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Vegetation of temperate inland salt marshes on their north-western border (North German Plain)

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Abstract: Temperate inland salt marshes, formerly used as meadows or pastures, are priority habitats in Europe and are threatened by intensifying anthropogenic activities. They are particularly important because of their biogeographical location on the North German Plain, which is the westernmost hotspot of continental halophytic vegetation in Eurasia. In spite of their remarkably long history of floristic research, there are disproportionately few studies dealing with plant communities. They are traditionally included in the *Puccinellion maritimae* and *Armerion maritimae* alliances with a typical distribution along the North and Baltic Sea coasts. The similarity with other inland salt marshes has been overlooked. We surveyed natural and secondary sites with euhalophytic vegetation in central Germany (Saxony-Anhalt and Thuringia) in 2018 and 2020 and analysed 105 phytosociological relevés. This resulted in the identification of three main groups (alliances) containing seven associations: annual hypersaline succulent communities of the alliance *Therosalicornion* (*Salicornietum europaeae*, *Halimioni pedunculatae-Puccinellietum distantis*, *Suaedetum maritimae*), wet saline meadows of the alliance *Juncion gerardi* (*Triglochino maritimae-Glaucetum maritimae*, *Scorzonero parviflorae-Juncetum gerardi* variant with *Glaux maritima*) and saline short-grass swards of the alliance *Puccinellion limosae* (*Puccinellietum limosae*, *Atriplex prostrata community*). For each association we defined the typical species composition and calculated Ellenberg indicator values depending on the ecological gradients of soil salinity, nutrients and moisture. To determine possible floristic similarities between the inland and coastal salt marshes, we compared our data with data from other areas of saline vegetation: the southern Baltic Sea coast, Kujawy (Poland), Pannonian Basin (Hungary) and Transylvanian Basin (Romania). We concluded that the salt marshes in inland Germany showed a stronger relation with salt marshes of the remote Pannonian and Transylvanian Basins, and they were well separated from the Baltic salt marshes. Thus, we suggest including inland salt marshes on the North German Plain into the syntaxonomical class of continental halophytic vegetation of *Festuco-Puccinellietea.*

Keywords: abandoned salt waste deposits, brackish meadows, central Europe, continentality, *Juncetea maritimi*, *Scorzonero-Juncetalia gerardi*, *Therosalicornietea*, vegetation classification

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Introduction

Saline habitats are tidal (coastal) or non-tidal (inland) wetlands formed mainly by herbaceous vegetation developing on salt-affected soils. In Europe they are widespread on all coasts, from the Arctic and Atlantic to the Mediterranean (Chytrý et al. 2020). Temperate inland salt marshes (Annex 1 code 1340, Eunis R.63, Red List E6.3) are very much more limited in their spatial extent than coastal salt marshes. They are confined to several discrete areas in central and eastern Europe (Eliáš et al. 2013, Janssen et al. 2016, Zlatković et al. 2019) on the North European Plain, with a frequent distribution in Germany (mainly Saxony-Anhalt, Thuringia and Brandenburg states) and Poland (Kujawy region) (Piernik 2012; Janssen et al. 2016). The vegetation of temperate inland salt marshes is very similar to the adjacent A2.5b Baltic coastal meadows (1630) and A2.5c Atlantic coastal salt marshes (1330), however, they are not influenced by seawater inundation, but occur in close vaccinity to salt-rich springs emerging from fossil salt deposits similar to those found in the Transylvanian Basin (Krézsek & Bally 2006, Dítě et al. 2021a). Inland saline vegetation is confined to areas with increased evaporation during dry and warm summers (Rivas-Martinez & Rivas-Saenz 2009). This is especially true for the Pannonian Basin, where halophytic species and characteristic plant communities are the most variable (Molnár & Borhidi 2003). Temperate inland salt marshes are under threat throughout their distribution. Regulation of water levels and abandonment results in a reduction in the area, decreased habitat quality and encroachment of ruderal species, e.g. *Elytrigia repens* (Pätsch et al. 2019a, Dítě et al. 2021b).

The remarkably long history of floristic research on inland salt marshes on the North German Plain dates back to the 16th century. For instance, the first mention of the relict halophytic species *Artemisia rupestris* from Brennburg is reported by Cordus in 1561 (sec. Bank & Kison 1999). The distribution of salt-tolerant species was already well-explored by the end of the 19th century and research continued throughout the 20th century (see the bibliography in Brandes 1999). Recently, the focus has shifted to the conservation of the remaining salt marshes (e.g. Pusch 2007, Schuster et al. 2010, Hartenauer et al. 2012). As is the case with the natural environment in general, the gradual destruction of salt marshes occurred even as knowledge about them has increased. As industrial development continued, the intensity of habitat deterioration increased until the 1980s, with consequences lasting until the present (Hartenauer et al. 2012). Many localities were reduced in size and several species have become extinct in Thuringia and/or Saxony-Anhalt, such as *Artemisia laciniata*, *Blysmopsis rufa* and *Eleocharis parviflora* (Jäger 1987, Frank et al. 2004). The number of halophytic specialists continues to decline in the existing natural areas (Krumbiegel & Hartenauer 2012, Frank & Schnitter 2016). Simultaneously with the decline in natural habitats, several halophytes spontaneously spread into anthropogenic habitats affected by mining (potash, kaolin and salts), around salt-polluted rivers and at some industrial sites (e.g. Garve & Garve 2000). Several species abundant in such places are already very rare in natural salt marshes, for instance *Salicornia europaea* and *Suaeda maritima*. Species that had already become regionally extinct (e.g. the relic *Hornungia procumbens*) are currently spreading (John 2000). The number of species recorded at secondary sites has increased over time, and today all halophytic species occurring in the area are growing in man-made habitats as well. At the same time, several allochthonous species (*Gypsophila perfoliata*, *G. scorzonerifolia*) have been spreading in such locations (Liebmann & Heinze 1980, Westhus & Westhus 1998, Garve & Garve 2000, John 2000).

Compared to the volume of published floristic data on halophytic flora in Germany, there are disproportionately few works dealing with halophytic plant communities. Past phytosociological studies dealt primarily with coastal salt marshes (e.g. Tüxen 1928 in the Baltic), which are still frequently and interdisciplinary studied on regional and supranational scales (e.g. Dijkema 1990, Bakker 2014, Pätsch et al. 2019b). The first survey of inland saline vegetation was provided by Altehage & Roßmann (1939), who describe several formations across a wide gradient of salt marsh vegetation and characterized their ecology. Within the annual succulent vegetation of the class *Therosalicornietea*, they characterized three zones: *Salicornia herbacea* zone, *Suaeda maritima* zone and *Obione pedunculata* (= *Halimione pedunculata*) zone. They describe the associations *Salicornietum herbaceae* and *Puccinellia distans-Obione pedunculata* Ass., from outer zones with less saline soils, the *Triglochin maritima-Scorzonera parviflora*-Ass. Later, Mahn & Schubert (1962) described the *Juncus geradi-Glaux maritima*-Ass. from salt meadows in Magdeburg. Both works only list associations without their classification into higher syntaxonomic units, which was done by Wilkoń-Michalska (1963) in her detailed study of the vegetation of inland salt-affected soils in the eastern part of the North-European Plain (Kujawy, Poland). She placed the hypersaline stands in the class *Salicornietea* Br.-Bl. et Tüxen 1943, order *Salicornietalia* Br.-Bl. (1931 n.n.) 1933, alliance *Thero-Salicornion* Br.-Bl. (1931) 1933 and association S*alicornietum patulae* W. Christiansen 1955. The brackish, tall-rush vegetation she classifies to *Juncetea maritimi* Br.-Bl. (1939) 1951, order *Juncetalia maritimi* Br.-Bl. 1931, alliances *Puccinellion maritimae* (W. Christiansen 1927) Tx. 1937 and *Armerion maritimae* Br.-Bl. et de Leeuw 1936 containing a new association *Triglochin maritimum-Glaux maritima* (the syntaxon names are cited verbatim from this publication). These higher units are all described from coastal salt marshes. The later classification of inland salt vegetation of Poland, including material for the Natura 2000 network (Matuszkiewicz 2001, Nienartowicz & Piernik 2004a, b), follows the same concept as Wilkoń-Michalska (1963).

Inland saline vegetation in Germany is also traditionally included in the higher syntaxa originally described for coastal vegetation. This is seen in regional studies from Thuringia (Pusch 1999, Heinrich et al. 2010, 2011, Schuster et al. 2010), Saxony-Anhalt (Schubert et al. 2001, Frank et al. 2004, Krumbiegel & Hartenauer 2012) and Brandenburg (Zimmermann 2010), and in the older and most up-to-date national vegetation surveys (Pott 1992, Schubert 2001, Bergmeier 2020). Saline soils in inland Germany and Poland undoubtedly support plant communities that are similar to those occurring on the North Sea and Baltic coasts (e.g. Leuschner & Ellenberg 2017). However, so far there have been no studies on their relation to saline vegetation in other important areas of temperate inland salt marshes in Europe (Pannonian Basin, Transylvanian Basin).

Our aim was to provide a comprehensive syntaxonomical overview of inland salt marshes on the North German Plain including: (i) a characterization of the ecological preferences of the surveyed euhalophytic vegetation based on Ellenberg indicator values, (ii) an analysis of data from inland and coastal salt marshes in adjacent regions (Baltic Coast, Pannonian Basin and Transylvanian Basin), (iii) a broad syntaxonomical discussion of the resulting types of vegetation in terms of a wider central-European perspective.

Thus, our study aims to resolve the question whether to allocate the inland salt marshes on the North German Plain to those of coastal saline vegetation or continental saline vegetation.

Methods

Study area

We surveyed 12 salt marsh complexes (in German: Binnensalzstellen) in central Germany (Fig. 1), where they occur on a loess belt stretching along the south-eastern rim of the North German Plain (part of the North European Plain). The highest abundance of inland salt marshes is found in the intensively used lowlands of the Saale River and its tributaries in Saxony-Anhalt. In the hilly, more humid state of Thuringia, salt marshes are more scattered and mostly found in the middle section of the Werra River. Together, they form an important hotspot of halophytic vegetation in temperate Europe.

The North German Plain stretches from the North Sea and the Baltic Sea in the North to the German Central Uplands in the south, and from the the Netherlands in the west to the border of Poland in the east. It was formed during the Pleistocene era as a result of the various glacial advances of terrestrial Scandinavian ice sheets and periglacial geomorphologic processes. The transitional climate determined the closeness of the sea and becomes increasingly continental towards the east (Rivas-Martinez & Rivas-Saenz 2009). For example, the Magdeburg Börde (Saxony-Anhalt), situated in the rain shadow of the Harz Mountains, is one of the driest regions in Germany, which is reflected in the presence of natural salt-affected areas. The mean annual temperature is between 8.4 and 9.6 °C with a mean annual precipitation of 542 mm (Fick & Hijmans 2017, see Supplementary Table S1). This area of the North German Plain belongs to the continental biogeographical region (https://www.eea.europa.eu/data-and-maps/figures/biogeographical-regions-in-europe-2).

