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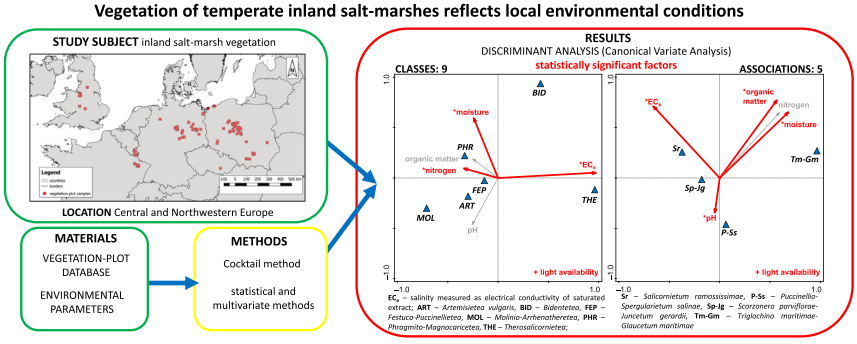
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HIGHLIGHTS

- Inland temperate salt marsh vegetation is diversified into different units.
- Vegetation syntaxonomical units depend on environmental properties.
- Salinity, moisture, light availability and nitrogen content drive the class level.
- Associations are determined by salinity, organic matter, soil pH and moisture.
- Environmental requirements provide direct implications for salt marsh management.

GRAPHICAL ABSTRACT



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ABSTRACT

Inland salt marshes are recognized as habitats of unique and valuable vegetation at the European scale. There is still a lack of generalization regarding its vegetation syntaxonomy and environmental requirements, which is needed for its effective protection. To falsify our hypothesis about vegetation dependence on environmental requirements we aimed at description of the syntaxonomical units present in temperate European inland salt marshes and identification of their main environmental drivers. In our work we focused on the vegetation from the northern part of temperate salt marshes to limit confusion related to the geographical ranges of species. We collected the database of 968 vegetation plots from different European countries and applied the Cocktail method to analyze the data. Based on results, expert knowledge, existing syntaxonomical classifications and information from the literature, we identified diagnostic, constant and dominant species for individual syntaxonomical units. Then, we compiled maps of the vegetation unit distribution, and identified the most important environmental factors for the analyzed vegetation using statistical and multivariate methods, including canonical variate analysis. We classified the analyzed vegetation into nine classes, including two typical for salt-marsh vegetation – the *Therosalicornietea* and *Festuco-Puccinellietea*. Within these two classes, we distinguished two alliances and a total of five associations. The classes differ the most in terms of species preferences to salinity, soil moisture, light availability and soil nitrogen content. In addition salt marsh associations differ also by soil reaction and soil organic matter content. This provides direct implications for salt marsh sustainable management.

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1. Introduction

Saline areas are inhabited by organisms that are adapted to high soil salinity (Flowers and Colmer, 2008; Pétillon et al., 2011). Plant species typical for saline habitats called halophytes can perform their whole life cycle at high salinity over 200 mM NaCl (Flowers and Colmer, 2008). However, many other species with wide ecological responses are also present there. Species salt tolerance is reflected in the numerous classifications that divide them into different categories, e.g., obligatory and facultative halophytes, indifferential and accidental species (Parida and Das, 2005; Wilkoń-Michalska, 1963). Grigore and Cojocariu (2021) compared several of such classifications. Currently, some of the species are used as bioindicators of soil salinity (Arora and Dagar, 2019; Piernik, 2003a). It is worth emphasizing that halophytes are species recognized as a sensitive indicator not only of salinity but also of soil moisture and they are extremely light-sensitive (Wilkoń-Michalska, 1970). Therefore, the environmental factors have a significant impact on the salt marsh species composition (Erfanzadeh et al., 2010; Piernik, 2012). This vegetation frequently is characterized by species zonation defined by dominance of some species and determined mostly by salinity and tides on coastal marshes and by salinity level on inland salt marshes (Lee et al., 2016; Piernik et al., 1996; Piernik et al., 2015). The saline habitats in Europe has been studied and documented for years (e.g., Lee, 1977; Wilkoń-Michalska, 1963; Zulka et al., 1997), and this process continues to this day, because they are undeniably an important elements in our local biodiversity (Dajić-Stevanović et al., 2019; Dítě et al., 2021, 2022; Fantinato and Buffa, 2019; Lubińska-Mielińska et al., 2022; Piernik, 2012).

The present research concerns vegetation-environment relations of the temperate European part of inland salt-marshes. Inland saline areas of temperate Europe are related to the presence of salt stratums uplifted near the surface, salt springs and salt, soda and potassium industry (Brandes, 1999; Lee, 1977; Piernik et al., 2015). They have to be supported continuously by saline water because of excess precipitation over evapotranspiration which washes salts out of the upper part of the soil profile (Waisel, 1972). Moreover, as many semi natural habitats they should be managed by extensive mowing and grazing (Nienartowicz and Piernik, 2004a) because of potential expansion of *Phragmites australis* or *Elymus repens* and habitat degradation (Piernik, 2006). As rare and valuable habitats they have been designated to be under protection by *Council of Europe Directive 92/43/EEC* (Council of Europe, 1992) and they have been included into the Natura 2000 network. Apart of protection within Natura 2000, in individual countries they are legally protected as parts of nature reserves, e.g., Valea Ilenei (Iaşi) in Romania (Grigore and Toma, 2014), Artern, Jerxheim, Barstorf in Germany (Brandes, 1999), or Owczary and Ciechocinek in Poland (Kostuch and Misztal, 2006; Lubińska-Mielińska et al., 2022). Although natural inland temperate salt marshes have been designated as priorities for the European Union and have been protected for years (Bank and Spitzenberg, 2001; Pusch, 2007), recently they have been listed as endangered in the *European Red List of Habitats* (Janssen et al., 2016).

The syntaxonomical classification of this vegetation, which is helpful in its management planning, is still under question. In the latest synthesis on vegetation of Europe, Mucina et al. (2016) integrated the units proposed for years by European vegetation researchers and presented a comprehensive syntaxonomical classification system based on the Braun-Blanquet approach (Braun-Blanquet, 1964). Unfortunately, the synthesis of Mucina et al. (2016) arranges vegetation only to the level of alliances. In order to analyze the vegetation of European inland salt marshes at the association level, it is necessary to refer to the older proposals of vegetation classification systems, which are often local or national in scope, e.g., systems by Matuszkiewicz (2017) and Pott (1992), which have already been thoroughly compared by Piernik (2020). As the research of recent years shows, unification of vegetation classification systems and their dissemination are more and more frequent and necessary. A comparative overview of the syntaxonomical units based on the *EuroVegChecklist* (Mucina et al., 2016) was made for vegetation in Germany by Bergmeier (2020). Recently, Landucci et al. (2020) carried out classification to the association level of European marsh vegetation. Pätsch et al. (2019) classified vegetation of saline and brackish grasslands of the Baltic Sea coast. Classification of the south European coastal part of salt marsh communities also already exists, based on Croatian data (Dítě et al., 2019). Danihelka et al. (2022) presented halophytic vegetation of southern Moravia and northern Lower Austria. However, there is still a gap in the current classification system for inland salt-marsh vegetation across whole temperate Europe, although some of it was analyzed on the basis of data from the North German Plain (Dítě et al., 2022). The effective protection of inland salt-marsh vegetation that will allow for broad-scale comparisons require the syntaxonomical classification system based on data from various European locations.

Another lack of information is related to the environmental requirements of vegetation syntaxonomical units. Few researchers investigated soil properties in vegetation patches and then vegetation-environment relations (e.g., Piernik et al., 1996; Piernik, 2005, 2012; Wilkoń-Michalska, 1963, 1970). Quite frequently they related vegetation patches according to the species dominance (e.g., Piernik, 2003a, 2003b; Piernik et al., 2015) only some of them referred vegetation units to vegetation associations in the sense of Braun-Blanquet system (Wilkoń-Michalska, 1963, 1970; Zlatković et al., 2019).

Therefore, we used the data collected and published by various researchers from Central and Northwestern Europe to classify vegetation according to the currently used nomenclature and to find environmental drivers for their differentiation. To falsify the hypothesis about vegetation syntaxonomical units dependence on environmental requirements we aimed at (1) identification of the vegetation classes present in temperate European inland salt marshes, (2) checking if they species composition is affected by saline environment, (3) classification of the typical salt-marsh vegetation classes to the associations level, and (4) identification of the main environmental variables influencing the differentiation of analyzed vegetation. Following Janssen et al. (2016), who distinguished three categories of inland salt marsh habitats in Europe, i.e. temperate inland salt marsh, Mediterranean inland salt steppe and continental inland salt steppe, in our work we focused on the vegetation from the northern part of temperate salt marshes to limit confusion related to the geographical ranges of species.

2. Methods

2.1. Vegetation-plot database

We have created a vegetation-plot database containing data from six countries in Central and Northwestern Europe: Czech Republic (CZ), France (FR), Germany (DE), Luxemburg (LU), Poland (PL) and the United Kingdom (UK). Into account were taken all vegetation plots (hereafter also called 'plots') collected in saline areas, in which the salt marsh species occurred. The data was obtained partly from collected bibliographic sources and partly from the *Polish Vegetation Database* (Kącki and Śliwiński, 2012). Several vegetation plots were derived from our own unpublished field observations. The list of 32 bibliographic sources and two items with unpublished data on vegetation plots are provided in Table A.1.

