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Breeding System, Insect Flower Visitation, and Floral Traits of Two Alpine *Cerastium* Species in Norway

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Abstract

Many alpine/arctic flowering plant species have presumably evolved the ability to self-pollinate as a reproductive assurance mechanism under harsh abiotic environmental conditions that restrict insect flower visitation. We compared self-pollination, pollen limitation, insect flower visitation, and dichogamy of low- and high-elevation populations of *Cerastium alpinum*, a species in established alpine communities, and *Cerastium cerastoides*, a pioneer species in disturbed habitats. *Cerastium alpinum* has large showy flowers, while *C. cerastoides* has smaller and paler flowers. The temporal separation of pollen release and stigma receptivity within a flower (dichogamy) was smallest in *C. cerastoides*, which was also more highly self-compatible. No pollen limitation on seed set occurred in any species, possibly due to their high selfing ability. Despite a substantially higher pollinator visitation to *C. alpinum* compared to *C. cerastoides*, the latter had the higher seed set. Pollen limitation, autogamy, and pollinator visitation did not differ between altitudes for either species. Differences in habitat and flower size, color, and development between the species are consistent with their different selfing ability.

Introduction

The evolution of self-pollination (autogamy) and the ability to self-fertilize (self-compatibility) are proposed to be adaptations that insure reproductive success under conditions of chronically low or temporarily unreliable cross-pollination (the reproductive assurance hypothesis) (Hagerup, 1951; Baker, 1955; Lloyd, 1992; Lloyd and Schoen, 1992). Insufficient cross-pollination appears to be common in flowering plants. In a literature review, Burd (1994) found that female reproductive success was limited by low pollen availability in 62% of species or populations examined, in at least some years. In another analysis, Larson and Barrett (2000) found that pollen limitation was less intense in self-compatible and autogamous species, compared to obligate outcrossing species. This finding supports the reproductive assurance hypothesis.

Low temperatures and short snow-free periods, which constrain the abundance and flight activity of insect pollinators (McCall and Primack, 1992; Totland, 1994), characterize arctic and alpine habitats. Thus, a relatively high proportion of arctic and alpine flowering plant species may have evolved autogamy and self-compatibility in response to poor cross-pollination opportunities. In an extensive review, Molau (1993) suggests that self-compatibility is very widespread among tundra plants. He also found that species growing in late-thawing habitats, such as snow beds, were more self-compatible than species in earlier emerging habitats. Self-compatibility should be accompanied by evolutionary adjustments of morphological or phenological traits of flowers that enhance self-pollination (Lloyd and Schoen, 1992). For example, the physical distance between stigma and anthers (herkogamy) is usually lower in highly autogamous phenotypes or taxa than in predominately outcrossing ones (Lloyd and Schoen, 1992; Takebayashi and Delph, 2000). Moreover, the temporal separation between anther pollen release and stigma receptivity (dichogamy) should also decrease with increasing autogamy (Bertin and Newman, 1993). However, to our knowledge few studies have actually documented a relationship between dichogamy and selfing rate at the among-population or among-species levels. Such studies could show that selection has favored traits that enhance self-pollination ability. If autogamous

pollination is an adaptation to insufficient pollinator service, there should be differences in the ability to self-pollinate between species or conspecific populations experiencing different pollinator visitation rates. However, few comparative studies at the species or population level on the relationships between pollinator visitation rates, pollen limitation, and selfing ability have been conducted to explicitly test this hypothesis.

Here we examine the relationships between flower visitation rates by insects, selfing ability, pollen limitation and dichogamy in two alpine *Cerastium* species that differ in flower size, flower coloration, and habitat. *Cerastium alpinum* has large and bright white flowers and grows in dry meadows and rock outcrops, while *C. cerastoides* have smaller and paler flowers, and grows in late-melting wet snowbeds. On the basis of these differences between the species, we predicted that *C. cerastoides* should be visited less frequently by insects, possess decreased dichogamy, be less pollen limited, and be more autogamous compared to *C. alpinum*. Specifically we ask: (1) if pollen limitation, autogamy, and selfing ability differs between the species, (2) if pollinator visitation rates differ between the species and between low- and high-altitude populations of each species, and (3) if dichogamy differs between the species.

