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Mikael Stenström

CONTROLS ON REPRODUCTIVE EFFORT AND  
SUCCESS IN *SAXIFRAGA OPPOSITIFOLIA*,  
AN ARCTIC-ALPINE PERENNIAL



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**CONTROLS ON REPRODUCTIVE EFFORT AND SUCCESS IN  
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MIKAEL STENSTRÖM



Göteborg 1998





Göteborg University  
Faculty of Natural Sciences

Dissertation

**CONTROLS ON REPRODUCTIVE EFFORT AND SUCCESS IN  
*SAXIFRAGA OPPOSITIFOLIA*, AN ARCTIC-ALPINE PERENNIAL**

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Avhandling för filosofie doktorsexamen i systematisk botanik  
(examinator: professor Lennart Andersson)  
som enligt matematisk-naturvetenskapliga fakultetens beslut  
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Göteborg 1998



STENSTRÖM, M. 1998. Controls on reproductive effort and success in *Saxifraga oppositifolia*, an arctic-alpine perennial

Botanical Institute, Systematic Botany, Göteborg University, Box 461, SE 405 30 Göteborg, Sweden.

#### ABSTRACT

The prospective warming of the atmosphere, due to anthropogenic emission of greenhouse gases, is predicted to be greatest at high latitudes. Experimental warming of tundra plant communities has been shown to induce an individualistic growth response in different species, with slow-growing, evergreen species standing the risk of suffering from shading from more competitive species. Dispersal by seeds into new available habitats can therefore become critical. The factors governing the sexual reproduction in most arctic-alpine plants is however poorly investigated. My studies aimed at elucidating these factors in the widespread arctic-alpine perennial *Saxifraga oppositifolia*, mainly at Latnjajaure in northern Swedish Lapland. I studied the natural variation in flowering, pollination, and seed production, as well as plant utilization and seasonal development in bumblebees, which had previously been observed to frequently visit the species. Manipulative studies included crossing experiments and selective exclusion of bumblebees. The response to warming was studied as a part of ITEX, The International Tundra Experiment. Using passive heating devices (open-top chambers) phenology, pollination, and seed production was monitored at three contrasting latitudes, in a collaborative effort with workers from Switzerland and Canada.

The results show that reproductive effort (flower production) in *S. oppositifolia* can be explained by a single environmental variable, the solar radiation accumulated during July to September in the season preceding flowering. The controls on reproductive success presented here are more complex, and can be divided into biotic (1) and abiotic (2) factors:

**1a.** Cross pollination produces substantially more seeds than either autodeposition or geitonogamy. Seed weight is however not affected by the pollen source. The flowers are protogynous, and pollination occurring during the female phase leads to higher seed set than during the male phase, due to declining stigma receptivity.

**1b.** Bumblebee visitation in the early part of the season increases cross pollination levels, and to some extent also seed production. Flies however seem to do the major share of pollination, and almost all flowers are eventually pollinated during all parts of the season. The occurrence of pollen limitation is probably due to geitonogamous pollen transfer by the flies. The large and mobile bumblebee population probably effects long-distance pollen transfer in the early part of the season, which could partly explain the high levels of intrapopulational genetic variation found by other workers.

**2a.** The pollination rate (number of flowers pollinated) on any given day is to a large extent determined by weather conditions, mainly insolation and windspeed. This is an indirect effect, acting by reducing insect activity, and thus linking biotic and abiotic factors. If pollen has been deposited, precipitation has little effect unless it occurs within three hours after pollination.

**2b.** Experimentally increasing temperature has little effect on phenology as well as reproductive success, neither in the Alps, the Scandinavian mountains, nor the Canadian high Arctic. Together with the strong dependence of flower production on insolation, this should make *S. oppositifolia* vulnerable to competition from more responsive species in a warmer climate.

*Keywords:* *Saxifraga oppositifolia*, arctic, alpine, tundra, reproductive ecology, reproductive effort, reproductive success, bumblebees, *Bombus*, climate change, greenhouse effect

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This thesis is based on the following papers, which will be referred to in the text by their Roman numerals:

- I. STENSTRÖM, M. and MOLAU, U. 1992. Reproductive ecology of *Saxifraga oppositifolia*: phenology, mating system, and reproductive success. *Arctic and Alpine Research* 24: 337-343.
- II. STENSTRÖM, M., GUGERLI, F., and HENRY, G.H.R. 1997. Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. *Global Change Biology* 3 (Suppl. 1): 44-54.
- III. STENSTRÖM, M. and BERGMAN, P. 1998. Bumblebees at an alpine site in northern Sweden: temporal development, population size, and plant utilization. *Ecography* 21(1) (in press).
- IV. STENSTRÖM, M. Seasonal variation in cross pollination levels and seed production in the arctic-alpine perennial *Saxifraga oppositifolia*. Submitted.
- V. STENSTRÖM, M. and MOLAU, U. Micrometeorological determinants of reproductive effort and success in the arctic-alpine perennial *Saxifraga oppositifolia*. Submitted.

Paper I is based mainly on research ideas by the co-author. I am responsible for the major part of field and laboratory work, statistical analysis, and compilation of the manuscript.

Paper II is based on ideas and planning by all three authors. Field work, data analysis, and compilation was also a collaborative effort.

Papers III and V were based on ideas by both two authors involved in each paper. I am responsible for the major part of fieldwork and data analysis. Compilation of the manuscripts was a joint effort.

For Paper IV, I am solely responsible.





*Till Anna*



"Although research proceeds from one step to another, the sequence taken is often not as logical nor as linear as the book that results. I had, in the beginning, no grand model or design in my mind, to be corroborated by a planned set of experiments in the field and in the laboratory. I pursued only small questions that seemed interesting in light of previously collected data. The central theme presented—the theme of economics based on energetics—emerged of its own accord."

Bernd Heinrich, *Bumblebee economics*

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## INTRODUCTION

### Arctic and alpine environments

Habitats at high latitudes and high altitudes exhibit many similarities in terms of physical conditions, such as low temperatures, short growing seasons, and low nutrient availability (Billings and Mooney 1968). While the well-known decrease in temperature from south to north corresponds to a similar decrease along altitudinal gradients, incipient solar radiation shows a very different pattern, especially when comparing the Arctic with more southerly alpine areas. The Arctic receives virtually no solar radiation for half the year, and instead has almost constant daylight for the other half. Alpine areas instead have regular diurnal variation in solar radiation (Ives and Barry 1974). The intensity of solar radiation also increases with altitude, so that alpine plants can experience extremely high radiation. Other differences include much higher total amounts of snowfall in alpine areas, as well as higher mean and maximum windspeeds (Ives and Barry 1974). When travelling from south to north, the mountain areas encountered will become more and more like the Arctic, in terms of physical conditions as well as vegetation (Jónsdóttir et al. 1996). The main study site, Latnjajaure in northern Swedish Lapland, in many respects resembles the true Arctic even though it is actually subarctic-alpine.

The most prominent feature of arctic and alpine landscapes is that they are devoid of trees. The word "tundra", derived from the Finnish "tunturi", originally designated the treeless plateaus of Lapland, but its use has later been widened to include both arctic and alpine landscapes beyond and above the treeline (Callaghan and Emanuelsson 1985). The delimitation of the Arctic has caused much dispute, but the treeline is now considered as the biologically most reasonable boundary (Bliss and Matveyeva 1992).

In arctic and alpine environments, comparatively very little exogenous heat is available, and this is often a limiting factor for plant growth and reproduction (Billings and Mooney 1968, Savile 1972, Jonasson et al. 1996). Low temperatures also results in short growing seasons, which is further reinforced by a persistent snowcover. At Latnjajaure only the period June–September has mean temperatures above 0°C, and many plants do not emerge from snow until July.

Another factor, which relates to temperature, is the degree of predictability in the climate. Using fractal and chaos theories, Ferguson and Messier (1996) showed that inter-annual climatic variation is less predictable in the Arctic than that at lower latitudes. The mean values for metereological variables



thus tell little about the extremely variable weather conditions in different years (Paper V, Table 1). This was summarized nicely by Urban Nordenhäll, who after eight years in the north said: "I'm still waiting for a normal year".

To the same extent as the weather being unpredictable, the location of snowbeds is a predictable factor. Topography in combination with prevailing winds during winter make snowbeds form in the same places year after year. This is reflected in the vegetation, where snowcover is an important factor when explaining species composition (Billings and Bliss 1959, Schaefer and Messier 1995). At the same time as protecting the plants from being blasted by windborn ice crystals during winter, the melting snow also provides moisture during the summer months. The input of nutrients is also largely concentrated to the snowmelt period, probably mostly emanating from decaying soil microbes (Jonasson and Michelsen 1996). On the down side, the snow shortens the growing season and cools the ground, both in solid form (by insulation and reflection of solar radiation) and as meltwater. For a thorough review of the importance of snow in the Arctic, see Chernov (1988). The phenology of arctic and alpine plants is also largely determined by the release from snow (Sørensen 1941, Holway and Ward 1963, Kudo 1991). The sequence of flowering of different species therefore looks more or less the same from year to year (Molau and Rosander 1995).

Nutrients, especially nitrogen, often limit plant growth in tundra plants (Billings and Mooney, Savile 1972, Jonasson and Michelsen 1996). The low availability is partly a consequence of low temperatures slowing down weathering and microbial processes. Although large amounts of nutrients can be stored in the organic component of the soil, they are however to a large extent immobilized by the soil microbes (Jonasson and Michelsen 1996).

## Arctic and alpine plants

### Life forms and vegetative growth

The most apparent characteristic of arctic-alpine plants is their low stature. This is especially evident in species capable of growing in exposed places with little snowcover in winter. As mentioned above, strong winds during wintertime transport ice crystals, which quickly destroy tall plants (Savile 1972). Cushions and mats are common life forms, and they often have tough, leathery leaves that are densely packed. A large proportion of the biomass is usually under ground (Billings and Mooney 1968). This "compact living", illustrated by species like *Diapensia lapponica*

and *Loiseleuria procumbens*, also has the advantage of conserving absorbed heat (Savile 1972; names throughout this thesis follow Nilsson 1987). Species growing in somewhat more sheltered positions, where at least some snow accumulates in winter, are often more upright, but still have leathery leaves. *Cassiope tetragona* and *Phyllodoce caerulea* are examples of this growth form. In places with even more snow, dwarf birch, *Betula nana*, is often the dominant species. Most of the willows (*Salix* spp.), and ericaceous dwarf shrubs (*Vaccinium* spp.) also belong to this category.

The life forms outlined above all grow in drier locations, forming what is commonly called fell-field and heath vegetation. Wetter places are often dominated by sedges (*Carex* spp.), or cottongrass (*Eriophorum* spp.), forming two common types of vegetation called wet sedge meadow and tussock tundra (Bliss and Matveyeva 1992). These types of vegetation often sit on top of permafrost.

Due to the short and cold growing season, annuals are very rare in arctic-alpine habitats (Billings and Mooney 1968, Callaghan and Emanuelsson 1985, Molau 1993a). Most species are long-lived perennials, but determining their ages is often a difficult matter. Counting annual rings is difficult in woody species due to the rings being very narrow and sometimes irregular (Callaghan and Emanuelsson 1985), and this method obviously does not work in herbaceous plants. With the use of other types of annual markers, the life span of many herbaceous species has been found to be in the interval 10-50 years (Callaghan and Emanuelsson 1985). More recent estimates have however pointed to much longer life spans. *Bartsia alpina* is reported to reach 200 years (Molau 1990). In cushion-forming species, where annual markers are not useful, measuring the radial growth rate is an alternative method. With an annual radial increase of as little as 0.6 mm, Molau (1997a) estimated that a 30 cm cushion of *Diapensia lapponica* is approximately 700 years old. Clones of both alpine and arctic *Carex* species have been determined to reach 2000 years (Steinger et al. 1996, Augner et al. unpubl.).

