# Morphometric variation in a hybrid zone between the weed, *Silene vulgaris,* and the endemic, *Silene uniflora* ssp. *petraea* (Caryophyllaceae), on the Baltic island of Öland

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**Abstract**: On the island of Öland the weed, *Silene vulgaris* (Moench) Garcke, and the endemic, *Silene uniflora* Roth ssp. *petraea*, hybridize when brought into contact by anthropogenic disturbance. Variation was studied in transects across a hybrid zone where a linear population of *S. vulgaris* crossed the native habitat of *S. uniflora* ssp. *petraea*. Plants were scored for 20 morphological characters. Although individual characters showed clinal trends between weed and endemic, all plants were assignable to one or other parental species. Only 14% of the 554 scored plants showed intermediacy in one or a few characters, and ordinations showed two separate groups of samples. The low number of intermediates is discussed in terms of character choice, habitat separation, disturbance history, and reproductive ecology. The results of the study are consistent with the earlier observation that the species have remained morphologically distinct on Öland, despite evidence of sparse introgression of allozymes from weed to endemic. Disturbance is necessary not only for the creation of intermediate (hybrid) habitats but also for the establishment of the weedy parent. The transient nature of *S. vulgaris* populations is likely to be important in limiting introgression into *S. uniflora* ssp. *petraea* under the present disturbance regime.

*Key words*: genetic assimilation, hierarchical partitioning of diversity, habitat disturbance, introgression, rare species, clines.

**Résumé** : Sur l'île de Öland, lorsqu'ils sont mis en contact par des perturbations anthropogènes, le *Silene vulgaris* (Moench) Garcke une mauvaise herbe, et l'espèce endémique *Silene uniflora* Roth ssp. *petreae,* s'hybrident. Les auteurs ont étudié la variation dans des transects traversant une zone d'hybridation, où une population linéaire de *S. vulgaris* traverse l'habitat de l'espèce indigène *S. uniflora* ssp. *petreae*. Les auteurs ont observé 20 caractères morphologiques. Bien que les caractères individuels montrent des tendances clinales entre la mauvaise herbe et l'espèce endémique, toutes les plantes peuvent être attribuées à l'une ou l'autre des espèces parentes. Seulement 14 % des 554 plantes observées apparaissent intermédiaires pour un ou quelques caractères et l'ordination montre deux groupes séparés d'échantillons. Les auteurs discutent le faible nombre d'intermédiaires en termes de choix du caractère, de la séparation des habitats, de l'historique des perturbations et de l'écologie de la reproduction. Les résultats de cette étude concordent avec des observations antécédentes à l'effet que ces espèces sont demeurées morphologiquement distinctes sur l'île de Öland, en dépit de l'existence d'une faible introgression allozymique de l'espèce adventice vers l'espèce endémique. La perturbation est nécessaire non seulement pour créer des habitats (hybrides) intermédiaires mais aussi pour l'établissement du parent adventice. La nature transitoire des populations du *S. vulgaris* est probablement importante pour limiter l'introgression chez le *S. uniflora* ssp. *petreae*, dans le cadre du présent régime de perturbation.

*Mots clés* : assimilation génétique, partition hiérarchique de la diversité, perturbation de l' habitat, introgression, espèce rare, clines.

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## Introduction

Interspecific hybridization is widespread among plants (Arnold 1992; Rieseberg and Wendel 1993), and hybridization is thought to have played a major role in plant evolution (Lotsy 1916; Anderson 1948; Stebbins 1959; Grant 1981). It has been suggested that hybridization has contributed to the evolutionary history of the majority of angiosperm species (Grant 1981; Stace 1987).

Hybrid zones and clines between interfertile taxa may arise as a result of secondary contact between previously isolated populations (Mayr 1942; Hewitt 1988). Many plant

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and animal hybrid zones in Europe and North America are thought to have a secondary origin and to have arisen as a result of species' range changes and migrational spread after the last ice age (Hewitt 1989, 1993). Hybrid zones and clines may also represent a primary response to varying selection pressures along environmental gradients (Endler 1977; Heywood 1986). Primary and secondary clines can give rise to identical patterns of variation (Endler 1977). Hybrid zones may also have a mosaic rather than clinal structure (Harrison 1990; Arnold and Bennett 1993).

Introgressive hybridization, with hybridization being followed by repeated backcrossing (Rieseberg and Wendel 1993), may result in the merging of two species (e.g., Anderson 1949; Bloom 1976; Rieseberg and Ellstrand 1993). Introgression may also provide a rich source of variation that is available for natural selection. Stebbins (1959) suggested that the genetic diversity generated by recombination following hybridization between adaptively differentiated populations was an important source of variation for major evolutionary advances. However, hybridization is not always followed by introgression. Competition may result in the extinction of one of the parent species (Harrison 1990). Alternatively, if each of the parent species has a higher relative fitness in their respective habitats, hybrid zones may be stable over long periods of time and the hybridizing species will remain distinct (e.g., Heiser 1947; Levin 1971; Jackson 1973; Potts and Reid 1990).

Stable hybrid zones may be maintained by selection or by a balance between selection and dispersal (Barton and Hewitt 1985). Two main types of model have been proposed to explain the phenomenon of stable hybrid zones. In the first, selection acts against the hybrids and dispersal does not affect the structure of the hybrid zone (Barton and Hewitt 1985; Hewitt 1988). The second type of model assumes an intermediate habitat zone where hybrids have a higher relative fitness than both parental species (Endler 1977). It has also been suggested that hybrids can only be successful in disturbed and unstable habitats (Anderson 1948; Heiser 1973; Grant 1981).

Many of the currently known examples of hybridization and introgression are the result of human disturbance that has either removed the distinction between different types of habitat or introduced alien species into the range of native species (Stace 1975; Harrison 1990; Levin et al. 1996). The greater the level of ecological disturbance, the greater the opportunities will be for hybridization and hybrid establishment (Levin et al. 1996), and hybridization as a result of human disturbance has been documented for many plants (e.g., Wiegand 1935; Baker 1948; Anderson 1948; Stace 1975; Levin 1967a, 1975; Arnold et al. 1990; Rieseberg and Wendel 1993). The probability of hybridization between previously allopatric taxa is increasing (Albert et al. 1997).

Rare species may be threatened when habitat disturbance promotes hybridization with widespread congeners (Rieseberg and Doyle 1989; Ellstrand 1992; Ellstrand and Elam 1993; Rhymer and Simberloff 1996). Locally adaptive variation in rare species may be lost as a result of interspecific gene flow (Cade 1983; Hewitt 1989; Rieseberg et al. 1989). Outbreeding depression may occur if two previously separated populations, adapted to different environmental conditions, are brought into contact and locally adapted gene complexes are broken down (Templeton 1986).

Many rare or vulnerable species occur in small populations and have declining population sizes (Barrett and Kohn 1991; Bijlsma et al. 1994). Interspecific gene flow may reduce the risk of extinction by lowering the likelihood of inbreeding depression. But interspecific gene flow may also increase the risk of extinction through hybridization (Rieseberg 1991; Ellstrand 1992; Ellstrand and Elam 1993; Levin et al. 1996). Populations of a rare species are more likely to be genetically contaminated or genetically assimilated by a related taxon if they are small and (or) isolated (Cade 1983; Rieseberg 1991; Ellstrand and Elam 1993; Young et al. 1996). Insular endemic taxa with non-specific pollinators are particularly vulnerable to extinction by hybridization (Levin et al. 1996).

The bladder campions *Silene vulgaris* (Moench) Garcke and *Silene uniflora* Roth ssp. *petraea* on the Baltic island of Öland provide an example of hybridization between an introduced weed and an endemic island taxon. The two taxa show a high degree of interfertility (Marsden-Jones and Turrill 1957), they are visited by the same suite of pollinators (Pettersson 1991; 1994), and they have overlapping flowering phenologies (Runyeon and Prentice 1996). *Silene uniflora* ssp. *petraea* occurs in small and spatially disjunct populations on shallow limestone soils. *Silene vulgaris* is widespread and occurs in large and extensive populations in anthropogenically disturbed habitats. Patterns of allozyme variation indicate that there is spatially extensive, but sparse, introgression of *S. vulgaris* alleles into *S. uniflora* ssp. *petraea* (Runyeon and Prentice 1996).

