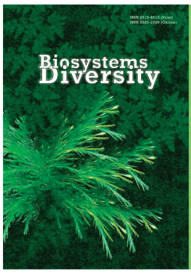

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Ecological and physiological peculiarities of bryophytes on a post-technogenic salinized territory

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Taxonomic, biomorphological and ecological structures of bryophytes, their reproductive strategy and the main mechanisms of tolerance in the conditions of salinization were investigated. Bryophytes are the pioneers that have colonized the territory of a tailing storage that holds liquid waste from potassium-magnesium concentrate production of the Mining and Chemical Enterprise "Polymineral". Due to excess salts, the soil solution in the shore area of the tailing pond acquires high osmotic pressure. Three experimental plots which differed significantly in the level of the substrate salinity were laid at the distance of 3, 6 and 9 m from the reservoir for experimental studies. Water extracts of the substrates from the test sites showed the highest concentrations for sulfates – 10.4–64.6 mg Eq/100 g of soil and chlorides – 7.6–43.3 mg Eq/100 g of soil. It was established that the investigated areas of the tailing storage territory differed in the biochemical activity of the substrate, which was evaluated by its redox potential. On the areas of the uncovered substrate it was the lowest – 230 mV, which indicates anaerobiosis in conditions of very high salinization and moisture. Higher ROP values were determined at the sites of bryophyte cover distribution – 295–330 mV. The aim of the study was to determine the features of taxonomic, biomorphological and ecological structures of bryophytes, their reproductive strategy and to establish the main mechanisms of adaptation to the conditions of salinization on the tailing storage territory. 24 species and 3 varieties of bryophytes, belonging to 12 families and 16 genera were found on the shore of the tailing storage pond. The results of biomorphological and ecological analysis of bryophytes indicate the uneven conditions of the habitats and their considerable ecological plasticity. Among the bryophytes, mesophytes, xeromesophytes and meso-eutrophs, eutrophs with a life-form of low dense and loose turf dominated. In salinization conditions, dioicous acrocarpous mosses prevailed, the fertile turf of which, depending on the influence of abiotic factors, differed significantly in the number of sexual shoots, their ratio and productivity. Bulbils were found only on the tips of *Bryum argenteum* shoots. Along with *Salicornia europaea* L., a euhalophyte, the leading role in the initial stage of overgrowth of the tailing storage area most often belonged to *Didymodon rigidulus*, *Bryum argenteum*, *Funaria hygrometrica* and *Barbula unguiculata*. The process of formation of bryophyte cover occurred along a gradient of decrease in salt concentration at the experimental sites. Adaptation of bryophytes to substrate salinity is due to a change in metabolic processes, which is manifested in an increase of the total content of carbohydrates and an increase of the cation exchange capacity of moss cell walls, which is the primary barrier that reduces the toxic effect of ions under salt stress.

Keywords: salt stress; tailings storage; moss reproduction; carbohydrates; cation exchange capacity; plant ecomorphogenesis.

Introduction

Due to the extraction of potassium and magnesium salts, specific man-made ecotopes were formed near the town Stebnyk in Lviv region. From the first half of the nineteenth century raw kainite (without enrichment) and table salt were produced in this area. After the building of the Stebnyk Chemical Processing Factory in 1967 the Potassium Plant produced potassium-magnesium mineral fertilizer. The technology of mineral processing was to dissolve potassium salt rocks with hot water to precipitate insoluble clay residue and to separate the highly concentrated brine from the sediment and crystallize potassium-magnesium concentrate from it. The production of potassium-magnesium concentrate was accompanied by the formation of a large amount of waste in the form of sludge – "tails", relatively stable fine suspensions. Clay material as well as the undissolved polyhalite, halite and the brine with high content of sodium chloride and potassium-magnesium salts got into the waste. The waste from the chemical processing plant was transported by pipeline to a tailings dump located in the northeast neighborhood of Stebnyk. The liquid phase of the Stebnyk tailings is in fact a secondary deposit of potassium-magnesium salts, which poses a potential environmental threat. After cessation of production, the demutation of plant cover at these territories is mostly spontaneous. Due to their high tolerance to the effect of ecological change, bryophytes play an important role in succession processes on devastated territories where other plants cannot initially grow (Lobachevska et al., 2005; Glime, 2006; Maestre et al., 2015). By inhabiting such disturbed territories, pioneer moss turfs form a new succession with changes in humidity (Shcherbachenko et al., 2015; Rabyk et al., 2017), mineral (Vilmundardóttir et al., 2018) and organic status of the substrate (Karpinets et al., 2016; Kyyak & Baik, 2016; Karpinets et al., 2017). The participation of bryophytes in the revitalization of plant cover of technogenic ecosystems is determined by their high tolerance to drying (Kyyak & Khorkavtsiv, 2015; Kyyak et al., 2017; Lobachevska & Sokhanchak, 2017), their ability to restore soil due to the structuring of its upper horizons (Carter & Arocena, 2000; Aronson & Alexander, 2013; Jackson, 2015), to prevent its erosion (Haig, 2016; Baughman et al., 2017; Stark, 2017), to absorb and retain moisture (Seitz et al., 2017; Batista et al., 2018; Delgado-Baquerizo et al., 2018), thereby reducing surface runoff (Greenwood & Stark, 2014; Zhao et al., 2014; García et al., 2016). Due to its specific properties of metabolism, moss turf has a significant effect on the soil chemical reaction, accelerating the exchange of cations in the biogeochemical cycle, affecting the circulation of organic carbon and nutrients through the release of mineral and organic compounds into soil solutions (Douma et al., 2007; Kyyak & Baik, 2016), synthesis of phenolic substances with a wide spectrum of antimicrobial action, which promotes the development of a substantial litter layer, in which the processes of mineralization are much slower, biogenic elements are accumulated and favourable conditions for the growth of the underground organs of vascular plants are created (Cortina-Segarra et al., 2016; Bueno de Mesquita et al., 2017). Bryophyte cover plays an important role in the nitrogen cycle not only in the substrate but also in altering its cyclization in the ecosystem (Reed et al., 2012; Ball & Guevara, 2014). Bryophytes largely determine the structure of the plant cover, protecting the seeds of vascular plants from the effects of extreme temperatures and increasing the viability of their seedlings (Whitehead et al., 2018).

