

Effects of fires on vascular plant and microalgae communities of steppe ecosystems

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The article is focused on a hypothesis verification: the higher plants, microalgae and cyanobacteria may be used in bioindication of steppe ecosystem restoration dynamics after fires. On the territory of the Askania Nova biosphere reserve (Ukraine) 4 stationary polygons were investigated: SP1 – steppe area which had not been exposed to fire for 20 years preceding our study, as well as areas where single fires occurred in 2001 (SP2), 2005 (SP3), and a site where fires occurred in 2001 and 2004 (SP4). The investigation revealed the dynamics of height and projected area of the higher vegetation according to seasons during two years (2010 and 2011), as well as abundance and biomass of microalgae and cyanoprokaryotes in the soil layer by the layer of the depth to 15 cm. It was found that the effects of pyrogenic load remain evident for several years after the fires, manifesting in decrease of the height and projected area of herbage, the number and biomass of algae and cyanobacteria in the soil, especially to the depth of 5 cm. Multivariate general linear models were used to test the significance of the dependence of quantitative characteristics of vegetation, microalgae, and cyanoprokaryotes on environmental predictors (season, year, soil layer, and fire). In the model, 75.2% of the grass height variability and 91.6% of the grass projected area variability could be explained by the predictors under consideration. In the series SP1 → SP2 → SP3 → SP4 the grass height and projected area decreased. The differences in the projected area of the grass stand were most evident in spring. The model explained 89.1% of the variation in abundance and 91.6% of the variation in biomass of Bacillariophyceae. The abundance of Bacillariophyceae was greater in the upper soil layer than in the lower layer and decreased with depth. The abundance of this group of algae decreased in the series SP1 → SP2 → SP3 → SP4 at depths of 0–5 and 5–10 cm. Changes in abundances of Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae) equaling 47.6% could also be explained by the model. The abundance of this group of algae was greatest in the upper soil layer. In the upper soil layer, the maximum abundance of Chlorophyta, Streptophyta, and Heterokontophyta (Xanthophyceae and Eustigmatophyceae) was recorded for Polygon SP1 and the minimum for Polygon SP3. Within the model, 48.0% of the variation in biomass of Chlorophyta, Streptophyta, and Heterokontophyta (Xanthophyceae and Eustigmatophyceae) was explained by the environmental predictors. The biomass trend was coherent with the population trend. A special feature was that there was a significant increase in biomass at 10–15 cm depth at Polygon SP3 compared to other polygons at this depth. The model was able to explain 61.8% of the variation in abundance and 66.7% of the variation in cyanobacteria biomass. The highest abundance of cyanobacteria was found in the upper soil layer of polygon SP1. Somewhat lower numbers of cyanobacteria were at polygons SP2 and SP4, and the lowest were found in the upper soil layer at polygon SP3. In turn, the highest number of cyanobacteria was found particularly at this polygon in the 5–10 cm layer. The biomass in the 0–5 cm layer was coherent with the abundance pattern of this group. The research results confirmed that the quantitative characteristics of the higher vegetation (height and projected area) as well as of microalgae and cyanobacteria (abundance and biomass) may be used in bioindication of the dynamics of post-pyrogenic processes in steppe ecosystems.

Keywords: grass height and projected area; abundance and biomass of microalgae and cyanobacteria; bioindication.

Introduction

Ecosystems formed by herbaceous vegetation are widely distributed in different continents and in a broad range of climatic conditions (Butterbach-Bahl et al., 2011; Zerbo et al., 2016). They provide a wide spectrum of ecological services (Smelansky & Tishkov, 2012; Lachashvili et al., 2017; Leßmeister et al., 2019). The study of their biodiversity, functioning regularities, resistance to various factors of natural and anthropogenic origin is currently considered among the priority scientific problems (Feng & Squires, 2020; Siebert et al., 2020; Freitag et al., 2021). The steppe ecosystems of Europe have a special position in the entire diversity of herbaceous ecosystems. These are ecosystems dominated by perennial xerophytic plants, mainly sod grasses of the genera *Stipa*, *Festuca*, *Agropyron*, *Koeleria*, etc. The diversity of European steppe ecosystems is determined primarily by the heterogeneity of climatic conditions and increasing continentality in the direction from north-west to south-east. The northernmost variant, meadow steppes, is firstly replaced by a strip of true steppes and then by desert steppes (Butterbach-Bahl et al., 2011). For true steppes, the predominance of herbaceous perennial xerophytes (*Stipa capillata* L., *S. ucrainica* P. Smirn., *S. lessingiana* Trin. Et Rupr., *Koeleria cristata* (L.)

