Syntaxonomy and ecological differentiation of the pioneer vegetation of Ukraine. 1. Classes: *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea, Crypsietea aculeatae, Therosalicornietea*

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Pioneer plant communities grow on newly-formed ecotopes of coastal and partially continental areas, on patches that have dried after the surface water flooding. They are affected by sea tides, wind-induced effect, salinity, denudation, accumulation and sharp changes in soil humidity. To these factors are added chemical and biological pollution, as well as anthropogenic pressure. Due to these reasons, such plant communities have a specific floristic composition, structure, functional regime and resilience mechanisms, which are different from coenoses of more stable habitats. On the basis of the analysis of more than 600 phytosociological relevés using TWINSPAN modified algorithm the current state of littoral and halophytic classes of pioneer vegetation in Ukraine has been established and their syntaxonomic structure identified. It has been determined that the level of pioneer phytocoenoses diversity in Ukraine is similar to that of Central Europe. The *Cakiletea maritimae* class is presented by 1 order, 1 alliance, and 4 associations; *Ammophiletea* – by 1 order, 1 alliance, and 8 associations; *Crithmo-Staticetea* – by 1 order, 2 alliances, and 3 associations; *Crypsietea aculeatae* – by 1 order, 3 alliances, and 4 associations, *Therosalicornietea* – by 1 order, 2 alliances, and 10 associations. Synoptic tables of vegetation classes are given and nine alliances are briefly characterized. Using DCA-ordination analysis of syntaxa in the association-rank level we identified that the main factors of ecological differentiation are soil humidity and aeration as well as the nitrogen content. For the pioneer plant communities, other significant impact factors are the extremality of environmental conditions, their unevenness and non-equilibrium, in particular, the mechanical action of the sea waves, the dynamic processes of denudation and accumulation, salinity, as well as the variability of damping during the year. This research contributes to the identification of the place of the distinguished syntaxa of Ukrainian pioneer vegetation in the European system.

Keywords: plant communities; classification; new-formed ecotope; ecological gradients; DCA-ordination; Ukraine.

Introduction

Pioneer phytocoenoses are the initial producers of organic substances and initiate the development of derivative plant communities; they also have very important biological and ecological functions. Geocomplexes where littoral vegetation is formed are places of origin and conservation of biodiversity. They are also habitats for many plant and animal species, the source of spreading of their genetic material (DNA). Newly-formed ecotopes are perfect migration pathways for alien species. Besides, these territories are the centers of formation of endemic vegetation complexes that are distinguished by genus endemicity, especially in the coastal areas. Considerable variability of environmental factors ensures the exceptional role of pioneer plant communities in the development of adaptation processes. There is a theory that pioneer phytocoenoses will have a faster reaction to global climate changes than other types of vegetation. This difference is due to the predominance of alternative mechanisms of regulation of seasonal cycles in pioneer plants (Sergienko & Sonina, 2011). Other studies also confirm the hypothesis that the coastal dune vegetation is exposed to local climate influence which has significant effects on both floristic composition and plant community structure. As a result, the coastal phytocoenoses are particularly prone to the effect of possible climate change which may change species composition and distribution as well as disturb the native plant communities' development (Del Vecchio et al., 2018). That is why research on this vegetation type is highly relevant.

The syntaxonomy of pioneer vegetation in Europe has been well developed. In particular, classification schemes and syntaxa characteristics have been determined for the territories of Slovenia (Valachovič, 1995),

France (Bardat et al., 2004), Italy (Biondi et al., 2014), Spain and Portugal (Rivas-Martínez et al., 2001), Bulgaria (Tzonev et al., 2009), Hungary (Borhidi, 2003), Germany (Berg et al., 2004), Romania (Sanda et al., 2008) etc. European high and middle-rank syntaxa are generalized in "Vegetation of Europe…" (Mucina et al., 2016).

In comparison to countries of Western Europe, syntaxonomic structure of the pioneer plant communities in Ukraine has not been fully developed yet. Studies of *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea* and *Therosalicornietea* phytocoenoses has been conducted mainly in the Crimea and the coastal areas of the Black and Azov Sea (Vicherek, 1971; Dubyna et al., 1995, 2003, 2007a; Dubyna & Neuhäuslová, 2003; Dubyna & Dziuba, 2005; Vojtyuk, 2005; Tyshchenko, 2006; Korzhenevskiy & Kvitnitskaya, 2014). The *Crypsietea aculeatae* class communities, due to their ephemeral character, remain less researched; territorially they are present in the regions of the forest-steppe zone in the basin of Dnieper River (Bairak, 1997; Dziuba et al., 2010). Syntaxomic structure of these classes has been analyzed in some generalizing scientific papers (Tymoshenko, 1999; Korzhenevskiy et al., 2003; Dubyna et al., 2004, 2007b). Brief information about the syntaxa of these classes also has been published in the "Prodrome of the Vegetation of Ukraine" (Dubyna et al., 2019a).

The vegetation of *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea, Crypsietea aculeatae* and *Therosalicornietea* classes grows on new-formed ecotopes of coastal and continental areas, on the territories that have dried after surface flooding. They are affected by sea tides, wind-induced effect, salinity, denudation, accumulation and rapid changes in soil humidity. To these factors are added chemical and biological

pollution, as well as anthropogenic pressure. Due to these reasons, such plant communities have specific floristic composition, structure, functional regime and resilience mechanisms which are different from coenoses of more stable habitats. Today they are in the focus of many ecological problems associated with the large-scale building of hydropower in recent years, afforestation of sandy dunes and melioration of saline soils.

Development of nature conservation in the country and participation of Ukraine in international conventions on the conservation of biodiversity with its involvement in the European process of establishment of a single syntaxomic system in Europe, on the basis of the international scientific cooperation, raise questions about coentotic identification of its vegetation. The paper examines the syntaxonomy of pioneer vegetation of Ukraine and consists of three parts. In the first, we consider the syntaxonomy of the pioneer plant communities of the coastal dunes and halophytic new-formed ecotopes which involves the *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea, Crypsietea aculeatae, Therosalicornietea* classes; in the second part we will try to find out the syntaxonomy structure of pioneer vegetation on continental alluvial sands; the third part looks into diversity of annual wetland herbaceous plants on river banks and seasonally flooded territories.

The main aims of this paper are detailing the syntaxonomic structure of pioneer littoral and halophytic vegetation of Ukraine and clarifying its current state. On the base of DCA-ordination analysis – identification of the leading factors of ecological differentiation phytocoenoses. This method is widespread in biology and ecology for quantitative assessment of ecological changes from the geological datasets (Correa-Metrio et al., 2014), studies of vegetation successions (Cao et al., 2019),

building of hierarchical syntaxonomic schemes (Çoban & Willner, 2019; Zhou et al., 2019; Willner et al., 2019), identification of the main ecological factors of plant communities' differentiation (Korolyuk et al., 2018; Lashchinskiy et al., 2019), assessment of the impact of the environment on the floristic richness of a phytocoenosis (Jansons et al., 2016; Yousaf et al., 2016; Slezák et al., 2017) and other tasks. Using this method for studying the differentiation of pioneer vegetation in ecological space by the 12 vectors-ecofactors supplements phytosociological researches and allows us to detect ecosystems' conditions by the indicators of biotic components (Didukh, 2012).

The problem questions about syntaxonomic content of *Crypsietea aculeatae* and *Therosalicornietea* classes have been discussed.

Materials and methods

The studied territory is located in the south part of Ukraine, in particular, on the coastlines of the Black and Azov Sea (for *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea* classes), and in the steppe and the southern regions of forest-steppe zone (for *Therosalicornietea, Crypsietea aculeatae* classes, Fig. 1). Orographically, the major part of the study area is occupied by the Black Sea Lowland. Its surface is mostly flat and has a general slope to the south. The Danube, Dnister and Dnieper rivers form broad arms, and there are lakes-estuaries in their valleys. The Pryazovya territory is a coastal cumulative terrace plain. Orographically it is a lowland with the heights 0.5–40.0 m above the sea level. Lakes, islands, estuaries, sand-shelly spits and dunes make the relief of this territory very specific.

Fig. 1. Location of study area in Ukraine

The location of the Northern Black Sea region and Pryazovya in the south-western part of the Eastern-European plain is marked by a significant amount of solar radiation. The total annual solar radiation fluctuates between 110 kcal/cm^2 in the north and 125 kcal/cm^2 in the south. The annual radiation balance changes from 50 to 60 kcal/cm^2 accordingly. The annual sum of temperatures above 10 ℃ is 2,800–3,600 ℃. The frostless period lasts for 160–220 days, the period of active vegetation is 160–195 days. The average annual air temperature rises from the northeast to the southwest from +7.5 ℃ to 4.0–11.0 ℃; average air temperature in January is from –7.0 ℃ to –1.0 ℃ and average air temperature in July rises from +21.5 ℃ to +23.0 ℃ in the southern direction. The amount of precipitation is from 450 to 350 mm, it is up to 300 mm in the north part of the study area. Most of the precipitations (60–70%) fall in the warm period of the year. The characteristic feature of the Northern Black Sea region is high evaporation: 700–800 mm in the north of the zone and 900–1000 mm in the south. The humidity index changes from 1.2 to 0.8, which contributes to the processes of soil salinity (Rudenko, 2007).

