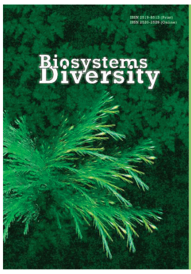

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Features of ecological differentiation of halophytic, steppe and petrophytic vegetation in the valley of the Liman Kuyalnik (Odesa Oblast)

D. V. Dubyna*, T. P. Dziuba*, L. P. Vakarenko*, A. A. Ennan**, H. M. Shykhaleeva**, H. M. Kiriushkina**

**M. G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine, Kyiv, Ukraine*
***Physical-Chemical Institute for Environment and Human Protection of Ministry of Education and Science and the National Academy of Sciences of Ukraine, Odesa, Ukraine*

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M. G. Kholodny Institute of Botany, NAS of Ukraine, Tereshchenkivska st., 2, Kyiv, 01004, Ukraine. Tel.: +38-099-079-01-08. E-mail: ddub@ukr.net

Physical-Chemical Institute for Environment and Human Protection of Ministry of Education and Science and the National Academy of Sciences of Ukraine, Preobrazhenska st., Odesa, 65000, Ukraine. Tel.: +380-48-723-75-61. E-mail: i.l.monitoring@ukr.net

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Assessment of key environmental factors that influence vegetation distribution and formation of plant communities is one of the most important challenges in modern phytocenology. Nowadays, several bioindication systems are applied to determine ecological specificity of plant communities and to establish the leading factors for their environmental differentiation. The system most widely used in Europe, that of H. Ellenberg, contains a numerical score on 6 ecological factors. On the example of vegetation of the valley of the Liman Kuyalnik, Y. Didukh developed the synphytoindication method based on evaluation of phytocenoses with respect to 12 ecological factors: 7 edaphic factors and 5 climatic factors; the method determines a more accurate and complete presentation of the analysis. In the valley of the Liman Kuyalnik (Odesa Oblast) the largest area is covered with halophytic and steppe vegetation. Halophytic vegetation (*Therosalicornietea*, *Festuco-Puccinellietea* classes, *Juncetea maritimi*, *Bolboschoenetea maritimi*) predominated in the shoreline areas of the valley, whereas steppe (*Festuco-Brometea*) and petrophytic (*Sedo-Scleranthetea*) vegetation dominated on the slope sites. With the application of DCA-ordination and synphytoindication methods it was established that distribution of plant communities in the hyper-space of the environmental conditions was most strongly correlated with edaphic factors, whereas microclimatic (light intensity) and climatic (thermo-regime) conditions had somewhat less influence on their differentiation. Water regime and level of soil salinity served as key factors for syntaxa of halophytic vegetation; moisture variability and salt regime, as well as soil moisture and carbonate content were key factors for the steppe vegetation, and thermo-regime was the main factor for petrophytic-steppe and petrophytic vegetation. The "eco-spaces" of these groups largely overlap. Halophytic cenoses are characterized by quite wide ecological ranges by most ecological factors. Steppe communities show much less ecological diversity. In the valley of the liman, all the steppe communities were characterized by stenotopicity in relation to most ecological factors; these factors complexly determine the specificity and diversity of biotopes within the valley, which are unique and require protection and the taking of appropriate measures, depending on the changes in activity of one or another limiting factor. Nowadays, the valley of the Liman Kuyalnik is in a state of environmental disaster. The established relationships in ecological differentiation of plant communities will be applied to further monitoring of biodiversity state, preservation and possible restoration of vegetation types that were native for this unique territory.

Keywords: synphytoindication; DCA-ordination; *Therosalicornietea*; *Festuco-Puccinellietea*; *Juncetea maritimi*; *Bolboschoenetea maritimi*; *Festuco-Brometea*; *Sedo-Scleranthetea*.

Introduction

Vegetation cover serves as an indicator of ecosystem state because it responds quickly the changes in environmental conditions (Burger, 2006; Parmar et al., 2016; Lykholat et al., 2018a); it gives the opportunity to make an environmental assessment of a certain territory using phytoindication scales (LaPaix et al., 2009; Ivanova & Zolotova, 2015) and to conduct phytomonitoring of the territory (Klimo et al., 2011; Lykholat et al., 2018b; Jetz et al., 2019; Lashchinskiy et al., 2019). Bioindication properties of biological communities are also used in assessment of level of anthropogenic pollution on aquatic (Ceschin et al., 2010) and terrestrial (Rowe et al., 2015; Baranovski et al., 2016; Faly et al., 2017; Valjavec et al., 2017; Hedwall et al., 2019) ecosystems. Synphytoindication analysis of plant communities involves phytosociological surveys of vegetation and allows the ecosystem state to be defined using the indexes of their biotic components (Didukh, 2012; Bagrikova, 2018). The synphytoindication method is based on the specificity of ecological ranges of plant species, taking into account their cenotic significance in relation to various environmental factors. Its effectiveness lies in the possibility of obtaining the required information without direct measurements,of covering all the diversity of syntaxa and reflecting their cumulative effect over a long period of time. Such surveys are also undertaken for more comprehensive comparative assessment analysis of some types of plant communities in relation to others, which is important for understanding their place in the system of vegetation cover of certain landscapes or regions (Didukh & Kuzemko, 2014; Pinto et al., 2016). In synphytoindication surveys, European phytocenologists usually use the indicative scale of G. Ellenberg, which contains numerical scores on 6 ecological factors: soil moisture (12 grades), soil nitrogen content (9), soil acidity level (9), light intensity/shading (9), thermo-climate (9) and continentality (9) (Ellenberg et al., 1991). Ecological ranges on syntaxa of different vegetation types in the Czech Republic (Chytrý et al., 2007, 2009, 2011, 2013), forest plots of Great Britain (Carpenter & Goodenough, 2014), France (Pinto et al., 2016) and of Central Europe (Szymura et al., 2014), alpine vegetation of the Tatra Mountains in Poland and Slovakia (Czortek et al., 2018) etc. have been calculated. Phytoindication scales of Y. P. Didukh allow one to conduct a more detailed analysis on 12 ecological factors.

The valley of the Liman Kuyalnik is located in the South-West part of Ukraine, the territory is meridionally elongated and separated from the Black Sea by a mound with a width up to 3 km (current territory of Odesa city). The Liman Kuyalnik reaches a length of 28 km from the river head (the mouth of the Great Kuyalnik River) to the mound, and its width varies from 2 to 4 km. The average depth is 3 m (0.5–7.0 m), salinity is about 300‰. It is a unique hyperhaline natural reservoir, located below sea level. On the slopes of the estuary valley, large areas of native steppe vegetation have remained, and on the shore areas sites of halophytic vegetation are located. In 2016–2018, surveys of the liman valley vegetation were carried out, as a result of which a large variety of plant communities was detected and their syntaxonomic structure (Dubyna et al., 2017a, 2018a, c) and special features of territorial differentiation were found (Dubyna et al., 2017b, 2018b).

