Preslia 95: 215–240, 2023
doi: 10.23855/preslia.2023.215

Preslia

Inventory of the halophytes in inland central Europe

Daniel Dítě[1], Róbert Šuvada[2], Tibor Tóth[3] & Zuzana Dítě[1,*]

[1]Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Dúbravská cesta 9, SK-84523 Bratislava, Slovakia; [2]Administration of the Slovenský kras National Park, Hámosiho 188, SK-04951 Brzotín, Slovakia; [3]Institute for Soil Sciences, Centre for Agricultural Research, Herman Ottó út 15, H-1022 Budapest, Hungary.
[*]corresponding author: zuzana.dite@savba.sk

Abstract: There is a long tradition in Europe of assigning ecological indicator values to plants and using these values in ecological research. A special case is that of the salt-tolerant species. Saline soils are extremely heterogeneous and their physical and chemical properties vary significantly with microrelief and between alternating dry/wet seasons. The complexity of such soils suggests using salt indicator values. This study resulted in the first multi-country database of vascular plants occurring in inland salt marshes and on salt steppes in temperate Europe based on expert revision of the literature and field experience. The inventory of the 190 salt-tolerant species was carried out according to their quantitative representation in saline and non-saline habitats. These species were each classified into one of three categories of salt tolerance (obligate halophytes, facultative halophytes, accessory/associated species) assigned salt numbers on a nine-point scale reflecting their individual preference for soil salinity based on their calculated halophytic value. Saline soils are reliably indicated by the presence of obligate halophytes; these specialists grow exclusively in natural saline habitats. Only 45 species are assigned to this group, while 61 species make up the group of facultative halophytes and 84 are accessory species with a wide ecological niche, occurring more or less accidentally in saline habitats. Their number is likely to increase since every plant (non-halophyte) recorded in a saline habitat can be considered to be an accessory species. The obtained salt numbers showed a close consistency with the recently used salinity indicator values estimated by Ellenberg, Borhidi and Breckle; in terms of categories of salt tolerance, only slight differences were detected.

Keywords: bioindication system for soil salinity, ecological preferences, facultative halophytes, habitat specialists, obligate halophytes, supranational classification

Introduction

Salt-tolerant plants are a specific group of organisms well adapted to complete their life cycle on saline substrates (Koyro et al. 2009). Saline habitats occur naturally worldwide, particularly in saltwater-affected coastal areas. In inland regions, they are distributed irregularly, most notably in arid and semiarid zones (Chapman 1960, Szabolcs 1974). In Europe, they cover a broad area west of the Caspian Sea and north of the Black Sea (Golub 1995), occurring in central Europe mainly in the Pannonian Lowland (Molnár & Borhidi 2003) and the North German Plain (Piernik 2012, Dítě et al. 2022b). A specific

Received: 31 Mar 2022; Revised: 1 Nov 2022; Accepted: 4 Jan 2023; Published: 5 Jun 2023

type of saline habitat is found adjacent to springs or seeps fed by brine from fossil salt deposits, e.g. in the Transylvanian Basin (Dítě et al. 2021a).

Salt-tolerant plants belong to the group of extremophytes that thrive in seemingly unsuitable habitats and are of considerable interest due to their evolutionary adaptation to the great abiotic stress associated with the environments they occupy. As with the academic interest in the origin, development and distribution of saline soils, the knowledge of salt-tolerant plants progressively increased in terms of their plant communities and ecological preferences. Their physiological capacity to adapt to the saline environment has been studied in great detail (e.g. Volkmar et al. 1998). In recent decades, there has been an increase in the interest in salt-tolerant plants as food and medicinal plants (e.g. Ventura et al. 2015). With the increasing focus on the flora and vegetation of salt-affected habitats, it became necessary to define species associated with saline soils. Grigore (2012) presents a chronological list of the definitions of the term "halophyte". The earliest of the 44 definitions dates back to Crozier (1892): "A plant containing a large quantity of common salt in its composition, and which thrives best in salty places". Clements (1907) defines the term succinctly as "species of saline and alkaline soils" (salt plants). The most recent definitions of these plants are as follows: "plants of saline habitats" (Holzapfel 2009) and "plants that tolerate excessive salt" (Quinn 2009). Physiological definitions of halophytes are based on an established concentration threshold limit value that separates glycophytes from halophytes.

With the increase in the knowledge of halophytes, various databases were established to store a diverse set of traits essential for agriculture, bioremediation and ecological restoration. Global estimates of halophytic plants today range between 350 and 2,600 taxa, and around 2% of all angiosperms are classified as halophytes (https://extremeplants.org/modelsystem/halophytes/#tabs-465-0-1). A comprehensive global database, eHALOPH, includes 1,554 species for which evidence of salt tolerance exists (Santos et al. 2016). The recent list compiled by Flowers & Colmer (2008) includes halophytes described as plants that can complete their life cycle in a salt concentration of at least 200 mM NaCl.

Plants that grow in saline soils in central-eastern Europe are classified most intensively in Romania where natural saline habitats are widespread; the first attempt was made by Prodan (1922), who later presented the findings in an extended form (Prodan 1939). He divided the species into three categories according to their affinity with saline soils: (I) obligate halophytes, (II) facultative halophytes, and (III) species tolerant of salinity. Similar categories were defined in Slovakia and Czech Republic by Krist (1940) and later Šmarda (1953), and in central Poland by Wilkoń-Michalska (1963). In western Europe, Iversen (1936) accurately defined four categories: obligate halophytes as species that need salt to thrive (physiologically based) or those that occur exclusively on saline soils (ecologically based), optional halophytes that have their optimum on saline soils but also occasionally occur on non-saline soils, accidental halophytes as species that may occur on saline soils, and glycophytes (non-halophytes) that avoid saline soils. Grigore & Cojocariu (2021) studied all the halophyte classifications and collated and reviewed 215 species that occur in Romania.

In addition to the plants' relation to soil salinity, halophytes are frequently grouped arbitrarily based on numerical salinity threshold values (Grigore 2021). In central Europe, the most widespread system used by vegetation scientists is that devised by Heinz Ellenberg (Ellenberg et al. 1991). It is based on estimations of ecological indicator values for particular species growing in central/western Europe (light, temperature, moisture, soil reaction, nutrients, salinity and continentality), which was recently adapted for use with the whole European flora by Tichý et al. (2023). Salt preference of plants is evaluated by their tolerance for chloride levels in the soil, ranging from (–0.1) 0.05 to 2.3% Cl. The unique indices scaled from 0 to 9 (S-values) are based on the review of Scherfose (1990) carried out in coastal salt habitats in Germany. His scale originates from chloride ranges in which the plants grow best under field conditions (ecological optimum). Inland salt-affected soils have different ionic composition; they are sodic (alkali), with carbonates, bicarbonates and sulphates (Na_2CO_3, $NaHCO_3$, Na_2SO_4, and $MgSO_4$) predominating, whereas the NaCl content in central-European saline habitats has a marginal role (Leuschner & Ellenberg 2017). However, for this inland area, the indicator values originate also from Ellenberg et al. (1991), and the salt scale from Scherfose (1990), e.g. in the Hungarian flora as the relative ecological indicator value SB (Borhidi 1995), in the flora of the Czech Republic (PLADIAS), as modified by Chytrý et al. (2018) or in the Romanian flora (Sârbu et al. 2013). An initial version of the salt index figure on a scale of 1–9 used in Romania by Breckle (1985) considers exclusively halophytes, has not been applied in the European flora, but is used in plant ecology research in Central Asia (e.g. Breckle & Wucherer 2012).

There is a disadvantage to determining the ecological indicator values by direct measurement of soil salinity as it significantly fluctuates throughout the growing season (Ungar 1974) and is dependent on the depth of the soil profile (Hütterer & Albert 1993). Due to the considerable temporal and horizontal variation, a bioindication system using plants may compensate for the unavailable exact values. An alternative method was tested for indicating the soil moisture requirements of the flora of European mires (Hájek et al. 2020), which confirmed that plant species composition (or type of vegetation) is more stable than the measured ecological variables because it accurately reflects even long-term environmental conditions. This approach could also be applied to other ecological variables.

This study focuses on a bioindication system for soil salinity for vascular plants, based on 20 years of field observation and annotated literature on temperate inland salt marshes and salt steppes in central Europe. The primary objectives were to (i) review and classify halophytic species into three categories of salt tolerance and (ii) to compile a list of obligate, facultative halophytes ranked on a nine-point scale according to their preference for soil salinity based on their relative frequency in saline and non-saline habitats. Finally, the obtained salt numbers of halophytes are compared with the other systems of EIV for salinity in central and central-eastern Europe (Breckle 1985, Ellenberg et al. 1991, Borhidi 1995).

Methods

Study area

The study area covers central Europe, where there is a high occurrence of natural and seminatural inland saline habitats (Fig. 1). In the northern half of the area studied (part of the North European Plain) temperate inland salt marshes (in German: Binnensalzstellen) are present in Saxony-Anhalt and Thuringia federal states and Polish region of Kujawy (Piernik 2012). The greatest concentration and variability in alkali steppes and salt marshes are in the Danube and Tisza river basins in the Pannonian Lowland (Austria, Czech Republic, Slovakia, Hungary, Romania and Serbia). Halophytic vegetation is

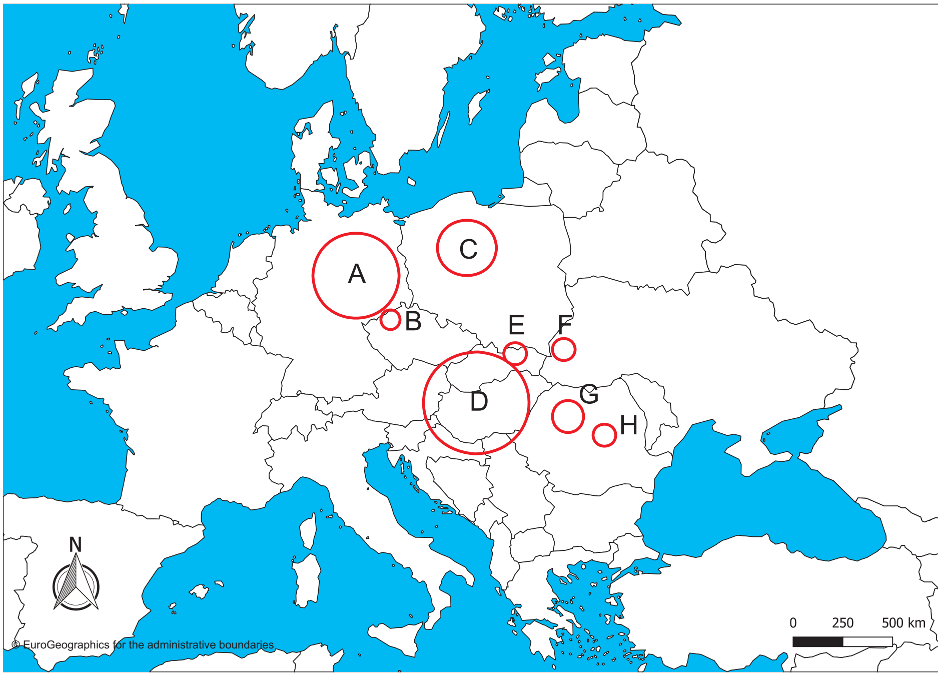


Fig. 1. Schematic illustration of central-European regions where inland saline habitats occur: A, C: North European Plain with Thuringia, Saxony-Anhalt and Brandenburg states (A), Kujawy (C); B: Most and Chomutov basins; D: Pannonian Lowland; E: Spiš basin; F: Drohobych; G: Transylvanian Plateau; H: Harghita region.

often confined to fossil salt deposits, e.g. on the Transylvanian Plateau in Romania (Dítě et al. 2021), or develops secondarily around abandoned salt mines like those in western Ukraine (Woch & Trzcińska-Tacik 2015). The subhalophytic vegetation growing around mineralized springs at tectonic breaks in the west of the Czech Republic (Toman 1976) was recently destroyed. Salt springs occur scattered in South Moravia (Vicherek 1973, Grulich 1987, Danihelka et al. 2022), in Slovakia (Spiš basin) in the Western Carpathians (Šmarda 1961, Dítě et al. 2004), in Poland near Krakow (Piernik 2012) and in Romania in the foothills of the Eastern Carpathians, where saline areas are associated with mineral-rich springs and mud volcanoes (Dítě et al. 2022a).

