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Anna Stenström

**From pollination to variation -
reproduction in arctic clonal plants
and the effects of simulated climate change**



**Botanical Institute
Göteborg University
Sweden**

Göteborg University
Faculty of Science

Dissertation

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and the effects of simulated climate change

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Sweden

Avhandling för filosofie doktorsexamen i Miljövetenskap med inriktning mot Systematisk Botanik (examinator: professor: Lennart Andersson) som enligt Naturvetenskapliga fakultetens beslut kommer att offentligens försvaras fredagen 19 januari 2001 kl. 13.00 i föreläsningssalen på Botaniska Institutionen, Carl Skottbergs gata 22B, Göteborg.



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Stenström A (2000) From pollination to variation - reproduction in arctic clonal plants and the effects of simulated climate change.

Botanical Institute, Göteborg University, Box 461, SE 405 30 Göteborg, Sweden

Abstract

In this thesis I study the reproduction in arctic clonal plants, using *Carex bigelowii* and the closely related taxa *C. ensifolia* ssp. *arctisibirica*, *C. lugens* and *C. stans* as model plants. I follow the cyclic process of reproduction through flowering, pollination, seed set and seedling recruitment, and through vegetative reproduction (clonal growth) and analyse the consequences for genetic and morphological variation. I also studied the effects of simulated climate change on some of the processes. Reproduction and responses to simulated climate change were studied at a subarctic-alpine site at Latnjajaure, northern Sweden and at a subarctic site at Thingvellir, Iceland. The response to simulated climate change was studied as a part of ITEX (The International Tundra Experiment) using passive heating devices (open-top chambers). Variation was studied at 17 sites along the north coast of Eurasia, most of them visited during the Swedish-Russian Tundra Ecology Expedition 1994.

My results show that the amount of flowering, flowering phenology and seed set in *Carex bigelowii* are largely dependent on the temperature at Latnjajaure, while flowering is not affected by temperature at the warmer site at Thingvellir (Paper I, VI and VII). Flowering and seed set decrease with latitude and is affected by lemming cyclicality in *C. ensifolia*, *C. lugens* and *C. stans* (Paper III). Vegetative reproduction is extensive in all the taxa and provides the individual clones with a longevity extending hundreds and even several thousands of years (Paper II and III). The relationship between vegetative reproduction and temperature differ between sites (Paper III and VII). During their long lives there is a high probability for at least some warm growing seasons that enable the plants to set viable seeds. These seeds germinate in the infrequent disturbances, giving rise to new clones (Paper I). This apparently happens so often that a high genetic variation and clonal diversity is seen in most populations of all the studied taxa (Paper IV). However, it takes a long time for genetic variation to develop as indicated by a lower genetic variation in populations deglaciated 10 000 years B.P. compared to populations deglaciated earlier. The dependence of flowering and the sexual process on weather is further seen in the decrease in clonal diversity at higher latitudes (Paper IV). The genetic distances between the populations are correlated to the morphologic distances, and morphology is also influenced by climate and herbivory (Paper V). Warmer climate is likely to increase reproduction and growth at colder sites, while decreasing growth at warmer sites in *C. bigelowii* (Paper VI, VII).

Keywords: *Carex*, clonal plant, graminoid, Arctic, Subarctic, sexual reproduction, vegetative reproduction, climate, genet age, genetic variation, clonal diversity, glaciation, morphological variation, climate change

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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 A (1999) Sexual reproductive ecology of *Carex bigelowii*, an arctic-alpine sedge. *Ecography* 22: 305-313.
- II. Jónsdóttir IS, Augner M, Fagerström T, Persson H & Stenström A (2000) Genet age in marginal populations of two clonal *Carex* species in the Siberian Arctic. *Ecography* 23: 402-412.
- III. Jónsdóttir IS, Stenström A, Fagerström T & Augner M Population variation in clonal sedges along the arctic coast of Eurasia: Effects of climate, weather and lemmings. Submitted.
- IV. Stenström A, Jonsson BO, Jónsdóttir IS, Fagerström T & Augner M (in press) Genetic variation and clonal diversity in four clonal sedges (*Carex*) along the arctic coast of Eurasia. *Molecular Ecology*, Blackwell Science Ltd.
- V. Stenström A, Jónsdóttir IS & Augner M Morphological variation in clonal sedges (*Carex*), in the Eurasian arctic: Effects of taxonomy, ecotype, lemmings and climate. Manuscript.
- VI. Stenström A & Jónsdóttir IS (1997) Responses of the clonal sedge, *Carex bigelowii*, to two seasons of simulated climate change. *Global Change Biology* 3 (Suppl. 1): 89-96.
- VII. Stenström A & Jónsdóttir IS Effects of simulated climate change on phenology and life history traits in *Carex bigelowii*, at two contrasting sites. Manuscript.

For Paper I, I am solely responsible.

In Paper II, III, IV and V, the planning and fieldwork was a joint effort of the authors. I took part in the analyses and compilation of the manuscripts in Paper II and III. In Paper IV, I am responsible for the majority of the laboratory work and data analyses, and I also compiled the manuscript. I am responsible for the data analyses and the compilation of the manuscript in Paper V.

Paper VI and VII, are based on ideas and were planned by both authors. I made most of the field work and data analyses. In Paper VI we compiled the manuscript together, while I compiled the manuscript in Paper VII.

Nog vet jag
att man bör tala
allvarligt
Klokt

Men vem såg då
de förunderliga små gräsen

Nils-Aslak Valkeapää
ur Vidderna inom mig

Till Mikael och Tove



From pollination to variation - reproduction in arctic clonal plants and the effects of simulated climate change.

Anna Stenström

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Introduction

Reproduction is essential for all organisms. But many organisms can reproduce in two different ways, viz. sexually or asexually. Asexual reproduction exists in many different kinds of organisms, e.g. in animals as bryozoan, aphids and lizards (Hughes & Cancino 1985), many fungi (Buss 1985), and in most of the plant species (Silander 1985). Most organisms that reproduce asexually do so facultatively (Mars-hall & Brown 1981, Hughes & Cancino 1985), but there are examples of ancient asexual lineages in both animals, plants and fungi, which seem to have existed for millions of years without any sexual reproduction (Judson & Normark 1996).

Sexual reproduction is thought to be evolutionary advantageous in the long term, as it introduces genetic variation through recombination, outbreeding and migration (Maynard Smith 1978, Silander 1985). In the short term, however, there is a cost of sexual reproduction that is absent in asexual reproduction: in a sexually produced offspring only half of the genes from one parent are transferred to the offspring. This has been called "the two-fold cost of meiosis" and infers that the proportion of parthenogenetic females would double in each generation as they do not have to produce males (Maynard Smith 1978). On top of this cost, sexual reproduction is thought to have a high reproductive cost compared to asexual reproduction, and there is also the risk of attaining sexually transmitted diseases (Silander 1985). Numerous theories have been presented to explain why sexual reproduction is advantageous in the short term. These theories can be divided into two groups, that sexual reproduction is advantageous as it spreads advantageous traits (e.g. parasite resistance) or that sexual reproduction is advantageous as it enables the removal of deleterious genes, but the theories are still debated (Hurst & Peck 1996). Asexual reproduction, on the other hand, makes the genet (the offspring of one zygote, consisting of one or several ramets (Harper 1977)) potentially immortal and therefore unlimited in both time and space (Schmid 1990, Wikberg 1995, Santelices 1999). Therefore the question to be asked might instead be: Why are not all organisms clonal?

There are many different ways of asexual reproduction, e.g. fragmentation, rootsuckers, bulbills, agamospermy (seed formation without meiosis), ramet formation by rhizomes or stolons (Silander 1985). In this thesis I will use the term

vegetative reproduction for asexual reproduction except asexual seed formation. Reproduction modes which makes the offspring physically connected to the mother plant are classified as linked asexual reproduction e.g. rootsuckers, rhizome and stolon formation, while fragmentation, bulbill formation and agamospermy result in physically distinct offspring and are called non-linked asexual reproduction (Silander 1985, Tiffney & Niklas 1985). However, these two groups are not definite but rather the endpoints in a continuum with the connections between mother and offspring having different longevity. Non-linked asexual reproduction has some features in common with sexual reproduction, e.g. it enables the plant to disperse offspring over a long distance and the possibility of parental care is rather low (Silander 1985, Lloyd 1987). Linked asexual reproduction gives the mother plant possibility of parental care, which is of great importance in areas where recruitment from seeds is difficult, as in some arctic environments (Billings 1987). It also increases the possibilities of the genet for local persistence.

