

## The pigment complex and photosynthetic activity in the annual cycle of *Polytrichum commune* in the forest belt of the Khibiny Mountains on the Kola Peninsula of Russia

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### Abstract

This paper presents data on the content and ratio of pigments, photosynthesis rate, and assimilation number throughout the annual cycle of *Polytrichum commune* in the forest belt of the Khibiny Mountains. It is shown that the activity of the pigment complex in the photosynthetic organs of *P. commune* is preserved and maintained over 2 years. The highest content of plastid pigments in this year's shoots was recorded in fall, in the past year's shoots in the summer. In winter, the content of chlorophylls in the photosynthetic organs of this year's shoots decreased in 1.5 times relative to the summer maximum, and carotenoids - in 1.4 times. In the past year's shoots, no significant changes in the content of the pigments were noted. During the active vegetation period, the photosynthetic intensity in this year's shoots is in 1.5 times as high as that in the past year's shoots. At the end of the growing season in the past year's shoots the value of LHC (76%) due to their immersion deep into the moss clumps and shading them with this year's shoots. Chlorophyll's efficiency (assimilation number) in *P. commune* shoots of different ages in early spring (April) is in 2 times as high as that in fall (October).

**Key words:** moss, this year's and the past year's shoots, annual cycle, chlorophylls, carotenoids, apparent photosynthesis, assimilation number

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### Introduction

Plant productivity in the Far North remains a relevant area of research in connection with global climate change and the need to forecast future changes in the vegetation patterns at high latitudes (Longton 1992, Martin and Adamson 2001), where bryophyte play a leading role. Mosses are found everywhere up to the Arctic desert, and are dominants and co-dominants in

many plant communities. In the Khibiny Mountains, mosses are an important component of the forest vegetation and play a significant role in the accumulation of organic matter and in the biological nutrient cycles of the ecosystems (Pereverzev 2012). Because of their unique physiology and morphology, mosses have an effective system of regulating water regime and are

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thus highly tolerant to environmental factors, allowing them to colonize habitats where spermatophytes are unable to succeed. Photosynthetic organs of mosses, similarly to those of evergreen plants, maintain their pigment complex active over a long time, extending the period of photosynthetic activity during the short growing season in the Far North (Lukyanova et al. 1986, Yatsco et al. 2009).

Bryophytes generally have chlorophyll concentrations typical of shade-loving plants (Tieszen and Johnson 1968). The total chlorophyll content in bryophytes varies in a wide range depending on habitat – from 0.67 to 11.56 mg g<sup>-1</sup> of dry weight (Martin 1980, Masarovičová and Elias 1987, Doera and Chaudhary 1991). A study of 39 species of mosses and 16 species of liverworts showed that the average chlorophyll content in mosses is 1.64 mg g<sup>-1</sup> of dry weight and 3.76 mg g<sup>-1</sup> of dry weight in liverworts; the chlorophyll (*a/b*) ratio was 2.29 and 1.99, respectively; the ratio of chlorophylls and carotenoids was 4.74 in mosses and 6.75 in liverworts (Marschall and Proctor 2004). The chlorophyll (*a/b*) ratio falls due to an increase in the proportion of chlorophyll *b*, which is typical for plants adapted to growing in shade. Most bryophytes have developed physiological adaptations to low light intensities, have low chlorophyll (*a/b*) ratios, which may vary significantly (1.0–2.5) depending on the availability of light, season, and degree of adaptation (Mishler and Oliver 1991). Bryophytes are capable of adapting

to low intensity of light by increasing the number of chloroplasts, which was shown for *Funaria hygrometrica* (Glime 2007). The total pigment content in forest mosses (Kansas, US) increases from early spring (1.45 mg g<sup>-1</sup> of dry weight) to canopy closure (4.36 mg g<sup>-1</sup> of dry weight), which is indicative of the indicator's wide range (Martin and Churchill 1982). In forest mosses in Slovakia, a narrower range of 2.14–2.85 mg g<sup>-1</sup> of dry weight was observed in July (Masarovičová and Elias 1987). In habitats where light is blocked by the snow cover for more than 6 months, a decreased level of chlorophyll is characteristic. In the Antarctic, bryophytes reduce both the content and the chlorophyll (*a/b*) ratio of during winter (Melick and Seppelt 1994). In some of the most common moss species of the Khibiny Mountains forest belt, a chlorophyll content range of 0.87–4.35 mg g<sup>-1</sup> of dry weight was found (Lukyanova et al. 2011). However, few studies exist on the annual dynamics of the photosynthetic activity of mosses in the Far North. Pigment content and ratio have been traditionally used by many researchers to detect the response of plants to changes in their environment (Tuzhilkina 2009).