The climate in central Europe is humid continental (Peel et al. 2007); in the lowland areas, it is generally hot in summer and cold in winter. The hottest and driest is the Pannonian Lowland where the annual average temperature is 10.5 °C, and the annual rainfall is 500–550 mm (Bihari et al. 2018). In the north-west (Germany and Poland), where the Atlantic has a moderating influence, the mean annual temperature ranges between 8.4–9.6 °C and the mean annual precipitation between 479–675 mm (Fick & Hijmans 2017), very similar to the Transylvanian Plateau where the mean annual temperature is 8.4–9.7 °C and the annual precipitation ranges from 520 to 650 mm (Kun et al. 2004). The submontane south-eastern part of the Transylvanian Basin (Harghita region) adjacent to the Carpathian bioregion has the highest annual precipitation.

In the area studied, there are two biogeographical regions, the Pannonian and the Continental. The eastern half of the Continental bioregion (e.g. the Wallachian Plain) was not included due to the prevalence there of a different flora extending from the Steppic bioregion, nor was the inland basins of the Balkans (Bulgaria, Northern Macedonia and southern Serbia) where the climate and vegetation are significantly influenced by the Mediterranean conditions.

Selection of species

The subjects of this study are terrestrial vascular plants growing in inland saline habitats in central Europe (Fig. 1). Although there are several recently naturalized neophytes (e.g. *Hordeum jubatum*, *Gypsophila perfoliata* and *G. scorzonerifolia*), the emphasis is on the native halophytic flora.

First, we compiled an inventory of species included in the most relevant surveys of temperate inland saline vegetation in Europe: the work of Prodan (1939) and Krist (1940) which list vascular plant taxa as (I) obligate halophytes, (II) facultative halophytes, and (III) salt-tolerant species/accessory species; further we reviewed the work of Bucur et al. (1957) and Wilkoń-Michalska (1963) and the species list of the most frequently used systems of ecological indicator values (EIV) for the central and central-eastern European flora by Ellenberg et al. (1991) and Borhidi (1995). Species with S-value 0 (zero) were omitted as they are not associated with saline soils (= glycophytes). This was supplemented by the selection of species that are mentioned in some other local/regional flora and vegetation studies conducted in the area studied (because they are numerous only the most relevant sources are cited in the References) and by drawing upon our 20 years of field experience and our set of 1,615 phytosociological relevés recorded in central-European saline vegetation, stored in TURBOVEG database (Hennekens & Schaminée 2001).

This resulted in a preliminary list of 364 species, which was reduced to 190. The species excluded were those that, according to the literature, our field experience and their EIVs, are not considered halophytes. In most cases, they have an S-value of 1, which is defined by Ellenberg et al. (1991) as “mostly on non-saline soils, occasionally occurring on somewhat saline soils”, and Borhidi (1995) as “salt tolerant plant but living mainly on non-saline soil”.

The final list of 190 plants clearly closely associated with saline soils was subjected to further analysis based on expert revision, the literature and field experience. All essential supporting data and analytical tables are incorporated in Supplementary Data S1 in five separate sheets (1 Types of habitat, 2 Scoring and calculation, 3 Category and Scale, 4 Comparing categories and scales, 5 Frequency).

For the ranges of the species, distribution maps and/or databases were used (Meusel & Jäger 1992, Bartha et al. 2015). The taxonomy and nomenclature of the 190 plant species analysed follow Euro+Med (2006), the nomenclature of the additional non-halophytic species in Supplementary Data S1: 5 Frequency is that used in the European species list defined in the TURBOVEG database.

Calculation of preference for salinity based on the affinity of species for particular habitats

The frequency of occurrences of the final list of 190 species was based on their affinity for particular types of habitat in central Europe. The content of habitats follows the European hierarchical floristic classification system for vascular plant communities (Mucina et al. 2016). These habitats were classified as saline and non-saline. The saline habitats are recognized as Temperate inland salt marshes (Annex 1 code 1340, Eunis R.63) and Continental inland salt steppes (Annex 1 code 1530, Eunis R.62) according to the European Nature Information System of Chytrý et al. (2020). Five habitats were classified as saline: hypersaline open swards (SO), soda pans (SP), salt marshes and alkali meadows (SM), salt steppes (ST) and seminatural subsaline grasslands (SS), the latter being the least saline and the means by which species indifferent to soil salinity can colonize halophytic plant communities, which are in transition to non-saline habitats. To the non-saline type of habitat, six habitats were assigned: freshwater marshes (W), seasonally flooded annual wetlands (AW), fens (F), temporarily wet meadows (WM), mesic hay meadows (M), dry grasslands (X) and ruderal man-made habitats (R). The content and classification of each habitat (plant communities or alliance rank) are included in Supplementary Data S1: 1 Types of habitat.

We scored each species according to its habitat affinity as recorded in central Europe and also within its entire distribution. For scoring we applied the same ordinal variables as in the methodology of the inventory of glacial-relic species by Dítě et al. (2018): 0 – the species never grows in a particular habitat (no affinity); 1 – the species has its optimum in other habitats, but grows rarely in a particular habitat (low affinity); 2 – the species' ecological niche spans several types of habitat, but it grows frequently in a particular habitat (high affinity); 3 – the species is characteristic/diagnostic of a particular habitat, being at its optimum there (very high affinity).

The ordinal variables were used to calculate the preference for salinity (halophytic value) for each species (abbreviated as 'Hal') using the following equation:

$$\mathrm{Hal} = \frac{\sum a}{\max A} \cdot \mathrm{Spec} - \frac{\sum b}{\max B} \cdot 2$$

a = the affinity of the species for saline habitats SM, SO, SP, ST; A = the set of summary values of all species' affinities for saline habitats SM, SO, SP and ST; b = the affinity of the species for non-saline habitats (W, AW, F, WM, MM, X, R); B = the set of summary values of all species' affinities for non-saline habitats (W, AW, F, WM, MM, X, R).

Spec = the species specificity (minimum value 1) based on the total number of saline habitats in which it occurs (N) and the affinity for the habitat SS (indicated as SS):

$$\mathrm{Spec} = 1.4 - \frac{N}{10} + \frac{SS}{10}$$

On rare occasions, various species can differ from the general pattern. In these instances, the halophytic value of a species with a strong preference for a single saline habitat is lowered by their occasional occurrence in non-saline habitats. For this reason, specificity (Spec) was added to the formula, which was calculated in a way that ensures that it has a minimum value of 1 and therefore has no negative effect on the species score $\frac{\sum a}{\max A}$ derived from other saline habitats. Since it is a multiplier, each tenth in Spec increases the gained scores from saline habitats SM, SO, SP and ST by 10%.This is thought to be a reasonable value, non-negligible but at the same time not too high, to avoid substantial changes in scores gained from the saline habitats associated with the species specificity. For better understanding of this adjustment a few examples are given below:

Carex extensa occurs only in habitat SM in Europe and its specificity is calculated as 1.4 – (1/10) + (0) = 1.3, which means that the specificity raises its score from saline habitats by 30%. *Salicornia perennans* occurs in three saline habitats (SO, SM, SP), its Spec value is calculated as 1.4 – (3/10) + (0) = 1.1, which means that its score from saline habitats only increases by 10%. *Salicornia perennans* is less specific than *C. extensa*, as it grows in a larger range of saline habitats.

When the species occurs in four saline habitats (SM, SO, SP, ST), Spec is calculated as 1.4 – (4/10) + (0) = 1. This indicates that the species is not confined to one particular type of vegetation. The Spec is 1 and therefore does not affect the score gained from saline habitats. The affinity level of species in habitat SS also affects the specificity value. Types of vegetation belonging to SS are at the end of the salinity gradient, often degraded or have a secondary origin (Mucina et al. 2016). These were not included in the calculation of saline habitats due to their separate position in terms of specificity.

Plantago maritima, a widespread halophyte, occurs in three types of saline habitat and four types of non-saline habitat in central Europe scored by the following ordinal variables (affinity with habitats; Supplementary Data S1: 2 Scoring and calculation):

Saline habitats				Non-saline habitats		
SM	SO	ST	SS	F	X	R
2	2	2	1*	1	1	1

* (incl. specificity calculation)

The maximum value of summary affinity to saline habitats (SM + SO + SP + ST) in the matrix of all species is 8, as in the *Puccinellia distans* agg. (included *Puccinellia peisonis*, *P. distans* subsp. *distans*, subsp. *limosa*). The maximum value of total affinity to non-saline habitats (W + AW + F + WM + MM + X + R) in the matrix of all species is 12 (*Agrostis stolonifera*). The calculated halophytic value for *P. maritima* is:

$$\mathrm{Hal}_{(\text{Plantago maritima})} = \frac{2+2+2}{8} \cdot \left(1.4 - \frac{3}{10} + \frac{1}{10}\right) - \frac{1+1+1}{12} \cdot 2 = 0.40$$

Then, the calculated halophytic value for 190 species was transformed into salt numbers on a nine-point scale (from 1 to 9) based on percentiles. They were used for compiling the list of halophytes in which the species are arranged in descending order according to their individual preference for soil salinity. This scale does not include zero, like the systems of EIV of Ellenberg et al. (1991) and that of Borhidi (1995), both of which elaborate the entire flora in the area they studied. When using EIV for salinity in ecological analyses, it is recommend that a salt number of 0 is assigned to all the other species not mentioned in the list. These are plants completely avoiding saline environments (non-halophytes, halophobes or glycophytes), like the salt index figures used by Breckle (1985) in Romania, in which species “almost not salt-tolerant, very rare in brackish soils” with a salt number (Salzzahl) 1 are not listed.

