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Original article

Syntaxonomy and ecological differentiation of the pioneer vegetation of Ukraine

Classes: *Isoëto-Nanojuncetea*, *Bidentetea*

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ABSTRACT

The studies of the pioneer vegetation of freshwater shorelines of water bodies are of particular interest owing to the specific ecology of these habitats and the short cycle for their development in which periods of flooding and subsequent drainage alternate. Using the methods of phytosociological classification and cluster analysis based on the interpretation of 414 phytosociological relevés, the syntaxonomic structure of the pioneer vegetation of freshwater shorelines of the water bodies of Ukraine has been established that are represented by the phytosociological classes *Isoëto-Nanojuncetea* and *Bidentetea*. The class *Isoëto-Nanojuncetea* includes 8 associations that belong to 2 alliances and 1 order and the class *Bidentetea* includes 10 associations belonging to 2 alliances and 1 order. Phytocoenoses of both classes are more typical for the Polissia region and the forest-steppe zone of Ukraine, where there are favourable habitats with a flat relief, low degree of dissection and a high level of soil humidity. Using a DCA ordination analysis of associations their position in ecological space was determined. It was established that the main factors of ecological differentiation for *Isoëto-Nanojuncetea* habitats are soil humidity, soil aeration, nitrogen content, as well as temperature regime. Differentiation in the hyperspace of abiotic factors of the class *Bidentetea* occurs mainly along the gradients of soil humidity, salt regime and acidity. The ecological distribution of syntaxa of this class is also significantly influenced by the concentration of mineral nitrogen compounds in the soil.

KEY WORDS: phytocoenoses, classification, newly formed ecotopes, DCA ordination, Ukraine

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1. Introduction

This article is the final one in a series devoted to the pioneer vegetation of Ukraine. Previously, we have analyzed the syntaxonomic structure and ecological differentiation of the classes: *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea, Crypsietea aculeatae, Therosalicornietea, Helichryso-Crucianelletea maritimae*, *Festucetea vaginatae* and *Koelerio-Corynephoretea canescentis* (DUBYNA ET AL., 2020a, b).

The pioneer vegetation of wetland habitats, in particular freshwater shorelines, has great biosphere importance. In particular, its phytocoenoses have anti-erosion, stabilization, water-cleaning, water protection, and other functions. The littoral zones of natural or man-made water bodies, where such vegetation is formed, are habitats for many species of plants and animals and channels for the distribution of their genetic material, in particular, for neophyte migration. Plant development period, short life cycles, and long-term survival in dormant propagules contribute to the uniqueness of these phytocoenoses and their highly dynamic habitats (Deil, 2005; Šumberová & Hrivnák, 2013). Most of the species and plant communities belonging to this vegetation type, especially the floodplain ephemeretum, are considered to be rare.

In Ukraine, the pioneer vegetation of the littoral zones of freshwater continental water bodies occupy river banks, shorelines of lakes and water reservoirs, the bottoms of periodically draining fish ponds, wet agricultural lands, depressions along roads and forest paths, sand and clay pits, forest glades, and other territories with a specific ecology of these habitats, when periods of flooding and drainage alternate. Vegetation of ephemeral wetlands also form in anthropogenically transformed habitats.

The syntaxonomy of the vegetation of ephemeral wetlands in Europe has been developed in sufficient detail. Classification schemes and characteristics are presented for the territories of Germany (Schubert et al., 2001; Berg et al., 2004), Poland (Matuszkiewicz, 2008), Czech Republic and Slovakia (Chytrý, 2011; Šumberová & Hrivnák, 2013), France (Bardat et al., 2004), Romania (Sanda et al., 2008), Italy (Biondi et al., 2014), Spain and Portugal (Rivas-Martínez et al., 2001), Bulgaria (Tzonev et al., 2009), Hungary (Borhidi, 2003; Makra, 2006) and some other countries. An overview of the syntaxonomic system of alliances, orders and classes of the annual herb vegetation in Europe is presented by Mucina et al. (2016).

In Ukraine, the pioneer vegetation of freshwater shorelines is represented by two classes: *Isoëto-Nanojuncetea* and *Bidentetea*. Due to the seasonal nature of their development, the syntaxonomy of these plant communities has not previously been sufficiently developed. In Ukraine, coenoses of the class *Isoëto-Nanojuncetea* were described for the first time by the Czech phytocoenologist J. Vicherek in 1968. For the territory of the Middle Dnieper River he identified a new association *Peplido alternifoliae-Juncetum tenageiae*. O. Senchylo and I. Goncharenko studied the littoral ecotone of the territory of the Dnieper Valley in the forest-steppe zone using the method of ecological profiling. These authors identified 3 subassociations of the most widespread within the *Isoëto-Nanojuncetea* class – *Cypero fusci-Limoselletum* (Senchylo et al., 1998; Senchylo & Goncharenko, 2008). Coenoses of this association were also described by V. Shevchyk et al. in the Dnieper Valley for the Kanivsky Nature Reserve (Shevchyk & Solomakha, 1996; Shevchyk et al., 1996). *Dichostyli-Gnaphalietum uliginosi* communities were recorded in the Danube Estuary within the territory of the Danube Biosphere Reserve (Dubyna et al., 2003). For the Ukrainian Rostochia Soroka (2010) marked the distribution of 5 associations: *Cyperetum flavescentis*, *Cypero fusci-Limoselletum*, *Centunculo-Anthoceretum punctati*, *Pepli-Agrostietum* and *Ranunculo-Myosuretum minimi*. In the upper part of the Tysa Basin (Ukrainian Carpathians) Felbaba-Klushyna (2010, 2017) described the *Juncetum bufonii* and *Cyperetum flavescentis* associations. The first one is also noted for other regions of the Carpathians, in particular, the Natural Reserves Skolivski Beskydy (Solomakha et al., 2004) and "Gorgany" (Klimuk et al., 2006). Shapoval (2006) in the territory of the depressions of the Left Bank of the Lower Dnieper described several syntaxa of the class *Isoëto-Nanojuncetea*, including new ones for science. In particular, the alliance *Myosuro-Beckmannion eruciformis*, associations *Middendorfio borysthenicae-Crypsietum alopecuroides* and *Myosuro-Beckmannietum eruciformis*. As a result of studies of the Udai valley within the territory of the Pyryatynsky National Natural Park Kovalenko (2014) identified 7 associations, including 2 which were described for the first time – *Psammophiliello-Juncetum nastanthi* and *Polygono recti-Juncetum juzepczukii*. The position of these syntaxa in the Braun-Blanquet system is still insufficiently clear and further research is nessesary. In the Western Bug valley, the distribution of 2 associations were recorded – *Juncetum bufonii* and *Cyperetum micheliani* (Kuzyarin et al., 2015). 3 assocations have been recorded in the Sluch valley – *Cyperetum micheliani*, *Pulicario vulgaris-Menthetum pulegii* and *Veronico anagalloidis-Lythretum hyssopifoliae* (Korotka & Pashkevych, 2017).

The plant communities of the class *Isoëto-Nanojuncetea* were also recorded in the valleys of Girskyi Tikych (Chorna, 2004) and Khorol (Gomlya, 2005), within the territories of the Carpathian Biosphere Reserve (Gadach et al., 1996), Polissia Natural Reserve (Didukh et al., 2008), Western Polissia (Konishchuk, 2009a,b), Zhytomyr Polissia (Orlov & Iakushenko, 2005; Iakushenko, 2005a,b). Phytocoenoses of annual wetland herbs were also found within urboecosystems of Kyiv (in the riverbed part of the Dnieper) (Alioshkina, 2011) and Chernigiv (on sandy habitats) (Lukash & Danko, 2020).

An overview of the syntaxonomy of *Isoëto-Nanojuncetea* has been provided in some generalist publications: for the Northern Black Sea region (Dubyna et al., 2004), Ukrainian Polissia (Onyshchenko, 2006), Polissia subprovince of the mixed forest zone (Konishchuk, 2013), water bodies and swamps of the forest-steppe zone of Ukraine (Chorna, 2013). The summary work was "Prodrome of the Vegetation of Ukraine" (Dubyna et al., 2019).

The class *Bidentetea* combines semi-natural pioneer plant communities. Therefore, in Ukraine many researchers have described such phytocoenoses as synanthropic ones. In the territory of Lviv KUCHERYAVYI ET AL. (1991) identified phytocoenoses of the association *Bidentetum tripartitae*. As a part of the ruderal vegetation of Big Yalta, LEVON (1996) identified 2 associations of the discussed class – *Bidentetum tripartitae*, and a new one to science – *Mentho longifolii-Pastinacetum umbrosi*. In the Dnieper Valley within Cherkasy, OSYPENKO & SHEVCHYK (2001) recorded coenoses of the *Bidentetum tripartitae* and *Bidentetum cernuae*. Later, *Bidentetea* coenoses are mentioned for the newly-formed alluvial ecotopes of the Danube Delta (DUBYNA ET AL., 2002, 2003), the northeastern regions of the forest-steppe zone (GONCHARENKO, 2003), Zhytomyr Polissia (YAKUSHENKO, 2004, 2005a,b), the floodplain ecosystems of the Western Bug Basin (KUZYARIN, 2005), the Khorol Valley (GOMLYA, 2005), the Regional Landscape Park "Kremenchuk Plavni" (GALCHENKO, 2006), the Ukrainian Roztochia (SOROKA, 2008), the floodplain of the Dnieper within Kiev (ALIOSHKINA, 2011), the littoral zones of the Kremenchuk reservoir (KONOGRAY, 2013), and the sandy habitats of Chernigiv (LUKASH & DANKO, 2020). The syntaxonomy of the class *Bidentetea* in the Dnieper Valley, within the forest-steppe zone of Ukraine, was considered by MAKHYNYA (2015). The regional works, where classes are discussed, are overview of the synanthropic vegetation of Ukraine (SOLOMAKHA ET AL., 1992), vegetation of the Northern Black Sea region (DUBYNA ET AL., 2004), Ukrainian Polissia (ONYSHCHENKO, 2006), Polissia sub-province of the mixed forest zone (KONISHCHUK, 2013), wetlands of the forest-steppe zone of Ukraine (CHORNA, 2013), habitats of the forest and forest-steppe zones of Ukraine (DIDUKH ET AL., 2011). The results of studies of the *Bidentetea* structure in Ukraine are summarized in the “Prodrome of the Vegetation of Ukraine” (DUBYNA ET AL., 2019).

