The Purple Saxifrage, *Saxifraga oppositifolia*, in Svalbard: two taxa or one?

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Several studies have demonstrated high levels of genetic (DNA), ecophysiological, ecological, and morphological variation within the species Purple Saxifrage, *Saxifraga oppositifolia*, in Svalbard. It has recently been proposed that *S. oppositifolia* is represented by two conspicuously different subspecies in this archipelago: ssp. *reptans*, a late-flowering, prostrate ecotype of snow-protected, damp habitats, and ssp. *pulvinata*, an early-flowering, cushion-like ecotype of dry, wind-exposed heaths and ridges. It has also been suggested that the subspecies may be differentiated at the tetraploid and diploid levels, respectively, which would promote reproductive isolation. These hypotheses are tested by examining variation in morphology, ecology, and pollen size and stainability in 150 plants of *S. oppositifolia* growing in 50 vegetation samples at four sites in the Kongsfjorden area. Although analyses of the various data sets demonstrated the large variation within the species, the material could not be separated into distinct groups. The morphological variation was continuous along local ecological gradients. The pollen grains were fully stainable and the pollen diameter data showed a unimodal distribution, suggesting that the plants analysed represent only one ploidal level. These results reject a hypothesis that the morphologically intermediate plants are hybrids between two taxa at different ploidal levels. Thus, the conspicuous variation in *S. oppositifolia* in Svalbard probably results from local, in situ ecoclinal differentiation. Although this variation clearly is without taxonomic significance, it is important in the broader context of arctic conservation biology and the potential impact of global warming on arctic vegetation.

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Introduction

It has been shown recently that, although fewer in number than in more southern areas, many arctic plants possess extraordinary high levels of variation. High levels of intraspecific variation in arctic plants have been documented in their ecological traits (McGraw & Antonovics 1983; McGraw 1995a, b), ecophysiology and morphology (Crawford et al. 1993), and molecular genetics (Brochmann et al. 1992a, b, c; Haraldsen & Wesenberg 1993; Nordal & Iversen 1993; Gabrielsen et al. 1995; Hagen et al. 1995; Tollefsrud et al. 1995; Bauert 1996; Brysting et al. in press). For polyploid species, which constitute the majority of arctic floras, use of a wide species concept is often necessary because many such species are composed of races of different hybrid origins that bridge the morphological discontinuities originally found between their diploid progenitors (Brochmann 1992b, 1995a, b). This type of evolution is probably associated with the turbulent climatic history of arctic areas, with repeated glaciations/deglaciations, massive plant migrations, and frequent hybridisation. In diploid arctic species, high levels of variation may be caused by differential selection along gradients in snow cover and duration of the growth season. Such factors vary considerably over short distances in the treeless arctic and alpine areas, and this is probably the main reason for the ecotypic differentiation observed in the arctic diploid *Dryas octopetala* (McGraw & Antonovics 1983; McGraw 1995b).

The high level of intraspecific variation in arctic plants has important implications for arctic conservation biology. It is widely accepted that genetic variation and ecotypic differentiation is necessary for the long-term persistence of a species, which is of particular relevance today with regard to potential global warming (Crawford et al. 1993; McGraw 1995b). It is paradoxical, however, that traditional conservation biology focuses on taxon numbers and rare taxa rather than on the genetic diversity occurring *within* widely defined, widespread taxa, which probably is a better approach to conserving arctic biodiversity.

The Purple Saxifrage, *Saxifraga oppositifolia* L., is a variable species with wide circumpolar distribution, extending also into the higher mountains southwards in Europe, Asia, and North America (Hultén & Fries 1986). It is a long-lived perennial with opposite, small leaves and conspicuous, pink or purple flowers appearing soon after snow-melt. Although this species, in likeness with most other arctic species, is self-compatible, it strongly depends on insect pollination for seed set (Stenström & Molau 1992). The plants grow in a wide range of habitats in the Arctic, including moist snow beds, heaths, dry ridges, and barren, recently unglaciated areas.

The broad morphological variation within the species has been noted by many scientists, and various attempts have been made to split it into several taxa (see e.g., Hayek 1905). The most recent taxonomic treatment of the intraspecific variation in *S. oppositifolia* is that of Webb & Gornall (1989), who closely follow Engler & Irmscher (1919). Webb & Gornall (1989) recognise one widely distributed and morphologically variable subspecies, ssp. *oppositifolia* (the only subspecies they recognise in the European Arctic), four subspecies endemic to the central and southern European mountains, and two additional subspecies occurring in the North American Arctic (and probably across the Beringia into eastern Asia (Hultén & Fries 1986).

The species also varies in chromosome number. Most populations investigated are diploid (2n = 26), but several tetraploid (2n = 52) populations have been reported from arctic areas in Europe, Asia, and North America (Hedberg 1967; Johnson & Packer 1968; Löve & Löve 1975). Two chromosome counts, both tetraploid, have been published for *S. oppositifolia* in Svalbard, one from the Isfjorden area (Flovik 1940) and one from the Ny Ålesund area (Chapman 1995). All studies from the rest of northern Europe have reported a diploid number (e.g., Skovsted 1934; Löve & Löve 1956). To what extent the chromosomal variation in *S. oppositifolia* is correlated with the morphological differentiation of the species is unknown.

Recently, there has been particular focus on the variation within *S. oppositifolia* in Svalbard. This focus has been accentuated by the publication of a colour photograph of a cushion-formed plant from Ny Ålesund on the front cover of the journal *Molecular Ecology* (Abbott et al. 1995), and by the recognition of two ecologically and morphologically divergent subspecies, one cushion-formed and one prostrate, in the new edition of Rønning's *Svalbards flora* (Rønning 1996). This variation in growth form within *S. oppositifolia* in Svalbard was already reported by Andersson & Hesselman (1900). Recent studies have demonstrated that there not only is large morphological and ecological variation in *S. oppositifolia* in the archipelago, but that the species also shows large variation in DNA markers (Abbott et al. 1995; Gabrielsen et al. 1995, Gabrielsen 1996) and ecophysiological traits (Crawford et al. 1993, 1994; Crawford & Abbott 1994).

The different growth forms observed in *S. oppositifolia* in Svalbard have also been suggested to be correlated with other characteristics (Crawford et al. 1993; Rønning 1996; Elven & Elvebakk 1996). The prostrate plants grow in snow-protected, damp habitats and have high photosynthetic rates, distant leaves with marginal cilia, and open flowers with narrow, non-overlapping petals, whereas the cushion-formed plants grow on dry, wind-exposed ridges and have low photosynthetic rates, dense, overlapping leaves entirely or mostly without cilia, and urn-shaped flowers with broad, overlapping petals.

