Morphological variation in Scandinavian populations of the diploid–tetraploid species pair *Anthericum ramosum* and *Anthericum liliago* (Anthericaceae)

Gabrielle Rosquist and Honor C. Prentice

Abstract: Both members of the diploid–tetraploid species pair *Anthericum ramosum* L. and *Anthericum liliago* L. occur as geographically disjunct isolates on the margins of their northern range in Scandinavia. Variation in floral morphology was studied in 33 populations of *A. ramosum* from four geographic regions and 25 populations of *A. liliago* from seven regions in Scandinavia. Tepal shape was characterized with the help of moment invariants, and intra- and interspecific variation in style and filament length was investigated. There were significant between-region and between-population differences in tepal shape and style and filament length within both species. However, despite the geographic disjunction of both species' distributions, there was considerable overlap in tepal shape between populations from the different regions. The hierarchical partitioning of tepal shape diversity was similar in the two species. Most of the total diversity was explained by regional and interpopulation components of diversity (48% and 35%, respectively, in *A. ramosum* and 61% and 22%, respectively, in *A. liliago*). The two species were clearly discriminated on the basis of tepal shape and style and outer filament lengths. A southern Swedish population, containing triploid hybrids between *A. ramosum* and *A. liliago*, was indistinguishable from other Scandinavian populations of *A. liliago* on the basis of tepal shape. However, a (allegedly hybrid) Danish population of *A. liliago* was intermediate between the two species in tepal shape.

Key words: polyploidy, geographic variation, tepal shape, hybridization, moment invariants.

Résumé : Les deux membres de la paire d'espèces diploïde–tétraploïde *Anthericum ramosum* L. et *Anthericum liliago* L. existent comme isolats géographiquement disjoints à la marge de leur zone de distribution, en Scandinavie. Les auteurs ont étudié la variation de la morphologie florale dans 33 populations de l'*A. ramosum* provenant de quatre régions géographiques, et 25 populations de l'*A. liliago* provenant de sept régions, en Scandinavie. La forme des tépales se caractérise avec l'aide d'invariants momentanés (moment invariants), et on a également examiné la variation intra- et inter-spécifique de la longueur du style et des filaments. Il y a des différences significatives entre les régions et entre les populations, dans la forme des tépales et de la longueur du style et des filaments, à l'intérieur de chacune des deux espèces. Cependant, malgré la disjonction géographique des distributions des deux espèces, on observe un recouvrement considérable dans la forme des tépales entre les populations des différentes régions. La répartition hiérarchique de la diversité des formes des tépales est semblable chez les deux espèces. La majeure partie de la diversité totale s'explique par des composantes régionales et inter-populations de la diversité (48% et 35% chez l'*A. ramosum* et 61% et 22% chez l'*A. liliago*). Les deux espèces se distinguent nettement sur la base de la forme des tépales et des longueurs du style et des filaments. Une population du sud de la Suède, comportant des hybrides triploïdes entre l'*A. ramosum* et l'*A. liliago*, est indistincte des autres populations scandinaves de l'*A. liliago*, sur la base de la forme des tépales. Cependant, une population danoise (considérée comme hybride) de l'*A. liliago* est intermédiaire entre les deux espèces, quant à la forme des tépales.

Mots clés : polyploïdie, variation géographique, forme des tépales, hybridation, invariants momentanés.

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Introduction

Many of the central and southern European plant species that reach their northern range limits in southern Scandinavia are restricted to open habitats and occur in a few geographically disjunct regions (Hultén 1971). It is unclear to what extent the marginal Scandinavian distributions of southern and central European species reflect the species' climatic, ecologi-

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cal, or physiological limits (Bengtsson et al. 1988). However, it is likely that the present-day distributions of many of these species have a strong historical component and are related to the postglacial availability of open sites within a predominantly forested landscape. There are notable concentrations of range-margin disjuncts in open grasslands and fissured limestone habitats on the islands of Öland and Gotland (Sterner 1922; Bengtsson et al. 1988; Ekstam et al. 1984). There are also concentrations of disjunct species in grasslands on unstable sandy soils along the southern and eastern coasts of the province of Skåne in southern Sweden (Olsson 1994).

The lilioid herbs *Anthericum ramosum* L. and *Anthericum liliago* L. (Anthericaceae (= Liliaceae s.l.)) are morphologically similar and have similar European distributions (Hultén and Fries 1986). Both the diploid *A. ramosum* and the tetraploid *A. liliago* have their northern range limits in southern Scandinavia, where each of the species occurs in a small number of geographically isolated regional populations (Hultén 1971; Hultén and Fries 1986). They are found in open grassland habitats on fissured limestone, unstable coastal or lakeside slopes, or freely drained sandy soils. Both species have been lost from many sites where they occurred earlier in the present century (e.g., Weimarck and Weimarck 1985; Wind 1993). Particularly in Denmark and southernmost Sweden, the loss of populations is a consequence of the increasing industrialization of agriculture and the associated decline in areas of traditionally grazed and unfertilized grasslands (cf. Rosquist and Prentice 2000).

The regional isolates of the two species are often geographically coincident (Hultén 1971). However, at present there are few sites where populations of the two species occur in sympatry. As has been observed in other diploid–polyploid species pairs (Thompson and Lumaret 1992), the flowering phenologies of Scandinavian *A. ramosum* and *A. liliago* are normally nonoverlapping. However, one *A. liliago* population in Skåne (southernmost Sweden) contains a high proportion of individuals that have a flowering time that is intermediate to that of the two species (Strandhede 1963). Phenologically intermediate individuals from this Skåne population have been shown to be triploid hybrids between *A. ramosum* and *A. liliago* (Strandhede 1963). A phenologically and morphologically aberrant population of *A. liliago* has also been reported from Sjælland (eastern Denmark).

