

Breeding System Evolution in the Arctic: a Comparative Study of *Campanula uniflora* in Greenland and Iceland

Authors: Hafdís Hanna Ægisdóttir, and Thóra Ellen Thórhallsdóttir

Source: Arctic, Antarctic, and Alpine Research, 38(3) : 305-312

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2006\)38\[305:BSEITA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2006)38[305:BSEITA]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-o-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Breeding System Evolution in the Arctic: a Comparative Study of *Campanula uniflora* in Greenland and Iceland

Hafðís Hanna Ægisdóttir*†

and

Thóra Ellen Thórhallsdóttir*

*Institute of Biology, Askja, University of Iceland, Sturlugata 7, 101 Reykjavík, Iceland.

†Corresponding author. Present address: Institute of Botany, University of Basel, Schönbeinstrasse 6, CH-4056 Basel, Switzerland. Hafdis-Hanna.Aegisdottir@unibas.ch

Abstract

The breeding system and floral development were compared in mid-range (West Greenland) and marginal (North Iceland) populations of *Campanula uniflora*, a widespread high arctic species which is rare in large parts of its range. Seed set and germination were compared among outcrossed, passively and actively selfed, and control flowers. There were no significant differences in seed set or seed quality among treatments or populations. Seed viability was high and germination rapid following GA³ pretreatment in both populations, but germination was delayed by a week in the Icelandic seeds. The populations showed similar flowering phenology with a short and synchronized flowering period. While the population in Greenland had a floral development typical of the genus *Campanula*, the Icelandic flowers can be classified as pre-anthesis cleistogamous. Both populations appeared to be predominantly inbreeding, despite being protandrous with pollen released before the flower opened. This method of pollen deposition is interpreted as a secondary mechanism of reproductive assurance, securing seed production. This indicates that an evolutionary switch has occurred, from selection for outbreeding in the ancestral group toward inbreeding in the only truly high arctic species in the genus.

Introduction

Important aspects of plant breeding system evolution include self-incompatibility, floral traits such as flower structure and phenology, as well as pollinator availability and behavior. Arctic environments severely constrain many of these factors. For example, pollinators are few with often greatly reduced activity, and the growing season may be too short for seeds to mature (Savile, 1972; Murray, 1995). Although virtually the whole suite of reproductive traits is represented among arctic plants, many have evolved towards apomixis or self-pollination (Bliss, 1962; Murray, 1987; Arroyo and Squeo, 1990; Philipp et al., 1990; Molau, 1993), and outcrossing diploids only constitute a small proportion of high arctic floras, e.g., that of Svalbard (Brochmann and Steen, 1999). The evolution of selfing is a common trend in angiosperms and has been interpreted as an adaptation toward reproductive assurance, i.e., securing reproductive success when conditions for outcrossing are unfavorable (Jain, 1976; Holsinger, 1992, 2000; Schoen et al., 1997; Barrett, 1998).

One approach toward understanding environmental constraints on reproduction is to compare reproductive patterns among close relatives, e.g., congeners and conspecific but geographically separated populations. Although the Arctic is beyond the climatic tolerance of most of the world's vascular flora, true arctic species have their center of distribution in the Arctic. Such species often have large mid-range populations but small and isolated populations at higher or lower latitudes, which can therefore be classified as marginal (e.g., Böcher et al., 1978; Hultén and Fries, 1986; Kristinsson, 1986).

The genus *Campanula* is found exclusively in the northern hemisphere, from Mexico to northern Greenland with a center of diversity in the Mediterranean region. It lives in a variety of habitats, including forests, meadows, and deserts as well as mountains (Nyman, 1993; Hickey and King, 1988). The reproductive biology of the genus is well known, with most species being self-incompatible and allogamous. Autogamy occurs, but is considered the least common type of breeding system (Shetler, 1979; Nyman, 1993). Most

Campanula species are protandrous, with unusual floral development, presenting the pollen as a layer around the style before the stigma becomes exposed. This serves as a secondary pollen presentation mechanism, facilitating pollen transfer to visiting insects. In some *Campanula* spp., the stigmatic lobes bend backward toward the style during late-female phase, picking up pollen that has not been removed by insects. This process facilitates the late self-fertilization of ovules that have not been fertilized by outcrossing (Fægri and Pijl, 1979; Nyman, 1993).

Campanula uniflora is the only truly arctic species of the genus *Campanula* (Hultén and Fries, 1986). In West Greenland, *C. uniflora* is widespread and quite common, while the Icelandic populations are few, isolated, and mostly very small (Böcher et al., 1978; Kristinsson, 1986). The aim of this study was to seek an understanding of arctic breeding system evolution by comparing (1) the breeding system of the arctic species with its non-arctic congeners, and (2) comparing floral development, phenology, seed set, and seed quality in a large, mid-range population (West Greenland) with a small and isolated marginal population (North Iceland).

Species

Campanula uniflora is mostly high arctic with an amphi-Atlantic distribution (Brochmann and Steen, 1999) reaching 80°N in Greenland (Böcher et al., 1978) and Svalbard (data provided by Herbarium Universitas Osloensis) (Fig. 1a). It is also found in Iceland, the Scandinavian mountains, Alaska, Franz Josef Land, and south to the Rocky Mountains of British Columbia. Isolated populations live in mountains in Utah and Colorado (39°N), (Hultén, 1941–1950). It is a herbaceous perennial with basal rosettes, and one to several leafy flowering stalks up to 15 cm tall, each carrying a single tubular blue flower. In North Iceland most plants carry a single flowering stalk while the Greenland plants often produce 3–4 flowers (personal observation). The fruit is a multiseeded capsule (Böcher et al., 1978; Kristinsson, 1986; Rønning, 1996).

