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RE-ASSESSING THE ECOLOGY OF RARE FLOOD-MEADOW VIOLETS (*VIOLA ELATIOR*, *V. PUMILA* AND *V. PERSICIFOLIA*) WITH LARGE PHYTOSOCIOLOGICAL DATA SETS

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Abstract: This study demonstrates how conventional ecological knowledge on species together with models resulting from functional traits can be tested and refined by tapping large data sources that have been made available through recent electronic compilations. The study is based on the comparison of three rare, closely related flood-meadow violet species, which have been supposed to have similar ecological behaviour and niche occupation. In contrast, the analysis of 335 Central European relevés using different methods of numerical ordination, classification and calibration revealed distinct differences in habitat preferences between the three species. Detrended correspondence analysis ordination, and multiple-response permutation procedures and TWINSPAN classification displayed the separation of *Viola persicifolia* from *V. elatior* and *V. pumila* along a moisture and base-richness gradient, while the latter two differed mostly in terms of mowing compatibility. Although the three violets are considered to be weak competitors they may be found under nutrient-poor as well as nutrient-rich site conditions. The distribution of C-S-R strategy types in relevés supported the hypothesis that at more fertile sites the violets crucially depend on disturbance by management or flooding events that create gaps and weaken strong competitors, while at less productive sites they may persist for a long time even under fallow conditions. The S/R strategy is shared by all three violets. Problems and perspectives arising with the use of phytosociological databanks as a source of ecological information are discussed.

Keywords: Calibration, Classification, C-S-R strategy types, Ellenberg indicator values, Indicator species analysis, MRPP, Ordination

Nomenclature: WISSKIRCHEN & HAEUPLER (1998)

INTRODUCTION

In recent years national phytosociological databanks have been compiled in several European countries (BRISSE & GRUBER 1996, CHYTRÝ 1997). Due to the vast number of relevés sampled by phytosociologists during the past century following a very similar protocol, such databanks potentially contain large amounts of ecological information. However, their current use is more or less strictly focused on phytosociological classification (RODWELL 1991, RODWELL et al. 1995, SCHAMINÉE et al. 1995). Only rarely have they been used for research on biodiversity patterns or for an explicit analysis of ecological gradients in species distribution (EWALD 2001). Since every phytosociological relevé is a measurement of species richness and habitat quality, they provide a lot of relevant information (AUSTIN 1999).

This applies in particular to poorly studied, rare and endangered species whose ecological preferences and niche separation are often still dubious (MATTHIES & POSCHLOD 2000).

This study demonstrates how phytosociological relevés stored in large databanks can be utilized as a source of ecological information at the species level. The main aspects addressed in this paper are as follows:

(1) Putting conventional phytosociological knowledge to the test: Can the sociological affinities expressed for instance by OBERDORFER (1983, 1994) and the ecological calibration of ELLENBERG et al. (1992) be confirmed and refined by tapping the large data sources that have been made available through recent electronic compilations?

(2) Testing hypotheses resulting from life history, morphological and functional traits (GRIME et al. 1988): Do the investigated species behave according to ecological theory in real plant communities? Are biological predictions confirmed by broad field evidence?

MATERIALS AND METHODS

Study species

The taxonomically closely related violets *Viola elatior* FR. (further abbreviated VE), *V. pumila* CHAIX (VPu) and *V. persicifolia* ROTH (= *V. stagnina* KIT.) (VPs), which are among the rarest and most endangered plant species in Central Europe (SCHNITTLER & GÜNTHER 1999), were chosen for the analysis. In Central Europe, where these species reach the western edge of their Western Eurasian distribution (MEUSEL et al. 1965), they are largely confined to climatically warm and dry lowland flood-meadow habitats along large river corridors such as the valleys of the Rhine, Elbe and Danube (HAEUPLER & SCHÖNFELDER 1988, BENKERT et al. 1996). Due to the loss of suitable habitats caused by flood control, drainage and modern agricultural land use the violets have become extremely rare (KORNECK et al. 1996) and are the subject of recovery programs in several European countries (PULLIN & WOODELL 1987).

OBERDORFER (1994) lists the violets as character species of the *Cnidion* alliance, which comprises lowland flood-meadows of sub-continental distribution (BALÁTOVÁ-TULÁČKOVÁ 1969), and mentions that they may also occur rarely in alluvial *Molinion* meadows. Thus, traditional phytosociology assumes that they share quite a similar ecological niche. The impression of ecological redundancy is also supported by the indicator values of ELLENBERG et al. (1992) that differ only slightly among the three species (Table 1).

The close evolutionary relationship among the three violet species is reflected by a high degree of similarity in morphology and life history (HEGI 1975). All three species are perennial hemicryptophytes with an erect stem lacking a basal rosette and bearing petiolate ovate-lanceolate leaves with long stipulae (especially VE and VPu). The three species differ mainly in chromosome number, growth height, seed size and seed weight (Table 1). Lateral clonal growth is of limited importance while seed production is very flexible and may be prolonged over the whole growing season, as in many other *Viola* species (BERG & REDBO-TORSTENSSON 1999), by cleistogamous flowering. Seeds are discharged from the capsules by a ballistic mechanism and may be hurled almost five meters in VE (MÜLLER-SCHNEIDER 1983). The hard-shelled seeds hold an elaiosome, which facilitates dispersal by ants. All three species build up long-term persistent seedbanks (MOORE 1983,

Table 1. Comparison of ecological, morphological and life history traits of *Viola elatior* (VE), *V. pumila* (VPu) and *V. persicifolia* (VPs), according to $^{1)}$ – ELLENBERG et al. (1992), $^{2)}$ – BRIEMLE & ELLENBERG (1994), $^{3)}$ – OBERDORFER (1994), $^{4)}$ own unpublished measurements. The first seven traits are expressed on a relative scale covering the whole Central European flora.

