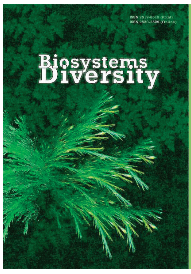

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Role of the bryophytes in substrate revitalization on a post-technogenic salinized territory

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This work aims to investigate the role of the bryophyte cover in substrate revitalization on a post-technogenic salinized territory. The influence of the moss cover on the organic carbon content, actual acidity, redox potential, and the content of the main ecological and trophic groups of microorganisms in the substrate of the tailings storage of the Stebnyk Mining and Chemical Enterprise "Polymineral" was investigated. Bryophytes significantly affect the tailings storage saline substrates. They colonize areas with a very strong and strong degree of salinity, which are unsuitable for other plants. It was indicated that pioneer moss species promote the accumulation of organic matter in saline substrates of the tailings storage. Under moss turfs, the amount of organic carbon increased 2.2–5.0 times, compared with its content in the uncovered substrate. The high variability of the organic matter content is determined by the species characteristics of mosses, primarily their life form. The dense-turf species *Didymodon rigidulus* and *Pthychostomum pseudotriquetrum* var. *bimum* accumulated the most organic matter. The thickness of the litter under the moss turf of these species was much greater than in *Barbula unguiculata* and *Funaria hygrometrica*, which form loose turf. We assessed the specificity of the accumulation of organic carbon in the turfs of the studied mosses. It founded that most organic matter accumulated in the dead parts of the moss turf. In the green parts of the shoots of these moss species the amount of organic carbon was 3–4 times less, which indicates a relationship between litter capacity and content of carbon in the substrate under moss turfs. We investigated the influence of mosses on the actual acidity of the tailings storage substrate. Moss turfs promote the increase of acidity of the aqueous solution of the tailings substrate by 0.2–0.5 units. The tailings storage substrates are characterized by a reduction regime. The redox potential of the substrate under moss cover significantly depended on the species characteristics of mosses. Under the moss cover, the redox potential increased by 1.2–1.4 times, compared with the index for the substrate without moss cover. We studied the influence of moss cover on microbial biomass and the quantity of some ecological-trophic groups of microorganisms in the substrates of the tailings storage. The amount of microbial biomass under moss turfs increased depending on the degree of the substrate salinization and the species characteristics of the mosses. In areas with a very high degree of salinization under the moss turfs of *Didymodon rigidulus* and *Funaria hygrometrica*, the microbial biomass index increased almost two times, compared with the uncovered substrate. We found a significant increase in the quantity of the main ecological and trophic groups of microorganisms (saprophytes, cellulose-destroying bacteria, oligonitrophils and nitrogen fixers) in the substrate under the moss cover. Thus, pioneer moss species have a complex effect on the saline substrate of tailings storage. They accumulate organic matter, increase the acidity of the upper layer, improve the redox regime of the substrate and promote the development of soil microbiota.

Keywords: tailings storage; mosses; organic carbon; actual acidity; redox potential; microorganisms.

Introduction

Bryophytes play a significant role in the revitalization of post-technogenic ecosystems (Belnap & Weber, 2013; Pointing, 2016; Alexander et al., 2016; Gao et al., 2018; Puczko et al., 2018; Cheng et al., 2019; Ćosić et al., 2020). Moss communities accelerate the disintegration of broken rocks and improve the hydrological regime and fertility of rock surfaces by absorbing water, dust particles, and nutrients from the atmosphere (Maik, 2005; Zheng et al., 2009; Jia et al., 2014). Bryophytes promote soil formation by accumulation organic carbon, organic acids and organogenic elements (Karpinets et al., 2014; Kyyak & Baik, 2016). They maintain balance of the subsoil alkalinity and acidity and improve its physical and chemical properties, create conditions for settlement of other plant species and promote the development of microbial communities (Li et al., 2007; Xiao et al., 2014; Jackson, 2015; Zhang et al., 2016; Bueno de Mesquita et al., 2017; Gecheva et al., 2017; Cao et al., 2020).

Quantitative and functional composition of microbiocenoses is an indicator of ecological changes in anthropogenically transformed environments (Maik, 2005; Li et al., 2007; Zheng et al., 2009). In recent years, the study of associations of mosses and microorganisms has been very relevant (Abed et al., 2010; Lindo & Gonzalez, 2010; Steven et al., 2014; Blay et al., 2017; Xiao & Veste, 2017; Maier et al., 2018; Cao et al., 2020). Moss-microbe associations are particularly relevant to terrestrial nitrogen (N) and carbon (C) cycling in northern ecosystems, where mosses are ubiquitously distributed and can be responsible for as much as 50% of ecosystem net primary productivity (Turetsky et al., 2012). Moss-associated N_2-fixing bacteria are often the primary source of ecosystem N inputs in boreal forests and arid lands (DeLuca et al., 2002; Yeager et al., 2007; Sorensen & Michelsen, 2011; Zhang et al., 2011; Lett & Michelsen, 2014). It is known that the development of bryophyte communities on the post-technogenic substrates promotes the accumulation of organic matter and nutrients, which has a positive effect on the soil microbiota development (De Luca, 2002; Gavazov et al., 2010; Stewart et al., 2011).

