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Facultative apomixis and hybridization in arctic *Potentilla* section *Niveae* (Rosaceae) from Svalbard

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The degree of sexual seed set and the ability to cross were investigated in three taxa of *Potentilla* section *Niveae* (*P. chamissonis*, *P. insularis* and *P. nivea*) from the Svalbard Archipelago. Emasculated and bagged flowers had little or no seed set, while 71% of the emasculated, bagged and pollinated flowers had some. The taxa are interpreted as pseudogamous apomicts. Parental plants and offspring were subjected to isozyme analysis. Most of the offspring were clones of the mother plant, but 1.7% had bands from the pollen donor. The sexual offspring were all produced by mother plants of *P. insularis*, which is interpreted as a facultative apomict. Surprisingly, crosses between different taxa gave higher seed to ovule ratios and numbers of sexually produced offspring than crosses within taxa. Some of the sexually produced hybrid offspring had the same kind of hairs on the petioles as their mother taxon, showing that hybrids may not be intermediate in hair characters, which are considered important in the delimitation of these taxa. The results of the present study indicate very close relationships among the investigated plants. © 2003 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2003, **142**, 373–381.

ADDITIONAL KEYWORDS: crossing experiments – isozymes – offspring analysis – pseudogamy – species delimitation.

INTRODUCTION

The subtle intricacies of *Potentilla* section *Niveae* make distinction and classification difficult even for the trained botanist. The complicated taxonomy, including a large number of postulated hybrids (Soják, 1986, 1989; Elven & Elvebakk, 1996), is probably in large part due to the reproductive system. Many *Potentilla* species are known to be facultative apomicts (Asker, 1977; Asker & Jerling, 1992; Eriksen, 1996; Eriksen & Fredrikson, 2000), which means that the offspring are mainly clones of the mother plants, although the plants have the possibility to produce some seeds sexually. The apomicts in *Potentilla* are often known to be pseudogamous, i.e. they depend on pollen to produce endosperm and thereby viable seeds. The proportion of sexually produced offspring seems to vary among species and populations (Eriksen, 1996). Additionally complicating the taxonomy, extensive morphological plasticity obscures boundaries between taxa (Eriksen & Nyléhn, 1999).

The delimitation of taxa and possibilities of hybrid speciation in *Potentilla* within the Svalbard Archipelago have been debated in recent years (Soják, 1986; Elven & Elvebakk, 1996; Eriksen *et al*., 1999; Hamre, 2000; Hansen, Elven & Brochmann, 2000). Three taxa are currently recognized within section *Niveae* in this geographical area: *P. chamissonis* Hultén, *P. insularis* Soják, and *P. nivea* L. ssp. *subquinata* (Lange) Hultén (Hansen *et al*., 2000). These taxa have recently been investigated utilizing morphometry, random amplified polymorphic DNAs (RAPDs) and isozymes (Hamre, 2000; Hansen *et al*., 2000), and found to be closely related. They were not clearly separated by isozymes, but a somewhat better delimitation was provided by RAPDs. A few putative hybrids were found. The mode of reproduction is not known.

Taxa in section *Niveae* have been delimited based on the different kinds of indumentum, particularly the petioles. Eriksen & Yurtsev (1999) studied hair types by scanning electron microscopy (SEM) and classified species according to indumentum traits. They tested putative hypotheses on hybridization, but did not find intermediacy in hair traits. The hereditability and

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genetical basis of the hair types are, however, not known. Eriksen & Yurtsev (1999) concluded accordingly that a study investigating the effect of hybridization on hair types is needed.

Before any conclusions can be drawn concerning the taxonomy of this intricate complex, it is important to have information on the reproductive system. In the present study the mode of seed production in the taxa *P. chamissonis*, *P. insularis* and *P. nivea* ssp. *subquinata* was investigated in order to establish whether they are obligately apomictic, pseudogamous, and/or have the ability to cross within and among taxa. Using SEM, the hair types in offspring produced sexually from crosses between different taxa were analysed, together with their parental plants, to determine whether hybrid origin can be traced by indumentum traits.

MATERIAL AND METHODS

Plant material

Plant material from *P. chamissonis*, *P. insularis*, *P. nivea* ssp. *subquinata*, and *P. crantzii* (Crantz) G.Beck ex Fritsch from section *Aureae*, was collected at Svalbard in 1996 (Table 1). The plants occur in a few places in the warmest parts of Spitsbergen on southfacing cliffs and scree slopes. They are rare and constrained to nutrient-rich soils. *P. nivea* ssp. *subquinata* is referred to henceforth as *P. nivea*.

