

Bryophytes on the devastated territories of sulphur deposits and their role in restoration of dump substrate

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Bryophytes possess a wide ecological diapason allowing them to populate substrates of technogenic origins which are scarcely suitable or completely unsuitable for viability of vascular plants. 49 bryophyte species, which belong to 2 divisions, 3 classes, 8 orders, 17 families, and 33 genera have been found on the dump territory of sulphur extraction of the mining-chemical enterprise “Sirka” (Yavoriv district, Lviv region). Seven transects, three on the north slope (base, slope, top), three on the south slope and one on the plateau were laid for sample selections. 20 investigated 0.5×0.5 m plots located 2 m apart were analyzed within each 10×10 m transect. Specific composition, life forms, projective cover, biomass of bryophytes, numbers of male, female and sterile plants, moisture content in the turfs, pH and physiological investigation of mosses were determined on each plot. The quantitative analysis of the biomorphological structure allowed us to establish the dependence of the spread of life forms on exposition and slope height; essential variability of the projective cover and moss biomass. Bryophyte cover plays an essential part in optimization of the moisture regime and surface layer temperature of technogenic substrates, improving the conditions of growth localities. We established that on the dump the dominant moss species are dioecious with a high level of reproductive effort (sexual and sexless), with short ontogenesis and age of first reproduction, which provides the chance to produce the maximum number of progeny in the minimum period and to form a complete moss cover. The analysis of seasonal moss photosynthesis dynamics has demonstrated the adaptability of moss photosynthetic apparatus to contrasting climatic conditions and the ability to support the intensity of photosynthetic processes on a rather stable level during the vegetative period. Our research showed that bryophytes play an important role in productivity of plant cover on the post-technogenic territories of sulphur extraction. It was found that bryophytes play a role in accumulation of organic carbon and biogenic elements in the substrate of the sulphur extraction dump. Carrying out research of specific composition dynamics and species activity is the precondition for revealing the essence of the dynamic processes taking place in the structure of the bryophyte communities on devastated territories and the influence of these processes on the formation of vegetation on dump complexes.

Keywords: mosses; life forms; reproduction; photosynthesis activity; organic carbon

Introduction

The restoration of territories devastated as a result of excavation of natural sulphur deposits is one of most important ecological problems in Western Ukraine. Technogenic changes in these territories are so profound that formation of artificial high-productive agrocenoses here is economically unjustified, requiring permanent subsidies in the process of exploitation. A new approach connected with the maximum utilization of regenerating possibilities of natural ecosystems for restoring resources and ecological functions of devastated territories – their “ecological restoration”, has been developed in the world practice of rehabilitation of technogenic geosystems. The use of the potential of plant communities adapted to anthropogenically changed substrates gives a chance to decrease significantly the intensity of denudation processes of technical soil and initiate soil forming processes in them. The conception of technogenic ecosystem restoration is ecologically grounded and economically justified (Moreno Mateos et al., 2012; Aronson & Alexander, 2013; Alexander et al., 2016; Cortina-Segarra et al., 2016; Tolvanen & Aronson, 2016).

As the result of open-cast mine exploitation of native sulphur extraction on the territory of Novoyavorivsk state mining-chemical enterprise “Sirka” (Lviv region, Ukraine), a number of dumps of various ages composed both of the rocks which take part in the zone’s soil formation and from bedding rocks which do not form soils (e.g. tertiary clays, sulphur containing limestones etc.) have been formed. The main problem in cultivating dump rocks is their hostility to biota and sometimes their toxicity. Bryophytes were among the first to settle on

the dump substrates and formed a thick, multispecific overgrowth (Shcherbachenko et al., 2015; Rabyk et al., 2017). The investigations of sexual and vegetative reproduction of monoecia and dioecia are important aspects for explaining the peculiarities of reproductive strategy of moss (Szövényi et al., 2009; McDaniel & Perroud, 2012; Bisang et al., 2014; Barrett, 2015; Bisang et al., 2017). Light intensity, temperature and substrate pH, forming different conditions for mosses’ development, influence the formation of gametangia and sporophyte development of bryophytes and lead to the variety of their reproductive cycles (Longton, 2006; Crowley et al., 2005; Crawford et al., 2009; Devos et al., 2011). Variability of reproductive phenology of moss is connected with temporal form changes and development of moss plants under the influence of microclimatic turf conditions and the season. By now it has been established (Söderström & During, 2005; Maciel-Silva & Válio, 2011; Baughman et al., 2017) that the scale of self-fecundation of monoecious moss species is evidently exaggerated, as their cross fecundation occurs more often than was considered earlier (Longton, 2006). Thus, the advantage of dioecious species first of all consists in cross fecundation, which owing to fast purification of the gene pool from harmful mutations and accumulation of useful changes gives the populations the opportunity to be adapted to changeable environmental conditions. The periods of sexless and sexual reproduction which provide them with considerably higher life activity, reproductive and genetic variability and effective colonization of devastated territories are alternated in the majority of dominant dioecious bryophyte species as the result of energy conservation strategy. Vegetative reproduction in bryophytes occurs in various forms, which are divided into three main types: vegetative organs, frag-

mentation and specialized sexless reproductive propagula (Glime, 2006). Mainly dioecious perennial moss species, which are rather often sterile, are propagated only in a vegetative way. The simplest and the most widespread method of vegetative reproduction consists in separation of young shoots as the result of the dying off of the branched maternal shoot below or the underground part of its stolons. Usually any isolated moss fragment is able to form the secondary protonema and new plants under rather favourable conditions. Brood propagula (fragile stems, branches, flagella, bulbids and rhizoid tubers) are distinguished among specialized reproductive organs. Brood propagula have apical cells and can germinate into shoots without forming protonema and gemmae (falling leaves, chloronemous and endogenous gemmae), which always start their growth with protonema formation because of the lack of apical cells (Duckett & Pressel, 2003).

Functioning of photosynthetic apparatus determines productivity of plant cover under the changeable conditions of the natural environment. Information on functioning of photosynthetic apparatus and productivity of bryophytes will give us the possibility to assess their role in preserving biodiversity and contribution to the total productivity of plant cover. Productivity and peculiarities of moss biology have been investigated in detail, taking Sphagnopsida, bryophytes of wood groups and bogs, tundra ecosystems, and chalky meadows of Europe as examples (Proctor, 2000; Grogan & Jonasson, 2006; Goffinet & Shaw, 2009; Street et al., 2011; Hanson & Rice, 2014). The role of bryophytes in populating and restoring technogenically devastated territories has practically not been investigated. It is known that carbon accumulation is determined by the ability of a phytocoenosis to absorb CO₂ in the process of photosynthesis and to some extent depends on the chlorophyll content in plants. Therefore, the study of photosynthetic intensity of mosses on the dump territory will provide an opportunity to establish their role in the productive process of plant cover on the technogenic substrates of sulphur production. Bryophytes are the first to colonise dump substrates, gradually forming dense, multispecific cover. The important role of mosses as pioneer plants is well-known (Bowden et al., 1999; Bueno de Mesquita et al., 2017). The gradually dying off of the pioneer bryophyte species prepares the substrate for other mosses and vascular plant populations. The way in which bryophytes change technogenic substrate has not been sufficiently investigated. It is known from the literature that moss cover essentially influences both the soil formation processes and the ecological conditions inside an ecosystem: hydrometric conditions in the rhizosphere, soil acidity, mineral regime, deposition and carbon cycle (Bowden, 1991; O'Neill, 2000; Shaw & Goffinet, 2000; Turetsky, 2003; Seedre & Chen, 2010; Jackson, 2015; Karpinec' et al., 2016; Gecheva et al., 2017; Stark, 2017; Xiao & Vesté, 2017). However, the question of the role of mosses in renaturalization of technical soil and on the territories of sulphur extraction remains underinvestigated.

The aim of this work was: to establish peculiarities of reproductive strategy of bryophytes on sulphur extraction dumps, determine the main types of sexual structure and development of fertile plants as well as morphological differences of sexless propagules of dominant species on sulphur extraction dumps; to investigate the influence of bryophyte cover on accumulation of biogenic elements in the dump's substrate and to determine the role of bryophytes in restoration of technogenic landscapes of sulphur deposits.

Materials and methods

The object of investigation was bryophytes from the dump (near the village of Lis) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state mining-chemical enterprise "Sirka". Field investigations were carried out by standard expedition-route method and by laying stationary experimental plots. Seven transects 10 × 10 m, three on the north slope (base, slope, top), three on the south slope and one on the plateau were laid for sample selections. The samples were selected by grid method (During & van Tooren, 1990). 20 investigated plots of 0.5 × 0.5 m located at the distance of 2 m apart were analyzed within each 10 × 10 m transect. Specific composition, life forms, projective cover and biomass of bryo-

phytes were determined on each plot. The investigations were carried out in summer and autumn in two years (2015–2016). Taxonomic processing of materials was carried out by the universally acknowledged comparative-morphological method using bryophyte identification guides (Ignatov & Ignatova, 2003, 2004). The nomenclature and the authors of the moss species are given according to Boiko (2014). The bryophyte life forms were determined by the system suggested by Glime (2006). Biomass of bryophyte cover was determined by the methods of During & van Tooren (1990). The samples of the same area for determining biomass were selected from every plot. Bryophytes, including died off parts, were separated from the soil fractions and washed in water. The dry weight of the sample was dried out during 48 hours at 70 °C. Moisture content in moss turfs was determined by weight method and was calculated in percentage from the weight of the absolute dry substance (Horodnii et al., 2005). The light intensity on the investigated plots was determined by means of a luxmeter YU-116. Actual acidity (pH) was determined potentiometrically in a water extraction for the soil solutions (1 : 5).

The number of male, female and sterile plants, percentage of sexual shoots, and sexual proportion as the quotient from division of the number of male plants into the total number of fertile plants were determined from every growth locality of arbitrarily chosen turfs 3 × 3 cm in size. For investigation of bryophytes' influence on accumulation of biogenic elements in the dump substrate, substrate samples under moss cover were chosen for the experiments and the surface substrate layer of 2–3 cm wide, where the bryophyte cover was of the greatest influence, was analysed. Samples of the base substrate (without plant cover) were used as control. The substrate was chosen in three places within the experimental plot; the average sample was mixed and formed.

Three dominant moss species: *Barbula unguiculata*, *Bryum argenteum*, *B. caespiticium* were chosen for physiological investigation. Chlorophyll content was determined in 80% acetone using the D. Arnon method (Shengqi et al., 2010). The mass quotient of vegetable material (50–100 mg) was homogenized in 80% acetone for this purpose. The obtained extract was centrifuged at 4 thousand revolutions per minute (r/m) during 15 minutes and was used for spectrophotometric determination (Specord 210 Plus) of optical density at various wavelengths: 663 nm (for chlorophyll *a*) and 645 nm (for chlorophyll *b*). The pigments content was expressed in mg/g of dry substance mass.

The photosynthesis intensity was determined by Nikolaychuk et al. (2000) methods without using chamber in freshly collected plant material. For this, a portion of freshly collected vegetable material (50 mg) was immersed in the test-tubes with 0.4 n of chrome mixture and was boiled in the water bath during 20 minutes without burning the sample. The experiment was repeated after two hours. After the test-tubes had cooled, the content was spectrophotometrically analyzed at λ = 590 nm. The photosynthesis intensity was expressed in mg CO₂/g of dry substance mass per hour. To determine the chlorophyll index (XI), the values of chlorophyll *a* and *b* content, and phytomass data of all groups components were used (Martin & Adamson, 2001). They were determined according to formula: $Ch_1 = (chl_a + chl_b) \times \text{phytomass}$ and expressed in g/m². Determination of organic carbon in the substrate was carried out by the I. Turyn method in the modification of B. Nikityn (Horodnii et al., 2005), which is based on oxidation of organic substance by chromium mixture in strongly acidic medium. The optical density of the solutions was measured spectrophotometrically on the spectrophotometer Specord 210 Plus at wave length 590 nm and was expressed in percentage.