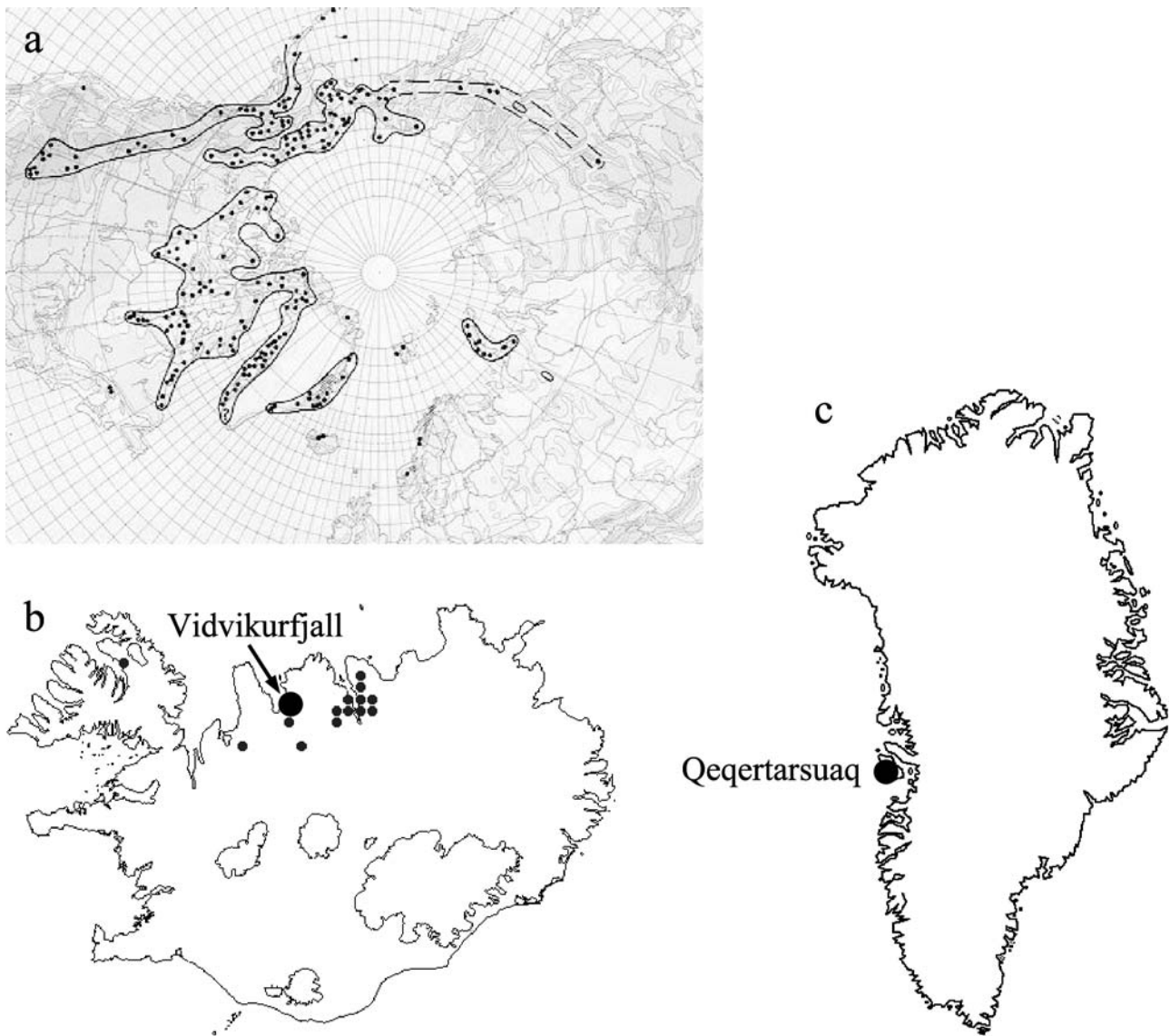


FIGURE 1. (a) Global distribution map of *Campanula uniflora* (Hultén and Fries, 1986), (b) distribution in Iceland (small black spots) and location of the population on Vidvikurfjall (large black spot) (Kristinsson, 2005), and (c) location of the Greenlandic population on Qeqertarsuaq.

Campanula uniflora is rare in Iceland, where it is restricted to small and isolated populations in the mountains of the north and northwest (Fig. 1b), with a center in the massive mountain range of the central north. One small population has been found on Vatnsdalsfjall mountain in Northwest Iceland and another close to Drangajökull glacier in the Vestfirðir peninsula (Kristinsson, 2005). *C. uniflora* is

quite common in some parts of West and Southwest Greenland but rare in North, South, and Southeast Greenland (Fig. 1c). Toward the north, it is common in dry lowland habitats but south of ca. 69°N it is almost exclusively found on mountains (Böcher et al., 1978).

Sites

QEQTARSUAQ, WEST GREENLAND

Qeqertarsuaq (Disko Island) is a 7500 km² island of layered basalt off the west coast of Greenland (Fig. 1c) (Böcher and Petersen, 1997). It has a low arctic climate (Table 1), moderated by the West Greenland current which is highly variable from year to year (Phillip et al., 1990).

The study site was a dry south-facing and partly vegetated scree slope near the Arctic Station of the University of Copenhagen (69°15.358'N, 53°31.344'W). *C. uniflora* was concentrated at the edge of vegetated patches but absent from dense vegetation. Common species in the area included *Cerastium alpinum*, *Bistorta vivipara*,

TABLE 1

Mean monthly summer and annual temperatures (°C) in Qeqertarsuaq and estimated mean temperature (°C) on Vidvikurfjall (Nielsen et al., 2001, and data provided by the Danish Institute of Meteorology, Copenhagen and the Icelandic Meteorological Office).

	Mean temp. (°C)	June	July	August	Year
Qeqertarsuaq	1991–1999	5.1	7.5	5.9	–5.0
	2000	5.8	7.4	6.8	–2.5
Vidvikurfjall	1991–2002	4.1	5.0	5.3	–0.8
	2001	3.3	5.8	4.8	–0.1

VIDVIKURFJALL, NORTH ICELAND

Vidvikurfjall is on the western side of the massive basaltic mountain range of the central north (Fig. 1b). A small population of *C. uniflora* was found at 750 m a.s.l. (65°43.846'N, 19°16.287'W), with only a few isolated plants higher up. The habitat at Vidvikurfjall is rockier than in Qeqertarsuaq, with sparser vegetation, and *C. uniflora* was commonly found together with *Racomitrium* mosses. Accompanying vascular plant species included *Carex bigelowii*, *Dryas octopetala*, *Cerastium alpinum*, *Silene acaulis*, *Armeria maritima*, *Saxifraga caespitosa*, *Bartsia alpina*, and *Ranunculus glacialis*.

Mean June, July, August, and annual air temperature (°C) at the site in Vidvikurfjall were estimated from the nearest weather station at Dalsmyrni (~4 km away, 65°45.433'N, 19°14.846'W), correcting for the 620 m difference in altitude by the approximation that temperature (°C) falls about 0.7°C/100 m altitude (Wallace and Hobbs, 1977) (Table 1).

Methods

PHENOLOGY

Flowering phenology was monitored from 1 to 20 July 2000 in 60 randomly selected plants in West Greenland. To test for the possible effect of hand-pollination on flower longevity, ten hand-pollinated plants were also monitored. In North Iceland, 40 randomly selected plants were monitored from 9 to 26 July 2001 with an additional sample of 35 plants (103 flower buds) added on 13 July. Flowering stages were recorded once (Iceland) or twice a day (Greenland) from bud stage to fruit initiation.