This paper examines the content of photosynthetic pigments and the photosynthetic activity of different ages shoots of *Polytrichum commune* in the annual cycle the Khibiny Mountains on Russia's Kola Peninsula.

## Material and Methods

### *Study site*

The study was carried out in the protected area of the Polar Alpine Botanical Garden-Institute (PABGI) in the forest belt of the Khibiny Mountains (67°34' N, 33°36' E). The physiological patterns (growing season and winter period) of plant shoots

of different ages were studied. Patterns during the winter period were studied in a model experiment. Due to the fact that the snow cover in the forest belt can be up to 2 m deep, which complicates sampling, mono-species moss turfs of *P. commune*

sized 50×50 cm were removed in fall and placed in close proximity to the study area (open, flat area above the lab's porch). In this connection, the snow cover depth in the actual forest belt in the PABGI and on

the experimental plot may differ (no more than 80 cm). On the experimental plot, the snow cover was completely lost 3 weeks earlier than in the forest belt (Fig. 1).

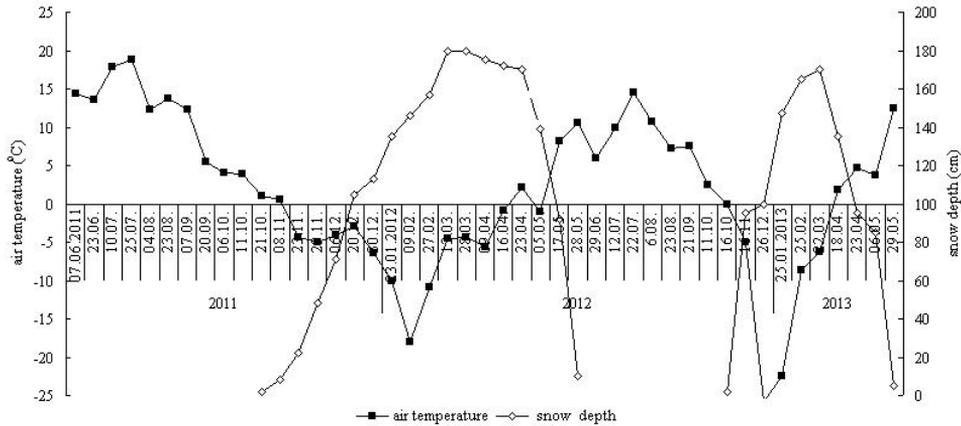


**Fig. 1.** The turfs of *P. commune* in model experiment (in late April).

#### *Weather data for the study period*

According to the available long-term observation data (from 2009 to 2018), the snow cover was lost between May 21 and June 12. The active growing season begins when the air temperature becomes above +10°C and, as a rule, lasts from early in the second decade of June to the second decade of September. First snow and night frosts often come at the end of September. On average, the vegetation season is 121 days long. Air temperature and snow depth

in the forest belt of the Khibiny Mountains during the study period are shown in Fig. 2. During the study period (2011-2013), the establishment of seasonal snow cover was observed in late October, maximum snow depth (170-180 cm) in March, and complete loss of snow cover by late May. Winter air temperatures below -15°C were infrequent. Maximum daily average air temperatures during the growing season did not exceed +19°C.



**Fig. 2.** Air temperature and snow cover height in the period June 2011 to June 2013 at the Khibiny forest belt (PABGI).

*Study subject*

*Polytrichum commune* Hedw. belongs to the Polytrichaceae family, is one of the largest acrocarpous moss species, and forms loose or thick dark green turfs. In the forest communities of the Khibiny Mountains, *P. commune* is a dominant or co-dominant species; in some habitats, it forms microgroups with a cover of 80–100%. Gametophyte annual shoots are clearly identified by the bend of the stem; in the climatic conditions prevalent in the Khibiny Mountains, shoots of the past two years are

photosynthetically active (green).

*P. commune*, being an endohydric species, is capable of retaining moisture in its tissues for a long time and is thus resistant to moisture loss. Average water content in *P. commune* tissues is 60–63%. During prolonged periods with no precipitation, the water content in *P. commune* tissues never falls below 40% (Ermolaeva and Shmakova 2017). In this study, shoots were classified into this year’s and the past year’s shoots.

