Diversity of plant communities with *Carex flava* agg. in Poland and their relationship with soil properties

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Abstract The *Carex flava* aggregate belongs to one of the most taxonomically difficult groups of sedges which colonize diverse habitats, from organic to sandy, from acidic to alkaline, usually humid and moist. The study included 129 vegetation plots and ten soil variables (organic matter, phosphorus, potassium, magnesium, calcium, carbonates, carbon, nitrogen, pH, and the ratio between organic carbon and nitrogen). The main aim was to determine the relationships between the various plant communities *C. flava* agg. occur in and their soil properties. With the aid of the two-way indicator species analysis and cluster analysis, we delimited nine vegetation types from the *Scheuchzeria palustris*-*Caricetea fuscae*, *Littorelletea uniflorae*, *Molinio-Arrhenatheretea* and *Alnetea glutinosae* classes differing in their response to soil properties. The CCA revealed pH, N, K, C, CaCO₃, P and Ca to be statistically significant, and to account for 11.55% of the total variance in species composition. The largest differences, both in terms of species composition and in soil condi-

tions, were revealed between communities with *C. lepidocarpa* and *C. demissa*. *Carex lepidocarpa* occurred in calcareous and extremely rich fens (*Caricion davallianae*) whereas *C. demissa* was found to occur in poor and moderately rich fens (*Sphagno-Caricion canescentis*, *Caricion canescenti-nigrae*). *Carex flava* grew mostly in calcareous, rich fens and wet grasslands (*Caricion davallianae*, *Calthion palustris*). *Carex viridula* was found in both calcareous, extremely and moderately rich fens and wet grasslands, and in nutrient-poor habitats such as dunes and sandy lake shores. The ecological niche of *C. viridula* is very wide and this species showed no affinity to any specific syntaxon.

Keywords sedges · soil properties · vegetation composition · wetlands

Introduction

The *Carex flava* complex belongs to one of the most taxonomically difficult groups because of a lack of clear morphological discontinuities (e.g. Havlíčková 1982; Crins and Ball 1989a,b; Pykälä and Toivonen 1994; Jiménez-Mejías et al. 2012) and the presence of numerous hybrids (Schmid 1982; Więclaw and Koopman 2013; Więclaw and Wilhelm 2014). The *Carex flava* complex in Europe is considered consisting of six species (Więclaw 2017). These taxa are usually small in size and have short rhizomes; they usually have a solitary subcylindrical male spike on top of the inflorescence, above globose to oblong female spikes with more

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or less inflated, ovoid-ellipsoid utricles with a distinct bifid beak (Chater 1980). In Poland, the *C. flava* group contains four taxa: *C. flava*, *C. lepidocarpa* subsp. *lepidocarpa*, *C. demissa* subsp. *demissa* and *C. viridula* var. *viridula* (Więclaw 2014a). *Carex viridula* var. *pulchella*, identified earlier in Poland by Zajac (1968), is most likely part of the continuum of variation within var. *viridula* resulting from effects of local habitat conditions (Więclaw 2017). The most important for the identification of taxa of the *C. flava* group are generative characters, particularly dimensions of the utricle and beak, from the longest in *C. flava* via *C. lepidocarpa* and *C. demissa* to the shortest in *C. viridula*, as well as the beak length/utricle length ratio, the diminishing order of which starts with *C. flava* to proceed via *C. demissa*, *C. lepidocarpa* to *C. viridula* (e.g. Pykälä and Toivonen 1994; Więclaw 2014a). In addition, two or more taxa of the *C. flava* aggregate may share a site; such mixed populations frequently contain hybrids (e.g. Więclaw and Wilhelm 2014; Schmidt et al. 2018).

Carex flava and *C. viridula* are frequent in Poland, whereas *C. lepidocarpa* is relatively rare. *Carex demissa* is found scattered across the country, mostly in the south (Więclaw 2014b). The relatively most common hybrids are *C. ×alsatica* [*C. demissa* × *C. flava*] and *C. ×subviridula* [*C. flava* × *C. viridula*]. In Poland, the taxa from the *C. flava* group usually grow in fens, wet meadows, along lake, sea and pond shores, along ditches, roadsides, in pastures, along streams and rivers, and less frequently in forests (Więclaw 2014b). They colonize diverse substrates, from organic to sandy and from acidic to alkaline, usually humid and moist (e.g. Davies 1956; Schmid 1984; Crins and Ball 1989b). Sedges of the *C. flava* complex can grow in different plant assemblages, usually representing the classes *Scheuchzerio palustris-Caricetea fuscae*, *Isoëto-Nanojuncetea*, *Littorelletea uniflorae*, *Molinio-Arrhenatheretea*, *Phragmito-Magnocaricetea* and *Alnetea glutinosae* (e.g. Hájková et al. 2010; Hájek and Hájková 2011; Šumberová 2011; Šumberová and Hrivnak 2013; Vončina 2017). For example, *C. flava* and *C. lepidocarpa* are regarded as species typical of communities included in the *Caricion davallianae*, for example *Caricetum paniceo-lepidocarpace* (Kwiatkowski 1999), *Carici flavae-Blysmetum compressi*, *Carici flavae-Eriophoretum latifolii* (Zamfirescu and Zamfirescu 2006), *Valeriano simplicifoliae-Caricetum flavae* (Pawłowski et al. 1960;

Hájek 1999; Hájek and Hájková 2002; Hájek et al. 2005) and *Carici flavae-Cratoneuretum* (Hájek et al. 2005). On the other hand, because of the morphological similarity of the sedges and difficulties in their identification, some phytosociological publications treat them as a broadly-defined aggregate; for example, Jarolímek and Šibík (2008) mentioned *Carex flava* agg. as diagnostic for the class *Scheuchzerio palustris-Caricetea fuscae* and the alliance *Caricion davallianae* (see also Hájek 2002; Peterka et al. 2017). Moreover, most phytosociological and ecological studies were focused on *C. flava* and *C. lepidocarpa*, and less so on *C. demissa* and *C. viridula* (e.g. Hájek 1999, 2002; Hájek and Hájková 2002). In addition, closely related species which are poorly morphologically differentiated can be easily overlooked or the differences observed may be regarded as a manifestation of habitat-dependent variation. Therefore, this study was aimed at identifying types of plant assemblages capable of supporting species of the *C. flava* complex and at determining relationships between soil properties and species composition and diversity of vegetation with *C. flava* agg.

The results presented are part of a comprehensive study on the taxa of the *C. flava* complex in Poland, with a particular reference to inter- and intra-specific differentiation, taxonomy and hybridisation within the group (Więclaw and Podlasiński 2013; Więclaw and Koopman 2013; Więclaw and Wilhelm 2014; Więclaw 2014a,b, Więclaw 2017).

Material and methods

Field sampling

Field data were collected in 2012–2014 in Poland from various habitats, for example from upland and lowland, coastal and inland, from calcareous, extremely and moderate-rich fens and wet grasslands to poor habitats such as dunes and sandy lake shores (Fig. 1; Online Resource 1). A total of 129 plots were sampled in patches with the presence of species from *C. flava* agg., specifically 16 with *C. demissa* subsp. *demissa*, 57 with *C. flava* s.str., 19 with *C. lepidocarpa* subsp. *lepidocarpa* and 37 with *C. viridula* var. *viridula*. The sedges were identified using the keys of Pykälä and Toivonen (1994) and Więclaw (2014a).

