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RESEARCH ARTICLE

Carbon-sequestrating function of soil microalgae and cyanobacteria as a key ecosystem service of steppe ecosystems

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Abstract

This paper presents empirical data on the contribution of soil microalgae and cyanobacteria in steppe ecosystems to the assimilation of atmospheric carbon dioxide. Our findings indicate that Cyanobacteria predominated within the soil phototrophic assemblages of these steppe ecosystems, while Chlorophyta, Streptophyta, and Heterokontophyta (Eustigmatophyceae, Xanthophyceae and Bacillariophyceae) played a secondary role. The abundance, biomass and carbon sequestration of soil microalgae and cyanobacteria exhibited distinct seasonal dynamics, peaking during the autumn period when the moisture conditions were optimal. Microclimatic conditions that developed within relief depressions further facilitated the growth of these microphototrophs. The active biomass of microalgae and cyanobacteria ranged from 10.52 kg RW ha^{-1} to 31.87 kg RW ha^{-1}. Net primary production (NPP) generated monthly by microalgae and cyanobacteria within the upper 0-5 cm soil layer reached up to 1.96 g m^{-2} $month^{-1}$ (expressed as equivalent carbon). This represents approximately 7% of the average primary biological productivity of vascular plants in natural steppe ecosystems. When considering the synthesized exogenous organic compounds released during life cycles and the rapid incorporation of this biomass into grazing food webs, the overall contribution of soil microalgae and cyanobacteria to atmospheric carbon sequestration may be substantially higher.

Keywords

Steppe ecosystems, carbon dioxide, productivity, seasonal dynamics, Cyanobacteria, Chlorophyta, Streptophyta, Heterokontophyta

Introduction

In recent years, the widespread occurrence of ecological crises in natural ecosystems has altered their structural characteristics and compromised their capacity to fully deliver key ecosystem services. The concept of ecosystem services is multifaceted, having evolved from early definitions centered on the benefits humans derive from ecosystems to more complex frameworks that incorporate ecosystem states, processes, and functions essential for human survival, including climate regulation and biodiversity conservation (Birkhofer et al. 2015). Among the most critical regulatory services that currently receive intense scientific attention is the regulation of atmospheric gas composition. Global climate change requires the identification and promotion of natural processes capable of maintaining the atmospheric gas balance required to support life. Sustainable management in the context of mitigating climate change requires a comprehensive understanding of the primary mechanisms governing the uptake, accumulation, emission and transformation of climatologically active greenhouse gases.

Carbon dioxide (CO_2) is considered the primary greenhouse gas that drives global warming. Although it possesses a lower global warming potential than methane (CH_4) or nitrous oxide (N_2O), its significance is dictated by its high atmospheric abundance, its ability to absorb and re-emit infrared radiation across multiple wavelengths, and its long atmospheric residence time. Photosynthetic organisms play the primary role in the capture of atmospheric carbon dioxide, its assimilation through photosynthesis, and its sequestration within organic biomass.

Ecosystems vary greatly in their capacity to sequester and retain carbon. Consequently, investigating the specific patterns of carbon sequestration and accumulation in different habitats is of paramount importance. Extensive research has confirmed the substantial role of forest ecosystems in the capture of carbon dioxide (Wigneron et al. 2024). Herbaceous ecosystems also represent a critical, yet historically understudied, component of the global carbon balance (Blagoveschensky et al. 2019). Steppe ecosystems cover relatively small land surface areas and develop under arid regional climates, yet exhibit a high carbon sequestration capacity (Golubyatnikov et al. 2023). However, anthropogenic pressures have significantly altered the sequestration potential of these grasslands. Many natural steppe ecosystems are highly degraded or transformed, currently existing at various stages of recovery or regressive ecological succession. (Refinery of our estimates of the contribution of steppe ecosystems to regional and global carbon sequestration requires targeted research across diverse and localized ecosystem types.

