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

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Introduction

The restoration of territories devastated as a result of excavation of natural sulphur deposits is one of the most important ecological problems in Western Ukraine. Technogenic changes in these territories are so profound that formation of artificial high-productive agroecoses 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; Tolvanes & Aronson, 2016).

As the result of open-cut 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 monoecious and dioecious moss are important aspects for explaining the peculiarities of reproductive strategy of moss (Szővényi 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, bulblets 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 Sphagnum species, bryophytes of wood groups and bogs, tundra ecosystems, and chalky meadows of Europe as examples (Prorok, 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 start their growth with protonema formation because of the lack of apical cells.

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 district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yazivsky sulphur deposit (Lviv region, Yavoriv district), subordinated to Novoyavorivsk sulphur deposit of the state (Gomul, Ukraine) of Yas...
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.](Image)

**Table 1**

| Species                              | Exposition | Locality |
|--------------------------------------|------------|----------|
| Amblystegium serpens (Hedw.)         | 3          | 3        | 3        | –         | –         | –         | –         | –         |
| Schimp.                              | 3          | 3        | 3        | 2(N)      | –         | –         | –         | –         |
| Antiochecium varium (Hedw.) Mitt.    | 3          | 3        | 3        | 2(N)      | –         | –         | –         | –         |
| Barbula unguiculata Hedw.            | 4          | 4        | 4        | 4         | 4         | 4         | 4         | 4         |
| Brachythecium glareosum (Bruch ex Spruce) Schimp. | 4          | 4        | 4        | 4         | 4         | 4         | 4         | 4         |
| Bryum argenteum Hedw.                | –          | 3        | –        | 3         | –         | –         | –         | –         |
| B. caespitisci Hedw.                 | 2          | 2        | 2        | 2         | –         | –         | –         | –         |
| B. dichotomum Hedw.                 | 2          | 2        | 2        | 2         | –         | –         | –         | –         |
| Ceratodon purpureus (Hedw.) Brill.   | 2          | –        | 2        | –         | 2         | 2         | 2         | 2         |
| Dicranelia heteromallia (Hedw.)      | 2          | 2        | 2        | 2(N)      | 2         | 2         | 2         | 2         |
| Schimp.                              | 3          | 3        | 3        | 2         | 2         | 2         | 2         | 2         |
| Didyomod rigidiolus var. gracilis (Schleich. ex Hook. & Grev.) | R. H. Zander | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 |
| –                                    | –          | 2        | 2        | 2         | –         | –         | –         | –         |
| D. fallax (Hedw.) Zander             | –          | 2        | 2        | 2         | –         | –         | –         | –         |
| Drepanocladus aduncus (Hedw.)        | –          | 2        | 2        | 2         | –         | –         | –         | –         |
| Warnst.                              | –          | 2        | 2        | 2         | –         | –         | –         | –         |
| Ditrichum puzilum (Hedw.) Hampe      | –          | 3        | 2        | 2         | –         | –         | –         | –         |
| Fissidens bryoides Hedw.             | 3          | 3        | 3        | –         | –         | –         | –         | –         |
| F. taxifolius Hedw.                  | 1          | –        | 1        | –         | –         | –         | –         | –         |
| Funaria hyggomtrica Hedw.            | 1          | –        | 1        | –         | –         | –         | –         | –         |
| Hygroamblystegium varium (Hedw.)     | 4          | 4        | 4        | 4         | 4         | 4         | 4         | 4         |
| Mnik.                                | 2          | 2        | 2        | 2         | –         | –         | –         | –         |
| Leptocladum riparium (Hedw.)         | 2          | 2        | 2        | 2         | –         | –         | –         | –         |
| Warnst.                              | 3          | 3        | 3        | 3         | 3         | 3         | 3         | 3         |
| Pellia endivifolia (Dicks.) Dumont.  | 3          | 3        | 3        | 3         | 3         | 3         | 3         | 3         |
| P. pseudotriquetrum (Hedw.)          | 3          | 3        | 3        | 3         | 3         | 3         | 3         | 3         |
| R. Speace & H. P. Ramsay             | 2          | 2        | 2        | 2         | –         | –         | –         | –         |
| Tortula medica Zander                | –          | 2        | 2        | 2         | –         | –         | –         | –         |
| Total                                | 17         | 12       | 17       | 16        | 12        | 6         | 12        | 6         | 12        |