Initially, the database consisted of 1231 vegetation plots. We carried out a thorough selection of plots and excluded duplicate data and plots collected at typically coastal sites. We have only left data on vegetation plots along the Polish coastline, sites within Kołobrzeg and Chrząszczewska Island, where the salinity is related to the underground supply, not to the influence of the seawater (Ćwikliński, 1977; Piotrowska, 1974). Finally, we analyzed 968 vegetation plots with the size range of 0,5–400 m^2, including 426 vascular plants (including plants marked only by genus name), from the period of 63 years collected in 1952–2015. Geographical distribution of all vegetation-plot samples in the database is shown in Fig. A.1.

Nomenclature of species in vegetation-plot database followed the authors of the bibliographic sources. In the file used for analyzes, the names of species were unified using the World Flora Online (World Flora Online, 2020; http://www.worldfloraonline.org/) and EuroMedPlant (Euro + Med, 2006 + [continuously updated]; http://www.europlusmed.org). The coordinates for all vegetation plots were used to present the results of classification on the

map of Europe. The maps were prepared using the QGIS 2.14.2 "Essen" software (QGIS Development Team - Version 2.14.2, 2016).

2.2. Data classification

We used the Cocktail method (Bruelheide, 1997, 2000) and computer expert system (Tichý et al., 2011). Cocktail method (Bruelheide, 1997, 2000; Kočí et al., 2003) ensures stable, repeatable, and consistent classification outcome, e.g., Kącki et al. (2020) or Landucci et al. (2020). We decided to use this method because it applies unambiguous definitions of individual plant units. Based on expert knowledge, existing syntaxonomical classifications and information from the literature, we identified diagnostic species for classes *Therosalicornietea* and *Festuco-Puccinellietea* and alliances *Salicornion ramosissimae* and *Juncion gerardi* and we created #TC functional groups (Mucina et al., 2016; Tichý, 2002). Using these groups we prepared formal definitions (Kočí et al., 2003). As a base we used a nested expert system created by Kącki et al. (2020). However, we applied a new formal definition for all classes of no-forest vegetation found in Poland including *Crypsietea aculeatae* Vicherek 1973 class which is not reported in Poland. Performing classification we defined diagnostic species (Dg) as those with fidelity equal to or higher than 25. The fidelity measure used here was the phi coefficient (Bruelheide, 2000; Chytrý et al., 2002). For constant species (Cs) we set the frequency threshold at 50 %. The coverage value threshold of the dominant species (Dm) was 25 % with a minimum frequency of 20 %. At the association level we applied the same criteria except Dg species, which were defined as those with fidelity equal to or higher than 25 and percentage frequency equal to/higher than 50 %. We used a hierarchically nested classification system in which a vegetation plot classified to a specific unit must also meet the formulas of higher syntaxonomical units (Kącki et al., 2020; Landucci et al., 2020). JUICE software (Tichý, 2002) was used for the analyzes.

The preliminary classification showed that 26 vegetation plots were classified simultaneously into two syntaxa, and no syntaxon was identified for 58 plots. Therefore, 84 vegetation plots were not included in the final classification. Groups representing classes with less than six plots were also omitted as outliers. Therefore, the next 10 plots cumulatively were not considered. In this way, the final groups were based on 874 plots.

Although the standard use of geographic stratification in the analysis of phytosociological databases (Chytrý et al., 2007; Knollová et al., 2005), we did not apply it. This would result in a loss of large amounts of data, because inland halophytic communities are relatively rare and local. Such solutions have been already practiced (e.g., Jarolímek and Šibík, 2008; Stupar et al., 2015).

Names of classes, orders and alliances follow the European syntaxonomical classification system by Mucina et al. (2016). The nomenclature of associations follow Matuszkiewicz (2017), Pladias online database (Chytrý et al., 2021; Pladias, 2022), and names recently adopted by Dítě et al. (2022). Lichens, bryophytes and algae, which some authors noted in the vegetation plots, were not taken into account, because of their marginal role in these habitat types and uneven distribution in the dataset. This is a common practice, although it may change soon (Berg et al., 2020). In addition, the European system of floristic classification (Mucina et al., 2016) includes all these groups separately.

2.3. Environmental data

Due to the lack of data obtained from the environment for all plots in our database, we used weighted averages for individual vegetation plots calculated on the basis of Ellenberg indicator values (Ellenberg et al., 1992) as estimated environmental parameters (Schaffers and Sýkora, 2000). For this purpose we used: light availability (L), temperature (T), moisture (M), reaction/soil acidity (R), nitrogen content/trophy (N) and salinity (S). To perform the calculations, it was necessary to transform the data from the Braun-Blanquet cover/abundance scale (Braun-Blanquet, 1964) to the van der Maarel (2007) ordinal scale as follows: r → 1, + → 2, 1 → 3, 2 → 5, 3 → 7, 4 → 8, 5 → 9.

As the second set of environmental data, we analyzed soil parameters from bibliographic sources: salinity expressed as electrical conductivity of saturated extract (EC_e), moisture, pH, total nitrogen and organic matter content. It was possible only for some vegetation plots ($n = 285$) from our database, where the authors provided such data with the same methodology.

2.4. Ordination and statistical analyzes

To find main drivers for vegetation differentiation we applied Canonical Variate Analysis (CVA) as discriminant analysis and the Canoco 5.0 package (ter Braak and Šmilauer, 2012). We used forward selection procedure and Monte Carlo permutation tests, and focused on conditional effects, which exclude the effect of the most correlated predictors (ter Braak and Šmilauer, 2012). The predictors are chosen in the order of their decreasing explained variation. We skipped simple effects, that summarize the independent effects of all explanatory variables, because we decided to compare this effect by non-parametric Kruskal-Wallis test with Dunn post-hoc comparisons using Statistica 13.0 software (StatSoft Inc., Tulsa, Oklahoma, USA).

3. Results

3.1. Vegetation units

Results of classification demonstrate presence of nine classes of vegetation in the inland saline areas (Table 1): *Ruppietea maritimae* (RUP), *Therosalicornietea* (THE), *Festuco-Puccinellietea* (FEP), *Polygono-Poetea annuae* (POL), *Artemisietea vulgaris* (ART), *Potamogetonetea* (POT), *Bidentetea* (BID), *Phragmito-Magnocaricetea* (PHR) and *Molinio-Arrhenatheretea* (MOL). Classes of typical salt-marsh vegetation, i.e. *Festuco-Puccinellietea* and *Therosalicornietea* were represented by the highest number of plots – respectively ca. 50 % and 14 % out of the analyzed 874 vegetation plots. Most of the vegetation plots assigned to the *Therosalicornietea* class represented one association: *Salicornietum ramosissimae* (Se). Plots in the *Festuco-Puccinellietea* class were assigned to four different associations: *Scorzonero parviflorae-Juncetum gerardii* (Sp-

Table 1
Classification results: syntaxonomical synopsis and the number of vegetation plots assigned to each syntaxonomical unit; for high-rank units the number of plots assigned is given followed by the number of plots assigned to lower units. Abbreviations: Cl. – class, O. – order, All. – alliance, Ass. – association. Main vegetation units are given in bold.

Code Mucina et al. (2016)	Syntaxon name	Number of plots
RUP	**Cl.: *Ruppietea maritimae* J. Tx. ex Den Hartog et Segal 1964**	**6**
THE	**Cl.: *Therosalicornietea* Tx. in Tx. et Oberd. 1958**	**137**
THE-01	O.: *Therosalicornietalia* Pignatti 1952	137
THE-01C	All.: *Salicornion ramosissimae* Tx. 1974	137
–	Ass.: *Salicornietum ramosissimae* Christiansen 1955	133
FEP	**Cl.: *Festuco-Puccinellietea* Soó ex Vicherek 1973**	**485**
FEP-05	O.: *Scorzonero-Juncetalia gerardi* Vicherek 1973	469
FEP-05A	All.: *Juncion gerardi* Wendelberger 1943	469
–	Ass.: *Scorzonero parviflorae-Juncetum gerardii* (Wenzl 1934) Wendelberger 1943	121
–	Ass.: *Agrostio stoloniferae-Juncetum ranarii* Vicherek 1962	6
–	Ass.: *Triglochino maritimae-Glaucetum maritimae* Wilkoń--Michalska, 1963 ex Dítě et al. ass. nov. 2022	56
–	Ass.: *Puccinellio-Spergularietum salinae* (Feekes 1936) R.Tx. at Volk 1937	134
POL	**Cl.: *Polygono-Poetea annuae* Rivas-Mart. 1975**	**10**
ART	**Cl.: *Artemisietea vulgaris* Lohmeyer et al. in Tx. Ex von Rochow 1951**	**14**
POT	**Cl.: *Potamogetonetea* Klika in Klika et Novák 1941**	**12**
BID	**Cl.: *Bidentetea* Tx. et al. ex von Rochow 1951**	**22**
PHR	**Cl.: *Phragmito-Magnocaricetea* Klika in Klika et Novák 1941**	**112**
MOL	**Cl.: *Molinio-Arrhenatheretea* Tx. 1937**	**76**

Jg), *Agrostio stoloniferae-Juncetum ranarii* (As-Jr), *Triglochino maritimae-Glaucetum maritimae* (Tm-Gm) and *Puccinellio-Spergularietum salinae* (P-Ss). The number of plots in individual associations is presented in Table 1.

