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Natural hybridization within the *Carex flava* complex (Cyperaceae) in Poland: morphometric studies

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Natural populations of hybrids and populations of parental species of the *Carex flava* aggregate, growing in seven localities in Poland, were studied. Statistical methods were used to analyse 30 morphological characters measured from 399 dried specimens. The results allowed us to recognize the following hybrids: *C.* × *alsatica* [*C. flava* × *C. demissa*], *C.* × *ruedtii* [*C. flava* × *C. lepidocarpa*], *C.* × *schatzii* [*C. lepidocarpa* × *C. viridula*] and *C. demissa* × *C. viridula*. We found that (i) the utricle and beak lengths in the hybrid are usually similar to those of the parents that have longer utricles and beaks, and that (ii) introgression typically occurs towards the parental taxon dominant in an area and that with an earlier flowering period. The morphological characters most useful in distinguishing between hybrids and their parental species in the *C. flava* aggregate are the size of the utricle and the beak as well as characters transgressive in the hybrids, associated with inflorescence length, location of female spikes, and length of male utricles and their peduncles.

Introduction

Hybridization is a common phenomenon in vascular plants and an important mechanism in their evolution (Barton & Hewitt 1989, Arnold 1997, Rieseberg 1997, Barton 2001, Wissemann 2005). Because of that, populations of spontaneous hybrids are particularly interesting for botanical research (e.g. Hardig *et al*. 2000, 2002, Blackstock & Ashton 2001, 2010, Blackstock & Jermy 2001, Szczepaniak *et al*. 2007, Koopman 2010). On the one hand, hybrids are thought to be morphologically intermediate in relation to their parental taxa (e.g. Diskin *et al*. 2006), while on the other, they are a mosaic of parental, intermediate and extreme characters (Rieseberg & Ellstrand 1993, Rieseberg 1995). In the latter case, it is assumed that some morphological characters are more useful for revealing the hybrid origin than others. Thus it is important to establish which morphological characters can be considered most valuable for recognizing hybrids, providing such characters do exist. Moreover, the expression of an extreme or a novel character is one of the possible outcomes of a genome mixture, a phenomenon known as transgressive segregation (Rieseberg 1995, Rieseberg *et al*. 1999, Soltis & Soltis 2009). Extreme "transgres-

sive" phenotypes are often found in recombinant hybrid populations (e.g. Devicente & Tanksley 1993, Rosenthal *et al*. 2005).

The frequency of spontaneous hybridization differs among plant families and genera, as demonstrated in multiple floras (Ellstrand *et al*. 1996, Rieseberg 1997). In *Carex*, hybridization generally occurs only in certain sections with critical groups, e.g. *Ceratocystis*, *Phacocystis*, and *Vesicariae* of the subgenus *Carex*, or *Heleonastes*, *Vulpinae*, and *Heleoglochin* of the genus *Vignea* (Sylvén 1958, Wallace 1975, Toivonen 1981, Cayouette & Catling 1992). Most of the *Carex* hybrids have completely sterile pollen, except for hybrids between some closely related species (or subspecies) in the section *Ceratocystis*, containing taxa of the *C. flava* group (Davies 1955, Schmid 1982, Stoeva & Štepánková 1990, Halkka *et al*. 1992, Jermy *et al*. 2007). According to Schmid (1982), species of the *C. flava* aggregate which reproduce by seeds often produce backcrosses resembling one of the parents. Therefore, hybridization results in an accumulation of introgressed swarms, selection favouring morphs or introgressants most resembling either of the parents (Schmid 1982). Even though hybridization takes place between all taxa of the *C. flava* aggregate, and many morphological characters overlap, the species themselves are nevertheless morphologically recognizable, and display clear ecological preferences (Schmid 1981, 1982, Hedrén 2002).

Taxonomy of the *C. flava* aggregate has been widely discussed in the literature (e.g. Davies 1953, Palmgren 1959, Schmid 1983, Crins & Ball 1989a, 1989b, Pykälä & Toivonen 1994, Hedrén 2002, Jiménez-Mejías *et al*. 2012a). The following four well-defined taxa at the species level are currently distinguished in north-central Europe: *C. flava*, *C. lepidocarpa*, *C. demissa* and *C. viridula* (Chater 1980, Koopman 2011). A controversial species *C. derelicta* has been reported from a single site in the Czech Republic (Štepánková 2008); the taxon was previously reported as *C. oederi* subsp. *pseudoscandinavica* (Havlícková 1982). Another debatable taxon, *C. nevadensis*, occurs in southwestern Europe (Luceño & Jiménez-Mejías 2007, Jiménez-Mejías *et al*. 2012a), and one more, *C. castroviejoi*, in Greece and Albania (Jiménez-Mejías & Luceño 2009, Jiménez-Mejías *et al*. 2012b).

The studies of Swiss sedge populations by Schmid (1983) yielded two species only: *C. flava s. stricto* and *C. viridula s. lato*, the latter including all the other taxa as subspecies. The nomenclature of those taxa in Europe is still subject to some confusion: for example, Hedrén (2002) maintained that the name *C. oederi s. lato* rather than *C. viridula* should be used, whereas Egorova (1999) used the names *C. viridula* and *C. serotina*.

In Poland, the most common species in the group are *C. flava* and *C. viridula* (Zając & Zając 2001). *Carex lepidocarpa* and *C. demissa* are rarer; however, the knowledge on the range of the latter taxon is still insufficient (Zając & Zając 2001). Occasionally, mixed populations with different taxa of the *C. flava* aggregate are encountered in Poland. When these taxa occur sympatrically, they often hybridize. Such mixed populations became a starting point for this analysis of the *C. flava* aggregate hybrid morphology. We address the following specific questions: (1) Can morphological characters be used to differentiate among hybrids as well as between hybrids and parental taxa? (2) Which morphological characters are most useful in identifying hybrids and parental taxa? (3) To what extent are hybrids similar to/different from the parental taxa? (4) Does introgression take place in the study taxa?

Material and methods

Field studies and collection of specimens

In 2009–2011, we conducted field studies on 90 natural populations of the *Carex flava* aggregate in Poland. We found hybrid specimens in as few as eight of the 90 localities surveyed. One locality had a single putative parent only, while seven sites had both parental species and their hybrids. We therefore focus on these seven localities (Table 1). This is a classic situation in which hybrid populations coexist with populations of both parents along the same environmental gradient (Cayouette & Catling 1992).

Three localities contained *C. flava*, *C. lepidocarpa* and *C.* × *ruedtii* [*C. flava* × *C. lepido-*

carpa]; *C. flava*, *C. demissa* and *C.* × *alsatica* [*C. flava* × *C. demissa*] were present in two (one featuring also *C. viridula* and *C. demissa* × *C. viridula*), whereas *C. lepidocarpa*, *C. viridula* and *C.* × *schatzii* [*C. lepidocarpa* × *C. viridula*] occurred at two sites. Throughout this paper, we follow Koopman (2011) in the hybrid nomenclature.

We collected a total of 399 *C. flava* aggregate specimens from the mixed populations for phenetic analyses (Table 1). To reduce the probability of collecting individuals from the same clone, our sampling sites within a population were 3–6 m apart. Voucher specimens from each population were deposited in SZUB.

Specimens from the locality supporting the putative hybrid and one of the parental species were disregarded in the morphological analyses. To find out if a specimen was indeed a hybrid (specimens are often fertile and morphometrically indistinguishable from one of the parents) and which taxon of the study group could be the other parent, it would be necessary to use both morphological and molecular information. As shown by Blackstock and Ashton (2010), it is very important in such situations to include both approaches (morphometric and molecular) when trying to identify hybrids within a critical group. In this work, unequivocal morphological identification of hybrids was possible when the field data (i.e. the co-occurrence of hybrids and parent taxa) were considered.

Estimates of fertility

We estimated the fertility of each specimen from the percentage of utricles with developed achenes. To this end, we used the following simplified fertility scale of Hedrén (2002): 1 = 0% developed achenes; 2 = 0% < developed achenes < 10%; 3 = 10% < developed achenes < 50%; 4 = less than 50% < developed achenes < 100%; 5 = 100% developed achenes.

Analyses were made on completely sterile or reduced-fertility (scoring 1–3) hybrids and specimens representing pure species, with all the utricles containing well-developed achenes

Table 1. Localities of the populations *Carex flava* agg. included in the morphometric analysis.

No.	Location	Number of individuals sampled	Taxa
1	Bieszczady Mountains (49°03´N, 22°42´E)	8	*C. flava*,
		22	*C. demissa*
		8	*C. viridula*
		22	hybrid: *C.* × *alsatica*
		9	hybrid: *C. demissa* × *C. viridula*
2	Ińsko Lakeland (53°13´N, 15°40´E)	16	*C. flava*
		28	*C. demissa*
		31	hybrid: *C.* × *alsatica*
3	Suwałki Lakeland (54°04´N, 23°27´E)	22	*C. flava*
		14	*C. lepidocarpa*
		20	hybrid: *C.* × *ruedtii*
4	Kaszuby Lakeland (53°33´N, 18°19´E)	8	*C. flava*
		18	*C. lepidocarpa*
		21	hybrid: *C.* × *ruedtii*
5	Szczecin Lowland (53°34´N, 14°42´E)	17	*C. flava*
		7	*C. lepidocarpa*
		10	*C.* × *ruedtii*
6	Myślibórz Lakeland (53°00´N, 14°51´E)	17	*C. viridula*
		32	*C. lepidocarpa*
		25	hybrid: *C.* × *schatzii*
7	Myślibórz Lakeland (52°59´N, 14°54´E)	16	*C. viridula*
		22	*C. lepidocarpa*
		6	hybrid: *C.* × *schatzii*

(scoring 5). This indicates that we encountered mainly F1 hybrids (scoring 1–2) and rarely F2 ones (scoring 3). Such a pattern is indicative of the first step of the hybridization process.