Natural sites of inland halophilous vegetation in central Europe are connected with areas supported by springs and groundwater rich in soluble salts (Balaske 2012). The origin of this saline water is associated with fossil salt deposits from relict seawater in the Zechstein sedimentary rock layers (Zhang et al. 2013). It has formed salt domes over the Central and Southern North Sea, expanding eastwards into Germany. The thickness of these salt formations differs locally and can extend to a depth of 800 m (Westhus et al. 1997). Depending on the weight of rocks lying on the salt deposits and on the primary thickness of the salt complex, numerous forms have developed, uplifted in the form of salt pillows, diapirs and salt domes (Dadlez & Jaroszewski 1994). The flow processes of salts (gypsum, rock salt, potash salt) were triggered by faults in the overlying rocks and tectonic unevennesses (Balaske 2012). Halokinesis began in the upper Triassic period and in some places has continued to the present day. These salt structures are present, for example within the Thuringian Basin, the Sub-Hercynian Basin in Germany and in the axial part of the Polish-German Basin (Stupnicka 1978). While primary salinization is caused by eruptions of groundwater percolating through layers of evaporites in the geological subsoil, secondary salinization is caused by industrial salt mining and processing, causing local and regional salinization, the latter due to discharge of wastewater into rivers. For more than 100 years, local salinization has also been caused by discharges of wastewater from these industrial processing sites into the rivers (Braukmann & Böhme 2011). Secondary salt marshes can also be hundreds of years old, because salt mining in

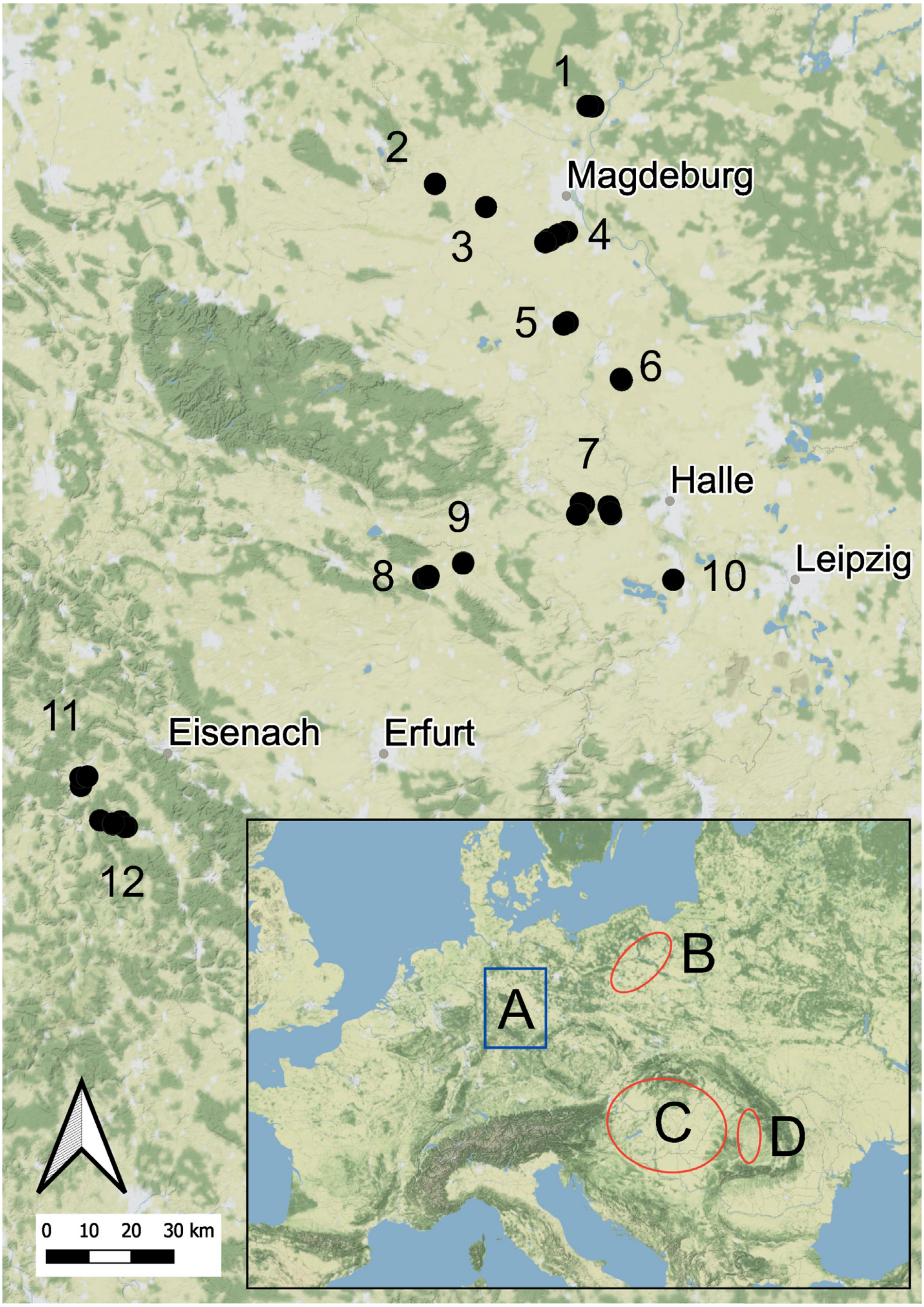


Fig. 1. Area studied and location of the inland salt marshes visited (black circles). A – central Germany, within that localities in Saxony-Anhalt: 1 – Zielitz; 2 – Wormsdorf; 3 – Remkersleben; 4 – Sülldorf – Osterweddingen – Dodendorf; 5 – Staßfurt – Hohenerxleben; 6 – Kleinwirschleben; 7 – Süßer See (Aseleben) – Röblingen am See – Langenbogen – Teutschenthal; 10 – Merseburg. Localities in Thuringia: 8 – Esperstedt, 9 – Artern, 11 – Dippach – Dankmarshausen; 12 – Dorndorf – Merkers – Kaiseroda – Tiefenort. Other regions with temperate inland salt marshes that were compared with the area studied: B – Kujawy, C – Pannonian Basin, D – Transylvanian Basin.

the region is a tradition dating back 1000 years, e.g. at Sülldorf. The frequent occurrence of primary salt marshes is proven by many historical local names, although at present the soils at these localities no longer show any signs of salinity (Schuster et al. 2010). Irrigation of natural salt marshes occurred as early as 1640 (Koert 1924, 1927 sec. Hartenauer et al. 2012). In these cases, the distinction between natural and secondary salt marshes is problematic.

Vegetation sampling

In late summer of 2018 and 2020, we sampled 105 phytosociological relevés at sites with euhalophytic vegetation, including vascular plants and bryophytes. Transitional vegetation in freshwater influenced areas (e.g. trampled nutrient-rich grasslands of *Loto-Potentillion anserinae*, meso-eutrophic reeds and mesic grasslands of *Arrhenatherion elatioris*) were not studied. We used the adapted nine-point Braun-Blanquet cover-abundance scale (Barkmann et al. 1964), which was converted to mid-percentage values for the analyses. All the relevés were recorded in plots of 4 × 4 m, which is the standard plot size for recording non-forest vegetation (Chytrý & Otýpková 2003).

Plant nomenclature follows Euro+Med (2021) and the names of higher syntaxa up to alliance rank are according to Mucina et al. (2016). Association names and syntaxa of lower rank are cited at their first mention in the same wording in which they were published in the original work regardless of the correctness of the International Code of Phytosociological Nomenclature (Theurillat et al. 2021).

Data processing

The relevés were stored in a TURBOVEG database (Hennekens & Schaminée 2001) and exported for classification to the JUICE program (Tichý 2002). We distinguished the higher vegetation units (orders) and the associations using hierarchical clustering (log-transformed percentage abundances, Bray-Curtis dissimilarity and beta-flexible clustering; beta = –0.25) in the PC-ORD 5.0 software (McCune & Mefford 2006). OptimClass1 (Tichý et al. 2010) was used to detect the optimum number of clusters. The coherence of these clusters was checked using Detrended correspondence analysis (DCA; log-transformed percentage abundances) with the 'Envelopes' 3D visualization function from R package Vegan (Oksanen et al. 2013). Their content was evaluated using the analysis of diagnostic, constant and dominant species in JUICE. As a fidelity measure, the phi coefficient was calculated with virtually equalized sizes of all relevé groups. Species were not considered as diagnostic when the occurrence concentration in the target clusters was not shown to be significant using Fisher's exact test at $P < 0.001$ (Chytrý et al. 2002). Diagnostic species in the combined synoptic table were based on two criteria: (1) phi coefficient value higher than 0.20 and (2) species frequency higher than 50%. The threshold frequency value for constant species was 50% and the threshold value of cover for dominant species was 25% with a frequency higher than 20%.

We performed additional analyses in order to compare our data with historical and recently published relevés within the orders *Therosalicornietalia* and *Scorzonero-Juncetalia gerardi*. Firstly, we analysed our dataset of 105 relevés (Supplementary Table S2) together with 78 relevés from the coastal meadows of the Baltic Sea recorded by Ricarda Pätsch (Supplementary Table S3) to detect the relation between inland and coastal salt marshes. Further more, for better data interpretation of the identified plant associations, we analysed 43 historical relevés from inland Germany published by Altehage & Roßmann (1939) and Wilkoń-Michalska (1963), along with 41 recent relevés published for the Pannonian and Transylvanian Basins by Dítě et al. (2015). To assign this heterogeneous set of historical relevés into our concept of associations, we used supervised K-means clustering with square root transformation of percentage covers in JUICE program. The additional analyses were checked using DCA (log-transformed percentage abundances) with the 'Spiderplot' and 'Envelopes' visualization function from R package Vegan (Oksanen et al. 2013). The indicator values (EIV) for moisture, nutrients and salt concentration of the soils were taken from Ellenberg et al. (1992) and displayed using boxplots. Statistically significant differences among groups displayed in boxplots were tested using ANOVA and the Tukey HSD test (alpha = 0.01) generated in the Statistica 7 programme (StatSoft, Inc. 2004).

The map was created using the program QGIS, version 3.2 (QGIS Development Team 2018) with the QuickMapServices plugin and a terrain background layer from Stamen Design with OpenStreetMaps data. Values of bioclimatic variables (Supplementary table S1) were calculated for each relevé from a set of global climate layers WorldClim2 (Fick & Hijmans 2017) at a spatial resolution of 30 seconds (~1 km^2).

Results

The euhalophytic vegetation studied in inland Germany is species-poor. Our 105 relevés recorded at 21 locations contained a total of 58 species of vascular plants at the 12 different sites shown in Fig. 1 (for site description of relevés see Supplementary Data S2). Despite low species richness, the plant communities consisted of several zones of vegetation easily detectable by their distinct physiognomies, which reflected microtopographical differences. The analysis distinguished three main groups of higher syntaxonomic rank (A, B, C) in which there were seven clusters (associations) (Fig. 2), plotted on the DCA ordination diagram (Fig. 3, 4). Along the main axis (DCA1), the annual succulent vegetation of group A belongs to class *Therosalicornietea*, order *Therosalicornietalia*, which includes three associations. The hemicryptophytic vegetation of groups B and C belong to the class *Festuco-Puccinellietea*, group B to the order *Scorzonero-Juncetalia gerardi* with two associations and group C to the order *Puccinellietalia*, also with two associations. Different ecological preferences (based on Ellenberg indicator values) for salinity, nutrients and moisture are clearly reflected in the associations identified (Fig 5).

Description of the groups of vegetation: species composition and ecological preferences

Group A. Class *Therosalicornietea*, order *Therosalicornietalia*, alliance *Therosalicornion*.

This group consists of pioneer vegetation of annual succulent plants in irregularly flooded flat depressions in inland salty areas and includes clusters no. 1, 2 and 3 (Table 1, Fig. 2). They occuppied the most salinized and wettest soils in the area studied and their preference for soil nutrient content varied from the lowest in cluster 1 to very high in cluster 3 (Fig. 5).

Table 1. Synoptic table with percentage frequency and modified fidelity index phi coefficient (upper-case numbers) for seven columns (associations). Diagnostic species for associations are indicated by bold font and highlighted by grey colour. 1 – *Salicornietum europaeae*; 2 – *Halimioni pedunculatae-Puccinellietum distantis*; 3 – *Suaedetum maritimae*; 4 – *Triglochino maritimae-Glaucetum maritimae*; 5 – *Scorzonero parviflorae-Juncetum gerardi* variant with *Glaux maritima*; 6 – *Puccinellietum limosae*; 7 – *Atriplex prostrata* community.