In the present study of variation in floral morphology in populations of *A. ramosum* and *A. liliago* at the northern limits of their ranges, we investigated whether the pronounced geographic disjunction is reflected in the structuring of interpopulation differentiation within species or in the hierarchical partitioning of morphometric diversity between populations and regions. We also compared the patterns of regional differentiation within the two species and examined whether the structure of the morphometric variation in either of the species can be interpreted in terms of scenarios of postglacial immigration (Hewitt 1996; Runyeon and Prentice 1997*a*). We compared the sizes of the reproductive organs in the two species to determine whether there were consistent size differences that agree with the prediction that polyploids will be larger than their diploid relatives (Stebbins 1971). Finally, we evaluated the morphological affinities between the phenologically aberrant *A. liliago* populations on

Fig. 1. The regional distributions of *Anthericum ramosum* (●) and *Anthericum liliago* (▲) in Denmark and Sweden. Regional codes: A, Jylland; B, Sjælland; C, Halland; D, Skåne; E, Blekinge; F, Öland; G, Östergötland; H, Gotland.
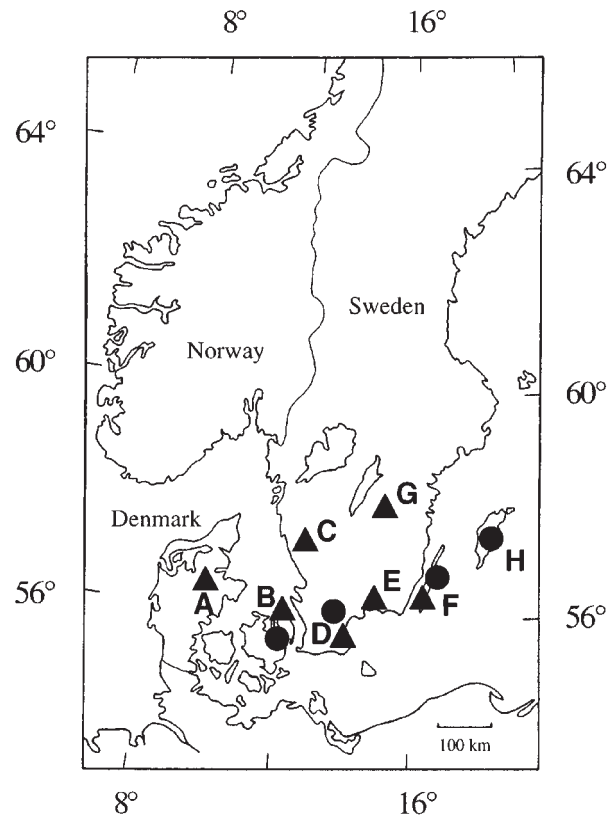
Sjælland and in Skåne and the other populations of *A. liliago* and *A. ramosum*. The late-flowering Skåne population of *A. liliago* occurs in a site where the two species are at the present day sympatric, and this population is known to contain triploid hybrids (Strandhede 1963). It has been suggested that the late flowering Sjælland *A. liliago* may also have a hybrid origin, although it is currently geographically isolated from other populations of both *A. ramosum* and *A. liliago*.

Materials and methods

The species

Anthericum ramosum and *A. liliago* are closely related, long-lived perennial herbs. Both species have white, diurnal flowers with six tepals arranged in two whorls of three. *Anthericum ramosum* is regarded as a diploid ($2n = 30, 32$) and has a branched inflorescence, while *A. liliago* is tetraploid ($2n = 60, 64$) in Scandinavia and usually has an unbranched inflorescence (Strandhede 1963; Tutin et al. 1980). Preliminary allozyme data suggest that *A. liliago* is an allotetraploid and that *A. ramosum* may be involved in its parentage (G. Rosquist and H.C. Prentice, data not shown). No other members of the genus are present in northern Europe. The mean number of flowers per inflorescence in Scandinavian material is 45 ($n = 23$) in *A. ramosum* and 19 ($n = 33$) in *A. liliago* (G. Rosquist, personal observations). The flowers of *A. liliago* are larger (35–40 mm in diameter) than the flowers of *A. ramosum* (20–26 mm in diameter) (Hegi 1909; Strandhede 1963). In Sweden, *A. liliago* flowers in June and *A. ramosum* flowers from late July to the end of August.

Table 1. Regions, populations, population codes, estimated population sizes (total number of ramets and number of flowering ramets), sample sizes (one flower per individual), and geographic locations (latitude and longitude) for 33 populations of *Anthericum ramosum* (from four regions) and 25 populations of *Anthericum liliago* (from seven regions) in Denmark (Dk) and Sweden (Sw).

| Species | Region | Population | Population code | Population sizes (no. of ramets) | | Sample size | Latitude, longitude |
				Total	Flowering		
A. ramosum	Sjælland (Dk)	Kregme Strand	KS	1 900	400	8	55°56′N, 12°03′E
		Frederikssund	FS	320	70	4	55°50′N, 12°06′E
		Skuldelevs Strand	SL	1 500	1 000	14	55°47′N, 12°04′E
		Kyndbyværket	KY	3 000	500	15	55°49′N, 11°54′E
		Ejby Ådal	EÅ	4 500	900	15	55°43′N, 11°51′E
	Skåne (Sw)	Söndre Klack 1	SK1	1 300	400	16	55°50′N, 14°04′E
		Söndre Klack 2	SK2	11 000	1 000	18	55°50′N, 14°04′E
		Söndre Klack 3	SK3	3 600	1 100	13	55°49′N, 14°05′E
		Sågmöllan 1	SM1	1 800	800	19	55°56′N, 14°05′E
		Sågmöllan 2	SM2	12 000	2 000	12	55°56′N, 14°05′E
		Sågmöllan 3	SM3	600	170	11	55°56′N, 14°04′E
		Everöd	ER	5 000	500	19	55°54′N, 14°06′E
		Horna	HO	1 100	400	18	55°57′N, 14°16′E
	Öland (Sw)	Gynge Alvar 1	GY1	25 000	5 000	15	56°31′N, 16°29′E
		Gynge Alvar 2	GY2	32 000	2 000	15	56°32′N, 16°29′E
		Gynge Alvar 3	GY3	10 000	1 500	15	56°32′N, 16°30′E
		Möckelmossen 1	MM1	15 000	5 000	15	56°31′N, 16°32′E
		Möckelmossen 2	MM2	8 000	1 000	15	56°31′N, 16°33′E
		Skarpa Alby 1	SA1	1 500	500	15	56°35′N, 16°35′E
		Skarpa Alby 2	SA2	25 000	5 000	15	56°35′N, 16°34′E
		Skarpa Alby 3	SA3	1 500	400	15	56°34′N, 16°34′E
		Vickleby 1	VB1	2 000	1 000	15	56°34′N, 16°29′E
		Vickleby 2	VB2	500	200	15	56°34′N, 16°30′E
		Vickleby 3	VB3	14 000	1 200	14	56°33′N, 16°30′E
	Gotland (Sw)	Hejdeby 1	HB1	12 000	2 000	15	57°38′N, 18°23′E
		Hejdeby 2	HB2	10 000	2 000	15	57°37′N, 18°25′E
		Hejdeby 3	HB3	100 000	3 000	15	57°38′N, 18°24′E
		Etelhem 1	EH1	4 500	1 000	11	57°19′N, 18°31′E
		Etelhem 2	EH2	6 500	1 500	15	57°19′N, 18°31′E
		Etelhem 3	EH3	3 500	400	13	57°20′N, 18°31′E
		Sundre 1	SE1	9 000	2 000	15	56°56′N, 18°11′E
		Sundre 2	SE2	500 000	50 000	15	56°56′N, 18°10′E
		Sundre 3	SE3	5 000	1 500	15	56°55′N, 18°11′E
A. liliago	Jylland (Dk)	Havskov Dal	HD	2 000	1 000	14	56°33′N, 09°29′E
	Sjælland (Dk)	Tibirke Bakker	TB	1 500	500	11	56°02′N, 12°16′E
	Halland (Sw)	Sällstorp	SS	250	35	6	57°15′N, 12°24′E
	Skåne (Sw)	Vik	VK	1 500	1 000	20	55°37′N, 14°17′E
		Rörum	RR	20	8	2	55°37′N, 14°14′E
		Stenshuvud	SH	700	100	13	55°39′N, 14°16′E
		Kivik	KV	3 000	2 000	20	55°41′N, 14°12′E
		Vitemölla	VM	300 000	100 000	20	55°42′N, 14°12′E
		Haväng	HA	250	110	6	55°43′N, 14°11′E
		Brösarps N. Backar	BNB	550	50	8	55°43′N, 14°04′E
		Drakamölla	DM	150	22	5	55°45′N, 14°08′E
		Maglehem	MH	3 000	900	20	55°46′N, 14°08′E
		Degeberga	DB	900	150	17	55°50′N, 14°05′E
		Stora Drivan	SD	550	150	17	55°51′N, 14°10′E
		S. Lyngsjön	LY	100	10	2	55°55′N, 14°04′E
	Blekinge (Sw)	Hoka Gård	HG	500	180	17	56°17′N, 14°51′E
	Öland (Sw)	Penåsa	PE	600	50	6	56°26′N, 16°28′E
		Millersten	MS	550	70	16	56°26′N, 16°30′E
		Penåsabäcken	PB	1 100	300	15	56°26′N, 16°30′E
		Ammatornsrör	AR	1 900	400	11	56°26′N, 16°30′E
		N. Ammatornsrör	NAR	2 500	750	16	56°27′N, 16°30′E
		Gösslunda	GL	1 800	400	10	56°29′N, 16°31′E
		Ismantorp	IT	600	70	6	56°45′N, 16°37′E
		Noaks Ark	NA	1 500	400	18	56°46′N, 16°37′E
	Östergötland (Sw)	Somvik	SV	200 000	40 000	24	58°04′N, 15°11′E