The slow growth rate of *Diapensia lapponica* is probably extreme, but nevertheless illustrates a common feature among arctic-alpine plants. Slow growth is imposed by low temperatures and short growing seasons, but also by low availability of nutrients (Savile 1972). Some species are adapted to constantly low levels, and will not increase growth very much even if nutrients are added, whereas other rapidly increase their biomass (Chapin and Shaver 1985). Different abiotic factors may also limit growth in different locations. Havström et al. (1993) found that



temperature was a limiting factor in *Cassiope tetragona* at high altitude and high latitude, but that nutrients were limiting at a site at low latitude and low altitude. Commonly more than half of the annual requirement of nutrients in arctic plants is translocated from overwintering organs (Jonasson and Michelsen 1996). The slow release of nutrients from the soil is also compensated by most plants having mycorrhiza (Jonasson and Michelsen 1996).

When discussing arctic and alpine plants in this thesis, I restrict myself to species occurring in both types of locality, thus called arctic-alpine (Billings and Mooney 1968). The alpine regions considered here are therefore in the temperate or subarctic zone. Alpine plants in tropical areas often have a very different appearance. The peculiar habit of columnar giant rosette plants in African alpine locations is one example, interpreted as an adaptation to the extreme fluctuations in temperature from day to night (Hedberg 1964)

## Reproductive strategies

The early observers of floral biology in the Arctic, such as Ekstam (e. g., 1895, 1897) and Warming (1909), held the view that the flowers had lost their importance for attracting insects, since the harsh climate, as experienced by humans, was assumed to preclude insect pollination. Asexual means of reproduction were long assumed by several workers to have largely replaced sexual means in arctic plants (see Murray 1987 for a critical review). Following ideas put forward by Russian workers, Kevan (1972) performed exclusion experiments to prove the dependence of arctic plants on insect visitation. He found that some species, e. g. *Pedicularis capitata*, were entirely dependent on insects to set any seed at all. A number of others, e., g., *Saxifraga oppositifolia* and *Dryas integrifolia*, were found to require insect visitation for full seed set. The dependence of many arctic-alpine plant species on insect visitation has later been confirmed by a number of studies (e. g., Tikhmenev 1984, Philipp et al. 1990, Molau 1993a). Murray (1987) provides a list of 78 species of insect-pollinated arctic plants. Still, the majority of the species in Kevan's (1972) study were able to set seed successfully without the aid of insects. Such species included *Cassiope tetragona* and *Papaver radicum*.

Diptera (flies, syrphids, and mosquitoes) and to a lesser extent bumblebees are generally considered as the most important pollinators in arctic-alpine plants (Hocking 1968, Kevan 1972, Kevan and Baker 1983, Chernov 1988, Pont 1993). The majority of plant species have unspecialized (open, cup- or bowlshaped)

flowers which can be visited by many types of insects (Chernov 1988). Species with flowers adapted for bee pollination are comparatively rare, most species belonging to the Fabaceae (*Oxytropis* spp., *Astragalus* spp.) and to the genus *Pedicularis* (Scrophulariaceae). In periods when these flowers are not available, bumblebees forage on species with more unspecialized flowers like *Saxifraga oppositifolia*, *Diapensia lapponica*, and *Dryas integrifolia* (Richards 1973, Bergman et al. 1996).

Wind pollinated plants, such as species of *Betula*, *Salix*, *Carex*, and *Eriophorum*, form a conspicuous element in tundra habitats. Since my studies involve insect pollination, I will concentrate the discussion in this thesis to that strategy. Actually, very little data exists on the reproductive ecology of wind pollinated plants in these environments (Jónsdóttir 1995, Jones et al. 1997, A. Stenström, manuscr.)

From this overview, it is obvious that many different reproductive strategies coexist among arctic-alpine plants. Molau (1993a) found a very convincing pattern among the reproductive systems when relating them to flowering phenology. Early-flowering species have their flower buds preformed to a high ontogenetic level at the end of the growing season preceding flowering (Sørensen 1941). Molau (1993a) found that early-flowering species (vernal phenophase) are primarily xenogamous (outcrossed) and have low seed output. This could be due to selective abortion, but also to unpredictable weather in the early part of the season. He termed these plants "pollen riskers", and this category includes species like *Saxifraga oppositifolia*, *Silene acaulis*, and *Ranunculus nivalis*. On the other end of the spectrum, late-flowering snowbed species (late aestival phenophase) are primarily autogamous and always have a high seed output. That is, if not winter sets in too early, in which case they will lose their entire seed crop. They were accordingly called "seed riskers" by Molau (1993a). This category includes species like *Saxifraga stellaris*, *Silene uralensis*, and *Ranunculus pygmaeus*. Together these six species illustrate that different phenological strategies may even be present within a single genus.

Another interesting pattern was found by Brochmann (1993) in diploid and polyploid arctic *Draba* species. Diploid species all had small, unscented flowers and high seed set from selfing. Large, scented, and protogynous flowers were only present in polyploids, and these species also had low seed set from selfing. The diploids had previously been found to be genetically depauperate (Brochmann et al. 1992), and allopolyploidy in these species can therefore be interpreted as an escape from the effects of inbreeding (Brochmann 1993).



## Factors governing reproductive effort

Reproductive effort, the investment into reproductive structures, can be subdivided into a male and female component in hermaphroditic plants (Lloyd 1980). In this thesis I however consider the two components together and simply regard reproductive effort as the number of flowers produced. I also restrict myself to sexual reproduction; vegetative reproduction is sometimes also included in the reproductive effort (Fitter 1986).

The preformation of flower buds in early-flowering arctic-alpine plants (Sørensen 1941) means that the current year's reproductive effort in these species will depend on the conditions during one or more preceding years. Carlsson and Callaghan (1994) found that flowering frequency in *Carex bigelowii* was correlated with the mean July temperature in the year before flowering. Experimentally increasing temperature also increases flowering frequency in this species (Stenström and Jónsdóttir 1997). Havström et al. (1995) however found no increase in flowering from warming in *Cassiope tetragona*, showing that other climatic variables than temperature may be more important for determining flower production.

## Factors governing reproductive success

Like reproductive effort, the reproductive success in hermaphroditic plants has a male and female component (Lloyd 1980). Male success depends on the amount of ovules fertilized, and female success on the amount of ovules that develop into seeds. I have concentrated on the female success, since the output of seeds is of great importance for survival in a changing climate. I therefore also mostly studied pollen transfer from the female point of view, i. e., the receipt of pollen on stigmas.

Limitations to seed production, due to the biotic and abiotic environment, include the availability and quality of pollen (pollen limitation), the amounts of nutrients and photosynthate available for reproduction (resource limitation), herbivores and diseases, and physical conditions of the environment (Lee 1988). Several factors may limit seed production simultaneously, but from extensive empirical evidence, resource limitation has forcefully been argued to be predominant in most angiosperms (Lee 1988, Haig and Westoby 1988, Kearns and Inouye 1993). Demonstrating pollen limitation is problematic, since increased seed output may deplete resources, causing lower seed set in coming years (see Kearns and Inouye [1993] for a review of both technical and theoretical problems). Nevertheless, Burd (1994)

found that there was evidence of pollen limitation in 62% of the species studied to date. Among those 258 species not a single arctic-alpine species was however included. The lack of data is surprising: if you were interested in whether pollen limitation may be important, predominantly outcrossing plants growing in a climate which supposedly limits insect activity would be an obvious choice. In my studies, I have tried to assess how the variation in pollen deposition and reproductive success relates to biotic and abiotic factors of the tundra environment.

Dividing species into categories according to their reproductive strategy (Molau 1993a) is a useful starting point when erecting hypotheses about which kinds of selective pressures act, or have acted, on reproductive traits in arctic-alpine plants. Information on how different biotic and abiotic factors affect reproductive success is however necessary to ascertain if these selective pressures really exist. The existence of an early-flowering strategy, e. g., implies that there are, or has been, selective pressures favouring early onset of flowering. Such pressures could include higher insect visitation frequencies in the early part of the season, and longer time available to complete fruit maturation. Workers studying seasonal variation in alpine species have often found decreasing seed output as season progresses, in some cases coupled to decreasing insect visitation (Galen and Stanton 1991, Totland 1994a, Totland 1997, A. Stenström *manuscr.*). Kudo (1993), studying the likewise alpine *Rhododendron aureum*, instead found that seed set was increased in late-flowering specimens, probably as a consequence of increased visitation from bumblebee workers as season progressed. For arctic plants there is no information of this kind available.

During any part of the flowering season in a species, direct and indirect effects of weather has the potential to reduce reproductive success. Direct effects include interference of pollen dispersal and germination by precipitation, and delayed fruit maturation by low temperatures (Corbet 1990). Indirectly, inclement weather can restrict insect activity, in flies (Totland 1994b) as well as in bumblebees and butterflies (Lundberg 1980, Bergman et al. 1996). Which meteorological variables are most important will depend on the type of pollinator. The large, furry, and endothermic bumblebees (Heinrich 1993) are able to forage even in subzero temperatures (-1.7°C; Richards 1973), but in flies activity ceases already at much higher temperatures (4°C; Totland 1994b). Wind is also expected to affect small insects such as flies more than bumblebees.

Small insects are often found basking inside flowers, where they can take advantage of the shelter



and reflected sunlight to keep up their body temperature (Kevan 1975). This is especially evident in species like *Papaver radicum* and *Dryas integrifolia*, which both exhibit heliotropism (flowers tracking the sun), and may lead to increased pollination (Kevan 1975, Krannitz 1996). The bowl-shaped corolla focuses the sun's rays on the gynoecium, where the increased temperature leads to more and heavier seeds being produced (Corbett et al. 1991, Krannitz 1996).

If flowering and seed formation has been successfully completed, germination and seedling establishment are the final critical steps. Most arctic-alpine plants lack innate seed dormancy (Bliss 1971), which allows germination whenever conditions are favourable, something that may happen very rarely (Bell and Bliss 1980). In many clonal species you rarely find any seedlings at all (Callaghan and Emanuelsson 1985), and establishment in such species probably only occurs in "windows of opportunity" when disturbance creates suitable microhabitats (Eriksson and Fröberg 1995). In species reproducing mainly sexually, seedlings may be common but high juvenile mortality leads to age class distributions with a constant and high decrease in frequency from the youngest to the oldest classes (Callaghan and Emanuelsson 1985). Formation of needle ice and drying out of the soil as summer progresses are factors that may be responsible for the high mortality of seedlings (Billings and Mooney 1968, Bliss 1971). Successful reproduction and establishment only occurring rarely is probably one of the selective pressures leading to the long life spans of tundra plants.