Different kinds of reproduction are thought to give different kind of patterns of genetic variation. Hamrick & Godt (1990) found, however, no difference in the amount of genetic variation between plants having only sexual reproduction and those having both sexual and asexual reproduction. On the other hand, in Hamrick & Godt's (1990) analyses the plant breeding system was one of two main determinants of the amount of genetic variation, the other was geographic distribution. Selfing plant species had less variation within populations and more differentiated populations than outcrossing plant species (Hamrick & Godt 1990). The pollination system was also important, wind pollinated plants had more variation within populations than insect pollinated plants (Hamrick & Godt 1990). In clonal plant populations, clonal diversity can also be used as a measure of genetic variation. Clonal diversity was for long thought to be low and most clonal plant populations were thought to be monoclonal, due to low sexual recruitment and high competitive exclusion (e.g. Stebbins 1950). Recent studies have shown that most populations of clonal plants are multiclonal, although many species show some monoclonal

populations (Ellstrand & Roose 1987, Widén *et al.* 1994, Diggle *et al.* 1998). Morphological variation, on the other hand, is an expression of phenotypic variation and is thus influenced both by the genotype, the environment and the genotype \times environment interaction, which makes it less directly dependent on reproduction than genetic variation (Silvertown & Lovett Doust 1993).

Aims

Sexual reproduction is a central theme in evolution theory, but evolution theory does not apply as well to organisms having asexual reproduction. E.g. the notion of potentially immortal genets in some organisms will have consequences for fitness theory, life history theory and thereby evolution theory (Sackville Hamilton *et al.* 1987, Tuomi & Vuorisalo 1989, Eriksson & Jerling 1990, Schmid 1990, Fagerström 1992, Wikberg 1995, Fagerström *et al.* 1998), which stresses the importance of studying both sexual and asexual reproduction in clonal plants. The aim of this thesis was to study the reproduction of arctic clonal plants, following this cyclic process through flowering, pollination, seed set, seedling recruitment and vegetative reproduction and the resulting variation, both at the genetic and morphological level. I also wanted to study the effects of simulated climate change on arctic clonal plants as many arctic plants are temperature limited.

Study organisms

The studies in this thesis are made on four arctic rhizomatous *Carex* taxa, *Carex bigelowii* Torr. ex Schwein, *C. ensifolia* Krecz. ssp. *arctisibirica* Yurtsev, *C. lugens* Holm and *C. stans* Drej.. *C. bigelowii* was used for pollination experiments (Paper I), while *C. ensifolia* and *C. stans* were used in the study of genet age (Paper II). In the population study *C. ensifolia*, *C. lugens* and *C. stans* were used (Paper III), while in the studies of genetic and morphological variation all the taxa were used (Paper IV and V). *C. bigelowii* was used in the climate change experiments (Paper VI and VII).

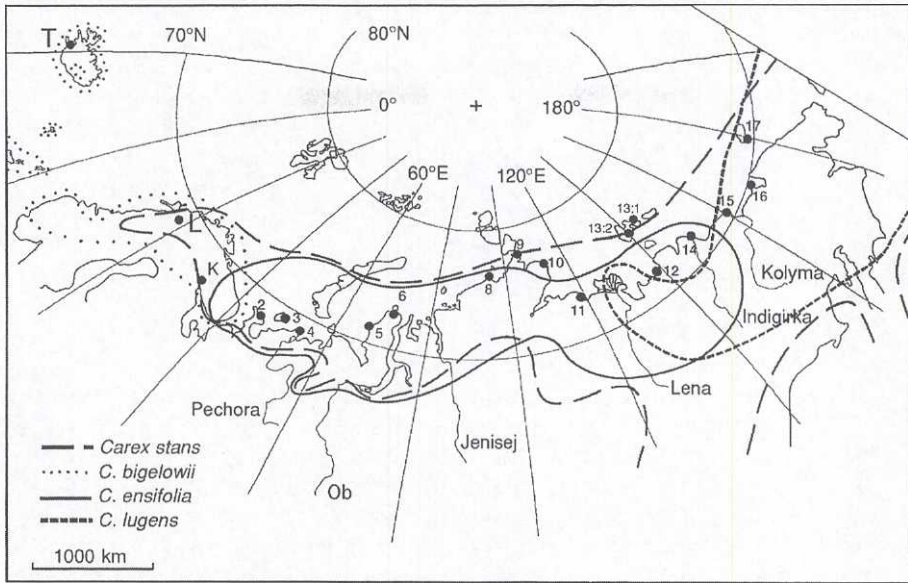


Fig. 1. Study sites and geographic ranges of the taxa used in the papers of this thesis. T=Thingvellir, L=Latnjajaure, K=Kola Peninsula. Sites with numbers were sampled during the Swedish-Russian Tundra Ecology Expedition 1994. Plant distributions drawn after Hultén (1962), Egorova *et al.* (1966) and Mossberg *et al.* (1992).

Carex bigelowii, *C. ensifolia ssp. arctisibirica* and *C. lugens* are members of the *C. bigelowii* complex, which is a circumpolar species-complex with debated taxonomy (Murray 1994; Fig. 1). *Carex stans* is a circumpolar taxon (Fig. 1). The name *C. stans* is mostly used in the high Arctic while *C. aquatilis* is used in the low Arctic (Murray 1994). *Carex stans* is the dominant taxa in wet to moist habitats in many tundra habitats (Shaver *et al.* 1979), while the *C. bigelowii* species complex prefer mesic to dry habitats (Jónsdóttir *et al.* 1999). However, in the absence of any of the *C. bigelowii* complex taxa, *C. stans* can also be found at mesic to dry habitats (Paper II). All of the studied taxa form extensive rhizome systems, but they hold different positions along the phalanx-guerrilla continuum of clonal growth-forms (*sensu* Lovett Doust 1981). In *C. bigelowii* the ramets may become 10 years old if they stay vegetative (Jónsdóttir 1991), but only the youngest ramet generations are photo-assimilating (Jónsdóttir & Callaghan 1988 and 1989). The ramets may flower when 2-4 years old and the shoot apex dies after flowering, since the apical meristem is used up (Carlsson *et al.* 1990).

Study sites

These studies were mainly conducted at two sites: Latnjajaure, Swedish Lapland and Thingvellir, Iceland. All pollination experiments (Paper I) and climate change experiments (Paper VI and VII) were performed at Latnjajaure and part of them at Thingvellir (Paper I and VII). However, to study population dynamics and genetic and morphological variation within and between populations requires a much larger number of populations (Paper III, IV and V) and for these studies additional populations were sampled during the Swedish-Russian Tundra Ecology Expedition-94. The plants for the study in Paper II were also sampled during the Tundra Ecology expedition at Faddeyevsky Island (site 13:1) and at North-eastern Taymyr Peninsula (site 10).

Latnjajaure Field Station (68° 21.6'N, 18° 31.5'E) is a subarctic-alpine site situated at 1000 m.a.s.l., which is about 300 m above the mountain birch treeline. The study area is placed in a gentle south-west-facing slope with a bedrock consisting of mica garnet schist mixed with acid

moraine (J. Kling pers. comm.). The vegetation is a mesic heath community (Paper VII). A constant snow cover of 10 cm or more in the Latnjajaure-valley developed between mid-October and mid-November in 1994-1998, and stayed until late May or early June in 1995-1998. During snowmelt, parts of the study area are standing in running melt water, creating large temperature gradients due to the microtopography.

The Thingvellir site (64°17'N 21°03'W) is maritime subarctic and situated at 120 m.a.s.l. on an 8000 years old post-glacial lava-field north of the lake Thingvallavatn. The study area is situated in a subsidence area between the fissures Hrafnagjá in the east and Almannagjá in the west, where both fissures are parts of the axial rift zone in south-west Iceland (Saemundsson 1992). The area was fenced from sheep grazing in 1928 (Jónasson 1992) and there are now scattered *Betula pubescens* trees and bushes of *Salix sp.* as the site is about 200 m. below the potential treeline (Thorsteinsson & Arnalds 1992). The bottom layer consists of a 5-30 cm thick carpet of the moss *Racomitrium lanuginosum*, with few vascular plant species growing in the moss (Paper VII).