Adaptation of bryophytes to the microclimatic conditions of their habitats is manifested in the growth form and morphological structure of moss turfs, which is an important ecological indicator. The distribution of bryophytes into ecological groups is mainly influenced by the macroclimatic factors and features of the microenvironment: light intensity (shading), humidity and temperature. The ecological mechanisms of bryophyte richness and the structure of their distribution, depending on the gradients of microclimatic conditions, still need further study (Lobachevska, 2014).

The peculiarity of the overgrowth of the tailings areas is the formation of pioneer succession stages from organisms of halophytic and salt-resistant ecological groups (Pakhomov et al., 2008; Kul'bachko et al., 2015). So far, no halophytes and specialized mechanisms of salt resistance have been found among the bryophytes compared to vascular plants. There is little information to this date on either the effect of salt stress on bryophytes or the mechanisms that ensure their spread and survival in salinity (Garbary et al., 2008), so it is important to clarify the features of their adaptive strategy in salinity conditions. Such data are important for modeling the response of an entire ecosystem to changing environmental conditions and help to elucidate the ecological role of bryophytes in restoring disturbed ecosystems.

The aim of the study is to determine the features of taxonomic, biomorphological and ecological structures of bryophytes, their reproductive strategy and to establish the main mechanisms of adaptation to the conditions of salinization on the territory of tailing storage of Mining and Chemical Enterprise "Polymineral".

Materials and methods

Research of the bryophyte species composition was carried out on the shore of the tailing storage of the Mining and Chemical Enterprise "Polymineral", namely technogenic reservoirs that were used to dump liquid waste of flotation ore enrichment and production of potassium-magnesium concentrate. The field survey method was used to study moss cover. Taxonomic processing of materials was carried out according to the conventional comparative-morphological method using bryophyte identification guides (Ignatov & Ignatova, 2003, 2004). Nomenclature and authors of moss species are given by Boiko (2014). The classification of mosses was carried out according to "Morphology, anatomy, and classification of the Bryophyta" (Goffinet et al., 2009). Ecological groups were determined according to the criteria proposed by Rikovsky & Maslovsky (2004). To determine the life forms and life cycle strategies of the bryophytes, the classification of Glime (2006) was used. The number of male, female and sterile plants, percentage of sexual shoots, sexual proportion as the quotient from of total number of fertile plants were determined from every growth locality of arbitrarily chosen turfs having the size 3 × 3 cm (Lobachevska & Sokhanchak, 2017). The actual acidity (pH) of the substrates was determined potentiometrically in the aqueous extract by the ratio of soil: solution 1 : 5 (Nikolaychuk et al., 2000).

For experimental studies, 3 pilot sites were laid on the tailings storage area at distances of 3, 6, and 9 m from the reservoir, which differed significantly in the level of substrate salinity: plot 1 – very strongly saline area, plot 2 – strongly saline wet area, plot 3 – strongly saline dry area.

Determination of the content of water-soluble ions in the upper layer of the tailings substrate (0–3 cm) was carried out by a complexometric method. The chemical ionic composition of the aqueous extracts filtrate prepared from the tested substrate samples was determined by standard methods: HCO_3^-, Cl^-, SO_4^{2-}, Ca^{2+} and Mg^{2+} (GOST 26424-27-85, 1985. Pochvy. Metody opredeleniya ionov v vodnoy vytyazhke [State standard 26424-85. Soils. Methods of ions determination in aqueous exhaust]).

The quantity of cations (Na^+ and K^+) was determined by the difference between the sum of anions (HCO_3^-; Cl^-; SO_4^{2-}) and the sum of cations (Ca^{2+}, Mg^{2+}) in mg Eq/100 g of soil. The redox potential of the substrate was determined using the Ezodo 5041 ORP meter. Cell walls of moss shoots were isolated by the method of Stassart (1981) using the 1% solution of Triton X-100. The cation exchange capacity of the cell walls was determined by the method of Blamey (1990). The method is based on alternate holding of plant samples in a solution of HCl (0.1 M) and KCl at a concentration of 1 M, pH 7.0. The amount of adsorbed hydrogen ions was detected by estimating the pH change of the KCl solution before and after exposure of the plant material. Cation exchange capacity was expressed in mg Eq/100 g of dry weight. The total carbohydrate content was determined by the phenol-sulfate method after acid hydrolysis of the samples (Sadasivam & Manickam, 2007).

The results were processed by standard methods with the calculation of x – mean value, SE – standard error. Differences between the variants were considered statistically significant at $P < 0.05$, 0.01, and 0.001. The difference between the variants of the study was proved by using the standard procedure of one-factor ANOVA.