Study Species

Cerastium alpinum L. is an insect-pollinated, perennial mat-forming herb. The hermaphroditic, five-petaled, actinomorphic flowers are bright white, and are ca. 20 mm in diameter (Clapham et al., 1987). Flowers are visited by several species of Muscidae, Anthomyiidae, and Empididae (Totland, 1993). Flowering is initiated relatively late after snow melt, around mid-July (Totland, 1993). It grows in a range of habitats, but it is most common in dry, south-facing slopes on rock outcrops or in dry meadow areas with a stable vegetation cover where snow melts early in the season. There is a large amount of intraspecific morphological variation within the *C. alpinum* complex (Grundt et al., 2000). Based on habitat type and hairiness, the plants in this study probably belong to *C. alpinum* spp. *alpinum*.

Cerastium cerastoides (L.) Britton is a perennial herb with many-branched, creeping stems. The hermaphroditic, five-petaled actinomorphic flowers are dull white, and are ca. 10 mm in diameter (Clapman et al., 1987). Flowers are visited by the same insects as *C. alpinum* (Ø. Totland, personal observation). Flowering is initiated relatively late in the season, around late July to early August. *Cerastium cerastoides* typically grows in moist snowbeds with a discontinuous vegetation cover. The two species have very similar distribution patterns in Europe (Jalas and Suominen, 1983). The two species have nearly identical number of ovules per flower (*C. alpinum*: mean = 45.7 ovules/flower, $SD = 5.8$, $N = 71$; *C. cerastoides*: mean = 45.5, $SD = 12.5$, $N = 71$). In both species, anthers are arranged in a whorl around, and at about the same height as, the styles.

Study Sites and Methods

STUDY SITES

The study sites were situated at Finse, Hardangervidda, southwest Norway (60°36'N, 7°30'E). We selected one low and one high-altitude population of each species. The low-altitude *C. alpinum* population was situated on a south exposed slope with early snow melt and low soil moisture, ca. 100 m southeast of the Alpine Research Center at Finse, at ca. 1200 m altitude. The low-altitude *C. cerastoides* site was on the south facing slope of Mount Kvannjølnuten in a flat meadow with medium time of snow melt (late June to early July) and high soil moisture, ca. 400 m east of Torbjørnstølen, at ca. 1220 m elevation.

The *C. alpinum* population at high altitude was on a large, wind-exposed ridge with early snowmelt and low soil moisture on the southwest-facing slope of Mount Sandalsnuten, at ca. 1520 m altitude. The high-altitude *C. cerastoides* population was on a flat area with late snow melt and regular disturbance by an adjacent river in a large snow bed between Mount Sandalsnuten and Mount Jomfrunuten at ca. 1420 m altitude. The sites at the two altitudes used for the same species are ca. 2.5 km apart and differ greatly in abiotic environmental conditions, such as ambient temperature, wind exposure, and snowmelt time. The plants of the same species used for the first and second period of the flowering season at the high altitude were intermingled in the same area.

FIELDWORK

Fieldwork was conducted from 11 July to 5 September 2000. At each study site and at each period, we selected 48 to 72 flowers (on separate individuals) of both species and randomly assigned each flower to one of four treatments: control, bagged, and manually self-pollinated by hand, and open and supplementary cross-pollinated by hand. To assess spontaneous self-pollination of the two species we bagged (mesh width ca. 2×2 mm) flowers in the bud stage to prevent insect visitation, and compared their seed set with that of simultaneously flowering naturally pollinated control flower. To examine the ability of the two species to produce seed after self-pollination, we bagged flowers and self-pollinated them by hand on one to three occasions, depending on the rapidity of the floral development. Hand pollinations were done when stigmas appeared receptive for pollen. We removed the bags immediately after the flowers had withered. To assess if seed set of individual flowers was limited by pollen availability, we supplementary hand cross-pollinated unbagged flowers with pollen from donor plants situated ca. 1 to 50 m away on one to three occasions, depending on the rapidity of the floral development. Hand-pollination was accomplished by picking pollen-laden anthers with forceps from donor flowers and gently brushing the anthers across the stigmas of recipient flowers. All experimental flowers were marked when still in their bud stage. On five occasions small insects had