Today, halophytic vegetation occupies a dominant position in the shoreline areas within the estuary valley. Due to catastrophic decrease in the water surface area of the estuary in recent decades, there has been observed an increase in the diversity of these plant communities and reduction of areas occupied by them. This type of vegetation is represented by 4 classes: *Therosalicornietea* (1 order, 2 unions, 5 associations), *Festuco-Puccinellietea* (4 orders, 5 unions, 15 associations), *Juncetea maritimi* (1 order, 1 union, 1 association) and *Bolboschoenetea maritimi* (1 order, 2 unions, 4 associations) (Dubyna et al., 2017a). Steppe and petrophytic-steppe vegetation dominates on the left-bank slopes and occupies large areas on the right-bank slopes of the valley. The syntaxonomic structure of the steppe vegetation includes 4 orders, 5 unions, 11 associations and 2 communities of indeterminate rank, belonging to the *Festuco-Brometea* class. In contrast to halophytic vegetation, degradation of native steppe plant communities, reduction of their diversity and the areas occupied by them were observed due to increased influence of anthropogenic factors. Petrophytic phytocenosis is represented by single community (*Sedum acre* comm.) referred by us to *Sedo-Scleranthetea* class.

The goal of the work was identification the environmental specifics of halophytic, steppe and petrophytic vegetation in the Liman Kuyalnik valley with application of DCA-ordination and synphytoindication methods. Such data are important for determining the key factors of ecological differentiation of the main vegetation types within the valley, development of protection measures for the vegetation and forecasting possible changes in its components.

Materials and methods

The materials for synphytoindication assessment of halophytic and steppe vegetation were based on more than 400 original descriptions made by authors in 2009 and 2016–2017 according to the methodological principles of the floristic geobotanical school. Their ordering was carried out by creating a database of geobotanical descriptions in the Turboveg 2.79 format. Interpretation of the phyto-sociological material was carried out using a modified algorithm of Two Way Indicator Species Analysis (Twinspan) method as the part of Juice 7.0 software package (Hill, 1979; Roleček et al., 2009). An adjustable stratification in the Juice program was carried out to obtain more reliable phytoindication results (Tichý, 2002), with the selection of descriptions based on the Euclidean distance calculation. In processing of *Festuco-Brometea* class we applied 198 descriptions, *Festuco-Puccinellietea* – 172, *Therosalicornietea* – 39, *Bolboschoenetea maritimi* – 11, *Juncetea maritimi* – 6, *Sedo-Scleranthetea* – 4.

The method of DCA-ordination (Determined Correspondence Analysis) (Hill & Gauch, 1980) based on the computer language R (Venables & Smith, 2009) integrated into the Juice software package was used in order to identify the main environmental factors of the plant communities' differentiation. This method allows us to assess the position of phytocenoses in ecological space and identify key environmental factors that determine the distribution of plant communities.

Calculation of environmental parameters was performed according to standardized point scales of synphytoindication ecological amplitudes developed by Didukh (2011); the scales allow one to conduct ordination analysis by 12 factors: 7 edaphic factors: soil moisture, moisture variability, soil aeration, available nitrogen content, soil acidity, salt regime, carbonate content, and 5 climatic factors: thermo-regime, ombroregime, continentality, cryoregime, and light intensity. Phytoindication analysis of the interactions between plant communities and environmental factors and the range of their distribution was carried out using the method of synphytoindication (Didukh, 2011), Juice program and basic statistical analysis in Statistica 7.0 package (StatSoft Inc., USA). Syntaxon ranges and optima for each of the 12 environmental factors were calculated with the Statistica 7.0 package (StatSoft, 2005). In ecological assessment of phytocenosis, average scores of all types of phytocenosis were used, which together represent average value. Data on *Festuco-Brometea* and *Festuco-Puccinellietea* classes were represented using "box-and-whisker". At the same time, the "boxes" represent a interquartile range (25–75% of the values observed), they correspond to the ecological optimum of the syntaxon, and the "whiskers" represent minimum and maximum values, and the middle point represents median. Where the number of descriptions did not allow representative presentation of statistically reliable results on the *Therosalicornietea*, *Bolboschoenetea maritimi*, *Juncetea maritimi* and *Sedo-Scleranthetea* classes, phytoindication results were tabulated.

Results

Analysis of DCA-ordination on 10 halophytic vegetation unions: *Scirpion maritimi* Dahl et Hadač 1941, *Typhion laxmannii* Nedelcu 1968, *Salicornion prostratae* Géhu 1992, *Suaedion acuminatae* Golub et Tchorbadze in Golub 1995 corr. Lysenko et Mucina 2015, *Juncion maritimi* Br.-Bl. ex Horvatić 1934, *Juncion gerardii* Wendelberger 1943, *Puccinellion limosae* Soó 1933, *Salicornio-Puccinellion* Mirkin in Golub et Solomakha 1988, *Plantagini salsae-Artemision santonicae* Shelyag-Sosonko et Solomakha in Lysenko, Mucina et Iakushenko 2011, *Glycyrrhizion glabrae* Golub et Mirkin in Golub 1995 (Fig. 1) showed that ecological differentiation of syntaxa was mainly determined by water regime, acidity and soil salinity. Along the DCA1 axis, phytocenoses were located from the most hygrophytic (*Scirpion maritimi*, *Typhion laxmannii*) to mesoxerophytic saline-steppe (*Glycyrrhizion glabrae*). In comparison with others, in more xerophytic unions such as *Plantagini salsae-Artemision santonicae* and *Glycyrrhizion glabrae*, thermo-regime is also an important environmental factor. Variability of soil moisture regime (DCA2 axis) was also of great importance for ecological differentiation of plant communities within the abovementioned unions. Light intensity of ecotopes acts as a less important factor (DCA3 axis). The widest range of distribution was typical for *Scirpion maritimi* union because it combines communities formed not only by typical terrestrial halophytes, but also by hydrophytes (*Potamogeton pectinatus* L., *Batrachium rionii* (Lagger) Nyman, etc.). *Junction gerardii*, *Puccinellion limosae* and *Plantagini salsae-Artemision santonicae* unions were also characterized by a significant ecological range. Within the Kuyalnik Estuary valley they occupy a transitional position between saline-marsh vegetation of *Bolboschoenetea maritimi* class and saline-steppe vegetation of *Festuco-Puccinellietea* class.