Results

Biomorphological and ecological structures of bryophytes, their reproductive strategy as well as the mechanisms of resistance to salinity need detailed study. Based on the results of the analysis of the water-soluble ion content in substrates on the territory of the tailings storage, it was established that the experimental plots differ significantly in the content of anions and cations. Among the anions, the highest concentrations were determined for sulfates – 10.4–64.6 mg Eq/100 g of soil, and chlorides – 7.6–43.3 mg Eq/100 g of soil, much lower – for bicarbonates – 2.2–9.7 mg Eq/100 g of soil (Table 1). Among the cations from water extractions, there were significantly more Ca^{2+} – 10.2–40.2 mg Eq/100 g soil, and Mg^{2+} – 8.8–38.7 mg Eq/100 g soil ions at all sites (Table 1).

The highest levels of ion content were recorded in the bare substrate, which explains the lack of plant cover on this area. In plot 1, the predominant ion content was: SO_4^{2-} ion – 32.7 mg Eq/100 g of soil, and Cl^- ion – 27.3 mg Eq/100 g of soil, indicating a very strong degree of substrate salinization. The dissemination of *Didymodon tophaceus*, a calcephilic species, under such conditions is apparently due to the liming of the shoreline tailing territory. In the aqueous extracts of the substrate of plot 2, somewhat lower indices of the ionic composition (SO_4^{2-} – 23.6, Cl^- – 12.4 mg Eq/100 g of soil) were determined, although these values also indicate very saline substrate, which has caused the predominance of mainly halophytes and salt-tolerant species of vascular plants, as well as mosses with low-dense and loose turf, which are characteristic of devastated territories, since the morphological structure of the turf, especially dense, is well adapted to absorption of atmospheric moisture. In plot 3, the content of SO_4^{2-} ions and Cl^- ions was significantly lower (10.4 and 7.6 mg Eq/100 g of soil, respectively), indicating a high degree of salinization. The species composition of the bryophyte communities in this area was the most diverse in terms of life forms and ecological features (Table 4).

Table 1
The content of water-soluble ions in the substrate of the tailing storage of the Stebnyk Mining and Chemical Enterprise "Polymineral" (mg Eq/100 g of soil, x ± SE, n = 5)

Place of the substrate samples collection	Na^++K^+	Ca^{2+}	Mg^{2+}	Sum of cations	HCO_3^-	Cl^-	SO_4^{2-}	Sum of anions
Substrate without plants (control)	38.7 ± 3.6	40.2 ± 3.1	38.7 ± 3.4	117.6	9.7 ± 0.8	43.3 ± 3.6	64.6 ± 5.8	117.6
Very strongly saline area (plot 1)	11.3 ± 0.9***	24.3 ± 2.3***	28.6 ± 2.5	64.2	5.9 ± 0.6**	27.3 ± 2.8***	32.7 ± 3.6***	65.9
Strongly saline wet area (plot 2)	6.7 ± 0.2***	17.6 ± 0.9***	15.8 ± 1.1***	40.1	3.7 ± 1.6***	12.4 ± 0.6***	23.6 ± 1.4***	39.7
Strongly saline dry area (plot 3)	1.2 ± 0.1***	10.2 ± 0.5***	8.8 ± 0.4***	20.2	2.2 ± 0.1***	7.6 ± 0.6***	10.4 ± 0.5***	20.2

Note: ** – difference compared to substrate without plants is statistically reliable at $P < 0.01$, *** – at $P < 0.001$.

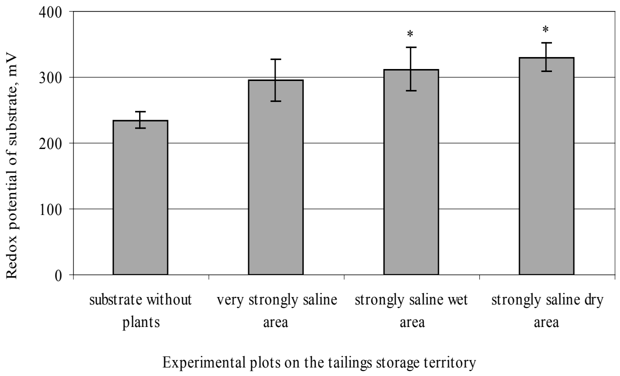

Fig. 1. Redox potential of the substrate on the experimental plots of the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral" (x ± SE, n = 5): * – difference compared to substrate without plants is statistically reliable at $P < 0.05$

It was found that the investigated plots at the tailings storage territory differed in biochemical activity of the substrate, which was evaluated by their redox potential. Soil samples for analysis were selected at the locality of *Didymodon rigidulus*. In the areas of the bare substrate, redox potential was the lowest (Fig. 1), indicating anaerobiosis in conditions of very strong salinization and moisture. Higher redox potential values are defined in the areas of distribution of the bryophyte cover. In the covered substrate that was the farthest from the water reservoir of the tailing, redox potential increased to 330 mV (Fig. 2).

In our investigations 24 species and 3 varieties of bryophytes (Table 2), belonging to two divisions (Marchantiophyta and Bryophyta), 2 classes (Bryopsida and Jungermanniopsida), 12 families and 16 genera were identified as a result of the studies of the bryophyte species composition on the shores of the tailing storage. The largest is the Pottiaceae family – 6 species (25%) belonging to 3 genera (19%): *Aloina*, *Barbula*, *Didymodon*. *Didymodon rigidulus* has two varieties – *D. rigidulus* var. *gracilis* (Schleich. ex Hook. & Grev.) R. H. Zander. and *D. rigidulus* var. *giganteus* (Schleiph. ex Warnst.) Ochyra & Bedn.-Ochyra, comb. nov. (Table 3).

