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КРАТКИЕ СООБЩЕНИЯ

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# PHOTOSYNTHESIS OF WIDESPREAD LICHEN SPECIES IN PINE FORESTS OF CENTRAL SIBERIA[1]

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Lichens and other terrestrial photosynthetic unicellular organisms of the planet consume nearly 14.3 billion tons of atmospheric $CO_2$. Due to climate change, such important components of the forest ground cover as lichens are very vulnerable. This study evaluates the photosynthetic activity in widespread lichens by measuring the indices of net photosynthesis, dark respiration, and prompt fluorescence. Hence, cryptogams of pine forests in Central Siberia near the Zotino tall tower observatory (ZOTTO) are characterized as highly active. *Cladonia stellaris* (Opiz.) Brodo and *Cladonia rangiferina* (L.) are the main representatives of ground cover species. The purpose of this study was to determine the photosynthetic activity in dominant species of ground cover lichens during a growing season. We found the seasonal dynamics of photosynthesis with the lowest values being observed in June, and the highest ones in August. Dark respiration peaks in June and is the lowest in September. Fluorescence values are within the range of 6.7 ± 0.3. The species under study that grow on podzol soils in pine forests show fast kinetic activation.

*Keywords: Cladonia stellaris, Cladonia rangiferina, photosynthetic activity, photosynthesis, carbon balance, fluorescence.*

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As of today, northern boreal forests act mainly as a carbon sink (Bianchi, 2021). They represent one of the largest terrestrial reservoirs of atmospheric carbon. Due to the forecasted climate change, ecosystems of the boreal biome may shift from a sink of atmospheric carbon (Winkler et al., 2021) to its source (Koven et al., 2021). Such an effect can be predicted due to $CO_2$ emissions from ecosystems being larger than $CO_2$ uptake during photosynthesis, which, in fact, signifies an increase in decomposition of organic matter and in root respiration (Ryu et al., 2019; Bonan, 2008).

Mosses, lichens, and other unicellular photosynthetic organisms absorb 7% of carbon dioxide from the Earth's atmosphere (Elbert et al., 2012). The absorptive capacity of bryophytes and lichens is greater in temperate and subtropical climate zones than equatorial or tropical ones. Boreal forests are characterized by ground vegetation rich in bryophytes and lichens. Dominating in the ground cover layer, poikilohydric plants functionally contribute to the carbon and nitrogen sequestration in the ecosystem, soil insulation, soil stability, and preservation of permafrost (Bianchi, 2021). They contribute to up to 50% of the gross $CO_2$ exchange in the ecosystem (Winkler et al., 2021; Bryant et al., 1997).

Given their important ecological roles in the taiga biome, it is surprising to know that only a few studies have attempted to parameterize the intrinsic abiotic factors that control the moss-lichen cover carbon dynamics, specifically under the ongoing climate change at high latitudes (Elbert et al., 2012; Whitehead, Gower, 2001). Regional studies of the carbon cycle are relevant due to discrepancies in estimates of balance in carbon fluxes obtained for Russian forests that are diverse in composition, structure, and productivity, and due to the resulting necessity to supplement and refine those estimates.

With this study, we focused on exploring the absorptive capacity of lichens in pine forests of Central Siberia. They are estimated to account for up to 30–94% of the total biomass of ecosystems (Goltsev et al., 2012). As one of the most important metabolic processes, photosynthetic activity can be examined during field studies (Panov et al., 2009). Its measurements are based on recordings of carbon assimilation

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**Table 1.** Forest inventory parameters for the pine forests under study

| Forests | DBH, cm | *H*, m | Density, trees $ha^{-1}$ | Stock, t C $ha^{-1}$ |
|---|---|---|---|---|
| Lichen-dominated pine forests | 14.4 | 11.4 | 358 | 82.6 |

rates and chlorophyll fluorescence. The ratio of different ways of using the absorption energy of light quanta may vary depending on the functional activity in a photosynthesis system, as well as on the lighting conditions, which affects the chlorophyll fluorescence intensity.