The Swedish-Russian Tundra Ecology Expedition-94 took place in June-August in 1994, visiting 17 sites along the north coast of Russia (Fig. 1). The expedition was based on the ship R/V Akademik Fedorov, using helicopters to go ashore for 24-48 hours. The expedition covered several arctic vegetation zones (or subzones) and the vegetation we encountered varied a lot between sites, but for our studies we always looked for a mesic to dry site in levelled terrain or gently sloping towards south or south-west.

The arctic and subarctic environment

The definition of the Arctic has caused much debate, but the most common boundary used today is the high latitude treeline (Bliss & Matveyeva 1992). The arctic environment is different from more southerly latitudes mainly because of the low winter and summer temperatures and a long photoperiod in the summer. Plants respond to low summer temperature

primarily by low growth rates and low photosynthetic activity (Fitter & Hay 1987). The weather in the Arctic is not only cold, but also less predictable among years than in more southern areas (Ferguson & Messier 1996). The low temperature also creates a short growing season (2-4 months), which is made even shorter by the snow cover. During winter the snow insulates the plants, but the differences in snow cover creates very steep gradients in water availability and the length of the growing season. Decomposition and the rate of soil microbial activity decrease at low temperature, giving low concentrations of nutrients in the ground (Marion & Miller 1982). The low temperatures also maintain a permafrost layer, limiting the plants to the uppermost layer of the soil (Billings 1987). Despite the large amounts of snow and ice present (in sub- and low Arctic), arctic plants in some areas suffer from drought due to low summer precipitation and frozen soil moisture (Fitter & Hay 1987). The wind is usually strong in the treeless arctic landscape. This can cause dehydration in the plants, but also abrasion by snow, ice or sand particles especially above the snow cover. Frost heave and needle ice formation cause mechanical problems for plants, especially seedlings, inhibiting seedling establishment in certain areas (Andersson & Bliss 1998).

Today 60% of the vegetation in the Northern Hemisphere is classified as Arctic or Subarctic (Billings & Mooney 1968). However, the situation has not always been like this, as during the ice ages large parts of the Arctic were glaciated. Many tundra plants have thus migrated over large distances to and from icefree areas (cf. Hewitt 1996). Other areas in the Arctic never became glaciated during the last ice age, e.g. northern Siberia east of the Taymyr Peninsula (Forman *et al.* 1999, Svendsen *et al.* 1999) and north-western Alaska (Billings & Mooney 1968). These areas served as refugia for many organisms during the ice age. Furthermore, the glaciated areas deglaciated at different times (Forman *et al.* 1999, Svendsen *et al.* 1999). Consequently, the Arctic is not a homogeneously young area, rather there exist large differences in vegetation age between areas. The different history among areas is likely to create differences in biodiversity and genetic variation, thereby affecting plant

performance and population structure today (Hewitt & Butlin 1997).

Alpine environments have many similarities with the arctic environment (Billings & Mooney 1968). However, when stating that the authors thought about alpine environments in temperate, boreal and subarctic areas. The contrast between arctic and alpine environments is greatest in tropical alpine environments, e.g. by tropical alpine environments having "winter every night and summer every day" (Hedberg & Hedberg 1979). But going northwards the alpine and arctic environments become more and more alike both in terms of vegetation and physical conditions. Therefore, at Latnjajaure, well above the mountain birch treeline, the environment is similar to the environment in the true Arctic even though it is strictly subarctic-alpine, while the Thingvellir site is below the treeline and thus subarctic. The environment encountered during the Tundra Ecology-94 expedition was variable, from low to high Arctic conditions (Hedberg *et al.* 1999). In this thesis I will not differentiate between conditions in subarctic-alpine and arctic environments. However, when discussing special high arctic or subarctic conditions I will specify that.

Climate change

General Circulation Models have predicted an increase in atmospheric temperature of 2°C from 1990 to 2100, due to increased levels of "greenhouse gases" (carbon dioxide, methane, chlorofluorocarbons (CFCs), and nitrous oxide; Houghton *et al.* 1996). There are uncertainties in climate sensitivity and future emissions, giving a range in the temperature increase predictions from 1-3.5°C. This temperature increase will not be evenly distributed around the earth though, the largest increase is predicted to occur in the Arctic (Houghton *et al.* 1996). However, it will be during late autumn and winter that the increased temperature will be larger than the world mean temperature increase. Precipitation is predicted to change due to climate change in high latitudes giving an increase in soil moisture in high latitudes during winter (Houghton *et al.* 1996).

Climate change experiments

In 1990, ITEX, The International Tundra Experiment was initiated with the goal to study the responses of tundra vegetation to natural variation in climate and experimental warming (Webber & Walker 1991, Henry & Molau 1997, Arft *et al.* 1999). A standardised design of warming experiments was agreed upon using open-top chambers (OTCs) which passively trap the solar energy (Marion *et al.* 1997). The climate change experiments in this thesis were conducted using the ITEX design with hexagonal OTCs (Paper VI and VII). Because *Carex bigelowii* is wind pollinated we thought that the pollination might be disturbed by the OTCs. We therefore hand pollinated the ramets in the OTCs and had double controls, one with hand pollinated ramets and one with untreated ramets (Paper VI and VII). The OTCs increased the temperature differently between years (Paper VII), but in all years the temperature increase was within the predictions from the Global Circulation models.

There have been some criticisms of passive greenhouses as simulations for climate change, mainly concerning those with a closed top (Kennedy 1995a and b). However, also the OTC design has unwanted side effects. One of the main criticism has been that although the mean temperature mimics Global Circulation models, the temperature variation does not. The open-top of the OTCs and the many gaps along the ground slightly decrease the amount of heating by the OTCs, but mainly decrease the temperature extremes that can occur (Marion *et al.* 1997). The temperature extremes can be excess warming during sunny days or a cooling effect during clear nights. At Latnjajaure during 1997 and 1998 and in all measured years at Thingvellir, there were cooling effects during the nights in the OTCs (Paper VII). The soil temperature increased in the OTCs with 0.8°C at Latnjajaure. The ground at Thingvellir is covered with a 5-30 cm thick layer of the moss *Racomitrium lanuginosum*, which insulates the soil. The temperature within the middle of the moss layer was decreased with 0.6°C in the OTCs. Desiccation might be a problem, but this is also minimised by the large open-top allowing the precipitation to enter. As an extra precaution, we

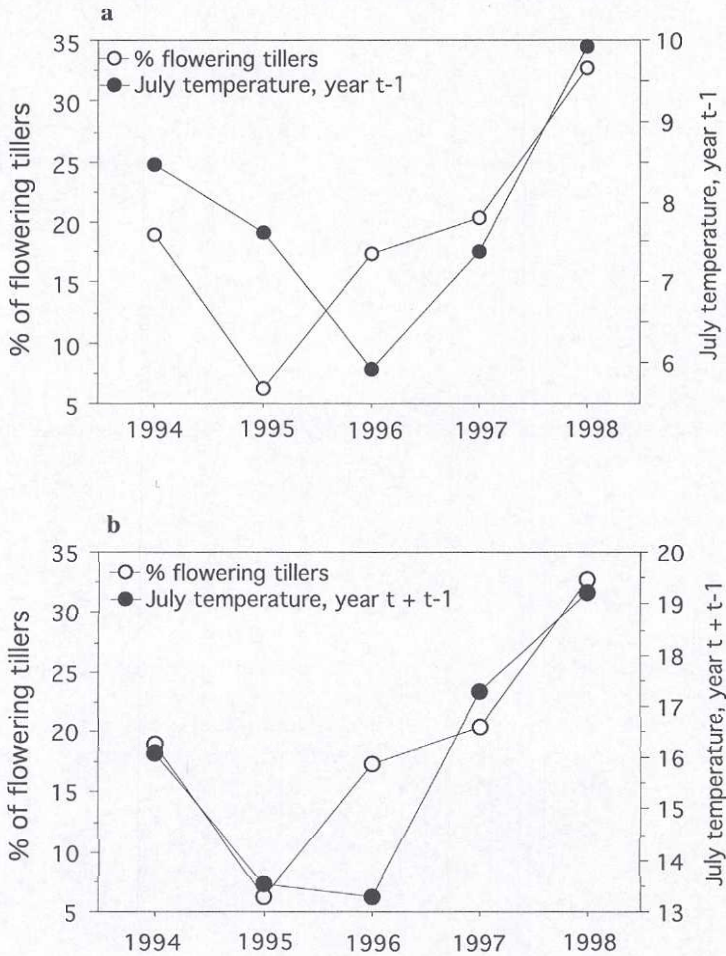


Fig. 2. Flowering frequency in *Carex bigelowii* at Latnjajaure compared to a) July temperature the year before flowering and b) the summed July temperature the year before and the year of flowering.

did not use the 10 cm edge chamber area for measurements, where no precipitation can fall. Using a passive heating device inevitable creates a lee-effect together with the heating. This is not possible to get around, and instead comparisons with more controlled experiments and natural variation can be used to help interpreting the results. However, in spite of the drawbacks the OTCs might have they have been shown to create the same responses in the plants as the natural between-year variation in the temperature (Hollister & Webber 2000).