Both species are insect pollinated and self-compatible (Rosquist 2001). The fruits are loculicidal capsules and the seeds lack specialized dispersal mechanisms (Rosquist 2001). Triploid hybrids ($2n = 3\times = 44, 45$) have been reported from one site in Skåne (southern Sweden) in an area where the two species co-occur at present (Strandhede 1963). Hybrid individuals have a flowering

time (late June to mid July) that is intermediate to that of *A. ramosum* and *A. liliago* (Strandhede 1963).

The geographic distributions of both *Anthericum* species are centred in central Europe, with marginal, northern populations in southern Scandinavia (maps in Hultén and Fries 1986). Within Scandinavia, both species have populations on Sjælland (Denmark) and in Skåne, on Öland and on Gotland (Sweden). *Anthericum liliago* also occurs in Jylland and on Fyn (Denmark) and in Halland, Blekinge, and Östergötland (Sweden). The two species are rare and occur in scattered populations in northern Germany and Poland, but they are more frequent in central Europe (Hultén and Fries 1986). In Scandinavia, both species grow in dry grass-lands on steep slopes or (on the islands of Öland and Gotland) in areas with fissured limestone.

Sites and sampling

Whole flowers for morphometric analysis were sampled from 33 populations of *A. ramosum* within four geographic regions and from 25 populations of *A. liliago* within seven regions (Fig. 1; Table 1). Totals of 475 and 320 individuals were sampled from *A. ramosum* and *A. liliago*, respectively, during the period 1995–1997 (Table 1). Within regions, populations of *A. ramosum* were separated from each other by 0.1 to 80.0 km (mean = 17.4 km). The local geo-graphic distribution of *A. liliago* populations within Scandinavia is even more restricted than that of *A. ramosum*. The sampled popula-tions of *A. liliago* were separated from each other by 0.2 to 38.2 km (mean = 14.3 km) within regions. For each species, we sampled one flower per individual from 15–20 individuals per population. Popu-lations of *A. ramosum* and *A. liliago* may be spatially restricted but contain many densely grouped ramets. Within populations, the sam-pled (flowering) individuals were separated from each other by at least 5 m to avoid sampling from closely related individuals. The re-stricted spatial extent, small size, or low number of flowering indi-viduals in some populations, especially of *A. liliago*, meant that some of the sample sizes were less than 15 (Table 1). Triploid hybrids be-tween *A. ramosum* and *A. liliago* have been previously reported from the Degeberga (DB) population of *A. liliago* in Skåne (Strandhede 1963). When sampling material from DB for the present investigation, we focussed on individuals with intermediate flowering phenology (presumed hybrids).

Permission to sample flowers from Denmark, where both spe-cies are nationally protected, was obtained from the Forest and Na-ture Board (Skov- og Naturstyrelsen) at the Danish Ministry for Environment and Energy. Permission to sample *A. liliago* flowers from Skåne and Blekinge in Sweden, where the species is also pro-tected, was obtained from the regional governments in the prov-inces of Kristianstad (now Skåne) and Blekinge.
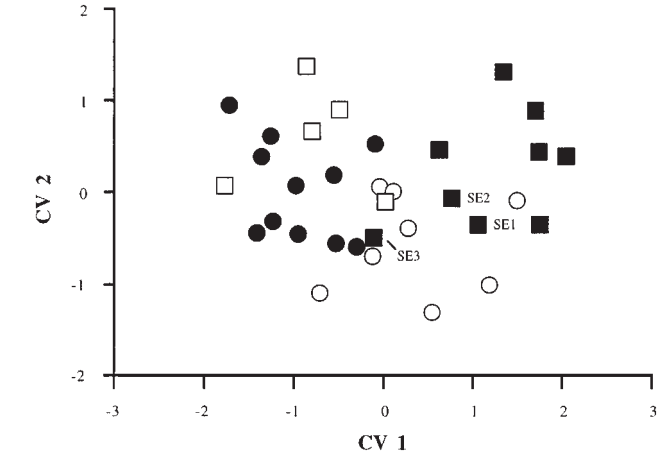
Tepal shape

Totals of 461 and 320 individuals were scored for tepal shape in *A. ramosum* and *A. liliago*, respectively. The three (in a few cases two or four) freshly sampled inner tepals from each flower were pressed and their outlines were captured by a video camera and transferred to a computer via an analogue-to-digital converter. The shape of each tepal was then described with the help of moment invariants (Dudani et al. 1977; White et al. 1988). The image ac-quisition and shape description was carried out with the program ARBO 1.74 (White et al. 1988).