Creation and development of phytosociological databases will not allow only (i) the clarification of the syntaxonomic structure of pioneer vegetation, but also (ii) the determination of the floristic composition and productivity of phytocoenoses; (iii) the possibility to study the population structure and patterns of the adaptive response of various ecobiomorphs in different ecological and coenotic conditions; (iv) the clarifiction of the dynamics of pioneer vegetation under conditions of increasing adaptive specialization; and (v) an assessment of the changes in communities in the spatio-temporal scale (DUBYNA ET AL., 2015). Ordination analysis of phytocoenoses that supplements syntaxonomic studies (RAHMAN ET AL., 2017; ÇOBAN & WILLNER, 2019) allows us (a) to identify the leading factors of the plant communities’ distribution within ecological space according to the main environmental gradients (KUZEMKO ET AL., 2016; KOROLYUK ET AL., 2018; LASHCHINSKIY ET AL., 2019); (b) to determine the state of ecosystems in terms of their biotic components (DIDUKH, 2012), the features of the spatial distribution of vegetation (TONG ET AL., 2019; ZHIYANG ET AL., 2020), the patterns of ecological and biological organization of the vegetation cover (WILDI, 2018), the relationships of vegetation parameters within local and regional ecological processes (CHATURVEDI & RAGHUBANSHI, 2018); and (c) to identify phytoindicators of climate change (BACHMAIR ET AL., 2016).

Based on the above mentioned features, the aims of this article are 1) to generalize the accumulated phytocoenotic materials on the syntaxonomy of vegetation of the *Isoëto-Nanojuncetea* and *Bidentetea* classes in Ukraine; 2) to develop their syntaxonomic structure; 3) to determine the ecological series of syntaxa and 4) to establish the main factors of ecological differentiation of phytocoenoses based on ordination analyses.

2. Materials and methods

2.1. Data collection

The phytosociological materials for this research work included 414 relevés from the territory of Ukraine made directly by the authors and documented in the literature. Our own relevés were made between 1989 and 2020 on plots of standard size 4 x 4 m, according to the method of floristic classification by J. Braun-Blanquet (BRAUN-BLANQUET, 1964; WESTHOFF & VAN DER MAAREL, 1973). In some cases, on narrow elongated banks of water bodies, the plots were 1 x 4 m or 2 x 5 m in size. At the same time, the requirements for a homogeneous structure of the vegetation cover were observed. The data set also included relevés given in the publications of VICHEREK (1968), SHEVCHYK & SOLOMAKHA (1996), SHEVCHYK ET AL. (1996), OSYPENKO & SHEVCHYK (2001), GOMLYA (2005), ORLOV & IAKUSHENKO (2005), SOLOMAKHA ET AL. (2005), GALCHENKO (2006), SHAPOVAL (2006), KLIMUK ET AL. (2006), SENCHYLO & GONCHARENKO (2008), SOROKA (2008), IAKUSHENKO ET AL. (2011), CHORNA (2013), KOVALENKO (2014), MAKHYNYA (2015), KOROTKA & PASHKEVYCH (2017), LUKASH & DANKO (2020). The database also included unpublished relevés from manuscripts and dissertations, kindly provided to us by D. Iakushenko, V. Konogray, I. Khomyak, O. Senchylo, O. Kovalenko, A. Kuzemko and A. Kuzyarin. All localities of the annual herb vegetation of Ukraine are presented on the distribution map (Fig. 1).

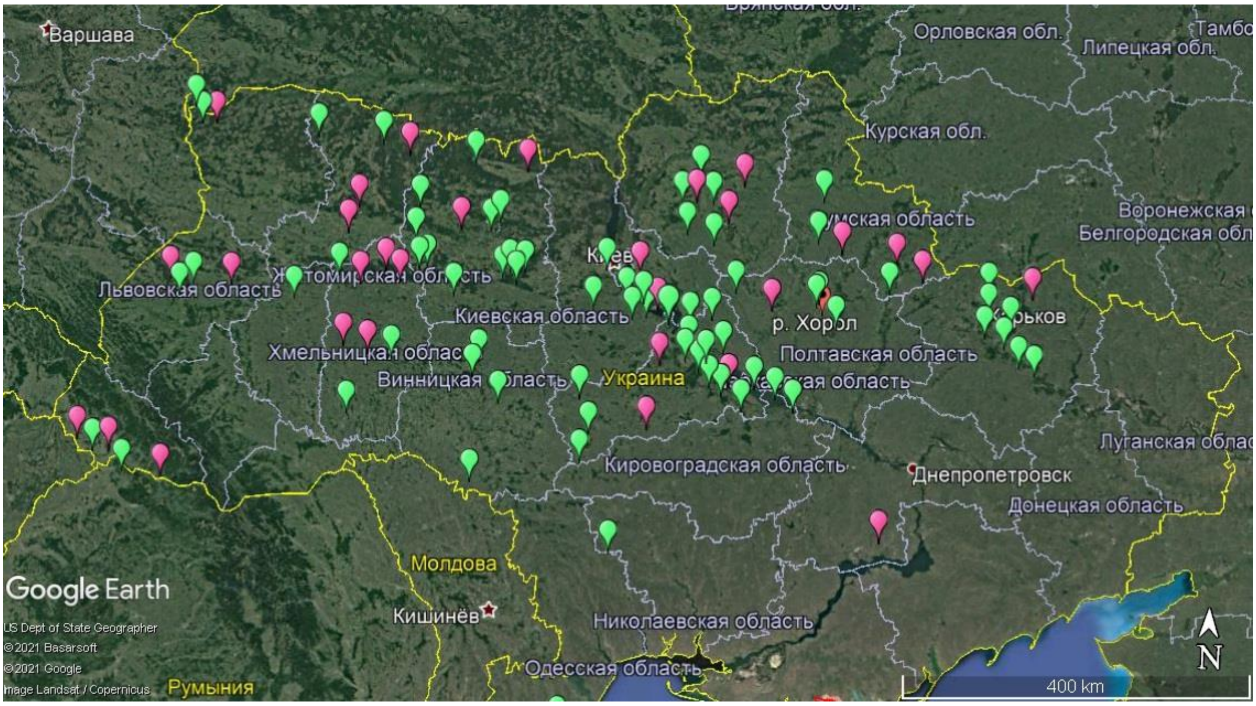

Fig. 1. A distribution map of the localities of annual herb vegetation in Ukraine (pink colour marks localities of the class *Isoëto-Nanojuncetea,* green colour – of the class Bidentetea)

2.2. Data analysis

All 414 relevés were entered into a database created in the TURBOVEG 2.79 format (HENNEKENS & SCHAMINÉE, 2001). They were combined with a database of aquatic, wetland and meadow vegetation, numbering 4932 vegetation plots in general. Relevés of related types of vegetation were included in the analysis to obtain a clearer separation of groups and to avoid subjective assessments. Then the relevés were exported to the JUICE program (TICHÝ, 2002).

The phytosociological data were interpreted using the JUICE 7.0.83 software package (TICHÝ, 2002). The processing of relevés was carried out using the method of two-factor indicator species analysis (TWINSPAN), in particular its modified version (HILL, 1979; ROLEČEK ET AL., 2009), as well as use of the PC-ORD software package (MCCUNE & MEFFORD, 2016). At first, using the modified TWINSPAN, the general database (5346 relevés) was processed in order to divide it into smaller groups based on their floristic differences. The "pseudo-species" cut levels were 0, 5, 15, 30%. The measure of cluster heterogeneity was the of Whittaker's beta (WHITTAKER, 1978) taken as the correlation measure between the total number of species in all relevés of a cluster to the average number per relevé. Then all groups with a list of diagnostic species corresponding to the classes *Isoëto-Nanojuncetea* and *Bidentetea*, according to MUCINA ET AL. (2016), were analized separately using the PC-ORD software. Sørensen's coefficient was chosen as a measure of similarity of clusters (SÖRENSEN, 1948), and the grouping was carried out according to the "flexible" beta method at –0.25. This made it possible to obtain phytocoenons that approximately corresponded to the rank of the association.

Identification of diagnostic species of association was carried out in accordance with the fidelity index (*phi* coefficient) (WILLNER ET AL., 2009), the threshold values of which were accepted at level 25. All groups of relevés were standardized to equal size, and insignificant values of fidelity were removed based on Fisher's extract test ($P<0.001$). At the last stage, the phytocoenones were identified based on the analysis of their floristic composition and comparison with diagnostic groups of syntaxa published in foreign and national publications (CHYTRÝ, 2011; MUCINA ET AL., 2016; DUBYNA ET AL., 2019 et al.).

The nomenclature of taxa is given according to "Vascular plants of Ukraine. A nomenclature checklist" (MOSYAKIN & FEDORONCHUK, 1999).

The DCA ordination method (HILL & GAUCH, 1980; TER BRAAK & SMILAUER, 2015) of the R-project program (VENABLES & SMITH, 2008) was used to identify the position of syntaxa in ecological space. The ecological parameters were calculated according to 12 factors: soil humidity (Hd), variability of damping (fH), soil aeration (Ae), soil nitrogen content (Nt), soil acidity (Rc), salt regime (Sl), soil carbonate content (Ca), temperature regime (Tm), ombroregime (Om), climate continentality (Kn), cryoregime (Cr) and light intensity (Lc) according to the phytoindication scales of DIDUKH (2011).

3. Results

Classification scheme

Isoëto-Nanojuncetea Br.-Bl. et Tx. in Br.-Bl. et al. 1952
- *Nanocyperetalia* Klika 1935
  - *Eleocharition soloniensis* Philippi 1968
    - *Middendorfio borysthenicae-Crypsietum alopecuroidis* Shapoval 2006 nom. inval. (art. 3o, 5)
    - *Stellario uliginosae-Isolepidetum setaceae* Libbert 1932
    - *Cyperetum flavescentis* Koch 1926
    - *Cyperetum micheliani* Horvatić 1931
    - *Juncetum bufonii* Felföldy 1942
  - *Verbenion supinae* Slavnić 1951
    - *Pulicario vulgaris-Menthetum pulegii* Slavnić 1951 (incl. *Myosuro-Beckmannietum eruciformis pulicarietosum vulgaris* Shapoval 2006 (art. 5))
    - *Eragrostidetum suaveolentis* Golub et al. 2007
    - *Veronico anagalloidis-Lythretum hyssopifoliae* Wagner ex Holzner 1973 (incl. *Psammophiliello-Juncetum nastanthi* Kovalenko 2013; *Polygono recti-Juncetum juzepczukii* Kovalenko 2013 (syntax. syn.))