Results and discussion

Flowering

Flowering is very variable between years in many arctic plants (e.g. Kalela 1962, Laine & Henttonen 1983, Shaver *et al.* 1986, Carlsson & Callaghan 1994). Our results show that in *Carex bigelowii* the number of flowering ramets varied 20-fold between plots and 4-fold between years at Latnjajaure (Paper VII). The flowering was much more stable between years at Thingvellir (Paper VII), and less variation in flowering at more southern latitudes has been attributed to

both a warmer climate and non-cyclic herbivores (Laine & Henttonen 1983). The variation in flowering has been explained by many different causes: variation in temperature (Carlsson & Callaghan 1994), internal rhythm of the plants due to delayed development and exhaustion of resources (Kalela 1962, Tast & Kalela 1971, Laine & Henttonen 1983) and grazing (Andersson & Jonasson 1986, Järvinen 1987).

Many arctic and alpine plants are thought to be temperature limited in their reproduction (Billings 1987). Carlsson & Callaghan (1994) have shown that during ten years of study the proportion of flowering ramets depended on the July temperature the year before flowering in *C. bigelowii*. During five years of study at Latnjajaure there was no such correlation (Latnjajaure: $F_4=1.84$, $P=0.27$, $R^2=0.50$; Fig. 2a). There was, however, an almost significant relationship between the proportion of flowering ramets and the summed July temperature of the year before flowering and the year of flowering at Latnjajaure ($F_4=8.81$, $P=0.06$, $R^2=0.56$; 2b). There were no further improvements of the regression by incorporating June or August temperatures. At Latnjajaure there was also a trend for flowering being increased by OTC treatment (Paper VII), a response found in a number of arctic clonal plants to warming treatment (Wookey *et al.* 1993, Arft *et al.* 1999). The same correlations between flowering frequencies and temperature were found when adding the flowering frequencies from the OTCs. There was no significant relationship between the July temperature the year before flowering and the flowering frequency, but a significant relationship between flowering frequency and the summed July temperature of the year before flowering and the year of flowering ($F_5=15.94$, $P<0.01$, $R^2=0.67$). This also provides a validation of the OTC treatment. However, absence of flowering response to warming has also been reported in arctic clonal plants (Parsons *et al.* 1995, Molau in press). At Thingvellir there was no effect of OTCs on flowering probably because *C. bigelowii* is not temperature limited at this warmer site (Paper VII) and no correlations could be made due to lack of weather data. In *C. bigelowii* the flowers are preformed the year before flowering, a very common phenomena in arctic plants (Sørensen 1941, Hansson 1997).

How well developed the preformed flower buds are at the end of the growing season varies from ramet to ramet and not all preformed buds will develop into flowering ramets (Hansson 1997). It can therefore be assumed that a warm summer will give a large number of preformed buds, and if the consecutive summer also is warm a large proportion of these preformed buds will develop to flowering ramets, giving the relationship between proportion of flowering ramets and July temperature the last two years found in *C. bigelowii* at Latnjajaure.

The large fluctuation in flowering has also been attributed to the plants internal rhythm (Tast & Kalela 1971, Laine & Henttonen 1983). According to this theory the plants need time after a large flowering episode to accumulate resources and to develop new meristems. When tested experimentally, flowering increased in a number of arctic clonal plants after application of nutrients (Henry *et al.* 1986, Parsons *et al.* 1995, Shaver & Chapin 1995), but it does not explain the variation between years in flowering. As the flowering ramets die after flowering one meristem is lost for the genet. After a large flowering episode the genet might then become limited in meristems, causing low amounts of flowering until new meristems and flowering buds developed. The long-term effect of the OTCs at Latnjajaure indicated that *C. bigelowii* might be meristem or nutrient limited in a warmer climate.

Carex bigelowii is grazed by many different herbivores e.g. reindeer (Warenberg 1982), sheep (Jónsdóttir 1991) and it is the plant most preferred by Norwegian lemmings (Moen 1990). *C. stans* is grazed by muskoxs, hares and collared lemmings (Klein & Bay 1994), as well as Norwegian lemmings (Rodgers & Lewis 1985). The proportion of flowering ramets in *C. bigelowii* was reduced by sheep grazing at two Icelandic sites (Jónsdóttir 1991). However, the grazing pressure from sheep is rather constant, while the population sizes of lemmings is known to fluctuate a lot between years in a cyclic way. The lemming population fluctuations are divided into four phases: low, increasing, peak and decreasing (Erlinge *et al.* 1999). In *C. ensifolia*, *C. lugens* and *C. stans* flowering varied between 0–32% (Paper III). The variation in flowering was

explained by the different lemming phases, with an increase during the increasing lemming phase compared to the other lemming phases (Paper III). If it is the microtines that affects the plants, the plants that affects the microtines or both organisms affecting each other have been heavily debated (Laine & Henttonen 1983, Andersson & Jonasson 1986, Järvinen 1987, Oksanen & Ericson 1987). The three different hypotheses explaining the variation in flowering with variation in temperature, the plants internal rhythm or grazing, might be correct for different species or for different populations within the same species. Thus, given the low amounts of grazing on *C. bigelowii* at Latnjajaure, temperature seems to be the main determinant of the amount of flowering there. At Thingvellir flowering is not limited by temperature or grazing, however, in accordance with the long-time effect of the OTCs at Latnjajaure flowering might be resource limited.

Phenology

Flowering phenology is known to be dependent on temperature, photoperiod and rainfall (Ratchke & Lacey 1985). Flowering in Norwegian populations of *Carex bigelowii* was stimulated by short day treatment and had an temperature optimum of 12–15°C (Heide 1992). Our results show that flowering phenology of *C. bigelowii* was accelerated by a higher temperature, but not an earlier snowmelt (Paper VI and VII). This is congruent with a large survey of arctic and alpine plants growing on Iceland including *C. bigelowii*, where June temperature was the main determinant of flowering phenology, not the time since snow melt (Thórhallsdóttir 1998).

There is a large variation in life history traits in arctic plants, which can not be explained by the r-K continuum or S-C-R triangle (Grime 1979, Molau 1993). Instead flowering phenology has been suggested as being an important factor determining reproductive strategies in arctic and alpine plants (Molau 1993). Species flowering early in the season are mainly outbreeders and have low seed:ovule ratios, while late flowering species are mainly inbreeders but have a high level of pollination (Molau 1993). The early flowering species, therefore, risk pollen limitation, while late flowering species risk their seeds

at an early onset of winter. *Carex bigelowii* was classified as early aestival and should therefore have an intermediate level of reproductive success. However, we found that the reproductive success was very variable between years (0.5–59%) and also between plots within site (Paper I). In most years though it was lower in *C. bigelowii* than for the early aestival group in general.

Carex bigelowii is protogynous (female flowers start to flower before male flowers; Paper VI and VII) at Latnjajaure, but protandrous at Thingvellir (Jonsson *et al.* 1996). This varied however between ramets with some ramets having completely separate gender phases, while others have almost completely overlapping gender phases. Our results show that the start of flowering of both female and male flowers are dependent on temperature, but male flowers are more temperature sensitive than the female flowers. This increased the gender phase overlap in the OTCs at Latnjajaure (Paper VI and VII). This might also explain the protandry at Thingvellir, as Thingvellir has a warmer climate than Latnjajaure. In a survey of *C. bigelowii* populations in Iceland and Sweden, protogyny increased and protandry decreased within a local altitudinal gradient (Svensson 2000). Thus in *C. bigelowii* male and female flowering phenology is dependent on temperature, but to a different degree, making also the degree of dichogamy temperature dependent.