Table 2
List of species and varieties of bryophytes found on the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral"

Divisio, Classis, Ordo, Familia, Genus	Species (variety)	Ecological group*	Life form**	Sexual type**	Life strategy**
Marchantiophyta, Jungermanniopsida, Jungermanniales, Cephaloziaceae, *Cephalozia*	*C. catenulata* (Hübener) Lindb.	mesotrophic mesophyte	smooth mat	dioicous	colonist
Bryophyta, Bryopsida, Funariales, Funariaceae, *Funaria*	*F. hygrometrica* Hedw.	eutrophic hygromesophyte	short loose turf	monoicous	fugitive
Dicranales, Fissidentaceae, *Fissidens*	*F. taxifolius* Hedw.	eutrophic mesophyte	short loose turf	heteroicous	colonist
Ditrichaceae, *Ceratodon*	*C. purpureus* (Hedw.) Brid.	oligomesotrophic xeromesophyte	short tight turf	dioicous	colonist
Dicranaceae, *Dicranella*	*D. varia* (Hedw.) Schimp.	mesotrophic mesophyte	short loose turf	dioicous	colonist
Pottiales, Pottiaceae, *Aloina*	*A. ambigua* (Bruch et Schimp.) Limpr.	eutrophic xeromesophyte	short loose turf	dioicous	perennial shuttle
	A. rigida (Hedw.) Limpr.	eutrophic xeromesophyte	short loose turf	dioicous	perennial shuttle
Barbula	*B.unguiculata* Hedw.	mesoeutrophic xeromesophyte	short loose turf	dioicous	colonist
Didymodon	*D. fallax* (Hedw.) Zander	eutrophic mesophyte	short loose turf	dioicous	colonist
	D. rigidulus Hedw.	mesoeutrophic xeromesophyte	short tight turf	dioicous	colonist
	D. rigidulus var. *gracilis* (Schleich. ex Hook. & Grev.) R. H. Zander	mesoeutrophic xeromesophyte	short tight turf	dioicous	colonist
	D. rigidulus var. *giganteus* (Schleiph. ex Warnst.) Ochyra & Bedn.-Ochyra, comb. nov.	mesoeutrophic xeromesophyte	short tight turf	dioicous	colonist
	D. tophaceus (Brid.) Lisa	mesoeutrophic mesohydrophyte	short tight turf	dioicous	colonist
Splachnales, Meesiaceae, *Leptobryum*	*L. pyriforme* (Hedw.) Wilson.	mesotrophic mesophyte	short loose turf	monoicous	colonist
Bryales, Bryaceae, *Bryum*	*B. argenteum* Hedw.	oligomesotrophic xeromesophyte	short loose turf	dioicous	colonist
	B. caespiticium Hedw.	mesoeutrophic xeromesophyte	short tight turf	dioicous	colonist
	B. intermedium (Brid.) Blandow.	mesotrophic mesophyte	short tight turf	monoicous	colonist
	B. pallescens Schleich. ex Schwägr.	mesotrophic mesophyte	short tight turf	monoicous	colonist
Ptychostomum	*P. pseudotriquetrum* (Hedw.) J. R. Spence & H. P. Ramsay.	eutrophic hygromesophyte	short tight turf	dioicous	colonist
	P. pseudotriquetrum var. *bimum* (Schreb.) Holyoak & N. Pedersen	eutrophic hygromesophyte	short tight turf	dioicous	colonist
Mniaceae, *Plagiomnium*	*P. cuspidatum* (Hedw.) T. J. Kop.	mesoeutrophic mesophyte	tall loose turf	monoicous	perennial stayer
Hypnales, Amblystegiaceae, *Amblysthegium*	*A. serpens* (Hedw.) Schimp.	mesoeutrophic mesophyte	loose weft	monoicous	colonist
Brachytheciaceae, *Brachythecium*	*B. campestre* (Müll. Hall.) Schimp.	mesotrophic mesophyte	loose weft	monoicous	colonist
	B. glareosum (Bruch. ex Spruce) Schimp.	mesoeutrophic mesophyte	loose weft	dioicous	perennial stayer
	B. rutabulum (Hedw.) Schimp.	mesoeutrophic mesophyte	loose weft	dioicous	perennial stayer
Oxyrrhynchium	*O. hians* (Hedw) Loeske	mesoeutrophic hygromesophyte	loose weft	dioicous	perennial stayer
Hypnaceae, *Calliergonella*	*C. cuspidata* (Hedw.) Loeske	eutrophic hygrophyte	loose weft	dioicous	perennial stayer

Note: * – were determined according to the criteria of Rikovsky & Maslovsky (2004); ** – the classification of Glime (2006) was used.

