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## Polyploid evolution in arctic-alpine
## *Draba* (Brassicaceae)

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Dissertation to be publicly defended at the University of Oslo for the degree of Doctor Philosophiae.

The mainly arctic-alpine genus *Draba* is well known for its complex morphological and chromosomal variation. This paper reviews a larger study of Nordic *Draba*, aimed to provide insights into evolutionary processes that confound taxonomic relationships in the genus. The populations analyzed were referred to 16 currently recognized species of the sections *Draba* (petals white), *Chrysodraba* (petals yellow), and *Drabella* (petals yellow), and investigated using enzyme electrophoresis, restriction site analysis of cpDNA and rDNA, and analysis of chromosome numbers, artificial and natural hybrids, reproductive biology, habitat differentiation, and morphology.

Section *Draba* comprises three diploids and seven polyploids (4x-10x) based on x = 8, sect. *Chrysodraba* comprises five polyploids (4x-16x) based on x = 8, and sect. *Drabella* comprises *D. crassifolia*, which probably is octoploid based on x = 5. Artificial $F_1$ hybrids were obtained in 19 interspecific combinations. Later-generation hybrids were obtained in seven of these combinations. The genetic data suggest that 1) all polyploids are genetic allopolyploids, i.e., they show disomic inheritance and are highly fixed-heterozygous; 2) several of the polyploids have originated recurrently, some of them even polyphyletically; 3) some of the alloploid populations may have originated from cross-incompatible, sibling species that all belong to a single diploid taxonomic species; 4) interspecific gene flow across chromosome number barriers is possible and probably occurs in natural situations; 5) each of three of the polyploids represents an independent alloploid lineage, whereas sect. *Draba* and two species of sect. *Chrysodraba* form an intricate phylogenetic network; 6) some of the polyploids have originated locally, others have migrated repeatedly into the Nordic area; and 7) the phenotypic expression of genes encoding taxonomically important morphological characters does not follow consistent patterns in hybrids; this result may explain the discrepancies between genetic and taxonomic relationships in this highly reticulate genus.

All species are sexual autogams, but there was large variation in autogamous seed set and traits promoting cross-pollination. The diploids are genetically depauperate, extremely inbreeding stress-tolerators occupying restricted ecological niches, whereas most of the polyploids have high levels of genetic variation, occupy a wide range of niches, and are either stress-tolerant competitors with a mixed mating system or primarily inbreeding ruderals. Mixed mating appears advantageous in the polyploids occurring in competitive habitats, although their fixed heterozygosity buffers the effect of selfing with respect to loss of variability. The ecological amplitude, heterozygosity, and biochemical diversity in the species were positively correlated and increased significantly with ploidal level. Two hypotheses are advanced to explain these correlations: 1) the general-purpose genotype hypothesis, which suggests that a high level of fixed heterozygosity in an allopolyploid genotype *per se* allows for exploitation of several different niches; and 2) the special-purpose genotype hypothesis, which suggests that repeated alloploidizations involving genetically divergent progenitors result in different fixed-heterozygous genotypes, each of which may exploit a particular niche.

The evidence for multiple polyploid origins, differentiation into sibling diploids, and interploidal gene flow in *Draba* add to a growing data base suggesting that polyploid complexes represent considerably more dynamic genetic systems than previously envisioned. In *Draba*, the principal evolutionary importance of these processes is probably that they serve as escapes from genetic and ecological depauperation caused by uniparental inbreeding at the diploid level. These processes inevitably result, however, in incongruities between taxonomic and evolutionary entities in the genus, supporting the use of a wide species concept.

Keywords: Enzyme electrophoresis, DNA restriction site analysis, Crossing experiments, Polyploidy, Fixed heterozygosity, Multiple origins, Gene flow, Breeding systems, Ecological amplitude, *Draba*.

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# CONTENTS

# DISSERTATION CONTENTS

This thesis is based on the following papers, which will be referred to by their roman numerals:

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

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

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

IV      Brochmann, C. 1993. Reproductive strategies of diploid and polyploid populations of arctic *Draba* (Brassicaceae). - Pl. Syst. Evol. (in press).

V       Brochmann, C. & Elven, R. 1992. Ecological and genetic consequences of polyploidy in arctic *Draba* (Brassicaceae). - Evol. Trends Plants 6 (in press).

VI      Brochmann, C., Borgen, L. & Stedje, B. 1993. Crossing relationships and chromosome numbers of Nordic populations of *Draba* (Brassicaceae), with emphasis on the *D. alpina* complex. - Nord. J. Bot. (in press).

VII     Brochmann, C., Stedje, B. & Borgen, L. 1992. Gene flow across ploidal levels in *Draba* (Brassicaceae). - Evol. Trends Plants 6 (in press).

VIII    Brochmann, C. 1992. Pollen and seed morphology of Nordic *Draba* (Brassicaceae): phylogenetic and ecological implications. - Nord. J. Bot. 12 (in press).

Some results have also been presented at international symposia:

1       Brochmann, C. 1988. Reproductive biology of arctic *Draba*: degrees of autogamy, population strategies, and evolutionary consequences. - "Arctic Botany Workshop", Tromsø, Norway, Sept. 28-30.

2       Brochmann, C., Borgen, L. & Stedje, B. 1989. Chromosome numbers and crossing experiments in Nordic populations of *Draba* (Brassicaceae). - "Evolution in Higher Plants: Patterns and Processes", Oslo, Norway, June 4-7; and "4th International Symposium of Plant Biosystematics: Biological Approaches and Evolutionary Trends in Plants", Kyoto, Japan, July 10-14.

3      Brochmann, C., Soltis, P.S. & Soltis, D.E. 1989.   Evolutionary trends in Nordic
       populations of *Draba* (Brassicaceae). - "4th International Symposium of Plant
       Biosystematics: Biological Approaches and Evolutionary Trends in Plants", Kyoto,
       Japan, July 10-14.

4      Brochmann, C., Soltis, P.S. & Soltis, D.E. 1990.  Multiple reticulations in a polyploid
       complex: recurring alloploidy in arctic-alpine *Draba*. - "ICSEB IV.  4th International
       Congress of Systematic and Evolutionary Biology", Maryland, USA, June 30 - July 7.

# INTRODUCTION

## POLYPLOID EVOLUTION

Polyploidy is a significant mode of speciation in vascular plants, and represents an extreme form of abrupt evolution by which new species may be formed after only a few generations (e.g., deWet 1980). Given the high proportion of extant angiosperm species which probably have experienced polyploidy in the course of their history (possibly about 50%; Grant 1963, 1981, Goldblatt 1980), it is not surprising that this feature of chromosomal evolution for a long time has attracted the attention of numerous evolutionary biologists (e.g., Winge 1917, Clausen et al. 1945, Stebbins 1947, 1950, 1980, 1984, 1985, Roose & Gottlieb 1976, deWet 1980, Ehrendorfer 1959, 1980, Lewis 1980, Grant 1981, Jackson & Hauber 1983, Levin 1983, Bothmer et al. 1987, 1988, 1989, Stebbins & Dawe 1987, Barrett & Shore 1989, D.E. Soltis & P.S. Soltis 1989, 1990, Bothmer 1990, Bayer et al. 1991). Polyploidy is typically associated with intra- or interspecific hybridization and serves as an efficient escape from hybrid sterility (e.g., Grant 1981). A crucial point in the traditional model of polyploid speciation is that hybrids not only re-establish full fertility through polyploidization, but that they also attain immediate reproductive isolation from their progenitors because of the chromosome number barrier (e.g., Stebbins 1950, Stace 1980, Stuessy 1990).

It has often been suggested that the principal evolutionary importance of polyploidy is as a means of stabilizing favourable new gene combinations derived from hybridization between races with different adaptive norms (e.g., Stebbins 1950, 1980, 1984, 1985, Lewis 1980). In allopolyploids, a combination of adaptive strategies inherited from different diploid progenitor species may be preserved as fixed heterozygosity (Stebbins 1985). Thus, a relationship between increased heterozygosity and potential for exploitation of ecological niches may account for the success of polyploidy as an evolutionary mechanism in plants. High levels of heterozygosity in polyploids may not only provide a possibility for invasion of a particular new habitat, but also of a wide range of habitats; i.e., genetic variation in polyploids may promote ecological flexibility (e.g., Lewis 1980, Levin 1983). Few empirical data are, however, available on the possible relationship between ecological and genetic variation in polyploids, and more studies of the adaptive significance of polyploidy are needed (Ehrendorfer 1980, Stebbins 1984, Bayer et al. 1991).

Most studies of the relationship between reproductive systems and ploidal levels in plants have focused on the close correlation between agamospermy and polyploidy (e.g., Gustafsson 1946, 1947a, b, Asker 1984, Bierzychudek 1985, 1987, 1989, 1990, Richards 1986). In sexual plant groups, it has frequently been argued that the probability for long-term establishment of polyploids is greatest if newly arisen polyploids are self-fertilizing, because selfing in a polyploid results in fertile progeny whereas backcrossing to its parents results in sterile progeny (e.g., Stebbins 1971, Grant 1981). In addition, genetic disadvantages of selfing may be reduced in polyploids because of the buffering effect of duplicated loci, and autogamous polyploids may, therefore, maintain higher levels of heterozygosity than autogamous diploids (e.g., Richards 1986, Barrett & Shore 1989). It has also been hypothesized that allopolyploids may tolerate more selfing than diploids because their 'genetic

load' of deleterious recessive alleles may be effectively tied up as fixed heterozygosity (e.g., Lande & Schemske 1985).

