percentage of normal pollen grains and the corresponding CV from the anthers in all the buds studied from the previous sites is shown in Fig. 11 a. For all three sites there is a significant correlation between the two parameters. This is taken as an indication of a pronounced environmental influence on pollen fertility, but this interpretation requires additional comments. In *D. integrifolia* flowers there is a gradient of developmental stages from the peripheral to the central anthers, and the various stages of pollen development exhibit variable sensitivity toward changes in the external environment and possibly in internal conditions, such as differential allocations of nutrients. Moreover, the analyzed anthers were picked at random so a possible age dependent variation could not be studied.

Analogous considerations must be made for explaining the relation between the average total numbers of pollen grains in a bud and the corresponding CV. There is no significant correlation between the data points in Fig. 11 b, but this should hardly be explained merely as a stronger genetic influence on pollen numbers. In general, pollen numbers reflect anther size which varies according to both the size of the plant and their position on the plant. In *D. integrifolia* the innermost and outermost anthers in a flower tend to be smaller than the middle one.

A possible correlation between the percentage of normal pollen grains and the total number of grains was studied, but a positive correlation was found only at site 6 (r: coefficient of correlation = 0.513). At the other sites 'r' was very close to zero. In addition, no correlation was found between numbers of stamens per flower and pollen production or fertility.

Pollen germination

From the counts of the total number of germinated pollen grains per stigma and the calculated proportion of carpels being pollinated (i.e. having one or more germinated pollen grains on the stigma) the relation between these two measures of pollination was studied (Fig. 12). It was not possible to find a mathematical model that describes the relation in a satisfactory way. The possibility of describing the basal mechanism of pollination by means of a Poisson distribution was considered. The *D. integrifolia* flower with its separate carpels which can be pollinated over a long period meets the fundamental requirements for a possible Poisson mechanism. With a few exceptions the distribution of germinated pollen on the stigmas in individual flowers does fit a Poisson distribution at a 5% level. When all flowers in a population are considered as a whole, however, there is clearly a tendency towards a systematic deviation. The observed mean numbers of pollen that lead to a certain percentage of pollinated carpels are always higher than the mean calculated from a Poisson distribution. This deviation may most likely be explained by a variable clustering of the pollen grains, either because the grains were deposited in small clumps or because deposition occurred more than once

Fig. 9. a: Flowers of *Dryas integrifolia* more or less eaten by larvae of *Sympistis labradoris* (the upper right flower unaffected). b: A fully grown larva of *S. labradoris*. c: Young larva of *S. labradoris* in flower of which the interior is eaten.

during the receptive period of the carpel. Casual observations on unfixed stigmas show that the attached grains occasionally occur in clumps, but competition for available space on the stigma surface is not likely to happen. In one instance more than one hundred germinated pollen grains were observed on a stigma. However, the feasibility of describing the distribution of grains within a flower by a Poisson distribution indicates that in general, there is very little clustering of germinated pollen grains.

Fig. 12 indicates that in cases where all carpels in a flower are pollinated there is typically a mean number

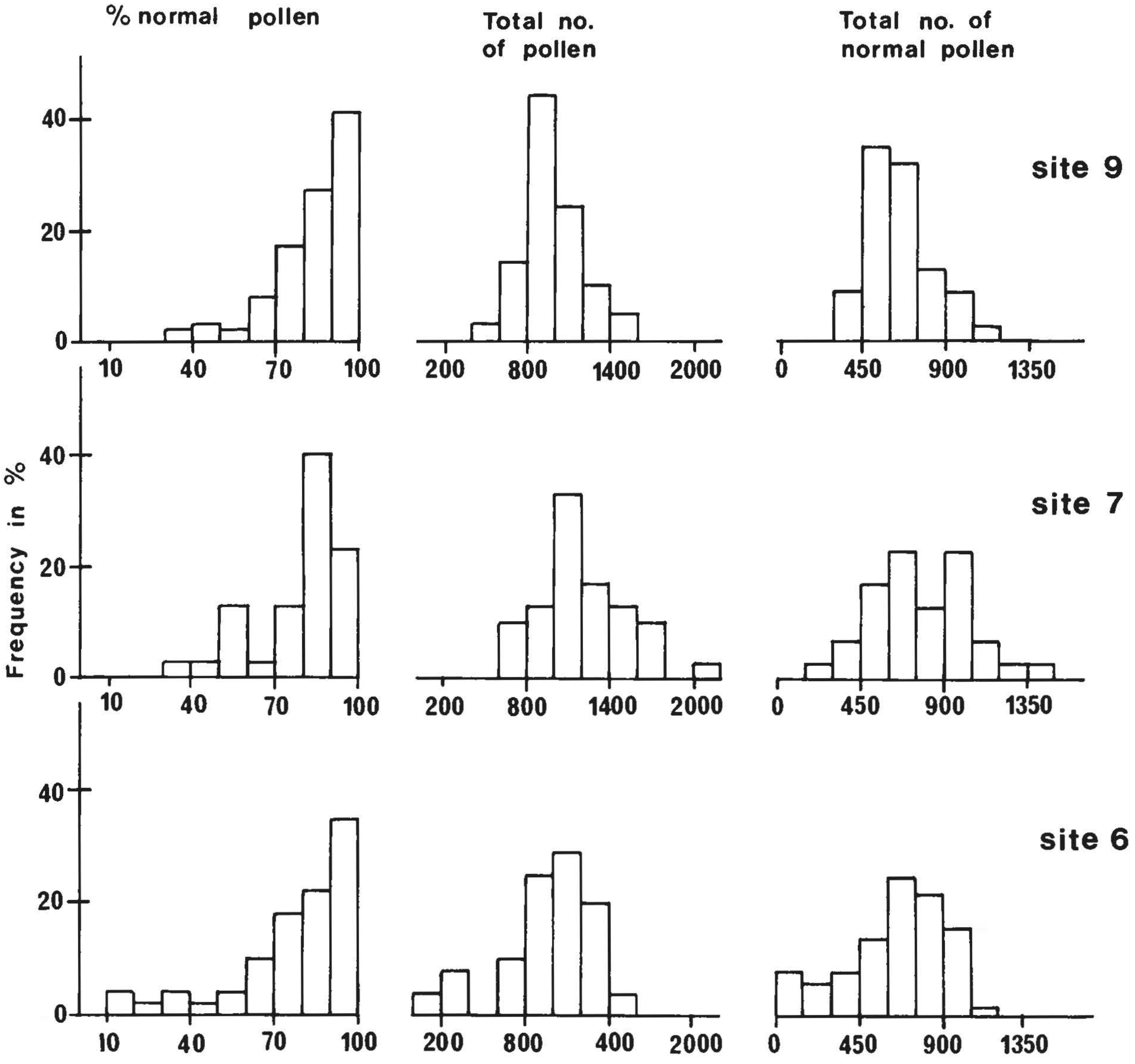


Fig. 10. Total number of pollen grains and number of morphologically normal pollen grains per anther in *Dryas integrifolia* populations.

of 10–20 germinated grains per carpel. Since the pollen/ovule ratio on the average is approximately 3000 (Table 4) a figure of 20 grains per carpel results in only approximately 0.7% of the total number of pollen grains being 'needed' in order to secure pollination of all carpels. Even if the reduced pollen fertility is taken into account the 'necessary expenditure' is still less than 1% of the number of normal pollen grains per flower. It must be pointed out, however, that the counted number of germinated grains is only a minimum estimate of the number deposited on the stigma. The actual germination pecentage of the deposited grains is not known.

In Fig. 13 the seasonal changes in the percentage of pollinated carpels are depicted along with the corresponding 'weather indicators' (p. 8). The course of the pollination curves can be interpreted in general as the combined effects of changes in the number of flowers during the flowering period in the three sites and fluctuations in weather conditions. The rise in the percentage of pollinated carpels from June 27 to July 2 at site 6 shows the beginning of the flowering period at this site. During this period the weather changed in a negative direction and then fairly rapidly in a positive direction in the following week. These changes were paralleled, after about two days delay, or 'reaction time' by first a decrease in the percentage of pollinated carpels at site 6 and 7 and then an increase at all three sites. The abrupt change in the weather in a negative direction from July

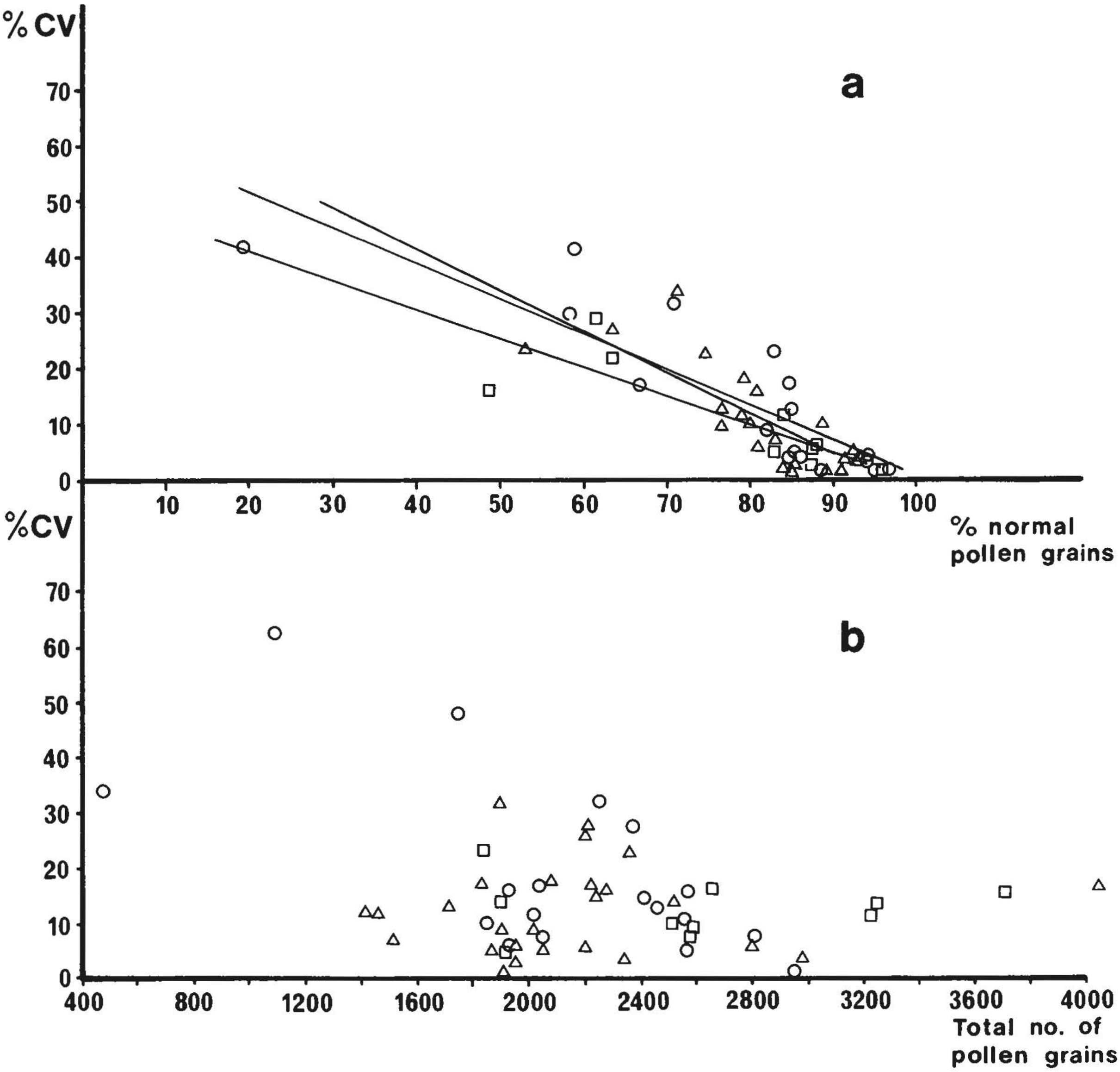


Fig. 11. The correlation between a: percentage normal pollen grains per anther, and b: total number of pollen grains, and the coefficient af variation of the number in each flower of *Dryas integrifolia* populations. ○: Site 6. □: Site 7. △: Site 9.

11 to July 12 led to a decrease in pollination from the 14th to the 17th at site 9 and probably to an extension of the flowering period, such that the improvement of the weather gave a final high pollination percentage. The end of the curves for the individual sites indicates that on the following day of collection it was not possible to find three open flowers on any individual.

Compatibility

The total results from the isolation and pollination experiments are summarized in Table 8. It appears that:

1. There was a very small variation in the percentage of total carpels that developed into seeds.
2. The lowest percentage of well-developed seeds was found in flowers which had been emasculated and isolated. Of the nine emasculated flowers the majority (7) set no seeds, whereas the remaining two had a high seed set, possibly because of strong winds during the period of isolation.
3. Apart from the flowers mentioned immediately above, all flowers which were not actively pollinated showed an average seed set of 68.4% of the number of carpels. Isolation per se had no influence on the seed set.

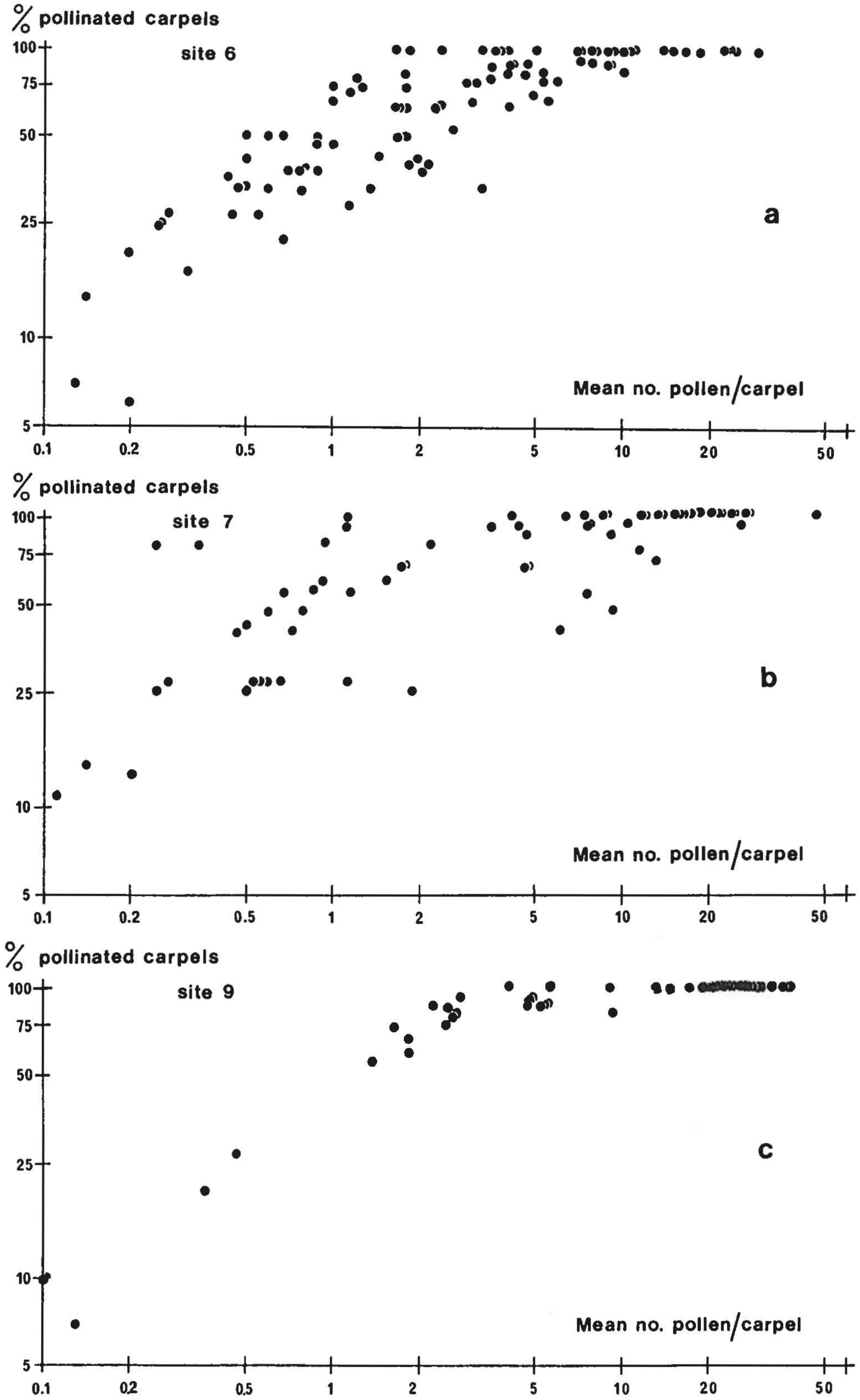


Fig. 12. The percentage of pollinated carpels per flower as a function of the mean number of germinated pollen grains per carpel in the same flower of *Dryas integrifolia*. a: Site 6. b: Site 7. c: Site 9.

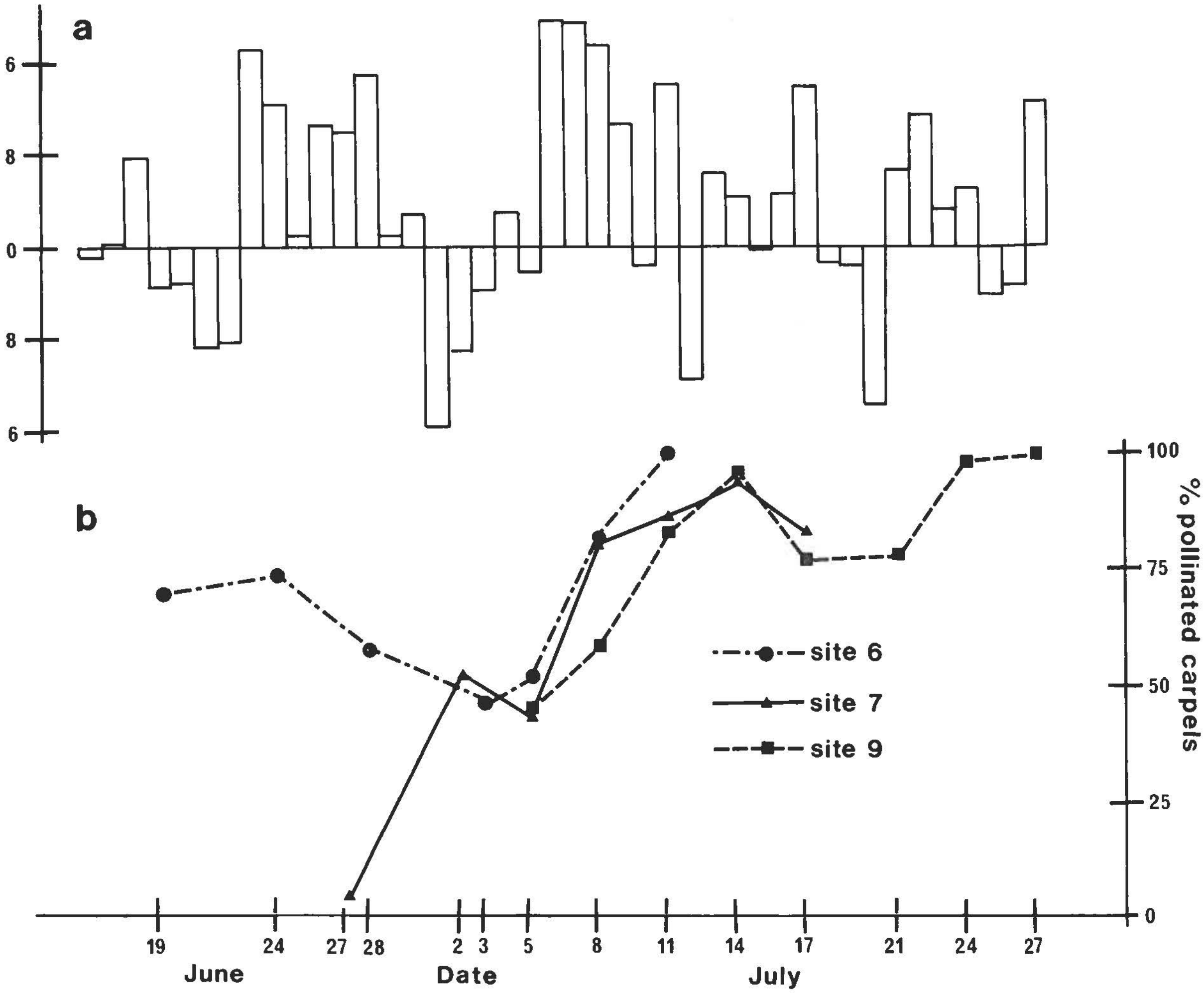


Fig. 13. A comparison between a: the "weather indicators" and b: the percentage of pollinated carpels per flower in *Dryas integrifolia* populations. Positive values of the weather indicators are above the zero-line.