Phytoindication analysis of associations within the *Bolboschoenetea maritimi* class by moisture gradient found mostly their hygrophytic pattern and stenotopicity by the width of ecological range (Table 1). Perhydrophitic conditions and hemi-stenotopicity were typical for communities within the *Typhetum laxmannii* (Ubrizsy 1961) Nedelcu 1968 association. They also show hemihydrocontrastophobicity in relation to changes in water regime (fluctuating of water level). Other plant communities in this class were hemihydrocontrastophilic and can be tolerant to seasonal drying of water bodies. In relation to substrate aeration, cenoses of this class are quite differentiated. Communities of *Bolboschoenetum maritimi* Eggler 1933 and *Typhetum laxmannii* associations were classified as aerophobic hemi-stenotopic, *Scirpetum tabernaemontani* Soó (1927) 1947 were classified as subaerophobic stenotopic, and *Eleocharitetum uniglumis* Almquist 1929 as hemi-aerophobic. In relation to soil salt regime, *Bolboschoenetum maritimi* association demonstrated glyco-trophicity and hemi-stenotopicity, *Typhetum laxmannii* – subhlyco-trophicity and hemi-stenotopicity, *Scirpetum tabernaemontani* and *Eleocharitetum uniglumis* – eutrophicity and stenotopicity. In relation to soil acidity, the most syntaxa within this class exhibit neutrophilicity and hemistenotopicity, and only the community of the *Bolboschoenetum maritimi* association was basiphilic because its tendency to conditions with alkaline environment. According to content of available nitrogen in soil, associations within this class were quite demanding and belong to nitrophilic group. They were also hemi-carbonate-trophic with a quite narrow ecological range and heliophylic because they grow in well-lit habitats (Table 1).

In relation to water regime, synphytoindication analysis of syntaxa in the *Therosalicornietea* class evidenced their predominantly hygromesophyte pattern and tendency to exist in moist habitats (Table 2). Only the communities within the *Bassietum sedoidis* (Ubrizsy 1949) Soó 1964 association can also occur in mesophytic conditions. In relation to water regime variability, syntaxa of this class showed hemihydrocontrastophobicity and can be tolerant to moderate changes in moisture throughout the year. Communities within *Bassietum sedoidis*, *Halimionetum pedunculatae* Şerbănescu 1965 and *Salicornio perennantis-Suaedetum salsae* Freitag, Golub et Yuritsyna 2001 associations were more tolerant to this factor. In relation to soil aeration, the communities demonstrated hemiaerophobicity with a fairly narrow range of values. Differentiation of plant syntaxa upon the gradient of soil richness-salinity was negligible. They all belong to halotrophic hemistenotopic communities and serve as indicators of chloride and sulfate-chloride (*Salicornio perennantis-Suaedetum salsae*) salinization soil type in the Kuyalnik Estuary valley. These communities also tend to alkaline or strongly alkaline soils. In relation to the content of mineral nitrogen in the soil they show heminitrophilicity and can developed on relatively nitrogen-poor soil. Communities of this class are acarbonatophilic and developed on coastal substrates with low content of limestone. By this factor, the widest range was observed in communities of the *Salicornietum prostratae* Soó 1927 association which grow both on clay-sandy noncarbonate soils and on substrates with a significant content of carbonates, especially in coastal places where process of limestone rocks weathering from the slopes was developed. In relation to the light intensity all the associations were heliophytic (Table 2).

In the territory of the liman, the *Juncetea maritimi* class was represented by a single association *Plantagini salsae-Juncetum maritimi* Shelyag-Sosonko et Solomakha 1987. Phytoindication analysis of the class showed that these communities develop in mesophytic, hemihydrocontrastophytic, hemiaerobic, glycotrophic, basyphytic, heminitrophytic, acarbonatophytic and heliophytic environmental conditions, and they are stenotopic by the majority of the factors (Table 3).

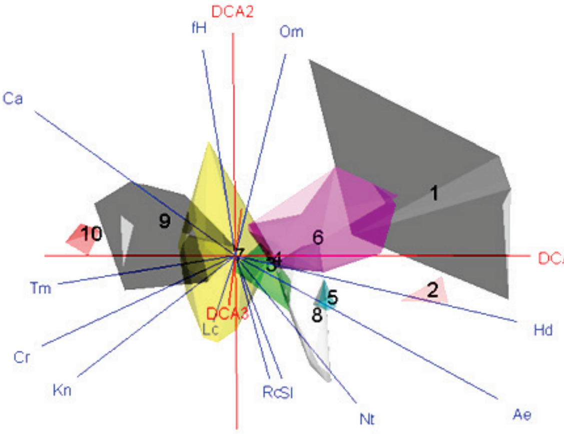


Fig. 1. Results of the DCA-ordination of halophytic vegetation unions: Hd – soil moisture, fH – moisture variability, Ae – soil aeration, Nt – available nitrogen content in soil, Rc – soil acidity, Sl – salt regime, Ca – carbonate content, Tm – thermo-regime, Om – ombroregime, Kn – continentality, Cr – cryoregime, Lc – light intensity; syntaxones: 1 – *Scirpion maritimi*; 2 – *Typhion laxmannii*; 3 – *Salicornion prostratae*; 4 – *Suaedion acuminatae*; 5 – *Juncion maritimi*; 6 – *Juncion gerardii*; 7 – *Puccinellion limosae*; 8 – *Salicornio-Puccinellion*; 9 – *Plantagini salsae-Artemision santonicae*; 10 – *Glycyrrhizion glabrae*; DCA1, DCA2, DCA3: ordination axes

Table 1
Distribution of plant communities within associations *Bolboschoenetea maritimi* class by ecological factors (in scores of Didukh (2011) ecological scales)

Association	Number of description	Ecofactors											
		Hd	fH	Rc	Sl	Ca	Nt	Ae	Tm	Om	Kn	Cr	Lc
Bolboschoenetum maritimi	1	13.67	7.00	12.67	14.17	6.50	6.83	9.17	9.67	8.67	9.33	8.67	8.33
	2	14.75	7.00	9.25	10.75	6.25	6.00	11.75	9.75	9.75	8.50	8.25	7.50
	3	16.60	6.20	9.80	11.10	5.60	6.90	10.60	9.00	10.90	7.90	8.70	7.80
Scirpetum tabernaemontani	4	13.83	9.67	7.17	9.50	5.50	6.50	8.00	8.33	11.67	8.83	8.17	8.00
	5	15.50	8.20	8.40	9.50	5.70	6.20	9.30	8.9	11.20	8.60	7.80	7.70
	6	16.40	6.80	8.60	9.30	5.90	6.20	10.00	9.00	11.10	8.60	7.90	7.60
	7	15.88	6.00	8.75	9.63	6.00	6.00	9.75	9.00	11.00	8.50	8.13	7.63
Eleocharitetum uniglumis	8	11.33	7.67	8.17	9.94	6.61	5.89	6.72	9.11	11.25	9.13	8.50	7.89
Typhetum laxmannii	9	19.00	4.00	9.50	10.00	5.00	6.50	13.00	9.00	11.50	7.50	8.00	8.50
	10	20.00	4.00	9.75	10.75	5.75	7.00	13.25	9.00	11.50	8.75	8.50	7.75
	11.00	14.90	6.20	10.10	11.60	6.00	6.60	10.40	9.50	10.80	8.00	8.60	7.90

Note: here and elsewhere in the tables: ecofactor names – see legend to Fig. 1.