The area of vegetation plots was in the range of 10–30 m². The species cover in each plot was estimated

Fig. 1 Locations of *Carex flava* agg. sampling sites. 1, 2, 3, 4... – number of relevé; relevés 1, 3, 5–15, 21, 26, 28–36, 38–47, 55–58 – samples with *C. flava* from fens and wet grasslands without *Valeriana dioica* subsp. *simplicifolia* (cluster VII); relevés 2, 4, 16, 27, 37 – samples with *C. flava* from *Alnus* forest (cluster VIII); relevés 17–20, 22–25, 48–51, 53, 54 – samples with *C. flava* from fens and wet grasslands with *Valeriana dioica* subsp. *simplicifolia* from the Bieszczady Mts (cluster VI); relevés 52, 66, 68–72 – samples with *C. demissa* from poor acidic fens (cluster Va);

relevés 59, 60–65, 67, 73 – samples with *C. demissa* from moderate-rich fens and fen grasslands (cluster Vb); relevés 74–92 – samples with *C. lepidocarpa* (cluster I); relevés 106–109 and 119–129 – samples with *C. viridula* from fens and wet grasslands (cluster II); relevés 93–105 – samples with *C. viridula* from sandy lake shores (cluster IIIa), relevés 110, 112–114 – samples with *C. viridula* from sites near a chalk mine (cluster IIIb), relevés 111, 115–118 – samples with *C. viridula* from dunes (cluster IV).

using a nine-grade scale (van der Maarel 1979). All the vascular plant and bryophyte species were recorded and their respective cover-abundances were coded as follows: 1 (one or a few individuals); 2 (rare and less than 1% cover); 3 (less than 5% cover; several specimens); 4

(less than 5% cover; abundant); 5 (5–12.5% cover); 6 (12.5–25% cover); 7 (25–50% cover); 8 (50–75% cover); 9 (75–100% cover). At each plot, three soil samples were collected with an Egner's soil sampler from the plant root zone (0–25 cm). The three samples were

combined to form a single soil sample, representing a given plot and used for chemical analyses.

Soil analysis

Soil samples were dried at room temperature, and then rubbed through a sieve to remove fractions larger than 1 mm. The following properties were determined in the thus-prepared material: organic matter content (as loss on ignition at 550°C), pH (potentiometrically in 1 M KCl), contents of assimilable nutrients (phosphorus P, potassium K, magnesium Mg and calcium Ca, using the American Society of Agronomy method; Sparks et al. 1996), carbonates (Scheibler's method; Tatzber et al. 2007) and total carbon C and nitrogen N (CHNS analyser, Costech Analytical Technologies Inc.; Sparks et al. 1996). The latter assay provides data for calculating the C/N ratio. The ratio between organic carbon and nitrogen (C/N) is one of the indicators of soil fertility. The lower the ratio, the more fertile the soil.

Data processing

Two multivariate statistical techniques were used to analyse the vegetation data: the two-way indicator species analysis (TWINSpan package, v. 2.3; Hill and Šmilauer 2005) and the cluster analysis (MVSP package, v. 3.1; Kovach 1985–1999). Each of these approaches provides a somewhat different view on the structure of the data, and when employed together they can be used to better understand the diversification of the vegetation. Clusters resulting from divisions (TWINSpan) with eigenvalues greater than 0.3 are treated as the final clusters which, however, do not necessarily constitute communities. The cluster classification (MVSP) was performed using the minimum variance, based on the squared Euclidean distance.

The statistical significance of differences between empirical distributions of the data analysed and the theoretical normal distribution was examined using the Shapiro–Wilk test. Since distributions of most data sets deviated from normality, the non-parametric U Mann–Whitney test, Kruskal–Wallis test and Dunn's multiple comparisons test were used to examine whether differences between sites of *C. flava* agg. species and between relevés (Shannon diversity index, the evenness and number of species) were significant. Calculations were performed using the software package Statistica v. 13.1 for Windows (StatSoft, Inc. 2013). The Shannon

diversity index and the evenness were calculated for each relevé using the MVSP package (Kovach 1985–1999).

Relationships between vegetation plots and environmental factors were determined using the software package CANOCO v. 4.51 (ter Braak and Šmilauer 2002). Vegetation distribution patterns in relation to environmental variables were explored using canonical correspondence analysis (CCA), after detrended correspondence analysis (DCA) detected a unimodal structure of the species data (the gradient length represented by the first ordination axis was greater than 3 *SD*). The Monte Carlo permutation test was further applied to test for statistical significance of environmental variables.

Nomenclature

The nomenclature of vascular plants, *Carex* taxa and mosses follows *World Flora Online* (WFO 2020), Koopman (2015) and Ochrya et al. (2003), respectively. The phytosociological units are in compliance with the syntaxonomic nomenclature of the vegetation of Europe (Mucina et al. 2016). Assignment to phytosociological units below the class level follows Matuszkiewicz (2018) and Dierßen (2001). The fen terminology is in accordance with Hajek et al. (2006). Specimens collected in the field have been deposited in the Herbarium Stetinensis (SZUB).

Results

Floristic composition and diversity of plant communities with taxa representing *Carex flava* agg

The TWINSpan resulted in eight final clusters (I–VIII; see Online Resource 2 and 3). The first division of the dataset separated plots with *C. lepidocarpa* and *C. viridula* from *C. flava* and *C. demissa*. The division was based on indicators: *C. viridula* with a coverage of 3 or more, and *C. lepidocarpa* with a coverage of 2 or more. All the relevés with *C. lepidocarpa* coverage of more than 2 were assigned to a single vegetation unit (cluster I) whereas the relevés with *C. viridula* coverage of 3 and more were divided into three groups (Online Resource 2). The division of the three groups was based on indicators: *Bryum pseudotriquetrum* with a coverage of 2 and more (cluster III) and *Pohlia nutans* with a coverage of 1 and more (cluster IV). Cluster II

contained relevés dominated by species of the classes *Scheuchzerio palustris*-*Caricetea fuscae* (e.g. *Carex nigra*, *C. panicea*, *Campylium stellatum*) and *Molinio-Arrhenatheretea* (e.g. *Molinia caerulea*, *Lythrum salicaria*, *Deschampsia cespitosa*). All the relevés with *C. demissa* were assigned to a single vegetation unit (cluster V), with a *C. demissa* coverage of 3 and more (Online Resource 3), as an indicator. The relevés with *C. flava* were divided into three clusters. Clusters VI and VIII were identified by the presence of *Valeriana dioica* subsp. *simplicifolia* and *Alnus glutinosa*, respectively. Cluster VI covers relevés taken exclusively in the mountainous area in south-eastern Poland whereas cluster VII groups relevés from both lowlands throughout the country and mountains and uplands, mainly in the South-West of Poland. These relevés are distinct by the absence of *Valeriana dioica* subsp. *simplicifolia*, while *V. dioica* s.str. is frequent (Online Resource 3).

The MVSP resulted in the division of the entire dataset into two main groups; the first one contained relevés with *C. lepidocarpa* and *C. viridula*, while relevés in the other group contained relevés with *C. flava* and *C. demissa* (Fig. 2a). Further analyses of the main groups showed that some relevés with *C. viridula* were included in the group with *C. lepidocarpa*, while some of the relevés with *C. flava* were assigned to the group with *C. demissa* (Fig. 2b, c). The MVSP demonstrated a separate nature of relevés with *C. viridula* from dunes (cluster IV versus clusters III and II), shores of water bodies and the vicinity of a chalk mine (cluster IIIa versus cluster IIIb), as well as relevés with *C. demissa* (cluster Va versus Vb) and those with *C. flava* (cluster VI versus cluster VII), see Fig. 2b,c; Online Resource 2 and 3).

Relevés with *C. lepidocarpa* (cluster I) were similar in terms of their floristic composition and proportions of species (Online Resource 2). Such a species composition is characteristic of the association *Caricetum paniceo-lepidocarpae*. It is dominated by diagnostic species such as *C. lepidocarpa* and *C. panicea*; there are also calciphilous vascular plants (e.g. *Carex flacca*, *Epipactis palustris* and *Parnassia palustris*) and mosses (e.g. *Campylium stellatum* and *Fissidens adianthoides*, see Online Resource 2). The number of species per relevé averaged 22; Shannon's diversity index and evenness averaged 4.22 and 0.96, respectively (Table 1).