BREEDING SYSTEM EXPERIMENTS

A breeding system experiment was set up in West Greenland in July 2000 with the following four treatments: (1) *control*: flowers left untreated to establish the natural level of seed set; (2) *passive selfing*: flowers bagged in bud inside insect excluders, made of white nylon curtain material with 1 mm mesh width, to establish whether seeds are produced in the absence of pollinators; (3) *active selfing*: flowers bagged in bud and subsequently hand-pollinated with own pollen by brushing anthers across the stigma when it was receptive for pollen (this treatment was carried out to assess whether insect visitation was required for self-pollination); and (4) *outcrossing*: flowers bagged in the bud stage and hand-pollinated with pollen from pollen donors located at least 3 m from recipients (this treatment was carried out to examine whether flowers produced more seeds when outcrossed). The treatments were applied to different flowers on a sample of 40 randomly chosen plants, each with 20 replicates on as many plants. To test for a possible treatment effect on resource allocation to other flowers, an additional control was added (15 randomly selected flowers on as many plants). Since there were no differences in seed production among these two control groups, we concluded that there were no confounding treatment effects. Fruits were bagged on 16–17 July and collected in mid-September 2000.

In the Icelandic population, active selfing and outcrossing treatments were not possible, and only control and passive selfing treatments were set up on 40 randomly selected plants (20 replicates per treatment) on 10–11 July 2001. Fruits were bagged on 26 July and collected on 8 September. Of the 20 original passive selfing replicates, 6 were lost due to predation and a heavy snowfall. After sorting and counting, seeds from both populations were kept at 4°C up to germination trials.

POLLEN LOADS ON STIGMAS

In West Greenland, pollen grains on stigmas were counted in the field through a binocular microscope on 30 randomly chosen flowers once a day for 5 days, starting on the first day of open flower. This was done by carefully lowering the microscope over the plant by slipping it through the circular hole left after removing the microscope's basal plate.

SEED GERMINATION

Since pre-trials with untreated seeds resulted in no germination, the following treatments were applied: (1) cold stratification (4°C) for 4 and 8 weeks; (2) cold stratification + Gibberellic Acid (GA³) in doses of 0.1, 1, or 10 mg L⁻¹; (3) cold stratification + scarification; (4) GA³ in doses of 0.1, 1, or 10 mg L⁻¹; (5) scarification only; and (6) control. Cold stratification had no and scarification very little effect. GA³ gave better results and after further tests it was decided to use a treatment of 1000 mg L⁻¹ GA³. Germination tests were run for 40 days, on 20 seeds from each of 10 flowers from each treatment in Greenland, but on 20 seeds from each of 12 passively selfed and 19 control flowers from Iceland.

The seeds were placed on filter paper in Petri dishes and moistened with a solution of 1000 mg/L of GA³. They were kept wet in an incubator with a 20-h photoperiod and 15°/10°C (day/night) temperature. Germination was recorded weekly.

STATISTICAL ANALYSES

Differences in seed sets among treatments and populations were tested with one way ANOVA and Student's *t*-test for normally distributed data (square-root transformed where appropriate, using $X' = (\sqrt{X} + 0.5)$ because of the small data sets and zero values), and Kruskal-Wallis and Mann-Whitney *U*-test for non-normally distributed data (Zar, 1999). The effect of hand-pollination on flower longevity was tested by Student's *t*-test and the differences in germination with *G*-test (Zar, 1999).

Statistical procedures were carried out in SigmaStat and SYSTAT (SAS, 1989; SYSTAT, 1999).

Results

PHENOLOGY

Flowering of *Campanula uniflora* started earlier in West Greenland in the summer of 2000 than in the North Iceland summer of 2001 but otherwise the populations showed similar phenology with a short and highly synchronized flowering period (Fig. 2).

In West Greenland, the population progressed from 0 to 100% flowering in just 14 days and individual flowers from bud to fruit in only 15 days (4–17 July) (Fig. 2). In North Iceland, the first flowers opened on 10 July (9 days later than in West Greenland, 2000) and 10 days later, 88.7% of the population had flowered. Fruit initiation was approximately 12 days later in North Iceland, 2001, than in West Greenland, 2000 (Fig. 2).

Flowers were short lived in both populations; in Iceland, flowers closed on average 5.5 ds after the petals became visible in the bud, and in Greenland only 3.9 ds later (Fig. 3). The temporal window for external pollen deposition was on average 2.2 ds in the Greenland flowers (stigma receptive to flower closure). In Iceland, own pollen has already cluttered the stigma prior to flower opening (Fig. 3, iii).

Flowers of hand-pollinated plants stayed open for a shorter time (mean = 2.85 days) than control plants (mean = 4.93 days) (*t*-test, $t = 5.91$; $p < 0.01$).

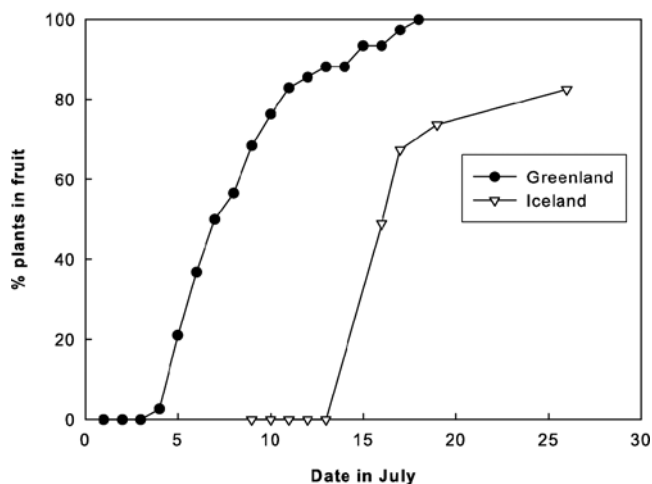
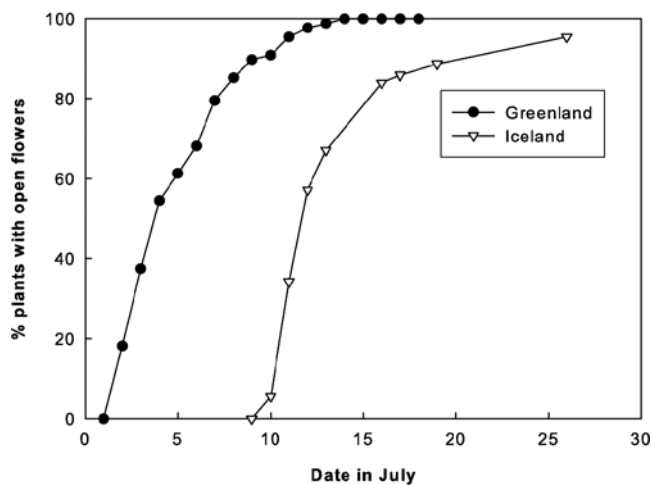


FIGURE 2. Phenological progression of *Campanula uniflora* populations in Qeqertarsuaq, West Greenland, summer 2000, and Vidvikurfjall, North Iceland, summer 2001, as percentage plants with open flowers (above) and percentage plants in fruit (below).