Recent studies highlight the important role of soil microscopic photosynthetic organisms (algae and cyanobacteria) in biological carbon fixation (Maier et al. 2018; Hamard et al. 2021). However, as emphasized in several recent reviews, its precise role in mitigating climate change remains poorly quantified on both regional and global scales (Jassey et al. 2022). Characterized by high growth rates, these organisms can contribute significantly to carbon dioxide uptake and the rapid conversion

of inorganic carbon into organic matter. Net primary production (NPP) is widely recognized as a key indicator of photosynthetic activity and carbon cycling for plants and aquatic algae (Pessarrodona et al. 2022; Golubyatnikov et al. 2023). However, standardized methodological approaches for evaluating the carbon sequestration function of soil microalgae and cyanobacteria have not yet been established. Currently, empirical biomass and production values measured within specific ecosystems serve as the primary baseline data to characterize carbon sequestration by soil phototrophs. Evaluating the role of soil microalgae and cyanobacteria in atmospheric carbon uptake and storage is essential to estimate the overall sequestration capacity of steppe ecosystems and developing targeted management strategies to improve it.

The aim of this study is to evaluate the seasonal sequestration dynamics and characteristics of soil microalgae and cyanobacteria in representative steppe ecosystems.

Materials and methods

Field investigations were conducted in steppe ecosystems located in the northwestern Azov region. The regional climate is moderately continental and semiarid, characterized by an annual precipitation range of 300-450 mm and a negative water balance (Marynych et al. 1985). The soils belong to the southern subzone of ordinary chernozems, represented primarily by chernozems and dark chestnut soils, which frequently exhibit solonetzic profiles (Marynych et al. 1985). The native steppe vegetation is dominated by associations of fescue-feather grass (*Festuca-Stipa*) with few species and their hemipsammophytic variants. Fragmented meadow steppes occur in topographic depressions within the Molochnaya River valley (Krasnova 1974).

For long-term monitoring, three stationary sample plots (STPs), measuring 500 m^2 each, were established (Figs 1, 2):

STP 1 (46.989327 N, 35.417032 E): Located on a watershed divide characterized by ravine topography near the settlement of Terpenie.

STP 2 (46.875062 N, 35.416293 E): Positioned at the transition zone between the watershed divide and the upper margin of the second terrace above the floodplain of the Molochnaya River, in the northeastern part of Melitopol.

STP 3 (46.874252 N, 35.423031 E): Situated on the first terrace above the floodplain of the Molochnaya River, in the northeastern part of Melitopol.

In STP 1 and STP 2, narrow-leafed xerophytic bunchgrasses predominated, including *Stipa capillata* L., *S. ucrainica* P. Smirn., *S. lessingiana* Trin. & Rupr., *Koeleria cristata* (L.) Pers., and *Festuca pseudovina* Hack. ex Wiesb. Herbaceous forbs were represented by *Carduus uncinatus* M. Bieb., *Crinitaria villosa* (L.) Grossh., *Dianthus guttatus* M. Bieb., *Verbascum phoeniceum* L., *Phlomis pungens* Willd., *Tanacetum millefolium* (L.) Tzvelev, and *Salvia tesquicola* Klokov & Pobed. Within the topographic depressions of STP 3, more hygrophilic forb species were recorded, such

as *Centaurea adpressa* Ledeb., *Medicago romanica* Prodán, *Falcaria vulgaris* Bernh., and *Salvia nutans* L. Additional botanical components included *Elytrigia repens* (L.) Nevski, *Carex melanostachya* M. Bieb. ex Willd., and *Poa angustifolia* L. The total projective plant cover at STP 1, STP 2, and STP 3 was 72.1%, 79.3%, and 91.2%, respectively.

Figure 1. Location of STP 1 on a watershed divide characterized by ravine topography near the settlement of Terpenie (Zaporizhzhia Oblast). Source: Yandex Maps.

Figure 2. Location of STP 2 and STP 3 on the terraces of the Molochnaya River valley in the northeast of Melitopol. Source: Yandex Maps.

To assess the sequestration characteristics of soil phototrophs, microalgal and cyanobacterial cell counts were determined directly in soil core samples collected following the standard methodology of Hollerbach and Shtina (1969). Soil samples were extracted from a depth of 0–5 cm in spring (April), summer (August), and autumn (November). Each composite sample consisted of 5 to 10 randomly collected cores with an individual surface area of 25 cm^2.

Cell counts and morphometric measurements were used to calculate the wet biomass (kg RW ha^{-1}) of the microalgal and cyanobacterial communities (Hollerbach & Shtina 1969). To estimate biomass productivity, daily soil sampling was performed over a 10-day period during each of the spring, summer, and fall seasons. To ensure comparability of the datasets, cell counts and biomass estimates were expressed per gram of absolutely dry soil. The gravimetric moisture content of the soil was determined in the laboratory by drying fresh soil samples at 105 °C for 5 hours.