Phenetic analyses

We examined a total of 30 morphological characters (27 quantitative and 3 qualitative) (Table 2). The measurements were taken under a stereomicroscope (Olympus SZ61; size of utricles, glumes, spikes, peduncles and width of leaves and bracts; to the nearest 0.01 mm) or with a ruler (plant height, length of leaves and bracts; to the nearest 0.1 cm). Qualitative characters were arranged into categories (Table 2).

We isolated five utricles and five glumes from the middle part of a female spike of each specimen, and five male glumes from the middle part of a male spike of each specimen. Average values of those characters (utricles and glumes) were used in the analyses. Utricles from the middle part of a spike are considered to be the least variable and are therefore the most commonly used in biometry (*see* Blackstock & Ashton 2010). We included also characters related to the arrangement of female spikes, despite reports of variability in *C. flava* (Heide 2004). When a study involves all members of a group, the female spike location is necessary as well; for example, in *C. demissa* the lower spike is usually basal, whereas *C. viridula* typically has the female spikes very closely clustered (e.g.

Table 2. Characters used in phenetic analyses.

No.	Character (unit)	Abbreviation
1	culm heigth (cm)	CH
2	cauline leaf length (cm)	CLL
3	cauline leaf width (cm)	CLW
4	culm height to leaf length ratio (1: leaves shorter than or equal to 1/2 the length of culm; 2: leaves 3/4 the length of culm; 3: leaves equal to the length of culm; 4: leaves longer than culm)	C/L
5	inflorescence length (cm)	IL
6	male spike length (cm)	MSL
7	male spike width (cm)	MSW
8	male spike peduncle length (cm)	MSPL
9	number of female spikes (no)	NFS
10	distance between two upper female spikes (cm)	DUFS
11	distance between two lower female spikes (cm)	DLFS
12	lowest female spike length (cm)	LFSL
13	lowest female spike width (cm)	LFSW
14	lowest female spike peduncle length (cm)	LFSPL
15	lowest female spike bract length (cm)	LFSBL
16	lowest female spike bract width (cm)	LFSBW
17	lowest female spike bract sheath length (cm)	LFSBSL
18	ratio of the length of the lowest bract to the length of inflorescence (1: bract shorter than inflorescence; 2: bract equal to inflorescence; 3: bract longer, but no more than twice the length of inflorescence; 4: bract much longer, more than twice the length of inflorescence)	B/I
19	uppermost female spike length (cm)	UFSL
20	uppermost female spike width (cm)	UFSW
21	second female spike bract length (cm)	SFSBL
22	second female spike bract width (cm)	SFSBW
23	utricle length (mm)	UL
24	utricle beak length (mm)	UBL
25	ratio of beak length to utricle length (%)	B/U
26	occurrence of achenes in the utricle (*see* Material and methods)	OAP
27	female spike glume length (mm)	FSGL
28	female spike glume width (mm)	FSGW
29	male spike glume length (mm)	MSGL
30	male spike glume width (mm)	MSGW

Havlícková 1982, Stoeva & Štepánková 1990, Hedrén 2002).

Following others who explored the taxonomic relationships among sedges (e.g. Naczi *et al*. 1998, Blackstock & Ashton 2001, Řepka 2003, Stoeva *et al*. 2005, Blackstock & Ashton 2010, Więcław & Koopman 2013), we performed multivariate analyses (PCA and DFA). We carried out those analyses for quantitative (continuous and discrete) and qualitative (ordered) characters combined.

We carried out a preliminary Principal Component Analysis (PCA) on the correlation matrix for all the taxa and hybrids. We used the PCA as a first-line tool to determine the relationships between the hybrids and their putative parents. It was possible to identify the parental taxa of a given hybrid, as the two pure parental taxa and those morphologically intermediate, sterile or reduced-fertility hybrids were both sympatric. Further, we carried out PCAs separately for each of the seven populations to reveal relationships between the hybrid and its parental taxa, and to elucidate their overall morphological variability (based on the complete data set comprising 30 characters).

To assess homogeneity among the investigated taxa, we used Discriminant Function Analysis (DFA) (based on the complete data set consisting of 399 individuals and 30 characters) which compares classifications defined *a priori* with expected ones (revealed by the discriminant analysis) in a classification matrix. Populations were assigned to *a priori* defined groups (species) based on the taxonomical concept of Pykälä and Toivonen (1994) and Hedrén (2002).

We used the following four pure species distinguished *a priori*: *C. flava* (71 specimens), *C. lepidocarpa* (93 specimens), *C. demissa* (50 specimens) and *C. viridula* (41 specimens) as well as four hybrids (based on information collected in the field, i.e. coexistence of both parents and hybrids, and fertility assessment): *C.* × *ruedtii* [*C. flava* × *C. lepidocarpa*] (51 specimens), *C.* × *alsatica* [*C. flava* × *C. demissa*] (53 specimens), *C.* × *schatzii* [*C. lepidocarpa* × *C. viridula*] (31 specimens) and *C. demissa* × *C. viridula* (9 specimens).

Subsequently, we calculated basic statistics [mean, standard deviation (SD) and coefficient of variation (CV)] from the data yielded by the measurements. Since most of the data were non-normally distributed (Shapiro-Wilk's test), we used a non-parametric Mann-Whitney *U*-test to examine whether differences between parental species and hybrids were significant. We performed the analysis using the Statistica ver. 8.0 for Windows (StatSoft Inc.) software package.

Results

Morphological relationships between hybrids and parental species

The PCA carried out on the entire dataset separated the pure taxa (Fig. 1). The first three principal components explain 57% of the overall variation (with the first, second and third components explaining 28%, 17% and 12%, respectively). The ordination space had four partially overlapping clusters corresponding to the parental taxa. Along the first principal component, formed primarily by characters of the utricle (UL, UBL, B/U) and the smallest bracts (LFSBL, LFSBW), distinct groups were formed by specimens of *C. flava* and the hybrid *C.* × *alsatica*, as well as, less conspicuously, *C.* × *ruedtii*, all with utricles larger than those in the remaining taxa (Fig. 1, Appendices 1 and 2; *see* Table 2 for character codes). The second principal component, formed primarily by NFS, MSPL and CH, distinguished three clusters of pure taxa (Fig. 1A, Appendices 1 and 2; *see* Table 2 for character codes). The two morphologically closest species *C. demissa* and *C. viridula*, and their hybrid, clustered together along the second principal component, and were distinctly separated from a cluster of *C. lepidocarpa* specimens. No separate clusters are visible along the third principal component. Some specimens of *C. flava*, *C. lepidocrpa*, *C.* × *alsatica* and *C.* × *ruedtii*, with relatively long inflorescences and long lowest peduncle sheaths, occupy the upper part of the ordination plot (Fig. 1B).

Carex × *alsatica* [*C. flava* × *C. demissa*]

We found this hybrid to be significantly different from *C. flava* in 17 characters and from *C.*

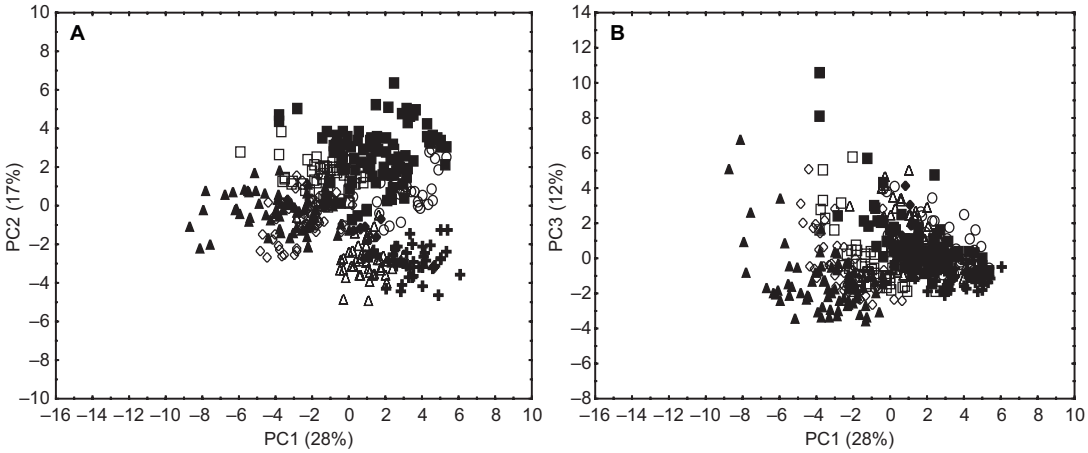

Fig. 1. Principal components analysis (PCA) of 30 standardized morphological variables from 399 specimens of *Carex flava*, *C. lepidocarpa*, *C. demissa*, *C. viridula*, *C.* × *alsatica*, *C.* × *ruedtii*, C. × *schatzii* and *C. demissa* × *C. viridula*. — **A**: PC1 and PC2; — **B**: PC1 and PC3. ▲ = *C. flava*, ■ = *C. lepidocarpa*, Δ = *C. demissa*, + = *C. viridula*, ◇ = *C.* × *alsatica*, □ = *C.* × *ruedtii*, ○ = C. × *schatzii*, ◆ = *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values greater than 0.50): CLW = –0.78, CLL = –0.67, LFSL = –0.62, LFSW = –0.70, LFSBL = –0.75, LFSBW = –0.77, UFSL = –0.65, UFSW = –0.69, SFSBL = –0.62, SFSBW = –0.59, UL = –0.76, UBL = –0.81, B/U = –0.70, FSGL = –0.76, MSGL = –0.57. Loadings for the second axis (only absolute values greater than 0.50): CH = 0.74, MSL = 0.56, MSPL = 0.70, NFS = –0.77, DLFS = –0.58, LFSL = 0.58, LFSW = 0.53, SFSBL = –0.54, SFSBW = –0.63. Loadings for the third axis (only absolute values greater than 0.50): IL = 0.87, DUFS = 0.51, DLFS = 0.55, LFSPL = 0.59, LFSBSL = 0.75, B/I = –0.55. For character codes *see* Table 2.

demissa in 21 characters (Table 3; for character codes *see* Table 2).

