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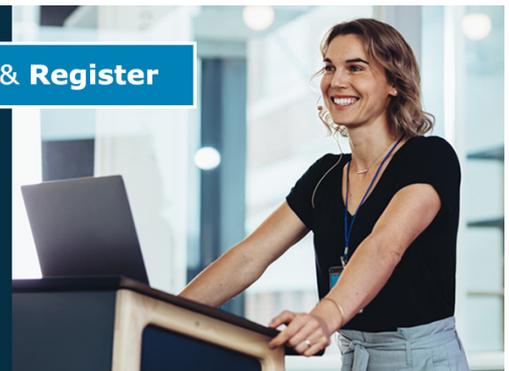
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Carbon photoassimilation by dominant species of mosses and lichens in pine forests of Central Siberia

D A Polosukhina¹, O V Masyagina² and A S Prokushkin^{1,2}

¹ Siberian Federal University, 660041, Krasnoyarsk, 79 Svobodny Prospect, Russia

² V N Sukachev Institute of Forest SB RAS, 660036, Krasnoyarsk, 50/28 Akademgorodok Street, Russia

dana_polo@mail.ru

Abstract. The stocks of phyto(bio)mass of a ground vegetation cover consisting of dwarf shrubs, lichens, and feathermosses are estimated in pine forests of Central Siberia (ZOTTO). CO₂ photoassimilation dynamics is analyzed for the dominant species of the moss-lichen layer throughout the growing season. In parallel, we assess the impact of abiotic environmental factors on the photoassimilation intensity.

1. Introduction

The boreal forests are characterized by ground vegetation rich in bryophytes and lichens. Dominating in the ground floor layer, mosses, lichens and their associated cyanobacteria functionally contribute to the ecosystem carbon and nitrogen sequestration, soil insulation, soil stability, and preservation of permafrost [1]. Poikilohydric plants contribute up to 50% of the ecosystem gross CO₂ exchange [2, 3].

Feathermosses and lichens play a significant role in well-drained sites and *Sphagnum spp.* are the most important contributors in wetland C uptake [5, 6]. Given their important ecological roles in taiga biome, it is surprising that only a few studies have attempted to parameterize the intrinsic abiotic factors that control the moss-lichen cover carbon dynamics, specifically under ongoing climate change in high latitudes.

Due to the climate change, the ecosystems of the boreal biome can shift from a sink of atmospheric carbon [7] to its source [8]. A negative balance of ecosystem C flux in the boreal biome is predicted due to excess of ecosystem respiration, i.e. an increased mineralization C flux from soils, over its photoassimilation by vegetation [9, 10]. The moss-lichen layer can play a key role in an ecosystem carbon accumulation, since it makes up 30-94% of the total biomass of ecosystems [11, 12]. Thus, the assessment of reserves and "vulnerability" of the considered vegetation layer of boreal forest to increase in temperature and carbon dioxide concentrations and changes in moisture regimes remains one of the main tasks in modern studies of the carbon cycle.

We hypothesized that the photosynthesis of mosses and lichens has seasonal dynamics during the entire growing season and they have different reactions to changing environmental factors (increase in the temperature, CO₂ concentration, and light level).

The main goal of this work was to determine the stocks of ground vegetation and photoassimilation activity of dominant species of the moss-lichen layer during the growing season.



2. Materials and methods

2.1 Study area

The study was conducted in Central Siberia near the Zotino tall tower observatory (ZOTTO, 60 ° N, 89 ° E) in lichen- and feathermoss-dominated pine forests (Figure 1). The territory belongs to the Ket-Sym lowland on the left bank of the Yenisei River. According to the forestry zoning of Siberia, "ZOTTO" is located within the middle taiga Sym-Dubeches forest district [12].