Salinity is predominantly sulfate and chloride-sulfate, in the south of the Black Sea Lowland it is chloride. There can be observed the development of secondary soil salinity processes when solonetzes turn back into

solonchaks. The reason for this is the epeirogenetic lowering of the coastline, raising the level of saline groundwater on irrigated areas as well as excessive grazing. Typical soils are chestnut, meadow-chestnut, drained, muddy-sand, muddy-shelly as well as solonets and solonchaks.

The northern coastline of the Black and Azov Sea is a moving shelf on the periphery of the continental plate subjected to oscillatory motions of considerable magnitude (Geologicheskaya istoriya, 1980). Moreover, during the last 70 years, a general tendency of annual Ocean level rise by 3.0 mm is observed, which is associated with the so-called "greenhouse effect" or anthropogenic warming on the planet (Buynevich et al., 2011). During the XX century, the Ocean level rise was 12 cm at minimum (The State..., 1990), and its rise in the second half of the XXI century is predicted to be more than 10 cm higher than contemporary level as a result of on-going global warming.

The original phytosociological relevés, conducted by the authors from 1994 to 2018 according to the Braun-Blanquet approach (Westhoff & van der Maarel, 1973), have become the main data for syntaxonomy development of the pioneer vegetation of Ukraine, as well as the vegetation plots in the scientific publications mentioned above. The standard size of the plots was mainly 4 x 4 m. In some cases, in particular, on outstretched

coastlines, the plots were 1 x 4 or 2 x 5 m. We have also followed the requirements of the homogeneous structure of the vegetation cover.

Data arrangement has been made by creating the phytosociological database using TURBOVEG software (Hennekens & Schaminée, 2001). The phytosociological material interpretation was made in a few steps. In the first stage it was made using Two-Way Indicator Species Analysis (TWINSPAN), in particular, its modified algorithm (Hill, 1979; Tichý, 2002; Roleček et al., 2009). The total dataset of halophytic and littoral pioneer vegetation of Ukraine, that included 6,505 relevés, was processed and divided into smaller groups according to their differences. "Pseudospecies" cut level was 0%, 5%, 15%, 25%. Whittaker's beta diversity index was chosen as a measure of the heterogeneity of the clusters (Whittaker, 1978). After this, every dendrite was analyzed separately and clusters distinguished which by groups of diagnostic species correspond to classes of pioneer vegetation. Within these clusters that included more than 600 relevés, the most homogeneous ones were identified as phytocoenons that have been accorded the rank of alliances. Then after the rejection of some vegetation plots, every cluster was analyzed using PC-ORD software. The Sörensen index was chosen as a measure of the homogeneity of the clusters (Sörensen, 1948), and relevés were grouped by the flexible beta method at 0.25. The use of PC-ORD algorithm at the final stages of conducting analysis made it possible to identify smaller groups that almost corresponded to the association-rank. The diagnostic species of a syntaxon were determined according to the phi coefficient (Willner et al., 2009), the accepted value is 0.25. Identification of the received phytocoenons was conducted based on the analysis of their diagnostic species using foreign and Ukrainian publications (Mucina et al., 2016). The method of DCA-ordination (Hill & Gauch, 1980; ter Braak & Smilauer, 2015) of R-project (Venables & Smith, 2008) integrated into a JUICE software package, was used to identify

the leading factors of ecological differentiation of plant communities. The ecological parameters were calculated by means of Y. Didukh's phytoindication scales (Didukh, 2011), which allows us to make an ordination analysis by 12 factors: soil humidity (Hd), variability of damping (fH), soil aeration (Ae), nitrogen content in soil (Nt), acidity (Rc), total salt regime (Sl), carbonate content in soil (Ca), thermal climate (Tm), humidity (Om), continental climate (Kn), cryoclimate (Cr), light (Lc). The nomenclature of taxa is given according to "Flora Europea" (Tutin et al., 1964–1980).

Results

The results of the phytosociological database cluster analysis made it possible to determine the place of the studied pioneer vegetation plant communities among the totality of all phytocoenotic data of halophytic and littoral vegetation of Ukraine (Fig. 2). It has been found out that *Ammophiletea* plant communities (cluster 13) have the most floristic similarity to the *Helichryso-Crucianelletea maritimae* phytocoenoses (clusters 14–16), which are often located directly behind them, occupying the hind-surf parts of the seaside shaft and stabilized coastal grey dunes. Also similar to each other are coenoses of the *Crithmo-Staticetea* (cluster 52) and *Cakiletea maritimae* (cluster 53) classes, which are located on the sea surf line. The plant communities of *Crypsietea aculeatae* (cluster 91) and *Therosalicornietea* (clusters 92, 93) classes also demonstrate a high floristic affinity because they are formed in ecological conditions, similar in several parameters – salt regime, soil humidity, variability of damping, etc. They form a group of dendrites with transitional coenoses to salt meadows of the *Festuco-Puccinellietea* class (cluster 94). Subsequently, each of the clusters was subjected to the same analysis to obtain phytocoenons of association rank and to identify connections between syntaxa.

Fig. 2. Hierarchical cluster analysis of relevés (PC-ORD)

Classification Scheme
    Cakiletea maritimae Tx. et Preising in Tx. ex Br.-Bl. et Tx. 1952
        Thero-Atriplicetalia Pignatti 1953
            Cakilion euxinae Géhu et al. 1994
                Cakilo euxinae-Euphorbietum peplidis Dubyna, Neuhäuslová et Shelyag-Sosonko 1994
                Lactuco tataricae-Cakiletum euxinae Korzhenevsky et Klyukin in Korzhenevsky 2001
                Cakilo euxinae-Salsoletum tragi Vicherek 1971
                Cakilo euxinae-Salsoletum ruthenicae Vicherek 1971
    Ammophiletea Br.-Bl. et Tx. ex Westhoff et al. 1946
        Ammophiletalia Br.-Bl. et Tx. ex Westhoff et al. 1946
            Elymion gigantei Morariu 1957
                Tournefortietum sibiricae Popescu et Sanda 1975
                Salsoletum sodae Slavnić 1948
                Elymetum gigantei Morariu 1957
                Artemisietum arenariae Popescu et Sanda 1975
                Asparago levinae-Calamagrostidetum epigei Vicherek 1971

Centaurea odessanae-Elymetum gigantei Vicherek 1971
      Elymo-Astrodaucetum littoralis Korzhenevsky, Volkova et Klyukin in Korzhenevsky 2001
      Crambetum maritimae Şerbănescu 1970
Crithmo-Staticetea Br.-Bl. in Br.-Bl. et al. 1952
  Crithmo-Staticetalia Molinier 1934
    Kochio prostratae-Limonion meyeri Korzhenevsky et Klyukin 1987
      Puccinellio distantis-Limonietum meyeri Korzhenevsky et Klyukin 1987
    Elytrigio bessarabicae-Lactucion tataricae Korzhenevsky ex Didukh et Mucina in Mucina et al. 2016
      Crithmo-Elytrigietum bessarabicae Korzhenevsky et Klyukin in Korzhenevsky 2001
      Lactuco tataricae-Elytrigietum bessarabicae Korzhenevsky et Klyukin in Korzhenevsky 2001
Therosalicornietea Tx. in Tx. et Oberd. 1958
  Camphorosmo-Salicornietalia Borhidi 1996
    Salicornion prostratae Géhu 1992
      Salicornietum prostratae Soó 1927
      Petrosimonio oppositifoliae-Salicornietum Korzhenevsky et Klyukin in Dubyna et al. 2007
      Bassietum hirsutae Şerbănescu 1965
      Petrosimonio oppositifoliae-Bassietum sedoidis Shelyag-Sosonko et al. 1989
      Ofaisto monandri-Salicornietum Dubyna et Neuhäuslová 2003
      Halimionetum pedunculatae Şerbănescu 1965
    Suaedion acuminatae Golub et Tchorbadze in Golub 1995 corr. Lysenko et Mucina 2015
      Salicornio perennantis-Suaedetum salsae Freitag, Golub et Yuritsyna 2001
      Suaedetum salsae Golub et Tchorbadze 1995
      Suaedetum confusae Golub et Tchorbadze in Golub 1995
      Petrosimonio brachiatae-Artemisietum santonicae Korzhenevsky et Klyukin 1991
Crypsietea aculeatae Vicherek 1973
  Crypsietalia aculeatae Vicherek 1973
    Cypero-Spergularion salinae Slavnić 1948
      Crypsietum aculeatae Wenzl 1934
    Heleochloion schoenoidis Br.-Bl. ex Rivas Goday 1956
      Heleochloëtum schoenoidis Ţopa 1939
      Polygono salsuginei-Crypsietum aculeatae Korzhenevsky et Klyukin in Korzhenevsky et al. 1997
    Lepidion latifolii Golub et Mirkin in Golub 1995
      Cynancho acutae-Lepidietum latifolii Dubyna, Neuhäuslová et Shelyag-Sosonko 1994

