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Carbon fluxes intensity from substrates and phototrophic consortiums of the photic zones in Montenegro caves

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Abstract

Carbon dioxide fluxes from substrates and consortiums were estimated for the first time in the photic zones of seven caves of Montenegro. The dependence of consortiums productivity with their species composition and structure, as well as determination of the priority source of carbon dioxide for the primary producers of trophic chains of the photic zones were revealed.

Five consortiums were distinguished in the fouling communities of the photic zones of seven karst caves of Montenegro: with the dominance of acrocarpous mosses, pleurocarpous mosses, green algae, cyanobacteria biofilms and sheath-forming cyanobacteria on various substrates. The closed chamber technique was used to calculate carbon fluxes. The net carbon flux, gross respiration of substrates and consortiums, and gross primary production of consortiums in the summer and winter were determined. The biomass of the phototrophic and heterotrophic components of the consortiums was estimated. Isotopic analysis of clay deposits and phytomass of bryophytes in the consortiums as well as on the surface was carried out. All of the investigated consortiums function as a carbon sink in both seasons, providing a negative balance to the atmosphere. Consortiums with the dominance of bryophytes possessed the greatest biomass, spores of micromycetes dominated in the heterotrophic component. The respiration of substrates was maximized on clay deposits, the respiration rate increased in winter. Phototrophic respiration and gross primary production were maximal in the consortiums of acrocarpous mosses and case-forming cyanobacteria in terms of dry phytomass. Increased content of the light carbon isotope ¹²C in the bryophytes phytomass in the photic zones compared to the bryophytes phytomass on the surface was established.

Key words: karst caves, ecotones, carbon balance, stable isotopes.

Introduction

Soil emission is considered as one of the most important indicators of the metabolism of terrestrial ecosystems (Karelin et al., 2014). Containing from 700 to 3000 Gt C in the upper meter layer (Kudeyarov et al., 2007) the soil represents a huge pool of terrestrial carbon, while gaseous CO₂ can accumulate in subterranean pores, cracks, and cavities. Studying the dynamics of CO₂ in caves is of increasing interest: carbon dioxide determines the hydrogeological characteristics of karst waters (Faimon et al., 2012), involved in the dissolution of karst rocks (Stumm & Morgan, 1996), plays a crucial role in calcite speleothems formation (Frisia et al., 2011) and speleothems corrosion (Tarhule-Lips & Ford, 1998).

For karst caves, the main sources of CO₂ are respiration of soil microbiota, atmospheric CO₂, and ventilation of subterranean CO₂ from pores and fissures (Spotl et al., 2005; Kowalczyk & Froelich, 2010; Benavente et al., 2010; Breitenbach et al., 2015). It is assumed that root respiration and respiration of rhizosphere microorganisms contribute to the CO₂ balance in the entrance zone (Kuzyakov, 2006). The CO₂ balance in the air of the caves is affected by several parameters: its contribution from the surface and the soil layer with air and infiltration waters, oxidative processes in the aeration zone, decomposition of organics of advective origin, thermal diffusion processes and CO₂ emission during the formation of carbonate sintered calcite formations, endogenous gas fluxes, oxidation of methane and other methane hydrocarbons and sulfate reduction (Bourges et al., 2001; Faimon et al., 2012). For caves used as tourism sites, the input of the CO₂ also includes the anthropogenic component (Faimon et al., 2006; Lang et al., 2015).

In the conditions of artificial lighting, communities of phototrophs are formed, which have different species composition, biomass, physiological activity, and affect the trophic chains of the cave. Such communities considered as an analog of the phototrophic fouling communities in the entrance zone of caves, where CO₂ emission and community productivity were estimated (Mulec et al., 2008; Mazina & Maximov, 2011; Mazina & Kozlova, 2019). Lighting directly (affecting humidity and temperature) and indirectly (due to the influence of metabolites of phototrophic communities) affects the microbiota of substrates. When assessing emissions, it is important to distinguish between fluxes of endogenous and exogenous CO₂ and to identify the contribution of directly allochthonous communities of lampenflora to assess their real significance for the trophic chains of the cave.

Accepting the thesis that the communities of the entrance zone are similar to the lampenflora communities, but more stable due to climax stage of succession, we can consider them as reference fouling communities and predict the dynamics of the lampenflora development based on their physiological and environmental parameters (Kozlova et al., 2019).

Phototrophic communities in the entrance zones are poorly studied, especially in terms of their ecophysiology, but they can be indicative of determining the carbon balance under constant microclimatic conditions.

This study aimed to identify the dependence of consortiums productivity with their species composition and structure, as well as a determination of the priority source of carbon dioxide for the primary producers of trophic chains in the photic zones of Montenegro caves.

Material and methods

Seven caves in Montenegro were the objects of the study: Untitled cave (42°17'32.46" N, 18°52'26.03" E), Obodska cave (42°21'07.61" N, 19°00'18.75" E), Golubinja cave (42°25'18.65" N, 18°47'58.22" E), Veluštica cave (42°25'58.32" N, 18°48'13.62" E), Vrbačka jama (42°25'58.98" N, 18°48'38" E), Jama ER-1 (42°25'56" N, 18°49'55.02" E), Njegoš cave (42°25'58.84" N, 18°49'53.72" E).

The photic zone of the caves has a complex landscape characteristic by humidity, light, and temperature gradients that determine the discreteness of the ecotopes and the mosaic of the presented phytocenosis. Represented by various micro- and macro groups the vegetation cover in the entrance zone considered as a continuous network of various interacting consortiums - the consortium continuum (Negrobov & Hmelev, 1999; Kozlova & Mazina, 2020).

At the border of the entrance zone of the caves and the surface, especially in large grottoes caves, humidity can decrease dramatically in summer, and bryophytes and other phototrophs stay in a dry inactive state, which does not reflect the state plants in the illuminated entrance zone of the caves. To conduct an adequate analysis of carbon fluxes, it is necessary to evaluate a physiologically active biota. Therefore, in

this study, only those consortiums developing in conditions of relative humidity not lower than 55% and on moist substrates (humidity was close to absolute and amounted to about 40%) were selected.