entered bags at the low-altitude *C. alpinum* population. These were removed immediately after being discovered, but the flowers were included in the statistical analyses.

At the low altitude, we initiated the experiment on 11 and 12 July on *C. alpinum* and *C. cerastoides*, respectively. The early-flowering group of *C. alpinum* at high altitude was initiated on 12 and 13 July, and the late-flowering group at 20 and 21 July. The early-flowering group of *C. cerastoides* at high altitude was initiated on 22 and 23 July, and the late-flowering group at 10 August. To ensure counting the complete seed number, we collected capsules for each population and period on the same day (ca. three weeks after flowering), irrespectively of their developmental stage. Unfortunately, some fruits were lost or destroyed during the experiment, probably due to strong winds and grazing animals. We counted developing seeds and undeveloped ovules within each capsule, and calculated seed to ovule ratio (s:o) of each flower as the ratio of seed number to total ovule number per flower.

We measured the insect flower visitation rate for each population and period, except for *C. cerastoides* at the low altitude and late-flowering *C. cerastoides* at the high altitude. On days with weather conditions that allowed insect flight activity, 9 to 30 flowers were observed repeatedly for 10-min periods (490 min in total) during the flowering period of the experimental plants. We counted every visit to the observed flowers by all insects. A flower visit was defined to occur when the insect landed on a flower. Visitation rate is expressed as the number of visits per flower during 10 min.

For each species, altitude, and period we observed 10 naturally pollinated, unmanipulated flowers every 1 to 3 d and described their floral development by the following five stages: A) flower closed, B) flower nearly open (the petals developed and started opening), C) flower open, but stigmas not receptive for pollen (stigmas bent down on the ovary in *C. alpinum*, or stuck together in one column in *C. cerastoides*, and the outer stamens shorter than the inner which have open anthers), D) flower open and stigmas receptive (the stigmas deployed and all stamens of more or less the same length and all anthers open), and E) flowers withered and stigmas not receptive.

STATISTICAL ANALYSES

SPSS, version 10.1, was used for all statistical analyses. We used three-factor ANOVAs to examine the effect of the three treatments on s:o of the two species. These models included the treatment, species, and an altitude-period factor as fixed factors. Separate ANOVAs were done for each of the three treatments, such that the treatment factor consisted of two levels (control vs. supplemental pollination; control vs. pollinator exclusion; control vs. pollinator exclusion and manual self-pollination). The altitude/flowering period factor consisted of the three levels: low altitude; high altitude and early season; high altitude and late season. This factor was also treated as fixed because we deliberately selected sites and flowering seasons that represented contrasting environmental conditions. The dependent variable, s:o, was arcsine-square root transformed prior to analyses.

We used *t*-tests to examine if visitation rates to flowers during 10-min periods differed between the two species, between altitudes, and between plants flowering at different times in the season. We were unable to quantify visitation rates for all combinations of species, elevation and flowering period, partly because of inappropriate weather conditions for pollinator activity. Therefore, to examine differences between the two species, we compared the visitation rate of late-flowering *C. alpinum* at high altitude with early-flowering *C. cerastoides* at high altitude. These two groups flowered simultaneously (see above). To contrast visitation rates at low and high altitude, we compared early-flowering *C. alpinum* at low altitude with early-flowering *C. alpinum* at high altitude. These two groups flowered

simultaneously (see above). To compare early- and late-flowering plants we compared visitation rates of early-flowering *C. alpinum* at high altitude with late-flowering *C. alpinum* at high altitude.