*Study methods*

The water content in fresh moss was measured by drying to an absolutely dry weight at 105°C. The content of photosynthetic pigments (chlorophylls – Chl *a* and Chl *b* and carotenoids – Car) was measured in ethanol extracts spectrophotometrically (Lichtenthaler and Wellburn 1983) with an UV-1800 (Shimadzu, Japan) at corresponding absorption maxima (Chl *a* – at 665 nm, Chl *b* – at 649 nm, and Car – at 470 nm). The proportion of chlorophylls in the light-harvesting complex (LHC, %) of

their total was calculated by assuming that all Chl *b* is held in the LHC and that the Chl (*a/b*) ratio in the LHC is 1.2 (Lichtenthaler 1987). Net (apparent) photosynthesis was measured using open-flow infrared gas analysis system (GAMMA-100, Russia). To quantify the relationship between the content of chlorophylls and the rate of photosynthesis, the assimilation number ( $A_n$ ) in mg of CO<sub>2</sub> per hour per 1 mg of chlorophyll was calculated (Andrianova and Tarchevsky 2000). The annual cycle of

photosynthetic pigments was studied from 2011 to 2013; CO<sub>2</sub> gas exchange was measured from 2009 to 2018 during the growing seasons (from June to October). In April-May, data were collected in a model experiment. During this period, mosses were extracted from under the snow for analysis. Productivity parameters (length and mass of the annual shoots) were measured during the growing season from 2009 to 2018 every 7-10 days (at least 50 replicate measurements). Physiological varia-

bles (water content, plastid pigments content and gas exchange rate) were measured on the day of sampling; the number of replications of the experiments was twice the biological frequency.

Air temperature measurements (1 meter above the moss turfs) were taken daily using iBDLR-3-UX loggers at the established weather observation times. Statistical processing of the data was done in Statistica 10.

## Results and Discussion

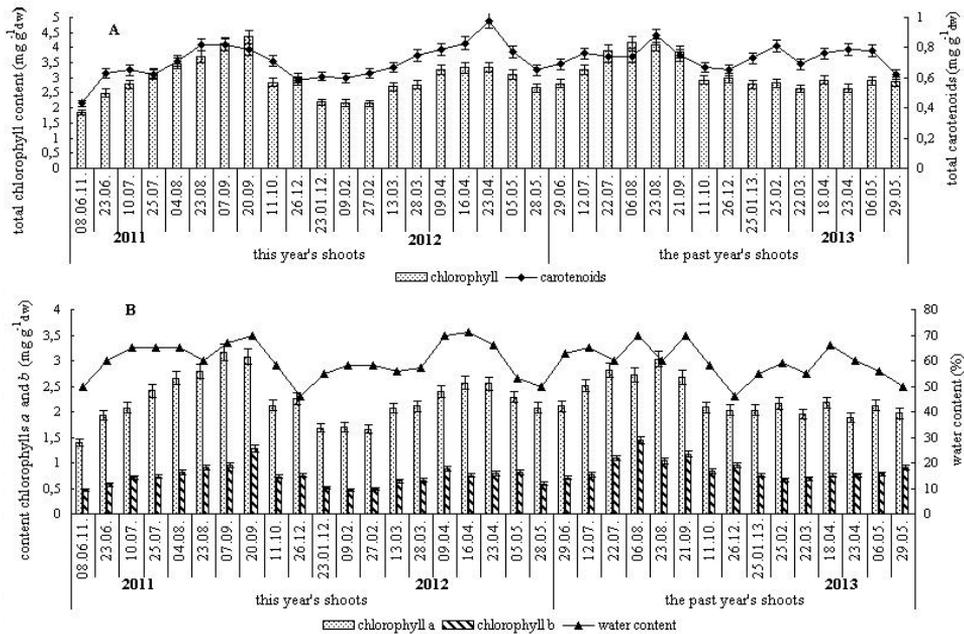
### *The content of photosynthetic pigments in shoots of different ages*