For comparing salt numbers resulting from the proposed approach with the salt indicator values of Breckle (1985), Ellenberg et al. (1991) and Borhidi (1995), frequency scatter plots, were produced analysing only those species that are included in each list.

Classification of halophytes into three categories of salt tolerance

The 190 species were classified into one of three categories of salt tolerance: obligate halophytes, facultative halophytes and accessory species regardless of their halophytic value or salt number. They were assigned to the categories based on their occurrence in the 12 defined habitats (Supplementary Data S1: 1 Types of habitat, 2 Scoring and calculation). Within the group obligate halophytes, two subcategories: regional and conditioned halophytes were defined based on their geographical range (Meusel & Jäger 1992, Bartha et al. 2015) and expert assessment.

For the visualization of the three categories/groups in ordination space, a principal component analysis (PCA) was used to display the 190 species characterized by 12 ordinal variables (vectors), which represent their affinity (frequency) for particular habitats. This classification of salt tolerance was compared with two relevant regional studies: Prodan (1939), which includes 114 halophytes, and Krist (1940), listing 108 halophytes. The number of species occurring in both datasets (N), adjusted coefficients of determination (r^2), Pearson correlation coefficient (r) and statistical significance of correlation (P) were calculated.

In addition, based on the percentage of individual salt tolerance categories, bar plots were used for examining in which habitats the obligate, facultative halophytes and accessory species occurred. Violin boxplots were used to show the level of salinization in the 12 habitats based on the calculated halophytic values for species that occur in them. All analyses were generated in the Statistica 7 program (StatSoft, Inc. 2004) and PAST 4.05 program (Hammer et al. 2001). The map was created using the program QGIS, version 3.2 (QGIS Development Team 2018).

Our private database of phytosociological relevés in inland saline habitats was used to present additional salt-tolerant species less frequently recorded on saline soils in central Europe by calculating their constancy values (Supplementary Data S1: 5 Frequency).

Results

The inventory of halophytes in central Europe has two aspects: (i) classification of halophytes into three categories of salt tolerance, (ii) compilation of a list of halophytes arranged according to their calculated halophytic value obtained from their incidence in saline and non-saline habitats. A salt number from 1 to 9 was assigned to each species, which reflects their individual preference for soil salinity. Table 1 presents the salt numbers and salt tolerance categories of the 190 species listed in alphabetical order and the outcomes, with all essential partial results summarized in Supplementary Data S1.

Classification of halophytes into three categories of salt tolerance

We reviewed the three categories of salt tolerance defined earlier by several authors (mentioned in the Introduction and Methods) and classified the species according to their quantitative occurrence in saline and non-saline habitats (Fig. 2.).

Table 1. Checklist of species in saline habitats in central Europe with the assigned salt number on a nine-point scale and category of salt tolerance (I – obligate halophyte, Ia – regional obligate, and Ib – conditioned obligate halophyte, II – facultative halophyte, III – accessory species) in alphabetical order.

Taxon	Salt number	Salt tolerance Category
Agrostis stolonifera	1	III
Achillea aspleniifolia	3	II
Achillea millefolium agg.	1	III
Allium vineale	1	III
Alopecurus pratensis	1	III
Althaea officinalis	2	II
Anacamptis palustris subsp. *palustris* / subsp. *elegans*	1	III
Apium graveolens	6	Ia
Argentina anserina	1	III
Armoracia macrocarpa	4	II
Artemisia laciniata	7	I
Artemisia maritima	7	I
Artemisia pontica	3	III
Artemisia rupestris	7	I
Artemisia santonicum	8	I
Atriplex littoralis (incl. *A. intracontinetalis*)	8	Ia
Atriplex prostrata	3	II
Atriplex tatarica	3	III
Bassia prostrata	3	II
Beckmannia eruciformis	5	II
Blackstonia acuminata	3	II
Blysmopsis rufa	7	Ib
Blysmus compressus	2	III
Bolboschoenus maritimus s.s.	5	II
Bromus hordeaceus	1	III
Bupleurum tenuissimum	8	I
Calamagrostis epigejos	1	III
Camphorosma annua	9	I
Cardamine parviflora	2	III
Carex distans	3	II
Carex divisa	4	II
Carex extensa	7	I
Carex hordeistichos	3	II
Carex melanostachya	2	III
Carex otrubae	2	III
Carex riparia	1	III
Carex secalina	6	II
Carex stenophylla	4	III
Carex viridula	1	III
Carex vulpina	1	III
Catabrosa aquatica	2	III
Centaurea jacea subsp. *angustifolia*	3	III
Centaurium littorale subsp. *compressum*	3	II
Centaurium pulchellum	1	III
Cerastium diffusum subsp. *subtetrandrum*	7	Ia
Cerastium dubium	3	II
Cirsium brachycephalum	4	II
Chenopodium album	1	III
Cirsium canum	2	III
Cladium mariscus	2	III
Crypsis aculeata	9	I
Crypsis alopecuroides	4	II

Taxon	Salt number	Salt tolerance Category
Crypsis schoenoides	6	II
Cynodon dactylon	2	III
Cyperus pannonicus	6	II
Eleocharis palustris	2	III
Eleocharis parvula	7	Ib
Eleocharis quinqueflora	3	III
Eleocharis uniglumis	1	III
Elytrigia repens	2	III
Festuca stricta subsp. *sulcata*	1	III
Festuca valesiaca subsp. *parviflora*	3	II
Gagea szovitsii	3	II
Galatella cana	5	II
Galatella linosyris	3	III
Galatella sedifolia	6	I
Galatella villosa	5	II
Galium verum	1	III
Glaux maritima	6	Ia
Gypsophila muralis	2	III
Halimione pedunculata	8	I
Hordeum geniculatum	8	I
Hordeum secalinum	3	II
Hornungia procumbens	6	Ia
Inula britannica	2	III
Iris spuria	5	II
Juncus articulatus	1	III
Juncus bufonius	1	III
Juncus compressus	1	III
Juncus gerardi	5	II
Juncus maritimus	8	I
Juncus ranarius	3	II
Juncus subnodulosus	1	III
Lactuca saligna	2	III
Leontodon saxatilis	2	III
Lepidium cartilagineum	9	I
Lepidium perfoliatum	4	II
Lepidium coronopus	2	III
Lepidium ruderale	1	III
Limonium gmelinii (incl. *L. hungaricum*)	8	Ia
Linum maritimum	7	I
Lotus angustissimus	8	Ib
Lotus maritimus	2	II
Lotus tenuis	3	II
Lythrum hyssopifolia	1	III
Lythrum tribracteatum	3	II
Matricaria chamomilla	3	II
Medicago lupulina	1	III
Medicago minima	2	III
Melilotus dentatus	5	II
Mentha pulegium	2	II
Myosurus minimus	3	III
Odontites vulgaris	2	III
Oenanthe silaifolia	2	III
Ononis spinosa	1	III
Oxybasis glauca	4	III
Oxybasis chenopodioides	6	Ia
Oxybasis urbica	3	III

Taxon	Salt number	Salt tolerance Category
Petrosimonia triandra	8	I
Peucedanum latifolium	8	I
Peucedanum officinale	3	II
Pholiurus pannonicus	9	I
Phragmites australis	1	III
Plantago cornuti	8	I
Plantago coronopus	5	Ia, Ib
Plantago major subsp. *intermedia*	2	III
Plantago maritima (subsp. *maritima*, subsp. *ciliata*)	7	II
Plantago schwarzenbergiana	8	I
Plantago tenuiflora	9	I
Poa angustifolia	1	III
Poa bulbosa	3	III
Polygonum aviculare	2	III
Prospero autumnale	3	II
Puccinellia distans agg.	9	Ia
Pulicaria dysenterica	3	II
Pulicaria vulgaris	1	III
Ranunculus baudotii	3	II
Ranunculus lateriflorus	4	II
Ranunculus pedatus	3	II
Ranunculus polyphyllus	3	II
Ranunculus sardous	2	III
Ranunculus sceleratus	1	III
Rorippa sylvestris subsp. *kerneri*	8	I
Rumex crispus	1	III
Rumex maritimus	2	III
Rumex pseudonatronatus	3	II
Rumex stenophyllus	3	II
Ruppia maritima	7	Ib
Salicornia europaea (incl. *S. appressa*)	9	I
Salicornia perennans	9	I
Salsola kali	2	III
Salsola soda	9	I
Samolus valerandi	3	II
Scorzonera cana	3	II
Scorzonera laciniata	1	III
Scorzonera parviflora	5	II
Scorzoneroides autumnalis	1	III
Sedobassia sedoides	4	II
Sedum caespitosum	7	Ib
Schedonorus arundinaceus	2	III
Schoenoplectus litoralis	7	Ib
Schoenoplectus pungens	5	II
Schoenoplectus supinus	2	III
Schoenoplectus tabernaemontani	3	II
Schoenus nigricans	3	II
Silene multiflora	5	II
Silene viscosa	3	III
Sonchus arvensis	1	III
Sonchus palustris	2	III
Spergularia marina	6	Ia
Spergularia media	6	Ia
Suaeda maritima	8	I
Suaeda pannonica	9	I
Suaeda prostrata	9	I

Taxon	Salt number	Salt tolerance Category
Suaeda salsa	7	Ia
Taraxacum bessarabicum	8	Ia
Teucrium scordium	1	III
Trifolium angulatum	6	I
Trifolium fragiferum	4	II
Trifolium micranthum	4	II
Trifolium ornithopodioides	6	II
Trifolium repens	1	III
Trifolium retusum	3	II
Trifolium striatum	3	II
Trifolium strictum	6	II
Trifolium subterraneum	3	II
Triglochin maritima	7	II
Triglochin palustris	3	III
Trigonella procumbens	3	II
Tripleurospermum inodorum	1	III
Tripolium pannonicum	9	I
Typha angustifolia	1	III
Typha latifolia	2	III
Verbena officinalis	2	III
Veronica acinifolia	3	III
Veronica anagalloides	1	III
Veronica arvensis	1	III
Veronica catenata	2	III
Veronica scardica	2	III
Vicia cracca	1	III

I. Obligate halophytes occur exclusively in saline habitats; 45 species belong here, while 29 of them are known only from natural saline habitats in central Europe (Supplementary Data S1: 2 Scoring and calculation). Two subcategories of obligate halophytes were defined (Ia, Ib). Their common feature, in addition to their high affinity for natural saline habitats, is the tendency to grow or even expand in non-saline or secondarily salt-affected habitats. The majority of these species are typical of roadsides treated with de-icing salt during winter in central Europe, e.g. *Puccinellia distans* agg., *Spergularia marina*, *S. media*, less frequently *Suaeda salsa* and *Limonium gmelinii*. A very small group of halophytes colonizes anthropogenic habitats like dump sites and sludge beds rich in nitrogen, such as e.g. *Atriplex littoralis* and *Oxybasis chenopodioides*. They are defined as conditioned obligate halophytes (Ia). Their presence does not necessarily indicate a saline habitat, as species of this subcategory may occur outside their primary range in areas where natural saline habitats do not occur, for instance, *Plantago coronopus*. This species is also a regionally obligate halophyte (Ib), a subcategory to which six other species belong. In central Europe, these plants are confined to saline habitats, but in other regions in their European range, they are common in non-saline (natural and seminatural) habitats. For instance, in dry grasslands it is *Lotus angustissimus*, in freshwater marshes and fens *Eleocharis parvula* and *Blysmopsis rufa* (Supplementary Data S1: 1 Types of habitat, 2 Scoring and calculation).