BREEDING SYSTEM

The Greenlandic flowers were strongly protandrous with pollen deposited by the anthers directly onto the style (Fig. 3, a, b). Later, the style elongated and the stigma became exposed (c, d). At the time of bud break, the anthers were half the length of the style (b). The back- and downward bending of the stigmatic lobes toward the style was repeatedly observed. Although also protandrous, the Icelandic plants had a distinctly different floral development (Fig. 3, i–iv). In nearly all cases pollen was deposited by the anthers directly onto the stigma and the top of the style in the closed bud (ii). When the bud opened the anthers bent over the immature stigma. The style subsequently elongated and the stigma, already cluttered with pollen, split open (iii, iv).

POLLEN LOADS ON STIGMAS

Pollen loads in West Greenland varied greatly. While many stigmas received none or very few pollen grains, a small number were cluttered with up to about 300 grains. Although some stigmas received pollen prior to stigma maturation, the number of pollen increased sharply when stigmas became mature (Fig. 4).

SEED SET

The number of mature seeds in the control plants did not differ significantly from the extra control plants (*t*-test, $t = -0.43$, $p = 0.67$),

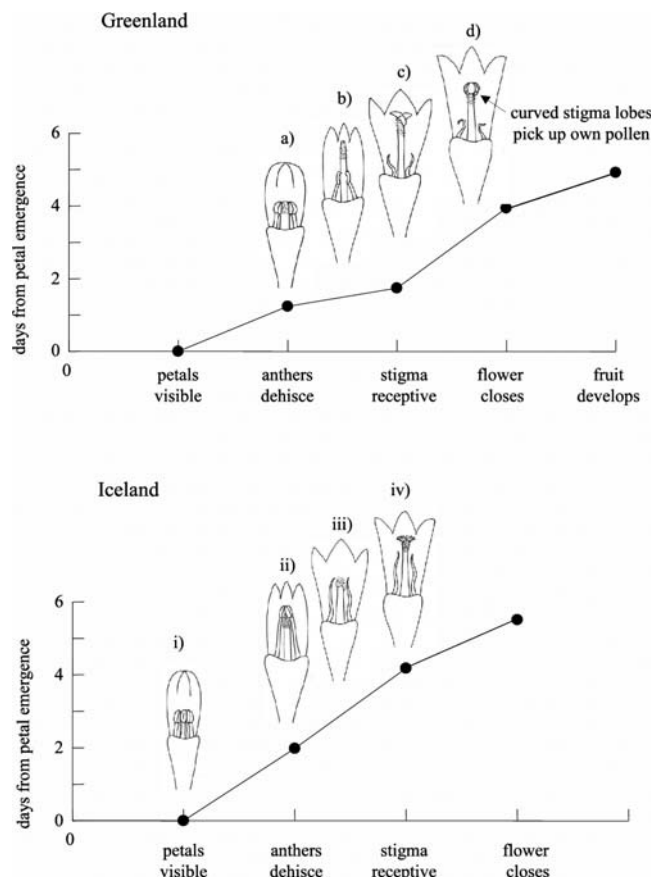


FIGURE 3. Floral development and flower-level phenology of *Campanula uniflora* in Qeqertarsuaq, West Greenland (above) and in Vidvikurfjall, North Iceland (below). Note the differences in anther length and position at pollen release (a, ii), resulting in pollen being deposited on the style in Greenland (b) but directly on the stigma in Iceland (iii, iv). Autogamy is secured in Iceland but facilitated toward the end of the flowering period in Greenland by the downward bending of the stigma lobes to contact own pollen left in the upper part of the style (d). Drawing: Th. E. Thórhallsdóttir.

which indicates that there was not a within-plants effect of the pollination treatments.

There were no significant differences in the number of mature or immature seeds/capsule between the two populations or among treatments (Fig. 5, Table 2). No aborted seeds were observed in Iceland and few in the Greenlandic fruits with no significant difference between treatments (Kruskal Wallis, $Z(K) = 2.79$; $p = 0.43$).

SEED GERMINATION

Seed viability in the Greenlandic population was very high and germination rapid (Fig. 6). In control treatments there was 100% germination, 98% in actively selfed, and 97% in outcrossed progeny. Significantly poorer germination (84%) in passively selfed progeny (*G* test, $\chi^2 = 10.06$, $p < 0.05$) could be attributed to one individual where only 3 seeds of 20 germinated, and when this plant was excluded from the analyses, there was no significant difference between treatments (*G* test, $\chi^2 = 3.5$). By day 8, 25–60% of the seeds had germinated and most by day 14 (Fig. 6).

Germination in North Iceland was also high with significant differences among seeds from control and passive selfed plants (*G* test, $\chi^2 = 6.63$, $p < 0.01$). Seeds germinated about a week later than in West Greenland. No seeds germinated after day 21 (Fig. 6).

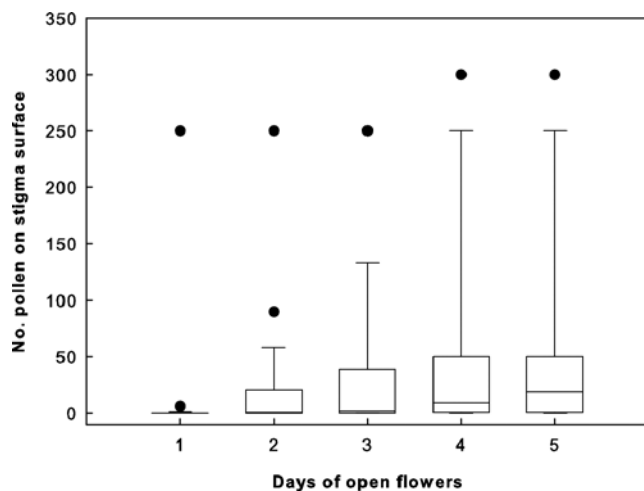


FIGURE 4. Number of pollen grains on stigmas from day 1 to day 5 of open *Campanula uniflora* flowers ($n = 30$), Qeqertarsuaq (West Greenland), summer 2000. Line within box = median, box = 25th–75th percentiles. Error bars above and below the box indicate 90th and 10th percentiles.

