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Respiratory Activity of Some Lichen Species–Representatives of Antarctic Flora

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Abstract—Data on the respiratory activity of 12 species of Antarctic lichens are presented. It is found that the respiration of foliose lichens is more intensive than the respiration of fruticose lichens. The O_2 uptake rate correlates positively with the nitrogen content in the biomass of thalli and depends on temperature. The thalli O_2 uptake rate increased 2.2–2.4 times with a temperature increase from 5 to 15°C. The reaction of respiration upon a further rise in temperature is species-specific. The decrease in the temperature coefficient of respiration (Q_{10}) with a temperature increase to 35°C is most pronounced in the endemic species *Usnea aurantiacoatra*, which is well-adapted to Antarctic conditions. The calculations show that, in summer, lichens are able to lose an amount of substrate equivalent to 0.8–1.4% of the thallus dry biomass in respiration daily. The total respiration cost of the lichen maintenance under snow during the winter can reach of 30–35% from their biomass. These results extend our knowledge on Antarctic lichens, and prediction their response to climatic change.

Keywords: lichens, Antarctica, respiration, nitrogen, temperature
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INTRODUCTION

Lichens are an ancient stable symbiotic association capable of surviving in extreme environmental conditions and restoring vital functions after influences that cause irreversible changes in the structure and cell metabolism of most other living organisms. Due to their resistance to extremely low temperatures and dehydration, as well as their ability to activate, absorbing vaporous water, lichens have successfully colonized ice-free areas of continental Antarctica and adjacent islands (Kappen, 2000), and are dominant in the flora of the continent (Peat et al., 2007). The history of systematic lichenological studies in Antarctica covers more than half a century. To date, the continental lichen flora has about 500 species of lichens (Øvstedal and Smith, 2001). Soviet and Russian lichenologists made a significant contribution to the study of the species diversity of the flora of Antarctic lichens (Andreev, 2014, 2018). Understanding of the Antarctic lichenobiot role and significance has been facilitated by progress in the development of environmental and physiological research observed in the last three decades (Kappen, 1985; Kappen, et al., 1991, 1996; Schroeter et al., 1992; Sancho and Pintado, 2004; Bartak et al., 2004; Green et al., 2012; Sadowsky and Ott, 2016).

Low temperatures are the main limiting factor for all organisms living in polar regions. Antarctica differs from the Arctic by a more severe climate. The summer is colder there, often with precipitation in the form of snow. At night, biota is often exposed to low negative temperatures. In the afternoon, average air temperatures are slightly above 0°C. With a short-term increase in air temperature to +5°C, lichen thalli can warm up to +35°C (Øvstedal and Smith, 2001). Quite strong solar radiation and wind and the abrasive action of mineral particles and ice crystals are essential for the life activity of lichens on the continent, and the proximity of birds and their colonies are essential in the coastal zone.

Lichens are phototrophic organisms. They carry out the photosynthetic assimilation of CO_2 due to a symbiosis with green algae and/or cyanoprokaryotes. Green algae supply the heterotrophic mycobiont with reduced carbon in the form of sugar alcohols (ribitol, sorbitol, and erythritol); cyanobacteria emit glucose (Elix and Stocker-Wörgötter, 2008). Mycobiont accounts for over 90% of the thallus biomass and makes a major contribution to the respiratory oxidation of assimilates and the carbon balance of a lichen as a whole (Palmqvist et al., 2008).

Compared with photosynthesis, the respiration of Antarctic lichens has not been studied enough. Studies of respiration can be identified as an independent problem, the relevance of which is caused by the need to expand the understanding of the fundamental pro-