For analysis of CO₂ exchange of phototrophs, consortium sections located in undisturbed areas, where the surface slope did not exceed 30 degrees with homogeneous projective cover and an area corresponding to the chamber area were selected.

Since the overgrowth of sheath-forming cyanobacteria mats was discrete and occupied small areas, often between mosses mounds, the suitable consortiums areas were found only in two caves - Veluštica and Untitled cave.

Fieldwork was carried out in July 2017 and January 2019.

Five characteristic consortiums were identified in the entrance zones of Montenegro caves by the dominant species that can be attributed to habitat-forming species (Kozlova & Mazina, 2020): mounds of acrocarpous mosses (am), mounds or «canopy» of pleurocarpous mosses (pm), fouling of green algae (ga), cyanobacterial biofilm (cb) and sheath-forming cyanobacteria mats (sc) on the different substrates: limestone (L), calcite (Ct), thin (a maximum of 5 mm) clay deposits on limestone or calcite and large clay deposits (5 mm and more) (Fig. 1).

Carbon dioxide fluxes from soils to the atmosphere were assessed as the sum of respiration of all soil organisms and the possible CO₂ flux from the lithosphere. Closed gas-exchange system method was used (Karelin et al., 2014).

The measurements were carried out using a plastic cylinder with a diameter of 9 cm, a height of 30 cm, dug into the ground to the depth of a loose substrate, but not more than 5 cm, or mounted on the surface of a dense substrate and sealed at the border of the substrate and the chamber (Karelin et al., 2020). A portable cap with an attached LI - 6200 analyzer sensor (Li-Cor Inc., Lincoln, Nebraska, USA) was hermetically sealed on the cylinder. Inside the chamber was a fan. An opaque and transparent chamber was used to measure carbon dioxide fluxes in the dark and at light. During the measurements, air temperature and atmospheric pressure were determined.

To calculate the change in the mass of carbon in the form of carbon dioxide in the chamber during the exposure, Mendeleev – Clapeyron equation was used (Safonov et al., 2012). The measurement time was 3-4 minutes; also, a series of measurements lasting 15 minutes was carried out.

The net carbon flux (measurements in the transparent chamber), gross respiration GR (measurements in the opaque chamber), and gross primary production GPP (net carbon flux minus gross respiration) were determined. The CO₂ fluxes of the consortiums were calculated as the difference between the emission from the area occupied by photoconsortiums and the emission of the corresponding substrate. For each consortium, at least 10 measurements were taken during daylight hours from 12 p.m. to 3 p.m.

After the measurements were completed, vegetation was collected within the base of the chamber, and separated into four fractions: 1) acrocarpous mosses; 2) pleurocarpous mosses; 3) green algae or cyanobacteria; 4) sheath-forming cyanobacteria. The mass of the absolute dry samples was weighted. Samples of phototrophs were also taken from small sites (2-3 cm²) to determine biomass. In most areas, measurements in summer and winter were carried out at adjacent points.

Substrate samples were placed into sterile sealed vials and transported in thermostatically controlled containers to the laboratory at cave temperature. These samples were also used to determine biomass.

To determine the daily carbon fluxes, 4 hours (2 after sunrise, 2 before sunset) were subtracted from daylight hours in July and January, assuming that at this time the flows were zero.

The phytomass determination was carried out by the gravimetric method after removal of carbonates and drying of the samples, recounting was carried out in g per 1 cm².

Fungal and bacterial biomass in substrates and under phototrophic consortiums was determined by light luminescence microscopy. For thin clay deposits and dense soils, scrapings were examined, for consortiums with the dominance of green algae and cyanobacteria, biofilms and mats were scraped; for bryophytes, the soil with the lower part of bryophytes was analyzed. White calcofluor and acridine orange were used to evaluate fungal mycelium and bacteria, respectively (Netrusov, 2005), the biomass was estimated per 1 g of dry soil.

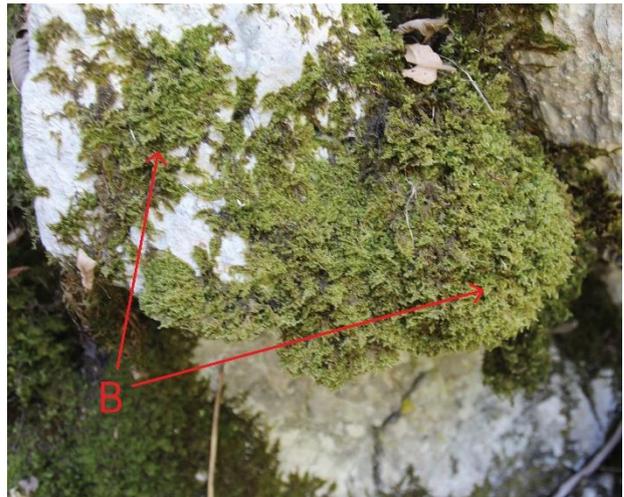
For isotope analysis, samples of bryophytes growing under natural light at the entrance zones of the caves, as well as samples of substrates, were taken (14 samples in total).

Mosses biomass was washed with distilled water to clean the samples from mineral components. Samples of substrate were treated with 1 M (1 mol / L) HCl solution to remove carbonates and then washed to neutrality with distilled water (Wang et al., 2015). All samples were dried and homogenized to a state of

fine dust. The weight of the sample for cave substrates was $\approx 3000-4000 \mu\text{g}$, the weight of the sample of one phototroph was $\approx 1500-1600 \mu\text{g}$. Each sample was analyzed in duplicate.