The class *Cakiletea maritimae* combines pioneer plant communities of nitrophilous annual herbs in strandlines of sandy and shingle beaches of the coasts that are formed in the tidal upper boundary of the surf. It includes 4 associations (Fig. 3, Table 1). They are common in the coastal areas of the Black and Azov Sea. The leading factors of territorial differentiation of syntaxa are the intensity of abrasive-accumulative activity of the sea, hydrological conditions, soil type, and its consistency.
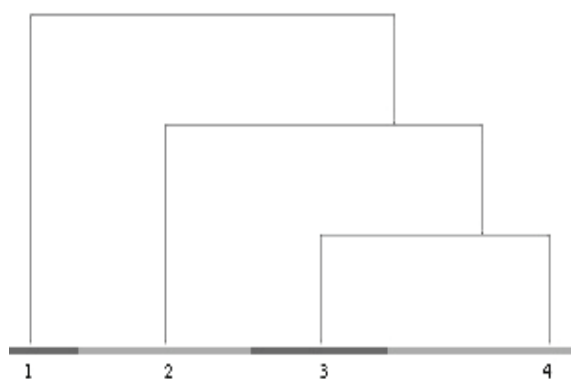

Fig. 3. Hierarchical cluster analysis of *Cakiletea maritimae* phytosociological relevés: *1* – association *Cakilo euxinae-Salsoletum tragi*, *2* – association *Lactuco tataricae-Cakiletum euxinae*, *3* – association *Cakilo euxinae-Euphorbietum peplidis*, *4* – association *Cakilo euxinae-Salsoletum ruthenicae*

Alliance *Cakilion euxinae* includes halo-nitrophilous plant communities of the Black and Azov Sea shores that are formed at the zone of storm washovers. The ordination analyses on the association-rank level made it possible to conclude that the main factors of their differentiation are the variability of damping, soil acidity, nitrogen and carbonate content in the soil, and cryoclimate (Fig. 4). The vectors by these gradients are the closest to the first ordination axis. Additionally, the soil aeration and total salt regime of ecotopes influence the ecological differentiation of coenoses.

Table 1
Synoptic table of the class *Cakiletea maritimae*

No. of syntaxa	1	2	3	4
Number of relevés	9	11	10	24
1	2	3	4	5
Euphorbia peplis	58.6	16.6	–	–
Astrodaucus littoralis	39.9	14.1	–	–
Leymus racemosus	–	75.3	–	–
Lactuca tatarica	–	72.4	–	–
Crambe maritima	21.7	60.2	–	–
Aeluropus littoralis	–	54.8	–	–
Polygonum aviculare	–	50.1	–	7.4
Atriplex calotheca	–	47.7	–	1.8
Xanthium strumarium s. italicum	–	44.8	–	6.6
Eryngium maritimum	–	41.9	–	9.1
Carex ligerica	–	37.8	–	–
Convolvulus arvensis	–	37.8	–	–
Elymus farctus s. bessarabicus	–	34.9	–	13.3
Gypsophila paniculata	–	26.4	–	–
Silene conica s. subconica	–	26.4	–	–
Secale sylvestre	–	26.4	–	–
Clypeola jonthlaspi	–	26.4	–	–
Elymus repens	–	26.4	–	–
Hordeum murinum	–	26.4	–	–
Suaeda altissima	–	26.4	–	–
Melilotus taurica	–	26.4	–	–
Melilotus alba	–	26.4	–	–
Puccinellia distans	–	26.4	–	–
Aster tripolium	–	26.4	–	–
Salsola kali s. tragus	–	–	86.6	–
Atriplex prostrata	–	–	79.8	–
Cynodon dactylon	–	–	–	44.7
Cynanchum acutum	–	–	–	36.1
Glaucium flavum	–	–	–	31.1
Argusia sibirica	–	–	–	31.1
Limonium gmelinii	–	–	–	31.1
Verbascum pinnatifidum	–	–	–	25.3
Aegilops cylindrica	–	–	–	25.3
Aegilops neglecta	–	–	–	25.3

	1	2	3	4	5
Bromus tectorum		–	–	–	25.3
Salsola kali		–	42.2	–	63.2
Leymus racemosus s. sabulosus		–	–	24.7	23.4
Gypsophila perfoliata		–	–	–	17.8
Asparagus litoralis		–	–	–	17.8
Rapistrum rugosum		–	–	–	17.8
Thlaspi perfoliatum		–	–	–	17.8
Eryngium campestre		–	–	–	17.8
Bassia sedoides		–	–	–	17.8
Centaurea arenaria s. odessana		–	–	–	17.8
Atriplex tatarica		–	–	–	17.8
Silene densiflora		–	–	–	17.8
Aster linosyris		–	–	–	17.8
Cichorium intybus		–	–	–	17.8
Cerastium fontanum s. vulgare		–	–	–	17.8
Elaeagnus angustifolia		–	–	–	17.8
Elymus nodosus		–	–	–	17.8
Medicago rigidula		–	–	–	17.8
Artemisia tschernieviana		–	–	11.0	17.2
Cakile maritima s. euxina		–	9.8	9.8	9.8
Ephedra distachya		–	18.6	–	2.7
Centaurea apiculata s. adpressa		–	18.6	–	2.7
Salicornia prostrata		–	18.6	–	2.7
Erysimum repandum		–	–	20.2	2.0
Polygonum maritimum		–	19.6	24.7	–

Notes: numbers mark syntaxa: *1 – Cakilo euxinae-Euphorbietum peplidis*; *2 – Lactuco tataricae-Cakiletum euxinae*; *3 – Cakilo euxinae-Salsoletum tragi*; *4 – Cakilo euxinae-Salsoletum ruthenicae*.

To *Ammophiletea* class belong the plant communities of coastal mobile sand dunes of the Black and Azov Sea shores. It represented by 8 associations (Fig. 5, Table 2). The phytocoenoses of the class are extended to the most dynamic relief forms that are called avandunes and are always on the transformation stage. They affected by sand blowing from already formed landforms as well as its accumulation from lower located beach areas. Alliance *Elymion gigantei* includes plant communities of the seaside shaft and coastal white dunes. Their regional specifics become apparent at the associations and subassociations-rank levels and are connected with the intensity of abrasive-accumulative activity of the sea, eolian processes as well as its place in landscape.

The results of ordination of syntaxa within the class have demonstrated that the main factor that identifies its ecological differentiation is the variability of damping, the vector by which it almost aligns with the first ordination axis. The belonging this gradient to the leading ones is determined by coastal location of the plant communities in the zone of regular wind-driven pressure of sea waves (Fig. 6).
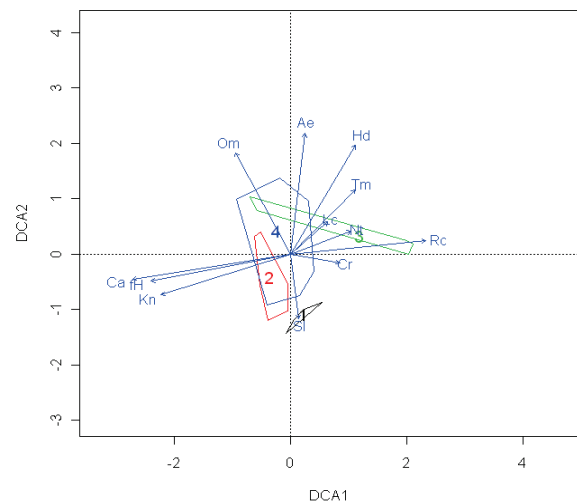

Fig. 4. Results of ordination analysis of the *Cakiletea maritimae* associations: the numbers mark syntaxa: *1 – Cakilo euxinae-Euphorbietum peplidis*; *2 – Lactuco tataricae-Cakiletum euxinae*; *3 – Cakilo euxinae-Salsoletum tragi*; *4 – Cakilo euxinae-Salsoletum ruthenicae*; here and after the Y. Didukh's scale (2011) have been used: Hd – soil humidity; Nt – nitrogen content in soil; Ca – carbonate content in soil; Rc – soil acidity; Sl – total salt regime; fH – variability of damping; Ae – soil aeration; Lc – light; Kn – continental climate; Om – humidity; Tm – thermal climate; Cr – cryoclimate; DCA1, DCA2 – ordination axis

Fig. 5. Hierarchical cluster analysis of *Ammophiletea* phytosociological relevés: *1 – association Tournefortietum sibiricae, 2 – Salsoletum sodae, 3 – association Artemisietum arenariae, 4 – association Elymetum gigantei, 5 – association Crambetum maritimae, 6 – association Asparago levinae-Calamagrostietum epigei, 7 – association Centaurea odessanae-Elymetum gigantei, 8 – association Elymo-Astrodaucetum littoralis*

Table 2
Synoptic table of the class *Ammophiletea*

No. of syntaxa	1	2	3	4	5	6	7	8
Number of relevés	25	10	20	6	10	13	17	14
1	2	3	4	5	6	7	8	9
Elymus farctus	88.2	–	–	–	–	–	–	–
Elymus repens s. elongatiformis	42.4	–	–	–	–	–	–	–
Euphorbia seguierana	37.8	–	–	–	–	–	–	–
Helichrysum arenarium	37.8	–	–	–	–	–	–	–
Festuca beckeri	36.7	–	4.1	–	–	–	–	–
Asparagus maritimus	–	94.2	–	–	–	–	–	–
Calamagrostis epigejos	–	87.8	–	–	4.6	–	–	–
Medicago sativa s. falcata	19.0	63.1	–	–	–	–	–	–
Syrenia montana	–	36.3	–	–	–	–	–	23.1
Galium tenderiense	17.4	31.5	–	–	–	–	5.7	–
Polygonum maritimum	–	–	60.7	–	–	–	–	–
Polygonum aviculare	–	–	60.7	–	–	–	–	–
Salsola kali	–	–	43.1	–	15.8	–	–	–
Cerastium pumilum	–	–	36.6	–	–	–	–	–
Plantago arenaria	–	–	35.8	–	–	–	5.7	–
Xanthium strumarium s. italicum	–	–	34.7	–	–	–	–	7.8
Holosteum umbellatum	–	–	29.8	–	–	–	–	–
Erophila verna	–	–	29.8	–	–	–	–	–
Carduus uncinatus	–	–	29.8	–	–	–	–	–
Alyssum turkestanicum	–	–	29.8	–	–	–	–	–
Suaeda prostrata	–	–	–	90.2	–	–	–	–