There are 5 species in the Bryaceae family (20.7%) that belong to two genera (12.6%): *Bryum* and *Ptychostomum*, in the species *P. pseudotriquetrum* (Hedw.) J. R. Spence & H. P. Ramsay the variety *P. pseudotriquetrum* var. *bimum* (Schreb.) Holyoak & N. Pedersen was found. The Brachytheciaceae family includes 4 species (16.5%) of two genera *Brachythecium* and *Oxyrrhynchium*. The remaining 9 families are monospecific. It was established that on the territory with the highest concentration of salts in the substrate (experimental plot 1) the following types of mosses prevail in pioneer moss communities: *Bryum argenteum*, *Didymodon rigidulus*, *Funaria hygrometica*, *Barbulata unguiculata*, *D. tophaceus*, *Bryum intermedium*, *Leptobryum pyriforme*, *Ptychostomum pseudotriquetrum* (Table 4). It happens due to frequent flooding by tailing water (pH = 7.0–7.2). *Didymodon rigidulus* and *Bryum argenteum* most often play a leading role in the formation of bryophyte cover at the initial stage of overgrowth of tailing storage substrates. The turfs of these species inhabit the most saline areas of the tailings storage, along with *Salicornia europaea* L., a euhalophyte.

In much drier areas (experimental plot 2), among halophytes and salt-resistant vascular plants (*Tripolium vulgare* Nees, *Sagina nodosa* Fenzl., *Puccinella distans* Parl., *Artemisia vulgaris* L.) *Ceratodon purpureus*, *Barbula unguiculata*, *Bryum argenteum*, *Didymodon rigidulus*, *B. intermedium*, *B. pallescens*, *Ptychostomum pseudotriquetrum*, *P. pseudotriquetrum* var. *bimum*, *Dicranella varia*, *Didymodon rigidus* var. *validus*, *D. fallax*, *Aloina ambigua*, *A. rigida*, *Fissidens taxifolius* and occasionally *Brachythecium campestre*, *B. glareosum*, *Cephalozia catenulata* occur predominantly in conditions of lower substrate salinity (pH = 7.2).

Table 3
Taxonomic structure of bryophyte communities on the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral"

Families	Genera		Species	
	number	%	number	%
Pottiaceae	3	19.0	6	25.0
Bryaceae	2	12.6	5	20.7
Brachytheciaceae	2	12.6	4	16.5
Amblystegiaceae	1	6.2	1	4.2
Cephaloziaceae	1	6.2	1	4.2
Dicranaceae	1	6.2	1	4.2
Ditrichaceae	1	6.2	1	4.2
Hypnaceae	1	6.2	1	4.2
Mniaceae	1	6.2	1	4.2
Meesiaceae	1	6.2	1	4.2
Fissidentaceae	1	6.2	1	4.2
Funariaceae	1	6.2	1	4.2
Total	16	100.0	24	100.0

Among resistant herbaceous communities (experimental plot 3, pH = 7.4), acrocarpous colonist pioneer moss species *Barbula unguiculata*, *Didymodon fallax*, *Ceratodon purpureus*, *Bryum caespiticium*, *B. intermedium*, as well as pleurocarpous mosses with the strategy of perennial stayer such as *Brachythecium campestre*, *B. glareosum*, *B. rutabulum*, *Plagiomnium cuspidatum*, *Calliergonella cuspidata*, *Oxyrrhynchium hians*, *Plagiomnium cuspidatum*, *Amblysthegium serpens* were common. By the ecological features of the localities (wetting conditions and substrate trophicity) bryophytes belong to different ecological groups. Moisture conditions are one of the important environmental factors affecting bryophyte resettlement. According to the distribution of the mosses within the areas with different levels of moisture, 5 major hygromorphs were identified. The mesophytic group of bryophytes, which are widespread in areas with moderate moisture levels (mesophytes – 44.4%, xeromesophytes – 32.5%, hygromesophytes – 15.1%; a total of 92.0%) was the most numerous.

Table 4
Colonization of bryophytes on the different plots of the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral"

Very strongly saline areas	Strongly saline wet areas	Strongly saline dry areas
Bryum argenteum	*Ceratodon purpureus*	*Barbula unguiculata*
Didymodon rigidulus	*Barbula unguiculata*	*Didymodon fallax*
Funaria hygrometrica	*Bryum argenteum*	*D. rigidulus*
Barbula unguiculata	*B. intermedium*	*Ceratodon purpureus*
Didymodon tophaceus	*B. pallescens*	*Bryum caespiticium*
Leptobryum pyriforme	*Didymodon rigidulus*	*B. intermedium*,
Bryum intermedium	*Ptychostomum pseudotriquetrum*	*B. argenteum*
Ptychostomum pseudotriquetrum	*P. pseudotriquetrum* var. *bimum*	*Amblysthegium serpens*
	Brachythecium campestre	*Brachythecium campestre*
	B. glareosum	*B.glareosum*
	Cephalozia catenulata	*B. rutabulum*
	Dicranella varia	*Calliergonella cuspidata*
	Didymodon fallax	*Fissidens taxifolius*
	Aloina ambigua	*Plagiomnium cuspidatum*
	A. rigida	*P. cuspidatum*
	Fissidens taxifolius	*Oxyrrhynchium hians*
8	16	16

The predominance of mesophytic conditions also led to the dominance of these hygromorphs of the bryophytes. Only one species of moss is represented by groups of hygrophytes – *Calliergonella cuspidata* (inhabits permanently moist habitats) and mesohygrophytes – *Didymodon tophaceus* (occurs under conditions of permanent moisture).

According to substrate trophicity , which is considered as one of the important factors of moss propagation, there are four groups of bryophytes: mesoeutrophics, eutrophics, mesotrophics, oligomesotrophics. The dominant groups are mesoeutrophics (36.8%) and eutrophics (30.2%), which are mosses that are characteristic of wet areas rich in mineral salts and humus (Fig. 2).