Relevés featuring *C. viridula*, taken along lake shores (cluster IIIa), were distinct by the presence of species

representing the classes *Montio-Cardaminetea*, *Potamogetonetea*, *Littorelletea uniflorae* and *Isoëto-Nanojuncetea*. Samples from the vicinity of the chalk mine (cluster IIIb) showed a low contribution of species representing the classes listed above (only *Cardamine amara*, *Bryum pseudotriquetrum* and *Drepanocladus polycarpus* were present) whereas species belonging to the *Phragmito-Magnocaricetea* (e.g. *Cladium mariscus*, *Carex disticha*, *Schoenoplectus tabernaemontani*) and *Molinio-Arrhenatheretea* (e.g. *Juncus subnodulosus*, *Linum catharticum*) occurred. Some relevés contained the calciphilous *Samolus valerandi* and *Campylium stellatum* (Online Resource 2). Plots dominated by *C. viridula*, occurring on exposed sandy shores (cluster IIIa), were classified as the assemblage *Ranunculo-Juncetum bulbosi*, variant with *C. viridula*. The assemblage was made up of several *Juncus* species (*J. articulatus*, *J. bufonius*, *J. bulbosus*) and a number of fen species such as *Agrostis canina* and *Hydrocotyle vulgaris* (Online Resource 2).

Patches featuring *C. viridula* observed in depressions between dunes (cluster IV) were characterized by the presence of species representing the classes *Oxycocco-Sphagnetalia* (e.g. *Drosera rotundifolia*, *Vaccinium oxycoccus*, *Aulacomnium palustre*) and *Nardetea strictae* (*Calluna vulgaris*, *Pohlia nutans*, *Empetrum nigrum*), and the order *Scheuchzerietalia palustris* (*Drosera anglica*, *Lycopodiella inundata*, *Sphagnum teres*). Relevés with *C. viridula* from wet grasslands and fens (cluster II) showed a presence of species from the class *Molinio-Arrhenatheretea* (e.g. *Lysimachia vulgaris*, *Ranunculus acris*, *Lotus pedunculatus*) and the order *Caricetalia fuscae* (e.g. *Hydrocotyle vulgaris*, *Carex nigra*, *Veronica scutellata*, see Online Resource 2). The fen and wet grassland relevés differed significantly from those of dunes in terms of the Shannon diversity index and the species richness ($P = 0.0193$ and $P = 0.0091$, respectively) as well as from those from lake shores ($P = 0.0048$ and $P = 0.0040$, respectively). The species richness in fen and wet grassland averaged 21 per relevé (Shannon index of 4.12) and 11 (Shannon index of 3.29) and 14 species (Shannon index of 3.56) in dune and lakeshore relevés, respectively.

The relevés with *C. demissa* were divided into two groups (Va and Vb; see Fig. 2c and Online Resource 3). Those included into cluster Va were distinct by the presence of species representing the classes *Nardetea strictae* (e.g. *Nardus stricta*, *Potentilla erecta*) and

Fig. 2 Results of hierarchical cumulative classification using Euclidean distance-based minimum variance techniques. **a** – Results for the entire dataset; **b** – Analysis for plots of *C. lepidocarpa* (cluster I) and *C. viridula* (II – samples from fens and wet grasslands, IIIa – sandy lakeshores, IIIb – sites near a chalk mine, and IV – dunes); **c** – Analysis for *C. demissa* (Va – samples from poor

acidic fen and Vb – moderate-rich fens and fen grasslands) and *C. flava* (VI – samples with *C. flava* from fens and wet grasslands with *Valeriana dioica* subsp. *simplicifolia* from Bieszczady Mts, VII – fens and wet grasslands without *Valeriana dioica* subsp. *simplicifolia*, and VIII – from *Alnus* forest).

Table 1 Diversity of species occurrence in phytocoenoses with *Carex flava* agg.; results of Kruskal–Wallis test and post hoc Dunn's multiple comparisons test, showing significance of differences in Shannon's index, evenness and number of species. F –*C. flava* s.str.; D – *C. demissa*; L – *C. lepidocarpa*; V – *C. viridula*; × – mean; *P* – statistical significance. The Significance level of *P* ≤ 0.05 is denoted in bold.

Shannon's method	Species				Kruskal-Wallis test		Dunn's multiple comparisons test					
	D × ±SD	F × ±SD	L × ±SD	V × ±SD	<i>H</i>	<i>P</i>	D-F <i>P</i>	D-L <i>P</i>	D-V <i>P</i>	F-L <i>P</i>	F-V <i>p</i>	L-V <i>p</i>
Index	4.61 ±0.39	4.84 ±0.31	4.22 ±0.59	3.78 ±0.52	70.34	0.000	0.464	0.389	0.000	0.000	0.000	0.141
Evenness	0.97 ±0.01	0.98 ±0.01	0.96 ±0.01	0.96 ±0.01	52.71	0.000	1.000	0.148	0.001	0.000	0.000	0.928
Num.Spec.	27 ±6.43	32 ±6.15	22 ±7.86	16 ±5.74	69.11	0.000	0.431	0.529	0.000	0.000	0.000	0.108

Oxycocco-Sphagnetum (*Sphagnum fallax*, *Polytrichum strictum*), as well as by a lower contribution of wet grassland species, compared to relevés in cluster Vb (Online Resource 3). The two groups identified by the MVSP were significantly different in their numbers of species (23 and 31 in clusters Va and Vb, respectively; *Z* = −2.2229; *P* = 0.0262), the Shannon diversity index (4.35 and 4.80 for clusters Va and Vb, respectively; *Z* = −2.1170; *P* = 0.0343) and evenness (0.97 and 0.98 for clusters Va and Vb, respectively; *Z* = −2.4346; *P* = 0.0149).

The *C. flava* relevés proved most species-rich, the Shannon index and the evenness being at their highest as well (Table 1). Relevés acquired in the Bieszczady Mountains (cluster VI) were significantly different from the remaining relevés (clusters VII and VIII) in terms of their Shannon index, evenness, and the number of species (5.07 vs 4.77 and 4.75, *P* = 0.0042; 0.98 vs 0.97 and 0.97, *P* = 0.0208; 38 vs 30 and 30, *P* = 0.0042, respectively). The Bieszczady Mts support a floristically rich variant of the *Valeriano simplicifoliae*-*Caricetum flavae* which featured, fairly frequently, *Valeriana dioica* subsp. *simplicifolia* and *Eriophorum latifolium*, while

in other regions the assemblages with *C. flava* featured fairly abundant *Valeriana dioica* s.str. All the relevés with *C. flava* showed an abundance of *Juncus articulatus* and small sedges such as *C. panicea* and *C. nigra* (Online Resource 3). Moreover, species primarily characteristic of wet grassland associations (e.g. *Anthoxanthum odoratum*, *Briza media*, *Cirsium palustre*, *Climacium dendroides*, *Festuca rubra*, *Geum rivale*, *Myosotis scorpioides* and *Ranunculus acris*) were also frequent. Some relevés from cluster VII were dominated by wetland species, for example *Blasmus compressus* (relevés 15 and 21), *Carex hartmanii* (40 and 41) and *Equisetum palustre* (12, 14 and 43, see Online Resource 3).

Distribution of plots and species along environmental gradients

The CCA results indicate that all the variables analysed accounted for 14.36% of the total variance in the species data (Table 2). The first axis and all the canonical axes were significant as tested by the unrestricted Monte Carlo permutation test (first axis: *P* = 0.026; all axes:

Table 2 Summary of CCA of vegetation samples collected at sites with the presence of species from the *C. flava* complex.