1	2	3	4	5	6	7	8	9
Puccinellia distans	–	–	–	90.2	–	–	–	–
Argusia sibirica	–	–	–	85.3	–	–	–	–
Salicornia prostrata	–	–	–	79.8	–	–	–	–
Polygonum arenarium s. arenarium	–	–	–	63.2	–	12.7	–	–
Bromus squarrosus	–	–	–	59.9	–	–	5.7	–
Melilotus alba	–	13.1	–	53.1	–	–	–	18.8
Bassia hirsuta	–	–	–	30.5	–	–	–	9.3
Artemisia tschernieviana	3.3	–	–	–	84.4	–	–	–
Elymus nodosus	–	–	–	–	60.7	–	–	–
Amorpha fruticosa	–	–	–	–	42.4	–	–	–
Petasites spurius	–	–	–	–	42.4	–	–	–
Salix viminalis	–	–	–	–	42.4	–	–	–
Elymus farctus s. bessarabicus	–	–	12.4	–	32.3	–	–	–
Picris hieracioides s. hieracioides	–	–	1.7	–	30.4	6.9	–	–
Elaeagnus angustifolia	–	–	–	–	29.8	–	–	–
Hippophae rhamnoides	–	–	–	–	29.8	–	–	–
Asparagus brachyphyllus	–	–	–	–	29.8	–	–	–
Artemisia santonicum	–	–	–	–	–	53.3	13.5	–
Limonium latifolium	–	–	–	–	–	52.9	–	–
Elymus elongatus	–	–	–	–	–	34.7	13.7	–
Plantago maritima	–	–	–	–	–	26.1	–	–
Cakile maritima	–	–	–	–	–	26.1	–	–
Euphorbia paralias	–	–	–	–	–	26.1	–	–
Seseli campestre	–	–	–	–	–	–	51.7	–
Elymus uralensis s. viridiglumis	–	–	–	–	–	–	32.3	–
Petasites albus	–	–	–	–	–	–	32.3	–
Erysimum repandum	–	–	–	–	–	–	32.3	–
Artemisia campestris s. campestris	–	–	–	–	–	–	–	62.9
Linaria genistifolia	–	18.9	–	–	–	–	–	57.2
Secale sylvestre	–	–	–	–	1.7	–	4.1	45.8
Suaeda confusa	–	–	–	–	–	–	–	43.9
Chondrilla juncea	–	–	–	–	–	–	–	43.9
Crambe maritima	18.6	17.1	24.6	1.9	–	–	–	39.8
Xanthium strumarium	–	–	–	–	–	24.6	1.3	39.4
Lepidium latifolium	–	–	–	–	–	–	5.1	37.5
Convolvulus arvensis	–	–	–	–	–	–	–	35.7
Chenopodium album	–	–	–	–	–	–	–	35.7
Bromus tectorum	–	–	–	–	–	–	8.1	28.4
Rumex confertus	–	–	–	–	–	–	–	25.1
Agropyron cristatum s. pectinatum	–	–	–	–	–	–	–	25.1
Atriplex tatarica	–	–	–	–	–	–	–	25.1
Glaucium flavum	–	–	–	–	–	–	–	25.1
Amaranthus blitoides	–	–	–	–	–	–	–	25.1
Althaea cannabina	–	–	–	–	–	–	–	25.1
Scorzonera parviflora	–	–	–	–	–	–	–	25.1
Elymus repens s. pseudocaesius	–	–	–	–	–	–	–	25.1
Gypsophila fastigiata	–	–	–	–	–	–	–	25.1
Matricaria perforata	–	–	–	–	–	–	–	25.1
Marrubium peregrinum	–	–	–	–	–	–	–	25.1
Melilotus officinalis	–	–	–	–	–	–	–	25.1
Centaurea arenaria s. odessana	49.9	–	–	–	18.1	–	–	42.0
Seseli arenarium	41.8	28.4	–	–	–	–	–	–
Consolida paniculata	34.3	31.5	–	–	–	–	–	–
Cynanchum acutum	31.5	57.9	–	–	–	–	23.9	–
Lactuca tatarica	27.9	37.0	10.5	–	–	–	–	–
Astrodaucus littoralis	–	–	51.5	–	–	–	–	38.8
Cakile maritima s. euxina	–	–	38.2	54.3	–	–	–	2.5
Euphorbia peplis	–	–	26.8	–	–	35.3	–	–
Salsola soda	–	–	–	37.4	–	66.7	–	–
Gypsophila perfoliata	–	–	–	28.0	28.0	–	–	7.8
Leymus racemosus	47.9	47.9	47.9	–	–	–	–	–
Leymus racemosus s. sabulosus	–	–	–	8.5	33.9	16.3	33.9	33.9
Galium humifusum	–	–	22.8	–	–	–	–	21.4
Seseli tortuosum	–	–	10.8	–	–	–	–	17.4
Linum austriacum	–	–	10.8	–	–	–	–	17.4
Verbascum pinnatifidum	–	–	10.8	–	–	–	–	17.4
Falcaria vulgaris	–	–	10.8	–	–	–	–	17.4
Alyssum hirsutum	–	–	20.5	–	–	–	–	13.1
Cichorium intybus	–	–	20.5	–	–	–	–	13.1
Syrenia cana	–	–	–	–	20.5	–	–	13.1
Astragalus onobrychis	–	–	20.5	–	–	–	–	13.1
Eryngium campestre	–	–	5.1	–	16.7	–	–	10.1
Salsola kali s. tragus	–	–	–	11.6	–	20.4	4.9	8.3
Carex ligerica	22.0	–	1.4	–	–	–	3.1	5.4
Conyza canadensis	–	–	–	22.4	–	–	13.4	4.9
Eryngium maritimum	19.6	–	10.3	23.0	–	–	–	–
Orobanche coerulescens	18.8	–	–	–	–	–	–	–

1	2	3	4	5	6	7	8	9
Thymus dimorphus	–	–	21.0	–	–	–	–	–
Phragmites australis	–	–	21.0	–	–	–	–	–
Lepidium perfoliatum	–	–	21.0	–	–	–	–	–
Asperula tenella	–	–	21.0	–	–	–	–	–
Coronilla varia	–	–	21.0	–	–	–	–	–
Medicago lupulina	–	–	21.0	–	–	–	–	–
Papaver dubium	–	–	21.0	–	–	–	–	–
Senecio vernalis	–	–	21.0	–	–	–	–	–
Holosteum umbellatum s. glutinosum	–	–	21.0	–	–	–	–	–
Arenaria serpyllifolia	–	–	21.0	–	–	–	–	–
Teucrium polium	–	–	21.0	–	–	–	–	–
Centaurea arenaria s. majorovii	–	–	21.0	–	–	–	–	–
Aeluropus littoralis	–	–	21.0	–	–	–	–	–
Plantago lanceolata	–	–	21.0	–	–	–	–	–
Erysimum diffusum	–	–	21.0	–	–	–	–	–
Myagrum perfoliatum	–	–	21.0	–	–	–	–	–
Sisymbrium polymorphum	–	–	–	–	–	–	22.8	–
Tragopogon brevirostris s. brevirostris	–	–	–	–	–	–	22.8	–
Elymus repens	–	–	–	–	–	–	22.8	–
Linum perenne	–	–	–	–	–	–	22.8	–
Artemisia salsoloides	–	–	–	–	–	–	22.8	–
Inula britannica	–	–	–	–	–	–	22.8	–
Cynodon dactylon	–	–	–	–	–	–	22.8	–
Polygonum species	–	–	–	–	–	–	22.8	–
Ephedra distachya	18.1	–	–	–	–	–	12.0	–
Picris hieracioides	–	–	–	–	21.7	–	10.6	–
Centaurea apiculata s. adpressa	–	–	–	–	21.7	–	10.6	–

Notes: the numbers marked syntaxa: *1 – Centaureo odessanae-Elymetum gigantei*; *2 – Asparago levinae-Calamagrostidetum epigei*; *3 – Elymo-Astrodaucetum littoralis*; *4 – Tournefortietum sibiricae*; *5 – Artemisietum arenariae*; *6 – Salsoletum sodae*; *7 – Elymetum gigantei*; *8 – Crambetum maritimae*.
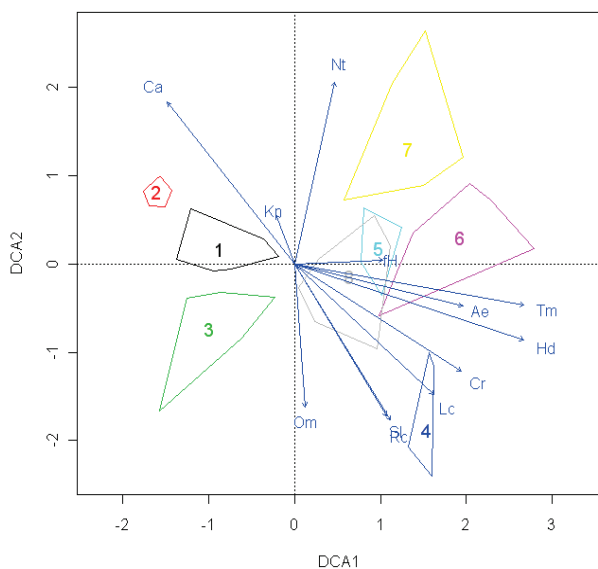