Pollination and seed set

The frequency of wind pollination increases at high latitudes and altitudes, being most efficient when there is little filtration through other vegetation as in tundra habitats (Whitehead 1983). However, many wind-pollinated plants have difficulties releasing pollen during rain, snow or fog (Whitehead 1983, Corbet 1990). This is also the case for *Carex bigelowii* (pers. obs.), and might explain the very low seed:ovule ratio found at Thingvellir (Paper I). *Carex bigelowii* is self-compatible and was able to set seeds from self pollination both at Latnjajaure (Paper I) and Thingvellir (Jónsdóttir 1995), but has been reported to be self-incompatible at other sites (Faulkner 1973). *Carex lugens* is also self-compatible (Tikhmenev 1979), while *C. stans* is only weakly self-compatible, with 2% seed set

reported in self-pollinated individuals (Standley 1985). However, in *C. bigelowii* (Paper I) and *C. lugens* (Tikhmenev 1979) ramets were normally crosspollinated in spite of their ability to self-pollinate. This is further confirmed by our genetic data, where *C. bigelowii* and *C. lugens* were in Hardy-Weinberg equilibrium indicating outbreeding (Paper IV). *Carex ensifolia* and *C. stans* showed heterozygote deficiency at some loci indicating a mixed mating system in these taxa (Paper IV). The seed:ovule ratio varied a lot between sites and years in *C. bigelowii* ranging between 0.005-0.59 at Latnjajaure and 0.005-0.007 at Thingvellir (Paper I). It also varied between sites in *C. ensifolia* and *C. stans*, while the three sampled populations of *C. lugens* had more equal seed:ovule ratios (Paper III). Due to the high variation in seed:ovule ratio it is hard to make comparisons with other taxa. However, seed:ovule ratios of 0.5-0.6 have been reported for alpine *Carex curvula* and *C. firma* populations, with values of 0.3 from a north-facing slope (Wagner & Reichegger 1997). These values are comparable to the highest found in *C. bigelowii* at Latnjajaure (Paper I).

There are many factors that may affect seed set, e.g. amount of pollen, temperature, length of the growing season, pathogens and seed predation. Like in many other wind pollinated plants, seed set in *C. bigelowii* is pollen limited, but this pollen limitation decreased during the season. Late in the season *C. bigelowii* became limited by temperature and time instead (Paper I). This agrees with the results in *C. ensifolia*, *C. lugens* and *C. stans* where the seed:ovule ratio decreased with latitude, showing that temperature is also important when comparing seed:ovule ratios of different populations (Paper III). In these populations the seed:ovule ratio was also higher during increasing lemming population phase compared to during the other lemming phases. During the increasing lemming phase the flowering was higher, thereby reducing the pollen limitation (Paper III). However, in this study the seed:ovule ratio also increased during peak lemming phase and with increasing July precipitation in 1994 which are harder to explain (Paper III). The inflorescences of *C. bigelowii* are infested by Diptera seed predators and smut fungi. However, these infestations did not reduce seed set during any of the study years (Paper VII).

My results confirm the results in the alpine sedges *C. curvula* and *C. firma* were longer growing seasons and higher temperature also gave higher seed set (Wagner & Reichegger 1997).

Seed weight is an important character for seedling establishment, heavier seeds having a greater chance of germination in a given species (e.g. Silvertown 1984, Lloyd 1987, Molau & Shaver 1997). My results show that seed weight in *C. bigelowii* was increased in a higher temperature and by a longer growing season (Paper I). An increase in seed weight in a higher temperature has been seen in a number of arctic clonal plants e.g. *Dryas octopetala* and *Eriophorum vaginatum* (Molau in press). Seed weight in *C. bigelowii* was also increased by nutrient addition (Jónsdóttir 1995). The chances of recruitment thereby increase through two ways in a higher temperature, as both the number and the weight of the seeds increase.

Genet establishment

Recruitment from seeds is infrequent in clonal plant populations (Harper & White 1974, Cook 1985, Eriksson 1993) and further limited by adverse climate conditions in arctic and alpine areas (Billings & Mooney 1968, Körner 1999). Although recruitment from seeds are thought to be low, most arctic and alpine plant species are represented in the seed bank including the clonal plants (McGraw & Vavrek 1989). E.g. where *Carex bigelowii* and *C. stans* are present in the vegetation they are usually also abundant in the seed bank (McGraw 1980, Gartner *et al.* 1983, Roach 1983, Ebersole 1989, Jónsdóttir 1995, Molau & Larsson 2000). Seed production and therefore seed rain is variable between years in the Arctic, but enough seeds are produced to create a seed bank although often smaller than in warmer areas (Ebersole 1989, Chambers 1995, Molau & Larsson 2000).

No seedling recruitment was found in closed vegetation in *C. bigelowii* populations at Latnjajaure (Paper I) which agrees with the results from other sites (Callaghan 1976, Carlsson & Callaghan 1990a, Jónsdóttir 1991, Jónsdóttir 1995). Seedlings were neither found in the OTCs at Latnjajaure, making it probable that it is not the low temperature that inhibits seedling recruitment. But when trying to

germinate *C. bigelowii* seeds (after stratification), 14% of the seeds from Thingvellir, and 0% (1995) and 0.002% (1996) of the seeds from Latnjajaure were successfully germinated. This difference might be due to the larger size of the seeds from Thingvellir, which is further supported by the fact that of the three germinated seeds from Latnjajaure two were from the OTCs which had heavier seeds (Paper I). Therefore, a future warmer climate might increase germination rates by enabling the plants to produce more viable seeds at sites that are too cold today.

Seedlings of *C. bigelowii* were, however, found at disturbances at both Latnjajaure (Paper I) and Thingvellir (Jónsdóttir 1995). This is not surprising, since many arctic clonal plants are known to produce large amounts of seedlings after disturbances (Chester & Shaver 1982, Gartner *et al.* 1983, Ebersole 1989). Disturbances play an important role in many arctic plant communities. These disturbances can be very different in size and frequencies, from small scale events e.g. trampling from herbivores and humans, small mammals digging and frost movements like needle ice formation in the soil, to large scale events e.g. masswasting and large scale human activities. Several seedling recruitment patterns in clonal plants have been identified, ranging from initial seedling recruitment with no further seedling recruitment occurring after the initial establishment of the population to frequently repeated seedling recruitment after the establishment of a population (Eriksson 1989). When disturbances are rare but necessary for establishment they can be looked at as "windows of opportunity", i.e. conditions for seedling establishment within established populations that occur rarely and under special circumstances (Jelinski & Cheliak 1992, Eriksson & Fröborg 1996). Disturbances thus enable plants to have repeated seedling recruitment although they grow in otherwise closed vegetation. However, to be able to have seeds in the right place when a disturbance occurs, the plants need to produce large amounts of seeds and/or long-lived seeds. This might explain that although most arctic clonal plants mainly reproduce vegetatively they have a relatively large allocation to sexual reproduction too.

Once established, the seedlings need to grow to survive in the population. In an alpine area seedling growth was increased by high levels of nutrients, high air temperatures and high soil temperatures, just as for adult plants (Chambers *et al.* 1990). Seedling survival, on the other hand, increased in higher temperatures, but decreased in fertilised plots (Chambers *et al.* 1990). However, the vegetation cover in the Arctic varies from constant plant cover in the low Arctic to patchy vegetation with a lot of bare ground in the high Arctic. It has been suggested that positive plant-interactions should be more common in the high Arctic e.g. seedlings having a greater chance of establishment and survival in cushion plants (Griggs 1956). If these positive interactions remain when the plants are established is not known. In the high Arctic, soil heave through e.g. needle ice formation restricts seedling establishment from bare soil (Andersson & Bliss 1998). In high arctic areas where seedlings did establish, they were mostly dependent on temperature and soil moisture (Bell & Bliss 1980). That seedling recruitment takes place repeatedly in the studied taxa is further supported by the high clonal diversity found in most of the studied populations (Paper IV). Clonal diversity has been studied in only a few arctic or alpine plant species, and is generally found to be high, although variable between species, between populations of the same species and within populations (Paper IV and references therein). In *Carex bigelowii* at Thingvellir, there were a lot of different clones but they formed distinct patches (Jonsson 1995). However, in populations from the Swedish mountains, ramet densities were more like the ones found at Latnjajaure and the genets were more intermingled (Jonsson 1995). Assuming only initial seedling recruitment, clonal diversity is expected to decrease with age of the population. However, in the populations studied in Paper IV there was no relationship between clonal diversity and population ages (time since glaciation). Instead, clonal diversity within the studied taxa decreased with latitude probably due to lower seed production and seedling recruitment compared to more southern populations (Paper IV). Thus even though seedlings are rarely found, seedling establishment probably takes place but at a rate

and spatial scale hardly detectable by most studies.