Table 8. Results of isolation and pollination experiments on *Dryas integrifolia*. The figures for "ovules" and "% good seeds" are averages per flower.
1: isolated (I) or not (O)
2: emasculated (E) or not (O)
3: active cross-pollination (C), self-pollination (S) or no treatment (O).

Site	Treatment			No. of flowers	Ovules	% good seeds
	1	2	3			
6	O	O	O	95	73.6	68.4
6	O	E	O	13	61.5	66.5
6	O	O	S	6	63.5	77.4
6	I	E	S	2	83.5	59.3
6	I	O	S	4	74.8	62.9
6	O	O	C	10	72.8	73.8
6	I	E	C	8	72.4	72.2
6	I	O	O	7	71.0	71.8
6	I	E	O	9	71.6	23.6
9	O	O	O	5	83.3	62.3
9	O	E	O	8	77.9	53.0
Total	O	O	O	100	74.1	68.1
-	O	E	O	21	67.7	61.4

4. Active selfing (OOS + IES + IOS) resulted in a seed set on average of 68.2% of the carpels.
5. Active outcrossing resulted in a seed set on average of 71% of the carpels.
6. A T-test on the results of seed set after selfing and outcrossing showed that the average seed set is not significantly different.
7. Emasculated flowers tended to have a lower seed set than non-emasculated flowers, but a T-test showed no significant difference due to a large standard deviation.

Seed production

Fruiting in *D. integrifolia* was abundant. The results for 1976 (Table 9) have been arranged in order of increasing shelter. At the most severe site, site 7 the mean of 52.5 seeds/head was the lowest found, and the trend is for numbers to increase with increasing shelter. It is notable

Table 9. Seed set in *Dryas integrifolia*.

Site	Year	No. of flowers	No. of fruits	Fruits/ flower	% seed set
7	1976	6	315	52.5	100
9	1976	44	2559	58.2	93.2
9	1977	5	260	52.0	62.5
6	1976	377	27367	59.8	82.6
6	1977	95	4778	50.3	68.4
12	1976	15	1202	80.1	-

on the other hand that the percentage of seeds developed is highest at the most exposed sites.

At the two sites for which we have counts from 1977, seed set was lower than in 1976 (Table 9).

Silene acaulis

Morphology (Fig. 14)

S. acaulis is a chamaephyte, the shoots forming more or less dense and convex cushions. The leaves are rigid, linear, c. 1 cm long; the internodes are very short. Often the whole cushion is covered by flowers, which are terminal, on short pedicels. Flower size (Table 10) as well as colour varies markedly. The flowers contain small amounts of nectar. Hermaphrodite and male flowers invariably have ten stamens.

Three flower morphs, female, male and hermaphrodite are found in the populations (Table 11). Usually they are found on separate plants, but rarely two sexes, generally hermaphrodite flowers together with either female or male flowers, are found on the same cushion. No definite pattern of disposition of the morphs on the same cushion was apparent. Further, there are three types of hermaphrodite cushions. In one type all of the flowers function as hermaphrodites, in a second some function as males only, and in a third some function as females only (Fig. 15). Female cushions come into flower earlier than male and hermaphrodite cushions (Table 12).

Table 10. Measurements (in mm ± S.E.) of calyx and corolla lobes of flowers from the three morphs of *Silene acaulis* (herm. = hermaphrodite).

Morph	Calyx	Corolla lobes	
	length	length	breadth
female	6.7 ± 0.07	3.5 ± 0.08	2.4 ± 0.08
male	6.8 ± 0.09	4.3 ± 0.08	2.7 ± 0.05
herm.	7.4 ± 0.09	5.1 ± 0.06	3.1 ± 0.05

Calyx and corolla lobes of flowers from the three morphs show significant differences in size (Table 10). All measurements except those of female and male calyx are significantly different (T-test, $p<0.001$). The ovaries of female plants contain a significantly higher number of ovules than those in the morphological hermaphrodites (Table 13).

The fruit is a capsule which opens with six teeth. The species has no vegetative propagation.

Flower phenology

The flower buds are produced the year before flowering (Warming 1920). The average duration of anthesis of flowers of the three morphs is shown in Table 14. The anthers open about one day after the flower has started opening. Our few observations indicate that rosettes

Table 12. Flowering phenology of *Silene acaulis*. The percentages of the three morphs among the flowering plants were noted on two dates at site 3 in 1976. The population contained 38% female, 52% male and 10% hermaphrodite flowering plants (Herm. = hermaphrodite, N = no. of flowering plants).

Date	Female	Male	Herm.	N
24/6	64	36	0	121
17/7	35	49	16	103

Table 13. Mean number of ovules ± S.E. per ovary on the three morphs of *Silene acaulis* (herm. = hermaphrodite).

Morph	Mean no. of ovules	No. of capsules
female	26.76 ± 0.49	126
herm.	24.09 ± 0.55	58
herm. → female	19.17 ± 3.52	6
herm. → male	25.49 ± 0.89	47

Table 11. Sex ratios in populations of *Silene acaulis* at five sites, 1976 and 1977 (3′= a site very close to site 3).

Site	Year	% female	% male	% hermaphrodite	% non-flowering	No. of plants
3	1976	29.7	40.7	7.7	22.0	91
13	1976	19.7	22.4	0.0	57.9	76
3′	1976	26.3	21.1	0.0	52.6	38
3′	1977	32.1	30.2	1.9	35.8	53
9	1976	53.8	7.7	0.0	38.5	13
7	1976	46.9	18.8	0.0	34.4	32


a


b

Table 14. Average length of anthesis (in days) of flowers on the three morphs of *Silene acaulis* (herm. = hermaphrodite).

Morph	No. of flowers	Open flowers	Open stamens	Exposed stigmas
female	12	7.4	–	6.0
male	21	4.7	2.9	–
herm.	7	8.6	2.6	3.0
herm. → male	14	6.8	4.2	3.0

which flower one year do not produce flowers the next year. The flowering period of the populations in 1976 was of three weeks' duration (site 3: June 23 – July 17; site 13: July 14 – Aug. 9).

Pollen production

The filaments of the outer and inner stamens in buds of *S. acaulis* differ in length and the anthers tend to open in two groups. Possible differences in the total number and the percentage of normal pollen grains between the first and later dehisced stamens were investigated. No significant differences were observed in the percentages of normal pollen from any of the three sites. The early and late stamens did not differ in total number of pollen grains in sites 3 and 7, but at site 13 there were significantly more grains ($P < 1\%$) in the early than in the late stamens. No difference in the total number of pollen grains and the percentage of normal pollen could be demonstrated between male and hermaphrodite plants.

The results of the pollen counts for sites 3, 7 and 13 are presented in the frequency histograms in Fig. 16. In addition to a great variation the graphs indicate a skew, and probably a bimodal or polymodal distribution as to both total number and number of normal pollen grains from sites 7 and 13 in particular. The histograms for the percentage of normal pollen deviate from a hypergeometric type of distribution which is usually seen (cf. Fig. 10) and most likely the distribution is bimodal at all three sites. The CV as a function of the mean percentage of normal pollen grains and mean total number of grains per anther was calculated as in *D. integrifolia* (Fig. 11). The distribution of the data pairs in Fig. 17 a could be interpreted as falling into two groups indicated by the regression lines. One group contains buds with a mean fertility above 49% and the other includes those with a mean fertility below 47%. In the first group at least there might be a proportionate decrease in CV with increasing mean percentage of normal pollen grains. A possible interpretation is that in all three populations there are two genotypes which differ as to the general level of pollen fertility. But for each genotype the percentage of normal pollen grains in a bud is modulated by environmental conditions.

The corresponding graph for the total number of pollen grains (Fig. 17 b) shows that in general, there is no correlation between the total number of grains and the corresponding CV. The data pairs from site 7, however, are described perfectly by the regression line drawn. No satisfactory interpretation of the distribution pattern has been found. As expected from Fig. 16, no correlation was found between the total number of pollen grains and the percentage of normal grains from any of the three sites. Although the *S. acaulis* populations probably have a bimodal distribution as to pollen fertility and are inhomogeneous as to the total number of pollen grains, a common mean has been estimated for each of the three sites (Table 39).

Pollen germination

Fig. 18 depicts the seasonal variation in the number of germinated pollen grains per stigma (b) and the percentage of pollinated flowers (a) together with the 'weather indicators' (c) from sites 3, 7 and 13. As in *D. integrifolia* the course of the curves is interpreted as a combined effect of changes in flower numbers during the flowering periods of the three populations and the climatic conditions. This is seen very clearly in the mean number of germinated grains per stigma branch at site 3. The exceptionally bad weather from June 29 to July 5 is followed by a decrease in pollination during the same period of time, which would normally be expected to correspond to the central part of the flowering period. A similar decrease in the curve for the percentage of pollinated flowers in the population is not obvious. The curve approaches the bell-shape expected for a distribution of numbers of flowers during the flowering period. The steep increase in both curves for site 13 from July 21 again parallels a rapid improvement in weather conditions. The value of 18.4 germinated pollen per stigma on August 4 is not in accordance with the previous interpretations. The high figure is due to exceptionally high numbers of germinated grains on a few stigmas, but no further explanation has been found.

As in *D. integrifolia* the possibility has been considered that the distribution of germinated pollen grains on the stigmas in a flower and even the distribution on the flowers of a cushion of *S. acaulis* follows a Poisson distribution. In neither of the cases was this type of function adequate. This is mainly due to an unequal distribution of the pollen grains between the individual stigma branches in a flower as well as between flowers in a cushion. The explanation in the first case could be a clumping of the pollen grains, and the fact that insects visit a limited number of flowers per cushion could be the explanation of the second case. Fig. 19 shows the relation between the mean number of germinated pollen grains per flower (collected on specific days and sites) = "G", and the percentage of flowers with at least

Fig. 14. *Silene acaulis*. a: Phenological observations in a hermaphrodite plant. b: Close-up of a hermaphrodite plant.


a
b

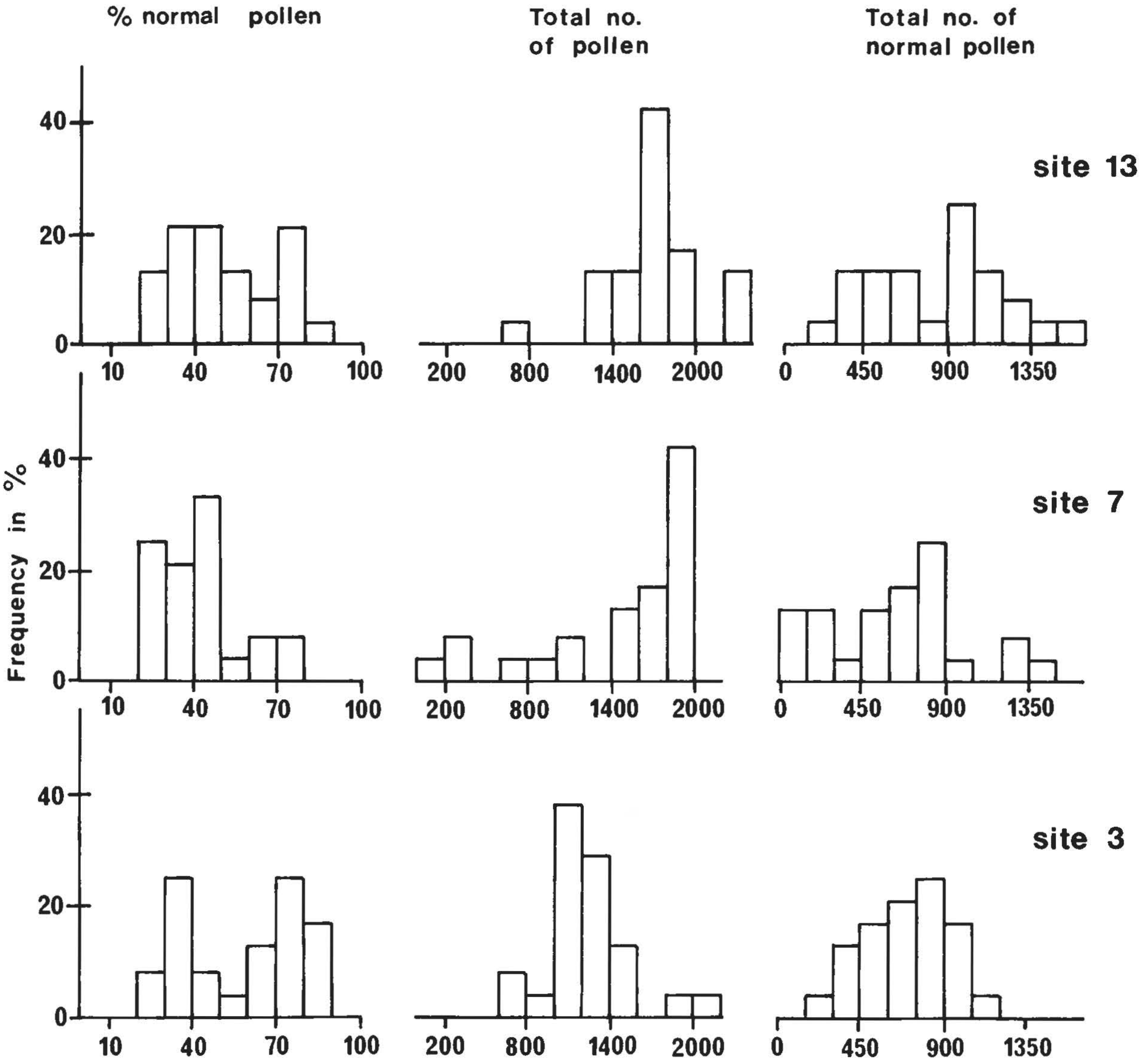


Fig. 16. Total number of pollen grains and number of morphologically normal pollen grains per anther in *Silene acaulis* populations.

one germinated pollen grain on the stigmas ("percentage pollinated flowers" = "F"). Sample series with no germinated grains at all have been excluded. The correlation can be described by the two lines $F = 27.8518 + 11.6345 \ln G$, and $\ln G = -0.6294 + 0.0408F$, $r = 0.689$ for 21 means. From the latter function it can be predicted that an average of 31.4 germinated pollen grains must be present on pollinated flowers to be able to expect all flowers to have at least one germinated grain. The P/O-ratio is 930.5 (site 3) and thus, approximately 3.4% of the pollen grains in the population are "needed" for pollination of all ovaries.

Compatibility

The total results from isolation and pollination experiments are summarized in Table 15. It appears that:

1. Isolated and emasculated flowers set no seeds.
2. Flowers which were isolated had a very low seed set.
3. Under insect-proof nets active self-fertilization was possible and no selfing depression was observed.
4. Emasculated flowers with open pollination had a seed set equal to reference flowers.

Fig. 15. *Silene acaulis*. a: Male plant. b: Plant with flowers intermediate between male and hermaphrodite.

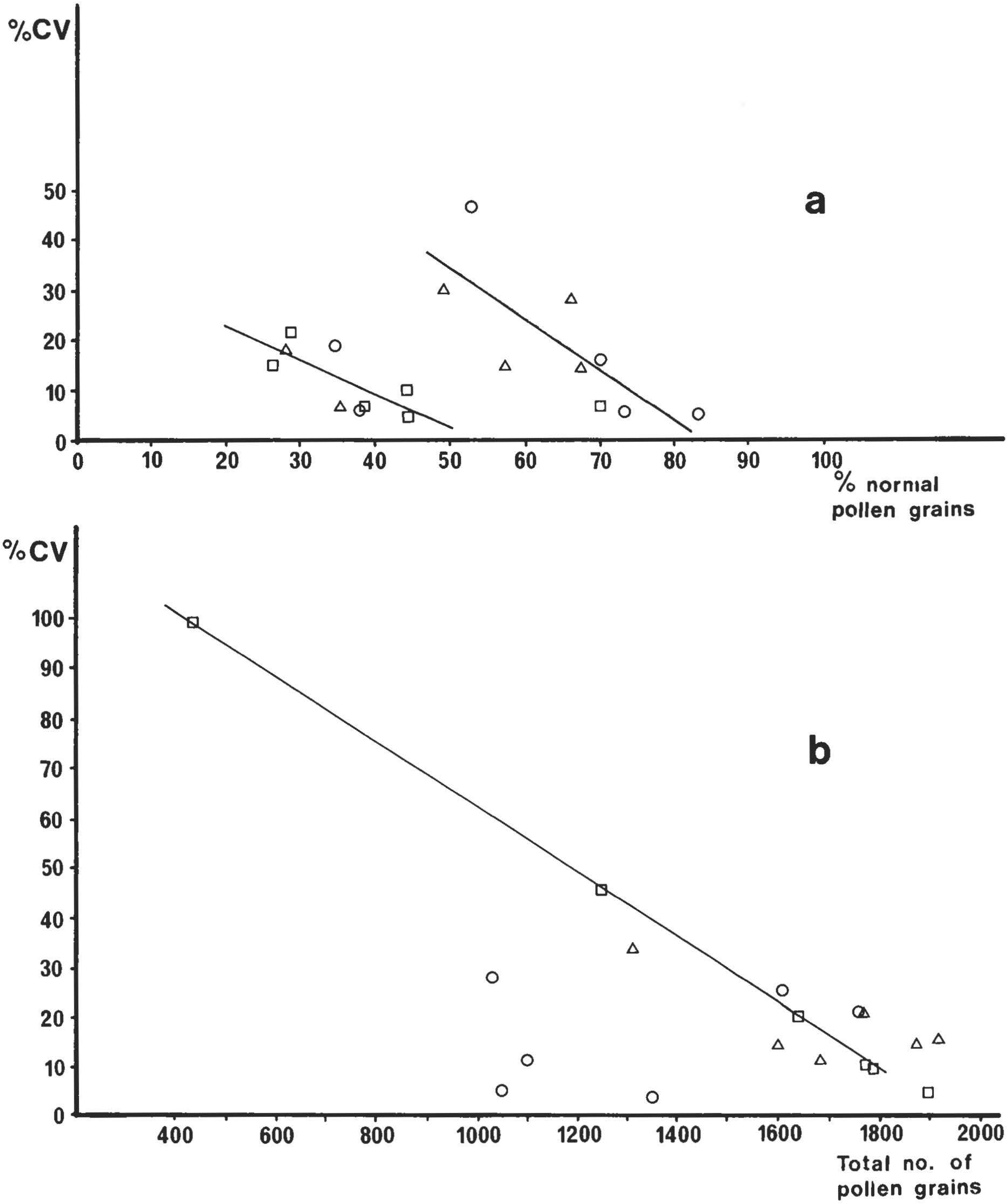


Fig. 17. The correlation between a: the percentage of normal grains and b: the number of pollen grains, and the corresponding coefficient of variation in *Silene acaulis* populations. ○: Site 3. □: Site 7. △: Site 13.