In calculating carbon dioxide assimilation, we assumed that 1 kg of dry biomass (DW) of microalgae and cyanobacteria sequesters an average of 1.88 kg of CO_2, with an average water content in living cells of 82% (Fedorov et al. 1974; Adamczyk et al. 2016). The results were converted and expressed as the amount of carbon immobilized within the biomass (kg C ha^{-1}) and as net primary production (NPP, g $Cm^{-2}month^{-1}$) (Pessarrodona et al. 2022; Jassey et al. 2022).

To ensure reproducibility, all experimental procedures were performed in triplicate. Statistical analyzes were carried out using Statistica (ver. 12.0), and data plotting was performed using Microsoft Excel (ver. 1903). Statistical significance was evaluated using one-way Analysis of Variance (ANOVA), with a significance threshold set at $p \leq 0.05$. Relationships between the biological and environmental variables measured were explored via Principal Component Analysis (PCA) using Statistica 12.0.

Results

Both prokaryotic Cyanobacteria and eukaryotic microalgae were identified in the upper soil layer (0–5 cm) of the steppe ecosystems (Figs 3, 4). Seasonal variation in precipitation and temperature was clearly reflected in the temporal dynamics of phototrophic cell density and biomass, with peak values recorded in autumn and spring (Figs 3a, 3c).

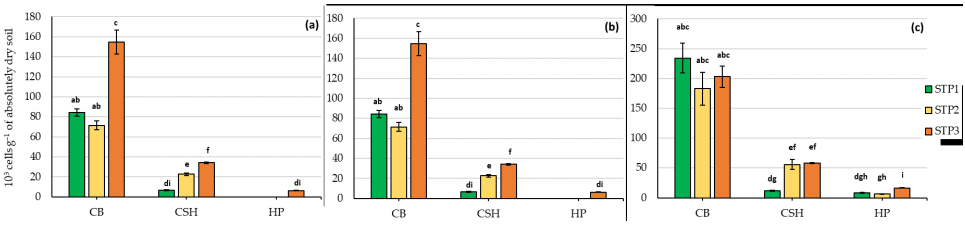

Figure 3. Abundance of soil microalgae and cyanobacteria within the upper 0–5 cm layer of the steppe ecosystems: (**a**) spring period, and (**b**) summer period, (**c**) autumn period. Note. Here and in Figures 4–5: CB – Cyanobacteria; CSH – Chlorophyta, Streptophyta, Heterokontophyta (Eustigmatophyceae, Xanthophyceae); HP – Heterokontophyta (Bacillariophyceae). Statistically significant differences are indicated at $p \leq 0.05$ (M ± SD, n = 3).

Spatial variation across the study plots was also pronounced. Consistently higher cell density and biomass values were recorded at STP 3, which was located within a topographic depression that retained higher moisture levels, thereby establishing a highly favorable microclimate for phototrophic growth. Cyanobacteria dominated the phototrophic community at all study sites.

The active wet biomass of microalgae and cyanobacteria ranged from 10.52 kg RW ha^{-1} to 31.87 kg RW ha^{-1} (Figs 4a–c).

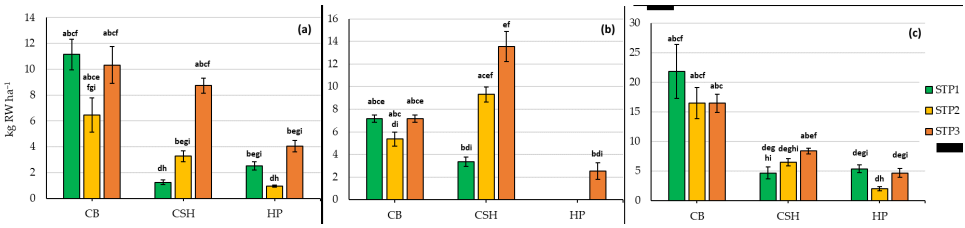

Figure 4. Biomass of soil microalgae and cyanobacteria within the upper 0–5 cm layer of the studied steppe ecosystems: (**a**) spring period, (**b**) summer period, (**c**) autumn period.