Vegetative reproduction

All clonal plants have, by definition, some sort of vegetative reproduction. Vegetative reproduction is relatively common in Arctic environments (e.g. Savile 1972, Jónsdóttir *et al.* 1996), but there is a shift in the frequency of different kinds of vegetative reproduction from the Subarctic to the high Arctic, with rhizomatous graminoids being common in the Subarctic and low Arctic (Bliss & Matveyeva 1992, Jónsdóttir *et al.* 1999). All the studied *Carex* taxa are rhizomatous with an extensive ability to reproduce vegetatively. They differ however in the length of the rhizomes both between populations and taxa, with *C. stans* having the longest rhizomes and *C. bigelowii*, *C. ensifolia* and *C. lugens* having consecutively shorter rhizomes (Paper V). The ramet differentiation in *C. stans* found in the population from Faddeyevskiy Island (Paper II) turned out to be very variable between populations (Paper V). Ramet differentiation has been reported from some populations of *C. bigelowii* (Carlsson & Callaghan 1990b), but we found no obvious ramet differentiation in *C. bigelowii*, *C. ensifolia* or *C. lugens* (Paper II and V). The numbers of new vegetatively produced ramets varied a lot both between years and sites in *C. bigelowii* (Paper VII), and at least between sites in *C. ensifolia*, *C. lugens* and *C. stans* (Paper III). We found that an increased temperature did not affect the number of new vegetative ramets produced at Latnjajaure, but decreased it at Thingvellir in *C. bigelowii* (Paper VII). In the other studied taxa, the number of new vegetative ramets in a population was negatively correlated with latitude (Paper III). This indicates either that while a single population can not take advantage of a warmer climate, different populations are adapted to different climates or that the studied taxa are influenced by temperature in different ways in different parts of the distributional area. In the warmer parts of the distribution an increased temperature is detrimental to ramet production, while in colder parts it is beneficial. In the middle parts, which Latnjajaure then should belong to, there was no effect at all. The number of new vegetative ramets produced was also correlated with the amount of lemming

grazing and lemming cyclicality in *C. ensifolia*, *C. lugens* and *C. stans* (Paper III). Thus in the studied *Carex* taxa, temperature and grazing affects allocation to both sexual and asexual reproduction, but the relationship is site-dependent.

Arctic clonal plants are thought to become very old, but have always been difficult to age. In the low Arctic with a continuous vegetation cover it is not possible to determine where one genet stops and another starts. Many clonal plants also grow in one end and die off in the other end, thereby slowly moving over the ground and making them theoretically immortal, but impossible to age. In the high Arctic, with more patchy vegetation cover, it becomes easier to identify clones and fairy-rings sometimes become apparent (Paper II). This makes it possible to measure their size and age them by aid of simulated growth models. The fairy-rings of *C. stans* we found were 15-150 years old, while the *C. ensifolia* genets were 3800-5000 years old (Paper II). The age of the *C. stans* genets are comparable to arctic dwarf-shrubs (Callaghan & Emanuelsson 1985), while the age of the *C. ensifolia* genets are comparable to the only other aged *Carex* I know of, *C. curvula* from the Alps, which was about 2000 years (Steinger *et al.* 1996). We do not know, though, whether these genet ages are representative also for non-marginal parts of the distributional area. Assuming that these ages are representative, it would have large implications for the genet dynamics. E.g. although the number of viable seeds produced by a genet is low or totally absent in a single growing season, the number of seeds produced during the life of the genet becomes be very large. The number of seedlings that need to be established per year to keep clonal diversity high becomes extremely small when a genet obtains a longevity of hundreds or thousands of years, making it very difficult to get a correct picture of the genet dynamics during the life time of a scientist.

Variation

Genetic variation in the Arctic has generally been assumed to be low, but not many plant species have been studied. In a review by Hamrick & Godt (1990) the most important factors governing genetic variation within a species were

the size of the distribution and the breeding system, showing that outbreeding species with a wide distribution had a large amount of genetic variation. They found no difference between plant species having only sexual reproduction compared to those having both sexual and asexual reproduction. However, there were no arctic plants included in this review. In a literature review Jonsson (1998) found significant differences between rhizomatous and caespitose (tufted) Cyperaceae species, with rhizomatous species having higher levels of genetic variation and lower levels of population differentiation than caespitose species. Neither in this review were there included any arctic populations, although a number of alpine and sub-arctic populations were included. We found high levels of genetic variation in *Carex bigelowii*, comparable to other outbreeding species with large distributions and other rhizomatous Cyperaceae (Paper IV). *Carex ensifolia*, *C. lugens* and *C. stans* had even higher levels of genetic variation than *C. bigelowii* and therefore higher levels than the other outbreeding species with large distributions or other rhizomatous Cyperaceae (Paper IV). When surveying the literature, we found 14 arctic, subarctic or arctic-alpine plants species previously studied for genetic variation by enzyme electrophoresis and therefore comparable to our study. Of these 14 species, *Silene acaulis* and *Poa alpina* had comparable levels of genetic variation to our study (Paper IV, Abbott *et al.* 1995, Philipp 1997). Both these species are widespread and assumed to be mainly outbreeding. The other 12 species had very low levels of genetic variation and included both endemic and selfing species as well as widespread and outbreeding ones (Paper IV). A wide distribution and an outbreeding breeding system might be a prerequisite for species to maintain high levels of genetic variation in the Arctic, but apparently there are other, unknown factors that can limit variation even in such species (Paper IV).

While the amount of genetic variation in a species mainly depends on geographical range and breeding system, the difference in genetic variation between populations within a species is affected by e.g. the population size, generation time and gene flow (Loveless & Hamrick 1984). These factors may vary with e.g. glaciation

patterns and latitude (Hewitt 1996), but in many studies it has been a problem though that they are correlated, making it impossible to say which factor is most important. The situation is, however, different in northern Eurasia where latitude is not correlated with glaciation patterns. In Paper IV, we were able to show that the level of genetic variation in the studied populations was lower in areas deglaciated 10 000 years B.P. compared to areas deglaciated 60 000 years B.P. or not glaciated at all during the last ice age. In this study there was no effect of latitude on the level of genetic variation (Paper IV). Populations in previously glaciated areas might have experienced small population sizes and low levels of gene flow after migration and establishment after glaciation, especially as their generation time might be very long (Paper II).

Distinct ecotypes are found among many arctic clonal plant populations (Shaver *et al.* 1979, Chapin & Chapin 1981, McGraw 1987, Fetcher & Shaver 1990). In general the degree of genotypic differentiation increase with isolation and therefore with the size of the distributional area and many arctic plants have large distributional areas (Bay 1992). *Carex bigelowii*, *C. ensifolia* and *C. lugens* are known to show very large variation in their morphology (Paper V, Egorova *et al.* 1966). In the studied populations there was a strong correlation between morphological distances between the populations and their genetic distances, and the genetics explained about 20% of the between-population variation in morphology (Paper V). A transplantation experiment revealed that some of the populations were still different after three years in a common environment, but these differences were much smaller than between the original populations (Paper V). This indicates that the environment has a strong influence on the morphology of these taxa, and that the plants are capable of plastic responses of their morphology. The environmental variables used to analyse the relationship between morphology and the environment explained 40-50% of the between-population variation within the *C. bigelowii* complex, indicating that the environment influence morphology to a great extent (Paper V). Temperature and lemming grazing were the most influential environmental factors for the leaf characters in the studied taxa.

Rhizome length was probably mostly influenced by the taxa, although there were significant differences between populations within taxa in rhizome length too (Paper V). That the environmental effect on the morphology was largely due to plasticity rather than ecotypic differentiation was further seen in the OTCs (Paper VI and VII). At Latnjajaure the leaves became longer and wider in the higher temperature, the same effect as was found when comparing different populations (Paper V, VI and VII). At Thingvellir, though, temperature had the opposite effect on the leaf characters in the OTCs indicating that growth in *C. bigelowii* might not be limited by low temperatures in this site. Thus, our study shows that genetic differentiation of populations in *C. bigelowii*, *C. ensifolia*, *C. lugens* and *C. stans* is reflected in their morphology, but the morphology of *C. bigelowii*, *C. ensifolia* and *C. lugens* is, however, even more influenced by the environment.