Fig. 6. Results of ordination analysis of the *Ammophiletea* associations: the numbers marked syntaxa: *1 – Centaureo odessanae-Elymetum gigantei*; *2 – Asparago levinae-Calamagrostidetum epigei*; *3 – Elymo-Astrodaucetum littoralis*; *4 – Tournefortietum sibiricae*; *5 – Artemisietum arenariae*; *6 – Salsoletum sodae*; *7 – Elymetum gigantei*; *8 – Crambetum maritimae*
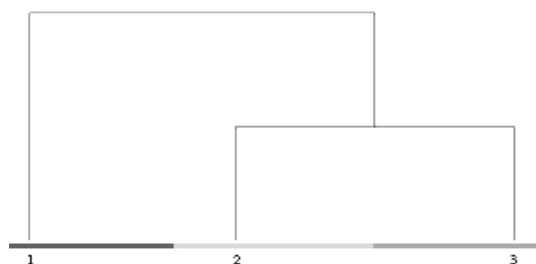

Fig. 7. Hierarchical cluster analysis of *Crithmo-Staticetea* phytosociological relevés: *1* – association *Puccinellio distantis-Limonietum meyeri*, *2* – association *Crithmo-Elytrigietum bessarabicae*, *3* – association *Lactuco tataricae-Elytrigietum bessarabicae*

The class *Crithmo-Staticetea* includes rocky and pebble beaches plant communities of the Black Sea abrasive shores that are formed by the influence of saline splatters. It contains 3 associations (Fig. 7, Table 3). The main factors of its territorial differentiation are relief of territory, soil humidity, total salt regime and structure of the substrate. Alliance *Kochio prostratae-Limonion meyeri* includes phytocoenoses of active and non-active cliffs that consist of limestones on the Kerch Peninsula of Crimea. Alliance *Elytrigio bessarabicae-Lactucion tataricae* this is plant communities of cliffs, rocky and pebble beaches that are composed of dense carbonates and are widespread on the Eastern coast of the Crimea.

Table 3

Synoptic table of the class *Crithmo-Staticetea*

No. of syntaxa	1	2	3
Number of relevés	10	33	9
1	2	3	4
Bassia prostrata	95.6	–	–
Holosteum umbellatum	85.3	–	–
Puccinellia distans	85.3	–	–
Goniolimon tataricum	78.0	–	–
Halimione verrucifera	70.7	–	–
Puccinellia festuciformis s. convoluta	63.2	–	–
Medicago sativa s. falcata	63.2	–	–
Allium flavum s. tauricum	55.5	–	–
Poa bulbosa	55.5	–	–
Bromus hordeaceus s. hordeaceus	55.5	–	–
Ephedra distachya	47.1	–	–
Limonium latifolium	47.1	–	–
Bromus tectorum	42.9	–	–
Plantago lanceolata	37.8	–	–
Aster linosyris	37.8	–	–
Limonium meyeri	35.0	–	–
Cynanchum acutum	29.6	–	23.2
Asparagus brachyphyllus	26.3	–	–
Taraxacum erythrospermum	26.3	–	–
Crithmum maritimum	–	71.2	–
Seseli dichotomum	–	50.0	–
Argusia sibirica	–	50.0	–
Gypsophila muralis	–	47.4	–
Senecio bicolor	–	44.7	–
Euphorbia paralias	–	41.9	–
Seseli gummiferum	–	39.0	–
Capparis spinosa	–	39.0	–
Dactylis glomerata s. hispanica	–	35.9	–

	1	2	3	4
Artemisia santonicum		–	31.8	–
Trachomitum sarmatiense		–	29.0	–
Parietaria lusitanica s. serbica		–	29.0	–
Bassia laniflora		–	25.0	–
Equisetum ramosissimum		–	25.0	–
Dorycnium pentaphyllum s. herbaceum		–	25.0	–
Galium humifusum		–	–	53.9
Atriplex calotheca		–	9.2	51.1
Cakile maritima s. euxina		–	–	50.0
Aeluropus littoralis		–	–	50.0
Phragmites australis		–	–	44.2
Astrodaucus littoralis		–	14.7	41.1
Galium spurium		–	–	40.0
Alyssum hirsutum		–	–	40.0
Crambe maritima		–	8.8	38.2
Crambe aspera		–	–	35.2
Asparagus litoralis		–	–	35.2
Marrubium peregrinum		–	–	35.2
Cichorium intybus		–	8.8	31.9
Melica ciliata s. monticola		–	–	31.0
Euphorbia peplis		–	–	31.0
Arthonia calcicola		–	–	27.7
Gypsophila paniculata		–	–	27.7
Hordeum murinum		–	–	27.7
Elymus repens		–	–	27.7
Xanthium strumarium		–	–	27.7
Convolvulus arvensis		–	–	27.7
Cardaria draba		–	–	27.3
Lactuca tatarica		–	27.7	58.2
Aster tripolium		–	1.0	16.4
Glaucium flavum		–	13.5	15.6
Elymus farctus s. bessarabicus		7.1	–	7.1
Melilotus alba		–	–	3.7
Centaurea solstitialis		–	14.3	–
Artemisia austriaca		–	14.3	–
Astragalus glaucus		–	14.3	–
Sonchus asper		–	20.3	–
Convolvulus lineatus		–	20.3	–
Centaurea arenaria s. odessana		–	20.3	–
Lappula squarrosa s. squarrosa		–	20.3	–
Cirsium arvense		–	20.3	–
Lactuca saligna		–	20.3	–
Eryngium maritimum		–	20.3	–

Note: the numbers marked syntaxa: *1 – Puccinellio distantis-Limonietum meyeri*; *2 – Crithmo-Elytrigietum bessarabicae*; *3 – Lactuco tataricae-Elytrigietum bessarabicae*.

According to the results of the ordination of *Crithmo-Staticetea* plant communities (Fig. 8) it has been found that their differentiation in the hyperspace of abiotic factors occurs along the gradient of ecotope light regime as well as climate aridity-humidity and soil humidity.

The class *Therosalicornietea* combines pioneer plant communities of annual halophyte succulents on wet, periodically flooded ecotopes with solonetzes and solonchaks. They are common in the steppe and in the south of the forest-steppe zone. They are more frequent in the territories where the sea has a direct influence, local depressions (pods), on flat areas near permanent and temporary water reservoirs, estuary shores (coast of the Black and Azov Sea, Prysyvashya). In the continental regions, these phytocoenoses grow on accumulative types of landforms – lowlands, river terraces and littoral zone of lakes (left bank river terraces of the Middle Dnieper). Also, *Therosalicornietea* plant communities are found on saline soils in the places of salt extraction in the Pre-Carpathian region. The class includes 10 associations (Fig. 9, Table 4). Coastal phytocoenoses (especially in Prysyvashya) are characterized by the predominance of hyper-halophytic species within their coenofloras, continental ones (on the left bank of the Dnieper River) – by the prevalence of salt meadow species. *Ofaisto monandri-Salicornietum* and *Petrosimonio oppositifoliae-Salicornietum* are endemic associations confined by the territory of Prysyvashya. Estuaries of large rivers (Dnieper, Dnister, Danube) define the territorial specificity because the water regime does not promote the spread of *Therosalicornietea* plant communities on those territories, as well as coastal spits of the Azov Sea because of their geomorphological peculiarities and more continental climate in comparison to the Black Sea Lowland. The Crimean Peninsula has phytocoenotic uniqueness where such associations as *Lepidietum crassifoliae* and *Petrosimonio brachiatae-Artemisietum santonicae* are described. The leading factors of territorial differentiation of syntaxa are relief of ecotopes, periods of offshore flooding, total salt regime, as well as their structure. The alliance *Salicornion prostratae* includes pioneer vegetation of the lowland territories on the seashores with muddy soils, on coastal zones of estuaries and on the salinized areas in the floodplains of rivers. *Thero-Suaedion* alliance represents terrophytic succulent vegetation of salinized wet territories of the seashores with the predominance of species of the genus *Suaeda*.
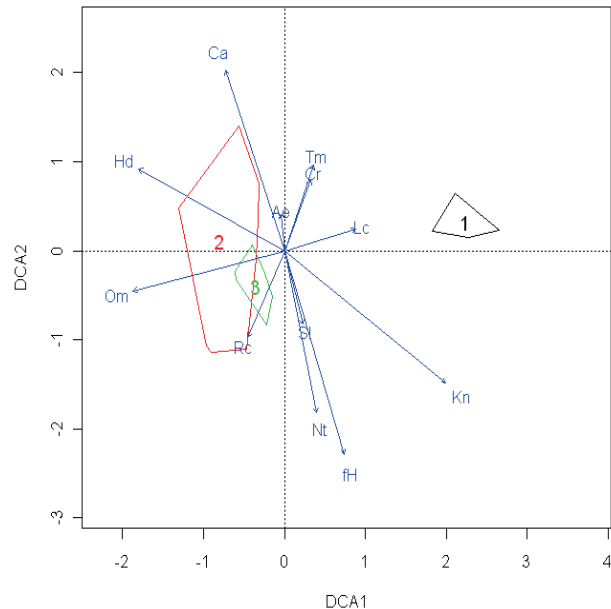