In the forest belt, in *P. commune* individuals emerging from under the snow, new shoots (1-2 mm) are immediately noticeable. This suggests that the growth starts under the snow, when its depth is not more than 20 cm. Light can penetrate through a snow layer that thick, and favorable greenhouse-like temperature conditions can develop (Tikhomirov 1952, Zyuzin 2006). Three weeks after the complete melting of the snow cover, shoots were about 6 mm long, which was 15% of the maximum annual shoots length at the end of the growing season (on average, 39 mm). In late June, when snowmelt runoff terminates, dry periods combined with

low temperatures often occur, which inhibits the growth of mosses. Maximum daily average growth rate in *P. commune* becomes possible when an effective temperature sum (above +5°C) of approximately 389°C has been accumulated, what was noted by a number of studies for other moss species (Bates 1989, Callaghan and Carlsson 1997). In the Khibiny Mountains, this can be observed already in the first decade of July. In late August, the shoots length is 90%, its mass 85% of the annual values. The growth processes terminate at the end of September, while photosynthetic activity may continue in the presence of favorable conditions.

***This year's shoots (Fig. 3. The period from 08.06.2011 to 28.05.2012):*** At the end of the first decade of June, the total content of plastid pigments in the photosynthetic organs of this year's shoots was the lowest and amounted to 1.8 mg g<sup>-1</sup> of dry weight for chlorophylls and 0.4 mg g<sup>-1</sup> of dry weight for carotenoids (Fig. 3 A). In the first decade of July, when the highest growth rate in *P. commune* was observed, the content of green and yellow pigments increased in 1.5 times relative in June. In

late August, the chlorophyll content nearly doubles, compared to the beginning of the growing season. The Chl (*a/b*) ratio in this year's shoots varies between 2.9 and 3.3, the proportion of chlorophyll in the LHC is 50-63%, the water content in the fresh moss is 60-70% (Fig. 3 B). The increase of chlorophylls amount is due largely to chlorophyll *a*. The content of carotenoids in this period reaches the maximum of 0.8 mg g<sup>-1</sup> of dry weight.



**Fig. 3.** The photosynthetic pigments content in *P. commune* shoots of different ages in the annual cycle: A – the total content chlorophyll and carotenoids; B – the content of chlorophylls *a* and *b* and water content. *Note:* dw – dry weigh.

At the end of September, when the formation of the annual shoots is completed (Ermolaeva et al. 2013, Ermolaeva and Shmakova 2017), the content of green pigments reaches its maximum during the growing season (4.4 mg g<sup>-1</sup> of dry weight). The Chl/Car ratio during the growing season (June-October) is within the range of 4.0 to 5.5. In this year's shoots in the end of growing season the concentration of chlorophylls and carotenoids increased to 2.4 and 1.9 times as high as beginning season, respectively.

In December, the content of chlorophylls in the photosynthetic organs of this year's shoots decreased in 1.5 times relative to the summer maximum, and carotenoids - in 1.4 times. The water content in the fresh moss is 46%. In January–February, the content of chlorophylls was 2.2 mg g<sup>-1</sup> of dry weight and remains stable until early March. The Chl/Car ratio during this period was an average of 3.5.

The decrease in the Chl/Car ratio compared to that in the growing season is due to a greater degree of reduction in the content of chlorophylls than carotenoids.

In early March, the relatively stable pigment complex of this year's *P. commune* shoots starts to change. According to the long-term data, in March-April in the Khibiny forest belt, the maximum depth of the snow cover can reach 180-200 cm, while in our model experiment, it did not exceed 120-130 cm. Earlier, we found that with changes in air temperature between 0 and -27°C (January-April), the temperature of the photosynthetic part of the moss turfs under the snow varies between 0 and -7.5°C (Shpak and Shmakova 2009). Bryophyte leaves are more resistant to freezing temperatures than those of flowering plants. Snow gives significant protection against freezing in winter; when it begins to melt, voids becomes filled with snow crystals and light penetration increases. This can be

a signal for bryophytes to start photosynthesis, growth, and development even before the snow melts (Marchand 1993). Only a small amount of light, especially in the blue and blue-green spectrum, can penetrate through the dense snow layer. In the same period in the Khibiny Mountains, the solar radiation influx increases from 3.7 in March to 8.1 kcal cm<sup>-2</sup> in April (Zyuzin 2006). In mid-April, the snow depth above the studied *P. commune* turfs (in the model experiment) did not exceed 30 cm. In March-April, the content of total chlorophylls and carotenoids in this year's shoots in 1.5-1.7 times as high as that the minimum value in winter. The Chl/Car ratio varies at this time from 3.4 to 4.1. Water content is 70%. The increase in the content of carotenoids and the shadow pigment Chl *b* in March-April can be considered as a defense reaction to increase the stability of the photosynthetic organs, which contributes to additional light capture and the delivery of additional energy to the reaction centers of Chl *a* (Czeczuga 1987, Popova et al. 1989, Slemnev et al. 2012). The defense protecting the photosynthetic organs from photo-destruction at low tem-