In the new edition of Rønning's *Svalbards flora* (Rønning 1996), the prostrate plants are referred to as *S. oppositifolia* ssp. *reptans* (Anderss. & Hesselm.) Rønning, and the cushion-formed plants are referred to as *S. oppositifolia* ssp. *pulvinata* (Anderss. & Hesselm.) Rønning. Although only tetraploid plants of *S. oppositifolia* have been recorded in Svalbard, it has been suggested that both diploid and tetraploid plants are present and that the difference in ploidal level may be correlated with growth form (Crawford et al. 1993; cf. also Löve & Löve 1951, 1975).

The aim of the present study was to determine if it is reasonable to divide *S. oppositifolia* in Svalbard into two ecologically, morphologically, and possibly also chromosomally, distinct taxa, or if the variation merely is ecoclinal, representing continuous morphological variation along local ecological gradients. Four different data sets were produced to answer this question: (1) Ecological parameters were measured or estimated to detect possible habitat differences correlated with growth form differences; (2) macro-morphological characters were measured in field-collected plants to detect any possible characters correlated with ecological traits and/or growth form differences; (3) pollen size was measured to reveal possible reproductive barriers owing to ploidal differences between growth forms (see Brochmann 1992a); and (4) pollen stainability was estimated to reveal if there was lowered fertility in morphologically intermediate plants, if such plants (potential hybrids) were detected.

Materials and methods

Ecological data

A total of 50 vegetation samples, each of 1 m^2, were analysed at four sites in the Kongsfjorden area where the postulated subspecies grow in close geographic proximity: (1) Brøggerhalvøya, Stuphallet, UTM VH 28–29 68–69, 12 samples (nos. 22–33, cf. Table 2); (2) Brøggerhalvøya, NW of Bayelva, UTM VH 3265, 16 samples (nos. 4–19); (3) Brøggerhalvøya, S of Ny Ålesund, UTM VH 34–35 63, 14 samples (nos. 1–3, 20, 21, 42–50); and (4) Blomstrandøya, London, UTM VH 3768, 8 samples (nos. 34–41). The vegetation samples were subjectively selected so that the samples at each site covered the range of variation observed in the vegetation where *S. oppositifolia* occurred, and so that at least one plant of *S. oppositifolia* occurred within each sample.

In each sample, the percentage cover of each vascular plant species (nomenclature follows Elven 1994) and the total cover of the vegetation, vascular plants, cryptogams, bryophytes, lichens, stones, and bare ground were recorded. In addition, the humidity conditions (1 = dry, 2 = intermediate, 3 = damp, 4 = moist) and degree of wind exposure (1 = protected, 2 = intermediate, 3 = exposed) were subjectively estimated from the topography and a general impression of the sample site. The aspect and slope (angle of inclination) were measured for each sample.

The vegetation samples and the surrounding areas were classified into five vegetation types following Brattbakk (1981): (1) *Dryas octopetala* heaths and ridges, (2) *Luzula arcuata*-lichen heaths, (3) *S. oppositifolia*-lichen heaths, (4) Talus slope vegetation, and (5) *Deschampsia alpina* snowbeds.

Morphological and pollen stainability data

A total of 150 plants of *S. oppositifolia* occurred within the vegetation samples. In the field, each plant was tentatively classified after growth form as typically prostrate or typically cushion-formed. It was, however, difficult to classify all plants into these two groups, and several plants were tentatively grouped as "intermediates".

Thirteen macroscopic morphological characters were scored for each plant. Seven characters were quantitative, three characters were qualitative, and

Table 1. Macroscopic characters used in morphometric analyses of *Saxifraga oppositifolia*. Five measurements were made of each character for each plant, and the median was used in further analyses. Characters included in the PCO analysis are indicated. Measurements in mm.

Character	Note	PCO
Internode length	the five longest internodes selected in each plant	x
Leaf width	maximum width	x
Leaf length		
Leaf index	leaf width/leaf length	x
No. of leaf cilia	number of cilia along one side of the leaf	
No. of leaf cilia pr. mm	number of cilia/leaf length	x
Petal width	maximum width	x
Petal length		
Petal index	petal width/petal length	x
Petal apex	1 – rounded, 2 – intermediate, 3 – acute	
Overlap of petals	1 – non-overlapping, 2 – tangent, 3 – overlapping	
Flower shape	1 – flattened, 2 – intermediate, 3 – urn-shaped	
Flower diameter	from petal apex to petal apex	x

Table 2. Floristic composition, frequency, and percentage cover of vascular plants in 50 vegetation samples including *Saxifraga oppositifolia*. Vegetation type no. 4–talus slope vegetation, no. 5–*Deschampsia alpina* snowbed. Two species groups in *Saxifraga* were scored collectively because of the early developmental stage of the plants (*S. cernua/hyperborea/rivularis* and *S. nivalis/tenuis*).

	1 *Dryas octopetala* ridge/heath													2 *Luzula arcuata* – lichen heath												
Species/sample no.	10	11	12	13	17	18	25	26	28	30	33	38	freq.	1	2	3	42	43	44	45	46	47	48	49	50	freq.
Saxifraga oppositifolia	2	4	2	3	4	2	10	50	8	10	15	10	1.0	50	5	2	10	5	4	3	25	5	5	4	5	1.0
Bistorta vivipara	1	1	1	1	—	1	1	7	2	2	1	1	0.9	—	—	—	—	1	—	—	—	—	—	1	—	0.2
Cardamine bellidifolia	—	—	—	—	—	—	—	—	—	1	—	1	0.2	1	1	—	—	—	—	—	—	—	—	—	—	0.2
Carex rupestris	—	—	—	—	—	1	5	—	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.0
Cerastium arcticum	—	—	—	1	1	—	—	1	1	1	1	—	0.5	1	—	—	1	1	1	1	—	1	1	1	—	0.7
Cerastium regelii	—	—	—	—	—	1	—	1	—	—	—	—	0.2	—	—	—	—	—	—	1	—	—	—	—	—	0.1
Cochlearia groenlandica	—	—	—	—	—	—	—	—	—	—	—	—	0.0	—	—	—	1	—	—	1	—	—	1	—	—	0.3
Deschampsia alpina	—	—	—	—	1	—	—	—	—	—	—	—	0.1	—	—	—	1	—	—	1	—	—	—	1	—	0.3
Draba lactea	—	—	—	1	—	—	—	1	—	—	—	—	0.2	1	—	—	1	—	1	—	—	—	—	—	—	0.3
Dryas octopetala	5	5	1	15	—	30	50	—	—	—	45	—	0.6	—	—	—	—	—	—	—	—	—	—	—	—	0.0
Equisetum scirpoides	—	—	—	—	—	—	—	—	—	—	—	—	0.0	—	—	—	—	—	—	—	—	—	—	—	—	0.0
Juncus biglumis	—	—	—	1	—	—	—	1	—	—	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	0.0
Luzula arctica	—	—	—	—	—	—	—	—	—	—	—	—	0.0	—	—	—	1	—	—	—	—	—	1	—	—	0.2
Luzula arcuata	—	—	—	1	—	—	—	1	—	—	—	—	0.2	5	3	1	1	5	3	1	2	7	3	3	—	0.9
Oxyria digyna	—	—	—	—	—	—	—	—	—	—	—	—	0.0	1	1	1	1	1	1	1	—	—	—	1	1	0.8
Pecicularis hirsuta	1	—	—	—	—	—	1	—	—	—	—	—	0.2	—	—	—	—	1	—	—	1	1	1	1	—	0.4
Poa alpina	—	—	—	—	—	—	—	—	—	1	—	1	0.2	—	1	1	—	—	—	—	—	—	—	—	—	0.2
Sagina nivalis	—	—	—	—	—	—	—	—	—	—	—	1	0.1	—	—	—	1	—	—	1	—	1	1	—	—	0.3
Salix polaris	1	—	1	1	—	1	1	2	2	1	1	1	0.8	1	—	6	1	4	15	—	25	15	3	5	5	0.8
Saxifraga cern./hyp./riv.	—	—	—	1	1	—	—	—	—	1	—	1	0.3	1	1	1	3	1	—	1	—	—	1	1	—	0.7
Saxifraga cespitosa	—	—	—	—	1	—	—	1	—	1	—	—	0.3	2	1	1	1	1	1	1	—	—	1	1	—	0.8
Saxifraga nivalis/tenuis	—	—	—	—	—	—	—	1	—	—	—	—	0.1	—	—	1	—	1	—	—	—	—	1	—	—	0.3
Silene acaulis	—	—	—	—	—	—	—	—	1	—	—	—	0.1	—	—	—	—	—	—	—	—	—	—	—	—	0.0
Silene uralensis	—	—	—	—	—	—	1	—	1	1	—	—	0.3	—	—	—	—	—	—	—	—	—	—	—	—	0.0