The main goal of this study was to determine the photosynthetic activity in dominant species of lichens during a growing season.

## MATERIALS AND METHODS

**Area and objects of study.** The study was conducted in Central Siberia near the Zotino tall tower observatory (ZOTTO, 60° N, 89° E) in lichen-dominated pine forests. The area belongs to the Ket-Sym lowland located on the left bank of the Yenisei River. According to the forestry zoning of Siberia, ZOTTO is located in the area of middle taiga forests in Sym-Dubeches district (Pleshikov, 2002).

The local climate is sharply continental. The sum of temperatures above 10°C amounts to 800–1200°C. The average annual air temperature is –3.8°C. The annual amount of precipitation is 536 mm (Panov et al., 2011).

The analysis of satellite data identified 11 classes of aggregated landscape types within a radius of 100 km of the international observatory ZOTTO (Klimchenko et al., 2011). The analysis results showed that forests cover about of 84% of the zone. Dark coniferous communities occupy the largest area. Feathermoss-dominated light coniferous forests account for 8.3%, and lichen-dominated pine forests account for 7.6%.

The plants develop on well-drained ferruginous illuvial podzols on fluvioglacial sands with no permafrost (Pleshikov, 2002; Gerasimov, 1964; Klimchenko et al., 2011). Vascular plants have Latin names according to S.K. Cherepanov (Cherepanov, 1994), mosses and lichens – according to the studies by M.S. Ignatov and E.A. Ignatova (Ignatov, Ignatova, 2003, 2004). *Pinus sylvestris* (L.) dominated forests are characterized by an almost all-over lichen layer (Panov et al., 2014; Trefilova et al., 2011). Forest inventory parameters for the pine forests under study are displayed in Table 1. According to our earlier data, the living ground cover of the forests is dominated by *Cladonia stellaris* (Opiz.) Brodo with 41% (145 ± 29 $g/m^2$), *Cladonia rangiferina* (L.) Nyl. with 32% (114 ± 10 $g/m^2$), and *Cetraria islandica* (L.) with 16% (57 ± 21 $g/m^2$). The share of shrubs accounts for 4%, and that of mosses accounts for only 1.5%. Grasses and dwarf shrubs are represented mainly by *Carex macroura* (Meinsh.), *Ledum palustre* (L.), and *Vaccinium vitis-idaea* (L.) (Polosukhina et al., 2020).

Hence, *Cladonia stellaris* and *Cladonia rangiferina* are the most common lichen species, for which $CO_2$ assimilation and chlorophyll fluorescence were measured. These bushy lichens of the genus *Cladonia* have a green alga trebouxia as the photobiont (Opredelitel' lishainikov USSR, 1977). The samples for measurements were the upper parts of the thalli, where, according to physiological characteristics, the photobiont is located (Bjerke, 2009).

**Gas exchange measurements.** Assimilation rates (A, μmol $m^{-2}$ $s^{-1}$) were measured once a month around 12:00 in June, August, and September during the growing seasons of 2021. Metabolic activity of lichens was examined by using a portable gas exchange system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) with a cuvette for Lichens/Mosses 3010-V32 (Manual, 2019). During the measurement, we recorded two fluxes: dark respiration (DR) and net photosynthesis (NP). First, we measured DR at PAR = = 0 μmol $m^{-2}$ $s^{-1}$. Then we recorded NP at PAR = = 1000 μmol $m^{-2}$ $s^{-1}$. The data was presented as the mean value ± standard error for every case (*n* = 15):

$$A = NP + DR.$$

To analyze the impact of external factors, we used the meteorological data of relative humidity (RH) and air temperature (Tair). The observations were retrieved from an eddy covariance station located nearby.