peratures and under excessive insolation in the early spring is the accumulation of various components of the violaxanthin cycle: for example, zeaxanthin in evergreen woody plants; neoxanthin in some evergreens of the grass-shrub layer (Yatsco et al. 2009). As observed by Tikhomirov (1952) on the Taimyr Peninsula, at the end of the winter period, due to the winter activity of mosses, a layer of granular powdery snow forms between the mosses and the denser snow cover. He believes that mosses might be photosynthetically active as soon as the polar night ends. Under the thermal action of light penetrating through the snow, «snow greenhouses» are formed.

In period, when the snow cover has completely melted away, the water content in fresh moss was 50-53%. Such low content is a protective mechanism against freezing damage by low temperatures and night frosts characteristic of the Khibiny Mountains in May. During the same period, we noted a decrease in the content of chlorophylls (Fig. 3A: 23.04-28.05.2012). Some researchers (Tuzhilkina and Veretennikov 1981) attribute this decrease to the beginning of growth processes.

**The past year's shoots (Fig. 3. The period from 29.06.2012 to 29.05.2013):** Starting in June (Fig. 3A), when new shoots start to form, this year's shoots are classified as the past year's shoots. In the past year's shoots, the content of chlorophyll in June (2.8 mg g<sup>-1</sup> of dry weight) is at the same level as after the winter in late May. Maximum concentration of chlorophyll in the past year's shoots (4.2 mg g<sup>-1</sup> of dry weight) was recorded in August. The Chl (*a/b*) ratio change from 3.2 in July to 1.9-2.9 in August-September; the chlorophyll content in LHC change from 52 to 76%, respectively. The change in the chlorophyll content in the past year's shoots is mainly due to the concentration of Chl *b*. This increase is the result of the immersion of the past year's shoots deep into the moss turfs and

shading them with this year's shoots. The Chl/Car ratio varies in the range of 4.1 to 5.6. The maximum carotenoids content was observed in August (0.9 mg g<sup>-1</sup> of dry weight). With the onset of cold weather in fall, the leaves start browning and the total content of green and yellow pigments decreases in 1.4 times relative to the summer maximum. Further, with the onset of the winter period, no major changes were observed in the pigment content in the past year's shoots.

Thus, the highest content of plastid pigments in this year's shoots was in fall and coincided with the end of the annual shoot growth. In the past year's shoots maxima content of plastid pigments was in summer. In winter the amount of pigments in both years' shoots was decreased com-

pared with summer. In the past year's shoots under the snow cover, no significant changes in the content of chlorophylls were noted. It is shown that the activity of the pigment complex in the photosynthetic organs of *P. commune* is preserved and maintained over the 2-year life cycle. The

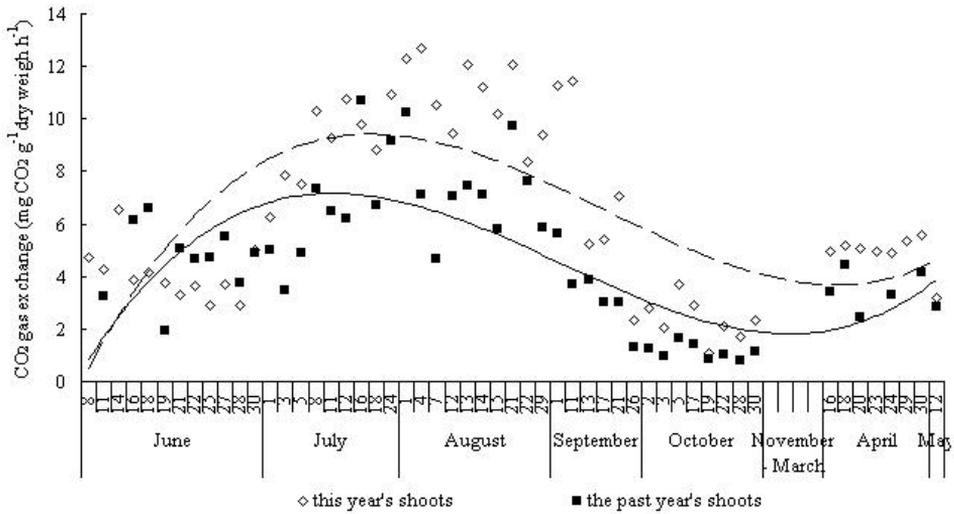
pigment complex in *P. commune* is characterized by a low content of chlorophylls and carotenoids, which is nevertheless comparable to that in evergreen and wintergreen vascular plants (Lukyanova et al. 1986, Yatsco et al. 2009, Sofronova et al. 2007).