Additional species (occurring in 1–3 samples only): *Draba alpina, D. corymbosa, D. oxycarpa, D. subcapitata, D. micropetala, Equisetum arvense, E. variegatum, Minuartia biflora, Papaver dahlianum, Saxifraga aizoides, S. hieracifolia, Stellaria longipes, Carex misandra, Phippsia* sp.

three characters were ratios between quantitative characters (Table 1). When possible, five measurements were made of each character for each plant, and the median of these five measurements was used in further analyses. The leaf characters were measured on the five longest shoots, on a leaf positioned 1 cm below the shoot apex. The flower characters were measured on the five best developed flowers on each plant.

Pollen size and stainability were measured in 36 plants, 12 plants from each of the three tentative growth form groups (typically prostrate, typically cushion-formed, or "intermediate"). Pollen grains were stained in cotton blue in lactophenol (Radford et al. 1974). The largest diameter of ten subjectively selected pollen grains of each plant was measured using a light microscope. Pollen fertility was estimated by counting the percentage of well-stained and regularly shaped pollen grains in a sample of 200 grains per plant.

Herbarium vouchers of 20 representative specimens of *S. oppositifolia*, selected among the 150 plants analysed, have been deposited at the Botanical Museum, University of Oslo.

Multivariate analyses and statistics

Descriptive statistics and correlations were performed using SPSS for Windows (Norusis 1993). The ecological data were analysed using detrended correspondence analysis (DCA; cf. Hill & Gauch 1980) based on floristic composition of the vegetation samples. The CANOCO program (Braak 1987) was used for these computations with standard parameter choice except that rare species were downweighted according to Eilertsen et al. (1990). Principal coordinate analysis (PCO; Gower 1966, 1967) and nonmetric multidimensional scaling (NMDS; Kruskal 1964) were performed using NTSYS-pc (Rohlf 1990) based on seven morphological characters, excluding qualitative multistate characters and characters with overlapping information (Table 1). The quantitative, continuous morphological characters were ln-transformed before analyses to eliminate

Table 2. Continued

3 *Saxifraga oppositifolia* – lichen heath																									4	5	Total
4	5	6	7	8	9	14	15	16	19	20	21	22	24	29	31	32	34	35	36	37	39	40	41	freq.	23	27	freq.
5	5	2	6	3	8	50	7	20	5	10	3	3	10	25	5	10	25	2	8	10	15	30	15	1.0	10	30	0.1
1	1	1	2	1	—	1	1	1	—	15	1	1	15	2	1	1	—	1	—	1	2	—	1	0.8	3	1	0.1
—	—	—	—	—	—	—	—	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1
—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	2	—	—	0.1	—	—	0.1
1	1	1	—	—	1	1	1	1	1	—	1	1	—	1	1	—	—	1	—	—	—	1	—	0.6	1	—	0.1
1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	0.2	—	1	0.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	0.0	—	1	0.1
—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	1	—	—	1	—	0.2	—	5	0.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.0	—	—	0.1
—	—	—	—	—	—	—	—	—	—	—	—	—	6	—	10	—	—	—	—	—	—	—	—	0.1	10	—	0.1
1	1	—	1	—	—	—	—	1	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	0.3	—	—	0.1
2	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	1	0.1
1	—	—	1	—	—	—	1	1	1	1	—	—	—	—	—	—	—	1	—	—	—	—	—	0.3	—	2	0.1
—	1	1	—	1	1	—	1	1	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	0.4	—	—	0.1
—	—	1	—	1	—	—	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	0.2	—	—	0.1
—	1	1	1	—	—	—	1	—	—	1	—	—	—	—	1	—	—	—	—	1	—	—	—	0.3	—	—	0.1
1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	2	2	0.3	—	1	0.1
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.0	—	—	0.1
4	5	3	4	1	30	1	3	—	3	10	3	—	1	—	1	1	—	—	1	1	10	1	2	0.8	—	1	0.1
1	1	—	—	1	—	1	1	1	1	—	1	—	—	—	—	—	1	—	1	—	—	1	1	0.5	—	—	0.1
—	—	—	1	1	1	—	—	1	1	1	1	—	—	—	—	1	—	1	1	—	—	1	—	0.5	—	1	0.1
—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.1	—	—	0.1
—	—	—	1	—	—	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	20	5	—	0.2	—	1	0.1
—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	1	0.1	—	—	0.1

the effect of size (cf. Brochmann 1987). All morphological characters were subsequently standardised by "ranging" (i.e., each character was scaled between 0 and 1, Gower 1971), and morphological dissimilarities between plants were calculated as average Manhattan distances (Rohlf 1990). Kendall's τ correlations (Kendall 1938) were calculated for the two first PCO axes, DCA axis 1, the morphological characters, and the ecological parameters.

Results

Ecology

Saxifraga oppositifolia showed a wide ecological amplitude in the Kongsfjorden area. The species occurred in a wide range of habitats varying from dry, wind-exposed, almost unvegetated ridges and slopes, via snow-protected, damp, densely vegetated heaths, to moist, densely vegetated snowbeds. A total of 38 vascular plant species was recorded in the 50 vegetation samples analysed (Table 2). Most samples were classified into three vegetation types, i.e., *Dryas octopetala* heaths and ridges (12 samples), *Luzula arcuata*–lichen heaths (12 samples), and *S. oppositifolia*–lichen heaths (24 samples; Tables 2 and 3). One sample was classified as talus slope vegetation, and one as *Deschampsia alpina* snowbed. The percentage cover of *S. oppositifolia* in each vegetation sample varied between 2% and 50%, and the cover of the species varied considerably within as well as between the main vegetation types (Table 2).