5. The highest seed set was found following either selfing or crossing by hand, irrespective of isolation.
6. Following open pollination hermaphrodite flowers set 2–3 times as many seeds as female flowers.
7. Flowers on hermaphrodite plants also carrying male flowers showed a seed set equal to that of "normal" hermaphrodite plants.

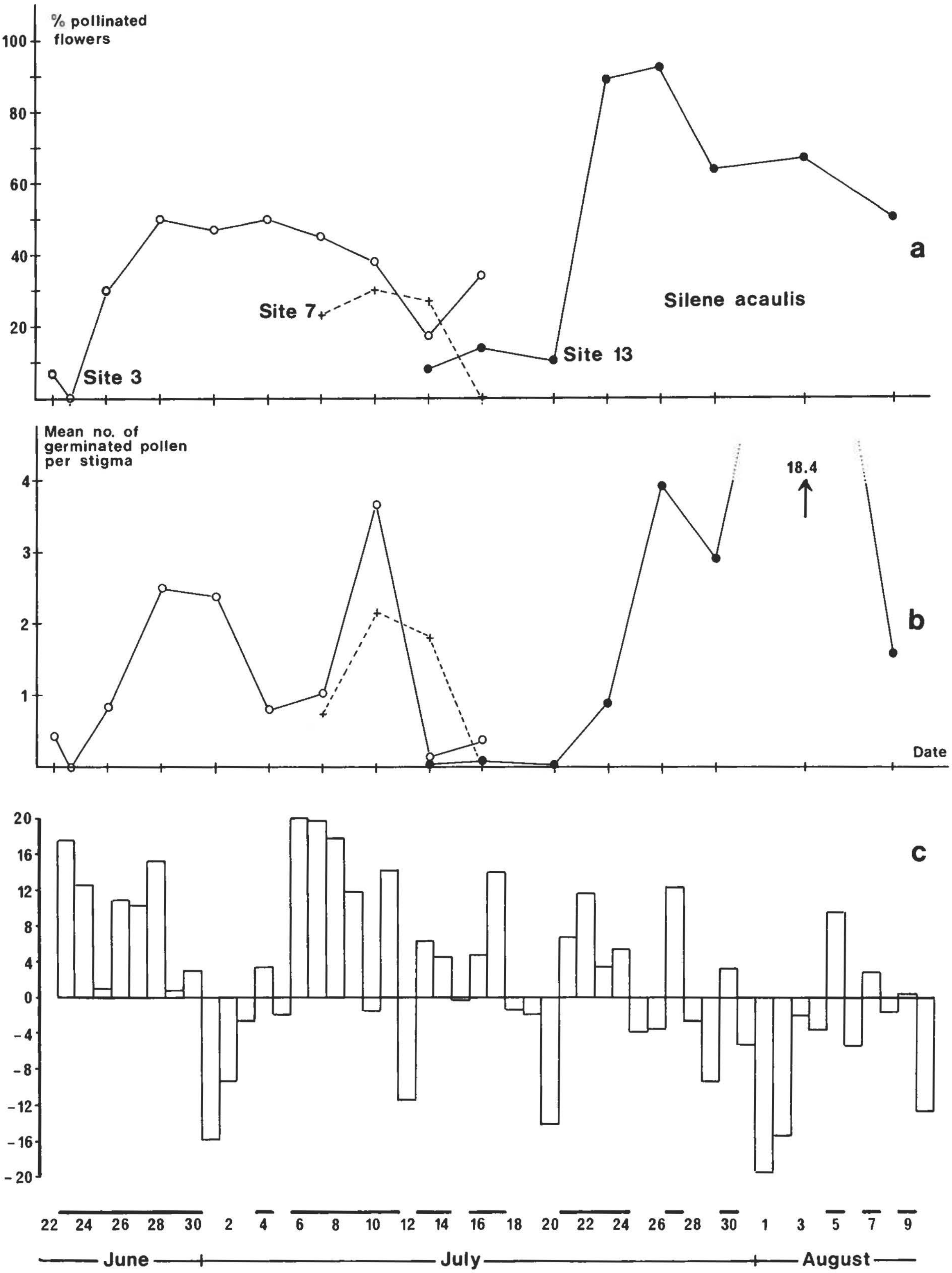


Fig. 18. A comparison between a: the percentage of pollinated flowers, b: the number of germinated pollen grains per stigma and c: "weather indicators" in *Silene acaulis* populations. Periods with positive weather indicators are shown at the bottom of the figure as horizontal bars.

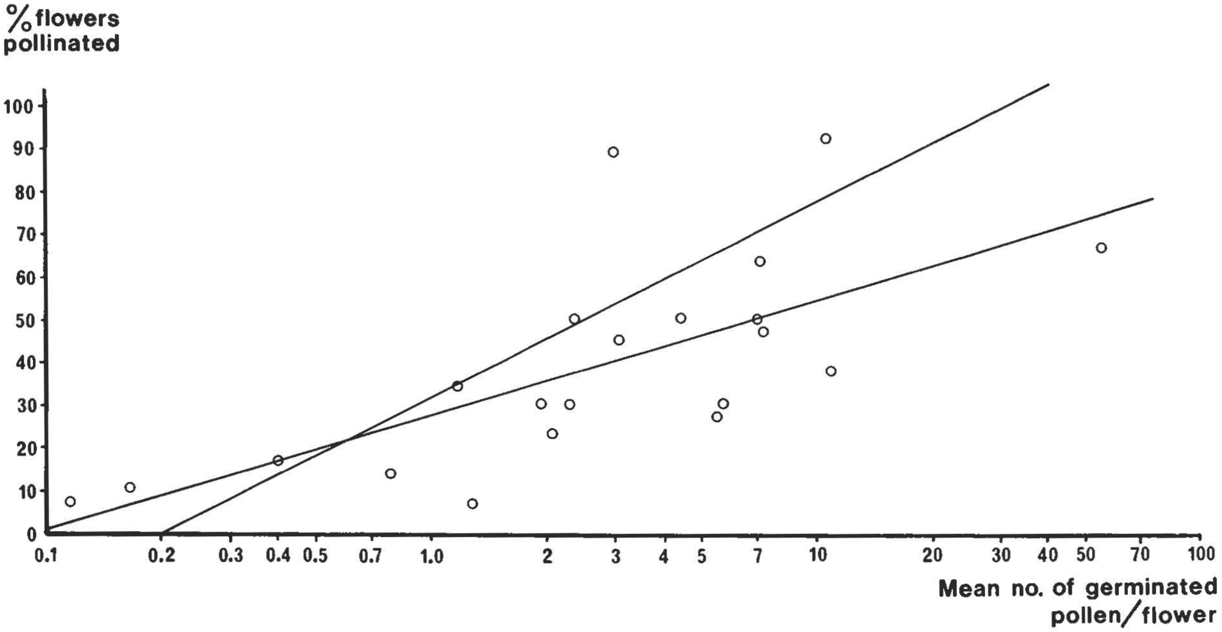


Fig. 19. The percentage of pollinated flowers as a function of the mean number of germinated pollen per flower in samples from cushions of *Silene acaulis*.

Seed production

In 1976 some capsules from 1975 remained at site 7. They had just ripened but not opened, and contained a mean of 8.67 seeds per capsule (Table 16). Immature unopened capsules from a nearby snowbed had a mean of 8.44 seeds per capsule. In 1976 seed set at site 7 was lower; 2.56 seeds per capsule. At site 3 the seed set in 1977 was lower than in 1976. This may be a consequence of reduced vigour resulting from the bad summer of 1976, and will be discussed later.

All these are low percentage seed sets compared with the number of ovules per flower, which is about 25 (Table 13).

Table 15. Average number of seeds per capsule in the three morphs of *Silene acaulis* after different treatments (herm. = hermaphrodites, numbers in brackets are number of flowers).
1: isolated (I) or not (O)
2: emasculated (E) or not (O)
3: active cross-pollination (C), self-pollination (S) or no treatment (O).

Treatment			Females	Herm.	Herm. → females	Herm. → males
1	2	3				
O	O	O	5.2 (44)	12.2 (9)	–	2.5 (65)
I	O	O	0.1 (30)	0 (2)	0 (2)	0.5 (6)
I	E	O	–	1 (2)	–	0 (18)
O	O	C	14.4 (21)	12.0 (2)	–	7.4 (11)
I	O	C	14.0 (28)	14.0 (2)	7.1 (7)	16.0 (2)
O	O	S	–	–	–	17.5 (2)
I	O	S	–	17.3 (4)	8.3 (12)	–
I	E	C	–	15.0 (1)	14.0 (3)	11.3 (3)
I	E	S	–	10.0 (1)	8.0 (2)	12.2 (6)
O	E	O	–	–	–	4.1 (8)

Ranunculus nivalis

Morphology (Fig. 20)

R. nivalis is a hemicryptophyte, the shoots forming small tussocks. The leaves are deeply divided into 3–5 lobes. The flowers are terminal and solitary, 15–20 mm in diameter. The calyx is loosely clothed in long dark brown hairs. Nectaries are pocket-like structures at the base of the petals. The mean number of stamens is 35.5 (n = 18, range 29–43). The numbers of carpels differed between sites. At sites 4 and 5 the median number was 57.4 ± 4.3, whereas at site 8 it was 73.4 ± 3.9. At both sites there were some individuals with carpel numbers much higher than the median, indeed quite different from the remainder of the flowers. The length of the stamens is about half the height of the gynoecium; this has a profound effect on the ability to self, as shown by the isolation and pollination experiments (p. 31). The flowers are placed 8–15 cm above ground, but during fruit ripening the pedicels elongate to a length of 15–25 cm. The fruits are achenes, each with a long beak. The species has no vegetative propagation.

The carpel numbers at site 8 tend toward a bimodal

Table 16. Seed set in *Silene acaulis*. Mean number of seeds per capsule (numbers in brackets are sample sizes).

Year	Site 3	Site 7	Snowbed
1975	–	8.67 (353)	8.44 (55)
1976	7.15 (727)	2.56 (79)	–
1977	4.25 (118)	–	–

Fig. 20. a: Flowers of *Ranunculus nivalis*. b, c, d: Flowers of *R. nivalis* visited by *Spilogona* sp., *Phaonia pallidisquama*, *Phytomyza vibeana*.

distribution. The presence of the few individuals with a very high carpel number and the causes of the possible bimodal distribution cannot be explained at present. The higher median number at site 8 may be a result of this being a favourable, sheltered locality.

Flower phenology

The buds develop during the autumn before the flowering season; they are protected by leaf sheaths (Sørensen 1941). When the buds open all the anthers are closed. In the process of opening the stamens bend toward the petals. It takes about three days from the opening of a bud until all the anthers are open. The entire anthesis lasts on average nine days (range 7–14). The flowers were thus found to be protandrous, possibly homogamous, as was stated by Jessen (1911). The flowering period is 2–3 weeks in June and July, depending on the differences in snow cover between sites. In 1976 the period was 14–30 June at sites 4 and 5, and 30 June to 20 July at site 8.

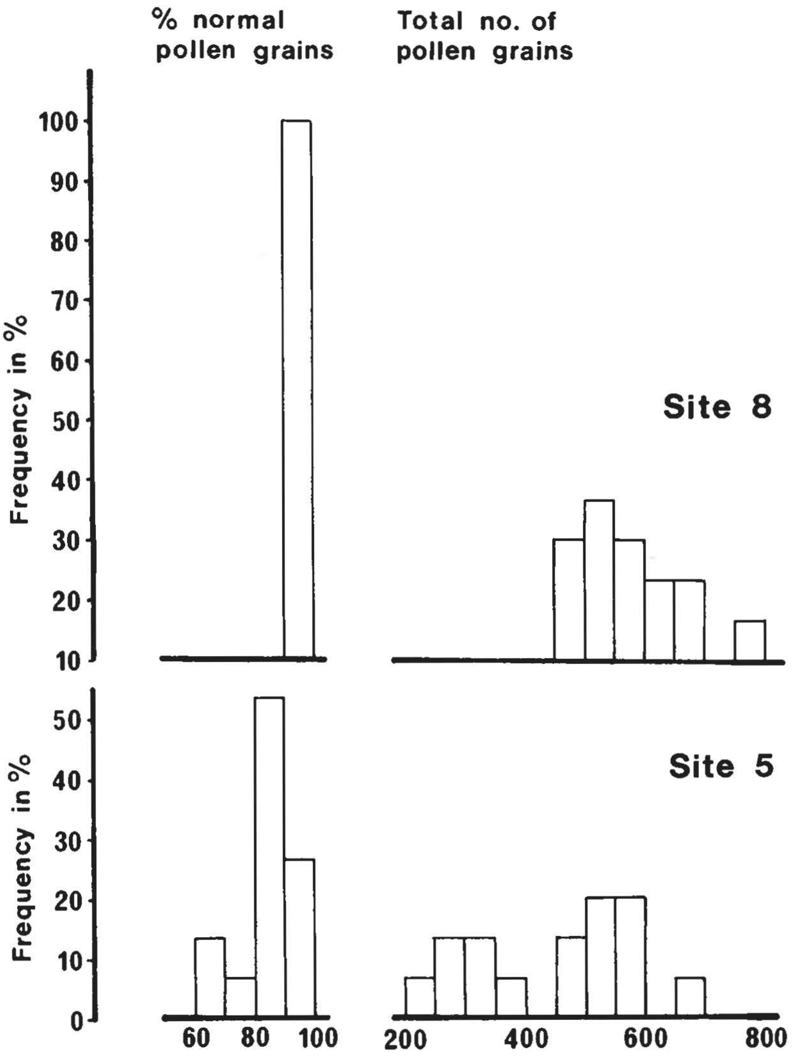


Fig. 21. Total number of pollen grains and the percentage of normal pollen grains per anther in *Ranunculus nivalis* populations.

Pollen production

The total number of pollen grains and the percentage of morphologically normal pollen grains were analyzed from five buds from each of the two sites 5 and 8. The frequency distribution of the two pollen parameters are presented in Fig. 21, and features worth noticing are the probable bimodal distribution as to total number of pollen at site 5 and the high pollen fertility at site 8.

The relation between bud means for the two pollen characteristics production and fertility, and the corresponding CV for these small samples are shown in Fig. 22. No correlation appears to be present in any of the two graphs and the variation among anthers in a bud may in this limited material be due to random fluctuations. A significant positive correlation is found when the total number of pollen grains are plotted against the percentage of normal pollen grains.

Pollen germination

Only a rather limited sample of open flowers was analyzed for pollen germination on carpels. Fig. 23 summarizes observations from sites 4 and 5 for a short part of the flowering period. Although flowering started more or less at the same time there is a difference between these populations in the percentage of pollinated carpels, and it may be relevant to note that the population at site 5 had a low pollen production.

Fig. 24 indicates that similarily to the situation in *D. integrifolia*, in which all carpels in a flower are pollinated, there are typically about five germinated pollen grains per carpel. Since the P/O-ratio is about 350 (site 8), five germinated pollen grains per carpel means that approximately 1.4% of the total number of pollen grains are "required" for pollination of all carpels. Since pollen fertility is high in this species (Fig. 21) about

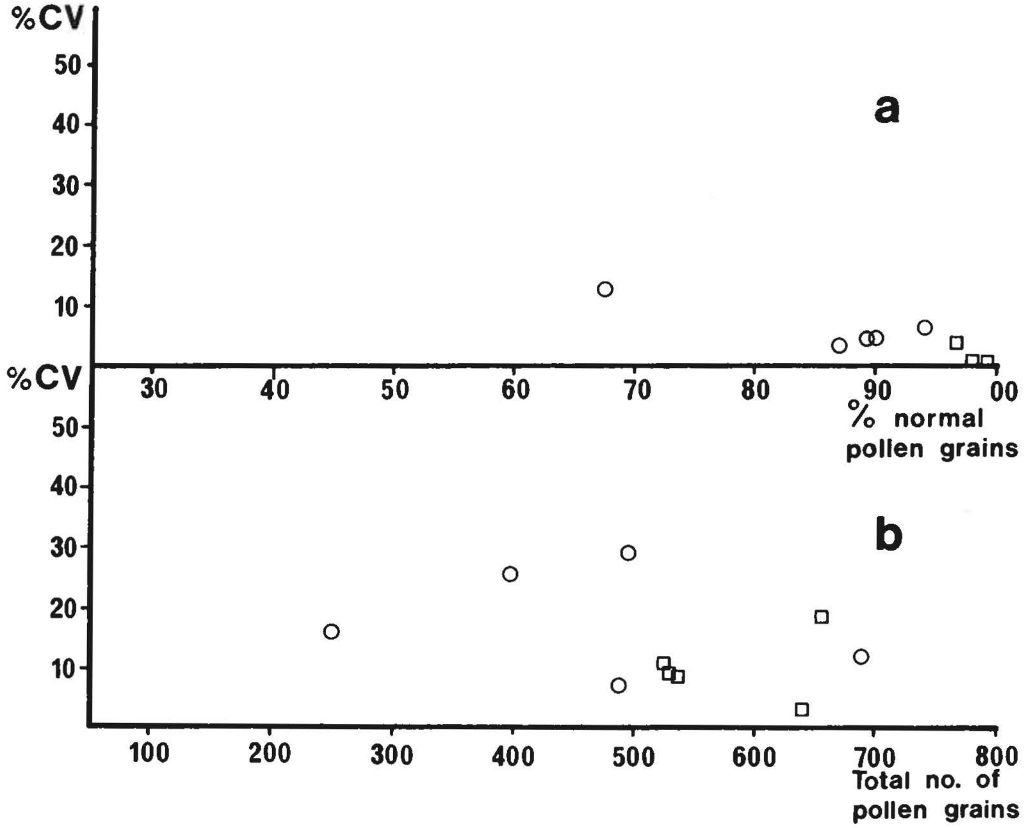


Fig. 22. The correlation between a: the percentage of normal grains and b: the total number of pollen grains, and the corresponding coefficient of variation in *Ranunculus nivalis* populations.

1.5% of the produced normal pollen grains per flower are "needed".

Compatibility

Because of the presence of a number of flies in some of our nets (possibly hatched inside them), the figures from isolation experiments are scanty (Table 17). The results from isolation and pollination experiments can be summarized as follows (Fig. 25):

1. All treated flowers produced fewer seeds than untreated flowers.
2. Isolated flowers produced very few seeds.
3. Emasculated flowers which were open for insect pollination produced about half the amount of seeds as did untreated flowers. This probably shows the effect of selfing caused by insects, which enhance self-pollination by their movements in flowers.

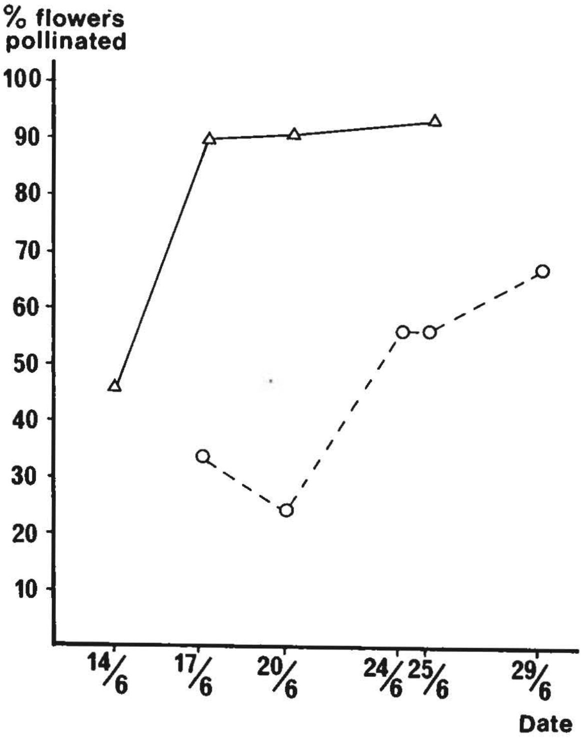


Fig. 23. Flowering phenology of *Ranunculus nivalis* populations. △: Site 4. ○: Site 5.