Style and filament length

Where possible, style and filament lengths were measured with a calibrated ocular micrometer on the same flowers that were scored for tepal shape. Totals of 466 and 319 individuals were scored for style and filament length in *A. ramosum* and *A. liliago*, respectively. The style and the six stamens from each sampled flower were mounted while fresh under a strip of Scotch magic tape on a glass

Fig. 2. Between-population differentiation in tepal shape in 33 populations of *Anthericum ramosum* based on a CVA of moment invariants. In the CVA, the groups were populations and the within-group replicates were individuals (mean values of three (2–4) inner tepals from one flower). The first and second CVs account for 51% and 19%, respectively, of the total between-population variance. Regional codes: □, Sjælland; ○, Skåne; ●, Öland; ■, Gotland. Population codes (cf. Table 1) are given for the populations that are discussed in the text.

slide. The six stamens within a flower are arranged in two whorls of three, and we calculated the mean lengths of the three inner and the three outer filaments for each flower. We also measured the length of the style (including the stigma) for each flower.

Data analysis

Patterns of morphological differentiation between populations and species

Patterns of between-population differentiation in tepal shape were analysed in three separate canonical variates analyses (CVAs), based on the 33 populations of *A. ramosum*, the 25 populations of *A. liliago*, and the pooled data (58 populations) from both species. The CVAs were based on the populations as groups, with individu-als as within-group replicates. Each individual was represented by the mean values of the inner tepals from one flower. The analyses were carried out using the routine CANDISC in the software pack-age from SAS Institute Inc. (1996).

The partitioning of tepal shape diversity

Wilks' Λ statistics from a series of CVAs were used to partition tepal shape diversity into its within- and between-region and -pop-ulation components within each of the species (White and Prentice 1988; Runyeon and Prentice 1997b). Wilks' Λ gives the proportion of the total diversity that is due to within-group diversity in CVA. Two CVAs were carried out for the partition analyses in each of the species. In these analyses, the within-group replicates were indi-viduals (mean data from 3 (2–4) tepals of one flower) and the groups were defined as regions (analysis R) or populations (analy-sis P) giving, respectively, Λ_R and Λ_P. Within each species, $1 - \Lambda_R$ gives the between-region component of the total morphological di-versity and $\Lambda_R - \Lambda_P$ gives the between-population component of the total diversity. The within-population diversity is given by Λ_P.

Styles and filaments

Differences in style length and outer and inner filament lengths between populations, regions, and species were tested with one-way analyses of variance (ANOVA), followed by multiple

Table 2. Mantel tests for associations between matrices of Mahalanobis' distances (MORPH, based on tepal shape) and matrices of geographic distances (GEO) and Rogers' genetic distances (GEN, based on allele frequencies at nine polymorphic loci; for *Anthericum ramosum* only) for 33 populations of *A. ramosum* and 25 populations of *Anthericum liliago* from Denmark and Sweden.

Pairwise matrix comparisons	*Anthericum ramosum*		*Anthericum liliago*	
	r	P	r	P
MORPH × GEN	0.326	0.001***	—	—
MORPH × GEO	0.232	0.002**	0.009	0.386ns
MORPH × GEO (TB excluded)	—	—	0.050	0.271ns
MORPH × GEO (TB and DB excluded)	—	—	0.046	0.295ns

Note: Matrix correlation coefficient (r) and one-tailed probability with >2000 permutations. ns, nonsignificant.

**$P < 0.01$.

***$P < 0.001$.

comparisions of means (based on Tukey's method for groups with unequal sample sizes). The statistical analyses of style and filament lengths were carried out with the program package STATISTICA (StatSoft Inc. 1994).

Comparision of distance matrices

For each species, the matrix of between-population Mahalanobis' distances (derived from the CVA analyses with populations as groups) for tepal shape was compared with the matrix of geographic distances between populations, using the generalized regression method of Mantel (Mantel 1967), based on a bootstrapping procedure with 2000 permutations. For *A. ramosum*, we also compared the matrices of morphometric and geographic distances with a matrix of genetic distances (Rogers' genetic distances based on within-population allozyme frequencies at nine polymorphic loci) derived from the same 33 populations that were included in the present study (Rosquist and Prentice 2000). The matrix comparisions were carried out with the program NTSYS-pc (Rohlf 1994).

Results

Patterns of differentiation and the partitioning of diversity within *A. ramosum*

Differentiation in tepal shape between populations within *A. ramosum*

The first two canonical variates (CVs) from a CVA of 33 populations of *A. ramosum*, based on moment invariant descriptors of tepal shape, are shown in Fig. 2. There is no clear separation of the populations in the four regions (Sjælland, Skåne, Öland, and Gotland). However, on CV1, all but one (SE3) of the Gotland populations are separated from the Öland and the Sjælland populations. There is also a tendency for the Skåne populations to be separated from the Sjælland populations by lower scores on CV2.

There was a positive association between the matrices of geographic distance and Mahalanobis' distance (based on tepal shape) between populations of *A. ramosum* (Mantel test, $P = 0.002$; Table 2). A positive association (Mantel test, $P = 0.001$; Table 2) was also found between the matrix of Mahalanobis' distances and a matrix of Rogers' genetic distances based on allozyme data (Rosquist and Prentice 2000).

Differentiation in style and filament length within *A. ramosum*

The lengths of the styles and the inner and outer filaments differ significantly ($P < 0.001$, in all analyses) be-

tween the 33 *A. ramosum* populations ($F_{[32,434]} = 14.97$, $F_{[32,434]} = 11.91$, and $F_{[32,434]} = 8.07$, from the ANOVAs for style, inner filament, and outer filament lengths, respectively) and between the four regions ($F_{[3,463]} = 82.65$, $F_{[3,463]} = 70.92$, and $F_{[3,463]} = 50.39$, for style, inner filament, and outer filament lengths, respectively). The mean values and the standard errors for style, inner filament, and outer filament lengths of *A. ramosum* flowers for the four regions (Sjælland, Skåne, Öland, and Gotland) are shown in Fig. 3. The Gotland individuals have significantly longer styles (14.79 ± 0.174 mm) and inner and outer filaments (11.32 ± 0.121 and 8.19 ± 0.082 mm, respectively) than individuals from the other three regions (Sjælland (13.15 ± 0.216, 9.78 ± 0.165, and 7.30 ± 0.133 mm, respectively), Skåne (13.53 ± 0.142, 9.71 ± 0.115, and 7.53 ± 0.085 mm, respectively), and Öland (11.79 ± 0.105, 9.23 ± 0.088, and 6.90 ± 0.062 mm, respectively)). The Gotland population SE3 differs significantly for all three characters (in the multiple comparison test of 33 populations) from the rest of the Gotland populations, but is not significantly different from the populations from Sjælland, Skåne, and Öland. Öland individuals have significantly shorter styles than individuals from the other three regions (Sjælland, Skåne, and Gotland) and shorter inner and outer filaments than those from Skåne. There were no significant differences in style or filament lengths between individuals from Sjælland and Skåne.