**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 (Antiochecium varium, Dicranella heteromallia, Didyomod fallax, Drepanocladus aduncus, Hygroamblystegium varium, Leptocladum riparium) and liverwort Pellia endivifolia occurred exceptionally in the base of the north slope and only 1 species (Ditrichum puzilum) 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, Didyomod rigidiolus var. gracilis) were only on the north side, 3 (Bryum dichotomum, Fissidens bryoides, Tortula medica) 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 heteromallia, Didyomod rigidiolus var. gracilis, Didyomod fallax, Funaria hyggomtrica, Pellia endivifolia), but 2 species were only on the south slope (Fissidens bryoides, Tortula medica).

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 heteromallia, Didyomod fallax, Pellia endivifolia, P. pseudotriquetrum, Fissidens taxifolius, Funaria hyggomtrica, Brachythecium glareosum. The frequent spring species was Didyomod rigidiolus 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 puzilum found there, while in autumn such species were found as Dicranella heteromallia, P. pseudotriquetrum.
In the upper layer of technogenic substrate the influence of moss turf was in general smaller (the difference between the substrate humidity was more essential on the south slope, although 16.4% higher than of the bare substrate). Thus, the influence of moss on growth localities were optimal for the growth and development of the highest indices of biomass and total bryophyte projective cover were determined. This testifies to the fact that microconditions of these localities were optimal for the growth and development of the Amblystegium varium, Didymodon rigidulus var. gracilis, Ceratodon purpureus, 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

| Exposition | Humidity, % | Biomass, g | Projective cover % |
|-------------|-------------|------------|--------------------|
| north slope |             |            |                    |
| base        | 41.3 ± 2.5**| 269 ± 2.5  |                    |
| slope       | 495 ± 4.5***| 789 ± 4.1  |                    |
| south slope |             |            |                    |
| base        | 394 ± 4.8** | 468 ± 4.5  |                    |
| slope       | 333 ± 2.2** | 512 ± 6.6  |                    |

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 turfs 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. Stenophytic 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

| Growth locality | Species name            | pH value of upper substrate layer |
|-----------------|-------------------------|----------------------------------|
| north slope     | base Ceratodon purpureus| 5.69 ± 0.03***                  |
|                 | Bryum caespiticum        | 6.96 ± 0.03***                  |
|                 | Barbula unguiculata      | 6.95 ± 0.03                     |
|                 | Bryum argenteum          | 6.94 ± 0.04                     |
|                 | Bryum caespiticum        | 6.96 ± 0.05***                  |
| top             | Barbula unguiculata      | 6.95 ± 0.04                     |
| south slope     | base Bryum caespiticum   | 6.73 ± 0.05                     |
|                 | Barbula unguiculata      | 6.87 ± 0.03                     |
|                 | Pellia endiviifolia      | 7.13 ± 0.04***                  |
|                 | Barbula unguiculata      | 6.98 ± 0.03***                  |
|                 | Bryum caespiticum        | 7.05 ± 0.05                     |
| top             | Barbula unguiculata      | 6.94 ± 0.03***                  |

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 subsol 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 ºC hotter. The amplitude of variability of the average temperatures for the substrate under bryophyte cover amounted to 17.3–30.3 ºC on the north and 20.1–33.2 ºC on the south slopes, but for the bare plots it was 17.7–34.1 ºC and 21.1–36.8 ºC 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 ºC on the north and 19.9–32.2 ºC on the south slopes, but the temperature of the bare substrate was 14.7–20.0 ºC and 18.7–31.3 ºC, 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 ºC) 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 (R²) 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](image)

![Fig. 3. Temperature dependence of surface substrate layers under moss cover (a) and without vegetation (b) on the light intensity](image)
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 monocious. In general, the number of dioecious species on the dump (27 species, 55%) exceeded that of monocious 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 monocious species: underground rhizoid tubers (Barbula unguiculata and Bryum caespiticium, B. dichotomum, Psychotostomum 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 branches 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. Two sporogonia each.