Pers, *Festuca pseudovina* Hack. ex Wiesb.) with inclusion of mesophytes and xeromesophytes is typical. Currently, the area of natural steppe vegetation is greatly modified by the human activity. A huge area of land is occupied by agriculture, industry, including mining, pipelines, transport routes, etc. As a result, only a small area of steppe natural vegetation has survived, mainly in protected areas. The Falz-Fein Biosphere Reserve Askania Nova is the largest steppe reserve in Europe (330.3 km²). Its history dates back to 1828. The vegetation complexes of the reserve were under the reserve regime for a long time, which makes it possible for us to consider the steppe ecosystems of the Falz-Fein Biosphere Reserve Askania Nova as reference ones.

Despite the strict protection, the steppes of the reserve are periodically affected by fires. Fire in herbaceous ecosystems is a quite common phenomenon of both natural and anthropogenic origin. The processes of post-pyrogenic restoration of such ecosystems are of considerable interest. This is important from the perspective of assessing possible losses of biodiversity (Reed-Dustin et al., 2016), reduction of ecosystem productivity (Bates et al., 2020), and soil fertility (Allen et al., 2011). Such studies are relevant due to the need for developing management strategies for steppe ecosystems after fires (Mata-González et al., 2018; Bates et al., 2019; Davies &

Dean, 2019; Nouwakpo et al., 2020). The significant fluctuations in the intensity of fires, frequency of their recurrence, seasonality with overlap with extreme climatic events (droughts), grazing, etc. considerably complicate the prediction of the post-pyrogenic effects and management of ecosystems during the recovery phase (Savadogo et al., 2017). The management significance of possible estimates and predictions may be improved by maximizing the extent of the studies on post-pyrogenic effects at the level of different groups of living organisms of steppe ecosystems (Kang et al., 2007; Gongalsky et al., 2012; Zaitsev et al., 2014; Muñoz-Rojas et al., 2016; Tang et al., 2018).

Vegetation cover plays a special role in assessing the structure and functions of ecosystems. The projected area is a fairly simple and informative indicator of vegetation condition (Bonham & Clark, 2005; Chen et al., 2009; Zhukov et al., 2019). The projected area is the value of the horizontal projection of aboveground plant organs. Other key ecosystem variables such as aboveground biomass, sawfly biomass, and leaf area index (LAI) may be reliably estimated using projected area (Chen et al., 2009). The projected area of soil vegetation is an important anti-erosion factor (Stred'anský et al., 2015). Developing a method to accurately determine projective vegetation cover to prevent soil erosion is important (Olmstead et al., 2004). The eye-catching determinations of projected area are context-dependent and subjective (Rasmussen, 2004), but are still widely used in practice (Jensen et al., 2004; Zhukov et al., 2018, 2019). The point-frame method was also developed (Krebs et al., 2003). This method is considered objective and is recommended as a standard protocol, but is very time-consuming, usually requiring 2–3 hours for measurements within a single site (Chen et al., 2009).