### Climate change and tundra vegetation

As discussed above, the low availability of exogenous heat, or other abiotic factors related to it, impose constraints on growth and reproduction in tundra plants. A warming of the climate, whether natural or anthropogenic, can therefore be expected to have a great effect in arctic and alpine environments. Global circulation models, used to predict the effect of increased concentrations of greenhouse gases due to human activities, indicate that warming will occur, and that it will be greatest at high latitudes (Maxwell 1992, Houghton et al. 1996). Even though there is considerable debate about the certainty of these predictions, assessing the importance of warming on tundra plants is an important task because of the potentially drastic consequences if the predictions do come true. Plants form the basis of the ecosystems, and changes in species composition will therefore

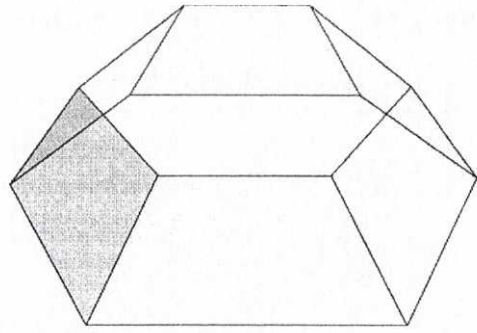


FIGURE 1. Open-top chamber (OTC), a passive device for increasing temperature in tundra plants. These devices, made of panels of transparent polycarbonate (construction by Urban Nordenhäll), were used in The International Tundra Experiment (ITEX) at Latnajokure. The ground surface area covered is ca. 1 m<sup>2</sup>, and in the experiments on *Saxifraga oppositifolia* four plants were monitored in each OTC.

affect populations of grazers (such as lemmings and reindeer), and ultimately the populations of predators. For the plants, the rate of climate change is a very important factor to take into consideration. Changes like the predicted 2–3°C in 50 years (Houghton et al. 1996) is probably not in the range previously experienced (Havström 1995); variation is usually on a much shorter time-scale (e. g., diurnal and seasonal variation) or a much longer one (e. g., glacial cycles).

Pioneering studies of the response of tundra plants to warming showed that the response is highly individualistic among species (Chapin and Shaver 1985) and that it may vary between different parts of a species' distribution (Havström et al. 1993). To be able to make reliable predictions about the future of tundra vegetation in a warmer climate, it is therefore necessary to study responses in multiple species and over a large geographical area. This was the reason for the initiation in 1990 of ITEX, The International Tundra Experiment, a collaborative effort to study the response to natural climatic variation and experimental warming in representative vascular plant species on a circumpolar basis (Henry and Molau 1997). Standardized methods for measuring phenology, growth, and reproduction were agreed upon, and a passive device for warming was designed (Fig. 1). These hexagonal open-top chambers (OTCs) increase the mean daily air temperature by 1.2–1.8 degrees (Marion et al. 1997). By having a large opening in the top, they avoid extremes in temperature as well as reduce the effects on sunlight and precipitation of more closed constructions. Open-top chambers were used in Paper II.



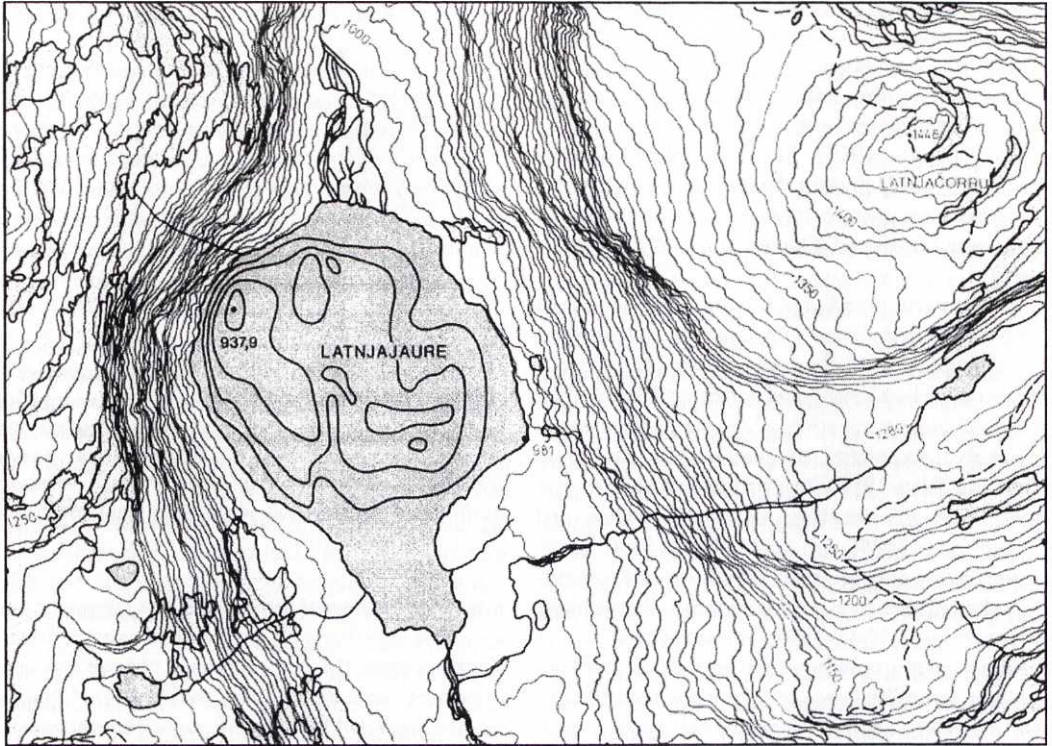


FIGURE 2. The study area. Latnjaure Field Station is on the east shore of the lake at the altitude mark (981 m a. s. l.). Most of the studies were conducted on the slopes just east of the lake. Scale 1:18 000 (1 cm = 180 m), contour interval 10 m. Stippled areas indicate snowbeds. Detail of original map of the entire drainage area by Johan Kling.

## OBJECTIVES

The aim of my studies was to determine some of the factors governing reproductive effort and success in the widespread arctic-alpine plant, *Saxifraga oppositifolia*. I therefore first had to get a general overview of its reproductive strategy, including phenological traits and mating system (Paper I). Following the predictions of a possible anthropogenic warming of the climate, the direct effects of increased temperature on flower production, phenology, and reproductive success needed investigating (Paper II). Since predictable snowmelt gradients and harsh but unpredictable weather conditions are salient features of arctic and alpine habitats, I also wanted to study the importance of these features on reproductive success in *S. oppositifolia* (Paper IV, V).

Bumblebees had been observed to visit *S. oppositifolia* in the early part of the season at several sites, but the importance of this visitation, compared to that by e. g. flies, had previously not been estimated. To be able to relate emergence and subsequent foraging in the bumblebees to pollination in *S. oppositifolia*, I also needed to investigate the seasonal development and change in use of food plants in the bumblebee

population at the study site (Paper III).

After descriptions of the study site and study species follows a summary of the papers which this thesis is based upon. Instead of merely repeating the major results and conclusions, I have tried to give a picture of the reasoning behind the studies, as well as of how they relate to each other. The last part of the thesis is a synthesis of the results.

## THE STUDY SITE

Most of the data in this thesis comes from fieldwork at Latnjaure Field Station, northern Swedish Lapland (Fig. 2). The station is owned and maintained by the Abisko Scientific Research Station, situated 15 km to the east. Research at Abisko has been conducted since 1912, mainly focussing on the subarctic birch forest community (see Karlsson and Callaghan [1996] for a review). Climate has been monitored since the start, and baseline data for a number of variables is therefore available. The activities at Latnjaure date back to 1965, when the station was built by the Institute of Limnology, Uppsala University. Their activities ended in the late seventies, and after several



years of inactivity at the site, research in plant ecology was initiated by Ulf Molau in 1990.

Latnjajaure Field Station is at 68°21'N, 18°29'E, situated ca 300 m above the treeline at an altitude of 981 m, on the east shore of Lake Latnjajaure (Latnjajávri is the spelling favoured by the Sami). The lake lies in a deep glacial valley, and to the west, north, and east the mountains reach over 1400 m. To the south there is first a gentle, undulating slope for ca 2 km, and then a 600 m drop into the Kårsavagge (Gorsavággi) valley. (Both these names are tautological, since "jávri" means lake and "vággi" means valley in Samic). Lake Latnjajaure is partly dammed by glacial morains, where the acidic and nutrient-poor substrate is dominated by species like *Empetrum nigrum*, *Betula nana*, *Diapensia lapponica*, and *Salix herbacea*. My studies were however conducted on the lowest part of the southwest-facing slope of Mount Latnjačorra (Fig. 2), which is dominated by base-rich schists, predominantly mica schist (Johan Kling, pers. comm.). The slope is terraced, and the drier parts with little snow in winter is covered by a species-rich *Dryas* heath, dominated by *Dryas octopetala* accompanied by species like *Silene acaulis*, *Rhododendron lapponicum*, *Salix reticulata*, and *Saxifraga oppositifolia*. Below the terrasses, parts of the otherwise acidic moraine has been covered by shingles of schist, flushed out when meltwater pools at higher altitude have suddenly emptied. One such event was observed after a period with rapid snowmelt in early June 1995; a fast-running creek suddenly appeared on the slope, eating away on the topsoil and depositing it on more even ground and on the still frozen lake. This rather special habitat provides an opportunity to work with specimens of *S. oppositifolia* growing on more level ground. If these catastrophic events did not happen from time to time, these plants would probably be overgrown by more competitive species.

The annual mean temperature at Latnjajaure is -2.6°C, with a range of -2.9 to -2.1 (1993-96). Summer temperatures vary considerably: the overall mean for July is 7.7°C, with means in different years ranging from 5.4 to 9.9°C (1990-97; Paper V, Table 1). Periods with snowfall and sub-zero temperatures, often accompanied by strong winds, can occur during any part of the summer.

## THE STUDY SPECIES

The genus *Saxifraga* includes about 440 species, mainly distributed in the Arctic and the north temperate zone (Webb and Gornall 1989). The different

species exhibit a wide array of different life forms, but the floral structure is very constant, with five petals and sepals, ten stamens, and two carpels. The main pollinators of the mostly open, upright flowers seem to be flies, beetles, and, less frequently, bees (Webb and Gornall 1989). Accounts of reproductive ecology of temperate species can be found in, e. g., Olesen and Warncke (1989a, b) and Lindgaard Hansen and Molau (1994), and for arctic-alpine species in Molau (1992, 1993a), Molau and Prentice (1992), and Gugerli (1997a).

The focal species of this study was the evergreen perennial *Saxifraga oppositifolia* L., which is probably the most widespread species in the genus (Webb and Gornall 1989). It has a virtually circumpolar distribution, and also occurs in mountain areas further south (Fig. 3). *Saxifraga oppositifolia* reaches furthest north of all flowering plants, thriving on northeast Greenland at 83°39'N. In polar deserts it is commonly the most abundant species (Bliss and Matveyeva 1992, Levesque 1997). It occurs on a number of different types of substrates, and is able to withstand extreme drought (Teeri 1972) as well as periodic flooding. In Scandinavia and Britain it is confined to calcareous, or at least base-rich conditions, but is indifferent further north. It is often a pioneer species on bare soil, such as glacial moraines (Piroznikov and Gorniak 1992) and scree slopes (Jones and Richards 1956).