	VE	VPu	VPs
Light (L)$^{1)}$	7	8	6
Temperature (T)$^{1)}$	7	7	7
Continentality (C)$^{1)}$	6	6	5
Moisture (M)$^{1)}$	8	7	8
Reaction of soil (R)$^{1)}$	8	6	6
Nutrients (N)$^{1)}$	2	4	3
Mowing compatibility (MO)$^{2)}$	4	4	4
Chromosomes$^{3)}$	2n = 40	2n = 40	2n = 20
Height (cm)$^{4)}$	20–50	5–20 (30)	10–25
Period of flowering$^{4)}$	1 May–10 June	20 April–30 May	1 May–5 June
Seed length x width (mm)$^{4)}$	2.1 × 1.2	1.8 × 1.0	1.5 × 0.8
Seed mass (g/1000 seeds)$^{4)}$	1.80	1.08	0.67

SCHOPP-GUTH 1997, HÖLZEL & OTTE 2001, HÖLZEL, unpubl. data) and may rapidly develop to the reproductive phase. Under suitable conditions the first seeds from cleistogamous flowers are released within only 12 weeks after germination (ECKSTEIN, HÖLZEL, unpubl. data).

Many authors (BÖGER 1991, QUINGER 1993) emphasize that the three investigated violet species are generally weak competitors. Following Grime’s model of plant functional types (GRIME et al. 1988) they should be confined to stressful habitats with low competition. However, biological properties such as a long-term persistent seed bank, rapid growth and flexible seed production through cleistogamous flowering support the idea of a ruderal component in their life strategy. Regarding growth height, seed size and weight, VE should be the most and VPs the least competitive species.

Using numerical ordination and classification techniques together with calibration methods, the following assumptions will be assessed:

(1) All three violets occur in the same plant communities with comparable floristic structure.

(2) All three violets share the same ecological preferences, which are in accordance with Ellenberg’s indicator values.

(3) All three violets occupy the same functional niches in plant communities according to Grime’s C-S-R strategy types.

Data set

Since phytosociological databanks are still not accessible over large parts of Central Europe, most of the relevés that contained one of the violet species had to be compiled from paper publications by a review of Central European literature (Table 2). Larger digital packages were obtained from the Dutch (E. Weeda) and Czech (M. Chytrý) national databanks. Additionally, recent unpublished material was contributed by B. Redecker, J. Danihelka, E. Weeda and the author. The majority of samples had a standard size between

Table 2. Origin of relevés used in the analysis and number ofsamples with *Viola pumila* (VPu), *V. elatior* (VE), *V. persicifolia* (VPs). Samples with co-occurrence of two violet species (seven times VE and VPu, two times VPu and VPs) are accounted twice.

Region	VPu	VE	VPs	Source
Aube, Seine and Marne River valleys, Champagne (Central France)	-	28	-	Didier & Royer (1988)
Upper Rhine valley, alluvium and lower terrace (Germany)	53	26	28	13 Böger (1991), 9 Göbel (1995), 25 Liepelt & Suck (1989), 10 Thomas (1990), 44 Hölzel unpubl.
Danube valley (Bavaria and Austria)	6	8	-	6 Ahlmer (1989), 6 Balátová-Tuláčková & Hübl (1974), 2 Hölzel unpubl.
Morava and Dyje River valleys (Austria and southern Moravia, Czech Republic)	39	9	24	3 Balátová-Tuláčková (1993), 7 Balátová-Tuláčková & Hübl (1974), 8 Croft & Preston (1997), Czech database (compiled by M. Chytrý et al.: 27 Danihelka, 2 Duchoslav, 3 Rydlo, 20 Šumberová)
Saale River (East Germany)	4	1	-	Knapp (1954)
Middle Elbe and Lower Havel River valleys (East Germany)	2	-	28	18 Burkart (1998), 7 Leyer (2002), 5 Redecker unpubl.
The Netherlands	-	-	39	Dutch database (compiled by E. Weeda)
Drömling fen (SE Lower Saxony, Germany)	-	-	3	Weeda et al. unpubl.
Spreewald fen (East Germany)	-	-	46	Müller-Stoll et al. (1992)

16 and 25 m^2, few were considerably smaller or larger. In all samples, the traditional or slightly modified (cover value 2 subdivided in 2m, 2a and 2b) Braun-Blanquet scale was used. Subspecies and varieties among the vascular plants were generally pooled into species or even species aggregates since the degree of identification varied considerably among authors. Only vascular plant records were used for the analysis, because the quality of recording cryptogams also varied strongly among authors. Vascular plant species with five or less occurrences ($< 2\%$ frequency) were omitted from the numerical analysis but were included in the calculation of the mean Ellenberg indicator values and calibrated mean C-S-R strategy values. This resulted in a reduction in the total number of vascular plant species from 508 to 243.

In total 335 relevés were included in the numerical analysis. Table 2 gives an overview of the geographical distribution and occurrence of the violets in the relevés. The recent Central European strongholds where all three species may occur together, namely in the northern part of the Upper Rhine Valley and along the floodplains of the Morava and Dyje Rivers in the southeast of the Czech Republic are well represented in the data set. In the northern and north-eastern parts of Central Europe VPs is predominant. A surprisingly high number of relevés with VE originates from the river valleys of the Champagne in Central France, at the extreme north-western distribution limit of this species.