Axis	I	II	III	IV
Eigenvalues	0.277	0.169	0.157	0.139
Species-environment correlations	0.875	0.810	0.838	0.756
Cumulative percentage variance of species data	3.2	5.2	7.0	8.7
Cumulative percentage variance of species-environment relation	22.5	36.2	49.0	60.3
Sum of all eigenvalues/ Total inertia				8.573
Sum of all canonical eigenvalues				1.231
Percentage of explained species data variance				14.36

$P = 0.006$). The results of forward selection in the CCA revealed seven variables (pH, N, K, C, CaCO_3 , P and Ca) to be statistically significant and to account for 11.55% of the total variance in species composition (Table 3).

In the ordination space (CCA), all the *C. lepidocarpa* relevés occupy the right-hand part of the diagram and are associated with relatively high pH values and soil Ca, Mg, CaCO_3 , C and N, as well as with a relatively high C/N ratio (Fig. 3; Table 4). The *C. lepidocarpa* habitat differed significantly from habitats of *C. demissa*, *C. flava* and *C. viridula* by being relatively rich in carbonates, calcium and magnesium in the soil, as well as showing a high soil pH (Table 5).

Relevés of *C. viridula* are scattered in the ordination space; however, most samples collected from dunes (cluster IV) and lake shores (cluster IIIa) are positioned in the left-hand side of the diagram and are associated with relatively low values of most soil parameters studied (Fig. 3; see also Table 5). The relevés taken from fens and wet grasslands (cluster II) are concentrated mainly in the central part of the diagram whereas samples collected from sites near the chalk mine (cluster IIIb) are placed in the right-hand part of the diagram together with samples of *C. lepidocarpa*. Statistically significant differences, primarily concerning pH and soil contents of organic matter, C, N, Mg, Ca and CaCO_3 were detected between relevés from dunes (IV) and fens and wet grasslands (II), as well as between dunes (IV) and sites near the chalk mine (IIIb), see Fig. 4a–h.

All the relevés with *C. demissa* occupy the left-hand part of the CCA diagram and are associated with

Fig. 3 Ordination diagram of vegetation samples and environmental variables along the first two CCA axes; cluster I – samples with *C. lepidocarpa*; cluster II – samples with *C. viridula* from fens and wet grasslands; cluster IIIa – samples with *C. viridula* from sandy lake shores; cluster IIIb – samples with *C. viridula* from sites near a chalk mine; cluster IV – samples with *C. viridula* from dunes; cluster Va – samples with *C. demissa* from poor acidic fens; cluster Vb – samples with *C. demissa* from moderate-rich fens and fen grasslands; cluster VI – samples with *C. flava* from fens and wet grasslands with *Valeriana dioica* subsp. *simplicifolia* from the Bieszczady Mts; cluster VII – samples with *C. flava* from fens and wet grasslands without *Valeriana dioica* subsp. *simplicifolia*; cluster VIII – samples with *C. flava* from *Alnus* forest; * – statistically significant variables, significance level $P \leq 0.05$. For abbreviations of soil properties, see Table 3.

relatively low values of most soil parameters studied (Fig. 3). The upper part of the diagram contains the relevés from poor acidic fens (cluster Va), while the relevés from moderate-rich fens (cluster Vb) are grouped in the central part. Significant differences between them concerned pH and the soil Ca content (Fig. 4d,g).

Table 3 Forward selection results with the test of variable significance for vegetation samples collected at sites with the presence of species from the *C. flava* complex. C – carbon concentration; N – nitrogen concentration; C/N – ratio between organic carbon and

nitrogen concentration; org. mat. – organic matter content; pH – soil pH; Ca – calcium concentration; CaCO_3 – carbonates concentration; Mg – magnesium concentration; P – phosphorus concentration; K – potassium concentration; * significance level $P \leq 0.05$.

Variables	LambdaA	Explained data variance [%]	F	P
pH*	0.23	2.68	3.60	0.002
N [%]*	0.15	1.75	2.45	0.002
K [mg/kg]*	0.15	1.75	2.36	0.002
C [%]*	0.15	1.75	2.35	0.002
CaCO_3 [%]*	0.11	1.28	1.69	0.024
P [mg/kg]*	0.10	1.17	1.55	0.022
Ca [mg/kg]*	0.10	1.17	1.54	0.028
org.mat. [%]	0.09	1.05	1.54	0.080
C/N	0.08	0.93	1.38	0.084
Mg [mg/kg]	0.07	0.82	1.18	0.202

Table 4 Soil properties at *Carex flava* agg. sites sampled. F – *C. flava* s.str.; D – *C. demissa*; L – *C. lepidocarpa*; V – *C. viridula*; C – carbon, N – nitrogen; $\bar{x}$ – mean; *SD* – standard deviation; range – minimum and maximum values; ** – for the pH measured on a log scale, only the range and extreme values (in brackets) are given. For abbreviations of soil properties, see Table 3.

Soil properties									
Taxa	C [%]	N [%]	C/N	Mg [mg/kg]	P [mg/kg]	range	$\bar{x} \pm SD$	range	range
F	14.8 ± 12.6	1.1 ± 1.0	13.9 ± 3.1	621.4 ± 920.5	18.6 ± 9.5	37.6–4,207.9		5.3–58.9	
D	9.2 ± 11.5	0.6 ± 0.9	16.9 ± 3.9	352.0 ± 448.2	16.2 ± 7.6	35.7–1,462.6		6.5–32.7	
L	22.4 ± 8.3	1.3 ± 0.9	26.4 ± 20.4	$1,618.5 \pm 1,036.5$	10.2 ± 5.7	102.0–3,366.7		0.0–19.6	
V	8.4 ± 13.4	0.5 ± 0.9	16.4 ± 16.4	495.7 ± 827.1	19.3 ± 15.0	26.8–3,736.9		4.4–52.5	
	pH	CaCO ₃ [%]	org. Mat [%]	Ca [mg/kg]	K [mg/kg]				
Taxa	range**	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	$\bar{x} \pm SD$	range		range	range
F	(4.3–)5.0–7.6	5.3 ± 13.4	25.4 ± 21.8	$8,627.2 \pm 12,730.9$	95.1 ± 59.6	226.4–62,834.9		21.4–248.8	
D	3.4–5.5(–7.2)	0.0	15.9 ± 19.8	$3,722.4 \pm 5,999.3$	108.9 ± 86.2	6.3–15,119.7		7.9–250.1	
L	(6.1–) 6.9–7.7	35.7 ± 36.1	35.4 ± 18.3	$48,745.8 \pm 44,086.3$	68.6 ± 89.1	2,256.9–110,048.9		20.1–319.0	
V	4.2–7.9(–8.2)	6.6 ± 17.5	10.6 ± 18.8	$10,397.7 \pm 25,733.6$	61.0 ± 80.0	41.4–136,017.0		16.2–319.0	

Plots of *C. flava* are scattered on the CCA diagram; however, relevés from the Bieszczady Mts (cluster VI) are situated in the upper part whereas the remaining relevés from fens and wet grasslands (cluster VII), as well as all the forest relevés (cluster VIII), are grouped in the lower part (Fig. 3). Statistically significant differences between the Bieszczady relevés and the other relevés were revealed for soil organic matter content, as well as for concentrations of carbon, nitrogen, magnesium and potassium (Fig. 4a–c,f,e).

Discussion

Vegetation types with taxa representing *Carex flava* agg

We delimited nine vegetation types with taxa included in the *Carex flava* group that differed in their species composition and response to soil properties.