*Silene uniflora* ssp. *petraea* appears to represent a classic example of an endemic species at threat from genetic assimilation by a widespread weed (*S. vulgaris*). However, the two species normally occupy ecologically distinct habitats and, despite the allozyme evidence for interspecific gene flow (Runyeon and Prentice 1996), morphologically intermediate individuals are rarely observed and hybrid swarms are transient and seldom extensive.

The present study explores the structure of phenotypic variation in morphological characters across a recently formed hybrid zone between *S. vulgaris* and *S. uniflora* ssp. *petraea* on Öland. An abandoned railway embankment, colonized by a linear population of *S. vulgaris*, cuts across an extensive area of the limestone "alvar" habitat occupied by *S. uniflora* ssp. *petraea*. This situation creates a natural experiment for the study of interspecific hybridization and gene flow between an introduced weed and an endemic taxon that is characteristic of an unique and ecologically extreme native habitat.

## Materials and methods

### *Silene vulgaris* and *Silene uniflora*

*Silene vulgaris* and *S. uniflora* are perennial herbs with a gynodioecious or gynomonoecious breeding system (Charlesworth and Laporte 1998). The two taxa are closely related and both are diploid ($2n = 24$) in northern Europe (Marsden-Jones and Turrill 1957; Jalas and Suominen 1986; Chater and Walters 1990). *Silene vulgaris* is native to Eurasia (Aeschimann 1983) but also occurs as a weed of cultivation in other parts of the world (Marsden-Jones and Turrill 1957). The species is widely distributed throughout Europe (Jalas and Suominen 1986) and is represented by several geographic subspecies (Aeschimann and Bocquet 1980). Only the weedy subspe-

cies, *vulgaris*, is present in northern Europe. *Silene uniflora* (= *Silene maritima* With.) is restricted to northwestern Europe (Jalas and Suominen 1986). Two allopatric subspecies are present in Sweden. The coastal *S. uniflora* ssp. *uniflora* is present along the whole of the west coast and along the northeastern Baltic coast but is absent from the southeastern Baltic coast and from the islands of Öland and Gotland. *Silene uniflora* ssp. *petraea* (Hartm.) Jonsell & H.C. Prentice is endemic to the Baltic islands of Öland and Gotland.

### *Silene vulgaris* and *Silene uniflora* on Öland

*Silene vulgaris* is common on Öland and forms extensive populations (often containing several thousands of individuals) in disturbed habitats such as road verges and field margins. *Silene uniflora* ssp. *petraea*, in contrast, is confined to the most open habitats within the steppe-like "alvar" (Königsson 1968) on limestone bedrock in the southern part of the island. It occurs in sparsely vegetated areas with thin, base-rich and heavily frost-disturbed soils. The populations of *S. uniflora* ssp. *petraea* are small (usually less than 50 individuals) and separated from each other by 1–3 km. (Runyeon and Prentice 1996).

The stems of *S. vulgaris* are erect (or ascending and then erect) and are up to 100 cm tall. The inflorescences contain 5–80 flowers (Clapham et al. 1989). The flowers are nodding, usually zygomorphic and have narrow, non-overlapping petals. The bracts of *S. vulgaris* are characteristically hyaline and the immature seeds are usually white. In contrast to *S. vulgaris*, the stems of *S. uniflora* ssp. *petraea* are procumbent to ascending. The inflorescences are one to three flowered, and the flowers are erect and usually actinomorphic. The petals vary in width and the degree of petal overlap also varies. An anthocyanin spot and (or) coronal scales are often present at the base of the petals. The bracts are characteristically herbaceous and immature seeds of *S. uniflora* ssp. *petraea* are often purple.

The two species overlap in their flowering period. *Silene vulgaris* flowers intensively for ca. 4 weeks from late June to July. *Silene uniflora* ssp. *petraea* flowers continuously but sparsely from early May until the first frosts in September or October. The main pollinators of both *S. vulgaris* and *S. uniflora* ssp. *petraea* are crepuscular moths (Pettersson 1991, 1992a).

### Hybridization

*Silene vulgaris* and *S. uniflora* are interfertile (Marsden-Jones and Turrill 1957; Walters 1975). On Öland, *S. vulgaris* and *S. uniflora* ssp. *petraea* normally occur in ecologically distinct habitats (Runyeon and Prentice 1996, 1997a). Hybrids are found in areas where anthropogenically disturbed habitats occur close to the alvar habitats occupied by *S. uniflora* ssp. *petraea*. The hybrids are fertile and may persist for several years. However, hybrid swarms are rare and transient, and morphologically intermediate individuals are usually few and scattered.

### The study site

The Great Alvar on Öland is a steppe-like, open area of ca. 260 km$^2$ with a mosaic of base-rich and weakly acidic soils overlying the limestone bedrock (Königsson 1968; Bengtsson et al. 1988). *Silene uniflora* ssp. *petraea* is confined to the most open alvar vegetation, on thin, base-rich soils that are derived from in situ weathering of the underlying limestone. These habitats are poorly drained, subject to frost action in the winter and spring, and to extreme drought in the summer. Such habitats are thought to have been open and treeless throughout the post-glacial period (Iversen 1958; Fries 1965; L.-K. Königsson, personal communication).

The Great Alvar is crossed by a narrow railway embankment that runs westwards from the village of Skärlöv (Fig. 1). The railway was abandoned in the 1950s. The embankment was cleared and surfaced with gravel (originating from outside the area) early

**Fig. 1.** Map showing the location of the hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* at Skärlöv on the Baltic island of Öland, Sweden.
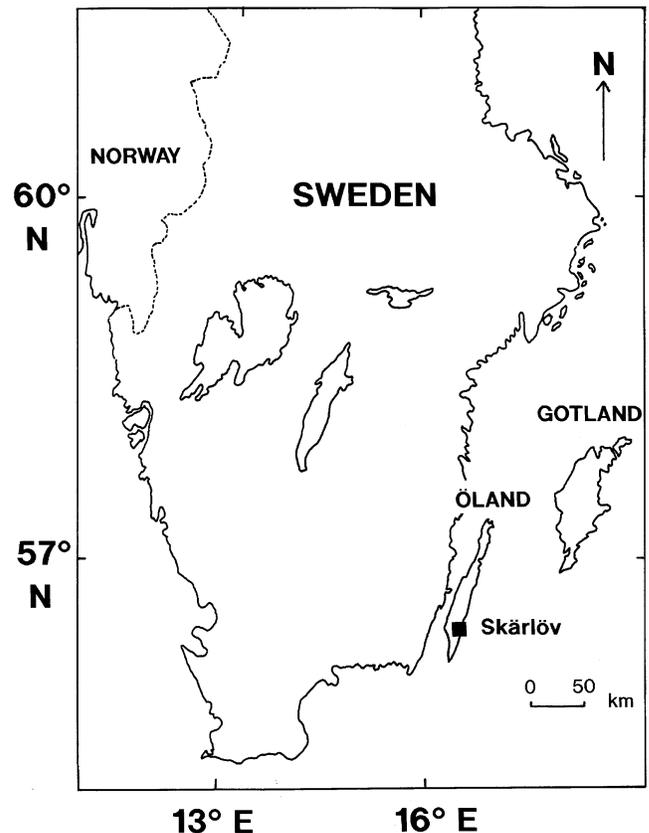


in 1989 and has been used subsequently as a track for cycling and walking. Many weedy species, including a large population of *S. vulgaris* consisting of several hundred individuals, colonized the embankment after the construction of the cycle track. A substantial proportion of the *S. vulgaris* individuals started to flower in 1989. The alvar on both sides of the embankment is open and frost-disturbed, and individuals of *Silene uniflora* ssp. *petraea* are found throughout the whole of this alvar area. The embankment is only ca. 2 m wide, and the change from a ruderal to a natural alvar habitat occurs over a few metres. *Silene uniflora* ssp. *petraea* individuals are found only a few metres from the linear *S. vulgaris* population. Individuals with some characters that are intermediate between the two species are scattered throughout the area and may be found several kilometres from the embankment. However, the *Silene* individuals along the embankment were all assignable to *S. vulgaris* on the basis of overall morphology, and all individuals outside the embankment were assignable to *S. uniflora* ssp. *petraea*.