The most conspicuously cushion-forming plants of *S. oppositifolia* were found at the driest, uppermost *Dryas* ridges. The *Dryas octopetala* vegetation type was, on average, the driest and most wind-exposed one among the main vegetation types (mean humidity 1.8; mean wind exposure 2.7), but the degree of humidity and wind exposure varied within this vegetation type along a gradient from ridges to slopes and heaths. The total vegetation cover (mean 52%) as well as the cover of bryophytes and lichens were, on

Table 3. Ecological parameters scored in 50 vegetation samples with *Saxifraga oppositifolia*, classified into vegetation types following Brattbakk (1981).

Vegetation type	No. of samples	Humidity 1 – dry, 4 – moist mean	sd	min	max	Wind exposure 1 – protected, 3 – exposed mean	sd	min	max	Slope (angle of inclination) mean	sd	min	max	Total vegetation cover (%) mean	sd	min	max	Vascular plant cover (%) mean	sd	min	max
Dryas octopetala ridge/heath	12	1.8	0.87	1	3	2.7	0.49	2	3	14	16.2	0	60	52	35.5	5	95	26	25.8	3	70
Luzula arcuata – lichen heath	12	2.3	0.49	2	3	2.0	0.00	2	2	1	1.8	0	5	82	23.0	35	100	22	17.3	4	60
Saxifraga oppositifolia – lichen heath	24	2.8	0.82	2	4	1.8	0.51	1	3	9	10.2	0	40	83	20.9	15	100	21	15.7	3	55
Talus slope vegetation	1	3.0	—	—	—	2.0	—	—	—	0	—	—	—	50	—	—	—	25	—	—	—
Deschampsia alpina snowbed	1	4.0	—	—	—	2.0	—	—	—	0	—	—	—	95	—	—	—	45	—	—	—

Vegetation type	No. of samples	Cryptogam cover (%) mean	sd	min	max	Bryophyte cover (%) mean	sd	min	max	Lichen cover (%) mean	sd	min	max	Stone cover (%) mean	sd	min	max	Bare ground cover (%) mean	sd	min	max
Dryas octopetala ridge/heath	12	31	28.5	1	85	21	25.9	1	75	11	13.5	1	45	36	35.9	1	95	14	25.8	0	92
Luzula arcuata – lichen heath	12	75	21.7	34	98	60	20.8	33	95	15	13.9	1	50	13	16.6	0	40	5	9.1	0	30
Saxifraga oppositifolia – lichen heath	24	71	21.5	10	99	44	22.1	10	98	27	20.6	1	90	10	13.6	0	50	8	16.1	0	70
Talus slope vegetation	1	25	—	—	—	5	—	—	—	20	—	—	—	25	—	—	—	25	—	—	—
Deschampsia alpina snowbed	1	50	—	—	—	35	—	—	—	15	—	—	—	5	—	—	—	0	—	—	—

Table 4. Descriptive statistics of macroscopic morphological characters analysed in *Saxifraga oppositifolia*, based on the median of five measurements per plant. See Table 1 for explanation of characters.

Character	No. of plants	Mean	SD	Min	Max
Internode length (mm)	146	2.8	1.66	0.3	8.1
Leaf width (mm)	146	1.9	0.26	1.3	2.7
Leaf length (mm)	146	3.3	0.45	2.1	4.5
Leaf index	146	0.57	0.06	0.44	0.73
No. of leaf cilia	145	8.6	2.0	4	15
No. of leaf cilia pr. mm	145	2.6	0.58	1.3	4.2
Petal width (mm)	132	4.2	1.15	1.5	8.6
Petal length (mm)	132	6.8	1.07	4.6	10.1
Petal index	132	0.60	0.11	0.33	0.85
Petal apex (1 – rounded, 3 – acute)	131	1.6	0.5	1	3
Overlap of petals (1 – non-overlapping, 3 – overlapping)	132	2.0	0.6	1	3
Flower shape (1 – flattened, 3 – urn-shaped)	132	1.9	0.6	1	3
Flower diameter (mm)	132	11.3	2.29	7	18

average, lowest in the *Dryas* vegetation type. The uppermost ridges were almost unvegetated (cover 5%), whereas the most humid *Dryas* heaths were densely vegetated (cover up to 95%). The vascular plant species most frequently observed in the *Dryas* vegetation type, except for the only dominating species *Dryas octopetala* and *S. oppositifolia*, were *Bistorta vivipara*, *Cerastium arcticum*, and *Salix polaris* (Table 2).

The most prostrate, creeping plants of *S. oppositifolia* were found in the most humid parts of the lichen heaths. The two lichen heath vegetation types were fairly similar except for quantitative differences in the occurrences of some species, in particular *S. oppositifolia*, *Luzula arcuata*, *Bistorta vivipara*, and *Oxyria digyna*, and in relative importance of bryophytes versus lichens (Tables 2 and 3). The lichen heaths were, on the average, densely vegetated (mean cover 82–83%), but had about the same cover of vascular plants as the *Dryas* vegetation type (means 21–22% and 26%, respectively). The cryptogam layer covered, on the average, 71–75% in the lichen heaths, versus 31% in the *Dryas* vegetation.

The DCA analysis based on the floristic composition of the 50 vegetation samples did not result in an interpretable pattern, probably caused by the species–poor samples with considerable overlap in species content, and this analysis is therefore not shown. Among the ecological parameters, only cryptogam cover and bryophyte cover were significantly ($p < 0.05$) correlated with DCA axis 1. Because no other parameters (e.g., humidity or total vegetation cover) were significantly correlated with DCA axis 1, these two parameters did not per se provide any meaningful ecological interpretation of the DCA axis. DCA axis 1 may nevertheless represent a humidity gradient. This might have been verified by a more accurate measure of humidity. Several ecological parameters were, however,

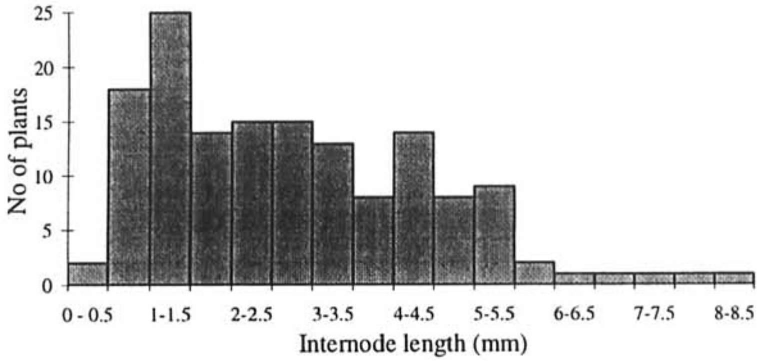

Fig. 1. Variation in internode length in *Saxifraga oppositifolia* from the Kongsfjorden area in Svalbard. n = 150 plants.