**Prompt fluorescence.** Prompt fluorescence parameters were measured using the fluorometer Junior-PAM (Walz, Germany). We conducted the study around 13:00–15:00. Using the standard light curve analysis software (Manual, 2020), we obtained data by parameters Y(II), ETR, and Fv/Fm. The Fv/Fm ratio was used to estimate the maximum quantum yield of photochemistry (Goltsev et al., 2012) and the efficiency of the PSII (Y(II)) reaction centers in the dark adapted state, which provides valuable information on the function of PSII (Maxwell, Johnson, 2000; Beer et al., 2001; Kovtun et al., 2021). Fv/Fm is defined as the ratio of a number of quanta involved in charge separation to the total amount of quanta absorbed by light-collecting complexes. Accordingly, the closer this parameter is to 1, the higher the efficiency of the photosynthetic apparatus in a given plant. The minimum and maximum fluorescence yields were measured after 24 hours of dark adaptation. We did this to eliminate the reaction of the light stage of photosynthesis. Data was presented as the mean value ± standard deviation for every case (*n* = 15). Electron transport rate

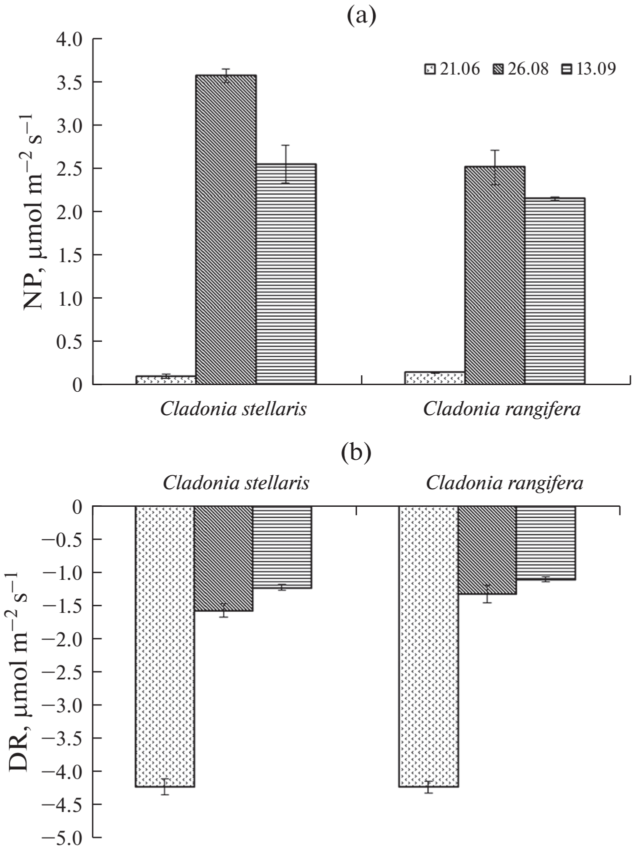


**Fig. 1.** Ecophysiological performance of *Cladonia stellaris* (left) and *Cladonia rangiferina* (right): (a) Net photosynthesis (NP) $\mu mol\ m^{-2}\ s^{-1}$; (b) Dark respiration (DR) $\mu mol\ m^{-2}\ s^{-1}$.

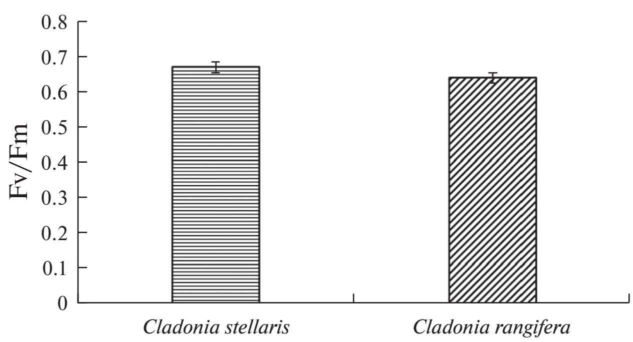


**Fig. 2.** Average summer values of Fv/Fm for lichens.

(ETR) characterizes the density of electron flow through an electron transport chain of thylakoid membranes (Maxwell, Johnson, 2000).