Partitioning of diversity in tepal shape within *A. ramosum*

Most (48%) of the total diversity in tepal shape within *A. ramosum* was accounted for by the between-regional component of variation (Table 3), 35% of the total diversity is due to variation between populations within regions, and 16% is due to variation between individuals within populations.

Patterns of differentiation and the partitioning of diversity within *A. liliago*

Differentiation in tepal shape between populations within *A. liliago*

The first two CVs from the CVA of the 25 populations of *A. liliago*, based on the moment invariant descriptors of tepal shape, are shown in Fig. 4. As in *A. ramosum*, there is no clear regional grouping of populations. The single population from Sjælland (TB) forms an outlier, with a low score on CV2. The Blekinge population (HG) has high scores on

CV1, while the populations from Jylland (HD), Halland (SS), and Östergötland (SV) are grouped together with the Öland and Skåne populations. The Skåne populations form a loose group on the right of the figure and the Öland populations are grouped on the left of the figure. The hybrid population DB (Skåne) is grouped together with the Öland populations on the left of the figure.

In contrast with *A. ramosum*, there was no positive association between the matrices of geographic and tepal shape distances, even when the outlying Sjælland (TB) population or both the TB and the hybrid Skåne (DB) populations were excluded from the matrix comparisons (Mantel test; Table 2).

Differentiation in style and filament length within *A. liliago*

There were significant differences ($P < 0.001$, in all analyses) in the lengths of the styles and the inner and outer filaments between the 24 *A. liliago* populations ($F_{[23,278]} = 12.5$, $F_{[23,278]} = 9.6$, and $F_{[23,278]} = 9.1$, from the ANOVAs for style, inner filament, and outer filament lengths, respectively) and the 7 regions ($F_{[6,295]} = 24.2$, $F_{[6,295]} = 16.4$, and $F_{[6,295]} = 10.0$, for style, inner filament, and outer filament lengths, respectively) when the hybrid Skåne (DB) population was excluded. If the DB population was included in the analyses, significant differences were also found between the 25 populations and seven regions ($P < 0.001$, in all analyses). The mean values and the standard errors for style lengths and outer and inner filament lengths for *A. liliago* flowers from the seven regions (Jylland, Sjælland, Halland, Skåne, Blekinge, Öland, and Östergötland) and for the hybrid population (DB) are shown in Fig. 5. *Anthericum liliago* individuals from Östergötland have the highest mean values of style (15.54 ± 0.411 mm) and outer and inner filament lengths (9.91 ± 0.185 and 8.33 ± 0.147 mm, respectively) of the seven regions (Fig. 5). Skåne material has significantly longer styles (14.54 ± 0.155 mm) and outer filaments (9.21 ± 0.109 mm) than Öland material (12.26 ± 0.141 and 8.15 ± 0.086 mm, respectively), and Öland has the lowest mean values for style length of all the regions. Individuals in the hybrid DB population only differed from the other Skåne individuals in mean style length (12.70 ± 0.393 mm).

Partitioning of diversity in tepal shape within *A. liliago*

The partitioning of tepal shape diversity in *A. liliago* was based on data from 24 populations (excluding the hybrid population DB). As in *A. ramosum*, most of the total diversity in tepal shape within *A. liliago* was accounted for by the between-regional component of variation (Table 3). The partitioning of the total morphological variation in *A. liliago* gave a regional diversity component of 61% and a between-population component of 22%. Seventeen percent of the diversity was accounted for by diversity between individuals within populations.

Patterns of morphological differentiation between the two species

Differentiation in tepal shape between *A. ramosum* and *A. liliago*

The first two CVs of the tepal shape CVA based on the pooled population data from *A. ramosum* and *A. liliago* are

Fig. 3. Between-region differences for 33 populations of *Anthericum ramomsum* in (A) mean style length, (B) mean outer filament length, and (C) mean inner filament length. Standard errors are indicated by bars. Pairs of regions that are not significantly different (one-way ANOVAs) are indicated by the same letters. Regional codes: Sj, Sjælland; Sk, Skåne; Öl, Öland; Go, Gotland.
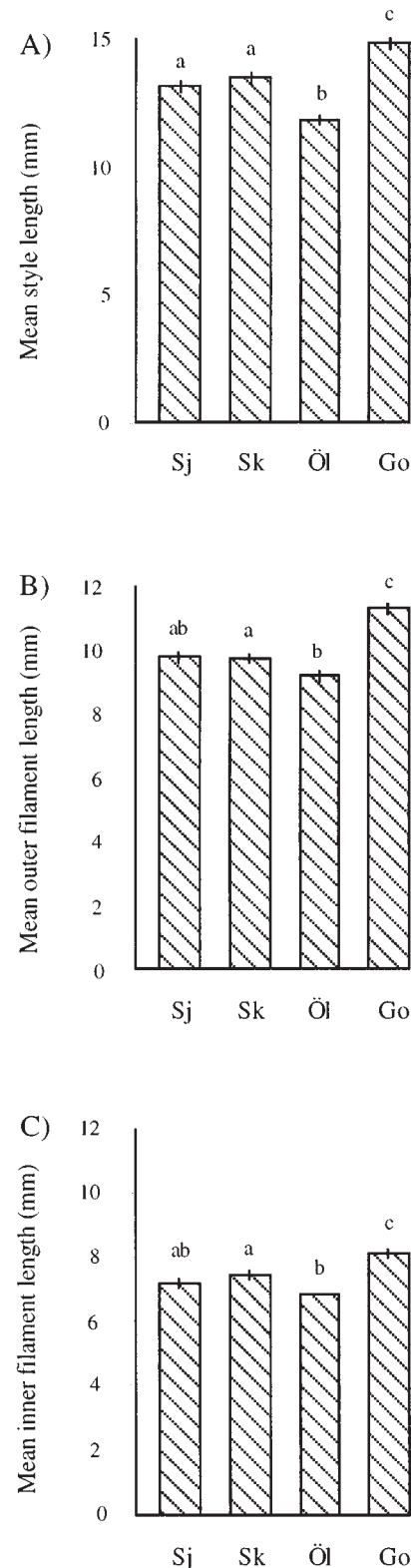
Table 3. The hierarchical partitioning of tepal shape diversity in *Anthericum ramosum* and *Anthericum liliago* and statistics from canonical variates analyses based on individuals as within-group replicates and regions or populations as groups.