Bryophytes are generally considered to be non-halophytes (Sabovljević & Sabovljević 2007), their behaviour under salinity conditions has not been studied. It is mostly accepted that bryophytes are absent from saline environments, but some species can tolerate high salt content in the substrate (Navarro et al., 2006; Lim et al., 2012). According to some examples, *Enthostodon hungaricus* (Boros) Loeske was recorded along alkali saline marshes and *Hennediella heimii* (Hedw.) R. H. Zander on saline banks (Ćosić et al., 2019). Some bryophytes form communities in mild saline environments (Ćosić et al., 2020). Naturally saline fens are occasionally found in the Canadian oil sands region or in the boreal zone in general. These fens were colonized by salt tolerant plant communities that include small proportions of mosses *Drepanocladus aduncus* (Hedw.) Warnst. and *Campylium stellatum* (Hedw.) C.E.O. Jensen (Trites & Bayley, 2009).

Therefore, it is important to investigate the role of bryophytes in saline ecosystems. The technogenic substrate of the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral" is relatively poor in nutrients and characterized by a high degree of moisture and salinity, low redox potential, which determines its low potential fertility and suitability for plant growth (Kyyak & Bunio, 2017; Fetsiukh et al., 2018). Bryophytes are some of the pioneers of overgrowing of the tailings storage saline substrates. They colonize areas with a very high and high degree of salinity, which are unsuitable for other plants (Kyyak & Kyyak, 2019). Species of mosses *Didymodon rigidulus* Hedw., *Funaria hygrometrica* Hedw. and *Barbula unguiculata* Hedw. play an important role in the initial stage of the overgrowing of the strongly saline areas of the tailings storage. The article aims to investigate the role of the moss cover on the organic carbon content, actual acidity, redox potential, and the content of the main ecological and trophic groups of microorganisms in the tailings storage substrate of Stebnyk Mining and Chemical Enterprise "Polymineral".

Material and methods

The object of our investigation was mosses from the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral" (Lviv region, Drohobych district). For investigations 4 moss species was chosen: *Didymodon rigidulus* Hedw., *Funaria hygrometrica* Hedw., *Barbula unguiculata* Hedw. and *Ptychostomum pseudotriquetrum* var. *bimum* (Schreb.) Turner. For investigation of the bryophytes' influence on substrate, substrate samples have been chosen under moss cover (2–3 cm) where the bryophytes has the greatest effect.

The investigations were carried out on the three plots on the territory of the tailings storage, which differed significantly by the salinity of the substrate : plot 1 – very heavily saline area, plot 2 – heavily saline wet area, plot 3 – heavily saline dry area. The samples of the uncovered substrate have been used as control.

The actual acidity (pH) of the substrate was determined in the aqueous extract by the ratio of soil:solution 1:5 using the Ezodo 5041 ORP meter (Nikolaychuk et al., 2000). The redox potential of the substrate was determined using the Ezodo 5041 ORP meter.

The content of water-soluble ions SO_4^{2-}, Cl^-, HCO_3^-, Mg^{2+} and Ca^{2+} in the substrate was determined by standard complexometric method (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 content of K^+ and Na^+ was defined by the difference between the sum of anions (Cl^-; SO_4^{2-}, HCO_3^-) and the sum of cations (Ca^{2+}, Mg^{2+}).

The content of organic carbon in the tailings substrate was carried out by I. V. Turyn and B. A. Nikityn method (Mineev, 1989), using chromium mixture. The optical density of solutions measured on the spectrophotometer Specord 210 Plus at the wavelength 590 nm.

We determined the influence of moss cover on the microbial biomass and the quantity of the most important ecological and trophic groups of microorganisms in the substrate of the tailings storage. Sample selection, soil suspension preparation, sowing on appropriate media and colony counting were performed according to generally accepted methods (Tepper et al., 1987). Saprophytes were detected on Luria-Bertani medium, cellulose-degrading bacteria – on Hutchinson medium with filter paper, oligonitrophils – on Ashby medium, and nitrogen fixers – on Fedorov medium. The count of microorganisms cells (CFU-colony-forming units) in 1 g of dry soil was carried out in Petri dishes on the agar surface of the solid medium, taking into account the dilution and relative humidity of the substrate. The number of cellulose-degrading bacteria was determined by the method of soil particles' overgrowing (Tepper et al., 1987). The biomass of microorganisms was evaluated by the rehydration method (Zvyagintsev, 1991).