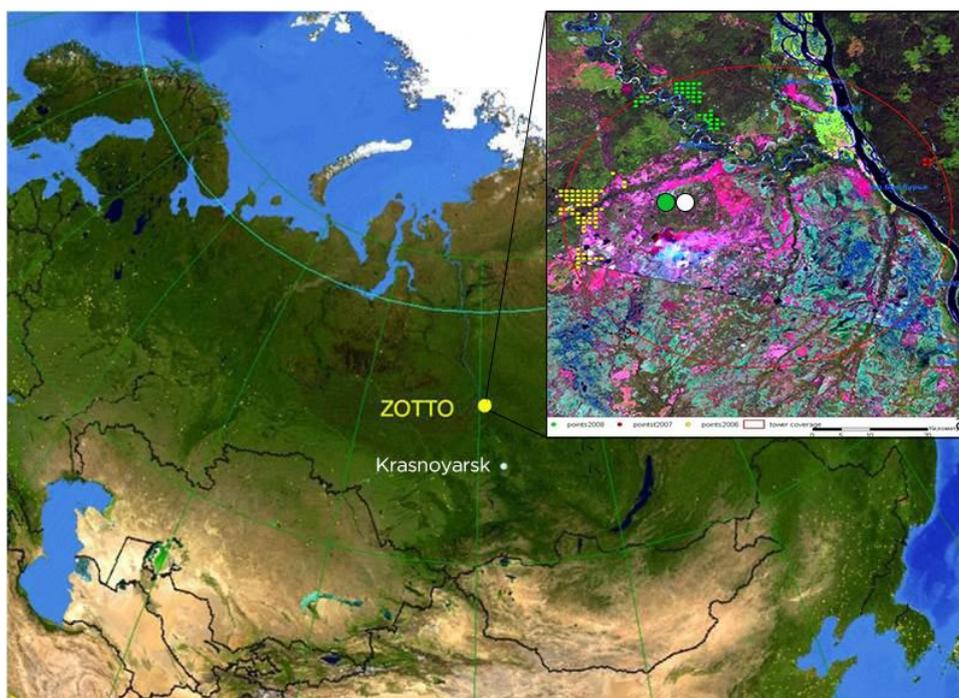


Figure 1. Maps of the Zotino tall tower observatory study area, green dot - green-moss pine forests, white dot - lichen pine forests.

The climate of the region is sharply continental. The sum of temperatures above 10 ° C is 800-1200° C. The average annual air temperature is -3.7 ° C. The annual amount of precipitation is 590 mm [13].

An analysis of satellite data identified 11 classes of aggregated land surface within a radius of 100 km of the ZOTTO international observatory [14]. The analysis results showed that the forest area was about 84%. Dark coniferous communities were determined to occupy the largest area. The light coniferous pine forests with the feathermoss-dominated account for 8.3% and the lichen-dominated pine forests, 7.6 %.

Sandy and sub-sandy soil types prevail in the soil cover (podzols); without permafrost [14]. The forest inventory parameters for the studied pine forests are defined (Table 1).

Table 1. Forest inventory parameters for the studied pine forests.

Forests	DBH, cm	H, m	Density, trees/ ha	Stock, t/ha
Lichen pine forests	14.4	11.4	358	82.6
Green-moss pine forests	19.8	15.7	565	156.7

2.2 Species diversity and definition of biomass stock

The species composition of the living ground cover and the occurrence of each individual species were determined. The nomenclature of the plants is given according to S.K. Cherepanov [15], and that of the mosses and lichens according to M.S. Ignatov and E.A. Ignatova [16, 17] and Oksner A. N. [18]. Based on the observation results, the frequency of occurrence calculated by the formula [19] is

$$R = \frac{A \times 100\%}{N} \quad (1)$$

where A is the number of sites in which this species is registered, and N is the total number of sites surveyed.

To assess the phyto (bio) mass stocks, the grass-shrub and moss-lichen layers were sampled in 100 replicates in each type of forest from 20x25 cm subplots ($S = 50 \text{ cm}^2$). Then each sample was oven-dried at 105°C for 24 hours.

The obtained data on the species diversity of the studied forests are presented below in the section on results and discussion. After this study, 3 dominant species of lichens and feathermoss were identified, for which CO₂ photoassimilation measurements were carried out. The species examined were *Cladonia stellaris* (Opiz.) Brodo, *Cladonia rangiferina* (L.) Nyl., *Cetraria islandica* (L.) Ach., *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp., and *Aulacomnium palustre* (Hedw.) Schimp.

