

Spring fen *Scheuchzerio-Caricetea nigrae* in the Polish Western Carpathians – vegetation diversity in relation to soil and feeding waters

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Abstract

The species composition of vegetation associated with the Carpathian fens primarily depends on the type of water present and the hydrological feeding of the soils that occur there. These, in turn, shape the fertility of the fens. Those with typically formed *Carici-Agrostietum caninae* and *Valeriano-Caricetum flavae* fundamentally differ in the properties of their soils and feeding waters. These include differences in mineral content, pH, CaCO₃ levels, degree of peat decomposition, electrical conductivity and oxygenation of the waters that feed the fens. *Carici-Agrostietum caninae* is a homogenous plant association adapted to extreme habitat conditions. It is characterized by a very narrow range of essential soil and feeding water parameters. *Valeriano-Caricetum flavae* is a highly diverse association. Considerable diversity both in terms of plant species and vegetation structure reflects very wide ranges in the properties of soil and feeding water. Vegetation patches of transitory character were also identified. These contained plant species characteristic of both associations. The character of the vegetation depends mainly on fen soil pH and the degree of mineralization of the feeding waters. It is only these parameters that allow intermediate patches to be clearly distinguished. The degree of peat decomposition, mineral content and water oxygenation all differ for *Carici-Agrostietum caninae* and *Valeriano-Caricetum flavae*, whereas the values for intermediate patches display a range of parameters typical of both investigated associations. Consequently, vegetation present in these patches reflects to a greater or lesser extent one of the two analyzed plant associations.

Keywords: *Carici-Agrostietum caninae*, *Valeriano-Caricetum flavae*, fens, soil and water properties, Western Carpathians, Poland

Introduction

The accumulation of organic matter derived from plants growing in fens results in the formation of peat in fen soils subjected to very wet conditions. Depending on the type of hydrological feeding present, fen waters vary greatly in terms of their mineral and ion composition [1,2]. As water flows through organic matter deposited during the formation of peat, it becomes enriched with minerals and thus, contributes to soil fertility. Fens of this kind can be divided into two groups, based on the type of hydrological feeding present. Firstly, soligenic fens are rich fens that form on a lime substratum, or moderately rich fens that develop on flysch bedrock of sub-Magura and mid-Magura layers, or on glacial deposits. The second group consists of poor fens that are fed by precipitation

waters, and these develop on a matrix lacking in carbonate. In the Polish Western Carpathians these are usually colonized by vegetation characteristic of *Valeriano-Caricetum flavae* and *Agrostietum caninae* associations [3]. Rich soligenic fen soils are characterized by their high degree of mineralization and the proportion of calcium cations involved in general mineralization. The concentration of calcium cations and the degree of mineralization of poor fen waters that display an ombrogenic type of feeding is many times lower [2,4]. On the basis of field investigations, a third group of fens was identified. Physical and chemical properties of their soils and waters were described as intermediate. These fens are called mesotrophic fens by Kornaś and Medwecka-Kornaś [5].

The aim of this work is to demonstrate that differences in the floristic composition of these plant communities reflect the physicochemical properties of the soil on which they grow.

Investigated area

Detailed analyses conducted during the period 2001–2006 investigated 20 selected fens distributed throughout the area of the Western Carpathians (the Tatra Mountains, the Subtatra Trough, the Spisko-Gubałowskie Foothills, the Pieniny Mountains, the Orawa-Nowy Targ Basin, the Gorce Mountains, Działy Orawskie Mountains, and the Babia Góra Range; Fig. 1). These fens were located at altitudes of between 530 and 925 m a.s.l., which, based on vegetation type, corresponds to a lower

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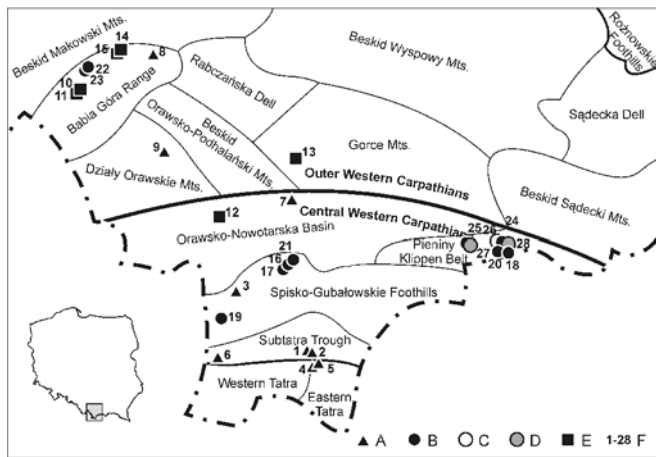


Fig. 1 Location of the investigated spring fens against the background of physiographic division of the Polish Carpathians after Kondracki [26]. A – *Carici-Agrostietum caninae*. B – *Valeriano-Caricetum flavae*. C – *Caricetum davallianae*. D – *Eleocharitetum pauciflorae*. E – intermediate patches. F – patch numbers: 1 – Murzasichle 2; 2 – Murzasichle 1; 3 – Podczerwone; 4 – Palenica Pańszczykowa, central part; 5 – Palenica Pańszczykowa, lower part; 6 – Polana Szczurówka; 7 – Pod lasem Grel; 8 – Zawoja Mosorne; 9 – Zubrzyca Górna; 10 – Norczak 1; 11 – Norczak 2; 12 – Baligówka; 13 – Pod Klikuszową; 14 – Markowe Rówienki 1; 15 – Markowe Rówienki 2; 16 – Maruszyna, upper part; 17 – Maruszyna, central part; 18 – Za Stronią below water seepage; 19 – Dzianisz; 20 – Młaka Franka; 21 – Maruszyna, lower part; 22 – Barańcowa 1; 23 – Barańcowa 2; 24 – Za Stronią above water seepage; 25 – Majerz; 26 – Roplichta; 27 – Majerz, along watercourse; 28 – Za Stronią, central part.

mountain forest zone [6]. Fens varied in size from several dozen to several hundreds of square meters. In most cases, fens formed enclaves within meadows, and were used in a similar manner. The vegetation was mowing at least once every 3–4 years. Some adjoined pastures were occasionally grazed.