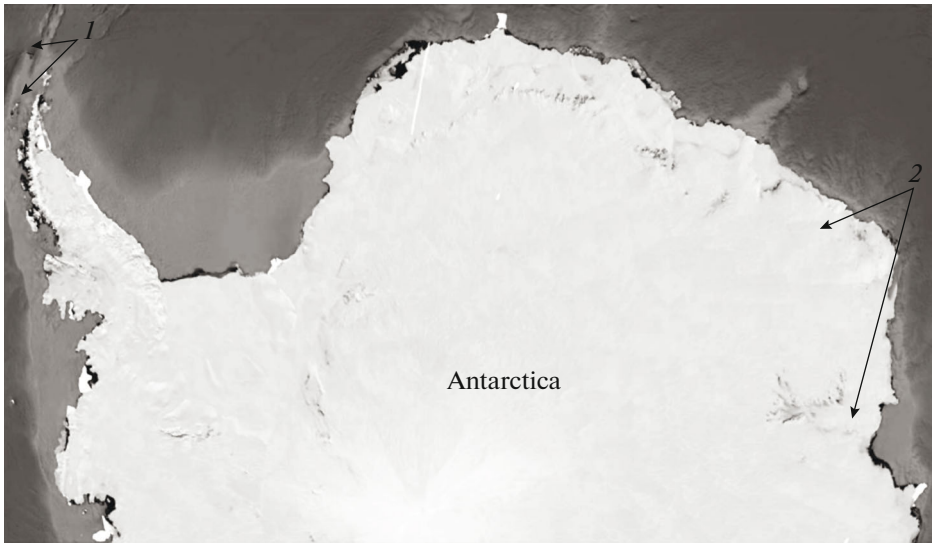

Fig. 1. Schematic representation of sites for collecting the samples of Antarctic lichen species (indicated by arrows). (*1*) Sampling sites on islands adjacent to the Antarctic Peninsula (61–62° S, 55–58° W), (*2*) sampling sites in eastern continental Antarctica (67–69° S, 45–73° W).

cess of living organisms life activity in the face of increasing climatic fluctuations and the threat of warming in the polar regions of the planet. The increase in the average annual temperature observed since the mid-1950s in Antarctica is 0.05°C per year (King and Turner, 1997).

The purpose of the work was to study the dependence of the respiratory activity of Antarctic lichen thalli on nitrogen content and temperature.

MATERIALS AND METHODS

Lichen samples were collected by M.P. Andreev (Komarov Botanical Institute, Russian Academy of Sciences (RAS)) in the summer period (January–April) in 2015 and 2016 in different regions of Antarctica: on the islands adjacent to the Antarctic Peninsula and in continental East Antarctica in the vicinity of the Molodezhnaya and Druzhnaya stations (Fig. 1, Table 1). The island territories belong to the cool Antarctic zone with a relatively warm maritime climate (Longton, 1988). The average annual temperature is –2.2°C; the summer period, with the average air temperature above 0°C, lasts about 4 months (Wen et al., 1998). Continental areas belong to a very cold Antarctic zone with an average annual temperature of –11°C. In summer, the average air temperature is –0.2°C (Andreev, 2013).

In total, 70 samples of 12 lichen species were selected, including 7 fruticose and 5 foliose species. In relation to the substrate, five species are epilithic, three species are epigeic, and four species are found on stones and soil. According to geographical distribution, five species (*Himantormia lugubris*, *Placopsis contortuplicata*, *Umbilicaria antarctica*, *Usnea antarctica*, and *Usnea aurantiaco-atra*) are endemic. Species of the genus *Usnea* are the most common and dominant in the sampling sites. Samples were delivered to the laboratory and stored in an air-dry state at a low positive temperature.

The nitrogen content was determined in dried ground samples on the elemental CHNS-O analyzer (EA-1110 Italy). The content of soluble protein was determined in a lyophilized material according to Bradford (1976).

Before determining the respiratory activity, the thalli were hydrated to full saturation with periodic drip irrigation and acclimated for a week in a Binder KWVF-720 climatic chamber (Germany) at a temperature of 15°C and a relative humidity of about 60%. Illumination was 60–80 μmol/(m^2 s), photoperiod (day/night) was 10/14 h.

The lichen respiration rate was determined polarographically by O_2 consumption using a Clarke electrode (Oxytherm system, Hansatech Inst., England) in a thermostatically controlled chamber at a temperature of 15°C and expressed in nmol O_2/g of dried mass min. Cuttings with an area of 2–3 mm^2 and a total mass of 15–20 mg were placed in a 3 mL reaction vessel containing 1.5 mL of HEPES buffer (Helicon, Russia) at a concentration of 50 mM, pH 7.2.

The temperature dependence of respiration was investigated in three lichens species (*Usnea sphacelata*, *Umbilicaria decussata*, and *Usnea aurantiaco-atra*). O_2 absorption was measured at 5, 15, 25, and 35°C.