Cluster no.	1	2	3	4	5	6	7
No. of relevés	21	28	8	18	7	12	11
Salicornia europaea	**100** $^{40.6}$	**93** $^{34.8}$	100	39	.	.	20
Tripolium pannonicum subsp. *tripolium*	38	**82** $^{32.5}$	25	72	.	62	20
Spergularia maritima	5	**79** $^{49.9}$	12	33	.	38	10
Suaeda maritima	33	**71** $^{29.6}$	**100** $^{53.8}$	.	.	31	20
Triglochin maritima	.	14	.	**78** $^{42.2}$	**100** $^{61.9}$	.	20
Juncus gerardi	.	21	.	**72** $^{42.0}$	**86** $^{54.4}$	8	.
Glaux maritima	.	.	.	**50** $^{26.8}$	**100** $^{75.7}$	8	.
Plantago major	.	.	.	.	**100** $^{78.9}$	8	40
Schedonorus arundinaceus	5	.	.	33	**71** $^{50.5}$	8	30
Plantago maritima	.	.	.	22	**71** $^{57.6}$	.	30
Carex distans	.	.	.	.	**57** $^{73.0}$	.	.
Agrostis stolonifera	.	.	.	.	**57** $^{52.9}$	15	20
Puccinellia distans agg.	33	64	.	61	.	**100** $^{44.7}$	60
Atriplex prostrata	10	50	62	78	29	**100** $^{32.5}$	100
Elytrigia repens	.	11	.	11	.	8	**50** $^{49.7}$
Juncus compressus	.	4	.	6	.	23	**50** $^{48.5}$
Phragmites australis	19	.	12	50	86	62	.
Alopecurus geniculatus	.	.	.	11	.	.	.
Althaea officinalis	.	.	.	.	.	.	10
Anacamptis palustris	.	.	.	.	29	.	.
Argentina anserina	.	.	.	.	14	.	.
Atriplex littoralis	10	4	.	.	.	.	.
Atriplex patula	.	4	.	.	.	.	.
Atriplex sagittata	14	14	38	.	.	.	.
Halimione pedunctulata	5	29 $^{41.0}$	.	6	.	.	.
Bolboschoenus maritimus agg.	.	4	.	6	29	31	20
Calystegia sepium	.	.	.	.	14	.	.
Carex acutiformis	.	.	.	.	14	.	.
Carex otrubae	.	.	.	.	29	.	.
Oxybasis glauca	.	.	.	.	14	.	30
Oxybasis rubra	.	4	.	.	14	.	10
Dactylis glomerata	.	.	.	.	.	8	.
Daucus carota	.	.	.	.	14	.	.
Drepanocladus aduncus	.	.	.	.	29	.	.
Eleocharis uniglumis	.	.	.	.	29	.	.
Festuca rubra	.	.	.	6	.	.	.
Hordeum jubatum	.	.	.	6	.	.	.
Hordeum secalinum	.	.	.	6	.	.	.
Hornungia pauciflora	.	4	12	.	.	.	.
Juncus articulatus	.	.	.	.	14	.	.
Lepidium ruderale	.	4	.	.	.	.	10
Lolium perenne	.	.	.	.	.	8	.
Lotus tenuis	.	.	.	.	43 $^{62.6}$	.	.
Lythrum salicaria	.	.	.	.	14	.	.
Melilotus dentatus	.	.	.	.	14	.	.
Mentha aquatica	.	.	.	.	29	.	.
Myosurus minimus	.	.	.	.	.	15	.
Polygonum aviculare	.	.	.	6	.	23	30

Cluster no.	1	2	3	4	5	6	7
No. of relevés	21	28	8	18	7	12	11
Ranunculus acris	.	.	.	.	14	.	.
Samolus valerandi	.	.	.	.	14	.	.
Schoenoplectus tabernaemontani	.	.	.	.	29	.	.
Scorzonera parviflora	.	.	.	.	29	.	.
Sonchus arvensis	.	.	.	6	.	.	.
Sonchus palustris	.	.	.	.	14	.	.
Spergularia marina	14	11	62	33	.	46	60
Taraxacum sect. *Palustria*	.	.	.	.	14	.	.
Taraxacum sect. *Ruderalia*	.	.	.	6	.	.	10
Trifolium fragiferum subsp. *fragiferum*	.	.	.	.	43 $^{62.6}$	.	.

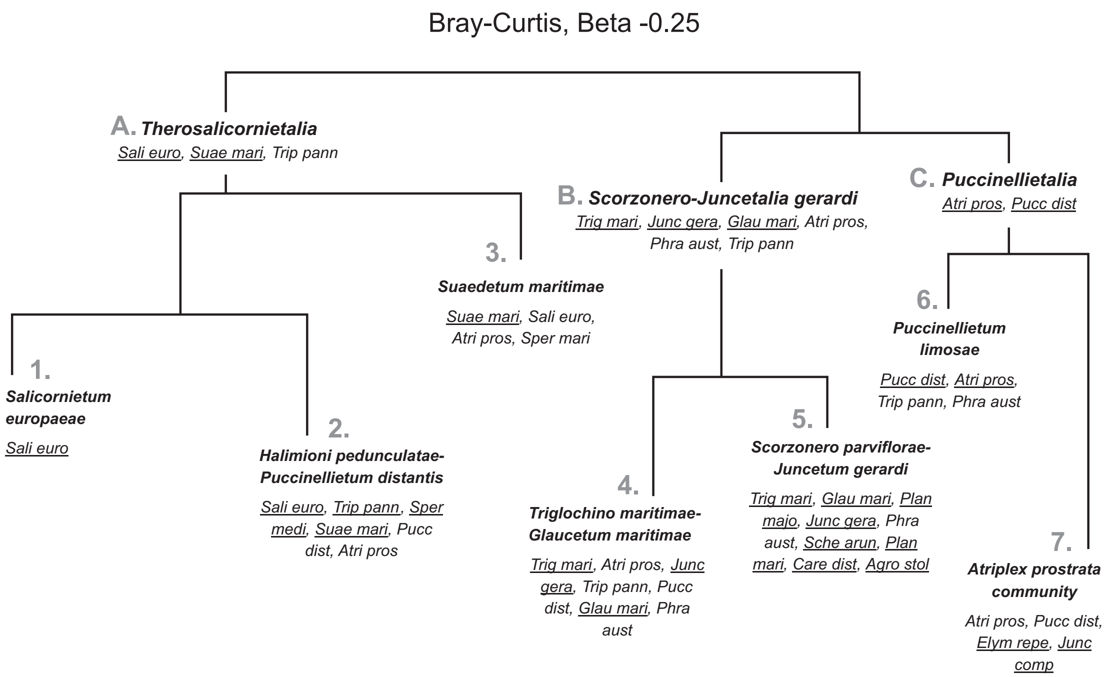


Fig. 2. Classification tree of the cluster analysis. Three higher syntaxa are orders (A, B, C) and seven lower syntaxa are associations (1–7) with abbreviations of their characteristic species. Underlined species are diagnostic, constant and dominant species based on the analysis in JUICE program.

Cluster 1: Association *Salicornietum europaeae* Tüxen 1974

Diagnostic, dominant and constant species: *Salicornia europaea*.

This vegetation is confined to the most extreme abiotic conditions within the salt marsh and has the highest preferences for soil salinity and temperature, and lowest preferences for nutrient content (Fig. 5). *Salicornia europaea* is the main component of these stands, while other species (*Puccinellia distans* or *Tripolium pannonicum* subsp. *tripolium*) occur only sporadically (cover < 1%). Rarely, mostly in man-made habitats, *S. europaea* forms dense species poor stands. These stands, with on average of 70% (35–98%) total

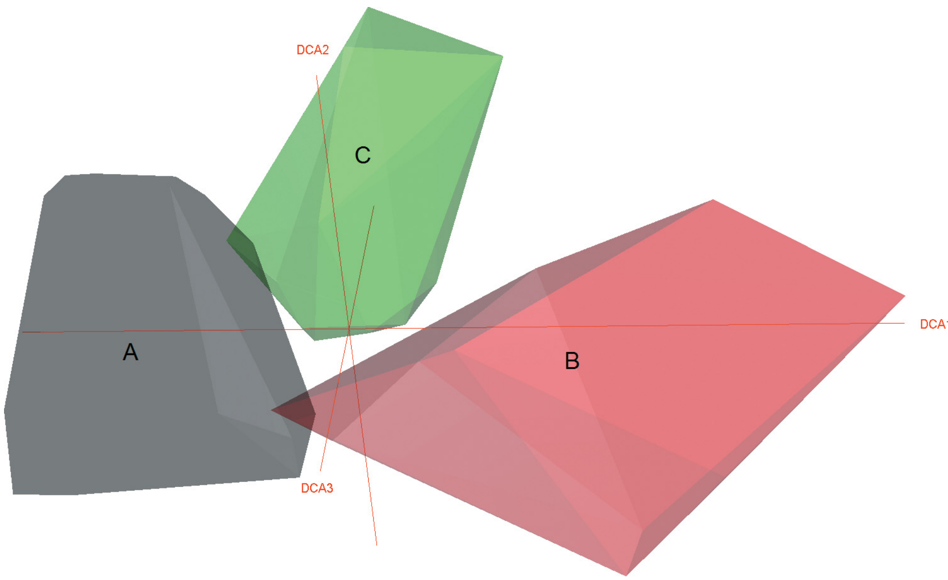


Fig. 3. Relationship between higher syntaxa (orders) in the ordination space of DCA with 3D "Envelopes" visualization. Cluster A – *Therosalicornietalia*, cluster B – *Scorzonero-Juncetalia gerardi*, cluster C – *Puccinellietalia*. The first three eigenvalues are 0.686, 0.333 and 0.259; DCA1 axis length is 5.395, DCA2 axis length 3.567 and DCA3 axis length 2.694.

cover form the inner zone of the salt marsh where the salt groundwater rises. At anthropogenic sites they occur in places with the highest accumulation of salts originating from industrial activities (slag heaps). These salts often create salt efflorescences on the surface of the soil.

Cluster 2: Association *Halimioni pedunculatae-Puccinellietum distantis* Altehage et Roßmann 1939 nom. corr. et nom. invers., subassociation *salicornietosum europaeae* Altehage et Roßmann 1939 nom. corr.

Diagnostic species: *Tripolium pannonicum* subsp. *tripolium*, *Salicornia europaea*, *Spergularia media*, *Suaeda maritima*. – Constant species: *Tripolium pannonicum* subsp. *tripolium*, *Atriplex prostrata*, *Puccinellia distans*, *Salicornia europaea*, *Spergularia media*, *Suaeda maritima*. – Dominant species: *Salicornia europaea*.

These stands have a lower preference for salt content and higher preference for nutrients (Fig. 5) than the vegetation in cluster 1. The species composition is more heterogeneous, the main components are *Salicornia europaea*, less frequently *Suaeda maritima* or *Halimione pedunculata* (Table 1). The total cover of vegetation was higher than 50%. This association was recorded mainly in natural salty habitats, with the most developed in the Sülze river valley (Dodendorf, Sülldorf) in flat salty depressions. It also occurs in secondary habitats contaminated by groundwater from close by heaps of salt (e.g. Kalihalde Teutschenthal or Kleinwirschleben).