Material and methods

Between one and three soil pits were made on each of the fens selected for analysis, in order to determine the basic morphological, chemical and physical properties of their soils. Piezometers were installed at the site of the soil pits, and water was sampled every month throughout the period March–December. Rich fens were investigated during 2000–2001, poor fens during 2003–2004 and mesotrophic fens during 2005–2006. The following criteria were measured for soil samples taken from investigated fens: pH was measured using the potentiometric method in water and 1M KCl, mineral content in organic horizons as a percentage weight loss following heating at 550°C [7], peat decomposition was assessed by means of the ten-degree von Post scale [8] and calcium carbonate content was calculated using the Scheibler method. The degree of oxygenation of water samples was measured by means of a CO-315 oxygen meter, together with electrical conductivity [9].

In order to identify and characterize plant associations, 27 phytosociological relevés were made in accordance with the method of Braun-Blanquet. The analyses were conducted during 2003–2006, but one phytosociological relevé made

in 2000, was also included. Depending on fen size and the diversity of its vegetation, one, two, and in some cases, even three phytosociological relevés were investigated for each fen. The investigated patches were selected so that the soil pit of each was at the center. In the case of larger, but homogenous patches, two or three closely situated soil pits occurred within a single phytosociological relevé.

Identification and distinction between plant communities followed Matuszkiewicz [3], Ratyńska et al. [10], Chytrý [11] and others (e.g. [5,12–17]). The syntaxonomic division of communities followed Ratyńska et al. [10]. Names of vascular plants and bryophytes followed Mirek et al. [18] and Ochrya et al. [19], respectively.

Phytosociological relevés were grouped using classic methodology and the sets obtained were compared with the results of hierarchical numerical classification [20–22]. Hierarchical numerical classification was conducted twice: 1 – based on the species present (0–1 scale), where dissimilarities between the relevés were computed using the Jaccard formula; and 2 – on the basis of coverage by species, using the 1–6 cover scale of Braun-Blanquet, where “+” = 0.5. In this case Manhattan was used. For trees and shrubs, the presence and degree of cover by individual species was given separately for each plant layer. Unweighted pair group method with arithmetic mean (UPGMA) was used for grouping. Differences in properties of soils and waters were determined by means of the Kruskal–Wallis test.

Results

Plant communities of the analyzed fens

Vegetation overgrowing fens in the Polish Western Carpathians comprises the *Scheuchzerio-Caricetea fuscae* class and consists of low sedge waterlogged meadows abundant in bryophytes and immersive low and transitory peatbogs [3].

The investigated fens can be divided into two alliances: *Caricion fuscae* and *Caricion davallianae*, each belonging to the *Caricetalia fuscae* order [10]. Patches of intermediate character were often observed among rich spring fens (*Caricion davallianae* alliance) [12]. When water relations were disturbed (e.g. by an irrigation system) these associations became transformed into meadow communities, mainly wet meadows of the *Molinietalia* order.

The investigated patches were divided into three groups (Tab. 1), based on species composition:

(i) Poor fens (*Caricion fuscae* alliance), represented by *Carici-Agrostietum caninae* association.

The mean number of species in the investigated patches was 25.6 (range = 15–33). The characteristic plants were *Agrostis canina*, *Carex canescens* and *C. echinata*. Species typical of the *Caricion fuscae* alliance – *Viola palustris*, *Polytrichum commune*, *Juncus filiformis* and *Ranunculus flammula* were also very numerous. Of those species characteristic of the *Caricetalia fuscae* order and the *Scheuchzerio-Caricetea fuscae* class, the most frequently encountered were *Carex nigra* and *Eriophorum angustifolium*. Plants typical of other biotopes usually consisted of a small number of species. The moss layer was usually well formed (50–100% cover in the investigated patches) *Polytrichum commune* and *Sphagnum angustifolium* were the most numerous species. *Carici-Agrostietum*, a homogenous plant association (Fig. 2), was clearly distinguishable from the surrounding plant communities.

(ii) Rich fens (*Caricion davallianae* alliance), were represented mainly by the *Valeriano-Caricetum flavae* association. One phytosociological relevè should be classified as *Caricetum davallianae*, two others as *Eleocharitetum pauciflorae* [11].