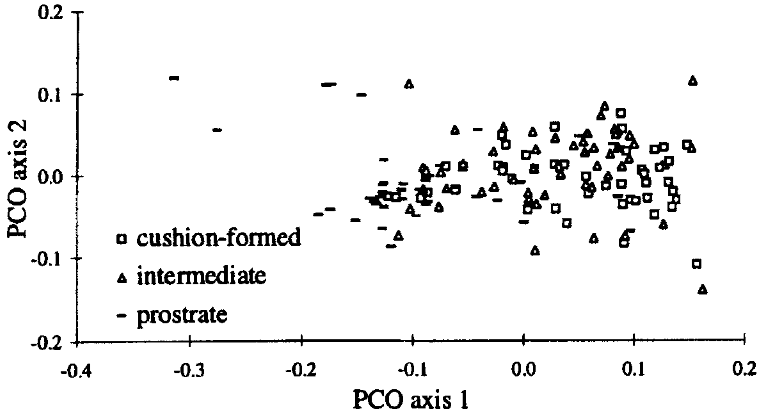

Fig. 2. PCO analysis (axes 1 and 2) of 146 plants of *Saxifraga oppositifolia* from the Kongsfjorden area in Svalbard based on seven morphological characters. The classification into growth forms (cushion-formed, intermediate, or prostrate) was not included prior to the analysis, but subsequently assigned to the plants subjected to the PCO analysis.

significantly correlated with individual morphological traits of *S. oppositifolia* as well as the PCO axes (see below).

Macromorphology

The plants analysed showed conspicuous variation in most individual morphological characters (Table 4). However, all quantitative characters showed a unimodal distribution, most distinctly so, and it was thus not possible to separate the material into two or more groups based on any individual characters.

Internode length, the character most closely associated with the growth form of the plants, varied from 0.3 mm (i.e., 3.3 leaves per mm of the stem) in the most cushion-formed plants to 8.1 mm (i.e., 0.1 leaf per mm of the stem) in the most prostrate plants, with an average of 2.8 mm for the 146 plants measured for this character. As for all morphological characters, the internode length showed a unimodal distribution (Fig. 1).

The leaves varied considerably in size and shape. The leaf length varied from 2.1 mm to 4.5 mm (mean 3.3 mm), the leaf width varied from 1.3 mm to 2.7 mm (mean 1.9 mm), and the leaf shape varied from narrowly to widely elliptic (mean leaf index 0.57). Leaf ciliation varied less than expected. All plants had ciliated leaves, varying from 1.3 to 4.2 cilia per mm of the leaf margin.

The variation in floral characters was particularly conspicuous. The petals varied nearly six-fold in width, from very narrow (1.5 mm) to very broad (8.6 mm), and more than two-fold in length (4.6–10.1 mm). The petals also varied considerably in shape, from very long, narrow, and non-overlapping (petal index 0.33) to nearly as broad as long and overlapping (petal index 0.85), and with an apex varying from rounded to acute. The shape of open flowers varied from flattened to distinctly urn-shaped.

Nor did the PCO analysis result in any distinct grouping of the plants, although the analysis revealed that there was a mainly one-dimensional, simple structure in the total morphological data set (Fig. 2). The first PCO axis had a high eigenvalue (1.40) and accounted for 78.3% of the total variance in the morphological data, and the first two PCO axes accounted for 95% of the variance. The result of the NMDS analysis (stress 0.22; not shown) was largely similar to that of the PCO analysis.

Most of the morphological characters were signifiantly correlated with PCO axis 1 (see also below; cf. Table 5). Internode length was most strongly correlated, and negatively so (τ) = –0.73, $p < 0.001$), indicating that the most prostrate plants (i.e., those with long internodes) had low values along PCO axis 1 and the most cushion-formed plants (i.e., those with short internodes) had high values along PCO axis 1. The tentative field classification of the plants after growth form as typically prostrate, "intermediate", or typically cushion-formed was superimposed on the PCO diagram (Fig. 2; note that this character was not included prior to the PCO analysis). Most of the plants classified as typically prostrate had low values (–0.3 to 0) along PCO axis 1, whereas most of the plants classified as typically cushion-formed had higher values (0 to 0.2), indicating that this subjective growth-form classification

Table 5. Kendall correlations between ecological variables, morphological variables, and PCO axis 1 coordinates for *Saxifraga oppositifolia*. ns = $p > 0.05$; * = $0.01 < p < 0.05$; ** = $0.001 < p < 0.01$; *** = $p < 0.001$.

1 Growth form																		
2 Internode length	0.36***																	
3 Leaf width	0.07 ns	0.23***																
4 Leaf length	0.09 ns	0.15**	0.47***															
5 Leaf index	0.04 ns	0.10 ns	0.29***	−0.22***														
6 No. of leaf cilia pr. mm	−0.36***	−0.39***	−0.08 ns	−0.14*	0.00 ns													
7 Petal width	0.22***	0.32***	0.27***	0.12 ns	0.12*	−0.14*												
8 Petal length	0.23***	0.37***	0.27***	0.21***	0.03 ns	−0.17**	0.61***											
9 Petal index	0.16*	0.19***	0.19**	−0.01 ns	0.21***	−0.09*	0.66***	0.27***										
10 Petal apex	−0.24**	−0.20**	−0.10 ns	0.05 ns	−0.16*	0.17*	−0.45***	−0.26***	−0.50***									
11 Overlap of petals	0.07 ns	−0.13 ns	0.19**	0.12 ns	0.10 ns	0.07 ns	0.24***	0.03 ns	0.36***	0.17*								
12 Flower shape	0.06 ns	−0.09 ns	−0.03 ns	0.08 ns	−0.03 ns	−0.05 ns	−0.27***	−0.26***	−0.19**	0.23**	0.17*							
13 Flower diameter	0.16*	0.30***	0.15*	0.13*	−0.01 ns	−0.13*	0.45***	0.55***	0.21***	−0.26***	−0.15*	−0.55***						
14 Humidity	0.22**	0.28***	0.09 ns	0.05 ns	0.10 ns	−0.25***	0.12 ns	0.12 ns	0.07 ns	−0.21**	−0.03 ns	0.08 ns	0.11 ns					
14 Wind exposure	−0.29***	−0.33***	−0.08 ns	−0.01 ns	−0.06 ns	0.26***	−0.19**	−0.21**	−0.14*	0.27***	0.00 ns	−0.03 ns	−0.13 ns	−0.52***				
16 Total vegetation cover	−0.05 ns	−0.01 ns	0.00 ns	−0.06 ns	0.03 ns	0.10 ns	0.12*	0.03 ns	0.12*	−0.22**	0.07 ns	−0.18*	0.14*	0.27***	−0.15*			
17 Stone cover	0.05 ns	−0.02 ns	−0.03 ns	−0.01 ns	−0.01 ns	−0.04 ns	−0.12*	−0.08 ns	−0.08 ns	0.15*	−0.07 ns	0.09 ns	−0.12 ns	−0.36***	0.15*	−0.66***		
18 Bare ground cover	0.09 ns	0.08 ns	0.06 ns	0.07 ns	0.00 ns	−0.16**	−0.05 ns	0.03 ns	−0.09 ns	0.17*	−0.03 ns	0.21**	−0.12 ns	0.10 ns	−0.11 ns	−0.55***	0.15*	
19 PCO axis 1	−0.41***	−0.73***	−0.21***	−0.20***	−0.05 ns	0.61***	−0.35***	−0.38***	−0.22***	0.24***	0.09 ns	0.08 ns	−0.33***	−0.30***	0.34***	0.02 ns	0.02 ns	−0.10 ns
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18