**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 caespiticosum 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 caespiticosum, tubers were laid on stolons of extremely branched rhizoid protonema (Fig. 6a).

**Fig. 6.** Sporangia of Bryum caespiticosum and Bryum dichotomum

**Bryum caespiticosum** 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 desiccation. It obviously gives Bryum caespiticosum 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 caespiticosum, B. argenteum, Decadella heteromalla, D. varia, Ceratodon purpureus, and less common Psychotostomum pseudotriquetrum, Bryum dichotomum, Didymodon heteromalla, D. varia, Ceratodon purpureus, and less common Psychotostomum pseudotriquetrum, Bryum dichotomum, Didymodon
rigidulus var. gracilis, in which male and female plants, as a rule, were in one turf, spore rather seldom. Among monocious mosses frequent sporogonium formation is mentioned only for Funaria hygrometrica, Amblystegium serpens and Brachythecium salebrosum (Hoffm. ex F. Weber & Mohr) Schimp.

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.
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](image)

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 monoeocious 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

| Growth locality | Number of plants, pieces | Fertile shoots, % | Sexual proportion | Sporogonia, % |
|-----------------|--------------------------|-------------------|-------------------|---------------|
| North slope     |                          |                   |                   |               |
| Base            | 54.5 ± 6.2               | 47.4 ± 8.2        | 156.9 ± 9.3       | 39.3 ± 2.3    | 0.46          | 80.7 ± 2.3   |
| Middle          | 86.3 ± 5.2***            | 48.0 ± 3.1        | 443.5 ± 9.8       | 34.0 ± 2.7    | 0.36          | 84.6 ± 3.0   |
| Top             | 85.1 ± 8.3               | 68.6 ± 9.5        | 297.4 ± 7.3       | 23.2 ± 1.9    | 0.36          | 86.7 ± 2.9   |
| South slope     |                          |                   |                   |               |               |               |
| Base            | 55.2 ± 5.4***            | 36.7 ± 4.0        | 266.3 ± 6.1       | 25.5± 1.4     | 0.39          | 30.8 ± 2.5   |
| Middle          | 21.7 ± 3.6               | 11.0 ± 2.1        | 214.5 ± 5.3       | 13.0 ± 0.7    | 0.34          | 48.5 ± 5.3   |
| Top             | 12.5 ± 2.1               | 183 ± 3.0         | 152.3 ± 3.7       | 16.5 ± 1.0    | 0.60          | 5.0 ± 1.0    |
| North slope     |                          |                   |                   |               |               |               |
| Base            | 30.9 ± 3.1***            | 3.1 ± 0.5         | 136.7 ± 3.0       | 19.5 ± 1.8    | 0.09          | 70.0 ± 8.2   |
| Middle          | 86.4 ± 7.3**             | 128.3 ± 10.1      | 315.3 ± 8.7       | 40.4 ± 3.5    | 0.60          | 89.6 ± 8.9   |
| Top             | 86.6 ± 6.8               | 78.3 ± 9.2        | 172.7 ± 5.8       | 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       | 17.7 ± 0.9    | 0.60          | 105.0 ± 9.7  |
| Middle          | 47.3 ± 2.7***            | 163.9 ± 19        | 124.3 ± 4.2       | 33.7 ± 2.8    | 0.25          | 105.8 ± 9.3  |
| Top             | 40.5 ± 7.1               | 490 ± 5.3         | 257.7 ± 8.3       | 24.4 ± 1.6    | 0.55          | 110.9 ± 9.5  |

*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 gametangia 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 CO2 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 CO2 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 meteor 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 CO₂/g of raw material/hour | April – May | June – July | August – September |
|------------------------------------|--------------------------------------------------------|-------------|-------------|-------------------|
| *Bryum caespiticium*                |                                                        |             |             |                   |
| 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 |                   |
| *Bryum argenteum*                 |                                                        |             |             |                   |
| plateau of the dump                | 3.50 ± 0.24                                            | 1.22 ± 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 |                   |
| *Barbula unguiculata*             |                                                        |             |             |                   |
| 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 caespiticum* was analysed and it was revealed that it looks like a double-apex curve. The photosynthesis maximum falls in the morning hours (8–10 o’clock), which is characteristic of polikolythic 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 insoluation level, was found (Fig. 9).