Carex lepidocarpa is a characteristic species of the assemblage *Caricetum paniceo-lepidocarpace* from the alliance *Caricion davallianae* (Kwiatkowski 1999). In Poland *C. lepidocarpa* grows only in calcareous sites (calcareous, extremely rich and rich fens). Those habitats are severely threatened due mainly to general and wide-scale disturbances in hydrological conditions (Wolejko et al. 2005; Šefferová Stanová et al. 2008; Grootjans et al. 2015). Moreover, *C. lepidocarpa* is sensitive to changes in hydrology and becomes increasingly rare. It is regarded as threatened in some Central European countries (Pykälä 1994).

Carex flava s.str. is found in calcareous, rich and moderate-rich fens and wet grasslands as well as in alder thickets and woods. In Poland, it grows on soils with a wide pH range, from (4.3–)5.0 to 7.6. *Carex flava* is one of the diagnostic species of the *Valeriano simplicifoliae-Caricetum flavae*, found in mountainous regions, throughout the flysch zone of the Slovak, Polish and Ukrainian Carpathians, and occasionally in Czechia (Pawłowski et al. 1960; Hájek 1999; Hájek and Hájková 2002, 2011; Hájek et al. 2002). In Poland, Koczur and Nicia (2013) reported a substantial variability in the assemblage, mainly produced by the wide range of the habitat parameters, notably the soil pH, varying from (5.8–)6 to (7.6–)8 (see also Mazurek and Nicia 2006); our study, however, showed the *Valeriano simplicifoliae-Caricetum flavae* to be a rather homogenous fen community (see also Hájek 1999), despite the habitat varying

Table 5 Results of Kruskal–Wallis test and post hoc Dunn's multiple comparisons test, showing significance of differences in soil properties at *Carex flava* agg. Sites sampled. F – *C. flava* s.str.;D – *C. demissa*; L – *C. lepidocarpa*; V – *C. viridula*; the significance level of $P \leq 0.05$ is marked with bold. For abbreviations of soil properties, see Table 3.

Soil properties	Kruskal–Wallis test		Dunn's multiple comparisons test					
	<i>H</i>	<i>P</i>	F-L <i>P</i>	F-V <i>P</i>	F-D <i>P</i>	L-V <i>P</i>	L-D <i>P</i>	V-D <i>P</i>
C [%]	34.16	0.000	0.105	0.000	0.366	0.000	0.000	1.000
N [%]	34.30	0.000	1.000	0.000	0.108	0.000	0.079	0.026
C/N	17.72	0.000	0.003	1.000	0.013	0.117	1.000	0.272
Ca [mg/kg]	38.77	0.000	0.005	0.003	0.101	0.000	0.000	1.000
Mg [mg/kg]	34.25	0.000	0.002	0.012	1.000	0.000	0.001	1.000
CaCO ₃ [%]	27.12	0.000	0.005	1.000	1.000	0.027	0.004	0.443
P [mg/kg]	10.39	0.016	0.008	1.000	1.000	0.196	0.349	0.945
K [mg/kg]	27.07	0.000	0.006	0.000	1.000	1.000	0.236	0.034
pH	38.33	0.000	0.000	1.000	0.006	0.002	0.000	0.00
org. Mat. [%]	38.52	0.000	0.651	0.000	0.341	0.000	0.027	0.4232

from acidic to slightly alkaline (from 5.0 to 7.6). The assemblage showed a fairly constant floristic composition, but a high number of species from the class *Molinio-Arrhenatheretea* points to its potential to become transformed into a grasslands community. In Czechia, the *Valeriano simplicifoliae-Caricetum flavae* is vicariant to the *Valeriano dioicae-Caricetum davallianae* in the mountainous regions of the Western Carpathians (Hájek and Hájková 2011). In Poland we found patches featuring *Carex flava* and *Valeriana dioica* s.str. as well as other species diagnostic for the *Valeriano dioicae-Caricetum davallianae*, for example *Carex panicea*, *Potentilla erecta*, *Succisa pratensis*, *Calliergonella cuspidata* (Hájek and Hájková 2011); however, *C. davalliana* was not found at any of our sites and the proportion of wet grasslands species was considerable. In Poland, *V. dioica* subsp. *simplicifolia* and *V. dioica* s.str. are vicariants; the former occurs mainly in the East and South-East whereas the latter is known from the central and western part of the country (Zajac and Zajac 2001). According to Zarzycki et al. (2002), the taxa are similar in their habitat requirements, but are different in terms of their continentalism and, to a lesser extent, in acidity preference: *V. dioica* subsp. *simplicifolia* is sub-continental and usually grows on alkaline soils (more seldom on soil with neutral pH), whereas *V. dioica* s.str. is a sub-Atlantic species and grows on neutral

pH soils. Our study confirmed the presence of the *Valeriano simplicifoliae-Caricetum flavae* in the Bieszczady Mountains, while the remaining patches with *C. flava* (outside of the Bieszczady) are heterogeneous and represent various associations, usually the wet grasslands ones from the class *Molinio-Arrhenatheretea*.

Carex demissa usually occurs in poor and moderate-rich fens as well as along forest roads and paths. In Poland, it was usually reported from acidic sites (pH 3.4–5.5) with usually a very low calcium concentration and with a carbonate-poor soil. It was only at a single

Fig. 4 Ranges of soil properties at *C. flava* agg. sites in Poland. ►

Large boxes indicate 25–75% of the interquartile ranges; small boxes are medians; circles denote outliers; asterisks mark extreme values. *Carex lepidocarpa* – cluster I; *C. viridula* – II, IIIa, IIIb, IV; *C. demissa* – Va, Vb, *C. flava* – VI, VII, VIII (the cluster numbers are compatible with Online Resource 2 and 3). The diagrams show statistically significant differences only within *C. viridula* (between four clusters), *C. demissa* (between two clusters) and *C. flava* (between three clusters) sites. The significance of differences between species sites is shown in Table 5. a – Carbon, $P = 0.0019$, $P_1 = 0.0416$, $P_2 = 0.0013$, $P_3 = 0.0023$, $P_4 = 0.0058$; b – Nitrogen, $P = 0.0016$, $P_1 = 0.0028$, $P_2 = 0.0005$, $P_3 = 0.0038$; c – Organic matter content, $P = 0.0262$, $P_1 = 0.0416$, $P_2 = 0.0009$, $P_3 = 0.0029$, $P_4 = 0.0083$; d – pH value, $P = 0.0021$, $P_1 = 0.0008$, $P_2 = 0.0050$; e – Potassium, $P = 0.0275$, $P_1 = 0.0000$, $P_2 = 0.0232$; f – Magnesium, $P = 0.0426$, $P_1 = 0.0293$, $P_2 = 0.0014$, $P_3 = 0.0009$, $P_4 = 0.0189$; g – Calcium, $P = 0.0107$, $P_1 = 0.0027$, $P_2 = 0.0003$, $P_3 = 0.0081$; h – Carbonates, $P = 0.0493$, $P_1 = 0.0055$, $P_2 = 0.0285$.

site, the northernmost one, about 700 m away from the Baltic Sea shore, that *C. demissa* was found growing on soil with a pH exceeding 7. In Central and Southern Europe, *C. demissa* is usually found on acidic and slightly acidic soils, for example in Switzerland (Schmid 1984), Bulgaria, Czechia, and Slovakia (Stoeva and Štěpánková 1990). In Northern Europe (e.g. in Finland), *C. demissa* is weakly calciphilous and occurs on nutrient-rich soils. According to Pykälä and Toivonen (1994), this lends support to the known observation of a species strengthening its requirements at the boundary of its range. In Poland, the structure and floristic composition of communities with *C. demissa* as well as the soil parameters, mainly pH, correspond with those typical of the *Carici echinatae-Sphagnetum* (cluster Va) and *Carici canescentis-Agrostietum caninae* (cluster Vb), see Hájek and Hájková (2002, 2011), Hájek et al. (2008), and Koczur and Nicia (2013). The habitat of the latter represents one of the most common types of fen grasslands on non-calcareous bedrock in Central Europe (e.g. Dítě et al. 2007; Hájek and Hájková 2011; Matuszkiewicz 2018).