### Sampling design

The embankment was used as a base line for the sampling of *Silene* individuals. In 1994, three 800-m-long cross transects (1–3, Fig. 2) were laid out across the embankment at 500-m intervals. Three parallel transects were laid out on each side of the embankment, 25 (A), 100 (B), and 400 m (D) from the embankment (*Silene* individuals were too sparse to allow sampling at 200 m). The parallel transects to the north and south of the embankment were denoted by the prefixes "N" and "S," respectively (Fig. 2). *Silene* individuals were sampled at the grid intersections ("sites") between the parallel and cross transects and the embankment. The sampling sites were labelled according to their relation to the embankment. For example, "S1A" denotes the site closest to the em-

**Fig. 2.** Schematic map showing the sampling design within the hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* on Öland. Three 800 m long cross transects (1–3) were laid out at 500-m intervals across the embankment (EM). Three parallel transects were laid out on each side of the embankment 25 (NA and SA), 100 (NB and SB), and 400 m (ND and SD) from the embankment. The sampling sites (circles) were located on the intersections of the parallel and cross transects. Two reference sites (squares) were sampled for each species: WST + EST for *S. vulgaris* and NOR + SOU for *S. uniflora* ssp. *petraea*. Solid symbols show sites with individuals assignable to *S. vulgaris*, and open symbols indicate sites with individuals assignable to *S. uniflora* ssp. *petraea*.
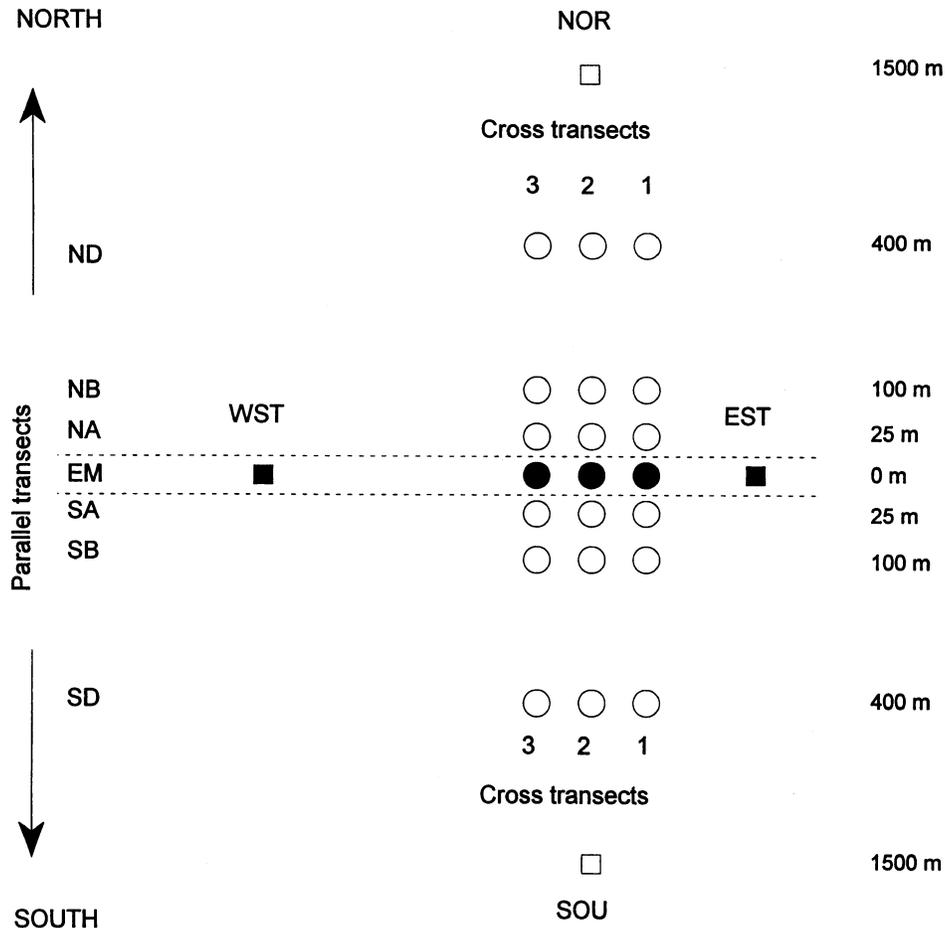


bankment on the southern side (parallel transect SA) situated in the most eastern cross transect (see Fig. 2).

Two sites outside the grid were also sampled as reference sites for each species. The two *S. uniflora* ssp. *petraea* reference sites (NOR and SOU) were located, respectively, ca. 1.5 km N and S of the embankment (at the ends of cross transect 2). The two *S. vulgaris* reference sites were located at the ends of the embankment (EST was ca. 1.5 km from site EM1 and WST was ca. 6 km from site EM3; see Fig. 2). The *S. vulgaris* individuals on the embankment were often separated from their neighbours by less than 1 m, whereas the *S. uniflora* ssp. *petraea* individuals occurred singly or in small patches, separated by more than 10 m. Approximately 20 individuals (mean 22.2) were sampled at each site. The first sampled individual was the individual that was nearest to the grid intersection. Subsequent individuals were chosen for sampling by working concentrically outwards from the first individual and following the rule that each sampled individual should be as near as possible to, but not less than, 5 m from the previously sampled individuals. A total of 554 individuals was sampled from the 25 sites (including the four reference sites).

## Morphometric measurements

A suite of 20 morphological characters (Table 1) was scored on each individual. The floral characters (Table 1, character Nos. 8–

20) were scored on three flowers per individual, where possible. However, many *S. uniflora* ssp. *petraea* individuals only produced one or two undamaged flowers. A total of 330 flowers was scored for *S. vulgaris* (119 individuals, mean 2.8 flowers/individual) and a total of 533 flowers for *S. uniflora* ssp. *petraea* (435 individuals, mean = 1.2 flowers/individual). Characters 1–14 were scored in the field, and characters 15–20 (petal characters) were scored in the laboratory. For the characters that were expressed as values on an integer scale from 1 to 3 (or 4), "*Silene vulgaris* character states" were given a value of 1 and "*Silene uniflora* character states" were given a value of 3 (or 4). Characters 2–20 were used in the statistical analyses. Character 1 ("purity") represents an a priori assessment of whether an individual showed any recognizable indication of morphological intermediacy.

The genetic control of character variation in the *S. vulgaris* group was studied by Marsden-Jones and Turrill (1957) who showed that even variation in vegetative characters such as stem orientation and colour of vegetative parts has a substantial genetic component. Greenhouse studies of *S. vulgaris* and *S. uniflora* ssp. *petraea* from Öland also show that the morphological differences (including differences in habit and in vegetative characters) between the two species persist when they are grown under standard conditions (Prentice and Giles 1993).

**Table 1.** Characters used in the investigation of morphological variation in a hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* on Öland.

| No. | Character | Measurement scale |
|---|---|---|
| 1 | Purity* | 1–3 (*Silene vulgaris*, intermediate characters, *Silene uniflora* ssp. *petraea*) |
| 2 | No. of flowers/inflorescence | Counts |
| 3 | Flower orientation | 1–3 (nodding to upright) |
| 4 | Bracts | 1–3 (hyaline to herbaceous) |
| 5 | Stem orientation | 1–4 (erect to procumbent) |
| 6 | Immature seed colour | 1–3 (white to purple) |
| 7 | Plant height | cm |
| 8 | Flower form | 1–3 (zygomorphic to actinomorphic) |
| 9 | Petal overlap | 1–3 (absent to pronounced) |
| 10 | Calyx length | mm |
| 11 | Calyx breadth at widest point | mm |
| 12 | Calyx tooth length | mm |
| 13 | Coronal scales (length) | mm |
| 14 | Carpophore length | mm |
| 15 | Petal breadth at widest point | mm |
| 16 | Petal breadth at narrowest point | mm |
| 17 | Spot at base of petal | 1–3 (absent to pronounced) |
| 18 | Petal dissection depth | mm |
| 19 | Petal claw length | mm |
| 20 | Petal claw breadth at widest point | mm |

**Note:** Where the characters are expressed as values on an integer scale, the "*Silene vulgaris* character state" has a value of 1 and the "*Silene uniflora* ssp. *petraea* character state" has a value of 3 (or 4).