As the species name implies, the leaves of this species are opposite. They are usually densely crowded, with bristle-like hairs on the margins, and with a lime-secreting hydathode at the tip (Webb and Gornall 1989). *Saxifraga oppositifolia* is very variable in its growth habit (Jones and Richards 1956, Crawford et al. 1995), which is also true for a number of other morphological characters such as the petal shape and color shade (Webb and Gornall 1989). It can grow either as dense cushions or as mats with long trailing shoots. The cushion form is more common in exposed sites, whereas the trailing form is more common in snowbeds and when mixed with other species. It has been suggested that the two forms are distinct, and have variously been given the rank of forms or subspecies (Jones and Richards 1956, Lid and Lid 1994). Crawford et al. (1995) regard the two forms as ecotypes, and have shown that they differ in metabolic rates, rate of shoot production, and extent of storage of water and carbohydrates. However, in a thorough survey of a number of morphological characters, Brysting et al. (1996) showed that the morphological variation has a unimodal distribution, with a gradual transition from tufted to creeping forms. Material from Svalbard was used in both these studies, and although I have made no quantitative measurements, it is fairly obvious that there is a



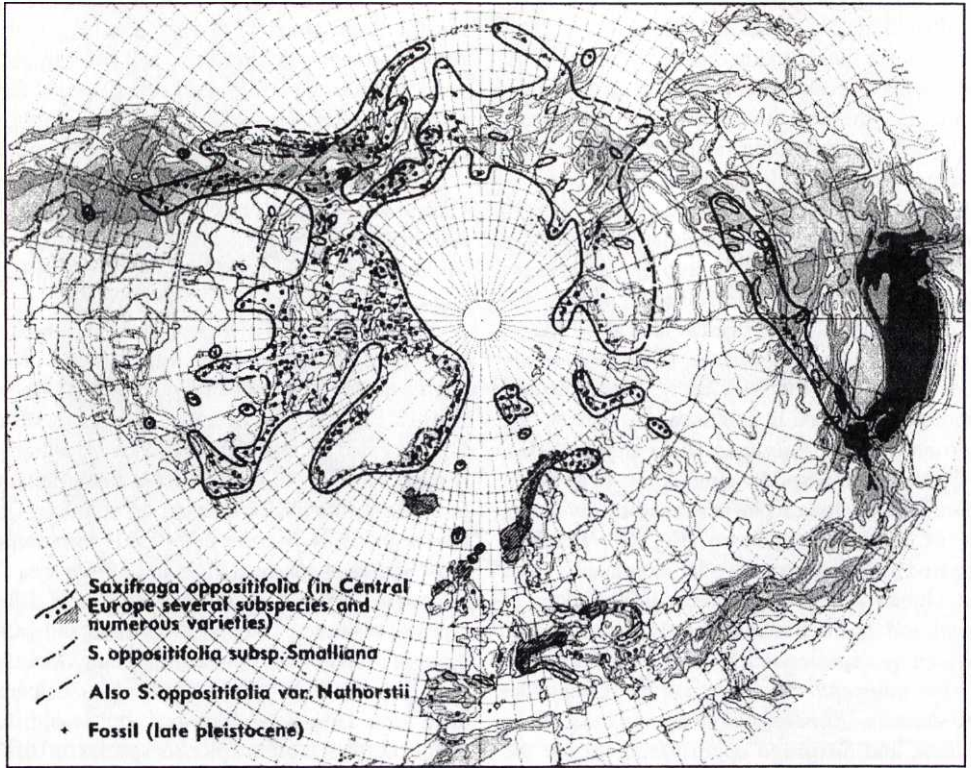


FIGURE 3. The worldwide distribution of *Saxifraga oppositifolia*. Map from Hultén (1970), reprinted with permission from the publisher.

gradual transition between the forms at Latnjajaure as well.

The variability in growth form and the irregular branching pattern makes it difficult to use any standard techniques to determine the age of genets of *S. oppositifolia*. A life span of 10 years or more is listed in Callaghan and Emanuelsson (1985), but this is most certainly an underestimation. No data exists on age class distributions. When dividing plants into simple size classes according to the degree of branching, and scoring specimens in 20 squares at each of three sites with different duration of snowcover, I found the distributions illustrated in Fig. 4. Note that the smallest size class was not always the most abundant, and even when it was, there was not that many of them compared to two other classes. As stated above, sexually reproducing tundra plants generally exhibit a rapid decline in the proportion of specimens from the youngest to the oldest age class due to high juvenile mortality (Callaghan and Emanuelsson 1985). Although the size classes used here are very rough, this data however indicate that establishment in *S. oppositifolia* may occur rather frequently.

The flowers of *S. oppositifolia* are terminal,

upright, and have light pink to purple petals. During flowering the pedicels are very short, not elongating until the seeds are mature. The ovary is bicarpellate, and the two stigmas are quite large (diameter ca. 0.5 mm). The pollen is bright orange, and together this means that it is fairly easy to determine if a flower has been pollinated. Unlike most other saxifrages, *S. oppositifolia* is protogynous (Webb and Gornall 1984). Pollen deposited while all flowers are still in the female phase is guaranteed to come from another genet, and the proportion of flowers pollinated before a plant starts to release its own pollen is therefore a minimum estimate of cross pollination (this approach was used in Paper IV). Throughout its distribution, *S. oppositifolia* is dependent on cross pollination for full seed set (Kevan 1972, Tikhmenev 1984, Gugerli 1997a). Like other saxifrages, it has a mechanism for autodeposition of pollen: at the end of anthesis, the stamens pivot at the point of attachment, with the anthers ultimately covering the stigmas. This should deposit any pollen left onto the stigmas, but very little seed set results from this mechanism compared to in many other arctic-alpine saxifrages (Molau 1993a).

Flowering in *S. oppositifolia* starts very early after snowmelt, a consequence of the flower buds



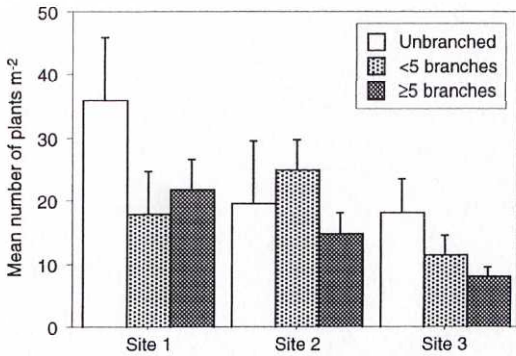


FIGURE 4. Size class distribution of *Saxifraga oppositifolia* at three sites with different duration of snowcover (means  $\pm$  SE). The size classes were defined by the degree of branching, and specimens were scored in 20 randomly placed squares, 50  $\times$  50 cm, in each site. Site 1 has the thinnest snowcover, and flowering usually starts in the end of May. At Site 3, flowering usually does not start until the end of June.

overwintering with all major parts already formed (Sørensen 1941). Reports on the prefloration period (time from snowmelt to flowering) range from 4 to 8 days (Cleve 1901, Resvoll 1917, Bliss 1971). In fact, it is usually the first species coming into flower in arctic habitats, and is often seen as a sign of spring by people living in these areas. Its extraordinarily wide tolerance to different environmental conditions nevertheless permits it to live in places with none or very thin snowcover as well as in snowbeds, which means that the flowering season can be very extended. At the study site the first flowers appear on south-facing cliffs in mid May, when almost all of the area is still snowcovered, and flowering does not end until the beginning of August.

Insect visitors to *S. oppositifolia* come from a number of different taxa. Previous records include Diptera (flies, mosquitoes, syrphids), Hymenoptera (bumblebees, sawflies), and Lepidoptera (Jones and Richards 1956, Hocking 1968, Kevan 1972, Bergman et al. 1996). The flowers secrete ample amounts of nectar (Hocking 1968) and have a strong sweet smell. Webb and Gornall (1989) claim that all European saxifrages are scentless, but this is obviously not true.

There are no special mechanisms for dispersal in saxifrages; the fruit is a dehiscent capsule, and the seeds simply fall out when the pedicels sway in the wind (Webb and Gornall 1989). *Saxifraga oppositifolia* can have fairly long (sometimes more than 5 cm) pedicels when the seeds are mature, but this mechanism can hardly disperse the small seeds more than some tens of centimeters. Considering its rapid colonization of, e. g., glacial moraines, dispersal by

water or wind (the light seeds can probably skid on top of the snow) is probably important (Jones and Richards 1956). The seeds are eaten by snowbuntings (*Plectrophenax nivalis*). Ulf Molau (pers. comm.) has observed seeds of various plants being stuck in the corners of the beak and in the small feathers near to it. He also observed the birds flying up to perch on rock ledges, where they clean themselves by rubbing their heads against the rock. This behaviour can probably account for some of the medium-range dispersal to seemingly inaccessible places. Long-range dispersal can probably occur by the seeds hitch-hiking on reindeer feet and muzzles. Molau (1990) experimentally showed that such secondary dispersal by adhesion to moist surfaces can increase dispersal distances dramatically.

There were several reasons for choosing *S. oppositifolia* as a study species. The main reason was that it was chosen as one of the primary ITEX species, as being an example of a long-lived, evergreen outcrosser. A circumpolar distribution with no geographic subdivisions was a prerequisite for the ITEX species that was also fulfilled for *S. oppositifolia*. Its floral morphology facilitates pollination experiments, and its very extended flowering season gives a good opportunity to study seasonal variation in pollination and reproductive success.

## SUMMARY OF PAPERS

### Paper I. The reproductive strategy of *Saxifraga oppositifolia*

The previously available information on the reproductive ecology of *S. oppositifolia* was scattered in the literature, and hardly no data was available for Scandinavia. Since we were going to start monitoring and temperature enhancement experiments using this species, we wanted to get adequate data on its flowering phenology and mating system. We monitored emergence phenology in permanently marked individuals in two sites, one on the fringe of a large solifluction lobe and one in a snowbed. The prefloration period (time from snowmelt to flowering) was  $10.2 \pm 3.0$  days (mean  $\pm$  SD), which was longer than the previous records of 4–8 days. Flowering smoothly followed the receding snow down into the snowbed, usually not more than 5 meters behind, showing that snowmelt triggers flowering as in other arctic-alpine angiosperms. The duration of the prefloration period varied between 5 and 16 days, probably due to how fast the ground heated up. A plant in a depression, receiving a constant input of



cold meltwater, probably requires longer time to start flowering than one in a dry place. There may of course also be a genetic component to this variation; the genets may not all preform their flower buds to the same ontogenetic level, or respond in the same way to the increase in temperature after snowmelt.

Observations of the intrafloral phenology showed that the obligate female phase lasts  $4.2 \pm 1.3$  days. When the anthers start releasing pollen, there is on average  $7.6 \pm 1.9$  days left until the flowers wilt, giving a total flower life span of  $11.7 \pm 1.8$  days. By pollinating flowers at different time intervals after flowering, we found that the receptivity of the stigmas is high when the flowers open, and then starts declining 5 days after opening. This is probably one of the reasons for the low autodeposition efficiency in this species; at the time of pollen release, the receptivity of the stigmas has already started to decrease, and when the anthers cover the stigmas at the end of flowering it is virtually zero.

To further elucidate the efficiency of different modes of pollination, we performed a crossing experiment. The following five treatments were applied to one flower each in 20 caged plants:

1. Autodeposition (untreated flower),
2. Hand selfing (equivalent to geitonogamy, pollen transfer between flowers within a genet),
3. Cross pollination with one donor,
4. Cross pollination with a mixture of three donors,
5. Cross pollination with three donors on three different occasions (within 24 h).

Unfortunately some rather serious errors were made when analyzing this data. When calculating seed number, seed yield (weight of all seeds in a capsule), and mean seed weight we included the zero values, i. e., the treated flowers which produced no seeds. The corrected result is shown in Fig. 5 (Fig. 6 in the paper). Table 1 (Table 7) is also corrected and contains the same data, together with the number of flowers resulting in capsules. There was very few genets that were able to set seed from autodeposition, and almost as few from hand selfing. The resulting fruits furthermore only contained a few seeds per capsule. These seeds were however as heavy as the ones produced from cross pollination. This shows that the pollen quality determines whether seeds will be produced or not, but not their weight. Including the zeros in the original calculation resulted in very low values on seed weight from autodeposition and hand selfing.