From the set of diagnostic species (Dg) we identified these specific for temperate inland salt marsh vegetation. The diagnostic species for classes *Therosalicornietea* and *Festuco-Puccinellietea* identified on investigated inland salt-marshes are demonstrated in Table A.2. For the *Therosalicornietea* class Dg species included *Salicornia europaea*, *Puccinellia distans*, *Spergularia marina* and *Spergularia media*. *S. europaea* was identified also as only one dominant (Dm) species. Constant species (Cs) included *S. europaea*, *P. distans* and *Tripolium pannonicum* (see also Table A.3). Vegetation representing this class was recorded in Poland, Germany and France. For the *Festuco-Puccinellietea* class the group of Dg species consisted only of *Juncus gerardii*. Additionally, *P. distans* was a Dm and Cs species. Vegetation representing this class is much more widespread than that of the *Therosalicornietea*, because it was recorded in all analyzed countries. Geographic distribution of *Therosalicornietea* and *Festuco-Puccinellietea* classes are presented in Fig. 1.

In the next step we focused on halophytic associations. Diagnostic species for all of them are presented in Table 2. For the *Salicornietum ramosissimae* only one Dg species was *S. europaea*. This species was also identified as dominant and additionaly as constant together with *P. distans* and *S. marina* (see also Table A.4). For *Puccinellio-Spergularietum salinae* association three species passed Dg rule including *S. marina*, *P. distans* and

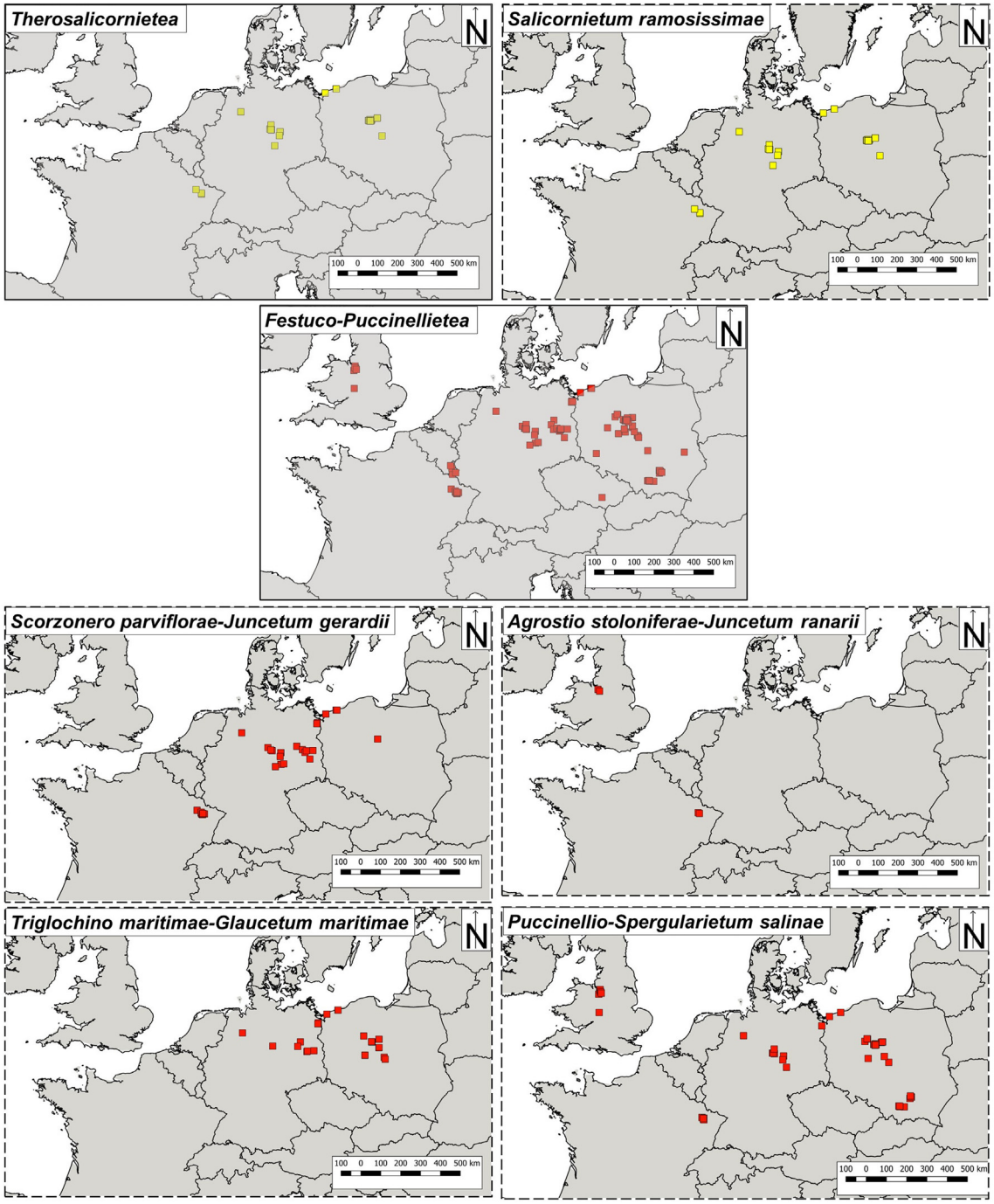


Fig. 1. Geographic distribution of *Therosalicornietea*, *Festuco-Puccinellietea* classes and associations identified on salt marshes based on the coordinates of individual vegetation sample plots.

Table 2
Shortened synoptic table with percentage frequency and fidelity index added in superscript for associations identified on salt marshes. The values for diagnostic species (with fidelity index ≥ 25 and percentage frequency ≥ 50 %) within associations are marked in gray, for constant species (with percentage frequency ≥ 50 %) have bold font, and for dominant species (with plant cover ≥ 25 % and percentage frequency ≥ 20 %) are marked with asterisk in superscript. Zero fidelity is assigned to species with insignificant fidelity to the cluster (Fisher's exact test at $p > 0.01$). Abbreviations: Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*, As-Jr – *Agrostio stoloniferae-Juncetum ranarii*.

↓ Species Associations →	Se	P-Ss	Sp-Jg	Tm-Gm	As-Jr
THEROSALICORNIETEA					
Salicornietum ramosissimae					
Salicornia europaea	**100$^{83.7*}$**	18^{---}	10^{---}	4^{---}	.$^{---}$
FESTUCO-PUCCINELLIETEA					
Scorzonero parviflorae-Juncetum gerardii					
Juncus gerardii	13^{---}	10^{---}	**100$^{62.5*}$**	39^{---}	33^{---}
Agrostio stoloniferae-Juncetum ranarii					
Juncus ranarius	.$^{---}$	9^{---}	4^{---}	5^{---}	**100$^{89.7*}$**
Tripolium pannonicum	49^{---}	29^{---}	**55$^{1.6}$**	36^{---}	**100$^{46.3}$**
Oxybasis rubra	1^{---}	4^{---}	1^{---}	.$^{---}$	**50$^{62.1}$**
Agrostis stolonifera	5^{---}	15^{---}	40^{5}	48$^{13.9}$	**67^{---}**
Triglochino maritimae-Glaucetum maritimae					
Triglochin maritima	23^{---}	10^{---}	48$^{12.2}$	**100$^{66.4*}$**	.$^{---}$
Glaux maritima	7^{---}	7^{---}	32^{---}	**93$^{72.8*}$**	.$^{---}$
Phragmites australis	16^{---}	15^{---}	36$^{7.4}$	**64^{38}**	17^{---}
Juncus compressus	2^{---}	15^{---}	7^{---}	**63$^{59.8}$**	.$^{---}$
Potentilla anserina	.$^{---}$	12^{---}	26$^{8.3}$	**61$^{51.3}$**	.$^{---}$
Puccinellio-Spergularietum salinae					
Spergularia marina	**50^{---}**	**100^{47*}**	13^{---}	2^{---}	**100^{---}**
Puccinellia distans	**80$^{7.8}$**	**100^{30*}**	36^{---}	**52^{---}**	**100^{---*}**
Atriplex prostrata s. l.	38^{---}	**72$^{32.6}$**	39^{---}	34^{---}	17^{---}

Atriplex prostrata. All of them were constant in this association, while *S. marina* and *P. distans* were also dominant. This association is the most widespread among associations in the *Festuco-Puccinielietea* class. It was recorded in Germany, the United Kingdom, Poland and France. For the *Scorzonero parviflorae-Juncetum gerardii* association only *J. gerardii* passed the criteria for Dg species. This species was also identified as Dm, and Cs

Table 3
Shortened synoptic table with percentage frequency and fidelity index added in superscript for vegetation classes identified on salt marshes with a complete list of diagnostic (Dg), constant (Cs) and dominant (Dm) species for *Therosalicornietea* and *Festuco-Puccinellietea* classes and identified salt marsh associations. Obligatory halophytes are marked in bold font and in gray, facultative halophytes in bold font (according to Wilkoń-Michalska, 1963). Abbreviations: PHR – *Phragmito-Magnocaricetea*, MOL – *Molinio-Arrhenatheretea*, ART – *Artemisietea vulgaris*, BID – *Bidentetea*, POL – *Polygono-Poetea annuae*, POT – *Potamogetonetea*, RUP – *Ruppietea maritimae*.