Environmental and biotic calibration

Cover-weighted averages of the indicator values given by ELLENBERG et al. (1992), the values for mowing compatibility by BRIEMLE & ELLENBERG (1994) and calibrated C-S-R strategy types by GRIME et al. (1988) were calculated for each sample. The calibration of unbalanced C-S-R radii for species was performed in the manner demonstrated by EJRNÆS & BRUUN (2000) and ECKE & RYDIN (2000). Only species categorized by GRIME et al. (1988) were included in the analysis; these comprised about 70% of the entire species pool and 90% of the most frequent and abundant species. The generation of C-S-R values for species not mentioned in GRIME et al. (1988) was avoided. Instead species without C-S-R values were made passive in the calculation. Percentages of annuals and woody chamaephytes per sample were also included in the analysis, since these are well known to be good biotic indicators for the presence or absence of disturbance (GRIME et al. 1988).

Data analysis

Numerical analyses were performed with the PC-ORD 4 package (MCCUNE & MEFFORD 1999). Multiple-response permutation procedures (MRPP) (ZIMMERMANN et al. 1985) were carried out to test sample differences between the three violet species in terms of floristic composition, mean Ellenberg indicator values and calibrated C-S-R strategy types. Differences between TWINSPAN clusters were tested in the same manner. MRPP is a useful technique to analyze differences between groups in ecological data since it does not require assumptions such as normality and equal variance (ZIMMERMANN et al. 1985). MRPP was performed using a recommended natural weighting factor and Sørensen distance measures (MCCUNE & MEFFORD 1999). Presence/absence data were used for the analysis of differences in floristic composition. Two similarity values are provided by MRPP: (i) *P*-value as a probability measure of significant differences between groups and (ii) *A*-value for within-group agreement, ranking from 1 (total within-group agreement) to 0 (heterogeneity within groups equals expectations by chance). With large sample sizes small *P*-values are easily obtained, so that the *A*-value for within-group homogeneity should also be considered for the interpretation of ecological significance (MCCUNE & MEFFORD 1999).

The indicator species analysis (DUFRÊNE & LEGENDRE 1997) was used to detect significant indicators for each violet species and to test the significance of indicator species within the TWINSPAN tree, as demonstrated by BRUUN & EJRNÆS (2000). The indicator value of a species is evaluated for a group of samples by the multiplication of its relative abundance within a particular group over all groups and its relative frequency within the particular group, both expressed as percentages. Significant differences between the indicator value of a species within a particular group and the expected average mean over all groups are tested by Monte Carlo statistics with a large number (1000) of random runs (MCCUNE & MEFFORD 1999).

Major gradients in the data set were explored by detrended correspondence analysis (DCA; HILL & GAUCH 1980), a method of indirect gradient analysis (JONGMAN et al. 1995). Running a DCA with detrending by 26 segments revealed a gradient length on the first axis of 4.594 standard deviation units indicating a strong unimodal response and thus the appropriateness of DCA (TER BRAAK & ŠMILAUER 1998). Ordination was performed on

Table 3. Comparison of the three flood-meadow violets by floristic composition, mean Ellenberg indicator values and calibrated Grime strategy types of relevés with MRPP. For each test an *A*-value for within-group agreement and the significance of dissimilarity between groups is given. High *A*-values (> 0.050) are given in bold. Due to multiple testing significance levels were set to $P < 0.001$ (*** – significant, ns – not significant). Significant values indicate deviation from the null hypothesis that the species do not differ in the given trait.

	VE/VPu/VPs	VE/VPu	VE/VPs	VPu/VPs
Floristic composition	**0.077*****	0.030***	**0.053*****	**0.069*****
All Ellenberg values	**0.117*****	0.013 ns	**0.083*****	**0.109*****
Moisture	**0.239*****	0.011 ns	**0.191*****	**0.229*****
Soil reaction	**0.233*****	0.025 ns	**0.192*****	**0.182*****
Nutrients	0.041***	0.001 ns	0.023***	0.043***
Mowing compatibility	0.029***	0.013 ns	0.005 ns	0.036***
Competition	0.008 ns	0.000 ns	0.010 ns	0.004 ns
Stress	0.016 ns	0.013 ns	0.002 ns	0.022***
Disturbance	0.013 ns	0.027 ns	0.003 ns	0.009 ns

square-root transformed Braun-Blanquet cover class means to prevent high species cover values from unduly influencing the ordination (VAN DER MAAREL 1979).

Correlations between sample scores derived from DCA ordination and environmental and biotic variables were tested using the Spearman rank correlation coefficient.

The classification of samples was carried out by a two-way indicator species analysis, TWINSPAN (HILL 1979). TWINSPAN is a divisive clustering method based on reciprocal averaging, the same algorithm that is used in DCA ordination (JONGMAN et al. 1995). Generally, the default program options were chosen, i.e., a maximum of five indicators per division, a maximum of six levels of division and a minimum group size for division of ten. Five pseudospecies cut levels were defined corresponding to the Braun-Blanquet cover values + to 5. The division process was stopped when further divisions resulted merely in groups of high spatial autocorrelation.