The results of synphytoindication analysis of syntaxa within the *Festuco-Puccinellietea* class by soil moisture factor (Fig. 2a) evidenced its importance in ecological differentiation of the communities. Most syntaxa within the class were mesophilic and stenotopic, however, communities of *Plantagini salsae-Artemision santonicae* and *Glycyrrhizion glabrae* unions were associated with submesophytic environmental conditions. By the gradient of water regime variability, the range of values was 5.5 points and shows hemihydrocontrastophilicity of most communities (Fig. 2b). Only communities of the *Tripolio pannonici-Phragmitetum* Golub et Yuritsyna 2001 association were characterized by hemihydrocontrastophobicity, i.e. they associated with location of the more stable and regular moisture over the year. The largest range of water regime was typical for *Puccinellietum distantis* (Rapaics 1927) Soó 1930 var. *Artemisia santonica* communities, which were transitional between the *Puccinellion limosae* and *Plantagini salsae-Artemision santonicae* unions. A significant differentiation of communities was observed in relation to soil aeration. Most syntaxa of the class were hemiaerophobic, i.e. associated with moderately aerated soils (Fig. 2c). *Puccinellio distantis-Juncetum gerardii* Dubyna et Dziuba in Dubyna et al. 2017, *Puccinellietum distantis* var. *typica*, *Astero tripolii-Phragmitetum* Krisch (1972) 1974 and *Tripolio pannonici-Phragmitetum* var. *typica* communities belong to subaerophobic. Communities of *Puccinellietum distantis* var. *Lactuca tatarica*, *Puccinellietum distantis* var. *Bassia sedoides* variants, as well as *Plantagini salsae-Artemision santonicae* and *Glycyrrhizion glabrae* unions were indicative of subaerophitic environment conditions and were characterized by a narrow amplitude by this factor. Syntaxa of the class were quite heterogeneous in relation to soil trophic conditions and to content of mineral salts in the soil (Fig. 2d). Communities of *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943, *Festucetum regelianae* Solomakha et Shelyag-Sosonko in Golub et al. 2003 associations, as well as *Plantagini salsae-Artemision santonicae* and *Glycyrrhizion glabrae* unions were characterized by eutrophicity; communities of *Puccinellio distantis-Juncetum gerardii*, *Puccinellietum distantis* var. *Lactuca tatarica* and *Tripolio pannonici-Phragmitetum* var. *Polygonum patulum* were characterized by subglycotrophicity; *Puccinellio distantis-Spergularietum salinae* (Feekes 1936) Tx. et Volk 1937 and *Tripolietum vulgaris* Korzhenevsky et Klyukin in Korzhenevsky, Klyukin et Korzhenevskaya 2000 were characterized by mesohalotrophicity. All of them were stenotopic by this factor. The remaining communities of this class were glycotrophic and hemistenotopic. The transitional pattern of *Puccinellietum distantis* var. *Artemisia santonica* communities, as already noted, also determines the significant amplitude of the values of this factor. In relation to requirements for reaction of soil solution, the communities were distributed as follows. Syntaxons *Scorzonero parviflorae-Juncetum gerardii*, *Puccinellio distantis-Juncetum gerardii*, *Festucetum regelianae*, *Puccinellietum distantis* var. *Lactuca tatarica*, *Tripolio pannonici-Phragmitetum* var. *Polygonum patulum* and communities of *Plantagini salsae-Artemision santonicae* and *Glycyrrhizion glabrae* unions were placed within the range of neutrophilic conditions (Fig. 2e). *Puccinellietum distantis* var. *Bassia sedoides* and *Astero tripolii-Phragmitetum* communities were basiphilic and hemistenotopic. The other communities were hyperbasiphilic, i.e. associated with highly alkaline soils. In relation to the content of mineral nitrogen in soil, most syntaxa belong to the heminitrophilic ecological group (Fig. 2f). Only the communities of waterlogged sites *Puccinellio distantis-Juncetum gerardii*, *Astero tripolii-Phragmitetum* and *Tripolio pannonici-Phragmitetum* were more demanding of nitrogen content and belong to the nitrophilic group. In relation to carbonate content in soil, most syntaxa show acarbonatophilicity (Fig. 2g). In relation to the light intensity, all the communities were heliophilic (Fig. 2h).

Table 2
Distribution of plant associations in communities of *Therosalicornietea* class by ecological factors