Carex × *alsatica* is characterized by a relatively large utricle and beak, which obviously is represented in the female spike width (*see* Appendix 1). The utricle and beak lengths can be arranged in the following decreasing order: *C. flava*, *C.* × *alsatica*, *C. demissa*. The ordering of the taxa is similar when we look at the ratio of beak length to the length of the entire utricle (the respective percentages for localities 1 and 2 were: 45%–49% *vs*. 42%–50% for *C. flava*, 40%–49% *vs*. 42%–46% for *C.* × *alsatica* and 36%–45% *vs*. 35%–42% for *C. demissa*). At the same time, the utriclular characters were the least variable (CV values below 10%; *see* Appendix 1).

As shown by the PCA for all morphological characters, the first three principal components explained 60% of the variation (Fig. 2). The parental species emerge in the ordination space as two distinct clusters. The *C. demissa* cluster contains only the material assigned to that taxon, while the *C. flava* cluster incorporates all material ascribed to *C. flava* and is slightly overlapping with the hybrids (Fig. 2). Moreover, the hybrid populations form two locality-dependent groups along the second principal component (Fig. 2A): the hybrid from northern Poland (locality 2) forms a group in the upper part of the plot, the lower part having a group of specimens from southern Poland (locality 1). The variables UL, UBL, LFSW, UFSW and FSGL have high factor loadings on the first component. IL, NFS, DLFS, LFSPL, LFSBL, LFSBW, LFSBSL and SFSBL are related to the second component (Fig. 2; for character codes *see* Table 2). Some individuals of *C.* × *alsatica* are characterized by a long inflorescence (mean 73 mm *vs*. 44 mm), lower, often basal female spike and 3–4 female spikes (the specimens from locality 1 have mostly 2–3 female spikes). In that respect they are more similar to *C. demissa*, whereas the utricle dimensions of hybrids from both localities are comparable, so they are intermediate in respect to the parental taxa. Some specimens of the hybrid from northern Poland (locality 2) form an intermediate group between the parental taxa on the plot, along the second principal component. However, the characters related to that component are variable (the

Table 3. Results of Mann-Whitney *U*-test showing difference between hybrids and their parental taxa (* $p \leq 0.05$). For character codes *see* Table 2.

	C. × *alsatica*				*C.* × *ruedtii*				*C.* × *schatzii*				*C. demissa* × *C. viridula*			
	C. flava		*C. demissa*		*C. flava*		*C. lepidocarpa*		*C. viridula*		*C. lepidocarpa*		*C. demissa*		*C. viridula*	
	Z	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*
CH	–6.85*	< 0.001	3.44*	0.001	3.42*	0.001	1.20	0.228	–2.76*	0.006	–7.58*	< 0.001	0.63	0.528	1.73	0.083
CLL	–4.54*	< 0.001	5.61*	< 0.001	–3.67*	< 0.001	3.83*	< 0.001	1.66	0.097	–5.36*	< 0.001	2.35*	0.019	1.68	0.092
CLW	–2.93*	0.003	3.56*	< 0.001	–3.03*	0.002	6.17*	< 0.001	–2.38*	0.017	–2.16*	0.031	–1.67	0.094	3.42*	0.001
C/L	0.04	0.969	1.07	0.287	–2.97*	0.003	4.14*	< 0.001	5.79*	< 0.001	–0.46	0.645	0.61	0.542	0.58	0.564
IL	3.47*	< 0.001	–3.84*	< 0.001	3.22*	0.001	–0.62	0.533	–2.93*	0.003	–2.15*	0.031	0.09	0.931	3.42*	0.001
MSL	2.49*	0.013	3.77*	< 0.001	2.49*	0.013	–0.39	0.693	–2.97*	0.003	–6.31*	< 0.001	3.22*	0.001	3.03*	0.002
MSW	0.83	0.406	2.13*	0.033	2.92*	0.003	0.61	0.541	–2.11*	0.035	0.456	0.648	0.65	0.514	3.17*	0.001
MSPL	5.55*	< 0.001	–1.78	0.074	6.56*	< 0.001	–2.67*	0.007	–6.32*	< 0.001	–3.30*	0.001	2.11*	0.035	2.89*	0.004
NFS	–0.08	0.939	–2.34*	0.019	–2.53*	0.011	2.86*	0.004	4.97*	< 0.001	1.61	0.107	–0.17	0.862	–0.34	0.736
DUFS	4.39*	0.002	0.70	0.482	1.03	0.302	–1.75	0.079	–4.04*	< 0.001	–0.71	0.479	2.19*	0.028	2.50*	0.012
DLFS	1.56	0.118	–4.02*	< 0.001	–0.74	0.457	2.17*	0.030	3.73*	0.001	1.21	0.226	–0.46	0.648	2.45*	0.014
LFSL	–1.95	0.051	5.73*	< 0.001	–0.45	0.652	4.38*	< 0.001	–4.87*	< 0.001	–6.19*	< 0.001	3.72*	< 0.001	3.22*	0.001
LFSW	–4.98*	< 0.001	8.65*	< 0.001	–3.47*	0.001	5.13*	< 0.001	–6.21*	< 0.001	–7.25*	< 0.001	–2.48*	0.013	1.11	0.268
LFSPL	0.07	0.166	0.38	0.702	–3.33*	0.001	2.59*	0.009	–1.32	0.188	0.16	0.869	–0.52	0.601	1.01	0.312
LFSBL	–1.39	0.166	1.35	0.176	–5.51*	< 0.001	4.22*	< 0.001	2.67*	0.008	–1.17	0.243	1.85	0.064	2.89*	0.004
LFSBW	–1.00	0.317	3.28*	0.001	–3.68*	< 0.001	6.92*	< 0.001	3.98*	< 0.001	1.85	0.064	0.83	0.408	3.08*	0.002
LFSBSL	3.57*	< 0.001	–2.87*	0.004	–1.99*	0.046	1.52	0.129	–2.42*	0.016	3.41*	0.001	–0.28	0.777	3.12*	0.002
B/I	–5.27*	< 0.001	3.94*	< 0.001	–6.75*	< 0.001	4.95*	< 0.001	5.09*	< 0.001	0.08	0.938	0.33	0.744	–2.84*	0.004
UFSL	–1.39	0.166	5.36*	< 0.001	–0.11	0.909	3.44*	0.001	–5.11*	< 0.001	–5.44*	< 0.001	0.59	0.557	3.42*	0.001
UFSW	–5.31*	< 0.001	8.39*	< 0.001	–2.09*	0.037	5.29*	< 0.001	–6.01*	< 0.001	–6.15*	< 0.001	–2.17*	0.029	2.36*	0.018
SFSBL	–0.87	0.382	0.41	0.682	–6.39*	< 0.001	5.24*	< 0.001	3.92*	< 0.001	–0.21	0.831	1.63	0.103	2.98*	0.003
SFSBW	1.45	0.148	–0.01	0.989	–6.46*	< 0.001	5.01*	< 0.001	4.34*	< 0.001	1.49	0.135	–0.41	0.679	3.27*	0.001
UL	–5.95*	< 0.001	8.73*	< 0.001	–1.84	0.066	7.13*	< 0.001	–5.49*	< 0.001	–7.24*	< 0.001	–0.09	0.931	2.98*	0.003
UBL	–5.72*	< 0.001	8.71*	< 0.001	–7.59*	< 0.001	7.62*	< 0.001	–5.25*	< 0.001	–6.32*	< 0.001	–3.55*	< 0.001	2.96*	0.003
B/U	–3.75*	< 0.001	8.09*	< 0.001	–8.43*	< 0.001	6.64*	< 0.001	–3.25*	0.001	–1.38	0.167	–4.02*	< 0.001	1.68	0.092
FSGL	–3.32*	0.001	8.56*	< 0.001	–3.28*	0.001	3.60*	< 0.001	–3.28*	0.001	–2.21*	0.027	4.04*	< 0.001	2.55*	0.011
FSGW	2.39*	0.017	2.78*	0.005	0.33	0.743	3.08*	0.002	–5.60*	< 0.001	1.04	0.296	0.01	0.972	3.08*	0.002
MSGL	1.31	0.189	5.43*	< 0.001	4.33*	< 0.001	6.30*	< 0.001	0.50	0.614	–3.03*	0.002	0.87	0.384	3.42*	0.001
MSGW	4.91*	< 0.001	0.79	0.425	2.64*	0.008	3.64*	< 0.001	–4.41*	< 0.001	1.64	0.100	–0.26	0.794	2.93*	0.003