↓ Species Classes →	PHR	MOL	ART	BID	POL	POT	RUP
Puccinellia distans	**31^{---}**	**18^{---}**	**21^{---}**	**55^{---}**	**100$^{41.7}$**	**.$^{---}$**	**.$^{---}$**
Atriplex prostrata s. l.	**47^{---}**	**16^{---}**	**50^{---}**	**100$^{49.4}$**	**10^{---}**	**.$^{---}$**	**.$^{---}$**
Phragmites australis	74$^{43.7}$	34^{---}	14^{---}	36^{---}	.$^{---}$	.$^{---}$	.$^{---}$
Agrostis stolonifera	43$^{19.4}$	51$^{26.8}$	29^{---}	27^{---}	.$^{---}$	.$^{---}$	.$^{---}$
Tripolium pannonicum	**17^{---}**	**4^{---}**	**14^{---}**	**14^{---}**	**.$^{---}$**	**100^{59}**	**.$^{---}$**
Potentilla anserina	37$^{20.7}$	67$^{50.5}$	7^{---}	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$
Juncus compressus	28^{---}	46$^{37.4}$	7^{---}	5^{---}	.$^{---}$	.$^{---}$	.$^{---}$
Triglochin maritima	**33^{---}**	**29^{---}**	**7^{---}**	**.$^{---}$**	**.$^{---}$**	**8^{---}**	**.$^{---}$**
Juncus gerardii	**21^{---}**	**4^{---}**	**21^{---}**	**5^{---}**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**
Glaux maritima	**15^{---}**	**17^{---}**	**14^{---}**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**
Spergularia marina	**10^{---}**	**1^{---}**	**7^{---}**	**27^{---}**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**
Oxybasis rubra	3^{---}	.$^{---}$	.$^{---}$	9^{---}	10^{---}	.$^{---}$	.$^{---}$
Juncus ranarius	6^{---}	5^{---}	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$
Salicornia europaea	**1^{---}**	**1^{---}**	**7^{---}**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**	**.$^{---}$**
Spergularia media	1^{---}	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$	.$^{---}$

together with *T. pannonicum*. Association was reported from Poland, Germany and France. For the *Triglochino maritimae-Glaucetum maritimae* association the set of five Dg species were identified: *Triglochin maritima*, *Glaux maritima*, *Phragmites australis*, *Juncus compressus* and *Potentilla anserina*, among which Dm species were *G. maritima* and *T. maritima*. All five were also constant in this association together with *P. distans*. The association was noted in the same countries as *Scorzonero parviflorae-Juncetum gerardii*, but except in France. The *Agrostio stoloniferae-Juncetum ranarii* association had three Dg species: *Juncus ranarius*, *T. pannonicum* and *Oxybasis rubra*. Dominant species in this association covered *J. ranarius* and *P. distans*, while constant species also included *S. marina* and *Agrostis stolonifera*. This association was recorded in the United Kingdom and France.

Results revealed that all analyzed vegetation units were affected by salinity. The variation of vegetation representing not typical halophytic classes has been presented in Table A.3. The occurrence of species with the highest diagnostic value for *Therosalicornietea* and *Festuco-Puccinellietea* classes in other syntaxonomical units is shown in Table 3. A total of 15 Dg, Cs and Dm species were distinguished for typical salt marsh classes and associations together and most of them were also present in other vegetation units. However, it is worth to focus on obligatory and facultative halophytes in this group (Wilkoń-Michalska, 1963). Among them obligatory halophytes *A. prostrata* and *T. pannonicum*, and facultative *P. distans* have the widest distribution within non-halophytic vegetation units. They were noted in plots belonging to five different classes. Even the most salt tolerant halophyte *S. europaea* passed to vegetation of *Artemisietea vulgaris*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea* classes. The highest number of halophytes passed to *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, followed by *Artemisietea vulgaris* and *Bidentetea* classes (Fig. A.2).

3.2. Vegetation-environment relations

In the first step we focused on the class level of vegetation. Canonical Variate Analysis (CVA) demonstrated that vegetation classes present on temperate inland salt marshes differ significantly in terms of species preferences to soil salinity, moisture, light availability and nitrogen content as presented in Fig. 2. The species preferences to soil salinity, and moisture explained over 14 % of variance between vegetation classes (Table A.5). Taking into account available soil data, analyzed syntaxonomical units differ the most in terms of salinity expressed as electrical conductivity of saturated soil extract, total nitrogen and soil moisture, which together explained over 10 % of soil parameters variation between vegetation classes (Table A.6).

The detailed statistical comparison of single environmental effects on vegetation units based on EIV (Fig. 3) showed that species belonging to the *Therosalicornietea* and *Ruppietea maritimae* classes are characterized by high salt tolerance, and together with *Potamogetonetea* by high reaction values. In addition, species belonging to these classes together with *Phragmito-Magnocaricetea* class are the most preferential to high soil moisture while belonging to the *Polygono-Poetea annuae* and *Artemisietea vulgaris* classes the least preferential. Considering light indicator value, the vegetation of *Therosalicornietea* class is the most preferential to high insolation. However, it is the least preferential to high nitrogen content in the soil. The preference for temperature value is the factor that differentiates the analyzed groups the least.

The results of statistical analyzes based on available soil data demonstrated that the highest salinity, measured as electrical conductivity of saturated extract, was characteristic for vegetation of *Therosalicornietea* and *Bidentetea* classes (*Ruppietea maritimi* class missing the soil data) (Fig. 4). The highest soil moisture, as expected, was recorded in the soils occupied by vegetation of *Phragmito-Magnocaricetea* class, whereas the highest soil nitrogen in patches of *Molinio-Arrhenatheretea* class. The analyzed classes of vegetation do not differ significantly in terms of pH and the content of organic matter in the soil. Detailed soil results are presented in Table A.7.

3.3. Environmental pattern of salt-marsh plant associations

Regarding plant associations we focused on vegetation typical for salt marshes from *Therosalicornietea* and *Festuco-Puccinellietea* classes. Results of discriminant analysis (Fig. 5) revealed that based on EIV the most important for vegetation differentiation were preferences of species to light availability and soil reaction correlated with salinity, followed by moisture and nitrogen and temperature. All together explained ca. 33 % of variability between associations (Table A.5). Taking into account available soil measurements the most important for association differentiation were salinity expressed as EC_e and organic matter content, followed by pH and soil moisture, explaining over 30 % of variance in soil parameters between associations (Table A.6).

The comparison of single environmental effects between associations based on EIV (Fig. 6) demonstrated that species, which build the associations *Salicornietum ramosissimae* and *Agrostio stoloniferae-Juncetum ranarii* are the

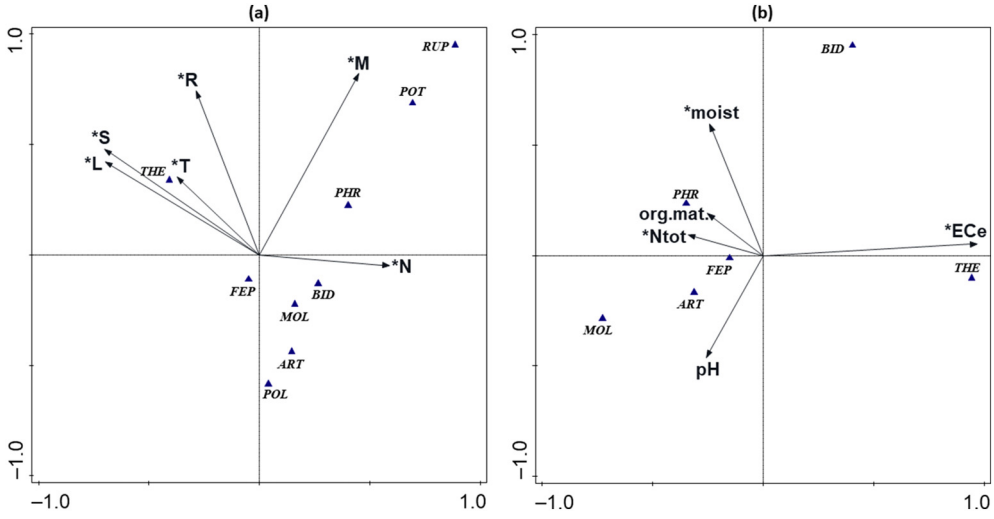


Fig. 2. Results of discriminant Canonical Variate Analysis (CVA): (a) relation between analyzed vegetation classes and environmental variables based on Ellenberg indicator values (EIV); (b) relation between analyzed vegetation classes and soil parameters. Distance between points is expressed as Mahalanobis distance. Statistically significant factors are marked by asterisk ($p < 0.05$). Abbreviations of vegetation classes: ART – *Artemisietea vulgaris*, BID – *Bidentetea*, FEP – *Festuco-Puccinellietea*, MOL – *Molinio-Arrhenatheretea*, PHR – *Phragmito-Magnocaricetea*, POL – *Polygono-Poetea annuae*, POT – *Potamogetonetea*, RUP – *Ruppietea maritimae*, THE – *Therosalicornietea*. Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content/trophy, R – reaction/soil acidity, S – salinity, T – temperature. Abbreviations of environmental parameters: ECe – salinity measured as electrical conductivity, moist – moisture, Ntot – total nitrogen, org.mat. – organic matter content.