Untitled cave, consortiums with the dominance of acrocarpous mosses on limestone, cave's wall (A)



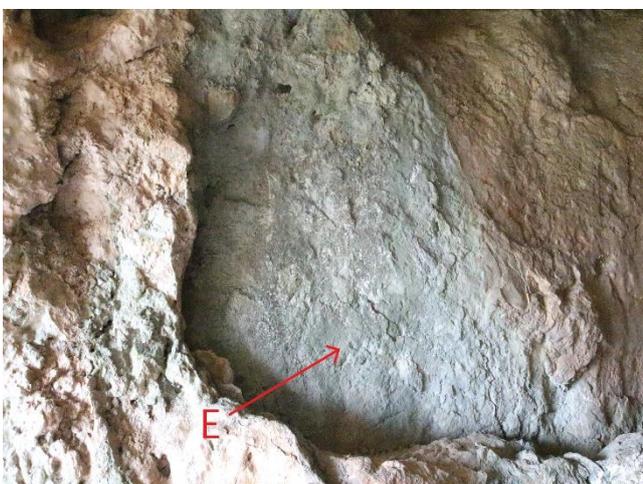
Njegoš cave, consortiums with the dominance of pleurocarpous mosses on limestone, cave's wall (B)



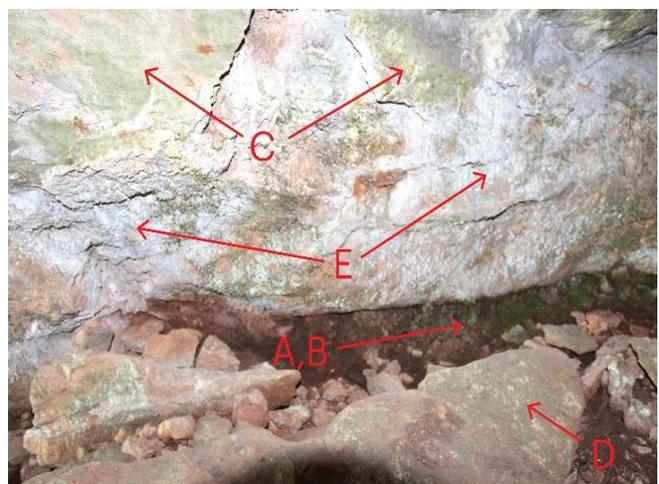
Njegoš cave, consortiums with the dominance of green algae on limestone, cave floor (C)



Veluštica cave, consortiums with the dominance of cyanobacterial biofilms, on clay deposits, cave floor (D)



Untitled cave, consortiums with the dominance of sheath-forming cyanobacteria mats on calcite and limestone, cave wall (E)



Veluštica cave, all of the studied consortiums

Figure 1. The consortiums of Montenegro caves.

Table 1. Types of consortiums in Montenegro caves.

Consortium	Dominant	Subdominant	Cave	Substrate	
acrocarpous mosses	<i>Amphidium lapponicum</i>	-	Golubinja	L, CL	
	<i>Amphidium mougeotti</i>		Golubinja; Njegoš	C, CL; L, CL	
	<i>Cynodontium tenellum</i>		Untitled cave; Jama ER-1	L, CL	
	<i>Ditrichum flexicaue</i>		Njegoš	L, CL	
	<i>Fissidens taxifolius</i>		Obodska	CL, C	
	<i>Plagiopus oederianus</i>		Golubinja	C, CL	
	<i>Tortella tortuosa</i>		Vrbacka jama	L, CL	
pleurocarpous mosses	<i>Amblystegium serpens</i>	-	Untitled cave	L	
	<i>Campylidium calcareum</i>		Vrbacka jama; Golubinja	C, CL; L, CL	
	<i>Conardia compacta</i>	<i>Humidophila contenta</i>		Untitled cave	L
	<i>Entodon schleicheri</i>	-	Vrbacka jama; Jama ER-1	L, CL	
	<i>Homalia trichomanoides</i>		Veluštica	CL, L, Ct	
	<i>Homalothecium philippeanum</i>		Vrbacka jama	L, CL	
	<i>Plagiothecium cavifolium</i>		Njegoš	L, CL	
	<i>Plagiothecium sp.</i>		Jama ER-1	L, CL	
	<i>Pseudoleskeellaceae sp.</i>		Obodska	CL, C	
	<i>Sciurohypnum latifolium</i>		Golubinja	C, CL	
	<i>Sciurohypnum plumosum</i>		Obodska	CL, C	
	<i>Sciurohypnum starkei</i>		Veluštica	CL	
	green algae	<i>Bracteacoccus minor</i>	-	Njegoš	L, CL, Ct
<i>Chlorella vulgaris</i>		-	Golubinja; Njegoš; Obodska	L, CL, C; L; CL	
		<i>Stichococcus bacillaris</i>	Untitled cave; Veluštica	L, CL; L	
<i>Parietochloris bilobata</i>		-	Untitled cave	L, CL	
<i>Stichococcus bacillaris</i>		-	Vrbacka jama; Jama ER-1	L, CL	
cyanobacterial biofilms	<i>Chroococcus minor</i> , <i>Gloeocapsa punctata</i>	-	Njegoš	L	
	<i>Gloeocapsa compacta</i> , <i>Jaaginema subtilissimum</i>	<i>Nostoc microscopicum</i>	Obodska	L, CL	
	<i>Leptolyngbya tenuis</i>	-	Veluštica	L, Ct, CL	
	<i>Leptolyngbya foveolarum</i>	-	Vrbacka jama	L, CL, C-Ct	
		<i>Gloeocapsa punctata</i>	Jama ER-1	L, CL	
	<i>Leptolyngbya foveolarum</i> ; <i>Leptolyngbya voronichiniana</i> ; <i>Aphanocapsa muscicola</i>	<i>Synechococcus elongatus</i>	Untitled cave	L, Ct	
	<i>Microcystis pulvereae</i>	-	Njegoš	L, Ct	
	<i>Nostoc microscopicum</i>	-	Obodska	L, CL	

..continued on the next page

TABLE 1.

sheath-forming cyanobacteria	<i>Spirulina sp.</i>	-	Golubinja	L
	<i>Calothrix gypsophila</i>	-	Veluštica	Ct, L
	<i>Scytonema julianum</i>		Untitled cave; Veluštica	Ct, L
	<i>Stigonema sp.</i>		Untitled cave	Ct, L

The ratios of stable carbon isotopes were measured in the Laboratory of Radiocarbon Dating & Electronic microscopy, Institute of Geography RAS, Moscow. The isotopic composition was determined using a Isoprime precisION stable isotope ratio mass spectrometer (UK) combined with the Vario Isotope Select elemental analyzer (Elementar, Germany).