To assess if the degree of protandry differs between the species we used a contingency test on the frequency of cases where the duration of the pre female stage (stage C above) was shorter, equal, or longer relative to the duration of the female stage (stage D above) of the flower. Unfortunately, sample sizes were too small (some markers were lost, some marked flowers did not develop, and some flowers developed too fast for us to determine duration of the five stages accurately) for us to contrast the two altitudes and the early- and late-flowering periods for each species. Therefore, because examination of the original data indicated that floral development was similar at the two altitudes and the two periods for both of the species, we pooled data from both altitudes and periods for the two species and contrasted only the two species.

Results

POLLINATION EXPERIMENTS

Supplemental hand pollination slightly increased s:o of both *Cerastium* species at all sites (Fig. 1). However, three-factor ANOVA showed that the supplemental pollination treatment had no significant effect on the s:o of either species, as revealed by an insignificant treatment effect and an insignificant treatment by species effect (Table 1). In addition, there was no treatment by site effect, or three-way interaction effect, showing that the general lack of a treatment effect of supplemental pollination on s:o was consistent across contrasting environmental conditions.

Pollinator exclusion had a negative effect on s:o at all sites for *C. alpinum* and at two sites for *C. cerastoides* (Fig. 1). Overall, pollinator exclusion reduced s:o by 46 % in *C. alpinum*, and by 27 % in *C. cerastoides*. Three-factor ANOVA showed that pollinator exclusion had a significant negative effect on s:o, and a non-significant treatment by species interaction revealed that the negative treatment effect was similar for both species (Table 1). The nonsignificant three-way interaction showed that the treatment effect was consistent across contrasting environmental conditions.

Caging and manual self-pollination reduced s:o of *C. alpinum* by an average of 38 % whereas the same treatment increased s:o of *C. cerastoides* by 11% (Fig. 1). This variable effect of manual selfing resulted in a nonsignificant overall treatment effect, but a significant treatment by species interaction in a three-factor ANOVA (Table 1). None of the other interactions were significant, showing that this interaction effect between species and treatment was consistent across contrasting environmental factors (Table 1).

FLOWER VISITATION RATES

Visitation rates to flowers were about five times higher to high-altitude *C. alpinum* than to simultaneously flowering high-altitude *C. cerastoides* (*C. alpinum*: mean = 0.73 visits per flower during 10 min, $SE = 0.14$, $N = 12$; *C. cerastoides*: mean = 0.14 visits per flower during 10 min, $SE = 0.03$, $N = 12$), a highly significant difference ($t = 4.48$, $P = 0.0001$). There was no significant difference in visitation rate to the low and high altitude *C. alpinum* populations (low altitude: mean = 0.74 visits per flower during 10 min, $SE = 0.15$, $N = 13$; high altitude: mean = 0.60 visits per flower during 10 min, $SE = 0.18$, $N = 12$, $t = 0.59$, $P = 0.56$). In addition, no significant difference in visitation rate was found between early- and late-flowering *C. alpinum* at the high altitude (early-flowering: mean = 0.60 visits per flower during 10 min, $SE = 0.18$, $N = 12$; late flowering: mean = 0.74 visits per flower during 10 min, $SE = 0.13$, $N = 12$, $t = 0.63$, $P = 0.54$). Although we were not