There was no significant difference in seed germination between the two localities for both controls and passive selfed plants (G test, $\chi^2 = 0.71$, $p > 0.05$, and $\chi^2 = 0.59$, $p > 0.05$, respectively).

Discussion

PROTANDROUS BUT STILL INBREEDING

In Greenland, *C. uniflora* had the same floral development as most other *Campanula* species, being strongly protandrous with pollen deposited by the anthers directly onto the style before the stigma became receptive (Fig. 3). Such a temporal separation of male and female maturation, dichogamy, is usually regarded as an outbreeding mechanism (Bhardwaj and Eckert, 2001; Silvertown and Charlesworth, 2001). Often, the temporal separation is not complete and in such species, self-fertilization is reduced but not prevented (Mallick, 2001). It is evident that in *C. uniflora*, considerable self fertilization took place. First, the backward bending of the stigmatic lobes toward the style, which was cluttered with pollen, was repeatedly observed in the field. Second, the median number of pollen grains on stigmas, immediately before the flower closed (18.5), was much lower than the median number of seeds per capsule (controls) in the same population (55). That indicates that the stigmatic lobes pick up pollen from the style during late-female phase with resultant self-fertilization. Complementary isozyme studies (Ægisdóttir, 2003) showed that both populations, but especially the Icelandic one, have very limited genetic variation, which reinforces the conclusion that the species is a habitual inbreeder.

Cleistogamy, recorded in over 200 species of flowering plants, represents the most extreme form of autogamy. The great majority of such plants produce dimorphic flowers, small and often highly modified cleistogamous flowers that never open and are obligate self-pollinators, and much bigger outcrossing chasmogamous flowers (Lord, 1981; Plitmann, 1995; Lu, 2002). Darwin (1877) was the first to suggest that the function of cleistogamy was to provide a large number of seeds at low cost and ensure fertilization under unfavorable conditions, a view now generally accepted (Plitmann, 1995). A correlation of cleistogamy with adverse environments has been found, e.g., in the Scandinavian mountains where autogamous and cleistogamous species occur predominantly at high elevations (Lindman, 1887).

Within the Campanulaceae, cleistogamy is known in *Specularia* but occurs rarely in *Campanula* (Shetler, 1979). Lord (1981) divided

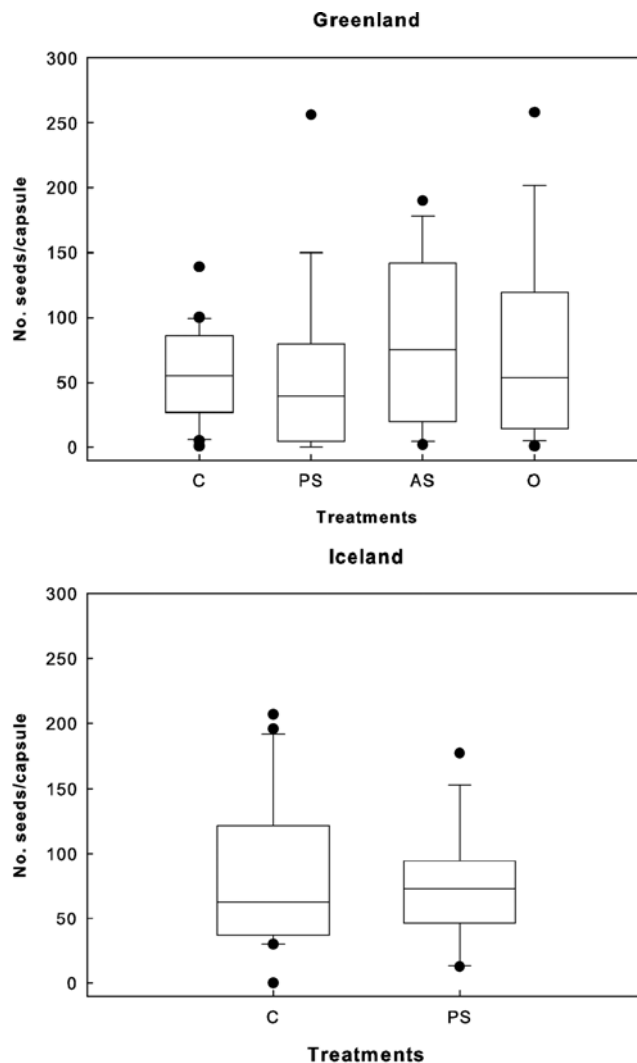


FIGURE 5. Number of mature seeds per capsule in control (C), passive selfed (PS), active selfed (AS), and outcrossed (O) *C. uniflora* plants in Qeqertarsuaq, West Greenland, 2000 (above), and Vidvikurfjall, North Iceland, 2001 (below). Line within box = median, box = 25th–75th percentiles. Error bars above and below the box indicate 90th and 10th percentiles.

cleistogamous species into four categories: pre-anthesis cleistogamy, pseudocleistogamy, complete cleistogamy, and “true” cleistogamy. Pre-anthesis cleistogamy refers to cases where bud pollination occurs followed by anthesis (Lord, 1981). This is uncommon and has mostly been observed in cultivated legumes, grasses, and other crop plants. *Campanula uniflora* in North Iceland can be categorized as a pre-anthesis cleistogamous species since pollen was deposited by the anthers directly onto the highest part of the style and the stigma itself before the bud opened. This behavior may effectively prevent cross-pollination by cluttering the stigma with own pollen before the flower opens (Frankel and Galun, 1977; Lord, 1981; Plitmann, 1995; Lu, 2002). Ours is not the first recording of such behavior in *C. uniflora* as it was described in Greenland and Norway by the Danish botanist Warming in 1886, although he did not specify the location of his populations. The evolution of cleistogamy in the Icelandic population of *C. uniflora* may be interpreted as a step toward reproductive assurance (large number of seeds at a low cost) in the small and marginal population at Vidvikurfjall, which has to deal with unpredictable weather conditions, lack of pollinators, and a short growing season.

TABLE 2

Comparisons of seed set among different treatments in Qeqertarsuaq and Vidvikurfjall were tested using one way ANOVA/Student's *t*-test (for mature seeds) and Kruskal-Wallis test/Mann-Whitney *U*-test (immature seeds), respectively. The comparison between number of control and passively selfed seeds in Qeqertarsuaq and Vidvikurfjall were tested using Student's *t*-test (mature seeds) and Mann-Whitney *U*-test (immature seeds).