Bidentetea Tx. et al. ex von Rochow 1951
- *Bidentetalia* Br.-Bl. et Tx. ex Klika et Hadač 1944
  - *Bidention tripartitae* Nordhagen ex Klika et Hadač 1944
    - *Polygonetum hydropiperis* Passarge 1965
    - *Bidentetum cernuae* Slavnić 1951
    - *Leersio-Bidentetum* (Koch 1926) Poli et Tx. 1960
    - *Bidentetum tripartitae* Miljan 1933
    - *Myosoto aquatici-Bidentetum frondosae* O. de Bolòs, Montserrat et Romo 1988
    - *Junco bufonii-Bidentetum connatae* (Timmermann 1993) Passarge 1996 (incl. *Bidentetum frondoso-connatae* Makhynya 2015 (syntax. syn.))
    - *Rumici maritimi-Ranunculetum scelerati* Oberd. 1957
  - *Chenopodion rubri* (Tx. in Poli et J. Tx. 1960) Hilbig et Jage 1972
    - *Chenopodietum rubri* Timár 1950
    - *Bidenti frondosae-Atriplicetum prostratae* Poli et Tx. 1960 corr. Gutermann et Mucina 1993
    - *Xanthio riparii-Chenopodietum rubri* Lohmeyer et Walther in Lohmeyer 1950

The class *Isoëto-Nanojuncetea* includes plant communities of low-growing annual herbs with an ephemeral life cycle (nanoephemeretum) in shallows of alluvial habitats of continental water bodies that are periodically flooded. They develop in conditions of rapid periodic seasonal changes in surface-soil humidity. The discussed phytocoenoses occupy mainly drying out streams, temporary water bodies, riverbanks, littoral zones of lakes, ponds and reservoirs. In Ukraine, the *Isoëto-Nanojuncetea* is represented by 8 associations that belong to 2 alliances and 1 order. Class is characterized by a lower level of coenotic diversity on the European scale. The main factors of territorial differentiation of these plant communities, are those that also determine their coenotic diversity, these are the type of relief of newly-formed ecotopes, the composition and thickness of alluvial sediments, as well as the hydrological regime of water bodies (water depth and flooding period). The formation of the coenoses is limited by excessive flooding and drainage, as well as human impact. The communities of the *Isoëto-Nanojuncetea* are more typical for the Polissia region and the forest-steppe zone of Ukraine, where suitable habitats (with a flat relief, a low degree of dissection and a high soil humidity) are common. In the steppe zone of Ukraine these aforementioned phytocoenoses are rare. Mainly here they occur on depressed landforms with slightly saline soils and flooding (Fig. 2–5).

The alliance *Eleocharition ovatae* includes ephemeral coenoses of therophytes and hemicryptophytes on eutrophic, or slightly saline substrates, in the littoral zones of rivers, lakes, ponds, and reservoirs. The alliance *Verbenion supinae* unites communities of low-growing annual or perennial herbs which have a short period of ontogeny and are of the stress-tolerator strategy type. They occupy sandy and sandy loamy nitrified soils, mainly those that are anthropogenically transformed. Blocks of diagnostic species are quite clear at the levels of associations (Fig. 6, Table 1).

In Europe, the *Isoëto-Nanojuncetea* is represented by 2 orders: *Isoëtetalia* Br.-Bl. 1935 and *Nanocyperetalia* Klika 1935, and 11 alliances. The diversity of climatic and edaphic conditions at the regional scale contributes to the formation of biogeographic differences in the communities of the floodplain nanoephemeretum.

Fig. 2. *Juncetum bufonii* on the littoral zone of the River Dnieper near the city of Kyiv (Kyiv region) (Photo by S. Iemelianova)

Fig. 3. *Pulicario vulgaris-Menthetum pulegii* on the floodplain meadow-pasture near the village of Rakoshyno (Mukachevo district, Zakarpattia region, 2015) (Photo by L. Felbaba-Klushyna)

Fig. 4. The phytocoenoses with the dominance of *Cyperus fuscus* on the periphery of the reservoir (near the village of Dyidovo, Beregiv district, Zakarpattia region, 12.08.2020) (Photo by L. Felbaba-Klushyna)

Fig. 5. *Juncus articulatus* on the periphery of the reservoir (near the village of Dyidovo, Beregiv district, Zakarpattia region, 110 m above sea level, 12.08.2020) (Photo by L. Felbaba-Klushyna)

Table 1. Synoptic table of the class *Isoëto-Nanojuncetea*

No. of syntaxa	1	2	3	4	5	6	7	8
Number of relevés	10	15	12	60	36	13	13	8
Middendorfia borysthenica	100.0	–	–	–	–	–	–	–
Juncus sphaerocarpus	100.0	–	–	–	–	–	–	–
Lythrum thymifolia	88.2	–	–	–	–	–	–	–
Ranunculus sceleratus	86.4	–	–	–	–	–	–	–
Persicaria maculata	76.9	–	–	–	–	–	–	–
Potentilla argentea	75.3	–	–	–	–	–	–	–
Rorippa brachycarpa	68.7	–	–	–	–	16.7	–	–
Rumex crispus	51.0	–	–	–	–	–	–	9.1
Xanthium albinum	50.0	–	–	2.9	–	9.8	–	–
Verbena supina	42.4	–	–	–	–	–	–	–
Veronica scutellata	–	75.3	–	–	–	–	–	–
Radiola linoides	–	66.6	–	–	–	–	–	–
Potentilla anserina	–	65.9	–	–	–	–	–	1.4
Alopecurus aequalis	–	60.7	–	–	–	–	–	–
Eleocharis uniglumis	–	49.1	–	–	–	–	–	–
Plantago uliginosa	–	46.2	10.0	17.5	7.4	–	–	–
Trifolium fragiferum	–	–	99.1	–	–	–	–	–
Carex distans	–	–	85.1	–	–	–	–	–
Scirpus melanospermus	–	–	77.1	–	–	–	–	–
Puccinellia distans	–	–	68.3	–	–	–	–	–
Sagina nodosa	–	–	66.7	–	3.3	–	–	–
Bolboschoenus planiculmis	–	–	63.2	–	–	–	–	–
Juncus gerardii	–	21.9	51.9	–	–	–	–	–
Juncus tenuis	–	–	50.0	–	13.6	–	–	–
Epilobium tetragonum	–	–	44.4	–	–	–	–	–
Scutellaria galericulata	–	–	36.3	–	–	–	–	–
Chenopodium rubrum	–	–	35.1	21.3	–	–	23.2	–
Iva xanthiifolia	–	–	32.5	5.3	–	–	–	–
Carex secalina	–	–	27.1	–	–	–	–	–
Elatine alsinastrum	–	–	–	44.1	–	–	–	–
Potentilla supina	–	–	–	36.3	–	–	–	14.0
Glyceria fluitans	–	–	–	34.9	0.9	–	–	–
Potentilla norvegica	–	–	–	32.2	–	–	–	–
Rumex maritimus	–	–	–	29.8	–	–	–	–
Lycopus europaeus	–	–	–	29.8	–	–	–	–
Persicaria hydropiper	–	–	7.3	25.8	7.3	–	–	–
Bidens tripartita	–	–	–	4.4	43.7	–	–	–
Setaria viridis	–	–	–	–	41.8	–	–	–
Juncus articulatus	–	–	–	22.9	29.6	–	–	–
Polygonum arenastrum	–	–	–	–	27.1	–	–	–
Juncus compressus	–	–	–	4.3	26.4	–	–	–
Lythrum virgatum	–	–	–	–	–	100.0	–	–
Beckmannia eruciformis	–	–	–	–	–	100.0	–	–
Mentha pulegium	–	–	–	–	–	91.0	–	–
Inula britannica	–	–	–	–	–	90.0	–	–
Polygonum aviculare	–	9.6	–	–	–	83.3	–	–
Aegilops cylindrica	–	–	–	–	–	65.5	–	–
Chaiturus marrubiastrum	–	–	–	–	–	65.5	–	–
Elytrigia pseudocaesia	–	–	–	–	–	59.5	–	–
Pulicaria vulgaris	2.0	–	–	–	–	58.0	12.6	–
Trifolium retusum	–	–	–	–	–	52.9	–	–
Ambrosia artemisiifolia	–	–	–	–	–	45.6	–	–
Alopecurus pratensis	–	–	–	–	–	45.6	–	–
Centaurea diffusa	–	–	–	–	–	45.6	–	–
Tripleurospermum inodorum	–	–	–	–	–	37.0	–	–
Solanum nigrum	–	–	–	–	–	37.0	–	–
Rorippa austriaca	14.7	–	–	–	–	26.3	–	–

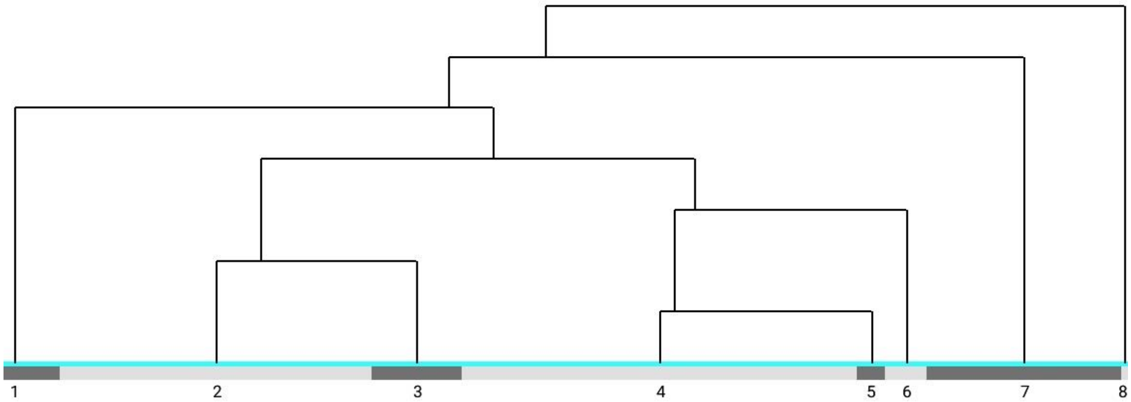

Fig. 6. Cluster analysis of the phytosociological data of the class *Isoëto-Nanojuncetea*
Clusters mark association: 1 – *Cyperetum flavescentis*, 2 – *Eragrostidetum suaveolentis*, 3 – *Veronico anagalloidis-Lythretum hyssopifoliae*, 4 – *Stellario uliginosae-Isolepidetum setaceae*, 5 – *Cyperetum michelliani*, 6 – *Juncetum bufonii*, 7 – *Pulicario vulgaris-Menthetum pulegii*, 8 – *Middendorfio borysthenicae-Crypsietum alopecuroidis*

According to the results of the ordination analysis of *Isoëto-Nanojuncetea* syntaxa (Fig. 7), it was established that the main factors for their ecological differentiation are: degree of soil aeration, variability of damping, as well as crio- and thermal regime of habitats, and concentration of nitrogen and carbonate compounds in the soil. The thermoregime, salt regime and light regime have especially affected the distribution of the associations *Myddendorfio borysthenicae-Crypsietum alopecuroides* and *Pulicario vulgaris-Menthetum pulegii*, which are described in the steppe zone of Ukraine and are the most thermophilic of the coenoses of the whole class. The ombroregime determines the ecological distribution of the communities of *Cyperetum micheliani* and *Juncetum bufonii* according to the amount of precipitation, which significantly affects the soil humidity. The variability of damping and the carbonate content of edaphotope, the vectors along which are the closest to the second ordination axis, became the additional gradients of syntaxa differentiation within the *Isoëto-Nanojuncetea*. The range of values for the main ecological factors and other abiotic gradients is presented in Table 2.