Molecular approaches have recently emerged as powerful tools in the analysis of polyploids, and may provide novel or complementary insights into polyploid evolution. The use of enzyme electrophoresis and restriction site analysis of chloroplast DNA (cpDNA) and nuclear ribosomal RNA genes (rDNA) has greatly increased our ability to distinguish between auto- and allopolyploids, identify the parental genomes of polyploids, and document multiple origins of polyploids (D.E. Soltis & P.S. Soltis 1990, P.S. Soltis et al. 1991). Notably, multiple origins of polyploids have recently been demonstrated in several genera based on molecular data, e.g., *Asplenium* (Werth et al. 1985), *Plagiomnium* (Wyatt et al. 1988), *Hemionitis* (Ranker et al. 1989), *Heuchera* (D.E. Soltis et al. 1989, Wolf et al. 1990), *Tragopogon* (D.E. Soltis & P.S. Soltis 1989, 1990), *Glycine* (Doyle et al. 1990), and *Senecio* (Ashton & Abbott 1992). Furthermore, enzyme electrophoresis provides fairly easily accessible genetic markers for estimating heterozygosity and breeding system characteristics (e.g., Hamrick et al. 1979, Hamrick 1989).


## THE TAXONOMIC COMPLEXITY IN *DRABA*: CURRENT EXPLANATIONS


*Draba* L. (Brassicaceae) is a taxonomically complex genus with about 350 species, of which most are perennials of arctic and alpine areas (Al-Shehbaz 1987). The genus contains numerous polyploid species (Bolkhovskikh et al. 1969, Löve & Löve 1975, Mulligan 1976, Goldblatt 1981, 1984, 1985, 1988, Goldblatt & Johnson 1990). The polyploids in particular present vexing taxonomic problems, and delimitation of species and infrageneric classifications in *Draba* have been continuously and vigorously debated among taxonomists for many decades (e.g., Ekman 1912, 1917, 1926, 1931, 1932a, b, 1936, Pohle 1925, Schulz 1927, Fernald 1934, Seidenfaden & Sørensen 1937, Tolmachev 1939, 1957, 1975, Hitchcock 1941, Hultén 1958, 1968, Walters 1964, Böcher 1966, Knaben 1966, Buttler 1967, Mulligan 1970, 1971a, b, 1972, 1974a, b, 1975, 1976, Al-Shehbaz 1987, Avetisjan 1979, Berkutenko 1979).

Several hypotheses have been presented to explain the intricate morphological and chromosomal variation in the genus. Extensive natural hybridization resulting in primary interspecific hybrids has been suggested to confound taxonomic relationships (e.g., Schulz 1927, Ekman 1932a, b, 1936, Hultén 1958, 1968). Other authors (e.g., Fernald 1934, Knaben 1966) have claimed, however, that many postulated hybrids merely represent variation within poorly circumscribed, polymorphic species. Apomixis, combined with interspecific hybridization and polyploidy, has also been suggested as a cause of the taxonomic confusion in the genus (Rollins 1966). It has also been hypothesized that the intricate patterns of variation may be explained by recurrent formation of similar polyploids, and that a given taxonomic species therefore may be of polytopic origin (Böcher 1966).

There is, however, limited experimental evidence available that can be used to evaluate these hypotheses, and the mode of formation (allopolyploidy versus autopolyploidy) and parentage of polyploid *Draba* are largely unknown. Crossing experiments between Canadian species of *Draba* invariably produced sterile $F_1$ hybrids, and it was concluded that interspecific hybridization is rare in nature and always results in sterile first-generation hybrids (Mulligan 1974b, 1975, 1976). Agamospermy has been documented in a few species only (Mulligan &

| Section Drabella DC. x = 5; petals yellow | Section Chrysodraba DC. x = 8; petals yellow | | Section Draba x = 8; petals white |
|---|---|---|---|
| **16x** | | D. corymbosa R. Br. ex DC. (SB) | |
| **10x** | | D. alpina L. s. str. (SN, NN, SB) | D. alpina complex; petals large | D. arctica J. Vahl (SB) |
| **8x** D. crassifolia Grah. (NN) | D. oxycarpa Sommerf. (SN, NN, SB) | D. alpina s. lat. | D. cacuminum E. Ekm. (SN, NN) D. daurica DC. (incl. D. dovrensis Fr.; SN, NN, SB) |
| **6x** | D. adamsii Ledeb. (SB) | | D. cinerea Adams (NN) D. lactea Adams (SN, NN, SB) D. norvegica Gunn. (SN, NN, SB) |
| **4x** | D. micropetala Hook. (SB) | D. adamsii complex; petals small | D. incana L. (SN, NN) |
| **2x** | | | D. fladnizensis Wulf. (SN, NN, SB) D. nivalis Liljebl. (SN, NN, SB) D. subcapitata Simmons (SB) |

Fig. 1. Survey of the currently recognized taxonomic species and sections of arctic-alpine *Draba* in the Nordic area, their ploidal levels, and their geographic distributions in the area investigated (SN - southern Norway, NN - northern Norway, SB - Svalbard, Spitsbergen).

Findlay 1970, Mulligan 1971a, 1972, 1976, Price 1980), whereas most species of *Draba* appear to be sexual autogams (Mulligan & Findlay 1970, Al-Shehbaz 1987).

## *DRABA* IN THE NORDIC AREA

The populations analyzed in this study were referred to 16 taxonomic species, representing all of the arctic-alpine species of *Draba* which currently are recognized in Scandinavia and the arctic archipelago of Svalbard (Bretten 1973, 1990, Rønning 1979, Lid 1985, Elven & Elvebakk in press; *D. dovrensis* is included in *D. daurica*, cf. Knaben & Engelskjøn 1967).
     Chromosome numbers have previously been determined in 13 species based on Nordic material (Engelskjøn 1979). Chromosome numbers in 82 populations representing all of the 16 species were obtained in the present study (Fig. 1; [VI]). Three species, *D. fladnizensis*, *D. nivalis*, and *D. subcapitata*, are diploids, and 13 species are polyploids ranging from

tetraploid to 16-ploid. The species have been referred (Schulz 1927, Walters 1964) to sect. *Draba* (ten white-flowered species), sect. *Chrysodraba* (five yellow-flowered species), and sect. *Drabella* (*D. crassifolia*; yellow-flowered). The basic chromosome number is x = 8 in the sections *Draba* and *Chrysodraba*. *Draba crassifolia* has 2n = 40 and has been proposed to be tetraploid based on x = 10 (e.g., Mulligan 1975) or pentaploid based on x = 8 (Böcher 1966). The number of duplicated electrophoretic loci observed in this species suggests, however, that it is octoploid based on x = 5 (Fig. 1; [III]).

Most Nordic species of *Draba* are circumpolar or belong to species complexes with a circumpolar distribution (Tolmachev 1975, Hultén & Fries 1986). Only one species, the octoploid *D. cacuminum*, is endemic to the Nordic area and has frequently been considered an example supporting the glacial survival theory (e.g., Ekman 1917, Rune 1950, Gjærevoll & Sørensen 1954, Gjærevoll 1973, Dahl 1989). The southern populations of this species have been referred to ssp. *cacuminum* and the northern ones to ssp. *angusticarpa* Elven, putatively representing geographically diverged remnants of a more continuously distributed ancestor (Elven & Aarhus 1984).

## THE PRESENT STUDY

This paper reviews an integrated study of populations of *Draba* from Norway and Svalbard based on data obtained from enzyme electrophoresis [I-III, partly V, VII], restriction site analyses of cpDNA and rDNA [II], cytology and crossing experiments [VI, VII], analysis of natural hybrids [VII], reproductive biology [IV], habitat differentiation [V], and, to a limited extent, comparative morphology of cultivated populations [I, VIII].

The study was initially aimed to clarify taxonomic relationships among Nordic species, in particular the poorly understood *D. alpina* complex, based on a traditional biosystematic approach. It soon became apparent, however, that the already extremely voluminous taxonomic literature on *Draba* reflected widely divergent opinions with respect to delimitation of species as well as intrageneric relationships (see references above), and that additional taxonomic studies would benefit from increased knowledge of the underlying processes responsible for the complex patterns of morphological and chromosomal variation in the genus. Thus, the main focus of the present study changed from the more purely taxonomic one to one attempting to provide an evolutionary framework for a better understanding of this complex variation, with the hope that this, in turn, will allow for application of more stable taxonomic concepts in *Draba*.

Of particular interest was the possible relationship between polyploid evolution and genetic variation, breeding systems, and ecological tolerance in *Draba*. We also attempted to clarify phylogenetic relationships among Nordic populations, although the geographic restriction of the study clearly would limit the possibility of unraveling the evolutionary history of many of these widespread species. The following main issues were addressed: 1) the mode of formation (allo- vs. autoploid) of the polyploids; 2) the progenitors of the polyploids; 3) the possibility for multiple origins of the polyploids; 4) the possibility for gene flow between species through semi-fertile hybrids; 5) the possible relationship between breeding system and genetic variation in diploids versus polyploids; 6) the possible relationship between ecological amplitude and genetic variation in diploids versus polyploids;

and 7) the inheritance of taxonomically important morphological characters in artificial hybrids and its significance for a) possible morphological identification of progenitors of polyploids and parents of natural hybrids, and b) taxonomic concepts in the genus.