Biomass productivity values ranged between 53.47 kg RW ha^{-1} month^{-1} and 217.52 kg RW ha^{-1} month^{-1} (Figs 5a–c). The lowest productivity values were recorded at all sites during the summer. Extremely high temperatures coupled with severe moisture deficits restricted the development of microalgal and cyanobacterial bacteria in the uppermost soil layer during this period.

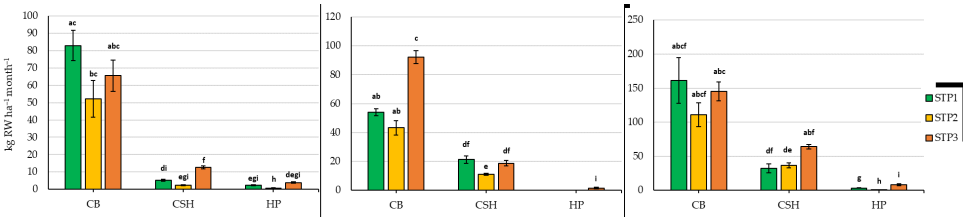

Figure 5. Biomass productivity of soil microalgae and cyanobacteria within the upper 0–5 cm layer of the steppe ecosystems: (**a**) spring period, (**b**) summer period, (**c**) autumn period.

The total amount of carbon immobilized within the phototrophic biomass reached 2.65–2.87 kg C ha^{-1} (Table 1). The monthly net primary production (NPP) of the microalgal and cyanobacterial communities within the upper 5 cm soil layer reached a maximum of 1.96 g C m^{-2} month^{-1}.

Table 1. Net primary production (NPP) and carbon sequestration of soil microalgae and cyanobacteria across the steppe ecosystems by season

Plot	Season	Carbon sequestered in biomass (kg C ha^{-1})	Net Primary Production (NPP) (g C m^{-2} $month^{-1}$)
STP 1	Spring	1.38	0.81
	Summer	0.95	0.68
	Autumn	2.87	1.77
STP 2	Spring	0.96	0.49
	Summer	1.32	0.49
	Autumn	2.25	1.33
STP 3	Spring	2.08	0.75
	Summer	2.09	1.01
	Autumn	2.65	1.96

The PCA performed on the entire suite of biological parameters revealed that the first two principal components accounted for 84.95% of the total variance (Fig. 6).

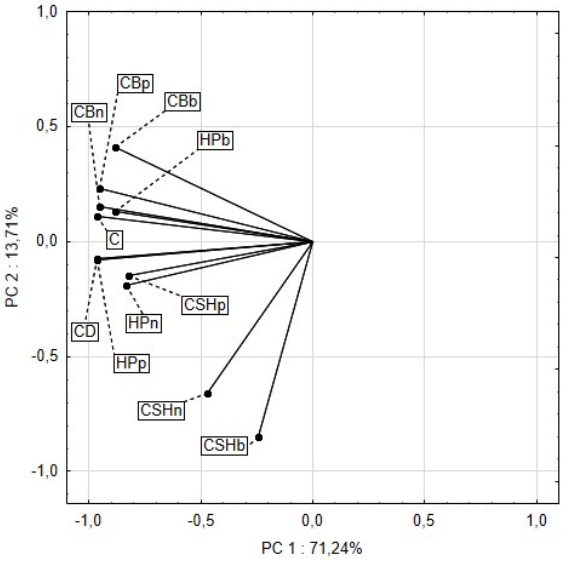

Figure 6. Principal Component Analysis (PCA) factor loading plot of the variables studied: CBn, CSHn, HPn – cell abundance; CBb, CSHb, HPb – biomass; CBp, CSHp, HPp – biomass productivity of Cyanobacteria (CB), Chlorophyta, Streptophyta, Heterokontophyta (Eustigmatophyceae, Xanthophyceae) (CSH), and Heterokontophyta (Bacillariophyceae) (HP), respectively; CD – carbon sequestered within microalgae and cyanobacterial biomass; C – monthly net primary production (NPP) of microalgae and cyanobacteria.

PC1 (71.24%) mainly reflected processes associated with the growth and carbon sequestration of Cyanobacteria and Bacillariophyceae. PC2 (13.71%) was associated with the growth and sequestration dynamics of eukaryotic green algae and xanthophytes (Chlorophyta, Streptophyta, Eustigmatophyceae and Xanthophyceae). The relative distribution of the sampling plots within the PC1 vs. PC2 space revealed distinct ecological patterns.