Association	Number of description	Ecofactors											
		Hd	fH	Rc	Sl	Ca	Nt	Ae	Tm	Om	Kn	Cr	Lc
Salicornietum prostratae	1	11.75	7.25	13.25	16.25	6.00	6.25	8.25	9.50	8.75	12.00	8.50	8.50
	2	12.50	6.75	14.25	15.50	6.25	7.25	8.25	9.25	8.50	10.00	8.75	8.50
	3	13.00	5.50	11.25	13.00	6.75	6.75	10.25	9.50	9.25	9.75	8.50	7.75
	4	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
	5	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
	6	12.75	6.00	12.75	15.75	8.00	5.50	8.00	10.00	9.75	9.75	8.00	8.50
	7	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
Bassietum hirsutae	8	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
	9	11.63	6.88	12.88	14.50	5.38	6.63	7.88	9.25	9.38	10.13	8.75	8.25
	10	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
	11	13.00	6.50	12.75	15.50	7.75	7.00	8.00	9.50	10.00	9.75	8.75	8.25
	12	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
	13	12.50	4.50	13.50	16.00	8.00	7.50	8.00	10.00	8.00	10.50	9.00	8.50
Bassietum sedoidis	14	11.33	6.50	13.00	15.67	7.83	6.67	7.17	9.50	9.17	11.00	8.00	8.33
	15	10.75	7.50	12.75	15.50	7.75	6.25	6.75	9.25	9.75	11.25	7.50	8.25
	16	11.67	7.17	11.50	13.67	7.00	6.17	8.67	9.17	10.00	10.50	7.67	7.83
	17	10.75	6.50	11.25	13.00	6.75	6.00	9.00	9.25	9.00	11.25	7.25	7.75
	18	11.33	8.00	13.50	15.33	6.67	6.50	7.33	9.00	9.50	10.67	7.83	8.33
	19	11.90	7.20	13.20	15.50	7.20	6.10	7.60	9.40	9.60	10.30	7.90	8.40
	20	11.75	7.88	13.13	15.38	7.00	5.75	7.50	9.25	10.00	10.25	7.63	8.38
	21	11.90	7.20	13.20	15.50	7.20	6.10	7.60	9.40	9.60	10.30	7.90	8.40
	22	11.90	7.20	13.20	15.50	7.20	6.10	7.60	9.40	9.60	10.30	7.90	8.40
	23	10.75	7.50	12.75	15.50	7.75	6.25	6.75	9.25	9.75	11.25	7.50	8.25
	24	10.75	7.50	12.75	15.50	7.75	6.25	6.75	9.25	9.75	11.25	7.50	8.25
Halimionetum pedunculatae	25	12.50	6.75	14.25	15.50	6.25	7.25	8.25	9.25	8.50	10.00	8.75	8.50
	26	12.88	7.38	13.13	15.38	7.00	6.13	8.13	9.38	10.13	9.50	8.25	8.38
	27	12.67	7.00	13.50	15.50	6.83	6.00	8.17	9.50	9.50	9.67	8.17	8.50
	28	12.50	7.50	11.50	12.83	6.92	6.58	8.42	9.25	9.60	9.00	8.00	8.00
	29	12.67	7.00	13.50	15.50	6.83	6.00	8.17	9.50	9.50	9.67	8.17	8.50
	30	12.67	7.00	13.50	15.50	6.83	6.00	8.17	9.50	9.50	9.67	8.17	8.50
	31	12.67	7.00	13.50	15.50	6.83	6.00	8.17	9.50	9.50	9.67	8.17	8.50
	32	12.67	7.00	13.50	15.50	6.83	6.00	8.17	9.50	9.50	9.67	8.17	8.50
	33	12.25	7.75	13.38	15.75	6.13	5.75	8.25	9.38	9.50	10.63	8.13	8.50
	34	12.13	7.25	12.88	14.13	6.88	6.25	7.75	9.63	9.25	9.00	7.63	8.38
	35	11.90	7.20	13.20	15.50	7.20	6.10	7.60	9.40	9.60	10.30	7.90	8.40
	36	11.17	7.67	13.50	15.50	6.83	5.50	7.33	9.33	9.33	10.67	7.33	8.50
	37	12.83	6.67	12.50	13.67	6.00	6.83	9.67	9.17	9.17	9.67	8.50	8.00
Salicornio perennantis-Suaedetum salsae	38	13.10	7.90	12.90	15.50	6.50	6.30	8.10	9.50	9.90	10.10	7.90	8.40
	39	12.50	7.64	11.93	14.21	6.57	6.71	7.57	9.71	9.93	9.86	7.71	8.36

Table 3
Distribution of plant communities within *Plantagini salsae-Juncetum maritimi* associations of *Juncetea maritimi* class by ecological factors

Number of description	Ecofactors											
	Hd	fH	Rc	Sl	Ca	Nt	Ae	Tm	Om	Kn	Cr	Lc
1	12.33	7.33	10.58	12.83	6.33	6.42	8.58	9.50	10.58	9.50	9.00	7.75
2	11.83	7.61	10.28	12.33	6.00	5.50	7.39	9.89	10.44	8.78	9.00	7.89
3	11.78	8.00	10.67	12.83	6.33	5.78	7.00	9.94	10.00	9.06	8.33	8.06
4	11.10	7.60	9.90	11.20	6.20	6.00	8.00	9.80	10.00	9.00	8.50	7.60
5	11.90	7.60	12.10	14.30	6.50	6.50	8.00	9.50	9.40	10.50	9.00	8.10
6	12.58	8.83	11.17	12.92	6.33	6.58	8.50	9.50	9.08	10.08	8.42	7.92

Interpretation of DCA-ordination results on steppe and petrophytic vegetation unions within the Liman Kuyalnik valley (Fig. 3) revealed that true steppe (*Festucion valesiacae* Klika 1931, *Stipo lessingianae-Salvion nutantis* Vynokurov 2014, *Tanaceto millefolii-Galatellion villosae* Vynokurov 2014), petrophytic steppe (*Potentillo arenariae-Linion czernjajevii* Krasova et Smetana 1999) and limestone slope unions (*Alysso-Sedion* Oberd. et T. Müller in T. Müller 1961, class *Sedo-Scleranthetea*) were clearly distinguished by the influence of ecological factors. The key environmental factors that influence formation of floristic and cenotic diversity of *Festucion valesiacae*, *Stipo lessingianae-Salvion nutantis* and *Tanaceto millefolii-Galatellion villosae* unions were moisture variability and salt regime, as well as soil moisture and carbonate content. These vectors were the nearest to the DCA2 axis. Communities of the *Festucion valesiacae* union have the greatest ecological amplitude. Temperature regime was the key factor for communities of *Potentillo arenariae-Linion czernjajevii* and *Alysso-Sedion* unions.