# SUMMARY OF PAPERS

PAPER I: Multiple origins of the octoploid Scandinavian endemic *Draba cacuminum*: electrophoretic and morphological evidence

The endemic status and disjunct distribution of the octoploid *Draba cacuminum* (Brassicaceae) have frequently been considered to support the glacial survival theory. Two subspecies, ssp. *cacuminum* (silicles broad) in southern Norway and ssp. *angusticarpa* (silicles narrow) in northern Scandinavia, have been described and suggested to be geographically diverged remnants of a more continuously distributed ancestor. To test an alternative hypothesis of independent origins of similar octoploids in different areas, we investigated populations of *D. cacuminum* and its possible progenitors using enzyme electrophoresis and morphological analysis. Electrophoretic analysis of progeny of *D. cacuminum* revealed high levels of fixed heterozygosity, demonstrating that the species is a genetic allopolyploid. Fixed electrophoretic differences among the populations and additivity of electrophoretic phenotypes indicate that the octoploid *D. cacuminum* has originated at least three times by alloploidizations involving different populations of the hexaploid *D. norvegica* and a diploid species, possibly *D. fladnizensis*. Electrophoretic and morphometric data suggest that populations of *D. cacuminum* with broad silicles have originated from populations of *D. norvegica* with broad silicles, and that populations of *D. cacuminum* with narrow silicles have originated from populations of *D. norvegica* with narrow silicles. However, the electrophoretic and morphometric variation within *D. cacuminum* did not correspond to the geographic origin of the populations, and the previously described subspecies could not be recognized. *Draba cacuminum* gives no relevant information on the glacial survival theory; the polyploidizations may have occurred in postglacial time as well as in pre-Weichselian periods.

PAPER II: Recurrent formation and polyphyly of Nordic polyploids in *Draba* (Brassicaceae)

It has been suggested that polyploids in *Draba* may have formed recurrently from different populations of the parental species (polytopy), and it is also possible that a given taxonomic species may actually comprise several polyploid races, each originating from different progenitor species (polyphyly). To unravel the taxonomic complexity of polyploid *Draba* in the Nordic area, three of the most morphologically variable species and their possible progenitors were investigated using enzyme electrophoresis and restriction site analysis of cpDNA and rDNA: *D. norvegica* (6x), *D. lactea* (6x), and *D. corymbosa* (16x). Electrophoretic analysis of progeny showed high levels of fixed heterozygosity in all three polyploids, demonstrating that all are genetic allopolyploids. Electrophoretic and rDNA data indicate that polytopic and/or polyphyletic origins have contributed to the complexity of these polyploids, whereas a lack of cpDNA variation limited the usefulness of this molecule for analysis of polyploid origins. The considerable electrophoretic variation observed in *D.*

*norvegica* suggests that these hexaploid populations have originated at least three and probably 13 times. Electrophoretic and rDNA data suggest that *D. lactea* and *D. corymbosa* are polyphyletic polyploids. Given the widespread geographic distributions of these species and their possible progenitors, and that the populations analyzed represent only a small fraction of their geographic distributions, it is likely that these species have formed numerous times in different areas.

PAPER III: Electrophoretic relationships and phylogeny of Nordic polyploids in *Draba* (Brassicaceae)

104 populations of 15 Nordic species (2x-16x) of the taxonomically complex genus *Draba* were investigated using enzyme electrophoresis. In contrast to the polyploids, which were genetic alloploids showing high levels of fixed heterozygosity and electrophoretic variation, the diploids were homozygous and genetically depauperate. This result suggests that alloploidy in arctic-alpine *Draba* may serve as an escape from genetic depauperation caused by inbreeding at the diploid level. Although some populations probably have local alloploid origins, electrophoretic data indicate that several polyploids have migrated repeatedly into the Nordic area. *Draba crassifolia* (2n = 40) is probably octoploid based on x = 5. A hypothesis on the evolutionary history of the polyploids based on x = 8 is presented. Diploids contributing to numerous polyploid genomes and multiple origins of polyploids may seriously have blurred taxonomic relationships. The relationships inferred from genetic data do not always correspond to those based on morphology; two morphologically very similar polyploids, *D. alpina* and *D. oxycarpa*, were, for example, genetically distant and probably represent independent lineages.

PAPER IV: Reproductive strategies of diploid and polyploid populations of arctic *Draba* (Brassicaceae)

To clarify a possible relationship between reproductive strategies and polyploid evolution in *Draba*, reproductive traits of 132 cultivated populations (2x-16x) of 15 arctic-alpine species were investigated. The populations were exclusively sexual and produced viable seed after spontaneous self-pollination, but showed large variation both in traits promoting cross-pollination and in autogamous fruit and seed set. Traits promoting cross-pollination, e.g., floral display, protogyny, and delayed selfing, were positively correlated, and these traits were negatively correlated with autogamous fruit and seed set. All diploid and many polyploid populations had high autogamous seed set and small, unscented, non-protogynous, and rapidly selfing flowers. In contrast, all populations with low autogamous seed set and large, scented, and strongly protogynous flowers with distinctly delayed selfing were polyploid. These results are consistent with enzyme electrophoretic data, suggesting that the diploids are extreme inbreeders and that the polyploids vary from extreme inbreeders to mixed maters. The reproductive data lend additional support to the hypothesis that allopolyploidy in arctic *Draba*

serves as an escape from genetic depauperation caused by uniparental inbreeding at the diploid level.

PAPER V: Ecological and genetic consequences of polyploidy in arctic *Draba* (Brassicaceae)

In this paper, we examined possible differences in ecological amplitude between the diploid and polyploid species of *Draba* in the Nordic area, and analyzed the possible relationship between habitat differentiation and breeding strategies. The habitats of 443 populations of three diploid and 13 polyploid species (4x - 16x) of *Draba* were classified into 17 habitat types based on relative importance of competition, stress, and disturbance, and positioned into Grime's CSR-triangle for plant strategies. The diploid species occupied largely similar, restricted niches and were predominantly selfing stress-tolerators setting few, small seeds. Most polyploid species occurred in a wide range of niches and were either moderately selfing, stress-tolerant competitors setting few, large seeds, or predominantly selfing ruderals setting many, small seeds. Although the alloploid condition buffers the effect of inbreeding with respect to loss of variability, the results suggest that mixed mating nevertheless is advantageous in polyploids occurring in habitats with high levels of competition. Ecological amplitude as well as heterozygosity and biochemical diversity in *Draba* increased significantly with ploidal level. The evolutionary success of allopolyploidy in this genus may, therefore, be based on increased ecological as well as genetic potential.

PAPER VI: Crossing relationships and chromosome numbers of Nordic populations of *Draba* (Brassicaceae), with emphasis on the *D. alpina* complex

101 populations of Nordic *Draba* were investigated for chromosome numbers and crossing relationships. The populations were referred to 16 currently recognized species of sect. *Draba*, sect. *Chrysodraba* (including the *D. alpina* complex with *D. alpina*, *D. oxycarpa*, and *D. corymbosa*), and sect. *Drabella*. The chromosome data suggest that all populations and species are homoploid. Three species are diploid, and 13 species are polyploids ranging from tetraploid to 16-ploid. *Draba alpina* is decaploid, *D. oxycarpa* is octoploid, and *D. corymbosa* is 16-ploid. The chromosome numbers of *D. micropetala* (n = 16, 4x) and *D. adamsii* (n = 24, 2n = 48, 6x) of sect. *Chrysodraba* and *D. cinerea* (n = 24, 6x) of sect. *Draba* were determined for the first time based on Nordic material. The relationships inferred from the crossing data largely agree with those inferred from previously published molecular data, but correspond poorly to relationships inferred from morphology. Interpopulational $F_1$ hybrids in *D. fladnizensis* were entirely sterile, suggesting that this predominantly inbreeding diploid species comprises at least two sibling species, possibly isolated by genic barriers. Sterile to semifertile $F_1$ hybrids with intermediate chromosome numbers were obtained in 19 interspecific combinations. $F_2$ hybrids were obtained in seven of these combinations. Both sect. *Chrysodraba* and the *D. alpina* complex are probably polyphyletic. The crossing data suggest that the morphologically very similar polyploids *D. alpina* and *D. oxycarpa* do not

have any diploid progenitors in common, and that sect. *Draba* forms an intricate alloploid complex that also includes *D. alpina* and *D. corymbosa* of sect. *Chrysodraba*. *Draba corymbosa* (16x) is probably an intersectional, polyphyletic alloploid derived from *D. alpina* (10x) and various hexaploids of sect. *Draba*. Crossing data also suggest that *D. norvegica* (6x) is one of the progenitors of the Nordic endemic *D. cacuminum* (8x). The phenotypic expression of genes encoding taxonomically important indument characters did not follow consistent patterns in interspecific hybrids. This result may explain the discrepancy between genetic and taxonomic relationships in Nordic *Draba*, and supports the use of wide taxonomic concepts in this highly reticulate genus.

PAPER VII: Gene flow across ploidal levels in *Draba* (Brassicaceae)

The traditional model of polyploid speciation suggests that a polyploid is reproductively isolated from its progenitors because of the chromosome number barrier. In the genus *Draba*, natural interploidal hybrids do occur but have been considered always to represent sterile first-generation hybrids. To re-examine this claim, we analyzed experimental and natural putative interspecific hybrids between Nordic allopolyploids in *Draba* using chromosomal, fertility, and enzyme electrophoretic data. Adult experimental $F_2$ hybrids were obtained in five interploidal combinations after selfing $F_1$ hybrids that had the expected, intermediate chromosome numbers. $F_2$ hybrids of *D. cacuminum* x *norvegica* (8x x 6x) ranged from completely sterile to fully fertile, and $F_3$ hybrids were obtained in this combination as well as *D. alpina* x *cacuminum* (10x x 8x) and *D. alpina* x *corymbosa* (10x x 16x). Chromosomal, fertility, and electrophoretic data suggest that three field-collected populations contain later-generation hybrids and/or backcrosses derived from *D. incana* x *norvegica* (4x x 6x), *D. daurica* x *nivalis* (8x x 2x), and *D. arctica* x *corymbosa* (10x x 16x), respectively. Progeny were raised after selfing several field-collected hybrids. The results demonstrate that interspecific hybridization across ploidal levels in *Draba* may result in re-establishment of fertility and probably of euploid chromosome numbers. We have earlier shown that the taxonomic complexity in *Draba* may be explained by recurrent formation of allopolyploids. Interspecific gene flow across ploidal levels provides an additional explanation for the taxonomic complexity in the genus.