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 (Chl), 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).

### Table 6

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

| Plant species               | Chlorophyll content (g_CO₂/\text{g} surface phytomass), mg | Supply of the phytomass, g/m² | Chlorophyll index, \text{g/m²} |
|----------------------------|-------------------------------------------------------------|--------------------------------|-------------------------------|
| Vascular plants            |                                                             |                                |                               |
| *Calamagrostis epigeios*   | 0.782 ± 0.051                                               | 12.22 ± 1.13                   | 0.0095 ± 0.0001               |
| *Cirsium arvense*          | 0.965 ± 0.081                                               | 1.74 ± 0.13                    | 0.0016 ± 0.0002               |
| Mosses                     |                                                             |                                |                               |
| *Bryum caespiticum*        | 1.231 ± 0.092                                               | 253.82 ± 21.15                 | 0.0361 ± 0.0211               |
| *Bryum argenteum*          | 1.053 ± 0.097                                               | 56.37 ± 3.15                   | 0.0593 ± 0.0034               |
| *Barbula unguiculata*      | 0.743 ± 0.056                                               | 182.53 ± 16.42                 | 0.1356 ± 0.0092               |

The chlorophyll index was determined for moss group on the dump plateau with moss *Bryum caespiticum*, 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 caespiticum*, *B. argenteum*), 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 caespiticum* 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 Chl, determined for plant groups with domination by vascular plants (for example, for shrubbery group Chl 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
Bryum argenteum reached 2 cm in some turfs of the north slope, the highest content of organic carbon was in the substrate under mosses (3.9–4.5%). On the base, the maximum content of organic carbon in the substrate under the moss cover was determined on the dump plateau (0.9–1.8%). In the territory of the dump, 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 differences 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 caespiticium 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).

Note: 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 structurally reorganized, 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 caespiticium and B. argenteum. In the substrate under moss cover formed by dense Bryum caespiticium 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 7

| Locality of substrate samples | Content of organic carbon, % | Content of nitrogen, % | Content of phosphorus, % |
|------------------------------|-----------------------------|------------------------|--------------------------|
| Collection under moss turfs  | Uncovered substrate (control) | North slope | South slope | North slope | South slope |
| Plateau of the dump          | 1.723 ± 0.082               | 1.645 ± 0.112         | 1.822 ± 0.091           |
| Top                          | 1.233 ± 0.091               | 1.922 ± 0.104         |
| Bryum caespiticum            | 4.335 ± 0.041***            | 2.567 ± 0.062**       | 2.324 ± 0.041**         |
| Slope                        | 2.843 ± 0.041***            | 2.458 ± 0.082**       | 2.043 ± 0.091**         |
| Top                          | 2.366 ± 0.052**             | 2.403 ± 0.091**       |
| Bryum argenteum              | 3.925 ± 0.061***            | 2.568 ± 0.074**       | 1.940 ± 0.113           |
| Plateau of the dump          | 2.735 ± 0.081***            | 2.433 ± 0.082**       | 2.115 ± 0.122**         |
| Top                          | 2.216 ± 0.113**             | 2.115 ± 0.122**       |
| Barbaula unguiculata         | 3.265 ± 0.114***            | 3.367 ± 0.312**       | 3.167 ± 0.095***        |
| Plateau of the dump          | 2.153 ± 0.132*              | 2.062 ± 0.051*        | 2.062 ± 0.073*          |
| Top                          | 2.236 ± 0.114*              | 2.062 ± 0.073*        |

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 Barbaula 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 conformity: 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.

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).

### Discussion

Lichens and mosses are the pioneer bryophyte species settling on the dump slopes and on the open growth places in tundra (During, 1992). The life forms of these species are the most complex, forming a dense rhizoid tomentum, which penetrates into the substrate and prevents it from disintegrating. The species Bryum argenteum played a special part in these processes. Besides, the species Bryum caespiticium 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 caespiticium. Penetrating into the substrate, moss rhizoids form a dense net, increasing porosity and promoting enrichment of the substrate with oxygen and moisture.