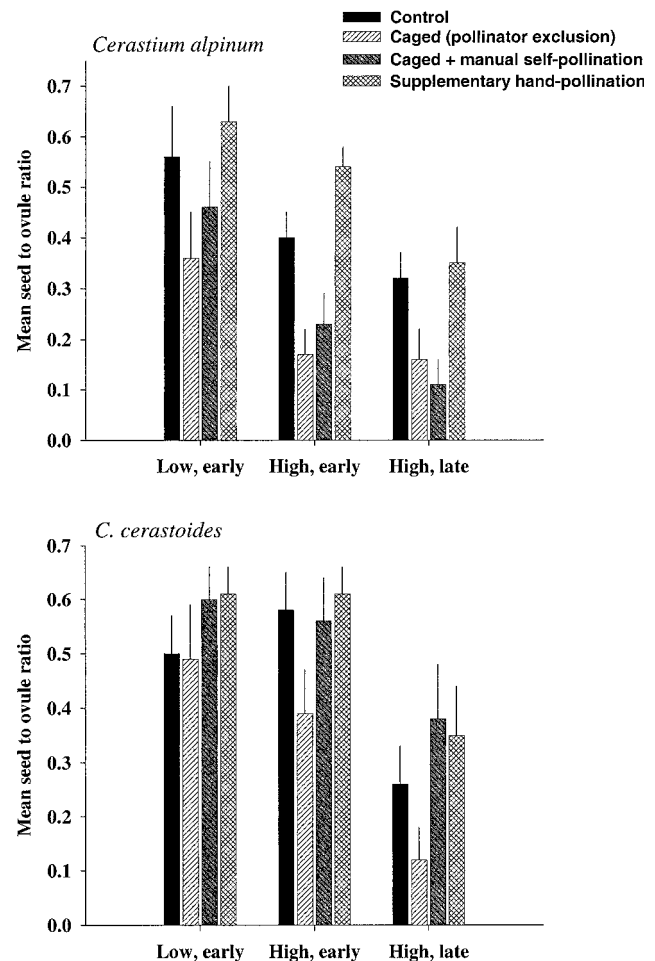


FIGURE 1. Mean seed to ovule ratio of *Cerastium alpinum* and *Cerastium cerastoides* in an experiment with control flowers (untreated), bagged flowers (insect visitation excluded), bagged flowers with manual self-pollination, and supplementary cross-pollinated unbagged flowers at two altitudes (high and low) and at two periods (early and late) at the high altitude. Vertical lines above bars are standard errors. Sample sizes for each bar range from 9 to 15 flowers.

able to identify flower visitors to species level, it is our impression that flowers of both species, at both altitudes, and at both periods were visited by the same dipteran families: Empididae, Muscidae, and Anthomyiidae.

FLOWER DEVELOPMENT

Nineteen percent of examined *C. alpinum* flowers and 6% of *C. cerastoides* flowers had longer male stage than male-female stage. Fifty percent and 19% of *C. alpinum* and *C. cerastoides* flowers, respectively, had an equal duration of the male and the male-female stages. Thirty-one percent and 75% of *C. alpinum* and *C. cerastoides* flowers, respectively, had a shorter male stage than male-female. A chi-square test on these proportions showed a significant difference between the two species in distribution across flower development stages (chisquare = 7.78, $P = 0.02$) showing that protandry, and thus dichogamy, is more pronounced in *C. alpinum* than in *C. cerastoides*.

Discussion

DIFFERENCES IN BREEDING SYSTEM BETWEEN SPECIES

Although pollinator exclusion showed that both *Cerastium* species were self-compatible, their reproductive success after selfing

TABLE 1

Three-factor fixed model ANOVAs on the effects of pollination treatments (supplemental pollination, pollinator exclusion, and manual self-pollination combined with pollinator exclusion), species (*Cerastium alpinum*, *C. cerastoides*) and site/flowering period on the seed to ovule ratio (arcsine-square root transformed) of two species at Finse in 2000. SS (III) = type III sums of squares, df = degree of freedom, MS = mean squares, F = F-ratio, P = significance level