RESULTS

Comparison of the violets

Comparison of the three violet species by MRPP (Table 3) revealed significant differences in floristic composition of relevés. However, there was a high within-group heterogeneity indicated by low *A*-values. Differences were most pronounced between VE and VPu on the one hand and VPs on the other hand. Regarding mean Ellenberg indicator values, differences between VE and VPu were no longer significant while those between the latter two and VPs were even more pronounced. This applied particularly to the values for moisture and soil reaction whereas the values for nutrients and mowing compatibility displayed a high within-group variation. The comparison of C-S-R functional types revealed no or negligible differences among the three violet species.

The comparison of VPu and VPs by indicator species analysis resulted in numerous significant positive indicators for each species (results at the species level not shown separately, but see almost identical species groups in Table 5). Positive indicators of VPs were mostly species indicating damp and/or acidic site conditions, while those of VPu were typical

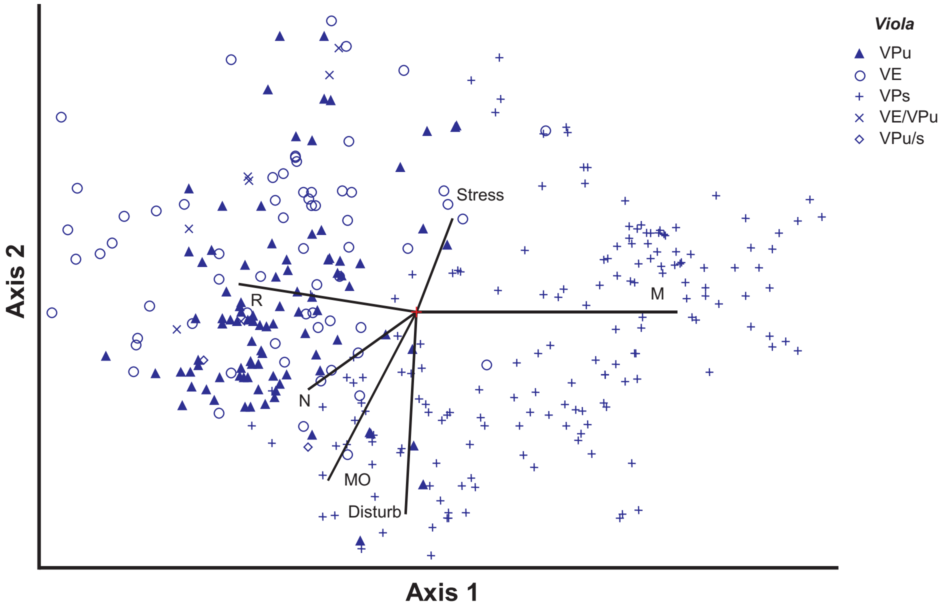

Fig. 1. Biplot of DCA ordination of 335 samples with flood-meadow violets. Vectors indicate correlation of DCA axis with Ellenberg indicator values and calibrated strategy types for stress and disturbance (vector length indicates the strenght of the correlation). Abbreviations see Table 1.

of base-rich sites with a mesic or highly variable moisture regime. A comparison of VE and VPs revealed similar results. In contrast, the comparison of VPu and VE showed a strongly asymmetric distribution of indicators. While VPu had numerous positive indicators, most of them characteristic of regularly managed meadows, there were quite few and only rather weak positive indicators in the case of VE. The positive indicators of VE included some tall forbs and woody chamaephytes typical of low management intensity or even fallow conditions, such as *Rubus caesius*, *Filipendula ulmaria*, and *Genista tinctoria*.

Gradient analysis

DCA ordination (Fig. 1) displayed a distinct separation of samples with VE and VPu, and those with VPs along the first DCA axis. The sample scores of DCA axis 1 were strongly correlated with the Ellenberg indicator values for moisture and soil-reaction and to a lower degree with those for temperature, continentality, nutrients and mowing compatibility (Table 4). Such a distinct separation of the violet species was not observed along the second DCA axis, with only VE showing a slightly stronger correlation. Indicator values for mowing compatibility, nutrients, stress and disturbance loaded strongly on DCA axis 2, and to a lower extent the proportion of annuals and woody chamaephytes per relevé were also correlated with this axis. Along the third DCA axis, there was no separation at all of the three violets. Indicator values for competitiveness, stress, continentality and nutrients were strongly correlated with this axis.

Table 4. Spearman rank correlations between DCA axes 1–3 and weighted mean Ellenberg indicator values, proportion of C-S-R strategy types and the occurrence of the violet species. High correlation coefficients (> 0.3) are given in bold; * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$, ns = not significant.

	Axis 1	Axis 2	Axis 3
Light	0.259***	**0.366*****	-0.127*
Temperature	**-0.383*****	0.063 ns	0.004 ns
Continentality	**-0.354*****	-0.005 ns	**0.529*****
Moisture	**0.856*****	0.004 ns	**0.328*****
Soil reaction	**-0.616*****	**0.338*****	0.296***
Nutrients	**-0.498*****	**-0.445*****	**0.505*****
Mowing compatibility	**-0.465*****	**-0.681*****	-0.022 ns
Competition	-0.197***	-0.026 ns	**0.613 *****
Stress	0.257***	**0.514 *****	**-0.510 *****
Disturbance	0.177**	**-0.723 *****	0.023 ns
% annuals	-0.248***	**-0.337 *****	-0.110 ns
% chamaephytes	-0.055 ns	**0.405 *****	0.054 ns
VPs	**0.751*****	-0.241 ***	-0.080 ns
VPu	**-0.546*****	-0.087 ns	0.065 ns
VE	**-0.410 *****	**0.318 *****	0.049 ns

Classification

The TWINSPAN classification resulted in eleven clusters (Tables 5 and 6). Clustering quality was checked by MRPP, revealing significant floristic differences among clusters ($P < 0.001$) and a high within-group agreement ($A = 0.243$). This was in accordance with the evaluation of the TWINSPAN tree by indicator species analysis, which confirmed many significant indicators for clusters at different hierarchical levels (Table 5). MRPP revealed significant ecological differences among clusters with respect to Ellenberg indicator values ($P < 0.001$, $A = 0.302$) and Grime strategy types ($P < 0.001$, $A = 0.198$). Hierarchical levels of clustering, along with information on syntaxonomy, synecology and management, are summarized in Table 6.