The isotopic composition of carbon was expressed in the δ -notation relative to the international standard (VPDB): $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where R is the ratio of the heavier isotope to the lighter one. Samples were analyzed with a reference gas calibrated against IAEA (caffeine IAEA-600 and cellulose IAEA-CH3). Casein B2155 and Urea B2174 were used as a laboratory standard. The analytical error in determining the isotopic composition of carbon and nitrogen varied within ± 0.2 ‰.

Results

The characteristics of the allocated consortiums are given in table 1. Substrates are indicated on which the listed types of consortiums were primarily found.

The maximum biomass was observed in mosses, the biomass of algae and cyanobacteria was comparable (Fig. 2). No significant changes in biomass in winter and summer were found.

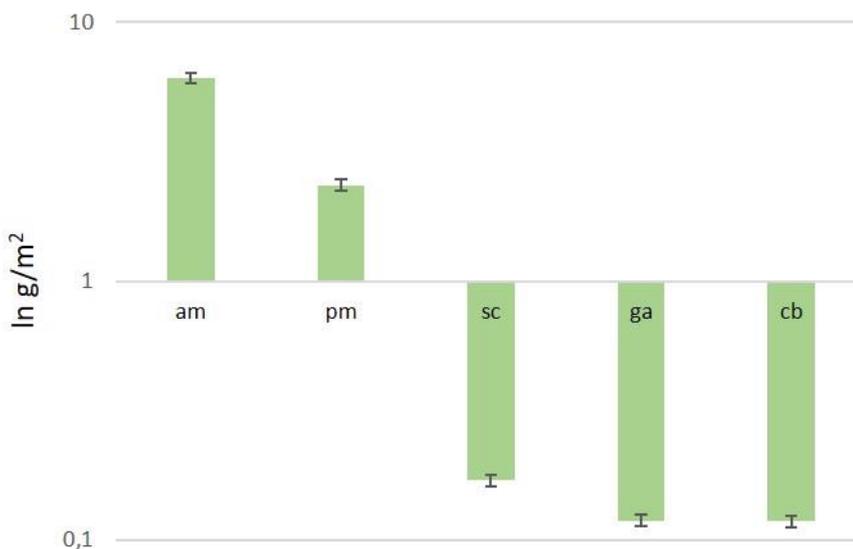


Figure 2. Phototrophic biomass in the consortiums of the photic zones in Montenegro caves.

A comparison of the respiration of various substrates showed that clay deposits of various thicknesses had the greatest respiration intensity, and it increased in winter (Fig. 3).

The maximum biomass in the heterotrophic component of the consortiums was observed in fungi, with spores predominating (Fig. 4). No significant changes in biomass in winter and summer were found. The maximum biomass of micromycetes was noted in bryophytes consortiums and was weakly dependent on the season.

Micromycetes also prevailed in substrates; the greatest changes were found in the amount of mycelium on dense substrates, in the consortiums, which may be due to the species and ecological forms of the communities (Fig. 5-6).

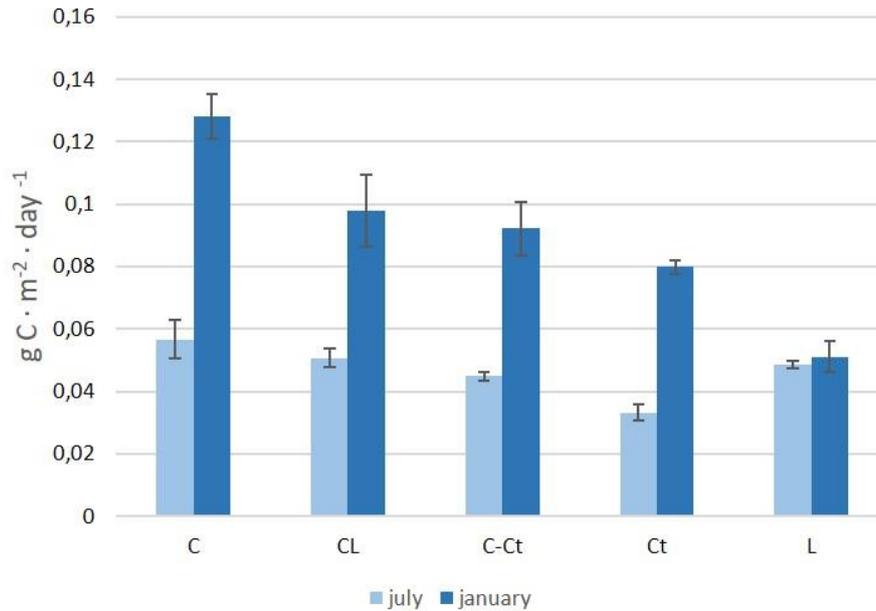


Figure 3. Substrate respiration of the photic zones in Montenegro caves.

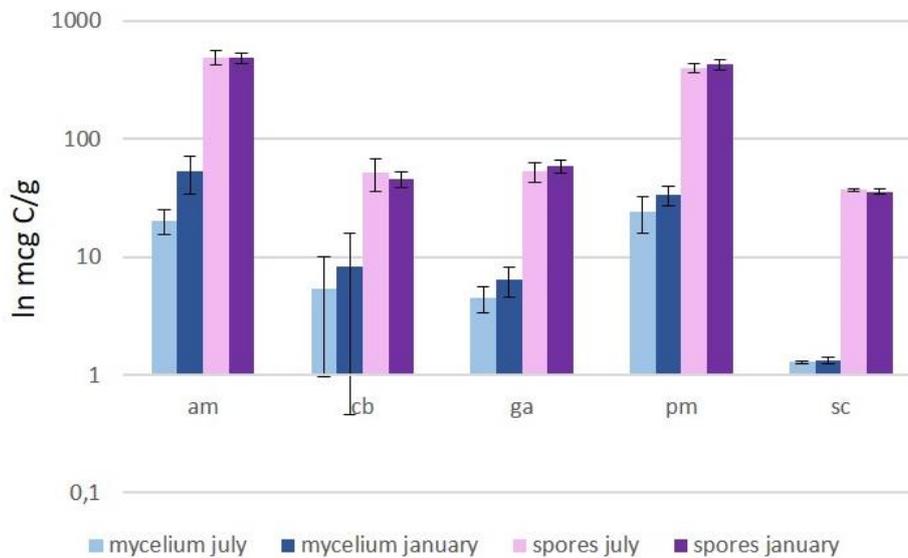


Figure 4. Micromycetes biomass in the consortiums of the photic zones in Montenegro caves.