2.3 Measurements and data analysis

2.3.1. CO₂ photoassimilation measurements during the growing season. The rate of CO₂ photoassimilation (A , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) was determined *in situ* by a Walz GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany) infrared gas analyzer with a moss cuvette (cuvette for Lichens/Mosses 3010-V32). The photosynthetic activity of lichens and feather mosses was measured during the growing season of 2018 in June, July, August, and September at 1 time per every month around the mid-day time.

2.3.2. The light, CO₂, and temperature responses of photosynthesis of examined species. For every time point, we also analyzed the dependence of the CO₂ exchange on temperature, photosynthetically active radiation (PAR), and CO₂ concentration. Three fresh samples of each examined species were used for the measurement. Only the live part was taken from the mosses.

We first determined the light-response curves. The cuvette conditions resembled the ambient conditions with a temperature set at 20 °C, the relative humidity following the ambient conditions (around 60 %), and a CO₂ concentration set at 400 ppm. Based on trial experiments, 9 steps of light intensity were set: 0, 50, 100, 200, 400, 600, 1000, 1500, and 2000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR. The samples were enclosed in the cuvette and the CO₂ gas-exchange was recorded when steady states were reached (usually after ~3 min).

The CO₂-response curves: the cuvette conditions resembled the ambient conditions with a temperature set at 20 °C, the relative humidity following the ambient conditions (around 60 %), and the PAR set at 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Based on trial experiments, 9 steps of CO₂ concentrations were set: 0, 50, 100, 200, 400, 600, 1000, 1500, and 2000 ppm. The samples were enclosed in the cuvette and the carbon exchange was recorded when steady states were reached (usually after ~3 min).

The temperature-response curves: the cuvette conditions resembled the ambient conditions with a CO₂ concentration set at 400 ppm, the relative humidity following the ambient conditions (around 60 %), and the PAR set at 1000 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Based on trial experiments, 5 steps of temperature were set: 0, 10, 20, 30, and 40°C. After the gas-exchange measurements, the samples were oven-dried at 100°C for 24 hours to obtain dry mass.

2.3.3. *Data analysis.* For analysis and processing of the observation data, licensed software GFS-Win was used. In addition, a number of programs were used for statistical processing and data analysis: Microsoft Excel 2008, Statistica 6.1.

3. Results and discussion

3.1 The species composition and phyto (bio) mass stocks

The forest floor vegetation strata in the lichen pine forest consisted of lichen species *Cetraria islandica*, *Cladonia gracilis* (L.), *C. rangiferina*, *C. stellaris*, *Cladonia uncialis* (L.); mosses *A. palustre* and *P. schreberi* and grasses and dwarf shrubs *Carex macroura* (Meinsh.), *Ledum palustre* (L.), *Vaccinium vitis-idea* (L.). Based on the calculation of the coefficient of variation R, the most common lichen associations are: *Cladonia stellaris* (63%), *Cladonia rangifera* (54%), and *Cetraria islandica* (48%). The total ground floor layer biomass was $354 \pm 25 \text{ g m}^{-2}$ (Figure 2). The lichens have the major biomass stocks, i.e. *C. stellaris* - 41% ($145 \pm 29 \text{ g/m}^2$), *C. rangifera* - 32% ($114 \pm 10 \text{ g/m}^2$), and *C. islandica* - 16% ($57 \pm 21 \text{ g/m}^2$). The share of shrubs accounted for 4%, and that of mosses only 1.5%.

The ground floor layer of the green-moss pine forests has the greater species diversity than in the lichen pine forest. The grass-dwarf shrub stratum is represented by *Empetrum nigrum* (L.), *L. palustre*, *Vaccinium myrtillus* (L.), *Vaccinium uliginosum* (L.), and *V. vitis-idaea*. The moss-lichen layer consisted of lichen species *C. gracilis*, *C. rangiferina*, *C. uncialis* and mosses of the following species *A. palustre*, *Dicranum elongatum* (Schleich.ex Schwägr), *Dicranum polysetum* (Sw.), *Dicranum spadice* (Zett.), *P. schreberi*, *Polytrichum commune* (Hedw.), *Ptilium crista-castrangis* (Hedw.), and *H. splendens*. Based on the calculation of the coefficient of variation R, the most common are *P. schreberi* (99%), *H. splendens* (85%), *A. palustre* (75%) in the moss-lichen cover; *V. myrtillus* (55%) dominates in the dwarf-shrub layer. The total stock of bio (phyto) mass in the pine dwarf-shrub-feathermoss pine forest was $646 \pm 40 \text{ g/m}^2$. The major stock was found in the following feathermoss species: *P. schreberi* - 35% ($294 \pm 36 \text{ g/m}^2$), *H. splendens* - 21% ($175 \pm 28 \text{ g/m}^2$), and *A. palustre* - 10% ($83 \pm 15 \text{ g/m}^2$).