PAPER VIII: Pollen and seed morphology of Nordic *Draba* (Brassicaceae): phylogenetic and ecological implications

Pollen and seed morphology were examined in 54 diploid and allopolyploid populations representing 15 Nordic species of *Draba*. The pollen size was strongly correlated with chromosome number, but it was unreliable for inferring the exact ploidal level of individual populations. Five main pollen types were recognized based on sculpturing of the exine. Two populations of *D. lactea* had conspicuously different exine sculpturing, supporting a previous hypothesis based on molecular data that this hexaploid is polyphyletic and has been derived

from various combinations of diploid species. The pollen morphological data are also consistent with the hypotheses that the 16-ploid *D. corymbosa* is an intersectional allopolyploid derived from the sections *Draba* and *Chrysodraba*, that the hexaploid *D. cinerea* is a progenitor of the decaploid *D. arctica*, and that *D. crassifolia* and *D. adamsii* represent isolated allopolyploid lineages. The seed size and weight were only weakly correlated with chromosome number, but showed a close relationship to habitat ecology. The largest seeds were observed in species typical of closed habitats, in which seedling establishment probably is limited by competition with mosses. The seed coat surface had a characteristic verrucate reticulum, but the differentiation among species was vague or absent. The seed size and colour, however, distinguished some species, e.g., in the *D. alpina* complex, which otherwise are morphologically very similar.

# GENERAL DISCUSSION AND CONCLUSIONS

The genetic data obtained from enzyme electrophoresis [I-III, VII], experimental and natural hybrids [VI, VII], and to a limited extent, DNA restriction site analysis [II] and comparative morphology of cultivated populations [I, VI, VIII] demonstrate that the evolutionary relationships among Nordic populations of *Draba* are extremely complex. Although the geographic restriction of the study limited the possibility of clarifying the complete evolutionary history of the polyploids, several basic features of polyploid evolution in the genus can be recognized. Data on reproductive traits [IV, VIII], habitat differentiation [V], and enzyme electrophoretic variation [III] further suggest that there is a close relationship between polyploid evolution and genetic variation, breeding systems, and ecological tolerance in *Draba*. Detailed discussions are given in the individual papers [I-VIII]. The following list summarizes the most important results and their implications, of which some are considered in more detail in succeeding sections of this chapter.

1) *Allopolyploidy* - All Nordic polyploids are allopolyploids in the genetic sense because disomic inheritance and almost exclusively fixed heterozygosity were observed in their progeny [I-III]. Thus, each polyploid genome contains non-homologous (or possibly partly homologous) sets of diploid genomes originally contributed from genetically divergent diploid ancestors.

2) *Multiple origins* – Several of the polyploid species have probably originated recurrently, some of them even polyphyletically, in the sense that they have originated repeatedly from different sets of progenitor species [I-III, VI, VIII]. It should be noted that an allopolyploid species per definition is polyphyletic in origin. In cases of multiple alloploid origins, however, the polyploids may have originated from different plants within the same populations or from different populations within the same species (i.e., polytopic origins), or from different species (i.e., polyphyletic origins in the present context).

3) *Sibling diploid species* - Some of the allopolyploid populations examined may have originated from sibling species that all belong to a single diploid taxonomic species [II, III, VI]. Only a few artificial crosses between diploid populations were attempted, but cross-incompatible populations or 'sibling' species were nonetheless demonstrated within the diploid *D. fladnizensis* [VI]. The electrophoretic data suggest that some populations of the genetically allohexaploid *D. lactea* may have originated from sibling diploid species [II]. Sibling diploids may be common in arctic *Draba* because mutations causing cross-incompatibility may become readily fixed in the diploid populations due to their high levels of inbreeding.

4) *Interploidal gene flow* - The interspecific crosses demonstrated that it is possible to obtain artificial later-generation hybrids across ploidal levels in *Draba* [VI, VII], and the analyses of natural populations suggest that interspecific hybridization and subsequent gene flow across ploidal levels also occur in natural situations [VI].

5) *Phylogeny* - *Draba crassifolia* of sect. *Drabella* is probably based on x = 5 and represents an evolutionary lineage in the genus very distant from that based on x = 8 (sections *Draba* and *Chrysodraba*). The species based on x = 8 show low levels of cpDNA and rDNA divergence, suggesting that they are closely related and that the polyploids have originated recently. Section *Chrysodraba* is probably polyphyletic. The small-flowered hexaploid *D. adamsii* (possibly together with the tetraploid *D. micropetala*) represents a distinct lineage,

whereas the large-flowered, high-polyploid *D. alpina* complex probably should be included in sect. *Draba* (cf. Fig. 1). Section *Draba* forms an intricate phylogenetic network that also includes *D. alpina* and *D. corymbosa* of sect. *Chrysodraba* [I-III, VI, VIII].

6) *Local alloploid origins and repeated immigrations* - The electrophoretic and rDNA data suggest that some of the polyploid populations have originated locally in the Nordic area (i.e., *D. cacuminum* and south-Norwegian *D. lactea*), whereas at least some of the polyploid species (e.g., *D. alpina*) have migrated repeatedly into the area [I-III]. The conspicuous lack of geographically structured variation within species of *Draba* in morphological characters (Tolmachev 1953) as well as at electrophoretic loci [I, III] is most easily explained by frequent migration of populations during major climatic changes. This conclusion agrees with that of a study of Quaternary vegetation history by Alm & Birks (1991), who argued that traditional descriptive plant geographers tend to have a view of the arctic flora that is too static, and Savile (1972), who suggested that arctic plants have considerably higher dispersal capacity than usually believed.

7) *Inheritance of morphological characters* - The phenotypic expression of genes encoding taxonomically important morphological characters does not follow consistent patterns in interspecific artificial hybrids [VI]. This result suggests that morphological characters should be used with caution when attempting to identify the parents of natural hybrids and the progenitors of polyploids in *Draba*, and supports the use of broad taxonomic concepts in this highly reticulate genus.

8) *Sexuality and self-compatibility* - All species are exclusively sexual and self-compatible, and set viable seed after spontaneous self-pollination [IV].

9) *Inbreeding and mixed mating* - In contrast to the diploids, which all are extreme, uniparental inbreeders, the polyploids probably vary from extreme, uniparental inbreeders to mixed maters [III, IV].

10) *Ecological and reproductive strategies* - The diploids are genetically depauperate, predominantly selfing stress-tolerators occupying restricted ecological niches, whereas most of the polyploids have high levels of genetic variation, occupy a wide range of niches, and are either moderately selfing, stress-tolerant competitors or predominantly selfing ruderals [IV, V]. Mixed mating appears, therefore, advantageous in polyploids occurring in competitive habitats.

11) *Ecological amplitude and genetic variation* - Ecological amplitude, heterozygosity, and biochemical diversity are positively correlated and increase significantly with ploidal level. Two hypotheses, the general-purpose genotype hypothesis and the special-purpose genotype hypothesis, are advanced to explain these correlations [V].

## MULTIPLE POLYPLOID ORIGINS AND INTERPLOIDAL GENE FLOW

This study provides experimental evidence supporting Böcher's intuitive hypothesis on multiple origins in *Draba* (Böcher 1966; [I-III]). The evidence for multiple origins of polyploids was primarily obtained from the electrophoretic variation observed within and among polyploid species [I-III], partly also from rDNA [II], crossing [VI], and morphological data [I, VIII]. An alternative explanation, i.e., evolution within species after a single polyploid origin, necessitates numerous parallel mutations at electrophoretic loci, which is very unlikely,

especially given the very low levels of restriction site divergence that were detected among species in cpDNA and rDNA [II].

Two major lines of evidence support the hypothesis of multiple origins. The first is that the variation within some polyploid species parallels the variation within their most probable progenitor species. The electrophoretic and morphometric variation within the octoploid Scandinavian endemic *D. cacuminum*, for example, parallels the variation within one of its probable progenitors, the hexaploid *D. norvegica* [I]. This result suggests that the intraspecific variation within *D. cacuminum*, rather than being caused by evolution within the species after its origin, is a consequence of multiple origins from differentiated progenitors: populations of *D. cacuminum* with broad silicles (the south-Norwegian subspecies 'cacuminum') have probably originated from populations of *D. norvegica* with broad silicles, whereas populations of *D. cacuminum* with narrow silicles (the North Scandinavian subspecies 'angusticarpa') have probably originated from populations of *D. norvegica* with narrow silicles. However, populations with broad silicles as well as populations with narrow silicles have probably originated in northern Norway, and the subspecies could not be recognized. Another example is that south-Norwegian *D. lactea* (hexaploid) and south-Norwegian *D. fladnizensis* (diploid) share an rDNA repeat length different from that shared among northern populations of these two species [II]. This result suggests that populations of *D. lactea* have originated locally in southern Norway with local *D. fladnizensis* as one of their progenitors, whereas northern populations of *D. lactea* have other origin(s).