Bacterial biomass increased in winter in all consortiums (Fig. 7). The great variability of values was found in biofilms of cyanobacteria and case-forming cyanobacteria. On clay substrates, a significant increase in the bacterial biomass in the winter period was found, which can be explained by the inflow of organic matter into the clay deposits of caves during the periods of rainfall (Fig. 8).

Phototrophic respiration was maximum in consortiums dominated by acrocarpous mosses and minimal in consortiums dominated by green algae (Fig. 9). Significant changes in respiration in winter and summer periods were not found.

The net carbon flux was maximum in the consortiums dominated by acrocarpous mosses, minimum in consortiums of green algae, and pleurocarpous mosses. It decreased slightly in winter, except for consortiums of sheath-forming cyanobacteria (Fig. 10).

The highest GPP rate was noted in the consortium of acrocarpous mosses, second in the consortiums of sheath-forming cyanobacteria, these are the only consortiums in which GPP increased in winter (Fig. 11).

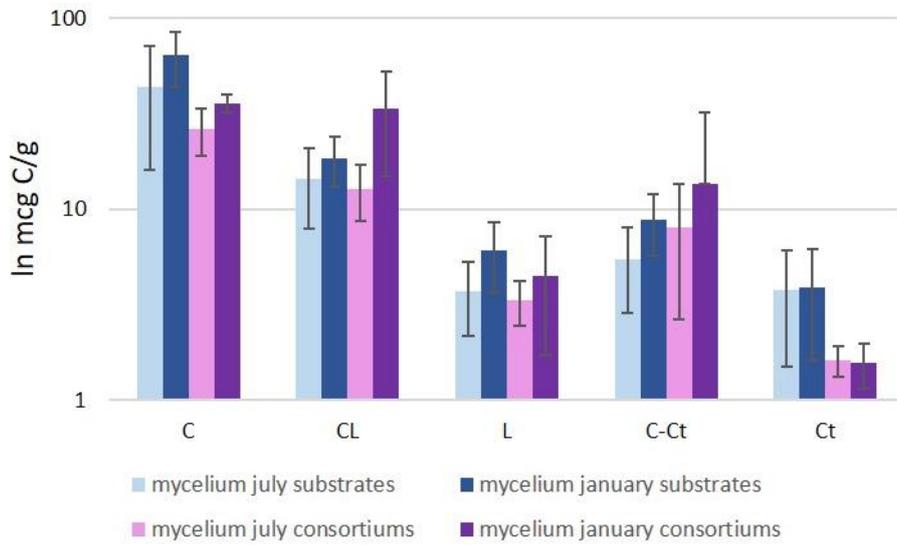


Figure 5. Mycelium biomass on substrates of the photic zones in Montenegro caves.

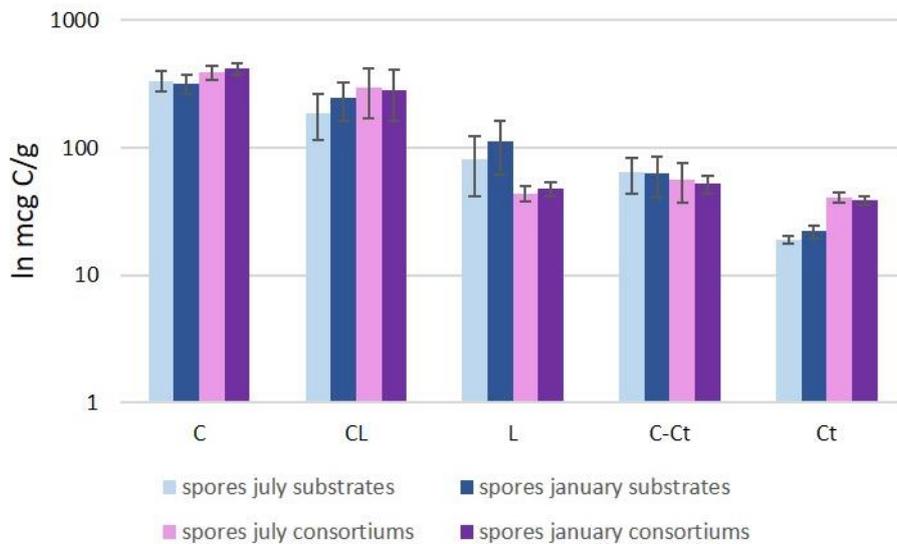


Figure 6. Spores biomass on substrates of the photic zones in Montenegro caves.

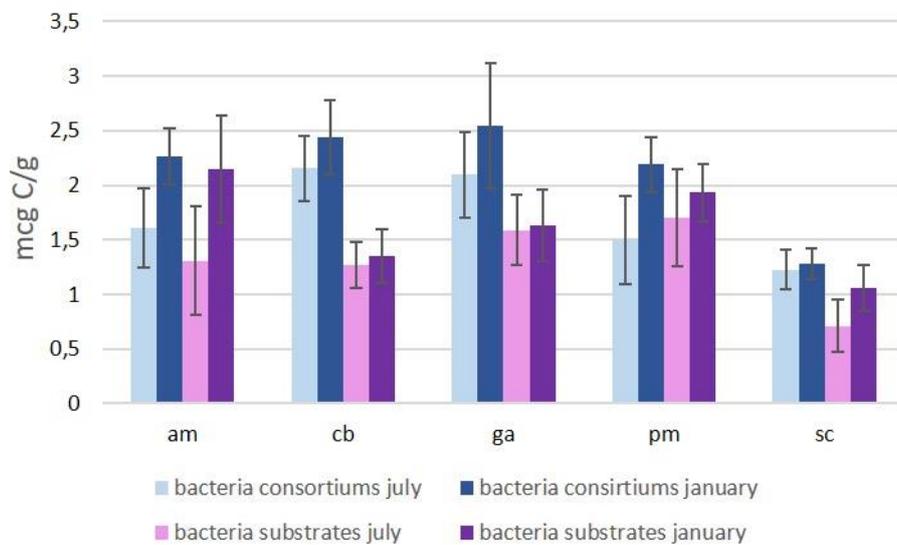


Figure 7. Bacterial biomass in the consortiums of the photic zones in Montenegro caves.