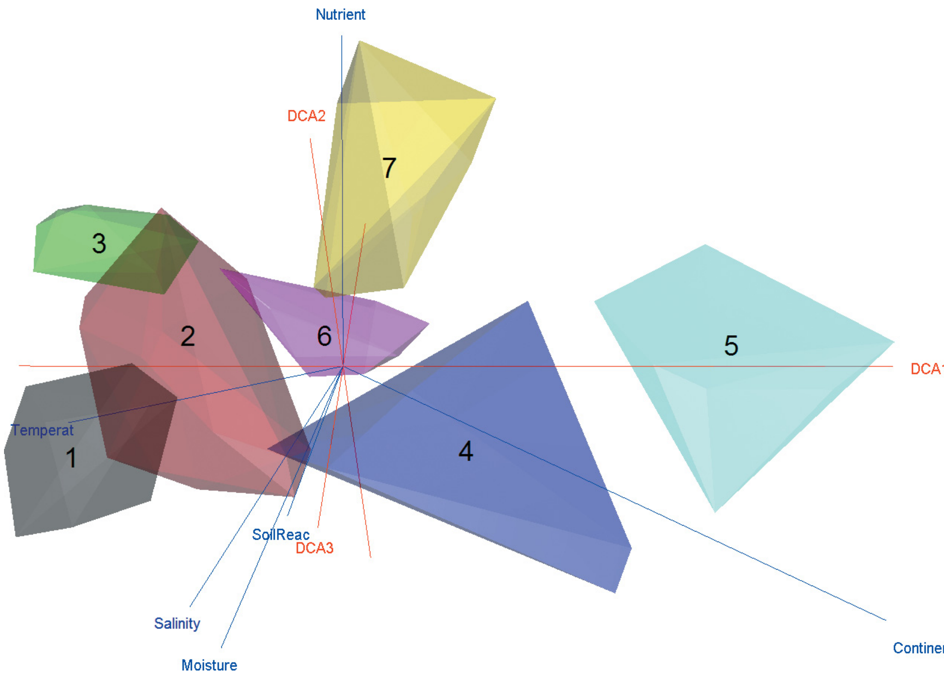


Fig. 4. Relationship between lower syntaxa (associations) in ordination space of DCA with 3D "Envelopes" visualization and displayed Ellenberg indicator values as passive vectors (nutrients, moisture, soil reaction, continentality, temperature, salinity). Cluster 1 – *Salicornietum europaeae*, cluster 2 – *Halimioni pedunculatae-Puccinellietum distantis*, cluster 3 – *Suaedetum maritimae*, cluster 4 – *Triglochino maritimae-Glaucetum maritimae*, cluster 5 – *Scorzonero parviflorae-Juncetum gerardi*, cluster 6 – *Puccinellietum limosae*, cluster 7 – *Atriplex prostrata* community. The first three eigenvalues are 0.686, 0.333 and 0.259; DCA1 axis length is 5.395, DCA2 axis length 3.567 and DCA3 axis length 2.694.

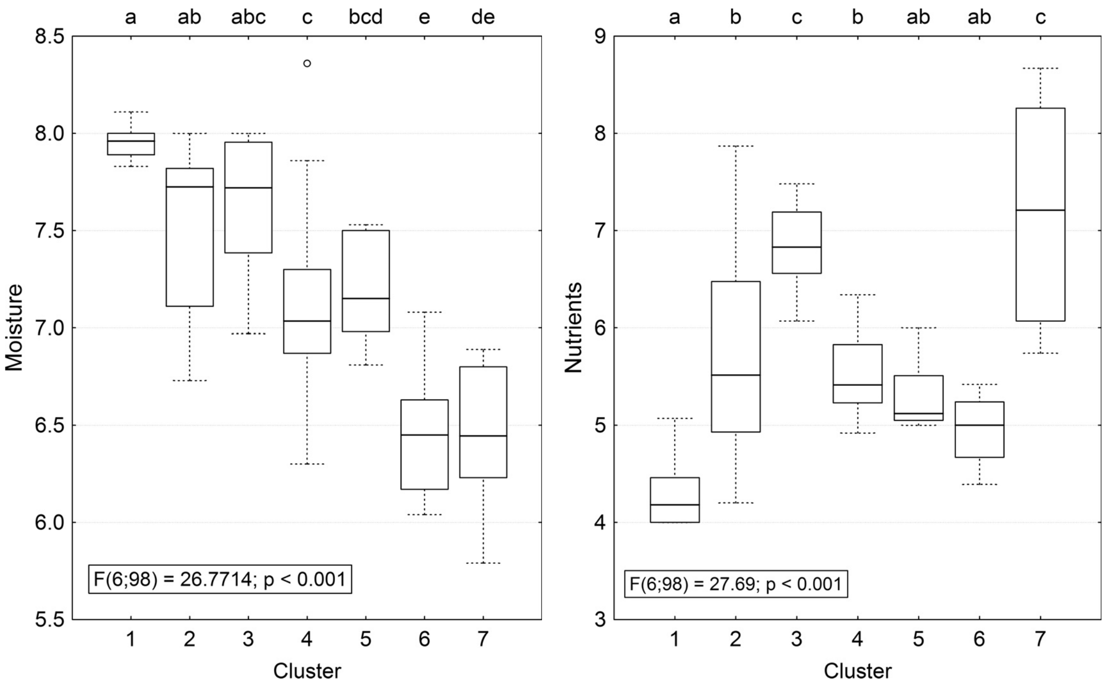
Cluster 3: Association *Suaedetum maritimae* (Conard 1953) Pignatti 1953

Diagnostic species: *Suaeda maritima*. – Constant species: *Atriplex prostrata*, *Salicornia europaea*, *Spergularia marina*, *Suaeda maritima*. – Dominant species: *Suaeda maritima*.

This vegetation occupies the edges of flat depressions. Its preferences for soil salinity and moisture are low, while that for nutrient content is higher (Fig. 5) than that of the neighbouring vegetation clusters 1 and 2. *Suaeda maritima* is dominant, characteristic but less important species are *Salicornia europaea* and *Spergularia marina* (Table 2). We recorded this association at three sites in secondary salt marshes (two around Zielitz, Kalihalde Teutschenthal).

Group B. Class *Festuco-Puccinellietea*, order *Scorzonero-Juncetalia gerardi*, alliance *Juncion gerardi*.

This group of hemicryptophytic tall-herbaceous plants occur in two-layered brackish marshes and prefers less saline and moderately wet soils with a medium nutrient content (Fig. 5). They occur in flat areas affected by shallow inundation in the first half of the growing season, at both primary and secondary salt marsh sites. Clusters 4 and 5 belong here (Table 1, Fig. 4).



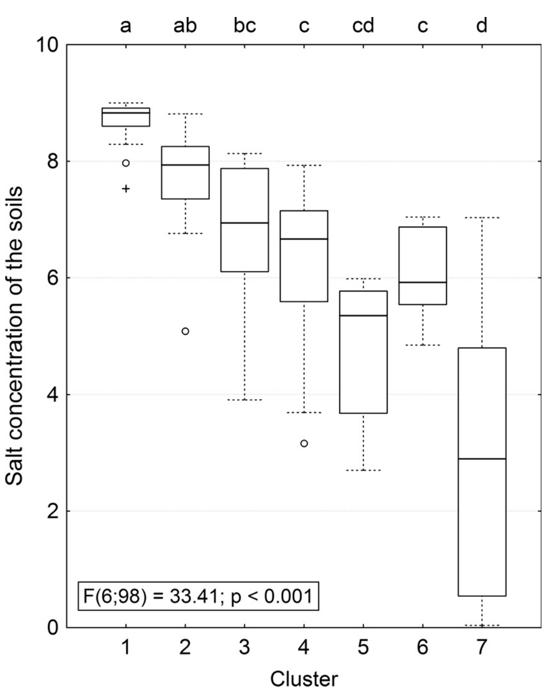


Fig. 5. Differences in Ellenberg indicator values for salinity, moisture and nutrients in the soils of the identified associations. Boxplots show median (bold line), interquartile range (boxes), non-outlier range (whiskers), outliers (empty circles) and extreme values (plus). Statistical significance based on ANOVA. The upper letters (a, b, c, d, e) indicate homogeneous groups according to Tukey's post-hoc test ($\alpha = 0.01$).

Cluster 4: Association *Triglochino maritimae-Glaucetum maritimae* Wilkoń-Michalska ex Dítě et al. ass. nov.

Diagnostic species: *Glaux maritima*, *Juncus gerardi*, *Triglochin maritima*. – Constant species: *Tripolium pannonicum* subsp. *tripolium*, *Atriplex prostrata*, *Glaux maritima*, *Juncus gerardi*, *Phragmites australis*, *Puccinellia distans*, *Triglochin maritima*. – Dominant species: *Triglochin maritima*.

This type of vegetation prefers soils of the highest salinity and moisture with a medium nutrient content of those in group B (Fig. 5). Dense stands (total cover > 80%) of *Triglochin maritima* and/or *Juncus gerardi* dominate, with the most important accompanying species *Puccinellia distans*. This association was recorded in natural salt marshes in the Sülze river valley (Saxony-Anhalt) and along the Werra river (Thuringia) affected by secondary salinization due to industrial activities. It was not found near slag heaps.

Cluster 5: Association *Scorzonero parviflorae-Juncetum gerardi* Wendelberger 1943 nom. cons., var. with *Glaux maritima*

Diagnostic species: *Agrostis stolonifera*, *Carex distans*, *Schedonorus arundinaceus*, *Glaux maritima*, *Juncus gerardi*, *Plantago major*, *Plantago maritima*, *Triglochin maritima*.
Constant species: *Agrostis stolonifera*, *Carex distans*, *Schedonorus arundinaceus*, *Glaux maritima*, *Juncus gerardi*, *Phragmites australis*, *Plantago major*, *Plantago maritima*, *Triglochin maritima*. – Dominant species: *Glaux maritima*.

This type of vegetation prefers moderately wet soils with a lower nutrient content and salinity than the types of vegetation in cluster 4 (Fig. 5). Species number is the highest of the clusters studied (Supplementary Table S2) as the habitat quality was high and the total cover was also the highest (on average 85%). The lower layer in these stands is formed by a carpet of *Glaux maritima* and the upper layer is not dominated by any particular species. It was recorded only in Saxony-Anhalt in natural salt marshes (Aseleben near Seeburg, Sülldorf, Merseburg).

Group C. Class *Festuco-Puccinellietea*, order *Puccinellietalia*, alliance *Puccinellion limosae*

This type of vegetation was also recorded in shallow depressions in the brackish marshes of *Juncion gerardi* described above (group B), but prefers lower moisture (Fig. 5). These desiccating salty patches were usually surrounded by poor mesic meadows dominated by *Elytrigia repens* and *Arrhenatherum elatius*. Clusters 6 and 7 belong here (Fig. 4, Table 1).

Cluster 6: Association *Puccinellietum limosae* Soó 1933

Diagnostic species: *Atriplex prostrata*, *Puccinellia distans*. – Constant species: *Tripolium pannonicum* subsp. *tripolium*, *Atriplex prostrata*, *Phragmites australis*, *Puccinellia distans*. – Dominant species: *Puccinellia distans*.

These species grow in short-grass swards and prefer soils with a high salinity and low nutrient content (Fig. 5). Within this species-poor, sparse vegetation, *Puccinellia distans* is dominant, followed by *Atriplex prostrata*. This community is rare, occurring usually at secondary sites, e.g. near Staßfurt and Merkers in the Bode river valley.

Cluster 7: *Atriplex prostrata* community

Diagnostic species: *Elytrigia repens*, *Juncus compressus*. – Constant species: *Atriplex prostrata*, *Elytrigia repens*, *Juncus compressus*, *Puccinellia distans*, *Spergularia maritima*. – Dominant species: *Atriplex prostrata*.

These stands were recorded on soils with the lowest salinity (Fig. 5), forming transitional stands in the outer belt of depressions in semi-natural mesic grasslands of *Arrhenatheretalia* that are periodically flooded. Salt-tolerant species like *Atriplex prostrata* (dominant with a cover > 75%), *Elytrigia repens* and *Juncus compressus* are typical indicators at ruderal sites. Obligate halophytes occur only marginally (*Puccinellia distans* and *Spergularia marina*), in such cases *Atriplex prostrata* is less abundant (Table 2). These stands are situated between the salt-affected vegetation of *Puccinellietum limosae* and adjacent mesic plant communities. Due to the low representation of halophytes, we do not regard this community as salt marsh vegetation. In some places, the community extends over large areas, e.g. in meadows at Esperstedt near Artern or in subsaline meadows at Tiefenort (both Thuringia). In secondary saline habitats around industrial heaps, this community is very rarely recorded.

Linking our own and published data

Additional analyses of data were carried out in order to determine the position of inland salt marshes on the North German Plain in the context of saline vegetation in temperate Europe. A clear difference was detected between the saline vegetation in inland Germany and that on the Baltic Sea coast (Fig. 6), which indicates inland salt marshes in Germany should not be included in the coastal plant communities of *Juncetea maritimi*, where they are currently classified (comp. Bergmeier 2020).