In the studied taiga ecosystems, it was found that the phytomass in the living ground layers varies from $354 \pm 25 \text{ g/m}^2$ in the lichen-dominated pine forests to $646 \pm 40 \text{ g/m}^2$ in the feathermoss-dominated pine forests (Figure 2). The statistical results were considered significant. The moss-lichen layer accounted for 78-96% of the total phytomass of the ground floor in the studied pine forests and was comparable to the photosynthetic phytomass of the tree canopy (pine needles). The grass-dwarf shrub stratum accounted for 4-22 % of the total phytomass of the ground floor in our plots.

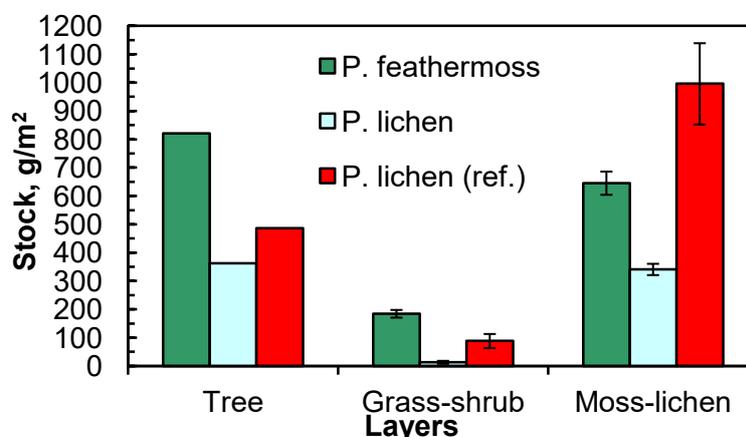


Figure 2. Stocks of organic matter of subordinate layers of vegetation and phytomass of the tree layer. The columns indicate the mean values of stock of each forest layer ($n = 100$) and the error bars represent the SEs. The statistical results were considered significant ($p \leq 0.050$).

For the lichen pine forests in the middle taiga subzone of the Urals, according to V.Z. Nagimov et al. 2009, the stock of dwarf shrubs and moss-lichen cover, in total, amounts to $1084 \pm 70 \text{ g / m}^2$ versus 486 g / m^2 in the tree canopy (pine needles) [20]. The living ground layer is an important component of the forest ecosystem. The assessment of the biomass stock is carried out in conjunction with the determination of the biological diversity within the subordinate layers of the vegetation cover. For the study area, a significant contribution of the moss-lichen layer to the stocks of the living ground cover is noted [1, 14, 21]. Thus, the mosses account for 39-47%, the lichens account for 39-43%, and the dwarf shrubs constitute 20-53% of the total phytomass of subordinate vegetation layers in the lichen and green moss pine forests, respectively [22, 23]. On average, for the boreal belt, according to O.V. Shpak, different species of the moss-lichen layer can accumulate from 194 to 1231 g of dry weight per m^2 [24].