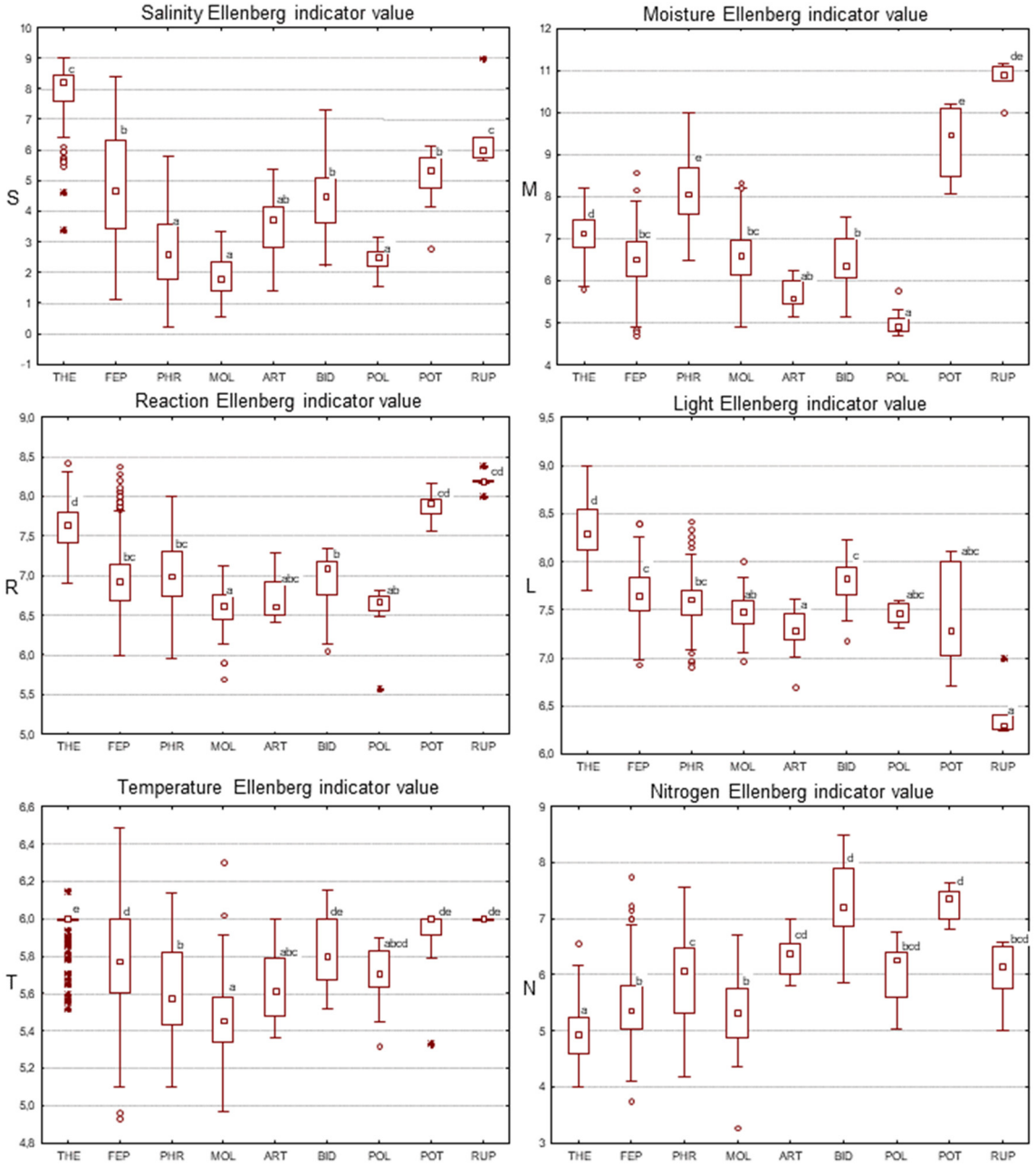


Fig. 3. Comparison of Ellenberg indicator values (EIV) for vegetation classes. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation classes: THE – *Therosalicornietea* ($n = 137$), FEP – *Festuco-Puccinellietea* ($n = 485$), PHR – *Phragmito-Magnocaricetea* ($n = 112$), MOL – *Molinio-Arrhenatheretea* ($n = 76$), ART – *Artemisietea vulgaris* ($n = 14$), BID – *Bidentetea* ($n = 22$), POL – *Polygono-Poetea annuae* ($n = 10$), POT – *Potamogetonetea* ($n = 12$), RUP – *Ruppietea maritimae* ($n = 6$). Abbreviations of environmental variables: S – salinity, M – moisture, R – reaction/soil acidity, L – light availability, T – temperature, N – nitrogen content/trophy.

most preferential to high soil salinity and light availability. *Salicornietum ramosissimae* association is also characterized by the greatest tolerance to high soil reaction. In the salinity gradient it is followed by *Puccinellio-Spergularietum salinae* association, but the set of species there turned out to be the least preferential to high values of soil moisture, but the most to high nitrogen content. Less salt tolerant *Scorzonero parviflorae-Juncetum gerardii* and *Triglochino maritimae-Glaucetum maritimae* associations differed in terms of light and temperature preferences, significantly lower in the second association, and of significantly higher there nitrogen indication.

Results obtained on the basis of available soil parameters confirmed that the highest soil salinity is typical for the *Salicornietum ramosissimae* association (Fig. 7 and Table A.8). However, on the second position has been placed *Scorzonero parviflorae-Juncetum gerardii* with significantly higher soil salinity and pH than in patches of *Triglochino maritimae-Glaucetum maritimae* association but significantly lower soil moisture and total nitrogen contents. *Puccinellio-Spergularietum salinae* association is noted in areas with the lowest content of organic matter and total nitrogen compared to other groups. Soil parameters were missing for *Agrostio stoloniferae-Juncetum ranarii.*

4. Discussion

4.1. Vegetation classification approach

The effective protection of inland salt-marsh vegetation that will allow for broad-scale comparisons require, as it was already mentioned, the

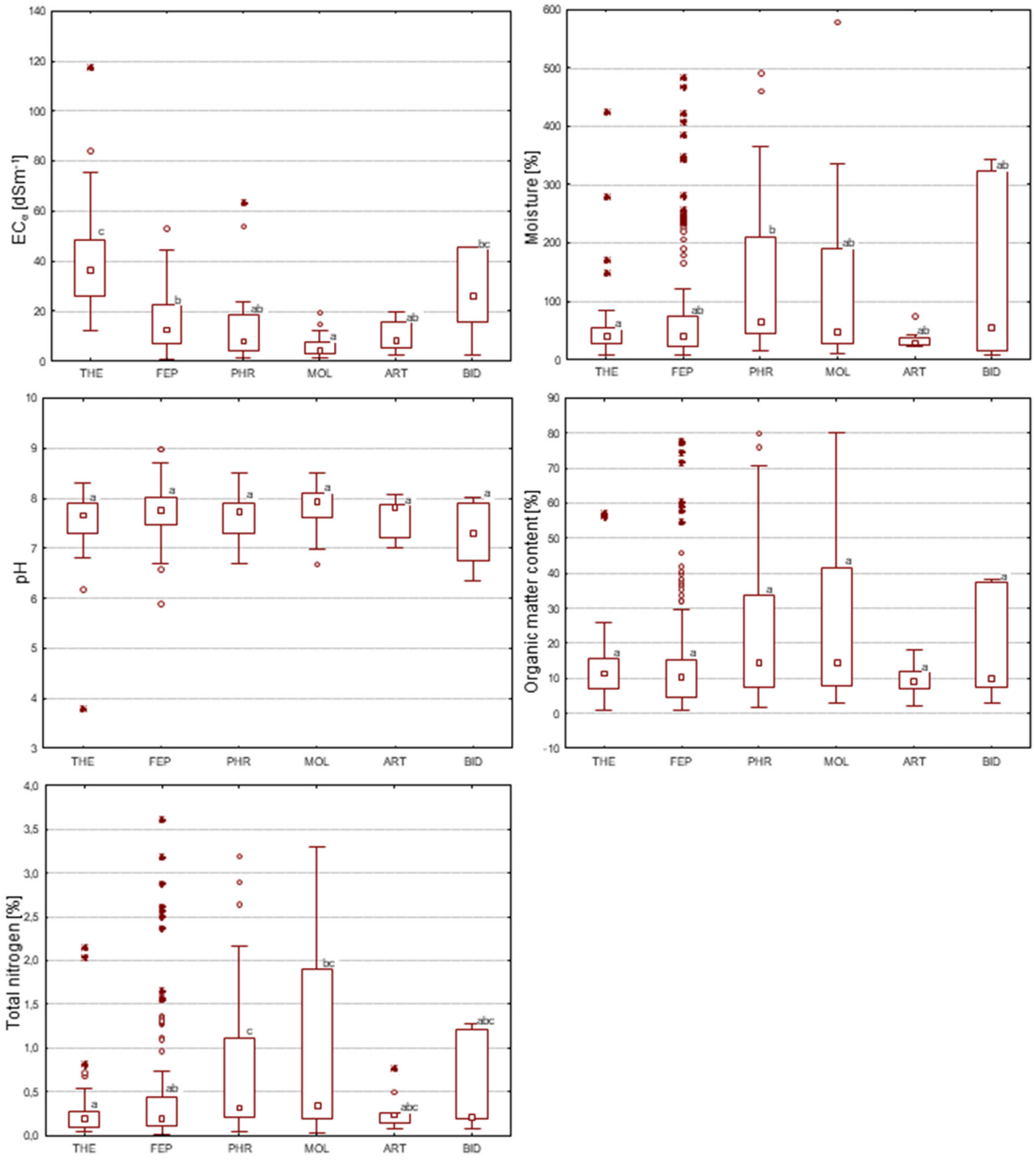


Fig. 4. Comparison of environmental parameters for vegetation classes. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation classes: THE – *Therosalicornietea* ($n = 54$), FEP – *Festuco-Puccinellietea* ($n = 134$), PHR – *Phragmito-Magnocaricetea* ($n = 38$), MOL – *Molinio-Arrhenatheretea* ($n = 24$), ART – *Artemisietea vulgaris* ($n = 9$), BID – *Bidentetea* ($n = 7$). Abbreviation of environmental parameter: EC$_e$ – salinity expressed as electrical conductivity.