II. Facultative halophytes also have a high affinity for saline habitats, but unlike obligate halophytes, they regularly occur in at least one non-saline habitat in central Europe. Their presence does not unequivocally indicate a saline habitat. In this category there are

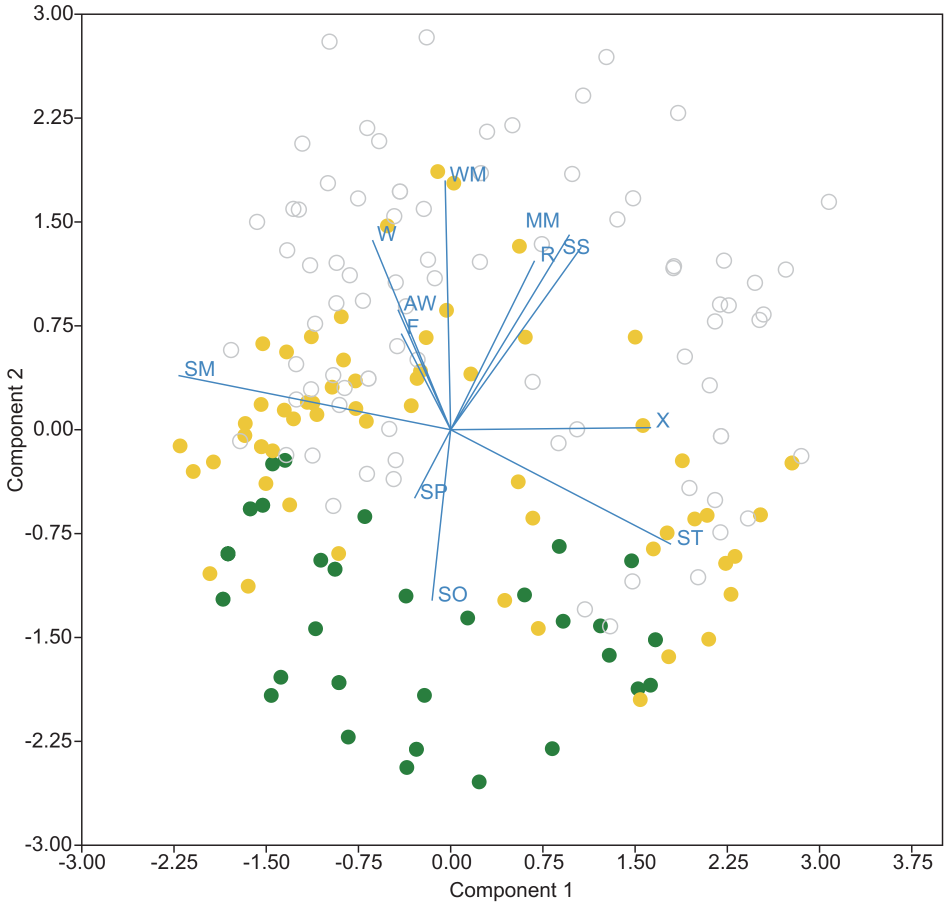


Fig. 2. Principal components analysis plot of 190 species divided into three categories: ● obligate halophytes; ● facultative halophytes; ○ accessory species. The species are characterized by 12 ordinal variables (quantified occurrence in five saline and seven non-saline habitats), displayed as biplots.

61 species (Supplementary Data S1: 2 Scoring and calculation). Facultative halophytes with a strong connection to saline habitats include species that, in addition to saline habitats, occur only in one non-saline habitat: in fens e.g. *Triglochin maritima* or in seasonally flooded annual wetlands e.g. *Cyperus pannonicus*. While the majority of facultative halophytes occur in one or more non-saline habitats, their main occurrences are in saline habitats in central Europe, e.g. *Juncus gerardi*, *Lotus maritimus*, *L. tenuis*, *Mentha pulegium*, *Ranunculus pedatus*, *R. polyphyllus* and *Trifolium fragiferum.* Seven facultative halophytes have two main phytosociological optima: *Prospero autumnalis* has one in salt steppes and the other in the non-saline environment dry grasslands. Except for this species and *Bassia prostrata*, the other facultative halophytes on the list have their second optimal occurrence in freshwater marshes (Supplementary Data S1: 2 Scoring and calculation).

III. Accessory species are not confined to saline habitats; indeed, their core occurrence is in one or more non-saline habitats. Six of them have optima both in saline and non-saline habitats, as do some facultative halophytes, but their affinity for non-saline habitats prevails, for instance, *Eleocharis uniglumis* (Supplementary Data S1: 2 Scoring and calculation). Eighty-four taxa were included in this category, although their number is certainly higher. It is difficult to decide which accessory species should be included, due to the wide ecological niches of species tolerating high salinity. For example, in the phytosociological database of central-European saline habitats a total of 305 accidentally occurring vascular plants are recorded having very different ecological preferences, of which the majority (280 species) have a frequency of lower than 1% (Supplementary Data S1: 5 Frequency). They can all be regarded as accessory (or associated species), based on the above definition.

Accessory species present in halophytic communities often originate from surrounding vegetation. For instance, for endangered *Orchidaceae*, such species include *Anacamptis palustris* subsp. *palustris* / subsp. *elegans* in freshwater marshes (Supplementary Data S1: 2 Scoring and calculation), *Ophrys sphegodes* in dry grasslands, *Anacamptis coriophora*, *A. morio*, *Orchis militaris* and *Spiranthes spiralis* in mesic and dry grasslands, and *Dactylorhiza incarnata* subsp. *incarnata*, *D. incarnata* subsp. *pulchella* and *Epipactis palustris* in fens.

Calculation of halophytic values for the salt numbers used to compile the list of halophytes on a nine-point scale

We sorted the list of 190 halophytes in decreasing order according to their halophytic value. Based on this, a nine-point scale of salt numbers (SN) was created that reflect the salt preference of each species (Supplementary Data S1: 3 Category and scale).

Of the species listed, 14% (27 in total) had the highest preference for salinity (SN 9 and 8) and all of these were categorized as obligate halophytes. They occur in more types of saline vegetation, but not in the least salt-affected habitat (SS), except for *Tripolium pannonicum* and *Artemisia santonicum* (Supplementary Data S1: 2 Scoring and calculation). The only conditioned obligate halophyte with SN 9 was the *Puccinellia distans* agg.; the majority of these species had a medium SN, e.g. *Spergularia salina*, *S. media* and *Glaux maritima* (6) and *Plantago coronopus* with SN 5. A relatively high preference for soil salinity (SN 7) was recorded for two facultative halophytes that occur rarely in one non-saline habitat: *Triglochin maritima* and *Plantago maritima*. 24 species in this category had a medium SN (4 to 6), e.g. *Crypsis schoenoides*, *Scorzonera parviflora*, *Juncus gerardi* and *Trifolium fragiferum*, whereas the majority of the facultative halophytes (31 species) had SN 3 (e.g. *Scorzonera cana*, *Althaea officinalis*) with the main occurrence being in the non-saline habitats as freshwater marshes, fens, and seasonally flooded annual wetlands (Supplementary Data S1: 2 Scoring and calculation). The lowest preference for salinity was recorded for accessory species, among which *Carex stenophylla* and *Oxybasis glauca*, had a high (SN 4) and 11 species had SN 3 (e.g. *Artemisia pontica* and *Cladium mariscus*). The remaining 69 accessory species had SN 1 or 2, e.g. *Odontites vulgaris*, *Inula britannica*, *Phragmites australis* and *Elytrigia repens*. These species are very common in inland saline habitats, but their high abundance in a large variety of non-saline habitats reduced their halophytic value (Supplementary Data S1: 2 Scoring and calculation).