Cyanobacteria (Cyanoprokaryota, Cyanophyta) are an extremely diverse group of prokaryotes. Their adaptive abilities, along with their potential to survive extreme conditions, make them cosmopolitans. They are found in virtually every habitat on Earth where life may exist. Cyanobacteria are extremely widespread: in seas, freshwater and hyperhaline water bodies, soils, snow and ice, hot springs, aerophytic conditions, etc. (Hoffman, 1999; Liu et al., 2016). Cyanobacteria are ranked first on the planet in resistance to extreme factors (Rampelotto, 2013). Cyanobacteria are characterized by a high ecological plasticity, so they occur in various, often even extreme habitats (Soares et al., 2013; Davydov, 2014; Pelechata et al., 2016), namely, in the marine environment (Hoffman, 1999; Engene et al., 2013; Arabadzhy-Tipenko, 2020), freshwater (McGregor et al., 2007; Okello et al., 2009; Okhapkin, 2015), soils (Davydov & Patova, 2018; Shekhovtseva & Mal'tseva, 2015; Maltseva et al., 2017; Maltsev & Maltseva, 2018), the biological soil crust, snow, cryoconites, etc. (Gaysina et al., 2019). The stress to which algae may be subjected is divided into two types: limiting stress caused by insufficient supplies of resources (such as insufficient light or nutrient deficiencies), and destructive stress (as a result of damage caused by adverse conditions) (Davison & Pearson, 1996). Some Cyanobacteria can live in soil and other terrestrial habitats, where they are important in the functional processes of ecosystems and nutrient circulation (Whitton & Potts, 2006; Chaurasia, 2015). Other species colonize surfaces by attaching to rocks or sediments, sometimes forming microbial mats (Golubic & Seong-Joo, 1999; Stal, 2012). The cyanobacteria have an impressive ability to colonize such barren substrates as volcanic ash, desert sand, and rocks (Dor & Danin, 1996). Another excellent feature of cyanobacteria is their ability to survive extremely high and low temperatures. Cyanobacteria are inhabitants of hot springs (Castenholz, 1977; Ward & Castenholz, 2006), mountain streams (Dufford et al., 1987), Arctic and Antarctic lakes (Zakhia et al., 2008), snow and ice (Laamanen, 1996). The cyanobacteria also form symbiotic associations with animals and plants (Amar Nath Rai, 2018). Cyanobacteria species show different optima with respect to environmental parameters such as temperature, light or nutrient content. Cyanobacteria are very well adapted to nutrient-poor conditions and limited light availability (Reynolds, 1984).

Heterokontophyta, Chlorophyta, Streptophyta comprise a numerous group of eukaryotic algae found in both aquatic (freshwater and marine) and terrestrial ecosystems. From the ecological point of view, this is a rather heterogeneous group of algae that includes both stenotopic and eurytopic species. They play an important role in the functional processes of ecosystems, are of great practical importance and much attention is

currently paid to the study of their diversity (Mamaeva et al., 2018; Liu et al., 2019; Kezlya et al., 2020; Kulikovskiy et al., 2020a, 2020b, 2020c; Maltsev et al., 2021a, 2021b).

In the study, we tested the following hypothesis: the higher plants, microalgae and cyanobacteria may be used in bioindication of recovery dynamics of the steppe ecosystems after fires. The objective of the study was analysis of the impact of fires in steppe ecosystems on the projected area and height of grasses, abundance and biomass of soil microalgae and Cyanobacteria.