agreed with the exact measurements of internode lengths. Notably, neither the growth-form classification nor the internode analysis resulted in distinct groups in the material; rather, the scores were distributed continuously along the two PCO axes.

Pollen size and stainability

The pollen diameter in individual plants varied from 20.0 to 32.2 µm, and the mean pollen diameter for the 36 plants analysed was 25.0 µm (sd 2.6). The pollen diameter showed a distinct unimodal distribution (Fig. 3). All plants except one had more than 80% stainable pollen (mean 92%, sd 8%, min 60%, max 95%; n = 36 plants).

Correlations among ecological traits, morphological traits, and PCO axes

Several of the individual traits were significantly correlated (Table 5). Among the ecological traits, humidity, vegetation cover, vascular plant cover, cryptogam cover, and bryophyte cover were positively correlated ($p < 0.01$). These traits were negatively correlated ($p < 0.01$) with stone cover, bare ground cover, and wind exposure. Among the morphological characters, leaf width, flower diameter, petal length, petal width, and petal index were positively correlated ($p < 0.01$).

Internode length was positively correlated ($p < 0.05$) with humidity, growth form, flower diameter, petal length, petal width, petal index, leaf length, and leaf width. The number of leaf cilia per mm, petal apex, and wind exposure were negatively correlated with internode length. Growth form was positively correlated ($p < 0.05$) with flower diameter, leaf length, leaf width, leaf index, vascular plant cover, lichen cover, and humidity, and negatively correlated ($p < 0.05$) with number of leaf cilia per mm, petal apex, and wind exposure.

Internode length and number of leaf cilia per mm were most strongly correlated with PCO axis 1 (Table 5). Internode length was negatively correlated, and the number of leaf cilia per mm was positively correlated with PCO axis 1. Floral characters and leaf width were negatively correlated with PCO axis 1. Except for internode length, similar, but weaker correlations were found for PCO axis 2. The significant correlations found for PCO axis 2 were leaf width (τ) = −0.13, $0.01 < p < 0.05$), number of leaf cilia pr. mm

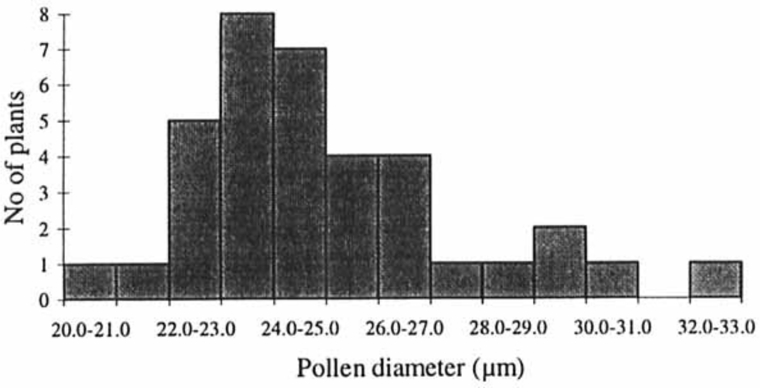

Fig. 3. Variation in pollen diameter in *Saxifraga oppositifolia* from the Kongsfjorden area in Svalbard. n = 36 plants (360 grains).

(τ) = 0.24, $p < 0.001$), petal width (τ) = –0.32, $p < 0.001$), petal index (τ) = –0.28, $p < 0.001$), and flower diameter (τ) = –0.25, $p < 0.001$).

The median pollen diameter was positively correlated with internode length (τ) = 0.53, $p < 0.001$) and growth form (τ) = 0.53, $p < 0.001$), and negatively correlated with PCO axis 1 (τ) = –0.58, $p < 0.001$).

Thus, the prostrate plants had larger pollen grains, longer internodes, fewer leaf cilia, larger leaves, larger flowers, larger, broader, and more rounded petals and occurred in wetter and less windy habitats than the cushion-formed plants.

Discussion

Neither the individual morphological characters nor the PCO analysis indicate that it is possible to divide the plant material into two distinct groups, as would be expected if the two growth forms of *S. oppositifolia* deserve status as separate taxa. Most characters vary continuously and show unimodal distributions. The growth form was not included as a character prior to the PCO analysis, but when the plants subsequently were labeled according to the tentative growth form classification, the three groups, prostrate, "intermediates" and cushion-formed, showed a continuous, overlapping distribution along PCO axis 1. In particular, the unimodal distribution of internode length (Fig. 1), a character which could be quantified exactly and which is closely associated with growth form, and the strong correlation between this character and PCO axis 1 (Table 5) strongly support the hypothesis that *S. oppositifolia* is represented by a single, but variable, taxon in Svalbard.

Several morphological traits besides internode length have been suggested to be diagnostic characters distinguishing between the two proposed subspecies of *S. oppositifolia* (Crawford et al. 1993; Elven & Elvebakk 1996; Rønning 1996): The prostrate growth form has been suggested to be correlated with occurrence of marginal leaf cilia, open flowers, and narrow, non-overlapping petals, whereas the cushion-like growth form has been suggested to be correlated with absence of leaf cilia, urn-shaped flowers, and broad, overlapping petals. Our results demonstrate, however, (1) that the number of cilia is negatively correlated with internode length (i.e., prostrate plants are more sparsely ciliated than cushion-formed plants), (2) that petal width is positively correlated with internode length (i.e., prostrate plants have broader petals than cushion-formed plants), and (3) that neither flower shape nor overlap of petals are correlated with internode length. We have thus shown that none of the cilia and floral characters separate the two growth forms in the way proposed by Crawford et al. (1993), Elven & Elvebakk (1996), and Rønning (1996).

It is well known that the pollen size may be useful to discriminate between different ploidal levels in plants, in particular between closely related populations at low ploidal levels (Ehrendorfer 1964; Ugborogho 1973; Brochmann 1992a). The stainable (and thus probably fully fertile) pollen grains and the unimodal distribution of pollen diameter observed in this study suggest that the plants analysed of *S. oppositifolia* represent a single ploidal level (diploid or tetraploid). Because cushion-formed, "intermediate", and prostrate plants were equally well represented among the investigated plants, the growth forms are thus probably not reproductively isolated by genetic barriers. Notably, the plants with intermediate morphology had fully stainable pollen. This result would not have been expected if the intermediates were triploid hybrids between a diploid and a tetraploid taxon. However, without chromosome counts it is not possible to determine if the plants analysed are diploids or tetraploids.