Statistical processing was performed using Statistica 10.0 software (StatSoft, United States). Measurements of all parameters were carried out in 3- to 8-fold biological replication. The normal distribution was

Table 1. Characteristics of lichens studied

Species	Life form	Ecological group	Photobiont
Cladonia squamosa Hoffm.	Fruticose	Epigeic	Green alga
Himantormia lugubris (Hue) I. M. Lamb	Fruticose	Epilithic and epigeic	Green alga
Physcia caesia (Hoffm.) Fürnr.	Foliose	Epilithic and epigeic	Green alga
Placopsis contortuplicata I. M. Lamb	Foliose	Epilithic and epigeic	Green alga + cyanobacteria
Pseudephebe minuscula (Nyl. ex Arnold) Brodo & D. Hawksw.	Foliose	Epilithic and epigeic	Green alga
Sphaerophorus globosus (Huds.) Vain.	Fruticose	Epigeic	Green alga
Stereocaulon alpinum Laurer ex Funck	Fruticose	Epigeic	Green alga + cyanobacteria
Umbilicaria antarctica Frey & I. M. Lamb	Foliose	Epilithic	Green alga
Umbilicaria decussata (Vill.) Zahlbr.	Foliose	Epilithic	Green alga
Usnea antarctica Du Rietz	Fruticose	Epilithic	Green alga
Usnea aurantiaco-atra (Jacq.) Bory	Fruticose	Epilithic	Green alga
Usnea sphacelata R. Br.	Fruticose	Epilithic	Green alga

determined using the Shapiro–Wilks criterion. A comparison of means was performed using ANOVA (Duncan's test). When calculating the correlation, the Pearson coefficient was used. All statistical calculations were carried out at a given level of significance $P \le 0.05$. The figures and tables show means and their standard errors.

RESULTS

The amount of nitrogen and protein in the thalli characterizes the nitrogen status of lichens. Judging by the data, the species differed in the content of total nitrogen (Table 2). The greatest accumulation of nitrogen, 10 mg/g or more of dried weight, was observed in four species. Three of them (*Placopsis contortuplicata*, *Umbilicaria decussata*, and *Pseudophebe minuscula*) are foliose lichens. The smallest amount of nitrogen is found in the thalli of fruticose lichens *Sphaerophorus globosus* and *Usnea aurantiaco-atra*.

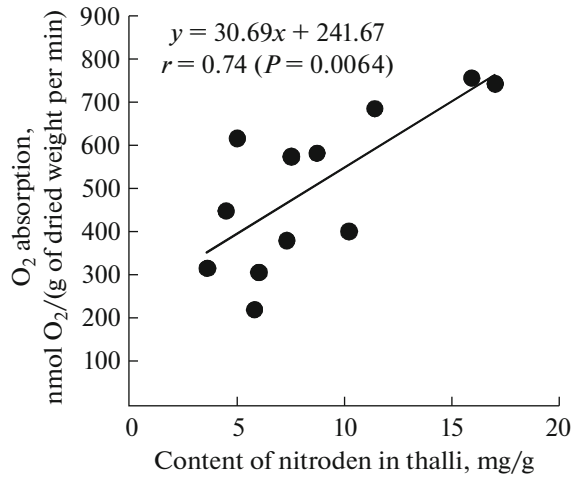

Fig. 2. O_2 absorption rate as a function of nitrogen content in thalli of Antarctic lichen species (r is the Pearson correlation coefficient at $P \le 0.05$).

The content of soluble protein ranged from 1.6 to 7.6 mg/g of dried weight and significantly correlated with the concentration of nitrogen. A high protein content was found in the fruticose *Cladonia squamosa* and *Himantormia lugubris* and in the foliose lichens thalli *Umbilicaria decussata* and *Placopsis contortuplicata*. The lowest concentration of soluble protein was found in the thalli of the fruticose lichens *Sphaerophorus globosus* and *Usnea aurantico-atra* and in the foliose lichen *Physcia caesia*.

In hydrated thalli preliminarily kept in a climatic chamber to fully restore their functional activity, the O_2 uptake rate at a temperature of 15°C varied from 220 to 750 nmol/(g of dried weight per min). *Pseudophebe minuscula* and *Placopsis contortuplicata* foliose lichens, whose thalli accumulated a significant amount of nitrogen, respired most intensely. The thalli of the fruticose lichens *Usnea antarctica*, *Himantormia lugubris*, and *Sphaerophorus globosus* were characterized by low respiratory activity. In general, foliose lichens respired 1.5 times more intensively and accumulated 2 times more nitrogen than fruticose lichens. The analysis showed that there was a statistically significant correlation between the nitrogen content in the thalli of the studied lichen species of Antarctica and their respiratory activity (Fig. 2).