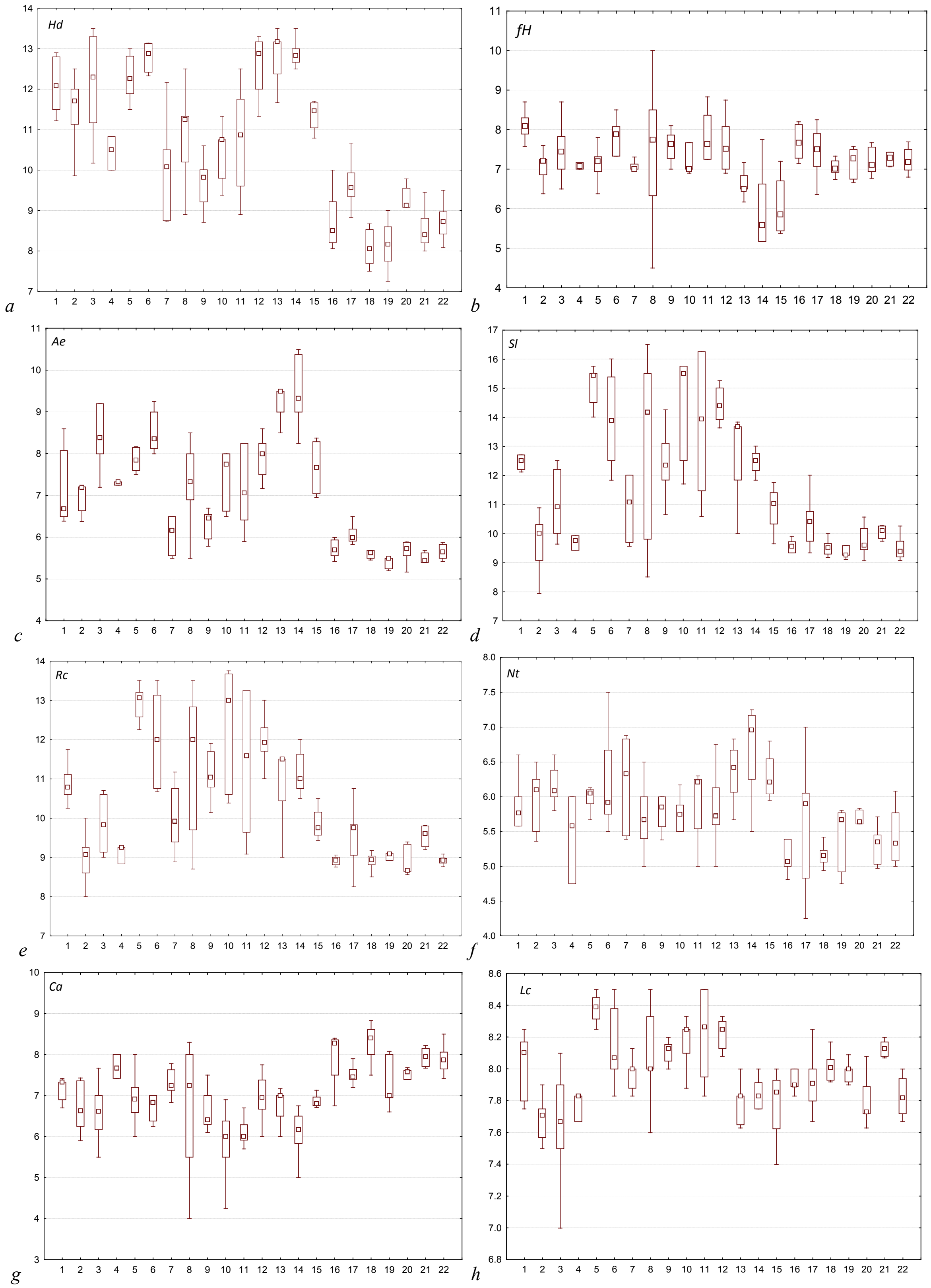
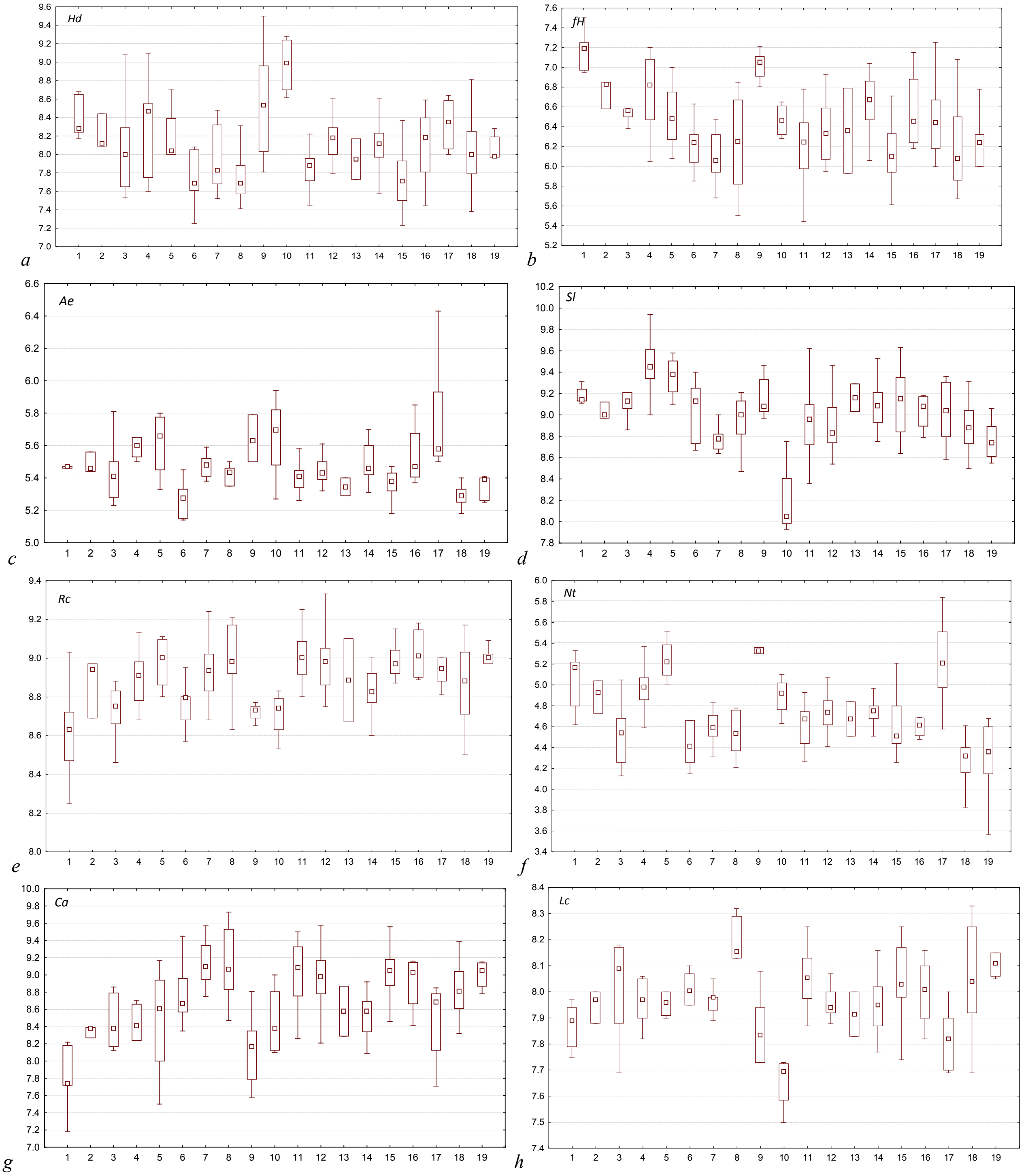