The pioneer bryophyte species settling on the dump slopes function as a separate life form, which guarantees adaptation to xeric conditions. Bryum argenteum connected with growth microlocations. For example, cushions are groups of tightly connected moss colonies (During, 1992). The life forms are closely connected with life functions as a separate life form, which guarantees adaptation to xeric conditions. Perhaps, the high insolation level on the south dump slope influences these life forms as for many moss species negative correlation between nitrogen and phosphorus accumulation and light intensity has been established (Proctor, 2002).

**Lycophytes 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 well 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 wetts 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 productivity 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 antarcticum (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 (Branley-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 re-store 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 life forms, makes it possible to elucidate the participation of the diaspore bank 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 nutritive 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 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 estab- lished 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 & Hedén, 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 gene- tic 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 micro-environment. It should be noted that for sporogonium formation, mosses need conditions which always correspond to the environment of their optimum growth. Sporogoniant 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 monoeccious 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 phology of the dominant moss species on the dump 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 buds-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 fertilization 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 monocious 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 Psychotomum 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 organization 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 gynoecia sometimes prevail even in monocious 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 their 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 monocious turfs on the dump is levied by the female plants mainly; in B. caespiticium and B. argenteum the ratio 1♀ : 1♂ 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 & Khorkavtsev, 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 acclimation 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 utilisers of temporal light heterogeneity, increasing carbon gain during short high-light events (Bottig & Fredeen, 2006; Grogan & Jonasson, 2006; Cui et al., 2009; Hanson & Rise, 2014; Kubisiek et al., 2014).

Bryophytes adapted to the wide range of light intensity and temperature regime are good for preparation of photosynthetic activity after the dry summer period (Cisitalan et al., 2000; Marschall & Proctor, 2004; Cui et al., 2009; Hanson & Rice, 2014; Kubisiek et al., 2014; Kyyak, 2015). Such peculiarities of bryophyte photosynthetic activity essentially increase the primary productivity of this plant groups where they are the pioneers (De Lucia et al., 2003; Proctor & Smirnoff, 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, pro- 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 insoluation level, moisture deficit), and the periodic transference of upper horizons of ground formation substrate down the slope as the result of morphodynam- ic 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 condi- tions 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, precipita- tion, dust and retain them during a long period of time in the undecom- posed part of dead shoots (De Lucia et al., 2003). It has been established that bryophytes promote enrichment of the dump substrate with bioge- nic elements. This process is governed by the high cation exchange capacity of mosses. This characteristic phenomenon takes place by a large negative charge carried extra cellulary 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. caes- piticium 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 publicati- ons (Brisibe 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 ele- ments necessary for plants (Bowden et al., 1999). It has been established in arctic ecosystems that some species of Sphagnum genus as well as Hylcomonium splendens (Hedw.) Schimp. and Pleurozium schreberi (Willd. ex Brid.) Mitt. accumulate three times more nitrogen and phos- phorus than Picea mariana (Mill.) Britton, Stems & Poggem. (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 increas- ed 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 organ- ic substance and in this way create the conditions for the development of other higher plants and soil biota. Conclusions

The quantitative analysis of bionomorphological 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 tem- perature 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 regene- rative ability and gametophyte fragmentation, use a large and more viable arsenal of various ways of sexual and sexless reproduction, pro- viding them with essentially higher viability, reproductive and genetic plasticity. Vegetative reproduction of dioecious species not only compens- ates their limited capacity for sexual reproduction under the condi- tions 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 differ- ent 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 capac- ity for vegetative or generative reproduction. The analysis of seasonal moss photosynthesis dynamics has de- monstrated the adaptability of moss photosynthetic apparatus to contrast- ing 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 producti- vity of plant cover on the post-technogenic territories of sulphur extrac- tion was shown. The obtained results indicated that high chlorophyll indices of moss cover on the dump territory were caused by the essen- tial mass of assimilating moss organs and high content of chlorophylls in them. This index is fully comparable with the values of Chl determi- ned 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 sub- strate with organic carbon and biogenic elements (nitrogen and phos- phorus). It was shown that the rate of accumulation of organic carbon and biogenic elements in the upper horizons of post-technogenic sub- strates on the dump territory is different and depends on the microclima- tic 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 high- est 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 oc- curred 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 substan- ces transport.

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