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

Results

On the tailings storage territory, plant communities are represented by halophytic and salt-resistant species. At these stages, representatives of autochthonous flora are absent, which indicates the unconformity of this area with the conditions of natural soils. Bryophytes are pioneers of the overgrowth of saline tailings storage substrates because their distribution is associated with pioneer groups of early stages of plant succession in these areas. Were selected three plots for the experiments, which differed significantly both in the chemical composition of the substrate (Table 1) and, accordingly, in the species composition of plants.

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

Substrate sampling location	Na^++K^+	Ca^{2+}	Mg^{2+}	Total number of cations	HCO_3^-	Cl^-	SO_4^{2-}	Total number of anions
Uncovered substrate (control)	28.6 ± 3.1	42.6 ± 3.8	39.8 ± 4.3	111.0	8.4 ± 1.2	36.1 ± 4.2	68.2 ± 7.5	112.7
Very heavily saline area (plot 1)	13.4 ± 1.7**	27.4 ± 3.3**	23.2 ± 2.7*	63.9	4.8 ± 0.5	24.1 ± 2.3	32.7 ± 4.1**	61.6
Heavily saline wet area (plot 2)	5.9 ± 0.3***	19.1 ± 1.1***	17.2 ± 1.4***	42.2	3.9 ± 0.2***	14.6 ± 1.1***	25.8 ± 1.9***	44.3
Heavily saline dry area (plot 3)	3.1 ± 0.3***	12.4 ± 1.3***	6.9 ± 0.5***	22.4	2.8 ± 0.2***	8.4 ± 0.7***	12.6 ± 1.3***	23.8

Note: * – difference compared to substrate without plants is statistically reliable at $P < 0.05$, ** – $P < 0.01$; *** – at $P < 0.001$.

Plot 1 – very heavily saline area, where halophyte *Salicornia europaea* L. mainly grows. Moss samples *Didymodon rigidulus* were collected here. Plot 2 – heavily saline wet area, where salt-resistant species (*Sagina nodosa* Fenzl., *Puccinella distans* Parl., *Artemisia vulgaris* L. and *Tripolium vulgare* Nees) were grown. Samples of mosses *Barbula unguiculata* and *Funaria hygrometrica* were collected here. Plot 3 – the furthest from the liquid phase of the tailings storage, where the lowest level of salinity is determined. Samples of the moss *Ptychostomum pseudotriquetrum* var. *bimum* were collected here.

Chemical analysis of the substrate samples at both sites showed the highest content of sulfates (Table 1), which indicates the sulfate type of salinity. The high content of SO_4^{2-} and Cl^- ions at the plot 1 indicated a very high level of the substrate salinity. At the plot 2 the content of Cl^- and SO_4^{2-} ions was almost twice as low, which indicated a strong degree of salinity. Mg^{2+} and Ca^{2+} ions significantly prevailed among the cations of aqueous extracts at both experimental plots. The total content of cations and anions was almost twice as high in the substrate of plot 1, which led to the settlement here mainly of salt-resistant species of vascular plants, and bryophytes with a low turf life form, which are tolerant to various adverse environmental factors. The role of pioneer moss species in the revitalization of the tailings storage substrate was investigated. Taking into account the peculiarities of the moss turfs growth, all organic matter, which is a potential source of humus substances was concentrated in the substrate layer, up to 3 cm deep. The carbon content in the upper layer of the bare substrate (control) of the tailings in the localities of the studied species of mosses was low (Table 2). In the underlying layer of the substrate under the moss turfs *Barbula unguiculata* and *Funaria hygrometrica*, the amount of organic carbon increased 2.2–3.0 times and under the turfs of *Didymodon rigidulus* and *Ptychostomum pseudotriquetrum* var. *bimum* – 4.5–5.0 times, compared with its content in the uncovered substrate.