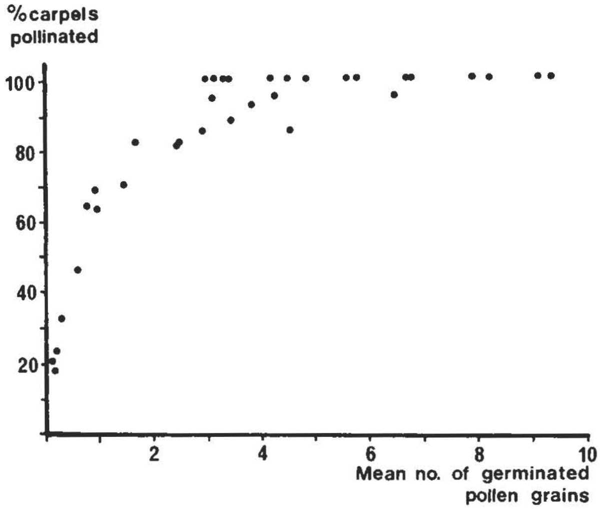


Fig. 24. The percentage of pollinated carpels per flower as a function of the mean number of germinated pollen grains per flower in *Ranunculus nivalis*.

Seed production

Seed counts were made from 1) random reference collections near the artificial pollination experiments, and 2) bulk collections of "well-filled" heads (Table 18).

Seed set was between 23 and 43 seeds per head in 1976, but in 1977 at site 8 it was halved. This may be a result of a general reduction in vigour due to the poor summer of 1976 when flower initiation took place.

The bulk collections of "well-filled" heads indicate that seed set of over 70% is possible in this species. Many heads set little or no seeds and this presumably reflects the low insect activity noted in *R. nivalis* populations (p. 45). However, in *R. glacialis* (Järvinen 1984) 31.3% of the carpels abort.

Table 17. Results of isolation and pollination experiments on *Ranunculus nivalis*, site 8. Figures are the average number of seed set per flower (N = number of flowers, "Phenology" = flowers for phenological studies).
1: isolated (I) or not (O)
2: emasculated (E) or not (O)
3: active cross-pollination (C), self-pollination (S) or no treatment (O).

Treatment 1 2 3	1976	N	1977	N
O O O	43.1	23	23.1	11
O E O	20.2	13	6.3	9
I O O	2.9	9	3.5	2
O O C	32.4	3	–	–
I O S	–	–	19.5	2
O E C	–	–	12.6	9
"Phenology"	24.0	8	–	–

Table 18. Seed production in *Ranunculus nivalis* at various sites in 1976 and 1977 (mean seed set ± S.E, N = number of analysed plants, * = bulk collections of "well-filled" gynoecia).

Site	1976		1977	
	N	Mean seed set ± S.E.	N	Mean seed set ± S.E.
8	23	43.1 ± 5.35	11	23.1 ± 5.25
5	9	23.1 ± 6.29	–	– –
4	21	27.1 ± 4.71	–	– –
4	*67	50.9 –	–	– –
below 8	*180	54.3 –	–	– –

Microclimate

Microclimatic measurements were carried out in order to (1) obtain an idea of the bioclimate of the plant species studied, and especially how temperature varied during clear weather spells, and (2) relate microclimatic conditions to the insects' flower visiting activity.

Tables 19–24 summarize temperature recordings, giving averages for "day" and "night" together with maximum and minimum values. Recordings from site 3 and *R. nivalis* sites were unsuccessful and are omitted. We worked at 69°N where the sun is continually in the sky for nearly two months during summer, but in Godhavn the high mountains to the north create a "night" when the sun dips behind them. The "night" has a different duration according to the position of the site, but lasts for at least six hours. The tables and figures show that the disappearance of the sun in the "evening" has a profound effect on the microclimate.

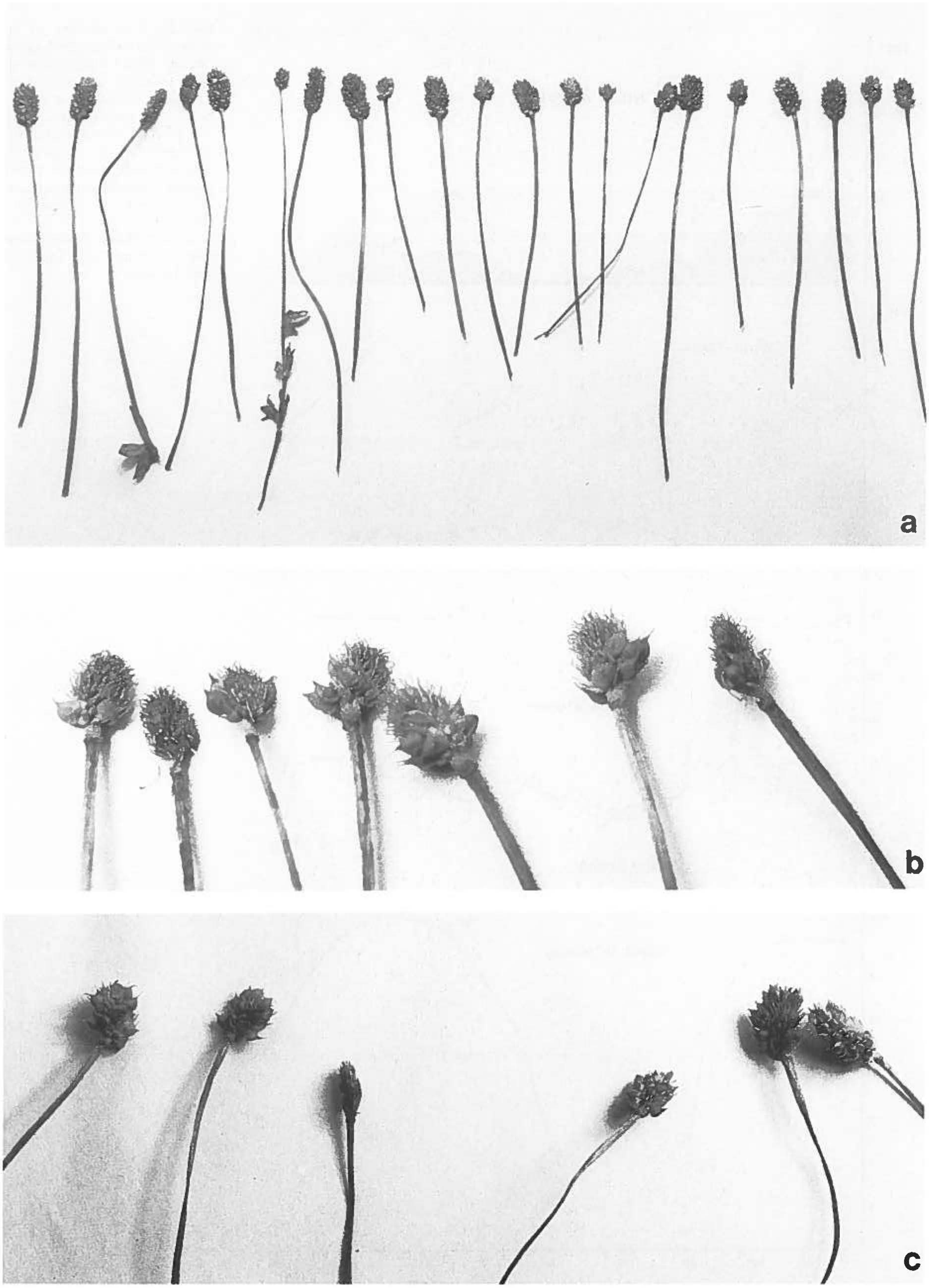
Figs 26–29 are selected examples of microclimatic recordings and insect counts from flowers in order to show how they are related.

Insect visits to flowers in relation to microclimate

Fig. 26 and Table 19 show recordings from two days in 1977 with almost clear skies and relatively high temperatures, but with different wind speeds. It is evident that the number of insects dropped to very low levels as the sun dipped behind the mountains in spite of the fact that the temperature within the flowers did not fall below 7°C. As soon as the sun reappeared, insects were again present in the flowers and their numbers increased as the sun rose.

July 8 was a windy day and in spite of otherwise ideal conditions the number of insect visits to flowers was much lower than on the preceding day. By comparing

Fig. 25. Isolation and emasculation experiment with *Ranunculus nivalis*. a: No treatment. b: Isolation, no treatment. c: Emasculation, no treatment.


a
b
c

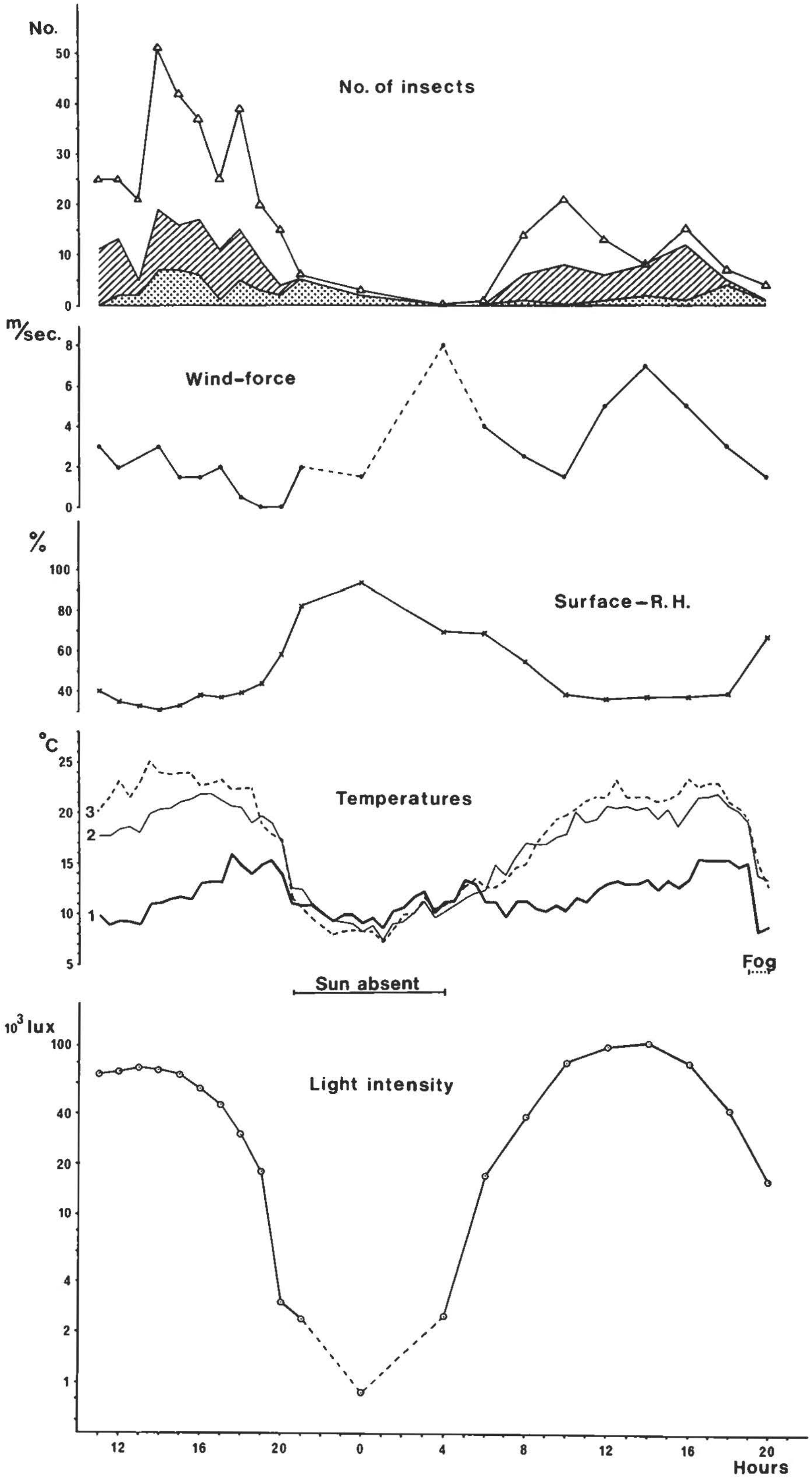


Fig. 26. The number of insects observed in 2915 flowers of *Dryas integrifolia* at site 7 during 21 inspection rounds in relation to microclimatic measurements, July 7–8 1977. Without signature: *Spilogona* spp; hatched: *Phaonia* spp; dotted: other insects. Temperature curves: 1) 120 cm above ground; 2) 2 cm above ground; 3) centre of *D. integrifolia* flower, 2 cm above ground. See Table 19 and the text.

Table 19. Temperature measurements of *Dryas integrifolia* plants at site 7, July 7–8 1977 (numbers of observations in brackets). The sky was clear on both days, but it was more windy on 8/7. The values from the two days are not strictly comparable, since registrations from 7/7 do not include morning data. See Fig. 26 and the text.

	Height above ground (cm)	"Day" 11.00–20.00		"Night" 20.30–4.00		"Day" 4.30–20.00	
		Mean (19)	Max.	Mean (16)	Min.	Mean (32)	Max.
Dryas flower	2	22.1	25.1	9.3	7.1	18.4	23.1
cushion surface	2	30.2	35.0	7.1	4.9	20.5	27.9
beneath cushion	0	16.9	18.5	10.7	8.0	12.9	16.5
Surroundings	120	12.1	15.8	10.2	8.5	12.1	15.1
	2	19.7	21.8	9.7	7.3	17.6	21.6
basaltic gravel	0	26.3	30.2	10.2	8.8	17.6	21.6

the number of insects found at 8, 10 and 12 p.m. when wind speed decreased and then increased again, it was apparent that insect numbers were directly affected by wind velocity. The small flies of the genus *Spilogona* were much more affected than the heavier *Phaonia*. *Spilogona* numbers dropped to zero during periods of highest wind speed (7–8 m/sec).

Fig. 27 and Table 20 show recordings during a quite similar weather spell in 1976, taken in a fell field among basaltic rocks at low altitude near the coast. A special

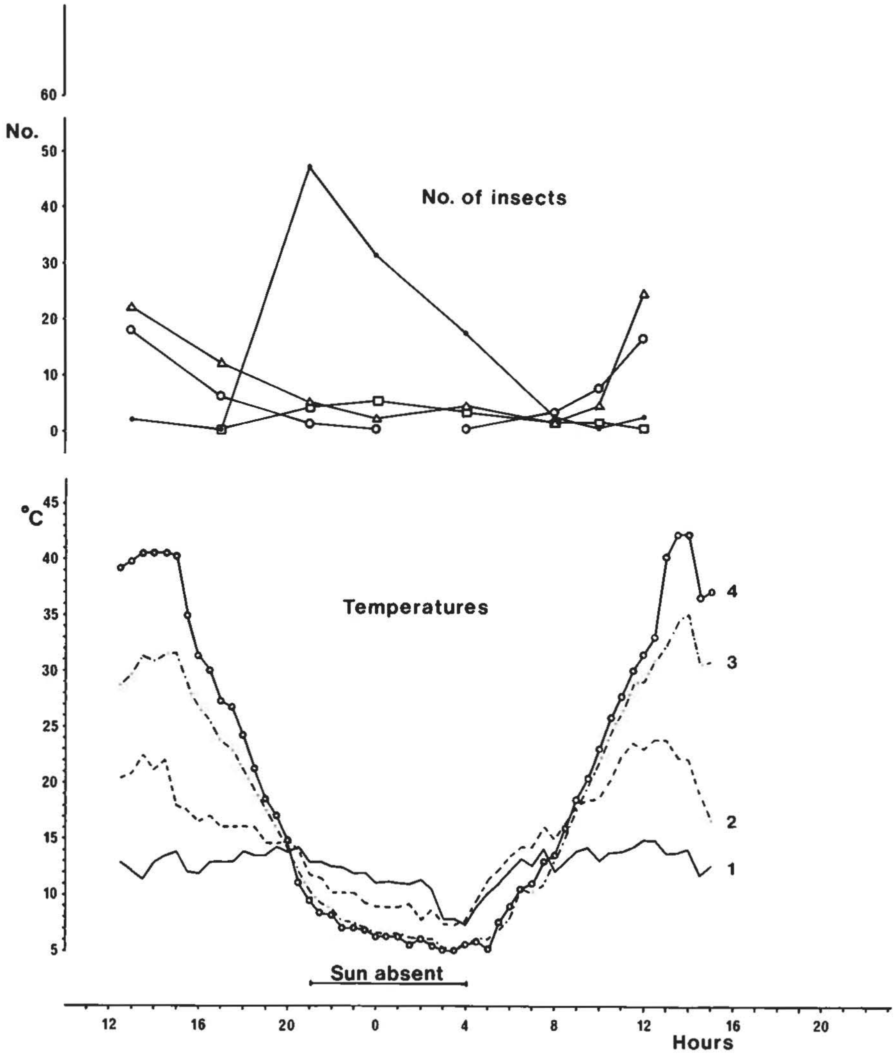


Fig. 27. The number of insects observed in c. 750 flowers of *Dryas integrifolia* in a fell field at c. 50 m altitude with a vegetation similar to site 7 during 8 inspection rounds, July 6–7 1976. △: *Spilogona* spp.; ○: *Phaonia* spp.; □: *Nysius groenlandicus;* ●: Chironomidae spp. Temperature curves: 1) 120 cm above ground; 2) centre of *D. integrifolia* flower, 3 cm above ground; 3) surface of *Silene* cushion, 3 cm thick. 4) surface of *D. integrifolia* cushion, 3 cm thick. See Table 20 and the text.

Table 20. Temperature measurements of *Dryas integrifolia* and *Silene acaulis* plants on a SW-facing slope at 50 m alt. (just above "Østerlien") July 6–7 1976 (numbers of observations in brackets). The vegetation is similar to that of site 7. The weather was clear, nearly calm except during 6–9 a.m. when there was strong wind. See Fig. 27 and the text.

	Height above ground (cm)	"Day" 4.30–20.30		"Night" 21.00–4.00	
		Mean (39)	Max.	Mean (15)	Min.
Dryas flower	3	17.7	23.7	9.2	7.3
cushion surface	3	25.6	42.2	6.5	5.0
Silene cushion surface	3	22.0	35.0	6.9	5.2
Surroundings	120	13.3	15.8	10.9	7.3
	3	17.4	21.9	9.2	6.9
plant litter	0	20.3	29.0	8.2	6.7
basaltic gravel	0	25.0	37.2	8.5	6.4

feature here was the settling of numerous chironomids and the common Greenlandic bug, *Nysius groenlandicus* in the flowers during the "night". The possible pollinating role of the chironomids is unknown and presumably the flowers were merely used as resting places during the cool hours when the sun was absent, as the insects appeared to be quite motionless. *N. groenlandicus* probably sucks nectar and feeds from the ripening fruits (J. Böcher 1972).

An example of insect activity during optimal weather conditions (10–11 July 1977) is shown in Fig. 28 and Table 21. In comparison, the next day, though warmer, was very windy and very few insects visited the flowers. During the period of high wind velocity after 10 a.m. on July 12 only moths (*Sympistis zetterstedtii*) and strong syrphids (*Helophilus* spp.) were flying from flower to flower, and after noon, when the sky gradually became overcast, only these insects were seen in the flowers. Once again it was obvious that as soon as the sun disappeared during the "night" the insects vanished from the flowers. This coincided with flower temperatures decreasing to below 10–12°C and light intensities to below c. 300 lux.

Fig. 29 and Table 22 give yet another indication of how sensitive the insects' flower visiting activity is to an increase in wind speed. Around noon on July 17 1976, the wind velocity (not included in the Figure) increased from 1–2 m/sec to about 4 m/sec and the insects, especially *Spilogopna spp.*, were no longer seen in the flowers. As soon as the wind decreased again the number of insects in the flowers increased rapidly. The flower temperature was fairly constant (14–15°C) from 9 a.m. to 7 p.m., but a haze around noon may have reinforced the effect of the wind.