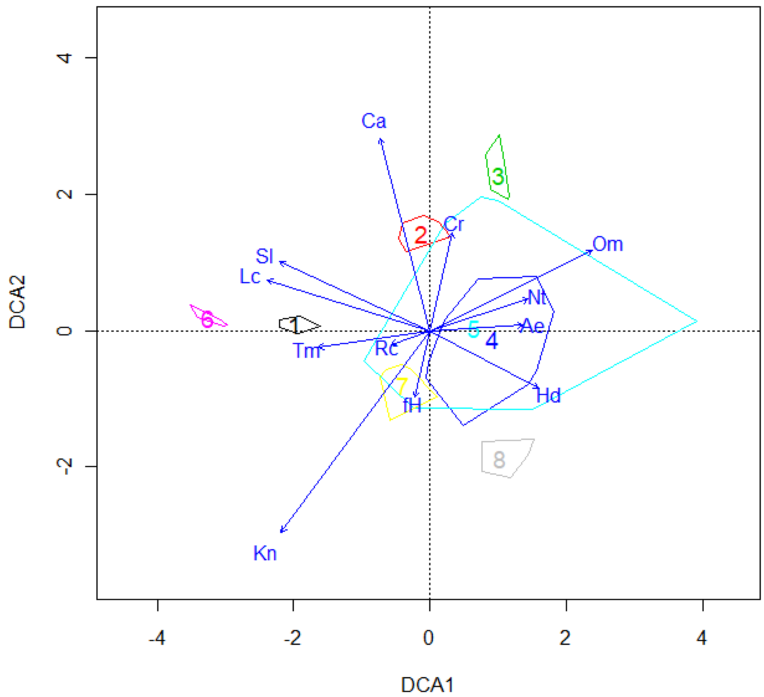

Fig. 7. Results of the ordination analysis of the syntaxa in the class *Isoëto-Nanojuncetea*
Numbers mark syntaxa: 1 – *Myddendorfio borysthenicae-Crypsietum alopecuroides;* 2 – *Stellario uliginosae-Isolepidetum setaceae*; 3 – *Cyperetum flavescentis*; 4 – *Cyperetum micheliani*; 5 – *Juncetum bufonii;* 6 – *Pulicario vulgaris-Menthetum pulegii;* 7 – *Eragrostidetum suaveolentis;* 8 – *Veronico anagaloidis-Lythretum hyssopifoliae*
Here and further the scale of ecological factors developed by Didukh (2011) was used: Hd – soil humidity; Nt – content of available nitrogen forms in the soil; Ca – content of carbonates; Rc – soil acidity; Sl – salt regime; fH –variability of damping; Ae – soil aeration; Lc – light intensity; Kn – climate continentality; Om – ombroregime; Tm – temperature regime; Cr – cryoregime; DCA1, DCA2 – ordination axes

Table 2. Mean, median, standard deviation and extremes of ecological factors values (in points of phytoindication scale) for each association

Class	*Isoëto-Nanojuncetea*								*Bidentetea*									
Association	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	9	10
Hd																		
MEAN	13.4	12.96	13.29	14.82	13.13	12.97	11.11	14.88	13.43	13.55	14.05	14.91	14.12	14.51	15.33	14.83	14.54	14.36
MEDIAN	13.42	12.94	13.45	14.69	13.24	12.85	10.93	15.11	14.23	13.7	14.07	14.9	14.4	14.63	15.82	14.88	14.55	14.36
SD	0.39	0.41	0.68	0.97	1.4	0.5	0.68	0.92	1.94	0.54	0.75	0.69	0.66	0.84	0.85	0.59	0.64	0.75
MIN	12.75	12.38	12	12.73	9.92	11.87	10	13.19	9.71	12.94	11.83	13.05	13.14	12.89	13.3	13.81	13.1	12.6
MAX	14.06	13.67	14.31	16.83	16.17	13.7	12.19	15.88	14.92	14	15.14	16.19	14.5	15.75	16.04	15.55	15.77	15.93
fH																		
MEAN	8.08	7.51	7.82	8.39	7.5	7.95	8.39	7.79	7.24	6.4	7.62	7.29	8.61	8.19	7.43	7.51	7.54	7.81
MEDIAN	8.03	7.56	7.66	8.45	7.67	7.96	8.22	7.77	7	6.7	7.62	7.32	8.75	8	7.31	7.44	7.55	7.9
SD	0.34	0.39	0.38	0.56	0.75	0.12	0.65	0.2	0.47	0.53	0.39	0.68	0.51	0.88	0.33	0.68	0.52	0.75
MIN	7.75	6.94	7.22	7	5.38	7.75	7.25	7.53	6.7	5.78	6.82	5.83	7.92	6.83	6.75	6.56	6.1	6.09
MAX	8.89	8.29	8.5	9.63	8.8	8.12	10	8.13	8.04	6.71	8.2	8.5	9	9.67	8.1	8.57	9	9.25
Rc																		
MEAN	8.35	6.54	8.01	7.43	7.11	7.63	7.04	7.67	8.09	8.51	7.85	7.16	8.24	7.74	7.78	7.85	7.62	7.54
MEDIAN	8.38	6.56	8.03	7.5	7.33	7.65	6.94	7.61	8.1	8.5	7.755	7.14	8.29	7.77	7.85	7.87	7.7	7.48
SD	0.28	0.42	0.32	0.39	0.68	0.18	0.61	0.22	0.23	0.08	0.27	0.34	0.46	0.35	0.29	0.38	0.46	0.41
MIN	7.75	5.67	7.36	6.5	5	7.38	6.21	7.43	7.68	8.44	7.5	6.55	7.75	6.75	6.88	7.21	6.5	6.81
MAX	8.88	7.07	8.42	8.25	8	8	8.75	8.06	8.56	8.6	8.25	7.69	8.63	8.3	8.1	8.25	8.7	8.75
Sl																		
MEAN	10.12	8.02	8.66	8.01	7.75	8.63	7.89	8.05	8.54	8.4	8.06	7.39	8.4	7.82	7.88	8.03	7.73	7.78
MEDIAN	10.25	7.94	8.57	7.975	7.83	8.63	7.93	8.15	8.48	8.25	8.09	7.37	8.51	7.82	7.9	7.87	7.7	7.74
SD	0.44	0.46	0.32	0.47	0.6	0.34	0.62	0.29	0.4	0.26	0.26	0.26	0.44	0.36	0.24	0.48	0.3	0.38
MIN	9.39	6.88	8.13	7	6	8.15	6.94	7.67	8.1	8.25	7.5	6.86	7.83	7.25	7.5	7.58	7.08	6.69
MAX	10.94	8.72	9.2	9.25	8.71	9.19	9	8.45	9.25	8.7	8.44	7.96	8.75	8.38	8.23	8.64	8.5	9
Ca																		
MEAN	6.25	6.34	6.8	5.6	5.75	6.12	5.75	5.68	5.94	6.05	5.53	5.49	5.35	5.83	5.52	5.62	5.61	5.67
MEDIAN	6.2	6.33	6.71	5.54	5.92	6.06	5.7	5.61	5.81	5.93	5.48	5.5	5.32	5.85	5.54	5.61	5.62	5.74
SD	0.28	0.12	0.4	0.39	0.52	0.21	0.5	0.21	0.45	0.24	0.32	0.22	0.26	0.41	0.25	0.25	0.27	0.29
MIN	5.89	6.17	6.15	4.42	4.83	5.75	5	5.54	5.46	5.9	5.05	4.94	5.13	4.9	4.85	5.25	4.94	5.05
MAX	6.69	6.57	7.7	6.36	6.75	6.5	6.5	6.19	6.86	6.33	6.33	5.91	5.64	6.5	5.8	5.94	6.31	6.2
Nt																		
MEAN	5.48	5.76	6.35	6.55	6.02	5.98	4.83	6.39	6.94	7.28	6.98	7.11	7.07	7.18	7.25	7.1	7.17	6.89
MEDIAN	5.47	5.79	6.32	6.62	6.11	5.96	4.81	6.41	7.07	7.36	7.03	7.19	7.13	7.33	7.2	7.1	7.25	6.88
SD	0.14	0.52	0.25	0.47	0.61	0.15	0.65	0.19	0.34	0.36	0.27	0.27	0.21	0.34	0.46	0.48	0.32	0.37
MIN	5.25	4.88	5.93	5.58	4.69	5.76	3.25	6.08	6.36	6.89	6.63	6.45	6.77	6.38	6.29	6.56	6.5	6.18
MAX	5.67	6.79	6.8	7.67	7.08	6.31	5.75	6.75	7.5	7.6	7.38	7.75	7.25	7.7	8.05	7.92	7.8	7.75
Ae																		
MEAN	7.65	7.87	7.91	9.26	7.9	7.83	5.91	8.92	8.58	8.66	8.89	9.66	9.02	9.03	9.8	9.43	9.23	9.15