**Data analysis.** To analyze and process the collected data, we used the licensed software GFS-Win and WinControl. In addition, we used several software solutions for statistical processing and data analysis like Microsoft Excel and Statistica. The two-way analysis of variance (ANOVA) was conducted to reveal significant differences in photosynthesis rates by species and by summer month.

## RESULTS AND DISCUSSION

**Ecophysiological traits of lichens.** The ANOVA results show a well-pronounced seasonal trend in the NP values of lichens ($p = 0.031$), yet no interspecies variability was revealed ($p = 0.279$). Hence, the lowest NP values were observed in June ($0.11 \pm 0.03\ \mu mol\ m^{-2}\ s^{-1}$), and the highest ones were observed in August ($3.58 \pm 0.08\ \mu mol\ m^{-2}\ s^{-1}$) (Fig. 1a). In our previous studies, *Cladonia* spp. also showed significant seasonal variability of assimilation rate with the lowest values in June and the peaking ones in August (Polosukhina et al., 2020). The measurements of *Cladonia stellaris* in Norway conducted by Bjerke (Bjerke et al., 2013) showed that the net photosynthesis reached the maximum value of $6\ \mu mol\ m^{-2}\ s^{-1}$.

The seasonal dynamics ($p = 0.001$) of the dark respiration rate was observed as well (Fig. 1b). The highest values were recorded in June ($-4.23 \pm 0.12\ \mu mol\ m^{-2}\ s^{-1}$), and the lowest in September ($-1.11 \pm 0.04\ \mu mol\ m^{-2}\ s^{-1}$). There was no significant interspecies variability in values ($p = 0.235$). According to the previous studies, the maximum DR rate for lichens reached up to $-8\ \mu mol\ m^{-2}\ s^{-1}$ in a Canadian old black spruce (*Picea mariana* (Mill.) B.S.P.) boreal forest ecosystem (Whitehead, Gower, 2001; Moser et al., 1983).

We found a positive correlation between NP and DR values. The correlation rates (r) for *Cladonia stellaris* (CS) and *Cladonia rangiferina* (CR) were 0.92 and 0.98, respectively. This result can be explained by the fact that the lichen thallus is four to ten times poorer in chlorophyll than higher plants (Bianchi, 2021; Kolomeichuk et al., 2020). In addition, algal cells are not always evenly distributed in the thallus. The intensive photosynthesis ensures a regular vital activity in lichens, since they have to endure frequent periods of a significant ecological depression (drying out) and are distinguished by a high plasticity of their entire metabolic apparatus, which allows them to live through those periods and quickly return to life even at low temperatures, low levels of carbon dioxide, etc., when other plants die or cease to function (Goltsev et al., 2012).

We analyzed the impact of environmental factors (Tair, RH) on the assimilation rates with the results shown in Table 2 ($p > 0.05$).

**Fluorescence variability.** The ANOVA analysis showed that there are no significant differences between the two species ($p = 0.605$) and different months of measurements ($p = 0.951$) in the Fv/Fm ratio. On average, Fv/Fm was $0.67 \pm 0.01$ for *Cladonia stellaris*, and $0.64 \pm 0.08$ for *Cladonia rangiferina*. However, for the species of the same genus, *Cladonia mitis Sandst* and *Cladonia uncialis* (L.) Weber ex F.H. Wigg, growing in a pine forest of the Bory Tucholskie National