Material and methods

The Falz-Fein Biosphere Reserve Askania Nova is located in the south of Ukraine in the zone of fescue-feather grass steppes. The measurements of the total projective cover and the height of the grass stand, abundance and biomass of soil microalgae and cyanobacteria were conducted seasonally (April, July, October) during 2010–2011 on four stationary polygons (SP) located in steppe ecosystems, where the protection regime had been in operation since 1898 (SP1–SP3) and since 1966 (SP4). SP1 (500 m² area, block 42) had not been exposed to fire during the twenty years preceding our study and was chosen as the control. SP2 (300 m² area, block 59), was exposed to fire in 2001. On SP3 (250 m² area, block 42), there was a fire in 2005. On SP4 (500 m² area, Pivnichna plot) there were fires in 2001 and 2004. The projective cover of grasses, taking into account all layers, was determined using a square grid of 1 m² divided by twine into separate cells of 10 cm². On each polygon, to determine the projective cover, we laid five 1 m² recording plots located in the corners of the polygon and one in the centre. Projective cover of grasses was expressed as percentage. The height of each layer was measured with a tape measure in each survey plot with the accuracy of 1 cm. Soil samples were examined for algae and cyanobacteria. Each sample was formed from 5–10 individual specimens with an area of 25 cm² collected randomly within the corresponding polygon. A total of 72 soil samples were collected to determine the abundance and biomass of algae and cyanobacteria. Algae were detected using an optical microscope XSP-128B at the magnification × 1000, and using oil immersion. The literature used for identification included Ettl & Gärtner (1995, 2014), and others (Ettl, 1978, 1983; Krammer & Lange-Bertalot, 1986, 1988; Ettl & Gartner, 1988b, 1988a; Komárek & Anagnostidis, 2005; Komárek, 2013). The referential system of Cyanobacteria was used in accordance to the reports (Komárek & Anagnostidis, 2005; Komárek, 2013), the rest of the groups – according to 'Syllabus of Plant Families' (Frey, 2015). Cell numbers of algae and cyanobacteria were determined by direct counting (Kalimichenko et al., 2018; Fomina, 2020). This method makes it possible not only to determine the total number of cells, but also to classify them according to morphological features into three groups: Cyanobacteria (first group), Bacillariophyceae (second group) and together Chlorophyta, Streptophyta, Xanthophyceae and Eustigmatophyceae from Heterokontophyta (third group). Biomass was determined by the volume-calculation method based on the number of cells and their size characteristics. The data were recalculated per 1 gram of absolutely dry soil. All measurements were performed in three repetitions.

Multivariate General Linear Models were used to test the significance of the dependence of quantitative characteristics of vegetation on environmental predictors (Software package Statistica). Two multivariate GLMs were performed. The first multivariate GLM was performed for plant cover height and projective cover. The variables season (three levels), year (two levels), polygon (four levels) and season×year, season×polygon, year×polygon (interaction between predictors) are treated as categorical predictors. The second multivariate GLM was performed for algae and Cyanobacteria abundance and biomass with the year (two levels), polygon (four levels), soil layer (three levels) and layer×year, layer×polygon, layer×polygon (interaction between predictors) as categorical predictors. The Planned Comparisons approach was used to test the differences between individual treatments.

Results

The predictors considered were statistically significant for explaining the height and projective cover of grass stands (Table 1). Within the mo-

del, 75.2% of grass height variability can be explained by the considered predictors ($R_{adj}^2 = 0.75$, $F = 22.3$, $P < 0.001$). The grass height increased in the same manner throughout the growing season (Fig. 1). In 2010, the rate of grass height increase during the season was higher than in 2011. In the order of polygons SP1 → SP2 → SP3 → SP4, the grass stand height decreased. The variation in grass height was most apparent in spring. A total of 91.6% of the variability of grass projective cover can be explained by the predictors considered ($R_{adj}^2 = 0.92$, $F = 77.7$, $P < 0.001$). The projective cover reached its maximum in summer. The projective cover was higher in 2011 than in 2010. In the order of polygons SP1 → SP2 → SP3 → SP4, the projective cover of grasses decreased. The differences in projective cover of the grass stand were most pronounced in spring.

Table 1

Multivariate GLM results examining the effect of polygon type, season and year as predictor on plant coverage height and plant projective cover

Effect	Wilks test value	F-ratio	Effect degree of freedom	Error degree of freedom	P-level
Intercept	0.001	45726.70	2	101	<0.001
Polygon*	0.077	87.30	6	202	<0.001
Year**	0.672	24.67	2	101	<0.001
Season***	0.324	38.51	4	202	<0.001
Polygon×Year	0.665	7.80	6	202	<0.001
Season×Polygon	0.254	17.14	12	202	<0.001
Year×Season	0.712	9.36	4	202	<0.001
Error	0.001	45726.70	2	101	<0.001

Note: * – polygon type (SP1–SP4); ** – year (2011 and 2012); *** – season (spring, summer, autumn).