Section *Niveae* is characterized by a white, woolly indumentum on the lower leaf surfaces. On the petioles, however, mostly long straight verrucose hairs are found in *P. chamissonis* and *P. insularis*, while a thick wool of intermingled floccose (inflated) hairs is found in *P. nivea*. In addition, *P. chamissonis* and *P. nivea* have mainly three leaflets, while *P. insularis* most often has five or, in some cases, more. *Potentilla crantzii* has three or five leaflets, lacks the relatively dense hair cover typical of section *Niveae*, and differs in other characters, e.g. style morphology. Most of the investigated taxa are reported as many-ploid with variable chromosome numbers. *Potentilla nivea* is reported with $2n = 14$, 28, 49, 54–56, 56, 63 and 70, *P. chamissonis* as varying from heptaploid to 11-ploid ($2n = 49$, 56, 77). *Potentilla crantzii* is reported with $2n = 28$, 42, 48, 49, 64, while the number in *P. insularis* is unknown (Lid & Lid, 1994; Hansen *et al*., 2000). The flowers are regular, bisexual and hypogynous with five yellow petals, approximately 20 stamens and numerous carpels. They are adapted for generalist pollinators (Fægri & van der Pijl, 1979), and insect activity is not uncommon (Kevan, 1972; Hansen *et al*., 2000; pers. observ.).

Isozyme analyses

The parental plants were transported from Svalbard to growth chambers at the University of Oslo in August 1996. The cultivation regime was 18 h of daylight, with diurnal/nocturnal temperatures of 14°C/6°C. The plants were vernalized for 3 months in the winter of 1996–97, and started to flower in April 1997.

Table 1. Collection data for populations of *Potentilla* from Svalbard used in the crossing experiments. Collectors: JN – Jorun Nyléhn, RE – Reidar Elven, IN – Inger Nordal, KTH – Kjell Tore Hansen, EH – Elin Hamre, TMG – Tove M. Gabrielsen. All plants were collected during 13–25 July 1996. UTM-coordinates are given

Pop. no.	Taxon	Collection data
7	*P. chamissonis*	Skansen. WH 231 190. JN, IN, KTH
35	*P. chamissonis*	Vestfjorden, Tysneset. WH 16 43. JN, EH, RE, IN.KTH
5	*P. insularis*	Hyperitthatten. WG 242 986. JN, EH, RE, IN, KTH
14	*P. insularis*	Templet, Skiltvakten. WH 360 066. EH, KTH, TMG
15	*P. insularis*	Templet. WH 363 052. EH, KTH, TMG
16	*P. insularis*	Templet. WH 371 047. EH, KTH, TMG
24	*P. insularis*	Gipshuken, above Anservika. WH 312 106. JN, RE
44	*P. insularis*	Kapp Thorsen. WH 135 101. JN, EH, RE, IN, KTH
49	*P. insularis*	Kapp Thorsen. WH 14 11. JN, EH, RE, IN, KTH
4	*P. insularis* & *P. nivea*	Hyperitthatten. WG 242 986. JN, EH, RE, IN, TH
21	*P. nivea*	Odindalen. WH 244 371. EH, RE
40	*P. nivea*	Endalen. Slope close to the road. WG 179 798. RE, IN
41	*P. nivea*	Skjørlokstupet. WG 291 970. JN, EH, KTH
42	*P. nivea*	Kapp Thorsen. WH 135 101. JN, EH, RE, IN, KTH
48	*P. nivea*	Kapp Thorsen. WH 14 11. RE
20	*P. crantzii*	Odindalen. WH 244 371. EH, RE
43	*P. crantzii*	Kapp Thorsen. WH 135 101. JN, EH, RE, IN, KTH

A total of 140 plants was analysed by means of isozyme electrophoresis during October 1996–February 1997 (Hamre, 2000). The laboratory procedures followed Wendel & Weeden (1989). All parental plants were classified according to variation in the enzymes GPI (glucose-6-phosphate isomerase) and TPI (triose-phosphate isomerase) prior to the pollination experiments (Fig. 1). *Potentilla nivea* showed no variation in these enzymes, while *P. chamissonis* varied in GPI, and *P. insularis* in TPI. *Potentilla crantzii* showed no variation in GPI and TPI, but was different from the other taxa in both.