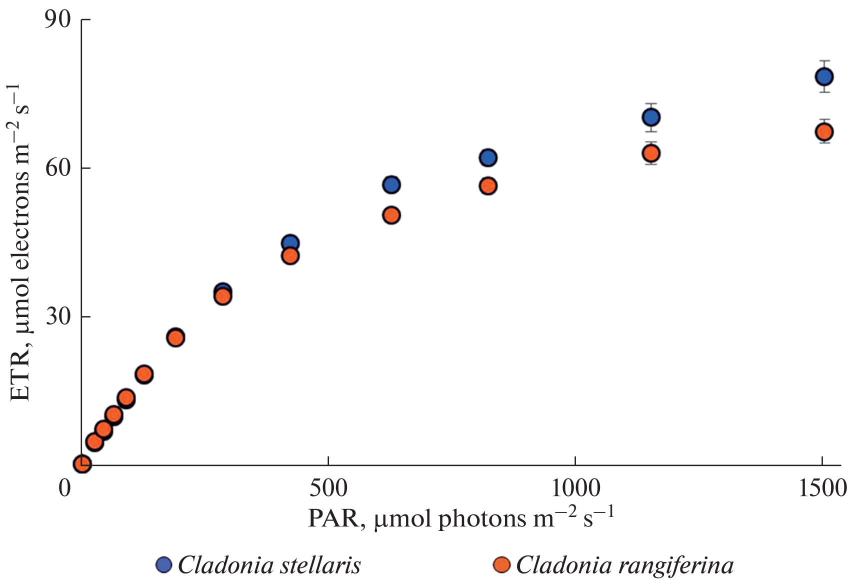


**Fig. 3.** Dependence of ETR on light intensity (Photosynthetically active radiation – PAR) in the species under study.

Park, the seasonal Fv/Fm dynamics showed the smallest values in June, and the largest ones in September (Węgrzyn et al., 2021). In general for lichens, the Fv/Fm ratio is usually ca. 0.60–0.72, while in higher plants it can reach ca. 0.91 (Bjerke, 2009). We tried to find a correlation between NP and Fv/Fm. For *Cladonia stellaris*, it turned out to be strongly negative ($r = -0.95$, $p = 0.92$), and for *Cladonia rangiferina,* it turned out to be strongly positive ($r = 0.89$, $p = 0.04$). In the Norwegian tundra, no correlation between NP and Fv/Fm was observed for deer lichens (Bjerke et al., 2017).

Some studies highlighted the importance of the time of day for Fv/Fm ratio estimations. So Fv/Fm is low from 9:00 to 12:00, and increases from 12:00 to 15:00 (Węgrzyn et al., 2021). To see how strong the light intensity may affect the photoassimilation system in lichens, we analyzed the ETR parameter (Fig. 3). At low light intensities (up to 285 μmol m$^{-2}$ s$^{-1}$), photochemical fixation is the same for different species. At medium and strong light intensities, the ETR parameter is larger for *Cladonia stellaris*. This indicates a higher intensity of photosynthesis in *Cladonia stellaris.* A strongly positive correlation between ETR and PAR was found with $r = 0.95$ ($p = 0.01$) for *Cladonia stellaris* and $r = 0.93$ ($p = 0.01$) for *Cladonia rangiferina*.

Another estimate of photosynthetic activity is dependence of the quantum yield of PSII on PAR (Fig. 4). This relationship shows the quantum yield of photochemical energy conversion in PSII (Y(II)), the quantum yield of non-regulated non-photochemical energy loss in PSII (Y(NO)), and the quantum yield of regulated non-photochemical energy loss in PSII (Y(NPQ)).

At a low intensity of photosynthetically active radiation (up to 200 μmol m$^{-2}$ s$^{-1}$) the Y(II) values in *Cladonia rangiferina* are higher, which indicates a more efficient distribution of absorbed light quanta towards photochemical reactions. The detected differ-