The content of total nitrogen in the substrate was determined by the K'endal' method (Horodnii et al., 2005), the phosphorus content was determined photocolourimetrically with the colouring intensity of phosphorus-molybdenum blue colour, the potassium content was determined on the photometer PFM-BP-3OM3 (Horodnii et al., 2005). All experiments were carried out three times.

The results are expressed as means ± SE. The reliability of the difference was evaluated using ANOVA.

Results

Life forms and groups of the bryophytes. 49 species belonging to 2 divisions, 3 classes, 8 orders, 17 families, 33 genera were found on the

investigated territory. Classification of bryophyte life forms on the devastated territories of sulphur production was carried out on the basis of analysis of the whole individual colonies, biomorphological structure was analysed by species spectrum, but also by the projective cover. It was found that low turf was formed by 47% (23 species), weft – 43% (21 species), small cushions – 6% (3 species), but dendroids and thallose mats involved only 2% each (1 species respectively) of all life forms. Having analysed biomorphological composition by projective cover on the dump, such prevailing life forms as low loose turf and tight turf, loose weft and thallose mat were singled out. The largest mean indices of projective cover were found for the species which form low loose turfs. It is natural that the cover of all life forms was higher on the north slope as the largest number of species was found there (Table 1). Differences in biomorphological composition depending on the exposition and position on the slope were observed as well (Fig. 1).

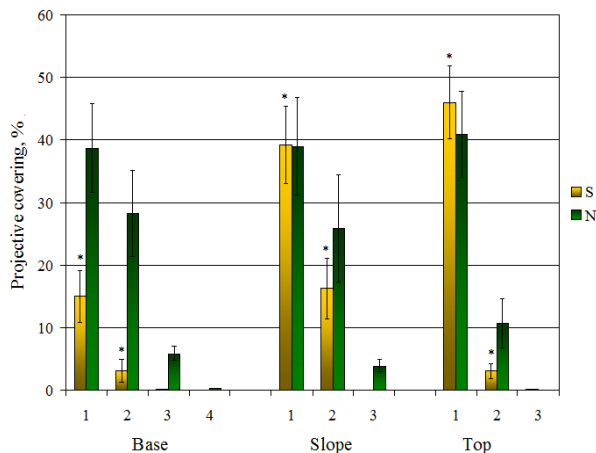


Fig. 1. Proportion of life forms relative to the position on the slope of dump: 1 – low loose turf, 2 – low tight turf, 3 – loose weft, 4 – thallose mat; S – south slope, N – north slope; data are means \pm SE for $n = 20$ plots; differences for south slope are indicated by $P < 0.05$ (One-Way ANOVA)

The projective cover of moss species which form low loose turf increased from the dump base to the top from the south slope (from 15.0% to 46.0%) and was the highest on the top of the south slope, while on the north slope the height, perhaps, did not matter (the difference between indices makes up only 2.2%). But on the other hand, the indices of species cover with tight turf and loose weft are smaller from the south slope (the average values are 7.5% and 0.2%), but from the north slope they increase from the top of the dump to the base (from 10.7% to 28.3% and from 0.1% to 5.9%). Low indices of the projective cover for liverwort *Pellia endiviifolia*, which forms a thallose mat (0.3%), were established in the base of the north slope.

The quantitative analysis of biomorphological structure allowed us to establish dependence of life forms' expansion on exposition and slope height. It was found that low loose turf prevailed on the north and south slopes, but from the south side the projective cover of species forming the life form depended on the position on the slope to a greater extent. This is connected with regime changes of illumination and moisture. The highest indices of projective cover of such type of life form as low loose turf were found on the top of the south slope, which confirms its greater adaptability to high level of insolation and lower level of moisture. The optimal conditions were for the species forming low tight turf of less intensive illumination and more stable humidity regime. Low indices of projective cover in general were established for species which formed loose wefts, but they were the highest in the base of north slope.

21 bryophyte species occurred very frequently in the bryophyte groups on the territory of the dump. Depending on exposition and position on the slope, bryophytes formed groups which consist of 6–17 species (Table 1). Four moss species (*Barbula unguiculata*, *Bryum argenteum*, *B. caespitium*, *Ptychostomum pseudotriquetrum*) occurred in all investigated transects and were dominants in the bryophyte community, while the share of other moss species was insignificant.

Table 1

Species composition of bryophyte groups on the dump

Species	Exposition		Locality			
	south	north	base	middle	top	plateau
<i>Amblystegium serpens</i> (Hedw.) Schimp.	3	3	3	–	–	–
<i>Anisothecium varium</i> (Hedw.) Mitt.	3	3	3	–	3(N)	–
<i>Barbula unguiculata</i> Hedw.	4	4	4	4	4	4
<i>Brachythecium glareosum</i> (Bruch ex Spruce) Schimp.	4	4	4	4	4	4
<i>Bryum argenteum</i> Hedw.	–	3	–	3	–	–
<i>B. caespitium</i> Hedw.	2	2	2	–	2(N)	2
<i>B. dichotomum</i> Hedw.	2	–	2	–	–	–
<i>Ceratodon purpureus</i> (Hedw.) Brid.	2	–	2	–	2	–
<i>Dicranella heteromalla</i> (Hedw.) Schimp.	2	2	2	–	2(N)	2
<i>Didymodon rigidulus</i> var. <i>gracilis</i> (Schleich. ex Hook. & Grev.) R. H. Zander	2	–	2	–	2	–
<i>D. fallax</i> (Hedw.) Zander	2	–	2	–	–	–
<i>Drepanocladus aduncus</i> (Hedw.) Wamst.	–	2	2	–	–	–
<i>Ditrichum pusillum</i> (Hedw.) Hampe	–	3	–	2	2	–
<i>Fissidens bryoides</i> Hedw.	3	–	3	–	–	–
<i>F. taxifolius</i> Hedw.	1	–	–	–	1	–
<i>Funaria hygrometrica</i> Hedw.	1	–	1	–	–	–
<i>Hygroamblystegium varium</i> (Hedw.) Mönk.	4	4	4	4	4	4
<i>Leptodictyum riparium</i> (Hedw.) Wamst.	2	–	2	–	–	–
<i>Pellia endiviifolia</i> (Dicks.) Dumort.	3	–	3	–	3	–
<i>Ptychostomum pseudotriquetrum</i> (Hedw.) J. R. Spence & H. P. Ramsay	3	3	3	3	3	3
<i>Tortula modica</i> Zander	–	2	–	2	2	–
Total	17	12	17	6	12	6

Notes: 1 – mosses found on the investigated territory only once; 2 – mosses with low observation frequency and projective cover which appeared periodically on the investigated transects; 3 – mosses and liverwort, frequency of occurrence and projective cover of which were low and increased; 4 – mosses with high indices of observation frequency and projective cover; N – moss grows only on the top of north slope; “–” – moss is absent.

On the north dump slope, 17 species were found, while on the south slope 12 species (Table 1). The largest number of species was at the dump base (17), 16 species were from the north side, and only 9 – from the south side. It has been established that 6 species (*Anisothecium varium*, *Dicranella heteromalla*, *Didymodon fallax*, *Drepanocladus aduncus*, *Hygroamblystegium varium*, *Leptodictyum riparium*) and liverwort *Pellia endiviifolia* occurred exceptionally in the base of the north slope and only 1 species (*Ditrichum pusillum*) was found at the base of the south slope. In the middle of the north dump slope, 7 moss species were found, and there were 8 species in the middle of the south dump slope. Among them, 5 species occurred independently of exposition, 2 species (*Brachythecium glareosum*, *Didymodon rigidulus* var. *gracilis*) were only on the north side, 3 (*Bryum dichotomum*, *Fissidens bryoides*, *Tortula modica*) were only on the south side. On the dump top, 13 bryophytes were found, among them bryophyte groups from the north side formed 11 species, and from the south side – only 6. Four moss species are common for these groups, 7 occurred only on the north slope (*Brachythecium glareosum*, *Ceratodon purpureus*, *Dicranella heteromalla*, *Didymodon rigidulus* var. *gracilis*, *Didymodon fallax*, *Funaria hygrometrica*, *Pellia endiviifolia*), but 2 species were only on the south slope (*Fissidens bryoides*, *Tortula modica*).

Various bryophyte species appeared on the investigated plots of the north slope depending on the season. For example, in autumn, the most frequent species were *Dicranella heteromalla*, *Didymodon fallax*, *Pellia endiviifolia*, *Ptychostomum pseudotriquetrum*, *Fissidens taxifolius*, *Funaria hygrometrica*, *Brachythecium glareosum*. The frequent spring species was *Didymodon rigidulus* var. *gracilis*. In the base of south slope, the number of species in spring-summer seasons was constant (6), but in autumn it amounted to 7. But only in summer were the species *Amblystegium serpens*, *Ditrichum pusillum* found there, while in autumn such species were found as *Dicranella heteromalla*, *Ptychostomum pseudo-*

triquetrum, *Ceratodon purpureus*, *Didymodon rigidulus* var. *gracilis*. On the south slope, the number of bryophyte species increased (from 4 to 8) during the period of investigation first, but in the period of unfavourable seasons it decreased to the initial value. On the south top, the greatest number of species was found in autumn, during other seasons their number amounted to 3–4. Moss-ephemerals with a short life cycle, the appearance of which would be restricted to a certain season, were not found. The occurrence of some bryophytes on the dump showed an exclusive relationship with exposition, for example, 5 species (*Hygroamblystegium varium*, *Dicranella varia*, *Bryum dichotomum*, *Fissidens taxifolius*, *Pellia endiviifolia*) grew only on the north side, and one moss (*Fissidens bryoides*) grows only on the south side.

Thus, during the period of investigation the increase of various bryophyte groups on the dump and spreading of separate moss species to new growth localities and at the same time disappearance of some species, which reached the site from adjacent undestroyed ecotopes, were found. Specific diversity and dynamics of bryophyte groups depends on the position on the dump top and the season. Constant changes in moss species number, substitution of one type of species for others, that is selection of species better adapted to the conditions in the localities, took place.

The influence of mosses on the moisture, acidity and temperature regime in the upper layer of technogenic substrate. The influence of bryophyte cover on the moisture of substrate layer surface was the most essential in summer under the conditions of high insolation and temperature. The humidity of moss turfs, substrate under moss and bare substrate were analysed (Table 2).

Table 2
The influence of bryophyte cover on the substrate humidity of sulphur dump ($x \pm SE$, $n = 20$)

Exposition		Humidity, %			Biomass, g	Projective cover %
		moss turf	substrate under mosses	substrate without plants		
north slope	base	41.3 ± 2.5**	41.5 ± 1.8**	29.4 ± 2.8	3.6 ± 0.4	26.9 ± 2.5
	slope	49.5 ± 4.5***	28.9 ± 1.3	26.1 ± 1.4	5.4 ± 0.7	78.9 ± 4.1
	top	49.2 ± 2.1**	37.2 ± 1.6***	20.8 ± 2.2	5.3 ± 0.5	62.9 ± 4.5
south slope	base	39.4 ± 4.8**	28.9 ± 2.3*	19.5 ± 3.5	2.8 ± 0.3	46.8 ± 4.5
	slope	33.9 ± 2.2***	26.3 ± 0.9**	20.5 ± 1.4	3.4 ± 0.3	51.2 ± 6.6
	top	15.9 ± 3.1**	8.0 ± 1.0**	4.2 ± 0.4	2.6 ± 0.4	25.3 ± 4.0

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

It has been established that humidity of the moss turfs was the highest on the top and in the middle of the north slope, for which the highest indices of biomass and total bryophyte projective cover were determined. This testifies to the fact that microconditions of these growth localities were optimal for the growth and development of the majority of bryophyte species. Essential influence of bryophytes on the humidity of the surface substrate layers was observed in the base and on the top of the north slope (humidity under moss turf was 12.1% and 16.4% higher than of the bare substrate). Thus, the influence of moss on the substrate humidity was more essential on the south slope, although the humidity of moss turfs was in general smaller (the difference between indices of humidity of substrate under mosses and the substrate without vegetation constituted from 5.0% to 7.9%). It was found that substrate under moss turf was higher than that of the bare humidity of substrate independently of the exposition and the position on the dump slope.