POLLINATION EXPERIMENTS

Pollination experiments were performed in a growth chamber in April–May 1997, seeds were collected in June 1997. In total, 58 flowers were bagged and emasculated: 22 *P. nivea*, 7 *P. chamissonis*, 19 *P. insularis*, nine *P. crantzii*, and one flower from a putative *P. insularis* × *nivea* plant. In addition, 72 flowers were bagged, emasculated and cross pollinated (Table 2). Whole anthers were picked with tweezers and applied to ripe stigmas. Each flower was pollinated on two consecutive days by the same pollen donor. Crosses were performed within and among the taxa in section *Niveae* (*P. insularis*, *P. chamissonis* and *P. nivea*). The number of reiterations in the different combinations of taxa are given in Table 2. When possible, crosses were undertaken between individuals of different genotypes. In addition, *P. crantzii* was used as a pollen donor to investigate the effect of more distantly related pollen. All crosses were independent, i.e. the same parental plants were not crossed more than once, with only one exception. The numbers of seeds and undeveloped ovules were counted and all seeds from flowers with 10 or more seeds were sown in February 1999. The number of germinated seeds was counted, and after 3 months of cultivation all surviving offspring were analysed by means of isozyme electrophoresis in June 1999.

SCANNING ELECTRON MICROSCOPY

The hair types in the offspring displaying bands from the pollen donor were analysed with SEM, together with their parental plants. Pressed leaves were mounted and coated with gold. Pictures were taken of the indumentum on the upper part of the petiole and the lower leaf surface of the end leaflet. Microscopy was performed using a JSM-6400.

RESULTS

POLLINATION TREATMENTS

On average, 69.3 ± 10.3 (SD) ovules were found in *P. nivea* (20 flowers), 64.4 ± 10.6 in *P. chamissonis* (seven flowers), and 80.8 ± 11.1 in *P. insularis* (23 flowers). One flower investigated in the putative *P. insularis* × *nivea* plant had 54 ovules.

Of the 58 bagged and emasculated flowers, most had a seed set of zero, the only exceptions being four flowers of *P. nivea* with between two and nine seeds, one flower of *P. chamissonis* with one seed, and one of *P. insularis* with 15.

Of the 72 flowers that were bagged, emasculated and cross pollinated, two flowers died, 19 had a seed set of zero, and 53 had some seed set (Table 2). Thus there was seed set in 71% of the pollinated flowers, and an average seed to ovule ratio (S:O) of 0.170 was

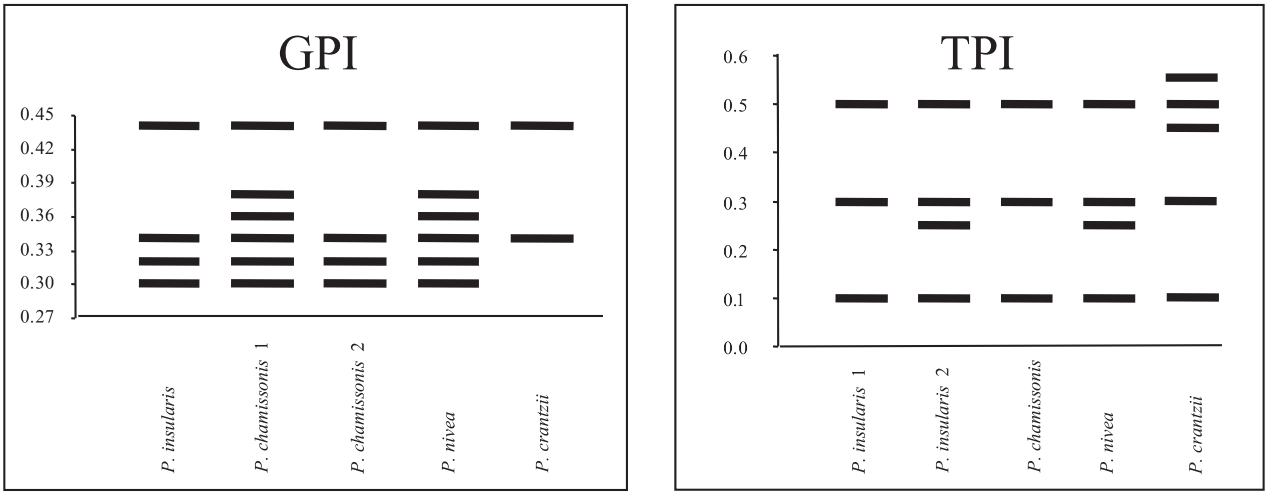


Figure 1. Enzyme patterns in the parental plants in the crossing experiments: *P. chamissonis*, *P. insularis* and *P. nivea* (section *Niveae*) and *P. crantzii* (section *Aureae*). Enzymes GPI and TPI.