Table 2
Influence of moss cover on biochemical parameters of tailings storage substrate of the Stebnyk Mining and Chemical Enterprise "Polymineral" (x ± SE, n = 5)

Place of the substrate samples location	pH of the substrste	Content of the organic carbon, %	Redox potential, mV
Substrate without plants (control)	7.23 ± 0.81	0.96 ± 0.08	253.0 ± 21.3
Under the turfs of *P. pseudotriquetrum* var. *bimum*	6.71 ± 0.59	4.88 ± 0.42***	344.0 ± 28.5*
Under the turfs of *D. rigidulus*	6.90 ± 0.78	4.50 ± 0.21***	359.0 ± 33.4**
Under the turfs of *B. unguiculata*	6.69 ± 0.75	2.45 ± 0.18***	337.0 ± 45.2*
Under the turfs of *F. hygrometrica*	6.84 ± 0.81	3.53 ± 0.38***	312.0 ± 25.6

Note: * – difference compared to substrate without plants is statistically reliable at P < 0.05, ** – P < 0.01; *** – at P < 0.001.

The salinity level of the substrate significantly affects the accumulation of organic carbon in the substrate under the moss cover. For *Barbula unguiculata*, which is the dominant moss species at the tailings storage territory, a reliable dependence between the number of anions (as an indicator of salinity) and the content of organic carbon in the substrate under the moss cover was shown (Fig. 1).

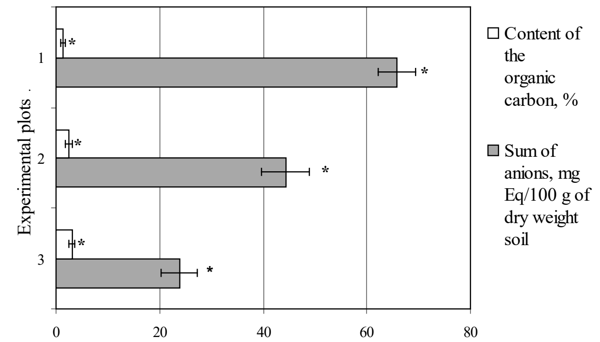

Fig. 1. The organic carbon content under the moss turfs *Barbula unguiculata* depending the sum of anions in substrate of the tailing storage territory of Stebnyk Mining and Chemical Enterprise "Polymineral": *1* – very heavily saline area; *2* – heavily saline wet area; *3* – heavily saline dry area; data are means ± SE for n = 5 samples; differences for samples are indicated by P < 0.05 (ANOVA)

The high variability of organic matter content is determined by the species characteristics of mosses, primarily their life form. The dense-turf species *Didymodon rigidulus* and *Ptychostomum pseudotriquetrum* var. *bimum* accumulated the most organic matter, the thickness of the litter under the moss turf of these species was much greater, than in *Barbula unguiculata* and *Funaria hygrometrica*, which form loose turf. It is shown that the highest percentage of the dead part (up to 75% in the moss turf) was in the samples of *Didymodon rigidulus* (Fig. 2). For *Funaria hygrometrica* and *Barbula unguiculata* the thickness of the dead layer in moss turf was significantly less.

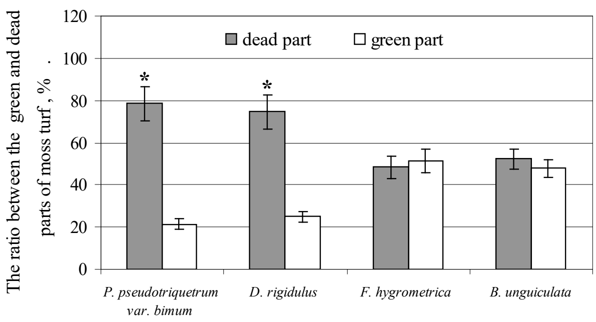

Fig. 2. Interrelation between photosynthesizing (green) and dead parts in the moss turfs from the territory of the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral" (x ± SE, n = 5): * – difference between green and dead parts of the moss turf is statistically reliable at P < 0.05

The specificity of the accumulation of organic carbon in the turfs of the studied mosses was assessed and it was found that most organic carbon accumulated in the dead parts of the moss turf. In the green parts of the shoots of these moss species, the amount of organic carbon was 3–4 times less (Fig. 3). These results indicate a relationship between litter capacity and content of the carbon in the substrate under moss turfs.

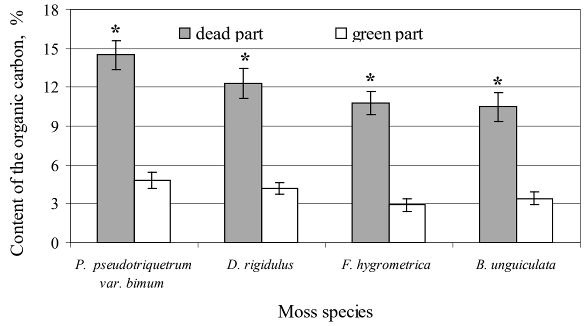

Fig. 3. The content of organic carbon in the green and dead part of moss shoots from the territory of the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral" (x ± SE, n = 5): * – difference between the content of organic carbon in green and dead parts of the moss turf is statistically reliable at P < 0.05

The cross-correlation-regressive analysis of the connection between litter capacity and content of organic carbon in the substrate under a mossy cover showed that the obtained dependence described by a linear equalization has a high coefficient of correlation (0.91), the level of approximation (R^2) presented 0.90. The accumulation of organic matter in the substrate under the moss cover correlates with the thickness of the dead layer in the moss turfs (Fig. 4).