MEDIAN	7.66	7.86	8	9.23	8	7.79	5.83	9.08	9.31	8.6	9	9.72	9.38	9.15	9.91	9.75	9.33	9.23
SD	0.29	0.33	0.46	1.33	1.58	0.28	0.43	0.79	1.41	0.31	0.59	0.7	0.99	0.59	0.63	0.75	0.47	0.56
MIN	7.13	7.33	7	6	5.5	7.33	5.4	7.42	6.21	8.39	7.33	7.45	7.55	7.85	8.1	7.94	8.23	7.88
MAX	8.08	8.33	8.57	14	11	8.33	6.67	9.86	9.69	9	9.86	10.75	9.75	10.17	10.61	9.95	10.3	10.67
Tm																		
MEAN	9.21	8.49	9.11	8.47	8.55	8.90	8.95	8.72	8.95	9.88	8.89	9.07	8.54	8.73	8.86	8.89	8.94	8.94
MEDIAN	9.13	8.5	9.13	8.46	8.67	8.88	8.83	8.72	8.88	9.94	8.79	9.05	8.5	8.69	8.94	8.88	8.86	8.84
SD	0.26	0.54	0.29	0.46	0.6	0.19	0.37	0.09	0.26	0.16	0.28	0.29	0.13	0.26	0.23	0.26	0.22	0.36
MIN	8.92	7.71	8.64	7.33	6	8.58	8.5	8.54	8.65	9.7	8.63	8.39	8.42	8.25	8.29	8.56	8.57	8.55
MAX	9.67	9.33	9.67	9.8	9.5	9.27	9.83	8.84	9.6	10	9.63	9.63	8.73	9.29	9.2	9.25	9.4	10.38
Om																		
MEAN	10.62	11.57	11.18	11.45	11.41	10.48	10.16	11.06	11.65	11.98	12.12	11.84	12.47	12.18	11.92	11.86	11.9	12.03
MEDIAN	10.63	11.63	11.17	11.42	11.33	10.46	10.25	11.19	11.65	11.83	12.13	11.85	12.5	12.29	11.87	12.02	11.92	12.07
SD	0.31	0.63	0.48	0.58	0.93	0.12	0.43	0.42	0.35	0.47	0.45	0.39	0.32	0.48	0.29	0.51	0.37	0.44
MIN	10.11	9.75	10.4	10.33	10	10.25	9.43	10.28	10.79	11.6	11.1	11.21	12.14	11.4	11.59	11.17	11.11	10.63
MAX	11	12.25	12	13	15	10.75	10.8	11.43	12.12	12.5	12.95	12.55	12.75	13.13	12.63	12.33	12.83	12.85
Kn																		
MEAN	9.49	8.21	7.68	8.45	8.29	9.54	10.19	9.12	9.06	9.13	8.56	8.89	8.58	8.63	8.84	9.02	8.81	8.82
MEDIAN	9.43	8.25	7.74	8.43	8	9.54	10	9.11	9	9.1	8.6	8.9	8.54	8.67	8.81	8.94	8.81	8.75
SD	0.23	0.27	0.29	0.51	1.2	0.24	0.96	0.21	0.19	0.35	0.18	0.21	0.12	0.17	0.21	0.48	0.19	0.27
MIN	9.23	7.67	7.2	6.5	5	9.14	9.29	8.82	8.87	8.79	8.25	8.38	8.5	8.29	8.6	8.56	8.44	8.39
MAX	10	8.67	8.14	9.5	11	10	13	9.44	9.56	9.5	8.96	9.2	8.75	9	9.41	9.83	9.21	9.83
Cr																		
MEAN	8.19	8.12	9.02	8.03	8.09	7.99	8.06	7.88	8.12	9.04	8	8.07	8.02	7.75	7.95	7.79	8.1	8.09
MEDIAN	8.15	8.13	9.06	8	8	8	8	7.91	8.15	8.9	7.93	8.05	8.13	7.67	8	7.76	8.13	7.96
SD	0.33	0.4	0.33	0.47	0.53	0.16	0.33	0.14	0.61	0.62	0.29	0.36	0.23	0.33	0.35	0.46	0.22	0.4
MIN	7.67	7.57	8.43	7	7	7.73	7.33	7.65	7.43	8.5	7.63	7	7.67	7.2	7.42	7.06	7.5	7.54
MAX	8.88	9	9.5	9	9.5	8.27	8.75	8.08	9.29	9.71	8.69	8.81	8.14	8.45	8.5	8.43	8.5	9.25
Lc																		
MEAN	7.69	7.75	7.6	7.37	7.38	7.64	7.88	7.2	7.42	7.57	7.36	7.14	7.57	7.36	7.33	7.33	7.33	7.33
MEDIAN	7.71	7.71	7.6	7.33	7.33	7.62	7.83	7.21	7.37	7.6	7.38	7.15	7.61	7.4	7.36	7.32	7.34	7.33
SD	0.09	0.15	0.09	0.3	0.26	0.07	0.11	0.14	0.14	0.06	0.18	0.18	0.1	0.19	0.09	0.23	0.11	0.12
MIN	7.56	7.5	7.43	6.67	6.8	7.5	7.67	7	7.28	7.5	6.96	6.67	7.42	6.92	7.17	7.06	7	7
MAX	7.83	8	7.8	8	8	7.77	8	7.38	7.65	7.61	7.63	7.5	7.63	7.75	7.45	7.71	7.6	7.67

Notes: numbers mark syntaxa Isoëto-Nanojuncetea: 1 – *Middendorfio borysthenicae-Crypsietum alopecuroidis*; 2 – *Stellario uliginosae-Isolepidetum setaceae*; 3 – *Cyperetum flavescentis*; 4 – *Cyperetum micheliani*; 5 – *Juncetum bufonii;* 6 – *Pulicario vulgaris-Menthetum pulegii*; 7 – *Eragrostidetum suaveolentis*; 8 – *Veronico anagalloidis-Lythretum hyssopifoliae*; Bidentetea: 1 – *Chenopodietum rubri*; 2 – *Xanthio riparii-Chenopodietum rubri*; 3 – *Bidenti frondosae-Atriplicetum prostratae*; 4 – *Junco bufonii-Bidentetum connatae*; 5 – *Rumici maritimi-Ranunculetum scelerathi*; 6 – *Polygonetum hydropiperis*; 7 – *Bidentetum cernuae*; 8 – *Bidentetum tripartitae*; 9 – *Leersio-Bidentetum*; 10 – *Myosotono aquatici-Bidentetum frondosae*

The class *Bidentetea* includes plant communities of tall annual wetland herbs in wet and nutrient-rich habitats both natural and man-made. The stands occupy the muddy alluvial sediments of river banks, ponds, reservoirs, canals, wet ditches, wet forest clearings, etc. The plant communities of the class are often present in habitats of forest and forest-steppe zones but are rarely in the steppe zone of Ukraine. In general, the distribution of 10 associations of *Bidentetea* were detected (Fig. 8-11). The main factors for their territorial differentiation are: the mechanical composition of the soil, the relief of newly-formed ecotopes, soil humidity, the duration of surface flooding, as well as the degree of anthropogenic impact.

The alliance *Bidention tripartitae* combines coenoses of annual wetland species, mainly belonging to the genera *Bidens* L., *Persicaria* Mill., *Ranunculus* L., *Rumex* L. and *Xanthium* L. They occur on wet loamy or clayey nutrient-rich soils. The alliance *Chenopodion rubri* includes communities of annual species of the genera *Atriplex* L. and *Chenopodium* L. on saline nitrified substrata. Blocks of diagnostic species at the level of associations are quite clear (Fig. 12, Table 3).

The class *Bidentetea* is spread throughout the territory of Europe. It is also represented by one order and two alliances: *Bidention tripartitae* and *Chenopodion rubri*, but differs in a large number of associations, which is caused by a variety of habitats as well as physico-geographical conditions of the different regions. For all European regions there are typical associations: *Rumici maritimi-Ranunculetum scelerati*, *Bidentetum cernuae*, *Bidentetum tripartitae*, *Polygonetum hydropiperis* and *Chenopodietum rubri*. Other ones are confined only to certain territories.

Fig. 8. *Junco bufonii-Bidentetum connatae* in the dried reclamation canal (near the village of Astei, Beregiv district, Zakarpattia region, 14.07.2012) (Photo by L. Felbaba-Klushyna)

Fig. 9. *Bidentetum cernuae* near the village of Synevyrska Polyana, Khust district, Zakarpattia region (31.08.2019) (Photo by M. Shevera)

Fig. 10. *Bidentetum tripartitae* on the left bank of the River Desenka (near the city of Kyiv, Kyiv region, 26.08.2019) (Photo by L. Makhynya)

Fig. 11. *Myosoto aquatici-Bidentetum frondosae* in the floodplain of the River Dnieper (near the village of Protsiv, Boryspil district, Kyiv region, 15.07.2019). (Photo by L. Makhynya)

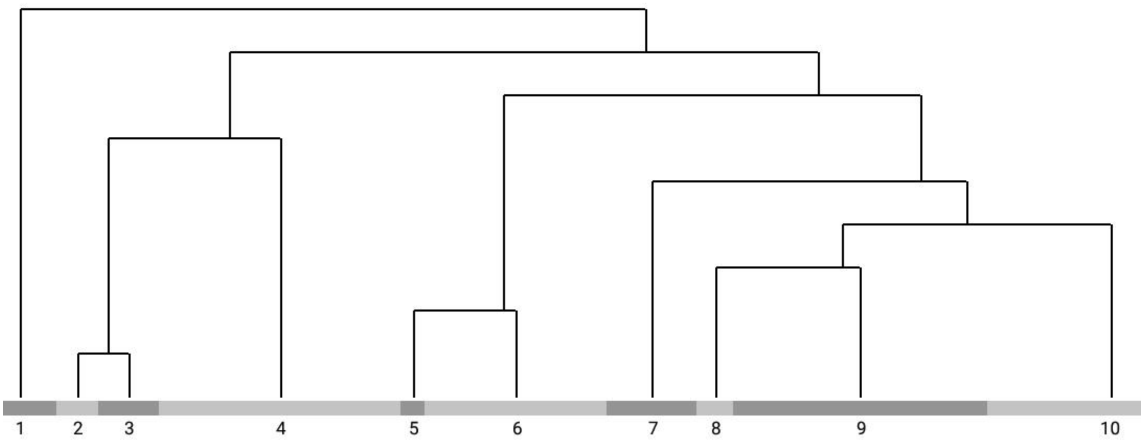

Fig. 12. Cluster analysis of the phytosociological data of the class *Bidentetea*. Clusters mark association: 1 –*Chenopodietum rubri*; 2 – *Xanthio riparii-Chenopodietum rubri*; 3 – *Bidenti frondosae-Atriplicetum prostratae*; 4 – *Junco bufonii-Bidentetum connatae*; 5 – *Rumici maritimi-Ranunculetum scelerathi*; 6 – *Polygonetum hydropiperis*; 7 – *Bidentetum cernuae*; 8 – *Bidentetum tripartitae*; 9 – *Leersio-Bidentetum*; 10 – *Myosotono aquatici-Bidentetum frondosae*