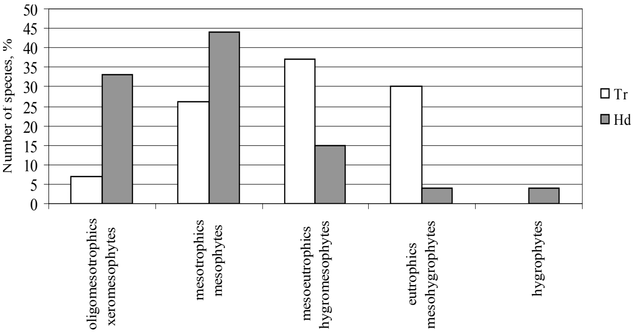

Fig. 2. Ecological structure of bryophytes by humidity (Hd) and trophic ability (Tr) on the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral"

The results of biomorphological composition of bryophytes indicate that the majority of projective cover consists of the life forms of short dense turf (10 species, 37%) in the locality of the experimental plot 1 with stable regime of moistening, and short loose turf (9 species, 33%) in the conditions of high light intensity but lower humidity of experimental plot 2, as well as loose weft (6 species, 22%) under moderate light conditions and sufficient moisture of experimental plot 3.

The identified bryophytes belong to three main sex types: 18 species (66%) of dioicous (unisexual) type, 8 species (29%) of monoicous (bisexual) type and 1 species (4%) of heteroicous (two- and one-sexual gametangia) type.

Of all the bryophytes, 67% of acrocarpous mosses formed sporogonium with capsules. *Bryum argenteum* dominated on the banks of the tailing storage (experimental plot 1), which had recently stopped being exposed to salt brine. Non-availability of gametangia or sporogonia was detected in the moss turfs and reproduction was due to the active formation of bulbils at the shoot tips. This is the only bryophyte species in which vegetative reproduction was determined using asexual specialized bodies. The polymorphic moss *Ceratodon purpureus* also occurred along the shores of the tailing storages (experimental plots 1 and 2), mostly in the sterile state, as it favours acidic substrates. Under high indices of pH (7.0–7.2) no formation of gametangia was observed. On experimental plots 1 and 2, the highest sexual reproduction activity (90% of plants in sporogonium turf) was noted for monoicous mosses *Funaria hygrometrica* (life strategy – fugitive) and *Leptobryum pyriforme* (life strategy – colonist). Among most sterile turfs of *Barbula unguiculata* and *Didymodon rigidulus* isolated shoots with sporogonia were rarely found. Based on the results of the analysis of sexual structure and productivity, most plants of *Barbula unguiculata* in the tailing storage (experimental plot 2) were female (80–84%) with predominantly one (up to 40%) and rarely with three (16–20%) perichaetia. Significant variability in the number of archegonia (from 4 to 36) was revealed in the perichaetia. In *Barbula unguiculata* turfs with sporogonia, sterile plants (67–69%) were predominant; no male specimens were found. All female plants were with sporophytes, with a rather low productivity (from 1 to 4 archegonia) for their gametangia. Many sterile plants (71–76%) were found in fertile turfs of *Barbula unguiculata*, and among fertile females accounted for 20–23% with 1 to 6 archegonia and a very few male plants were identified (6–8%).

The change of the directionality of metabolic processes in bryophytes for adaptation to salt stress is expressed in the accumulation of osmoprotectors, among which sugars are important. It was found that the studied moss species in the tailing storage differed in their total carbohydrate content (Fig. 3).

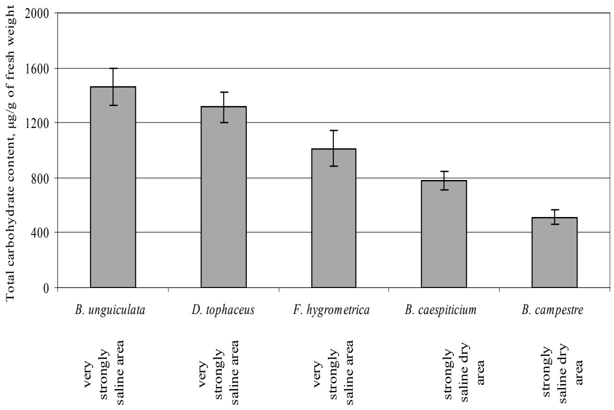

Fig. 3. Carbohydrate content in the moss shoots from experimental plots on the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral", which differed in the salinization level (x ± SE, n = 5)

The highest abundance was determined in *Barbula unguiculata* and *Didymodon tophaceus* from the very strongly saline area. The total content of carbohydrates was lower in mosses from the herbaceous community. That is, carbohydrate accumulation depended on both the species characteristics of mosses and the level of salt stress.

Support for plant growth under salinization conditions is connected with both the regulation of water and osmotic homeostasis and the change in cell wall properties. Cell wall polymers are the primary barrier that reduces the toxicity of many ions under salt stress. This barrier function depends primarily on the cation exchange capacity of the cell walls (CEC). The results of the cell wall CEC measurements in the studied moss indicate a significant variability of the indicator (3.04–11.59 mg Eq/100 g mass of dry weight), apparently due to both the level of substrate salinity and the specific features of the moss (Fig. 4). The least significant difference for the CEC at the probability level of 95% with accordance to the results of ANOVA equaled 0.61 mg Eq/100 g of dry weight.