Two major clusters, A and B, were clearly resolved along the PC1 axis (Fig. 7).

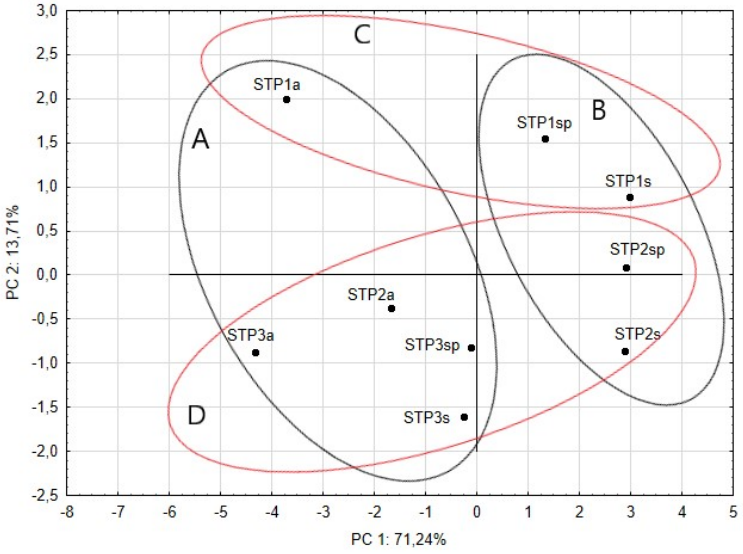

Figure 7. PCA score plot of the stationary sample plots (STPs): STP1sp, STP2sp, STP3sp – spring observations across the respective STPs; STP1s, STP2s, STP3s – summer observations across the respective STPs; STP1a, STP2a, STP3a – autumn observations across the respective STPs.

Separation of the plots into these clusters highlights the joint influence of macroclimatic seasonal shifts and localized microclimatic characteristics. The geomorphological characteristics of STP 1 and STP 2 resulted in drier topsoils during spring and summer. These observations were grouped together in Cluster A. In contrast, Cluster B grouped observations associated with more favorable moisture regimes: the autumn sampling for STP 1 and STP 2, and all seasonal samplings for STP 3 due to its position in a low-lying relief depression. Along the PC2 axis, the ecosystems formed distinct clusters C and D, reflecting the varying relative contribution of the Chlorophyta-Streptophyta-Heterokontophyta group (Eustigmatophyceae, Xanthophyceae) at the sites.

Discussion

Steppe ecosystems develop under semi-arid conditions characterized by distinctive biogeochemical cycling. Aridity exerts a powerful limiting effect on both photosynthetic carbon uptake and organic matter decomposition rates, which collectively govern net carbon emissions. Consequently, steppe soils are capable of long-term carbon accumulation and retention (Golubyatnikov et al. 2023). Carbon assimilated by vascular steppe vegetation is primarily partitioned belowground into root systems. This represents a fundamental divergence from forest ecosystems, where carbon storage is concentrated aboveground in woody biomass (Zamolodchikov 2012; Shvidenko, Schepaschenko 2014).

Photosynthetic soil cyanobacteria and microalgae represent an essential component of the edaphic community (Hollerbach & Shtina 1969). Their species richness, abundance, and biomass vary significantly across different terrestrial ecosystems (Maltseva et al. 2017; Maltsev et al. 2017; Patova et al. 2023; Sukhanova et al. 2025).

Phototrophic communities in steppe soil are characterized by a dominant role for Cyanobacteria, particularly representatives of the genera *Microcoleus* Desmazières ex Gomont, *Symploca* Kützing ex Gomont, *Schizothrix* Kützing ex Gomont, and *Phormidium* Kützing ex Gomont (Kuzyakhmetov 1991; Şalaru 1994; Shcherbyna et al. 2014). Along the environmental gradient from moderately dry to hyperarid desertified steppes, the dominance of cyanobacteria typically increases (Shushueva, 1985). Surface crusts formed by the *Nostoc commune* Vaucher ex Bornet & Flahault and *Microcoleus vaginatus* Gomont are frequently observed. Eukaryotic green algae (Chlorophyta) are second in terms of diversity and abundance; they occasionally exhibit high taxonomic richness, but rarely exceed cyanobacteria in cell density (Shushueva 1984; Kuzyakhmetov 1991).