The second line of evidence supporting the hypothesis of multiple polyploid origins is based on the observed high levels of intraspecific genetic variation *per se*. Multiple origins may be inferred directly from the intraspecific genetic variation observed in a polyploid species even if its progenitors cannot be recognized with certainty. The electrophoretic variation observed within the hexaploids *D. norvegica* (Fig. 2) and *D. lactea*, for example, cannot be explained by a single polyploid origin even if their progenitors are assumed to have been maximally heterozygous [II]. The number of lineages that can be derived from a single raw polyploid is limited by the fact that each diploid parent can have contributed a maximum of two different alleles at each locus. Thus, based on the electrophoretic variation observed within the populations examined, *D. norvegica* must have originated at least three times (Fig. 2) and *D. lactea* at least two times.

After the molecular analyses [I-III] were completed, however, the analyses of artificial and natural hybrids demonstrated that gene flow through semifertile, interploidal hybrids also may introduce novel genetic variation into established alloploid species of *Draba* [VI, VII]. This result was unexpected because artificial crosses between Canadian species of *Draba* always resulted in entirely sterile first-generation hybrids (Mulligan 1974b, 1975, 1976).

The high levels of fertility demonstrated in several artificial hybrids in the present study are particularly intriguing because the $F_1$ hybrids always had the expected, intermediate chromosome numbers which demonstrated that normal, reduced gametes were contributed from their parents [VI]. Notably, some interploidal second-generation hybrids were more fertile than first-generation hybrids and even re-established full fertility, as demonstrated in artificial $F_2$ hybrids obtained after selfing heptaploid $F_1$'s of *D. cacuminum* (octoploid) x *norvegica* (hexaploid; Fig. 3; [VII]). It is, however, not only possible to produce later-generation hybrids artificially in *Draba*, but it is also likely that interspecific gene flow in fact occurs across chromosome number barriers in natural situations [VII]. Enzyme electrophoretic, chromosomal, fertility, and progeny data suggest that field-collected hybrids collected at three natural sites represent later-generation segregates and/or backcrosses derived
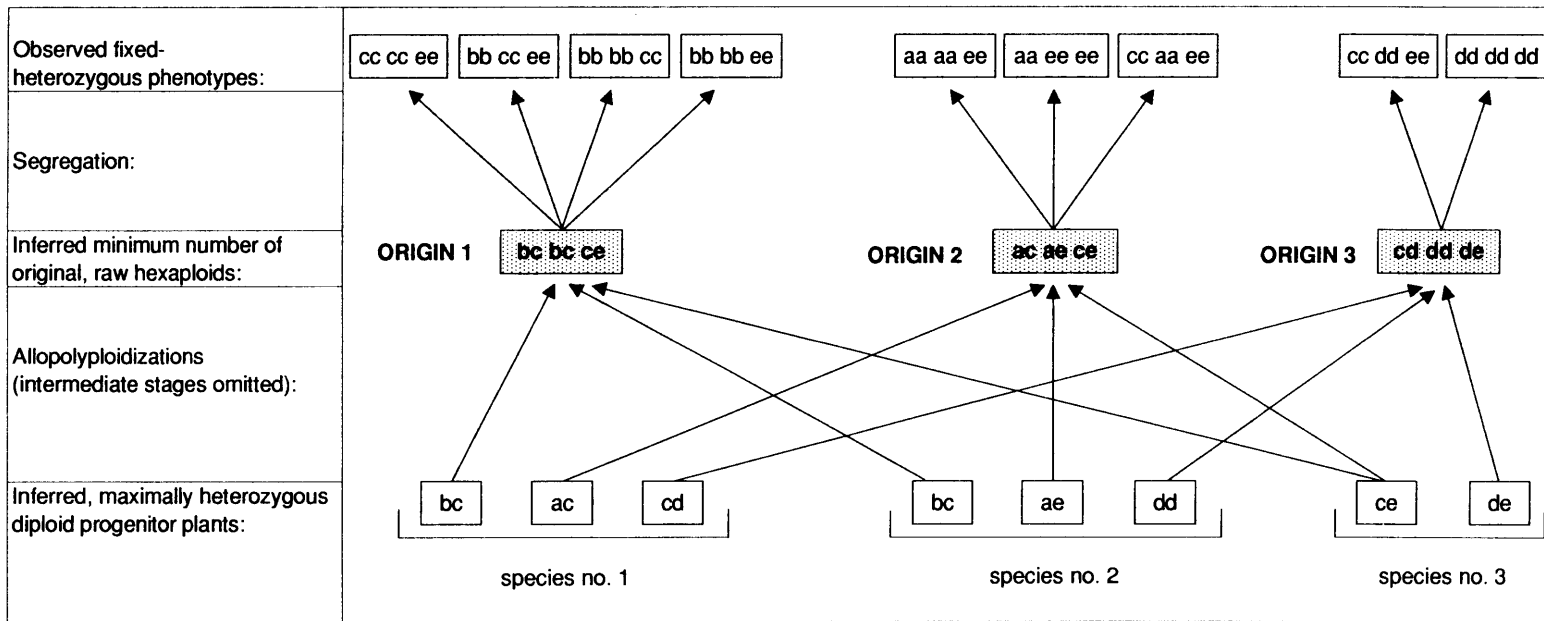
Fig. 2. Minimum number of origins of the allo-hexaploid *Draba norvegica*, inferred from the number of different fixed-heterozygous electrophoretic phenotypes observed at the most polymorphic "locus" ("*Pgi-2*") in Nordic populations, and allowing for maximal heterozygosity in the hypothetical diploid progenitor plants. For simplicity, allelic designations are used for the homomeric enzyme bands. Modified from [II].
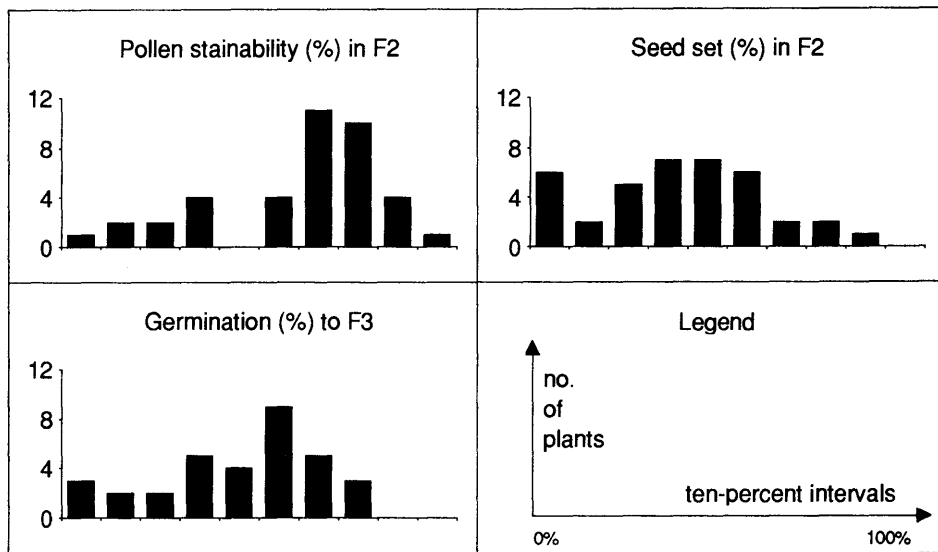
Fig. 3. Fertility of artificial F$_2$ hybrids of *Draba cacuminum* (octoploid) x *norvegica* (hexaploid), raised from seeds obtained after spontaneous selfing in heptaploid F$_1$ hybrids. Based on data from [VII].

from *D. incana* x *norvegica* (tetraploid x hexaploid), *D. arctica* x *corymbosa* (decaploid x 16-ploid), and *D. daurica* x *nivalis* (octoploid x diploid).

Although the limited chromosomal data [VII] do not provide definite evidence for re-establishment of stable, euploid chromosome numbers in plants derived from interploidal hybridization, the re-establishment of full fertility demonstrated in some later-generation hybrids suggests that their meiosis is regular. This result probably reflects that first-generation hybrids produce a mixture of balanced and variously unbalanced gametes which in some cases result in progeny with balanced genomes.

Interspecific gene flow resulting in novel genetic variation in a polyploid species of *Draba* may appear alternative to the hypothesis of multiple polyploid origins. Multiple alloploidizations (involving unreduced and reduced gametes; cf. deWet 1980) and interploidal gene flow between already established alloploid species (probably involving unreduced and variously reduced gametes) do not, however, necessarily represent basically different explanations for the complex patterns of variation in *Draba*. Both explanations involve processes such as crosses between genetically divergent populations, fusion of gametes with different chromosome numbers, and re-establishment of fertility in subsequent generations. Further studies of chromosome numbers and segregation in later-generation hybrids are necessary to clarify these processes. The available evidence nevertheless suggests that many polyploids in *Draba* are 'compilospecies', i.e., species which are genetically aggressive and repeatedly plunder related diploids and polyploids of their heredities (cf. Harlan & deWet 1963).

## PHYLOGENY OF NORDIC POLYPLOIDS

The electrophoretic data suggest that *D. crassifolia* (sect. *Drabella*) has the basic chromosome number x = 5 and represents an evolutionary lineage in the genus very distant from that of the x = 8 species [III]. Figure 5 presents a tentative and schematic hypothesis on the phylogeny of the species based on x = 8, i.e., sections *Draba* and *Chrysodraba*. This hypothesis is primarily based on enzyme electrophoretic [I-III] and crossing data (Fig. 4; [VI, VII]), and, to a limited extent, data from rDNA [II] and pollen morphology [VIII]. The genetic relationships inferred from the electrophoretic data are remarkably consistent with and also supplement those inferred from crossing data, but do not always correspond to taxonomic relationships (e.g., Schulz 1927, Tolmachev 1975; see [III]).