Table 2. Crossing experiments: number of crossed flowers in the different combinations of taxa. Proportions of flowers with seed set and average seed to ovule ratios (S:O) are given. The ratios are calculated from the proportion of crosses resulting in seed set, i.e. excluding flowers with zero seed set. Flowers with ten or more seeds were used in the germination experiment. The proportions of seeds germinating and of germinated seeds that survived for 3 months are given. The numbers of crossed flowers and offspring analysed by means of isozymes in the different combinations of taxa are given, together with the number of apomictically and sexually produced offspring. *Columns:* A, Number of crossed flowers; B, Proportion of flowers with seed set; C, Average S:O; D, Proportion of seeds germinating; E, Proportion of offspring surviving 3 months; F, Number of crossed flowers analysed; G, Number of offspring analysed; H, Number of offspring produced with apomixis; I, Number of offspring produced with outcrossing

Mother	Father	A	B	C	D	E	F	G	H	I
chamissonis	*chamissonis*	3	0.667	0.148	0.529	0.556	1	5	5	0
chamissonis	*insularis*	4	0.250	0.016					12	0
chamissonis	*nivea*	4	0.750	0.259	0.203	0.857	1	12		
chamissonis	*crantzii*	2	0.500	0.032					22	0
insularis	*chamissonis*	11	0.636	0.179	0.347	0.523	3	22		
insularis	*insularis*	7	0.714	0.056					88	3
insularis	*nivea*	8	1	0.301	0.666	0.810	6	91	2	0
insularis	*crantzii*	3	1	0.232	0.139	0.333	1	2	13	0
nivea	*chamissonis*	11	0.909	0.115	0.503	0.571	4	13	27	0
nivea	*insularis*	12	0.667	0.157	0.647	0.762	3	27		
nivea	*nivea*	2	0.500	0.070						
nivea	*crantzii*	4	0.250	0.324	0					
niv × *ins*[1]	*chamissonis*	1	1	0.111						

[1] Putative *P. nivea* × *P. insularis* hybrid.

Table 3. The average seed set in crosses within taxa compared with crosses between closely related taxa (CRT) (within section *Niveae*) and more distantly related taxa (DRT) (plants from section *Niveae* pollinated with *P. crantzii*)

	Within taxa	CRT	DRT
Proportion of crosses resulting in seed set	0.667	0.745	0.556
Average S:O	0.081	0.183	0.210
Proportion of seeds germinating	0.529	0.497	0.104
Proportion of offspring surviving 3 months	0.556	0.687	0.333

calculated from the flowers with seed set. The average S:O ratios, germination rates, and proportions of plants surviving for 3 months, were calculated for the different groups of cross pollinations within and among taxa (Tables 2, 3). Table 3 highlights the effect of using more distant pollen. The proportion of flowers with fruit set was highest in the crosses between different taxa within section *Niveae*, lowest when *P. crantzii* was the pollen source. The S:O ratios within fertilized flowers increased slightly as the pollen donor became less related to the mother plant, and were in fact highest in the crosses in which *P. crantzii* was used as pollen donor. They were higher in crosses between different taxa in section *Niveae* than within taxa. Crosses within section *Niveae* gave a higher germination rate and the seeds survived better than those produced with *P. crantzii* as the pollen donor.

ISOZYME VARIATION IN OFFSPRING

In total, 172 offspring survived, and were analysed by means of isozyme electrophoresis (Table 2). Of these, 169 shared banding patterns with the mother plant with no paternal contribution, and were thus produced apomictically. Only three had enzyme bands also from the pollen donor. Thus only 1.7% of the analysed offspring were produced sexually. The analysed offspring from mother plants of *P. chamissonis* and *P. nivea* were all produced apomictically, but 2.7% of the offspring produced by mother plants of *P. insularis* were produced sexually. The cross pollinations that resulted in some sexually produced offspring were: (1) between *P. insularis* from population 24 and *P. nivea* from population 40, and (2) between *P. insularis* from population 44 and *P. nivea* from population 48 (Table 1). Thus the parental plants were from different locations; although populations 44 and 48 were both collected at Kapp Thorsen, they were separated by a distance of 1 km in which the taxa were not found.