CARBON FLUXES OF THE PHOTIC ZONES IN MONTENEGRO CAVES

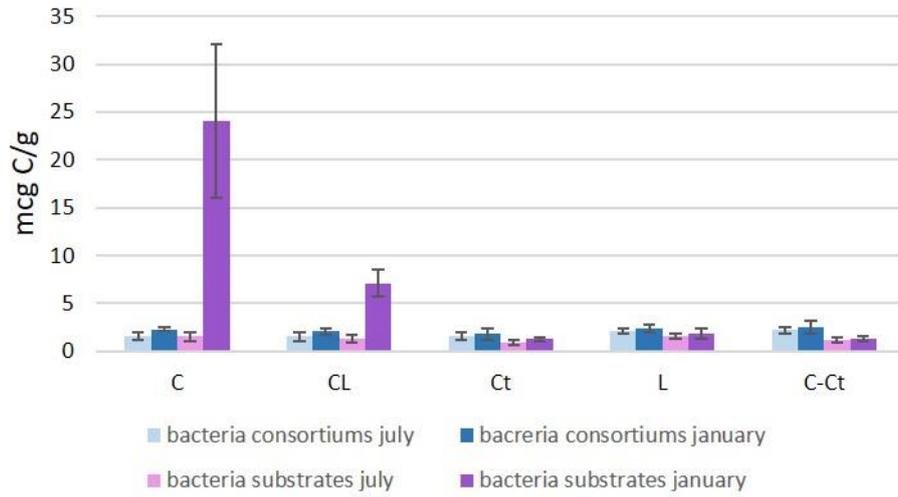


Figure 8. Bacterial biomass on substrates of the photic zones in Montenegro caves.

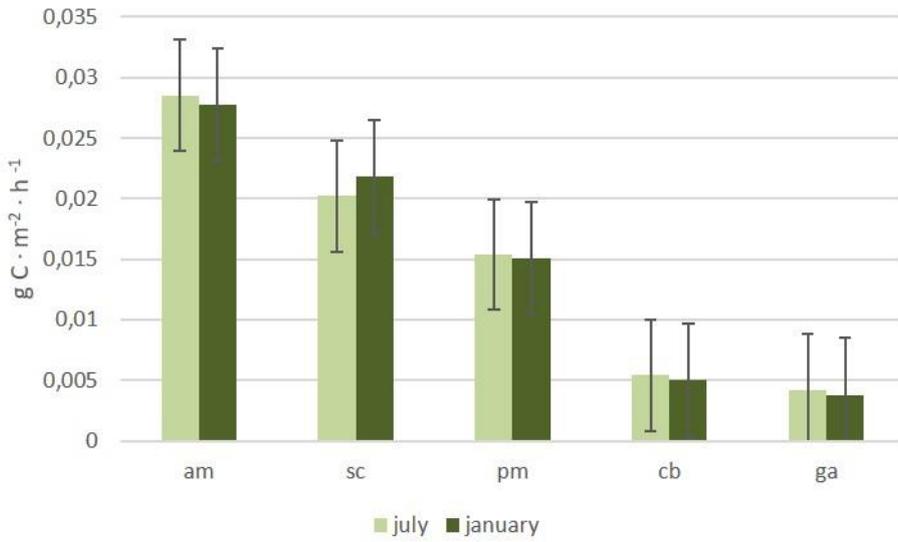


Figure 9. Phototrophic respiration in the consortiums of the photic zones in Montenegro caves.

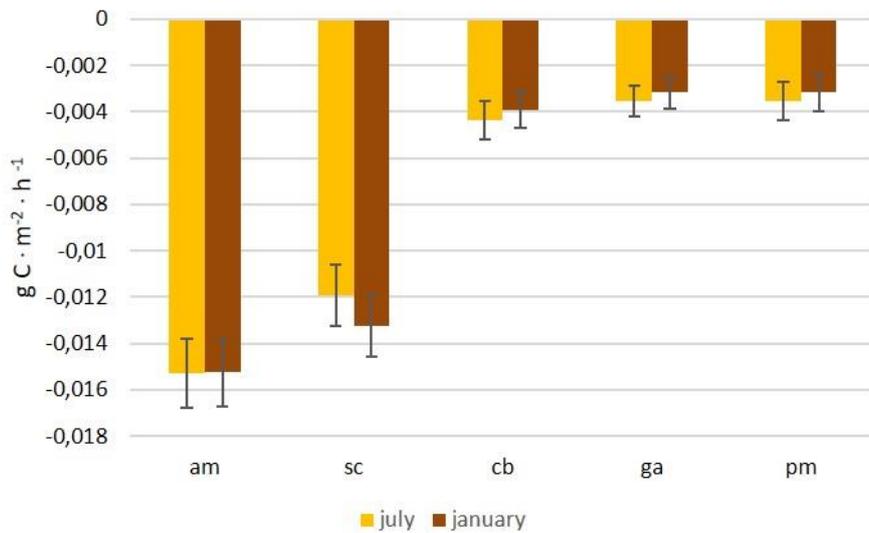


Figure 10. Net carbon flux of the photic zones in Montenegro caves.