In general, clusters displayed a distinct separation of the three violets by habitat. Strongholds of VE included irregularly disturbed ruderal forest edges (Cluster 1) and fallows (Cluster 2) or very extensively managed stands of *Molinion* meadows (Cluster 3), where an overlap with VPu (Cluster 2) could be observed. However, VPu was most often found in fairly eutrophic, regularly managed *Cnidion* meadows with a comparably dry but highly variable moisture regime (Clusters 4 and 5). In wet *Cnidion* meadows and corresponding moist tall-sedge stands and flood swards (Clusters 6 and 7) VPu was almost completely replaced by VPs. A stronger overlap of both species could only be observed in cluster 6. VPs was the only violet species found in moist, meso- to oligotrophic fen and swamp grassland communities (Clusters 8–10), which exist under more-or-less strongly acidic site conditions.

DISCUSSION

Ecological profiles of the violets

The high degree of ecological similarity that had been supposed by many authors (Ellenberg et al. 1992, Quinger 1993, Oberdorfer 1994) was not supported by the

Table 5. Indicator species analysis of the TWINSPAN tree. For each species the percentage frequency within a cluster is given (0 not shown). The first column shows the maximum indicator value (IV, grey shaded clusters) over all clusters. All indicator values shown in the table are according to Monte Carlo permutation tests significant at $P < 0.001$. Species with non significant or low indicator value (IV max. < 20) are not shown. Allegedly symmetric indicators (IV max. > 55) are printed in bold. Mean Ellenberg indicator values and mean percentage proportions of Grime strategy types for clusters are given in the header.

Cluster		1	2	3	4	5	6	7	8	9	10	11
No. of relevés		14	28	28	41	47	26	31	40	49	17	14
Moisture		5.5	6.7	5.9	6.0	5.5	6.9	6.7	7.5	7.5	8.4	8.1
Soil reaction		7.4	7.6	7.2	6.9	6.7	6.7	6.2	5.3	5.1	4.5	7.1
Nutrients		5.5	3.8	4.3	5.0	4.9	5.4	5.4	4.0	3.1	4.5	4.9
Mowing		4.7	4.4	5.8	6.0	5.9	5.9	6.6	5.6	4.3	3.0	3.8
Competition		50	45	40	43	40	47	45	40	33	35	58
Stress		27	37	33	25	30	20	18	23	45	45	30
Disturbance		23	18	27	32	30	33	37	37	22	20	12
	IV											
Viola elatior	71	93	50	96	12	13	4	13				7
Viola pumila	58	14	57	7	90	79	31	3				7
Viola persicifolia	86			4		13	69	84	100	100	100	86
Galium aparine	74	86	4		7	9	8					7
Rubus caesius	57	79	29	4	12	9	8					21
Geum urbanum	57	57				2						
Crataegus monogyna	53	64	11		29	9				2		
Cornus sanguinea	40	43			5	4						
Convolvulus arvensis	37	50	4	18	10	6		10				
Agrimonia eupatoria	34	50	18	14	22	4		3				
Urtica dioica	33	36			2	2	12	3				21
Prunus spinosa	33	36	4		2	2						
Quercus robur	28	43	7			6		3		6	35	7
Vincetoxicum hirundinaria	22	29	21		2							
Fraxinus excelsior	21	36			10	17	15		3			
Inula salicina	76	14	82	79	29	28	8					29
Carex tomentosa	52	7	54	57	39	9	12					
Genista tinctoria	32		46	21								21
Cirsium tuberosum	32		11	54								
Carex flacca	31	7	32	32	10							14
Briza media	26		11	43		6				2		
***Galium verum* agg.**	56	21	50	89	61	45	8	13	5			
Sanguisorba officinalis	45	7	86	39	61	57	27	13	8	14	6	36
Silaum silaus	42		50	68	39	32	8	10				
Colchicum autumnale	39		14	57	17	62	4					
Serratula tinctoria	37		50	7	66	45	38	3		2		29
Galium boreale	30		11	25	12	68	15	6				
Ranunculus polyanthemos agg.	26	21	39		34	30						
Allium angulosum	20		54	25	20	4	19		3	4		7
Centaurea jacea	59		14	89	66	55	27	13	5	33		7
Ranunculus acris	58	7		86	49	66	42	6	20	45		
Festuca pratensis	54		11	82	51	57	38	29	20	8		
Plantago lanceolata	50		21	71	59	62	54	19	23	31		