unified syntaxonomical classification system based on data from various European locations. In our research, following the concept of Braun-Blanquet (Braun-Blanquet, 1964; Mucina et al., 2016), we made an effort first to classify vegetation to syntaxonomical units, then to assess their environmental dependence. At the first stage, apart from already known from saline areas vegetation representing *Therosalicornietea* and *Festuco-Puccinellietea* classes we identified as integral parts of inland salt marshes classes representing other vegetation types. However, this vegetation has its own specificity. We noticed that species thought as limited to narrow environmental conditions can present relatively wide ecological responses. They can play an important role in classification difficulties on one hand and on the second can shape vegetation variety. All 15 species, including eight halophytes, being Dg, Cs and Dm for halophytic classes and associations of *Therosalicornietea* and *Festuco-Puccinellietea*, entered other vegetation units. Among them obligatory halophyte *T. pannonicum* together with *A. prostrata* and facultative *P. distans* had the widest distribution within non-halophytic vegetation units and were noted in plots belonging to five different classes. Even the most salt tolerant halophyte *S. europaea* passed to vegetation of *Artemisietea vulgaris*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea* classes. This wide response curve of species is consistent with findings of Piernik (2003a, 2012), who demonstrated that even obligatory halophytes can be recorded on non- or slightly saline soils. Recent studies on *S. europaea* also showed that although the lack of salinity and the salinity of over 800 mM NaCl (≈ 80 dS $\times$ m^{-1}) conditions are extreme for this plant and limit its functional traits, they still do not completely stop its development (Cárdenas-Pérez et al., 2022). Moreover,

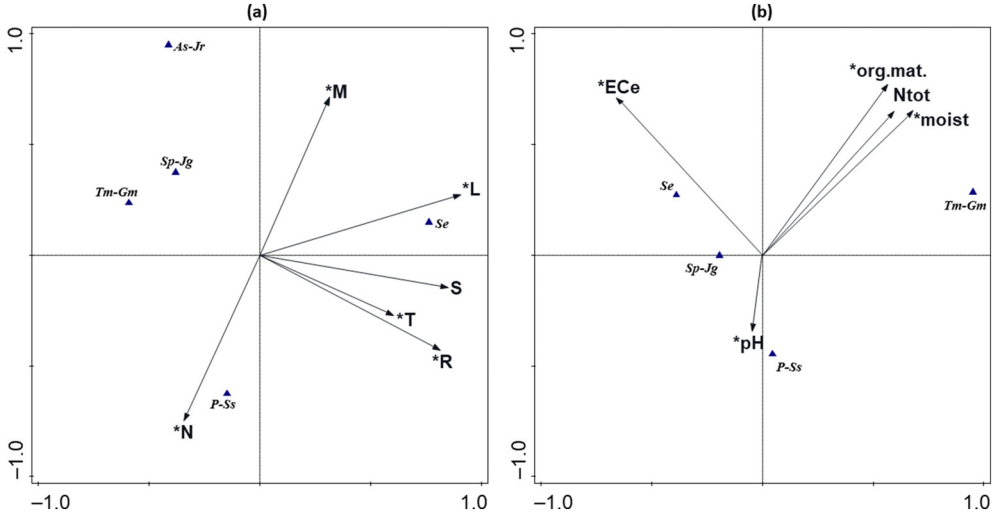


Fig. 5. Results of discriminant Canonical Variate Analysis (CVA): (a) relation between analyzed associations and environmental variables based on Ellenberg indicator values (EIV); (b) relation between analyzed associations and soil parameters. Distance between points is expressed as Mahalanobis distance. Statistically significant factors are marked by asterisk ($p < 0.05$). Abbreviations of vegetation associations: As-Jr – *Agrostio stoloniferae-Juncetum ranarii*, Se – *Salicornietum ramosissimae*, P-Ss – *Puccinellio-Spergularietum salinae*, Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii*, Tm-Gm – *Triglochino maritimae-Glaucetum maritimae*. Abbreviations of environmental variables: L – light availability, M – moisture, N – nitrogen content/trophy, R – reaction/soil acidity, S – salinity, T – temperature. Abbreviations of environmental parameters: EC_e – salinity measured as electrical conductivity, moist – moisture, Ntot – total nitrogen, org.mat. – organic matter content.

data from America shows high competitive ability, speed spread and high seed production of *P. distans* (Cusick, 1982; Tarasoff et al., 2007). Research from the United Kingdom shows that *P. distans* and *S. marina* permanently occupy roadsides due to salinity caused by the use of salt to defrost roads, although other species such as *Plantago maritima* are disappearing with time (Scott and Davison, 1985). The highest number of halophytes passed to *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, followed by *Artemisietea vulgaris* and *Bidentetea* classes. This is due to the high tolerance of these species to fluctuations in the soil salinity level and this decides about specificity of investigated vegetation. On the other hand the presence of vegetation from not typical salt marsh vegetation classes is due to relatively high salt resistance of many glicophytic species including diagnostic, constant and dominant. As demonstrated by Piernik (2012) the group of the most frequent species on inland salt marshes includes *Festuca rubra* which is according to Kącki et al. (2013) Dg and Cs species for *Molinio-Arrhenatheretea* class. Ecotype of this species was noted on inland salt marshes even at very high salinity (EC_e up to 25 dS × m^{-1}). In the most frequent group of species is present also *P. australis*, Dg and Dm species for *Phragmito-Magnocaricetea* class, noted in saline sites between EC_e 2.5 and 118 dS × m^{-1} (Kącki et al., 2013; Piernik, 2012). Three more species from the most frequent group are typical for *Artemisietea vulgaris* class, i.e. *E. repens* (Dg, Cs, Dm), *Cirsium arvense* (Dg, Cs) and *Achillea millefolium* (Cs). Also three species for *Bidentetea* class, i.e. *Plantago intermedia* (Dg), *Chenopodium glaucum* (Dg, Dm) and *A. prostrata* (Cs). All of them were recorded on even extremely saline soils (Piernik, 2012). That is why, not only vegetation classes typical for saline sites can be present on saline soils. However, all this creates difficulties with vegetation classification. The latest revision of the *Phragmito-Magnocaricetea* class classification even uses species of saline habitats as a functional species group to refine the definitions of some marsh vegetation associations (Landucci et al., 2020). Often, associations reacting to local environmental conditions form transitional patches with slightly different species compositions and complicate systematic classification. Despite the current simplicity of using numerical classifications, the final decisions about vegetation units are still subjective, but all these decisions are statistically sound (Tichý, 2002). As our research has shown, this problem largely concerns inland salt marshes. More than 28 % of the finally analyzed plots have been classified into seven atypical for saline areas classes. However, they should also be taken into consideration as an integral part while management and protection is planning.

4.2. Environmental drivers for vegetation

Our results positively verified the main research hypothesis on vegetation syntaxonomical units dependence on environmental requirements. Vegetation of inland salt marshes is very diverse, which reflects the syntaxonomic division at the class level as it was already discussed. We proved that its arrangement is determined by gradients of environmental factors, the most important of which are salinity, soil moisture and the availability of light. All statistically significant environmental factors, both applied as soil measurements or EIV, are able to explain respectively from 10 to 24 % of variation between groups (Tables A.5 and A.6). This is satisfactory taking into account high vegetation variability, different biogeographical locations and other factors that may affect vegetation formation as different species interactions or strategies and finally not taken into consideration environmental factors, as management type (Piernik, 2012; Piernik et al., 2015; Ulrich et al., 2018, 2019). Our results not only prove already reported field observations, e.g., that *Therosalicornietea* class is the most related to the highest soil salinity, then *Festuco-Puccinellietea* class but also demonstrate that *Phragmito-Magnocaricetea* class can cover vegetation not only resistant to high soil moisture but also to relatively high salinity and preferring relatively high nitrogen soil content. This is important, because high nitrogen availability can enhance species salt tolerance (e.g., Sikder et al., 2020). Definitely the last salt tolerant is vegetation from *Molinio-Arrhenatheretea* class, but on inland salt marshes its environmental requirements seems to overlap with *Phragmito-Magnocaricetea* class. It can mean that in our data the group of *Phragmito-Magnocaricetea* could include former meadows overgrown by *P. australis* as a result of its abandonment (Bosiacka et al., 2011). It is worth noting that vegetation from different classes usually coexist within particular locations. The coexistence of such diverse groups in the salinity gradient is known as zonation of salt marsh vegetation and it is formed not only by vegetation form *Therosalicornietea* and *Festuco-Puccinellietea* classes (Piernik et al., 1996; Piernik, 2006). It has been demonstrated also for continental halophytic grassland vegetation of Southeastern Europe (Dajić Stevanović et al., 2016). Moreover, zonation is also known for other organisms in saline areas, e.g., arthropods (Finch et al., 2007). This shapes the salt marsh biodiversity depending among others on the environmental gradients length (Ulrich et al., 2018).