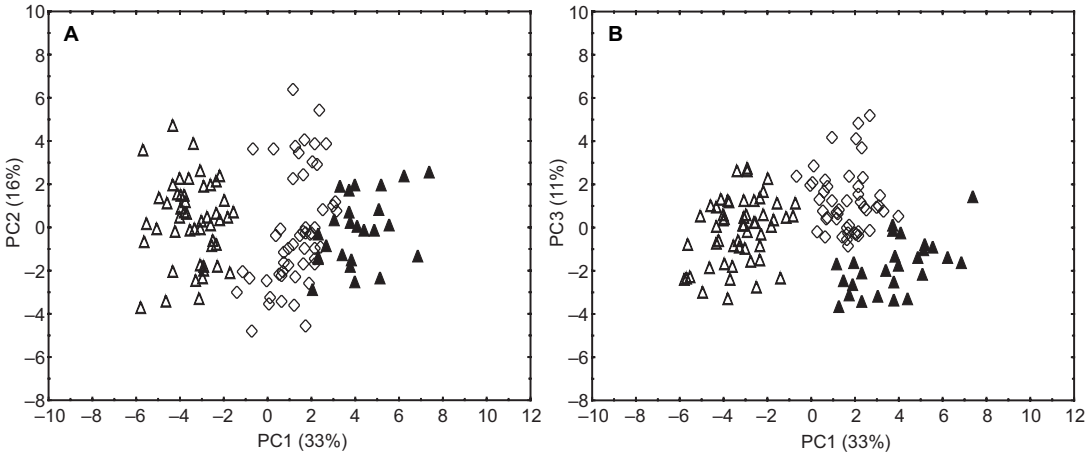

Fig. 2. Principal components analysis (PCA) of 30 standardized morphological variables from 127 specimens of *Carex flava*, *C. demissa* and *C.* × *alsatica*. — **A**: PC1 and PC2; — **B**: PC1 and PC3. ▲ = *C. flava*, Δ = *C. demissa*, ◇ = *C.* × *alsatica*. Loadings for the first axis (only absolute values greater than 0.50): CH = 0.68, CLW = 0.59, CLL = 0.79, DLFS = –0.52, LFSL = 0.77, LFSW = 0.93, B/I = 0.68, UFSL = 0.73, UFSW = 0.93, SFSBW = 0.67, UL = 0.94, UBL = 0.93, B/U = 0.78, FSGL = 0.90, MSGL = 0.54. Loadings for the second axis (only absolute values greater than 0.50): IL = 0.74, NFS = 0.58, DLFS = 0.74, LFSPL = 0.65, LFSBL = 0.76, LFSBW = 0.63, LFSBSL = 0.62, SFSBL = 0.70. Loadings for the third axis (only absolute values greater than 0.50): MSL = 0.51, MSPL = 0.74, DUFS = 0.68, OAP = –0.51, FSGW = 0.61, MSGW = 0.58. For character codes *see* Table 2.

coefficient of variation in the locality 2 hybrid ranges from 11% to 79%; Table 4). Along PC3, there is no locality-related variability among *C.* × *alsatica* (Fig. 1B). Associated with the third component are mainly MSPL and DUFS, and to a lesser extent also MSL, NFS and OAP (the hybrid produces no fruits). In *C.* × *alsatica*, a pedunculate male spike is common (in some specimens, the peduncle length attains extreme values) and female spikes are usually located close to each other (*see* Appendix 1).

Carex × *ruedtii* [*C. flava* × *C. lepidocarpa*]

Twenty-three morphological characters of this hybrid are significantly different from those of both *C. flava* and *C. lepidocarpa* (Table 3; for character codes *see* Table 2). Like *C. flava*, *C.* × *ruedtii* has relatively large utricles and long beaks (Appendix 2); however, the beak length to the utricle length ratio in the hybrid is usually similar to that in *C. lepidocarpa* (30%–40%) (31%–44% in *C.* × *ruedtii*, and 41%–49% in *C. flava*).

Table 4. Discriminant function analysis (DFA) classification matrix of OTU's from the complex *Carex flava*. F = *C. flava*, L = *C. lepidocarpa*, D = *C. demissa*, V = *C. viridula*, R = *C.* × *ruedtii*, A = *C.* × *alsatica*, S = *C.* × *schatzii*, D × V = *C. demissa* × *C. viridula*.

Group	Number of observations (percentage classified into group).							
	F	L	D	V	R	A	S	D × V
F	71 (100)	0 (0)	0	0 (0)	0	0 (0)	0 (0)	0 (0)
L	0 (0)	93 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
D	0 (0)	0	50 (100)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
V	0 (0)	0 (0)	0 (0)	41 (100)	0 (0)	0 (0)	0 (0)	0 (0)
R	0 (0)	2 (3.9)	0 (0)	0	49 (96.1)	0 (0)	0 (0)	0 (0)
A	0 (0)	0	0 (0)	0	0 (0)	53 (100)	0 (0)	0 (0)
S	0 (0)	1 (3.3)	0 (0)	1 (3.3)	0 (0)	0 (0)	29 (93.4)	0 (0)
D × V	0 (0)	0	1 (11.1)	1 (11.1)	0 (0)	0 (0)	0 (0)	7 (77.8)

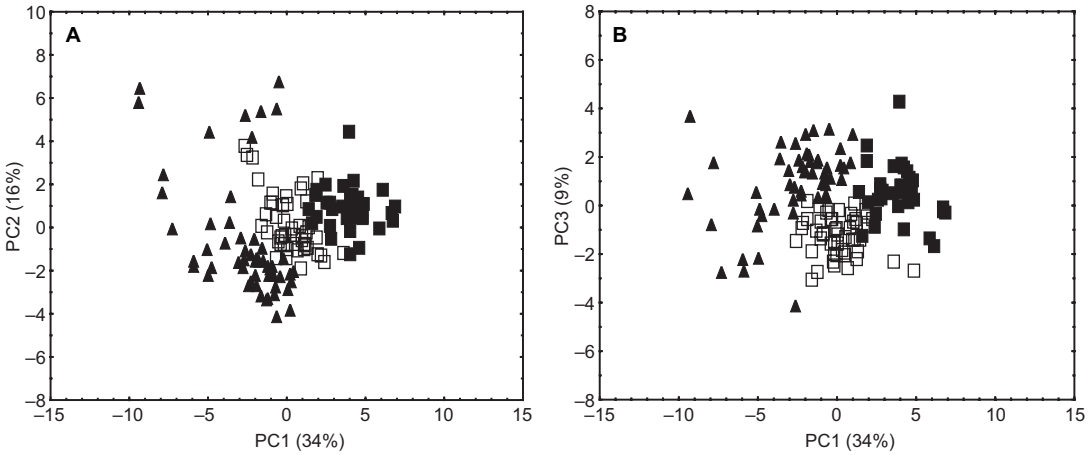

Fig. 3. Principal components analysis (PCA) of 30 standardized morphological variables from 137 specimens of *Carex flava*, *C. lepidocarpa* and *C.* × *ruedtii*. — **A**: PC1 and PC2; — **B**: PC1 and PC3. ▲ = *C. flava*, ■ = *C. lepidocarpa*, □ = *C.* × *ruedtii*. Loadings for the first axis (only absolute values greater than 0.50): CLW = –0.84, CLL = –0.68, MSPL = 0.53, NFS = –0.74, DLFS = –0.56, LFSL = –0.64, LFSW = –0.64, LFSPL = –0.54, LFSBL = –0.86, LFSBW = –0.91, LFSBSL = –0.52, B/I = –0.66, UFSL = –0.54, UFSW = –0.60, SFSBL = –0.66, SFSBW = –0.77, UL = –0.75, UBL = –0.73, B/U = –0.56, FSGL = –0.70. Loadings for the second axis (only absolute values greater than 0.50): IL = 0.87, MSL = 0.55, DLFS = 0.55, LFSPL = 0.59, LFSBSL = 0.62, B/I = –0.53, B/U = –0.60. Loadings for the third axis (only absolute values greater than 0.50): OAP = 0.59. For character codes *see* Table 2.

In contrast to *C. flava*, specimens of *C.* × *ruedtii* usually have pedunculate male spikes (although the mean peduncle length in these hybrids is usually smaller than that in *C. lepidocarpa*) as well as short and narrow bracts of the second female spike; bracts of the lowest female spike are usually equal to or slightly longer than the inflorescence (characters specific to *C. lepidocarpa*). Occasionally (e.g. in locality 5), we found hybrids with extreme values of CH, CLL, IL, MSL, MSPL, DUFS, LFSL, UFSL. These eight characters (30.8%) were positively transgressive (*see* Appendix 2).

The first three principal components explain 59% of the overall variation (Fig. 3). The ordination space shows two distinct clusters corresponding to the parental taxa. The hybrid specimens form an intermediate cluster overlapping to some extent with the parental taxa clusters. Most characters analyzed are associated with the first component, with the highest factor loadings in the utricle size (UL, UBL, B/U), bracts (LFSBL, LFSPW, SFSBL, SFSBW) and leaves (CLL, CLW). MSL, MSW and MSGL are associated with the second component (Fig. 3; for character codes *see* Table 2). The upper part of the plot, along PC2, shows a cluster of four hybrid specimens from locality 5 which are partially fertile and are characterized by long pedunculate male spikes (Fig. 3A). In the right-hand part of the plot, several specimens of C. *lepidocarpa* and two of *C.* × *ruedtii* form a separate group along PC1 (Fig. 3B). These specimens have only one female spike. It is rare to find an inflorescence with a single female spike in the *C. flava* complex; such inflorescences are observed mainly in *C. lepidocarpa*. *Carex flava* specimens with the longest utricles and beaks are grouped along PC1 to the left of the plot (Fig. 3B).