*An a priori assessment of whether an individual showed any recognizable indication of morphological intermediacy.

**Vegetation cover**

The vegetation cover (excluding the *Silene* individual) was recorded within a circle with a radius of 0.5 m around each sampled individual. Separate (percentage) cover values were estimated for total vegetation, herbs, grasses, and cryptogams (mosses and lichens).

**Statistical analyses**

A series of canonical variate analyses (CVA) was used to study the relationships between the sites in the contact zone. Characters 2–20 (Table 1) were included in the analyses and the procedure CANDISC in SAS (SAS Institute Inc.1994) was used for the CVAs.

As well as using CVA to display the patterns of overall morphometric differentiation between sites, CVA was also used to partition the total morphological diversity into its within- and between-species, -transect, -site, and -individual components. Four separate CVAs were carried out and flowers were used as the within-group replicates in each of the analyses. The proportion of the total variance due to within-group variance in a CVA is given by Wilks' lambda ($\Lambda$). In the first CVA, (analysis P, giving $\Lambda_P$), the two species (all the individuals were assignable to either *S. vulgaris* or *S. uniflora* ssp. *petraea*) were used as groups. In the second CVA (analysis D, giving $\Lambda_D$) the distances from the embankment were used as groups (five groups: embankment (including the *S. vulgaris* reference sites); parallel transects A, B, and D; and the *S. uniflora* ssp. *petraea* reference sites). A further two CVAs were carried out with the groups defined, respectively, as sites (giving $\Lambda_S$) and individuals (giving $\Lambda_I$). The $\Lambda$ values from the four analyses were used to produce two hierarchical partitions of morphological diversity (cf. Prentice and White 1988). The first hierarchy included species, sites, and individuals. The proportion of the total diversity due to variation between species is given by $1 - \Lambda_P$, the proportion of the diversity between sites within species is given by $\Lambda_P - \Lambda_S$, the proportion of the diversity between individuals within sites is given by $\Lambda_S - \Lambda_I$, and the within-individual component of diversity is given by $\Lambda_I$. The second hierarchy included transects, sites, and individuals. Here the proportion of the total diversity due to the distance-

classes is given by $1 - \Lambda_D$, the between-site diversity component by $\Lambda_D - \Lambda_S$, the within-site component by $\Lambda_S - \Lambda_I$, and the within-individual component of diversity by $\Lambda_I$.

Associations between the matrices of morphometric and geographic distances between the 25 sampling sites were tested for using the generalized regression method of Mantel (1967) and the relative neighbourhood graph (RNG) method of Lefkovitch (1984). One thousand permutations were used for the Mantel test. A likelihood statistic for marginal independence (assuming a $\chi^2$ distribution, 1 df) was used to compare the number of coinciding neighbours in the RNGs with random expectations. The morphometric distance matrix used in the comparisons was the Mahalanobis' distance ($D^2$) matrix from the CVA based on sites as groups.

Variation in the vegetation cover values (mean within-site total cover, herb cover, grass cover, and cryptogam cover) between sampling sites was analyzed using correspondence analysis (CA) and the program CANOCO (ter Braak 1987).

## Results

**Morphological characters**

*Silene vulgaris* and *S. uniflora* ssp. *petraea* are differentiated on the basis of numerous morphological traits. The most obvious differentiating characters between the two species are flower number and orientation. *Silene vulgaris* has nodding flowers, a higher number (>5) of flowers per inflorescence, and larger leaves than *S. uniflora* ssp. *petraea*.

All the scored individuals could be assigned to either *S. vulgaris* or *S. uniflora* ssp. *petraea* on the basis of their overall phenotype. However, 80 (14%) of the 554 sampled individuals were characterized, a priori, as showing some indication of phenological intermediacy (character 1, purity; Table 1). The subjective evaluation of "purity" included vegetative characters, such as leaf size, that were not included in

the statistical analyses. Only 16% of the individuals from the embankment (assignable to *S. vulgaris*) were scored as being intermediate (character 1). The highest proportion of discernably intermediate individuals (29%) was found in the parallel transects nearest to the embankment (NA + SA; Fig. 2), and the proportion of intermediates declined with distance from the embankment to 3.6% in the *S. uniflora* ssp. *petraea* reference sites (NOR + SOU).

Variation in the morphological characters across the hybrid zone is summarized in Fig. 3 (mean data for the reference sites, the embankment and the six parallel transects are available from the authors on request). *Silene vulgaris* (from the embankment) is clearly distinct from the *S. uniflora* ssp. *petraea* (outside the embankment) in the majority of the characters. However, although relatively few individuals were scored a priori as showing signs of intermediacy, many of the characters show at least a tendency towards clinal variation in the mean values for the samples of *S. uniflora* ssp. *petraea* in the area outside the embankment. Characters such as flower number (Table 1, character 2) and flower orientation (character 3) emphasize the distinction of *S. vulgaris* and show a weak, but more-or-less regular decline in *S. vulgaris* character states to the north and south of the embankment. Other characters, for example stem orientation (character 5) and immature seed colour (character 6), show similar, but less orderly, clinal trends. The clinal trends are not always symmetrical on the north and south sides of the embankment. The petal spot (character 17), a *S. uniflora* ssp. *petraea* character, is more pronounced in parallel transect SB than in NB, the degree of petal lobe overlap (character 9) is less in parallel transect SD than in ND, the coronal scales (character 13) are unusually short in SD but unusually long in NB compared with the other parallel transects. Parallel transect ND showed aberrant patterns in several characters. For example, mean stem orientation (character 5) was ascending (slightly *S. vulgaris*-like), the colour of the immature seeds (character 6) was paler (*S. vulgaris*, mostly white; *S. uniflora* ssp. *petraea*, mostly purple) and the calyces (character 10) were shorter in ND than in any of the other *S. uniflora* ssp. *petraea* parallel transects (Fig. 3). Three characters, petal lobe overlap (9), calyx length (10), petal claw breadth (20), showed peaks for the "*vulgaris*" characteristics in the parallel transect SA, adjacent to the embankment. Thirteen out of the 19 characters show extreme mean values (*vulgaris* character states) in the embankment group of sites (EM + WST + EST) whereas only 6 characters showed extreme ("*petraea*") values in the *S. uniflora* ssp. *petraea* reference sites (NOR + SOU).

The first two canonical variates (CVs) of a CVA based on 19 morphological characters (with sites as groups) are shown in Fig. 4. *Silene vulgaris* and *S. uniflora* ssp. *petraea* form clearly separate groups in the diagram. The three most negative and positive character loadings for the first three CVs are shown in Table 2. The characters "number of flowers per inflorescence," "petal dissection," and "plant height" decrease along CV 1, whereas "flower form," "bracts," and "flower orientation" increase along the first CV. "Flower form" and "petal spot" decrease, whereas "calyx breadth" and "calyx tooth length" increase along CV 2. Within the *S. uniflora* ssp. *petraea* group of sites, two of the three sites from parallel transect ND (N2D and N3D) are found in the lower part of the diagram, somewhat separated from the other sites (cf. Fig. 4).

A plot of Mahalanobis' distances ($D^2$, obtained from the CVA with sites as groups in Fig. 4) from the two *S. uniflora* ssp. *petraea* reference sites NOR and SOU is shown in Fig. 5. The distances are the mean $D^2$ from NOR and SOU to the *S. vulgaris* sites on the embankment (cross transects 1–3 and reference sites EST and WST) and the means from NOR and SOU to each of the eight parallel transects (see Fig. 2). The mean Mahalanobis' distances are greatest between the *S. uniflora* ssp. *petraea* reference sites (NOR and SOU) and the *S. vulgaris* sites on the embankment. The mean distances between NOR and SOU, respectively, and parallel transect ND are larger than the distances between NOR and SOU and the other parallel transects.

The Mantel test comparison of the between-site matrices of geographic and morphometric (Mahalanobis') distances showed a significant association between the two matrices (correlation coefficient 0.313, $P < 0.001$), whereas the RNG $\chi^2$ test statistic (1.588) was nonsignificant.