3.2 Gas-exchange measurements during the growing season

CO_2 gas exchange is more intense in bryophytes during the entire growing season. The greatest variation in the values was noted in June for the studied feathermoss species and amounted to $1.63 \pm 0.05 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in *Aulacomium palustre*, and reached a maximum of $2.39 \pm 0.02 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in *Pleurozium schreberi* (Figure 3). From July to September, among the studied species, the highest photoassimilation was observed in the species *A. palustre*, and the lowest one in *H. splendens*. The maximum values of photoassimilation are noted in August for all studied species and are $2.39 \pm 0.09 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *A. palustre*, $2.72 \pm 0.01 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *H. splendens*, and $2.66 \pm 0.13 \mu\text{mol m}^{-2} \text{ s}^{-1}$ for *P. schreberi*. The mean magnitude of A ($2.39 \pm 0.02 \mu\text{mol m}^{-2} \text{ s}^{-1}$) correlates with the range of the previous studies of *P. schreberi* ($1.0\text{--}4.8 \mu\text{mol m}^{-2} \text{ s}^{-1}$) [1,24,25,26,27,28] and was comparable to other measurements of boreal forest floor mosses [29]. Based on the results of a two-way analysis of variance, the revealed features of photoassimilation in bryophytes depend on the species specificity ($p=0.04$) and practically do not differ in summer ($p = 0.12$). The considered species of mosses are ectohydric species, i.e. the absorption of water and minerals occurs by their surface [24, 25].

The intensity of photoassimilation in the lichens is somewhat lower than that noted for mosses, but it is most pronounced in the growing season. This result can be explained by the fact that the lichen thallus is four to ten times poorer in chlorophyll than higher plants [1, 24]. In addition, the algal cells are not always evenly distributed in the thallus. Such an intensity of photosynthesis ensures normal vital activity of lichens, since they endure frequent periods of significant ecological depression (drying out) and are distinguished by high plasticity of the entire metabolic apparatus of lichens, which allows them to endure these periods and quickly return to life even in conditions of low temperature, low carbon dioxide content, etc. in which other plants die or cease to function [31].

The lowest values are recorded in June, then an increase in photoassimilation is observed (July-August), and a decrease occurs in September. During the entire growing season, the highest values are observed in *Cladonia stellaris*, and the lowest ones in *Cetraria islandica* (Figure 3). The maximum is observed in August for all studied species, for example, for *C. stellaris* $1.81 \pm 0.10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ *C. rangiferina* $1.91 \pm 0.07 \mu\text{mol m}^{-2} \text{ s}^{-1}$ *C. islandica* $1.55 \pm 0.14 \mu\text{mol m}^{-2} \text{ s}^{-1}$. The values correspond to the measurements of previous studies [5, 31]. Based on the results of two-way analysis of variance, the factor of the species specificity ($p = 0.09$) and the during factor ($p = 0.02$) are statistically significant.

Thus, the moss-lichen layer dominants maintained high photoassimilation activity throughout the growing season. The smallest seasonal variation is characterized by the dominant species of the moss layer of feathermoss pine forests - *Pleurozium schreberi*, and the largest one by the dominant species of the lichen layer of the lichen pine forests - *Cladonia stellaris*.

At the beginning and end of the growing season, decreased values of the intensity of photosynthesis are observed, which is also noted in a number of other studies [24-31]. The intensity of CO_2 photoassimilation in the seasonal dynamics in the moss-lichen cover in the forests of Siberia which, apparently, is associated with the local variation in the photosynthetic characteristics.