Flower temperature

It has been demonstrated (Hocking 1968, Kevan 1970, 1972, 1975) that in sunshine the temperatures of arctic flowers, especially heliotropic flowers of *D. integrifolia*, rise above the ambient air temperature. This was confirmed in the present study by the use of thread-shaped probes placed in the centre of the flowers (Tables 19–21, 23, 24). When a needle-shaped probe was used (in 1976, Table 20) a slight increase in temperature above ambient could be shown only in some cases.

Table 24 compares the temperature increase in sunshine of flowers of *D. integrifolia* and *Potentilla vahliana* in relation to ambient air temperature. The flower temperatures are shown to be greatly affected by wind. The

Table 21. Temperature measurements of *Dryas integrifolia* on a SW-facing site close to site 9 and with a similar vegetation, c. 185 m alt., July 10–12 1977 (numbers of observations in brackets). 10–11/7 were clear with little wind, 12/7 more windy and overcast. The values from 10/7 are not strictly comparable to the values from the next two days since registrations commenced at 1.30 p.m. that date. See Fig. 28 and the text.

	Height above ground (cm)	"Day" 13.30–19.30		"Night" 20.00–3.30		"Day" 4.00–19.30		"Night" 20.00–3.30		"Day" 4.00–19.30	
		Mean (13)	Max.	Mean (16)	Min.	Mean (32)	Max.	Mean (16)	Min.	Mean (32)	Min.
Dryas flower	5	24.7	28.9	9.0	7.6	20.7	27.3	0.9	8.5	20.1	25.1
cushion surface	5	32.9	42.4	7.2	5.0	26.3	40.2	8.3	6.1	19.9	31.5
beneath cushion	0	18.5	19.3	12.8	9.6	15.2	19.8	3.8	11.2	13.9	15.5
Surroundings	120	15.5	18.3	10.4	9.7	14.2	16.7	2.3	11.0	17.4	21.7
	5	20.4	21.5	9.4	8.0	18.1	22.2	1.0	9.0	18.7	25.0
basaltic gravel (humid)	0	24.3	26.5	10.9	8.2	19.9	26.8	1.8	9.5	17.3	23.5

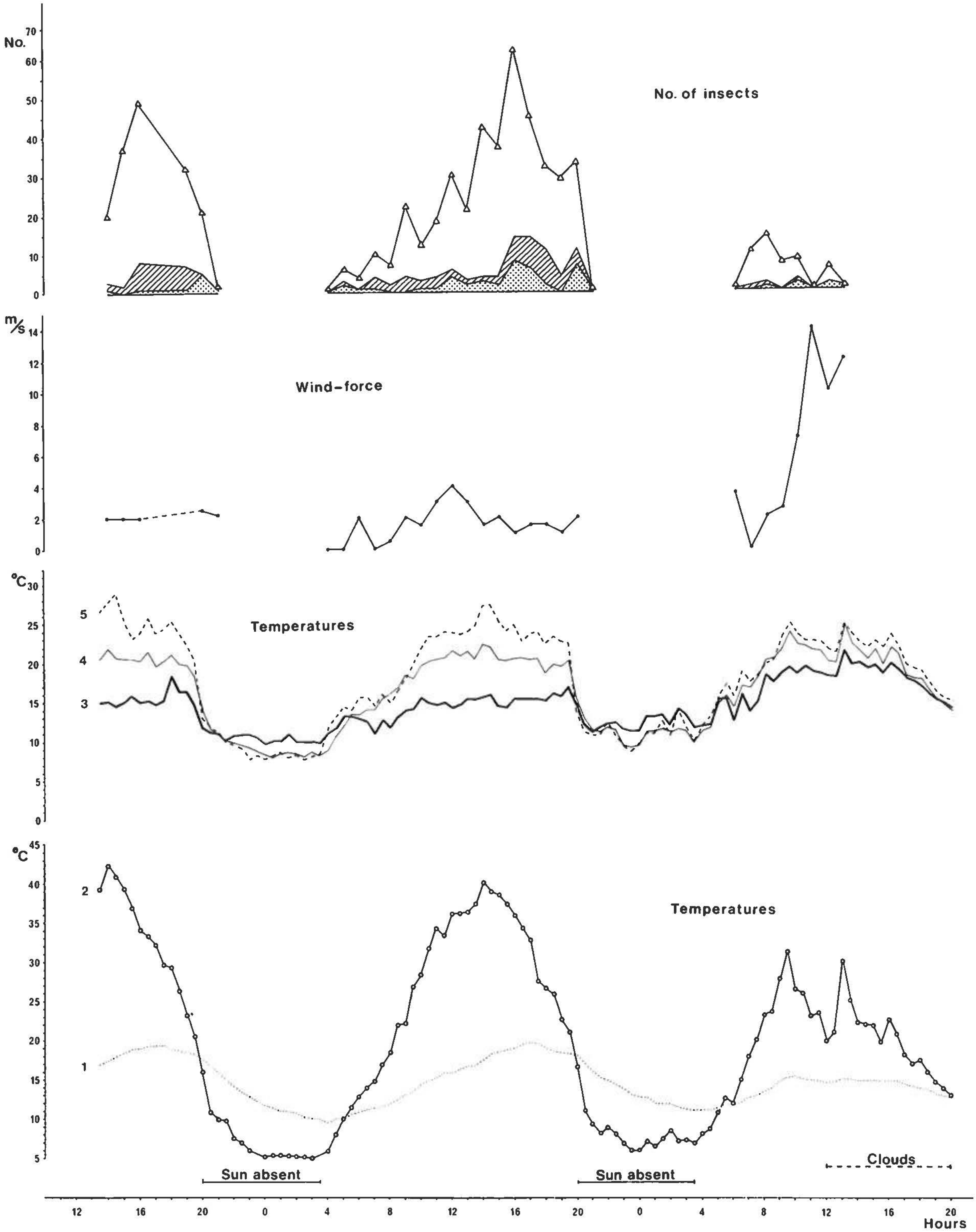


Fig. 28. The number of insects observed in c. 1660 flowers of *Dryas integrifolia* immediately NE of site 9 during 32 inspection rounds, July 10–12 1977. Without signature: *Spilogona* spp.; hatched: *Phaonia* spp.; dottet: other insects. Temperature curves: 1) Beneath *D. integrifolia* cushion, 5 cm thick; 2) surface of *D. integrifolia* cushion, 5 cm thick; 3) 120 cm above ground; 4) 5 cm above ground; 5) centre of *D. integrifolia* flower, 5 cm above ground. See Table 21 and the text.

Table 22. Temperature measurements of *Dryas integrifolia* and *Silene acaulis* July 1976 on a NW-facing slope near site 9 with a quite similar vegetation, c. 190 m alt (numbers of observations in brackets). 16/7 was clear and nearly calm, but 17/7 was hazy and windy (2–4 m/sec.) around noon. The aspect of the locality means that maximum temperatures are found late in the afternoon (note that there are only few readings from the "day" of 16/7. See Fig. 29 and the text.

	Height above ground (cm)	"Day" 17.00–19.30		"Night" 20.30–3.30		"Day" 4.00–20.00	
		Mean (7)	Max.	Mean (15)	Min.	Mean (33)	Max.
Dryas flower	4	13.3	14.7	2.6	0.5	12.1	15.2
cushion surface	2	20.8	23.3	2.3	−0.5	17.1	22.9
Silene, cushion surface	2	25.2	25.6	4.9	1.3	14.0	23.0
Surroundings	120	9.5	10.3	4.4	2.8	9.0	11.7
	5	14.7	15.5	3.6	1.5	12.0	15.2
	2	15.8	16.7	3.9	1.6	12.8	16.4
basaltic gravel	0	23.4	26.7	4.9	1.8	17.1	23.7

Table 23. Temperature measurements from the centre of flowers of *Dryas integrifolia*, July 10–12 1977, site 9. Mean of 17 measurements during 10 a.m.–6 p.m.

	10/7	11/7	12/7
In *Dryas* flower 5 cm above ground	25.5	24.1	22.3
Ambient air	20.7	20.5	21.0
Difference	4.8	3.6	1.3
Wind speed (m/sec.)	2–2.5	1.5–4	7–14

Table 24. Comparison of temperatures in the centre of flowers of *Dryas integrifolia* and *Potentilla vahliana* and in the ambient air at the same height above ground, July 7–8 1977, site 7. Mean of 15 measurements during 11 a.m.–6 p.m.

	Dryas (2 cm above ground)		*Potentilla* (5 cm above ground)	
	7/7	8/7	7/7	8/7
In flower	22.9	21.6	20.1	18.7
Ambient air	20.0	20.1	18.0	18.5
Difference	2.9	1.5	2.1	0.2
Wind speed (m/sec.)	0.5–3	1.5–7	0.5–3	1.5–7

greatest increase above ambient air temperature, 8.2°C, was found in *D. integrifolia* on July 10 at 1.30 p.m. at site 9.

In the area of Godhavn the flowers of *D. integrifolia, Papaver radicatum* and *Potentilla vahliana* are not able to manifest perfect heliotropy, because the absence of the sun for at least six hours "confuses" them so that they are disoriented when the sun reappears, and it takes some time for them to readjust. Furthermore, the flowers of *Potentilla* spp. bend downwards and partly

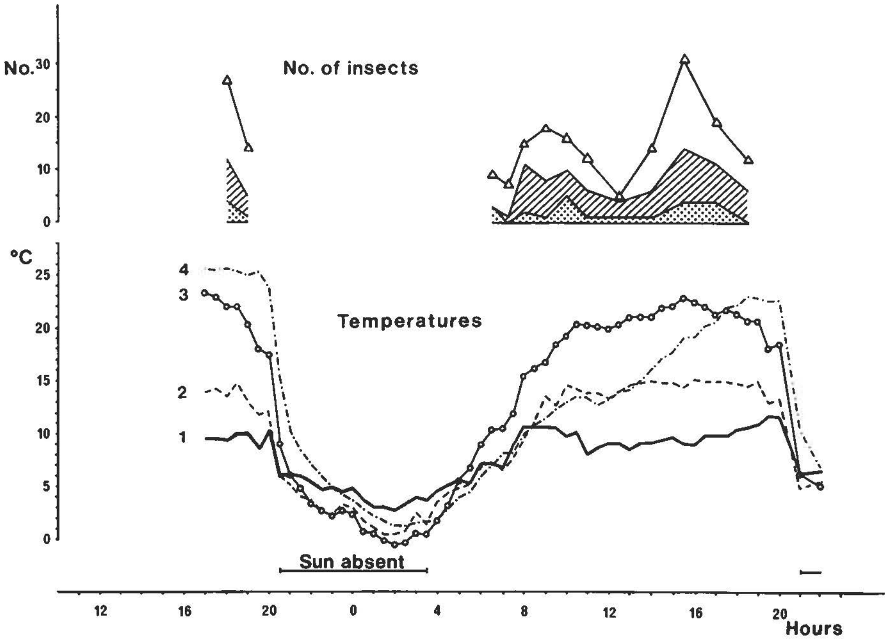


Fig. 29. The number of insects observed in c. 885 flowers of *Dryas integrifolia* on a NW-facing slope immediately N of site 9 during 13 inspection rounds, July 16–17 1976. Without signature: *Spilogona* spp.; hatched: *Phaonia* spp.; dotted: other insects. Temperature curves: 1) 120 cm above ground; 2) surface of *D. integrifolia* cushion, 2 cm thick; 3) ground surface (basaltic gravel); 4) surface of *Silene* cushion, 2 cm thick. See Table 22 and the text.

close during the "night" or when the sky is overcast, and it takes a couple of hours for them to rise and reopen during the "morning". These phenomena deserve further study.

Cushion temperature

The heating of the vegetative parts of arctic plants in sunshine is well known and has recently been studied by Mølgaard (1982) who also mentions previous investigations in this field. Several recordings of the temperatures of *D. integrifolia* mats showed that in sunshine temperatures can be very high, frequently even warmer than on an immediately adjacent exposed dry soil surface. In contrast, during the "night" in clear weather the surface temperature of *D. integrifolia* mats was always lower than anywhere else in the micro-landscape studied (Tables 19–22 and Figs 26–29).

Measurements from the surface and from just beneath a cushion indicate very efficient insulating properties which prevent the violent temperature fluctuations on the surface from penetrating the mat. On one occasion (July 10 1977, 2 p.m., Fig. 28) a gradient of 25°C (42.4°C on the surface, 17.4°C beneath) was found through a 5 cm thick mat, and during the "night" the surface was on average 5°C colder than beneath.

The thermal characteristics of *S. acaulis* cushions are similar to those of *D. integrifolia* mats, but the insulating properties appear to be less pronounced. In Tables 20 and 22 small individuals of both species of similar size and position are compared. On average *D. integrifolia* was 5°C warmer than *S.acaulis* during the "day" and the maximum value (38.7°C) was 9°C higher in *D. integrifolia*. However, a very thick and dense *S. acaulis* cushion is thermally similar to *D. integrifolia* mats, even though it does not attain such high maximum temperatures. Table 20 gives an example from a S-facing slope during optimal weather conditions. A higher maximum value in *S. acaulis* was found only on a NW-facing slope where *D. integrifolia* was horisontally oriented and *S. acaulis* was facing NW (Table 22).

Naturally, the temperature of sessile or nearly sessile flowers on these prostrate plants (especially *S. acaulis*) must be greatly influenced by the cushion surface temperature, irrespective of the physical properties of the flowers themselves.

Entomological observations

A survey of the total observations of insects in flowers is presented in Table 25.

It should be noted that only counts from the "sun period" are included in the following tables. From the previous section it appears that during the "night" the number of insects seen in flowers decreased considerably, often to zero. For details about the insects' flower visiting activity during the day, see p. 32.

Table 25. Total observations of insects in flowers of *Ranunculus nivalis* (R.n.), *Dryas integrifolia* (D.i.) and *Silene acaulis* (S.a.).

	R.n.	D.i.	S.a.
Heteroptera:			
Nysius groenlandicus (Zetterstedt)		x	x
Lepidoptera:			
Clossiana (Argynnis) chariclea Schneider	x	x	x
Colias hecla Lefebre			x
Eumichtis (Crino) sommeri Lefebre		x	x
Sympistis (Anarta) zetterstedti Staudinger		x	x
Sympistis (Anarta) spp.			x
Autographa (Plusia) gamma Linnaeus			(x)
Pyla (Salebria) fusca Haworth			x
Hymenoptera:			
Pristiphora sp.	x		
Olesicampe extrema (Holmgren)		x	
Bombus polaris Curtis		x	
Diptera:			
Mycetophilidae spp.	x	x	x
Aedes nigripes Zetterstedt		x	
Chironomidae spp.	x	x	x
Tipula arctica Curt		x	x
Empididae:			
Rhamphomyia nigrita Zetterstedt	x	x	
Rhamphomyia hirtula Zetterstedt		x	x
Syrphidae:			
Melanostoma lundbecki Collin		x	
Metasyrphus punctifer Frey		x	
Parasyrphus tarsatus (Zetterstedt)	x	x	x
Syrphus torvus Osten Sacken			x
Helophilus borealis Stæger	x	x	x
Helophilus groenlandicus O. Fabricius		x	
Phoridae:			
Megaselia groenlandica Lundbeck		x	x
Phoridae spp.	x		
Agromyzidae:			
Phytomyza vibeana Griffiths	x		
Calliphoridae:			
Protophormia terraenovae (Robineau-Desvoidy)		x	x
Muscidae:			
Phaonia pallidisquama (Zetterstedt)	x	x	x
Phaonia (Lophosceles) minima Malloch		x	
Spilogona arctica (Zetterstedt)	x		
Spilogona dorsata (Zetterstedt)	x	x	x
Spilogona sanctipauli Malloch	x	x	x
Spilogona spp.	x	x	x
Fucellia ariciiformis (Holmgren)		x	
Cordilurinae spp.			x
Hylemya (Delia) echinata (Séguy)		x	x

Dryas integrifolia (Figs 30–32)

The flowers of this species are very attractive to insects of diverse taxa (Kevan 1970). The quantitative results differed remarkably little (Tables 26, 27) so that 1.5% appears to be a reasonable estimate of the mean number of flowers in a population being visited at any one moment, and the same applies to the mean value of about 0.5 visits per flower per hour. The maximum values differed rather more. *Spilogona sanctipauli* and *Phaonia pallidisquama* together were responsible for over 80% of the total visits.

Table 26. Summary of observations of visiting insects per flower of *Dryas integrifolia* during inspection rounds (site 7a: see Table 20, Fig. 27).

Site	Date	No. of flowers (approx.)	No. of inspection rounds	Percentage of flowers visited	
				Mean	Max.
7 a	6–7/7–76	750	5	1.6	2.9
9	16–17/7–76	885	13	1.5	3.4
7	5–7 & 7–8/7–76	2915	21	0.5	1.4
9	10–12/7–77	1660	21	1.6	3.7
9	15/7–77	600	1	1.5	–

Total number of visiting insects (1331) distributed into taxonomical groups:

Spilogona spp. 1)	66.3%
Phaonia spp. 2)	20.5%
Muscidae spp.	1.1%
Syrphidae spp. 3)	3.2%
Empididae spp. 4)	1.7%
Aedes nigripes (females) 5)	0.2%
Chironomidae spp.	4.7%
Sympistis zetterstedtii	1.2%
Eumichtis sommeri	0.3%
Clossiana chariclea	0.2%
Ichneumonidae spp.	0.1%
Nysius groenlandicus	0.5%

1) About 90% *Spilogona sanctipauli.*
2) Probably exclusively *Phaonia pallidisquama.*
3) Mostly *Parasyrphus tarsatus.*
4) Mostly *Rhamphomyia hirtula.*
5) Possibly mixed with *Aedes nearcticus.*

With regard to *S. sanctipauli* it is interesting that nearly 90% of the insects caught on the flowers were males. An explanation is offered by the fact that the males use the flowers as observation posts from which to start off to catch females flying past. Following unsuccessful attempts the male usually returns to the look-out flower or another flower close to it. It alights in the centre of the flower and after a short period of confused wandering about among the pistils and stamens it finally comes to rest, basking on a petal. Very often this species is seen "diving" among the stamens in order to reach the nectar; more rarely it eats pollen. (Fig. 30).

Phaonia pallidisquama visits the flowers to feed and bask. Nine times as many females as males of this species were caught in the flowers (the reverse of *S. sanctipauli*), presumably because of the greater need for nutrition on the part of the egg-producing females. The males of this species do not use flowers as look-out posts. *P. pallidisquama* often spends long periods (more than ten minutes) in each flower, following a cyclical sequence, dividing the time between pollen-feeding, nectar-feeding and basking. The foraging on pollen is carried out in a specialized way; the anthers are squeezed between the front legs which are rubbed rapidly against each other, thus transporting the pollen to the mouthparts (Fig. 32).

Syrphidae (mainly *Parasyrphus tarsatus,* Fig. 32 e) also consume pollen from *D. integrifolia* flowers. The other visitors appear to be exclusively interested in the nectar. It is curious that the very common and ubiquitous calliphorid, *Phormia terraenovae,* was only rarely seen visiting *D. integrifolia.*

Table 27. Summary of observations of visiting insects per flower of *Dryas integrifolia* during time intervals.