**Table 2.** Assimilation rate (NP, DR) correlation and meteorological factors

| Lichen | Factors | Date | | |
|---|---|---|---|---|
| | | 21.06.2021 | 26.08.2021 | 13.09.2021 |
| *Cladonia stellaris* | DR/Tair | –0.494 | –0.263 | 0.378 |
| | DR/RH | 0.414 | 0.288 | –0.450 |
| | NP/Tair | –0.711 | –0.096 | 0.378 |
| | NP/RH | 0.633 | 0.172 | –0.134 |
| *Cladonia rangiferina* | DR/Tair | –0.101 | 0.063 | –0.223 |
| | DR/RH | 0.196 | –0.103 | 0.198 |
| | NP/Tair | 0.156 | –0.555 | 0.084 |
| | NP/RH | –0.251 | 0.550 | –0.081 |

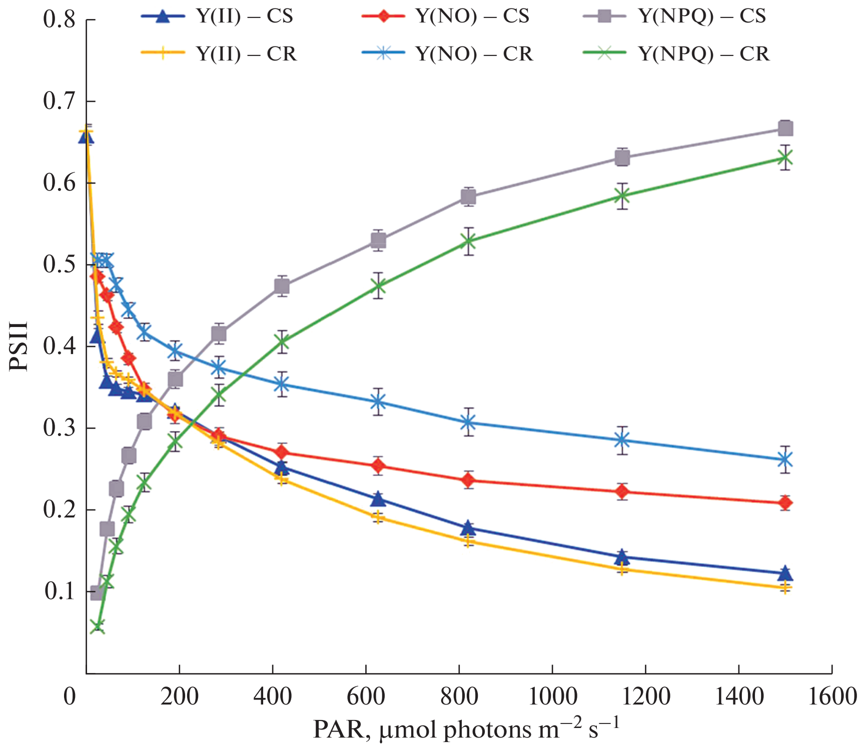


**Fig. 4.** Dependence of PSII quantum yield on PAR in lichen: quantum yield of photochemical energy conversion in PSII (Y(II)), quantum yield of non-regulated non-photochemical energy loss in PSII (Y(NO)) and quantum yield of regulated non-photochemical energy loss in PSII (Y(NPQ)).

ence is 3%. In the sector of the main intensity of PAR, the values of Y(II) are leveled with increasing illumination. *Cladonia stellaris* directs more light quanta to photochemical reactions – on average, their values are 7% higher than for *Cladonia rangiferina*. The Y(II) values show the difference between these two species of 16.4%.

Y(II) corresponds to the fraction of energy that is photochemically converted to PSII. The remainder 1 – Y(II) constitutes the total quantum yield of all loss processes, Y(loss), which is separated into two distinct components, Y(NO) and Y(NPQ), whose relative amounts provide valuable information on the photosynthesis features of a given plant. Y(NO) reflects the fraction of energy that is passively dissipated as heat and fluorescence, mainly due to closed PSII reaction centers. Y(NPQ) corresponds to the proportion of energy dissipated as heat by the adjustable NPQ photoprotective mechanism.

For two parameters of the non-photochemical distribution of light quanta, we divide the light intensity into 3 ranges (μmol $m^{-2}$ $s^{-1}$):

1 – low light intensity, 0 to 190,

2 – average light intensity (typical for given conditions), 285 to 625, and

3 – high light intensity, 820 to 1500.