The vegetation of these fens was abundant in species, (mean number of species = 37; range = 19–48). *Valeriano-Caricetum flavae* characteristic species, which occur here quite permanently, are *Valeriana simplicifolia*, *Eriophorum latifolium*, *Carex flava* and the much rarer *C. lepidocarpa*. *Carex davalliana* dominated the patch classified as *Caricetum davallianae*. However, it was present in much smaller numbers in the remaining patches. *Eleocharis quinqueflora* and *Triglochin palustre* grew exclusively in *Eleocharitetum pauciflorae* patches. Species characteristic of the *Caricion davallianae* alliance, such as *Epipactis palustris*, *Dactylorhiza majalis* and *Carex flacca* were numerous. Of those species characteristic of the *Caricetalia fuscae* order and *Scheuchzerio-Caricetea fuscae* class, the most frequently encountered were *Carex panicea* and *C. nigra*. Plants primarily characteristic of meadow associations (*Briza media*, *Calliargonella cuspidata*, *Caltha laeta*, *Cirsium palustre*, *C. rivulare*, *Climacium dendroides*, *Crepis paludosa*, *Cruciata gabra*, *Equisetum palustre*, *Galium uliginosum*, *Linum catharticum*, *Myosotis palustris*, *Plagiomnium elatum*, *Potentilla erecta*, *Ranunculus acris*) were numerous represented and even dominated in many relevès. Some rushes species (*Equisetum fluviatile*, *Carex paniculata*) were also frequent in these associations. The moss layer was very well developed, and displayed 30–100% cover, depending on the degree of hydration. Species of wet habitats were the most frequent whereas species characteristic of the *Scheuchzerio-Caricetea fuscae* class appeared to abort in 50% of the investigated patches. A characteristic phenomenon indicating considerable water movement was the shared presence of both spring species (*Montio-Cardaminetea* class) and species characteristic of *Caricion lasiocarpae* (i.e., *Calliargon giganteum*, *Tomentypnum nitens*). These are indicators of local acid conditions and occurred only occasionally.

Dominant among rich fens, *Valeriano-Caricetum flavae* is a heterogeneous, strongly diversified association (Fig. 2), forming a number of variants. Different species dominated in individual patches, and plants recognized as characteristic for the described association, alliance, order, or some plants typical of wet meadows or rushes plants were often the dominant taxa.

(iii) Patches of transitional character with species characteristic of both identified groups.

Patches classified as intermediate were among those which were most abundant in species, the mean number of species being 38.8, with individual phytosociological relevès displaying a range of 26–51. They are identified by the presence of species characteristic of the *Carici-Agrostietum caninae* association and the *Caricion fuscae* alliance (*Agrostis canina*, *Carex echinata*, *Viola palustris*), and those typical of the *Valeriano-Caricetum flavae* association, and the *Caricion davallianae* alliance (*Carex flava*, *Dactylorhiza majalis*, *Epipactis palustris*, *Eriophorum latifolium*, *Valeriana simplicifolia*). As in the case of *Valeriano-Caricetum flavae*, species typical of other communities, primarily meadow and rushes communities, were present in some numbers. The moss layer showed great diversity and displayed a cover range of 10–90%. Species characteristic of both moist and wet habitats were present here, including both species typical of rich fens and springs. A characteristic feature was the small overlap of species characteristic of the *Caricion lasiocarpae* alliance (*Calliargon giganteum*, *Sphagnum teres*, *S. warnstorffii*).

Tab. 1 Plant communities of spring fens (*Scheuchzerio-Caricetea nigrae*).

Number of relevés	I	II	III	1–28
	1–9	10–15	16–28	
Ch. <i>Caricion fuscae</i>				
<i>Carex echinata</i>	V (+3)	V (+)	I (+-1)	III
<i>Agrostis canina</i>	V (+3)	I (1)	I (+)	II
<i>Viola palustris</i>	IV (+-3)	I (1)	I (+)	II
<i>Carex canescens</i>	IV (+-3)	-	-	II
<i>Polytrichum commune</i>	III (2-5)	-	-	I
<i>Juncus filiformis</i>	III (1-2)	-	-	I
<i>Ranunculus flammula</i>	III (+-2)	-	-	I
Ch. <i>Caricion davallianae</i>				
<i>Valeriana simplicifolia</i>	I (+)	IV (+-1)	V (+-4)	IV
<i>Dactylorhiza majalis</i>	I (+)	IV (+-1)	IV (+-2)	III
<i>Epipactis palustris</i>	-	I (1)	V (1-3)	III
<i>Eriophorum latifolium</i>	-	III (+-1)	IV (+-3)	III
<i>Carex flava</i>	-	III (+-1)	III (+-2)	II
<i>Carex flacca</i>	-	-	IV (+-2)	II
<i>Carex lepidocarpa</i>	II (+)	I (+)	I (1)	I
<i>Pinguicula vulgaris</i>	-	I (+)	II (+-1)	I
<i>Bryum pseudotriquetrum</i>	-	I (+)	I (2)	I
<i>Parnassia palustris</i>	-	I (+)	-	I
<i>Carex davalliana</i>	-	-	II (+-4)	I
<i>Eleocharis quinqueflora</i>	-	-	II (1-2)	I
<i>Triglochin palustre</i>	-	-	II (+)	I
<i>Dactylorhiza incarnata</i>	-	-	I (1)	I
<i>Polygala amarella</i>	-	-	I (+)	I
Ch. <i>Caricetalia fuscae</i>				
<i>Carex nigra</i>	V (1-3)	V (2-3)	III (+-1)	IV
<i>Carex panicea</i>	II (+-2)	V (+-2)	V (+-2)	IV
<i>Epilobium palustre</i>	II (1-2)	III (+)	I (1)	II
<i>Juncus articulatus</i>	I (+)	III (+-1)	II (+-2)	II
<i>Pedicularis palustris</i>	-	I (+)	I (1)	I
<i>Drepanocladus aduncus</i>	-	-	I (3)	I
<i>Veronica scutellata</i>	I (+)	-	-	I
Ch. <i>Caricion lasiocarpae</i>				
<i>Calliargon giganteum</i>	-	II (1-2)	I (+)	I
<i>Sphagnum teres</i>	-	I (1)	-	I
<i>Sphagnum warnstorffii</i>	-	I (+)	-	I
<i>Tomentypnum nitens</i>	-	-	II (+-2)	I
Ch. <i>Scheuchzerietalia palustris</i>				
<i>Sphagnum angustifolium</i>	III (3-5)	I (+)	-	II
<i>Straminergon stramineum</i>	II (3)	I (1)	-	I
<i>Sphagnum fallax</i>	II (1-2)	-	-	I
Ch. <i>Scheuchzerio-Caricetea nigrae</i>				
<i>Hamatocaulis vernicosus</i>	II (1)	II (+-4)	II (+-3)	II
<i>Eriophorum angustifolium</i>	III (+-3)	I (1)	-	I
<i>Limprichtia revolvens</i>	-	-	II (2-3)	I
Ch. <i>Montio-Cardaminetea</i>				
<i>Cardamine amara</i>	-	II (+)	I (+)	I
<i>Palustriella decipiens</i>	-	III (+-4)	I (2-3)	I
Ch. <i>Phragmitetea</i>				
<i>Galium palustre</i>	IV (+-2)	III (+)	II (+-2)	III