It is possible to assert based on the obtained results, that the pioneer moss species promote the accumulation of organic matter in saline substrates of the tailings storage. Probably a significant part of organic matter under the moss cover is not represented by humus compounds but by the undecomposed organic remains (mainly, products of moss turf dying). These may be due to the slow rate of mineralization of plant remains due to specific hydrological conditions, the reductive regime of the substrate, and the immaturity of communities of microorganisms which play a major role in the decomposition of organic matter.

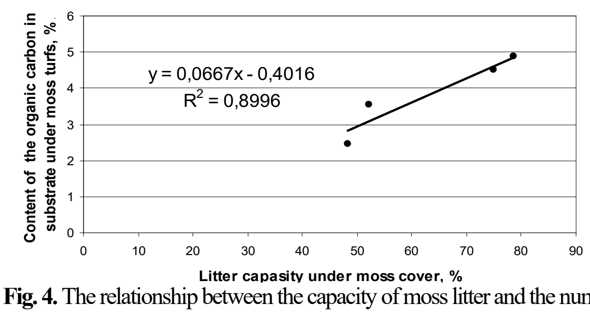

Fig. 4. The relationship between the capacity of moss litter and the number of carbon in the substrate under the moss cover in the territory of the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral"

We investigated the effect of moss turfs on the actual acidity of the tailings storage substrate. A neutral pH value (7.1–7.3) was determined for the uncovered substrate of strongly saline areas. Moss turfs of all studied species promoted the increase of acidity of the aqueous soil solution of the upper layer of the tailings substrate by 0.2–0.5 units, thus providing increases of the metabolic processes activity in the substrate. Compared with the bare substrate, the most significant increase of the acidity was found under turf of *Barbula unguiculata* and *Ptychostomum pseudotriquetrum* var. *bimum*, the change in pH was less expressed under *Funaria hygrometrica* and *Didymodon rigidulus* turfs. That is, in the moss cover an acidic environment was created due to the circulation of solutions with a high concentration of water-soluble organic acids, ammonia nitrogen, phosphorus, potassium, calcium and magnesium, which contributes to acidification not only in turf but also in the upper substrate layer. Thus, the greater the thickness of the moss litter, the more significant the effect of moss cover on the substrate actual acidity.

In the alkaline environment of the tailings storage substrate, metabolic processes occurred at low values of redox potential. In the bare tailings storage substrate, the redox potential rate was low, indicating significant anaerobiosis and the recovery regime of the tailings substrate. Under the moss cover, the redox potential of the substrate increased 1.2–1.4 times (Table 2). It was indicated that the redox potential significantly depended on the species characteristics of mosses. The highest rates were determined for dense turf species of *Didymodon rigidulus* and *Ptychostomum pseudotriquetrum* var. *bimum*, which form a quite thick layer of bedding (2–3 cm), compared with other investigated moss species. Under the moss cover formed by plants of these species, the substrate loosens and acquires a coarse-grained structure due to the secretions of moss turfs. Its porosity increases, which contributes to the enrichment of the substrate with oxygen and eliminates the effect of substrate anaerobiosis. It is one of the causes of the technogenic substrate's recovery.

The influence of moss cover on microbial biomass and the quantity of some ecological-trophic groups of microorganisms in the substrates of the tailings storage were studied. We found that the quantity of the bacteria biomass in the substrate samples from the experimental areas at the tailings storage was in the range of 3.19–11.27 μg C/g dry weight soil (Table 3). In the bare substrate with a very high degree of salinity the lowest biomass indexes were fixed. The amount of microbial biomass under moss turfs increased depending on the degree of the substrate salinization and the species characteristics of mosses. In areas with a very high degree of salinization under the moss turfs of *Didymodon rigidulus* and *Funaria hygrometrica*, the microbial biomass index increased to 5.09–6.10 μg C/g dry weight soil. We recorded higher values under perennial turfs of *Ptychostomum pseudotriquetrum* var. *bimum*, which grew furthest from the liquid phase of the tailings storage, with a twice as low degree of the substrate salinity.