Comparison	Treatment and sample size				Statistical significance	
	C	PS	AS	O	Mature seeds	Immature seeds
W Greenland	20	17	16	17	N.S	N.S
N Iceland	20	14			N.S	N.S
Greenland vs. Iceland	20 + 20				N.S	N.S
Greenland vs. Iceland	17 + 14				N.S	N.S

SEED QUALITY

Previous attempts to germinate *C. uniflora* have apparently failed, e.g. of seed from Svalbard (Eurola, 1972), Greenland (Sørensen, 1941), and the Rocky Mountains, U.S.A. (Bonde, 1965). In all cases, very few or no untreated, cold stratified, or scarified seeds germinated. Here, germination approached 100% after pretreatment with 1000 mg L⁻¹ of GA₃ (Fig. 6). *C. uniflora* seeds are classified as having physiological dormancy (Baskin and Baskin, 1998), and this can be broken by chemicals, including GA₃. The rapid germination exhibited by *C. uniflora*, e.g., the Greenlandic population where nearly all seeds had germinated after 14 days (Fig. 6), is not typical of arctic plants that generally have low germination percentages, are slow to initiate germination, and may take 2–3 weeks for full emergence of root and shoot (Bliss, 1997).

INSECT VISITS

On Mount Olympus, Greece, where *Andrenidae* and *Megachilidae* bees dominate the pollinator fauna, *Campanula* spp. were mostly pollinated by solitary bees (Blionis and Vokou, 2001). Pollination by flies has also been noted in *C. velebitica* and *C. cochleariifolia* in Bulgaria (Kozuharova, 2000), whereas bumblebees (*Bombus* spp.) were observed collecting pollen from flowers of *C. rotundifolia* in an alpine meadow in Switzerland (Cresswell and Robertson, 1994) and in the Rocky mountains (Bingham and Orthner, 1998). A bumblebee (*B. hortorum*) feeding on nectar has been observed in *C. uniflora* flowers in Abisko, northern Sweden (Erik Sjödin, personal communication).

In West Greenland, red mites, probably *Trombidium* spp., were commonly found in the flowers but no flies were observed visiting. Since pollen load on stigmas increased greatly with flower age in a few flowers (Fig. 4) and as a red mite was observed in one flower whose stigma was cluttered with pollen, it is suggested that those mites were able to transfer pollen from the style to the mature stigma of the flowers of *C. uniflora*. The pollen adhered to the mites but they were not observed transferring pollen between flowers.

PHENOLOGY

In both West Greenland and North Iceland the flowering of *C. uniflora* was highly synchronized. The Greenland population progressed from 0 to 100% flowering in just 14 days, and in Iceland 88.7% of the population had already flowered by day 10 (Fig. 2). This is much shorter than the average flowering period (27 days) reported for the genus *Campanula* (Blionis et al., 2001) and probably reflects

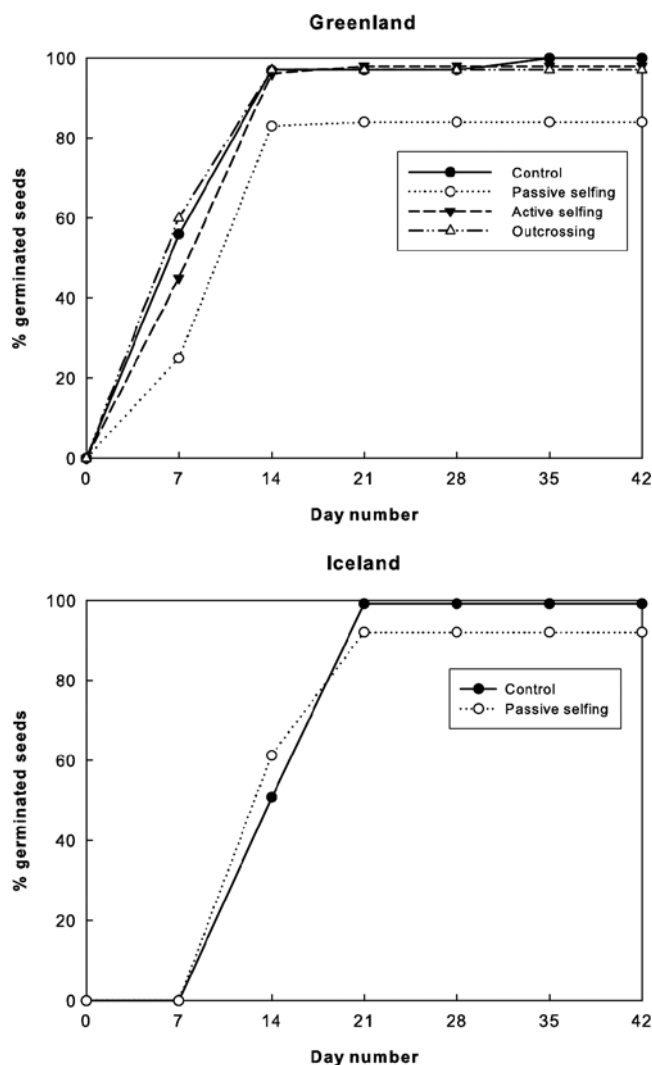


FIGURE 6. Percentage germination of *C. uniflora* seeds from control (C), passively selfed (PS), actively selfed (AS), and outcrossed (O) plants in Qeqertarsuaq, West Greenland (above), and Vidvikurfjall, North Iceland (below).

adaptation to a short growing season. Although synchronous flowering is quite common in arctic and alpine environments (Bliss, 1956, 1971; Totland, 1993), it is not always the case. As an example, *Saxifraga hirculus* has an exceptionally poorly synchronized flowering period in the central highlands of Iceland (Leplar, 2002).

Untreated *C. uniflora* flowers in West Greenland stayed open significantly longer than hand-pollinated plants. This may be interpreted as a form of compensation to offset the low frequency of pollinator visits; in fact, no flying insects were ever observed visiting the flowers. Such a response to variable pollinator visitation rates is well known and has been recorded in other *Campanula* species. A correlation between the length of the female phase and pollen deposition was found in *C. rapunculoides* (Richardson and Stephenson, 1989) and on Mount Olympus, Greece, insect visitation rates to *Campanula* spp. decreased with elevation while flower longevity increased (Blionis and Vokou, 2001). Similarly, has it been shown in a study of alpine and foothill populations of *C. rotundifolia* that the alpine *Campanula* were not pollinator limited since more effective pollination and greater flower longevity in the alpine populations compensated for lower visitation rates (Bingham and Orthner, 1998; Bingham and Ranker, 2000).