Microalgae and cyanobacteria colonize both the immediate soil surface and deeper soil horizons. Downward transport is primarily passive, driven by percolating water through soil micropores, root growth channels, moss protonemata, and soil faunal activity. The hydrological regime strongly influences this vertical distribution. For example, heavy downpours or seasonal washing can wash surface-dwelling cells deep into the soil profile (Hollerbach & Shtina 1969). Accurate assessments of photosynthetic carbon capture must account for this vertical migration, although the vast majority of phototrophs in arid steppe soils remain concentrated within the uppermost millimeters. Under arid conditions, these microphototrophs, together with other micro- and macroorganisms, form biological soil crusts (biocrusts) (Maier et al. 2018; Tamm et al. 2018). Biocrusts perform crucial ecological functions, including soil stabilization and nutrient enrichment. However, their precise quantitative role in carbon assimilation in arid and semi-arid regions remains insufficiently explored.

In our study, Cyanobacteria consistently dominated over eukaryotic microalgae. This dominance was most pronounced in STP 1 and STP 2. The ratio of cyanobacterial biomass productivity to that of eukaryotic microalgae (Chlorophyta,

Streptophyta, Eustigmatophyceae and Xanthophyceae) was 8.1:1 on STP 1, 9.5: 1 in STP 2, and 4.1:1 on STP 3. Historically, the diversity ratio of Cyanobacteria to eukaryotic green algae has been used as an indicator of habitat aridity, with higher ratios reflecting drier conditions (Novichkova-Ivanova 1980). Our productivity data similarly reflect this gradient, with the lowest ratio recorded at the topographically depressed and wetter STP 3.

The absolute amount of carbon dioxide captured by soil phototrophs in the steppe ecosystems is comparable to the estimates reported for forest soils (Maltseva et al. 2024). The maximum monthly NPP of the microphototrophs in the top 5 cm of soil (1.96 g $Cm^{-2}month^{-1}$) corresponds to approximately 7% of the monthly adjusted average NPP of vascular plants in natural steppes (Golubyatnikov et al. 2023).

However, it should be emphasized that current estimates of carbon sequestration by soil microalgae and cyanobacteria are highly conservative. Although measuring biomass increments over discrete time intervals is the most direct method available, it does not capture the full scope of photosynthetic carbon processing. Eukaryotic algae and cyanobacteria release a substantial portion of their photosynthetically fixed carbon into the surrounding soil matrix as extracellular organic matter (Liu et al. 2016; Brisson et al. 2021). The release of these active exometabolites can account for up to 70% of the total carbon assimilated by photosynthesis (Tambiev & Lukyanov 2011). Furthermore, soil phototrophs are rapidly consumed by diverse micro- and mesofauna. For example, Enchytraeidae feeding exclusively on soil algae are capable of consuming 131 to 140 kg of organic matter per hectare annually (Kabirov & Gaisina 2009). Therefore, the actual biogeochemical role of microalgae and cyanobacteria in carbon cycling is significantly greater than that can be resolved by traditional biomass-based methods.

The transfer of phototrophic carbon to grazing food webs helps stabilize organic carbon within the larger soil biota. The decomposition of senescent microalgal and cyanobacterial biomass yields humic and fulvic acids, the core building blocks of soil humus (Hollerbach & Shtina 1969). Given the characteristically slow rates of organic matter decomposition in semi-arid steppe soils, these microphototrophs make an important, ongoing contribution to humus accumulation and long-term carbon storage.

Conclusions

Soil microalgae and cyanobacteria in steppe ecosystems assimilate atmospheric carbon dioxide during growth, providing a vital regulatory ecosystem service. This carbon-sequestrating function exhibits distinct seasonal dynamics, peaks during the moist autumn period. Local microclimatic conditions in topographic depressions can sustain elevated phototrophic activity during otherwise dry seasons. The net monthly primary production of soil phototrophs in the upper 5 cm of soil reaches 1.96 g $Cm^{-2}month^{-1}$, representing approximately 7% of the average monthly NPP of

vascular steppe vegetation. When accounting for the release of extracellular organic matter (which can reach up to 70% of total assimilated carbon) and rapid trophic transfer through soil food webs, the true volume of carbon captured by these organisms is significantly greater than that which current methodology can directly measure. Future research incorporating isotopic labeling and advanced exometabolite profiling is required to further refine the quantitative contribution of soil phototrophs to the global carbon cycle.

Acknowledgements

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