All the three offspring in which the father contributed to the genome had *P. insularis* as mother and *P. nivea* as father (Fig. 2). These sexually produced offspring were found in two crosses, both of which resulted in a relatively large number of offspring (27 and 24, respectively; Fig. 3). The number of offspring in the other crosses, where all offspring were found to be clones of the mother plant, ranged from 0 to 16 with a mean of 5.3. The crosses resulting in some sexually produced offspring also differed in germinability and survival: an average of 0.82 seeds germinated and 0.89 plants survived in the crosses resulting in some sexually produced seeds, while an average of 0.40 seeds germinated and 0.53 survived among those germinating from the strictly apomictic crosses.

HAIR TYPES IN OFFSPRING

Hair types in the offspring with bands from the pollen donor were analysed with SEM, together with their parental plants. The indumentum on the upper part of the petiole and the lower leaf surface of the end leaflet was photographed (Fig. 4, Table 4). The offspring from both crosses were mainly similar to the *P. insularis* mother plant in hair characters. The floccose wool on the petiole characteristic of *P. nivea* was lacking in all offspring. In addition, the straight hairs on the lower leaf surface were verruculose in the *P. insularis* mother and in the offspring of cross 1 (Table 4), but verrucose in the *P. nivea* father. However, there was one exception: the hairs in the wool under the leaves of the *P. insularis* mother in cross 2 were only slightly inflated, but both offspring had much more inflated hairs, resembling those of the *P. nivea* father.

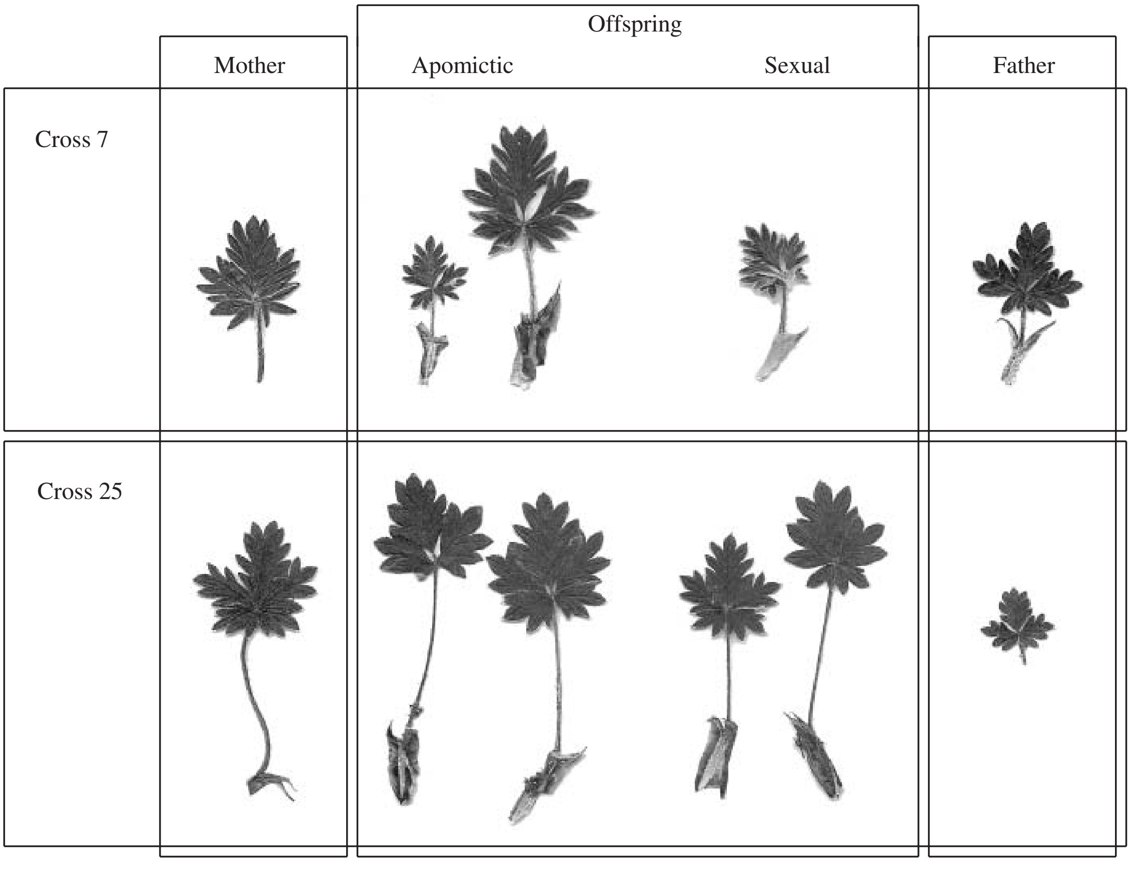


Figure 2. Scanned leaves from the two crosses that resulted in some sexually produced offspring, one leaf from each plant. To the left, *P. insularis* mother plants. To the right, *P. nivea* father plants. Offspring in between, left with *P. insularis* isozyme banding patterns and produced apomictically; right, with added isozyme bands from *the P. nivea* father and thus produced sexually.