Fig. 8. Results of ordination analysis of the *Crithmo-Staticetea* associations: the numbers marked syntaxa: *1 – Puccinellio distantis-Limonietum meyeri*; *2 – Crithmo-Elytrigietum bessarabicae*; *3 – Lactuco tataricae-Elytrigietum bessarabicae*
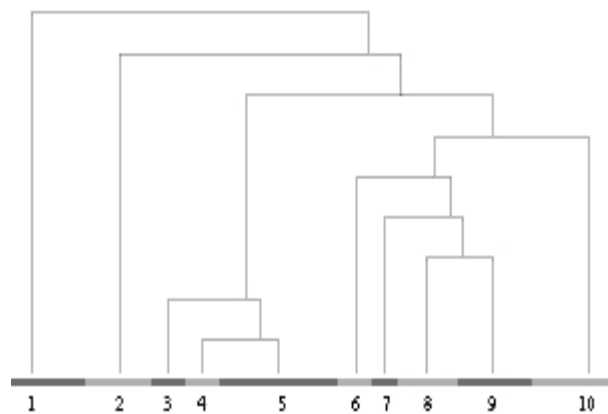

Fig. 9. Hierarchical cluster analysis of *Therosalicornietea* phytosociological relevés: *1 –* association *Petrosimonio brachiatae-Artemisietum santonicae*, *2 –* association *Petrosimonio oppositifoliae-Bassietumsedoidis*, *3 –* association *Suaedetum salsae*, *4 –* association *Salicornio perennantis-Suaedetum salsae*, *5 –* association *Ofaisto monandri-Salicornietum*, *6 –* association *Bassietum hirsutae*, *7 –* association *Suaedetum confusae*, *8 –* association *Salicornietum prostratae*, *9 –* association *Petrosimonio oppositifoliae-Salicornietum*, *10 –* association *Halimionetum pedunculatae*

DCA-ordination of *Therosalicornietea* class vegetation has demonstrated that their ecological distribution is mainly determined by continental climate (Fig. 10). The additional factors of ecological differentiation are the total salt regime, acidity as well as cryoclimate.

Table 4
Synoptic table of the class *Therosalicornietea*

No.of syntaxa	1	2	3	4	5	6	7	8	9	10
Number of relevés	150	6	11	16	37	11	54	6	14	18
1	2	3	4	5	6	7	8	9	10	11
Cynanchum acutum	30.2	–	–	–	–	–	–	–	–	–
Poa bulbosa	–	56.7	16.0	–	–	–	–	–	9.9	–
Polygonum species	–	55.7	–	–	–	–	–	–	–	–
Halimione verrucifera	–	55.7	–	3.7	14.8	–	–	–	7.0	–
Bassia sedoides	–	52.3	–	–	–	–	–	19.6	–	–
Elymus elongatus	–	50.1	–	–	–	–	–	–	–	–
Petrosimonia oppositifolia	–	48.2	–	–	–	–	–	–	22.8	–
Elymus repens	–	46.3	7.4	–	–	–	–	–	–	–
Puccinellia festuciformis s. convoluta	–	35.6	–	18.9	12.1	–	3.5	–	11.8	13.4
Bromus squarrosus	–	33.3	13.9	–	–	–	4.9	–	–	–
Juncus gerardi	–	30.8	–	–	19.8	–	10.5	–	–	–
Bassia hirsuta	–	–	77.4	2.8	–	2.3	–	–	–	–
Atriplex prostrata	–	–	39.6	–	–	–	5.9	13.3	–	–
Lepidium ruderale	–	–	38.5	–	–	–	–	–	–	–
Ofaiston monandrum	–	–	–	99.3	–	–	–	–	–	–
Pholiurus pannonicus	–	7.3	–	78.9	–	–	–	–	–	–
Frankenia hirsuta	–	2.8	–	53.2	18.0	–	–	–	–	–
Tetradiclis tenella	–	–	–	48.0	–	–	–	–	–	–
Limonium suffruticosum	–	–	–	42.1	9.6	–	8.8	–	–	–
Bassia prostrata	–	–	–	40.6	–	–	–	–	–	–
Salsola laricina	–	–	–	39.6	8.7	–	0.7	–	–	–
Halimione pedunculata	3.6	16.0	5.9	–	52.9	–	6.4	–	–	–
Puccinellia distans	–	–	–	–	43.5	3.9	9.2	–	–	–
Artemisia taurica	2.2	–	–	–	38.1	–	3.8	–	–	–
Agrostis gigantea s. maeotica	–	–	–	–	35.1	–	–	–	–	–
Suaeda baccifera	–	–	–	–	31.4	–	–	–	–	–
Lepidium syvaschicum	–	–	–	–	28.5	–	1.7	–	–	–
Cardaria draba	–	–	–	–	27.1	–	–	–	–	–
Saussurea salsa	–	–	–	–	–	–	39.1	–	–	–
Spergularia marina	–	–	5.3	–	15.7	–	27.3	–	–	–
Cakile maritima s. euxina	–	–	–	–	–	–	–	39.1	–	–
Puccinellia gigantea	7.4	–	18.7	–	–	10.4	–	31.2	–	–
Aeluropus littoralis	–	–	22.7	–	2.4	–	18.7	26.5	–	–
Apera spica-venti s. maritima	–	–	–	–	14.5	–	1.0	25.6	–	–
Lepidium cartilagineum s. cartilagineum	–	–	–	–	–	–	–	–	91.1	–
Cerastium pumilum s. pumilum	–	–	–	–	–	–	–	–	44.4	–
Lepidium campestre	–	–	–	–	–	–	–	–	36.1	–
Palimbia rediviva	–	–	–	–	–	–	–	–	36.1	–
Scorzonera laciniata	–	–	–	–	–	–	–	–	36.1	–
Vicia lathyroides	–	–	–	–	–	–	–	–	36.1	–
Anthemis cotula	–	–	–	–	–	–	–	–	36.1	–
Cerastium pumilum s. glutinosum	–	–	–	–	–	–	8.5	–	29.4	–
Erophila verna	–	–	–	–	–	–	–	–	25.4	–
Ranunculus marginatus v. trachycarpus	–	–	–	–	–	–	–	–	25.4	–
Petrosimonia brachiata	–	–	–	–	–	–	–	–	–	99.3
Atriplex calotheca	–	–	–	–	–	3.5	–	–	–	66.1
Salsola kali s. tragus	–	–	–	–	–	–	–	–	–	55.7
Petrosimonia triandra	–	–	–	–	–	–	–	–	–	55.7
Artemisia santonicum	–	14.0	–	0.4	9.1	–	–	–	3.7	50.1
Salsola soda	–	–	–	4.0	–	–	10.8	–	–	38.8
Gypsophila perfoliata	–	30.9	34.7	–	–	–	–	–	–	–
Limonium czurjukiense	–	29.2	–	26.7	15.3	–	–	–	–	–
Limonium meyeri	–	25.8	10.5	0.3	3.1	–	27.2	–	–	–
Limonium bellidifolium	10.8	–	–	32.4	26.3	–	4.7	–	–	–
Suaeda maritima s. salsa	–	–	2.8	21.4	–	48.1	48.1	–	–	–
Suaeda confusa	–	–	–	–	–	–	–	54.4	17.0	54.4
Limonium gmelinii	–	–	–	–	–	–	–	–	38.0	39.8
Camphorosma monspeliaca s. monspeliaca	–	35.2	–	–	–	–	–	–	33.3	53.0
Atriplex tatarica	–	13.7	–	–	5.8	0.5	18.6	–	–	23.4
Suaeda prostrata	–	–	–	16.9	12.2	–	–	–	16.2	8.6
Bromus sterilis	7.7	–	–	–	–	–	–	–	–	–
Lythrum volgense	7.7	–	–	–	–	–	–	–	–	–
Suaeda altissima	11.0	–	–	–	–	–	–	–	–	–
Taraxacum bessarabicum	11.0	–	–	–	–	–	–	–	–	–
Calamagrostis epigejos	11.0	–	–	–	–	–	–	–	–	–
Xanthium strumarium	–	–	–	–	–	–	12.9	–	–	–
Polygonum maritimum	–	–	–	–	–	–	12.9	–	–	–
Conyza canadensis	–	–	–	–	–	–	12.9	–	–	–
Crepis sancta	–	–	–	–	–	–	12.9	–	–	–
Salsola acutifolia	13.4	–	–	–	–	–	–	–	–	–
Althaea officinalis	2.8	–	–	–	–	–	10.6	–	–	–