### Partitioning of morphological diversity

The partitioning of the total morphometric diversity is shown in Table 3. In the first hierarchy, including species, sites, and individuals, the between-species component of diversity accounts for the majority (89%) of the total morphometric diversity and is approximately nine times higher than the between-site component of diversity (10%). Only 1% of the total morphometric diversity is due to within-site variation.

The second hierarchy included distance classes, sites, and individuals. Ninety-two percent of the total morphometric diversity is accounted for by differences between distance classes (Table 3). Five percent of the total diversity is explained by differences between sites (within distance classes), and the remaining 1% is due to within-site diversity. Within-individual variation does not account for any of the diversity.

There are significant ($P < 0.05$) between-group differences for all 19 morphometric characters in the site CVA (analysis S) and for 18 of the characters in the distance class (analysis D) CVA (Table 3). All characters except petal claw length and calyx tooth length differed significantly ($P < 0.05$) between groups in the species CVA (analysis P). Thirteen of the characters show significant between-individual differences in analysis I (Table 3). Two hundred and six of the total 300 between-site Mahalanobis' distances were significant ($P < 0.05$).

### Vegetation characteristics

Variation in vegetation characteristics, including the height of the surrounding vegetation and vegetation cover, is shown in Fig. 6. The values are given as means for each of the two *S. uniflora* ssp. *petraea* reference sites (NOR and SOU), means over each of the six parallel transects, and as a mean over the five *S. vulgaris* embankment sites (including the reference sites EST and WST). The *S. vulgaris* sites on the embankment are characterized by tall vegetation; high percentages of total, herb, and grass cover; and a relatively low cryptogam cover. The highest cryptogam covers are found along parallel transects SA and NA, situated 25 m from the embankment (Fig. 6). The *S. vulgaris* sites and the *S. uniflora* ssp. *petraea* sites form two clearly separated groups in the correspondence analysis of vegetation cover in Fig. 7.

**Fig. 3.** Plots summarizing variation in 19 morphological characters scored within the hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* on Öland. The character values are means (over sites) for the distance classes on the three northern and three southern parallel transects, the embankment sites (including the *S. vulgaris* reference sites) and the two *S. uniflora* ssp. *petraea* reference sites (NOR and SOU), respectively. EM, embankment; SA and NA, 25 m from embankment; SB and NB, 100 m from embankment; SD and ND, 400 m from embankment (see Fig. 2). Characters 3, 4, 6, 8, 9, and 17 are expressed as values on a integer scale from 1 to 3, and character 5, on a scale of 1 to 4 (from "*S. vulgaris* character state" to "*S. uniflora* ssp. *petraea* character state").
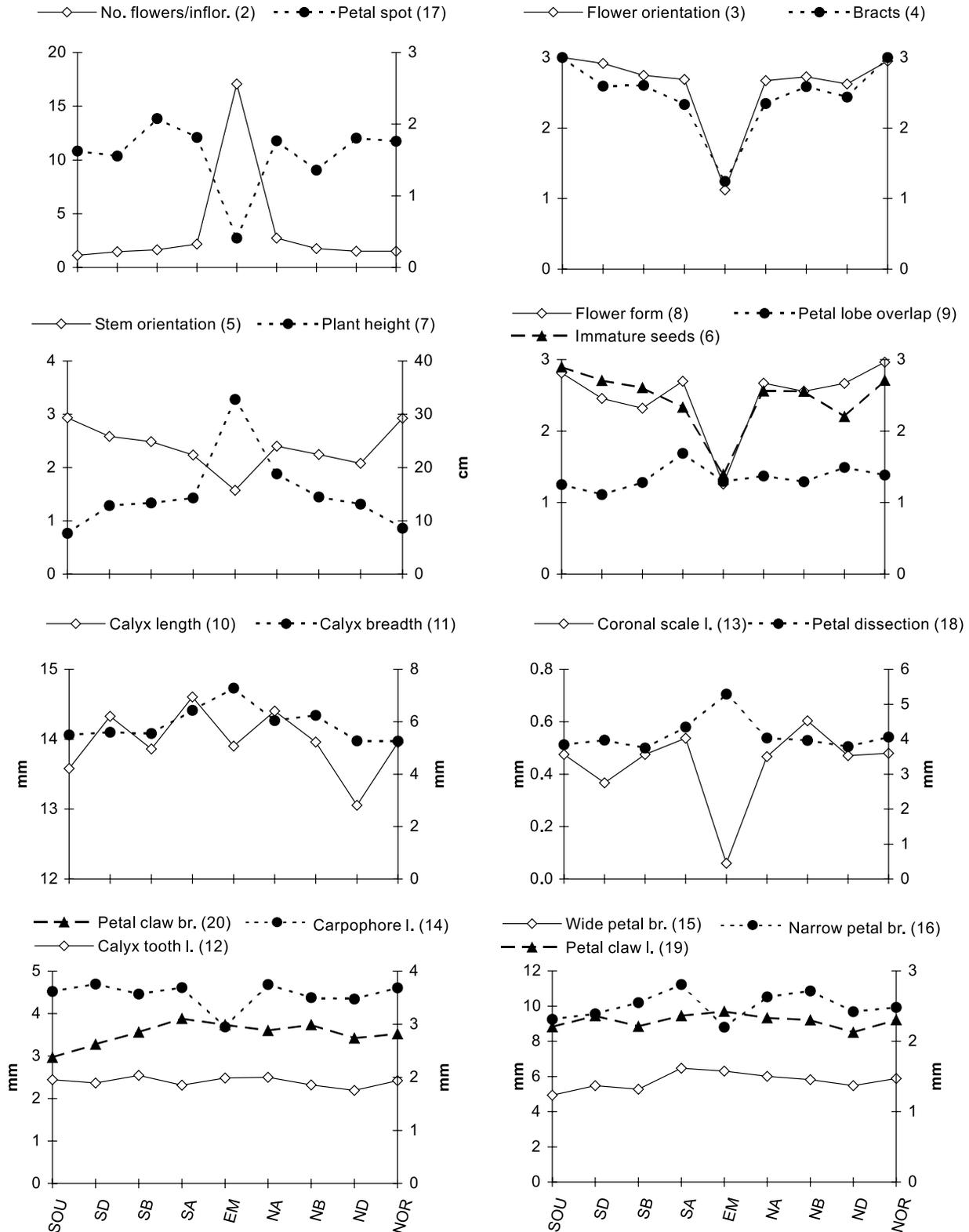
**Fig. 4.** Plot of CVs 1 and 2 from a CVA of 19 morphological characters (with sites as groups). Solid symbols show sites with individuals assignable to *Silene vulgaris*, and open symbols show sites with individuals assignable to *Silene uniflora* ssp. *petraea*: the reference sites are indicated by squares. Sites N1B, N3A, S2D, and S3D are closely grouped on the plot, and their position is indicated by an asterisk. See Fig. 2 for site codes and positions. The CVs are in standard deviation units; CV 1 accounts for 77% and CV 2, for 6% of the total between-site variance.
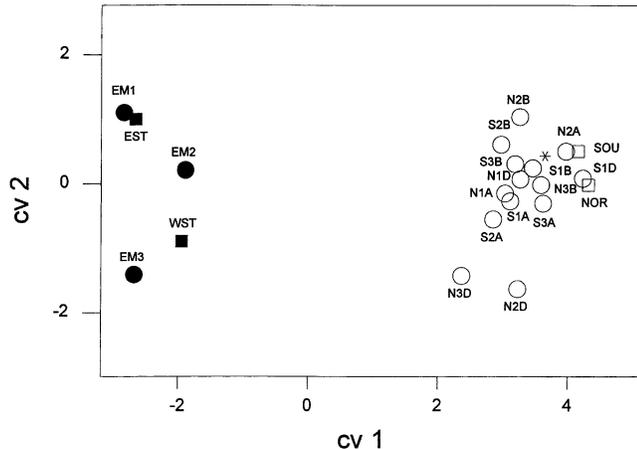