Table 3

Influence of moss cover on the microbial biomass and the quantity of some ecological-trophic groups of microorganisms in the tailings storage substrate of Stebnyk Mining and Chemical Enterprise "Polymineral" ($x \pm SE$, $n = 5$)

Place of the substrate samples' location	Microbial biomass, μg C/g of dry weight soil	The number of saprophytes, CFU/g of dry weight soil	The number of cellulose-degr-ading bacteria, % of soil particles overgrowing	The number of oligonitrophils, CFU/g of dry weight soil	The number of nitrogen fixers, CFU/g of dry weight soil
Substrate without plants (control)	3.19 ± 0.35	$1.9 \cdot 10^3 \pm 0.09 \cdot 10^3$	–	$2.2 \cdot 10^3 \pm 0.19 \cdot 10^3$	$1.2 \cdot 10^3 \pm 0.09 \cdot 10^3$
Under the turfs of *D. rigidulus*	5.09 ± 0.48**	$2.3 \cdot 10^4 \pm 0.18 \cdot 10^4$***	–	$3.1 \cdot 10^4 \pm 0.24 \cdot 10^4$***	$1.8 \cdot 10^4 \pm 0.21 \cdot 10^4$***
Under the turfs of *F. hygrometrica*	6.10 ± 0.72**	$4.5 \cdot 10^4 \pm 0.35 \cdot 10^4$***	24.5 ± 2.2	$4.7 \cdot 10^4 \pm 0.53 \cdot 10^4$***	$3.2 \cdot 10^4 \pm 0.38 \cdot 10^4$***
Under the turfs of *B. unguiculata*	7.13 ± 0.82***	$5.8 \cdot 10^4 \pm 0.61 \cdot 10^4$***	32.2 ± 3.0	$4.1 \cdot 10^4 \pm 0.32 \cdot 10^4$***	$6.1 \cdot 10^4 \pm 0.44 \cdot 10^4$***
Under the turfs of *P. pseudotriquetrum* var. *bimum*	11.27 ± 1.92***	$8.8 \cdot 10^4 \pm 0.81 \cdot 10^4$***	56.4 ± 3.1	$6.4 \cdot 10^4 \pm 0.52 \cdot 10^4$***	$7.3 \cdot 10^4 \pm 0.65 \cdot 10^4$***

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

Differences in microbial biomass indexes correlated with the results of investigations of the influence of substrate salinity on the ecological and trophic groups of microorganisms. It was established that the most numerous were the group of microorganisms that use organic forms of nitrogen – saprophytes. Their growth is significantly inhibited in the bare substrate due to unfavourable aeration conditions, moisture excess and low content of plant remains, so the number was $1.9 \cdot 10^3$ CFU/g of dry weight soil. Bryophytes significantly influenced the saprophytes' number. Under the turfs of *Didymodon rigidulus* and *Funaria hygrometrica*, their quantity increased more than 10 times. The largest number of saprophytes was fixed under the *Ptychostomum pseudotriquetrum* var. *bimum* turfs.

The influence of moss cover on the quantity of cellulose-degrading bacteria, which are the main indicators of the soil fertility, was studied. Since the development of this microorganism group largely depends on the presence of plant remains, substrate aeration and nitrogen nutrition, we did not detect them in the non-turf substrate. Moss cover promoted the development of cellulose-degrading bacteria. Colonies of these microorganisms were not detected in conditions of very high salinity under the *Didymodon rigidulus* turfs, so the degree of salinity of the substrate is also important. In a conditions of slightly lower substrate salinity under the turfs of *Funaria hygrometrica* and *Barbula unguiculata*, their quantity was 24.5–32.2% of fouling. The highest quantity of cellulose-degrading bacteria was determined at the lower salinity of the substrate under *Ptychostomum pseudotriquetrum* var. *bimum* turfs. The turfs of this species have a significant layer of dead plant mass (2.0–2.5 cm thickness). Also, *Ptychostomum pseudotriquetrum* var. *bimum* plants form a thick rhizoid felt, which, penetrating the substrate, increases its porosity and enriches it with oxygen. A significant increase of the cellulose-degrading bacteria quantity under *Ptychostomum pseudotriquetrum* var. *bimum* turfs occurs due to salinity decrease, improvement of the structure, and water-air characteristics of the substrate under the moss turfs, as well as due to an increase of the quantity of plant remains.

Oligonitrophilic microorganisms complete the organic substances mineralization, their development depends on the aeration and redox potential of the substrate and the presence of easily accessible organic substances. The number of oligonitrophils in the non-covered substrate was $2.2 \cdot 10^3$ CFU/g of dry weight soil. Under the moss cover, their number was in the range of $3.1 \cdot 10^4$–$6.4 \cdot 10^4$ CFU/g of dry weight soil. There was an increase in the quantity of this ecological-trophic group of microorganisms by a gradient of substrate salinity and, accordingly, improvement of the substrate redox potential was noted.