Conclusions

Flowering and seed set of *Carex bigelowii*, *C. ensifolia*, *C. lugens* and *C. stans* are largely dependent on climate, weather and lemming grazing (Paper I, III, VI and VII). Vegetative reproduction in these taxa is extensive and also influenced by climate, weather and lemming grazing (Paper III and VII). The extensive vegetative reproduction enables clones of *C. ensifolia* and *C. stans* to become hundreds to thousands years old (Paper II). During their long lives there are some warm growing seasons which enable the plants to set viable seeds. These seeds germinate in the infrequent disturbances, giving rise to new clones (Paper I). This happens so often that a high genetic variation and clonal diversity is seen in most populations of all the taxa (Paper IV). It however takes time as genetic variation is lower in populations deglaciated 10 000 years B.P. compared to populations deglaciated earlier. The dependence of flowering on the weather is further seen in the decrease in clonal diversity at higher latitudes (Paper IV). The genetic distances between the populations are shown in the morphology, which is also influenced by climate and herbivory (Paper V). Climate change is likely to increase reproduction and growth in colder sites, while decreasing

growth at warmer sites in *C. bigelowii* (Paper VI, VII).

Svensk sammanfattning

Den här avhandlingen handlar om vad som påverkar förökningen och variationen (genetisk och i utseendet) hos arktiska klonväxter. Dessutom har jag studerat hur växthuseffekten kan komma att påverka de här processerna. Man kan inte studera alla växter på en gång och därför har jag använt styvstarr och några närbesläktade arter som modellväxter. Varför studerar man då reproduktion hos styvstarr? För att förklara detta får jag börja med Charles Darwin. Han kom på grunderna till evolutionsteorin, vilket är den teori som har haft mest betydelse för den biologiska forskningen. Evolutionsteorin går i stora drag ut på att alla individer är olika och de individer som är bäst anpassade får flest avkommor. Därmed kommer deras gener att sätta sin prägel på kommande generationer (Darwin 1859). Klonväxter är växter som kan föröka sig asexuellt eller, vilket är det vanligaste, både sexuellt och asexuellt. Eftersom förökningen hos klonväxter komplicerar begreppen hos evolutionsteorin är det viktigt att studera den. Dessutom ville jag studera följderna av växthuseffekten på styvstarr, eftersom den är en mycket vanlig växt. Den betas av t.ex. lämlar och renar och effekter på styvstarr kan därför tänkas påverka andra delar av ekosystemet.

Studierna i den här avhandlingen har jag gjort dels på styvstarr (*Carex bigelowii*) och dels på norrlandsstarr (*Carex stans*). Systematiken hos de här arterna är omdebatterad och styvstarr delas ibland upp i tre arter: styvstarr (*Carex bigelowii*) samt *Carex ensifolia* och *Carex lugens* som saknar svenska namn. I den här svenska sammanfattningen använder jag namnet styvstarr för både *Carex bigelowii*, *Carex ensifolia* och *Carex lugens*. De mesta studierna har jag gjort i Latnjajaure i Abisko-fjällen och i Thingvellir på Island, men för att kunna studera variationen måste man ha många populationer att jämföra (Fig. 1). Därför samlade vi in många olika populationer under den svensk-ryska Tundraekologiexpeditionen 1994. Då åkte vi med den ryska isbrytaren R/V Akademik Fedorov längs den ryska ishavskusten och flög med helikopter till

olika lokaler i land. Där var vi sedan i 1-2 dygn och samlade in material innan vi flög tillbaka till fartyget.

Växters sätt att föröka sig

De flesta växter kan föröka sig både genom sexuell och asexuell förökning till skillnad från majoriteten av djur. Sexuell förökning är det vi normalt tänker på som förökning även hos växter, d.v.s. då växten bildar blommor. För att befruktning ska kunna ske måste ett pollenkorn landa på blommans märke och en pollenslang växa ned till fröämnet i blomman. Till skillnad från t.ex. frisimmande spermier så kan inte pollenkornen själva ta sig till märket, utan måste lifta med någon eller något annat. Hos vissa växter liftar pollenkornen med insekter, men det finns även växtarter som använder fåglar eller fladdermöss. Styvstarrans pollenkorn transporterar sig med hjälp av vinden. Att använda vinden istället för djur har både för- och nackdelar för växten. En vindpollinerad växt måste producera många fler pollenkorn än en insektpollinerad växt eftersom vinden inte är lika träffsäker som insekterna. Däremot behöver vindpollinerade växter inte tillverka stora blomblad eller nektar för att locka till sig några djur. Vindpollinerade växter är vanligast i öppna miljöer där det inte finns några träd som stoppar pollenet och i miljöer med låg artdiversitet, t.ex. på savanner, prärier eller i fjällen. När befruktningen sker blandas generna som finns i pollenkornet och fröämnet. Fröna får därför gener från både pollenkornet och fröämnet, precis som människors barn får gener från båda sina föräldrar.

Asexuell förökning (eller vegetativ förökning) kan t.ex. vara groddknoppar som hos ormröt, rotskott som hos asp, revor som hos jordgubbar eller skott från jordstammar som hos styvstarr. Den vegetativa avkomman blir genetiskt helt lik moderplantan och växter som kan föröka sig vegetativt kallas därför klonväxter. Ett område med styvstarr kan därför se ut som en gles gräsmatta med en massa skott, men precis som i gräsmattan kan man inte se hur skotten hänger ihop. För växten har sexuell och vegetativ förökning olika för- och nackdelar. Sexuell förökning ger mer genetisk variation än vegetativ förökning, men har å andra sidan större kostnader för växten. Vid vegetativ förökning blir alla avkommor genetiskt lika moderplantan, men en individ kan

potentiellt sett bli hur stor och hur gammal som helst. Det här är fördelaktigt i ett kort perspektiv, men inte i ett långt perspektiv eftersom variationen som evolutionen arbetar med minskar. Det har därför kommit många teorier som försökt förklara varför så många arter bara har sexuell förökning, men ingen har ännu helt lyckats förklara det (Hurst & Peck 1996).

Arktis

Arktis är området längst uppe i norr runt nordpolen och omfattar norra Ryssland, Alaska och Kanada samt hela Grönland och ett antal öar. Inom biologin brukar man bara räkna området ovanför trädgränsen till det riktiga Arktis, medan fjällbjörkskogen kallas "Subarktis". Miljön ovan trädgränsen på fjäll och i bergsområden liknar mycket miljön i Arktis och många av växtarterna som växer där är samma i båda områdena. Framför allt berg i närheten av Arktis, som de svenska fjällen, får en mycket liknande miljö och brukar därför kallas arktiskt-alpina. Det jag skriver om Arktis gäller därför även för arktiskt-alpina miljöer.

Alla växter som lever i Arktis är tvungna att stå ut med ett kallt klimat och en kort snöfri period varje år. Under den snöfria perioden är temperaturen ofta låg, även om den är mycket högre nära marken hos växterna än två meter upp. Det kalla klimatet gör att all nedbrytning går mycket långsamt och därför är marken oftast näringsfattig. Vädret under växtsäsongen varierar mycket och det är inte ovanligt med minusgrader och snö när växterna blommar. Vinden är dessutom ofta stark och den torkar ut växterna, men kan också ge direkta skador när vinden är full av iskristaller som slipar växterna. Den korta växtsäsongen gör att växterna måste börja blomma snabbt, men arter som börjar blomma tidigt riskerar att bli dåligt pollinerade (Molau 1993). Arter som blommar sent blir ofta bättre pollinerade, men riskerar istället att inte hinna producera några frön alls om vintern kommer tidigt. Frosthävningar och nålis gör att groddplantor kan ha svårt att etablera sig, de lyfts helt enkelt upp ur jorden. Jordrörelserna kan vara så kraftiga att det på vissa fläckar inte kan växa någonting.

Klimatförändringar

Människans utsläpp av koldioxid, metan, lustgas och freoner påverkar hela jordens klimat

genom växthuseffekten. Energi från solen driver väder och klimatsystemen på jorden. Av den inkommande solinstrålningen reflekteras omkring 1/3 och resten absorberas av atmosfären, oceanerna, is, land och vegetationen. Men på lång sikt balanseras instrålningen av utgående infraröd strålning från jorden och atmosfären. Kortvågig strålning kan passera genom atmosfären relativt obehindrat. Genom den naturliga växthuseffekten absorberas delvis långvågig strålning från jorden och återreflekteras av växthusgaserna. Eftersom den utgående långvågiga strålningen balanserar den inkommande solstrålningen blir jorden och atmosfären varmare än de annars skulle ha varit. Människans utsläpp av växthusgaserna gör dock att mer utgående långvågig strålning absorberas än vad som skulle ha gjorts annars och jorden värms därför upp lite extra.