## Discussion

At first sight, *S. uniflora* ssp. *petraea* appears to represent a classic example of a geographically restricted, insular endemic taxon that is under threat of genetic assimilation by an introduced, weedy taxon. The weed (*S. vulgaris*) and the endemic *S. uniflora* ssp. *petraea* are closely related, interfertile, share the same efficient and strongly flying pollinators, and have overlapping flowering phenologies (Pettersson 1991, 1992*a*; Runyeon and Prentice 1996). On the island of Öland, the two species hybridize in situations where they are brought into contact by human disturbance. The fact that the endemic, *S. uniflora* ssp. *petraea*, occurs in numerically small and disjunct populations is also expected to increase its vulnerability to interspecific hybridization (cf. Ellstrand 1992; Ellstrand and Elam 1993; Levin et al. 1996). Allozyme data provide evidence of spatially extensive introgression of genes from the weed to the endemic: alleles characteristic of *S. vulgaris* are sparsely scattered in individuals of *S. uniflora* ssp. *petraea*, even in populations that are far from *S. vulgaris* populations (Runyeon and Prentice 1996). However, despite allozyme evidence for long-distance introgression of *S. vulgaris* alleles into *S. uniflora* ssp. *petraea*, field observations indicate that morphologically intermediate individuals are rare on Öland (Runyeon and Prentice 1996).

The present study of phenotypic variation was carried out in an area where anthropogenic disturbance had introduced, five seasons earlier, a linear population of *S. vulgaris* into an area of native habitat containing *S. uniflora* ssp. *petraea*. All the individuals in the study area could be unambiguously assigned either to *S. vulgaris* or *S. uniflora* ssp. *petraea* on the basis of overall phenotype. Individuals assignable to *S. vulgaris* were restricted to the linear embankment, and there was an abrupt transition to the adjacent (natural) alvar

habitats, where all the individuals were assignable to *S. uniflora* ssp. *petraea*. However, within the alvar habitat of *S. uniflora* ssp. *petraea* there was a scattering of individuals that had the general appearance of *S. uniflora* ssp. *petraea* but that showed intermediacy in one or a few characters. Some intermediate plants were also present on the embankment, but these plants were confined to the middle of the cycle track, growing in open gravel.

The mean values for individual traits show that the degree of character intermediacy decreases in samples of *S. uniflora* ssp. *petraea* with increasing distance from the *S. vulgaris* population (Fig. 3). Although the use of mean trait values may overemphasize intermediacy (Rieseberg and Ellstrand 1993), the number of *S. uniflora* ssp. *petraea* individuals scored a priori as showing traces of intermediacy also decreased with distance from *S. vulgaris* (from 29% in sites at 25 m from the embankment to 3.6% in the reference sites of *S. uniflora* ssp. *petraea* at 1500 m). However, the total number of intermediates was low (14%) and intermediate plants were intermediate only in one or a few characters. The CVA in Fig. 4 shows a clear distinction between samples assignable to *S. vulgaris* and those assignable to *S. uniflora* ssp. *petraea*, and the diversity component due to these two groups of individuals accounted for the majority of the total diversity (Table 3).

### Intermediate versus parental characters

Several studies have shown that the numbers of intermediate and parental characters expressed in hybrids vary considerably between species (e.g., Levin 1967*b*; Kephart et al. 1988; McDade 1990; Rieseberg and Ellstrand 1993). It is possible that $F_1$ hybrids between *S. vulgaris* and *S. uniflora* ssp. *petraea* express a preponderance of parental characters. However, artificial $F_1$ hybrids between the two taxa typically have an overall phenotype that is obviously intermediate between that of their parents rather than showing basically parental phenotypes with traces of intermediacy in some characters (H.C. Prentice, unpublished observations). The fact that most of the "intermediate" individuals in the study area are only intermediate in a few characters and otherwise resemble one or other of the parental taxa suggests that they may represent later-generation hybrids or backcrosses rather than $F_1$ hybrids. Some hybrid taxa have also been shown to express extreme characters that do not resemble either parent (Rieseberg and Ellstrand 1993; Rieseberg 1995). In *Silene,* however, all of the 19 morphological characters were either parental or intermediate in all individuals.
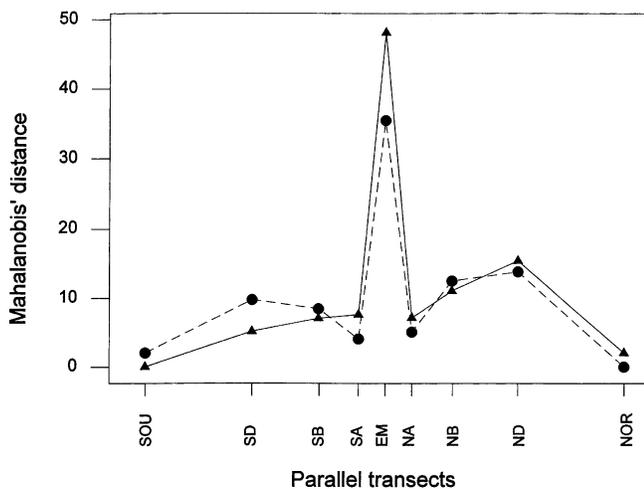
Character choice in studies of hybridization may also influence the degree of character intermediacy that is detected in hybrids (Rieseberg and Ellstrand 1993; Rieseberg 1995). The choice of quantitative (multigene) characters is expected to emphasize hybrid intermediacy, whereas the choice of discrete or qualitative characters is likely to lead to a higher proportion of parental character states being detected in hybrids (Rieseberg and Ellstrand 1993). Although morphological variation (particularly in quantitative traits) may be under multigenic control (Lynch and Walsh 1998), variation in a range of types of morphological characters, including growth habit, flower orientation, and plant height, have a simple genetic background in many plant species (Gottlieb 1984). Both

**Table 2.** The three lowest and the three highest character loadings for canonical variates (CVs) 1–3 in a CVA of morphological variation in a hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* (cf. Fig. 4).

| Character* | CV 1 | Character* | CV 2 | Character* | CV 3 |
|---|---|---|---|---|---|
| No. of flowers/inflorescence (2) | −0.78 | Flower form (8) | −0.31 | Immature seed colour (6) | −0.28 |
| Petal dissection (18) | −0.61 | Petal spot (17) | −0.15 | Stem orientation (5) | −0.28 |
| Plant height (7) | −0.58 | Petal overlap (9) | −0.05 | No. of flowers/inflorescence (2) | −0.17 |
| Flower form (8) | 0.83 | Plant height (7) | 0.36 | Petal breadth (narrowest) (16) | 0.41 |
| Bracts (4) | 0.83 | Calyx breadth (11) | 0.40 | Petal breadth (widest) (15) | 0.45 |
| Flower orientation (3) | 0.94 | Calyx tooth length (12) | 0.50 | Petal overlap (9) | 0.57 |

*Character numbers (see Table 1) are given in parentheses.

**Fig. 5.** Plot of pairwise Mahalanobis' ($D^2$) distances between each of the two *Silene uniflora* ssp. *petraea* reference sites (NOR and SOU), the sites on the six parallel transects and the *S. vulgaris* sites on the embankment. Distances from NOR are shown by a broken line with circles, and distances from SOU are shown by a solid line with triangles. The Mahalanobis' distances to each of the six parallel transects are means for cross transects 1–3, and the distances to the embankment are means for cross transects 1–3 plus the two *Silene vulgaris* reference sites (EST and WST; cf. Fig. 2). EM, embankment; SA and NA, 25 m from embankment; SB and NB, 100 m from embankment; SD and ND, 400 m from embankment; NOR and SOU, 1500 m from the embankment.