The positive effect of moss cover on the number of nitrogen fixers in the tailings storage substrate was revealed. The number of nitrogen-fixing bacteria in the substrate under the moss turfs was almost ten times larger than their quantity in the substrate without plants.

Discussion

One of the major abiotic factors that reduce plant productivity worldwide is salt stress (Munns & Tester, 2008; Ćosić et al., 2020). Increased salt content in the substrate has an adverse effect on plant growth and development. Salts have various osmotic and ionic effects on vascular plant growth, development and function, but very few data can be found on how salt affects bryophytes. Bryophytes are generally considered to be non-halophytes (Oliver et al., 2005; Sabovljević & Sabovljević 2007; Wang et al., 2012). There are no data on what the mechanisms for survival of these species have been under such unfavourable conditions.

Bryophytes play an important role in an ecosystem in many ways. Bryophytes have a great capacity to stabilize soil, mosses in particular are very effective and successful as soil binders and nutrient trappers. They have high water holding capacity and ability to tolerate desiccation. Bryophytes are spread by apical growth and even after their subsequent decay, the apex grows in a mat in favourable condition, which helps to hold the water and soon the young ones. They form a moist wet ground to form a cushion; which ultimately helps growth of other vascular seedlings later. This maintains the high humidity regime in ecosystems (Bates, 1990).

The nutrient supply determines fertility of soils and suitability for plant colonization. Bryophytes are involved in the circulation of nutritious in ecosystems (Brisbee et al., 2001). They absorb nutritious substances from precipitation and atmospheric air, and keep them in the undecomposed part of the moss turfs (Turetsky et al., 2012; Kyyak & Baik, 2016). This can be explained by the growing conditions of mosses (high level of the humidity, high actual acidity, low temperature) and physical and chemical peculiarities of the moss cells (high cation exchange capacity and high concentrations of phenolic compounds and lipids in the cell walls) (Lobachevska et al., 2005; Seedre & Chen, 2010; Lobachevska, 2014; Kyyak & Khorkavtsiv, 2016). In addition to the storage of mineral nutrients, bryophytes are able to accumulate carbon. Storage of organic carbon as photosynthate, predictably, can be found in leaves, but labelled carbon soon accumulates in other places as well. In particular, in mosses from boreal forest *Hylocomium splendens* (Hedw.) Schimp., *Polytrichum commune* Hedw. and *Sphagnum subsecundum* Nees it accumulated in the brown tissues (Glime, 2006). In our investigations most organic matter was found in the dead part of moss turfs.

On the territory of the tailing storage, pioneer moss species colonize substrates that are unsuitable for other plant species. After some time, bryophyte communities form an organogenic horizon. We established dependence between the content of organic matter in the substrate under moss turfs and the thickness of the moss litter. The maximum quantity of the carbon was determined under *Ptychostomum pseudotriquetrum* var. *bimum* and *Didymodon rigidulus* turfs, which form dense turfs. The litter thickness under the turf of these species is much greater than in *Barbula unguiculata* and *Funaria hygrometrica*, which form loose turf.

It can be argued based on the obtained results that the pioneer moss species contribute to the accumulation of organic matter in the saline substrates of the tailings storage. Probably a significant part of organic matter under the moss cover is represented not by humic compounds, but by undecomposed organic remains (mainly, products of moss turf dying). It is conditioned by the slow mineralization of plant remains as a result of special water regime, high salt concentrations, reduction substrate regime and immaturity of microorganisms communities, which play a significance role in destructions of organic remains.

The dead part of the moss turfs has high acidity, so the moss bedding has high absorption capacity and contains large concentrations of macro- and microelements necessary for the plant growth. For example, mosses alone account about 75% of the annual accumulation of phosphorus (Bowden et al., 1999). Sometimes bryophytes reduce mineral availability to other organisms and become successful competitors. During precipitation, mosses absorb some elements very well. This is due to the high cation exchange capacity of many mosses (Glime, 2006). It has been shown that an acidic environment is created in the moss cover due to the circulation of solutions with a high concentration of water-soluble organic acids, ammonia nitrogen, phosphorus, potassium, calcium and magnesium, which promotes acidification not only in turf but also in the upper substrate layer (Karpinets et al., 2014; Kyyak & Baik, 2016).

Due to this, mosses can influence the soil acidity and improve its physical and chemical properties. Moss turfs of all investigated species promoted the increase of the aqueous soil solution acidity of the upper layer of the tailings storage substrate by 0.2–0.5 units, thus providing increases in the metabolic processes activity in the substrate.