In Iceland, *Campanula uniflora* is geographically peripheral and has the ecological hallmarks of a marginal population, being restricted to a few small and highly isolated patches. In contrast, the population at Qerqertarsuaq is central in a more or less continuous range along western Greenland. Although we only studied two populations and therefore lack replication within site types, the differences reported here between the two fit well with the theory and empirical data on central vs. peripheral populations. Autogamy is more common at the edge of species' ranges (Silvertown and Charlesworth, 2001), and the Icelandic population seems to have evolved toward a particularly extreme form of active self-fertilization and one that may virtually exclude cross-fertilization (Fig. 3). A slower rate of germination, as found in the Icelandic compared with the Greenlandic population (Fig. 6), has also been reported for an isolated compared to a more central population of *Saxifraga aizoides* in the Swiss Alps (Meier and Holderegger, 1998). Likewise, although considerably further north, mean monthly temperatures at Qerqertarsuaq (West Greenland) exceeded those of Vidvikurfjall (North Iceland) in all three summer months (Table 1). Thus, it is possible that the differences among the two populations reflect the harsher climatic and less favorable biotic conditions (lack of pollinators) in the Icelandic population. The later flowering of *C. uniflora* in Iceland may be interpreted in this light, but Þórhallsdóttir (1998) found a strong correlation between warm early summer temperatures and the timing of onset of flowering in the central highland of Iceland.

CONCLUSION

While most *Campanula* spp. are allogamous and self-incompatible (Shetler, 1979; Nyman, 1993), the arctic *C. uniflora*, although retaining vestigial features promoting outcrossing, is completely self-compatible and inbreeding. The floral development of the Icelandic plants may even effectively prevent outcrossing. Still, no negative inbreeding effects were detected in seed set or seed quality. We conclude that these traits, e.g., the difference in the breeding system of an arctic *Campanula* compared to its non-arctic congeners as well as the difference in reproductive strategies between the West Greenland (mid-range) and the Icelandic (marginal) population can be explained as a regional adaptation of the species to meet the harshness of the arctic environments.

Acknowledgments

The authors thank Chloe Leplar for assistance in the field in Greenland and Gudmundur Ingi Gudbrandsson for collecting fruits from Vidvikurfjall, Iceland. We would also like to thank Assistant Professor Marianne Philipp at the Botanical Institute, University of Copenhagen, and the board of the Arctic Station, University of Copenhagen, and Hólar College, North Iceland, for providing working facilities for the study. Finally, we would like to thank Dr. David Du Puy and the two reviewers for giving valuable comments on the manuscript. This work was part of a larger project—"The capability of Arctic plant species to respond to rapid environmental changes"—for which we gratefully acknowledge the support of the Nordic Council of Ministers, Nordic Arctic Research Programme.

References Cited

Ægisdóttir, H. H., 2003: Æxlunarvístfræði, útlits- og erfðabreytileiki fjallabláklukku (*Campanula uniflora*) á Íslandi, Grænlandi og Svalbarda [e. Reproductive ecology, morphological, and genetic variation in *Campanula uniflora* in Iceland, Greenland and Svalbard]. M.Sc. thesis. Institute of Biology, University of Iceland, 89 pp.

- Arroyo, M. T. K., and Squeo, F., 1990: Relationship between plant breeding systems and pollination. In Kawano, S. (ed.), *Biological Approaches and Evolutionary Trends in Plants*. London: Academic Press, 205–227.
- Barrett, S. C. H., 1998: The evolution of mating strategies in flowering plants. *Trends in Plant Science*, 3: 335–341.
- Baskin, C. C., and Baskin, J. M., 1998: *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. California: Academic Press, 666 pp.
- Bhardwaj, M., and Eckert, C. G., 2001: Functional analysis of synchronous dichogamy in flowering rush, *Butomus umbellatus* (Butomaceae). *American Journal of Botany*, 88: 2204–2213.
- Bingham, R. A., and Orthner, A. R., 1998: Efficient pollination of alpine plants. *Nature*, 391: 238–239.
- Bingham, R. A., and Ranker, T. A., 2000: Genetic diversity in alpine and foothill populations of *Campanula rotundifolia* (Campanulaceae). *International Journal of Plant Sciences*, 161: 403–411.
- Blionis, G. J., and Vokou, D., 2001: Pollination ecology of *Campanula* species on Mt. Olympos, Greece. *Ecography*, 24: 287–297.
- Blionis, G. J., Halley, J. M., and Vokou, D., 2001: Flowering phenology of *Campanula* on Mt. Olympos, Greece. *Ecography*, 24: 696–706.
- Bliss, L. C., 1956: A comparison of plant development in micro environment of arctic and alpine tundras. *Ecological Monographs*, 26: 303–337.
- Bliss, L. C., 1962: Adaptation of arctic and alpine plants to environmental conditions. *Arctic*, 15: 117–144.
- Bliss, L. C., 1971: Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics*, 2: 405–438.
- Bliss, L. C., 1997: Arctic Ecosystem of North America. In Wielgolaski, F. E. (ed.), *Ecosystems of the World 3, Polar and Alpine Tundra*. Amsterdam: Elsevier, 551–683.
- Böcher, J., and Petersen, P. M., 1997: Greenland. In Wielgolaski, F. E. (ed.), *Ecosystems of the World 3. Polar and Alpine Tundra*. Amsterdam: Elsevier, 685–720.
- Böcher, T. W., Fredskild, B., Holmen, K., and Jakobsen, K., 1978: *Grønlands Flora*. København: P. Haase and Søns Forlag, 326 pp.
- Bonde, E. K., 1965: Further studies on the germination of seeds of Colorado alpine plants. *University of Colorado Studies, Series in Biology*, 14: 16 pp.
- Brochmann, C., and Steen, S. W., 1999: Sex and genes in the flora of Svalbard—implication for conservation biology and climate change. In Nordal, I., Razzhivin, V. Y. (eds.), *The Species Concept in the High North—a Panarctic Flora Initiative*. Oslo: The Norwegian Academy of Science and Letters, 33–61.
- Cresswell, J. E., and Robertson, A. W., 1994: Discrimination by pollen-collecting bumblebees among differentially rewarding flowers of an alpine wildflower *Campanula rotundifolia* (Campanulaceae). *Oikos*, 69: 304–308.
- Darwin, C., 1877: *The Different Forms of Flowers on Plants of the Same Species*. New York: Appleton and Co., 276 pp.
- Euroala, S., 1972: Germination of seeds collected in Spitsbergen. *Annales Botanici Fennici*, 9: 149–159.
- Fægri, K., and van der Pijl, L., 1979: *The Principles of Pollination Ecology*. Third edition. Oxford: Pergamon Press, 244 pp.
- Frankel, R., and Galun, E., 1977: *Pollination Mechanisms, Reproduction and Plant Breeding*. Berlin: Springer-Verlag, 281 pp.
- Hickey, M., and King, C., 1988: *100 Families of Flowering Plants*. Second edition. Cambridge: Cambridge University Press, 619 pp.
- Holsinger, K. E., 1992: Ecological models of plant mating systems and the evolutionary stability of mixed mating systems. In Wyatt, R. (ed.), *Ecology and Evolution of Plant Reproduction*. New York: Chapman and Hall, 169–191.
- Holsinger, K. E., 2000: Reproductive systems and evolution in vascular plants. *Proceedings of the National Academy of Sciences of the United States*, 97: 7037–7042.
- Hultén, E., 1941–1950: *Flora of Alaska and Yukon*. Lund: Lunds University Arsskrift, vols. 1–10, 1902 pp.
- Hultén, E., and Fries, E., 1986: *Atlas of North European Vascular Plants North of the Tropic of Cancer I–III*. Königstein: Koeltz Scientific Books.