Table 3. Synoptic table of the class *Bidentetea*

No. of syntaxa	1	2	3	4	5	6	7	8	9	10
Number of relevés	12	3	14	41	4	30	15	6	42	40
Malva neglecta	100.0	–	–	–	–	–	–	–	–	–
Chenopodium glaucum	100.0	–	–	–	–	–	–	–	–	–
Polygonum aviculare	77.8	–	–	–	–	–	–	–	5.4	–
Rorippa amphibia	53.4	–	–	–	–	–	–	11.4	–	–
Polygonum lapathifolium	45.7	–	–	–	–	–	17.2	–	–	–
Cichorium intybus	45.5	–	–	–	–	–	–	–	–	–
Oenanthe aquatica	42.4	–	–	–	–	–	12.3	–	–	–
Sparganium erectum	36.7	–	–	–	–	–	16.5	–	–	–
Iva xanthiifolia	35.9	–	–	–	–	–	–	–	–	1.4
Sonchus arvensis	35.9	–	–	–	–	–	–	–	–	1.4
Atriplex patula	35.9	–	–	–	–	–	–	–	–	1.4
Rumex hydrolapathum	33.5	–	–	–	–	–	17.3	24.5	–	–
Daucus carota	33.3	–	–	6.3	–	–	–	–	–	–
Epilobium palustre	31.8	–	–	3.4	–	2.1	9.1	–	10.6	–
Capsella bursa-pastoris	31.2	–	10.4	–	–	–	–	–	–	–
Ranunculus sceleratus	29.8	–	4.2	–	7.4	–	14.9	–	–	–
Caltha palustris	29.0	–	–	–	–	15.2	–	–	–	–
Sisymbrium loeselii	27.5	–	–	–	–	–	–	–	–	–
Potentilla reptans	27.5	–	–	–	–	–	–	–	–	–
Artemisia campestris	27.5	–	–	–	–	–	–	–	–	–
Fallopia convolvulus	27.5	–	–	–	–	–	–	–	–	–
Galinsoga parviflora	27.5	–	–	–	–	–	–	–	–	–
Stellaria palustris	27.5	–	–	–	–	–	–	–	–	–
Tripolium pannonicum	–	80.2	–	–	–	–	–	–	–	–
Apium graveolens	–	80.2	–	–	–	–	–	–	–	–
Arctium lappa	–	67.1	–	–	–	–	–	–	–	–
Xanthium albinum	–	64.4	0.2	–	–	–	–	–	8.0	7.2
Humulus lupulus	–	58.1	–	–	–	–	2.1	5.6	0.6	–
Rumex pseudoalpinus	–	55.7	–	–	–	–	–	–	–	–
Polygonum patulum	–	53.4	–	–	–	–	–	–	–	–
Plantago major	–	50.5	–	–	–	–	–	–	9.1	5.2
Echinochloa crus-galli	–	48.0	–	–	9.2	–	–	16.9	–	–
Sonchus oleraceus	–	47.7	4.7	–	–	–	–	–	–	–
Elytrigia repens	–	40.8	–	–	–	–	–	16.4	–	–
Calystegia sepium	–	27.6	5.7	11.7	–	–	–	–	5.7	–
Bidens frondosa	9.8	26.8	12.2	16.9	–	–	13.2	–	23.6	21.7
Scutellaria galericulata	–	–	42.0	1.9	–	–	1.0	–	–	–
Equisetum palustre	–	–	33.8	17.0	–	–	–	–	–	8.5
Chenopodium album	0.1	–	33.2	13.6	–	–	–	–	–	2.1

ag.										
Tanacetum vulgare	–	–	32.7	–	–	–	–	–	–	2.1
Leontodon autumnalis	–	–	31.7	–	–	–	–	–	–	15.8
Achillea pyrenaica	–	–	30.6	–	–	–	–	–	11.0	15.4
Rorippa palustris	–	–	28.8	–	11.4	–	–	–	12.5	13.8
Eleocharis acicularis	–	–	27.4	–	–	–	14.4	–	0.5	0.9
Trifolium arvense	–	–	25.4	–	–	–	–	–	–	–
Filipendula denudata	–	–	25.4	–	–	–	–	–	–	–
Carduus acanthoides	–	–	25.4	–	–	–	–	–	–	–
Bidens connata	–	–	–	95.9	–	–	–	–	–	–
Juncus bufonius	–	–	–	64.9	–	–	–	–	12.2	8.6
Thelypteris palustris	–	–	–	47.3	–	–	–	–	–	–
Cicuta virosa	–	–	–	42.3	–	–	–	–	–	–
Typha latifolia	–	–	–	36.6	–	–	–	–	–	–
Urtica dioica	–	–	–	36.0	–	8.6	–	–	22.5	–
Equisetum sylvaticum	–	–	–	25.8	–	–	–	–	–	–
Rumex maritimus	–	–	–	–	98.2	–	–	–	–	–
Juncus effusus	–	–	–	–	75.2	–	–	–	–	–
Festuca ovina	–	–	–	–	48.0	–	–	–	–	–
Lepidium ruderale	–	–	–	–	48.0	–	–	–	–	–
Salix viminalis	–	–	–	–	45.4	–	–	–	–	–
Agrostis capillaris	–	–	–	–	41.6	6.7	–	–	–	–
Taraxacum officinale ag.	–	–	–	–	33.5	3.7	–	–	–	5.0
Scirpus sylvaticus	–	–	–	–	33.0	24.9	–	–	–	–
Ranunculus repens	–	–	11.4	–	23.0	41.9	–	–	–	–
Polygonum minus	–	–	–	–	–	35.9	–	–	–	1.4
Poa annua	–	–	–	–	–	35.3	–	–	–	4.6
Rorippa sylvestris	–	–	–	–	–	34.9	–	–	–	–
Chamomilla suaveolens	–	–	–	–	–	34.9	–	–	–	–
Polygonum hydropiper	–	–	3.8	8.0	–	32.4	5.7	–	19.7	12.3
Deschampsia cespitosa	–	–	–	–	–	31.4	–	–	–	2.4
Polygonum mite	–	–	–	–	–	30.2	–	–	–	–
Lolium perenne	–	–	–	–	–	30.2	–	–	–	–
Cirsium arvense	–	–	–	–	–	26.3	–	–	–	12.6
Bidens radiata	3.0	–	–	–	–	–	65.4	–	–	–
Myosoton aquaticum	–	–	–	–	–	–	54.2	–	7.2	–
Bidens cernua	–	–	–	–	–	–	44.7	–	19.8	11.6
Scirpus lacustris	3.5	–	1.8	–	–	–	39.1	–	1.8	–
Glyceria maxima	–	–	–	–	–	–	38.4	15.0	–	2.1
Polygonum amphibium	19.3	–	–	–	–	–	35.3	–	–	–
Sium latifolium	5.7	–	–	4.1	–	–	34.6	–	0.1	–
Carex acuta	–	10.3	–	14.9	–	–	32.2	–	4.4	–
Lythrum salicaria	19.0	12.0	–	–	–	–	28.9	–	7.9	–
Phragmites australis	–	–	–	4.9	–	–	25.5	7.2	15.0	–
Eragrostis pilosa	–	–	–	–	–	–	–	55.7	–	–
Poa palustris	5.1	–	–	–	–	–	–	43.4	–	–
Epilobium parviflorum	–	–	–	–	–	–	–	39.1	–	–
Achillea cartilaginea	–	–	–	–	–	–	–	39.1	–	–
Agrostis gigantea	–	–	–	–	–	–	–	39.1	–	–
Polygonum bistorta	–	–	–	–	–	–	–	39.1	–	–
Amorpha fruticosa	–	–	–	–	–	–	–	39.1	–	–
Berula erecta	–	–	–	–	–	–	–	39.1	–	–
Urtica galeopsifolia	–	–	–	–	–	–	–	39.1	–	–
Scutellaria hastifolia	–	–	–	–	–	–	–	39.1	–	–
Festuca pratensis	–	–	–	–	–	–	–	36.0	1.2	–
Lycopus exaltatus	–	–	–	–	–	–	–	35.9	–	1.4
Carex acutiformis	–	–	–	–	–	3.2	–	34.9	–	–
Phalacroloma annuum	–	–	–	0.7	–	–	–	33.4	0.5	–
Rumex acetosella	–	–	–	–	–	–	–	27.5	8.5	4.2
Butomus umbellatus	17.6	–	–	–	–	–	11.9	27.1	–	–
Leersia oryzoides	–	–	–	23.3	–	–	–	–	40.7	–
Ambrosia artemisiifolia	–	–	–	–	–	–	–	–	36.1	–
Mentha spicata	–	–	12.0	5.5	–	–	–	–	5.2	27.2