Tab. 1 (continued)

Number of relevés	I	II	III	1-28
	1-9	10-15	16-28	
<i>Equisetum fluviatile</i>	II (+-2)	III (+-2)	III (+-5)	II
<i>Poa palustris</i>	-	II (+)	II (+-1)	II
<i>Carex paniculata</i>	-	-	III (1)	II
<i>Carex rostrata</i>	-	I (3)	II (+-2)	I
Ch. Molinietales				
<i>Equisetum palustre</i>	II (+-1)	V (+-3)	V (1-4)	IV
<i>Cirsium rivulare</i>	II (+-1)	III (1-2)	V (1-2)	IV
<i>Caltha laeta</i>	II (+-1)	IV (1-2)	IV (+-3)	III
<i>Myosotis palustris</i>	III (+-1)	V (+-2)	III (+-1)	III
<i>Cirsium palustre</i>	II (+-1)	V (+-1)	II (+-1)	III
<i>Crepis paludosa</i>	I (1)	III (1-3)	III (+-3)	II
<i>Lychnis flos-cuculi</i>	II (1)	IV (+-1)	II (+)	II
<i>Juncus effusus</i>	III (+-3)	II (+-1)	I (+-1)	II
<i>Galium uliginosum</i>	II (+-1)	II (+-1)	II (+-2)	II
<i>Deschampsia caespitosa</i>	III (+-2)	I (1)	I (+)	II
<i>Juncus conglomeratus</i>	IV (+-2)	-	-	II
<i>Scirpus sylvaticus</i>	II (+-2)	II (1)	I (3)	II
<i>Climacium dendroides</i>	II (+)	III (+-1)	II (1)	II
<i>Lysimachia vulgaris</i>	-	I (3)	II (+-2)	I
<i>Angelica sylvestris</i>	II (1)	-	I (+-1)	I
<i>Caltha palustris</i>	-	I (2)	II (+-2)	I
<i>Carex cespitosa</i>	-	I (2)	I (+)	I
Ch. Arrhenatheretalia				
<i>Lotus corniculatus</i>	III (+-2)	I (1)	II (+-1)	II
<i>Galium mollugo</i>	I (1)	I (1)	II (+)	II
Ch. Molinio-Arrhenatheretea				
<i>Ranunculus acris</i>	III (+-1)	II (+)	IV (+-1)	III
<i>Rumex acetosa</i>	II (+)	IV (+-1)	II (+-1)	III
<i>Lathyrus pratensis</i>	I (+)	I (+)	III (+)	II
<i>Prunella vulgaris</i>	-	II (+)	III (+)	II
<i>Vicia cracca</i>	II (+-1)	III (+)	II (+-1)	II
<i>Holcus lanatus</i>	I (+)	II (1)	II (+-1)	II
<i>Juncus inflexus</i>	-	I (2)	II (+-3)	II
<i>Trifolium pratense</i>	I (+)	II (+)	II (+)	II
<i>Lysimachia nummularia</i>	-	-	II (+-1)	I
<i>Mentha longifolia</i>	-	II (+)	II (+-2)	I
<i>Poa pratensis</i>	I (1)	II (+-1)	I (+)	I
<i>Festuca pratensis</i>	I (1)	I (1)	I (+-1)	I
<i>Rhinanthus minor</i>	-	II (+-1)	I (+-1)	I
Ch. Nardo-Callunetea				
<i>Potentilla erecta</i>	IV (+-1)	V (+-1)	V (1-2)	V
<i>Nardus stricta</i>	III (+-1)	I (+)	-	I
<i>Luzula campestris</i>	-	IV (+-1)	-	I
Others				
<i>Briza media</i>	II (+)	V (+-2)	IV (+-2)	IV
<i>Calliergonella cuspidata</i>	II (1-2)	V (+-1)	IV (+-3)	III
<i>Cruciata glabra</i>	-	V (+-1)	IV (+-2)	III
<i>Anthoxanthum odoratum</i>	III (+-3)	V (+-2)	I (+-1)	II
<i>Picea abies</i>	II (+-2)	I (1)	II (+-1)	II
<i>Rhytidadelphus squarrosus</i>	II (1-2)	II (1-3)	II (+-2)	II
<i>Trifolium medium</i>	I (+)	I (+)	II (+-1)	II
<i>Linum catharticum</i>	-	II (+)	IV (+-1)	II
<i>Geum rivale</i>	-	II (+-1)	II (+-1)	II

Relationship between spring fen vegetation, the soil reaction, and electric conductivity of feeding waters

Analysis of the acquired data revealed that both described groups of plant associations, identified on the basis of differences in their floristic composition, occurred in biotopes differing in pH. They also differed in the degree of mineralization of feeding water, as shown by electric conductivity measurements (Fig. 3). These differences were statistically significant (Tab. 2).