DISCUSSION

SEED SET FOLLOWING DIFFERENT POLLINATION TREATMENTS

The seed set in the emasculated and caged flowers was mainly zero, but a few seeds were set in six flowers. This might be due to a slight degree of pollen dehiscence before emasculation. Most of the emasculated flowers with some seed set belonged to *P. nivea*, in which the stamens opened earlier than in the other investigated taxa, before opening of the flowers (pers. observ.).

In total, 71% of the pollinated flowers gave some seed set, with an average S:O ratio of 0.170, and the investigated taxa (*P. chamissonis*, *P. insularis* and *P. nivea*) are interpreted as being dependent on pollen to set seed. Thus the taxa are probably pseudogamous, which is consistent with previous reports on the reproductive biology in *Potentilla* (Müntzing, 1928; Smith,

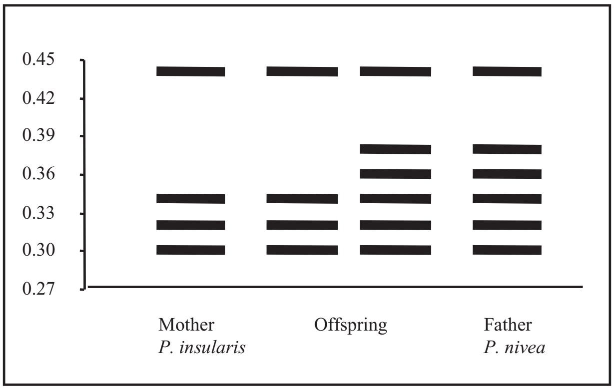
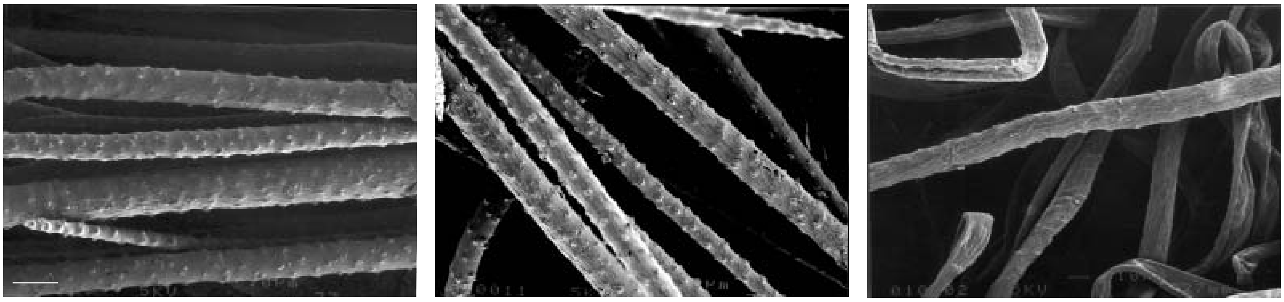


Figure 3. GPI banding patterns in crosses no. 7 and 25. Both had a *P. insularis* mother and a *P. nivea* father, and similar enzyme patterns appeared. One of the 27 offspring in cross no. 7 also had isozyme bands from the father, as did two of the 24 in cross no. 25. The remainder were identical to the *P. insularis* mother plants.


Mother *P. insularis*

Hybrid offspring

Father *P. nivea*

Figure 4. Hair types on the petioles analysed with SEM. Plants from one of the crosses that resulted in sexually produced offspring. Left, the *P. insularis* mother plant. Middle, offspring that received isozyme bands from the pollen donor. Right, the *P. nivea* father. Scale bar = 20 μm.