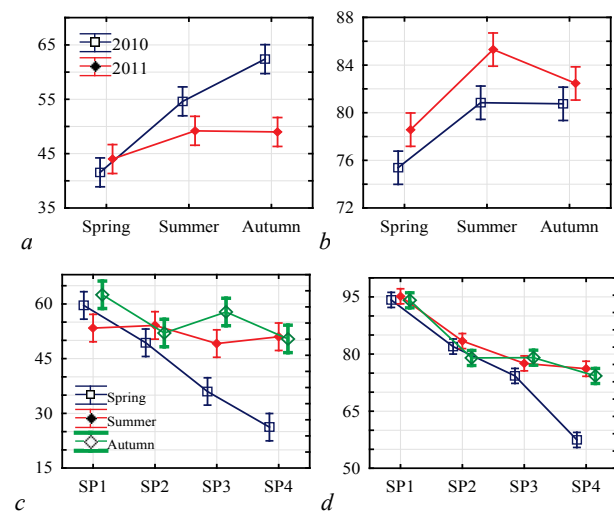


Fig. 1. The dependence of the plant cover height (cm, a, c) and plant projective cover (%), b, d) from the season (c, d), year (a, b) and burn effect (c, d): the vertical line indicates the standard deviation (SD)

The variables considered were statistically significant predictors of the abundance and biomass of algae and cyanobacteria (Table 2). Within the model, 89.1% of the variation in Bacillariophyceae abundance was explained ($R_{adj}^2 = 0.89$, $F = 286.2$, $P < 0.001$). The abundance of Bacillariophyceae was greater in the upper soil layer than in the lower ones and decreased with depth (Fig. 2). The abundance of this group of algae decreased in the series SP1 → SP2 → SP3 → SP4 at the depths of 0–5 and 5–10 cm. At the depth of 10–15 cm the differences in Bacillariophyceae abundance were not statistically significantly different. Within the model, 91.6% of the variation in Bacillariophyceae biomass was explained by the considered predictors ($R_{adj}^2 = 0.92$, $F = 379.7$, $P < 0.001$). The highest biomass of Bacillariophyceae was in the upper soil layer. The biomass of this group of algae was the highest in the SP 1 polygon at the depth of 0–5 cm. Differences in Bacillariophyceae biomass in other polygons were statistically not significant at the same soil depths.

The 47.6% variation in abundance of Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae) can be explained in the model ($R_{adj}^2 = 0.48$, $F = 32.7$, $P < 0.001$). The abundance of this group of algae was greatest in the upper soil layer. In the upper soil layer,

the maximum abundance of Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae) was recorded for polygon SP1, and the minimum was recorded for polygon SP3. At greater depths, differences in the abundance of this group of algae were not statistically significantly different within the same soil layer. Within the model, 48.0% of the variation in the biomass of Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae) can be explained by the predictors considered ($R_{adj}^2 = 0.48$, $F = 33.2$, $P < 0.001$). The dynamics of biomass was coherent with the dynamics of abundance. The peculiarity was that at the depth of 10–15 cm in polygon SP3 there was a significant increase in biomass compared to other polygons at this depth.

Table 2

Multivariate GLM results examining the effect of layer, polygon type, season and year as predictor on algae and cyanobacteria

Effect	Wilks test value	F-ratio	Effect degree of freedom	Error degree of freedom	P-level
Intercept	0.09	1661.0	6	1043	<0.001
Layer*	0.09	394.0	12	2086	<0.001
Season**	0.71	33.2	12	2086	<0.001
Year***	0.79	46.7	6	1043	<0.001
Polygon****	0.41	59.9	18	2951	<0.001
Layer×Season	0.63	21.7	24	3640	<0.001
Layer×Year	0.65	41.8	12	2086	<0.001
Season×Year	0.69	35.3	12	2086	<0.001
Layer×Polygon	0.23	50.8	36	4583	–
Season×Polygon	0.58	16.7	36	4583	–
Year×Polygon	0.71	20.9	18	2951	–

Note: * – layer (0–5, 5–10, 10–15 cm); ** – season (spring, summer, autumn); *** – year (2011 and 2012); **** – polygon type (SP1–SP4).