Cluster		1	2	3	4	5	6	7	8	9	10	11
No. of relevés		14	28	28	41	47	26	31	40	49	17	14
Dactylis glomerata	46	43	25	61	49	47	12	3				
Trifolium pratense	40	7		36	51	43	35	6	15	10		
Arrhenatherum elatius	39	36		50	37	45		6	3			
Achillea millefolium agg.	39	7	11	21	46	57	19	16	3	8		
Lotus corniculatus	38		21	75	39	34	12	26	3	2		14
Leucanthemum vulgare agg.	37		11	54	59	38	35	29		8		
Galium album	26	7	7	25	20	43	12			2		
Veronica chamaedrys	33	7		7		45						
Fragaria viridis	32				2	32						
Vicia hirsuta	22				7	26	4					
Campanula patula	20			4	5	36	8	6	3	2		
Carex praecox	43	7			17	47	54	13	3			
Vicia tetrasperma	31			4	5	43	31	3				
Myosotis ramosissima	22					30	12		3			
Stellaria graminea	20					23	27	3	3	4		
Ranunculus auricomus agg.	38	7			7	53	35	42	28	8		
Anthoxantum odoratum	37			7		34	23	16	70	43	29	
Galium palustre agg.	50		21	7	10		42	48	55	45	88	57
Lythrum salicaria	45		32	21	12	6	46	16	40	86	76	64
Mentha arvensis	45		4		10	4	42	35	52	53	59	29
Iris pseudacorus	33		7	4	5		31	13	40	51	24	43
Carex acuta	32		14		2	9	69	26	43	35	12	14
Phalaris arundinacea	31		14	11	17		69	48	38	29	12	64
Potentilla anserina	31	7	11		22	6	35	58	35	29	47	7
Ranunculus repens	75	7	25	61	66	30	85	90	95	67	6	29
Poa palustris	42	7	4		10	9	65	48	25	2		7
Trifolium repens	40	7		18	10	13	27	65	38	10	6	
Carex vulpina	33						62	32	15			
Stellaria palustris	32						23	32	40	12		
Rumex crispus	26			21	24	9	54	45	5			
Veronica serpyllifolia	23					17	23	39	13			
Myosotis scorpioides agg.	21		4				23	16	30	10	6	7
Senecio aquaticus	20			11	5			39	23	10		
Gratiola officinalis	46					11	50	10	3			
Plantago major subsp. *intermedia*	39						19	45	5			
Alopecurus geniculatus	34							35	5			
Poa trivialis	34	29	11	36	27	9	31	77	18	2		
Ranunculus flammula	72						4	16	83	76	41	
Agrostis canina	54							26	55	57	88	7
Hydrocotyle vulgaris	52								10	69	100	
Galium uliginosum	41			4				3	15	69	24	14
Juncus effusus	39					2	4	6	48	45	6	
Peucedanum palustre	38								10	49	71	
Cirsium palustre	35			4				3	28	47	24	
Juncus conglomeratus	34			4			4	3	33	37	29	7
Lotus uliginosus	31						4	3	20	49	6	
Carex nigra	29								30	24	41	

Cluster		1	2	3	4	5	6	7	8	9	10	11
No. of relevés		14	28	28	41	47	26	31	40	49	17	14
Salix cinerea	28					2			10	43	35	14
Frangula alnus	27		14						5	45	47	7
Caltha palustris	22							3	25	27	12	14
*Potentilla palustri*s	20								5	35	12	
Juncus acutiflorus	68								8	2	71	
Lycopus europaeus	58			4			4	3	13	33	71	14
Cirsium dissectum	51			4	4						22	65
Parnassia palustris	47										47	
Eriophorum angustifolium	43								3	12	47	
Calamagrostis canescens	43								10	22	47	
Carex flava agg.	36								13	12	53	
Erica tetralix	32									4	35	
Juncus bulbosus	23								10	6	35	
Viola palustris	23								3	2	24	
Euphorbia palustris	68		14		10	2						86
*Carex acutiformi*s	43	7	21		15	2	4		8	20	12	71
Gentiana pneumonanthe	29		4			4				16	18	36
Scutellaria galericulata	20								5	18	6	29
Carex panicea	67		46	18	17	2			20	84	82	57
***Molinia caerulea* agg.**	56		57	11	5	17		3	8	80	71	21
Lysimachia vulgaris	49		64	18	39		23	26	40	31	94	93
Succisa pratensis	45		43	36	5	9				63	41	21
Thalictrum flavum	43	7	43	29	15	2	8	19	23	59	24	86
Potentilla erecta	41		14	4		4		3	8	55	71	21
Phragmites australis	35	7	21		7	2				22	76	64
Silene flos-cuculi	48			11	39	51	77	58	78	24		7
Rumex acetosa	42	7	4	4	39	81	35	39	50	39		
Deschampsia cespitosa	40		36	32	59	23	46	61	55	63		7
Lysimachia nummularia	39	29	18	43	51	49	77	45	38	29	6	
Cardamine pratensis agg.	39		7	25	7	47	81	35	65	31	6	
Holcus lanatus	30			46	10	4	8	23	65	55	6	
Prunella vulgaris	29	21	7	43	54	19	15	6	23	59	6	14
Potentilla reptans	64	43	54	61	93	53	81	65	5		6	14
Elymus repens	55	43	29	43	80	57	38	71				
Glechoma hederacea	36	29	7	32	46	28	38	74	10	4		7
Alopecurus pratensis	79	21	11	29	85	83	96	87	45	8		
Lathyrus pratensis	55	14	32	39	76	77	50	45	8		6	7
Taraxacum officinale agg.	52	57	14	50	56	60	69	77	43	31	35	
Cirsium arvense	48	21	32	4	39	62	81	58	15		6	64
Poa angustifolia	41	29	21		78	23	19	48	5			
Cnidium dubium	38		14		17	55	65	52	5	2	12	
Veronica arvensis	33			4	7	64	31	26	5			
Cerastium holosteoides	33			11	34	45	38	29	13	8		
Carex hirta	29	7	4	25	32	47	38	3	3			
Equisetum arvense	28	21	11	11	51	36	15	6		4	29	

present study. In contrast, the numerical analyses revealed a distinct separation of the three flood-meadow violets along environmental gradients.