Another error is present in the statistical analysis of the difference between the treatments. Because hand selfing and autodeposition produced seeds in so

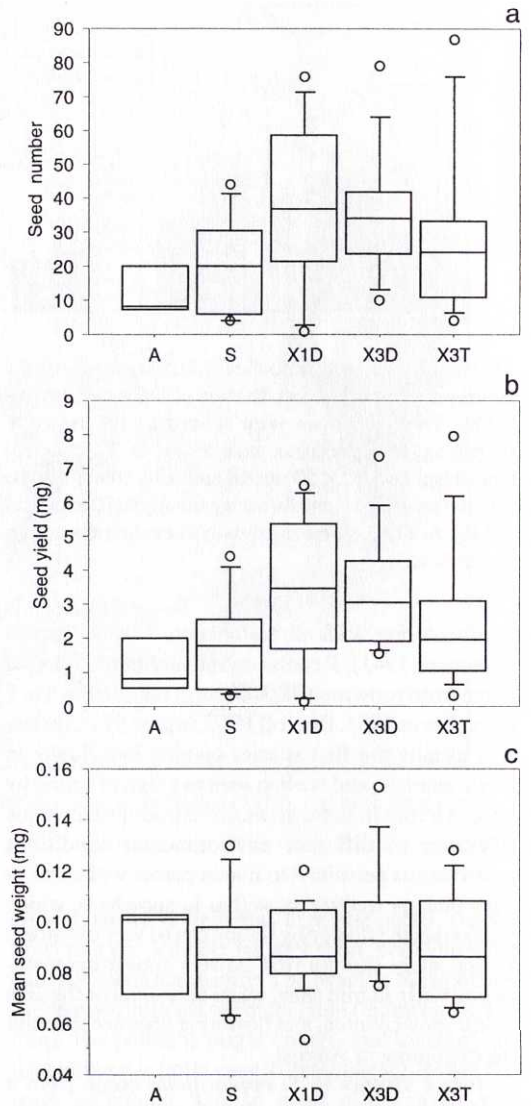


FIGURE 5. (Figure 6 in Paper I, corrected). Box plots of seed number (a), seed yield (b), and mean seed weight (c) for different pollination treatments in *Saxifraga oppositifolia*. A: Autodeposition, S: Selfing, X1D: Cross pollination with one donor, X3D: Cross pollination with a mixture of three donors, X3T: Cross pollination with three different donors on three different occasions.

few of the experimental plants, the sample size in the different treatments became very unequal. This is a serious problem which cannot be circumvented by the use of a non-parametric method like the Kruskal-Wallis test which we applied. The problem is that the power is much reduced with so few samples in some of the groups (Underwood 1997). A statistical test is therefore not useful in this case, but the outcome of the experiment was clear enough anyhow.

The two remaining treatments in the experiment,



TABLE 1. (Table 7 in Paper I, corrected). Seed number seed yield, and mean seed weight for different pollination treatments in *Saxifraga oppositifolia* (means  $\pm$  SD).

Treatment	Seed number	Seed yield (mg)	Mean seed weight (mg)	n <sup>a</sup>
Autodeposition	13.0 $\pm$ 9.5	1.2 $\pm$ 1.0	0.088 $\pm$ 0.023	3
Selfing	20.1 $\pm$ 15.3	1.8 $\pm$ 1.5	0.088 $\pm$ 0.023	7
Cross 1 donor	38.2 $\pm$ 24.0	3.3 $\pm$ 2.2	0.089 $\pm$ 0.017	13
Cross 3 donors	36.0 $\pm$ 19.2	3.4 $\pm$ 1.8	0.098 $\pm$ 0.023	11
Cross 3 times	30.1 $\pm$ 26.2	2.6 $\pm$ 2.2	0.089 $\pm$ 0.021	10

<sup>a</sup>Number of 20 treated flowers which set seed.

cross pollination with three donors at the same or different occasions, showed little difference between each other and also compared to cross pollination with a single donor. This was interpreted as that a single bumblebee visit would bring enough pollen for full seed set. This conclusion however implies that the pollen from this single visit entirely covers the stigma, as was the case in the experiment. While this may hold true for some bumblebee visits, it is hardly the case for flies.

We also tried to assess if pollen availability is a limiting factor for reproductive success in this species. In ten genets we cross pollinated half of the flowers (with three different donors) and left the others as controls. The treated flower produced almost twice as many seeds as the controls. Again the statistical analysis of the data was however erroneous. A standard mixed-model ANOVA was used, but since this experiment also conforms to a randomized blocks design a mixed model ANOVA without replication should have been used (Underwood 1997). This is because the randomized blocks design carries with it the assumption of no interaction between treatment and block (i. e., genet in this case). This flaw however does not change the conclusion, that seed set in *S. oppositifolia* can be pollen limited, at least some part of the season and in some years. More data was however needed to encompass the within- and among-year variation in pollination efficiency (see Paper IV).

To conclude, this study showed that *S. oppositifolia* is a facultative outcrosser, but that seed set is strongly favoured by outcrossing compared to both autodeposition and geitonogamy. This is in agreement with previous results (Kevan 1972, Tikhmenev 1984). Gugerli (1997a) later showed that this also holds true for the Alps. The intrafloral phenology promotes outcrossing, and the rapid onset of flowering gives ample time to complete seed maturation.

## Paper II. Direct effects of increased temperature

This study was performed at three sites very distant from each other: Val Bercla in the Swiss Alps, Latnjajaure in northern Swedish Lapland, and Alexandra Fiord on Ellesmere Island in the Canadian High Arctic. The aim was to compare the response to experimental warming in different parts of the distribution of *S. oppositifolia*. Open-top chambers were erected and we thereafter monitored flowering phenology, pollination, and seed production for two (Val Bercla) or three seasons. Observations at Latnjajaure and Val Bercla strictly followed the ITEX manual (Molau 1993b). The experimental site in Alexandra Fiord was on a polar semi-desert plateau far away from the lodging, and monitoring was therefore done every 4–10 days.

It turned out that the response to warming in *S. oppositifolia* was very slight at all three sites, for phenology as well as seed production. Pollination occurred somewhat earlier in the heated plants, indicating that the OTCs do not hinder pollination. (This could otherwise be expected after seeing bumblebees approaching the flowers at high speed, only to crash into the polycarbonate walls of the OTCs.) There were some indications that flowering was prolonged in the OTCs, rather than accelerated as expected, probably because of increased protection from wind and snow. There was no consistent effect on seed production. At Val Bercla and Latnjajaure there was a decreasing trend in the number of flowers per plant, a trend that was more pronounced in the heated plants. Whether this effect, if it was a real one, was due to the warming or to some side-effect of the OTCs will be discussed later.

The following experimental design was used to make sure that the lack of an effect on seed production was not an artefact of reduced insect visitation. Six new plots were established at Latnjajaure, and three of them were furnished with OTCs. Four plants were marked in each plot, and on each plant 5 flowers were cross pollinated by hand and emasculated. There was



no difference in seed number between heated and control plants in this experiment either.

The lack of response to temperature enhancement in *S. oppositifolia* means that it is likely to face serious problems in a warmer climate. This is because more responsive species, like *Carex bigelowii*, has been shown to rapidly increase growth in similar experiments (Stenström and Jónsdóttir 1997). *Saxifraga oppositifolia* seldom occurs in closed vegetation, which indicates that it is sensitive to shading (Jones and Richards 1956; see also Paper V). If the climate gets warmer, it will therefore probably be dependent on dispersing to higher latitudes or altitudes, or to areas opened up by retreating glaciers.

### Paper III. The bumblebee population at Latnajaure

The impetus for this study came from a need to find out precisely when and to which extent bumblebee queens forage on *S. oppositifolia*, in order to relate this to the levels of cross pollination during different parts of the season (Paper IV). By continuing capturing throughout a whole season, we would also be able to time the different events in the colony development of the bumblebees. We also wanted to know how many queens actually forage in the area. When I assisted in the study by Bergman et al. (1996) on the weather dependency of insect activity, we all guessed that we were observing a small number of rather stationary queens, even hesitating to catch a single one for the purpose of measuring body temperature.

Some of the data on plant utilization in this study was collected already in 1991 by Peter Bergman. Capturing during an entire season was however conducted in 1995. We captured bumblebees along a circular path on the slopes above the field station, adjusting the route according to where flowering was most intense. A captured bumblebee was treated in the following way. We first noted which species and caste it was, and which plant species we had captured it on. In all specimens we removed the corbicular pollen loads, if present. Queens were equipped with individual markings; a number tag on the scutellum (a hairless patch on the dorsal side of the thorax). In addition to capturing, we monitored flowering phenology of all species at four sites with different duration of snowcover. This was done to be able to compare the phenology of the plants with the utilization by bumblebees.

The first bumblebee queens were captured in the end of May, and for the three weeks to follow, they foraged almost exclusively on *S. oppositifolia*. Ten days after the first capture, the first queen with pollen

in her corbiculae was captured, indicating that they had started to establish nests. The pollen loads mostly consisted of *S. oppositifolia*; the first brood is thus fed mostly on this species. In the middle of June visits to *S. oppositifolia* started to decrease, and *Rhododendron lapponicum* instead became the favoured species. In late June, the species which was to become completely dominant food source for the bumblebees came into flower. This was *Astragalus alpinus*, and for the greater part of July this was the species getting most visits, and with the highest amounts in the pollen loads. The data from 1991 consisted of a large number of pollen loads collected during one week in the middle of July, together with records on the plant species visited. In that period as well, *Astragalus* dominated the pollen loads. The species which the bumblebees were most frequently captured on was however *Bartsia alpina*, closely followed by *Astragalus*. Visits to *Bartsia* was common in 1995 too, but not nearly as common as to *Astragalus*. In 1991 there were also visits to *Phyllodoce caerulea* and *Pedicularis lapponica*. There were hardly any flowers around at all of these two species in 1995. In August several *Vaccinium* species come into flower, and this showed up in the visitation records and as pollen from the Ericaceae in the corbicular loads. Interestingly, *Silene acaulis*, which is very common at the site, was only visited occasionally and mostly in the latest part of the season when few other species are still flowering. This has also been observed by Richards (1973), who documented a fairly similar sequence of visitation on Ellesmere Island. *Silene acaulis* is mostly visited, and probably also pollinated, by butterflies, an unusual condition in arctic-alpine plants (Andersson and Bergman, manuscript).

The dominance of the typical bee-flower *Astragalus* as a food plant, even though a number of other species are much more common, indicates that arctic-alpine bumblebees are no more generalistic than their temperate counterparts, as was suggested by Richards 1973. Specialization on the level of an individual bee is indicated by the fact that the pollen loads usually contained 91–100% pollen from a single species, even though 2–5 species were usually present. This is in accordance with the "majoring-minoring" behaviour described by Heinrich (1976).

*Bombus alpinus* was the species we most frequently encountered for the greater part of the season. The other common species was *B. hyperboreus*, which is an obligate nest parasite on the former species (and also on *B. polaris*, which is uncommon at Latnajaure but replaces *B. alpinus* in the Arctic; Richards 1973). The timing of capture of queens of *B. alpinus* with pollen in their corbiculae, and of workers and males of the same species, led us to conclude that only one



batch (or possibly two overlapping batches) of workers are produced by this species at Latnajaure. A single batch of workers being produced is also the case for *B. polaris* on Ellesmere Island (Richards 1973) and in Alaska (Vogt et al. 1994). This leads to few workers being produced, which will probably reduce the importance of bumblebees as pollinators compared to temperate areas.