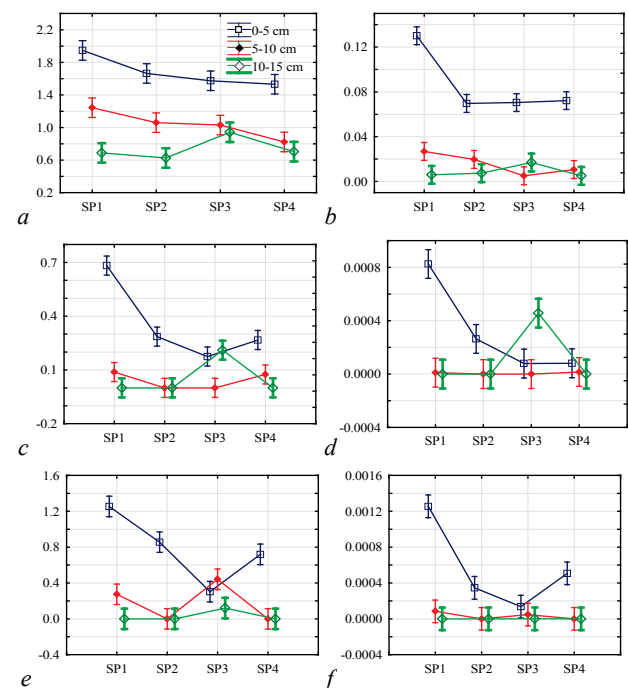


Fig. 2. Dynamics of abundance (logarithmic data: a – Heterokontophyta (Bacillariophyceae), c – Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae), e – Cyanobacteria) and biomass (logarithmic data: b – Heterokontophyta (Bacillariophyceae), d – Chlorophyta, Streptophyta, Heterokontophyta (Xanthophyceae and Eustigmatophyceae), f – Cyanobacteria) as a function of soil layer and pyrogenic impact based on the results of the General Linear Model (taking into account the impact of season, year, and their interaction); the vertical line indicates the standard deviation (SD)

The model was able to explain 61.8% of the variation in abundance and 66.7% of the variation in biomass of Cyanobacteria ($R_{adj}^2 = 0.62$, $F = 57.2$, $P < 0.001$ and $R_{adj}^2 = 0.67$, $F = 70.6$, $P < 0.001$). The highest abundance of Cyanobacteria was found in the upper soil layer in polygon SP1. Somewhat lower abundance of Cyanobacteria was in polygons SP2 and

SP4, and the lowest abundance was found in the upper soil layer in polygon SP3. In turn, it was this polygon, in the 5–10 cm layer, where we saw the highest Cyanobacteria abundance. Differences in Cyanobacteria biomass in layers 5–10 and 10–15 cm were not statistically significantly different in either layers and polygons. The biomass in 0–5 cm layer was coherent with the pattern found for the abundance of this group.

Discussion

Fires in herbaceous ecosystems can be both spontaneous, due to natural or anthropogenic factors, and purposeful, as a regulatory mechanism of the management system (Allen et al., 2011; Seger et al., 2014; Bates et al., 2020; Nouwakpo et al., 2020). Regardless of its origin, the pyrogenic load causes changes in ecosystems and, first of all, in the composition and structure of the phytosystems. As the studies showed, the pyrogenic impact on the steppe ecosystems continues to manifest itself during the next few years in the reduction of the projected area and height of the grass stand. This pattern was also recorded earlier (Zedler, 2007; Stavi, 2019). The consequence of this is a more pronounced contrast of temperature regime and humidity in the post-pyrogenic areas, to which only typically steppe species can successfully adapt. The mesophilic component in the narrowed ectopic conditions became less important. This is quite consistent with the conclusions that fire changes the course of natural transformation of the herbaceous ecosystem, associated with the intensification of the role of the mesophytic constituent and ligno-zytic component (Korotchenko & Peregrym, 2012). For European steppes, in the absence of large ungulates, a tendency towards overgrowth with shrubs and, in some cases, with forest trees has been observed (*Caragana frutex* (L.) K. Koch., *Rhamnus cathartica* L., *Acer tataricum* L., *Prunus stepposa* Kotov, *Ulmus minor* Mill., *Fraxinus excelsior* L.) (Wesche et al., 2016). Fires can act as a barrier to the mesophytization of the steppe and allow the steppe stages to persist for a longer time. The positive effect of regulated burning on the restoration of steppe vegetation has been also noted in the invasion of arboreal vegetation into sagebrush steppe communities in North America (Davies & Dean, 2019; Davies et al., 2019; Nouwakpo et al., 2020). Our results indicate that the greatest differences in height and projective vegetation cover were observed in spring and subsequently during the growing season these differences evened out. The spring period is the most favourable for the development of mesophilic fraction of flora. In spring, the most favourable living conditions are formed for plant species that are demanding in terms of water content in soil and are not adapted to live in extreme thermal regimes. Obviously, such species are most affected by fires. The restoration rate of the mesophilic fraction is significantly delayed compared to the restoration rate of the xerophilic fraction of the flora.