- Jain, S. K., 1976: The evolution of inbreeding in plants. *Annual Review of Ecology and Systematics*, 7: 469–495.
- Kozuharova, E., 2000: Pollination ecology of some rare and endemic plant species in Pirin Mts.—SW Bulgaria. In Ozhatay, N. (ed.), *Plants of the Balkan Peninsula: Into the Next Millennium*, vol. 1. The Proceedings of the 2nd Balkan Botanical Congress held at Istanbul, Turkey, 14–18 May 2000.
- Kristinsson, H., 1986: *Plöntuhandbókin*. Reykjavík: Örn og Örlygur, 304 pp.
- Kristinsson, H., 2005: *Flóra Íslands*, website with distribution maps of the Icelandic flora. Náttúrufræðistofnun Íslands (<http://www.ni.is/flora>).
- Leplar, C. G., 2002: *Æxlunarkerfi, útlits- og erfðabreytileiki gullbrár (Saxifraga hirculus) og svörun vid loftslagsbreytingum* [e. Breeding system, morphological- and genetic variability of *Saxifraga hirculus*]. M.Sc. thesis. Institute of Biology, University of Iceland, Reykjavík, 111 pp.
- Lindman, C. A. M., 1887: Blüten und Bestäubungseinrichtung im skandinavischen Hochgebirge. *Botanische Centralblatt*, 30: 156–160.
- Lord, E. M., 1981: Cleistogamy: a tool for the study of floral morphogenesis, function and evolution. *The Botanical Review*, 47: 421–449.
- Lu, Y., 2002: Why is cleistogamy a selected reproductive strategy in *Impatiens capensis* (Balsaminaceae)? *Biological Journal of the Linnean Society*, 74: 543–553.
- Mallick, S. A., 2001: Facultative dichogamy and reproductive assurance in partially protandrous plants. *Oikos*, 95: 533–536.
- Meier, C., and Holderegger, R., 1998: Breeding system, germination and phenotypic differences among populations of *Saxifraga aizoides* (Saxifragaceae) at the periphery of its alpine distribution. *Nordic Journal of Botany*, 18: 681–688.
- Molau, U., 1993: Relationships between flowering phenology and life history strategies in tundra plants. *Arctic and Alpine Research*, 25: 391–402.
- Murray, D. F., 1987: Breeding systems in the vascular flora of Arctic North America. In Urbanska, K. M. (ed.), *Differentiation Patterns in Higher Plants*. New York: Academic Press, 239–262.
- Murray, D. F., 1995: Causes of arctic plant diversity: origin and evolution. In Chapin, F. S., and Körner, C. (eds.), *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Heidelberg: Springer, 21–31.
- Nielsen, N., Humlum, O., and Hansen, B. U., 2001: Meteorological observations in 2000 at the Arctic Station, Qeqertarsuaq (69°15'N), central West Greenland. *Danish Journal of Geography*, 101: 155–157.
- Nyman, Y., 1993: *Biosystematics and Reproductive Strategies in Campanula (Campanulaceae)*. Ph.D. thesis. Department of Systematic Botany, University of Göteborg.
- Philipp, M., Böcher, J., Mattsson, O., and Woodell, S. R. J., 1990: A quantitative approach to the sexual reproductive biology and population structure in some arctic flowering plants: *Dryas integrifolia*, *Silene acaulis* and *Ranunculus nivalis*. *Meddelelser om Grønland. Bioscience*, 34: 60 pp.
- Plitmann, U., 1995: Distribution of dimorphic flowers as related to other elements of the reproductive strategy. *Plant Species Biology*, 10: 53–60.
- Richardson, T. E., and Stephenson, A. G., 1989: Pollen removal and pollen deposition affect the duration of the staminate and pistillate phases in *Campanula ranunculoides*. *American Journal of Botany*, 76: 532–538.
- Rønning, O. I., 1996: *The Flora of Svalbard*. Oslo: Norsk Polar-institutt, Polarhåndbog no. 10: 184 pp.
- SAS Institute, 1989: *SAS/STAT User's Guide*. Version 6, fourth edition. Cary, North Carolina: SAS Institute, Inc.
- Savile, D. B. O., 1972: *Arctic Adaptations in Plants*. Ottawa: Canada Department of Agriculture, Research Branch, Monograph no. 6: 81 pp.
- Schoen, D. J., Morgan, M. T., and Bataillon, T., 1997: How does self-pollination evolve? Inferences from floral ecology and molecular genetic variation. In Silvertown, J., Franco, M., Harper, J. L. (eds.), *Plant Life Histories: Ecology Phylogeny and Evolution*. Cambridge: Cambridge University Press, 77–102.
- Shetler, S., 1979: Pollen-collecting hairs of *Campanula* (Campanulaceae). I. Historical review. *Taxon*, 28: 205–215.
- Silvertown, J., and Charlesworth, D., 2001: *Introduction to Plant Population Biology*. Fourth edition. Oxford: Blackwell Science, 347 pp.
- Sørensen, T., 1941: Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland*, 125: 1–305.
- SYSTAT for Windows, 1999: *Systat 9.0*. Chicago: SPSS Inc.
- Thórhallsdóttir, Th. E., 1998: Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia*, 114: 43–49.
- Totland, Ø., 1993: Pollination in alpine Norway: flowering phenology, insect visitors, and visitation rates in two plant communities. *Canadian Journal of Botany*, 71: 1072–1079.
- Wallacer, J. M., and Hobbs, P. V., 1977: *Atmospheric Science (an introduction survey)*. California: Academic Press Inc., 467 pp.
- Warming, E., 1886: Om Bygningen og den formodede bestøvningssmaade of nogle grønlandske Blomster. *Oversigt over det Konglige Danske Vidensk. Forhandling*. Copenhagen, 152 pp.
- Zar, J. H., 1999: *Biostatistical analysis*. Fourth edition. Upper Saddle River, New Jersey: Prentice Hall, 663 pp.

Ms accepted August 2005