Both sect. *Chrysodraba* and the *D. alpina* complex (*D. alpina*, *D. oxycarpa*, and *D. corymbosa*; cf. Fig. 1) are probably polyphyletic (Figs. 4, 5). The crossing data as well as electrophoretic data suggest that both the hexaploid *D. adamsii* and the octoploid *D. oxycarpa* of sect. *Chrysodraba* represent independent alloploid lineages, whereas the decaploid *D. alpina* and the 16-ploid *D. corymbosa* of sect. *Chrysodraba* are closely related to sect. *Draba*. The most unexpected result was that the morphologically very similar polyploids *D. alpina* and *D. oxycarpa*, which both have large, yellow flowers and frequently are referred to a single taxonomic species, probably have no diploid progenitors in common [III, VI].

The hexaploid *D. adamsii* has a deviating pollen morphology [VIII], and no artificial hybrids were obtained between this and other species (Fig. 4; [VI]). These results as well as its electrophoretic phenotypes and conspicuously narrow petals suggest that *D. adamsii* represents the most distant lineage among the x = 8 polyploids. This lineage may also comprise the tetraploid *D. micropetala* (not analyzed; Fig. 1). In contrast, *D. oxycarpa* formed $F_1$ hybrids with several other species, and has a pollen morphology very similar to that of *D. alpina* as well as several species of sect. *Draba*. These results suggest that *D. oxycarpa*, although it probably has been derived from a separate group of diploids, most likely is more closely related to the other x = 8 species than is *D. adamsii*.

Section *Draba* probably forms an intricate neopolyploid complex that also includes *Draba alpina* and *D. corymbosa* of sect. *Chrysodraba* (Figs. 4, 5). In this complex, $F_1$ hybrids as well as $F_2$ and $F_3$ hybrids were obtained in many interspecific combinations. Most of these polyploids have probably originated recurrently, and are closely related through partly shared genomes mainly derived from a common stock of closely related diploid species (Fig. 5). The electrophoretic as well as crossing and pollen data suggest that *D. corymbosa* forms a high-polyploid bridge connecting the two sections. This species has probably originated polyphyletically from hybrids between *D. alpina* and several different species of sect. *Draba*. Thus, the results indicate that the *D. alpina* complex of sect. *Chrysodraba* rather should be included in sect. *Draba* (Figs. 1, 4, 5).

## INHERITANCE OF MORPHOLOGICAL CHARACTERS

The inheritance of taxonomically important characters in the artificial, interspecific $F_1$ and $F_2$ hybrids was complex [VI]. In overall morphology, most of the interploidal hybrids showed
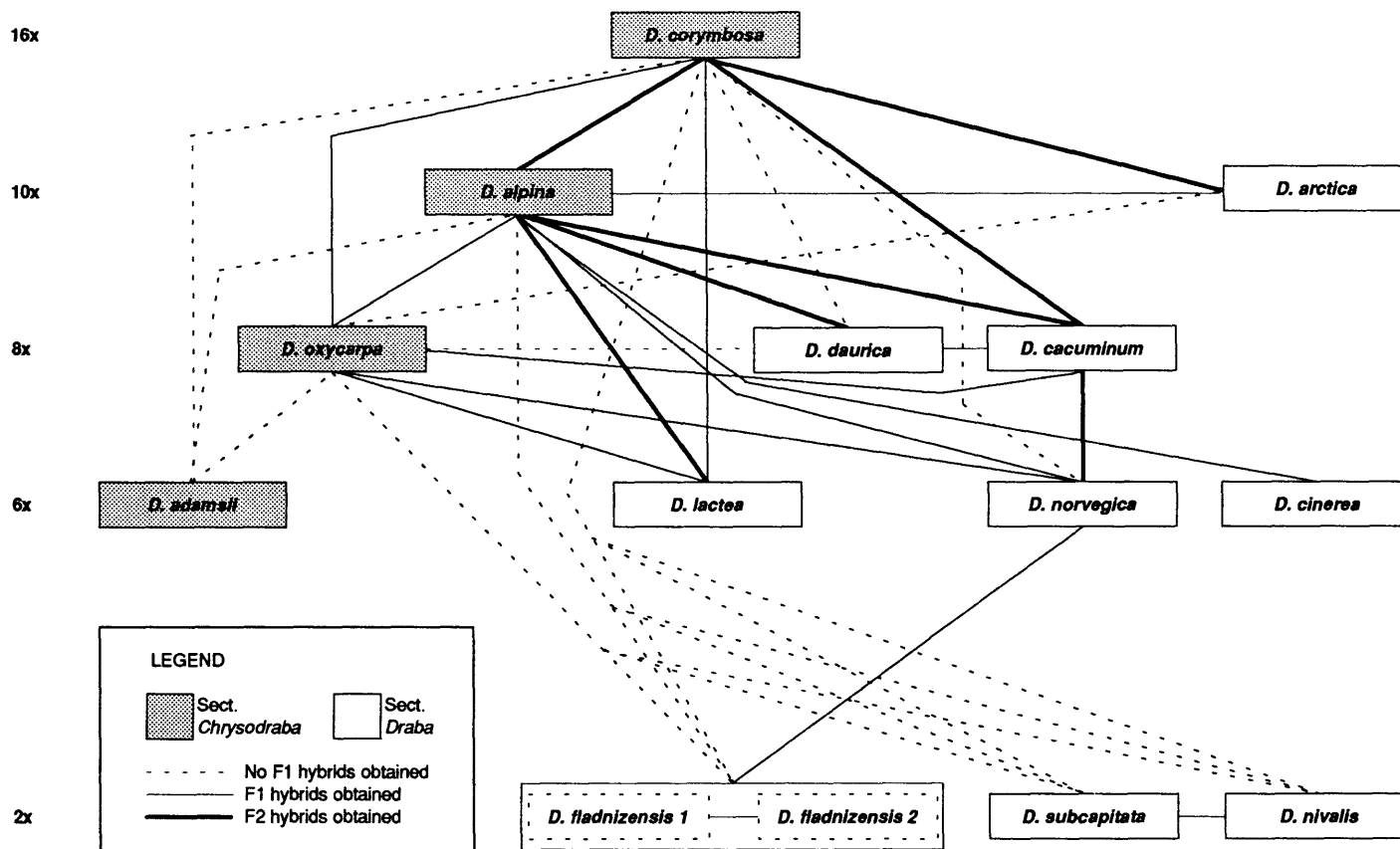
Fig. 4. Crossing relationships among Nordic species of *Draba*. Two cross-incompatible, sibling species are indicated within the diploid *D. fladnizensis*. Modified from [VI].
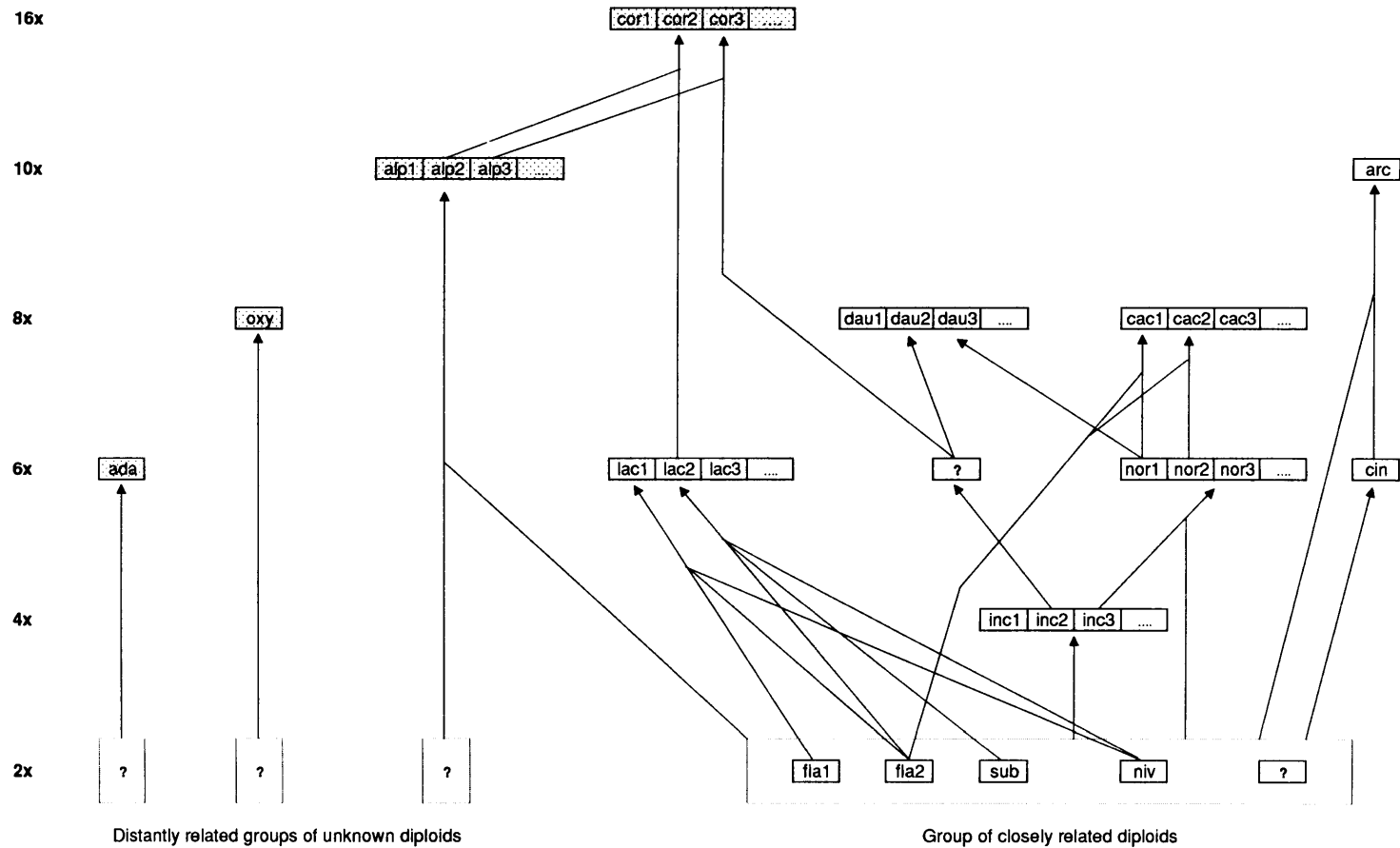
Fig. 5. A tentative, incomplete hypothesis on the phylogeny of Nordic polyploids of *Draba* with the basic chromosome number x = 8 (sections *Chrysodraba* (shaded) and *Draba*), based on enzyme electrophoretic, rDNA, crossing, and pollen morphological data. Multiple origins of polyploid species are indicated as, e.g., 'cac1, cac2' etc. in *D. cacuminum*. 'fla1' and 'fla2' designate two sibling species within the diploid *D. fladnizensis*. Species names are abbreviated by the first three letters (see Fig. 1). The tetraploid *D. micropetala* was not analyzed. For simplicity, intermediate ploidal stages in the origin of individual polyploids are not indicated if no explicit evidence was obtained. Modified from [III].