Source	SS (III)	df	MS	F	P
Supplemental pollination ($R^2 = 0.87$)					
Treatment	0.011	1	0.011	0.13	0.72
Species	0.001	1	0.001	0.01	0.93
Site/period	1.994	2	0.997	11.39	0.00003
Treatment × Species	0.006	1	0.006	0.07	0.80
Treatment × Site/period	0.188	2	0.094	1.07	0.35
Species × Site/period	0.374	2	0.187	2.13	0.12
Treatment × Species × Site/period	0.039	2	0.019	0.22	0.80
Error	11.557	132	0.088		
Pollinator exclusion ($R^2 = 0.80$)					
Treatment	1.883	1	1.883	18.37	0.00003
Species	0.157	1	0.157	1.54	0.22
Site/period	2.830	2	1.415	13.80	0.000003
Treatment × Species	0.085	1	0.085	0.83	0.36
Treatment × Site/period	0.150	2	0.075	0.73	0.48
Species × Site/period	0.759	2	0.379	3.70	0.027
Treatment × Species × Site/period	0.044	2	0.022	0.21	0.81
Error	14.145	138	0.102		
Manual self-pollination and pollinator exclusion ($R^2 = 0.84$)					
Treatment	0.199	1	0.199	2.07	0.15
Species	1.016	1	1.016	10.57	0.001
Site/period	2.674	2	1.337	13.92	0.000003
Treatment × Species	0.818	1	0.818	8.51	0.004
Treatment × Site/period	0.123	2	0.062	0.64	0.53
Species × Site/period	0.401	2	0.201	2.09	0.13
Treatment × Species × Site/period	0.177	2	0.088	0.92	0.40
Error	12.873	134	0.096		

differed considerably. The most obvious difference occurred in response to the pollinator exclusion combined with manual self-pollination treatment which significantly reduced s:o of *C. alpinum*, whereas s:o of *C. cerastoides* was unaffected or slightly increased. This result clearly demonstrates that *C. cerastoides* is more self-compatible than *C. alpinum*. This may suggest that selfing resulted in inbreeding depression that reduced seed set in *C. alpinum*, whereas in *C. cerastoides* no effect of inbreeding depression on seed set is indicated. It is possible that populations of the pioneer *C. cerastoides* historically have experienced higher amounts of selfing than populations of *C. alpinum*. As a pioneer species, *C. cerastoides* may frequently experience biparental inbreeding, due to substantially reduced population sizes (bottlenecks) during colonization events. Higher selfing rate in *C. cerastoides* may have more completely purged deleterious recessive alleles, thereby reducing genetic load and negative effects of selfing in this species (Lande and Schemske, 1985; Charlesworth and Charlesworth, 1990; Parker et al., 1995; Husband and Schemske, 1996; Byers and Waller, 1999). It is also possible that prezygotic selfing barriers (e.g., Waser and Price, 1993; Manicacci and Barrett, 1996; Dorken and Husband, 1999) exists to a larger extent in *C. alpinum* than in *C. cerastoides*, and that this may contribute to explain the difference found in self-compatibility between the species.

The ability to self-pollinate (autodeposition efficiency, cf. Molau, 1993) did presumably not differ significantly between the two species, as shown by the nonsignificant interaction term between the pollinator exclusion treatment and species. This lack of a clear difference in the autodeposition efficiency between the species is surprising given the differences in the degree of dichogamy (the temporal separation of timing of pollen release and stigma receptivity: Fægri and van der Pijl,

1979; Bertin and Newman, 1993), which was significantly less in *C. cerastoides* than in *C. alpinum*. Thus, our results may indicate that dichogamy does not always accelerate the selfing rate by autodeposition. A few studies have found a relationship between dichogamy and self-pollination in comparisons of species, conspecific populations, or individuals of the same population (Schoen, 1982; Holtsford and Ellstrand, 1992; Bertin and Newman, 1993; Brunet and Eckert, 1998). Because of the smaller flower size of *C. cerastoides* compared to *C. alpinum*, the difference in dichogamy between the species is also associated with differences in herkogamy (spatial separation of anther and stigma) between the two species. Thus, both reduced herkogamy and reduced dichogamy could have facilitated autodeposition to a greater extent in *C. cerastoides* than in *C. alpinum*, but apparently this was not the case. It is possible that the relatively small temporal overlap in pollen dispersal and stigma receptivity in *C. alpinum* is nevertheless sufficiently high to explain the similar autodeposition efficiency in the two species. Autodeposition efficiencies of *C. alpinum* at Finse (range from 42 to 64%) were substantially higher than those found by Grundt et al. (1999) in populations at lower altitudes in Norway (range from 30–34%).