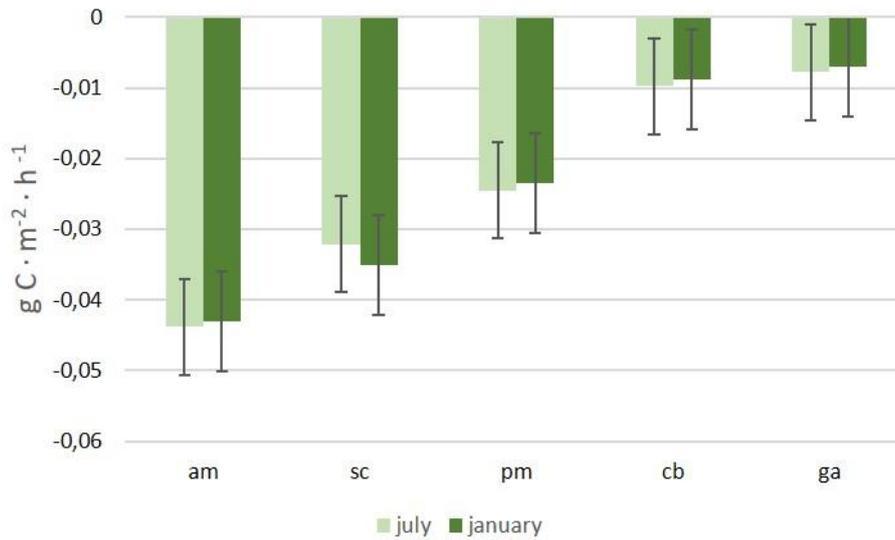


Figure 11. GPP of consortiums of the photic zones in Montenegro caves.

However, recalculation per unit weight of the consortiums dry phytomass revealed that the greatest GPP observed in sheath-forming cyanobacteria, and the minimal in mosses (Fig. 12).

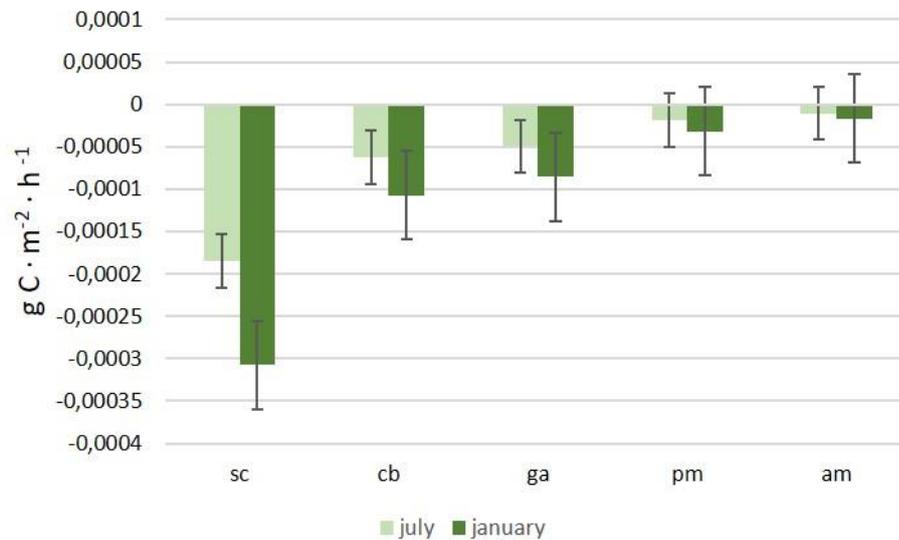


Figure 12. GPP per unit weight of dry phytomass of consortiums of the photic zones in Montenegro caves.

The value of daily net carbon flux indicates that investigated consortiums were functioning as a carbon sink in both seasons, providing a negative balance to the atmosphere (Fig. 13).

As a result of the analysis of the isotopic ratios $\delta^{13}\text{C}$ of bryophytes on the surface and in the photic zones, it was found that in the samples from the photic zones the ratio is shifted towards the light carbon isotope ^{12}C (Fig. 14).

Discussion

The greatest biomass of phototrophs in the consortiums of the entrance zones of Montenegro caves was observed in bryophytes and the minimal – in the cyanobacterial biofilms. The heterotrophic component of the consortiums is represented by micromycetes, the biomass of bacteria increased in winter. Phototrophic

respiration was maximal in the consortium of acrocarpous mosses and sheath-forming cyanobacteria, minimal respiration was noted in green algae. Phototrophic respiration slightly decreased in winter, except for the consortiums of sheath-forming cyanobacteria.

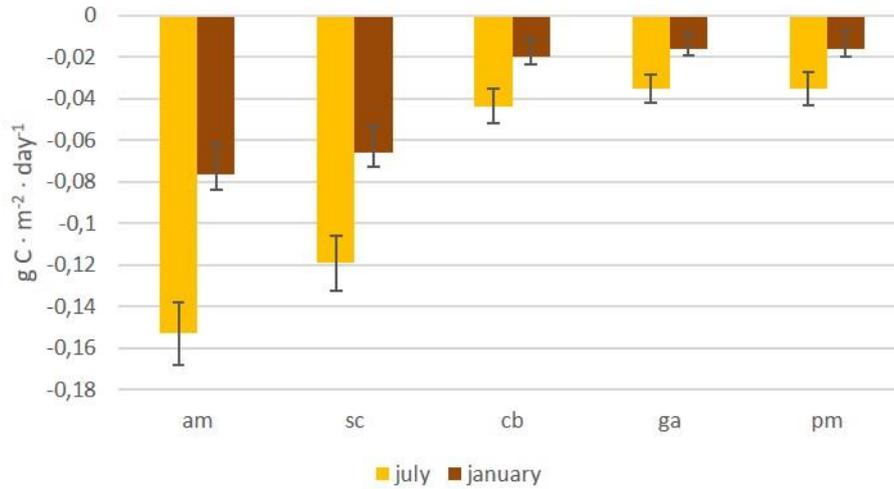


Figure 13. Daytime net carbon flux of the photic zones in Montenegro caves.

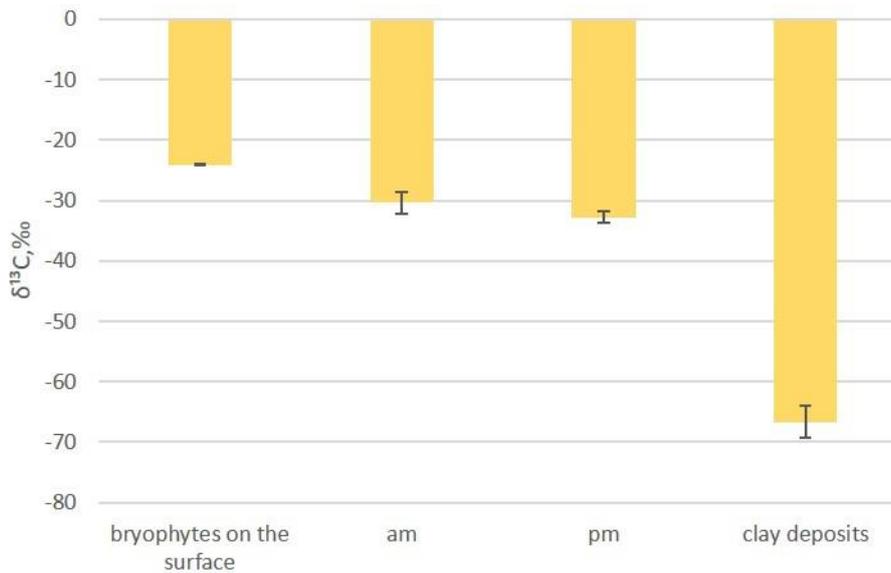


Figure 14. The results of isotopic analysis of bryophytes phytomass of the photic zones in Montenegro caves.