Carex viridula usually grows in open habitats (e.g. wet grasslands, fens, dunes, lake and pond shores) and is capable of colonising variable and unstable sites (Davies 1956; Schmid 1984; Stoeva and Štěpánková 1990; Więclaw 2014a,b, 2017). The sedge has been reported from various plant assemblages, mainly the classes *Isoëto-Nanojuncetea*, *Littorelletea uniflorae* and *Scheuchzerio palustris-Caricetea fuscae* (e.g. Šumberová 2011; Šumberová et al. 2011).

In Poland, *C. viridula* is regarded as one of the species characteristic of the *Cyperetum flavescens* from the class *Isoëto-Nanojuncetea*, which appears spontaneously on emergent bottom and shores of water reservoirs (Popiela 1997; Matuszkiewicz 2018). However, our study found *C. viridula* to grow, along lake shores, in *Ranunculo-Juncetum bulbosi* communities from the class *Littorelletea uniflorae* (see also Szańkowski and Kłosowski 2006; Hrivnák et al. 2011; Šumberová et al. 2011). All the sites with *C. viridula* located along lake shores were supported by the bryophyte *Bryum pseudotriquetrum*, which is common in wet and moderately infertile sites (Ellenberg et al. 1991). According to Dierßen (2001) this species can also occur on slightly acidic habitats such as fens and lake shores.

Communities featuring *C. viridula* and occurring in humid dune depressions along the Polish Baltic Sea

coast are similar to marsh assemblages of the class *Scheuchzerio palustris-Caricetea fuscae*. Theurillat et al. (2015) distinguished, within the class *Scheuchzerio palustris-Caricetea fuscae*, the alliance *Caricion viridulo-trinervis*, which covers low-sedge vegetation of wet, phosphorus-limited dune slacks of Atlantic coasts of Western Europe (see also Peterka et al. 2017). On the other hand, Sival and Grootjans (1996) frequently recorded *C. viridula* on dune slacks of the island of Schiermonnikoog in the northern part of the Netherlands in a pioneer assemblage with *Littorella uniflora*, *Samolus valerandi*, *Radiola linoides* and *Juncus bulbosus*. In Poland, the relevés made in between-dune depressions were distinct in showing the presence of the bryophyte *Pohlia nutans*, common and often abundant on wet or dry, acidic, peaty, sandy or gravelly soil on heaths and moors, in sand dunes, acidic grassland, bogs, and woods. It avoids base-rich or calcareous sites (Ellenberg et al. 1991).

Carex viridula is fairly frequently found also in fens and wet grasslands across a wide spectrum of soil conditions (e.g. Więclaw and Podlasiński 2013), in communities representing both the class *Scheuchzerio palustris-Caricetea fuscae* and the *Molinio-Arrhenatheretea*. According to Hájek et al. (2008), *C. viridula* reached a high cover in disturbed moderately rich fens in Bulgaria and occurred with some calciphilous species, for example *Eriophorum latifolium* and *Parnassia palustris*. In Poland, *C. viridula* can also grow at sites with a high soil calcium carbonate level (see also Więclaw and Podlasiński 2013) and is capable of colonizing heavily disturbed sites (Więclaw 2017). Thus, the ecological niche of *C. viridula* is very wide, compared to that of *C. flava*, *C. lepidocarpa* and *C. demissa*. *Carex viridula* grows in various plant communities without any tight syntaxonomic affinity.

Ecological differentiation within closely related species

In Poland, the *Carex flava* complex includes four closely related sedge species (Więclaw 2014a), which, as shown in this study, occupy diverse habitats and have diverse ecological requirements. In general, many closely related taxa may be distinctly different in their ecological preferences (e.g. Dakskobler et al. 1999; Hölzel 2003; Koutecká et al. 2011; Budzhak et al. 2016). A clear differentiation, both in the community composition, soil properties, and habitat types was revealed within the *Bolboschoenus maritimus* group (Hroudová

et al. 1999). According to Hroudová et al. (1999), the closely related taxa of the *Bolboschoenus maritimus* group show a much stronger ecological than morphological differentiation (no distinct diagnostic characters). Our investigation has shown that *C. lepidocarpa* and *C. demissa* are the most ecologically isolated species of the *C. flava* complex. The former was found on calcareous and extremely rich fens (*Caricion davallianae*) whereas the latter was reported from poor and moderately rich fens (*Sphagno-Caricion canescentis* and *Caricion canescenti-nigrae*). However, earlier morphological studies on the *C. flava* group in Poland showed *C. lepidocarpa* and *C. demissa* to be fairly distinctly separated morphologically, mainly in the dimensions of the generative characters (Więclaw 2014a). Similarly, taxa within the *Festuca varia* group were well separated both morphologically and ecologically, syntaxonomic studies on the group showing the presence of five vicariating regional associations and one edaphically determined association, growing on ecologically different sites (Wallossek 1999). Other studies, addressing species of the *Molinia caerulea* complex in Central Europe (*Molinia caerulea* s.str. and *M. arundinacea*), showed differences in their morphology and chromosome number (Dančák et al. 2012) as well as in habitat preferences (Budzhak et al. 2016). Comparative studies on three related species of the genus *Viola*, combined with their phytosociology and environmental parameters showed the species to differ in terms of their association with the soil moisture gradient and chemistry (Hölzel 2003). Koutecká et al. (2011) reported results of phytosociological research which clearly separated three *Myosotis* species from the *Myosotis palustris* group into different types of habitats and plant communities. They found only two locations with the simultaneous presence of two *Myosotis* species (*M. caespitosa* and *M. nemorosa*). These examples show closely related species to differ fairly distinctly in terms of micro-species morphology and to be clearly separated by ecological preferences. This pattern is, however, not so pronounced within the *C. flava* complex.

Our study showed the *C. flava* taxa to be capable of sharing a habitat, except for *C. lepidocarpa* and *C. demissa*, distinctly separated ecologically in Poland. *Carex lepidocarpa* and *C. flava* s.str. Can co-occur on calcareous and rich fens (*Caricion davallianae*). They are clearly different morphologically (e.g. Schmid 1984; Crins and Ball 1989a,b; Pykälä and Toivonen 1994;

Więclaw 2014a), but mixed populations frequently support hybrids, whereby an unequivocal species identification is challenging (Więclaw and Wilhelm 2014). The ecological amplitude of *Carex flava* s.str. is wider than that of *C. lepidocarpa*; the former species can also grow on wet grasslands and moderate-rich fens, where frequently co-occurs with *C. demissa* and their hybrid (*C. ×alsatica*). *Carex flava* s.str. and *C. demissa* are rather well separated morphologically, but the problem of intermediate hybrids present in their mixed populations appears here as well (Więclaw and Wilhelm 2014).

Carex viridula is encountered both in calcareous, extremely and moderately rich fens, wet grasslands, and in very poor habitats such as dunes and sandy lake shores. *Carex viridula* frequently co-occurs with both *C. lepidocarpa* and *C. flava*, and much more seldom with *C. demissa* (Więclaw 2014a,b) and hybridizes with all three mentioned species (Więclaw and Wilhelm 2014; Schmidt et al. 2018). *Carex viridula* is morphologically different from both *C. flava* and *C. lepidocarpa*, mainly in its much smaller utricles and shorter beaks, but is morphologically very close to *C. demissa* (e.g. Pykälä and Toivonen 1994; Hedrén 2003; Więclaw 2014a). Noteworthy is the fact that *Carex viridula* is the only species of the *C. flava* complex which grows on sandy lake shores and in dune depressions.