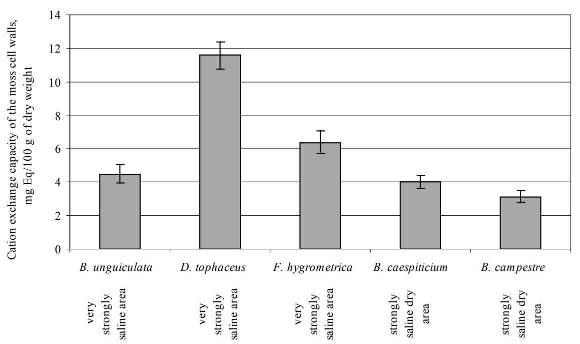

Fig. 4. Cation exchange capacity of the moss cell walls on the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral", which differed in the salinization level (x ± SE, n = 5): differences for mosses are indicated by $P < 0.05$ (one-way ANOVA)

For example, in conditions of very strong substrate salinization, CEC of *Barbula unguiculata* plants was 4.49 mg Eq/100 g of dry matter, *Funaria hygrometrica* – 6.38 mg Eq/100 g of dry weight, at the same time in the calciphile moss species *Didymodon tophaceus* this index reached 11.59 mg Eq/100 g of dry weight. It is known that in most calciferous species of bryophytes, the magnitude of the CEC is 3–5 times higher than in other mosses (Cosić et al., 2018). Due to the high cation exchange capacity of moss cell walls, in cells a barrier is created against the penetration of toxic concentrations ions into the cell. The lower values of CEC are defined in shoots of moss on a substrate with lower salinity: in *Bryum caespiticium* – 4.01 mg Eq/100 g of dry weight, *Brachythecium campestre* – 3.14 mg Eq/100 g of dry weight. (Fig. 4). That is, the CEC of the cell walls depends on the bryophytes' species specific features and the intensity of salt stress and protects the cells from the toxic effects of many ions under saline conditions.

Discussion

Mosses on the territory of the tailing storage of the Stebnyk Mining and Chemical Enterprise "Polymineral" are among the pioneers of overgrowth of the saline tailing substrate. They are colonizing the areas with very strong and strong levels of salinization, which are rarely inhabited by other plants. The predominance of the content of sulfate ions, according to the classification of soils by Bazylevych and Pankova (1970) by the degree of salinization, indicates the sulfate type of salinity of the substrate on the shoreline territory of the tailing storage. In general, the obtained results indicate that, by the specificity of redox processes, tailings substrates can be characterized as substrates with a reductive regime that gradually improves by a gradient of reduction of salinity and moisture of the substrate, as well as an increase in the projective cover of bryophytes. The creation of reductive conditions in the absorption complex of the substrate is mainly due to the accumulation of reducing mineral compounds, which leads to the suppression of the processes of nitrification and deterioration of the phosphate regime.

The processes of formation of bryophyte communities occur along a gradient of salt concentration decrease. A peculiarity of the overgrowth of the investigated areas is the formation of pioneer communities of halophytic and salt-resistant ecological plant groups. Among the bryophytes, there are no halophytes, no specialized mechanisms of salt resistance, unlike in vascular plants, but these plants are also pioneers of overgrowth of the tailing storage saline substrates, forming bryophytic communities near halophytes. *Didymodon rigidulus* and *Bryum argenteum* most often play a leading role in the formation of bryophyte cover at the initial stage of colonization of the tailing storage substrates. The turfs of these species inhabit the most saline areas of the tailing storage, along with the euhalophyte *Salicornia europaea* L.

The Pottiaceae family, whose representatives reflect the ecological and coenotic conditions of sandy outcrops on the banks of the tailing storage, occupy the first place in the bryoflora spectrum. The second-ranked Bryaceae family consists mainly of representatives of the *Bryum* genus, well adapted to diverse environmental conditions, eurytopic species that, through different life strategies, are actively involved in moss cover formation on devastated areas. The Brachytheciaceae family occupies the third place in the bryoflora. Its representatives reflect the diversity of ecocoenotic conditions of the study area. The presence of many mono-species families and mono-species genera indicates that the shores of the tailing storage are significantly influenced by technogenic factors, so moss species with a wide ecological amplitude (eurytopic and indifferent to various environmental factors) migrate from adjacent territories.

Moisture of the substrate is of secondary importance to poikilohydric bryophytes since they do not absorb water from the soil for growth and development as vascular plants, but rather obtain it from the surface of frost, the tops of shoots and leaves after rain, and from fog or dew. However, salt brine from the tailing storage often floods the shore plant cover, causing salt stress and dehydration of the plants.

Hyperosmotic shock and ion imbalance occur in moss cells under the influence of high concentrations of salt ions. In adverse conditions, bryophyte communities are dominated by short-turf xeromesophytic moss species, which are more adapted to lack of moisture due to their xeromorphic features and increased physiological resistance to drought. Osmotic pressure compensation under salinization conditions is due to the accumulation of appropriate osmoprotectors and osmolytes, which have almost no effect on the intracellular pH and maintain the normal activity of many cellular enzymes in the cytosol. In bryophytes, one of the most important mechanisms of adaptation to osmotic stress is to increase the concentration of soluble carbohydrates, which is accompanied by an increase in the osmotic potential of the cell. Enhanced hydrolysis of polymeric forms of carbohydrates, including low molecular weight oligosaccharides, and accumulation of soluble carbohydrates provides internal regulation of water potential and promotes active absorption of water by the plant organism, which is important under salinization conditions (Greenwood & Stark, 2014; Gao et al., 2017). Soluble sugars (primarily sucrose and raffinose) have an anti-denaturation effect on the protein-lipid complex of membranes. They attach to the polar terminal groups of membrane phospholipids and thus stabilize the membrane structure of moss cells under stressful conditions. In addition, high concentrations of sugars in the cell provide vitrification of the cytoplasm and membranes, which gives the cell structures stability and minimizes protein denaturation (Lobachevska et al., 2005; Wang et al., 2008; Bates et al., 2009). Carbohydrates also intercept reactive oxygen species and inhibit the processes of free radical oxidation of biological molecules during the development of oxidative stress induced by salinity. In addition to its protective and antioxidant effects, some carbohydrates can play a signaling role (Flowers et al., 2014; Kyyak & Khorkavtsiv, 2016; Lobachevska et al., 2019).