Soils bearing patches of *Carici-Agrostietum caninae* were characterized by low pH values (Fig. 3) in KCl (mean = 3.73; range = 3.29–4.73), whereas their feeding waters displayed low mineralization, as indicated by their electric conductivity

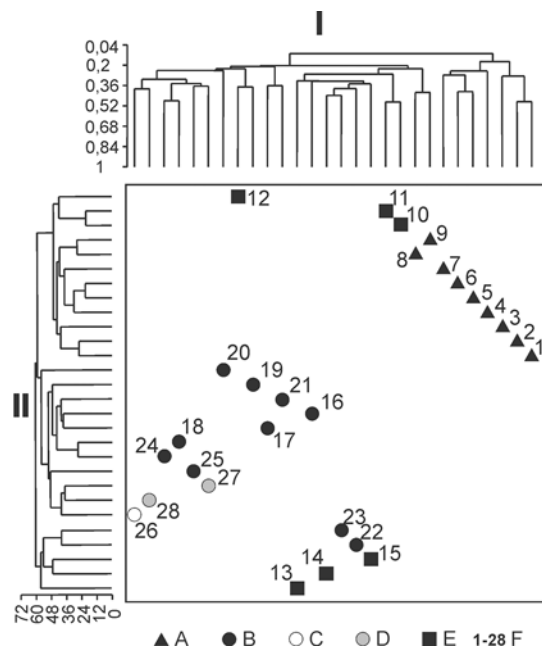


Fig. 2 Classification of spring fen relevés: I – dendrogram based on the presence/absence of species, II – dendrogram showing species coverage. A – *Carici-Agrostietum caninae*. B – *Valeriano-Caricetum flavae*. C – *Caricetum davallianae*. D – *Eleocharitetum pauciflorae*. E – intermediate patches. F – patch numbers.

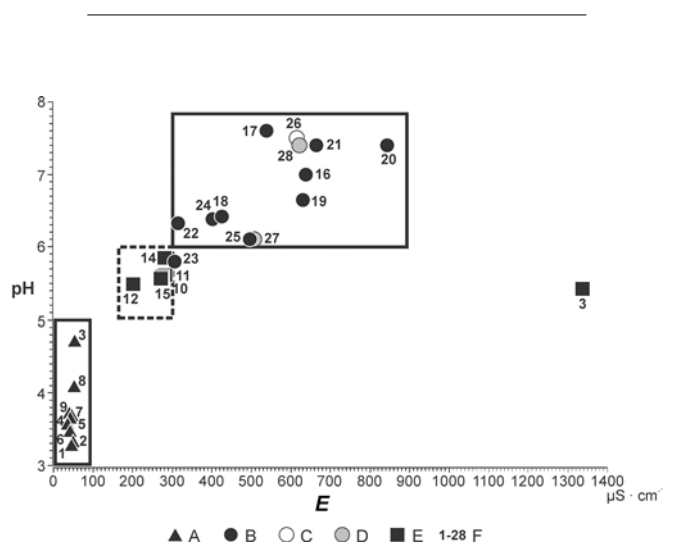


Fig. 3 Differentiation of spring fens based on soil pH and electrical conductivity (E) of their feeding waters. A – *Carici-Agrostietum caninae*. B – *Valeriano-Caricetum flavae*. C – *Caricetum davallianae*. D – *Eleocharitetum pauciflorae*. E – intermediate patches. F – patch numbers.

Tab. 1 (continued)

Number of relevés	I	II	III	1-28
	1-9	10-15	16-28	
<i>Listera ovata</i>	-	III (+-1)	II (+-1)	II
<i>Plagiomnium elatum</i>	-	I (2)	IV (+-4)	II
<i>Plagiomnium rostratum</i>	-	III (1-2)	III (+-5)	II
<i>Rhytidiadelphus triquetrus</i>	-	III (+-2)	III (+-2)	II
<i>Tussilago farfara</i>	-	-	III (+-1)	II
<i>Aulacomnium palustre</i>	I (+)	I (1)	I (1)	I
<i>Ranunculus auricomus</i>	II (+)	I (+)	I (+)	I
<i>Rhinanthus serotinus</i>	I (1)	II (+-1)	I (+-1)	I
<i>Salix aurita</i>	II (1)	I (1)	I (+)	I
<i>Salix silesiaca</i>	II (+)	I (1)	I (+-1)	I
<i>Equisetum sylvaticum</i>	II (+)	III (1-4)	-	I
<i>Senecio subalpinus</i>	II (+-1)	II (+)	-	I
<i>Chaerophyllum hirsutum</i>	-	III (+-1)	I (1-2)	I
<i>Equisetum variegatum</i>	-	II (+-2)	II (+-1)	I
<i>Festuca ovina</i>	III (+-1)	-	-	I
<i>Gymnadenia conopsea</i>	-	-	II (+-1)	I
<i>Eupatorium cannabinum</i>	-	-	II (+-2)	I

I – poor fens (including *Carici-Agrostietum caninae*); II – moderately rich fens; III – rich fens (include *Valeriano-Caricetum flavae*, *Caricetum davallianae* and *Eleocharitetum pauciflorae*).