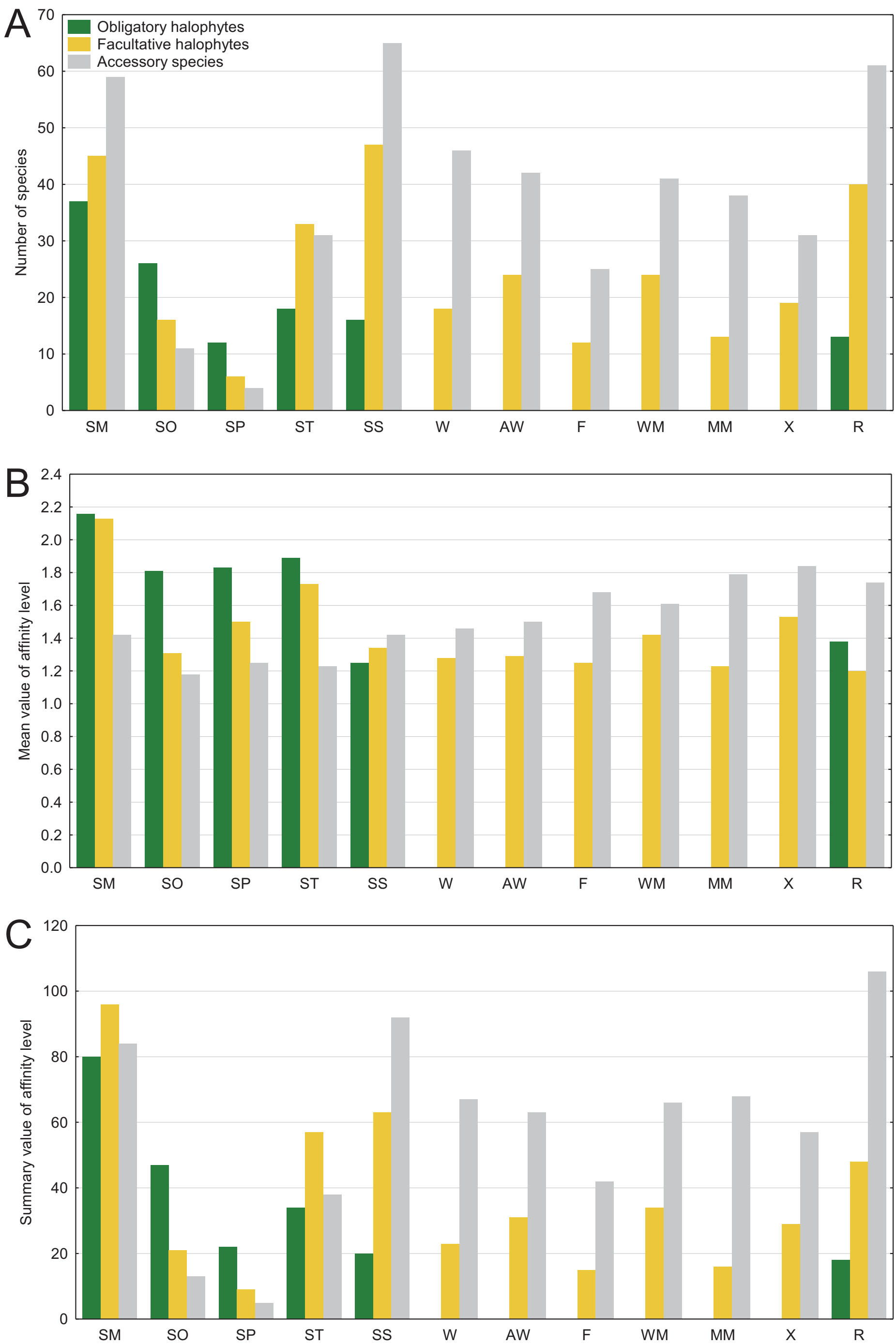


Fig. 3. Bar plots showing the (A) number of obligate, facultative and accessory species; (B) mean value of affinity level and (C) summary value of affinity level of species with saline and non-saline habitats. SM – salt marshes and alkaline meadows, SO – hypersaline open swards, SP – soda pans, ST– salt steppes SS – seminatural subsaline grasslands, W – freshwater marshes, AW – seasonally flooded annual wetlands, F – fens, WM – temporarily wet meadows, M – mesic hay meadows, X - dry grasslands, R - ruderal habitats.

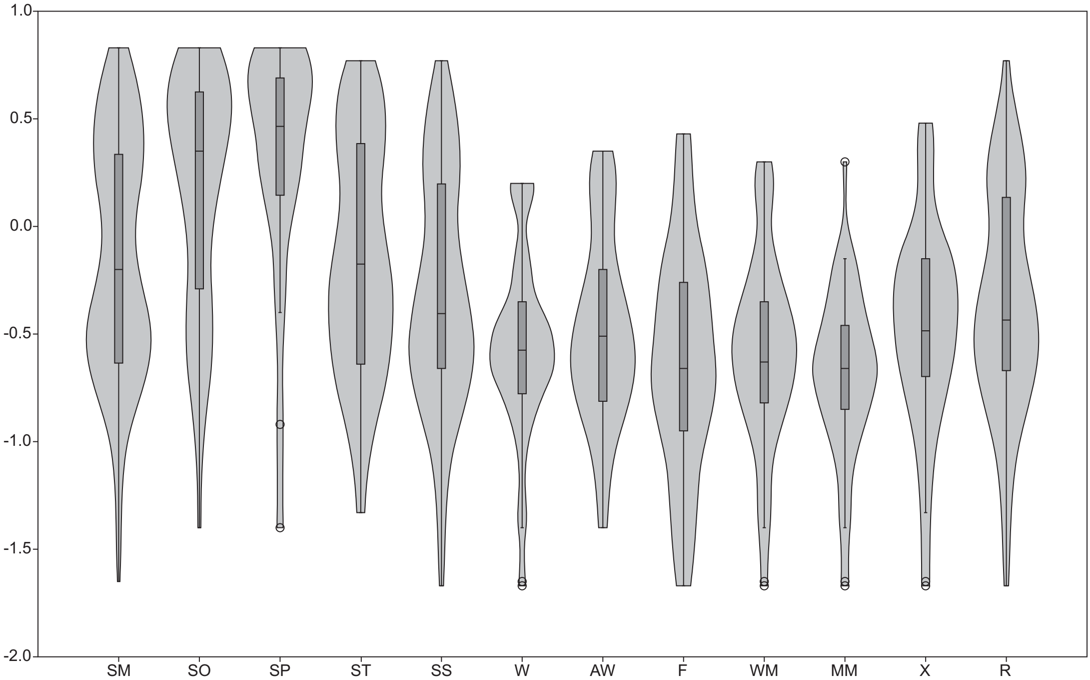


Fig. 4. Combined violin and box plots with the calculated halophytic value of the species occurring in the individual habitats showing the kernel density, 25–75 percent quartiles (using a box), median (horizontal line inside the box), minimum and maximum values (horizontal lines) for each sample. See Fig. 3 for habitat codes.

Further, the percentage of salt tolerance categories in the 12 habitats were analysed according to the affinity level of the species (0 to 3, see Methods) for the habitats. More than 70 obligate and facultative halophytes were recorded in salt marshes and alkaline meadows (SM), which is the highest total number of species occurring in this habitat (Fig. 3A). SM had a higher absolute number and mean value of obligate halophytes (37 and 2.2, respectively) than the strictly saline habitats, i.e. hypersaline open grasslands (SO) and soda pans (SP) (Fig 3B). Moderate fluctuations in water level and medium to low soil salinity of SM are also suitable for many accessory species and almost 60 species in this category were recorded there (Fig 3A). The more extreme ecological conditions (specifically, the drying of the surface and high soil salinity) in habitats SO and SP explain why obligate halophytes are the dominant species in these habitats, and that SO and SP had the lowest number of accessory species (Fig. 3). Among the non-saline habitats, only the ruderal habitats (R) hosted some obligate halophytes. Facultative halophytes occurred in all of the listed habitats.

A similar pattern was seen when the level of salinization of the 12 habitats was analysed based on the halophytic values of the species occurring in them. Habitats SO and SP had the highest number of species with a mean value > 0.4 (Fig. 4). Habitats SM and ST (salt steppes) also contained species with high halophytic values, but species with low halophytic values were also detected. In non-saline habitats other than the ruderal (R) one, only species with low mean halophytic value (–0.5) were recorded. The same pattern was recorded in habitats SS and R, which is associated with the high anthropogenic disturbance.

Table 2. Table comparing the salt numbers with ecological indicator values by Breckle (1985), Ellenberg et al. (1991) and Borhidi (1995) and the comparison of this classification of the categories obligate halophyte, facultative halophyte and accessory species with that in regional lists (Prodan 1939, Krist 1940). The only species analysed were those present in all of the lists cited. N – the number of species occurring in both datasets, r^2 – adjusted coefficients of determination, r – correlation coefficient, P – statistical significance of correlation.

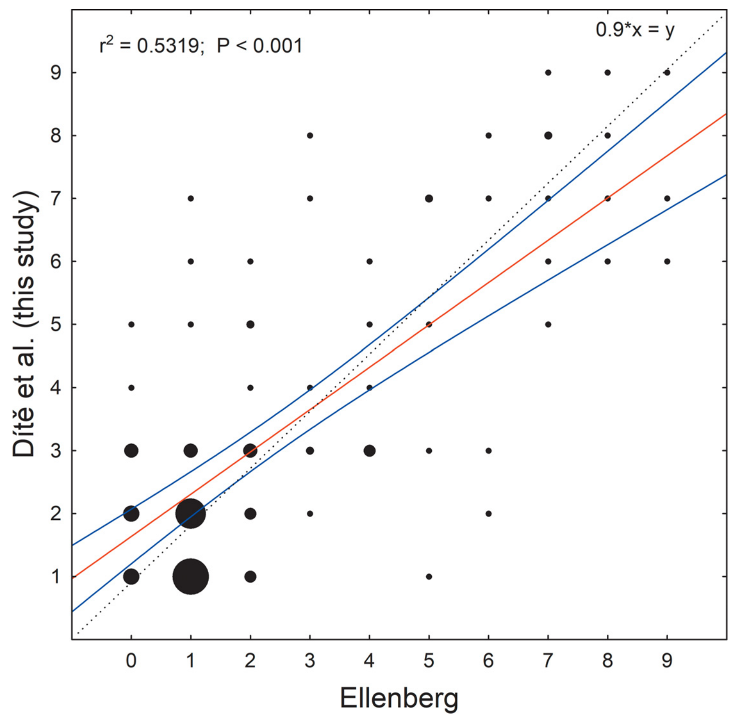
	Dítě (scale/rank)	Ellenberg (scale)	Borhidi (scale)	Breckle (scale)	Prodan (rank)	Krist (rank)
Dítě (scale/rank)	x	N=108 P<0.001 r^2=0.532 r=0.729	N=153 P<0.001 r^2=0.498 r=0.706	N=141 P<0.001 r^2=0.571 r=0.756	N=114 P<0.001 r^2=0.500 r= 0.707	N = 108 P<0.001 r^2=0.582 r=0.763
Ellenberg (scale)	N=108 P<0.001 r^2=0.532 r=0.729	x	N=140 P<0.001 r^2=0.646 r=0.804	N=111 P<0.001 r^2=0.679 r=0.824	x	x
Borhidi (scale)	N=153 P<0.001 r^2=0.498 r=0.706	N=140 P<0.001 r^2=0.646 r=0.804	x	N=145 P<0.001 r^2=0.438 r=0.662	x	x
Breckle (scale)	N=141 P<0.001 r^2=0.571 r=0.756	N=111 P<0.001 r^2=0.679 r=0.824	N=145 P<0.001 r^2=0.438 r=0.662	x	x	x
Prodan (rank)	N=114 P<0.001 r^2=0.500 r=0.707	x	x	x	x	N=103 P<0.001 r^2=0.419 r=0.763
Krist (rank)	N=108 P<0.001 r^2=0.582 r=0.763	x	x	x	N=103 P<0.001 r^2=0.419 r=0.763	x

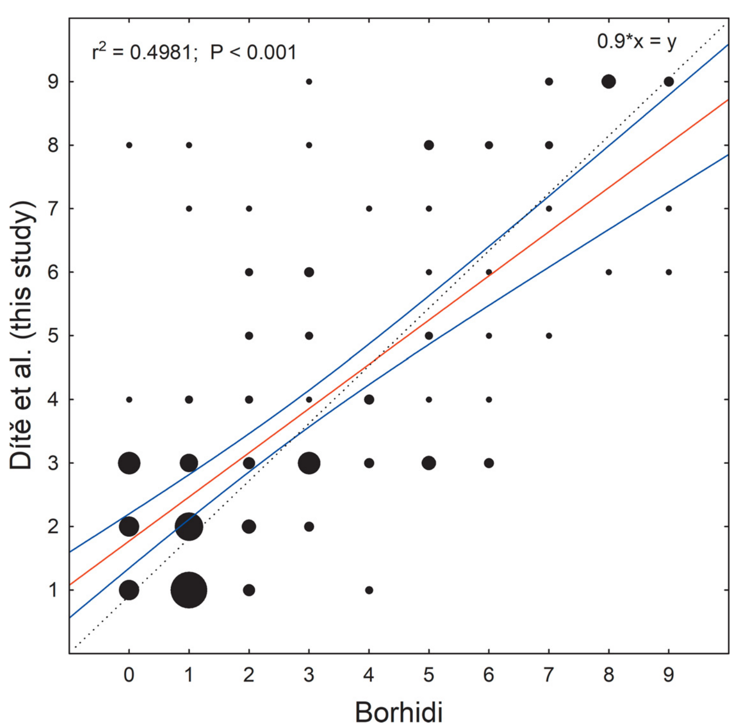
Comparing salinity indicator values and salt tolerance categories

The evaluation of salt preferences of halophytes using the habitat approach is in accordance with that based on the EIV of salinity used by Breckle (1985), Ellenberg et al. (1991) and Borhidi (1995) (Table 2, Fig. 5, Supplementary Data S1: 4 Comparing categories and scales). Pairwise Pearson correlation coefficients of the correlation between Breckle's salt numbers and those reported in this study ($r = 0.76$, $P < 0.05$) are statistically significant, which indicates that the indicator values based on databases focusing on salt-tolerant plants are consistent.