**Table 3.** CVA summary statistics and the partitioning of morphological diversity within a hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea*.

| Grouping | |
|---|---|
| **No. of significant (5%) descriptors** | |
| Species (analysis P) | 17 |
| Distance classes (analysis D) | 18 |
| Sites (analysis S) | 19 |
| Individuals (analysis I) | 13 |
| **No. of axes significant (5%) vs. no. of axes extracted** | |
| Species (analysis P) | 1 of 1 |
| Distance classes (analysis D) | 3 of 4 |
| Sites (analysis S) | 9 of 19 |
| Individuals (analysis I) | 18 of 19 |
| **Wilks' lambda ($\Lambda$)[†]** | |
| Species ($\Lambda_P$) | 0.1130 |
| Distance classes ($\Lambda_D$) | 0.0805 |
| Sites ($\Lambda_S$) | 0.0091 |
| Individuals ($\Lambda_I$) | 0 |
| **Partitioning of the total diversity (%): species, site, and individual components** | |
| Between species ($1 - \Lambda_P$) | 88.7 |
| Between sites, within species ($\Lambda_P - \Lambda_S$) | 10.4 |
| Between individuals, within sites ($\Lambda_S - \Lambda_I$) | 0.9 |
| Within individuals ($\Lambda_I$) | 0 |
| **Partitioning of the total diversity (%): distance, site, and individual components** | |
| Between distance classes ($1 - \Lambda_D$) | 92.0 |
| Between sites, within distance classes ($\Lambda_D - \Lambda_S$) | 7.1 |
| Between individuals, within sites ($\Lambda_S - \Lambda_I$) | 0.9 |
| Within individuals ($\Lambda_I$) | 0 |

**Note:** The descriptors were characters 2–20 (Table 1), and four CVAs were carried out on the data set. In analyses I, S, and P, groups were individuals, sites and species, respectively. In analysis D, the groups were distance classes, in relation to the embankment baseline (group 1, EM + EST + WST; groups 2–4, parallel transects A, B, and D; group 5, NOR + SOU; see Fig. 2). The total diversity is partitioned into between-species, -site, and -individual components and between-distance-class, -site, and -individual components.

[†]All the Wilks' lambda values are significant ($P < 0.001$).

qualitative and quantitative morphological characters were scored in the present study. Most, but not all, of the characters that show the clearest distinction between the samples from *S. vulgaris* sites from the embankment and the other (*S. uniflora* ssp. *petraea*) sites are qualitative characters (cf. Table 1, Fig. 3).

## Disturbance, hybrid zone history, and the availability of intermediate habitats

Anderson (1948) suggested that hybrids can survive only in "hybridized habitats." He argued that a first-generation hybrid between two species with different habitat requirements will be adapted to a uniform, intermediate habitat. Each individual produced from the following generations of hybridization will, however, have its own specific habitat requirements (Anderson 1948). Anderson (1948) also pointed out that the heterogeneous habitats required for survival of

different generations of hybrids should mainly be found in areas of human disturbance. The role of anthropogenic habitat disturbance as a catalyst for hybridization has been taken up in many recent studies of hybridization (cf. Wyatt and Broyles 1992; Arnold and Bennett 1993; Levin et al. 1996).

Anderson (1948) suggested that, because the heterogeneous habitats that are suitable for the establishment of a

**Fig. 6.** Plots of vegetation characteristics within a hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea* on Öland. The values are means (over sites) for the distance classes on the three northern and three southern parallel transects, the embankment sites (including the *S. vulgaris* reference sites) and the two *S. uniflora* ssp. *petraea* reference sites (NOR and SOU). EM, embankment; SA and NA, 25 m from embankment; SB and NB, 100 m from embankment; SD and ND, 400 m from embankment. Site codes and positions are given in Fig. 2.
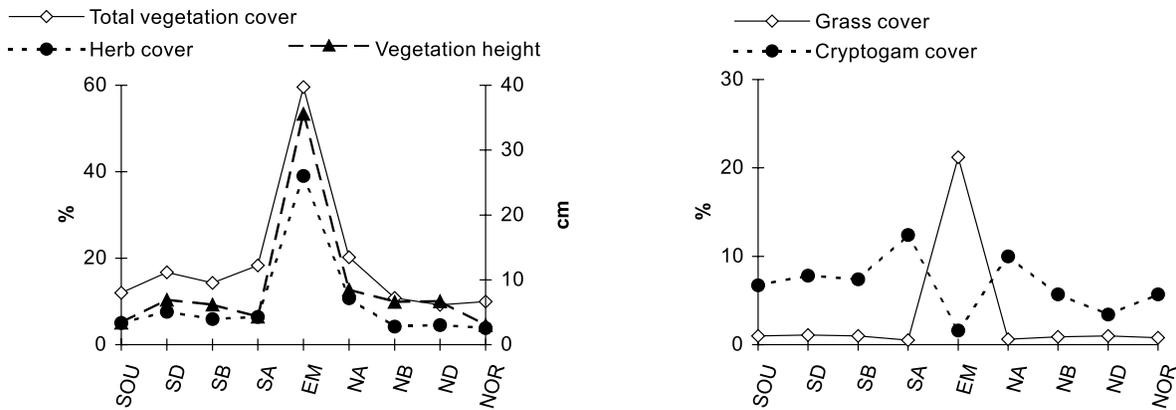


**Fig. 7.** Plot of the first two axes of a correspondence analysis based on total vegetation cover, herb cover, grass cover, and cryptogam cover at the sampling sites within a hybrid zone between *Silene vulgaris* and *Silene uniflora* ssp. *petraea*. Solid symbols show sites with individuals assignable to *S. vulgaris*, and open symbols show sites with individuals assignable to *S. uniflora* ssp. *petraea*; the reference sites are indicated by squares. Axis 1 accounts for 16% and axis 2, for 3% of the total between-site variation.
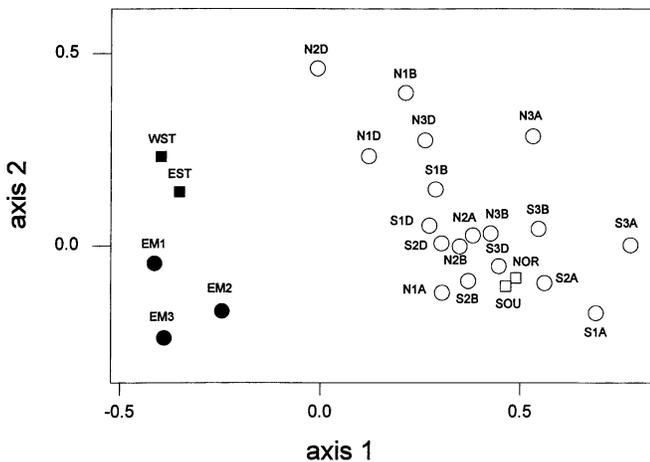


range of different hybrid generations are relatively rare, selection should favour hybrids with ecological phenotypes that are similar to one of the parents. Support for Anderson's prediction comes from, for example, studies of a hybrid zone in *Arctostaphylos* (Ball et al. 1983; Ellstrand et al. 1987). In the *Silene* hybrid zone, the resemblance of the intermediate individuals to one or other of the parental species and the fact that the number of intermediates declines with distance from the embankment is consistent with the spatial limitation of disturbed, intermediate habitats and the predominance of the parental habitats.

If the establishment of hybrids is dependent on the availability of disturbed habitats, the numbers of hybrids should decrease over time with decreasing levels of disturbance (Levin

et al. 1996), and the disappearance of local disturbance has been shown to lead to a decline in the number of hybrid individuals (cf. Heiser's (1979) study of *Helianthus*). Baker's (1948) classic work on hybridization between the introduced weed *Silene latifolia* Poiret (= *Melandrium album* (Mill.) Garcke = *Silene alba* (Mill.) E.H.L. Krause) and the native woodland *Silene dioica* (L.) Clairv. (= *Melandrium dioicum* (L.) Coss. & Germ.) in Britain also provides an illustration of the importance of a continuing disturbance regime for the continued establishment of hybrids. Baker observed widespread hybridization between the two *Silene* taxa and predicted the assimilation of *S. dioica* by the introduced *S. latifolia* (Baker 1947, 1948). Yet, 50 years later, extensive hybrid swarms between these species are rare in England (H.C. Prentice, personal observations) and *S. dioica* remains distinct. Baker's observations were made during the Second World War when military construction work and an expansion of arable agriculture created extensive habitat disturbance: such extensive disturbance has not continued during the post-war years.