Most striking were the differences between VPu and VE, and VPs, especially in terms of moisture regime and soil reaction (Table 3 and 5; Fig. 1), which are in accordance with independent measurements of soil properties in other studies (BALÁTOVÁ-TULÁČKOVÁ & HÜBL 1974, GÖBEL 1995, BURKART 1998, HÖLZEL 1999, LEYER 2002). The confinement of VE and VPu to base-rich sites might be the main reason for their entire absence from the diluvial northern Central European lowland, where non-calcareous, fairly acidic sediments ($pH < 6$) are predominant, even under alluvial conditions (BURKART 1998, LEYER 2002).

Differences between VPu and VE mostly concern management intensity, with VE preferring irregularly disturbed edge situations and avoiding early and/or regularly mown meadows. While MRPP at the species level detected no significant differences (Table 3), DCA ordination, TWINSPAN clustering and indicator species analysis revealed clear support for this assumption. In this context the application of different complementary ordination and classification techniques proved to be particularly useful. Differences in management intensity are sometimes reflected better by the occurrence of individual species than by total floristic composition, especially in early stages of succession after abandonment or along ecotones between meadows and forest edges. Tall growth seems to be a competitive advantage for VE to survive at sites with low or irregular disturbance, however this is paid for by a low mowing compatibility.

Although many authors emphasize a strong confinement to nutrient-poor habitats (ELLENBERG et al. 1992, QUINGER 1993), an unexpectedly broad range of site conditions was revealed in this study in terms of soil nutrient status and productivity. In comparatively fertile alluvial sites (mostly alliance *Cnidion*; Table 5 and 6, Clusters 4–7), the violets crucially depend on regular disturbances by mowing or grazing, which weaken strong competitors, while in comparatively unproductive, nutrient-poor sites (mostly alliance *Molinion*) they may persist for a long time even under fallow conditions (Table 5 and 6, Clusters 2, 9, 10, 11). In the forest edge community with VE (Cluster 1), disturbance comprises occasional anthropogenic scarring of the topsoil. This situation was almost perfectly reflected in the distribution of Grime's C-S-R-types in ordination space and among clusters (Fig. 1, Table 5). The importance of the ruderal strategy was positively correlated with increasing nutrient availability, mowing compatibility and the proportion of annuals, whereas the stress-tolerant strategy showed the opposite reaction. In contrast, the comparison of C-S-R types at the species level revealed no significant differences between the three violets (Table 3), indicating that they occupy comparable functional niches but in different plant communities. As weak competitors, the violets seem to be generally facilitated by turf disturbances. Sudden emergence following major disturbances (e.g. sod-cutting) after long periods of absence from established vegetation has been reported by several authors (PULLIN & WOODELL 1986, QUINGER 1993, CROFT & PRESTON 1996, HÖLZEL 1999, ROMAHN & KIECKBUSCH 2001, WEEDA 2002). Long-term persistent seed banks, rapid growth and flexible seed production by cleistogamous flowering are biological properties that enable the violets to colonize temporary gaps with low competition. Such periodically open site conditions are most likely to occur in continental lowland flood-meadows, where annual and inter-annual variations of

Table 6. Descriptions of plant communities as classified by TWINSPAN and predominant *Viola* species within clusters. Syntaxonomical, synecological and management characteristics are derived from Ellenberg indicator values for clusters and indicator species groups (Table 5) as well as from additional information in original papers.

Cluster number	TWINSPAN hierarchy	Syntaxonomy	*Viola*	Synecology / mangement
a) Alluvial sites with highly fluctuating watertable				
1	0000	*Artemisietea*	VE	Nitrophilous tall-forb stands along irregularly disturbed alluvial forest edges
2	0001	*Molinion*	VE/VPu	Unmanaged alluvial meadow fallows at oligotrophic, calcareous sites with a highly variable moisture regime
3	00100	*Molinion*	VE	Like 2 but more mesotrophic with late or irregular mowing or extensive pasture
4	00101	*Cnidion* (dry)	VPu	Regularly mown alluvial meadows at calcareous, meso- to eutrophic sites with a highly variable moisture regime
5	0011	*Cnidion* (dry)	VPu	Like 4 but at non calcareous, slightly acidic and drier, mostly sandy sites
6	010	*Cnidion* (wet)/*Magnocaricion*	VPs/VPu	Wet to moist alluvial meadows and tall-sedge stands at eutrophic non calcareous alluvial sites, extensively or irregularly mown
7	011	*Cnidion* (wet)/*Agropyro-Rumicion*	VPs	Wet to moist alluvial meadows and flood swards at eutrophic non calcareous alluvial sites, meadow pastures or exclusively grazed
b) Fen and gley sites with a more constant watertable				
8	100	*Calthion*/*Agropyro-Rumicion*	VPs	Mesotrophic wet meadows and flood swards on acidic peat or gley soils with permanently high groundwater table, regularly mown
9	101	*Junco-Molinion*	VPs	Like 8, but at oligotrophic sites with very late or irregular mowing
10	110	*Caricion fuscae*	VPs	Like 9, but more damp, acidic and mostly unmanaged
11	111	*Filipendulion*/*Phragmitetea*	VPs	Unmanaged damp, mesotrophic tall-forb and reed stands at mostly calcareous alluvial sites, recently only submerged by clear ascending groundwater