The effects of fires in the steppe are not the only changes in the characteristics of the vegetation, but also the transformation of soil microbial communities (Shcherbyna et al., 2017). The fires significantly change the properties of the soil as a living environment and affect the soil vegetation cover. The grass vegetation significantly affects the light and water regime of the soil. In the absence of vegetation cover and dead plant litter, we should expect a significant overcooling of the upper soil layers in winter, and in summer the soil would be subjected to a significant overheating. The vegetation cover also protects the soil from water and wind erosion and reduces moisture evaporation. A number of Cyanobacteria species are adapted to live at extremely high or low temperatures (Mutalipassi et al., 2019). A low temperature by itself does not necessarily damage the organism, but the formation of ice crystals can be fatal to it due to mechanical damage or changes in the concentrations of osmotically active solvents (Fogg et al., 1973; Fogg, 1999). The stress may occur during sudden changes in temperature (Holmstrup et al., 1999; Sinetova & Los, 2016). The microclimate temperature in the immediate proximity of the algae can differ significantly from the temperature in the broader environment. Therefore, it is necessary to distinguish between cooling and freezing. At high temperatures, the proximal cause of stress may be oxygen deficiency, oxygen being much less soluble in warm water than in cold water (Brook, 1980; Hemlata & Fatma, 2009).

In arid ecosystems, the soil surface is covered with biological soil crusts (BSC), which are composed of algae and cyanobacteria (Bowker

et al., 2004; Aguilar et al., 2009; Mager & Thomas, 2011; Dettweiler-Robinson et al., 2013; Warren et al., 2020). Their importance is associated with both a wide range of ecosystem services and the perspective of using valuable algae and cyanobacteria as a natural resource for practical use (Maltsev et al., 2020), mass production of biomass, preparation of inoculum, and soil inoculation (Liu et al., 2010; Lababpour, 2016; Antoninka et al., 2018), monitoring and control of primary successions in various man-made ecotopes and sandy habitats (Maestre et al., 2002; Myers & Davis, 2003; Barger et al., 2006; Crittenden et al., 2007) and secondary successions, including after pyrogenic destruction of various ecosystems (Allen et al., 2011; Warren et al., 2015, 2020; Aanderud et al., 2019). The biological soil crusts (bio-crusts) are the upper soil communities consisting of many groups of organisms: bacteria, cyanobacteria, microalgae, microfungi, mosses, lichens, protozoa and invertebrates (Belnap & Eldridge, 2001). Closely related to soil particles, these groups provide vital ecological functions in soil ecosystems. They contribute to nutrient cycling, increase the soil stability, reduce evaporation, and increase the soil moisture (Chamizo et al., 2016). Globally, biocrusts contribute 40% to 85% of biological nitrogen fixation by terrestrial organisms and 15% of global net terrestrial primary production (Rodriguez-Caballero et al., 2018). Biocrusts are often pioneer communities in ecosystems that are degraded as a result of natural or anthropogenic activities, for example, habitats affected by fires or that emerged after glacial retreat, mining areas, etc. Biocrusts induce the formation of soil and promote the restoration of natural vegetation (Baumann et al., 2018; Samolov et al., 2020; Tucker et al., 2020). The trophic structure of the biocrust determines the quantity and quality of nutrients entering the soil. The primary producers, mostly cyanobacteria, fix atmospheric carbon and nitrogen, which then become available to other soil biota. The soil under the crust can contain more than 300% more carbon and 200% more nitrogen than soil without the biocrust (Johnson et al., 2007; Pointing & Belnap, 2012). The nutrient enrichment of sub-crust soils promotes the localized growth of heterotrophic organisms, including bacteria, fungi, and nematodes (McLendon & Redente, 1992; Darby et al., 2007; Crenshaw et al., 2008). The ecosystemic role of BSC is related first of all to the formation of primary organic matter rich in nitrogen due to nitrogen-fixing cyanobacteria, provoking activity of heterotrophic microflora, soil animals, improvement of physical and chemical properties of soils (Zhang et al., 2006; Aznar et al., 2016). BSC is understood to have an effect on the germination ability of seeds of many vascular plant species (Rivera-Aguilar et al., 2005; Escudero et al., 2007; Langhans et al., 2009). Inhibitory effects of BSC on vascular plant species, especially from arid ecosystems, were reported (Prasse & Bornkamm, 2000; Hawkes, 2004). Therefore, many researchers emphasize the importance of detailed and long-term studies of BSCs and their functional role in biotic and abiotically changing environments (Aguilar et al., 2009; Mager & Thomas, 2011).