1	2	3	4	5	6	7	8	9	10	11
Carex extensa	15.5	–	–	–	–	–	–	–	–	–
Bromus hordeaceus s. hordeaceus	–	–	–	–	15.6	–	–	–	–	–
Artemisia austriaca	–	–	–	–	15.6	–	–	–	–	–
Odontites verna s. serotina	17.3	–	–	–	–	–	–	–	–	–
Cerastium semidecandrum	–	–	–	–	11.1	–	6.9	–	–	–
Alyssum desertorum	–	–	–	–	22.1	–	–	–	–	–
Puccinellia festuciformis	–	–	–	–	22.1	–	–	–	–	–
Plantago tenuiflora	–	–	–	–	22.1	–	–	–	–	–
Agropyron desertorum	–	–	–	–	–	–	22.4	–	–	–
Triglochin maritima	23.3	–	–	–	–	–	–	–	–	–
Cynodon dactylon	0.2	–	–	–	–	–	20.9	–	–	–
Limonium tomentellum	0.2	–	–	–	–	–	20.9	–	–	–
Polygonum arenarium s. arenarium	–	–	–	23.8	–	–	–	–	–	–
Melilotus alba	2.6	–	–	–	–	–	19.6	–	–	–
Spergularia media	23.7	–	–	–	–	–	2.9	–	–	–
Crypsis aculeata	–	–	–	–	–	24.7	2.1	–	–	–
Frankenia pulverulenta	–	–	–	–	20.6	–	7.4	–	–	–
Scirpus maritimus s. maritimus	18.1	–	–	11.9	–	–	0.5	–	–	–
Aster tripolium s. pannonicus	6.3	–	–	–	23.9	–	6.7	–	–	–
Plantago maritima	6.8	–	–	7.3	–	–	24.9	–	–	–
Juncus maritimus	–	–	–	–	7.9	9.7	23.1	–	–	–
Phragmites australis	7.4	–	15.7	–	–	–	8.7	13.7	–	–
Halocnemum strobilaceum	–	12.1	–	14.8	4.6	2.4	2.6	–	–	–
Aster tripolium	23.3	–	9.5	–	–	–	6.6	14.9	–	–
Salicornia prostrata	22.5	–	15.9	18.0	12.7	22.5	–	10.5	–	–

Note: numbers mark syntaxa: *1 – Salicornietum prostratae; 2 – Petrosimonio oppositifoliae-Salicornietum; 3 – Bassietum hirsutae; 4 – Ofaisto monandri-Salicornietum; 5 – Halimionetum pedunculatae; 6 – Salicornio perennantis-Suaedetum salsae; 7 – Suaedetum salsae; 8 – Suaedetum confusae; 9 – Lepidietum crassifoliae; 10 – Petrosimonio brachiatae-Artemisietum santonicae.*
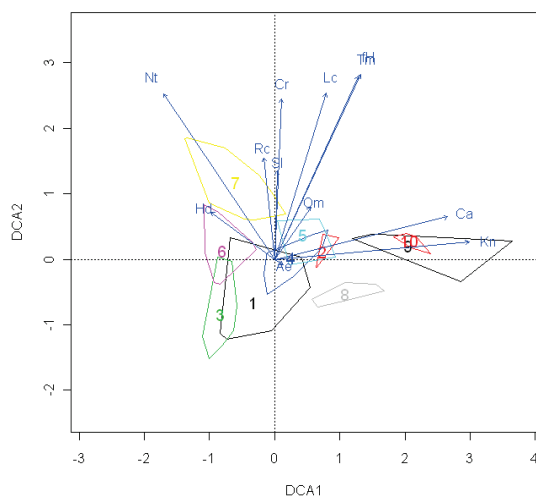

Fig. 10. Results of ordination analysis of the *Therosalicornietea* associations: the numbers mark syntaxa: *1 – Salicornietum prostratae; 2 – Petrosimonio oppositifoliae-Salicornietum; 3 – Bassietum hirsutae; 4 – Ofaisto monandri-Salicornietum; 5 – Halimionetum pedunculatae; 6 – Salicornio perennantis-Suaedetum salsae; 7 – Suaedetum salsae; 8 – Suaedetum confusae; 9 – Lepidietum crassifoliae; 10 – Petrosimonio brachiatae-Artemisietum santonicae*

Fig. 11. Hierarchical cluster analysis of *Crypsietea aculeatae* phytosociological relevés: *1 –* association *Cynancho acutae-Lepidietum latifolii, 2 –* association *Crypsietum aculeatae, 3 –* association *Heleochloëtum schoenoidis, 4 –* association *Polygono salsuginei-Crypsietum aculeatae*

Table 5
Synoptic table of the class *Crypsietea aculeatae*

No. of syntaxa	1	2	3	4
Number of relevés	11	4	20	21
1	2	3	4	5
Taraxacum bessarabicum	68.8	–	–	–
Salicornia prostrata	67.7	–	–	–
Scirpus maritimus s. maritimus	64.5	–	–	–
Puccinellia festuciformis s. festuciformis	62.0	–	–	–
Suaeda prostrata	55.6	–	–	7.6
Triglochin maritima	54.8	–	–	–
Spergularia marina	54.8	–	–	–
Halimione pedunculata	53.2	–	–	–
Agrostis stolonifera	46.9	–	–	–
Juncus gerardi	33.7	15.5	–	–
Limonium bellidifolium	26.4	–	–	–
Sonchus arvensis	26.4	–	–	–
Scorzonera parviflora	26.4	–	–	–
Limonium meyeri	26.4	–	–	–
Camphorosma annua	26.4	–	–	–
Polygonum aviculare	–	83.2	–	–
Crypsis schoenoides	–	70.7	23.6	–
Echinochloa crus-galli	–	65.5	–	–
Puccinellia distans	–	64.7	6.6	–
Atriplex prostrata	–	60.3	–	–
Xanthium strumarium s. italicum	–	44.7	–	–
Taraxacum officinale	–	44.7	–	–
Plantago major s. intermedia	–	44.7	–	–

The class *Crypsietea aculeatae* includes ephemeral comparatively species-poor obligate halophytic and weakly nitrophilic pioneer plant communities that grow on open slightly alkaline soils with rapid changes in humidity and total salt regime. The class numbers 4 associations (Fig. 11, Table 5). They are widespread on the banks of slightly saline and saline water bodies (estuaries, lakes, local natural or anthropogenic depressions) in the steppe zone. Their territorial differentiation is determined by the moisture-drainage regime, total salt regime, and type of the soil. The alliance *Cypero-Spergularion salinae* includes phytocoenoses with the predominance of *Crypsis schoenoides* on wet saline habitats, mainly in natural or anthropogenic depressions. The alliance *Heleochloion schoenoidis* includes plant communities with the predominance of *Crypsis schoenoides* of negative relief forms of natural (pods) or non-natural origin on saline ecotopes. The alliance *Lepidion latifolii* is the vegetation with the predominance of *Lepidium latifolium* on saline territories that are periodically flooded and are located in the continental regions of Eastern Europe.
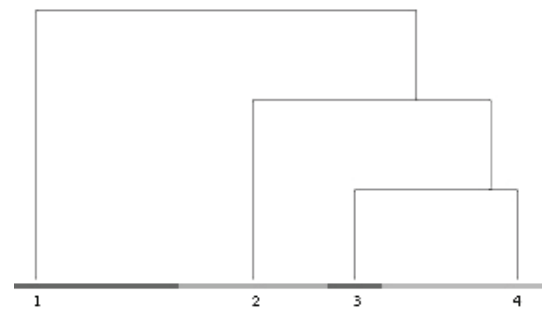
	1	2	3	4	5
Daucus carota	–	44.7	–	–	
Limonium tomentellum	–	44.7	–	–	
Pholiurus pannonicus	–	44.7	–	–	
Ambrosia artemisiifolia	–	44.7	–	–	
Lepidium ruderale	–	44.7	–	–	
Artemisia santonicum	–	34.2	–	18.2	
Beckmannia eruciformis	–	33.2	2.6	–	
Atriplex tatarica	–	29.4	–	8.7	
Limonium gmelinii	–	–	100.0	–	
Polygonum salsugineum	–	–	100.0	–	
Rumex stenophyllus	–	–	86.6	–	
Eleocharis palustris	–	–	65.5	–	
Alisma lanceolatum	–	–	65.5	–	
Salsola kali s. tragus	–	–	57.0	–	
Juncus maritimus	–	–	48.8	–	
Typha laxmannii	–	–	44.7	–	
Ventenata dubia	–	–	27.7	–	
Lepidium latifolium	–	–	–	100.0	
Cynanchum acutum	–	–	–	73.2	
Lactuca tatarica	–	–	–	66.7	
Sinapis alba	–	–	–	63.7	
Atriplex littoralis	–	–	–	63.7	
Bromus squarrosus	–	4.6	–	56.3	
Polygonum arenarium s. arenarium	–	–	–	56.2	
Bassia hirsuta	2.7	–	–	48.5	
Plantago arenaria	–	–	–	48.0	
Bassia sedoides	–	–	–	48.0	
Melilotus alba	–	–	–	48.0	
Elymus repens	–	4.7	–	43.1	
Polygonum scythicum	–	–	–	38.7	
Argusia sibirica	–	–	–	38.7	
Erysimum repandum	–	–	–	33.3	
Elymus elongatus	–	–	19.9	32.4	
Plantago maritima	–	–	–	27.1	
Bromus japonicus	–	–	–	27.1	
Chondrilla juncea	–	–	–	27.1	
Puccinellia gigantea	–	–	–	27.1	
Crypsis aculeata	57.7	–	57.7	–	
Aster tripolium	29.4	50.6	–	–	
Centaurea apiculata s. adpressa	–	–	–	19.0	
Cuscuta monogyna	–	–	–	19.0	
Agrostis gigantea	–	–	–	19.0	
Crambe maritima	–	–	–	19.0	
Eleocharis uniglumis	–	–	–	19.0	
Leymus racemosus s. sabulosus	–	–	–	19.0	
Seseli tortuosum	–	–	–	19.0	
Phragmites australis	17.5	–	–	9.7	
Pulicaria dysenterica	–	–	19.5	–	
Pulicaria paludosa	–	–	19.5	–	

Notes: the numbers mark syntaxa: *1 – Crypsietum aculeatae*; *2 – Heleochloëtum schoenoidis*; *3 – Polygono salsuginei-Crypsietum aculeatae*; *4 – Cynancho acutae-Lepidietum latifolii*.