On the basis of the obtained results, the conclusion has been drawn that pleurocarpous mosses are spread mainly in moist shaded places, absorb much more moisture than acrocarpous, which are characteristic of open localities mainly with lower air and substrate humidity. Thus, the ability of pleurocarpous and thallose bryophytes to absorb and retain moisture quickly is the adaptation which gives them a chance to use irregular and momentary increases of dew moisture.

In contrast to loose turfs which are well ventilated, dense moss turfs, thanks to the great number of living and dead leaves and rhizoid stolons, in open localities with sharp changes in moisture and environment temperature decrease evaporation of retained water by capillaries from their surface, at the same time changes in the level of water and temperature regimes make them more balanced and independent of the changeability

of growth locality microconditions. Dump rocks of sulphur extraction are clay, pH of which is neutral 6.9–7.3. As bryophytes are pioneers of settling devastated territories, they are the first to start to influence and change the substrate during the growth and formation of groups. It has been established that bryophyte species the spreading of which does not depend on pH substrate prevailed on the dump. Stenopic acidophilic bryophyte species occurred on the dump only in extremely moist growth localities (*Pellia endiviifolia*, *Dicranella heteromalla*), where thanks to fast accumulation of a great quantity of dead moss mass, high concentrations of water ions were formed. Alkaline medium with pH 7.13 changed to acidic-alkaline one with pH 6.24 on the top of the north slope (Table 3).

Table 3
Variability of acidity indices of technogenic substrate upper layer on the dump ($x \pm SE$, $n = 3$)

Growth locality	Species name	pH value of upper substrate layer	
		upper layer of substrate	substrate under moss turf
north slope			
base	<i>Ceratodon purpureus</i>	5.69 ± 0.03***	5.49 ± 0.02
	<i>Bryum caespiticium</i>	6.96 ± 0.03***	6.65 ± 0.04
	<i>Barbula unguiculata</i>	6.95 ± 0.03	6.87 ± 0.03
middle	<i>Barbula unguiculata</i>	6.94 ± 0.04	6.85 ± 0.03
	<i>Bryum argenteum</i>	6.96 ± 0.04***	6.65 ± 0.03
	<i>Bryum caespiticium</i>	6.93 ± 0.03***	6.56 ± 0.04
top	<i>Bryum caespiticium</i>	6.96 ± 0.05***	6.65 ± 0.03
	<i>Barbula unguiculata</i>	6.95 ± 0.04	6.89 ± 0.03
south slope			
base	<i>Bryum caespiticium</i>	6.73 ± 0.05	6.68 ± 0.04
	<i>Barbula unguiculata</i>	6.87 ± 0.03	6.80 ± 0.03
	<i>Pellia endiviifolia</i>	7.13 ± 0.04***	6.24 ± 0.05
middle	<i>Bryum caespiticium</i>	6.98 ± 0.03***	6.69 ± 0.04
	<i>Barbula unguiculata</i>	7.05 ± 0.05	7.09 ± 0.05
top	<i>Bryum caespiticium</i>	6.94 ± 0.03***	6.72 ± 0.04
	<i>Barbula unguiculata</i>	7.15 ± 0.03**	6.98 ± 0.04

Note: see Table 2.

Pleurocarpous bryophyte species, which at the moment of investigation formed poorly developed wefts, were characterized by small pH amplitude of the growth localities while the majority of acrocarpous bryophyte species were spread on the substrate with the reaction from acidic to basic, that is in growth localities with highly variable pH. We found that under loose moss turfs, atmospheric moisture together with moss assimilates penetrated into deeper substrate layers changing the substrate pH (per 0.2–0.3 units) to a depth of 2–3 cm. Dense moss turfs which are characterized by the formation of a rhizoid layer promote the essential change in pH and in the moisture of the upper substrate layer. Essential pH changes (0.3–0.4 units) have been established in localities with the most developed rhizoid layer on the dump top as the result of intensive decay of dead turf parts. High acidity indices – pH 5.1–5.7 have been fixed in moss mats.

It has been established that moss cover increases the acidity of the water subsoil solution of the mainly neutral substrate of the upper layer of the sulphur extraction rock dump by 0.2–0.4 units, in this way promoting increase in activity of exchange processes and vital function of pioneer species. The largest variability of pH values (6.46–6.98) of the water substrate solution on the dump slope, mainly the north one, has been pointed out. It is, perhaps, connected with substantial changes of microclimatic conditions, first of all, the water regime. Compared to bare substrate, the most essential increase in acidity was established under moss turfs on the top in the south slope, in particular where the rhizoid layer was the most developed, to pH 6.65–6.70 and to a lesser extent in the base – pH 6.80–7.00. Thus, the circulation of water solution with high content of ammonia nitrogen, phosphorus, potassium, sodium and magnesium as well as acidic water dissolved organic substances was raised with the increase of moss cover and the layer of moss mat, which as the result of high absorption and ion exchanging moss cells acidified the environment not only in turfs, but in the upper substrate layer.

In the period of drought, as the result of substantial moisture loss of moss plants and substrate, the acidity in the upper layer did not change essentially. The highest variability of water content in plants and sub-

strate as well as acidity indices of water subsoil solution were fixed for growth localities in the middle part of both slopes. The indices of alkaline-acidic substrate balance under moss turfs and sites without plants changed depending on the position on the dump slope: the lowest variability of pH values on the top was 0.04 units, the largest variability was in the base of the south slope – 0.14–0.18 units, and on the north slope it was 0.23–0.52 units. Under *Pellia endiviifolia*, the pH index of aqueous solution varied by 0.89 units (Table 3).

The influence of bryophyte cover on temperature regime of surface layers of technogenic substrates was investigated in summer and in autumn. It was established that temperature indices on the north and south slopes were different in summer: the substrate under moss cover and bare substrate on the south slope was on average 2 °C hotter. The amplitude of variability of the average temperatures for the substrate under bryophyte cover amounted to 17.3–30.3 °C on the north and 20.1–33.2 °C on the south slopes, but for the bare plots it was 17.7–34.1 °C and 21.1–36.8 °C respectively (Fig. 2a).

The largest variability of temperature values of bare substrate and substrate under moss turfs was established in the middle of the dump slope, first of all on the north slope, which is perhaps connected with essential changes in microclimatic conditions namely, water regime. The most essential temperature difference was determined under *Barbula unguiculata* and *Bryum caespiticium* moss turfs compared to the bare substrate on the north slope, where mosses formed a strong rhizoid

layer. Substrate temperature variability under bryophytes was approximately 57% smaller than temperature variability of bare substrate, therefore the temperature of substrate plots under bryophytes was more stable than in the plots without plant cover. In autumn the amplitude of the average temperature variability for the substrate under moss cover was 15.8–21.4 °C on the north and 19.9–32.2 °C on the south slopes, but the temperature of the bare substrate was 14.7–20.0 °C and 18.7–31.3 °C, respectively (Fig. 2b).

The temperature of substrate under moss turfs was even higher than that of bare substrate, as the bryophyte cover levelled the temperature variation during sharp changes of the weather conditions. The maximum temperature difference (2 °C) was determined under dense moss turf of *Bryum caespiticium* and bare substrate in the middle of the north slope. It is natural that there is dependence between light intensity and substrate temperature. Correlative-regressive analysis of relation of temperature of the surface layers of substrate under moss turfs and bare substrate to the light intensity showed that the obtained dependencies are linear equations and have different correlation coefficients. The approximation level (R^2) amounted to 0.4 and 0.6, respectively, that is, in the first case 40% of the temperature change was caused by the change in light intensity, and in the second case – by 60%, respectively (Fig. 3a, b). The correlation coefficient amounted to 0.65 in the first case; and in the second case it was 0.77. Thus, a smaller temperature dependence of the surface substrate layers under moss cover on light intensity than the substrate without plants was found.

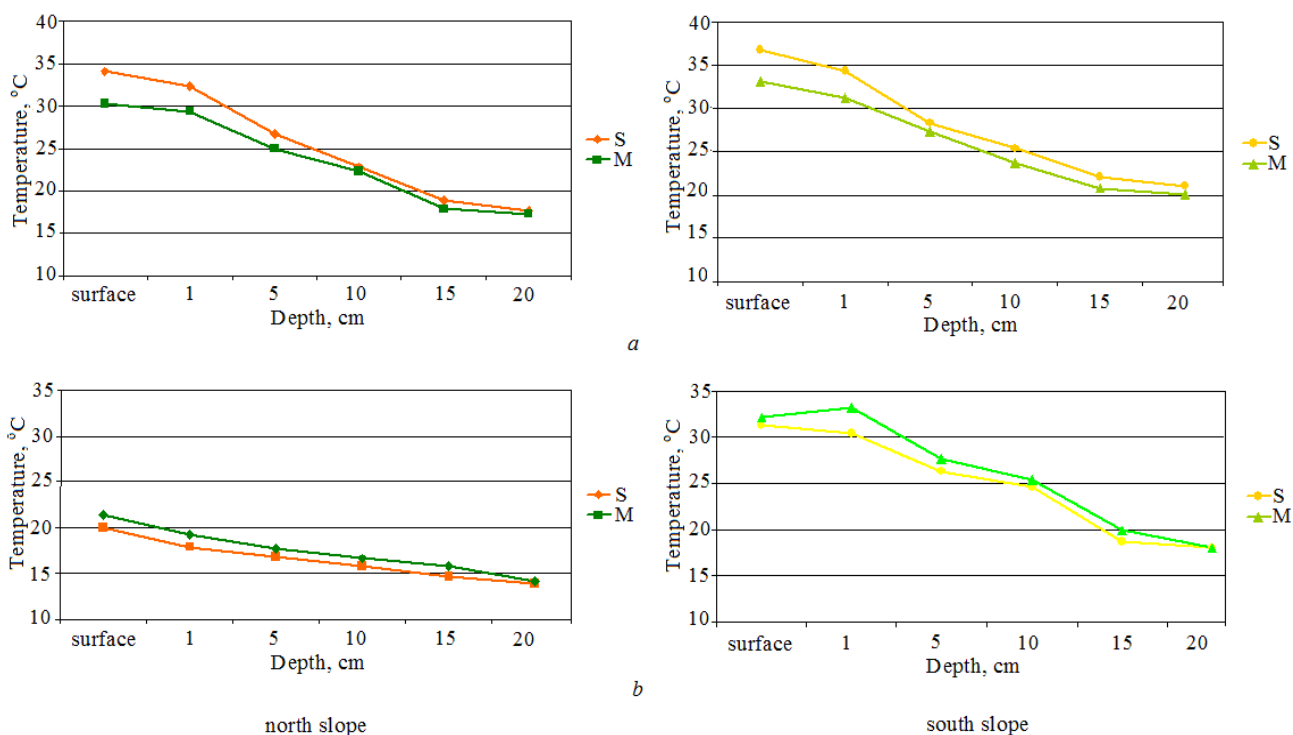


Fig. 2. Temperature regime of the substrate surface layers on the north and south dump slopes: a – summer, b – autumn; S – soil without plants, M – soil under moss turf