flooding and periods of drought trigger considerable spatial and temporal vegetation dynamics along elevation gradients (DISTER 1980, BURKART 1998, HÖLZEL 1999, LEYER 2002). Adaptation to this particular disturbance regime of flood meadows may be the main reason for the conspicuous confinement to large river corridors in Central European lowlands, which is a distribution pattern observed in many other plant species (KORSCH 1999, BURKART 2001). Besides flooding dynamics, climatic conditions causing summer drought seem to be essential in case of VE and VPu, an assumption supported by the restriction of these species to regions with low precipitation (< 600 mm) and high summer temperatures (monthly average in July > 17 °C, KORSCH 1999). In continental eastern Europe, where such climatic conditions are ubiquitous, the confinement to large lowland river corridors disappears (BURKART 2001) and both species may be found in steppe and forest-steppe habitats, giving credence to their "xeric origin" (HEGI 1975).

VPs is the only species that is not confined to alluvial habitats with a high variability in soil water potential. It is equally or even more often found on peaty or mineral groundwater soils in fen and swamp areas, not directly influenced by fluvial dynamics (Table 5 and 6). However, under these more stable conditions VPs is restricted to relatively nutrient-poor habitats with low productivity (*Molinion* meadows, short-sedge and rush communities). Equally, the confinement to large river corridors with warm and dry climatic conditions is less pronounced, which is reflected by a more northern distribution (HULTÉN & FRIES 1986) with single outposts even under strongly oceanic conditions such as in Norway (RØREN 1993), England (PULLIN & WOODELL 1987) and Ireland (PULLIN 1986).

Judging from our results one can conclude that all three violets follow the same S/R strategy depending on the productivity of habitat, while ecological separation is mostly caused by the environmental gradients, moisture and soil reaction along with the biotic trait resprouting ability. Beside the high degree of selfing and cleistogamous flowering, separation by habitat may be another reason why hybridization among them and with other violet species such as *Viola canina* rarely occurs – even in areas where the violets live closely together (RØRREN et al. 1994, KIRSCHNER & DANIHELKA 1997).

Phytosociological databanks – a potential source of sound ecological information?

Through the analysis of phytosociological relevés from the entire Central European range of the three flood-meadow violets it was possible to outline a picture of habitat preferences and ecological behaviour of these poorly-studied species. However, basic problems related to the use of phytosociological relevés in databanks as a source of ecological information should not be overlooked.

One major problem is that easily accessible databanks still do not exist in many countries, even those such as Germany with a long phytosociological tradition, recent vegetation surveys and tens of thousands of potentially available relevés (EWALD 2001). Great effort and investment are needed to make these data readily available to the scientific community and to practitioners dealing with nature conservation or landscape planning issues. Individual compilation and editing of relevés together with the standardization of taxa, remains a laborious and time-consuming process. The diffusion of standard phytosociological databank software such as TURBOVEG (HENNEKENS & SCHAMINÉE 2001) could ease such work in the future.

Although the high level of similarity in sampling procedure is certainly one of the strongest points of the phytosociological approach, the actual degree of standardization is mostly limited to a complete list of vascular plants and the common use of a traditional or slightly modified Braun Blanquet cover/abundance scale. Even the obligatory points of the impressive template for phytosociological relevés recently given by MUCINA et. al. (2001) are frequently not fulfilled by many authors. As experienced in this study, cryptogams as well as site-related metadata are often poorly and inconsistently documented.

A more fundamental problem relates to the representativeness of phytosociological relevés. As CHYTRÝ (2001) pointed out, phytosociologists tend to record species-rich, “well developed” and “homogeneous” stands, while species-poor types, ecotones and “disturbed” sites are largely neglected, although these may be predominant in certain landscapes or contain highly specialized rare and endangered species. For the analysis of ecological preferences of a certain species this could mean that important habitats and sections of ecological gradients may be completely overlooked, while others could be over-represented. In the present study, for instance, not a single relevé of the ruderal forest edge community with VE was found in the existing phytosociological literature, although this is undoubtedly one of the most important or even the predominant habitat type of this species in Central Europe (QUINGER 1993, KIRSCHNER & DANIHELKA 1997, HÖLZEL 1999). One can assume that a better representation of this habitat type in the dataset would probably have revealed a higher shade tolerance of VE in comparison with VPu and VPs. Based on the earlier phytosociological literature (e.g. OBERDORFER 1983), one might get the impression that the three violets are more or less confined to nutrient-poor habitats, an assumption that is also supported by the Ellenberg indicator values. This analysis shows that to be no more than a sampling artefact, however, since eutrophic flood-meadows were simply neglected by Central European phytosociologists until the mid 1980s. As in the case of species richness estimations from phytosociological relevés (CHYTRÝ 2001) or the unification of national classification approaches (BRUELHEIDE & CHYTRÝ 2000), biased data are obviously the most serious limiting point.

Regardless of the arising methodical problems, the present study clearly establishes that phytosociological databanks may be utilized as a substantial source of ecological information on species. Comparable studies could for example provide quick and large-scaled overviews of habitat preferences and basic underlying ecological gradients in the distribution of rare and endangered species. Such information may be essential as a starting point for further detailed ecological and population biological research on a particular species or to identify key habitats for species of international conservation concern, such as those in the European Union Habitats Directive. To achieve the goal of funding and maintaining phytosociological databanks it is vital that their main purpose be extended and connected to other fields of ecological research beyond national and international vegetation surveys (AUSTIN 1999, EWALD 2001).

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