According to the specifics of redox processes, the tailings storage substrates are characterized by a reduction regime. The creation of a reducing regime in the substrate leads to inhibition of nitrification processes and negative changes in the phosphate regime. Our investigations have shown that pioneer species of mosses significantly influence the substrate redox potential. First, we should note the important role of dense turf moss species *Didymodon rigidulus* and *Ptychostomum pseudotriquetrum* var. *bimum*. Under the turfs of these species, the substrate loosens and acquires a coarse-grained structure, increases its porosity, which contributes to oxygen enrichment of the substrate and thus eliminates the effect of anaerobiosis, which is one of the reasons for the technogenic substrate recovery regime at the tailings storage territory. It is shown that under the moss cover, the redox potential of the substrate increased by 1.2–1.4 times, compared with the index for the substrate without moss cover.

Mosses associate with a broad diversity of microbes, including, bacteria, fungi, and other microbial eukaryotes (Lindo & Gonzalez, 2010). These moss-microbe associations are particularly relevant to terrestrial nitrogen (N) and carbon (C) cycling in northern ecosystems, where mosses are ubiquitously distributed and can be responsible for as much as 50% of ecosystem net primary productivity (Turetsky et al., 2012). The importance of moss-microbial communities to terrestrial biogeochemistry and unique features of bryophyte biology make moss communities a useful system for investigating the interactions between host species identity, microbial community structure, and ecosystem function (Kip et al., 2010; Wang et al., 2015; Jean et al., 2020). It is known that bryophyte communities promote the development of associative nitrogen fixers (Bragina et al., 2013; Stuiver et al., 2014; Cutler et al., 2017). It was established that bryophytes provide congenial habitat for nitrogen-fixing Cyanophyceae, e.g., *Nostoc*, *Scytonema*, etc. Moss-associated cyanobacteria are an important source of nitrogen in the boreal forest and arid lands (Zhang et al., 2011; Lett & Michelsen, 2014). Some microorganisms inhabit the surface of mosses and play an important role in adaptation of their owners to extreme environmental conditions (Opelt & Berg 2004; Liu et al., 2014; Tian & Li, 2016; Cao et al., 2020). Two *Methylobacterium* strains were found on the surface of leaves of the gametophyte moss *Funaria hygrometrica*. It was indicated that this bacteria activated the process of bud formation in moss protonemata and growth of protonemal filaments (Hornschuh et al., 2006). On the surface of *Sphagnum* mosses endophytic methanotrophic bacteria were found. It was established that these bacteria provided carbon for photosynthesis via oxidation of methane to carbon dioxide (Raghoebarsing et al., 2005; Liu et al., 2014).

It is known that the number of soil microorganisms is affected primarily by vegetation, organic matter content, the environment reaction and the presence of mineral elements (Xiao & Veste, 2017). The development of soil microbiota was significantly inhibited in the substrate of the tailings storage. The main reasons for slowing down the process of microbiocenosis formation are the high degree of salinization and humidity of the substrate, low redox potential, and anaerobiosis. We found the increase of soil microflora quantity on the investigated plots of the tailings storage territory. It shows self restoration of technologically changed substrates, in which mosses play an important role as stimulators of development and enrichment of heterotrophic and nitrogen-fixing microflora specific composition. It has been shown that on the substrates covered with bryophytes the quantity and specific variability of microorganisms increases.

Thus, pioneer species of bryophytes significantly improve the structure and properties of the substrate, contribute to the accumulation of organic matter and nutrients, increase the acidity of the upper layer of the substrate, which increases the quantity of some ecological and trophic groups of microorganisms (saprophytes, cellulose-destroying bacteria, oligonitrophils and nitrogen fixers). These microorganisms change the mineral status of the substrate, and the site becomes suitable for the settlement of other vegetation.

Conclusions

Pioneer moss species have a complex effect on the saline substrate of the tailings storage: initiate the processes of the upper horizons structuring, accumulate organic matter and increase the acidity of the upper layer, which has a positive effect on the redox regime of the substrate and the activity of pioneer plant species. In the substrate of the tailings storage of Stebnyk Mining and Chemical Enterprise "Polymineral" the development of soil microbiota is significantly inhibited. The high degree of salinization and moistening of the substrate, low redox potential, and anaerobiosis are the main reasons for slowing down the process of the microbiocenosis formation. Bryophytes improve the structure and quality of the substrate, due to which mutually beneficial biotic relationships between microflora and plants form. We found a significant increase in the quantity of the main ecological and trophic groups of microorganisms (saprophytes, cellulose-destroying bacteria, oligonitrophils and nitrogen fixers) in the substrate under the moss cover.

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