The published classifications of the salinity scale estimated by the ecological behaviour obtained from phytosociological tables, taking into account site factors and available data on germination (Ellenberg et al. 1991, Leuschner & Ellenberg 2017), assigned similar salt numbers to those recorded in this study (Supplementary Data S1: 4 Comparing categories and scales). The highest correlation was recorded for the low salt numbers in each EIV system (Fig. 5). Among the species with a high SN, the smallest deviation was between the results presented and the list in Borhidi (Fig. 5B). Greater differences were recorded for a few species (Supplementary Data S1: 4 Comparing categories and scales), some examples of which are given in Table 3.

Concerning the three categories of salt tolerance (obligate and facultative halophytes, and accessory species), the similarity with the regional lists is also high (Table 2). There are a few dissimilarities, such as, the species *Galatella cana*, *Plantago maritima*, *Triglochin maritima*, *Carex divisa* and *C. hordeistichos*, which according to Krist (1940) are obligate halophytes, whereas they are evaluated in this study as facultative halophytes (Supplementary Data S1: 4 Comparing categories and scales); in addition, the species *Trifolium retusum*, *Galatella sedifolia*, *G. villosa*, *Achillea aspleniifolia* and *Scorzonera*


r² = 0.5319; P < 0.001
0.9*x = y
Dítě et al. (this study)
Ellenberg
0
1
2
3
4
5
6
7
8
9


r² = 0.4981; P < 0.001
0.9*x = y
Dítě et al. (this study)
Borhidi
0
1
2
3
4
5
6
7
8
9

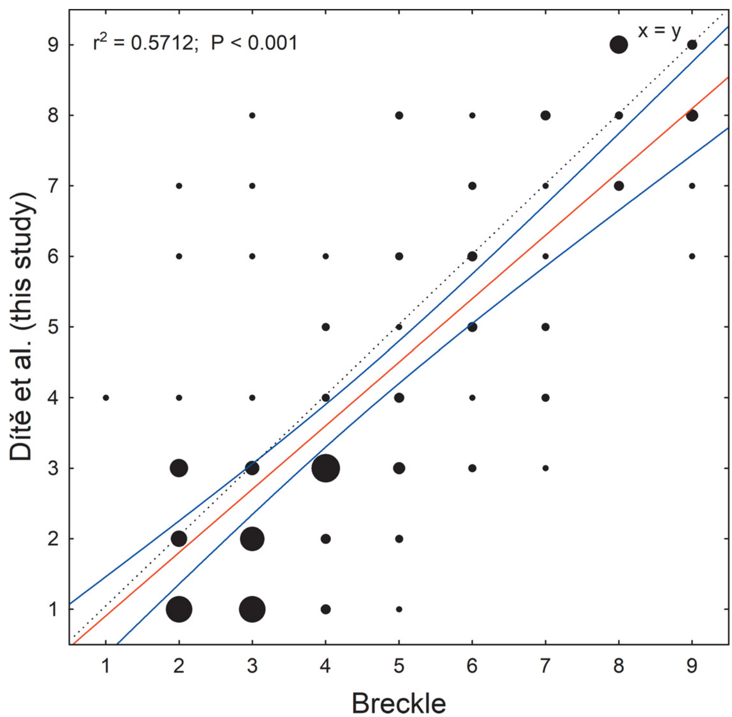


Fig. 5. Frequency scatter-plots of salt numbers recorded in this study compared with salinity indicator values of (A) Ellenberg et al. (1991), (B) Borhidi (1995) and (C) Breckle (1985) for species occurring in both datasets. Regression line (red), confidence regression band (0.95; blue), 0.9x = y line (black dotted), adjusted coefficients of determination (r^2) and statistical significance of correlation (P) are shown. The size of the black circles depends on the number of species with the same value.

Table 3. Selected species that differed greatly in the salt numbers attributed to them in this study compared to those based on ecological indicator values published before.

	Dítě et al.	Ellenberg et al. (1991)	Borhidi (1995)	Brecke (1985)
Crypsis aculeata	9	–	3	9
Bupleurum tenuissinum	8	3	3	5
Taraxacum bessarabicum	8	–	1	7
Oxybasis chenopodioides	6	1	2	4
Carex secalina	6	2	2	3
Eleocharis uniglumis	1	5	4	2–5

cana are classified as obligate halophytes by Prodan (1939), but as facultative halophytes in this study. *Oxybasis chenopodioides* is an obligate halophyte in this study, but a facultative halophyte by Prodan (1939) (Table 2, Supplementary Data S1: 4 Comparing categories and scales). An overall comparison of these regional classification systems with the results of this study is not possible as the sizes of the areas studied and number of species in the lists (114 and 108) differ.

Discussion

Reduced number of strict halophytes

The results underline the very high specialization of halophytes. Of the approximately 5,000 species occurring in the area studied (estimate based on the number of species in individual countries and species-area relationships) only 27 are halophytes sensu stricto, occurring exclusively in natural saline habitats. Even if conditioned and regional obligate halophytes (19) are included, these taxa make up only a small percentage of this species group in central Europe. Similar low numbers of obligate halophytes are reported on coasts, e.g. in the central-European North and Baltic Sea regions: of the ~250 taxa recorded only in salt marsh and beach vegetation only 30–40 are considered to be true halophytes, i.e. plants that are mainly found in saline habitats (Leuschner & Ellenberg 2017). This group includes 10 species of *Chenopodiaceae*, nine *Poaceae*, eight *Cyperaceae* and eight *Juncaceae*.

The classification presented, which is based on a habitat approach, differs from the earlier interpretation of obligate and facultative halophytes (Prodan 1939, Krist 1940). Numerous species previously considered to be obligate halophytes were reclassified as facultative halophytes, due to their prevailing occurrence in non-saline habitats, e.g. *Crypsis schoenoides*, which grows in annual wetlands and ruderal habitats (Eliáš et al. 2008), as well as *Juncus gerardi*, *Plantago maritima*, *Triglochin maritima*, *Scorzonera parviflora* (Dítě et al. 2018), *Galatella cana* (Eliáš et al. 2020) and *Cyperus pannonicus* (Király 2009); more details can be found in Supplementary Data S1: 4 Comparing categories and scales. Many species are considered salt-tolerant, whereas in fact they prefer soils affected by other extreme abiotic conditions, e.g. a high nitrogen content, soil reaction or very clayey soil texture, or another mineral-rich substrate other than high concentration of soluble salts.

The scaling based on the incidence in individual types of vegetation (habitats) largely correlates with the salinity indicator values of Breckle (1985), Ellenberg et al. (1991) and Borhidi (1995), with less than 10 species differing significantly in salt numbers. Ellenberg indicator values for the central-European flora are routinely used for estimating site conditions based on species composition when values for the environmental variables are not available (Diekmann 2003). Despite their limitations (Zelený & Schaffers 2012), they remain a very popular tool in vegetation science and are also used for assessing ecological conditions for invertebrates (Horsák et al. 2007).

The difficult aspects of scaling species according to soil salinity, however, should not be dismissed. Scherfose (1990) points out several ambiguities associated with the determination of salinity numbers, such as what level of salinity are plants exposed to. Depending on the weather and depth of the groundwater, there is either an upward or downward non-linear salt gradient in the soil, especially the solonchak type (Hütterer & Albert 1993). The sporadically measured seasonal salt content of the soil can therefore only be a rough indication of the actual salinity experienced by the plants. The salt content of any soil (including solonchak and solonetz) is temporally variable and follows instantaneous changes in mainly two processes. That is, a decrease following precipitation, due to the leaching of salts to deeper layers and an increase after evaporation/evapotranspiration, when saline groundwater rises by capillary attraction close to the surface (Haj-Amor et al. 2017). Moreover, the salt preference of most halophytes vary widely (Grigore 2021).

Only a few species require very saline soils. Many others occur on soils ranging from those with a high salt concentration to those with low salinity, apparently in severely degraded saline vegetation, where these species prevail among non-halophytes. For example, *Artemisia santonicum* and *Limonium gmelinii* at the northernmost sites in the Pannonic salt steppes survive in degraded stands with predominant *Elytrigia repens*, *Carex praecox*, etc. (Dítě et al. 2021b).

The characterization of the salt content of soils based on field measurements is effortful task constrained by several conditions. Salt preference of species e.g. in inland salt marshes in the North German Plain depend on technically demanding soil analyses (Piernik 2012). Not only does the wide ecological amplitude in salinity complicate the assignment of a salt index to a species, but there is also an inevitable uncertainty as to which salinity the plants are exposed to at a particular site, since the salinization in the soil profile is dependent on seasonal flooding and the weather fluctuations. Another complication involves selecting an appropriate time for the measurements since soil salinity constantly changes throughout the area studied (Douaik et al. 2005, Table 1). Not only salinity but also the salt composition and texture show depth and lateral variability due to precipitation and leaching, reflecting the horizontal variation in the chemical composition of the groundwater (Szendrei et al. 2014). The interpretation of the salt tolerance values based on only one kind of salt, such as NaCl (Scherfose, Ellenberg, Borhidi EIVs), is not straightforward as the composition of salts differs from place to place. Different salts exert different osmotic pressures and differ in their toxic effect on plants. Furthermore, the presence of distinct soil textures modifies the effect of salt, i.e. the same salinity in a coarse textured soil is more harmful than in a fine textured soil (Richards 1954). Severe drying out of the topsoil during hot summers, less common in coastal lagoons, causes large temporal and spatial fluctuations in soil moisture content of inland salt habitats (Tóth 2010, Fig1D).

Conclusions

The classification of halophytes into three categories of salt tolerance and assignment of salt numbers (1–9) for 190 halophytes based on their individual preferences for soil salinity in central Europe was determined by quantifying their occurrences in particular plant communities (habitats). This approach resulted in similar salt numbers for species to those seen in the regularly used classification systems of salinity indicator values, which are often based on subjective estimations. The system of determining the salt indicator values presented might be an alternative way of determining the level of soil salinization, which does not involve measuring ecological site conditions and costly soil analyses. Halophytic value and salt number can be determined for other species not present on the list by using the calculation table in the proposed methodology. The number of accessory species in the list is likely to increase as every plant (non-halophyte) recorded in a saline habitat can be considered to be an accessory species. The current information on the distribution and habitat preferences of plants is not exhaustive and is constantly evolving. It is simultaneously subjected to continual modification as plants can adapt to the rapidly changing climate and environments (area shifts and migration of species).