DCA-ordination results of the *Crypsietea aculetae* plant communities showed that they differentiate mostly along the gradients of nitrogen content in the soil and variability of damping, vectors of which are the closest to the first ordination axis (Fig. 12). Additionally, the leading factors for *Crypsietum aculeatae* plant communities are the total salt regime and soil acidity, for *Heleochloëtum schoenoidis* coenoses – cryoclimate.

Discussion

Therefore, the syntaxonomic structure of *Cakiletea maritimae* class in Ukraine includes 4 associations, which belong to 1 order and 1 alliance; *Ammophiletea* have 8 associations, 1 order and 1 alliance; *Crithmo-Staticetea* – 1 order, 2 alliances and 3 associations. Like both western and eastern European coastal vegetation of these classes, it is marked by a low level of phytocoenotic diversity (Sanda et al., 2008; Tzonev et al., 2009; Biondi et al., 2014) which is caused by extreme conditions of these habitats. The specificity of coastal plant communities in Ukraine is identified on the associations-rank level and conditioned by the action and intensity of coastal processes of the Ukrainian part of the Black and Azov Sea as well as the climatic conditions of the region. The communities of *Kochio prostratae-Limonion meyeri* Korzhenevsky et Klyukin 1987 and *Elytrigio*

bessarabicae-Lactucion tataricae Korzhenevsky ex Didukh et Mucina in Mucina et al. 2016 alliances are typical only for the Crimean Peninsula.

The classes of *Therosalicornietea* and *Crypsietea aculeatae* are also characterized by middle European level of phytocoenotic diversity (Borhidi, 2003; Chytrý, 2007; Sanda et al., 2008). *Crypsietea aculeatae* numbers 1 order, 3 alliances and 4 associations, *Therosalicornietea* – 1 order, 2 alliances and 10 associations.
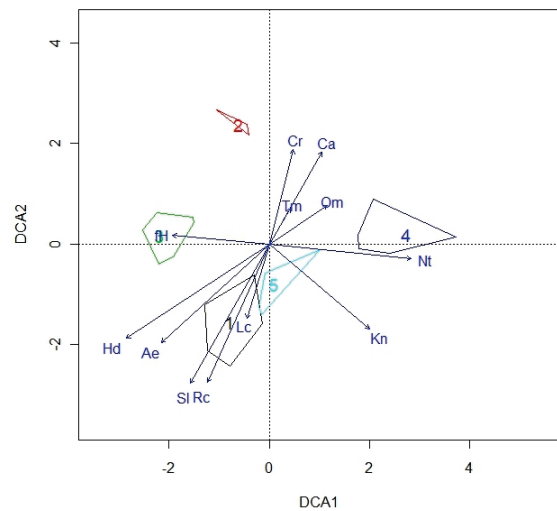

Fig. 12. Results of ordination analysis of the *Crypsietea aculeatae* associations: *1 – Crypsietum aculeatae*; *2 – Heleochloëtum schoenoidis*; *3 – Polygono salsuginei-Crypsietum aculeatae*; *4 – Cynancho acutae-Lepidietum latifolii*

Today the question of *Isoëto-Nanojuncetea* and *Crypsietea aculeatae* plant communities' correlation is being discussed in Europe. Italian, Spanish and French phytosociologists consider the class *Crypsietea aculeatae* as a syntaxomic synonym of *Isoëto-Nanojuncetea* (Rivas-Martínez et al., 2001; Bardat et al., 2004; Biondi et al., 2014). Bulgarian scientists include syntaxa of the order *Crypsietalia aculeatae* to belong to the *Isoëto-Nanojuncetea* class (Tzonev et al., 2009). Rodwell et al. (2002) share the same point of view, identifying three alliances within this class: *Cypero-Spergularion salinae, Polygono salsuginei-Crypsion aculeatae* and *Puccinellion peisonis*. Romanian phytosociologists think that communities of the *Cypero-Spergularion* alliance belong to the *Puccinellio-Salicornietea* class, which has a wider conception for them (Sanda et al., 2008), and Hungarian scientists relate it to *Thero-Suaedetea* Vicherek 1973 class (Borhidi, 2003). Our studies showed that phytocoenoses of these two classes can be quite clearly distinguished by the total salt regime and diagnostic species.

The most discussed questions about the conception and structure of the *Therosalicornietea* class relate to the taxonomy of the genus *Salicornia*. Depending on the distribution of its species (*Salicornia pusilla* J. Woods, *S. ramosissima* J. Woods, *S. europaea* L., *S. obscura* P. W. Ball & Tutin, *S. nitens* P. W. Ball & Tutin, *S. fragilis* P. W. Ball & Tutin, *S. dolichostachya* Moss, *S. procumbens* Smith) (Davy et al., 2001), several alliances are identified on the territory of Europe (Mucina et al., 2016). However, class *Thero-Suaedetea* is distinguished in Hungary, Italy, Spain, and France. In Romania pioneer communities of the order *Salicornietalia* Br.-Bl. (1928) 1933 on solonchaks belongs to the *Puccinellio-Salicornietea* Țopa 1939 class (Sanda et al., 2008).

Numerous studies confirm the importance of the soil humidity, edaphic and climatic characteristics of the habitats (Jarvis et al., 2016; Kuzemko et al., 2016; Pinto et al., 2016; Ermakov et al., 2017; Bagrikova, 2018), that affect phytodiversity and structure of pioneer vegetation. We agree with the assertion that the ecological specificity of a pioneer plant communities is driven by a combination of several factors (Chytrý et al., 2007, 2013; Didukh, 2012; Didukh et al., 2015). However, for the pioneer plant communities, considerable influence is exerted by the extremality of the environmental conditions. This involves first of all their irregularity such as the mechanical action of the sea surf and the impact of waves, the dynamic processes of denudation and accumulation, total salt regime, as

well as the extremely variable regime of soil humidity. In this aspect, it is possible to make parallels with the variability of ecological gradients for subalpine vegetation, which also develops in extreme ecotopes (Čarni et al., 2011; Dyakov, 2014). These features cause the extreme vulnerability of pioneer vegetation to biotic and abiotic changes (Dubyna et al., 2019), determine the weakness of its coenotic connections and low anthropotolerance (Dubyna et al., 2015, 2016a, b), which requires immediate action for conservation of this specific and unique type of phytocenosis.

Conclusion

Littoral and halophytic pioneer vegetation in Ukraine of *Cakiletea maritimae, Ammophiletea, Crithmo-Staticetea, Therosalicornietea* and *Crypsietea aculeatae* classes are represented by 29 associations, 9 alliances and 5 orders. The leading factors of territorial and ecological differentiation of littoral and halophytic pioneer vegetation in Ukraine have been identified. It has been determined that the intensity of abrasive-accumulative action of the sea, soil type, and its density explains the territorial distribution of *Ammophiletea, Cakiletea maritimae* and *Crithmo-Staticetea*. At the same time, relief of ecotopes, soil structure and period of flooding have a great impact on *Therosalicornietea* and *Crypsietea aculeatae* plant communities.

The conducted ordination analysis of coastal and halophytic pioneer vegetation in Ukraine at the classes and alliances-rank levels has shown that the leading factors of its ecological differentiation are soil humidity and soil aeration as well as nitrogen content. On the basis of the results of ordination of syntaxa within the classes, we have defined the main factors that correlate with the specifics of the habitats where the pioneer vegetation evolves. It has been found that the ecological differentiation within the *Ammophiletea* class is caused by the variability of damping, *Therosalicornietea* – by the total salt regime, soil acidity as well as continental climate and cryoclimate, *Cakiletea maritimae* – by the variability of damping, cryoclimate, soil acidity, nitrogen and carbonate content in the soil, *Crithmo-Staticetea* – by the light regime and climate humidity, and *Crypsietea aculeatae* – by the nitrogen content in the soil and its aeration.

These studies give the opportunity to determine the place of the syntaxa of pioneer vegetation in Ukraine within the European Vegetation Classification. The results of the conducted research can be useful for the formation of the preservation and ecological network in Ukraine, compilation of The Prodrome of the Vegetation of Europe, the next volumes of the editions "Vegetation of Ukraine" and "Green Data Book of Ukraine", for further research of succession and adaptation processes in rapidly changing environmental conditions, establishment of development patterns in regeneration geological systems as well as identifying the ways to manage them.

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