	Anthericum ramosum	*Anthericum liliago*
No. of populations	33	24
No. of descriptors	7	7
Significant (5%) descriptors		
Regions as groups (analysis R)	7	5
Populations as groups (analysis P)	7	7
Regions as groups (analysis R)		
No. of axes significant at 5%	3	2
No. of axes extracted	3	6
Populations as groups (analysis P)		
No. of axes significant at 5%	4	3
No. of axes extracted	7	7
Wilks' Λ		
Regions as groups, analysis R (Λ_R)	0.5185***	0.3896***
Populations as groups, analysis P (Λ_P)	0.1645***	0.1704***
Partitioning of the total tepal shape diversity		
Between regions ($1 - \Lambda_R$)	0.482	0.610
Between populations within regions ($\Lambda_R - \Lambda_P$)	0.354	0.219
Between individuals within populations (Λ_P)	0.164	0.170

Note: The total diversity in tepal shape is partitioned into its within- and between-region and -population components for *A. ramosum* and *A. liliago* (see the text for further details). The hybrid Skåne population (DB) is excluded from the *A. liliago* analysis.

***$P < 0.001$.

Fig. 4. Between-population differentiation in tepal shape in 25 populations of *Anthericum liliago* based on a CVA of moment invariants. In the CVA, the groups were populations and the within-group replicates were individuals (mean values of three (2–4) inner tepals from one flower). The first and second CVs account for 49% and 24%, respectively, of the total between-population variance. Regional codes: ■ , Jylland; □, Sjælland; ◐ , Halland; ○, Skåne; △, Blekinge ; ●, Öland; ▲, Östergötland. Population codes (cf. Table 1) are given for the populations that are discussed in the text. A hybrid population between *Anthericum ramosum* and *A. liliago* DB (Skåne) is included in the analysis.
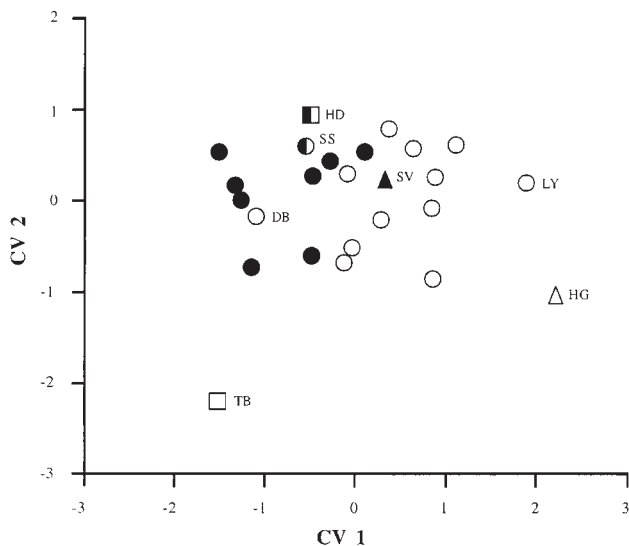
shown in Fig. 6. The populations of *A. ramosum* and *A. liliago* are clearly separated, with all 33 populations of *A. ramosum* grouped on the left of the figure and 23 of the 25 populations of *A. liliago* grouped on the right of the figure. Two *A. liliago* populations fall outside the main group of *A. liliago* populations. Population TB (Sjælland) is positioned between the groups of *A. ramosum* and *A. liliago* populations, and population LY (Skåne) is an outlier to the group of *A. liliago* populations on the far right of the figure.

Figure 7 is based on the CVA in Fig. 6, but with each population represented by one, randomly chosen tepal from one individual. The tepals of *A. ramosum* are smaller and broader in relation to their length than the *A. liliago* tepals. The tepal from the outlying *A. liliago* Sjælland population (TB) is intermediate in size and shape between the two species.

Interspecific comparisons of style and inner and outer filament lengths show that *A. liliago* has significantly longer styles ($F_{[1,756]} = 12.53$, $P < 0.001$) than *A. ramosum*, while *A. ramosum* has significantly longer outer filaments ($F_{[1,756]} = 132.32$, $P < 0.001$). There were no significant differences in inner filament lengths between the two species.

Discussion

Differentiation and diversity within *A. ramosum*: tepal shape and allozymes

The pattern of differentiation in *A. ramosum* tepal shape is more continuous and shows a less distinct regional structure than the mosaic pattern that was detected in an earlier study of allozyme variation in the same set of populations (Rosquist and Prentice 2000). Neither the earlier allozyme study nor the present investigation of floral morphology in *A. ramosum* reveal patterns of regional differentiation that

can be easily interpreted in terms of scenarios of postglacial immigration. However, allozyme frequency data do suggest that the populations from northern and southern Gotland may have had separate historical origins (Rosquist and Prentice 2000).

Allozyme data often reveal a more discrete structure of geographic differentiation than morphological characters (e.g., Allen et al. 1995; Lönn and Prentice 1995), and Lewontin (1984) provides a general explanation of why morphological characters (controlled by several or many loci) may be expected to detect a more subtle pattern of population differentiation than single-locus characters. In addition, in studies such as the present investigation of tepal shape based on morphological phenotypes, patterns of differentiation will reflect both environmental and genetic components of variation. Thus, it is more likely that environmentally related variation will be detected in phenotypic characters than in single-locus characters, such as allozymes, that are under direct genetic control.

Despite the fact that there is a somewhat overlapping pattern of regional differentiation in tepal shape in *A. ramosum*, the hierarchical analysis of tepal shape diversity showed that the between-region component of diversity accounted for the majority of the total diversity (Table 3). Only 16% of the total diversity was accounted for by the within-population component of diversity. In contrast, the hierarchical partition of allozyme diversity showed a between-regional component of 13% and a within-population component of 75% (Rosquist and Prentice 2000). Studies that compare patterns of variation and the structure of diversity in allozyme and morphometric characters show that geographic pattern is not necessarily a good predictor of the structure of genetic diversity, and that there is not necessarily a correspondence between the diversity partitions reflected in morphological and allozyme characters. Several studies show that the rank ordering of the diversity partition may be similar between different sets of characters, regardless of whether the characters show different patterns of geographic differentiation (e.g., Schwaegerle et al. 1986; Prentice and Andersson 1997). However, other studies support the present comparison of allozymes and tepal shape of *A. ramosum*, where allozymes tend to show a relatively large within-population and a relatively low between-population (or between-region) component of diversity compared with that shown in morphological characters (e.g., Prentice 1992; Runyeon and Prentice 1997*b*).