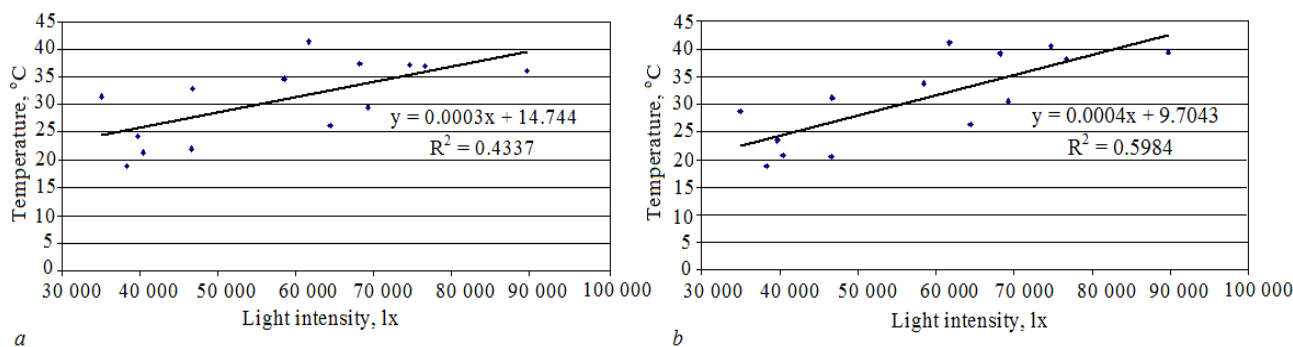


Fig. 3. Temperature dependence of surface substrate layers under moss cover (a) and without vegetation (b) on the light intensity

It has been established that temperature of substrate under moss cover was more stable than the temperature of bare substrate, which can promote optimization of exchange processes and colonisation of the sulphur extraction dumps by other higher plants. Thus, the formed moss turfs are able to transform temperature regime essentially, to cool the surface substrate layers in summer and to keep heat longer in autumn.

Peculiarities of vegetative reproduction of moss on the dumps of sulphur deposits. The bryophytes belonged to two main sex types: dioecious and monoecious. In general, the number of dioecious species on the dump (27 species, 55%) exceeded that of monoecious ones (22 species, 45%). However, all 5 dominant bryophyte species were dioecious.

Only 7 of the bryophyte species: 1 species of liverwort (*Pellia endiviifolia*) and 6 moss species, mainly dioecious ones (86%) had organs of vegetative reproduction. Vegetative renewal by protonema fragments and the formation of daughter plants as ramets is widespread in mosses. Protonema fragmentation was observed both under natural conditions and during investigation of tolerance of *Tortula modica* to water conditions in experimental culture. The conclusion was drawn that in such a way self-cloning of species may proceed and small natural turfs of *T. modica* may be individual clones which play an important part in dynamic processes of species development in the altered environment.

Specialized organs of sexless reproduction characterised six dioecious and one monoecious species: underground rhizoid tubers (*Barbula unguiculata* and *Bryum caespiticium*, *B. dichotomum*, *Ptychostomum pseudotriquetrum* and *Leptobryum pyriforme* (Hedw.) Wils.), bulbils (in leaf axils *Bryum argenteum*, *B. dichotomum* and at the thallus ends of *Pellia endiviifolia*). It has been established, that on the dump almost all dominant moss species formed underground rhizoid tubers, except *Bryum argenteum*, which very often formed bulbils on the tops of shoots.

Correlation between spore sizes and their capacity for sexless reproduction was established. Wide-spread on the dump were species of *Bryum* which form small spores (8–10 µm in *B. dichotomum* and 10–15 µm in *B. argenteum*), with low viability propagate with propagula – modified, very shortened budshoots (Fig. 4). Oval axillary bulbils often occur in *B. argenteum*. For *B. argenteum* under the drier conditions of the north slope, essential strengthening of stem branching and the formation of numerous bunches on their tops from the brood buds, which fall off easily, has been mentioned, but in more humid places this has been found in the form of larger end branches, which are broken easily.



Fig. 4. Axillary brood-bulbils under bud-like androecia of *Bryum dichotomum*

Short, extremely branched light green lobes which break off easily are often found at the ends of liverwort *Pellia endiviifolia* thallus, and having fallen off they germinate into new plants (Fig. 5).

Green-brown, egg-shaped and oblong egg-shaped bulbils with small leaves, which after falling off are quickly developed into new shoots

without protonema spreading out, are formed in leaf axil shoots of upper leaves of *Bryum dichotomum*. It has been noted that in the open sunny places in the dump there were brood bodies formed not only on the tops of sterile plants. Thus, the essential part of brood bodies was observed on male plants, in particular a large number of them were found in mixed turfs with male and female plants. It was established that in the drier conditions of the dump's south slope, an essentially larger number of brood bodies was formed in *Bryum argenteum* and *B. dichotomum* than on the north slope. Such reproduction peculiarities of dominant moss species are, perhaps, connected with the considerably higher productivity of the androecium than that of the gynoecium; more antheridia than archegonia were formed in *Bryum caespiticium* and *Barbula unguiculata* on the north slope, but in *Bryum argenteum* and *B. dichotomum* they were formed on the south slope, where female plants of *B. argenteum* more often had two sporogonia each.



Fig. 5. Male thallus of liverwort *Pellia endiviifolia* with light green lobes

Bright orange colouring was a characteristic feature of underground formed tubers of all analysed moss species. The colour of tubers after washing them from the substrate gradually became red-brown. The formation of multicellular brown rhizoid tubers was found in young shoots, as usual, at the distal end of the main rhizoids. Rhizoid tubers (round or pear-shaped with rather thick walls) promote settling of moss turfs at the initial stages of growth succession of destroyed soils. The number of tubers is caused, first of all, by temperature variability between slopes and the turf microconditions – high gametophore density, shading and humidity of the moss mat on the top compared to the slope.

In early spring, there were twice as many shoots with rhizoid tubers as in autumn (in *Barbula unguiculata* ~ 54%) mainly on sterile gametophores. In *B. unguiculata* and *Bryum caespiticium*, tubers were laid on stolons of extremely branched rhizoid protonema (Fig. 6a).

Bryum caespiticium formed dense turf with an especially dense rhizoid layer on the top and the middle part of the south dump slope under unstable conditions of high insolation and substrate dessication. It obviously gives *Bryum caespiticium* the possibility to survive unfavourable periods more successfully than under the conditions of loose turf *Barbula unguiculata*.

In *Leptobryum pyriforme* round to oval rhizoid tubers (Fig. 6b) are formed from 5–6 large cells mainly on rather long rhizoid branches. As in small capsules *L. pyriforme*, there are not many large spores, which are spread to insignificant distances, the mass formation of brood organs promotes moss survival and its preservation.

Sporophytes were represented by 18 moss species (36.7%) on the dump, among which 10 species are dioecious. Common dioecious moss species: *Barbula unguiculata*, *Bryum caespiticium*, *B. argenteum*, *Dicranella heteromalla*, *D. varia*, *Ceratodon purpureus*, and less common *Ptychostomum pseudotriquetrum*, *Bryum dichotomum*, *Didymodon*

rigidulus var. *gracilis*, in which male and female plants, as a rule, were in one turf, spore rather seldom. Among monoecious mosses frequent sporogonium formation is mentioned only for *Funaria hygrometrica*, *Amblystegium serpens* and *Brachythecium salebrosum* (Hoffm. ex F. Weber & Mohr) Schimp.

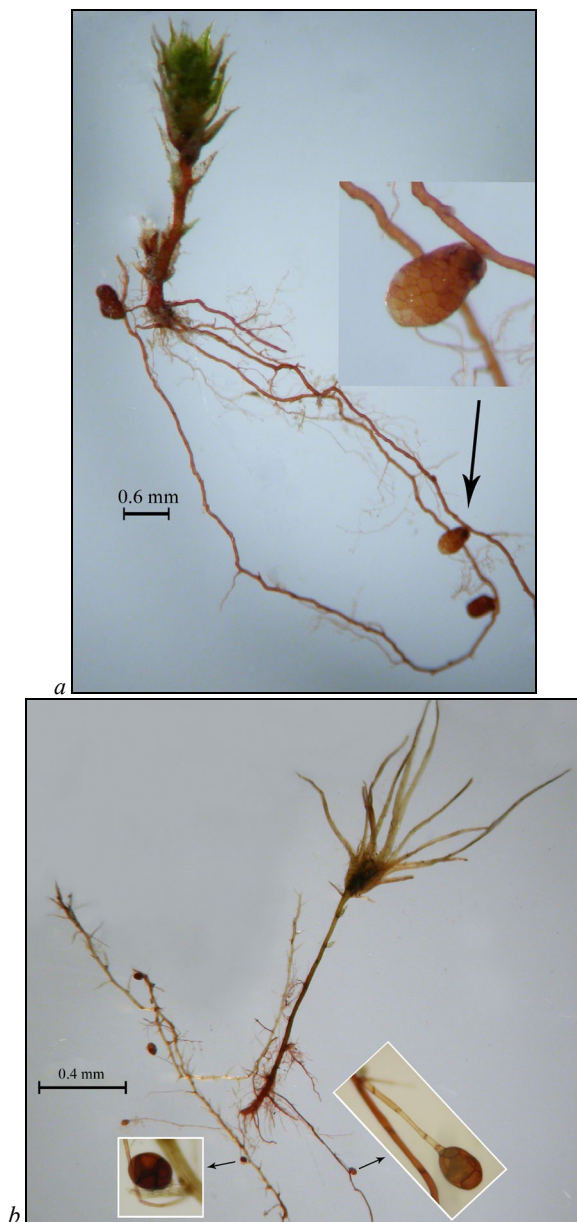


Fig. 6. Underground rhizoid tubers of *Bryum caespiticium* (a); *Leptobryum pyriforme* with tubers on rhizoid branches and leaf axils on underground ethylated shoots (b)

Sexual turf structure (reproductive bryophyte phenology). To elucidate the peculiarities of sexual reproduction of individual dominant moss species with various sexual productivity, comparative investigations of their reproductive phenology from different localities of the dump was carried out. Morphological analysis of fertile plants allowed us to determine the peculiarities of the structure and localization of gametangia.

It was established that on the dump, dominant dioecious moss species were dimorphic, they differed in ripening rate and the capacity for reproduction. Female plants, as a rule, were larger, they supported sporophyte development vigorously. Therefore they retained viability longer after full ripening (Fig. 7).

Generative renewal of *Barbula unguiculata* prevailed with some deviations on all dump plots comparing to summer months to the autumn-winter period: almost 50–55% of plants were with ripe sporogonia, but the plants of *Bryum* genus species were with young sporogonia.

An essentially high number of plants with sporogonia, 20–22%, was determined on the north slope and 12–15% on the south slope for *Amblystegium serpens* in comparison to summer months. In the droughty periods of summer and autumn the side offshoots, which grew much quicker than the paternal stems and thus guaranteed the growth of assimilation and total turf area, were thickly formed on the shoots of *A. serpens*. Under extreme peak conditions where high temperature and heightened sun radiation prevail, *Bryum caespiticium* and *Barbula unguiculata* practically did not form sporogonia (only 3–10% from the total number of shoots), viability and renewal of moss turfs were compensated by the formation of a great number of brood rhizoid tubers, which were represented by undeveloped buds, which suppressed development and essential reserve of nutritious substances. Rhizoid tubers were mainly formed on the top of the south dump slope only in moss turfs with a well developed rhizoid layer. The position of stems and leaves was changed in the droughty conditions of the south slope, they were rolled, the fragility of shoots of separate leaves and turf fragments increased, as a result, brood organs are separated and spread to the neighbouring territories. Thus, drought promotes separation and spread of brood organs.