Supplementary materials

Data S1. Analytical tables with input data for species. 1 Types of habitat, 2 Scoring and calculation, 3 Category and Scale, 4 Comparing categories and scales, 5 Frequency

Supplementary materials are available at www.preslia.cz

Acknowledgments

We greatly appreciate the critical comments and feedback of Milan Chytrý and Michal Hájek (Brno, Czech Republic) during the manuscript preparation, Ricarda Pätsch (Brno, Czech Republic) for providing literature that is difficult to access and Scott Burgess (Ludlow, UK) for his language revision. Last but not least we are thankful to Pavol Eliáš Jr. (Slovakia), † Vít Grulich (Czech Republic), András István Csathó, Gergely Király, Attila Mesterházy (Hungary) and Ranko Perić (Serbia) for sharing their private observations on species distribution and habitat preferences; and finally to the staff of the Seewinkel National Park for their technical assistance during the fieldwork in Austria. The study was financially supported by the VEGA Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic, project no. 2/0001/20, title "Islands of continental saline vegetation in temperate Europe – what they have in common and in what they differ?".

References

Bartha D., Király G., Schmidt D., Tiborcz V., Barina Z., Csiky J., Jakab G., Lesku B., Schmotzer A., Vidéki R., Vojtkó A. & Zólyomi Sz. (2015) Distribution atlas of vascular plants of Hungary. – University of West Hungary Press, Sopron.

Bihari Z., Babolcsai G., Bartholy J., Ferenczi Z., Gerhát-Kerényi J., Haszpra L., Homoki-Ujváry K., Kovács T., Lakatos M., Németh Á., Pongrácz R., Putsay M., Szabó P. & Szépszó G. (2018) Climate. – In: Kocsis K. (ed.), National atlas of Hungary. Natural environment, p. 58–69, MTA CSFK Geographical Institute, Budapest.

Borhidi A. (1995) Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. – Acta Botanica Hungarica 39: 97–181.

Breckle S.-W. (1985) Die siebenbürgische Halophyten-Flora-Ökologie und ihre pflanzengeographische Einordnung. – In: Heltmann H. & Wendelberger G. (eds), Naturwissenschaftliche Forschung über Siebenbürgen. III. Beiträge zur Pflanzengeographie des Südost-Karpatenraumes, p. 53–105, Böhlau, Köln, Wien.

Breckle S.-W. & Wucherer W. (2012) Halophytes and salt desertification in the Aralkum area. – In: Breckle S.-W., Wucherer W., Dimeyeva L. & Ogar N. (eds), Aralkum: a man-made desert. Ecological Studies, Vol. 218, p. 271–299, Springer, Berlin, Heidelberg.

Bucur N., Dobrescu C., Turcu G. H., Lixandru G. H., Teşu C., Dumbravă I. & Afusoaie D. (1957) Contribuţii la studiul halofiliei plantelor din păşuni şi fâneţe de sărătură din Depresiunea Jijia-Bahlui (partea a I-a) [Contributions to the study of halophytes in pastures and salt marshes in the Jijia-Bahlui Depression (Part Ia)]. – Studii şi Cercetări (Biol şi Şt Agricole), Academia R. P. Române. Filiala Iaşi 8: 277–317.

Chapman V. J. (1960) Salt marshes and salt deserts of the world. – Leonard Hill (Books) Ltd., London, Interscience Publishers, Inc., New York.

Chytrý M., Tichý L., Dřevojan P., Sádlo J. & Zelený D. (2018) Ellenberg-type indicator values for the Czech flora. – Preslia 90: 83–103.

Chytrý M., Tichý L., Hennekens S. M., Knollová I., Janssen J. A. M., Rodwell. J. S., Peterka T., Marcenò C., Landucci F., Danihelka J., Hájek M., Dengler J., Novák P., Zukal D., Jiménez-Alfaro B., Bruelheide H., Mucina L., Aćić S., Agrillo E., Attorre F., Bergmeier E., Biurrun I., Boch S., Bölöni J., Bonari G., Braslavskaya T., Campos J. A., Casella L., Ćuk M., Ćušterevska R., Čarni A., Demina O., Didukh Y., Dítě D., Dziuba T., Gégout J. C., Giusso del Galdo G., Goral F., Graf U., Indreica A., Jandt U., Jansen F., Jansen J., Jašková A., Kalníková V., Kavgacı A., Khanina L., Korolyu A. Y., Kozhevnikova M., Kuzemko A., Küzmič F., Laiviņš M., Lavrinenko I., Lavrinenko O., Lebedeva M., Maciejewski L., Onyshchenko V., Haase A. P., Pielech R., Prokhorov V., Rašomavičius V., Rodríguez Rojo M. P., Rūsiņa S., Schrautzer J., Stančić Z., Šibík J., Šilc U., Škvorc Ž., Tikhonova E., Tonteri T., Uogintas D., Valachovič M., Vassilev K., Willner W., Yamalov S., Evans D., Lund M. P., Spyropoulou R., Tryfon E. & Schaminée J. H. J. (2020) EUNIS Habitat Classification: expert system, indicator species and distribution maps of European habitats. – Applied Vegetation Science 23: 648–675.

Clements F. E. (1907) Plant physiology and ecology. – Henry Holt and Company, New York.

Crozier A. A. (1892) A dictionary of botanical terms. – Henry Holt and Company, New York.

Danihelka J., Chytrý K., Harásek M., Hubatka P., Klinkovská K., Kratoš F., Kučerová A., Slachová K., Szokala D., Prokešová H., Šmerdová E., Večeřa M. & Chytrý M. (2022) Halophytic flora and vegetation in southern Moravia and northern Lower Austria: past and present. – Preslia 94: 13–110.

Diekmann M. (2003) Species indicator values as an important tool in applied plant ecology: a review. – Basic Applied Ecology 4: 493–506.

Dítě D., Eliáš P. Jr. & Sádovský M. (2004) Recentný výskyt halofytov v Liptovskej a Spišských kotlinách (severné Slovensko) [Recent occurrence of halophytes in Liptovská kotlina Basin and Spišské kotliny Basin (northern Slovakia)]. – Bulletin Slovenskej botanickej spoločnosti 26/Suppl. 10: 117–121.

Dítě D., Hájek M., Svitková I., Košuthová A., Šoltés R. & Kliment J. (2018) Glacial-relict symptoms in the Western Carpathian flora. – Folia Geobotanica 53: 277–300.

Dítě D., Šuvada R. & Dítě Z. (2021a) Habitat shaped by ancient salt: inland halophytic plant communities of the Transylvanian Basin (Romania). – Folia Geobotanica 56: 109–123.

Dítě Z., Šuvada R. & Dítě D. (2022a) Isolated occurrence of halophytic vegetation on mineral springs in the Eastern and Western Carpathians. – Folia Geobotanica 57: 231–246.

Dítě D., Šuvada R., Kliment J. & Dítě Z. (2022b) Vegetation of temperate inland salt marshes on their north-western border (North German Plain). – Preslia 94: 111–141.

Dítě Z., Šuvada R., Tóth T., Eliáš P. Jr., Píš V. & Dítě D. (2021b) Current condition of Pannonic salt steppes at their distribution limit: what do indicator species reveal about habitat quality? – Plants 10: 530.

Douaik A., van Meirvenne M. & Tóth T. (2005) Soil salinity mapping using spatio-temporal kriging and bayesian maximum entropy with interval soft data. – Geoderma 128: 234–248.

Eliáš P. Jr., Dítě D., Grulich V. & Sádovský M. (2008) Distribution and communities of *Crypsis aculeata* and *Heleochloa schoenoide*s in Slovakia. – Hacquetia 7: 5–20.

Eliáš P. Jr., Dítě Z. & Dítě D. (2020) Poznámky k výskytu hviezdovca sivého (*Galatella cana*) na Slovensku [Contribution to occurrence of *Galatella cana* in Slovakia]. – Bulletin Slovenskej botanickej spoločnosti 42: 129–137.

Ellenberg H., Weber H. E., Düll R., Wirth V., Werner W. & Paulißen D. (1991) Zeigerwerte von Pflanzen in Mitteleuropa. – Scripta Geobotanica 18: 1–248.

Euro+Med (2006+) Euro+Med PlantBase: the information resource for Euro-Mediterranean plant diversity. – URL: http://www.europlusmed.org.

Fick S. E. & Hijmans R. J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. – International Journal of Climatology 37: 4302–4315.

Flowers T. J. & Colmer T. D. (2008) Salinity tolerance in halophytes. – New Phytologist 179: 945–963.

Golub V. B. (1995) Halophytic, desert and semi-desert plant communities on the territory of the former USSR. – Russian Academy of Sciences, Institute of Ecology of the Volga River Basin, Togliatti.

Grigore M. N. (2012) Romanian salt tolerant plants. Taxonomy and ecology. – Tehnopress, Iaşi.

Grigore M. N. (2021) Definition and classification of halophytes as an ecological group of plants. – In: Grigore M. N. (ed.), Handbook of halophytes: from molecules to ecosystems towards biosaline agriculture, p. 3–50, Springer, Cham.

Grigore M. N. & Cojocariu A. (2021) A tentative list of Romanian halophytes: taxonomy, distribution, and ecology. – In: Grigore M. N. (ed.), Handbook of halophytes: from molecules to ecosystems towards biosaline agriculture, p. 471–567, Springer, Cham.

Grulich V. (1987) Slanomilné rostliny na jižní Moravě (katalog historických lokalit) [Halophytes in southern Moravia (catalogue of historical sites)]. – Český svaz ochránců přírody, Břeclav.

Haj-Amor Z., Hashemi H. & Bouri S. (2017) Soil salinization and critical shallow groundwater depth under saline irrigation condition in a Saharan irrigated land. – Arabian Journal of Geosciences 10: 1–13.

Hájek M., Dítě D., Horsáková H., Mikulášková E., Peterka T., Navrátilová J., Borja J. A., Hájková P., Tichý L. & Horsák M. (2020) Towards the pan-European bioindication system: assessing and testing updated hydrological indicator values for vascular plants and bryophytes in mires. – Ecological Indicators 116: 106527.

Hammer Ø., Harper D. A. T. & Ryan P. D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. – Palaeontologia Electronica 4: art. 9,
URL: http://palaeo-electronica.org/2001_1/past/issue1_01.htm.

Hennekens S. M. & Schaminée J. H. J. (2001) TURBOVEG, a comprehensive data base management system for vegetation data. – Journal of Vegetation Science 12: 589–591.

Holzapfel C. (2009) Deserts. – In: Jørgensen S. V. (ed.), Ecosystem ecology, p. 222-240, Academic Press, Amsterdam.