The maximum respiration of the substrates was reached on clay deposits, the minimum was observed on calcite and limestone. The net carbon fluxes were maximum in acrocarpous mosses and sheath-forming cyanobacteria. GPP rates reached minimum values in consortiums with the dominance of pleurocarpous mosses, maximum - in consortiums with the dominance of acrocarpous mosses. The production of sheath-forming cyanobacteria increased in the winter.

The respiration rate of clay deposits was more intense with an increase in the abundance of micromycetes and bacteria and soil moisture in the winter season. The inflow of water into the soils of the cave's photic zone occurs due to rainfall and the internal movement of water. Obodska and untitled caves function as vauclusian spring due to periodic irrigation with flows from caves, formed with intense rainfall in the autumn- in most caves with spring period. Temporary flows and drips are formed in most caves with heavy rainfall.

Moisture consumption occurs due to intrasoil runoff and evaporation. The intensity of evaporation depends on the temperature and humidity, which are stable in the caves in comparison with the surface and

also on solar radiation, which is reduced in the caves. Humidity, temperature and illumination are associated with the morphology of the entrance, the characteristics of the substrates, and water and air flows in the cave. All these parameters characterize the environment in which phototrophs determine the physiological processes in the consortiums, including productivity.

Not only abiotic parameters should be taken into account, but also the amount of living above-ground phytomass (Karelin et al., 2013). According to our data, the most productive are consortiums with the dominance of sheath-forming cyanobacteria.

Temperature, moisture, and some other environmental factors are known to regulate soil respiration (Ryan & Law, 2005; Fernandez et al., 2006; Deng et al., 2012; Weil & Brady, 2017). Respiration rates increase exponentially with temperature (Enquist et al., 2003). Typically soil respiration demonstrates maximum at intermediate soil moisture values, and decreasing under drier or wetter conditions (Davidson & Janssens, 2006; Moyano et al., 2013). Due to the stable microclimate parameters (Salvidio et al., 2020) conditions of a stable balance between humidity and temperature of air and soil are achieved in caves. This ensures the maximum moisture content of the substrates at a stable underground temperature. Under these conditions, maximum respiration can be expected, which is confirmed by the conducted studies.

When modeling the lower tier ecosystems emission rate, it is recommended to take into account the carbon stock of the upper soil layer (Chen et al., 2010). Since the rocks and dripstones are the least similar to soils and have a minimum content of organic carbon in this study, the analysis of carbon content in soils was not carried out. Clay deposits under the phototrophic consortiums can be considered as soloids or soil-like bodies (Goryachkin et al., 2019) which have a higher content of organic carbon and, as a result, a higher respiration rate compared to substrates without consortiums. It is assumed that in winter, the cave's substrates achieve an optimal moisture.

In arid region soils, where extreme temperatures are observed at noon in summer, biological activity decreases, therefore, minimal respiration occurs in this time as well as in the daily and seasonal cycles (Smagin, 2005). Moisture in these regions severely limits primary production (Whitford, 2002, Housman et al. 2006), even small and short-duration rainfall strongly affects the structure and function of microbial and plant communities, including bryophytes productivity (Ogle & Reynolds, 2004, Cable et al., 2008). The caves of Montenegro reflect the situation of arid zones - a decrease in respiration in summer, especially in caves where the air humidity is low, such as Golubinja and Veluštica caves.

For the south taiga spruce forest, the maximum CO₂ fluxes are usually observed in July, while at the beginning (May) and at the end of the season (November) they are minimal (Karelin et al., 2014). The terrestrial ecosystems of the southern regions are characterized by the seasonality of carbon dioxide fluxes: for example, in the southernmost monitoring point in Europe, Greek deciduous forests function as a sink of carbon from late April to early November, and the rest of the year - as a source (Proutsos et al., 2017). Despite the absence of representatives of Magnoliophyta and woody plants in the composition of phototrophic communities of Montenegro caves, they function as a carbon sink in July and January. Considering that these periods reflect the lowest and highest moisture content and temperature of the photic zone, it can be assumed that they function as a sink throughout the year.

It is noted that photosynthesis and productivity of bryophytes capture mainly carbon dioxide released during soil respiration (Delucia et al., 2003). This statement is confirmed in this study by analyzing the ratios of stable isotopes of bryophytes phytomass. The enrichment of bryophytes phytomass in the photic zones of the caves with the light carbon isotope ¹²C compared to bryophytes phytomass on the surface can be explained by the predominant fixation of carbon of autochthonous biogenic origin under conditions of limited air circulation in the photic zones. The accumulation of ¹²C by plants in open spaces is difficult due to continuous air circulation, which ensures the mixing of isotopes with the atmosphere; in confined spaces with stagnant air, plants are more enriched in the light isotope of carbon (Wickman, 1952). Similar data were obtained in other caves (Turchinskaya et al., 2019).

Under the stable temperature and humidity, a seasonal change in substrates respiration, bacterial biomass, net carbon flux and GPP of phototrophic consortiums were revealed. The most variable indicator between winter and summer seasons was the bacterial biomass, which is associated with an increase of winter humidity, as well as with the presence of organic matter (Rigobelo & Nahas, 2014). Phototrophic consortiums function as a carbon sink both in winter and summer. For consortiums of sheath-forming cyanobacteria, an increase in productivity in winter and the highest GPP and phytomass storage were detected.

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