It should be noted that the differences in respiration rates between the species were less pronounced when recalculating the intensity of O_2 consumption per unit of nitrogen. Respiration was noticeably higher in species with a low nitrogen status.

Table 2. Respiratory activity and content of nitrogen and soluble protein in lichen thalli

Species	Content of nitrogen, mg/g	Content of soluble protein, mg/g	O_2 absorption rate, nmol/(g of dried mass min)	O_2 absorption rate, nmol/(mg N min)
Cladonia squamosa	7.3 ± 0.8	7.0 ± 0.1^{c}	382 ± 15^{a}	0.42 ± 0.02^{a}
Himantormia lugubris	6.0 ± 1.2	5.6 ± 0.3^{d}	309 ± 49^{ad}	0.38 ± 0.06^{a}
Physcia caesia	5.0 ± 0.9	2.4 ± 0.4^{ab}	618 ± 39^{bc}	0.98 ± 0.07^{c}
Placopsis contortuplicata	15.9 ± 2.9	7.6 ± 0.04^{c}	759 ± 51^{c}	0.39 ± 0.04^{a}
Pseudophebe minuscula	17.0 ± 3.0	No data	745 ± 20^{c}	0.29 ± 0.01^{a}
Sphaerophorus globosus	3.6 ± 0.7	2.0 ± 0.2^{b}	319 ± 45^{ad}	0.76 ± 0.14^{bc}
Stereocaulon alpinum	10.2 ± 1.1	3.4 ± 0.4^{a}	404 ± 9^{a}	0.36 ± 0.01^{a}
Umbilicaria antarctica	8.7 ± 1.0	3.4 ± 0.003^{a}	584 ± 37^{be}	0.46 ± 0.03^{a}
Umbilicaria decussata	11.4 ± 2.0	6.6 ± 0.2^{c}	687 ± 66^{bc}	0.39 ± 0.04^{a}
Usnea antarctica	5.8 ± 1.2	4.0 ± 0.04^{ab}	223 ± 9^{d}	0.41 ± 0.02^{a}
Usnea aurantiaco-atra	4.5 ± 0.9	1.6 ± 0.3^{a}	451 ± 64^{ae}	0.89 ± 0.12^{c}
Usnea sphacelata	7.5 ± 1.4	3.0 ± 0.1^{ab}	577 ± 15^{be}	0.58 ± 0.02^{ab}

The means of nitrogen and soluble protein content and O_2 uptake rates of two independent series of measurements in 2015 and 2016 are presented. The O_2 uptake rate was measured at 15°C. For the soluble protein content and O_2 consumption, and in all other tables, ± Δ is the standard error of the means. For nitrogen, ± Δ is the limit of the absolute error interval at $P = 0.95$, according to the method of determination. Different superscript symbols indicate the statistical significance of interspecific differences in the studied indicator ($n = 5–10$ for each species) (ANOVA, Duncan's test, $P \le 0.05$).

For respiration, temperature is the most significant factor. We studied the O_2 uptake rate in the thalli of three typical for Antarctica lichen species at 5, 15, 25, and 35°C. As is seen in Fig. 3, the respiration activity of the *Usnea sphacelata* and *Umbilicaria decussata* thalli increased almost exponentially with increasing temperature. At 15°C, thalli respiration rate was 2.2–2.4 times more intensely than at 5°C (Table 3). With a further increase in temperature, the magnitude of the temperature coefficient of respiration Q_{10} in *Usnea sphacelata* decreased markedly. In *Umbilicaria decussata*, such a decline began in the range of 15–25°C. The most pronounced decrease in the value of Q_{10} in the temperature range of 15–35°C was noted in *Usnea aurantiaco-atra*. At a temperature of 35°C, respiratin rate of *Usnea aurantico-atra* was 1.6 times more intensely than at 15°C, whereas thalli of *Usnea sphacelata* and *Umbilicaria decussata* increased their respiration rate 2.3–2.5 times.

Thus, the results of our studies showed that foliose lichens exceeded the fruticose forms in the respiratory activity; the O_2 uptake rate correlated with the nitrogen content in thalli and depended on temperature.