To sum up, detailed knowledge on closely related species, combining results of taxonomic and environmental studies, allows us to fairly precisely determine the ecological amplitude of narrowly-defined species. The combination of an ecological and taxonomic approach may lead to a better understanding of the evolutionary ecology of plants.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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References

- Budzhak VV, Chorney II, Tokariuk AI, Kuzemko AA (2016) Numeric syntaxonomical analysis of communities of the *Molinia caerulea* complex in Southwestern of Ukraine. *Hacquetia* 15:63–77
- Chater AO (1980) *Carex* L. In Tutin TG, Heywood VH, Burges NA, Moore DM, Walters SM, Webb DA (eds) *Flora Europaea* 5 (*Alismataceae* to *Orchidaceae*). Cambridge University Press, Cambridge, pp. 290–323
- Crins W J, Ball PW (1989a) Taxonomy of the *Carex flava* complex (Cyperaceae) in North America and northern Eurasia. I. Numerical taxonomy and character analysis. *Canad J Bot* 67: 1032–1047
- Crins WJ, Ball PW (1989b) Taxonomy of the *Carex flava* complex (Cyperaceae) in North America and northern Eurasia. II. Taxonomic treatment. *Canad J Bot* 67:1048–1065
- Dančák M, Duchoslav M, Trávníček B (2012) Taxonomy and cytogeography of the *Molinia caerulea* complex in central Europe. *Preslia* 84:351–374
- Dakskobler I, Seliškar A, Vreš B (1999) *Stellaria nemorum* L. and *S. montana* Pierrat (*Caryophyllaceae*) in the forest communities of Slovenia. *Folia Geobot* 34:115–125
- Davies EW (1956) The ecology and distribution of *Carex flava* and its allies in the British Isles. *Bot Not* 109:51–74
- Dierßen K (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophyt Biblioth* 56:1–289
- Dítě D, Hájek M, Hájková P (2007) Formal definitions of Slovakian mire plant associations and their application in regional research. *Biologia* 62:400–408
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobot* 18:1–248
- Grootjans A, Bulte M, Wolejko L, Pakalne M, Dullo B, Eck N, Fritz Ch (2015) Prospects of damaged calcareous spring systems in temperate Europe: Can we restore travertine-marl deposition? *Folia Geobot* 50:1–11
- Hájek M (1999) The *Valeriano simplicifoliae-Caricetum flavae* association in the Podhale Region (Western Carpathians, Poland): notes on syntaxonomical and successional relationships. *Fragm Florist Geobot* 44:389–400
- Hájek M (2002) The class *Scheuchzerio-Caricetea fuscae* in the Western Carpathians: indirect gradient analysis, species groups and their relation to phytosociological classification. *Biologia* 57:461–469
- Hájek M, Hájková P (2002) Vegetation composition, main gradient and subatlantic elements in spring fens of the north-western Carpathian borders. *Thaiszia* 12:1–24
- Hájek M, Hájková P (2011) Vegetace slatinišť, přechodových rašelinišť a vrchovištních šlenků (Vegetation of fens, transitional mires and bog hollows) In Chytrý M (ed) *Vegetace České republiky. Vodní a mokřadní vegetace (Vegetation of the Czech Republic. Aquatic and Wetland Vegetation)* 3. Academia, Praha, pp 614–701
- Hájek M, Hájková P, Apostolova I (2008) New plant associations from Bulgarian mires. *Phytol Balcan* 14 :377–399
- Hájek M, Hájková P, Rybníček K, Hekera P (2005) Present vegetation of spring fens and its relation to water chemistry. In Pouličková A, Hájek M, Rybníček K (eds) *Ecology and palaeoecology of spring fens of the West Carpathians* 5. Palacký University Press Olomouc, Academy of Sciences of the Czech Republic, Masaryk University Brno, pp 69–95
- Hájek M, Hekera P, Hájková P (2002) Spring fen vegetation and water chemistry in the Western Carpathian flysch zone. *Folia Geobot* 37:205–224
- Hájek M, Horsák M, Hájková P, Dítě D (2006) Habitat diversity of Central European fens in relation to environmental gradients and an effort to standardise fen terminology in ecological studies. *Perspect Pl Ecol Evol Syst* 8:97–114
- Hájková P, Hájek M, Blažková D, Kučera T, Chytrý M, Řezníčková M et al (2010) Louky a mezofilní pastviny (Meadows and mesic pastures) In Chytrý M (ed) *Vegetace České republiky. Travná a keříčková vegetace (Vegetation of the Czech Republic. Grassland and heathland vegetation)* 1. Academia, Praha, pp 165–280
- Havlíčková J (1982) *Carex flava*-complex in the Czech lands. I. Analysis of the variability of morphological characters. *Preslia* 54:201–222
- Hedrén M (2003) Patterns of allozyme and morphological differentiation in the *Carex flava* complex (Cyperaceae) in Fennoscandia. *Nordic J Bot* 22:257–301
- Hill MO, Šmilauer P (2005) *Twinspan for Windows version 2.3*. Centre for Ecology and Hydrology, University of South Bohemia, Huntingdon & České Budějovice
- Hölzel N (2003) Re-assessing the ecology of rare flood-meadow violets (*Viola elatior*, *V. pumila*, *V. persicifolia*) with large phytosociological data sets. *Folia Geobot* 38: 281–298
- Hrivnák R, Kochjarová J, Otáhel'ová H (2011) Vegetation of the aquatic and marshland habitats in the Orava region, including the first records of *Potametum alpinum*, *Potametum zizii* and *Ranunculo-Juncetum bulbosi* in the territory of Slovakia. *Biologia* 66:626–637
- Hroudová Z, Zákravský P, Frantík T (1999) Ecological differentiation of central European *Bolboschoenus* taxa and their relationship to plant communities. *Folia Geobot* 34:77–96
- Jarolímek I, Šibík J (eds) (2008) *Diagnostic, constant and dominant species of the higher vegetation units of Slovakia*. Veda, Bratislava
- Jiménez-Mejías P, Martín-Bravo S, Luceño M (2012) Systematics and taxonomy of *Carex* sect. *Ceratocystis* (Cyperaceae) in Europe: a molecular and cytogenetic approach. *Syst Bot* 37: 382–398
- Koczur A, Nicia P (2013) Spring fen *Scheuchzerio-Caricetea nigrae* in the Polish Western Carpathians – vegetation diversity in relation to soil and feeding waters. *Acta Soc Bot Poloniae* 82:117–124
- Koopman J (2015) *Carex Europaea. The genus Carex L. (Cyperaceae) in Europe* 1. Accepted names, hybrids,