(mean = 45.0; range = 36–53 $\mu\text{S cm}^{-1}$). Such extreme biotopic conditions result in the formation of a distinctive flora in poor fens, and a small degree of penetration of the association by alien species. They also result in a visible difference that enables a distinction to be made between this and neighboring associations that are already present on mineral soils. Hierarchical analysis of phytosociological relevés of *Carici-Agrostietum caninae* revealed the presence of a close group, that is particularly obvious in dendrogram II, based on species coverage (Fig. 2). It corroborates a small degree of differentiation of the analyzed patches and the considerable floristic distinctness of the association.

Soils colonized by *Valeriano-Caricetum flavae*, *Caricetum davallianae* and *Eleocharitetum pauciflorae* associations displayed higher pH values (Fig. 3) within the 6.1–7.6 range in KCl (mean 6.77) and considerable mineralization of their feeding waters, as indicated by high electric conductivity for the range 306–842 $\mu\text{S cm}^{-1}$ (mean 538.5). Measurements for patches

classified as *Caricetum davallianae* and *Eleocharitetum pauciflorae* fell within the same ranges (Fig. 3). Quite a wide range of the described biotopic parameters, comprising both weakly acid soils through neutral to alkaline, resulted in considerable variation in the *Valeriano-Caricetum flavae*. Intermediate soil conditions of some patches favored the penetration of the association by species typical of other, mainly meadow, rushes and tall herb communities. The outcome was the presence of a considerable number of plants typical of wet meadows, and blurred boundaries to the majority of fens, caused by their transition into surrounding meadow or tall herb communities. Hierarchical numerical analysis of phytosociological relevés of *Valeriano-Caricetum flavae* revealed that they do not form such tight groups as the *Carici-Agrostietum caninae* association, indicating their considerable similarity to transitional patches. This is best seen in dendrogram I, which is based on the species present (Fig. 2), and where a single group contains patches classified as typical *Valeriano-Caricetum flavae*, as well as intermediate patches. This demonstrates the great diversification of the association. Patches classified as *Caricetum davallianae* and *Eleocharitetum pauciflorae* partly overlapped with *Valeriano-Caricetum flavae*.

One patch classified as *Valeriano-Caricetum flavae* showed a slightly lower pH of 5.80 when measured in KCl (Fig. 3), yet, simultaneously, the electric conductivity of its feeding waters was close to the lower limit of the range (306 $\mu\text{S cm}^{-1}$). Vegetation growing on this patch did not differ significantly from that on other patches. Together with the adjoining patch, it inclined towards intermediate fens (Fig. 2). However, the combination of characteristic species associated with this patch, and the predominance of plants typical of *Valeriano-Caricetum flavae*, made it possible to classify it as this association.

Fen soils having transitory vegetation features are characterized by their possession of intermediate parameters. They belong to weakly acid soils, with a mean pH value of 5.59 (range = 5.42–5.85) in KCl (Fig. 3), and their feeding waters are moderately abundant in mineral compounds, as indicated by their mean electric conductivity of 261.2 (range = 201–281 $\mu\text{S cm}^{-1}$). The ranges of pH values typical for this fen group fall exactly between those ranges typical of the two described plant communities. Whereas the upper limit of electrical conductivity is clearly visible, the lower limit does not conform to that considered typical of *Carici-Agrostietum caninae*. This is important, since typical patches of poor fens are characterized by a unique homogeneity with regard to water electrical conductivity.

The narrow range given here contains those patches with species typical of both poor and rich fens in almost equal

Tab. 2 Changes to essential properties of surface horizon soils and feeding waters, proposed initially as typical of the investigated plant communities, and that allow them to be distinguished from each other.

Essential properties of soils and waters	<i>Carici-Agrostietum caninae</i>	Intermediate fens	<i>Valeriano-Caricetum flavae</i>	χ^2	df	P
pH	3–5	5–6	6–8	24.67	2	0.0000
Electrical conductivity ($\mu\text{S cm}^{-1}$)	30–60	200–300	300–900	24.67	2	0.0000
CaCO ₃ concentration (g kg ⁻¹)	0	0	0–700	-	-	-
Mineral content (%)	6–33	{22–73}	34–75	15.237	2	0.0005
Water oxygenation (mg O ₂ dm ⁻³)	0.1–0.3	{0.15–2.5}	0.5–5	14.857	2	0.0006
Peat decomposition	H2–H4	{H5–H7}	H6–H9	12.697	2	0.0018

Values which do not allow distinction between individual fen groups (overlapping ranges typical of other groups) are given in curly brackets.

measure. However, a degree of diversification was observed in this small group, indicating a slight prevalence of species characteristic of one of the associations. Hierarchical numerical analysis (Fig. 2) demonstrated that when dendrogram II was based on species abundance, these patches became segregated into two different groups containing relevés from poor and rich fens. This diversification can be correlated with variation in other soil parameters, such as mineral content, degree of peat decomposition and differences in the oxygenation of waters feeding individual patches (Fig. 4).

Moreover, one of these investigated patches differed from all the rest and was distinguished by its extremely high electric conductivity value ($1337 \mu\text{S cm}^{-1}$). Such elevated values were due to exceptionally high concentrations of chlorides resulting from disturbance of the natural environment by anthropogenic factors. This particular patch is located on a slope below and at a distance of approx. 100 m from the Cracow to Zakopane national road. Despite these considerable changes to the natural environment, the vegetation present on the aforementioned fen did not differ much from that found on the others. Possibly, in future, the situation will change as increased salting adversely affects some of the more sensitive species, eventually causing them to vanish. Mainly facultative halophytes (inter alia: *Carex nigra*, *C. panicea*, *Equisetum palustre*, *Juncus articulatus*) will tend to survive, together with some of the meadow species [23]. Currently they constitute about 30% of vascular plants present on this spot, however in future these proportions may change.