Taking into consideration analyzed plant associations, the most important role in their pattern is played by the salinity, availability of light,

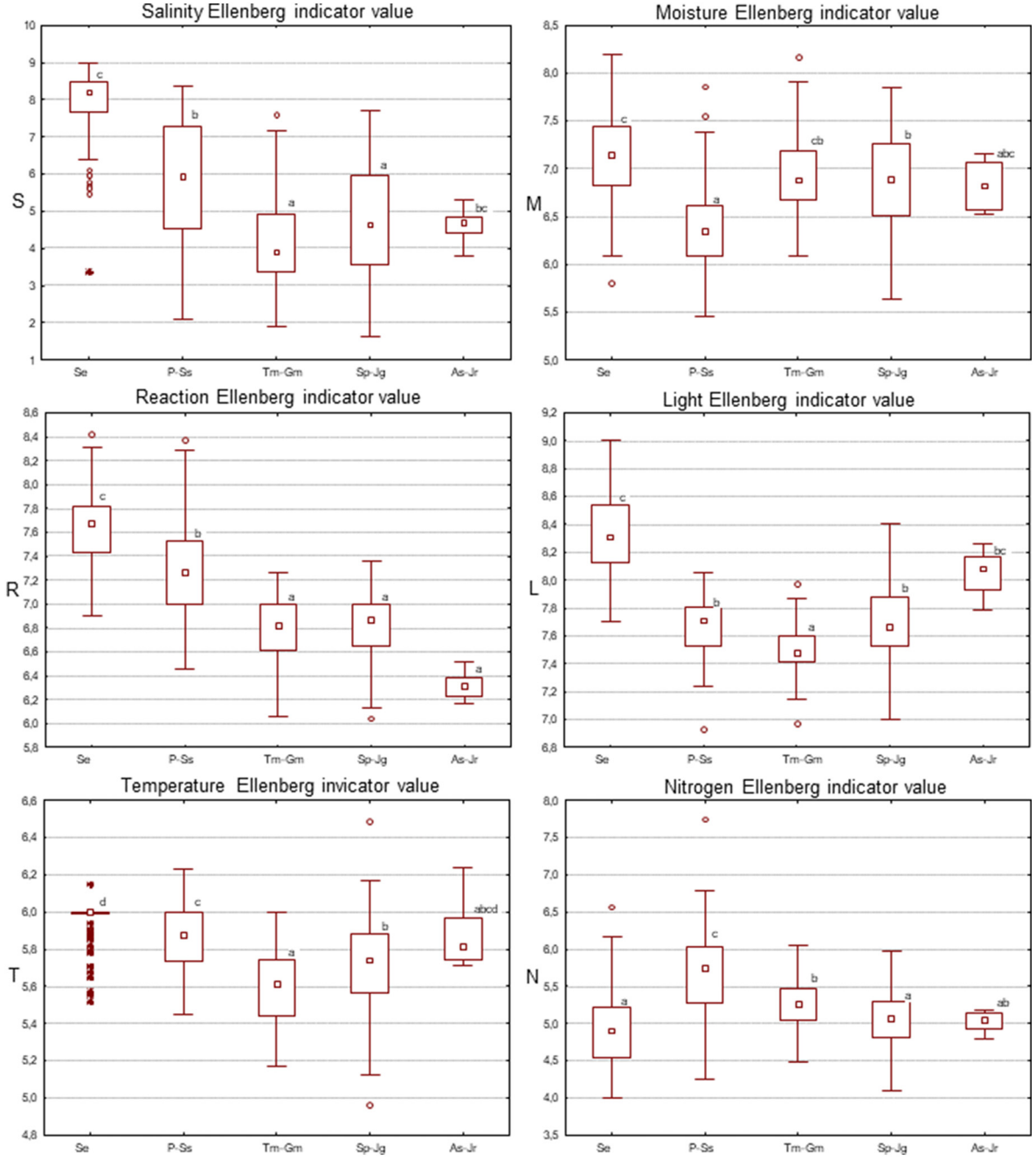


Fig. 6. Comparison of Ellenberg indicator values (EIV) for vegetation associations. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation associations: Se – *Salicornietum ramosissimae* ($n = 133$), P-Ss – *Puccinellio-Spergularietum salinae* ($n = 134$), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* ($n = 56$), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* ($n = 121$), As-Jr – *Agrostio stoloniferae-Juncetum ranarii* ($n = 6$). Abbreviations of environmental variables: S – salinity, M – moisture, R – reaction/soil acidity, L – light availability, T – temperature, N – nitrogen content/trophy.

moisture, reaction and the content of organic matter in the soil. It is worth emphasizing that discriminant analysis based on EIV representing long term environmental conditions and on soil measurements representing temporal measurements overlap in this case. The results demonstrate that environmental parameters explain respectively 33 and 30 % of the total variance between associations. The results obtained for individual associations based on EIV are confirmed in the literature from other inland sites in Europe (Dítě et al., 2021, 2022). *Salicornietum ramosissimae* is characterized by the highest EIV of salinity, moisture and soil reaction in comparison to other associations. This high soil salinity typical for this association has been also confirmed by analysis based on soil measurements. The next in the salinity gradient is placed *Puccinellio-Spergularietum salinae*, characterized also by relatively low moisture requirements and relatively high nitrogen preferences. It frequently follows *Salicornietum ramosissimae* as the next vegetation zone in the salinity gradient (Piernik et al., 1996; Piernik, 2006). However, based on soil parameters it is not so visible, probably due to possible high fluctuations in soil salinity e.g., after rains and presence of this association in the industrial, not stable habitats (Piernik, 2003b; Piernik and Hulisz, 2011). There is relatively little known about *Triglochino maritimae-Glaucetum maritimae* association which has been described firstly by Wilkoń-Michalska (1963) by the name *Triglochin maritimum-Glaux maritima* as occurring in inland salt meadows in Poland.

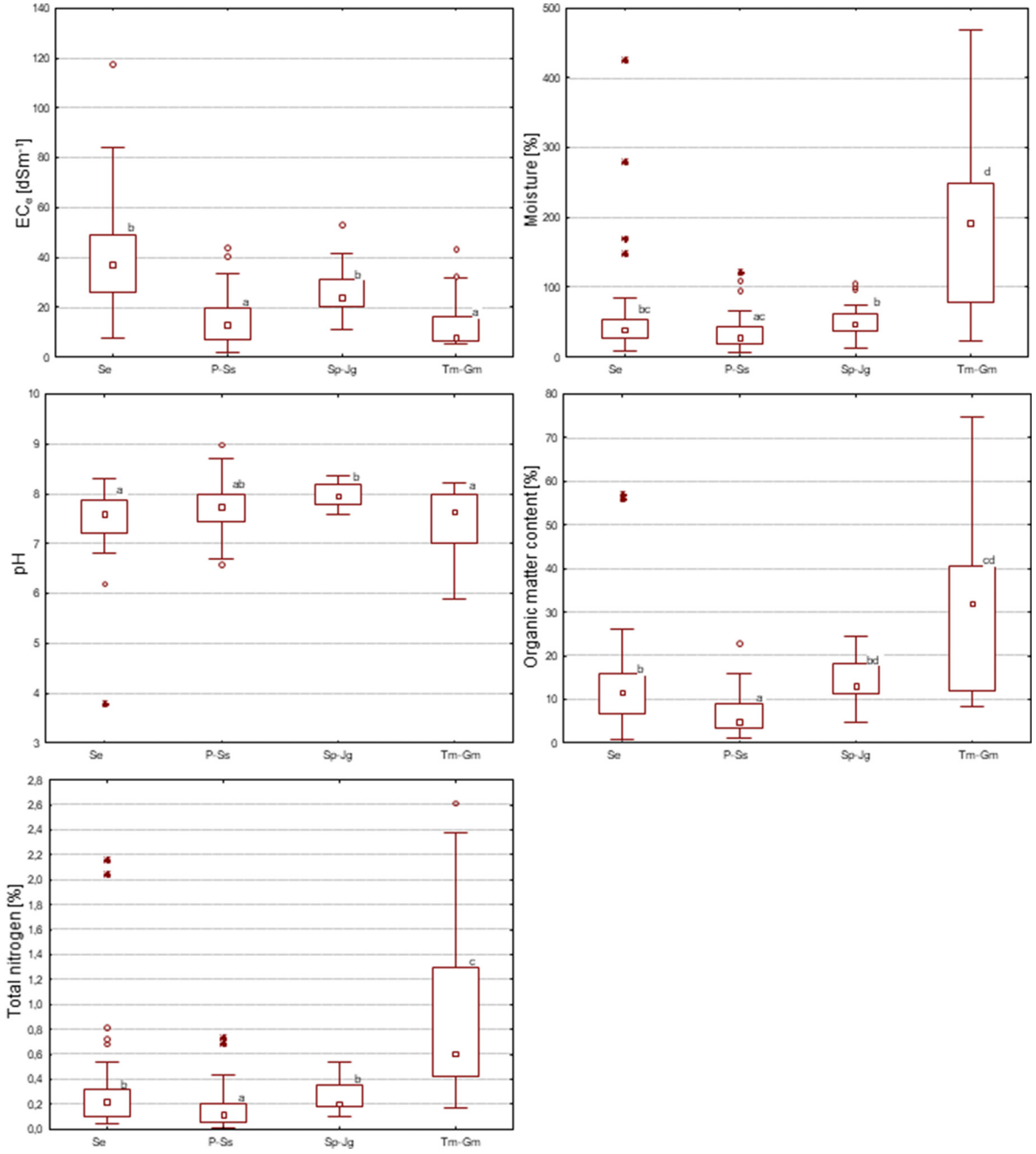


Fig. 7. Comparison of environmental parameters for vegetation associations. Significantly different groups according to Kruskal-Wallis test with Dunn post hoc comparisons are denoted by different letters at $p < 0.05$. Abbreviations of vegetation associations: Se – *Salicornietum ramosissimae* ($n = 50$), P-Ss – *Puccinellio-Spergularietum salinae* ($n = 45$), Sp-Jg – *Scorzonero parviflorae-Juncetum gerardii* ($n = 23$), Tm-Gm – *Triglochino maritimae-Glaucetum maritimae* (n = 23). Abbreviation of environmental parameter: EC$_e$ – salinity expressed as electrical conductivity.