Mentha arvensis	30.1	–	–	–	–	–	28.4	21.6	–	–
Galium palustre	28.8	–	–	–	–	–	31.3	–	–	–
Phalaris arundinacea	27.7	–	–	–	–	–	35.4	8.5	–	–
Atriplex prostrata	–	65.7	65.7	–	–	–	–	–	–	–
Agrostis canina	–	–	41.7	–	–	–	–	–	1.7	35.7
Potentilla anserina	–	–	36.5	–	0.4	14.7	–	–	–	27.6
Chenopodium rubrum	–	–	26.6	–	32.2	–	–	–	–	–
Bidens tripartita	–	–	18.6	–	11.3	1.2	–	28.2	26.6	4.6
Juncus capitatus	–	–	–	–	–	–	–	–	13.9	21.3
Galium verum	–	–	–	–	–	–	–	–	–	21.3
Trifolium repens	–	–	8.5	–	–	7.6	–	–	–	19.2
Carex riparia	–	–	–	–	–	–	–	–	–	15.0
Convolvulus arvensis	–	–	–	–	–	–	–	–	–	15.0
Xanthium strumarium	–	–	–	–	–	–	–	–	–	15.0
Malva pusilla	–	–	–	–	–	–	–	–	–	15.0
Trifolium pratense	–	–	–	–	–	–	–	–	–	15.0
Cyperus fuscus	–	–	–	–	–	–	–	–	–	15.0
Arctium tomentosum	–	–	–	–	–	–	–	–	–	15.0
Equisetum arvense	–	–	–	–	–	–	–	–	–	15.0
Althaea officinalis	–	–	–	–	–	–	–	–	–	15.0
Populus nigra	–	–	–	–	–	–	–	–	–	15.0
Tragopogon borysthenicus	–	–	–	–	–	–	–	–	–	15.0
Lactuca serriola	–	–	–	–	–	–	–	–	–	15.0
Cynodon dactylon	–	–	–	–	–	–	–	–	–	15.0
Anthriscus sylvestris	–	–	–	–	–	–	–	–	–	15.0
Galeopsis bifida	–	–	–	–	–	–	–	–	–	15.0
Beckmannia eruciformis	–	–	–	–	–	–	–	–	–	15.0
Triglochin palustre	–	–	–	–	–	–	–	–	–	15.0
Geranium robertianum	–	–	–	–	–	–	–	–	–	15.0
Cardamine impatiens	–	–	–	–	–	–	–	–	–	15.0
Rorippa austriaca	–	–	–	–	–	–	–	–	–	15.0
Rumex crispus	–	–	–	–	–	–	–	–	–	15.0
Rubus idaeus	–	–	–	–	–	–	–	–	–	15.0
Ballota nigra	–	–	–	–	–	–	–	–	–	15.0
Ranunculus polyanthemos	–	–	–	–	–	–	–	–	–	15.0
Trifolium fragiferum	–	–	–	–	–	–	–	–	–	15.0
Rumex thyrsiflorus	–	–	–	–	–	–	–	–	–	15.0
Potentilla erecta	–	–	–	–	–	–	–	–	–	15.0
Calamagrostis canescens	–	–	–	–	–	–	–	–	–	15.0
Impatiens glandulifera	–	–	–	–	–	–	–	–	–	15.0
Veronica anagallis-aquatica	–	–	–	1.9	–	–	–	–	14.0	14.9
Polygonum persicaria	–	–	6.6	–	–	11.6	–	2.1	15.6	14.7
Rumex acetosa	–	–	–	1.6	–	3.8	–	–	7.4	14.3
Veronica longifolia	–	–	8.4	–	–	–	–	–	17.9	14.1
Armoracia rusticana	–	–	18.0	–	–	–	–	–	–	11.5
Inula britannica	–	–	24.0	–	–	–	–	–	20.5	10.7
Setaria viridis	20.3	–	–	–	–	–	–	–	–	10.7
Odontites vulgaris	–	–	9.3	–	–	–	–	–	14.2	10.0
Filipendula vulgaris	–	–	–	–	–	–	–	–	9.1	9.6
Carduus crispus	–	–	–	–	–	–	–	–	9.1	9.6
Gratiola officinalis	–	–	22.6	–	–	–	–	–	3.7	9.1
Lycopus europaeus	7.6	–	11.5	19.1	–	–	22.0	2.0	9.9	8.7
Alopecurus geniculatus	–	–	–	–	–	12.0	–	–	–	8.4
Echinocystis lobata	14.8	–	12.0	–	–	–	–	–	–	6.9
Myosotis scorpioides	2.5	–	7.0	2.9	–	5.7	12.1	–	4.8	5.7
Carex hirta	21.0	–	5.0	–	–	9.8	–	–	–	5.6
Glyceria fluitans	–	–	–	–	–	20.1	–	–	–	5.5
Amaranthus retroflexus	–	–	21.1	–	–	–	–	–	–	5.2
Vicia cracca	–	–	21.1	–	–	–	–	–	–	5.2

Setaria pumila	–	–	–	13.2	–	–	–	–	4.8	5.2
Conium maculatum	–	–	–	13.2	–	–	–	–	4.8	5.2
Agrostis stolonifera	–	–	–	4.4	–	4.7	0.2	13.7	7.3	4.7
Campanula glomerata	–	–	–	3.8	–	–	–	–	18.1	3.9
Stellaria media	–	–	–	–	–	6.3	16.3	–	–	3.8
Artemisia vulgaris	–	–	7.2	3.0	–	6.4	6.4	–	–	3.2
Solanum dulcamara	7.9	–	–	14.7	–	10.8	–	–	–	2.1
Glechoma hederacea	–	–	–	18.9	–	–	–	–	12.6	1.4
Eupatorium cannabinum	–	–	4.3	–	–	–	14.4	–	23.6	0.9
Achillea collina	18.1	–	3.4	–	–	12.9	–	–	3.4	0.1
Mentha aquatica	–	17.0	5.9	8.7	9.3	–	–	1.5	–	–
Symphytum officinale	9.3	–	–	–	–	0.0	–	24.8	–	–
Anagallis arvensis	–	–	–	–	–	–	–	–	14.7	–
Angelica sylvestris	–	–	–	–	–	–	–	–	14.7	–
Potentilla argentea	–	–	–	–	–	–	–	–	14.7	–
Coronilla varia	–	–	–	–	–	–	–	–	14.7	–
Bolboschoenus maritimus	–	–	–	–	–	–	–	–	14.7	–
Galium album	–	–	–	–	–	–	–	–	14.7	–
Acorus calamus	–	–	–	–	–	–	–	–	14.7	–
Geranium palustre	–	–	–	–	–	–	–	–	14.7	–
Zizania aquatica	–	–	–	–	–	–	–	–	14.7	–
Geum urbanum	–	–	–	14.8	–	–	–	–	–	–
Aristolochia clematitis	–	–	–	14.8	–	–	–	–	–	–
Equisetum hyemale	–	–	–	14.8	–	–	–	–	–	–
Ranunculus acris	–	–	–	14.8	–	–	–	–	–	–
Alopecurus aequalis	–	–	–	–	–	17.3	–	–	–	–
Melandrium album	–	–	–	–	–	17.3	–	–	–	–
Poa trivialis	–	–	–	–	–	17.3	–	–	–	–
Geranium pusillum	–	–	–	–	–	17.3	–	–	–	–
Anthoxanthum odoratum	–	–	–	–	–	17.3	–	–	–	–
Betula pubescens	–	–	–	–	–	17.3	–	–	–	–
Scrophularia nodosa	–	–	–	–	–	17.3	–	–	–	–
Verbascum nigrum	–	–	–	–	–	17.3	–	–	–	–
Salix alba	–	–	–	–	–	17.3	–	–	–	–
Ranunculus flammula	–	–	–	–	–	17.3	–	–	–	–
Lythrum portula	–	–	–	–	–	17.3	–	–	–	–
Galeopsis tetrahit	–	–	–	–	–	17.3	–	–	–	–
Lysimachia nummularia	–	–	18.3	10.4	–	5.0	–	–	1.7	–
Epilobium angustifolium	–	–	–	–	–	–	–	–	20.8	–
Prunella vulgaris	–	–	–	–	–	–	–	–	20.8	–
Peucedanum palustre	–	–	–	–	–	–	–	–	20.8	–
Crepis tectorum	–	–	–	–	–	–	–	–	20.8	–
Lythrum virgatum	–	–	–	21.0	–	–	–	–	–	–
Poa pratensis	–	–	–	–	–	12.2	–	–	8.0	–
Catabrosa aquatica	–	–	–	–	–	12.2	–	–	8.0	–
Conyza canadensis	–	–	19.0	10.1	23.7	–	–	–	–	–
Trifolium hybridum	–	–	–	–	–	–	24.6	–	–	–
Epilobium species	–	–	–	–	–	–	24.6	–	–	–
Sisymbrium officinale	–	–	–	–	–	24.6	–	–	–	–
Myosotis species	–	–	–	–	–	–	24.6	–	–	–
Rumex confertus	–	–	4.9	–	–	–	15.1	–	20.7	–
Ranunculus reptans	–	–	–	–	–	–	20.3	–	5.2	–
Chelidonium majus	–	–	–	–	–	–	20.3	–	5.2	–
Glyceria plicata	–	–	–	–	–	20.3	–	–	5.2	–
Berteroa incana	–	–	21.2	–	–	–	–	–	4.9	–
Typha angustifolia	–	–	–	–	–	–	15.1	–	16.5	–
Solanum nigrum	–	–	–	23.1	–	–	–	–	9.2	–
Lysimachia vulgaris	–	–	13.5	3.1	–	7.1	2.1	–	9.9	–
Urtica urens	–	–	–	8.5	–	–	13.3	–	8.2	–

Verbascum phlomoides	–	–	–	14.6	–	–	–	–	20.3	–
Tussilago farfara	–	–	13.9	–	–	21.3	–	–	–	–
Epilobium hirsutum	16.2	–	–	–	–	20.3	–	–	–	–
Sonchus palustris	–	–	–	7.4	–	–	11.8	–	13.0	–
Galium aparine	–	–	10.5	17.5	–	–	0.2	13.7	–	–
Oenothera biennis	–	–	8.5	8.9	–	–	–	–	22.8	–
Alisma plantago-aquatica	6.8	–	–	12.5	–	3.1	24.9	–	–	–
Stachys palustris	–	–	–	2.1	–	–	–	23.0	14.6	–
Sagittaria sagittifolia	22.5	–	–	10.4	–	–	5.0	–	1.7	–
Senecio vulgaris	–	–	5.8	23.1	–	–	5.0	–	5.8	–
Calamagrostis epigeios	–	–	6.0	–	18.4	–	4.9	8.8	3.2	–

Notes: numbers mark syntaxa: 1 – *Chenopodietum rubri*; 2 – *Xanthio riparii-Chenopodietum rubri*; 3 – *Bidenti frondosae-Atriplicetum prostratae*; 4 – *Junco bufonii-Bidentetum connatae*; 5 – *Rumici maritimi-Ranunculetum scelerathi*; 6 – *Polygonetum hydropiperis*; 7 – *Bidentetum cernuae*; 8 – *Bidentetum tripartitae*; 9 – *Leersio-Bidentetum*; 10 – *Myosotono aquatici-Bidentetum frondosae*

According to the results of the ordination and gradient analysis of *Bidentetea* plant communities, it was found that their differentiation occurs mainly along gradients of soil acidity and light regime of their habitats (Fig. 13, Table 2). In addition, the ecological distribution of syntaxa of the class is significantly affected by the concentration of mineral nitrogen compounds in the soil, variability of damping and the ombroregime. The associations *Rumici maritimi-Ranunculetum scelerathi* and *Polygonetum hydropiperis* are especially sensitive to these factors. In the ecological differentiation of the communities *Xanthio riparii-Chenopodietum rubri* the gradient of the thermoregime is of significant importance.