The significant correlations obtained between some of the ecological parameters and internode length as well as growth form indicate that the cushion-formed plants are most common on dry, wind-exposed ridges, whereas the prostrate plants usually are found in less exposed and more damp habitats. This is in agreement with the observations by Crawford et al. (1993), Rønning (1996), and Elven & Elvebakk (1996). The PCO and correlation analyses demonstrate, however, that the morphological variation in *S. oppositifolia* is continuous along local ecological gradients. Plants in the driest and most wind-exposed habitats have shorter internodes, smaller and more densely ciliated leaves, and smaller flowers than plants growing in successively more damp habitats. These characters probably all reflect response to drought. Similar, genetically based clinal variation along local humidity gradients has recently been demonstrated in the genus *Frankenia*, suggested to be caused by one or a few genetic factors that control organ size and are subjected to differential selection with respect to drought tolerance (Brochmann et al. 1995).

It is likely that the observed morphological and ecological variation in *S. oppositifolia* is genetically based, but this cannot be determined with certainty without molecular genetic data, manipulation of environmental factors, or reciprocal transplant experiments. However, we observed that prostrate and cushion-formed plants occasionally grow in close proximity within the same, apparently homogeneous habitat. This observation may suggest that the growth form is genetically determined, and that the different genotypes sometimes are able to disperse and establish in suboptimal habitats. Notably, similar conspicuous differences in morphology and photosynthetic capacity that are genetically based have been demonstrated along similar environmental gradients for *Dryas octopetala* in Alaska (McGraw & Antonovics 1983; McGraw 1995a).

In conclusion, the present study clearly demonstrates the high levels of morphological and ecological variation within *S. oppositifolia* in Svalbard, but gives no support for maintaining the two growth forms as the separate subspecies *reptans* and *pulvinata* as proposed by Rønning (1996). It seems rather most reasonable to refer all of the populations of *S. oppositifolia* occurring in Svalbard to the widespread and variable, typical subspecies *oppositifolia*, in agreement with Webb & Gornall (1989), who note that this subspecies is "usually fairly lax in growth (except in very exposed situations)" (p. 106). The differentiation within *S. oppositifolia* in Svalbard is clearly of no taxonomic significance, but probably caused by local ecoclinal evolution occurring independently in different sites and geographic areas. The close geographic proximity of the extreme forms, a considerable overlap in flowering time, and the existence of many, fully fertile plants that cannot easily be classified as either prostrate or cushion-formed suggest that the plants at each site represent single panmictic populations rather than different taxa evolved by sympatric sub-speciation. Genetic diversity and ecological versatility within species seem to be common phenomena in many arctic plants, without necessarily being of taxonomic significance (McGraw 1995; Murray 1995). Such variation is, however, of significance in a broader context of arctic conservation biology and the potential impact of global warming on arctic vegetation.

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References

Abbott, R. J., Chapman, H. M., Crawford, R. M. M. & Forbes, D. G. 1995: Molecular diversity and derivations of populations of *Silene acaulis* and *Saxifraga oppositifolia* from the high Arctic and more southerly latitudes. *Molec. Ecol. 4,* 199–207.

Andersson, G. & Hesselman, H. 1900: Bidrag til kännedomen om Spetsbergens och Beeren Eilands kärlväxtflora. *Bih. K. Svenska Vet.-Akad. Handl. 26, III, 1,* 1–88.

Bauert, M. R. 1996: Genetic diversity and ecotypic differentiation in arctic and alpine populations of *Polygonum viviparum*. *Arct. Alp. Res.* 28, 190–195.

Braak, C. J. F. ter 1987: *CANOCO—a FORTRAN program for canonical community ordination by (partial)(detrended)(canonical) correspondence analysis, principal components analysis and redundancy analysis (version 2.1).* TNO Inst. appl. Comp. Sci., Stat. Dept. Wageningen, Wageningen.

Brattbakk, I. 1981: *Brøggerhalvøya, Svalbard. Vegetasjonskart 1:10.000.* K. Norske Vitensk. Selsk. Mus. Bot. Avd., Trondheim.

Brochmann, C. 1987: Evaluation of some methods for hybrid analysis, exemplified by hybridization in *Argyranthemum* (Asteraceae). *Nord. J. Bot. 7,* 609–630.

Brochmann, C. 1992a: Pollen and seed morphology of Nordic *Draba* (Brassicaceae): phylogenetic and ecological implications. *Nord. J. Bot. 12,* 657–673.

Brochmann, C. 1992b: Polyploid evolution in arctic-alpine *Draba* (Brassicaceae). *Sommerf. Suppl. 4,* 1–37.

Brochmann, C. 1995a: Arktisk biodiversitet er underestimert: ny innsikt fra evolusjons- og molekylærgenetiske studier. *Univ. Trondheim Vitensk.mus. Rapp. Bot. Ser. 1995 3,* 18–20.

Brochmann, C. 1995b: Conservation biology and polyploid evolution in the Arctic: insights from molecular and reproductive studies. *Abstract, VI International Symposium IOPB, "Variation and Evolution in Arctic and Alpine Plants",* Tromsø, Norway.

Brochmann, C., Lobin, W., Sunding, P. & Stabbetorp, O. 1995: Parallel ecoclinal evolution and taxonomy of *Frankenia* (Frankeniaceae) in the Cape Verde Islands, W Africa. *Nord. J. Bot. 15,* 603–623.

Brochmann, C., Soltis, D. E. & Soltis, P. S. 1992a: Electrophoretic relationships and phylogeny of Nordic polyploids in *Draba* (Brassicaceae). *Plant Syst. Evol. 182,* 35–70.

Brochmann, C., Soltis, P. S. & Soltis, D. E. 1992b: Multiple origins of the octoploid Scandinavian endemic *Draba cacuminum*: electrophoretic and morphological evidence. *Nord. J. Bot. 12,* 257–272.

Brochmann, C., Soltis, P. S. & Soltis, D. E. 1992c: Recurrent formation and polyphyly of Nordic polyploids in *Draba* (Brassicaceae). *Amer. J. Bot. 79,* 673–688.

Brysting, A. K., Elven, R. & Nordal, I. In press: The hypothesis of hybrid origin of *Poa jemtlandica* supported by morphometric and isozyme data. *Nord. J. Bot.*

Chapman, H. M. 1995: P. 10 in Stace, C. A. (ed.): IOPB chromosome data 9. *IOPB Newsletter 24.*

Crawford, R. M. M. & Abbott, R. J. 1994: Pre-adaptation of arctic plants to climate change. *Botanica Acta 107,* 271–278.