DISCUSSION

The nitrogen content in the thalli of 12 lichen species varied from 3.6 to 17 mg/g of dried weight. The data we obtained are consistent with the scarce literature data on the nitrogen status of Antarctic lichens (Palmqvist et al., 2002; Lee et al., 2009). Earlier, when studying the elemental composition of a large group of representatives of the boreal lichen flora, we showed that nitrogen concentration is higher in associations of lichens and cyanoprokaryotes (Tabalenkova et al., 2016). Among the Antarctic lichens, three-component lichens *Stereocaulon alpinum* and *Placopsis contortuplicata* were characterized by a significant accumulation of nitrogen. However, two other species (*Umbilicaria decussata* and *Pseudophebe minuscula*) with a high content of nitrogen are chlorolichens. *Sphaerophorus globosus* and *Usnea aurantiaco-atra*, the species with the lowest nitrogen content, are also chlorolichens.

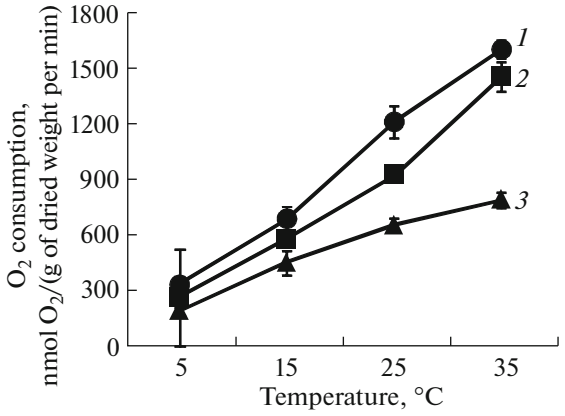

Fig. 3. Temperature dependence of the O_2 consumption rate by lichens: (*1*) *Umbilicaria decussata*, (*2*) *Usnea sphacelata*, and (*3*) *Usnea aurantiaco-atra*.

Table 3. Values of temperature coefficient Q_{10} of three Antarctic lichens species at different temperature ranges

Species	$Q_{10\ (5–15°C)}$	$Q_{10\ (15–25°C)}$	$Q_{10\ (25–35°C)}$
Umbilicaria decussata	2.2 ± 0.3	1.9 ± 0.4	1.4 ± 0.1
Usnea sphacelata	2.2 ± 0.2	1.6 ± 0.1	1.6 ± 0.1
Usnea aurantiaco-atra	2.4 ± 0.5	1.0 ± 0.1	1.2 ± 0.1

Since there were no cyanolichens (species containing only cyanobacteria) among the Antarctic lichens studied, it is difficult to estimate the significance of the photobiont type for the nitrogen status of the Antarctic lichens.

The relationship between the nitrogen content in thalli and the concentration of soluble protein was statistically significant ($r = 0.70$ at $P = 0.02$). The relatively low content of soluble proteins in the species of Antarctic lichens that we studied (less than 1% of the dried weight of thalli) can be explained by the fact that, before being removed, the thalli were in a state close to anabiosis for a long time (about 4 months). The fraction of soluble protein includes enzymes that play an important role in the overall metabolism, and their renewal is an energy-intensive process.

Respiration is the process of extracting the energy contained in the respiratory substrate with the formation of many metabolites necessary for growth and maintaining the functional activity and integrity of living organisms (Golovko, 1999). As the data analysis showed, there is a statistically significant correlation between respiration rate and nitrogen content in the thalli of the Antarctic lichens species (Fig. 2). Intensive respiration of foliose lichens can be associated with their more active (when compared with fruticose forms) metabolism and growth intensities. Studies on the linear growth of lichens suggest that the growth rate of foliose forms is higher when compared with fruticose ones (Hale, 1973). The growth rate of lichens depends on the availability of nitrogen and the ability to use it (Palmqvist et al., 2008). The relationship of respiration with the efficiency of nitrogen use by lichens is evidenced by the data on the rate of respiration calculated per nitrogen. For nine studied lichen species, there were no statistically significant differences in the O_2 uptake rate (nmol O_2/(mg N min), and only in three lichen species with a low nitrogen content the O_2 uptake rate was significantly higher (Table 2).

In addition to the presence of moisture in the environment, temperature has a significant effect on lichen respiration. The means of annual temperature of the surface layer of air in the habitats of the Antarctic lichens that we studied varies from −2 to −10°C. In summer, the air temperature means are about 2°C. However, during the day, thalli can warm up to temperatures above 20°C (Pannewitz et al., 2003; Sadowsky and Ott, 2016).