*C*arex × *schatzii* [*C. lepidocarpa* × *C. viridula*]

We found this hybrid to differ from *C. lepidocarpa* in 15 characters, and from *C. viridula* in 26 characters (Table 3; for character codes *see* Table 2). The utricle and beak lengths in *C.* × *schatzii* are intermediate between those in *C. lepidocarpa* and *C. viridula* (Appendix 3). The utricle length to beak length ratios are similar in all three taxa, averaging 33% to 36%. The configuration and number of female spikes (usually two, less often three spikes remote), the presence

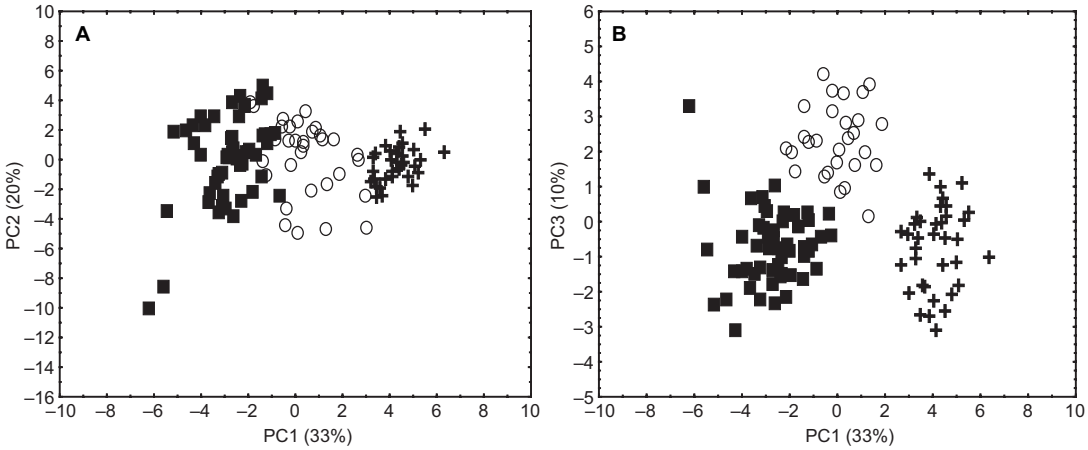

Fig. 4. Principal components analysis (PCA) of 30 standardized morphological variables from 118 specimens of *Carex lepidocarpa*, *C viridula* and *C.* × *schatzii*. — **A**: PC1 and PC2; — **B**: PC1 and PC3. ■ = *C. lepidocarpa*, + = *C. viridula*, ○ = C. × *schatzii*. Loadings for the first axis (only absolute values greater than 0.50): CH = –0.81, C/L = 0.68, MSL = –0.78, MSPL = –0.77, NFS = 0.76, DLFS = 0.53, LFSL = –0.82, LFSW = –0.91, LFSBW = 0.60, B/I = 0.61, SFSBW = 0.67, UL = –0.93, UBL = –0.92, B/U = –0.55, FSGL = –0.66, FSGW = –0.60. Loadings for the second axis (only absolute values greater than 0.50): IL = –0.72, DUFS = –0.62, LFSPL = –0.72, LFSBL = –0.85, LFSBW = –0.68, LFSBSL = –0.70, USFL = –0.66, UFSW = –0.56, SFSBL = –0.68, SFSBW = –0.53. Loadings for the third axis (only absolute values greater than 0.50): CLW = –0.72, OAP = –0.71, MSGW = 0.52. For character codes *see* Table 2.

of a long male spike peduncle and relatively narrow bracts in the hybrid makes it similar to *C. lepidocarpa*. Locality 7 had hybrid specimens with female spikes arranged at considerable distances from one another, and therefore possessing extremely long inflorescences (IL, DUFS and DLFS) (*see* Appendix 3).

The first three principal components account for more than 63% of the overall variation. The first principal component shows high factor loadings of UL, UBL, LFSL, LFSW, MSL, NFS and CH (Fig. 4; for character codes *see* Table 2). These characters are determined primarily by the parental taxa, while the hybrid is represented by specimens with intermediate values of the characters (numerous transitional forms) and by specimens morphologically closer to *C. lepidocarpa* than to *C. viridula* (Fig. 4A). Characters of the inflorescence length (IL, DUFS, LFSPL) and bract size (LFSBL, LFSBW, LFSBSL) are associated with PC2 (Fig. 4A). The plot shows a few individuals of *C. lepidocarpa* placed away from other specimens in the group on account of their long (over 17 cm) inflorescences (Fig. 4). Along PC3, *C.* × *schatzii* forms a group separated from both parental species and is not intermediate. As the third principal component is largely related to the presence of achenes in the utricle (OAP) (–0.71), specimens of *C.* × *schatzii* with reduced fertility form a separate cluster (Fig. 4B).

Carex demissa × *Carex viridula*

Specimens of this hybrid are quite similar to *C. demissa* differing from it in only 10 morphological characters. On the other hand, the hybrid is different from *C. viridula* in 22 variables (Table 3; for character codes *see* Table 2). The hybrid's utricle size is similar to that in *C. demissa*, the hybrid beaks being substantially shorter (Appendix 4). Seven characters (26.9%) (CLL, MSL, MSPL, LFSL, LFSPL, LFSBL, SFSBL) attained extreme values. The hybrid specimens have relatively long and pedunculate male spikes, long, narrow and pedunculate lower female spikes, as well as long bracts (*see* Appendix 4).

The first three principal components explain over 63% of the overall variation. In the plot, almost all the hybrid specimens are grouped within the *C. demissa* cluster (Fig. 5). While

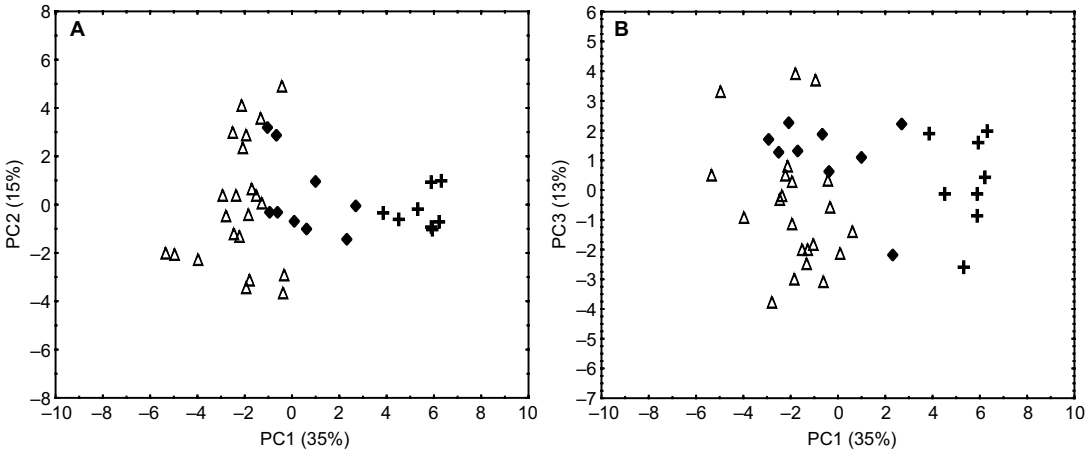

Fig. 5. Principal components analysis (PCA) of 30 standardized morphological variables from 39 specimens of *Carex demissa*, *C. viridula* and *C. demissa* × *C. viridula*. — **A**: PC1 and PC2; — **B**: PC1 and PC3. Δ = *C. demissa*, + = *C. viridula*, ◆ = *C. demissa* × *C. viridula*. Loadings for the first axis (only absolute values greater than 0.50): CLW = –0.73, IL = –0.66, MSW = –0.59, DLFS = –0.60, LFSL = –0.57, LFSW = –0.65, LFSBL = –0.67, LFSBW = –0.77, LFSBSL = –0.69, B/I = 0.65, UFSL = –0.78, UFSW = –0.73, SFSBL = –0.77, SFSBW = –0.86, UL = –0.74, UBL = –0.79, B/U = –0.62, FSGW = –0.70, MSGL = –0.58, MSGW = –0.60. Loadings for the second axis (only absolute values greater than 0.50): MSL = 0.72, MSPL = 0.64, NFS = –0.53, DUFS = 0.66, DLFS = –0.55, LFSL = 0.57, OAP = –0.61. Loadings for the third axis (only absolute values greater than 0.50): NFS = 0.62, LFSBL = 0.53, UBL = –0.51, B/U = –0.52. For character codes *see* Table 2.

most of the characters analyzed are associated with the first component, the highest factor loadings on the second component are those of CLL, MSL, LFSL, OAP, B/U and FSG. The third principal component is primarily related to IL, LFSBSL and B/I (Fig. 5; for character codes *see* Table 2).

Morphological separation of taxa and hybrids by Discriminant Function Analysis

The first two discriminant functions explain more than 88% (59% and 29%) of the total variance in the data. The first discriminant function consists primarily of IL, DLFS, LFSBW and UBL. The second discriminant function is determined mostly by variables of utricle size (UL, UBL, B/U) and stem height (Fig. 6; for character codes *see* Table 2). The first discriminant function differentiates taxa with a relatively short inflorescence, wide bracts and long beaks (*C. flava* and *C.* × *alsatica*) from the remaining ones. The DFA plot shows groups of *C. flava* and *C.* × *alsatica* specimens located to the left, the mean canonical values being negative (Fig. 6). The second function discriminates between *C. viridula* specimens, with shortest stems and smallest utricles, and those of *C. demissa* and *C. demissa* × *C. viridula*.