The development of algal populations is regulated not only by physical and chemical factors (Richardson et al., 1998), but also biological factors, such as predation (Maar et al., 2002; Elloumi et al., 2008) and competition between species (Mallin & Paerl, 1994; Pinckney et al., 1998). However, the availability of nutrients remains the main factor controlling the composition and biomass of algal communities (Ortega-Mayagoitia et al., 2003; López-Flores et al., 2006). These abiotic parameters vary in time and directly or indirectly influence the composition and abundance of algae flora (Koffi, 2009). As reported earlier, the species composition of algae and cyanobacteria of Askania Nova steppe ecosystems changes after fires (Shcherbyna et al., 2017). The pyrogenic load leads to a decrease in the abundance and biomass of algae and cyanobacteria in the soil of steppe ecosystems. The most significant changes were observed to the depth of 5 cm and persisted for several years after the fire. This indicated a rather slow process of recovery of quantitative indicators of algae and cyanobacteria communities in BSC after pyrogenic load. Bacillariophyceae were the most abundant (and biomass) both in the control plot and the post-pyrogenic plots, with cyanobacteria in the second place. According to other studies, cyanobacteria in steppe and other arid ecosystems can exceed other groups of microalgae by abundance (Bu et al., 2014; Antoninka et al., 2018). At the same time, there are reports that cyanobacteria may be more susceptible to fire than other BSC components (Bowker et al., 2004). The results show that algae and cyanobacteria are very sensitive to post-pyrogenic loads. A decrease in quantitative indicators was

observed, which is also directly related to the change in the volume of their ecosystem functions. The extent to which this affects the processes of humus accumulation observed under pyrogenic load, the functioning of other soil microorganisms, and the biological activity of soils in general cannot be unequivocally assessed at this stage of research. This may be the subject of further research and be of great importance both for detailing the processes of post-pyrogenic transformation of herbaceous ecosystems, and for evaluating the totality of consequences when using fires to regulate the development of herbaceous ecosystems.

Conclusion

In steppe ecosystems the height and projected area of higher vegetation, the abundance and biomass of soil microalgae and cyanobacteria change significantly after fires. The consequences of pyrogenic load remain noticeable for several years, seen in decrease of height and projected area of herbage, abundance and biomass of algae and cyanobacteria in the soil, especially to the depth of 5 cm. The statistically significant dependencies obtained between the studied characteristics and environmental predictors (season, year, soil layer, fire) within the framework of multidimensional general linear models confirm that quantitative characteristics of higher vegetation (height and projected area), microalgae and cyanobacteria (abundance and biomass), may be used in bioindication of the dynamics of postpyrogenic processes in steppe ecosystems.

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