### *CO<sub>2</sub> gas exchange rate in shoots of different ages*

The main growth form in mosses is a gametophyte without pronounced developmental phases; therefore, seasonal gas exchange differs from that of vascular plants in that there are no clear dynamics. Seasonal changes are mainly associated with fluctuations of environmental factors. In the June, when the low air temperatures and no shading, the primary role in the assimilation of carbon dioxide in *P. commune* belongs to the past year's shoots, whose photosynthetic rates are within the range of 2 to 6 mg CO<sub>2</sub> g dry weight<sup>-1</sup> h<sup>-1</sup> (Fig. 4). In the first decade of July, when the maximum growth rate was observed, photosynthetic rates in this year's shoots was higher than in the past year's shoots. During the period of active vegetation (July-August), the primary factor limiting the photosynthetic activity in *P. commune* is water content, rather than air temperature. As the annual shoots forms, the photosynthetic rate gradually increases, reaching the highest values (12 mg CO<sub>2</sub> g dry weight<sup>-1</sup> h<sup>-1</sup>) in August. In this period, the photosynthetic rate in this year's shoots is in 1.6 times as high as that in the past year's shoots. At the end of August, browning of the foliage can be observed in the past year's shoots. Starting in the third decade of September, when the annual shoots has fully formed (length and mass no longer change), average daily air temperatures are consistently below +10°C, water regime no longer plays a decisive role, and the net photosynthesis range becomes narrow-

er than in summer. In the second half of October, when, as a rule, the average daily air temperatures is near 0°C, the photosynthetic rate in this and the past year's shoots does not exceed 1-2 mg CO<sub>2</sub> g dry weight<sup>-1</sup> h<sup>-1</sup>.

Growth processes in mosses can start as early as under the snow. The potential level of photosynthesis in *P. commune* shoots extracted from under the snow was investigated in a model experiment. According to our data, the earliest start of photosynthetic activity in this species was observed at the end of March, when the snow depth was 15 cm and 200 lux of light was transmitted through the snow. The temperature in the chamber was -3.3°C, while the ambient temperature ranged from -4.2 to -1.6°C. In mid-April, the air temperature is within the range of 0 to +6°C and *P. commune* was photosynthetic activity. The photosynthesis rate in the second half of April can be up to 5 mg CO<sub>2</sub> g dry weight<sup>-1</sup> h<sup>-1</sup> in this year's shoots and up to 4.4 mg CO<sub>2</sub> g dry weight<sup>-1</sup> h<sup>-1</sup> in the past year's shoots (Fig. 4: 16.04.-12.05.). The water content in fresh moss was in the optimal range (60-68%). During this period, as a rule, the average daily temperature was above 0°C. Photosynthetic efficiency in April can be the same as in July, but at a lower air temperature. We found that photosynthetic activity in this year's shoots (overwintered) in April-May is higher than of the past year's shoots.



**Fig. 4.** Seasonal dynamics of CO<sub>2</sub> gas exchange in *P. commune* shoots of different ages: this year's shoots – open symbols (dotted line); the past year's shoots – closed symbols (solid line).

Despite the ambiguity of the relationship between the content of chlorophyll in the photosynthetic organs and the rate of CO<sub>2</sub> uptake, we found it possible to use the value of the assimilation number ( $A_n$ ) as a variable characterizing the photosynthetic rate in different ages shoots of *P. commune*. Using data on the content of chlorophyll and the net gas exchange rate, we estimated the  $A_n$  of the shoots in different periods of the annual cycle (Table 1). Mosses, being poikilohydric plants, depend on the availability of water and do not have phenological development phases; therefore,  $A_n$  can be examined depending on the climatic conditions of the seasons of the year in nature. Multiple methods exist for identifying seasonal climatic patterns. For example, in areas with a persistent snow cover, the annual cycle can be conventionally divided into growing season and cold winter season (Kuryina et al. 2013). According to the method proposed in that paper, the beginning of the annual cycle is the date when the average daily air temperature has below 0°C and the snow cover has appeared, while the end of the

cold season is the date when the snow has melted away. Annual vegetation season is the period from the date when the snow has melted away to the date when the average air temperature was above +5°C (effective temperature), the active vegetation season starts when the average daily temperature was above +10°C, and fall starts when the average daily air temperature has dropped below +10°C.