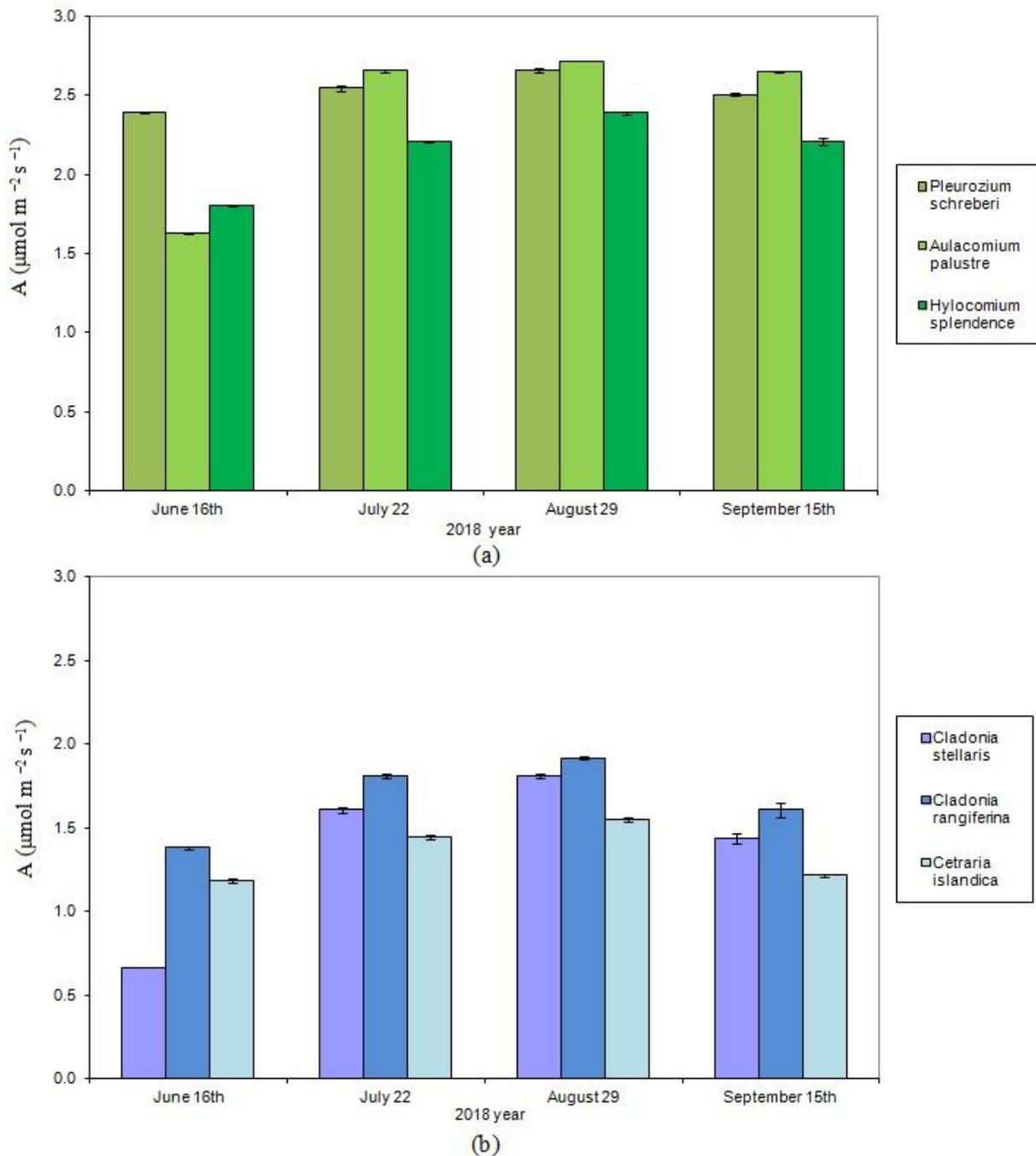


Figure 3. Photoassimilation activity (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) of the dominant moss (a) and lichen (b) species in pine ecosystems during the growing season. The columns indicate the mean values of A ($n = 5$) and the error bars represent the SEs.

3.3 The response of photosynthesis of feathermosses and lichens to environmental factors

Due to their poikilohydric nature, the capacity of moss and lichen species photosynthetic gas exchange is dependent on the water content, light, CO_2 concentration, and temperature [24, 25, 29-31]. The rates of photosynthesis and respiration increase with increasing temperature, reach a peak, and then the processes are inhibited [1, 24]. The optimum temperature for photosynthesis of mosses and lichens from different habitats varies over a wide range [1]. As a rule, the moss-lichen synusia are active at

temperatures above zero degrees Celsius [24]. However, lichens, especially the Arctic species, can also be activated at subzero temperatures, from atmospheric humidity, although gas exchange at these temperatures is low [1, 5, 24-31].

Cladonia stellaris and *Pleurozium schreberi*, acting as absolute dominants in the living ground layer, reflect the general trends in the course of photosynthesis for the studied species of mosses and lichens, depending on changes in the environmental factors. There were no differences in the temperature dependence of CO₂ photoassimilation between feathermosses and lichens (Figure 4a and 4d). At a temperature of 0 °C in the studied species of the moss-lichen cover, the predominance of CO₂ emission over its absorption was noted. With an increase in the temperature, an increase in the intensity of assimilation was observed, and no inhibition by high temperatures (up to +40 °C) was noted. The maximum intensity of assimilation at 40 °C for *Cladonia stellaris* was $2.78 \pm 0.14 \mu\text{mol m}^{-2} \text{s}^{-1}$, and for *Pleurozium schreberi* $2.95 \pm 0.12 \mu\text{mol m}^{-2} \text{s}^{-1}$.