When capturing and marking queens, it soon became evident that they were much more numerous than we had expected. At the end of the summer we had marked 154 queens: 124 of *B. alpinus*, 30 of *B. hyperboreus*, 3 of *B. balteatus*, and 1 of *B. lapponicus* (the latter two species mostly occur on lower elevation). During the summer we recaptured 26 of the marked individuals, and using the Schumacher and Eschmeyer method (Krebs 1989) we calculated the size of the population of queens to 350 individuals. The high numbers are surprising when considering how seldom we encountered foraging queens in the field.

The low visitation frequencies and high number of individuals at Latnajaure implies that the queens range over large areas. This is in contrast with meadows in the Netherlands, where queens are able to find sufficient resources in a rather small area where they stay all summer (M. Kwak, pers. comm.). The high mobility of bumblebee queens at Latnajaure could potentially bring about extensive gene flow through long-distance pollen transport.

#### **Paper IV. Seasonal variation in pollination and seed production**

In this study I wanted to test the hypothesis that the seasonal change in visitation to *S. oppositifolia* from bumblebee queens, as presented above, affects the levels of cross pollination, and ultimately seed production. To do so, I first monitored pollination at sites with different duration of snowcover for three seasons. Three sites were used in 1992 and 1993, and four in 1995. During the entire study I also captured insects visiting *S. oppositifolia*, to get a view of the variety of potential pollinators.

As predicted, the minimum cross pollination level (proportion of flowers pollinated before onset of pollen release) decreased as season progressed, with significant decline in two of three years and a similar trend in the third. In 1995 this decline coincided precisely with the decrease in visitation and pollen load content. The pattern for seed production was however not as convincing. Only in one of the three years it was seed production higher at the earliest site; in the two other there were no significant differences

among the sites. To find out if the additional cross pollination effected by the bumblebee queens actually increases seed production, I set up an experiment with selective cages in 1996 and 1997. These cages had a mesh width of 6 mm, which excludes bumblebee queens but should allow smaller insects such as flies to enter. The cages were erected over 20 plants at each of three sites, with 20 plants left untouched as controls. This was a factorial experiment, with treatment as well as site as fixed factors (since the sites represented a gradient and not only a sample of all potential sites; Underwood 1997). I should probably also have included cages with openings large enough to permit the passage of bumblebees, to act as procedural controls (Underwood 1997). Interpretation of the outcome of the experiment was however possible anyhow.

In the first year the exclusion had an effect on seed:ovule ratio at the two earliest sites, with the largest effect in the middle site. Thus, bumblebee visitation increased seed production in the beginning and middle of June, but not in the end of June. In the second year, there was a constant decline in the effect of the cages on seed:ovule ratio from the earliest to the latest site. Thus, the pattern conformed more closely with the expected one in the second year, with bumblebee visitation increasing seed production most in the earliest part of the season. Snow was more unevenly distributed in this year, which prolonged the flowering season. The first site was set up already in the end of May, and the third not until the middle of July.

The fruit:flower ratio was constantly lower in the caged plants in both years. However, in neither year was the interaction between site and treatment significant even for seed:ovule ratio, indicating that the change in effect during the season was not very large. This in turn means that the visitation from bumblebee queens increases seed production to a rather moderate extent. Visitation from flies and other small insects is enough to raise the level well above that previously observed from autodeposition. The total pollination level, i. e., the proportion of flowers pollinated at the end of flowering, was usually near 100% at all sites and in all years. Even though the flies probably transfer more pollen between flowers on the same individual than do bumblebees, the fact that the seed:ovule ratio was still around 0.20 indicates that they do contribute to some cross pollination as well. Seed:ovule ratios from pure geitonogamy, as shown in Paper I (Fig. 5b) was usually below 0.15.

In addition to bumblebees, insect visitors during the study included several species of flies, a wasp, a sawfly, a stonefly and a beetle. The larger flies, belonging to the families Anthomyiidae and Muscidae,



are quite often seen on the flowers, whereas visitors from other orders were seen only occasionally. Although no quantitative census was made, it nevertheless seems likely that the larger flies contribute most to the pollination of *S. oppositifolia* at Latnjajaure. Bumblebee visitation probably has a greater effect on gene flow than on seed production.

### **Paper V. Micrometereological determinants of flowering, pollination, and seed set**

The final paper of this thesis contains an eight-year dataset (1990–97) on flowering in permanently marked individuals of *S. oppositifolia* at Latnjajaure. We used this data to elucidate which climatic factors determine flower production in this species. For most of the study period (1991–96) we also monitored flowering phenology in the marked specimens, to get a view of the variation among years. The second aim of this study was to find out which meteorological variables determine the pollination rate. The data used for this purpose came from the daily observations in 1995 of pollination in 20 plants at each of four sites with different duration of snowcover (Paper IV). The pollination rate was calculated for each day as the proportion of remaining unpollinated flowers (from the day before) having received pollen. As discussed in the introduction, weather in arctic and alpine habitats is very unpredictable. If pollination has taken place, rapidly deteriorating weather could still reduce seed set by interfering with the germination of pollen grains on the stigmas (Corbet 1990). We therefore performed an experiment with simulated rain on hand pollinated flowers to estimate the time interval sensitive to precipitation.

The relationship between flower production and climate in the preceding season (since the flower buds are preformed) was a lot simpler than we had expected. Using linear regression, we found that the solar radiation accumulated during July, August, and September during the preceding year was the single most useful variable for determining flower production in *S. oppositifolia* at Latnjajaure. The regression explained 96% of the variation in flower production (expressed as the deviation from the mean for all years included). The importance of solar radiation is also illustrated by the fact that a 17% difference in radiation produced an 89% difference in flowering among years.

The time period of accumulated radiation used in the linear regression coincides with the snowfree period of the plants. They get snowfree at the end of June, and are usually snowcovered again in the beginning of October. The flowering phenology was

almost synchronous at the two sites used (described in Paper I), but was shifted between years as a consequence of different extent of the snowcover. In 1992 there was a severe spell of snow and strong winds in the middle of flowering. This destroyed a lot of flowers at the most exposed of the two sites, and also delayed onset in specimens not yet in flower. Together this produced a double-peaked phenology curve in that year.

The picture for pollination rate was slightly more complicated than for flower production. Multiple regression showed that accumulated solar radiation and mean windspeed were the two variables with highest predictive value. Neither in this case was temperature, measured at 1.5 m, an important variable. Precipitation did not have enough predictive power to be included in the model either. There was however no pollination on days with more than 7.3 mm of precipitation. A threshold value also existed for mean windspeed; above 12.3 ms<sup>-1</sup> (which means twice the value in gusts), no pollination was observed. In the study by Bergman et al. (1996), bumblebee activity ceased at mean windspeed of 8 ms<sup>-1</sup>. The method used here thus indicates that some insects are active even at higher windspeeds. It could also mean that the plants which received pollen at high windspeeds were located in sheltered spots, where insects could remain active.

The experiment with simulated rain showed that the time period sensitive to precipitation is quite short. Seed set was decreased significantly in flowers flushed with water 1.5 h after pollination, but after 3 hours the effect was no longer significant. After 6 hours there was no effect at all, which means that the pollen had germinated and was firmly attached to the stigmata. Considering that the stigmata are receptive for about 5 days (Paper I), this means that there should be ample time during the life span of a flower to receive pollen. That is if it has not been destroyed by drifting snow, like happened in many of the permanently marked plants in 1992. The flowers are insensitive to low night-time temperatures, and they seem to recover well after rain (pers. obs.). But snow is an entirely different matter, especially if accompanied by strong winds. The abrasion of ice crystals quickly destroys the petals, and leaves the flowers unattractive for pollinators. I have however not tested whether the stigmata are still receptive after such events.

In this paper we also presented a comparison of flowering pattern in five other common species at the site, representing different life forms. Flower production in the two evergreen species, *Diapensia lapponica* and *Cassiope tetragona*, showed the same pattern in the year-to-year variation as the likewise



evergreen *S. oppositifolia*. The herbaceous *Ranunculus nivalis* also showed the same pattern. Correspondence was however not as good with the semi-evergreen *Dryas octopetala*, indicating that variables other than radiation is important in this life-form. Flowering in *Eriophorum vaginatum* showed no correspondence at all. In the monocarpic (dying after flowering) tillers of this species, flowering frequency is determined by the temperature 3–4 years back (Shaver and Molau, unpubl.); its being completely out of phase with *S. oppositifolia* was therefore expected.

Several other species than *S. oppositifolia* are thus sensitive to even a moderate reduction in solar radiation. Increased growth, and thereby increased shading, from graminoids in a warmer climate could therefore lead to reduced flower production in these species (Stenström and Jónsdóttir 1997, Molau 1997b). Experimental shading has been shown to reduce flowering frequency in *Cassiope tetragona* (Havström et al. 1995). *Saxifraga oppositifolia* has a reputation of being a rapid colonizer, but if flowering decreases, so will seed production and thereby its ability to escape from competition.

## DISCUSSION

### The past: glacial survival and genetic variation in *Saxifraga oppositifolia*

*Saxifraga oppositifolia* is the only species in its section (*Porhyrion* Tausch) having reached the Arctic. In doing so, it has become the probably most widespread species in the large and varied genus *Saxifraga* (Webb and Gornall 1989). It has an extraordinary tolerance to environmental stress factors, such as low temperatures, short growing seasons, and drought (Teeri 1972, Crawford et al. 1995). In being so widespread, you would expect it to have a high capability of seed production in the absence of insects, to be able to colonize new lands without having to rely on pollinators. But this is not the case: throughout its range, *S. oppositifolia* is almost completely dependent on insect visitation to produce any considerable amount of seeds (Kevan 1972, Tikhmenev 1984, Gugerli 1997a, Paper I). During past migrations, such as occurred during the periods of advance and retreat of epicontinental glaciers, the pollinators must therefore have followed in its path. The long life span of individual plants means that they could probably afford to sit around for a while until the pollinators reached them. Whether the arctic plants spent the last glaciation in ice-free refugia within the ice-sheet (the nunatak hypothesis; Dahl

1987) or if they all immigrated after the ice had retreated (the tabula rasa hypothesis; Nordal 1987) has been a matter of much debate. Recently, patterns of genetic variation in *S. oppositifolia* has provided arguments favouring both standpoints. Abbott et al. (1995), using chloroplast DNA, found a higher number of genotypes in Svalbard than in Norway. They interpreted this as *S. oppositifolia* possibly having survived the glaciation in High Arctic refugia. In a more extensive study on the variation in RAPD markers, Gabrielsen et al. (1997) however found the highest amounts of intra-population variation in southern Norwegian populations. There was less variation in northern Norway, and even less in Svalbard. The geographical structuring of the variation suggested that *S. oppositifolia* immigrated from large, variable periglacial populations when the ice retreated. They also claimed that the lower levels of variation in the High Arctic populations was due to lower pollinator activity and shorter flight distances, but no supporting data was provided.