the expected similarity to the parent contributing the highest number of genomes. In a 16-ploid x hexaploid combination (*D. corymbosa* x *lactea*), however, the hybrids were conspicuously similar to the low-ploid parent. This result suggests that these hybrids in fact represent backcrosses between an alloploid derivative (*D. corymbosa*) and one of its progenitors (*D. lactea*; Fig. 5).

Most important, however, were the observations of the inheritance of individual morphological characters. Yellow petal colour, which has been used as a basic character at the sectional level in *Draba* (Schulz 1927), behaved almost completely recessively in the crosses between yellow- and white-flowered plants. Many of the $F_1$ hybrids had purely white petals, others had purely white petals in fully open flowers but slightly yellowish ones at early floral stages [VI]. No yellow flowers were observed in the few flowering artificial $F_2$ hybrids observed in these combinations, but observations of natural hybrids suggest that plants in later hybrid generations may regain more yellowish petals [VII]. This result, as well as the crossability and molecular data (Figs. 4, 5), suggests that petal colour has limited value as a taxonomic marker at the sectional level, and that the yellow-flowered *D. alpina* complex should be included in sect. *Draba*.

At the species level, the taxonomic tradition in *Draba* has relied primarily on indument characters such as the frequency and structure of stellate, branched, and simple hairs of various parts (e.g., Schulz 1927, Tolmachev 1975, Mulligan 1976). In contrast to petal colour, the phenotypic expression of genes encoding various indument characters did not follow consistent patterns in the interspecific hybrids. The most peculiar pattern was observed in the hybrids derived from one population of the octoploid *D. cacuminum*. Although this population had the dense, heterotrich silicle indument typical of the species, $F_1$ hybrids involving this population always had the silicle indument of the other parent. The inheritance of the peduncle indument did not, however, show the same pattern as silicle indument. A cross between this population of *D. cacuminum*, which had a densely heterotrich peduncle as well as silicle indument, and *D. norvegica*, which had glabrous peduncles and silicles, produced $F_1$ hybrids with heterotrich peduncles as *D. cacuminum* but glabrous silicles as *D. norvegica*. The $F_2$ hybrids showed highly asymmetric segregation for both characters, and 25 of 35 $F_2$ hybrids had glabrous peduncles as well as silicles [VI].

The results probably reflect complex effects of gene duplications in the polyploid hybrids, and provide an explanation for the inconsistencies between the genetic relationships inferred from crossing data and molecular data (Figs. 4, 5) and taxonomic relationships inferred from morphology (e.g., Schulz 1927, Walters 1964). The results suggest that morphological characters should be used with caution when attempting to identify the parents of natural hybrids or progenitors of polyploids, and support the use of a wide species concept in this highly reticulate genus.

## BREEDING SYSTEMS AND ECOLOGICAL STRATEGIES

The electrophoretic data demonstrated that the diploids are genetically depauperate with high levels of homozygosity and low levels of intra- as well as interpopulational variation [III]. The situation is conspicuously different in the polyploids, which are highly fixed-heterozygous and show high levels of interpopulational (but usually not intrapopulational) variation. These
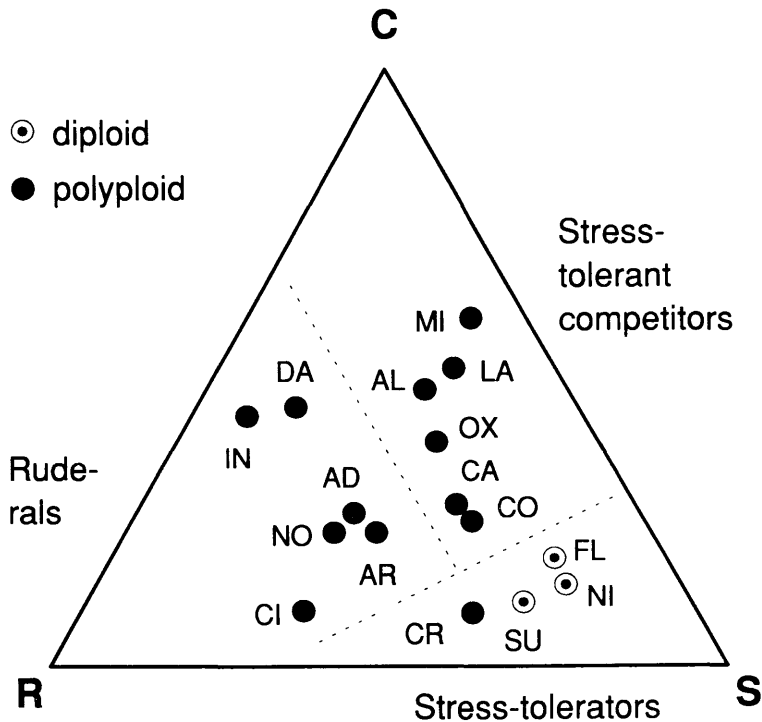
Fig. 6. Ecological strategies of diploid and polyploid species of *Draba* inferred from their habitat preferences. The mean position of each species along the gradients of competition (C), stress (S), and disturbance (R) is based on the proportion of its populations observed in different habitat types. Three main ecological strategies are indicated. Species names are abbreviated by the first two letters (see Fig. 1). Modified from [V].

results suggest that the diploids are extreme inbreeders, and are consistent with high levels of inbreeding also in the polyploids. Rates of outbreeding are, however, difficult to estimate for allopolyploids because of their fixed heterozygosity, which may conceal allelic segregation at overlapping electrophoretic loci. Thus, several of the polyploids may have higher rates of outbreeding than the diploids even if allelic segregation only was observed in progeny of the polyploids *D. oxycarpa* and *D. corymbosa* [III]. The analysis of reproductive traits in *Draba* [IV, partly VIII] provides, therefore, an important supplement to genetic data on breeding system differentiation. Notably, this analysis revealed that the diploids are predominantly autogamous, whereas the large and strongly correlated variation observed in autogamous seed set and traits promoting cross-pollination in the polyploids suggests that they vary from predominantly autogamous to mixed auto-allogamous [IV].

The variation in reproductive traits shows a much closer relationship to habitat differentiation than to geographic origin of populations or phylogenetic relationships among species (Figs. 6, 7; [V]). Three main ecological strategies (cf. Grime 1979, 1988) were recognized in Nordic species of *Draba* based on their habitat preferences (Fig. 6). All three diploid species (sect. *Draba*) and the distantly related polyploid *D. crassifolia* (sect. *Drabella*)
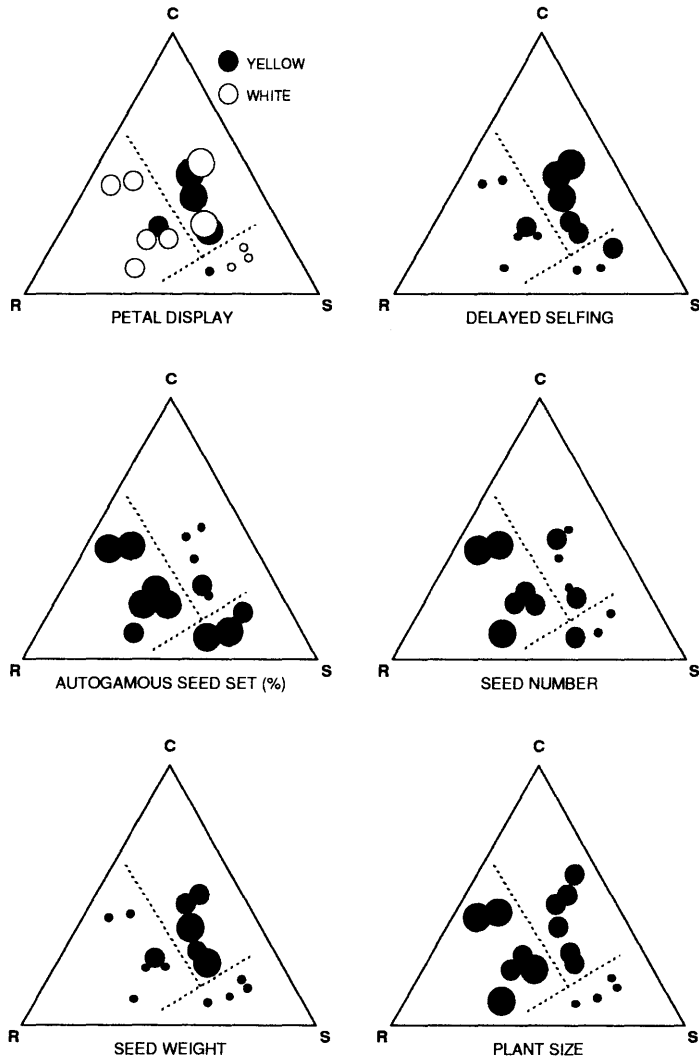
Fig. 7. The relationship between ecological and reproductive strategies of species of *Draba*. See Fig. 6 for key to the species. Based on data from [IV], [V], and [VIII]; modified from [V].

are stress-tolerators occurring in habitats with discontinuous vegetation and high levels of environmental stress. In contrast, all remaining polyploids are either stress-tolerant competitors with their main occurrence in densely vegetated habitats, or ruderals with their main occurrence in open, naturally unstable habitats (Fig. 6).