In the Khibiny Mountains, the annual cycle begins at the end of October, when the snow cover is usually established and the daily temperature has below 0°C. During this period, the  $A_n$  in this year's shoots is in 1.4 times as high as that in the past year's shoots. This is followed by a 5-month long winter period with polar night and deep snow and, accordingly, no photosynthetic activity. April is one of the last months of the cold part of the annual cycle in the Khibiny Mountains; in late April, the climatic conditions initiate snowmelt and mosses resume their photosynthetic activity. This is evidenced by the value of  $A_n$ , which in April is in 1.8-2 times as high as that in October, despite the similar tem-

Annual cycle period	Shoots	Assimilation number, (A <sub>n</sub> ) mg CO <sub>2</sub> mg chlorophyll <sup>-1</sup> h <sup>-1</sup>
October (daily average air temperature below 0°C)	1	1.0
	2	0.7
April (snowmelt, daily average air temperature around or above 0°C)	1	1.8
	2	1.4
May (release from snow cover, daily average air temperature above +5°C)	1	0.8
	2	0.9
June (daily average air temperature above +10°C)	1	1.6
	2	2.5
July (active vegetation)	1	3.1
	2	2.0
August (active vegetation)	1	3.5
	2	2.1
September (growth stops, daily average air temperature below +10°C)	1	1.2
	2	1.0

**Table 1.** Chlorophyll efficiency in *Polytrichum commune* shoots of different ages. Note: 1 – this year's shoots; 2 – the past year's shoots.

perature conditions. In May, when the snow cover has melted away, air temperatures rise, but the accumulated meltwater quickly evaporates and mosses become limited by water in their photosynthetic activity, which is significantly reduced. The A<sub>n</sub> is almost the same in shoots of different ages and is comparable in magnitude with the fall values. By the third decade of June, new shoots have formed, but their photosynthetic organs are still not as efficient as those of the past year's shoots, which in the fall and spring were still considered this year's shoots. In this connection, the photosynthetic efficiency of the past year's shoots in June is in 1.6 times as high as that in this year's shoots. July and August are active vegetation periods under the studied conditions, when mosses are char-

acterized by high growth rates subject to a favorable combination of temperature and water availability. At this time, the past year's shoots begin to reduce their photosynthetic efficiency and become shaded by this year's shoots, whose photosynthetic activity was in 1.6-1.7 times as high as that of the past year's shoots. It was in this period that the highest values of photosynthetic rate and A<sub>n</sub> were recorded. In September, moss growth terminates and the final stage of the annual vegetation season begins. In fall, the assimilation number decreases in 2.9 (this year's shoots) and in 2.1 (the past year's shoots) times as low as to the maximum. By the beginning of a new annual cycle, the past year's shoots lose photosynthetic activity faster.

## Conclusion

The photosynthetic apparatus of *Polytrichum commune* preserves the pigment complex for two years, which can be considered as one of the ways adaptations to growing in a cold climate. The high stability of the photosynthetic apparatus is indicated by the ability of the species to quickly restore and maintain photosynthetic activity after frost and release from snow cover. The ability to preserve the photosynthetic apparatus in winter compensates for the low growth rate. Comparability of main parameters of the photosynthetic apparatus of *P. commune* with that of some deciduous and evergreen under-shrub species testifies to the great contribution of this plant group to the productivity of northern ecosystems (Shmakova et al. 1996). As in evergreen vascular plants, a

decrease in the content of chlorophyll and an increase in the content of carotenoids were observed in mosses in the autumn-winter period, which contributes to a greater resilience of the photosynthetic apparatus and protects chlorophylls from destruction.

This endohydric species is characterized by a highly flexible pigment complex, allowing to occupy habitats with a broad range of light conditions. The highest photosynthetic activity was observed in July-August, and in this year's shoots it was in 1.5 times as high as that in the past year's ones. An early start of photosynthetic activity was observed in this moss as early as at the end of the cold part of the annual cycle (in April).

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