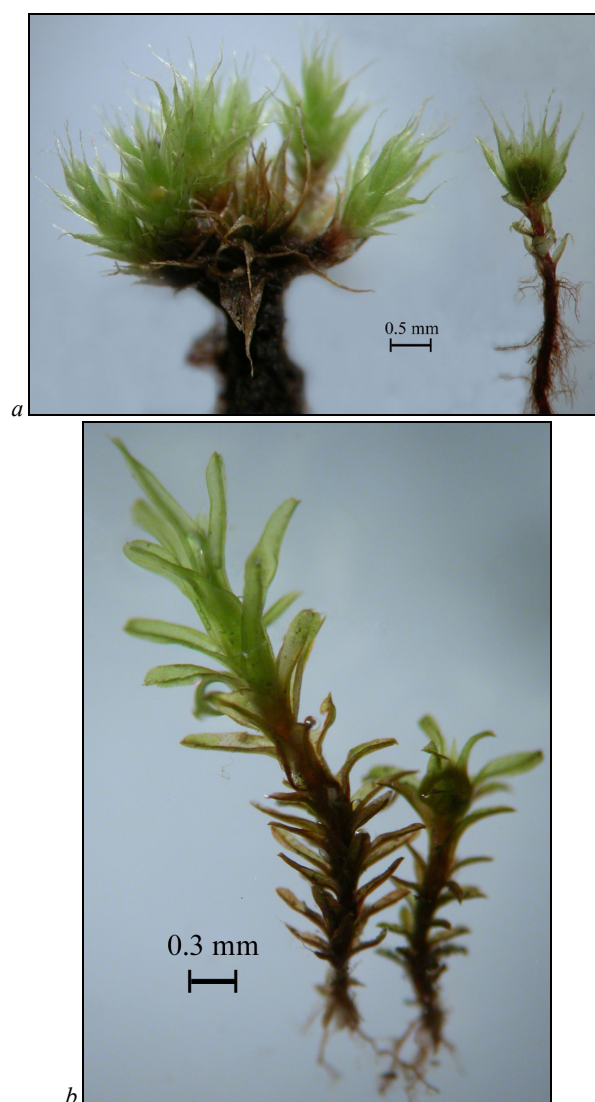


Fig. 7. Female and male plants of *Bryum caespiticium* Hegw (a) and *Barbula unguiculata* Hedw. (b)

Female plants, occupying considerable space, obtain more light, water and nutrient substances. In this way they create better conditions for ensuring sporophyte viability and moss reproduction. Female plants are more competitive thanks to a high renewal rate with new meristematic apices – innovations and larger projective cover (Fig. 8a). Male plants happened to propagate more actively being sexless, as in *Bryum*

species (Fig. 8). Mass formation of bulbils was found not only on sterile plants, but on the males, more seldom on the female plants and especially densely on sexually mixed turfs.



Fig. 8. Unisexual male turf of *Bryum argenteum*

The ratio of female and male fertile shoots in *B. unguiculata* varied within 1 : 1 – 3 : 1 depending on locality (Table 4). On the north slope, male plants made up 12.7% in the *B. unguiculata* turfs, on the south slope they made up 8.3%; female gametangia were found on 17.5% of gametophores on the north slope and 11.2% – on the south slope, 70%

of shoots were sterile on the north slope and 80.5% – on the south one. The share of shoots with sporogonia was rather high and amounted to 64% on the north slope and 33% on the south slope, but it varied essentially from the top to the foot of both dump sides (17.8–72.1%; Table 4). The advantage of female fertile shoots was noted for the scattered fertile *Bryum argenteum* turfs on both dump slopes, but the large percentage was the result of the sporogonia in the moss turfs of the formation of predominantly some sporogonia from one perichaecium.

A greater number of female gametangia than the male ones was found on the north dump slope in the turfs of dominant dioecious acrocarpous mosses (Table 4), while in monoecious pleurocarpous species, perigonia quantitatively prevailed over perichaetia. The results of analysis of the sexual structure of *Bryum caespiticium* and *B. argenteum* turfs show that in both mosses more fertile plants were formed on the north dump slope (30.2% and 39.7% respectively) than on the south one (19.5% and 24.7%). The indices of sex correlation show the advantages of male plants in the *B. argenteum* turfs. On the north slope, 90% of female plants formed sporogonia in the *Bryum caespiticium* turfs, but on the south slope there were only 20% of sporogonia. In *Bryum argenteum* stable to drought afflicted conditions, ripe capsules were formed on the north and south slopes, but the percentage of shoots with two sporophytes decreased sharply. It was established that besides mixed species, turfs mainly with male and female plants were often found in dioecious species. However, the great number of male plants in unisexual turfs was levelled by the advantage of female plants as a whole. For *B. argenteum*, the ratio ♀ : ♂ constituted 1, while for *B. caespiticium* it was ♀ : ♂ = 1.4. In ripe *Barbula unguiculata* turfs under drought-afflicted conditions (especially on the south slope) the sex ratio constituted 2♀ : 1♂, which testifies to the higher tolerance of female plants to extreme temperatures.

Table 4

Sexual turf structure of dominant dioecious moss species ($\bar{x} \pm SE$, $n = 3$)

Growth locality	Number of plants, pieces				Fertile shoots, %	Sexual proportion	Sporogones, %
	♀	♂	sterile	total			
<i>Bryum caespiticium</i>							
north slope							
base	54.5 ± 6.2	47.4 ± 8.2	156.9 ± 9.3	257.7 ± 18.2	39.3 ± 2.3	0.46	80.7 ± 2.3
middle	86.3 ± 5.2***	48.0 ± 3.1	443.5 ± 9.8	577.3 ± 27.5	23.2 ± 1.9	0.36	84.6 ± 3.0
top	85.1 ± 8.3	68.6 ± 9.5	297.4 ± 7.3	450.9 ± 20.1	34.0 ± 2.7	0.44	86.7 ± 2.9
south slope							
base	55.2 ± 5.4**	36.7 ± 4.0	266.3 ± 6.1	357.5 ± 19.3	25.5 ± 1.4	0.39	30.8 ± 2.5
middle	21.7 ± 3.6*	11.0 ± 2.1	214.5 ± 5.3	246.7 ± 15.6	13.0 ± 0.7	0.34	48.5 ± 5.3
top	12.5 ± 2.1	18.3 ± 3.0	152.3 ± 3.7	182.2 ± 11.7	16.5 ± 1.0	0.60	5.0 ± 1.0
<i>Bryum argenteum</i>							
north slope							
base	30.9 ± 3.1***	3.1 ± 0.5	136.7 ± 3.0	169.3 ± 3.3	19.5 ± 1.8	0.09	70.0 ± 8.2
middle	86.4 ± 7.3**	128.5 ± 10.1	315.3 ± 8.7	529.5 ± 17.0	40.4 ± 3.5	0.60	89.6 ± 8.9
top	86.6 ± 6.8	78.3 ± 9.2	172.7 ± 5.8	336.4 ± 8.1	48.8 ± 4.0	0.47	91.7 ± 10.0
south slope							
base	16.2 ± 2.4*	24.8 ± 3.0	186.4 ± 6.0	226.1 ± 7.6	17.7 ± 0.9	0.60	105.0 ± 9.7
middle	47.3 ± 2.7***	16.3 ± 1.9	124.3 ± 4.2	187.4 ± 6.3	33.7 ± 2.8	0.25	105.8 ± 9.3
top	40.5 ± 7.1	49.0 ± 5.3	275.7 ± 8.3	36.6 ± 12.7	24.4 ± 1.6	0.55	110.0 ± 9.5
<i>Barbula unguiculata</i>							
north slope							
base	62.8 ± 8.0***	22.4 ± 3.6	148.2 ± 5.2	232.2 ± 9.4	36.2 ± 3.2	0.26	50.2 ± 4.1
middle	142.3 ± 8.7	138.1 ± 7.3	68.4 ± 6.6	348.5 ± 17.3	81.3 ± 6.4	0.49	72.1 ± 6.3
top	110.5 ± 7.9***	50.8 ± 6.0	80.7 ± 6.0	240.2 ± 10.1	66.6 ± 5.7	0.31	48.3 ± 3.8
south slope							
base	68.6 ± 7.4**	40.3 ± 4.2	130.6 ± 7.1	238.3 ± 9.5	45.4 ± 3.2	0.37	47.7 ± 5.0
middle	82.3 ± 6.2***	46.1 ± 3.3	110.0 ± 9.9	236.4 ± 8.6	53.4 ± 3.3	0.36	32.2 ± 2.8
top	70.5 ± 8.1**	40.3 ± 3.9	56.8 ± 7.2	166.5 ± 7.7	66.3 ± 4.1	0.36	17.8 ± 7.4

Note: * – difference compared number of female and male plants is statistically reliable at $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

It was noted that the drought-afflicted conditions of the summer-autumn period depressed the development of sporophyte mosses. The growth and differentiation of capsules were inhibited in *Barbula unguiculata*, but in *Bryum caespiticium* the development of setae before the capsule formation was stopped. In 12 randomly chosen growth localities of *Barbula unguiculata*, gametophores with sporogonia prevailed on the north slope (56%), but on the south slope there were 46% of sterile plants and 32% of gametophores with sporogonia. First of all, sterility is caused by depression of gametangia development stages and the low level of archegonia fertilization. On the open south slope with high illumination and temperature, the number of fertile plants was 69% lower

compared to the north slope, where the conditions are more moderate.

Photosynthetic activity of the mosses. The results of analysis of photosynthesis intensity of dominant moss species on the dump territory confirmed the dependence of this index both on the peculiarities of the specific plants and on the concrete ecological conditions. The maximum intensity was determined in mosses which grew in the dump base (Table 5). The lowest CO_2 assimilation indices were determined in the samples collected from the dump top. There is a tendency of lowering photosynthesis level from the dump base to the top.

The largest assimilation values of CO_2 were found in mosses *Bryum caespiticium* and *B. argenteum*. Perhaps, it is connected with specific

character of their life forms as they form short dense or loose turf, which keep water well. A somewhat lower level of photosynthesis intensity compared to the two previous species was established for *Barbula unguiculata*. This species often occurs on open localities with high light intensity, which considerably changes the CO₂ assimilation values. As the photosynthesis intensity depends on the main meteorological factors: temperature and water regime, light intensity, the maximum photosynthetic activity was determined in April – May and August – September. The lowest assimilation values CO₂ occur in dry summer months.

Table 5
Photosynthesis intensity of the mosses on the territory of sulphur extraction dump (x ± SE, n = 5)

Locality of moss samples collection	Photosynthesis intensity, mg CO ₂ /g of raw material/hour		
	April – May	June – July	August – September
<i>Bryum caespiticium</i>			
plateau of the dump	3.64 ± 0.35	1.46 ± 0.16	3.44 ± 0.36
base	3.57 ± 0.38	1.45 ± 0.17	3.23 ± 0.35
slope	2.54 ± 0.23	1.16 ± 0.12	2.85 ± 0.24
top	2.06 ± 0.19	1.16 ± 0.11	2.66 ± 0.22
<i>Bryum argenteum</i>			
plateau of the dump	3.50 ± 0.24	1.32 ± 0.15	3.57 ± 0.28
base	3.56 ± 0.28	1.20 ± 0.09	3.16 ± 0.33
slope	2.56 ± 0.22	1.24 ± 0.13	2.56 ± 0.21
top	2.29 ± 0.21	1.18 ± 0.11	2.15 ± 0.22
<i>Barbula unguiculata</i>			
plateau of the dump	3.14 ± 0.35	1.14 ± 0.14	2.81 ± 0.18
base	3.04 ± 0.32	0.84 ± 0.09	2.66 ± 0.21
slope	2.31 ± 0.26	0.89 ± 0.09	2.28 ± 0.21
top	2.22 ± 0.27	0.80 ± 0.08	2.23 ± 0.19

Daily dynamics of photosynthesis intensity in the moss *Bryum caespiticium* was analysed and it was revealed that it looks like a double-peak curve. The photosynthesis maximum falls in the morning hours (8–10 o'clock), which is characteristic of poikilohydric moss species, for which moisture is the limitation factor of photosynthetic processes. The second peak of photosynthesis activity falls in the late afternoon/early evening (17–18 o'clock). Under the conditions of maximum light intensity (12–14 o'clock) the decrease of photosynthesis intensity, as the result of disbalance of water and temperature regime under the conditions of high insolation level, was found (Fig. 9).