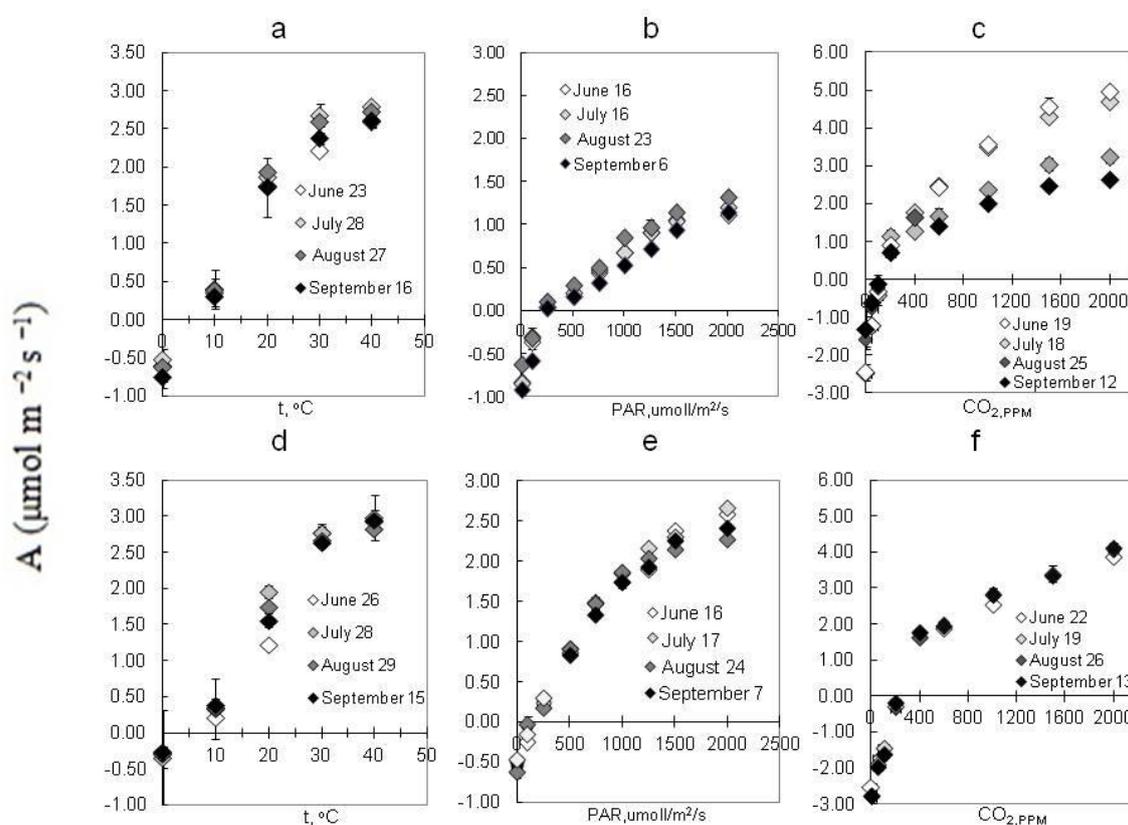


Figure 4. Response of photoassimilation intensity (A , $\mu\text{mol m}^{-2} \text{s}^{-1}$) of *Cladonia stellaris* (Opiz) and *Pleurozium schreberi* (Brid.) Mitt. to air temperature (a and d), PAR (b and e), CO₂ concentration (c and f) on different days of the growing season. The points indicate mean values of A ($n = 3$) and the error bars represent the SEs. The statistical results were considered significant ($p \leq 0.050$).