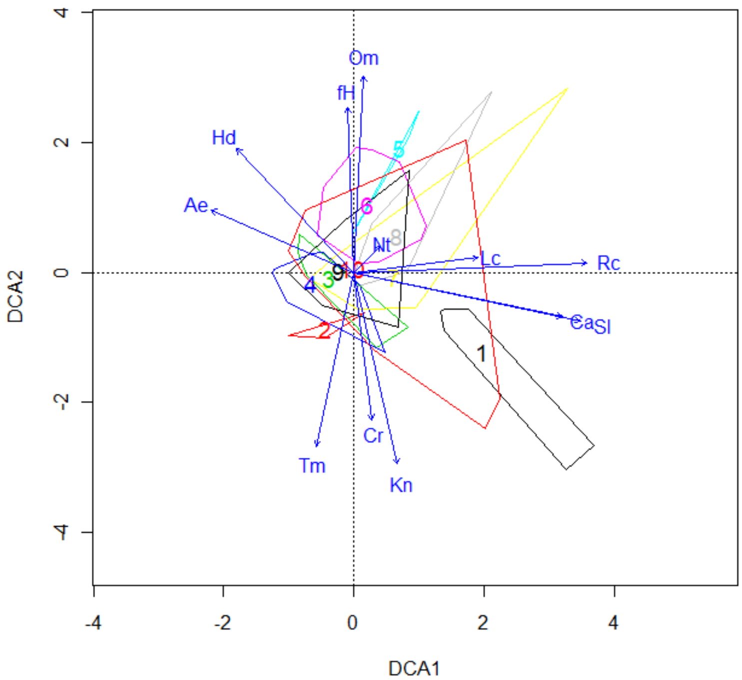

Fig. 13. Results of the ordination analysis of syntaxa in the class *Bidentetea*

Numbers mark syntaxa: 1 – *Chenopodietum rubri*; 2 – *Xanthio riparii-Chenopodietum rubri*; 3 – *Bidenti frondosae-Atriplicetum prostratae*; 4 – *Junco bufonii-Bidentetum connatae*; 5 – *Rumici maritimi-Ranunculetum scelerathi*; 6 – *Polygonetum hydropiperis*; 7 – *Bidentetum cernuae*; 8 – *Bidentetum tripartitae*; 9 – *Leersio-Bidentetum*; 10 – *Myosotono aquatici-Bidentetum frondosae*

4. Discussion

The pioneer vegetation of the classes *Isoëto-Nanojuncetea* and *Bidentetea*, due to their seasonal development and short life cycles, is a subject for discussion. French, Italian, Spanish and Portuguese syntaxonomists characterize both classes as pioneer ephemeral vegetation (Rivas-Martínez et al., 2001; Bardat et al., 2004; Biondi et al., 2014). Russian scientists classify communities of the class *Isoëto-Nanojuncetea* as shoreline aquatic vegetation (Golovanov & Abramova, 2012). Hungarian and Bulgarian scientists include these discussed phytocoenoses in wetland vegetation (Borhidi, 2003; Tzonev et al., 2009). Czech phytocoenologists have also classified *Isoëto-Nanojuncetea* and *Bidentetea* as a part of wetland vegetation (Chytrý, 2011). In the "Vegetation of Europe ..." (Mucina et al., 2016), the class *Isoëto-Nanojuncetea* is assigned to the vegetation of freshwater springs, shorelines, and swamps. At the same time, the class *Bidentetea* is included in anthropogenic vegetation. It should be noted that the class *Bidentetea* are often presented in ruderal vegetation, due to its high level of synanthropization (Osypenko & Shevchyk, 2001; Borhidi, 2003; Abramova & Golovanov, 2016; Ermakov, 2012; Dubyna et al., 2019). The last reason is not sufficiently substantiated in our opinion. The phytocoenoses of this mentioned class grow in specific conditions of newly-formed ecotopes, favourable for the invasion of alien species. That's why plant communities of the class *Bidentetea* have relationships with phytocoenoses of nitrophylic weeds of the order *Chenopodietalia albi* (that belong to the class *Stellarietea mediae*), given that the excess nitrogen in the littoral zone is favourable for the distribution of nitrophylic species (Bissels et al., 2005). This also leads to the uncertain and debatable syntaxonomical status of the alliance *Chenopodion rubri*, which is sometimes included in the classes *Chenopodietea* or *Stellarietea mediae* (Galchenko, 2006). However, phytocoenoses of *Bidentetea* occupy both wetlands that are natural, or semi-natural, ruderalized habitats and have their specific floristic composition with *Bidens tripartita*, *B. cernua*, *B. frondosa*, *Leersia oryzoides*, *Persicaria hydropiper*, *P. lapathifolia*, *Ranunculus sceleratus*, *Rumex maritimus* (Stępień & Rosadziński, 2020).

A debatable point is also the correlation between the communities of the classes *Isoëto-Nanojuncetea* and *Crypsietea aculeatae*. Italian, Spanish, and French phytosociologists consider that the class *Crypsietea aculeatae* is a syntaxonomic synonym of the class *Isoëto-Nanojuncetea* (Bardat et al., 2004; Biondi et al., 2014; Rivas-Martínez et al., 2001). Bulgarian scientists relate the order *Crypsietalia aculeatae* to the class *Isoëto-Nanojuncetea* (Tzonev et al., 2009). Rodwell et al. (2002) have the same point of view and distinguish 3 alliances: subsaline vegetation in the class *Isoëto-Nanojuncetea*: *Cypero-Spergularion salinae*, *Polygono salsuginei-Crypsion aculeatae* and *Puccinellion peisonis*. In our opinion both of the classes mentioned are different syntaxa of the highest rank, firstly, according to the salt regime of the soil. However, in the future, the syntaxonomic position of some syntaxa remains to be clarified, in particular, the association *Middendorfio borysthenicae-Crypsietum alopecuroidis* (Shapoval, 2006) and the alliance *Myosuro-Beckmannion eruciformis* (Shapoval 2006), described from the area of depressions within saline soils in the steppe zone of Ukraine. The results of phytosociological analysis show that their floristic composition is closer to the alliance *Beckmannion eruciformis* Soó 1933. In this regard, further research is necessary in this direction as well as to establish the correct syntaxonomy nomenclature of the class *Isoëto-Nanojuncetea* in Europe (Tomaselli et al., 2020).

Unlike the *Isoëto-Nanojuncetea*, the syntaxonomy of the *Bidentetea* class is more determined and stable. The plant communities of the class, which is widespread throughout Europe, are combined in one order *Bidentetalia tripartitae* and two alliances: *Bidention tripartitae* and *Chenopodion glauci* (Mucina et al., 2016).

In addition to taxonomic and syntaxonomic differentiation, analysis of the structure of the annual herb vegetation of shorelines and littoral zones of water bodies of Ukraine made it possible to identify functional information through the distribution of communities in ecological space. In fact, our results are consistent with previous studies (Šumberová & Hrivnák, 2013; Altenfelder et al., 2014), demonstrating that the main factor in the ecological differentiation of these phytocoenoses is the soil humidity regime. In addition to soil humidity, the variability of communities is largely determined by the salt regime and soil acidity. Although, by definition of the *Bidentetea* class coenoses these are confined to nutrient-rich soils, only some of the plant communities demonstrate an increased requirement for the content of assimilated nitrogen compounds. In the ecological-phytocoenotic series of the nanoephemeral plant communities the arrangement of associations occurs mainly in the direction of the variability of damping, soil aeration, and the nitrogen content of the substrate. In contrast to the countries of Central Europe, the significant length of the territory of Ukraine in the meridional direction determines the variability of the *Isoëto-Nanojuncetea* communities and this also occurs along a gradient of the temperature regime of the habitats, which confirms the influence of climatic parameters on the distribution and floristic composition of the communities of the aforementioned class (Deil, 2005).

Our research has shown that the use of generalized, large-scale phytosociological databases can be a valuable tool for identifying the current state of these discussed plant communities on a continental scale. Thus, this knowledge can contribute to the improvement of the European vegetation classification of littoral zones of continental water bodies, providing information on diagnostic species, their syntaxonomic structure, and the geographical and ecological features of phytocoenoses formed in unique habitat conditions.

From the point of biodiversity conservation, our research could also be used for monitoring in the context of climate change. Increases in temperature and changes in precipitation can significantly change the composition and abundance of species, which can lead to associated changes in the distribution of local plant communities (Moomaw et al., 2018). Wetlands are particularly vulnerable to changes in climate (Fay et al., 2016; Grieger et al., 2020), as well as to other human impacts on the environment. These discussed vegetation complexes are very sensitive to ecological and human disturbances. That is why they can be good bioindicators for monitoring and preserving newly-formed ecotopes (Ernandes et al., 2017). Also, for the plant communities of shorelines and littoral zones, a significant threat is the invasion of alien species, which, over time can be quite large-scale and even lead to structural transformations and formation of new a syntaxa (Hrivnák et al., 2016; Korotka & Pashkevych, 2017). As has already mentioned by other authors (Bagella et al., 2016; Tomaselli et al., 2020), these unique plant communities are very vulnerable and easily affected by these different impacts. They occur in habitats № 3130 (oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and / or of the *Isoëto-Nanojuncetea*) and № 3270 (rivers with muddy banks with *Chenopodion rubri* p.p. and *Bidention* p.p. vegetation) that are protected by Council Directive 92/43 / EEC. Therefore, it is necessary to pay more attention to their study and preservation.

5. Conclusions

The pioneer vegetation of the freshwater shorelines and littoral zones of the water bodies of Ukraine is represented by 2 classes: *Isoëto-Nanojuncetea* and *Bidentetea*. The syntaxonomical structure of the *Isoëto-Nanojuncetea* class includes 1 order, 2 alliances and 8 associations. The level of its coenotic diversity is lower than the European average, which is possibly due to a lack of research into these habitats in our country. The syntaxonomy of the class *Bidentetea* includes 1 order, 2 alliances, and 10 associations. The level of its coenotic richness is average for European countries. It has an average European level for its coenotic diversity. Plant communities of both classes are more typical for the Polissia region and the forest-steppe zone of Ukraine, where there are favourable habitats with a flat relief, a low degree of dissection and a high level of soil humidity. The coenotic diversity and territorial differentiation of the communities of these discussed classes are mainly caused by the hydrological regime of water bodies, in particular the duration of flooding, and the structure and thickness of alluvial sediments. Further studies will make it possible to supplement and clarify the syntaxonomic structure of the *Isoëto-Nanojuncetea* class, in particular, the position of the alliance *Myosuro-Beckmannion eruciformis* which Shapoval (2006) described from the area of depressions with saline soils in the steppe zone of Ukraine.

On the basis of the ordination analysis of the syntaxa, it was established that in the ecological differentiation of the communities of the classes *Isoëto-Nanojuncetea* and *Bidentetea* the main factors are the water regime and the concentration of mineral nitrogen compounds in the soil. In the first class, the variability of coenoses is also determined by the degree of soil aeration, as well as by the temperature regime of habitats. Differentiation of the plant communities in the *Bidentetea* class in ecological space and the formation of their ecological-coenotic series also occur along the gradients of the salt regime and acidity of the substrates.

Our research has shown that ordering, supplementing and combining materials in the form of phytosociological databases can be used for a large-scale analysis of the current state of different plant complexes. Thus, it can contribute to the improvement of the classification of European vegetation. The results of this work will be also useful for preserving the biodiversity of these pioneer phytocoenoses.

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