Fig. 2. Distribution of communities of *Festuco-Puccinellietea* class by ecological factors: *a* – soil moisture; *b* – moisture variability; *c* – soil aeration; *d* – salt regime; *e* – soil acidity; *f* – available nitrogen content in soil; *g* – carbonate content; *h* – light intensity; on the x-axis the numbers indicate syntaxon: *1 – Plantagini salsae-Juncetum gerardii*; *2 – Scorzonero parviflorae-Juncetum gerardii*; *3 – Puccinellio distantis-Juncetum gerardii*; *4 – Festucetum regelianae*; *5 – Puccinellio distantis-Spergularietum salinae*; *6 – Puccinellietum distantis* var. *typica*; *7 – Puccinellietum distantis* var. *Lactuca tatarica*; *8 – Puccinellietum distantis* var. *Artemisia santonica*; *9 – Puccinellietum distantis* var. *Bassia sedoides*; *10 – Puccinellio distantis-Petrosimonietum triandrae*; *11 – Puccinellio distantis-Petrosimonietum oppositifoliae*; *12 – Tripolietum vulgaris*; *13 – Astero tripolii-Phragmitetum*; *14 – Tripolio pannonici-Phragmitetum* var. *typica*; *15 – Tripolio pannonici-Phragmitetum* var. *Polygonum patulum*; *16 – Limonio meyeri-Artemisietum santonicae*; *17 – Artemisietum santonicae* var. *Puccinellia distans*; *18 – Artemisietum santonicae* var. *Festuca valesiaca*; *19 – Artemisietum santonicae* var. *Bromus japonicus*; *20 – Poo bulbosae-Artemisietum santonicae*; *21 – Taraxaco bessarabicae-Artemisietum santonicae*; *22 – Anisantho tectori-Glycyrrhizetum glabrae*; on the y-axis the numbers indicate scores of environmental scales of Didukh (2011)



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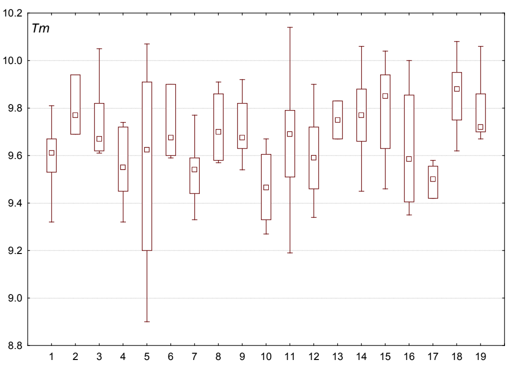

Fig. 4. Distribution of communities in *Festuco-Brometea* class by ecological factors: *a* – soil moisture; *b* – moisture variability; *c* – soil aeration; *d* – salt regime; *e* – soil acidity; *f* – available nitrogen content in soil; *g* – carbonate content; *h* – light intensity; *i* – thermal regime; on the x-axis the numbers indicate following syntaxons: *1 – Salvio nemorosae-Festucetum valesiacae* var. *typica*; *2 – Salvio nemorosae-Festucetum valesiacae* var. *Stipa lessingiana*; *3 – Salvio nemorosae-Festucetum valesiacae* var. *Thymus dimorphus*; *4 – Salvio nemorosae-Festucetum valesiacae* var. *Artemisia austriaca*; *5 – Salvio nemorosae-Elytrigietum intermediae*; *6 – Ephedra distachya* comm.; *7 – Astero oleifolii-Ephedretum distachyae*; *8 – Bothriochloetum ischaemi*; *9 – Aegilopsetum cylindricae*; *10 – Vinco herbaceae-Caraganetum fruticis*; *11 – Stipo lessingianae-Salvietum nutantis typicum*; *12 – Stipo lessingianae-Salvietum nutantis caraganetosum fruticis*; *13 – Stipa pulcherrima* comm.; *14 – Ephedro distachyae-Stipetum capillatae typicum*; *15 – Ephedro distachyae-Stipetum capillatae stipetosum lessingianae*; *16 – Stipo ucrainicae-Agropyretum pectinati*; *17 – Festuco valesiacae-Galatelletum biflorae*; *18 – Pimpinello titanophilae-Thymetum dimorphi typicum*; *19 – Pimpinello titanophilae-Thymetum dimorphi paronychietosum cephalotae*; on the y-axis the numbers indicate scores of environmental scales Didukh (2011)

Table 4
Distribution of *Sedum acre* communities of *Sedo-Scleranthetea* class by ecological factors

Number of description	Ecofactors											
	Hd	fH	Rc	Sl	Ca	Nt	Ae	Tm	Om	Kn	Cr	Lc
1	8.17	7.25	8.75	9.25	7.08	4.75	5.50	9.33	10.58	9.75	8.42	8.00
2	7.83	7.04	8.63	8.50	8.25	4.25	5.29	9.33	10.96	9.75	8.79	8.13
3	8.30	7.70	9.00	8.30	8.00	3.20	5.10	8.80	11.30	9.00	8.80	8.20
4	8.58	7.33	8.42	8.17	7.92	4.08	5.17	9.08	11.67	8.67	8.75	8.08

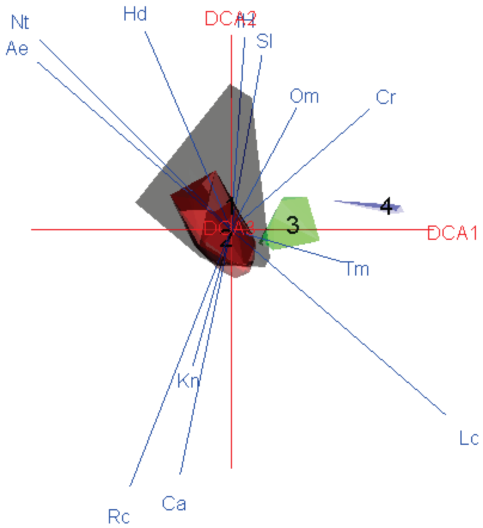

Fig. 3. Results of the DCA-ordination of steppe (*Festuco-Brometea*) and petrophytic (*Sedo-Scleranthetea*) vegetation unions: Hd – soil moisture, Fh – moisture variability, Ae – soil aeration, Nt – available nitrogen content in soil, Rc – soil acidity, Sl – salt regime, Ca – carbonate content, Tm – thermo-regime, Om – ombroregime, Kn – continentality, Cr – cryoregime, Lc – light intensity; unions: *1 – Festucion valesiacae*; *2 – Stipo lessingianae-Salvion nutantis*; *3 – Tanaceto millefolii-Galatellion villosae*; *4 – Potentillo arenariae-Linion czernjajevii*; *5 – Alysso-Sedion*; DCA1, DCA2, DCA3: ordination axes