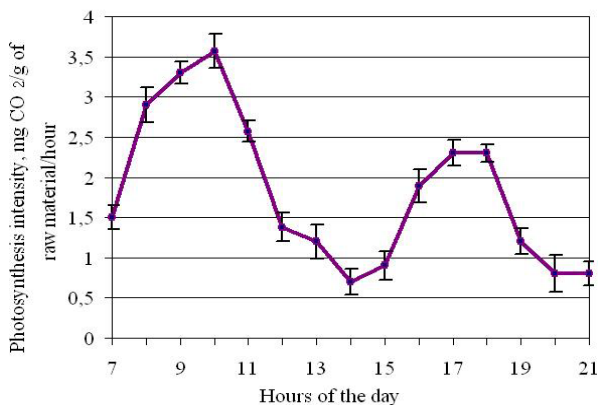


Fig. 9. Daily dynamics of photosynthesis intensity of the moss *Bryum caespiticium* on the territory of sulphur extraction dump

One of the limiting factors of carbonic acid gas interchange is the ability of bryophyte leaves to absorb water, as the connection between the values of photosynthesis intensity and the moisture content in moss turfs has been established (Fig. 10). Thus, taking the moss *Bryum argenteum* as an example, the highest indices of photosynthetic activity (2.29 mg CO₂/g of raw material mass per hour) were determined for vegetable samples with moisture content 50%. Under the lowest values of plants' saturation with water a sharp drop of photosynthesis activity almost to zero value takes place.

The basis of the production process of plants is the energy transformation and the formation of organic substances in the photosynthesis process. In this connection, the contribution of bryophytes to the primary

productivity of plant cover on the territory of sulphur production was estimated. Chlorophyll index (ChI), which serves as universal parameter for comparing plant components of various morphology and systematic position, was used as the production index. The values of the content of chlorophylls *a* and *b* and phytomass data of all group components were used for its determination (Table 6).

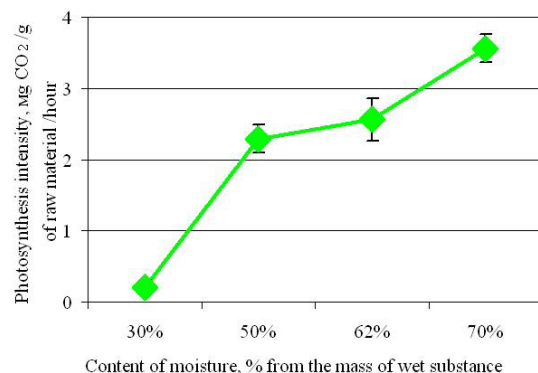


Fig. 10. Influence of moisture content in the *Bryum argenteum* moss turf on the photosynthesis intensity on the territory of sulphur extraction dump

Table 6
Chlorophyll index of plant cover on the plateau of the sulphur extraction dump (x ± SE, n = 5)

Plant species	Chlorophyll content (a+b), mg/g of the dry substance mass	Supply of the surface phytomass, g/m ²	Chlorophyll index, g/m ²
Vascular plants			
<i>Calamagrostis epigeios</i>	0.782 ± 0.051	12.22 ± 1.13	0.0095 ± 0.0001
<i>Cirsium arvense</i>	0.965 ± 0.081	1.74 ± 0.13	0.0016 ± 0.0002
Vascular plants – sum total	–	13.97	0.0111 ± 0.0002
Mosses			
<i>Bryum caespiticium</i>	1.231 ± 0.092	253.82 ± 21.15	0.3681 ± 0.0211
<i>Bryum argenteum</i>	1.053 ± 0.097	56.37 ± 3.15	0.0593 ± 0.0034
<i>Barbula unguiculata</i>	0.743 ± 0.056	182.53 ± 16.42	0.1356 ± 0.0092
Mosses – sum total	–	492.73	0.5630 ± 0.0048

The chlorophyll index was determined for moss group on the dump plateau with moss *Bryum caespiticium*, the share of which amounted to 52% from all phytomass. The projective moss cover on the investigated plot reached almost 100%. The specific plant composition is represented by 5 species, including 3 species of mosses (*Barbula unguiculata*, *Bryum argenteum*, *B. caespiticium*) and two species of vascular plants (*Calamagrostis epigeios* (L.) Roth and *Cirsium arvense* (L.)). The structure of the surface phytomass is represented mainly by assimilating organs and amounts to ~ 506.4 g/m², among which the share of bryophytes constitutes 97% (Table 6). It was found that the store of the surface phytomass is essentially larger in dense turf moss species (*Bryum caespiticium* and *B. argenteum*) on account of the number of pieces per area unit. It was established that the value of chlorophyll index of moss cover on the dump plateau is rather high and amounts to 0.563 g/m², which is caused by the essential mass of assimilating mass organs and high content of green pigments. This index is fully comparable with the values ChI, determined for plant groups with domination by vascular plants (for example, for shrubby group ChI it amounts to 0.5–0.6 g/m²). The obtained results show the important role of bryophytes in the production processes on technogenic territories of sulphur extraction. Thus, the analysis of seasonal and daily moss photosynthesis dynamics demonstrated the adaptability of the photosynthetic apparatus of moss to contrasts in climatic conditions on the dump territory and the ability to support the intensity of photosynthetic processes on a rather stable level during the vegetative period.

Thus, ecological and physiological assessment of dominant moss species on the dump territory of sulphur extraction of mining-chemical enterprise “Sirka” indicate the important role of bryophytes in the productivity of plant cover on the posttechnogenic landscapes of sulphur

extraction and the necessity to continue investigations of peculiarities of functioning of plant communities with bryophytes domination.

Role of bryophytes in accumulation of organic carbon and biogenic elements. The pioneer bryophyte species settling on the dump slopes which were used in investigations caused both mechanical and chemical influence on the substrate. First of all, they fixed the movable slopes' substrate mechanically and prevented it from disintegrating. The species that form the life form of dense and loose turf – *Bryum caespitium* and *B. argenteum*, played a special part in these processes. Besides, the species *Bryum caespitium* forms a dense rhizoid tomentum, which penetrates densely into the substrate, providing plants with additional fixation on the slopes. It was found during the investigations that the rhizoid tomentum reached 2 cm in some turfs of *Bryum caespitium*. Penetrating into the substrate, moss rhizoids form a dense net, increasing porosity and promoting enrichment of the substrate with oxygen and moisture.

The content of organic carbon in the upper layer of the bare substrate (without plant cover) was 0.9–1.8% in the territory of the dump (Table 7). Besides, a tendency to decrease in the content of organic carbon from the dump base to the top by 25.4–50.2% was found. First of all, this is caused by the peculiarities of the conditions on the dump top, which are the least favourable for the growth of plants as the result of wind and water erosion of substrate, as well as moisture deficit, which leads to the slowing down of renaturalization processes of rock substrates. Such difference in quantity of organic carbon on the dump top can be caused by washing out of the surface substrate layer from the top to the dump base. The maximum content of organic carbon in the substrate under moss cover was determined on the dump plateau (3.9–4.5%). On the north slope, the highest content of organic carbon was in the substrate under mosses *Bryum caespitium* and *B. argenteum* (2.7–2.8%), which was almost 72.3% higher compared to the amount of carbon in the bare substrate from this dump plot (Table 7).

Table 7

Content of organic carbon in the substrate under moss cover on the territory of sulphur extraction dump ($x \pm SE$, $n = 5$)

Locality of substrate samples collection under moss turfs	Content of organic carbon, %	
	north slope	south slope
<i>Uncovered substrate (control)</i>		
Plateau of the dump	1.723 ± 0.082	
Base	1.645 ± 0.112	1.822 ± 0.091
Slope	1.661 ± 0.102	1.624 ± 0.102
Top	1.233 ± 0.091	0.922 ± 0.104
<i>Bryum caespitium</i>		
Plateau of the dump	4.535 ± 0.041***	
Base	2.567 ± 0.062***	2.324 ± 0.041**
Slope	2.843 ± 0.041***	2.458 ± 0.082***
Top	2.366 ± 0.052***	2.043 ± 0.091***
<i>Bryum argenteum</i>		
Plateau of the dump	3.925 ± 0.061***	
Base	2.568 ± 0.074***	1.949 ± 0.113
Slope	2.735 ± 0.081***	2.433 ± 0.082***
Top	2.216 ± 0.113**	2.115 ± 0.122***
<i>Barbula unguiculata</i>		
Plateau of the dump	3.265 ± 0.114***	3.367 ± 0.312***
Base	2.153 ± 0.132*	2.062 ± 0.051*
Slope	2.236 ± 0.114**	2.026 ± 0.073*
Top	1.955 ± 0.095***	1.566 ± 0.092**

Note: * – difference compared to control (uncovered substrate) is statistically reliable at $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$.

The quantity of carbon was 34.6% higher under *Barbula unguiculata* turf compared to its content in the substrate without turf. A similar tendency of change in organic carbon content in the substrate under the investigated moss species was observed in the slope base as well. The smallest quantity of organic carbon under moss turfs was found on the top, although compared to its quantity in bare substrate on this dump plot, its content increased almost by 58.6–91.8%, which shows the essential contribution of bryophytes to accumulation of organic substances even under unfavourable ecological conditions.

The results of determining the content of organic carbon in the substrate under moss cover on the south dump slope show a similar confor-

mity: the highest content was in the substrate under mosses on the slope and in the dump base, and the lowest content is on the top. On the basis of the obtained results, it is possible to confirm that the process of soil formation occurs with participation of bryophytes on the dump territory.

One of the main characteristics of soils determining their fertility and capacity for settlement by plants is their supply with nutrients. Technogenic dump substrate of sulphur extraction is practically not structuralized, it is characterized by insufficient absorption and water retention properties, being poorly supplied with the main nutrition elements (nitrogen, phosphorus, potassium), which in complex defines its low potential fertility and adaptability to plant life activity.

We have established that mosses also influence accumulation of nitrogen and phosphorus in the substrate on the dump territory of sulphur extraction. The highest indices of their content were determined in the substrate under mosses *Bryum caespitium* and *B. argenteum*. In the substrate under moss cover formed by dense *Bryum caespitium* turf, the gross nitrogen content increased by 79.3–247.1%, phosphorus content increased by 33.3–45.7% compared to their quantity in bare substrate (Table 8).