Then it has been proved with the current name by Dítě et al. (2022) on inland salt marshes on the North German Plain. Our results confirm this finding. Unfortunately, these authors did not find any statistical differences in EIV properties between this association and known already from Germany *Scorzonero parviflorae-Juncetum gerardii*. From our data for *Triglochino maritimae-Glaucetum maritimae* has been classified 56 plots, located both in Poland and Germany, while for *Scorzonero parviflorae-Juncetum gerardii* 121 plots located mostly in Germany. Based on EIV we found differences in nitrogen preferences higher for the first association and light and temperature higher for second confirming *Scorzonero parviflorae-Juncetum gerardii* preferences to the warmer climate of western Europe. For direct soil comparisons we had only 23 plots in each group. However, we confirmed that patches of *Triglochino maritimae-Glaucetum maritimae* are typical for organic soils with high organic matter and high total nitrogen content, while *Scorzonero parviflorae-Juncetum gerardii* prefer mineral soils. Moreover, we found significantly higher soil salinity and pH for *Scorzonero parviflorae-Juncetum gerardii*. This is in line with our results on species composition because we found distinct differences between these units, i.e. higher number of diagnostic species for preferring lower salinity *Triglochino maritimae-Glaucetum maritimae*. Unfortunately, we had only six plots classified as *Agrostio stoloniferae-Juncetum ranarii* association and none with soil data. That is why the environmental interpretation for this vegetation unit should be postponed for the future more extended research.

4.3. Biogeographic distribution of typical halophytic vegetation

The *Therosalicornietea* class is widespread in Europe. Apart from the sites considered in our study, which partially correspond to the areas analyzed by Dítě et al. (2022), research was carried out also, e.g., in Romania (Dítě et al., 2021), Croatia (Dítě et al., 2019), Italy (Tomaselli et al., 2020) and generally in Southeastern Europe (Dajić Stevanović et al., 2016). The class is also listed outside our continent, e.g., in Central Asia, near the salty lakes and at the dry bottoms of intermountain depressions of eastern Siberia (Korolyuk et al., 2017). All of these confirm this class as azonal vegetation. Locally quite common is *Salicornietum ramosissimae* association from this class, which occurs not only throughout almost the entire area of our research, but also, e.g., in coastal areas in southern Europe, Croatia (Dítě et al., 2019).

The *Festuco-Puccinellietea* class is definitely more widespread than the *Therosalicornietea*. It shows a greater variety of species, more complex dependence on the local environment and thus a more complex syntaxonomic system. Generally it represents halophytic-steppe communities on the solonetz soils of the inner regions of Eurasia (Yuritsyna, 2021). It occupies, e.g., slightly saline, moist and wet substrates along the depressions and inter-ridge lowlands in the floodplains of rivers and along the highways (Bulokhov, 2018). In the past, this class was not described in the inland salt marshes of Europe with a temperate climate. However, Mucina et al. (2016) provoked a new syntaxonomical approach of temperate inland salt marsh vegetation classified to the *Juncetea maritimi* class before. In the new vegetation classification system they distinguished three classes containing the vegetation of natural salt marshes: *Therosalicornietea*, *Juncetea maritimi* and *Festuco-Puccinellietea*. The *Therosalicornietea* class as pioneer vegetation of annual succulent halophytes is not under question. The *Juncetea maritimi* class is declared to contain perennial grasslands, herb-rich vegetation of coastal and inland-salt marshes but any order or alliance is dedicated to cover inland part of salt-marsh vegetation. The *Festuco-Puccinellietea* class in this system comprises two groups of orders from which one covers vegetation typical of flooded, moist/wet (mainly solonchak) soils in order *Scorzonero-Juncetalia gerardi* Vicherek 1973 and alliance *Juncion gerardi* Wendelberger 1943, which could include inland temperate salt marsh vegetation. Consequently, a similar approach is presented by other researchers in the temperate salt marshes of Europe (e.g., Dítě et al., 2021, 2022). Moreover, Dítě et al. (2022) based on data from the southern Baltic Sea coast and inland German salt marshes, proved the difference between inland salt marsh vegetation denoted as *Festuco-Puccinellietea* class and coastal vegetation representing *Juncetea maritimi* class. They are based on limited data sets not including environmental parameters and therefore, this syntaxonomical doubt can be thought as still open for future research and discussion. Regardless, the most common in this class is *Puccinellio-Spergularietum salinae* association. This name has been around for years and the authors of the plots in our database used it most frequently, see Table A.9. Interestingly, it was not noted in the latest study of salt marshes in North German Plain by Dítě et al. (2022), who classified this vegetation, rather to the *Puccinellietum limosae* Soó 1933 and *Atriplex prostrata* community, despite the large share of *S. marina*. The *Scorzonero parviflorae-Juncetum gerardii* association is also widespread in European inland salt marshes as shows research from the Balkans (Dítě et al., 2015) or individual countries – Romania (Dítě et al., 2021). In our dataset *Triglochino maritimae-Glaucetum maritimae* association has been documented only in Poland and Germany, as confirmed by the results of Dítě et al. (2022). Currently association is rather not listed in southern or western Europe, incl. in Romania (Dítě et al., 2021). This may be related to the local extinction of *T. maritima* and *G. maritima* (Danihelka et al., 2022), which was earlier noted also in inland positions of western Europe. The *Agrostio stoloniferae-Juncetum ranarii* association was recorded in our data set only on inland salt marshes in the United Kingdom and France. This association is typical of slightly moist, saline soils with frequently disturbed surfaces. It is reported also from dry areas of northern Bohemia (Ohře river basin) and southern Moravia (Eliáš et al., 2012; Novák and Šumberová, 2007).

4.4. Conservation and protection implications

As it was already mentioned inland salt marsh vegetation is protected under the Natura 2000 network. Two habitats, 1310 - *Salicornia* and other annuals colonizing mud and sand and *1340 - Inland salt meadows (*Glauco-Puccinellietalia*), were created. The vegetation included by us in the *Salicornietum ramosissimae* association is classified as representing habitat 1310 (Nienartowicz and Piernik, 2004b). The remaining analyzed associations from the *Festuco-Puccinellietea* class represent habitat *1340 (e.g., Nienartowicz and Piernik, 2004a). As it was proved by us, the most important environmental factors shaping inland salt marsh vegetation is salinity and moisture, frequently related to each other, because salty ground water can serve as the source of soil salinity both in natural and industry habitats (Piernik and Hulisz, 2011). Therefore, this vegetation is sensitive to any water regulations that can also change soil pH and organic matter decomposition. Moreover, the research by Čížková et al. (2020) showed that the water level has an impact on the abundance of individual species of halophytes in salt marshes. Some species grow both on moist and dry soils, such as *T. pannonicum* or *S. marina*, some on rather dry soils like *Melilotus dentatus*. Another significant factor is light availability, which proves necessity of management by regular mowing, as well as grazing livestock, which results in gnawing and trampling on plants and creation free spaces for annual species as *S. europaea* or *S. marina* (Bakker and De Vries, 1992). Grazing is most important for short species of halophytes such as *S. europaea*, *Suaeda maritima* and *G. maritima* (Jensen, 1985). Research shows that moderate grazing generally increases plant richness and diversity, while lack of grazing and overgrazing reduces the plant diversity and richness of salt marshes (Bouchard et al., 2003; Kiehl et al., 1996). That is why, it is also important to consider the appropriate density and species of herbivores, e.g., cattle, horses or sheep (Milotić et al., 2010; Nolte et al., 2014). Moreover, some species can be sensitive to mowing or grazing. As research on *Bolboschoenus martimus*-dominated vegetation in Europe show it covers inland wetlands in a broad range of both freshwater and saline habitats (Hroudová et al., 2009; Ljevnaić-Mašić et al., 2020). Therefore, it copes well with the salinity and high humidity of the soil, but is very threatened by mowing and grazing (Ljevnaić-Mašić et al., 2020). It should be taken into consideration if it is a target species for some areas.

The cessation of mowing or grazing usually results in a gradual overgrowing of the light-requiring halophyte associations (Wilkoń-Michalska, 1970) and formation of communities with higher species. In the case of high soil moisture, these are often reed communities of the *Phragmito-Magnocaricetea* class. As our results show, this may be a common and easy effect, because we classified over 12 % of samples into this class. The spreading of *P. australis* is a common and important problem (Burdick et al., 2001). Tall shoots of this species cover halophilous vegetation, which initially remain in the form of patches scattered in vast reeds, but then disappear (Bosiacka et al., 2011). Finally, it is worth emphasizing that the most important thing in effective protection is the appropriate involvement of people responsible for the protected areas, who will ensure the systematic conduct of active treatments (e.g., Lubińska-Mielińska et al., 2022). After all, there are known for years effective actions that imitate the traditional way of land use, which guarantee not only the maintenance, but also the improvement of the condition of the salt marsh vegetation (Brandes, 1999).

5. Conclusions

Our results demonstrates that in addition to *Therosalicornietea* and *Festuco-Puccinellietea* other vegetation classes, such as *Ruppietea maritimae*, *Polygono-Poetea annuae*, *Artemisietea vulgaris*, *Potamogetonetea*, *Bidentetea*, *Phragmito-Magnocaricetea* and *Molinio-Arrhenatheretea*, are an integral part of temperate inland saline habitats and include halophytic species. These classes differ the most in terms of species preferences to salinity, soil moisture, light availability and soil nitrogen content. In addition, identified typical salt marsh associations differ also by soil reaction and soil organic

matter content. This indicates a large diversity of the analyzed vegetation type, but also its sensitivity to changes in environmental conditions. Targeting biodiversity conservation and restoration these requirements should be taken into account.

CRediT authorship contribution statement

SLM – prepared first draft of publication, prepared and managed database, performed classification analyses, ZK – design the definitions of syntaxonomical units and performed classification, DK – supported classification designing and interpretation, JP – collected part of the data from France, CE – collected the part of the data from Germany, AP – supervised the project, prepared the rules for syntaxonomical units, collected part of the data from Poland and performed statistical vegetation-environment analysis. All authors substantially contributed to the final version of the manuscript.

Data availability statement

After acceptance of publication data will be available from the authors under request.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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