Site	Date	No. of flowers	No. of observation periods	No. of visits/flower/hr.	
				Mean	Max.
6	28/6, 29/6, 4/7–76	35, 50, 40	10, 20, 15 min	0.5	0.9
7	9/7–76	40	9 × 10 –	0.5	1.5
7 x)	9/7–76	23	9 × 10 –	0.3	1.3
9	16–17/7–76	50	13 × 10 –	0.7	4.1
9	10–12/7–77	50	30 × 10 –	0.8	4.1

Total number of insect visits (320) distributed into taxonomical groups:

Spilogona spp. 1)	68.4%
Phaonia spp. 2)	17.8%
Parasyrphus tarsatus	3.4%
Phoridae spp. 6)	0.3%
Empididae spp. 4)	0.3%
Chironomidae spp.	4.7%
Aedes nigripes (females) 5)	4.1%
Tipula arctica	0.3%
Sympistis zetterstedtii	0.6%

1) About 90% *Spilogona sanctipauli.*
2) Probably exclusively *Phaonia pallidisquama.*
4) Mostly *Rhamphomyia hirtula.*
5) Possibly mixed with *Aedes nearcticus.*
6) Probably *Megaselia groenlandica.*
x) Data for *Potentilla vahliana* (visited by 8 *Spilogona* spp., 1 *Phaonia* sp., 1 *Phormia terraenovae,* 1 Chironomidae sp.).

Fig. 30. Flowers of *Dryas integrifolia* visited by *Spilogona sanctipauli*. a-b: Diving for nectar. c-d: Basking.

The insect visitation on *Potentilla vahliana* (Table 28, Fig. 5) is similar to that on *D. integrifolia* regarding species composition, visiting frequency and behaviour of insects in the flowers. Accordingly, as the two species commonly occur together in fell fields in this part of Greenland and bloom at the same time, they may be competing for insect visitors. Chironomidae are found more often in the flowers of *P. vahliana* than in those of *D. integrifolia*, especially during the "night" when the flowers of *P. vahliana* are partly closed ("sleeping movements") and offer shelter in addition to food to the delicate insects.

Fig. 31. Flowers of *Dryas integrifolia* visited by Nematocera and Empididae. a: A chironomid sp. hiding among stamens. b: Female of *Aedes nigripes* imbibing nectar. c-d: *Ramphomyia hirtula* resting and "diving" for nectar.

Fig. 32. Flowers of *Ranunculus nivalis* (a) and *Dryas integrifolia* (b, c & d) visited by *Phaonia pallidisquama* feeding on pollen. e) *Parasyrphus tarsatus* ingesting pollen in flower of *D. integrifolia*.

Fig. 33. a: *Silene acaulis,* male plant with *Phaonia pallidisquama* ingesting pollen. b: *S. acaulis,* female plant with basking *Spilogona* sp. c: *S. acaulis,* male plant visited by *Delia echinata.*

Silene acaulis (Fig. 33)

On several occasions Lepidoptera spp. (most frequently *Clossiana chariclea* and *Sympistis zetterstedtii*) were observed on the flowers of this species (Table 25), but no quantitative data were obtained. A number of flowering cushions was included in the routes (see Methods), but no insects were seen on them, suggesting a low frequency of visitation. This impression was confirmed by the inspection of 100 flowering cushions during ideal weather conditions (Table 29). No Lepidoptera were seen, but some flies which were usually merely basking on the flowers were noted. Only three individuals were seen moving into the flowers (*Delia echinata, Spilogona* sp. and *Smittia* sp.).

Table 28. Summary of observations of visiting insects per flower of *Potentilla vahliana* during inspection rounds (site 7a: see Table 20, Fig. 27).

Site	Date	No. of flowers (approx.)	No. of inspection rounds	Percentage of flowers visited	
				Mean	Max.
7 a	6–7/7–76	650	5	1.8	4.0
7	7–8/7–76	555	21	0.5	2.0

Total number of visiting insects (324) distributed into taxonomical groups:

Spilogona spp. 1)	36.7%
Phaonia spp. 2)	23.5%
Fucellia spp. 7)	3.1%
Muscidae spp.	3.1%
Phormia terraenovae	0.3%
Syrphidae spp. 3)	1.5%
Empididae spp. 4)	1.2%
Chironomidae spp.	25.9%
Ichneumonidae spp.	0.9%
Nysius groenlandicus	3.7%

1) About 90% *Spilogona sanctipauli*.
2) Probably exclusively *Phaonia pallidisquama*.
3) Mostly *Parasyrphus tarsatus*.
4) Mostly *Rhamphomyia hirtula*.
7) Probably *Fucellia ariciiformis*.

On other occasions *Parasyrphus tarsatus* was seen feeding on pollen. *Spilogona sanctipauli* uses the flowers as observation posts (cf. *D. integrifolia*), and *Spilogona spp.* were seen frequently dipping into the flowers. *Delia echinata,* however, appears to be the most regular visiting fly to *S. acaulis.* Often it was observed walking restlessly over the cushions, dipping into flower after flower. The butterflies *Colias hecla* and *Clossiana chariclea* were also occasional nectar feeders on *S. acaulis.*

In many instances cushions with ripe capsules were densely populated by the seed-eating lygaeid bug *Nysius groenlandicus.* This must undoubtedly cause a serious reduction in the number of viable seeds (J. Böcher 1972). On July 21 1976 a *S. acaulis* cushion covering 1260 cm^2 was inhabited by 93 individuals of the bug.

Ranunculus nivalis (Figs 20, 34)

Generally this species seemed to be unattractive to insects (Table 30). In spite of fine sunny weather it was possible to pass hundreds of flowers without seeing a single visiting insect, but on certain occasions the flowers were suddenly seen to be well frequented by *Spilogona* spp. and *Phaonia pallidisquama. Clossiana chariclea* was once seen visiting a row of flowers successively. This happened particularly late during the flowering period of the species, in situations where a thick snow cover had delayed flowering.

Table 29. Observations of insects visiting *Silene acaulis* 16/7 & 18–19/7–77. Insects were noted on 100 flowering cushions covering a total area of c. 30.000 cm^2 and carrying a total of c. 14.500 flowers, (i.e. c. 0.5 flowers/cm^2 cushion) at a location close to and similar to site 13.

Spilogona spp. 1)	22
Delia echinata	9
Muscidae spp.	2
Megaselia groenlandica	7
Helophilus borealis	1
Chironomidae spp.	9

1) Mostly *Spilogona sanctipauli.*

On close examination of the flowers small Chironomidae were frequently found hiding among the stamens and pistils. Often small swarms of chironomids were seen hovering above the flowers and alighting on them and on other parts of the plants. The possible pollinating role of these insects is unknown.

Phytomyza vibeana was found exclusively in the flowers of *R. nivalis,* and besides Chironomidae, comparatively many Mycetophilidae were caught on *R. nivalis.*

Population structure and resource allocation

Long-term observations of populations of known age structure are necessary for the proper determination of the characteristics of the populations in the field. Few of these are available for perennials, and they are not available for arctic plants. We had to rely on "instant" samples and we have no satisfactory measure of age for the three species under discussion. (cf. Callaghan & Emanuelsson 1985). We measured sizes of plants and

Table 30. Summary of observations of visiting insects per flower of *Ranunculus nivalis* during time intervals.

Site	Date	No. of flowers	No. of observation periods	Mean no. of visits/ flower/hr.
4	24/6–76	70	15 min.	0.1
8	4/7–76	60	15 -	0.0
8	2/7–77	90, 56	2×15 -	0.6

Total number of insect visits (46) distributed into taxonomical groups:

Spilogona spp. 1)	80.4%
Chironomidae spp.	19.6%

1) Mostly *Spilogona sanctipauli* and *S. dorsata.*

Fig. 34. Flowers of *Ranunculus nivalis* visited by *Spilogona sanctipauli* (a-b), a: Probably ingesting pollen. b: Basking, and by *Sciarinae sp.* (c-d), c: Resting. d: Diving for nectar.

constructed size-class histograms, which can often be more meaningful than age-class histograms (Werner & Caswell 1977).

Dryas integrifolia

Shrub demography is less understood than that of trees or herbs. Shrubs are long-lived and have a slow turnover but they do not have the economic importance of trees and have therefore been neglected in population studies. Several of the species studied have been from arid regions (Chew & Chew 1965, Roughton 1972, Crisp & Lange 1976, West et al. 1979). In the Arctic, growth rates are so slow (Wager 1938) that even small plants may be decades old, and shrubs may live for centuries.

Our observations of *D. integrifolia* (Fig. 35) demonstrate distinct differences between populations. Those at sites 3, 6 and 9 are similar and typical of populations undergoing reasonably regular natality and having a

Table 31. Allocation (per cent) to different parts of plants in different sized individuals of *Dryas integrifolia*.

Total dry weight (g)	Assimilating tissue	Non-assimilating tissue	Roots	Flowers
0.0088	3.4	72.7	23.9	0
0.1211	28.6	54.7	15.8	0
0.8379	21.4	41.4	36.5	0.7
0.8399	27.0	60.1	12.9	0
2.6706	25.8	66.8	10.0	0
3.3446	18.1	74.6	6.9	0.4
9.3996	10.4	66.3	23.3	0
9.6183	11.3	82.0	6.5	0.2
13.7529	8.4	66.3	25.3	0
47.7867	4.6	75.8	19.5	0.04
165.7461	4.4	83.7	12.0	0.16

declining rate of mortality with increasing age with a consequent long "tail" of large plants. Nonetheless, they show signs of not quite regular recruitment as all three populations have deficits of seedlings and very small individuals, and the careful search that was conducted leaves us in no doubt that this deficit is real. Populations at sites 6 and 9 show peaks in the 36–40 cm and 48–52 cm size classes which may represent past episodes of better than normal recruitment. In both there is also a gap below the largest size classes which may also represent a long period with low recruitment. Alternatively, they may indicate very long survival of few individuals.

The site 7 population is quite distinct. No real decline in numbers occurs in any size class until the 52–56 cm diameter class is reached. It has similar gaps among the larger size classes, and is further distinguished by the presence of a few very large individuals.

Silene acaulis

This cushion species is also long-lived. We have data from four sites (Fig. 36). The populations at sites 3 and 13 both occur in areas of high vegetation cover and show regular natality and decreasing rates of mortality. Those at sites 7 and 9 are in marked contrast with peak numbers in quite large size classes, no seedlings and very few small plants. Again, there are gaps betweeen groups of large size classes, especially at site 7.

One population of *S. acaulis* was observed in two successive years (Fig. 37) near site 3 in a gravelly outwash which was damp and occasionally waterlogged. All the plants in the population which covered an area of 16 m^2 were recorded in both years, thus enabling a direct comparison. In 1976, 78 of the plants (35%) were at the seedling or single rosette stage. In 1977 all the seedlings and all but one single rosette had disappeared, and the population dropped from 219 to 121 individuals. Most individuals could be identified from the previous year's notes and there appeared to be no loss of plants more than 1 cm in diameter.

Both in this species and in *D. integrifolia* the relationship between plant size and flowering was explored (Tables 31, 32), and they exhibit similar patterns with the number of flowers reaching a peak in small size classes and then declining.

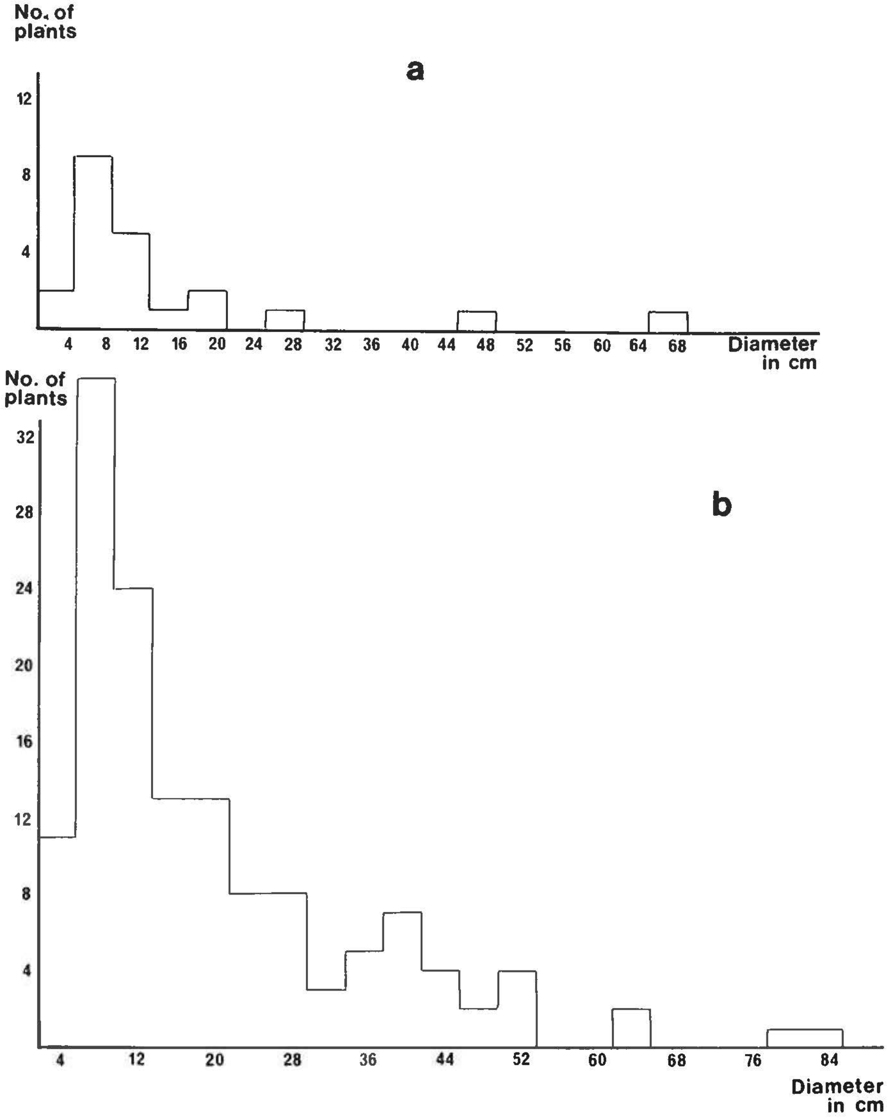
Ranunculus nivalis

We have characterised this species' populations by classifying the individuals into categories with non-flowering plants and with flowering plants subdivided according to flower number. These are best regarded as "life-states" (in the sense of Rabotnov 1978). The largest class is of one-flowered individuals (Fig. 38). It is pos-

Table 32. Allocation (per cent) to different parts of plants in different sized individuals of *Silene acaulis* (ros. = rosette).

Total dry weight (g)	Size	Assimilating tissue	Non-assimilating tissue	Roots	Flowers
0.0255	1 ros.	35.8	32.5	32.8	0.0
0.0373	1 ros.	9.4	44.6	45.6	0.0
0.0379	2 ros.	14.7	70.7	15.6	0.0
0.6087	3 ros.	8.5	81.0	10.6	0.0
0.6616	3 ros.	7.5	84.1	8.4	0.0
0.6718	4 ros.	15.2	70.7	14.1	0.0
0.1618	2×1 cm	9.4	73.7	17.9	0.0
0.2025	1.5×1 cm	7.1	72.5	20.4	0.0
0.2147	–	4.8	83.4	11.5	0.0
1.7858	4×4 cm	7.8	86.3	5.9	0.0
1.8410	4×3 cm	8.1	84.4	7.6	0.0
2.1226	5×4 cm	10.9	77.2	7.3	2.8
2.8880	–	14.3	76.9	6.0	2.9
4.6200	7×6 cm	11.1	77.7	8.8	2.4
21.5000	–	10.3	81.7	6.0	2.0
163.7000	–	5.3	80.1	13.6	1.0

Fig. 35. Population structure of *Dryas integrifolia*. a: Site 3. b: Site 6. c: Site 7. d: Site 9 (c and d on following page).



sible that individuals remain at this stage for several years while replenishing the energy expended in the first flowering.

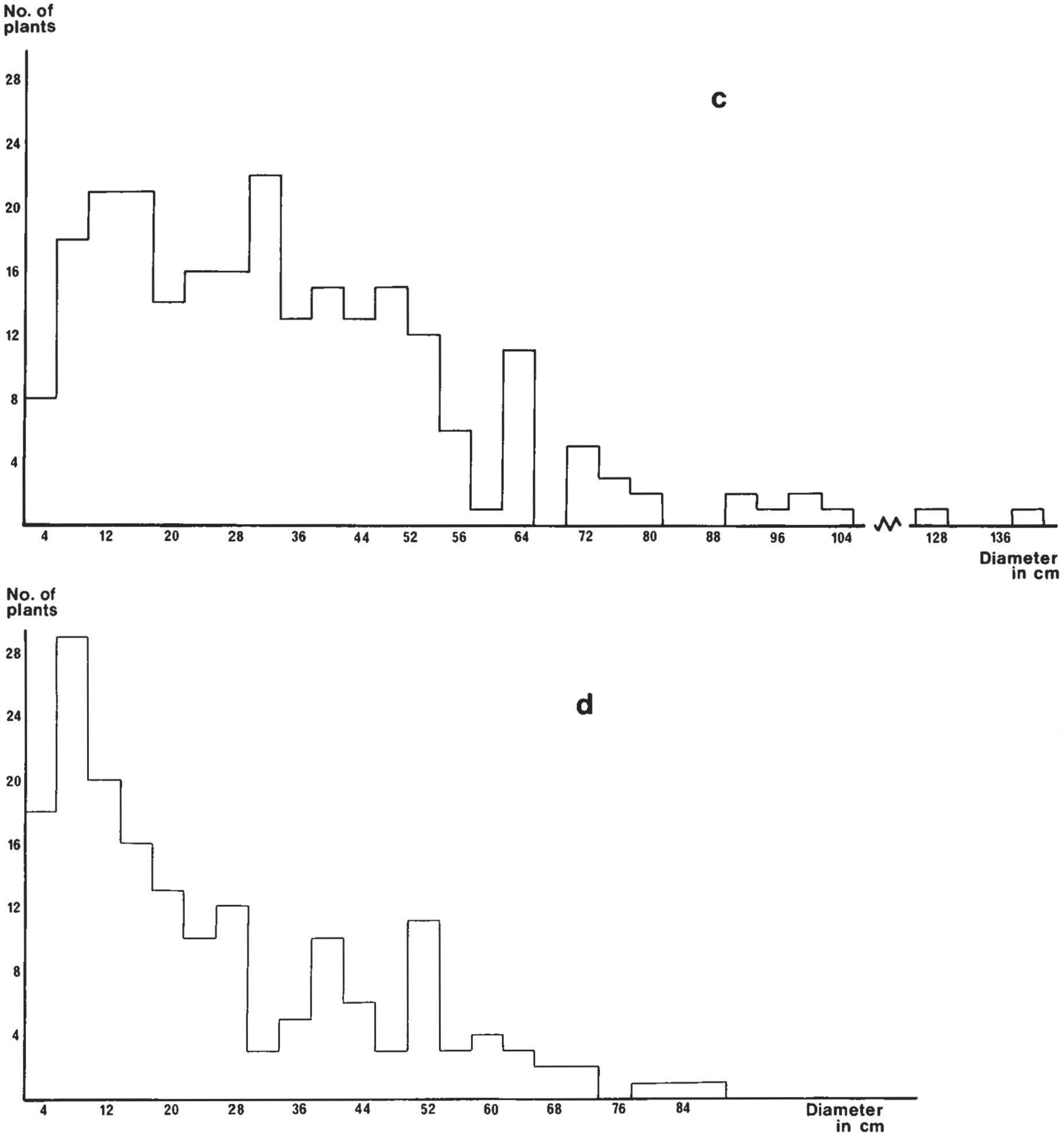
Allocation of resources

The data from the harvest of individuals of different sizes are presented in Tables 31–33 as absolute values and as percentages of total dry weight.

In *D. integrifolia* the assimilating tissue is a very small proportion of small plants, but increases to 25% before declining to a steady 4% in large plants. The amount allocated to inflorescences is very low at all stages. In contrast, the very small *S. acaulis* plant has a third of its dry weight as assimilating tissue, after which c. 10% ends in this category. Inflorescences comprise again a rather small proportion of total dry weight.

Table 33. Allocation (per cent) to different plant parts in plants of different sized individuals of *Ranunculus nivalis*.