Further comparison with historical relevés in the *Therosalicornietalia* and *Scorzonero-Juncetalia gerardi* orders also support the continental character of salt marshes on the North German Plain. The relationship between the associations of the annual succulent vegetation (group A) and historical relevés belonging to *Therosalicornietalia* by Altehage & Roßmann (1939) is shown in Fig. 7. The species composition of relevés no. 62–66 (p. 162, Tab. 8 in Altehage & Roßmann l.c.) is in accordance with our records and corresponds to cluster 1, and relevé no. 69–72 (p. 164, Tab. 9 in Altehage & Roßmann l.c.) to cluster 2. *Suaedetum maritimae* (cluster 3) was detected as a distinct type of vegetation.

The similarity of wet saline meadows on the North German Plain and the Pannonian Basin is mentioned in several studies (Weinert 1957, Borhidi et al. 2012). We tested this hypothesis on a subset of our data consisting of relevés from clusters 4 (Table 2, relevés 58–75) and 5 (Table 2, relevés 76–82) from inland Germany. To compare this vegetation with that of other wet saline meadows, we complemented the subset by adding recently published data on the alliance *Juncion gerardi*, association *Scozonero parviflorae-Juncetum gerardi* from the Pannonian and Transylvanian Basins (Dítě et al. 2015, Table 1, relevés 19–60). The results unambiguously confirmed the similarity of the stands of *Juncion gerardi* in these geographical regions (Fig. 8). Stands of cluster 5 overlap with published records of *Scozonero parviflorae-Juncetum gerardi*, while stands of cluster 4 (*Triglochino maritimae-Glaucetum maritimae*) form a different group.

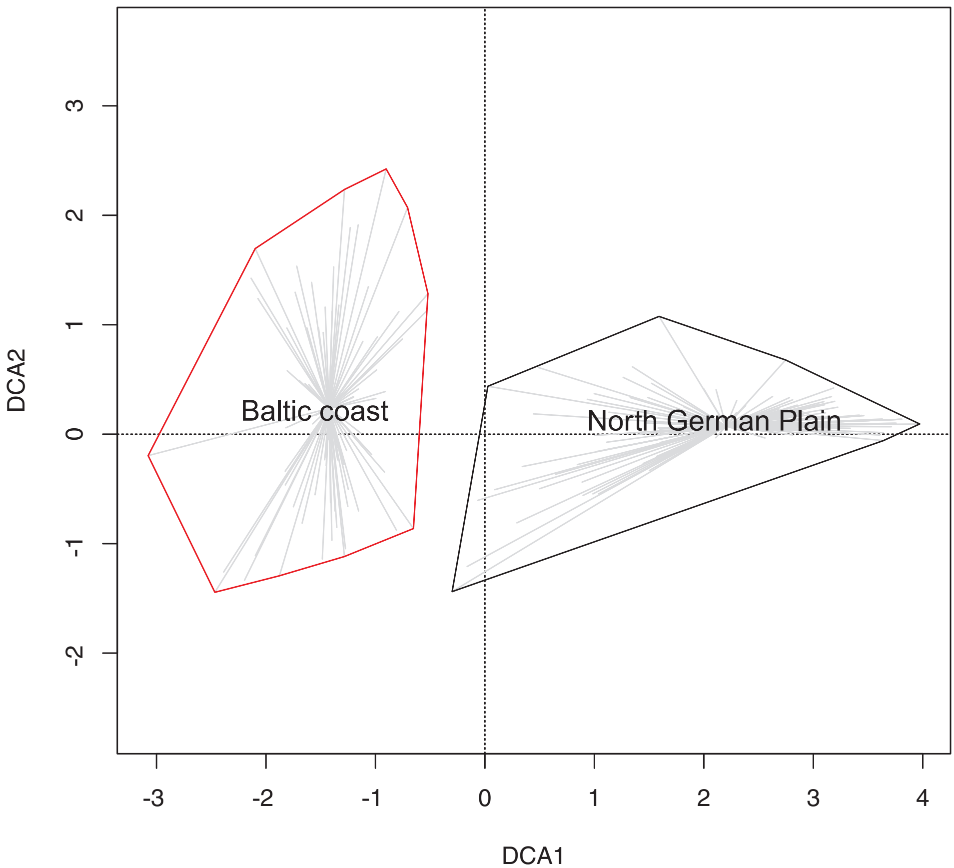


Fig 6. Relationship between 105 relevés recorded in inland Germany by DD and ZD and 78 relevés recorded by RP from the Baltic coast in ordination space of DCA with "Spiderplot" and "Envelopes" visualization. The first two eigenvalues are 0.809 and 0.390; DCA1 axis length is 7.048, and DCA2 axis length 3.867.

Furthermore, we determined whether the relevés of clusters 4 and 5 differed from historical records published for the same area (inland Germany). The dataset contained original relevés of communities named *Triglochin maritimum-Scorzonera parviflora*-Ass. from Altehage & Roßmann (1939): Tab. 10, relevés 76–98 and Zespół *Triglochin maritimum-Glaux maritima* from Wilkoń-Michalska (1963), Tab. 9, relevés 1–20. Two groups of clusters were identified by the DCA (Fig. 9). In the first (left side in ordination space) are our records of *Scorzonero parviflorae-Juncetum gerardi* (cluster 5), fourteen relevés of Altehage & Roßmann (1939): Tab. 10, no. 79, 82, 84–97 and eleven relevés of Wilkoń-Michalska (1963): Tab. 9, no. 1–4, 6–8, 15, 18–20. The second group (the right side of DCA) contains our relevés of *Triglochino maritimae-Glaucetum maritimae* (cluster 4), the remaining relevés from Altehage & Roßmann (1939): Tab. 10, no. 76–78, 80, 81, 83, 98 and the remaining relevés from Wilkoń-Michalska (1963): Tab. 9, no. 5, 9–14, 16, 17.

Finally, the newly identified association in inland Germany (*Scorzonero parviflorae-Juncetum gerardi*) was subjected to a detailed analysis (Fig. 10) of its variability within a larger geographical context than when it was studied previously in the Pannonian and

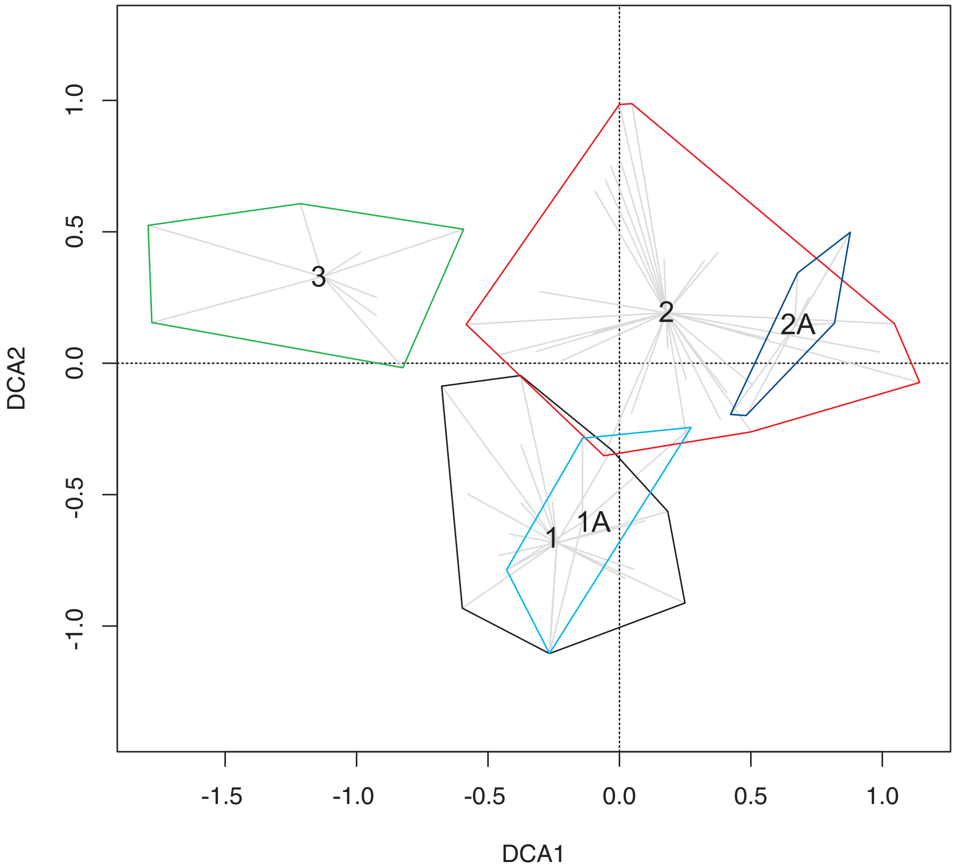


Fig. 7. Relationship between the distinguished associations (clusters) of the annual hypersaline succulent vegetation (class *Therosalicornietea*) and historical relevés of this vegetation in ordination space of DCA with "Spiderplot" and "Envelopes" visualization. Numerals denote centroids of clusters formed by classified relevés. Cluster 1 – *Salicornietum europaeae*, cluster 1A – *Salicornietum europaeae* in Altehage & Roßmann (1939), cluster 2 – *Halimioni pedunculatae-Puccinellietum distantis*, cluster 2A – *Puccinellia distans-Obione pedunculala* Ass. in Altehage & Roßmann (1939), cluster 3 – *Suaedetum maritimae.* The first two eigenvalues are 0.333 and 0.268; DCA1 axis length is 2.935, and DCA2 axis length 2.092.

Transylvanian Basins (Dítě et al. 2015). In the stands on the North German Plain, some Pannonic and continental species are absent (e.g. *Carex divisa*, *Cirsium brachycephalum*) and simultaneously there is a frequent occurrence of *Glaux maritima*, which in the Pannonian and Transylvanian Basins is very rare. This analysis revealed a third, "western" variant of ass. *Scorzonero parviflorae-Juncetum gerardi*, variant with *Glaux maritima*, which is clearly distinct from the variants *typicum* and *Tripolium pannonicum* subsp. *pannonicum* detected by Dítě et al. (2015). Notable is the close proximity of two relevés from Aseleben (no. 76, 77 in Table 2) to the var. with *Tripolium pannonicum* from Pannonia. The stands studied at this site were classified as *Juncus gerardi-Scorzonera parviflora*-Gesellschaft by Weinert (1957). Another site with the border floristic element in Germany (*Scorzonera parviflora*), with a very similar species composition, was recorded near this locality, in Unterröblingen (John & Stolle 2011).