Supplemental cross-pollination did not significantly increase s:o in any species, sites, or periods, showing that s:o in the two *Cerastium* species was not constrained by the availability of cross pollen. This occurred despite the fact that we only pollinated one flower per plant, and thus maximized the opportunity to detect pollen limitation if it occurred (Zimmerman and Pyke, 1988). In an extensive literature survey, Larson and Barrett (2000) found that pollen limitation was lower in self-compatible and autogamous species than in self-incompatible and nonautogamous species. Thus, our results are

consistent with their findings (see also Burd, 1994), and suggest that a high self-pollination ability is a reproductive assurance mechanism because it makes seed set largely independent of pollinator activity. Some studies show that pollinator activity in alpine and arctic habitats constrains seed set through reduced pollen availability (Galen, 1985; Stenström and Molau, 1992; Miller et al., 1994; Totland, 1997, 2001). Our results show that this may not be universally true, at least not in the case of highly autogamous species. It is noteworthy that, although self-compatibility differed significantly between the *Cerastium* species, the s:o of both was not detectably limited by cross-pollen availability. Probably the substantially higher flower visitation rate to *C. alpinum* compared to *C. cerastoides* explains this result. Thus, even the modest level of autogamy in *C. alpinum*, combined with relatively high pollinator visitation, probably results in the deposition of enough pollen for the fertilization of all the ovules that an individual can provision.

Our results indicate that both *Cerastium* species have a mixed mating strategy since both species are self-compatible and autogamous. Mixed mating strategies within the flowering plants appear to be more common than previously thought (Vogler and Kalisz, 2001), and may be favored under conditions where pollinator population abundances and flower visitation rates are highly variable. Such pollinator unpredictability could select for the capacity for a combination of both self- and outcross pollination.

DIFFERENCES IN BREEDING SYSTEM BETWEEN ALTITUDES AND FLOWERING PERIODS

None of the two-way or three-way interactions involving the treatment and the site-flowering period factor were significant, showing that treatment effects for both species were consistent across the sites/flowering seasons that we used. The few other studies that have compared the autogamy rate of populations along elevation gradients have provided equivocal results; some have detected differences (Hessing, 1989; Schoen and Brown, 1991; Hill et al., 1992; Eriksen et al., 1993; Utelli and Roy, 2000) whereas others have not (Sobrevila, 1989; Gugerli, 1998). There may be several reasons for the lack of differences between altitudes for the two species examined here. First, we only analyzed autogamy, selfing rate, and pollen limitation during one single season, and it is possible that differences in treatment responses would occur in other seasons with different environmental or pollination conditions. Second, to our surprise, the results indicated that flower visitation rates did not differ between the altitudes or between flowering periods in the examined season. Such differences have been found previously in our study area (Totland, 1993, 2001). With equal flower visitation rates at the two altitudes and flowering periods, it is unlikely that any differences in autogamous seed production would emerge, unless there are differences between the populations at different altitudes or between plants flowering at different periods within a season, in traits that promote selfing, such as dichogamy or herkogamy. However, because of gene flow through seed and pollen, such differentiation in floral traits may be unlikely between populations situated so close (ca 2.5 km apart and with several populations in between) or between plants of the same population that flower at different times. Third, similar selection pressures operating on the breeding system, together with gene flow between populations at different altitudes, may prevent local genetic differentiation of the breeding system.

The differences in flower phenology and morphology, and selfing ability between the species may represent adaptive suites of traits to contrasting environmental conditions. However, since the two species are likely distantly related within the genus it is also possible that the differences are simply due to phylogenetic constraints. More data on how natural selection operates on floral traits are needed for a more

complete understanding of the evolutionary history of these two arctic/alpine *Cerastium* species.

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