The results of studying the temperature dependence of the three lichens species respiration rate (Fig. 3, Table 3) showed that, in the range of 5–15°C, changes in the respiration rate obey the Van't Hoff rule, which says that in the thermally optimal zone the rate of metabolic processes increases 1.5–2.5 times with a temperature increase of 10°C. With a further increase in the temperature of the thalli, the magnitude of temperature coefficient Q_{10} decrease was the most pronounced in *Usnea aurantiaco-atra*. A significant decrease in Q_{10} indicates an exponential transition to a parabola and an approach to the point (zone) of the respiration temperature optimum (Semikhatova and Chirkova, 2001). It is believed that a decrease in Q_{10} at high temperatures indicates the inhibition of metabolism in general and/or individual growth-related processes. Limitations on respiration by the availability of the substrate necessary to maintain a high oxidation rate cannot be excluded. A stronger decrease in the Q_{10} coefficient under the effect of temperatures above 15°C on the thalli of *Usnea aurantiaco-atra* when compared with the two other lichen species may be explained by the fact that the species lives only within the Antarctic Belt. *Usnea sphacelata* and *Umbilicaria decussata* are bipolar species, and perhaps they are evolutionarily more adapted to the effects of elevated temperatures.

According to some authors (Colesie et al., 2018), Antarctic lichen species are not capable of thermal acclimation of respiration to reduce respiratory costs during prolonged exposure to warmer growth conditions.

Based on the results of respiration measurement, we can estimate the daily cost of the respiratory substrate of lichens in the summer period at an average temperature of about 5°C. According to the balance equation of respiration, the absorption of 1 mg of O_2 is equivalent to the oxidation of 0.375 mg of C or 0.9375 mg of glucose (Voznesensky et al., 1965). According to our calculations, lichens can use the amount of the substrate accounting for 0.8–1.4% of their biomass for the daily respiration (Table 4). At a temperature of 15°C, respiratory costs increase by an average of 2.2 times. If we consider that thalli can warm up to 20°C and more during the day, then the expenses of the substrate for lichen respiration will reach 3–5% of their biomass. Such values are comparable with respiratory costs in higher plants (Golovko, 1999). Obviously, an increase in the temperature of the environment caused by the warming of the climate in Antarctica can significantly affect the carbon and energy balance of lichens.

The extrapolation of the temperature dependence curves of lichens respiration to zero temperature indicates that the O_2 uptake rate in the thalli of *Usnea sphacelata* and *Umbilicaria decussata* is 2 times, and in

Table 4. Daily cost of the respiratory substrate in three species of Antarctic lichens at a temperature of 5°C

Species	nmol O_2/(g min)	mg O_2/(g day)	mg C/(g day)	mg glucose/(g day)
Umbilicaria decussata	332 ± 15	15.3 ± 0.7	5.7 ± 0.3	14.3 ± 0.6
Usnea aurantiaco-atra	189 ± 20	8.7 ± 0.9	3.3 ± 0.4	8.2 ± 0.9
Usnea sphacelata	262 ± 17	12.1 ± 0.8	4.5 ± 0.3	11.3 ± 0.7

the thalli of *Usnea aurantiaco-atra* is 3 times lower than the absorption rate at 5°C. During the winter period, lichens are in the active state for a long time under snow in the dark at near-zero and negative temperatures (Kappen, 1993, 2000). According to our calculations, despite the low respiratory activity, the loss of the respiratory substrate during the winter (June to August) of the Antarctic lichens can reach 30–35% of the thalli biomass.

Therefore, the results of the studies revealed species-specific differences in the nitrogen content and respiratory activity of the Antarctic lichen thalli. The presence of a high correlation relationship between respiration and the nitrogen status of the lichen association is shown. In general, foliose lichens accumulated more nitrogen in the biomass and respired more intensely than the fruticose lichens. The absorption rate of O_2 in the thalli depended on temperature. In the temperature range of 5–15°C, the value of the temperature coefficient Q_{10} was 2.2–2.4. Increasing the temperature of thalli to 35°C led to a decrease in Q_{10}, which was most significant in *Usnea aurantiaco-atra*. During the summer, thalli can use a substrate amount equivalent to 0.8–1.4% of their biomass for respiration. The obtained data are new, relevant for characterizing the functional activity of the lichenbiota of Antarctica, and may be useful for predicting changes in its state under conditions of significant fluctuations and climate warming.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest. The authors declare that they have no conflict of interest.

Statement of the welfare of animals. This article does not contain any studies involving animals or human participants performed by any of the authors.

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