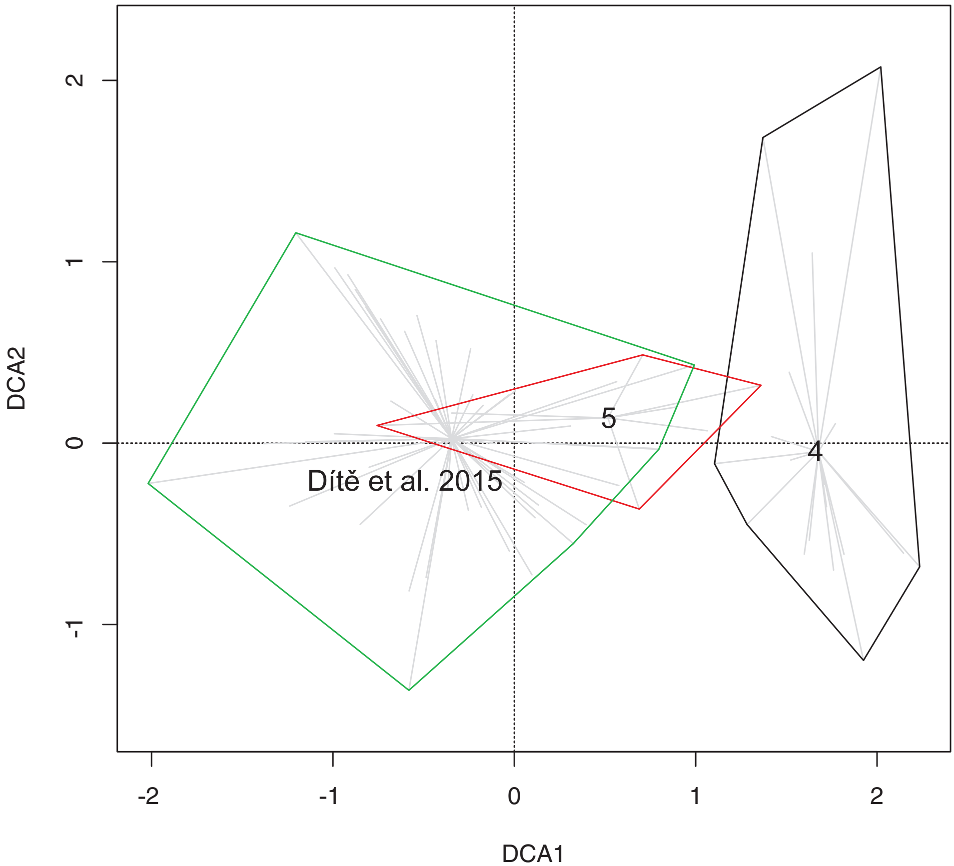


Fig. 8. Relationship between the different associations (clusters) in wet saline meadows (*Juncion gerardi*) and recent relevés of this vegetation in ordination space of DCA with "Spiderplot" end "Envelopes" visualization. Numerals denote centroids of clusters formed by classified relevés. Cluster 4 – *Triglochino maritimae-Glaucetum maritimae*, cluster 5 – *Scorzonero parviflorae-Juncetum gerardi*, cluster "Dítě et al. 2015" – published relevés of *Scorzonero parviflorae-Juncetum gerardi* from the Pannonian and Transylvanian Basins. The first two eigenvalues are 0.537 and 0.298; DCA1 axis length is 4.253, and DCA2 axis length 3.437.

Discussion

Class *Therosalicornietea*, order *Therosalicornietalia*, alliance *Therosalicornion*

Salicornietum europaeae

Pioneer vegetation of annual succulents on hypersaline soils in mainland Germany (Thuringia and Saxony-Anhalt) was studied in detail by Altehage & Roßmann (1939). They describe several associations, e.g. *Salicornietum herbaceae* dominated by *S. herbacea* (spec. coll.). They mention two other taxa (*S. strictissima* and *S. apressa*, p. 161–163), although their phytosociological tables contain only *S. herbacea*. The problematic nomenclature of the *Salicornia* genus was inherited by the nomenclature of plant communities, which we reviewed under note 1 in Supplementary Data S1. Relevés with the

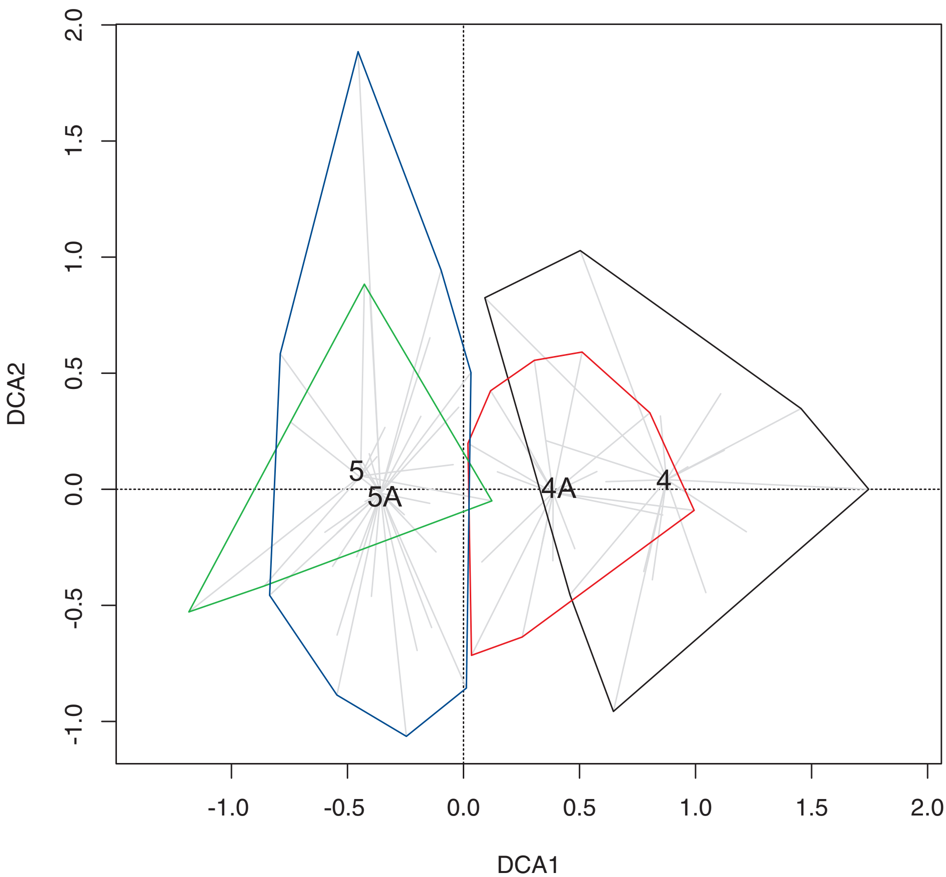


Fig. 9. Relationship between the different associations (clusters) in wet saline meadows (*Juncion gerardi*) and historical relevés published by Altehage & Roßmann (1939) and Wilkoń-Michalska (1963) divided to present the vegetation concept in ordination space of DCA with "Spiderplot" and "Envelopes" visualization. Numerals denote centroids of clusters formed by classified relevés. Cluster 4 – *Triglochino maritimae-Glaucetum maritimae*, cluster 4A – historical relevés assigned by K-means to *Triglochino maritimae-Glaucetum maritimae*, cluster 5 – *Scorzonero parviflorae-Juncetum gerardi*, cluster 5A – historical relevés assigned by K-means to *Scorzonero parviflorae-Juncetum gerardi.* The first two eigenvalues are 0.292 and 0.228; DCA1 axis length is 2.929 and DCA2 axis length 2.949

same vegetation and edaphic conditions, using the taxon name *Salicornia herbacea* var. *patula* and syntaxon name *Salicornietum patulae* Wi. Christiansen 1955 are published from Kujawy (Poland) by Wilkoń-Michalska (1963, p. 70–71, Tab. 5). This community is recorded in both primary and secondary salt marshes, while pure stands are reported occurring around a soda factory. Those stands also correspond to cluster 1 in our study. Regarding recent data on hypersaline vegetation, Piernik (2012) published 43 relevés recorded at Kujawy, Saxony-Anhalt and Thuringia, (Tab. VIII.I). She divides *Salicornia*-dominated vegetation into five types: *Salicornia europaea*-, *Salicornia europaea-Phragmites australis*-, *Salicornia europaea-Triglochin maritimum-Spergularia media*-, *Salicornia europaea-Spergularia salina*- and *Salicornia europaea-Aster tripolium*-community. Each is classified according to the system of Matuszkiewicz (2001) in the

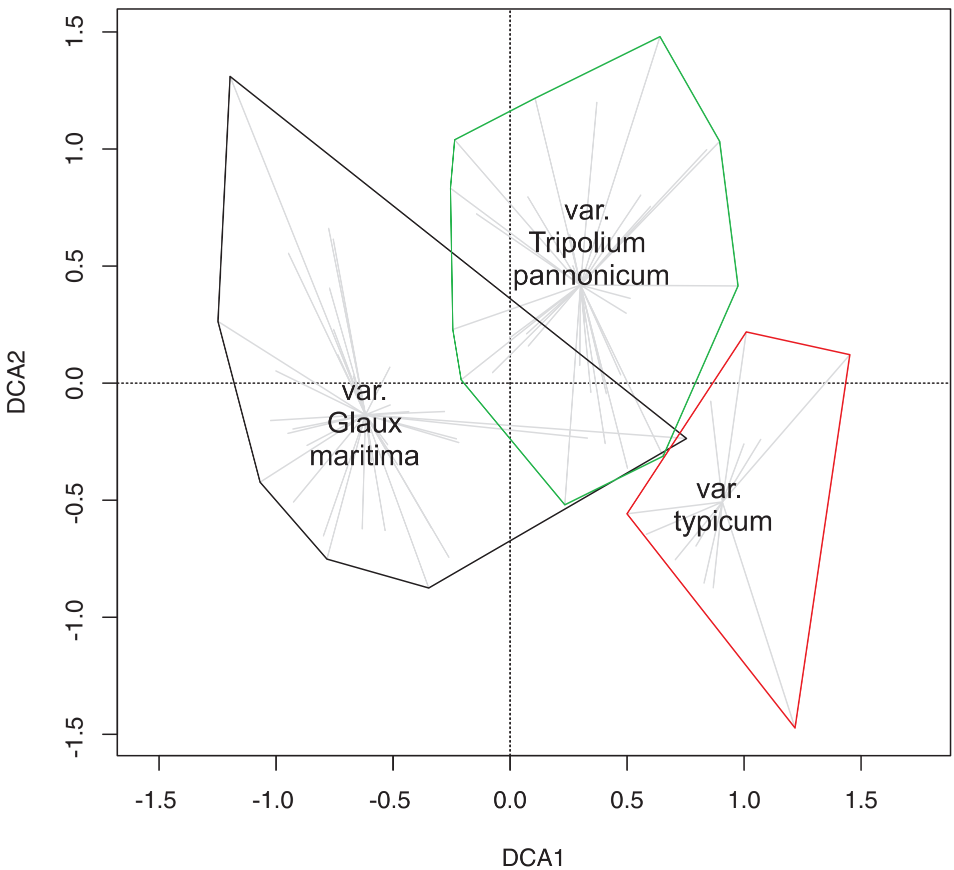


Fig. 10. Relationship between the variants of association *Scorzonero parviflorae-Juncetum gerardi* in ordination space of DCA with "Spiderplot" and "Envelopes" visualization. Numerals denote centroids of clusters formed by classified relevés. Cluster "var. *Glaux maritima*" – relevés of *Scorzonero parviflorae-Juncetum gerardi* recorded by DD and ZD in inland Germany, cluster "var. typicum" – relevés of *Scorzonero parviflorae-Juncetum gerardi* var. typicum in the Pannonian Basin published by Dítě et al. 2015, cluster "var. *Tripolium pannonicum*" – relevés of *Scorzonero parviflorae-Juncetum gerardi* var. with *Tripolium pannonicum* in the Pannonian and Transylvanian Basins published by Dítě et al. 2015. The first two eigenvalues are 0.334 and 0.246; DCA1 axis length is 2.700, and DCA2 axis length 2.953.

association *Puccinellio distantis-Salicornietum brachystachyae* (Wilkoń-Michalska 1963) R. Tx. 1974 and according to the system of Pott (1992) in *Salicornietum ramosissimae* Christiansen 1955. Our data in cluster 1 regarding species composition correspond to the *Salicornia europaea* and *Salicornia europaea-Phragmites australis* communities. The other types listed in this work correspond to cluster 2 in our study.

Halimioni pedunculatae-Puccinellietum distantis

Altehage & Roßmann (1939) describe another association, *Puccinellia distans-Obione pedunculata* Ass. from inland Germany. We assume that this type of vegetation was rare even then, as they record it at only two sites (Numburg, Artern). It was the contact vegetation of *Salicornietum*, occurring on soils with a wider salinity range. Three types were distinguished: (i) on the most saline soils initial species-poor stands with *Salicornia*, subordinate species: *Halimione pedunculata*, *Puccinellia distans*, *Spergularia media*, *Suaeda maritima*, *Tripolium pannonicum* subsp. *tripolium* and *Triglochin maritima*, (ii) at sites at high altitudes with low salinity, the optimal stage of *Puccinellia distans-Obione pedunculata* subassociation with *Salicornia herbacea* where *Puccinellia distans* and *Tripolium pannonicum* subsp. *tripolium* dominate (see Altehage & Roßmann 1939, p. 164, Tab. 9, relevés 69–72); these records are identical with cluster 2 in our analysis (Fig. 7), (iii) on soils with the lowest salinity, they describe a subassociation with *Spergularia salina*, where salt-demanding species are absent. In accordance with the current taxonomic nomenclature and the rules and recommendations of the ICPN, it is necessary to correct the name of the association and subassociation, together with their typification:

Halimioni pedunculatae-Puccinellietum distantis Altehage et Roßmann 1939 nom. mut. nov. et nom. invers. (art. 42, 45)

Original form of the name: *Puccinellia distans-Obione pedunculata*-Ass. (Altehage & Roßmann 1939: 164, Table 9)

Taxonomic sources: Uotila (2011), Creuwels & Pieterse (2021)

Nomenclatural type: Altehage & Roßmann 1939, Table 9, rel. 71, lectotypus hoc loco

All relevés of cluster 2 can be assigned to subass. *salicornietosum europaeae* Altehage et Roßmann 1939 nom. mut. nov. (art. 41b, 45).