Morphological differentiation and diversity within *A. liliago*: comparison with *A. ramosum*

Anthericum liliago has an even more fragmented and disjunct Scandinavian distribution than *A. ramosum* (Hultén 1971). The two regions (Skåne and Öland) that have the highest concentration of populations (which are represented by several populations in our investigation) form loose and intergrading groups in the analysis of tepal shape (Fig. 4) and the pattern of between-population differentiation is more or less continuous. The hybrid Skåne population (DB) is separated from the rest of the Skåne populations and falls within the main group of the Öland populations. The LY population (Skåne), which forms an outlier in the ordination, was only represented by data from two individuals. However, the HG population from Blekinge and the TB popula-

Fig. 5. Between-region differences for 25 populations of *Anthericum liliago* in (A) mean style length, (B) mean outer filament length, and (C) mean inner filament length. Standard errors are indicated by bars. Pairs of regions that are not significantly different (one-way ANOVAs) are indicated by the same letters. Regional codes: Jy, Jylland; Sj, Sjælland; Ha, Halland; Sk, Skåne; Bl, Blekinge; Öl, Öland; Ög, Östergötland. Population codes are given where a region is represented by a single population. The hybrid population DB (Skåne) is treated as a separate "region."
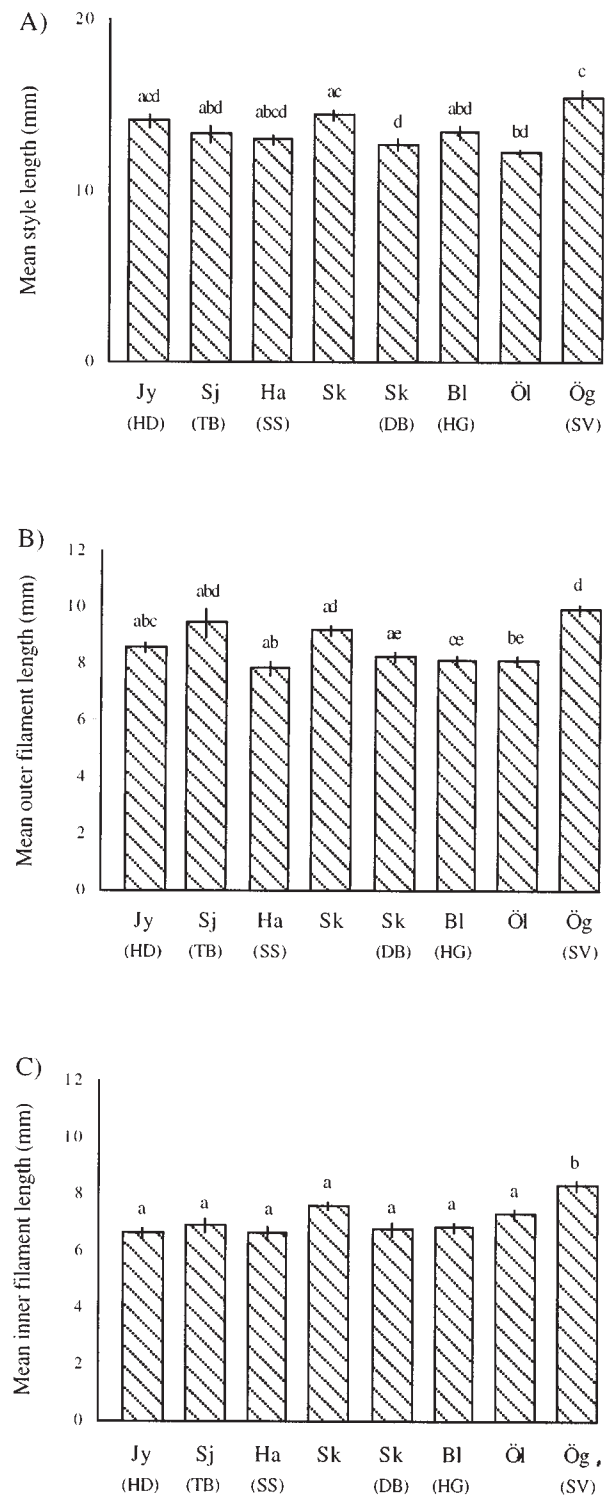
Fig. 6. Between-population differentiation in tepal shape in 58 populations of *Anthericum ramosum* and *Anthericum liliago* based on a CVA of moment invariants. In the CVA, the groups were populations and the within-group replicates were individuals (mean values of three (2–4) inner tepals from one flower). The first and second CVs account for 89% and 5%, respectively, of the total between-population variance. Regional codes: (◧, Jylland; □, Sjælland; ◖, Halland; ○, Skåne; △, Blekinge ; ●, Öland; ■, Gotland; ▲, Östergötland. Population codes (cf. Table 1) are given for the populations that are discussed in the text. A hybrid population between *A. ramosum* and *A. liliago* DB (Skåne) is included in the analysis.

Fig. 7. Tepal shape variation in *Anthericum ramosum* and *Anthericum liliago*. One randomly chosen tepal from each population is superimposed on the CVA of the between-population differentiation in tepal shape (moment invariants) for the 58 populations of *A. ramosum* and *A. liliago* in Fig. 6. A hybrid population between *A. ramosum* and *A. liliago* DB (Skåne) is included in the analysis.
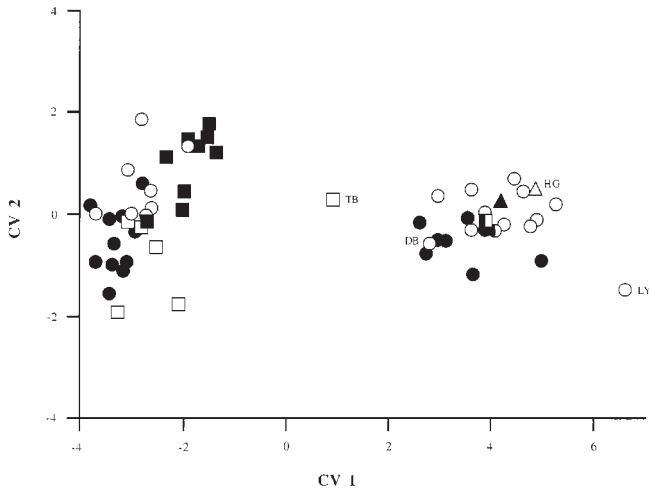
tion from Sjælland, which occupy clearly outlying positions in relation to the rest of the populations, are both large and represented by data from ca. 15 flowering individuals (Table 1). The geographically isolated populations SV, HD, and SS (see Fig. 1 and Table 1) are not separated from the main group of populations on the basis of tepal morphology, and there is no overall tendency for populations from adjacent geographic regions to form large-scale geographic groups. In contrast with *A. ramosum*, there was no significant association between geographic and morphological distances (even after the removal of the outlier TB and the hybrid DB population). But the sampling design in *A. ramosum* included several populations within each of the regions, whereas most regions in *A. liliago* are only represented by one or two populations.