Table 8

Gross nitrogen and phosphorus content under moss cover on the territory of sulphur extraction dump ($x \pm SE$, $n = 5$)

Locality of substrate samples collection under moss turfs	Content of nitrogen, %	Content of phosphorus, %
<i>Uncovered substrate (control)</i>		
Plateau of the dump	0.102 ± 0.011	0.094 ± 0.011
North slope	0.094 ± 0.012	0.092 ± 0.012
South slope	0.092 ± 0.011	0.081 ± 0.011
<i>Bryum caespitium</i>		
Plateau of the dump	0.354 ± 0.022***	0.137 ± 0.013*
North slope	0.226 ± 0.013***	0.129 ± 0.010*
South slope	0.165 ± 0.021*	0.108 ± 0.014
<i>Bryum argenteum</i>		
Plateau of the dump	0.206 ± 0.024**	0.116 ± 0.013
North slope	0.137 ± 0.013*	0.104 ± 0.012
South slope	0.224 ± 0.033**	0.118 ± 0.010*
<i>Barbula unguiculata</i>		
Plateau of the dump	0.136 ± 0.009*	0.116 ± 0.015
North slope	0.129 ± 0.009*	0.114 ± 0.013
South slope	0.103 ± 0.011	0.087 ± 0.015

Note: see Table 7.

Under *Bryum argenteum* turfs, the nitrogen quantity increased by 45.7–143.5%, phosphorus – by 13.0–40.7%. Under *Barbula unguiculata* turf, nitrogen content in the substrate increased by 11.9–33.3%, but the control difference in phosphorus was not authentic.

Discussion

Microclimatic conditions on the dump territory also influence accumulation of nitrogen and phosphorus in the substrate, as the highest content of these elements was determined in the substrate on the dump plateau, but the lowest content was on the south dump slope, that is, the dependence on the conditions of plant localities is observed. Perhaps, the high insolation level on the south dump slope influences these indices as for many moss species negative correlation between nitrogen and phosphorus accumulation and light intensity has been established (Proctor, 2002).

Life forms and groups of the bryophytes. The life form is the general organization of growth form, type of branching groups of individuals and their modifications (During, 1992). The life forms are closely connected with growth microlocations. For example, cushions are groups of straight stems formed in dry open places. Thickness of stems guarantees their protection from drying out. Therefore, the colony functions as a separate life form, which guarantees adaptation to xeric conditions. Modification of the life form under the influence of the growth location is shown in *Hylocomium splendens* (Hedw.) Schimp., which forms weft under the conditions of moderate forest moisture or turfs on the open growth places in tundra (During, 1992; Glime, 2006). Water and light are decisive factors in making life forms. Shoots with

thick leaves pressed to the substrate facilitate motion and accumulation of water and are considered to be the most adaptable to moisture conservation (Proctor, 2002). They cause the least air turbulence compared to wefts and turfs. Measuring of air flows showed that under the conditions of low wind speed, cushions are close to the objects with flat surface as to the indices of water loss (they make up approximately square root from wind speed). It has been proved that roughness of the surface of the life form increases turbulence of the adjoining wind layer. It has been found (Proctor, 2002) that hairy tops of leaves which overhang the surface of the turf or cushion form an additional layer of inert wind between moist leaves and wind flows, decreasing conductivity of the adjoining layer in *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr. per 20–35%, preventing the loss of water in this way. The important characteristic of all life forms is their ability not only to absorb, but to retain moisture. It has been proved that the turf of *Schistidium antarctici* (Cardot) L. I. Savicz & Smirnova has a higher water content, relative to dry mass, than the cushion of the same species, but the speed of water loss is much higher in the turf form (Bramley-Alves et al., 2014). So, the life form is the general structure of the individual group, which is formed in specific growth places (Glime, 2006).

The influence of mosses on the moisture, acidity and temperature regime in the upper layer of technogenic substrate. Water content in cells of poikilohydric bryophytes is not constant and depends to great extent on the degree of the environmental moisture. Owing to the lack of transpiration regulation mechanisms in mosses, stomata and lignin cuticle, they absorb water quickly and lose it from all their surface. Showing high resistance to drought and various signs of xeromorphism (the decrease of plants' height, the leaves' size etc.), mosses quickly restore water balance even in dry summer periods. The ability to regulate water regime and the average water content in moss shoots in species is a specific sign of bryophytes, which to a great extent is determined by the form of turf growth. As mosses mainly grow in numerous, thick groups (from 17 to 1500 shoots/cm²) of one or several species (During, 1990) their development is limited first of all by water supply, the duration of the high water potential period, necessary for photosynthesis. In its turn, it depends on the quantity of water inside and between the shoots in the turf which is characterized by full structure and thickness.

Peculiarities of moss vegetative reproduction on the dumps of sulphur deposits. It is considered (Casanova-Katny et al., 2016) that high regenerative ability, which has been lost by more complex higher surface plants organized in more complicated manner, has evolved as a primitive adaptation sign in bryophytes. With the development of various gametophyte adaptations, specialized types of sexless propagule as to their structural-functional organization have become more complicated, extremely widespread and more important for their reproduction under unfavourable climatic conditions. As vegetative reproduction plays an important part in the life strategy of species and bryophyte adaptation to extreme and unstable conditions of the environment (Proctor, 1990; Sinclair et al., 2012; Casanova-Katny et al., 2016), the study of cell sizes and form, colour, the number and place of various types formation of specialized sexless, reproductive propagule and their morphogenesis makes it possible to elucidate the participation of the diaspore bank in populating and forming moss groups, the support and regulation of moss population on devastated territories. Besides, brood organs are more often used as an important diagnostic sign in taxonomy and molecular bryophyte investigation for tissue culture and biotic layer formation in order to stabilize dunes and surfaces of deserts (Söderström & During, 2005).

Sexual structure of turf and sporophyte development (reproductive bryophyte phenology). The combination of various strategies of sexless and sexual moss reproduction with the formation of numerous diaspores promotes the spread of bryophytes on heterogeneous technogenically transformed territory and their successful expansion across considerable distances. Dispersion to greater distances mainly takes place by spores, while sexless propagula are important for local spreading and population support, when the reproduction is sexless, in particular. It has been established that dioecious species are more viable as most of them use a considerable arsenal of various ways of reproduction; besides high regenerative ability, gametophyte fragmentation, they have organs of sex-

less reproduction, supplementing or fully substituting sexual reproduction. The results of our investigation testify to the participation of rhizoids and rhizoids tubers as an imperceptible but important phase of the life cycle of dioecious species of moss colonists in the realization of a life strategy tolerant to extreme conditions of the natural environment on devastated territories: thanks to the fast pace of spreading and the long time bank conservation of viable diaspores. In our opinion, rhizoidal tubers, formed under such conditions, function mainly as organs of nutritious substance accumulations, are more resistant to temperature and moisture changes, and contain more reserve substances than unicellular spores, promoting the formation of a larger number of new plants and more active colonization of destroyed substrates. In this way dioecious species supplement or fully substitute sexual reproduction. Thus, on the basis of the investigations carried out, it may be confirmed that dioecious moss species prevail on the dump. They are characterized by considerable flexibility of development and raised genetic polymorphism, which widely realize various possibilities of sexual and vegetative reproduction, making mosses more viable and promoting successful colonisation of devastated territories.

Perhaps, sexual dimorphism of dioecious species is an aspect of their adaptability formed in the process of evolution and is connected with physiological-biochemical plant differences (Fuselier & McLetchie, 2004; Khryanin, 2007). The advantages of cross fertilization are based on rather rapid genopool purification from harmful mutations and accumulation of useful changes, which gives a chance for populations to adapt to changeable environmental conditions. Up till now it has been established that the scale of self-fertilization of monoecious moss species is obviously exaggerated, and that cross fertilization occurs more often than had been considered earlier (Söderström & During, 2005). Both vegetative and generative reproduction is typical of the majority of dioecious acrocarpous mosses on the dump. Moss spore formation needs a large energetic input (Bisang & Ehrlen, 2002; Bisang & Hedelén, 2005). Energy is also necessary to form specialized reproductive structures such as bulbils rhizoid tubers. It seems as if gametophytes and sporophytes compete for limited plant resources, but sexless structures as a rule, don't need the corresponding seasonal conditions for their development, which would guarantee reliable reproduction. Vegetative reproduction of dioecious species not only compensates their limited capacity for sexual reproduction under the conditions of time – space sex division but besides gametophyte fragments renewal, it can be the source of considerable changeability (Stark, 2002). Thus, thanks to the strategy of energy conservation, the majority of dominant dioecious bryophyte species alternate periods of sexless and sexual reproduction, providing them with essentially higher viability, reproductive and genetic flexibility for effective colonization of devastated territories. Mosses grow mainly in groups forming more or less dense turfs, which causes the formation of microconditions in single turfs, namely, their own microenvironment. It should be noted that for sporogonium formation, mosses need conditions which always correspond to the environment of their optimum growth. Sporogonium formation is undoubtedly the most important for successful distribution of species.

Among possible reasons for the rarity of sporophyte formation in separate turfs of dominant dioecious species, the following points should be mentioned: suppression of gametangia formation with one or both sexes and of their fertility, perhaps, as the result of various types of sensitivity to the influence of unfavourable environmental factors and different energetic losses on perigonia and perichaetia formation and sex manifestation; deviation in sex correlation and spreading of monoecious turfs as the result of colonial growth; low percentage of sexually mixed turfs in connection with rarity of male gametangia. Thus, substantial differences in sexual structure and reproductive phenology of the dominant moss species on the dump 1 of Yazivske sulphur deposit have been established. The species differ in reproductive ability, growth and morphometric shoots indices depending on growth microconditions (wash out and humidity gradient). On the top, *Bryum caespiticium* forms bud-shaped stems, while in the dump base they are more stretched; in moist places on the north slope, *Bryum argenteum* forms more dense turfs mainly with male plants, and shoots with great number of bulbils in loose turfs on the top of the south slope. Variability

of sexual correlation, sexual productivity and reproductive stages depending on the growth locality – in the base, middle part and the slope top have been determined.

Hence, the high level of sexual demorphism, various rates of gametangia ripening and their capacity for reproduction with diaspores are the main factors influencing sexual correlations and promote cross fecundation in dioecious species in this way supporting the high level of genetic variability of moss, with the type of colonists' life strategy under the conditions of devastated territories. As male plants are more sensitive to unfavourable natural conditions (Longton, 1992, 2006), perhaps, in mixed turfs female plants can ensure their additional protection and conditions for their higher productivity. Male plants show a greater capacity for clone growth, dispersal and capture of new territories; therefore, they form monoecious turfs, which can exist for a long time. This leads to deviation of sex ratio among ripe plants of dioecious moss species. A considerable number of sterile plants was observed in male turfs. This is, perhaps, connected with preservation of energetic resources, as the formation of male organs needs more input (Stark et al., 2009), than that of females. On the other hand, essential losses of male gametes on the way to female gametangia take place.

The analysis results of sexual structure of *Bryum caespiticium*, *B. argenteum*, *B. dichotomum* and *Ptychostomum pseudotriquetrum* turfs show that fertile plants were formed more intensively on the north dump slope than on the south one. It has been established that depending on exposition and location on the dump, turfs of dominant dioecious species differ considerably in the number of sexual shoots: their ratio, productivity as well as their capacity for vegetative or generative reproduction. The tendency to prevalence of female plants has been established for many dioecious bryophyte species in spite of the fact that the sex ratio 1♀ : 1♂ is expected in meiosis in accordance with chromosome sexual determination. Thus, the sexual structure of dominant moss species and their sexual productivity is changeable, its formation depends on the turf sizes, the conditions of slope moisture, competitive expansion of neighbouring bryophyte species. The formation of a greater number of female plants in the turf is a rather widespread phenomenon among dioecious mosses (Lobachevska & Sokhanchak, 2017) and gynoecea sometimes prevail even in monoecious species (Goffinet & Shaw, 2009). This is the result of short-term adaptation chosen by selection for decrease of out-breeding over expenditure or the manifestation of adaptation to suboptimal conditions, as for example was established for arctic species *Polytrichum alpestre* (Longton, 1998). Some authors explain the absence of male plants (During 1979; Goffinet & Shaw, 2009) by increased sensitivity of male sex to the changes of media conditions. In general, the time of the first reproduction and the rate of individual atrophy essentially influence the sex ratios (Boiko, 1999; Jesson et al., 2011).