Original form of the name: *Obione pedunculata-Puccinellia distans*-Ass., Subass. v. *Salicornia herbacea* (Altehage & Roßmann 1939, Table 9, rels. 69–72).

Nomenclatural type: identical with the type of the association name.

Schubert (2001) presents the available data (p. 231) in a table with constancy values of vegetation corresponding to *Halimioni pedunculatae-Puccinellietum distantis*. He named the vegetation *Salicornietum ramosissimae* Christ. 1955 (syn.: *Salicornietum patulae* Christ. 1955 – *Salicornietum brachystachae* – *Salicornietum europaeae*, incl. *Puccinellio distantis-Salicornietum* R. Tx. 1974). The name *Salicornietum ramosissimae* is the single association name in the *Therosalicornietea* class used in the recent literature on inland salt habitats on the North German Plain. It is assigned to the alliance *Salicornion ramosissimae* R.Tx. 1974 (see the relevant sources in the Introduction). Monocoenoses of *Salicornia* species (clusters 1 and 2) are also the most salt-demanding vegetation in other inland salt marshes in temperate Europe. In the Pannonian Basin, according to the recent European vegetation checklist (Mucina et al. 2016), it is represented by *Salicornia perennans* Willd. (syn. *S. prostrata* Pall., nom. illeg. superfl.). The individual areas of inland salt marshes differ in the commonly used names of the *Salicornia* species and in the commonly used names of the communities with *Salicornia*. In the latest surveys of vegetation on the Pannonian Basin, *Salicornietum prostratae* Soó 1964 is the most frequently used name (e.g. Mucina 1993, Borhidi 2003, Šumberová 2007, Borhidi et al. 2012, Dítě et al. 2017). The same syntaxon is used for the vegetation in Transylvania and on the Black Sea coast in Romania (Pop et al. 2002, Sanda et al. 2008) and in the recently discovered secondary salinas at potash mines in western Ukraine (Woch & Trzcińska-Tacik 2015).

Suaedetum maritimae

Altehage & Roßmann (1939), in their study of hypersaline pioneer vegetation of annual succulent plants, record *Suaeda maritima* at two sites. It is called the *S. maritima* zone, neighbouring stands of *Salicornietum herbaceae* as distinct vegetation at sites at slightly higher altitudes affected by shorter inundations. They compare their findings with published data from the Neusiedl Lake area (Austria) (sec. Bojko 1932) and from the southern part of European Russia (sec. Keller 1928). The ecology of both types of vegetation (*Salicornietum herbaceae*, *S. maritima* zone) is assumed to be similar to that of the salt marshes in inland Germany, despite floristic differences. They also mention the coastal stands of *S. maritima* around the Wadden Sea (Skallingen, Denmark), where *S. maritima* stands are similarly asssociated with low altitude sites with *Salicornia procumbens* (cf. Altehage & Roßmann 1939). From Artern they record vegetation dominated by *S. maritima* (Tab. 8, rel. 66 in Altehage & Roßmann 1939). Due to the low occurrence of a *S. maritima* zone, they did not consider it to be a distinct and separate association and incorporated it in the ass. *Salicornietum herbaceae* (p. 162, 163, Tab. 8). Piernik (2012) published vegetation with *Suaeda maritima* from Germany (Tab. VIII.I, relevés 39–43) under the name *Puccinellia distans-Suaeda maritima-Spergularia media*. *Suaeda maritima* with a cover of up to 25%, and accompanying species *Puccinellia distans*, *Spergularia media* and the glycophytes *Daucus carota*, *Elytrigia repens* or *Schedonorus arundinaceus*. This is indicative of low soil salinity and degradation of the halophytic vegetation and is recorded on salt mine dumps near Beienrode and Hecklingen. In accordance with the system of Matuszkiewicz (2001), she assigns this vegetation to *Puccinellio-Spergularietum salinae* (Feekes 1936) R.Tx. et Volk 1937, alliance *Puccinellion maritimae* (Christiansen 1927) R. Tx. 1937 and according to the system of Pott (1992) to ass. *Spergulario-Puccinellietum distantis* Feekers 1943, alliance *Puccinellio-Spergularion* Beeftink 1965. In both cases, these syntaxa were described from salt marshes on seacoasts.

Although stands with *Suaeda maritima* were present in natural salt marshes in the past (see for instance Altehage & Roßmann 1939), we have not found any other published records for inland salt marshes on the North German Plain identical with *Suaedetum maritimae*. We rarely recorded this species in natural salt marshes, and then with low cover, mostly in the Sülze river valley. Although the occurrence of this association in natural habitats is possible, it is confirmed only in the vicinity of heaps and mineral processing factories. Today, it is the only known halophytic plant community that only occurs in secondary salt marshes. Due to lack of data, we use the name for coastal vegetation with *Suaeda maritima* in the German literature (Rausch 2021): *Suaedetum maritimae* (Conard 1953) Pignatti 1953. Vegetation dominated by *S. maritima* in inland salt marshes in temperate Europe requires further study.

Suaedetum maritimae as a distinct type of vegetation of the class *Therosalicornietea* and alliance *Therosalicornion* (cluster 3 in our results) was also confirmed when we compared our data with the data published by Altehage & Roßmann 1939 (Fig. 7). As in the case of vegetation with *Salicornia herbaceae* (clusters 1 and 2), the association *Suaedetum maritimae* in inland Germany is similar to vegetation with *Suaeda prostrata* (and partially *S. pannonica*) in inland salt marshes in other regions in temperate Europe. Despite the fact that both *S. prostrata* and *S. maritima* are valid names (Euro+Med 2021), the name *Suaeda maritima* has been inconsistently used in both historical and recent studies (for several examples from the Pannonian Basin and from coastal marshes of the Wadden Sea see note 2 in Supplementary Data S1).

Class *Festuco-Puccinellietea*, order *Scorzonero-Juncetalia gerardi*, alliance *Juncion gerardi*

While the hypersaline vegetation of succulent halophytes occurs in small patches in salt-affected habitats, brackish meadows and marshes (clusters 4 and 5), they cover larger areas. At some localities with an overall low soil salinity, it is often the only type of salt marsh vegetation present. Although it is species-poor (despite being the richest type of salt marsh vegetation on the North German Plain) and relatively homogeneous, several associations have been described. Altehage & Roßmann (1939) published relevés from Saxony-Anhalt and Thuringia with dominant species *Glaux maritima*, *Juncus gerardi*, *Plantago maritima*, *Triglochin maritima*, *Tripolium pannonicum* subsp. *tripolium* and named this vegetation *Triglochin maritima-Scorzonera parviflora*-Ass. In addition to the subass. *typicum*, they describe two variants of the subass. with *Phragmites communis* (var. *Drepanocladus aduncus* and var. *Trifolium fragiferum* (p. 168–169, Tab. 10) on waterlogged, less saline soils with a prevalence of glycophytes.

Scorzonera parviflora, one of the characteristic species of *Juncion gerardi* (Borhidi et al. 2012) is extremely rare in inland Germany where it is at the north-western limit of its distribution (Meusel & Jäger 1992) and has been historically confirmed at about five localities (Weinert 1957, Knapp et al. 1978, Barthel & Pusch 1993, John 1994, Hartenauer et al. 2012). The authors emphasize the continentality of these stands by putting the name of this species in the association name. They note a closer relationship with inland solonchak meadows in the Pannonian region than to brackish vegetation on the sea coast. Weinert (1957) reports the communities *Juncus gerardi-Scorzonera parviflora*-Gesellschaft and *Juncus gerardi-Scorzonera parviflora*-Geselschaft faz. v *Plantago maritima* in meadows around lake Süßer See (Aseleben, Saxony-Anhalt). He also highlights the peculiar species composition of this community, which is indicative of the overall continental character of salt marshes in inland Germany.

Wilkoń-Michalska (1963) described the community *Triglochin maritimum-Glaux maritima* zespół occurring in inland salt meadows in Poland. She notes it is very similar to *Armerietum maritimae* (W. Christiansen 1927) Br.-BI. et de Leeuw 1936 in the alliance *Armerion maritimae* Br.-Bl. et de Leeuw 1936, which is species-poor brackish vegetation on the North Sea coast. Its easternmost limit to its distribution is the German Baltic coast, where it is also known as *Festucetum rubrae littoralis* Tüxen 1937. On the Polish Baltic coast, the characteristic species composition of this alliance/association (e.g. *Armeria maritima*, *Parapholis filiformis*, *Artemisia maritima* and *Cochlearia danica)* and other Atlantic species occur only marginally (cf. Wilkoń-Michalska 1963). Despite that, based on the presence of other typical species such as *T. maritima*, *G. maritima*, *J. gerardi* and *T. pannonicum* subsp. *tripolium*, this community is included in *Armerion maritimae*.

In a recent survey of European habitats (Janssen et al. 2016), temperate inland salt marshes to which these sites belong are also classified as *Puccinellion maritimae* and *Armerion maritimae*.

Wilkoń-Michalska (1963) compared *Triglochin maritimum-Glaux maritima* with four communities from different geographical regions: *Artemisietum maritimi* (sea coasts), *Triglochin maritima-Scorzonera parviflora* (Saxony-Anhalt, Thuringia), *Juncus gerardi-Scorzonera parviflora* (Neusiedler See, Pannonia) and *Astereto-Triglochinetum* Soó 1947 (Transylvania). For details see note 3 in Supplementary Data S1.

In the area of the degraded lake Salziger See (Saxony-Anhalt) Weinert (1989) reports the occurrence of *Juncus gerardi*, *Puccinellia distans*, *Spergularia marina* and *Tripolium pannonicum* subsp. *tripolium*, which according to this author are indicators of secondary saline vegetation and are characteristic species of the association *Astero-Puccinellietum distantis* Weinert 56 ms. emend. Weinert 89 (syn.: *Puccinellia distans-Aster tripolium*-Ass. Weinert 56 ms., S. 63, *Astero-Puccinellietum distantis* Weinert in Rothmaler, Schubert, Vent 1976). He analysed twelve historical relevés (Table 1, p. 224–225) with heterogeneous vegetation, in which the constant species are *T. pannonicum* subsp. *tripolium* and *P. distans* accompanied by species with a wide variety of ecological preferences.

Alliance Juncion gerardi on the North German Plain, syntaxonomical treatment

Additional synthesis (Figs 8, 9) revealed a strong relationship between salt meadows and brackish marshes on the North German Plain and in the Pannonian Basin. These findings raised several unresolved syntaxonomical issues. Based on a comparison of certain records of the association *Triglochin maritimum-Scorzonera parviflora* Altehage & Roßmann (1939), including the nomenclatural type (see below), with our records of the association *Scorzonero parviflorae-Juncetum gerardi* (see Fig. 9, left) we merged them into one association (according to art. 25 of the ICPN). For this association the earlier published valid name should be used (= *Scorzonero parviflorae-Triglochinetum maritimi* Altehage & Roßmann 1939 nom. invers.). OFN: *Triglochin maritima-Scorzonera parviflora*-Ass. (Altehage & Roßmann 1939: 68, Table 10).