The hierarchical structure of tepal shape diversity within *A. liliago* was similar to that in *A. ramosum*, with the majority of the total diversity (61%, compared with 48% in *A. ramosum*) explained by the between-region component of diversity and a relatively low within-population component of diversity (17%, compared with 16% in *A. ramosum*). The high regional component of diversity in both species is consistent with their strongly disjunct regional distributions in Scandinavia.

Morphological relationships between *A. ramosum* and *A. liliago*

Populations of *A. ramosum* and *A. liliago* form two discrete and well-separated groups on the basis of tepal shape (Figs. 6 and 7). Tepal shape provided a reliable character for discriminating between the two species and the tetraploid *A. liliago* also has larger tepals than diploid *A. ramosum*
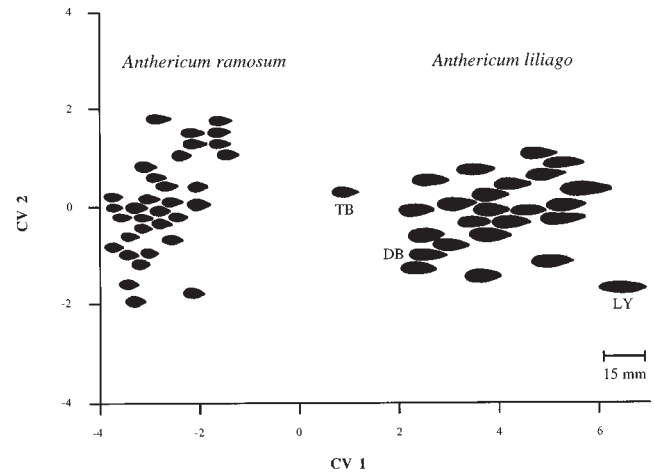
(Fig. 7; Strandhede 1963). It has been suggested that because genome size is related to cell size, polyploids are, in general, expected to be larger than related diploid taxa (Stebbins 1971), and many studies have reported larger sizes of plants, inflorescences, flowers, and pollen grains in polyploid compared with diploid taxa (e.g., *Phlox drummondii* (Garbutt and Bazzaz 1983), *Asphodelus fistulosus* (Ruiz Rejón et al. 1990), *Vaccinium uliginosum* (Jacquemart and Thompson 1996), *Arrhenatherum elatius* (Petit and Thompson 1997), and *Lotus corniculatus* (Gauthier et al. 1998)). In *Anthericum*, although the tepals are larger and the styles longer in the tetraploid (*A. liliago*) than in the diploid (*A. ramosum*), the lengths of the outer filaments are significantly longer in the diploid than in the tetraploid. Consequently, the relative lengths of tepals, styles, and filaments differ between the two species. The styles in the diploid (*A. ramosum*) protrude beyond the relatively short tepals, resulting in species-specific differences in the presentation of anthers and stigmas to visiting insects.

Polyploidization may be associated with changes in guilds of pollinating insects (Segraves and Thompson 1999). Selection by pollinators influences local and regional differentiation in floral morphology within species (Galen 1996; Johnson and Steiner 1997). The fact that the Öland populations of both species have the shortest styles and filaments suggests that there may be regional differences in the guilds of pollinators that visit both *A. ramosum* and *A. liliago*. It is reasonable to expect that selection by pollinators has contributed to the patterns of inter- and intra-specific differences in floral morphology in *A. ramosum* and *A. liliago*. Both species are visited by bumble bees, honey bees, and syrphids (G. Rosquist, personal observations). However, we have no detailed information on the species' pollination biology.

Polyploidization may be accompanied by a shift in flowering phenology (e.g., Thompson and Lumaret 1992). It has been suggested that a delay in the flowering season of a

polyploid in relation to its diploid progenitor would be expected if cell division and growth rates are slower in polyploids than in diploids (Stebbins 1971). Most studies of phenology in diploid–tetraploid pairs of taxa have been made on autopolyploids (*A. liliago* is thought to have had an allopolyploid origin (G. Rosquist and H.C. Prentice, data not shown)). In *Phlox drummondii* (Garbutt and Bazzaz 1983) and *Plantago media* (van Dijk et al. 1992) the polyploid cytotypes have been shown to flower later than the diploid cytotypes. However, in *Arrhenatherum elatius* (Petit et al. 1997) and *Dactylis glomerata* (Lumaret et al. 1987), as in *Anthericum*, the polyploids flower earlier than the diploids.

The *A. liliago* population TB (from Sjælland), which was an outlier in the *A. liliago* tepal shape ordination (Fig. 4), occupies a position between the groups of *A. ramosum* and *A. liliago* populations in the pooled-species ordination (Fig. 7). Danish botanists have also observed that this population is morphologically intermediate between *A. ramosum* and *A. liliago* and that it's time of flowering is intermediate between the two species (S.E. Sandermann Olsen and F. Skovgaard, personal communication). The fruit set of individuals in the TB population is said to be low, and it has been suggested that this population may represent a hybrid between *A. ramosum* and *A. liliago*. However, there are no other populations of *A. liliago* on Sjælland at the present day and the nearest *A. ramosum* population is about 114 km distant. Cytological data from Sjælland individuals are needed to clarify the status of the TB population.

In contrast with the TB population (Sjælland), the DB (Skåne) population of *A. liliago*, which has been shown to contain triploid hybrid individuals (Strandhede 1963), has a similar tepal shape to other *A. liliago* populations, although it is distinct from other Skåne populations (Fig. 4). Hybrids within the DB population have been reported as being female sterile (Strandhede 1963; G. Rosquist, personal observation) but male fertile with 10% to 50% morphologically well-developed pollen grains (Strandhede 1963). The ability of the hybrids to produce some fertile pollen may allow gene flow, across ploidy levels, between the two species. Gene flow between ploidy levels is usually unidirectional, from $2\times$ to $3\times$ to $4\times$ (Levin 1978). The site where the DB population occurs is one of the few Scandinavian localities that currently contains both *A. ramosum* and *A. liliago* individuals. The hybrid individuals in the DB population have a flowering time that is intermediate between the early flowering *A. liliago* and the later flowering *A. ramosum*. There are recent reports of other late-flowering *A. liliago* individuals or populations from Skåne (K.A. Olsson, personal communication; G. Rosquist, personal observation) and from Öland (Ålind and Öberg 1999). It is possible that these individuals or populations may also contain hybrids, particularly in the northern part of Skåne and on Öland, where populations of the two species show a limited degree of sympatry.

Acknowledgements

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