Calcium carbonate content in spring fen soils

Carici-Agrostietum caninae association and patches bearing transitory vegetation occur on soils lacking carbonate. The presence of calcium carbonate was found only in the soils of rich fens (Fig. 5). However, even here, it was not present in all investigated patches.

The CaCO_3 concentrations of analyzed rich fen soils showed great diversity. However, the results obtained were not unanimous but fell into three ranges or groups, as shown below (Fig. 5):

(i) Fens where calcium carbonate is high or very high (range = $351\text{--}653 \text{ g kg}^{-1}$) – *Valeriano-Caricetum flavae* and *Caricetum davallianae* patches as well as one patch of *Eleocharitetum pauciflorae* belong here.

(ii) Fens with low concentrations of CaCO_3 (range = $50\text{--}85 \text{ g kg}^{-1}$) – *Valeriano-Caricetum flavae* patches belong here.

(iii) Fens lacking carbonate or containing trace amounts of CaCO_3 (range = $0\text{--}0.1 \text{ g kg}^{-1}$) – *Valeriano-Caricetum flavae* patches and one patch of *Eleocharitetum pauciflorae* belong here.

Contrary to expectations, these enormous differences in the calcium carbonate content of the soil did not significantly affect the species composition and structure of plant communities. Patches lacking carbonate, and those containing only trace amounts of CaCO_3 , can be distinguished by a slightly greater amount of *Carex nigra*. It would also seem that *Eriophorum latifolium* is more characteristic of habitats with lower concentrations of calcium carbonate. Conversely, *Pinguicula vulgaris* and *Triglochin palustre* prefer habitats containing large amounts of CaCO_3 . Differences between patches lacking carbonate and others are more obvious, in that they more closely resemble intermediate patches, as has been shown by hierarchical numerical analysis (Fig. 2).

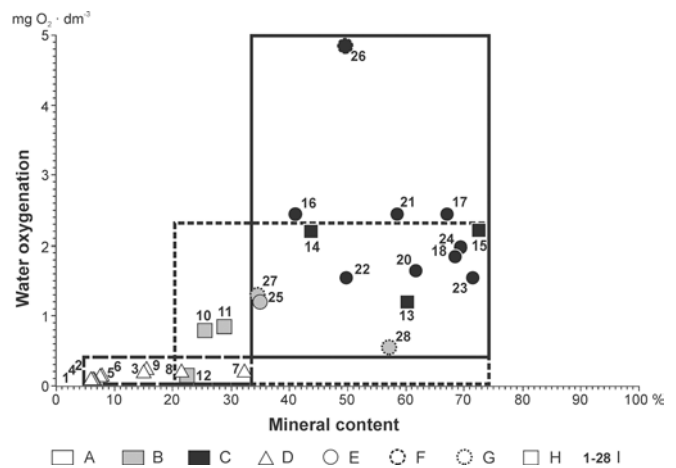


Fig. 4 Differentiation of spring fens and degree of peat decomposition (H) based on mineral content and water oxygenation. A – H2–H4. B – H5–H6. C – H7–H9. D – *Carici-Agrostietum caninae*. E – *Valeriano-Caricetum flavae*. F – *Caricetum davallianae*. G – *Eleocharitetum pauciflorae*. H – intermediate patches. I – patch numbers.

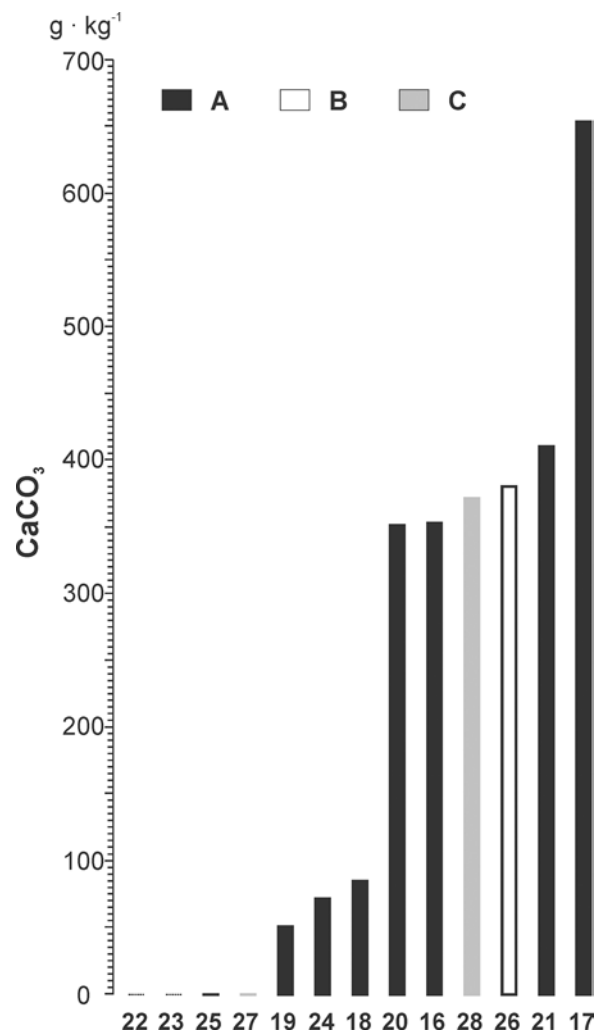


Fig. 5 Calcium carbonate concentrations in rich fen soils with *Caricion davallianae* vegetation. A – *Valeriano-Caricetum flavae*. B – *Caricetum davallianae*. C – *Eleocharitetum pauciflorae*.