Synphytoindication analysis of syntaxa of the *Festuco-Brometea* class in relation to soil moisture factor (Fig. 4a) indicates that they belong to subxerophytic conditions and have a slight differentiation by this factor. Only communities of two associations *Aegilopsetum cylindricae* Buia et al. 1969 and *Vinco herbaceae-Caraganetum fruticis* Korotchenko et Didukh 1997 are submesophytic. In relation to variability of water regime, all the steppe communities were developed under hemihydrocontrastophitic conditions with highly irregular moisture content in the rooting zone of the soil, with insignificant rainfall and melt water penetration usual for slope ecotopes (Fig. 4b). In relation to soil aeration, these communities were subaerophilic (Fig. 4c), they develop on well-aerated soils with a high content of limestone weathering products. In relation to soil trophicity and its chemical properties, steppe communities of the liman valley were eutrophic, neutrophilic, eunitrophilic (with the exception of the *Vinco herbaceae-Caraganetum fruticis* communities that have some signs of nitrophilicity) and hemicarbonatophilic (Fig. 4d, e, f, g). The lowest levels of carbonates in the soil (7.7–8.2) were observed for *Salvio nemorosae-Festucetum valesiacae* Korotchenko et Didukh 1997 var. *typica* communities, mostly formed on loess slopes and on the sites near slopes of the liman shore and border with salt marshes and salines. In relation to light intensity all the communities were heliophilic (Fig. 4h), and in relation to the thermal regime they were mesothermic (Fig. 4i). Steppe plant communities of the valley were characterized by a stenotype type of ecological range by almost all environmental factors considered.

Phytoindication analysis of a single syntaxon in *Sedo-Scleranthetea – Sedum acre* comm. class indicates its membership to subxerophilic, hemicontrastophilic, subaerophilic, eutrophic, neutrophilic, heminitrophilic and heliophilic ecogroups (Table 4). Distribution of these communities by carbonate content in the soil showed a somewhat paradoxical result: belonging of the communities to group of acarbonatophiles due to the very wide range of this factor, which typical for dominant of the communities, *Sedum acre* L., which grows both on sand and on carbonate slopes.

Discussion

Analysis of DCA-ordination is increasingly used in surveys of plant communities, particularly for identification of distribution patterns of phytocenoses in the multidimensional space of ecological factors (Didukh & Kuzemko, 2014; Evangelista et al., 2016; Ermakov et al., 2017). On the example of river valleys, using DCA-ordination, an assessment of cenotic β-diversity differentiation was conducted in relation to the change of key ecological factors (Didukh et al., 2015), and ecological specificity of biotopes (Chusova, 2018), and so on were studied. The ordination analysis carried out by us provided assessment of ecological range and pattern of ecological differentiation of cenoses of halophytic, steppe and petrophytic vegetation in the Liman Kuyalnik valley. The analysis showed that distribution of plant communities most closely correlated with edaphic factors; microclimatic (light intensity) and climatic (thermal regime) factors have somewhat less effect on their differentiation, which is consistent with phytosociological studies of other authors (Tölgyesi et al., 2014; Li et al., 2017; Czortek et al., 2018). On halophytic vegetation, the greatest influence of importance of soil moisture and salinity was revealed. This is particularly typical in communities of coastal vegetation (Jarvis et al., 2016), as well as in other regions of saline soil vegetation distribution (Chytrý et al., 2007; Lysenko, 2016). Differentiation of steppe vegetation on the territory of the liman is determined by variability of moisture and salt regime, which varied in gradient of slope height, as well as soil moisture and carbonate content. Within the relatively small territory of the liman, phytoindication indexes of climatope (such as continentality, cryoregime and ombroregime) have not shown a significant effect on phytocenoses distribution. Then, climatic factors were identified as one of key climatic factors for distribution of steppe vegetation on large areas (Cheng & Nakamura, 2007; Vynokurov, 2014; Ermakov et al., 2017; Lashchinskiy et al., 2019). Our surveys have demonstrated the strong effect of thermal regime on petrophytic cenoses' distribution in the ecological space because the degree of rocky slopes' warming and exposure on the very steep slopes of the valley is essential for development of these cenoses. The steppe phytocoenoses of the estuary valley are characterised by zonal fescue-feather grass steppes and can be used as active bioindicators of zonal vegetation in the south of Ukraine. Alternatively, *Sedum acre* communities were not effective bioindicators, they show a wide synecology.

Localized ecological systems are known to pass dramatically and irreversibly from one state to another when they forced to cross critical thresholds; it highlights the need to improve biological forecasting by identification of early warning signs of critical transitions at global as well as regional scales (Barnosky et al., 2012; Asif et al., 2018). Nowadays, the valley of the Liman Kuyalnik is in a state of ecological disaster (Dubyna et al., 2018b; Ennan et al., 2018). The established relationships in ecological differentiation of plant communities will be applied to further monitoring of the biodiversity state, preservation and possible restoration of vegetation types that are, or were, native for this unique territory.

Conclusion

Results of phytoindication analysis of plant communities in the Liman Kuyalnik valley by the main environment indicators showed considerable ecological diversity of vegetation syntaxa. Their differentiation by ecological factors is mainly determined by water regime, from the most hygrophytic (*Bolboschoenetea maritimi*) to steppe subxerophitic and petrophytic (*Festuco-Brometea*, *Sedo-Scleranthetea*). In halophytic plant communities, soil acidity and salt regime also have a leading role. Distribution of plant communities most strongly correlated with edaphic factors, whereas microclimatic (light intensity) and climatic (thermo-regime) conditions have somewhat less influence on their differentiation.

Halophytic cenoses were characterized by quite wide ecological ranges with most ecological factors. Steppe communities showed much less ecological diversity. The key environmental factors that influence the formation of floristic and cenotic diversity of *Festucion valesiacae*, *Stipo lessingianae-Salvion nutantis* and *Tanaceto millefolii-Galatellion villosae* unions were moisture variability and salt regime, as well as soil moisture and carbonate content. The "eco-spaces" of these groups largely overlap. Temperature regime was the key factor for communities of *Potentillo arenariae-Linion czernjajevii* and *Alysso-Sedion* unions. In the liman valley, all the steppe communities were characterized by stenotopicity in relation to most ecological factors; these factors complexly determined the specificity and diversity of biotopes within the valley, which are unique and require protection and the taking of appropriate measures, depending on the changes in activity of one or other limiting factor.

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