The classification matrix (Table 4) synthesizes information on the phenetic coherence of the individual taxa. The specimens examined are well-separated phenetically: 78%–100% of the correctly classified specimens correspond to those samples whose classification by the discriminant functions coincides with the *a priori* identification. All the pure species were correctly classified in 100%. The percentage of correctly classified hybrid specimens (excluding the completely sterile *C.* × *alsatica* individuals, correctly classified in 100%) was 78%–96% (Table 8). The analysis algorithm placed only a few specimens, *a priori* classified (based on their reduced fertility) as hybrids, in parental taxa groupings. This was due to the hybrids possessing morphological characters similar to those in one of the parental species; for example, two specimens of *C.* × *ruedtii* were placed in a group formed by individuals of *C. lepidocarpa* (Table 8). The *C. demissa* × *C. viridula* hybrid had the lowest rate of correct classification. The reason is the

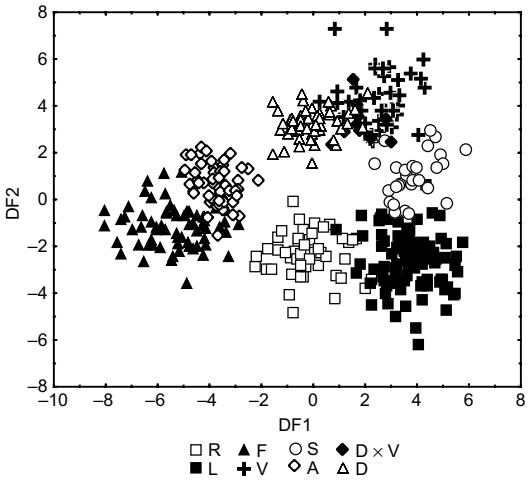

Fig. 6. Discriminant scores for individuals of *C. flava* agg. F = *C. flava*, L = *C. lepidocarpa*, D = *C. demissa*, V = *C. viridula*, R = *C.* × *ruedtii*, A = *C.* × *alsatica*, S = *C.* × *schatzii*, D × V = *C. demissa* × *C. viridula*. The scores of all individuals are projected onto the two-dimensional space defined by discriminant functions one and two. Loadings for the first axis DF1 (only absolute values greater than 0.50): UBL = –0.54, LFSBW = –0.55, IL = 1.06, DLFS = –0.73. Loadings for the second axis DF2 (only absolute values greater than 0.50): CH = –0.54, UL = –1.29, B/U = –0.69. For character codes *see* Table 2.

absence of clear-cut morphological boundaries, both between the two parental taxa and among the parents and the hybrids. An additional reason is the low number (9) of the hybrid individuals examined.

Discussion

Utricle and beak sizes are important in distinguishing between the taxa of the *C. flava* aggregate (e.g. Havlíčková 1982, Crins & Ball 1989a, 1989b, Schmid 1983, 1986, Pykälä & Toivonen 1994, Hedrén 2002). In hybrids these characters are the least morphologically variable and can be used successfully to differentiate hybrids from one another and from their parents. Measurements and analyses indicate that the utricle and beak dimensions in hybrids are intermediate in comparison with the parental taxa. However, the length of the utricle and that of its beak in the hybrid are usually similar to those of the parent having longer utricles and beaks. Thus, the individuals of *C.* × *ruedtii* and particularly *C.* × *alsatica*, have relatively long utricles and beaks which, in numerous *C.* × *alsatica* individuals, are even as long as those in pure *C. flava*. Similarly, the dimensions of those elements in hybrid *C. demissa* × *C. viridula* are similar to those found in pure *C. demissa*. The mean size of utricle and beak decrease in the following order: *C. flava*, *C.* × *alsatica*, *C.* × *ruedtii*, *C. lepidocarpa*, *C.* × *schatzii*, *C. demissa*, *C. demissa* × *C. viridula*, *C. viridula*. The beak length to the utricle length ratio (B/U) is also a distinctive characteristic of the taxa studied, its value decreasing from *C. flava* to *C. viridula* (except for *C. demissa* and *C. lepidocarpa*, in which the direction is reversed). A similar trend in the utricle and beak sizes was found in the hybrids of *C. hostiana* × *C. flava* aggregate by Więcław and Koopman (2013). Moreover, the utricles of hybrids are usually faded; they become pale yellow or pale green immediately after formation, and are slightly flattened and often empty because of the undeveloped nuts.

Carex × *alsatica* specimens were completely sterile, and for the most part intermediate of both parental species or, less often, morphologically similar to (but not identical with) *C. flava* (Fig. 1). The similarity to *C. flava* was mostly observed in vegetative traits, as well as the dimensions of the utricle and beak (in many hybrid specimens of intermediate size, but with a tendency to reach a far greater size than in *C. demissa*), and the size of female spikes. Hybrids can resemble immature *C. flava*; however, the utricles of the latter contain small, green, immature nuts. At one site in northern Poland (locality 2) some *C.* × *alsatica* had inflorescences with female spikes arranged in a similar manner as in *C. demissa* (the lower spike below mid-length of the stem).

Schmid (1982) studied natural populations and cultivated individuals of *C. flava* × *C. demissa* in Switzerland. Natural hybrids turned out to be completely sterile, pollen fertility of the experimental hybrids being 0%–2% (Schmid 1982). Therefore, mixed natural populations of *C. flava* and *C. demissa* may be expected to contain sterile hybrids, most of which are intermediate relative to the two parental species, or morphologically resembling *C. flava*.

All the individuals of *C.* × *ruedtii* examined were morphologically intermediate in respect to both parental taxa or, less often, morphologically similar to *C. lepidocarpa*. In addition to completely sterile hybrid specimens, there were also individuals having utricles with mature nuts (3 on the fertility scale), especially in locality 5 with numerous hybrids with extreme character values.

According to Schmid (1982), the pollen fertility of natural *C. flava* × *C. lepidocarpa* hybrids in Switzerland was low (0%–2%), up to 3% being found in artificial hybrids. Blackstock and Ashton (2010), who investigated *C. flava* × *C. lepidocarpa* hybrid populations in England, reported their morphological similarity with *C. lepidocarpa*. The English hybrids grew together with a population of pure *C. lepidocarpa*, while *C. flava* was absent. All the Polish localities sampled had more numerous specimens of *C. lepidocarpa* than of *C. flava*. Therefore, it seems that the low-pollen-fertility hybrids backcross with the more common *C. lepidocarpa*, as in the Polish localities sampled or as in those in England lacking *C. flava* (Blackstock & Ashton 2010).

The *C.* × *schatzii* specimens were either intermediate in respect to the parental taxa or morphologically similar to *C. lepidocarpa*, but hybrids with extremely long inflorescences were found as well. Numerous hybrid specimens looked like small *C. lepidocarpa*, with widely-spaced female spikes and a pedunculate male-spike typical of the species. Utricles of some hybrids contained well-developed nuts, suggesting the specimens to be F_n hybrids or backcrosses, which suggests introgression towards *C. lepidocarpa*. Schmid (1982) reported the seed set in the artificial *C. lepidocarpa* × *C. viridula* hybrids to vary between 6% and 12%, and the pollen fertility to be 25%–37%. Although Schmid (1982) did not investigate the fertility of natural hybrids of the two taxa, he assumed that they might be less fertile than the experimental ones. The flowering time of both parental taxa should also be considered. In the studied group, *Carex lepidocarpa* is the earliest to flower, while *C. viridula* is the latest (Vonk 1979). However, the late-flowering *C. lepidocarpa* populations may come into anthesis simultaneously with, or even later than, the earliest flowering *C. viridula* populations (Vonk 1979). Therefore, spontaneous crossing of these species is possible, and the resultant partially fertile hybrids may backcross with populations of *C. lepidocarpa* in full flower more often than with populations of *C. viridula* which have just entered anthesis.

Carex demissa × *C. viridula* hybrids were partially fertile and morphologically very similar to *C. demissa*. Several hybrids probably represented a later generation, with a few extreme traits. In his experimental crosses of *C. demissa* and *C. viridula*, Schmid (1982) reported seed set to range from 18% to 25%, but he did not specify the level of pollen fertility. *Carex demissa* is the third among the members of the *C. flava* aggregate to enter the flowering period, while, as mentioned earlier, *C. viridula* is the last (Vonk 1979). For that reason, introgression will probably proceed towards *C. demissa*.

Natural hybrids in the *C. flava* aggregate can be distinguished by their complete or partial sterility, intermediate traits, characters of either of the parental taxa, and extreme trait values. It must be stressed that in this paper we are presenting the analysis of mainly quantitative characters (relevant to distinguishing between closely related taxa of the *C. flava* aggregate), therefore the hybrids show predominantly intermediate traits. However, we found also a few extreme characters, as those often appear in subsequent generations of hybrids (Rieseberg & Ellstrad 1993, Schwarzbach *et al*. 2001). According to Rieseberg *et al*. (1999), studies of quantitative traits in segregating hybrid populations sometimes reveal the presence of phenotypes that are extreme in respect to those of either parental line. In this study, we were able to identify some characters that were positively transgressive for *C. flava* aggregate hybrids. These characters are mainly those of the inflorescence length, spacing of female spikes, and length of male spike and its peduncle. Perhaps those characters will gain in distinctness in subsequent hybrid generations. It is therefore possible that the characters will become typical of the hybrids only and will facilitate their morphological identification. In addition, the tendencies found in the utricle and beak sizes and the analysis of the remaining morphological characters suggest the following

likely direction of introgression: *C.* × *alsatica* → *C. flava*, *C.* × *schatzii* → *C. lepidocarpa* and *C. demissa* × *C. viridula* → *C. demissa*. It is difficult to draw an unequivocal conclusion regarding *C.* × *ruedtii*; the utricle and beak sizes point to introgression towards *C. flava*, whereas the remaining morphological characters, particularly those of the inflorescence and female spike spacing as well as the flowering period, indicate a higher probability of introgression towards *C. lepidocarpa*. While the latter possibility is indicated by studies on an English hybrid population (Blackstock & Ashton 2010), the former seems more plausible based on the research carried out in Switzerland (Schmid 1982). It is plausible, in addition, that the resultant backcrosses become similar to the parental sedges prevalent in a particular locality and characterized by an earlier flowering period, as is the case with *C.* × *schatzii*, *C. demissa* × *C. viridula* and probably with *C.* × *ruedtii* too.