The time at which a hybrid zone is sampled, in relation to disturbance history, will influence the observed characteristics of the zone (Rieseberg and Ellstrand 1993). The timing of sampling may thus influence conclusions about the vulnerability of native or endemic species to assimilation or contamination by introduced congeners. The low number of intermediates that was observed in the *Silene* contact zone is likely to be, at least in part, due to the fact that hybridization followed a single episode of habitat disturbance, 5.5 years before sampling. The subsequent vegetation succession has not only led to the progressive loss of intermediate habitats adjacent to the embankment but also to the loss of the open habitats that allowed the establishment of the *S. vulgaris* population.

Discussion of disturbance in relation to hybrid swarms has mostly focussed on the availability of intermediate habitats that are suitable for hybrids (e.g., Levin et al. 1996). It has been pointed out also that disturbance may favour hybrids by reducing the availability of parental habitats (Levin et al. 1996). However, little attention has been paid to the fact that disturbance may be critical for the establishment and persis-

tence of one of the parental species. In situations where hybridization is between an introduced taxon and a native or endemic taxon, the introduced taxon may often be behaving as a weed and be dependent on disturbed habitats.

In situations where both the weedy parent and early generation hybrids depend on disturbed habitats, the spatial and temporal dynamics of hybridization and introgression may depend as much on the persistence or transience of the weedy parental population as on the availability of intermediate habitats for the hybrids. Individual episodes of hybridization may be short lived because of the transient nature of populations of the ruderal parent. The decline in hybridization between *S. latifolia* and *S. dioica* in post-war England reflects a decline in the type of disturbed habitat required by *S. latifolia* as well as by the hybrids (cf. Baker 1948).

*Silene vulgaris* behaves as an early successional weed over much of its range and is dependent on disturbed habitats (e.g., Aeschimann 1983). Local populations are transient in the absence of continued disturbance. Individuals of *S. vulgaris* along the old railway embankment were mapped in 1988, six months before the construction of the cycle track (H.C. Prentice, unpublished data). No *S. vulgaris* individuals were present along the 1-km stretch of the embankment that formed the baseline for the transects in the present study. The nearest (isolated) *S. vulgaris* individual was 3 km W of transect 1. In 1997, three years after the present study, less than 10 (the majority non-flowering) individuals of *S. vulgaris* were found within the study area, and the verges of the cycle track were densely vegetated.

After the initial and spatially limited disturbance along the embankment, vegetation succession rapidly reduced the habitat available for *S. vulgaris*. The population in the study area declined from several hundred to less than 10 flowering individuals over 8 years. The window for the production of F$_1$ hybrids with *S. uniflora* ssp. *petraea* is likely to have been restricted to the first few years after the disturbance. The low numbers of intermediate individuals and the lack of genuine intermediacy is likely to reflect the fact that both the habitat of *S. vulgaris* and intermediate habitats suitable for early generation hybrids were already in short supply by the time the hybrid population was sampled.

### The habitats of *Silene vulgaris* and *Silene uniflora* ssp. *petraea*

The habitats of the sampled individuals are clearly separated into two groups (Fig. 7). The alvar habitat of the endemic *S. uniflora* ssp. *petraea* is one of the few natural habitat types in Sweden that are thought to have remained treeless throughout the postglacial period (L.-K. Königsson, personal communication). The windswept alvar is characterized by base-rich, shallow, and poorly drained soils. The soils are waterlogged for long periods during the autumn and spring and are subject to extreme frost disturbance. The soil is often bone dry in the summer and sporadic, severe droughts lead to the widespread loss of vegetation cover (Runyeon and Prentice 1997*b*). Populations of *S. uniflora* ssp. *petraea* are also decimated by the most severe droughts (Pettersson 1992*b*). Vegetation is sparse (cf. Fig. 6), and the few perennial vascular plants are mostly dwarf shrubs with a procumbent growth form and small leaves (cf. Bengtsson et al. 1988). Paradoxically, the naturally open alvar habitat represents a

more extreme form of disturbance than the anthropogenic, ruderal habitat of *S. vulgaris*. The ruderal habitat occupied by the established population of *S. vulgaris* is characterized by deeper soils, relatively tall, closed vegetation and higher percentage cover of herbs and grasses than the adjacent alvar habitats (Fig. 6).

*Silene uniflora* ssp. *petraea*, with its small leaves, procumbent stems, few flowers, and prolonged flowering season, is well-adapted to the harsh and unpredictable alvar environment. In contrast, the habit of *S. vulgaris*, with large leaves and tall, branched, many-flowered inflorescences, is ill suited to the alvar environment.

The observed spatial structure of variation in the contact zone is consistent with the expectation that there is strong selection on the overall phenotypes of *S. vulgaris* and *S. uniflora* ssp. *petraea* in the two parental habitats. Intermediate habitats were spatially limited and temporally short lived, and hybrids with predominantly parental phenotypes are likely to have been strongly favoured (cf. Anderson 1948; Ellstrand et al. 1987). Ideally, reciprocal transplants should be carried out to investigate the relative fitness of the two species and hybrids in parental and intermediate habitats (cf. Rieseberg 1995; Emms and Arnold 1997). However, the design of biologically realistic experiments is hindered by the fact that *S. uniflora* ssp. *petraea* has complex (and genetically determined) germination requirements (Prentice and Giles 1993; Runyeon and Prentice 1997*b*) and by the fact that transplants of seedlings or older plants into the inhospitable alvar habitat have a high probability of failure unless supported by supplementary watering.

### Barriers to hybridization between *S. vulgaris* and *S. uniflora* ssp. *petraea* on Öland

The pronounced distinction between the parental habitats, the transient nature of *S. vulgaris* populations, and the limited and short-lived availability of suitable, intermediate habitats for early generation hybrids are probably the main barriers to unlimited hybridization between the two species on Öland. However, other reproductive or ecological barriers may also be involved in restricting hybridization and introgression. Despite high levels of crossability, interfertility, and hybrid fertility within the *S. vulgaris* complex (Marsden-Jones and Turrill 1957; Walters 1975; H.C. Prentice, unpublished data), it is possible that there are single-stage or cumulative (pre- or post-zygotic) reproductive barriers that influence the relative success of seed production and (or) the relative fitnesses of pure and hybrid progeny in crosses involving *S. vulgaris* and *S. uniflora* ssp. *petraea* (cf. Arnold and Bennett 1993; Rieseberg et al. 1995; Hodges et al. 1996). This possibility is currently being investigated. We also lack information on the relative fitness of reciprocal crosses between the two species.

Although the flowering period of *S. vulgaris* is included within that of *S. uniflora* ssp. *petraea* and the species share the same pollinators (Pettersson 1991; 1992*a*), the phenological characteristics of the two species are likely to promote intraspecific pollination (Runyeon and Prentice 1996). Relatively little pollen from the sparsely flowering *S. uniflora* ssp. *petraea* is likely to contribute to the pollination of the mass-flowering *S. vulgaris*. (Runyeon and Prentice 1996), and only a proportion of the total seed production of *S. uniflora*

ssp. *petraea* is generated during the short flowering period of *S. vulgaris*. In addition, predation by *Hadena* moths may remove the majority of the capsules produced by *S. uniflora* ssp. *petraea* during the early part of the flowering season (Pettersson 1994; H.C. Prentice, unpublished data). Early capsule predation promotes reflowering, and late-produced seed of *S. uniflora* ssp. *petraea* does not show a reduction in germinability (Pettersson 1994).

## Conclusions

Despite the potential for interspecific gene flow between the introduced weed, *S. vulgaris*, and the endemic, *S. uniflora* ssp. *petraea*, the present study supports earlier field observations that individuals with intermediate morphological phenotypes are rare. Anthropogenic disturbance adjacent to alvar areas is sporadic, and populations of *S. vulgaris* are short-lived. Differences between the two parental habitats are pronounced and intermediate habitats are spatially restricted and transient. Hybrids with inappropriate morphological phenotypes are unlikely to persist in either parental habitat. Under the present regime of occasional disturbance, a range of ecological and phenological factors appear to prevent the wholesale intergradation of the weed and the endemic. Allozyme data provide evidence that there is some introgression of genes from the weed to the endemic (Runyeon and Prentice 1996). However, hybridization does not appear to pose a major threat to the survival and integrity of the endemic *S. uniflora* ssp. *petraea* under the present disturbance regime.

## Acknowledgements

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