- synonyms, distribution, chromosome numbers. Ed. 2 (2nd reprint), Margraf Publishers, Weikersheim
- Koutecká E, Koutecký P, Lepš J (2011) Comparison of community composition and site conditions between three closely related *Myosotis* species IV. In Koutecká E (ed) *Ecological comparison of three closely related species from Myosotis palustris group*. PhD. Thesis [in English/Czech], University of South Bohemia, Faculty of Science. České Budějovice, Czech Republic, pp 117–135
- Kovach WL *MVSP PLUS version 3.1*. Pentraeth (1985–1999)
- Kwiatkowski P (1999) *Caricetum paniceo-lepidocarpaceae* - a plant association new to Poland. *Fragm Florist Geobot* 44:375–388
- Matuszkiewicz W (2018) *Przewodnik do oznaczania zbiorowisk roślinnych Polski (Guide to the determination of plant communities in Poland)*. Ed. 3 (3rd reprint), Wydawnictwo Naukowe PWN, Warszawa
- Mazurek R, Nicia P (2006) Micromorphological properties of low sedge mountain fen soils. *Polish J Environm Stud* 15:80–85
- Mucina L, Bültmann H, Dierßen K, Theurillat J-P, Raus T, Čarni A et al (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, be, lichen, and algal communities. *Applied Vegetation Science* 19(Suppl. 1):3–264
- Ochyra R, Żarnowiec J, Bednarek-Ochyra H (2003) *Census catalogue of Polish mosses*. Institute of Botany, Polish Academy of Sciences, Cracow
- Pawłowski B, Pawłowska S, Zarzycki K (1960) *Zespoły roślinne kośnych łąk północnej części Tatry i Podtatrza (Les associations végétales des prairies fauchables de la partie septentrionale des Tatras et de la Région subtatruque)*. *Fragm Florist Geobot* 6:95–227
- Peterka T, Hájek M, Jiroušek M, Jiménez-Alfaro B, Aunina L, Bergamini A et al (2017) Formalized classification of European fen vegetation at the alliance level. *Appl Veg Sci* 20:124–142
- Popiela A (1997) Zbiorowiska namulkowe z klasy *Isoëto-Nanojuncetea* Br.-Bl. et Tx. 1943 w Polsce (Occurrence of the *Isoëto-Nanojuncetea* Br.-Bl. et Tx. 1943 class communities in Poland) *Monogr Bot* 80:1–59
- Pykälä J (1994) The ecology and distribution of *Carex lepidocarpa* subsp. *lepidocarpa* in Finland. *Ann Bot Fenn* 31:261–274
- Pykälä J, Toivonen H (1994) Taxonomy of the *Carex flava* complex (Cyperaceae) in Finland. *Nordic J Bot* 14:173–191
- Schmid B (1982) Karyology and hybridization in the *Carex flava* complex in Switzerland. *Feddes Repert* 93:23–59
- Schmid B (1984) Niche width and variation within and between populations in colonizing species (*Carex flava* group). *Oecologia* 63:1–5
- Schmidt L, Fischer M, Oja T (2018) Two closely related species differ in their regional genetic differentiation despite admixing. *AoB PLANTS* 10:ply007
- Sival FP, Grootjans AP (1996) Dynamics of seasonal bicarbonate supply in a dune slack: effects on organic matter, nitrogen pool and vegetation succession. *Vegetatio* 126:39–50
- Sparks DL, Page AL, Helmke PA, Loeppert RH (1996) *Methods of soil analysis part 3 - chemical methods*. SSSA Book Ser. 5.3. Soil Science Society of America, American Society of Agronomy, Madison.
- StatSoft, Inc. (2013) *Electronic Statistics Textbook*. Tulsa, OK: StatSoft. Available at <http://www.statsoft.com/textbook>
- Stoeva MP, Štěpánková J (1990) Variation patterns within the *Carex flava* agg. in Bulgaria and Czechoslovakia. *Preslia* 62:1–24
- Šefflerová Stanová V, Šeffler J, Janák M (2008) *Management of Natura 2000 habitats. 7230 Alkaline fens. Technical Report 200820/24 Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora DAPHNE*. Institute of Applied Ecology, Slovakia
- Šumberová K (2011) Vegetace jednoletých vlhkominálních bylin (Vegetation of annual wetland herbs) In Chytrý M (ed) *Vegetace České republiky. Vodní a mokřadní vegetace (Vegetation of the Czech Republic Aquatic and Wetland Vegetation)* 3. Academia, Praha, pp 309–338
- Šumberová K, Hrivnák R (2013) Formalised classification of the annual herb vegetation of wetlands (*Isoëto-Nanojuncetea* class) in the Czech Republic and Slovakia (Central Europe). *Phytocoenologia* 43:13–40
- Šumberová K, Navrátilová J, Čtvrtlíková M, Hájek M, Bauer P (2011) Vegetace oligotrofních vod (Vegetation of oligotrophic water bodies) In Chytrý M (ed) *Vegetace České republiky. Vodní a mokřadní vegetace (Vegetation of the Czech Republic. Aquatic and Wetland Vegetation)* 3. Academia, Praha, pp 268–309
- Szańkowski M, Kłosowski S (2006) Habitat variability of the *Littorelletea uniflorae* plant communities in Polish *Lobelia* lakes. *Hydrobiologia* 570:117–126
- Tatzber M, Stemmer M, Spiegel H, Katzlberger C, Haberhauer G, Gerzabek M (2007) An alternative method to measure carbonate in soils by FT-IR spectroscopy. *Environm Chem Lett* 5:9–12
- ter Braak CJF, Šmilauer P (2002) *CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4.5)*. Microcomputer Power. Ithaca, NY, USA.
- Theurillat J-P, Mucina L, Hájek M (2015) Validations of high-rank syntaxa in *Potamogetonetea* and *Scheuchzerio-Caricetea fuscae*. *Lazaroa* 36:67–73
- van der Maarel E (1979) Transformation of cover-abundance values in phytosociology and its effect on community similarity. *Vegetatio* 39:97–114
- Vončina G (2017) *Młaki eutroficzne polskich Karpat [Eutrophic fens in the Polish Carpathians]*. The Committee of Organismal Biology of Polish Academy of Sciences - Institute of Biology of Jagiellonian University. Warszawa – Kraków
- Wallossek C (1999) The acidophilous taxa of the *Festuca varia* group in the Alps: new studies on taxonomy and phytosociology. *Folia Geob Phytotax* 34:47–75
- WFO (2020) *World Flora Online*. Published on the Internet; Available <http://www.worldfloraonline.org>. (Accessed on 23 Mar 2020)
- Więclaw H (2014a) *Carex flava* aggregate (section *Ceratocystis*, Cyperaceae) in Poland: taxonomy, morphological variation, and soil conditions. *Biodivers Res Conservation* 33:3–47

- Więclaw H (2014b) *Carex flava* aggregate (section Ceratocystis, Cyperaceae) in Poland: distribution maps and locality lists. *Biodivers Res Conservation* 33:49–84
- Więclaw H (2017) Within-species variation among populations of the *Carex flava* complex as a function of habitat conditions. *Pl Ecol Diversity* 10:443–451
- Więclaw H, Koopman J (2013) Numerical analysis of morphology of natural hybrids between *Carex hostiana* DC. and the members of *Carex flava* agg. (Cyperaceae). *Nordic J Bot* 31:464–472
- Więclaw H, Podlasiński M (2013) Morphological differences between natural populations of *Carex viridula* (Cyperaceae): effects of soil conditions. *Ann Bot Fenn* 50: 13–22
- Więclaw H, Wilhelm M (2014) Natural hybridization within the *Carex flava* complex (Cyperaceae) in Poland: morphometric studies. *Ann Bot Fenn* 51:129–147
- Wojewko L, Herbichowa M, Potocka J (2005) Typological differentiation and status of Natura 2000 mire habitats in Poland. *Stapfia* 85, zugleich Kataloge der OÖ. Landesmuseen *Neue Serie* 35:175–219
- Zajac A (1968) *Carex serotina* Mér. subsp. *pulchella* (Lönnr.) v. Ooststr., w Polsce. *Fragm Florist Geobot* 14:205–211
- Zajac A, Zajac M (eds) (2001) *Distribution Atlas of Vascular Plants in Poland*. Laboratory of Computer Chorology, Institute of Botany, Jagiellonian University, Kraków, pp. 714
- Zamfirescu O, Zamfirescu ȘtR (2006) Diversity analysis of plant communities with *Carex flava* from the Ceahlău mountain. *Contr Bot* 41:61–66
- Zarzycki K, Trzcińska-Tacik H, Różański W, Wołek J, Korzeniak U (2002) *Ecological indicator values of vascular plants of Poland*. In Mirek Z (ed) *Biodiversity of Poland*. 2, W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, pp. 183

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