Gabrielsen et al. (1997) argued that the generally high levels of intrapopulation variation reflect the fact that *S. oppositifolia* is predominantly outcrossed, but that the high levels could not be explained by gene flow alone. As shown in Paper IV, bumblebee visitation can increase the level of cross pollination in early-flowering parts of a population. In May and early June most of the landscape is still covered with snow, and the areas with flowering specimens of *S. oppositifolia* can be separated by hundreds of meters or even several kilometers. This forces the queens to make long transport flights between foraging bouts. Some of the pollen deposited will therefore probably be brought from remote populations, potentially causing an important influx of new genes. In Paper III, we presented some observations that indicate that the queens do forage over large areas. Whether the queens are even confined to Latnjavagge is an open question; I would say that they are not. In 1996 we repeated capturing and marking of queens, with the difference that we did it at two different locations simultaneously (M. Stenström, unpubl. data). Very few queens were recaptured, but two of those had moved between locations about 1 km apart. One of the locations was near the top of the ridge separating Latnjavagge from the next valley to the east. The queen captured there had flown from the vicinity of the field station, and could easily have moved on to the other valley. Moreover, as long as the queens have not established nests, they do not have to return to the same place to unload their cargo of pollen and nectar. This means that directional pollen flow could be even more pronounced in the early part of the season. The exceptional conditions during the early part of the



flowering season of *S. oppositifolia*, together with it having access to highly mobile pollinators, was not taken into account by Gabrielsen et al. (1997). I would think that these factors could explain a substantial amount of the intrapopulational variation found in this species. To prove that long-distance pollen flow actually takes place is however a very complicated matter, but definitely one that merits further effort.

### **The present: controls on reproductive effort and success in *Saxifraga oppositifolia* in different parts of its distribution**

Since *S. oppositifolia* is so extremely widespread, you can not expect that the controls on reproductive effort and success will be the same everywhere. Seasonal variation (Paper IV), e. g., should be less pronounced in landscapes with a less ragged topography, since this will result in less marked snowmelt gradients. If temperatures are very low also in summer, even a small accumulation of snow will extend the flowering season. On the Chelyuskin Peninsula, the northernmost tip of the Eurasian continent, *S. oppositifolia* was observed to flower from June to August, even though snowmelt gradients were not very pronounced. Pollination at this site however seemed to be very inefficient: only a single flower in 40 specimens scored had received any pollen, despite the weather being exceptionally favourable. I would guess that fragmentation from frost heaving has a large part in the very extensive cover of *S. oppositifolia* found there. In contrast, almost every single flower was pollinated in 20 specimens scored on Wrangel Island, which has a less severe climate. Bumblebees were frequent on Wrangel, and so were other insects. During the stop at the Chelyuskin Peninsula I did not observe a single insect. These observations were all made by the author during the Swedish-Russian Tundra Ecology Expedition in 1994.

Weather, acting directly by destroying flowers or indirectly on insect activity, is likely to be a limiting factor for pollination in all parts of the species distribution. Even though the study site has 24 hour daylight for a large part of the growing season, the steep sides of the valley hinders direct sunlight for many of those hours. Whether solar radiation governs the pollination rate also in open tundra landscape further north is an open question. Windspeed is however likely to be as important everywhere. In any case, our data suggest that solar radiation probably plays a more important role in the reproduction of tundra plants than previously believed, both for reproductive

effort and for reproductive success (Paper V). The intensity of sunlight has a much stronger influence on ground surface temperature, which is more relevant to the plants as well as to small insects, than air temperature (Molau 1995). In the case of reproductive effort in *S. oppositifolia*, the effect of solar radiation is probably not only increased temperature in the plant tissues. It should also affect the rate of photosynthesis, with an increased supply of stored energy available for flower production after a sunny season. If temperature alone had been important, we should have observed higher flower production in the warming experiments. This was not the case even at the High Arctic site. There is however a risk that the OTCs reduced the light input to such an extent that it may have affected flower production. Measurements by U. Johansson (Univ. of Lund) show that the polycarbonate used at Latnjajaure reduces light in the photosynthetically active range by about 20%. The large opening in the top of the OTCs should make this reduction less important, but considering that even a small change in accumulated radiation will affect flowering in *S. oppositifolia*, measurements of light input to the OTCs should probably be made anyhow.

My studies show that natural day-to-day variation in temperature (Paper V), as well as experimental warming (Paper II), has little effect on pollination rates and reproductive success in *S. oppositifolia* at Latnjajaure. It is therefore not surprising that Gugerli (1998) found no evidence of increased pollen limitation at higher altitude. Seed set from selfing did not increase with altitude either. In *Ranunculus acris*, Totland and Birks (1996) however found that altitude explained a large part of the variation in seed set and seed weight. Gugerli (1998) concluded that environmental conditions in arctic and alpine habitats not always select for higher selfing rates. Gugerli (1998) suggests that the presence of large amounts of intrapopulational variation, as will be the result of outcrossing, could be advantageous in these highly stochastic environments. Not constituting real proof, it is nevertheless suggestive that one of the most widespread arctic-alpine plants, *S. oppositifolia*, has very high levels of variation within populations (Gabrielsen et al 1997).

Pollen limitation in *S. oppositifolia* has been shown to exist both in the Alps (Gugerli 1997a) and in north Scandinavia (Paper I), at least during some parts of the season. Almost all flowers of *S. oppositifolia* at Latnjajaure eventually get pollinated (Paper IV). The amount of pollen is therefore not the limiting factor, but rather the quality of the pollen and when it is deposited. These two factors are closely connected, in that cross pollination is more likely to occur during the female phase. When pollen is starting to be



released, geitonogamy is likely to occur. Flies are probably more responsible for this pollen transfer among flowers on a genet, since they tend to stay longer and visit more flowers per plant than bumblebees (pers. obs.). The pollination by flies (and possibly other small insects) in the bumblebee-proof cages (Paper IV) was probably mostly geitonogamy, since the seed set was only slightly above that found from hand selfing (Paper I). Interestingly, the only variable which was affected by the pollen source was seed number, not seed weight (Paper I). Both variables are affected in the subarctic-alpine *Bartsia alpina* (Molau et al. 1989). There seems to be no lower limit for the number of ovules developing into seeds in a fruit: it ranges from a single one up to virtually all. In *Bartsia*, a lower limit of 10 seeds per capsule exists (Molau et al. 1989).

Flower production in *S. oppositifolia* at Latnjajaure was explained almost entirely by the amount of sunshine in the season preceding flowering. Since high solar radiation also increases pollination rate, sunny summers should also entail high seed production. If resources are depleted by a high seed output, a decline, rather than an increase, in flower production the year after a sunny season could be expected. This was however not the case. Whether seed production is reduced after a year with high seed output I do not know. Two or more good seasons in a row, which is necessary for maximizing both reproductive effort and success, however occurs very rarely at the study site. With all these facts at hand, my conclusion is that pollen limitation is more important than resource limitation in this species. I would expect that to be the case also for other arctic-alpine outcrossers.

The arctic saxifrages which most closely resembles *S. oppositifolia* in habit are probably *S. cespitosa* and *S. aizoides*. *Saxifraga cespitosa* is gynodioecious, with hermaphroditic as well as purely female flowers (Molau and Prentice 1992). The hermaphroditic individuals have a high selfing efficiency; outcrossing is probably ensured by the high proportion (39%) of female individuals. This species has white flowers which have been reported to be pollinated by small flies (Molau and Prentice 1992); there are no records of bumblebees visiting this species. In fact, *S. oppositifolia* is probably unique among arctic-alpine saxifrages in being an important food source for bumblebee queens. It is also the only arctic species with purple flowers, a color often found in bee-pollinated species (Faegri and van der Pijl 1979). The yellow or orange flowers of *Saxifraga aizoides* are probably also pollinated by flies. This species occurs together with *S. oppositifolia* in moist places at the study site, but does not start flowering until the end of

July. No visits to this species from bumblebees were recorded in the study described in Paper III, nor was any *Saxifraga* pollen present in the corbicular loads that late in the season. Like other late-flowering species, *S. aizoides* has a high selfing efficiency (Molau 1993a). Thus, whereas *S. oppositifolia* occupies a whole range of snowmelt gradients, *S. aizoides* is restricted to the late-thawing parts. The latter species is probably not as tolerant to the drought and snow abrasion characterising ridges and hilltop; it has larger, softer leaves which are not as densely packed as those of *S. oppositifolia*. Accordingly, *S. aizoides* has a more restricted distribution, not reaching as far north as *S. oppositifolia*.

*Saxifraga biflora*, a late-flowering species of the same section as *S. oppositifolia*, occurs in the Alps (Webb and Gornall 1989). Gugerli studied the reproductive ecology of both species (1997a) as well as the hybridization between them (1997b). As expected, *S. biflora* has a higher selfing efficiency than *S. oppositifolia*, although *S. biflora* is protogynous as well. Geitonogamy in *S. biflora* also leads to higher seed set than in *S. oppositifolia*. Pollen limitation accordingly seems to be less of a problem for *S. biflora*.

### The future: *Saxifraga oppositifolia* and climate change

When hypothesizing about controls on different aspects of plant reproduction in tundra habitats, it is important not to assume that your own perception of the climate is shared by the plants (Murray 1987). Even though the Arctic was colonised by plants only very recently when viewed on a geological timescale, many of the species we see today had existed in mountainous and periglacial areas for long periods before that. These plants share a number of characteristics that allow them not only to subsist, but to thrive, in conditions that we humans sometimes perceive as unbearable. It is therefore important to consider more than just the obvious features of the habitat. The presence of unexplained variation in, e. g., seed production among and within seasons (Paper IV) may be due to my inability to understand all the factors that may limit the success of the flowers of a purple saxifrage. Solar radiation probably being more important than temperature for determining reproductive effort in several tundra plants is one example. Knowing that you have been as objective as possible is especially important when predicting the fate of the tundra in a warmer climate, since such data may ultimately be used by policy-makers. As far as my data goes, a reduction of the emission of



greenhouse gases is probably necessary to ensure the long-term survival of *S. oppositifolia*, and probably also for several other slow-growing tundra plants with low competitive ability, in the Scandinavian mountains. The crucial data still missing is the rate of dispersal in these species: will they be able to escape from competition or not?

## CONCLUSIONS

The studies presented in this thesis show that reproductive effort (flower production) in the arctic-alpine perennial *Saxifraga oppositifolia* can be explained by a single environmental variable, the solar radiation accumulated during July to September in the season preceding flowering. The controls on reproductive success presented here are more complex, and can be divided into biotic (1) and abiotic (2) factors:

**1a.** Cross pollination produces substantially more seeds than either autodeposition or geitonogamy. Seed weight is however not affected by the pollen source. The flowers are protogynous, and pollination occurring during the female phase leads to higher seed set than during the male phase, due to declining stigma receptivity.

**1b.** Bumblebee visitation in the early part of the season increases cross pollination levels, and to some extent also seed production. Flies however seem to do the major share of pollination, and almost all flowers are eventually pollinated during all parts of the season. The occurrence of pollen limitation is probably due to geitonogamous pollen transfer by the flies. The large and mobile bumblebee population probably effects long-distance pollen transfer in the early part of the season, which could partly explain the high levels of intrapopulation genetic variation found by other workers.

**2a.** The pollination rate (number of flowers pollinated) on any given day is to a large extent determined by weather conditions, mainly insolation and windspeed. This is an indirect effect, acting by reducing insect activity, and thus linking biotic and abiotic factors. If pollen has been deposited, precipitation has little effect unless it occurs within three hours after pollination.

**2b.** Experimentally increasing temperature has little effect on phenology as well as reproductive success, neither in the Alps, the Scandinavian mountains, nor in the Canadian High Arctic. Together with the strong

dependence of flower production on insolation, this should make *S. oppositifolia* vulnerable to competition from more responsive species in a warmer climate.

## SUMMARY IN SWEDISH

Den här avhandlingen handlar om vilka faktorer som styr blomning och fröbildning hos purpurbräcka, *Saxifraga oppositifolia*. Purpurbräcka är en arktisk-alpin växtart, dvs den förekommer i de norra polartrakterna men även i bergsområden längre söderut, som t ex i våra svenska fjälltrakter.