Nomenclatural type: Altehage & Roßmann 1939, Table 10, rel. 91, lectotypus hoc loco.

Since the name *Scorzonero parviflorae-Juncetum gerardi* has been conventionally used for a long time, we propose to retain this name according to Art. 52 (Theurillat et al. 2021): *Scorzonero parviflorae-Juncetum gerardi* Wendelberger 1943 nom. cons. When merging the remaining records of the *Triglochin maritimum-Scorzonera parviflora*-Ass. Altehage et Rossmann 1939 and Zespół *Triglochin maritimum-Glaux maritima* Wilkoń-Michalska (1963) with our records of cluster 5 (Fig. 9, right), none of the original names can be used for two reasons (Art. 25): (i) The association name *Scorzonero parviflorae-Triglochinetum maritimi* after syntaxonomic revision is a syntaxonomical synonym of the association *Scorzonero parviflorae-Juncetum gerardi* (see above). Moreover, none of the remaining relevés contain the name-giving taxon *Scorzonera parviflora* (Art. 3f). (ii) The Zespół *Triglochin maritimum-Glaux maritima* Wilkoń-Michalska (1963) was described without validation (Art. 3c). Although in several later works (mostly Polish) it appears in association rank as *Triglochino-Glaucetum maritimae* Wilkoń-Michalska 1963 (Matuszkiewicz 2001), this name has not yet been validated according to Art.6. After validation, it is named as follows:

***Triglochino maritimae-Glaucetum maritimae* Wilkoń-Michalska ex Dítě et al. ass. nov.**

OFN: Zespół *Triglochin maritimum-Glaux maritima* (Wilkoń-Michalska 1963, p. 86 & Table 9) (Art. 3c).
Nomenclatural type: Wilkoń-Michalska 1963, Table 9, rel. 10, holotypus.
Syn.: *Triglochin maritimum-Scorzonera parviflora*-Ass. Altehage & Rossmann 1939 p. p. (excl. typus)

Both the associations *Triglochino maritimae-Glaucetum maritimae* and *Scorzonero parviflorae-Juncetum gerardi* form part of the inland salt meadow vegetation of the *Juncion gerardi* alliance. Its range extends from Central Asia through southern Russia and Ukraine (Golub et al. 2003) westwards to the Transylvanian (Dítě et al. 2021a) and Pannonian Basins (Wendelberger 1943, 1950). Central Germany is at the westernmost border of the alliance *Juncion gerardi*, and also of the supposed association *Scorzonero parviflorae-Juncetum gerardi* (Borhidi 2003, Borhidi et al. 2012). The results of our synthesis (Fig. 8, 9) confirmed the presence of these two associations on the North German Plain, which considerably extends the distribution of the *Juncion gerardi* alliance to the west.

Class *Festuco-Puccinellietea*, order *Puccinellietalia*, alliance *Puccinellion limosae*

Puccinellietum limosae

Short-grass saline swards occurring on the North German Plain are often included in the association *Spergulario-Puccinellietum distantis* Feek (1934) 1943, alliance *Puccinellio-Spergularion* Beefting 1965, units of which are described from coastal habitats. For syntaxonomical notes, see Supplementary Data S1, note 4. Data on this vegetation are sparse compared to the previous types of vegetation. The stands in inland Germany are characterized by a high abundance of *Atriplex prostrata*, which is the diagnostic species of *Puccinellia*-swards in South Moravia (Šumberová et al. 2007), which is on the NW border of the Pannonian Basin. In the main part of the Pannonian Basin, the diagnostic value of *A. prostrata* is lower and it is more common in ruderal vegetation on slightly salt-affected soils. *Atriplex littoralis*, another halophyte more characteristic of the *Puccinellia*-swards on disturbed saline soils in Pannonia/Transylvania (Borhidi et al. 2012), is very rare in inland Germany: we confirmed its presence at only one site (Dippach in Thuringia). Several other Pannonian and continental species are missing from inland salt marshes in Germany as their geographical range does not extend as far as the North German Plain. Their absence is not relevant as these species are not characteristic of the association *Puccinellietum limosae*, but come via contact with zones of vegetation of other associations of the alliance *Puccinellion limosae* (Dítě et al. 2014), for instance, *Camphorosma annua* (as. *Camphorosmetum annuae* Soó 1930), *Pholiurus pannonicus*, *Plantago tenuiflora* (as. *Plantagini tenuiflorae-Pholiuretum pannonici* Wendelberger 1943) and *Hordeum geniculatum* (as. *Hordeetum hystricis* Wendelberger 1950). Considering the common features and differences listed above, the typical species composition of *Puccinellia*-swards on the North Germna Plain do not substantially differ from stands in the Pannonian and Transylvanian Basins. We suggest including these stands in the ass. *Puccinellietum limosae* Soó 1933 (alliance *Puccinellion limosae*).

In the Pannonian Basin, *Puccinellia*-swards are most typically found in shallow depressions with a fluctuating water regime and high soil salinity (Vicherek 1973, Borhidi 2003) or in littoral zone of salty lakes (Dítě et al. 2017) and they also occupy degraded (ploughed) salty soils. At relatively well-preserved sites, vast monocoenoses of *Puccinellia distans* agg. are typical (e.g. Hortobágy, Kiskunság in Hungary, Vojvodina in Serbia) with subordinate species *Tripolium pannonicum* subsp. *pannonicum*, *Spergularia marina* and *S. media*. Stands recorded in inland Germany are most closely related to the subassociation *spergularietosum marginatae* described from South Moravia (Czech Republic) by Vicherek (1973). It occupies flat periodically flooded depressions and secondary salinized areas affected by trampling.

Atriplex prostrata community

It occurs in the outer zone of the least salt-affected areas within salt marshes where they transform into semi-natural mesic grasslands and are not as intensively studied as the previous types of vegetation. There are a few relevés published by Krisch (1967) from subsaline meadows of secondary origin in the Werra-river valley (Merkers and Dorndorf) under the name *Atriplex hastata*-Gesellschaft (Tab. VII, No. 268–271). These records are similar to the vegetation in our cluster 7. The author reports massive germination of *Atriplex prostrata* in all halophytic habitats during the first half of the growing season, but the majority of them dessicate later. Piernik (2012) reports from the Kujawy region the following types of vegetation: *Spergularia salina*-*Elymus repens* and *Atriplex prostrata* ssp. *prostrata* var. *salina* (p. 126, Table IX.I). This vegetation has similar ecology to the community *Atriplicetum prostratae* Wenzl 1934 corr. Gutermann et Mucina 1993 (alliance *Cypero-Spergularion salinae*, class *Crypsietea aculeatae*). Both develop in depressions flooded in spring on moderately saline soils where the dominant species is *Atriplex prostrata*. In the Pannonian Basin it is typical of the nitrogen-rich moderately salt-affected soils with the accompanying species *Tripolium pannonicum* subsp. *pannonicum* or *Suaeda pannonica*. These periodically flooded stands are closely related to the association *Bidenti frondosae-Atriplicetum prostratae* Poli et J. Tüxen 1960 corr. Gutermann et Mucina 1993 belonging to the class *Bidentetea tripartitae* Tüxen et al. ex von Rochow 1951; for a more detailed classification further study is required. We consider the stands recorded in inland Germany to be an instance of a degraded stage of *Puccinellietum limosae* transforming into ruderal-mesic meadows with decreased soil salinity.

Conclusions

The vegetation of *Juncion gerardii* and *Puccinellion limosae* on the North German Plain are very similar to the continental salt marshes in the Pannonian and Transylvanian Basins and very different from the Baltic coastal meadows. Based on these findings, we suggest including them into the syntaxonomical class of continental halophytic vegetation of *Festuco-Puccinellietea.* They are at the northernmost limit of inland saline vegetation and extend from eastern Europe to Central Asia. In addition to the phytosociological viewpoint the re-classification is supported by the environmental conditions. Soil salinity and moisture are crucial ecological factors in both coastal and inland salt habitats, but coastal salt marshes are subject to seawater inundation, whereas the salt in inland salt marshes comes from geological sources (Veldkornet et al. 2015). Coastal and inland saline vegetation has a number of species in common (see for instance the distribution maps in Meusel & Jäger 1992) with ecological optima both at the coast and inland, therefore some vegetation units are also identical (e.g. *Puccinellietum limosae*, *Scorzonero parviflorae-Juncetum gerardi*). Coastal saline habitats include also plants with a solely coastal distribution range: *Limonium vulgare*, *Parapholis strigosa*, *Puccinellia maritima* (Pätsch et al. 2019b), although some of them may very rarely occur inland in limited numbers or at single localities: *Carex extensa* (Király et al. 2013) and *Linum maritimum* in the Pannonian Basin (http://burgenlandflora.at/pflanzenart/linum-maritimum/) and *Artemisia maritima* in central Germany. Several species that occur mainly on the coasts, on the North German Plain are not true coastal species (e.g. *Halimione pedunctulata*, *Blysmus rufus*), as their main distribution is in continental parts of Eurasia (Meusel & Jäger 1992). Therefore, the occurrence of these species in inland salt marshes does not indicate coastal plant communities.

Supplementary materials

Table S1. – Values of the bioclimatic variables for 109 relevés from a set of global climate layers WorldClim2.
Table S2. – Table of phytosociological relevés recorded in inland salt marshes in Germany.
Table S3. – Table of phytosociological relevés recorded on the Baltic Sea coast.
Data S1. – Syntaxonomical notes containing information, which supplements that in the Discussion.
Data S2. – List of localities of phytosociological relevés recorded in inland salt marshes in Germany.

Supplementary materials are available at www.preslia.cz

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Vegetace vnitrozemských slanišť na jejich severozápadní hranici v Severoněmecké nížině

Vnitrozemské slané louky jsou prioritním stanovištěm evropského významu, v současnosti jsou však ohrožena intenzivním využíváním krajiny a narušováním jejich vodního režimu. Poloha v Severoněmecké nížině jako nejzápadnějším výskytu kontinentální slanomilné vegetace v Eurasii jim dává zvláštní biogeografický význam. Navzdory dlouhému floristickému výzkumu existuje relativně málo studií zabývajících se jejich rostlinnými společenstvy. Vegetace slaných luk této oblasti je tradičně zařazena svazů *Puccinellion maritimae* a *Armerion maritimae*, které jsou rozšířeny podél pobřeží Severního a Baltského moře, a jejich podobnost s vnitrozemskými slaništi byla dosud přehlížena. V letech 2018 a 2020 jsme zkoumali přirozené a sekundární lokality vnitrozemských slanišť ve středním Německu (Sasko-Anhaltsko a Durynsko). Analýza 105 fytocenologických snímků identifikovala tři hlavní skupiny (svazy), obsahující sedm asociací: jednoletá sukulentní společenstva svazu *Therosalicornion* (*Salicornietum europaeae*, *Halimioni pedunculatae-Puccinellietum distantis*, *Suaedetum maritimae*), vlhké slané louky svazu *Juncion gerardi* (*Triglochino maritimae-Glaucetum maritimae*, *Scorzonero parviflorae-Juncetum gerardi*, varianta s *Glaux maritima*) a krátkostébelné trávníky svazu *Puccinellion limosae* (*Puccinellietum limosae*, společenstvo s *Atriplex prostrata*). Pro každou asociaci jsme definovali charakteristické druhové složení a vypočítali hodnoty Ellenbergových indikačních hodnot pro vlhkost a obsahu solí a živin v půdě. Vegetaci studované oblasti jsme porovnali s historickými a recentními údaji o slanomilné vegetaci jiných oblastí: jižní pobřeží Baltského moře, Kujawy (Polsko), Panonská pánev (Maďarsko) a Transylvánská pánev (Rumunsko). Slaniště vnitrozemského Německa vykazovala bližší vztah ke slaništím odlehlé Panonské a Transylvánské pánve a byla dobře oddělena od pobřežních slaných luk Pobaltí. Vnitrozemské slané louky Severoněmecké nížiny navrhujeme přeřadit do syntaxonomické třídy kontinentální halofytní vegetace *Festuco-Puccinellietea*.

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