The cell wall plays a significant role in the formation of plant salt resistance. It is a complexly organized, dynamic cell compartment, which, due to the presence of fixed negatively charged groups, provides modification of the outer solution as a result of the exchange reactions between the ion-exchange groups of the polymer matrix and the medium ions. In fact, the cell wall is the primary protective barrier of the cell against excess ions in salinity conditions. It has been found that the cation exchange capacity of the mosses' cell walls is significantly higher compared to vascular plants and is determined by 70–90% of carboxylic groups of polyuronic acids, primarily galacturonic acid, and partially carboxyl groups bound to cellulose and hemicellulose (Greenwood & Stark, 2014). Protein components are also involved in the adsorption of cations, accounting for 10–30% of the ion-exchange capacity of cell walls not associated with pectin. The cell walls of mosses also have a small anion-exchange capacity, which is probably due to the fixed organic cations of the cell wall matrix – free amino groups of proteins (Janicka-Russak & Kabata, 2015). Substrate salinization usually leads to an increase in CEC of bryophytes regulated by the enzyme methylpectinesterase (Cosić et al., 2018). This enzyme demethylates pectins and thus contributes to the increase of cell wall cation exchange capacity. Its activity depends on the presence of polyamines in the apoplast and, therefore, on the nitrogen nutrition of the plants.

It should be noted that in natural ecosystems, mosses rarely occur under salinization conditions. For example, in Canada, in the oil sands region, natural salt marshes with a high concentration of Na salts formed groups of salt-tolerant plants, among which *Bryum pseudotriquetrum* (Hedw.) G. Gaertn, B. Mey. & Scherb., *Campylium stellatum* (Hedw.) C. E. O. Jensen and *Drepanocladus aduncus* (Hedw.) Warnst. were found (Trites & Bayley, 2009). The species composition of bryophytes in the territory of natural salt steppes in Austria has been investigated (Zechmeister, 2005); *Entosthodon hungaricus* (Boros) Loeske, *Pottia heimii* (Hedw.) Hampe, *Drepanocladus aduncus* (Hedw.) Warnst., *Phascum cuspidatum* var. *mitriforme* Limpr., *P. cuspidatum* Hedw., *Funaria hygrometrica* Hedw. and *Bryum algovicum* Sendtn. ex Müll. Hal. Some mosses, such as *Fontinalis dalecarlica* Bruch & Schimp., *Campylium stellatum* (Hedw.) C. E. O. Jensen and *Schistidium maritimum* (Turner ex Scott, Robert) Bruch & Schimp have a high ability to survive under permanent irrigation by seawater on coastal cliffs, althoughugh bryophytes rarely occur in seawater (Garbary et al., 2008).

Therefore, despite the distribution of bryophytes under salinization conditions, they lack evolutionarily formed specific mechanisms of salt resistance, such as, for example, halophytes, which have adapted to salinity through the formation of specialized subcellular, biochemical and molecular mechanisms, whereas bryophyte adaptation to salt stress is bound with effective mechanisms of desiccation resistance, the important criteria of which (as well as salt resistance) are the ability to osmoregulation, the stability of water and osmotic potentials of plant cells. Although there are only 210 desiccation-resistant species documented among bryophytes, it is considered (Greenwood & Stark, 2014) that most terrestrial bryophytes are to some extent adapted to water deficit, which obviously led to their tolerance to a variety of osmotic stresses. This tolerance is largely ensured by the presence of high concentrations of osmolytes and increased cation exchange ability of cell walls in moss cells.

Conclusion

Bryophytes in the tailing storage area can be classified by the ecological features of the habitat (under the conditions of moisture and substrate trophicity): the majority of mosses are dioicious species (mesophytes, xeromesophytes, hygromesophytes and mesoeutrophs, eutrophs, mesotrophs) with short dense and loose turf life form. The results of the analysis of ecological and biological structure of bryophytes indicate uneven conditions of the habitats and their considerable ecological plasticity. Fertile turfs of dioecious acrocarpous mosses *Barbula unguiculata*, *Didymodon rigidulus*, *D. fallax*, *Ceratodon purpureus*, *Bryum caespiticium*, *B. intermedium* differed significantly in the number of sexual shoots, their ratio, productivity, which is a manifestation of the energy saving strategy: higher number of female plants and the increase of genetic variability of the formed diaspores compared to the male ones, the formation of which requires greater energy costs. The adaptation of bryophytes to salinization is due to a change in the directionality of metabolic processes, which is manifested in an increase of the total content of carbohydrates, which promote to increase the cells' osmotic potential and stabilize their membrane structures under stressful conditions. The increased cation exchange capacity of cell walls is the primary barrier protecting moss cells from excess ions under salinization conditions and an important mechanism for their stress tolerance formation.

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