Total dry weight (g)	Stage	Assimilating tissue	Roots + rhizomes	Flowers
0.0121	Young non-flowering	11.3	88.7	0.0
0.149	Non-flowering	24.7	75.3	0.0
0.019	1 flower	53.4	40.3	6.3
0.024	–	42.4	44.6	13.0
0.069	–	56.3	26.8	16.9
0.034	–	48.5	34.1	17.3
0.085	–	48.0	41.7	10.3
0.100	–	39.6	46.6	13.8
0.123	–	44.5	38.8	16.7
0.127	2 flowers	57.8	30.1	15.2
0.119	–	52.3	30.9	16.8
0.210	–	45.3	38.8	15.9
0.306	3 flowers	40.8	42.3	17.2



R. nivalis is very different. There is an initial massive investment (nearly 90%) in below-ground tissue, but in flowering individuals the below-ground and assimilating tissues are more or less equal at about 40%. In contrast to the other species *R. nivalis* allocates a large proportion of its resources to flowering at all stages.

Seedling establishment

Seedlings are few in all the species and the low numbers of very small plants suggests that seedling mortality is high. This is in agreement with some published data (e. g. Bliss 1971). The presence in 1976 of capsules of *S. acaulis* containing ripe seeds from 1975 enabled us to set up a seedling establishment experiment at sites 7 and 13. The seeds were sown in plastic cylinders 22.6 cm in diameter and 5 cm deep. They gave some protection from the persistent downslope soil movement. Three were used at site 13 and four at site 7. They were sunk into the soil so that the upper edge protruded 0.5 cm above the surface. In each cylinder we sowed 49 seeds on a 7 x 7 grid on August 9 1976.

The experiments were revisited in 1977. There was no germination in two of the plots at site 7. Some germina-

Table 34. Germination and survival of seedlings of *Silene acaulis* at sites 7 and 13, 1977. Each plot had 49 seeds. Figures are number of seedlings present.

	Site 13			Site 7			
Plot	A	B	C	D	E	F	G
1 July	9	8	5	4	0	0	8
4 July	9	10	11	6	0	0	10
5 July	10	9	12	4	0	0	10
7 July	12	8	11	4	0	0	6
14 July	10	12	12	5	0	0	5
20 July	10	14	12	6	0	0	1
	Peaty soil					Gravel	

tion occurred in the others, but the seeds had often moved within the cylinders. The site 13 sowings were on peaty substrates and here movement was less.

The results (Table 34) show that all the seedlings which appeared in the peaty soils survived until our last day of observation, but all but one of those in the gravel had died by July 20. The summer was dry and the seedlings had wilted. Other seedlings appeared in the area at both sites and many of these also died in mid-July.

Discussion

This paper deals with a broad range of topics in relation to three species. In order not to lose sight of the specific information regarding each species and each section of our results, these will be dealt with in turn, and we shall conclude with a general discussion in which we shall discuss the wider implications of the work.

Dryas integrifolia

D. integrifolia could be regarded as the most important of the three species discussed here because of its abundance in every habitat, its value as a resource for insects and its wide distribution in the Nearctic. The genus *Dryas* has been studied by several biologists (Elkington 1965, Hulten 1959, Kevan 1972, McGraw & Antonowics 1983), but much of this work has either been carried out on *D. octopetala* or has been taxonomic, and the taxonomic problems in defining the species do not concern us, since only *D. integrifolia* occurs on Disko.

While published accounts have discussed one or a few aspects of the biology of the species, no one has looked

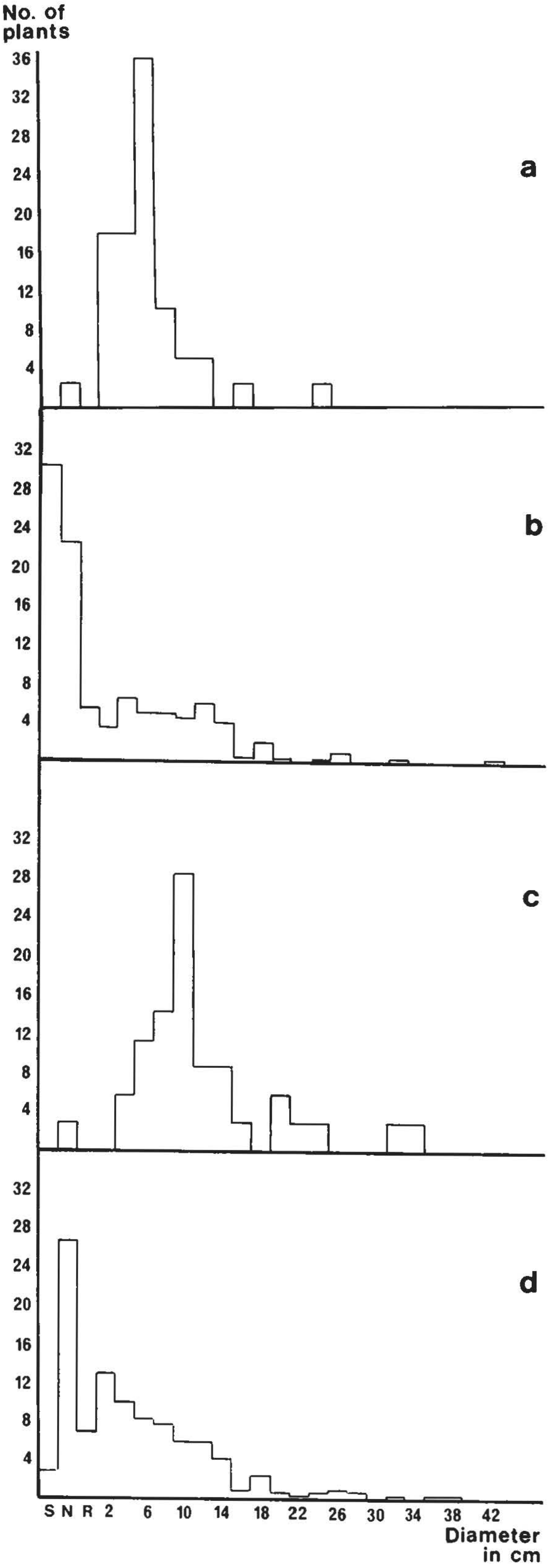


Fig. 36. Population structure of *Silene acaulis*. a: Site 9. b: Site 13. c: Site 7. d: Site 3 (S = seedlings; N = one rosette; R = 2–3 rosettes).

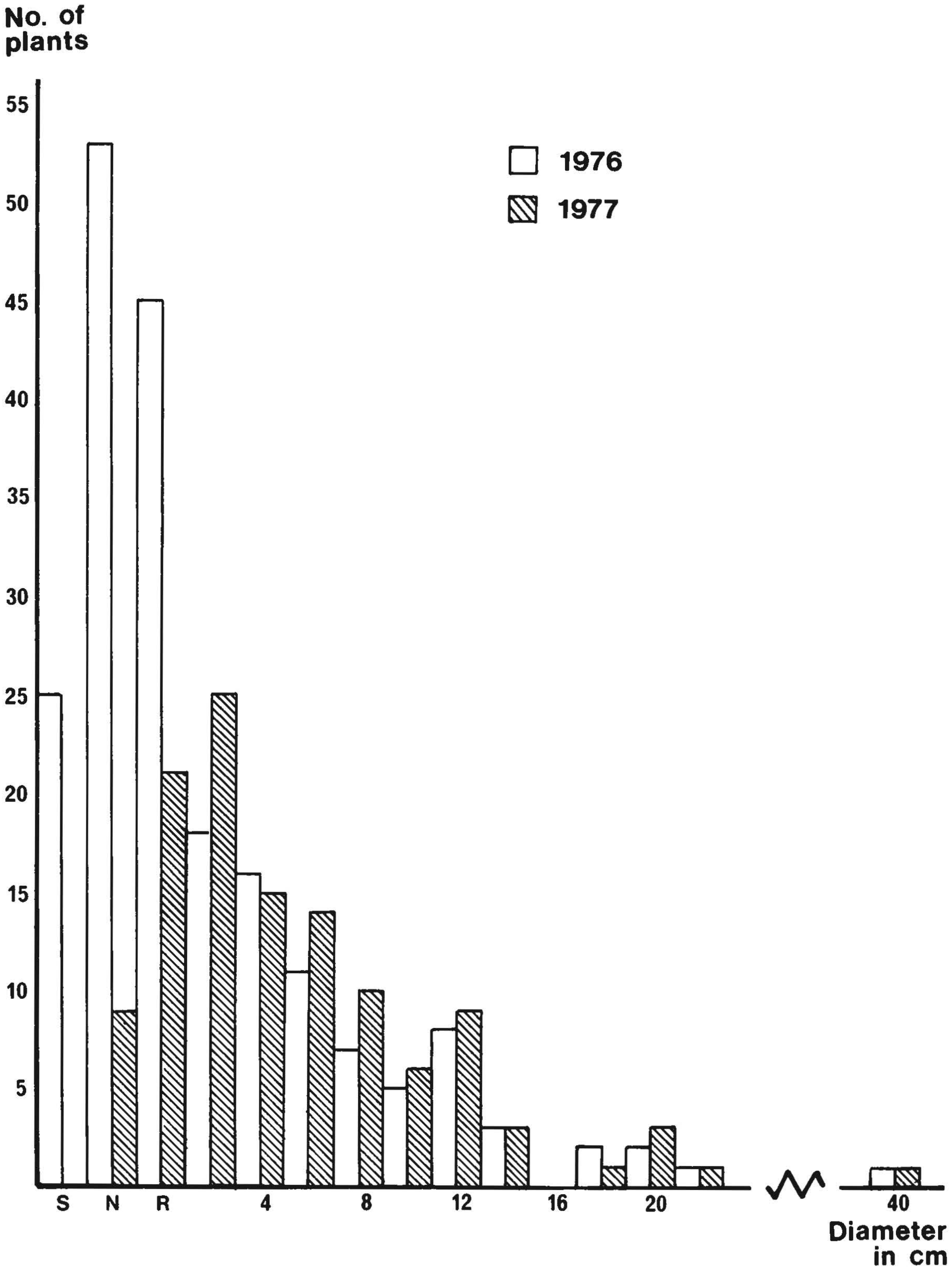


Fig. 37. Population structure of *Silene acaulis* in the same area in two consecutive years (S = seedlings; N = one rosette; R = 2–3 rosettes).

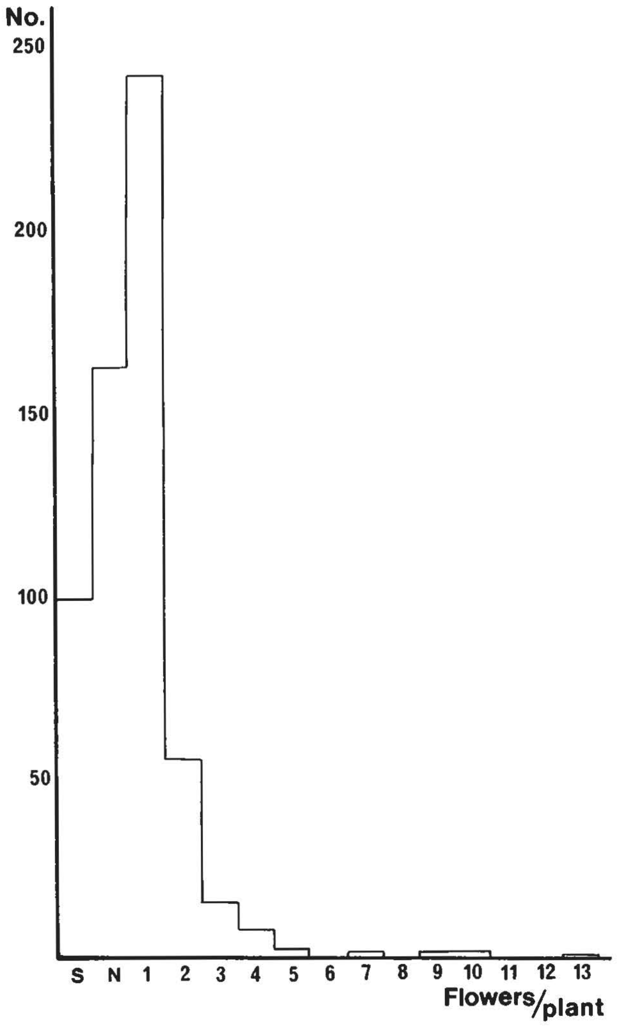


Fig 38. Population structure of *Ranunculus nivalis* (S = seedlings; N = one rosette).

at its reproduction as a whole and in quantitative terms. The main object of our study was to attempt to quantify all aspects of the species' reproduction, and ultimately to produce a reproductive budget.

Even within the limited geographical area of our study, there was considerable variation between sites, e. g. as to flowering periods and numbers of reproductive structures (Tables 4, 5, 7, 38). The sites can be arranged subjectively in order of severity based on their degree of exposure, soil instability and vegetation cover with site 6 being the most favourable and site 7 the least. This scaling is reflected in the decreasing number of individuals per m^2 (Table 38) and in the number of stamens and carpels per flower at the three sites (Table 4). The percentage of flowering individuals and the number of flowers per plant are, however, clearly higher at site 7 than at site 9. Moreover, the highest number of pollen grains per anther was counted at the former site . This leads to a P/O-ratio nearly 30% above that of site 9.

The significance of this higher ratio is unclear. We made the estimate (p. 17) that an average of approximately 20 pollen grains per stigma is adequate to ensure pollination of all carpels, and number af pollen grains per se are hardly limiting for fertilisation at any of the sites.

One explanation of the larger number of pollen grains per anther at site 7 might lie in the ontogeny of the flower. A smaller floral apex probably resulting from the more severe environment will lead to a reduced number of stamens and carpels, but at the same time offers an opportunity for individual organs to grow bigger. We should bear in mind that the explanations for differences of the kind we have demonstrated do not necessarily have any evolutionary significance, and knowing so little about the genetic background of the species we should be cautious in seeking evolutionary answers. However, we cannot exclude the possibility that it might be an advantage in a more severe habitat to increase the pollen/ovule ratio, thus increasing the likelihood of fertilisation.

At site 7 the P/O-ratio is higher and the proportion of male flowers is lower than at site 9. These may be alternative means of achieving a sufficient high level of pollen grains in the population.

As to the higher proportion of flowering individuals and the higher number of flowers per plant at site 7 compared with site 9, we regard this as consistent to a common physiological reaction towards "extreme" environments, of which site 7 is an example. This reaction may be seen as partly compensating for reduced plant density.

In spite of the fact that self-pollination is possible in *D. integrifolia* the pollen/ovule ratio is more in accordance with those of outbreeders in Cruden's (1977) list. It is worth noting that the closely related *D. octopetala* is self-incompatible (McGraw & Antonowics 1983). Unfortunately, we do not have comparable figures for *D. octopetala* pollen/ovule ratios, but we would expect the change toward self-compatibility to occur more easily than changing pollen/ovule ratios.

Seed set varies from site to site and although there is a reduced absolute number of seeds per flower it is remarkable that the highest seed set in relation to the number of carpels per flower is at the most exposed site. Nevertheless, this is in accordance with the point discussed above, namely the possible advantage of increasing the pollen/ovule ratio.

Kevan (1972) studied local differences in seed set in *D. integrifolia* on Ellesmere Island and found that percentage seed set, as measured by the percentage of well-developed seed heads, varied from 84% along water courses with sedgy areas, down to 38% in dry areas, and ranged between these extremes in intermediate habitats. He interpreted the results as reflecting the suitability of different habitats for pollinators and hence their abundance.

Since Kevan gave no quantitative information about insect activity it is not possible to make a direct comparison. Our data (Tables 26, 27) suggest that insect activity differs little between sites. We cannot at this juncture suggest any obvious reason for the differences in seed set between our sites. We can assert that insect activity is unlikely to be the main reason, since despite greater activity in 1977 seed set was lower at all our sites.

Silene acaulis

This species is well known for its sexual trimorphism (Hegi 1979, Böcher et al. 1968). Shykoff (1988), however, studied a population of *S. acaulis* which was gynodioecious. We consider females, males and hermaphrodites to be genetically fixed. Observations of many hundreds of plants have never shown an individual with a mixture of male and female flowers. Among the scanty hermaphrodites, one can find plants with a few female, and more frequently a few male flowers – the hermaphrodite plants are somewhat labile with respect to their sexuality.

The proportion of the sexes vary from site to site (Table 11). We have arranged the sites subjectively in order of increasing severity and there appears to be an increase in the proportion of females along this gradient. We have no definite explanation of this and the limited literature on sex ratios v. environment is inconclusive (Putwain & Harper 1972, Wade et a1.1981). We could detect no difference in average size between male and female cushions.

Female predominant sex ratios have been investigated by Lloyd (1973). His model predicts that the maximal seed set for dioecious species will occur when females predominate, providing that pollinators visit each flower more than once. The mechanism by which an unequal sex ratio can be established in *S. alba* has been shown to be differential gamete success (Correns 1928, Mulcahy 1967). The difference in success between male and female gametes is suggested to be caused by an accumulation of non-functional genes in the y-chromosome.

Unfortunately, we have no estimate of the number of insect visits per flower for this species, but we know that visits are rarely observed and that only a fraction of the flowers are pollinated (Table 35). The number of germinated pollen grains per pollinated flower (Table 35) increases from site 3 to site 7. If the number of grains found on the stigmas are on average below the number needed for maximal seed set, no pollen tube competition should occur, resulting in a 1:1 sex ratio, which is approximately the case at site 3. At site 7 the highest average number of germinated pollen grains per pollinated flower is found (Table 35) and thus, a higher gamete competition possibly occurs, resulting in a female predominant sex ratio. At site 13 the same average number of germinated pollen grains per pollinated flower is found, but the percentage of females is about fifty, indicating a non-existing gamete competition. In all cases the number of germinated pollen grains is lower than the number of ovules per flower, which might mean that no gamete competition takes place at all. On the other hand, the number of ovules developing to mature seeds is much lower (2.8–5.2 per flower) than the number of ovules. This low number might be determined by the low number of pollen grains per flower, or by a limited amount of other resources. In both cases a possibility for sexual selection exists (mostly at the more severe sites; Willson & Burley 1983), and as the system also includes hermaphrodites it seems to be worth a special study.

Table 35. Number of germinated pollen grains per flower of *Silene acaulis* at three sites.

Site	No. of flowers	% pollinated flowers	Mean no. of germinated pollen grains per pollinated flower
3	306	33	12.2
13	180	45	16.4
7	121	13	17.7

In any single population the female plants come into flower first (Table 12) and continue to flower after the males have finished. This is the usual pattern of flowering phenology in gynodioecious plants (Philipp 1980).

Male flowers are open for fewer days than either females or hermaphrodites (Table 14). Hermaphrodite flowers which perform two functions are open longest. Their average period of stigma exposure, however, is only half that of the females. This difference could result from more rapid pollination and a following more rapid withering of the styles in the hermaphrodite flowers than those of the females. That stigmas of female flowers are exposed for a long time (six days) could have at least two further, rather similar adaptive explanations: 1) They come into flower first, thus enhancing the possibility of long-distance pollination due to the long exposure of the stigma, and 2) even during the main flowering period the female is given a greater variety of pollen grains and the chance to choose (Willson & Burley 1983).

The persistence of hermaphrodite plants in this species may lie in the "insurance value" which increases the likelihood of at least some reproduction even if the females fail to set seed.

The pollination and isolation experiments showed that we can increase seed set of individual flowers by a factor of three using artificial pollination. This could be interpreted as a result of lack of pollinators, as is often stated, and it cannot be ruled out here, as we recorded rather few insect visitors to *S. acaulis*. On the other hand, high pollination levels in nature may not result in much higher seed set, because the plants may not be able to allocate adequate resources to allow all flowers to produce large numbers of seeds. In the cushions where we pollinated the flowers such resource allocation problems may not exist, since we pollinated only a few in relation to the total number of flowers on each cushion.