The analysis results of vital cycles of dominant moss species show that they, first of all are able to avoid unfavourable conditions that is, the stages of their life cycle are adapted to different conditions. It is best observed in the drought resistant moss *Barbula unguiculata*, which forms loose turf during the year. Life cycles of two-year species of the genus *Bryum* differ in the high flexibility of specific reproductive structures, adaptive reactions of life forms and the resistance to drying out that gives them the chance to occupy various ecological niches. Thus, moss species dominate on the dump thanks to combination of extremely high phenotypic plasticity and their exceptional ability for survival. On the basis of the results of analysis of the reproductive phenology of the main colonists *Barbula unguiculata* and *Bryum caespiticium*, it has been established that they belong to two alternative groups as to the duration and phenological properties of sporophyte development, which needs high humidity, while dissemination of spores needs drier conditions. Fecundation in *Barbula unguiculata* occurs in the spring-summer period with continuous sporophyte development, spores are spread from early summer to the following spring. So, the species dominates on the damper north dump slope. *B. caespiticium* had the advantages on the drier south slope, because ovule fecundation occurs in the summer period, embryos mainly pass the winter but sporophytes sometimes ripen in autumn or the next spring. It has been established that depending on the locality on the dump – in the base, middle part and on the

top of the slope, the turfs of dominant dioecious species differ considerably in the number of sexual shoots, their ratios, productivity, reproductive stages, and capacity for vegetative or generative reproduction. Besides sexually mixed turfs, plots of mainly female or male plants have been fixed. However, on the whole, the presence of a great number of male plants in monoecious turfs on the dump is levelled by the female plants mainly: in *B. caespiticium* and *B. argenteum* the ratio ♀ : ♂ is 1.4.

Photosynthetic activity of the mosses on the devastated territories of sulphur extraction. The important process which determines vital functions of all green plants is carbonic acid assimilation. It is known that clear dynamics with maximum interchange intensity of gases which is tied to place of reproductive development is displayed by flowering plants in seasonal aspect (Martin & Adamson, 2001; Cui et al., 2009). In connection with the unique specific character of mosses' gametophyte organization (small sizes, weak rhizosphere development, primitive conductive system and other morphophysiological properties), it can be supposed that this plant group has other, distinctive from flowering plants, peculiarities of photosynthetic apparatus functioning. The analysis of moss photosynthesis intensity on the territory of the dump showed the dependence of this index both on the species peculiarities, adaptability to the locality conditions and on morphological moss characteristics. First of all, the species life form has an important meaning, as the highest values of CO₂ assimilation are established for those species which form short dense and friable turf (*Bryum caespiticium* and *B. argenteum*). The species with such life form are characterized by higher tolerance to unfavourable ecological conditions (Goffinet & Shaw, 2009; Lüttge et al., 2011; Hanson, Rise, 2014; Kyyak, 2014; Kyyak & Khorkavtsiv, 2015; Kyyak et al., 2017). The decrease of photosynthesis intensity in the direction from the base to the dump top has been established for all investigated moss species. Perhaps, high insolation and unstable moisture regime on the dump slope were the main reasons for variations in the photosynthetic apparatus of the mosses.

In a number of publications it has been shown that bryophyte photosynthesis after dark acclimatisation is induced much faster than in tracheophytes, reaching 50% of maximum gross photosynthesis in about 90 seconds. Such rapid induction is comparable only to tracheophytes, whose stomata do not limit CO₂ uptake. Times taken to reach 90% of gross photosynthesis were also substantially shorter in bryophytes (~220 s) than those reported for most tracheophytes (500–2000 s). Shade-grown mosses did not reveal lower photosynthetic capacity than sun grown ones. For example, shade-grown *Hypnum cupressiforme* induced photosynthesis slightly faster than that from forest gaps. It was concluded that bryophytes are efficient utilizers of temporal light heterogeneity, increasing carbon gain during short high-light events (Botting & Fredeen, 2006; Grogan & Jonasson, 2006; Cui et al., 2009; Hanson & Rise, 2014; Kubašek et al., 2014).

Bryophytes adapted to the wide range of light intensity and temperature regime are good for reparation of photosynthetic activity after the dry summer period (Csintalan et al., 2000; Marschall & Proctor, 2004; Cui et al., 2009; Hanson & Rice, 2014; Kubašek et al., 2014; Kyyak, 2015). Such peculiarities of bryophyte photosynthetic activity essentially increase the primary productivity of these plant groups where they are the pioneers (De Lucia et al., 2003; Proctor & Smirnov, 2011; Street et al., 2012). It has been established that the productivity value (chlorophyll index) of moss cover on the dump plateau is rather high, which is caused by the essential mass of assimilating moss organs and high content of green pigments in them.

Role of bryophytes in accumulation of organic carbon and biogenic elements in the substrate of the sulphur extraction dump. Bryophytes are able to grow in stressful conditions like cold, drought, shade and in nutrient poverty conditions and play a dominating role in such ecosystems by subsequently influencing factors such as soil temperature, nutrient input, etc. The role of bryophytes in an ecosystem is governed by four properties: their ability to establish soils, to trap and hold moisture, to exchange cations and to tolerate desiccation.

We know that bryophytes colonize barren lands which have poor nutrients and where no other plants may grow. After a long interval, these bryophyte colonies build up an organic layer on that barren land which helps the growth of microorganisms. These microbes change the

mineral status of the substratum and the site become suitable for the establishment of other vegetation (Douma et al., 2007). In our investigation it was shown that the rate of organic carbon accumulation in the upper horizons of the post-technogenic substrate on the dump territory is different, it depends on the microrelief, microclimatic conditions, on the projective cover of bryophytes and their species composition. The quantity of organic carbon increased in the bedding substrate layer under moss turfs on all dump levels compared to its content in the substrate without turfs. The high variability of organic substance content is determined by both specific moss peculiarities and the microconditions on the dump territory. The highest content of organic carbon in the upper dump horizons has been established under moss turfs of *Bryum caespiticium* and *B. argenteum*. The lowest indices of organic carbon content have been determined on the dump top, which may be caused by both tension of ecological factors on this plot (high insolation level, moisture deficit), and the periodic transference of upper horizons of ground formation substrate down the slope as the result of morphodynamic processes characteristic of technogenic landscapes. It is obvious that essential variability of organic carbon accumulation rate can be caused by the fact that the essential part of organic substance on the dump territory is represented by humus compounds and undecomposed organic remnants (mainly by the dying off of products of moss turfs and by the introduced falling of vascular plants). This can point to the slow mineralization of plant remnants as the result of specific hydrological conditions and unripeness of microorganism groups, which are the main destructors of organic remnants (Douma et al., 2007).

It is known that bryophytes play an important part in the circulation of nutrient substances in ecosystems, in spite of the relatively small share of their biomass compared to vascular plants (Goffinet & Shaw, 2009). Mosses can absorb nutrient substances from atmospheric air, precipitation, dust and retain them during a long period of time in the undecomposed part of dead shoots (De Lucia et al., 2003). It has been established that bryophytes promote enrichment of the dump substrate with biogenic elements. This process is governed by the high cation exchange capacity of mosses. This characteristic phenomenon takes place by a large net negative charge carried extra cellularly on the cell walls of mosses, and plays a role in absorption of some nutrient cations (De Lucia et al., 2003). Peculiarities of moss species have essential influence on the process since the highest indices of organic carbon, nitrogen and phosphorus content were fixed in the substrate under the moss *B. caespiticium* with dense turfs. An important role is also played by concrete ecological conditions on slopes of the dump. The role of bryophytes in accumulation of nitrogen in the soil is discussed in numerous publications (Brisbee et al., 2001). It has been established that the dead part of moss cover has rather high hydrolytic acidity, thanks to this factor the moss bedding is characterized by essential absorption ability and can contain not only hydrogen ions in great quantities, but also other elements necessary for plants (Bowden et al., 1999). It has been established in arctic ecosystems that some species of *Sphagnum* genus as well as *Hylocomium splendens* (Hedw.) Schimp. and *Pleurozium schreberi* (Willd. ex Brid.) Mitt. accumulate three times more nitrogen and phosphorus than *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (Goffinet & Shaw, 2009). In our experiments in the substrate under moss cover formed by the dense turf of the species *Bryum caespiticium*, the gross nitrogen content increased by 79.3–247.1%, phosphorus content increased by 33.3–45.7% compared to their quantity in bare substrate.

Thus, at the early stages of soil formation, bryophytes as pioneer plants play the key role in this process promoting accumulation of organic substance and in this way create the conditions for the development of other higher plants and soil biota.

Conclusions

The quantitative analysis of biomorphological structure allowed us to establish the dependence of spread of life forms on exposition and slope height. The essential variability of the projective cover and moss biomass indices depending on exposition and position on the dump slope was found but it was established that bryophyte cover plays an essential part in optimization of moisture regime and surface layer temperature of the technogenic substrates, improving the conditions of

growth localities. For effective colonization of devastated territories, the majority of dominant dioecious bryophyte species, besides high regenerative ability and gametophyte fragmentation, use a large and more viable arsenal of various ways of sexual and sexless reproduction, providing them with essentially higher viability, reproductive and genetic plasticity. Vegetative reproduction of dioecious species not only compensates their limited capacity for sexual reproduction under the conditions of time – space sex division, but besides gametophyte fragments renewal, it can be the source of considerable changeability. The results of analysis of vital cycles of the dominant moss species show that different vital cycles differ in the high plasticity of specific reproductive structures, adaptive reactions of life forms and the resistance to drying out that gives the chance to occupy various ecological niches. Thus, moss species dominate on the dump thanks to a combination of phenotypical and genetic plasticity and their exceptional ability for survival. It has been established that depending on exposition and location on the dump, turfs of dominant dioecious species differ considerably in the number of sexual shoots: their ratio, productivity as well as their capacity for vegetative or generative reproduction.

The analysis of seasonal moss photosynthesis dynamics has demonstrated the adaptability of moss photosynthetic apparatus to contrasting climatic conditions on the dump territory and the ability to support the intensity of photosynthetic processes on rather a stable level during the vegetative period. The important role of bryophytes in the productivity of plant cover on the post-technogenic territories of sulphur extraction was shown. The obtained results indicated that high chlorophyll indices of moss cover on the dump territory were caused by the essential mass of assimilating moss organs and high content of chlorophylls in them. This index is fully comparable with the values of ChI determined for plants groups with vascular plants' domination. The important role of bryophytes in the processes of primary soil formation was found. It was established that bryophytes promote enrichment of the dump substrate with organic carbon and biogenic elements (nitrogen and phosphorus). It was shown that the rate of accumulation of organic carbon and biogenic elements in the upper horizons of post-technogenic substrates on the dump territory is different and depends on the microclimatic conditions, projective bryophyte cover and species composition. It has been established that moss cover increases acidity of aqueous solution of the upper layer of the technogenic soil, in this way promoting activity of exchange processes and vital functions of pioneer species. The highest variability of pH values of water aqueous subsoil solution on the dump slope, mainly on the north one was registered. This is, perhaps, connected with substantial changes of their microclimatic conditions, first of all of water regime.

Thus, negligible increase in acidity of the upper substrate layer occurred on the dump by means of moss cover. Perhaps, optimal weak – alkaline conditions are established in this way, which are favourable for oxidation – reduction processes of ground minerals transformation, weak acids ionization (e.g. growth substances) absorption and substances transport.

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