Crawford, R. M. M., Chapman, H. M., Abbott, R. J. & Balfour, J. 1993: Potential impact of climatic warming on arctic vegetation. *Flora 188,* 367–381.

Crawford, R. M. M., Chapman, H. M. & Hodge, H. 1994: Anoxia tolerance in high arctic vegetation. *Arct. Alp. Res. 26,* 308–312.

Ehrendorfer, F. 1964. Notizen zur Cytotaxonomie und Evolution der Gattung *Artemisia. Österr. Bot. Zeitschr. 111,* 84–142.

Eilertsen, O., Økland, R. H., Økland, T. & Pedersen, O. 1990: Data manipulation and gradient length estimation in DCA ordination. *J. Veg. Sci. 1,* 261–270.

Elven, R. 1994. *6. utg. av Lid & Lid, Norsk flora.* Det Norske Samlaget, Oslo.

Elven, R. & Elvebakk, A. 1996: Part 1. Vascular plants. Pp. 9–53 in Elvebakk, A. & Prestrud, P. (eds.): A catalogue of Svalbard plants, fungi, algae, and cyanobacteria. *Norsk Polarinst. Skr. 198.*

Engler, H. G. A. & Irmscher, E. 1919: Saxifragaceae: *Saxifraga. Das Pflanzenreich 69,* 449–709.

Flovik, K. 1940: Chromosome numbers and polyploidy within the flora of Spitzbergen. *Hereditas 26,* 430–440.

Gabrielsen, T. M. 1996: *RAPD variation and phylogeography of Nordic populations of Saxifraga oppositifolia.* Cand. scient. thesis, Univ. of Oslo.

Gabrielsen, T. M., Bachmann, K., Jakobsen, K. S. & Brochmann, C. 1995: RAPD variation in an arctic-alpine, mainly diploid outbreeder: *Saxifraga oppositifolia. Abstract, VI International Symposium IOPB, "Variation and Evolution in Arctic and Alpine Plants",* Tromsø, Norway.

Gower, J. C. 1966: Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika 53,* 325–338.

Gower, J. C. 1967: Multivariate analysis and multidimensional geometry. *Statistician 17,* 13–28.

Gower, J. C. 1971: A general coefficient of similarity and some of its properties. *Biometrics 27,* 857–874.

Hagen, A., Schjøll, O., Brochmann, C., Elven, R., Nordal, I. & Borgen, L. 1995: Genetic variation in the polyploids *Cerastium alpinum* and *C. arcticum* (Caryophyllaceae): morphology, isozymes and RAPDs. *Abstract, VI International Symposium IOPB, "Variation and Evolution in Arctic and Alpine Plants",* Tromsø, Norway.

Haraldsen, K. B. & Wesenberg, J. 1993: Population genetic analyses of an amphi-Atlantic species: *Lychnis alpina* (Caryophyllaceae). *Nord. J. Bot. 13,* 377–387.

Hayek, A. 1905: Monographische Studien über die Gattung *Saxifraga,* 1. Die Sektion *Porphyrion* Tausch. *Denkschr. kaiserl. Akad. Wissensch., Wien, 77,* 611–709.

Hedberg, O. 1967: Chromosome numbers of vascular plants from arctic and subarctic North America. *Arkiv Bot. II, 6,* 309–326.

Hill, M. O. & Gauch, H. G. 1980: Detrended correspondence analysis: an improved ordination technique. *Vegetatio 42,* 47–58.

Hultén, E. & Fries, M. 1986: *Atlas of North European vascular plants north of the Tropic of Cancer.* Koeltz, Königstein.

Johnson, A. W. & Packer, J. G. 1968: Chromosome numbers in the flora of Ogotoruk Creek, N. W. Alaska. *Bot. Not. 121,* 403–456.

Kendall, M. G. 1938: A new measure of rank correlation. *Biometrika 30,* 81–94.

Kruskal, J. B. 1964: Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika 29,* 1–27.

Löve, Á. & Löve, D. 1951: Studies on the origin of the Icelandic flora. II. Saxifragaceae. *Svensk Bot. Tidskr. 45,* 368–399.

Löve, Á. & Löve, D. 1956: Cytotaxonomical conspectus of the Icelandic flora. *Acta Horti Gotob. 20,* 65–291.

Löve, Á. & Löve, D. 1975: *Cytotaxonomical atlas of the arctic flora.* Cramer, Vaduz.

McGraw, J. B. 1995a: Patterns and causes of genetic diversity in arctic plants. Pp. 33–43 in Chapin III, F. S. & Körner, C. (eds.): *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences.* Springer, Berlin.

McGraw, J. B. 1995b: Prevalence and significance of ecotypic variation in arctic and alpine plants. *Abstract, VI International Symposium IOPB, ''Variation and Evolution in Arctic and Alpine Plants"*, Tromsø, Norway.

McGraw, J. B. & Antonovics, J. 1983: Experimental ecology of *Dryas octopetala* ecotypes. I. Ecotypic differentiation and life cycle stages of selection. *J. Ecol. 71*, 879–897.

Murray, D. F. 1995: Causes of arctic plant diversity: origin and evolution. Pp. 21–32 in Chapin III, F. S. & Körner, C. (eds.): *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Springer, Berlin.

Nordal, I. & Iversen, A. P. 1993: Mictic and monomorphic versus parthenogenetic and polymorphic—a comparison of two Scandinavian mountain grasses. *Opera Bot. 121*, 19–27.

Norusis, M. J. 1993: *SPSS for Windows. Base systems user's guide. Release 6.0.* SPSS Inc., Chicago.

Radford, A. E., Dickison, W. C., Massey, J. R. & Bell, C. R. 1974: *Vascular plant systematics*. Harper & Row, New York.

Rohlf, F. J. 1990: *NTSYS-pc. Numerical taxonomy and multivariate analysis system. Version 1.60.* Exeter Software, New York.

Rønning, O. I. 1996: *Svalbards Flora. Ed. 3.* Norsk Polarinstitutt, Oslo.

Skovsted, A. 1934: Cytological studies in the tribe Saxifrageae. *Dansk Bot. Arkiv 8*(5): 1–52.

Stenström, M. & Molau, U. 1992: Reproductive ecology of *Saxifraga oppositifolia*: phenology, mating system, and reproductive success. *Arct. Alp. Res. 24*, 337–343.

Tollefsrud, M. M., Bachmann, K., Jakobsen, K.S. & Brochmann, C. 1995: RAPD variation in an arctic-alpine, polyploid inbreeder: *Saxifraga cespitosa*. *Abstract, VI International Symposium IOPB, "Variation and Evolution in Arctic and Alpine Plants"*, Tromsø, Norway.

Ugborogho, R. E. 1973: North American *Cerastium arvense* L. I. Cytology. *Cytologia 38*, 559–566.

Webb, D. A. & Gornall, R. J. 1989: *A manual of Saxifrages and their cultivation*. Timber Press, Portland.