Man har gjort många olika modeller för att se vad de ökade utsläppen kommer att leda till och de har gett delvis olika resultat. Alla modeller är dock överens om att den största temperaturökningen kommer att ske i Arktis. Det rör sig bara om ca 2°C ökning från 1990 till 2100, men det är en snabbare temperaturökning än vad jorden har upplevt under de senaste 10 000 åren (Houghton *et al.* 1996). Många växter i Arktis är begränsade av temperaturen, det är helt enkelt för kallt för att de ska kunna växa och föröka sig så mycket som de annars skulle kunna. Därför kan man förvänta sig att en ökning av temperaturen påverkar växterna mer i Arktis än i varmare områden. Förutom den direkta förändringen av temperaturen så kan också snösmältningen, molnigheten, markfuktigheten m.m. förändras, men detta är väldigt svårt att förutsäga p.g.a. alla återkopplingar.

Mina resultat

Blomningen hos styvstarr ökar i en högre temperatur i Latnjajaure, men påverkas inte på Thingvellir (Artikel VII). Blomningen varierar även mycket mellan åren i Latnjajaure, men ligger på en stabilt låg nivå på Thingvellir (Artikel VI och VII). Detta visar att blomningen är begränsad av temperatur i Latnjajaure, men av andra orsaker än temperatur på Thingvellir som har ett varmare och mindre variabelt klimat (Artikel VII). Styvstarr kan sätta frön vid självpollinering, men blir oftast korspollinerad (Artikel I).

Alla blommor sätter inte frön p.g.a. pollenbrist, för låg temperatur och att växtsäsongen är för kort (Artikel I). Det är också stor skillnad i andelen av blommorna som sätter frön i Latnjajaure och på Thingvellir. I Latnjajaure varierar frösättningen mycket mellan åren, medan den i Thingvellir är lika låg varje år (Artikel I). I Arktis är många lämmelpopulationer cykliska, d.v.s. populationsstorleken går regelbundet upp och ned. Man brukar urskilja fyra olika faser i de här svängningarna: ökningsfas, toppfas, nedåtgående fas och en låg fas (Erling *et al.* 1999) och antalet blommande skott beror också på vilken fas lämmelpopulationen är i. När lämmelpopulationen ökar så finns det många blommande skott jämfört med i de andra lämmelfaserna (Artikel III).

Vid vilken tidpunkt som styvstarr börjar blomma beror på temperaturen. Detta har jag kunnat visa genom att höja temperaturen, varpå styvstarr började blomma tidigare (Artikel VI och VII). Styvstarr har skilda han- och honblommor. I Latnjajaure börjar honblommorna blomma först (Artikel VI och VII), men i Thingvellir börjar hanblommorna blomma först (Jonsson *et al.* 1996). Vid en förhöjd temperatur påverkas hanblommorna mer än honblommorna i Latnjajaure så att deras blomningsperioder överlappar mer än de gör vid en lägre temperatur (Artikel VI och VII). Detta ökar risken för självpollinering. Styvstarr är oftast korspollinerad, trots att den kan självpollinera sig (Artikel I). Att den oftast korspollineras stämmer också med strukturen i den genetiska variationen (Artikel IV). När växten väl blivit pollinerad ska den producera frön. Ju tyngre fröna blir desto större chans har de att klara av att gro. Hos styvstarr ökar frövikten vid en högre temperatur och en längre växtsäsong (Artikel I).

Jag lyckades aldrig hitta groddplantor av styvstarr i kontinuerlig vegetation, men det är ett vanligt resultat (Callaghan 1976, Jónsdóttir 1995). Däremot kom det upp groddplantor när jag störde vegetationen (Artikel I). I naturen förekommer störningar t.ex. på grund av djur som trampar eller gräver, människor som går och på grund av nålis. Att groddplantsetablering verkligen förekommer stämmer också med att de flesta populationer som jag studerat genetiskt innehöll flera kloner (Artikel IV). Om det inte

förekom någon groddplantsetablering så borde antalet kloner minska med åldern på populationen genom att de antingen konkurrerar ut varandra eller att vissa kloner slumpmässigt dör. Men i de populationer som jag studerade var det ingen skillnad på antalet kloner i områden där isen drog sig tillbaka för 10 000 år sedan, 60 000 år sedan eller områden som inte varit nedisade under den senaste istiden (Artikel IV). Däremot var antalet kloner lägre ju längre norrut vi kom (Artikel IV). Detta beror nog på att det är kallare längre norrut. Då blommar styvstarrar mer sällan, får färre frön och fröna blir lättare och detta ger färre groddplantor och därmed färre antal kloner. Genom att klonerna kan bli väldigt gamla: 3800-5000 år gamla hos styvstarr och 15-150 år gamla hos norrlandsstarr (Artikel II) så behöver de inte ha många groddplantor som klarar sig varje år. Det räcker med att någon groddplanta klarar sig, kanske ett ovanligt varmt eller annars gynnsamt år. Därför förekommer säkert groddplantsetablering, bara så sällan att man inte upptäcker den inom normala forskningsprojekt.

Produktionen av vegetativa skott varierade mellan år och olika populationer. I Latnjajaure så påverkades inte antalet vegetativa skott av en temperaturökning men i Thingvellir så minskade antalet vegetativa skott vid en högre temperatur (Artikel VII). Antalet nya vegetativa skott var också fler när det finns fler lämlar och när lämmelpopulationen ökar (Artikel III).

Man har länge trott att klonväxter skulle ha mindre genetisk variation än växter som bara förökar sig sexuellt. Men i en studie av alla då undersökta växter av Hamrick & Godt (1990) så visade det sig att det inte fanns någon skillnad. Istället var det utbredningsområdets storlek och om en växt var självpollinerad eller korspollinerad som avgjorde hur mycket genetisk variation den hade. I deras studie ingick det dock inga arktiska växter. Styvstarr och norrlandsstarr är korspollinerade och har stora utbredningsområden och borde därför ha mycket genetisk variation, vilket de också har (Artikel IV). Däremot så var den genetiska variationen lägre i områden där isen drog sig tillbaka för 10 000 år sedan jämfört med de områden där isen drog sig tillbaka för 60 000 år sedan eller som inte var nedisade under den senaste istiden (Artikel IV).

Styvstarrar varierade väldigt mycket i hur den ser ut mellan olika populationer, till skillnad från norrlandsstarrar (Artikel V). Hos styvstarr kunde 20% av skillnaden i utseende mellan populationerna förklaras med den genetiska skillnaden mellan populationerna (Artikel V). Däremot berodde 40-50% av skillnaderna i utseende på skillnader i miljöfaktorer. Temperaturen och antalet lämlar påverkade skotthöjden och bladbredden mest. Ju kallare det var och ju fler lämlar det fanns, desto kortare och smalare blev bladen. Bladen blev också smalare ju mindre nederbörd det kom i en population. Klyvöppningarna blev fler om temperaturen var högre, antalet lämlar mindre och nederbörden högre. Storleken på klyvöppningarna reagerade dock tvärtom, när det fanns många klyvöppningar var de små och fanns det få så var de stora. Jordstammarna blev kortare ju längre österut de växte och ju färre lämlar det fanns (Artikel V).

Sammanfattningsvis kan man säga att styvstarrars förökning påverkas mycket av klimatet, vädret och lämmelbetet (Artikel I, III, VI och VII) och den kommer i stora delar av sitt utbredningsområde (dock inte de varmaste) att gynnas av en ökande temperatur p.g.a. växthuseffekten, i alla fall på kort sikt (Artikel VI och VII). Styvstarrar kan bli mycket gammal (Artikel II) och lyckas under sin livstid att sätta tillräckligt med groddplantor för att populationerna ska innehålla många kloner (Artikel IV). Antalet kloner kan också tänkas öka i en ökande temperatur. Styvstarrar har en hög genetisk variation (Artikel IV) och ett utseende som mest påverkas av miljön, men även till viss del av genetiken (Artikel V).

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