The first range is characterized by a large uncontrolled dissipation of energy, which averages 50% of the entire energy distribution, gradually decreasing as the light intensity increases. The difference between *Cladonia stellaris* and *Cladonia rangiferina* is 14% with larger values observed in *Cladonia rangiferina*.

The dynamics is the same for all ranges, but the difference between the two species increases, showing 29.9% for the average light intensity and 27.7% for the high light intensity.

In this case, the controlled dissipation of excess energy has the reverse dynamics. The values at the low light intensity differ by 44.7% in favor of *Cladonia stellaris*, but this difference gradually decreases with 16.7% for the average light intensity and only 8% for the high light intensity.

As Y(II) values approach zero at high quantum flux densities, high Y(NPQ) values indicate high photoprotective mechanisms capacity, while high Y(NO) values reflect the plant's inability to protect itself from damage by excessive lighting. For a given set of environmental conditions, successful regulation usually targets the maximum Y(II) values, and the remaining Y(loss) targets the maximum Y(NPQ)/Y(NO) ratio. At the saturating light intensity, high Y(NO) values and low Y(NPQ) or Y(NPQ)/Y(NO) values reflect insufficient power of photo-protective mechanism reactions, which may eventually result in damage by excessive lighting. High Y(NO) values after dark adaptation signify this.

## CONCLUSION

This study has attempted to characterize the photosynthetic apparatus of lichens by quantifying net photosynthesis, dark respiration, and prompt fluorescence parameters. *Cladonia stellaris* and *Cladonia rangiferina* maintained a high photosynthetic activity throughout the summer of 2021. At the same time, the highest values of photosynthesis were observed in August, and the highest values of respiration were recorded in June. Both species – *Cladonia stellaris* and *Cladonia rangiferina* – showed fast kinetic activation. The parameters of prompt fluorescence correlate with the existing estimates. The completely different nature of the correlation between prompt fluorescence and assimilation intensity poses new challenges for us. Our future studies will focus on estimating the influence of different light wavelengths on photosynthetic activity in the subordinate forest layers.

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# ФОТОСИНТЕЗ ШИРОКО РАСПРОСТРАНЕННЫХ ВИДОВ ЛИШАЙНИКОВ В СОСНОВЫХ ЛЕСАХ ЦЕНТРАЛЬНОЙ СИБИРИ

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Лишайники и другие наземные фотосинтезирующие одноклеточные организмы планеты потребляют почти 14.3 млрд тонн атмосферного $CO_2$. В связи с изменением климата такие важные компоненты лесного напочвенного покрова, как лишайники, очень уязвимы. В данном исследовании оценивается фотосинтетическая активность широко распространенных лишайников путем измерения показателей чистого фотосинтеза, темнового дыхания и быстрой флуоресценции. Таким образом, криптогамы сосновых лесов Центральной Сибири в районе обсерватории Зотинская высокая башня (ZOTTO) характеризуются как высокоактивные. *Cladonia stellaris* (Opiz.) Brodo и *Cladonia rangiferina* (L.) являются основными представителями видов напочвенного покрова. Целью данного исследования было определение фотосинтетической активности у доминирующих видов напочвенных лишайников в течение вегетационного периода. Выявлена сезонная динамика фотосинтеза, причем самые низкие значения наблюдаются в июне, а самые высокие – в августе. Темновое дыхание достигает максимума в июне и является самым низким в сентябре. Значения флуоресценции находятся в диапазоне $6.7 \pm 0.3$. Исследуемые виды, произрастающие на подзолистых почвах в сосновых лесах, демонстрируют быструю кинетическую активацию.

*Ключевые слова: Cladonia stellaris, Cladonia rangiferina, фотосинтетическая активность, фотосинтез, баланс углерода, флюоресценция.*