Vilka är då skälen till att ägna nästan sju år åt att studera denna enda växtart? Det finns egentligen två huvudskäl. För det första är den sexuella förökningen hos arktisk-alpina växter dåligt utforskad. Tidigare trodde man att de allra flesta arterna antingen litade helt till vegetativ förökning (t ex med groddknoppar, utlöpare och jordstammar), och att om sexuell förökning förekom så skedde den genom självbefruktning eller apomixis (dvs fröbildning utan föregående befruktning). Inte förrän i början av sjuttioalet framkom det bevis på att ett stort antal arter faktiskt är beroende av insektsbesök för att sätta ordentligt med frön. Vilka faktorer som styr frösättningen är dock inte utrett för mer än ett fåtal av dessa arter.

Det andra huvudskälet har att göra med förändringar i jordens klimat. De ökande utsläppen av så kallade växthusgaser (varav koldioxid är den mest kända) genom förbränning av fossila bränslen förutspås leda till en ökning av jordens medeltemperatur med 2–3 grader de närmaste 50 åren. Det låter kanske inte så mycket, men för arktiska och alpina växter är det en drastisk förändring. Det beror på att mängden tillgänglig värmeenergi i dessa områden är så liten och att detta ofta begränsar hur mycket växterna kan växa till och föröka sig. De klimatmodeller som används för att beräkna ökningen i temperatur visar också att uppvärmningen kan bli ännu större i polartrakterna. Eftersom växterna utgör basen för ekosystemen så kan uppvärmningen få stora konsekvenser, inte bara för växterna utan också för de djur som livnär sig på dem. I sista hand påverkas även rovdjuren, till vilka vi även kan räkna oss själva. Rennäringen kan t ex påverkas starkt av förändringar i sammansättningen av växtarter i fjällen.

Purpurbräcka tillhör visserligen inte de arter som är viktiga för betesdjur som renar och lämlar. Genom att den är så vittspridd (Fig. 3) valdes den ändå till en av studiearterna inom ITEX, The International Tundra Experiment. Målsättningen med ITEX var från början att utröna effekten av klimatförändringar på ett urval av viktiga växtarter med cirkumpolär utbredning.



Forskningsprogrammet började i liten skala, men har nu växt till att inkludera över 20 fältstationer i arktiska och alpina tundraområden, med deltagare från 13 olika länder. Genom att standardisera experiment-uppläggning och mätmetoder har vi kunnat få fram resultat som kan jämföras mellan områden, för att därigenom få en bättre bild av klimatförändringars effekt på växtsamhällena.

Mina undersökningar är främst gjorda vid Latnjajoure Fältstation (allmänt kallad Latnja), som ligger i en dal på 981 meters höjd i västra Abisko fjällarna (Fig. 2). Stationen ägs av Abisko Naturvetenskapliga Station. Latnja ligger i den mellanalpina regionen (ca 300 höjdmeter över trädgränsen) och har en årsmedeltemperatur på  $-2,6^{\circ}\text{C}$  och en medeltemperaturer i juli på  $7,7^{\circ}\text{C}$ . Det betyder att växtsamhällena på kalkfattig mark i dalbotten utgörs av låga ris och örter som t ex kråkris, dvärgbjörk, fjällgröna och dvärgvide. Purpurbräcka växer dock helst på kalkrik mark, och det finns det på bergssidorna. Där dominerar arter som fjällsippa, lapsk alpros, fjällglim och nätvide.

Purpurbräcka har ett krypande växtsätt och har blommorna sittande i skottspetsarna. Blommorna varierar i färg från ljus rosa till mörk purpur. De besöks av många olika typer av insekter, men främst avflugor och humlor. Tidigare undersökningar gjorda i arktiska områden har visat att purpurbräcka har mycket liten förmåga att sätta frö genom självbefruktning och alltså är beroende av insektsbesök. Min första undersökning (Artikel I) visade att det stämmer också för svenska fjällen. Stänger man ute insekter bildas det mycket få frön och pollinerer man för hand med pollen från samma individ blir det nästan lika få. Frövikten påverkas dock inte av om pollenet kommer från den egna plantan eller utifrån. Blommorna är protogyna, dvs när blomman öppnar är märkena mottagliga för pollen medan ståndarna öppnar sig först senare. Hos purpurbräcka varar den honliga fasen i omkring fyra dagar. När ståndarna väl öppnar sig har mottagligheten hos märkena redan börjat gå ner. I slutet av blomningen faller ståndarna in över märket, men då är märkena antagligen inte längre mottagliga alls. Förskjutningen av den honliga och haliga fasen gynnar förmodligen korsbefruktning; den förhindrar åtminstone självbefruktning.

Purpurbräckan börjar blomma väldigt snart efter att snön har smält: i Latnja tar det omkring 10 dagar (Artikel I). Att den kan komma igång så snabbt beror på att blomknopparna är nästan färdiga redan hösten innan de skall slå ut. Det gör i sin tur att hur många blommor en planta har en viss säsong beror på hur förhållandena var under föregående säsong. Det ligger nära till hands att tro att temperaturen när blommorna anläggs är det som bestämmer antalet. Hos purpurbräcka i Latnja visade det sig att det istället är

instrålningen (mängden solenergi) under föregående säsong som bestämmer hur många blommor det blir. Det fick vi fram genom att vi hade följt ett antal fast uppmärkta plantor under åtta säsonger (Artikel V).

Även försöken med förhöjd temperatur visade att purpurbräcka inte verkar vara speciellt starkt begränsad av värmetillgången (Artikel II). Vi simulerade ett förändrat klimat med miniväxthus (s k open-top chambers; Fig 1.) och undersökningen genomfördes förutom i Latnja i Alperna (Schweiz) och i kanadensiska högarktis (Ellesmere-ön). Varken fenologi (följden av olika händelser i tex blomningen) eller fröproduktion påverkades nämnvärt av uppvärmningen. Många andra arter både blommor och sätter frön snabbare, samt producerar mer frön, när de utsätts för ökad temperatur.

Det som påverkar frösättningen hos purpurbräcka är istället en kombination av insekternas aktivitet och andra väderfaktorer än temperatur. Från mitten av maj till mitten av juni besöks purpurbräcka av humledrottningar (Artikel III). Så tidigt är det få andra arter som blommor, och humlorna får huvuddelen av sitt behov av både nektar (som bränsle) och pollen (som mat till larverna) från purpurbräcka. Senare på säsongen växlar humlorna över till andra arter, främst fjällvedel. Nya plantor av purpurbräcka fortsätter dock att smälta fram ur snödrivorna långt fram på säsongen vilket gör att dess blomningssäsong sträcker sig ända in i augusti vissa år. Det orange pollenet synst tydligt på det stora märkena och tack vare att blommorna är protogyna kan man se hur många som blir pollinerade under den honliga fasen, vilket ger ett minimimått på graden av korspollinering (Artikel IV). Det visade sig att de som blommor tidigt på säsongen blir korsbefruktade i högre grad än de som blommor sent. Detta är en följd av att de tidiga får besök av humlor;flugor verkar inte vara lika duktiga på att transportera pollen mellan olika plantor. Genom att använda burar som stängde ute humledrottningarna, men inte flugorna, kunde jag också visa att humlebesöken också ökar frösättningen tidigt på säsongen. Ökningen var dock inte så stor, så det verkar som flugorna ändå står för det mesta av purpurbräckans pollinering.

Den korspollination som humlorna ger upphov till kan ändå vara betydelsefull, eftersom den bidrar till en omblandning av generna i populationerna. Tidigt på säsongen måste humlorna flyga mellan snöfria fläckar med blommande bräckor som kan ligga hundratals meter, eller t o m kilometer, från varandra. När vi studerade vilka växter som humlorna födosöker på under olika tider på säsongen märkte vi samtidigt alla drottningar vi fångade. Genom att jämföra antalet märkta humlor med hur många av dem vi fångade igen (s k fångst-återfångstmetod)



kunde vi uppskatta hur många humledrottningar som fanns i området (Artikel III). Det visade sig att det fanns omkring 350 stycken. Med tanke på att vi kunde få jobba en hel dag med att få ihop mer än 10 stycken är det förvånande många; det måste betyda att de rör sig över stora områden. Förmodligen sprider alltså humledrottningarna purpurbräckans pollen över stora avstånd. Detta genflöde är förmodligen en del av förklaringen till att norska forskare funnit att huvuddelen av den genetiska variationen finns inom populationer, istället för mellan populationer som skulle ha varit fallet om pollenspridningsavstånden hade varit korta.

För att ta reda på hur vädret påverkar pollinationen kan man gå omvägen om insekterna och se hur aktiva de är i olika väder. Vi valde istället att se direkt på hur många blommor som fått pollen på märkena en viss dag, och sedan relatera det till hur vädret varit (Artikel V). Det visade sig då att instrålning och vindstyrka var de faktorer som gav den bästa överensstämmelsen med hur många blommor som blev pollinerade. Instrålningen bestämmer hur varmt det blir nära marken, där ju insekterna oftast håller till, och vindhastigheten bestämmer hur svårt det är för dem att flyga. Varken nederbörd eller temperatur (på 1,5 m höjd) hade någon större inverkan. Precis som för vind fanns det dock ett tröskelvärde för nederbörden: över en viss mängd regn (eller snö) eller när vinden var för hård blev det ingen pollinering. För vinden låg gränsen dock så högt som 12 m/s, vilket betyder det dubbla i byarna. Efter att pollinering skett kan man tänka sig att regn eller snö stör pollengröningen. Genom att först pollinera blommor och sedan spruta vatten på dem efter olika tidsintervall fann vi dock att pollenet bara är känsligt i omkring tre timmar. När pollenet väl har grott spelar det ingen roll för frösättningen om det regnar. Snödrev kan dock förstöra blommorna innan pollinering hinner ske.

Sammantaget kan man säga att medan reproduktionsansträngningen (antalet blommor) hos purpurbräcka styrs av en enda miljövariabel, så styrs reproduktionsframgången (antalet frön som produceras) av en samverkan av flera, bl a tiden på säsongen när blomningen sker och vädret under själva blomningen. En generell ökning av temperaturen ökar dock inte reproduktionsframgången. Arter som t ex styvstarr ökar snabbt sin tillväxt med ökad temperatur, och purpurbräcka riskerar därför att utsättas för ökad konkurrens. Även en måttlig minskning av ljusstillgången sänker blomproduktionen kraftigt och arten riskerar därför att få se sin fröproduktion minska istället för öka i ett varmare klimat. Det minskar också dess chanser att undkomma konkurrens genom att sprida sig till nya områden.

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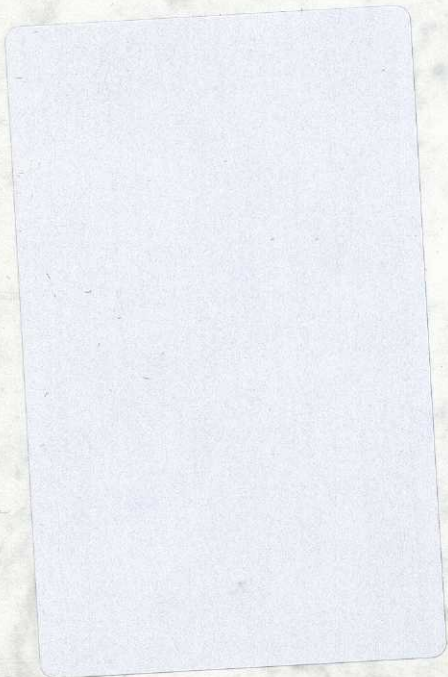


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