The situation studied in this work — the presence of both parental taxa and their hybrids — becomes more complicated if one or both parental taxa are absent from the locality, and the hybrid shows a high fertility rate and well-developed nuts. As shown by Blackstock and Ashton (2010), genetic tests are then needed to establish the origin of a *C. flava* aggregate hybrid. Therefore, we plan to continue research on those hybrids using molecular assays to complement the morphological data discussed in the present paper.

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Appendix 1. Morphological variation between *Carex* × *alsatica* and parental species (*C. flava* and *C. demissa*). Basic statistics M = mean (UL, UBL, FSGL, FSGW, MSGL, MSGW are in mm; B/U is expressed in %; others are in cm), SD = standard deviation, CV = coefficient of variation (%). For character codes *see* Table 2.

Char.	Locality 1									Locality 2								
	C. × *alsatica*			*C. flava*			*C. demissa*			*C.* × *alsatica*			*C. flava*			*C. demissa*		
	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV
CH	25.20	5.76	23	47.39	9.19	19	23.30	5.72	25	30.17	3.74	12	45.12	5.61	12	25.61	3.83	15
CLL	9.67	1.72	18	15.40	1.97	13	8.10	1.61	20	15.66	2.72	17	19.58	3.39	17	10.09	1.87	19
CLW	0.29	0.04	13	0.32	0.05	14	0.26	0.03	11	0.30	0.03	10	0.33	0.04	13	0.28	0.03	12
IL	4.43	2.02	46	3.38	0.75	22	9.08	5.92	65	7.32	4.57	62	3.68	0.82	22	10.44	5.17	50
MSL	1.48	0.26	17	1.38	0.29	21	1.34	0.27	21	1.65	0.26	15	1.56	0.23	14	1.54	0.25	16
MSW	0.16	0.02	10	0.15	0.01	9	0.16	0.02	12	0.17	0.02	10	0.17	0.02	13	0.16	0.02	11
MSPL	0.53	0.29	54	0.22	0.03	14	0.48	0.31	64	0.34	0.18	52	0.21	0.07	32	0.56	0.27	49
DUFS	0.78	0.42	54	0.38	0.11	29	0.60	0.37	62	0.66	0.21	32	0.49	0.44	90	0.76	0.33	43
DLFS	2.79	2.32	83	1.47	0.52	35	7.02	5.75	82	4.64	4.26	92	1.50	0.54	36	7.44	4.96	67
LFSL	1.16	0.14	12	1.28	0.12	9	0.91	0.08	9	1.35	0.13	10	1.38	0.15	11	1.14	0.16	14
LFSW	0.85	0.06	7	0.96	0.07	7	0.68	0.05	7	0.88	0.04	5	0.98	0.08	8	0.68	0.05	7
LFSPL	0.19	0.11	57	0.26	0.18	69	0.22	0.09	43	0.51	0.22	42	0.45	0.22	48	0.32	0.14	46
LFSBL	7.45	1.83	25	10.66	1.60	15	8.41	1.87	22	13.68	3.62	26	12.58	3.00	24	10.51	2.12	20
LFSBW	0.24	0.03	12	0.26	0.04	17	0.23	0.03	15	0.27	0.03	11	0.27	0.04	14	0.24	0.02	9
LFSBSL	0.65	0.38	58	0.29	0.17	59	1.29	0.78	60	1.07	0.85	79	0.41	0.20	50	1.09	0.40	36
UFSL	1.05	0.14	14	1.12	0.16	15	0.84	0.15	18	1.10	0.15	13	1.16	0.17	15	0.95	0.11	11
UFSW	0.82	0.07	9	0.95	0.06	7	0.64	0.07	11	0.85	0.05	6	0.94	0.08	9	0.66	0.04	6
SFSBL	4.06	0.94	23	5.03	1.51	30	4.57	1.25	27	6.13	1.66	27	5.94	2.02	34	5.51	1.68	30
SFSBW	0.16	0.03	17	0.17	0.06	32	0.16	0.04	26	0.17	0.03	17	0.15	0.04	28	0.17	0.03	17
UL	4.50	0.32	7	5.24	0.27	5	3.27	0.18	6	4.46	0.17	4	4.98	0.37	7	3.27	0.18	6
UBL	2.06	0.19	9	2.45	0.16	6	1.36	0.12	9	1.98	0.09	4	2.33	0.26	11	1.27	0.11	8
B/U	45.00	1.90	4	46.00	1.60	3	41.00	2.07	5	44.00	0.94	2	47.00	2.33	5	40.00	1.97	5
FSGL	2.85	0.19	7	3.26	0.23	7	2.28	0.09	4	2.98	0.20	7	3.08	0.26	8	2.36	0.18	8
FSGW	1.64	0.10	6	1.57	0.11	7	1.56	0.10	7	1.51	0.10	6	1.45	0.10	7	1.42	0.14	10
MSGL	3.64	0.14	4	3.61	0.33	9	3.45	0.24	7	3.67	0.23	6	3.75	0.28	8	3.45	0.26	8
MSGW	1.58	0.13	8	1.37	0.10	7	1.63	0.10	6	1.45	0.09	6	1.35	0.12	9	1.45	0.10	7

Appendix 2. Morphological variation between *Carex* × *ruedtii* and parental species (*C. lepidocarpa* and *C. flava*). Basic statistics M = mean (UL, UBL, FSGL, FSGW, MSGL, MSGW are in mm; B/U is in %; the others are in cm), SD = standard deviation, CV = coefficient of variation (%). For character codes see Table 2.

Char.	Locality 3									Locality 4									Locality 5								
	C. × *ruedtii*			*C. lepidocarpa*			*C. flava*			*C.* × *ruedtii*			*C. lepidocarpa*			*C. flava*			*C.* × *ruedtii*			*C. lepidocarpa*			*C. flava*		
	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV
CH	52.46	10.60	20	57.27	9.47	17	53.11	9.28	17	53.97	9.37	17	49.39	9.36	19	37.30	4.11	11	55.75	12.20	22	42.73	10.44	24	34.66	6.85	20
CLW	0.27	0.03	11	0.22	0.02	8	0.30	0.03	11	0.29	0.04	15	0.24	0.03	13	0.31	0.07	21	0.37	0.06	16	0.24	0.03	14	0.42	0.07	17
CLL	13.62	3.19	23	11.51	1.69	15	17.95	5.07	28	15.87	3.06	19	12.43	1.58	13	17.75	2.07	12	20.13	6.16	31	16.21	3.26	20	19.69	2.84	14
IL	4.58	1.33	29	4.84	1.17	24	4.14	1.16	28	5.15	1.34	26	6.00	2.51	42	3.39	1.28	38	10.27	2.87	28	6.97	3.08	44	7.10	5.45	77
MSL	1.76	0.33	18	1.85	0.24	13	1.65	0.26	16	1.58	0.37	23	1.69	0.24	14	1.39	0.23	17	2.06	0.35	17	1.78	0.23	13	1.61	0.33	20
MSW	0.16	0.02	12	0.18	0.02	11	0.15	0.02	12	0.18	0.02	8	0.17	0.02	10	0.15	0.02	12	0.19	0.02	13	0.17	0.02	13	0.19	0.02	11
MSPL	0.90	0.49	55	1.79	0.70	39	0.44	0.18	41	0.95	0.42	44	1.29	0.74	57	0.34	0.16	46	1.79	1.43	80	1.12	0.76	68	0.34	0.11	32
DUFS	1.15	0.56	49	1.67	0.87	52	1.86	0.86	46	1.08	0.32	30	2.37	2.31	98	0.36	0.17	47	2.99	2.66	89	1.77	0.67	38	0.41	0.24	59
DLFS	2.17	1.37	63	0.00	0.00	0	0.34	0.16	46	2.46	0.83	34	3.02	0.91	30	2.01	0.79	39	4.28	2.29	53	3.78	2.95	78	4.45	5.07	114
LFSL	1.36	0.11	8	1.28	0.08	6	1.40	0.22	16	1.31	0.09	7	1.13	0.14	12	1.26	0.15	12	1.64	0.21	13	1.37	0.19	14	1.46	0.20	14
LFSW	0.88	0.04	5	0.81	0.05	6	0.89	0.04	5	0.85	0.05	6	0.77	0.07	9	0.92	0.05	6	0.86	0.08	10	0.77	0.12	16	0.94	0.10	11
LFSPL	0.35	0.35	98	0.40	0.39	97	0.67	0.35	52	0.35	0.24	68	0.54	0.50	93	0.50	0.23	47	1.13	0.70	62	0.94	1.22	131	1.10	1.00	90
LFSBL	7.09	2.70	38	4.59	2.35	51	12.58	3.25	26	8.56	2.40	28	6.11	1.56	26	11.93	1.78	15	12.72	3.45	27	8.86	3.58	40	15.16	4.77	31
LFSBW	0.20	0.03	15	0.10	0.04	40	0.25	0.04	16	0.23	0.03	11	0.17	0.03	16	0.25	0.05	21	0.28	0.04	15	0.18	0.03	15	0.34	0.08	25
LFSBSL	0.24	0.12	49	0.22	0.28	124	0.45	0.26	56	0.41	0.18	45	0.46	0.35	76	0.47	0.29	62	1.05	0.77	74	0.71	0.54	76	1.10	1.13	103
UFSL	1.21	0.12	10	1.15	0.11	9	1.19	0.11	9	1.14	0.08	7	1.05	0.16	15	1.13	0.11	9	1.34	0.26	19	1.05	0.26	25	1.15	0.15	13
UFSW	0.88	0.06	7	0.79	0.05	6	0.87	0.05	6	0.86	0.03	4	0.79	0.08	10	0.92	0.05	6	0.90	0.15	17	0.77	0.15	19	0.91	0.08	8
SFSBL	2.65	1.41	53	1.06	0.74	70	6.75	1.84	27	3.20	1.58	49	1.95	1.08	55	6.61	1.62	25	4.44	2.47	55	1.74	1.09	63	4.29	0.83	19
SFSBW	0.08	0.04	52	0.04	0.02	46	0.15	0.03	19	0.09	0.04	45	0.06	0.03	53	0.14	0.05	36	0.11	0.03	24	0.07	0.01	21	0.15	0.03	18
UL	4.44	0.26	6	3.85	0.25	6	4.43	0.25	6	4.39	0.20	5	3.88	0.22	6	4.46	0.09	2	4.30	0.43	10	3.81	0.26	7	4.77	0.47	10
UBL	1.88	0.12	6	1.44	0.14	10	2.06	0.13	6	1.75	0.12	7	1.28	0.13	10	2.10	0.05	3	1.56	0.22	14	1.25	0.11	9	2.12	0.16	8
B/U	42.00	1.66	4	37.00	1.76	5	46.00	1.18	3	40.00	1.50	4	33.00	1.91	6	47.00	0.93	2	38.00	2.92	8	33.00	2.48	7	45.00	1.81	4
FSGL	2.60	0.26	10	2.52	0.24	9	2.65	0.21	8	2.67	0.09	3	2.52	0.13	5	2.84	0.07	3	2.86	0.42	15	2.57	0.10	4	3.38	0.46	13
FSGW	1.42	0.11	7	1.43	0.09	6	1.49	0.10	7	1.45	0.05	4	1.44	0.06	4	1.46	0.12	8	1.59	0.07	5	1.53	0.18	12	1.56	0.14	9
MSGL	3.31	0.07	2	3.35	0.04	1	3.38	0.22	7	3.76	0.21	6	3.33	0.02	1	3.31	0.07	2	3.92	0.53	14	3.79	0.28	8	3.73	0.38	10
MSGW	1.53	0.12	8	1.49	0.06	4	1.62	0.05	3	1.79	0.14	8	1.58	0.01	1	1.60	0.05	3	1.72	0.14	8	1.56	0.12	8	1.53	0.14	9