The effect of temperature on photosynthesis depends on the intensity of illumination. At low illumination, photosynthesis does not depend on temperature ($Q_{10} = 1$) [16, 21, 26]. Therefore, at a low level of illumination photosynthesis proceeds at the same rate at 15 ° and 25 ° C [1, 24]. *Pleurozium schreberi* stands from different taiga ecosystems in interior Alaska found light compensation and saturation of photosynthesis (20 °C) [1, 28]. On the other hand, in *Hylocomium* the

rates of net photosynthesis at light saturation generally increased when the temperature raised from 5 °C to 20 °C [1, 27, 29, 30].

At the same time, differences in photoassimilation between the green mosses and lichens were revealed depending on photosynthetically active radiation. The mosses showed a 2-fold larger response of the CO₂ assimilation intensity to an increase in the PAR as compared to lichens (Figure 4b and 4e). For *Pleurozium schreberi*, the highest value at PAR = 2000 μmol m⁻² s⁻¹ was 2.67± 0.03 μmol m⁻² s⁻¹, and for *Cladonia stellaris*, 1.31±0.01 μmol m⁻² s⁻¹. The point of compensation in *Cladonia stellaris* varied during the season: in June it was observed at PAR = 249 μmol m⁻² s⁻¹, and in September it decreased to 199 μmol m⁻² s⁻¹. In *Pleurozium schreberi* a compensation point was observed in June at PAR = 161 μmol m⁻² s⁻¹ and in September at PAR = 147 μmol m⁻² s⁻¹. The results are in accordance with the results from other subarctic and subalpine regions [1, 24, 28]. For the lichens, lower values of the intensity of photoassimilation are noted. The photosynthetic light-response curves for the study species showed log growth with increasing light. According to other studies, this trend persists for both bryophytes and lichens [1,4, 24-31].

The rate of photosynthesis of both moss and lichen showed log growth with increasing CO₂ levels up to 2000 ppm (Figure 4c and 4f). When analyzing the dependence of photosynthesis on the CO₂ concentration for *Cladonia stellaris*, an increase in photoassimilation was noted, which in June and July at CO₂ = 2000 ppm was about 4.94 ±0.01 μmol m⁻² s⁻¹, but decreased at the end of the season. In *Pleurozium schreberi*, influence of seasonal changes in the yield of photosynthesis on the concentration of CO₂ were not observed, amounting to about 4.13±0.12 μmol m⁻² s⁻¹ at CO₂ = 2000 ppm. The observed effect is typical for both tropical and arctic mosses [1, 3, 4, 24-31]. The widespread sub-Arctic bryophytes and lichens even after midwinter warming events retain a similar trend [4].

4. Conclusions

In summary, we found that the stocks of phyto (bio) mass in the moss-lichen layer of pine forests of the study area are comparable to the photosynthesis phytomass of the tree layer. The moss-lichen layer accounts for 78-96% of the total phytomass of the ground cover in pine forests of Central Siberia. The dominant species in the living ground cover of pine ecosystems are *Cladonia stellaris*, *Cladonia rangiferina*, *Cetraria islandica*, *Pleurozium schreberi*, *Hylocomium splendens*, *Aulacomium palustre*, and *Vaccinium myrtillus*.

Our hypothesis that the photosynthesis of mosses and lichens has seasonal dynamics during the entire growing season has not been confirmed. In contrast to lichens, the seasonal dynamics of photosynthesis in mosses is weak. The smallest seasonal variation is characterized by the dominant species of the moss layer of green moss pine forests - *Pleurozium schreberi*, and the largest one - by the dominant species. The dominants of the moss-lichen layer retained high photoassimilation activity throughout the growing season when the studies were carried out (June-September 2018). The contribution of bryophytes to the total photoassimilation of carbon dioxide by the moss-lichen layer of pine ecosystems is higher than that of lichens. This is due to the larger amounts of photosynthesis of mosses and their significant stocks.

The rate of photosynthesis of mosses and lichens showed log growth with increasing light, CO₂ concentrations and temperature. The response of the studied species to changes in the environmental factors was a log growth. The species differences in the compensation points for the CO₂ concentration (the range of variation: 170 to 260 ppm), light (147-247 μmol / m²s), and temperature (5 - 6 °C) have been shown. The thus revealed features of photosynthesis of moss-lichen synusia in taiga biomes characterize their adaptability to the ongoing climate changes: an increase in the temperature and CO₂ concentrations.

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