Horsák M., Hájek M., Tichý L. & Juřičková L. (2007) Plant indicator values as a tool for land mollusc autecology assessment. – Acta Oecologica 32: 161–171.
Hütterer F. & Albert R. (1993) An ecophysiological investigation of plants from a habitat in Zwingendorf (Lower Austria) containing Glauber's salt. – Phyton (Horn) 33: 139–168.
Iversen J. (1936) Biologische Pflanzentypen als Hilfsmittel in der Vegetationsforschung. – Levin und Munksgaard, Kopenhagen.
Király G. (ed.) (2009) Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok [New Hungarian herbal. The vascular plants of Hungary. Identification keys]. – ANP Igazgatóság, Jósvafő.
Koyro H. W., Geissler N. & Hussin S. (2009) Survival at extreme locations: life strategies of halophytes. – In: Ashraf M., Ozturk M. & Athar H. R. (eds), Salinity and water stress. Improving crop efficiency, p. 167–177, Springer Science + Business Media B.V., Dordrecht.
Krist V. (1940) Halofytní vegetace jihozápadního Slovenska a severní části Malé uherské nížiny [Halophytic vegetation of south-western Slovakia and northern part of the Little Hungarian Plain]. – Práce Moravské přírodovědecké společnosti 12: 1–100.
Kun A., Ruprecht E. & Szabó A. (2004) Az Erdélyi-medence bioklimatológiai jellemzése [The bioclimatological characteristics of the Transylvanian Basin, Romania]. – Múzeumi Füzetek 13: 63–81.
Leuschner C. & Ellenberg H. (2017) Salt marshes and inland saline habitats. – In: Ecology of Central European non-forest vegetation: coastal to alpine, natural to man-made habitats, p. 3–60, Springer, Cham.
Meusel H. & Jäger E. J. (eds) (1992) Vergleichende Chorologie der Zentraleuropäischen Flora. Band III. – Gustav Fischer Verlag, Jena.
Molnár Z. & Borhidi A. (2003) Hungarian alkali vegetation: origin, landscape history, syntaxonomy, conservation. – Phytocoenologia 33: 377–408.
Mucina L., Bültmann H., Dierßen K., Theurillat J. P., Raus T., Čarni A., Šumberová K., Willner W., Dengler J., Gavilán García R., Chytrý M., Hájek M., Di Pietro R., Iakushenko D., Pallas J., Daniëls F. J. A., Bergmeier E., Santos Guerra A., Ermakov N., Valachovič M., Schaminée J. H. J., Lysenko T., Didukh Y. P., Pignatti S., Rodwell J. S., Capelo J., Weber H. E., Solomeshch A., Dimopoulos P., Aguiar C., Hennekens S. M. & Tichý L. (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. – Applied Vegetation Sciece 19 (Suppl. 1): 3–264.
Peel M. C., Finlayson B. L. & McMahon T. A. (2007) Updated world map of the Köppen-Geiger climate classification. – Hydrology and Earth System Sciences 11: 1633–1644.
Piernik A. (2012) Ecological pattern of inland salt marsh vegetation in Central Europe. – Nicolaus Copernicus University Press, Toruń.
Prodan I. (1922) Oecologia plantelor halofile din România, comparate cu cele din Ungaria şi Şesul Tisei din regatul SHS [The ecology of halophilic plants in Romania, compared to those in Hungary and the Tisza Plain in Yugoslavia]. – Buletinul de informaţii al Grădinii Botanice şi al Muzeului Botanic dela Universitatea din Cluj 2: 37–52, 69–84, 101–112.
Prodan I. (1939) Flora pentru determinarea şi descrierea plantelor ce cresc în România, Ediţia a II-a [Flora for the determination and description of plants growing in Romania, Ed. 2]. – Cartea Românească, Cluj.
QGIS Development Team (2018) QGIS geographic information system. – Open Source Geospatial Foundation Project, URL: http://qgis.osgeo.org.
Quinn J. A. (2009) Desert biomes. – Greenwood Press, Westport.
Richards L. A. (1954) Diagnosis and improvement of saline and alkali soils. – Agriculture handbook No. 60, U.S. Department of Agriculture, U.S. Government Printing Office, Washington.
Santos J., Al-Azzawi M., Aronson J. & Flowers T. J. (2016) eHALOPH a database of salt-tolerant plants: helping put halophytes to work. – Plant & Cell Physiology 57: e10.
Sârbu I., Ştefan N. & Oprea A. (2013) Plante vasculare din România: determinator ilustrat de teren [Vascular plants of Romania: an illustrated field guide]. – Editura Victor B Victor, Bucarest.
Scherfose V. (1990) Salz-Zeigerwerte von Gefäßpflanzen der Salzmarschen, Tideröhrichte und Salzwassertümpel an der deutschen Nord- und Ostseeküste. – Jahresbericht Niedersächsisches Landesamt für Wasser und Abfall Forschungstelle Küste 39: 31–82.
Šmarda J. (1953) Halofytní květena jižní Moravy [Halophytic flora of southern Moravia]. – Práce Moravskoslezské akademie věd přírodních 25: 121–168.
Šmarda J. (1961) Vegetační poměry Spišské kotliny [Vegetation conditions of the Spiš basin]. – Vydavateľstvo Slovenskej Akademie Vied, Bratislava.
StatSoft, Inc. (2004) STATISTICA (data analysis software system), version 7. – URL: www.statsoft.com.
Szabolcs I. (1974) Salt affected soils in Europe. – Martinus Nijhoff, The Hague, The Netherlands.

Szendrei G., Tóth T. & Kovács-Pálffy P. (2014) Sulphate and chloride salt efflorescences and their relationships with groundwaters and soils in Hungary. – Agrokémia és Talajtan 63: 29–38.
Tichý L., Axmanová I., Dengler J., Guarino R., Jansen F., Midolo G., Nobis P. M., Van Meerbeek K., Aćić S., Attorre F., Bergmeier E., Biurrun I., Bonari G., Bruelheide H., Campos J. A., Čarni A., Chiarucci A., Ćuk M., Ćušterevska R., Didukh Y., Dítě D., Dítě Z., Dziuba T., Fanelli G., Fernández-Pascual E., Garbolino E., Gavilán R. G., Gégout J. C., Graf U., Güler B., Hájek M., Hennekens S. M., Jandt U., Jašková A., Jiménez-Alfaro B., Julve P., Kambach S., Karger D. N., Karrer G., Kavgacı A., Knollová I., Kuzemko A., Küzmič F., Landucci F., Lengyel A., Lenoir J., Marcenò C., Moeslund J. E., Novák P., Pérez-Haase A., Peterka T., Pielech R., Pignatti A., Rašomavičius V., Rūsiņa S., Saatkamp A., Šilc U., Škvorc Ž., Theurillat J. P., Wohlgemuth T. & Chytrý M. (2023) Ellenberg-type indicator values for European vascular plant species. – Journal of Vegetation Science 34: e13168.
Toman M. (1976) Halofilní květena severozápadních Čech [Halophilous flora of northern Bohemia]. – Preslia 48: 60–75.
Tóth T. (2010) Medium-term vegetation dynamics and their association with edaphic conditions in two Hungarian saline grassland communities. – Grassland Science 56: 13–18.
Ungar I. A. (1974) Inland halophytes of the United States. – In: Reimold R. & Queen W. (eds), Ecology of halophytes, p. 235–305, Academic Press, New York.
Ventura Y., Eshel A., Pasternak D. & Sagi M. (2015) The development of halophyte-based agriculture: past and present. – Annals of Botany 115: 529–540.
Vicherek J. (1973) Die Pflanzengesellschaften der Halophyten- und Subhalophytenvegetation der Tschechoslowakei. – Academia, Praha.
Volkmar K. M., Hu Y. & Steppuhn H. (1998) Physiological responses of plants to salinity: a review. – Canadian Journal of Plant Science 78: 19–27.
Wilkoń-Michalska J. (1963) Halofity Kujaw [Halophytes of Kujawy]. – Studia Societatis Scientianarum Torunensis, Seria D, Botanica 7: 3–122.
Woch M. W. & Trzcińska-Tacik H. (2015) High occurrence of rare inland halophytes on post-mining sites in western Ukraine. – Nordic Journal of Botany 33: 101–108.
Zelený D. & Schaffers A. P. (2012) Too good to be true: pitfalls of using mean Ellenberg indicator values in vegetation analyses. – Journal of Vegetation Science 23: 419–431.

Halofyty vnitrozemských slanisk střední Evropy

V Evropě existuje dlouhá tradice přiřazování ekologických indikačních hodnot rostlinným druhům a jejich využití v ekologickém výzkumu. Zvláštním případem jsou druhy tolerantní vůči zasolení. Zasolené půdy jsou extrémně heterogenní a jejich fyzikální a chemické vlastnosti se výrazně liší v rámci mikroreliéfu a mezi sezónně se střídajícími suchými a vlhkými obdobími. Pro charakterizaci biotopů jsou ekologické indikační hodnoty vhodnější, než hodnoty přímo naměřeného obsahu soli v půdě, které vyžadují přísné určení hloubky odběru a jsou zatíženy případnými krátkodobými fluktuacemi. Naše práce představuje první nadregionální databázi cévnatých rostlin vyskytujících se na vnitrozemských slaniskách a slaných stepích temperátní Evropy, založenou na expertní revizi literárních údajů a dat z dlouhodobého terénního výzkumu. Inventarizace 190 druhů odolných vůči zasolení byla provedena podle jejich kvantitativního zastoupení v zasolených a nezasolených biotopech. Na základě zastoupení v jednotlivých biotopech jsme tyto druhy zařadili do tří kategorií tolerance vůči zasolení (obligátní a fakultativní halofyty, akcesorické druhy). Zároveň jsme každému druhu přiřadili číselnou hodnotu na devítibodové stupnici, odrážející individuální preference k slaniskovým biotopům (salinity půdy). Na slané půdy, respektive slaniskové biotopy, spolehlivě upozorňuje přítomnost obligátních halofytů; tito specialisté rostou výhradně v přirozených zasolených biotopech. Do této skupiny bylo zařazeno pouze 45 druhů, zatímco skupinu fakultativních halofytů tvoří 61 druhů a akcesorických druhů s širokou ekologickou nikou, vyskytujících se na zasolených stanovištích víceméně náhodně, je 84. Jejich počet je neuzavřený, protože jakoukoli rostlinu zaznamenanou v slaniskové vegetaci lze považovat za akcesorický druh. Zařazení druhů na škále salinity v rozmezí 1 až 9 ukázalo blízkou shodu s indikačními hodnotami publikovanými v minulosti Ellenbergem, Borhidim a Brecklem; byly zjištěny pouze drobné rozdíly.

How to cite: Dítě D., Šuvada R., Tóth T. & Dítě Z. (2023) Inventory of the halophytes in inland central Europe. – Preslia 95: 215–240.

Preslia, a journal of the Czech Botanical Society

www.preslia.cz