Table 4. Hair types analysed by SEM. Plants from the two crosses that resulted in sexually produced offspring, the offspring that received isozyme bands from the pollen donor and their parental plants. One of these crosses resulted in one sexually produced offspring, the other in two (the rest were produced apomictically). 'Verrucose' refers to straight hairs with distinct papillae, 'verruculose' to straight hairs with smaller papillae. 'Floccose' refers to intermingled, long, wool-like and more or less inflated hairs

	P. insularis mother	Offspring		*P. nivea* father
Cross 1				
petiole	verrucose	verrucose		verrucose, a few verrucose and floccose
lower leaf surface	verruculose and floccose	verruculose and floccose		verruculose, and floccose
Cross 2				
petiole	verrucose	verrucose	verrucose	verrucose, a few verruculose, and floccose
lower leaf surface	verrucose, a few verruculose, and floccose	verrucose, a few verruculose, and floccose	verrucose, a few verruculose, and floccose	verrucose, a few verruculose, and floccose

1963; Acharya Goswami & Matfield, 1974; Asker, 1977; Asker & Jerling, 1992; Eriksen, 1996; Holm & Ghatnekar, 1996).

Pollen from any of the donor taxa resulted in some seed set, whether from the same taxon, from a closely related taxon (within section *Niveae*) or a more distantly related one (*P. crantzii* from section *Aureae*). Pollination from another taxon in section *Niveae* gave the highest proportion of flowers with seed set, and the lowest was given with *P. crantzii* as pollen donor (Tables 2, 3). The average S:O ratios, however, increased slightly as the relationship between the parents became more distant. Thus the ratio was highest in crosses with *P. crantzii* as pollen donor. Seeds produced with *P. crantzii* as pollen donor had, on the other hand, much lower germination rates than seeds from crosses within section *Niveae*. In addition, offspring from crosses with *P. crantzii* survived to a much lower degree. Although the number of replicates were small, these differences were distinct. Thus the effect of using only *P. crantzii* as pollen donor was negative on offspring production. The possibility of producing some offspring with pollen from a distantly related donor (such as *P. crantzii*) might, however, contribute to increased seed set in natural populations. In the scattered, isolated occurrences of the studied plants the possibility of reproduction in the absence of conspecifics is surely an advantage.

Eriksen (1997) reported ovule number as one of the most significant differences between taxa investigated in section *Niveae* in Alaska. In the present study one of the taxa (*P. insularis*, average of 80.8) had a somewhat higher ovule number than the other two (*P. nivea*, average of 69.3, *P. chamissonis* of 64.4), but the values are much closer to one another than those reported from Alaska (Eriksen, 1997). The plants named *P. nivea* ssp. *subquinata* at Svalbard had almost three times as many ovules as those named *P. nivea* in Alaska. These results might indicate close relationships among the three taxa investigated at Svalbard, and perhaps also that the use of the name *P. nivea* in different arctic regions should be reconsidered, or perhaps that ovule number is not consistent and useful in taxonomic treatments on a larger geographical scale.

SEXUALLY PRODUCED OFFSPRING

Most of the offspring had the same isozyme patterns as their mother plants, except a few produced by *P. insularis*. Thus at least *P. insularis* seems to be a facultative apomict. Fewer offspring were produced and analysed in *P. chamissonis* and *P. nivea* than in *P. insularis*; thus a larger number of analyses might have revealed some sexually produced seeds also in these taxa. Obligate apomixis is generally rare (Asker & Jerling, 1992).

Potentilla insularis had larger flowers than the others investigated; in addition, the stamens opened somewhat later than in *P. chamissonis* and especially *P. nivea*. Thus this taxon seems more adapted to cross pollination than the others (cf. Fægri & van der Pijl, 1979). Furthermore, greater variation in RAPDs (Hansen *et al*., 2000) and isozymes (Hamre, 2000) was found in *P. insularis* than in *P. nivea* and *P. chamissonis*, suggesting that it is more sexual.

A few other studies have reported on the ability to cross in facultative apomictic *Potentilla* species. Eriksen & Nyléhn (1999) reported that 2% of the offspring in crosses between *P. hyparctica* Malte and *P. hookeriana* Lehm. in Alaska were morphologically intermediate between the parents. Holm & Ghatnekar (1996) found that one among 50 (= 2%) of the offspring in crosses between hexaploid *P. argentea* L. plants were produced sexually. Although few in number, these studies are highly consistent.