Ranunculus nivalis

The demography of other species of *Ranuculus* has been studied elsewhere and this enables us to make some comparisons which are not possible for *D. integrifolia* and *S. acaulis*. The data, however are limited. There is none available on flower phenology, pollen production or germinated pollen on stigmas. Recently, Järvinen (1984) compared *R. glacialis* with the three north temperate buttercup species *R. acris, R. bulbosus* and *R. repens* (Sarukhan & Harper 1973, Harper 1977). We have data for *R. nivalis* which can be matched with theirs (Table 36).

R. nivalis, in terms of density, flower production and achene production produces results of the same order as the other species, in most respects in between the extreme arctic/alpine *R. glacialis* and the three temperate species. *R. nivalis* has no vegetative propagation, and it produces many achenes of small size (1.1 x 1.0 mm) from a relatively low number of flowers. Compared to *R. glacialis,* which Järvinen considers a colonizing species, *R. nivalis* is found in much more stable and sheltered habitats, and this may be reflected in the lower number of achenes per square metre.

Microclimate

Our data illustrate the well-known phenomenon that even in an arctic environment the climate near the ground is very much warmer than the "macroclimate" (e.g. Sørensen 1941, Downes 1965, Kevan & Shorthouse 1970, Dreisig 1981). This amelioration of the climate is especially important in the Arctic, making possible plant growth and insect activity.

Sunshine is of paramount importance. As soon as the sun dips behind the mountains insects cease to frequent flowers, undoubtedly because of the rapidly decreasing temperature. Our data (Figs 26–29 and Tables 19–22) confirm that the number of active insects is highly dependent on climatic conditions (see esp. Figs 28, 29), and also that there is replacement of some insect groups by others during the "day" and "night" alternation. In this context it is worth noting that during spells of cool overcast weather, and particularly when it is raining, insects are inactive and shelter beneath vegetation. After such a spell they emerge rapidly, and within a few minutes of the appearance of the sun, large numbers of insects can be seen visiting flowers.

Another important factor affecting activity is wind speed. Even in warm sunny weather a wind-speed of more than 4 m/sec. is enough to prevent most visits to flowers.

The heating of the heliotropic flowers of *D. integrifolia* above ambient air temperature in sunshine was again demonstrated (cf. Hocking 1968, Kevan 1970, 1972, 1975). This has recently been shown to influence seed set as well (Kjellberg et al. 1982). The flowers are situated close to the mat surface which, due to excellent insulating properties, is generally warmer than any other place in the micro-landscape. The heat conducted from the mat to the flowers probably has a greater effect on the flower temperature than that generated within the flower itself. This applies even more to the nearly sessile flowers of *S. acaulis.* Heliotropic flowers held on long pedicels, such as those of *Papaver radicatum,* depend much more on heat generated within the flowers themselves (Kevan 1975). The importance of temperature for seed set has been demonstrated in *Cirsium acaule* by Pigott (1968).

Entomological observations

It is notable that the distribution of taxa of insect visitors to the flowers studied (Table 25) is in close agreement, even at the species level, with the observations by Kevan (1970, 1972) from the high arctic locality, Lake Hazen on Ellesmere Island at nearly 82° N.

Of the three species studied the flowers of *D. integrifolia* were by far the most attractive to insects, and

Table 36. Comparison of reproductive characteristics of five species of *Ranunculus.*

Species	Individuals/m^2	Flowers/m^2	Flowers/flowering individual	Achenes/flowering individual	Achenes/m^2	Vegetative propagation
R. acris	c. 50	40–110	3.2–5.0	10	1000	+
R. bulbosus	c. 50	70–110	3.7–4.0	15	500	none
R. glacialis	c. 10	13	3.2	500	2300	none
R. nivalis	29.45	25.7	1.53	65.9	1110	none
R. repens	c. 150	10–50	1.3–1.4	1	100	++

the mean number of visits (0.5/hour) is more than enough to ensure adequate pollination, even taking into consideration the fact that not all insects will carry pollen or cause it to be transferred from anthers to stigmas by their movements in the flowers. The same is true of *Potentilla vahliana*. Though the systematic observations of *S. acaulis* were negative, other observations (Table 29) showed that there are fairly frequent visitors, and we often noted Lepidoptera visiting cushions and probing the flowers for nectar. The seed set obtained in this species indicates that there must be a reasonable level of visitation.

R. nivalis was regularly visited by Chironomidae and they may be important pollinators. Despite long periods during which no insects were seen on the flowers there were "falls" of large numbers of insects from time to time, and these may be quite sufficient to ensure pollination. Experience here and elsewhere suggests that sporadic visits to flowers may account for a high proportion of pollinations, and one must be lucky to be at the site at the moment they occur.

We were interested in the possibility of competition for pollinators between the adjacent and concurrently flowering *D. integrifolia* and *Potentilla vahliana*, but during our period of observations the insect activity was very high and no competition could be demonstrated. Shortage of insects can occur in the Arctic as shown by Kevan (1972), and competition has been demonstrated both in natural (e.g. Mosquin 1971) and agricultural contexts (e.g. Free 1968). In places where insects are less abundant than they are on Disko it could well be significant.

Population structure and allocation

The causes of the irregular recruitment that is indicated by the size class diagrams (Figs 35–38) could have been intermittent failure of seed production, failure of seedling establishment or loss of young individuals during unfavourable periods, or a combination of these effects. The loss of a whole cohort of *S. acaulis* in one population illustrated in Fig. 37 is a clear indication that massive loss of young individuals does occur.

The distribution of size classes in *D. integrifolia* at site 7 is most distinctive. It is the most exposed site, steeply sloping and undergoing rapid solifluction. Markers on the site moved considerably between 1976 and 1977, and we observed active downslope soil movement on one day of heavy rain in 1976. Establishment may be especially difficult on this site , and possibly the slow and variable vegetative growth may blur the distinctions between size classes.

At all sites there are gaps in the large size classes, and since these are the groups least likely to suffer high mortality, these gaps may well represent periods when recruitment was low or absent. Episodic recruitment has been observed in arctic areas by Wager (1938) and Petersen (1981), and in an area where establishment is generally difficult it is possible that there are sometimes long intervals between successful episodes of recruitment. Both *D. integrifolia* and *S. acaulis* indicate that this may have been the pattern of population increase in the past. We are dealing here with plants whose life spans may extend to centuries, and it would not be surprising to find that new individuals are added to the populations at long and maybe irregular intervals.

The evidence for *R. nivalis* is more equivocal. Given the sheltered habitat at site 8, fed by a "warm" stream and with no problems of water deficit, recruitment may be more regular and frequent – certainly the present population structure seems to suggest that this is so.

The consideration of resource allocation must include two aspects; the proportions of resources allocated to different tissues at different ages of the plant, and the ages or sizes at which flowering is at a maximum. In the latter respect *R. nivalis* differs markedly from the other two species. Being a shorter-lived herbaceous perennial it appears to be capable of allocating a large proportion of its resources to flowering, presumably aided by its high allocation to assimilating tissue throughout its life.

For two of the species, *D. integrifolia* and *S. acaulis*, there are some data on resource allocation on Ellesmere Island (Maessen et al. 1983). The differences between our sampling methods do not make comparison easy. They sampled randomly along preset lines, whereas we deliberately chose our plants to obtain a wide range of sizes, and thus assess the changes in components of resource allocation during life. If we "lump" our data into population samples the coefficient of variation is so high as to render the information almost valueless. In order to attempt a comparison we selected some individuals from the middle size ranges and calculated mean values and CVs for them. The resulting comparisons (Table 37) are instructive, despite the reservations concerning the comparison of data collected in different places and in different ways.

In *D. integrifolia* the percentage allocation to both assimilating tissues, inflorescences and below-ground tissues is much higher on Disko than on Ellesmere Island. In *S. acaulis* the most puzzling difference is the relative allocation to flowers and assimilating tissues. On Disko, 3% is allocated to flowering and 10% to assimilating tissue, whereas on Ellesmere Island the comparable figures are 1.56% to flowers and 1.36% to assimilating tissue.

It is a pity that these two studies are not more easily comparable. Our aim was to study change in allocation during the life history, and time did not allow for replication of samples at different sizes. Maessen et al. (1983) have not documented the differences in sizes of their plants. Nevertheless, even these limited comparisons suggest that there are considerable differences between the plants at these two localities.

What is clear from our data as to allocation to differ-

Table 37. Relative allocation of resources (dry weight, g) to different plant components in high arctic (Ellesmere Island) and low arctic (Disko) populations of *Dryas integrifolia* and *Silene acaulis* (non-assimilating tissue includes both non-photosynthesizing live and attached dead tissue, * is the CV for "attached dead" only in the Ellesmere Island samples).

Species and no. of samples	Component	Ellesmere	CV	%	Disko	CV	%
Dryas	Inflorescence	0.065	18	0.175	0.064	17	0.819
6 (Ellesmere)	Assimilating	0.708	48	1.910	0.901	27	11.500
5 (Disko)	Non-assimilating	33.590	27*	90.390	5.49	59	70.350
	Below-ground	2.800	26	7.53	1.360	105	17.400
Silene	Inflorescence	0.030	30	1.565	0.085	30	3.163
22 (Ellesmere)	Assimilating	0.026	15	1.360	0.293	56	10.900
5 (Disko)	Non-assimilating	1.749	38*	91.240	2.113	41	78.640
	Below-ground	0.112	61	5.842	0.196	61	7.294

ent components as well as to numbers of flowers in relation to plant size is that these long-lived perennials go through a phase in "early middle age" during which they have sufficient resources to allocate some (but never a very substantial proportion of them) to flowering. After this they decline, and progressively less resources are available for flowering. Many large individuals, especially of *D. integrifolia,* flower rarely if at all. The situation is less extreme for *S. acaulis,* which is able to continue to allocate more resources to flowering than *D. integrifolia* because of its large commitment to foliage throughout life.

The large non-flowering plants simply occupy space during their long period of decline, and since they are non-flowering they are no longer able to contribute to the gene pool. Occasionally, one may find a very large plant covered with flowers. What enables such a plant to suddenly produce many flowers is not clear, but it does suggest that even these individuals may sometimes continue to make a contribution to the sexual reproduction of the population. Possibly the persistence of non-flowering individuals has two advantages. The peaty substrate beneath the slowly disintegrating cushions of *D. integrifolia* provides a good site for seedling establishment and hence perpetuation of the species at that spot. The occupation of area may be seen as advantageous in that it pre-empts that space for the species and prevents others from growing there. Since they do not propagate vegetatively there is no possibility for the kind of regeneration of vigour documented by Kershaw (1960) in *Alchemilla alpina.* What would be useful here are long-term observations of individual plants. Just how variable is an individual in the amount of flowering it permits from year to year? How much is this affected by climatic fluctuations? This is a fascinating area where much too little is known. Even the painstaking work of Aleksandrova (1988) dealt with only one season.

Conclusions

The reproductive budget

One of the purposes of the present project was to compile a "reproductive budget" (Woodell et al. 1977) for the species to demonstrate quantitatively how much emphasis arctic species place on sexual reproduction (Tables 38–40). We conclude that at all stages in the reproductive cycle there is a high resource investment in sexual reproduction.

When analyzing the reproductive cycle, we must distinguish between three levels of reproductive capacity: **potential**, **actual** and **realized** (Table 41). **Potential** reproductive capacity is a measure of the number of seeds obtainable under ideal conditions, and it should be the same as the number of ovules. This definition is slightly different from that of Callaghan & Emanuelsson (1985). **Actual** reproductive capacity is a measure of the number of seeds produced (Salisbury 1942). **Realized** reproductive capacity is a measure of the number of established individuals in the field from these seeds.

From scrutiny of the reproductive budgets it becomes obvious that with one exception, *Silene acaulis*, where the amount of pollen deposited on stigmas may be limit-

Table 38. Reproductive budget for *Dryas integrifolia.* All figures are per square meter.

	Site 6	 7	 9
Number of individuals	1.19	0.66	1.03
Flowering plants	0.72	0.41	0.29
Flowers	6.83	2.53	0.96
Ovules	493.4	131.6	67.2
Stamens	626.1	189.8	83.2
Pollen grains	1329398.1	497334.8	177866.8
Normal pollen grains	1073010.1	394680.0	143819.5
Mature fruits	408.4	132.8	55.8
Seedlings	0.0	0.1	0.1
Young plants	0.06	0.4	0.3

Table 39. Reproductive budget for *Silene acaulis*. All figures are per square meter (Herm. = hermaphrodite).

	Site 3				Site 7		Site 13	
	Male	Female	Herm.	Total	Male	Female	Male	Female
Flowering plants	7.4	5.4	1.4	14.2	0.15	0.38	0.34	0.30
Flowers	237.0	112.2	12.8	362.0	11.6	34.9	10.44	10.82
Ovules		3002.5	308.4	3310.9		933.9		260.7
Stamens	2370.0		128.0	2498.0	116.0		104.0	
Pollen grains	2922992.1		157866.2	3080858.3	169770.6		176601.0	
Mature seeds		583.4	156.2	739.6		89.3		
Seedlings				0.2	0.025		1.12	
Young plants				0.8	0.005		0.28	

ing, the crucial factor in all three species seems to be the realized reproductive capacity, i.e. seedling establishment and possibly seed germination. In this respect our conclusions are similar to those of many other studies which show that in all habitats seedling establishment is the point at which populations of perennial species come under the most intense pressure (Harper 1977).

Thus, despite the generally held belief discussed in the Introduction that sexual reproduction is limiting in the Arctic, we have shown that arctic plants are subject to the same limitations on population establishment as are perennial plants in other areas. Others have recently come to this conclusion (McGraw & Shaver 1982, Chapin & Shaver 1985, Billings 1987, Murray 1987).

The population structure of arctic plants might differ from that of plants in less extreme environments in that recruitment is episodic. Our data for the population structure of *Dryas integrifolia* and *Silene acaulis* suggest that in some, or maybe many years, the realized reproductive capacity is zero. Such populations could be regarded as balancing on a "reproductive knife edge". During favourable periods, establishment of new individuals is possible, but there are periods, possibly prolonged, during which no recruitment can occur. In contrast, most studies of temperate species indicate that annual, or at least frequent recruitment is standard. The exceptions are certain shrubs and trees where new cohorts may be separated by periods during which little or no recruitment takes place. Gap-phase colonization in forests might come into this category.

In a harsh environment a species on a "knife edge" may be pushed in the wrong direction, towards extinction, by prolonged adverse spells. The drop in actual reproductive capacity from 1976 to 1977 which was a result of the poor summer of 1976 indicates how sensitive these widespread species are to environmental fluctuations. A decrease in the number of flowers or ovules per flower as was observed between 1976 and 1977 (Table 9) is indicative of a decline in potential reproductive capacity. A decrease in seed set per flower, like that in *S. acaulis* between 1976 and 1977 (Table 16) is indicative of a decline in actual reproductive capacity. The lower reproductive capacity in 1977 seems paradoxical in view of the warmer and drier weather in 1977, and the fact that insect activity in that year was at least as good as in the previous year. The explanation must lie in the delayed effects of the poor summer of 1976, during which not only the flower buds for 1977 were initiated, but also food reserves were being laid down.

Animals, especially migratory species, can respond to environmental fluctuations rapidly. For instance, *Anthus spinoletta rubescens* bred on Disko in 1977, where it had not been seen for over a century (Woodell 1979). It appears to respond rapidly to good summers by breeding north of its usual range. Plants cannot respond in this way, and as we have seen, the environmental effect is delayed as the environment programs the plants' reproductive capacity for the following year. Presumably, it would take only a slight permanent climatic deterioration to bring about the destabilization of these populations.

Table 40. Reproductive budget for *Ranunculus nivalis*. All figures are per square meter.

	Site 8
Flowering plants	16.2
Flowers	25.8
Ovules	1890.1
Stamens	988.7
Pollen grains	551354.4
Mature seeds	594.8
Seedlings	4.7
Young plants	8.2

Table 41. The relation between potential, actual and realized reproductive capacity in *Dryas integrifolia, Silene acaulis* and *Ranunculus nivalis*. The figures are averages from all the sites, 1976.

	Reproductive capacity		
	Potential	Actual	Realized
D. integrifolia	100	88.9	0.08
S. acaulis	100	29.0	0.001
R. nivalis	100	75.1	0.32

It may be that in these circumstances the ability to persist as individuals, or to spread vegetatively, comes into its own in the Arctic. A possible example is *Chamaenerion angustifolium* which is found on Disko, flowers in most years, but is said never to set seed in Greenland. It presumably did so in a period of warmer climate but now survives only vegetatively.

Exploitation

The effectiveness of the exploitation of the investment in the breeding system can be elucidated by examining the pollen/ovule ratios obtained from the reproductive budgets (Tables 38–40). Pollen/ovule ratios have been related to the breeding system (Cruden 1977). The ratios obtained in the present study and the characteristics of the breeding systems of our species are not in agreement with the relationships proposed by Cruden. All our species are facultative xenogamous, and the pollen/ovule ratios are either too high (*D. integrifolia:* 2647–3779) or too low (*S. acaulis:* 182–934 and *R. nivalis:* 292).

The pollen/ovule ratio in *R. nivalis* at site 8 is 291.7, and the corresponding ratio for *D. integrifolia* at site 6 is 2694.4. This means that *D. integrifolia* produces nine times as many grains per carpel as *R. nivalis.* At the same time, the "minimum expenditure" is about 20 germinated pollen grains per pollinated ovule for *D. integrifolia* and about 5 for *R. nivalis.* This means that *R. nivalis* utilizes 1.7% of the total number of pollen grains, whereas *D. integrifolia* exploits only 0.7%. So *R. nivalis* utilizes 2.4 times as many of the pollen grains produced as does *D. integrifolia.*

The effective exploitation can be calculated by dividing the number of pollen grains by the number of seeds produced. *R. nivalis* uses 927.0 pollen grains per seed. The corresponding figure for *D. integrifolia* at site 6 is 3255.1. So *D. integrifolia* spends 3.5 times as many pollen grains per seed as does *R. nivalis.* This is a reduction from the nine times as many grains per carpel mentioned above. Compared to *D. integrifolia, R. nivalis* apparently has a more effective exploitation of pollen, but not so effective as to make up for the lower number of grains produced per carpel.

The fact that *D. integrifolia* pollen grains are readily eaten by insects, and thus resulting in a higher cost in terms of pollen grains produced per carpel implies a higher actual reproductive capacity in this species than in *R. nivalis.* This may be caused by the insects staying longer in the flowers of *D. integrifolia* and depositing a higher number of pollen grains per flower.

Variation

The reproductive budgets show that each species varies from site to site. Our results also show variation throughout the season. It would be desirable if we could distinguish between environmental and genetic causes behind the observed phenotypic variation in virtually all characters. The analysis of variance on number of pollen grains in *D. integrifolia* shows that the genetic differences between plants influence the results most. Further, the bimodal distribution of pollen fertility within some of the populations points to genetic heterogeneity. There is only one clear-cut difference that is purely environmental: the trend in all three species at all sites towards fewer flowers and a lower seed set per flower, both overall and as a percentage of total ovules in 1977 compared with 1976.

Our results have shown that there is considerable variation in reproductive capacity between years, between sites and between plants. Population turnover is very slow, and recruitment is episodic. In this context, one might well ask the question: what value is a reproductive budget? We find it valuable to quantify the reproductive cycle in order to be able to compare different systems. Unfortunately, there are hardly any data available anywhere of the kind we have presented here, and certainly not from the Arctic. What we can say as a result of these data is that we can finally reject the opinion that sexual reproduction is less important or non-functioning in the Arctic. A substantial investment of resources occurs in sexual reproduction. Seeds mature regularly. The crucial stage is establishment from seeds, and this may take place only in some years.

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