Appendix 3. Morphological variation between *Carex* × *schatzii* and parental species (*C. lepidocarpa* and *C. viridula*). Basic statistics M = mean (UL, UBL, FSGL, FSGW, MSGL, MSGW are in mm; B/U is in %; the others are in cm), SD = standard deviation, CV = coefficient of variation (%). For character codes see Table 2.

Char.	Locality 6									Locality 7								
	C. × *schatzii*			*C. lepidocarpa*			*C. viridula*			*C.* × *schatzii*			*C. lepidocarpa*			*C. viridula*		
	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV	M	SD	CV
CH	23.52	5.63	24	55.68	10.32	19	13.28	9.89	75	34.63	3.47	10	60.41	9.39	16	24.57	4.45	18
CLL	5.82	1.36	23	13.61	3.44	25	7.39	4.87	66	13.85	3.41	22	13.17	2.22	17	14.06	5.27	37
CLW	0.24	0.04	15	0.26	0.04	16	0.22	0.02	7	0.25	0.04	16	0.26	0.03	12	0.23	0.04	18
IL	4.88	2.08	43	7.64	3.57	47	3.16	0.92	29	7.42	2.99	36	5.18	1.44	28	4.38	1.42	32
MSL	1.35	0.22	16	2.18	0.34	16	1.15	0.18	16	1.57	0.26	17	1.74	0.29	17	1.28	0.20	16
MSW	0.20	0.02	12	0.19	0.02	9	0.19	0.02	11	0.15	0.01	6	0.17	0.02	9	0.15	0.02	10
MSPL	1.18	0.74	63	2.62	1.47	56	0.29	0.08	28	1.53	1.54	80	1.52	1.01	67	0.32	0.14	44
DUFS	1.94	1.65	85	3.25	2.63	81	0.48	0.38	79	2.26	2.63	116	2.08	0.87	42	0.52	0.24	46
DLFS	4.22	2.52	60	3.86			1.39	0.78	57	4.87	1.22	25	3.11			2.20	1.39	63
LFSL	1.08	0.09	8	1.58	0.23	15	0.89	0.11	12	1.24	0.21	17	1.29	0.16	13	0.98	0.13	13
LFSW	0.71	0.06	8	0.85	0.07	8	0.57	0.04	8	0.67	0.05	8	0.85	0.04	5	0.60	0.05	8
LFSPL	0.51	0.37	73	0.79	0.76	96	0.25	0.11	44	0.43	1.11	78	0.53	0.64	121	0.27	0.13	47
LFSBL	4.78	1.87	39	7.72	3.38	44	6.13	2.45	40	10.37	5.09	38	5.02	2.00	40	10.65	2.53	24
LFSBW	0.14	0.04	28	0.14	0.05	32	0.21	0.01	7	0.19	0.03	13	0.12	0.04	35	0.20	0.03	15
LFSBSL	0.92	0.66	72	0.82	0.85	104	0.58	0.37	64	0.79	0.94	52	0.32	0.25	81	0.86	0.59	69
UFSL	0.93	0.10	11	1.35	0.21	15	0.74	0.09	12	0.97	0.20	21	1.08	0.12	11	0.77	0.09	12
UFSW	0.71	0.05	8	0.85	0.06	8	0.57	0.04	7	0.64	0.05	8	0.82	0.04	5	0.57	0.04	7
SFSBL	2.22	0.88	72	2.25	2.03	90	3.36	1.37	41	3.44	2.09	61	0.93	0.60	65	3.70	1.50	40
SFSBW	0.05	0.02	45	0.05	0.03	53	0.10	0.04	35	0.08	0.03	42	0.04	0.02	53	0.09	0.03	29
UL	3.43	0.30	9	4.19	0.28	7	2.72	0.22	8	3.27	0.22	7	4.03	0.25	6	2.99	0.26	9
UBL	1.24	0.15	12	1.52	0.16	10	0.90	0.13	14	0.98	0.16	16	1.45	0.10	7	0.95	0.12	13
B/U	36.00	2.13	6	36.00	2.69	7	33.00	2.93	9	30.00	3.61	12	36.00	2.70	8	32.00	1.67	5
FSGL	2.37	0.23	10	2.71	0.21	8	2.15	0.20	9	2.54	0.23	9	2.30	0.18	8	2.26	0.14	6
FSGW	1.52	0.15	10	1.46	0.13	9	1.24	0.13	11	1.41	0.09	6	1.48	0.10	7	1.30	0.07	5
MSGL	3.24	0.28	9	3.56	0.22	6	3.33	0.33	10	3.53	0.08	2	3.37	0.22	6	3.32	0.22	7
MSGW	1.64	0.14	8	1.65	0.12	7	1.46	0.21	14	1.52	0.09	6	1.64	0.15	9	1.53	0.11	7

Appendix 4. Morphological variation between *C. demissa* × *C. viridula* and parental species. Basic statistics M = mean (UL, UBL, FSGL, FSGW, MSGL, MSGW are in mm; B/U is in %; the others are in cm), SD = standard deviation, CV = coefficient of variation (%). For character codes see Table 2.

Char.	Locality 1								
	C. demissa × *viridula*			*C. demissa*			*C. viridula*		
	M	SD	CV	M	SD	CV	M	SD	CV
CH	23.89	3.30	14	23.30	5.72	25	19.74	4.27	22
CLL	8.62	1.57	16	8.10	1.61	20	7.94	0.02	12
CLW	0.24	0.01	6	0.26	0.03	11	0.19	1.64	21
IL	7.98	4.11	51	9.08	5.92	65	2.75	0.71	26
MSL	1.73	0.20	12	1.34	0.27	21	1.29	0.21	17
MSW	0.16	0.01	9	0.16	0.02	12	0.13	0.01	10
MSPL	0.58	0.38	56	0.48	0.31	64	0.48	0.05	10
DUFS	0.66	0.24	32	0.60	0.37	62	0.38	0.21	55
DLFS	5.32	4.11	77	7.02	5.75	82	0.98	0.54	55
LFSL	1.10	0.09	8	0.91	0.08	9	0.83	0.11	14
LFSW	0.61	0.06	10	0.68	0.05	7	0.59	0.03	5
LFSPL	0.29	0.19	64	0.22	0.09	43	0.12	0.02	18
LFSBL	9.40	1.07	11	8.41	1.87	22	6.08	2.15	35
LFSB	0.23	0.03	12	0.23	0.03	15	0.18	0.02	13
LFSBSL	1.17	0.52	44	1.29	0.78	60	0.30	0.22	74
UFSL	0.83	0.10	11	0.84	0.15	18	0.62	0.07	12
UFSW	0.60	0.03	5	0.64	0.07	11	0.55	0.04	7
SFSBL	5.13	0.65	13	4.57	1.25	27	2.76	1.33	48
SFSBW	0.15	0.02	16	0.16	0.04	26	0.07	0.03	48
UL	3.26	0.30	9	3.27	0.18	6	2.88	0.09	3
UBL	1.14	0.09	8	1.36	0.12	9	0.92	0.08	9
B/U	35.00	3.60	10	41.00	2.07	5	32.00	2.64	8
FSGL	2.32	0.12	5	2.28	0.09	4	2.39	0.41	17
FSGW	1.56	0.13	8	1.56	0.10	7	1.28	0.11	9
MSGL	3.50	0.11	3	3.45	0.24	7	3.06	0.30	10
MSGW	1.61	0.09	5	1.63	0.10	6	1.44	0.11	8