Both of the experimental pollinations resulting in some sexual seed set had more offspring with better survival than the rest, where only apomictically produced offspring were detectable. It seems clear that some combinations of mother and father plants were more compatible than others. Why, though, were these ‘successful combinations’ found between taxa (*P. insularis* and *P. nivea*) and not within? The relatively low number of replicates might be part of the explanation. However, crossing among taxa in section *Niveae* also had positive effects on the S:O ratios compared to crossing within taxa. Eriksen (1996) reported different ploidy levels within populations of other taxa in section *Niveae* from Alaska, and these are reported from *P. chamissonis* and *P. nivea* (Hansen *et al*., 2000). This might prevent successful crossing within as well as between taxa.

Another line of explanation follows on from the fact that outcrossed seeds are generally more vigorous than selfed (Eriksen, 1996), partly as a consequence of a larger endosperm (Haskell, 1960). Thus the pollen donor might have positive influence on both sexually and apomictically produced offspring. Mazzucato *et al*. (1995) found that the facultative apomict *Poa pratensis* L. tends to outcross when sexually reproducing. The results of the present study indicate that this might also be the case in the investigated *Potentilla* taxa. Outcrossing and apomixis better maintain heterozygosity and genetic variation within individuals than selfing (Marshall & Weir, 1979; Kellogg, 1990). The occurrence of sexual seed set only in the crosses with many surviving offspring might indicate that the plants ‘assure’ some seed set by apomixis, and when pollen of good quality is available, some of the seed set is sexual.

Since the investigated taxa do not, by and large, cooccur at Svalbard, the possibilities for hybridization are small. In addition, manipulation with cross pollen on emasculated flowers differs considerably from natural pollination. However, in one locality two taxa (*P. insularis* and *P. nivea*) were found growing together with a few putative hybrids (Hansen *et al*., 2000). Interestingly, both crosses in the present study resulting in some sexually produced offspring were between a *P. insularis* mother and a *P. nivea* father. Thus hybridization seems to be possible, although rare, in the Svalbard Archipelago.

Hair types in delimitations of taxa

The successful crosses were between parental plants with different hair types. The present study provides data on the heritability of hair types, as advocated by Eriksen & Yurtsev (1999). The three sexually produced offspring had the same hair types as their *P. insularis* mother plants, i.e. they lacked the floccose wool on the petiole characteristic of, and used in the classification of, their *P. nivea* fathers. Although the wool on the lower leaf surface of the offspring in cross 2 (Table 4) resembled that of their *P. nivea* father (their *P. insularis* mother had wool that was only slightly inflated), this observed difference is within the variation otherwise found in *P. insularis* at Svalbard (Hamre, 2000). Following Rieseberg & Ellstrand (1993), hybrids are no more likely to have intermediate traits than to have traits in common with one of their parental plants; thus hybrids might have the same hair types as one of their parental taxa. Eriksen & Yurtsev (1999) concluded that if the postulated hybrid origins of the material they examined were correct, the hereditability of hair types must be complicated and include suppression of hair types in hybrids. This is partly supported by our data.

Eriksen & Yurtsev (1999) proposed a classification of section *Niveae* based on hair morphology. They subdivided the section into three groups; taxa from two of these were investigated in the present study (*P. insularis* and *P. chamissonis* from one, *P. nivea* from another). Despite being proposed as belonging to basically different lineages within section *Niveae*, the investigated taxa seem very closely related, with the same compatibility in crosses between as within taxa. This is supported by molecular data reported by Hansen *et al*. (2000) and Hamre (2000). Thus the results of the present study suggest close relationships generally within the *Niveae* complex. Different indumentum types alone may not be sufficient for proper classification. In addition, leaflet number, which has been regarded an important character in separating taxa and indicating hybridization (cf. Soják, 1986, 1989), has been shown to be unreliable due to morphological plasticity (Eriksen & Nyléhn, 1999). Section *Niveae* is widespread in arctic habitats, and plants in the different arctic regions should be investigated and compared prior to drawing any taxonomic conclusions.

CONCLUSIONS

The investigated taxa in *Potentilla* section *Niveae* were found to be mainly apomictic, although some sexual seed production was found in *P. insularis*. All taxa are probably pseudogamous. Crosses between different taxa in section *Niveae* exhibited higher S:O ratios and produced a greater number of sexually produced offspring, compared with crosses within taxa. Some of the sexually produced offspring had the same kind of hairs on the petiole as their *P. insularis* mother plants, which indicates that hybrids might not be intermediate in hair characters. Hybridization is possible, but is expected to be rare in the Svalbard Archipelago where most populations are isolated and contain only one *Niveae* taxon. The results of the present study indicate very close relationships among the investigated taxa in section *Niveae* at Svalbard.

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