Other properties of soils and their influence on the vegetation of spring fens

The described plant associations, identified on the basis of differences in their floristic composition, are the result of not only differences in the acidity and CaCO_3 concentrations of the soils in which they grow, and the electrical conductance of their feeding waters, but also, the degree of peat decomposition, mineral content and oxygenation level of the feeding water. These differences are statistically significant (Tab. 2).

Carici-Agrostietum caninae association grows on peat exhibiting a low degree of decomposition (H2–H4) and having a low mean mineral content of 13.1% (range = 6.0–33.3%). Its feeding waters are extremely poorly oxygenated, having a mean value of 0.17 (range = 0.10–0.26 mg O_2 dm⁻³; Fig. 4).

Valeriano-Caricetum flavae, *Caricetum davallianae* and *Eleocharitetum pauciflorae* associations grow on peat exhibiting a high degree of decomposition (H6–H9) and having a higher mean mineral content of 56.77 (range = 34.6–74.1%). The feeding waters show great diversity in terms of their oxygenation levels, which vary widely (mean = 1.99; range = 0.55–4.85 mg O_2 dm⁻³; Fig. 4). Despite these large differences, in the degree of water oxygenation, this factor did not have any significant effect on plant species composition (compare Fig. 2, Fig. 4).

Peat exhibiting a low or medium degree of decomposition (H5–H7) occurs in the substratum of fens covered by transitional type of vegetation, the degree of decomposition depending on its floristic composition. Mineral content fluctuates widely from 22.3 to 72.5% (mean = 42.12; Fig. 4), and enters the ranges typical for both *Carici-Agrostietum caninae* and *Valeriano-Caricetum flavae*. The values of fen-feeding water oxygenation are similar, and fluctuate from 0.15 to 2.21 mg O_2 dm⁻³ (mean = 1.23). It would seem that the boundaries between the ranges for mineral content and water oxygenation typical for both investigated associations, are crucial for their vegetation structure. Fens with vegetation of intermediate characteristics are closer to *Carici-Agrostietum caninae*, or to *Valeriano-Caricetum flavae*, depending on the values of the described parameters (compare Fig. 2, Fig. 4).

Discussion

Fens bearing typically formed *Carici-Agrostietum caninae* and *Valeriano-Caricetum flavae* associations differ fundamentally in relation to the properties of their soils and feeding waters. Mineral content, pH, CaCO_3 concentration and the degree of peat decomposition, as well as electrical conductivity and the oxygenation of fen-feeding waters do not tally. Parameter ranges typical for each of these two associations can easily be determined as an initial step in their characterization (Tab. 2). *Carici-Agrostietum caninae* is a uniform association adapted to extreme biotopic conditions. It is characterized by its very narrow range of soils and feeding-water parameter values. *Valeriano-Caricetum flavae* is a most diverse association. The considerable diversity of its species composition and plant structure reflects a very wide range of basic soil and feeding water parameters. The character of its vegetation depends mostly on fen soil pH and the degree of mineralization of its feeding water. It is only these parameters that seemingly distinguish patches that bear vegetation of intermediate character. They cannot be identified easily based on the degree of peat decomposition, mineral content and level of water oxygenation. These parameters are different for *Carici-Agrostietum caninae* and

Valeriano-Caricetum flavae, whereas intermediate patches are able to grow in the typical ranges characteristic of both investigated associations. Moreover, the vegetation of these patches is able to diversify to such an extent that the latter resembles one of the two investigated associations.

The results obtained in this study generally agree with those obtained for other studies of spring fens in the Carpathians [24,25], although we identified fewer plant communities. The chemical properties of both soil and water in *Carici-Agrostietum caninae* correspond with those typical of *Carici echinatae-Sphagnetum sphagnetosum fallacies*, a community identified in the Czech Republic and Slovakia [11,24]. The parameters exhibited by *Valeriano-Caricetum flavae* are also similar. Patches of intermediate pH represent *Carici echinatae-Sphagnetum sphagnetosum flexuosi*, but their electrical conductivity is typical of *Valeriano-Caricetum flavae* [24].

The concentration of calcium carbonate in some spring fens was found to be very high and considerably exceeded those concentrations reported from spring fens for other areas of the Western Carpathians [25]. These differences were due to two factors. Firstly, in our study, the concentration of calcium carbonate was determined for soil, whereas other authors based their results on the analysis of water. Secondly, our study included fens located both on flysch and on calcareous substrate. However, earlier studies were restricted to fens of the flysch region.

Plant species characteristic of *Sphagno warnstorffii-Eriophoretum latifolii* and *Caricion lasiocarpae* alliances (*Sphagnum teres*, *S. warnstorffii* and *Tomentypnum nitens*) represented only a small proportion of plants from both the *Valeriano-Caricetum flavae* and fens with the intermediate type of vegetation. *Sphagno warnstorffii-Eriophoretum latifolii* occurs in the investigated area [17], but was not present in those fens selected for this study. None of the conductivity values obtained fell within the range characteristic of this plant association [24].

Some characteristics discovered in our study have previously been reported from the Western Carpathians [24], e.g., the wide tolerance of *Eleocharitetum pauciflorae* to the CaCO_3 content of soil, its floristic similarity to *Valeriano-Caricetum flavae* and the similar ranges of basic soil parameters. We also demonstrated that a high proportion of spring species present in the moss layer is typical of fens located on slopes with running water.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: collecting data (vegetation sampling), data analyzes and interpretation, writing the manuscript, table and figures arrangement: AK; research designing, collecting data (soil and water sampling, chemical analyzes), writing the manuscript: PN.

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