The stress-tolerators are dwarf species with inconspicuous petal display, non-protogynous and rapidly selfing flowers (before flower opening in *D. crassifolia*), high autogamous seed set (%), and few, small seeds. The ruderal polyploids are large plants with

intermediate petal display, non-protogynous and rapidly selfing flowers (often during flower opening), high autogamous seed set, and many, small seeds. In contrast, the stress-tolerant competitive polyploids are intermediately sized plants with large petal display, protogynous flowers, strongly delayed selfing (up to five days after flower opening), low autogamous seed set, and few, large seeds (Fig. 7). Thus, the stress-tolerant competitors partition their seed output into few, large seeds rather than many, small seeds, suggesting that a large amount of seed storage tissue is necessary to ensure seedling establishment in closed habitats.

The results suggest that mixed mating is advantageous in polyploids occurring in habitats with high levels of competition. Even if the polyploid condition buffers the effect of selfing with respect to loss of variability, the polyploids in competitive habitats probably benefit from a balanced combination of genetic recombinaton and stabilization of successful genotypes, which is achieved via the mixed mating strategy.


## GENETIC AND ECOLOGICAL VARIATION IN DIPLOIDS VS. POLYPLOIDS


To clarify a possible relationship between genetic and ecological variation and polyploid evolution in *Draba*, the data on habitat differentiation [V] were compared to the enzyme electrophoretic data [III]. The polyploids have greater genetic variation than the diploids at two levels: 1) variation among populations, and 2) heterozygosity, which expresses genetic variation within individual plants. The heterozygosity at electrophoretic loci (H; see [V] for definition) increases significantly with ploidal level, and ranges from 0.0 in the diploids (no heterozygotes detected) to 2.00 in the most fixed-heterozygous polyploid plant (the 16-ploid *D. corymbosa*, mean H = 1.71; Fig. 8). The ecological amplitudes of the polyploid species are significantly wider than those of the diploids (Fig. 8). In contrast to the diploid species, which are almost exclusively confined to the uppermost parts of the ridge-snowbed gradient, most polyploids occur in a wide range of habitats, e.g., luxuriant meadows, scree slopes, polygon fields, exposed ridges, and snowbeds [V].

Two alternative or possibly complementary hypotheses are advanced to explain that polyploid species of *Draba* have wider ecological amplitude, and therefore, possibly greater ecological tolerance, than diploid species [V]: 1) The general-purpose genotype hypothesis - According to this hypothesis, a high level of genetic variation as fixed heterozygosity (and thus, high biochemical diversity) in an allopolyploid genotype *per se* allows for exploitation of several different niches. An allopolyploid may accordingly possess a 'general-purpose' genotype, i.e., a genotype with an ecological tolerance exceeding that of its diploid progenitors (cf. Bierzychudek 1989). 2) The special-purpose genotype hypothesis - According to this hypothesis, repeated alploidizations involving genetically divergent progenitors result in different fixed-heterozygous genotypes, each of which may exploit a particular niche. Further studies of genetic and ecological differentiation within species of *Draba* are needed to discriminate between these hypotheses.
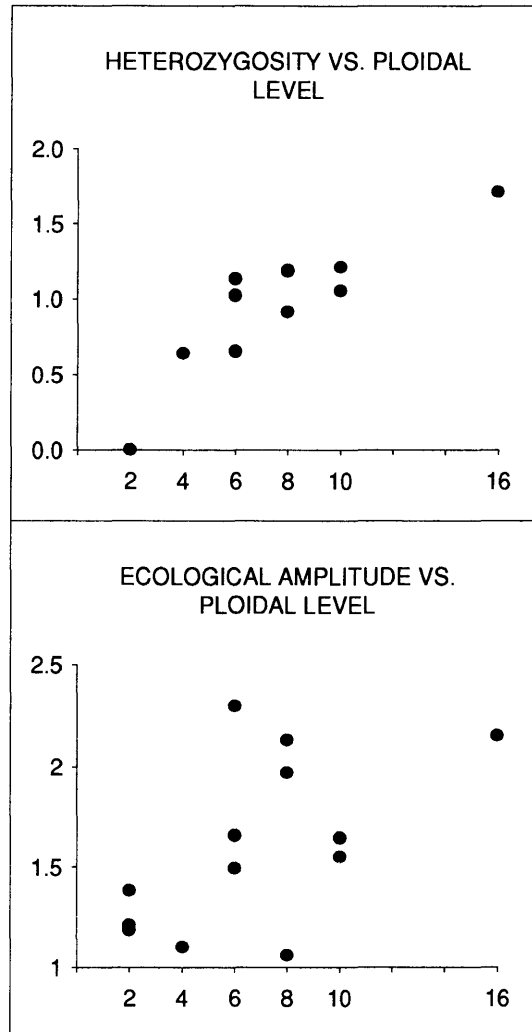
Fig. 8. The relationship between polyploidy, heterozygosity, and ecological amplitude for three diploid and ten polyploid (4x-10x, 16x) species of *Draba*. The heterozygosity is zero in all three diploids. Based on mean heterozygosities at seven electrophoretic loci in 101 populations and Shannon-Weaver diversities for 437 populations. Modified from [V].

ALLOPOLYPLOIDY AS AN ESCAPE FROM GENETIC AND ECOLOGICAL DEPAUPERATION

The data obtained in this study provide compelling evidence for a far more complex evolution in arctic-alpine *Draba* than previously envisioned. Allopolyploidizations are probably much

more frequent than estimated from the number of polyploid taxonomic species in the genus, and the potential gene flow between established polyploid species as well as alloploid formation from sibling diploids add additional levels of complexity to polyploid evolution in *Draba*. The confounding taxonomic relationships in the genus may be explained by 1) the high levels of reticulate evolution, and 2) the unpredictable phenotypic expression of duplicated genes encoding taxonomically important morphological characters. Even if a given polyploid species actually is polyphyletic, it may be difficult, if not impossible, to establish a taxonomy that correctly reflects the evolutionary history of its populations.

The evolutionary patterns in *Draba* may also be common in other genera in arctic and alpine floras, which have a turbulent history characterized by frequent climatic changes accompanied by plant migrations and secondary contacts between genetically divergent populations (cf. Stebbins 1985). The large number of widespread polyploid species in arctic and alpine floras and the possibility for multiple origins of these polyploids have several important implications, e.g., for interpretation of present-day distributional patterns and for the discussion of centres of origins of the arctic flora.

The evidence for multiple alloploid origins, differentiation into sibling diploids, and interploidal gene flow in *Draba* adds to a growing data base suggesting that polyploid complexes represent considerably more dynamic genetic systems than suggested from traditional models of polyploid speciation. Individual alloploid lineages may be evolutionary 'dead-ends' or unable to undergo adaptive evolution because their variation is tied up as fixed heterozygosity. Many polyploid species, however, probably represent continuously evolving assemblages that also comprise hybridizing alloploid lineages and are repeatedly furnished by novel alloploid lineages derived from diploid or lower polyploid sources. In recent years, evidence has accumulated not only on multiple origins of polyploids (e.g., Werth et al. 1985, Wyatt et al. 1988, Ranker et al. 1989, D.E. Soltis & P.S. Soltis 1989, 1990, D.E. Soltis et al. 1989, Doyle et al. 1990, Wolf et al. 1990, Ashton & Abbott 1992), but also on gene flow across ploidal levels (e.g., Lord & Richards 1977, den Nijs et al. 1985, Lumaret & Barrientos 1990), re-diploidization and 'cyclic di-polyploid evolution' (e.g, deWet 1971, 1980, den Nijs & Sterk 1980, 1984, den Nijs & Hulst 1988), and selective chromosome elimination (e.g., Bothmer et al. 1983, Bothmer 1990).

The data obtained on breeding systems, genetic variation, and ecological variation in *Draba* provide a possible explanation for the evolutionary success of polyploid evolution in the genus. In diploid *Draba*, regular, extreme inbreeding by self-pollination secures sexual reproduction under the severe ecological conditions in arctic and alpine areas, but inevitably results in genetic depauperation and thus, probably also decreased ecological potential. In allopolyploid *Draba*, however, considerable genetic variation is tied up as fixed heterozygosity which is maintained in spite of inbreeding. The principal evolutionary importance of processes such as recurring alloploidy and gene flow between genetically divergent populations is probably as means of enriching the genetic and ecological diversity in the entire complex. This study suggests, therefore, that allopolyploid evolution in arctic-alpine *Draba* serves as an escape from genetic and ecological depauperation caused by inbreeding at the diploid level.

# ACKNOWLEDGEMENTS

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