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STRUCTURE AND FUNCTIONAL PROPERTIES OF THE ORTHOTROPIC AND THE PLAGIOTROPIC SHOOTS OF *CLIMACIUM DENDROIDES* AND *POLYTRICHUM COMMUNE* (BRYOPHYTA)

СТРУКТУРА И ФУНКЦИОНАЛЬНЫЕ СВОЙСТВА ОРТОТРОПНЫХ И ПЛАГИОТРОПНЫХ ПОБЕГОВ *CLIMACIUM DENDROIDES* И *POLYTRICHUM COMMUNE* (BRYOPHYTA)

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Abstract

The structure, functional properties and productivity of two moss species, *Polytrichum commune* and *Climacium dendroides*, forming the plagiotropic rhizomatous shoots were studied in the middle taiga subzone. Mosses accumulated 30-100 g DW / m^2; plagiotropic shoots constituted 40-50% of the total biomass. The differences between the orthotropic (assimilating) and the plagiotropic (heterotrophic) shoots of *C. dendroides* are stronger than those in *P. commune*. Plagiotropic rhizomatous shoots of *C. dendroides* differ from its orthotropic assimilating shoots in more cell layers in stem epidermis, thicker inner cortex, low respiration rates (0.1-0.2 mg CO_2 / g DW h), accumulation of oligosaccharides (50% of the total carbohydrates). The differences in these parameters in *Polytrichum* are not observed or minimal. Relationships of the respiration rate and the water balance of the studied species with their shoot morphology were shown. *P. commune* is characterized by higher rates of net photosynthesis, higher ratio of net photosynthesis to water evaporation, higher accumulation of dry mass and assimilating surface area as compared to *C. dendroides*

Резюме

Изучена структура, функциональные свойства и продуктивность двух видов мхов *Polytrichum commune* и *Climacium dendroides*, формирующих плагиотропные побеги и произрастающих в условиях средней тайги. Мхи накапливали 30-100 г сухой массы на м^2, 40-50% которой составляли плагиотропные побеги. Значительные различия между ортотропными (ассимилирующими) и плагиотропными (гетеротрофными) побегами показаны для *C. dendroides*. Плагиотропные корневищеподобные побеги *C. dendroides* характеризуются значительным развитием эпидермиса, утолщением внутренней коры, низкой скоростью дыхания (0.1-0.2 мг CO_2 / г сухой массы ч), накоплением олигосахаридов (50% от суммы углеводов), в отличие от ортотропных ассимилирующих побегов. Показана связь метаболической активности и водного обмена с формой роста бриофитов. *P. commune*, характеризующийся ковровой формой роста, имел более высокую фотосинтетическую способность, эффективность использования воды, продуктивность и площадь ассимилирующей поверхности по сравнению с *C. dendroides* с древовидной формой роста. У растений *P. commune* выявлена более высокая скорость испарения воды и отношение видимого фотосинтеза к испарению воды.

KEYWORDS: *Polytrichum commune*, *Climacium dendroides*, orthotropic and plagiotropic shoots, productivity, nonstructural carbohydrates, respiration rate, photosynthesis, water use efficiency

INTRODUCTION

Mosses in the northern ecosystems are dominants and codominants of many plant communities, they play an important role in the energy and carbon balance, distribution of mineral elements and regulation of the water balance (Proctor, 2000, 2009; Goncharova & Ben'kov, 2005; Shpak, 2008; Masyagina *et al.*, 2010; Turetsky *et al.*, 2012). Mosses often are edificators, especially in wetlands and mountain tundra and in forests where they often form a continuous cover. The portion of bryophytes in the total ground phytomass of bogs can reach 80%.

Bryophytes are characterized by perennial gametophytes with specific branching, development of the mechanical and conducting tissues, and leaf morphology (Potemkin, 2007). Despite of their small sizes, the morphology of mosses is quite diverse and complex. Shoots of mosses may be classified into orthotropic (vertical) and plagiotropic (horizontal) by growth, and

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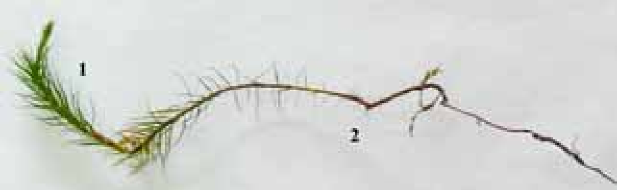


Fig. 1 (above). System shoots of *Polytrichum commune*. 1 – Orthotropic shoots, 2 – plagiotropic shoots.

Fig. 2 (right). System shoots of *Climacium dendroides*. 1 – Orthotropic shoots, 2 – plagiotropic shoots, 3 – branching shoots, 4 – shoot of tillering.

into monopodial and sympodial by origin (Ignatov & Ignatova, 2003).

Polytrichum commune Hedw. and *Climacium dendroides* (Hedw.) F. Weber & D. Mohr, which are in the focus of this paper, both form plagiotropic rhizomatous shoots growing within litter. However the origin of these shoots is different. In *Polytrichum commune,* the rhizomatous shoots originate from orthotropic shoots (Abramov & Volkova, 1998), which turn to horizontal position with age, loosing leaves and developing more or less dense rhizoid tomentum (Fig. 1). In *Climacium* they appear as a result of sympodial branching, arising at base of orthotropic dendroid shoot. In most cases, such innovation at first grows plagiotropically; developing only strongly reduced scaly leaves, while later it turns to orthotropic growth, developing dendroidly branched plants. The branching in this species is fairly variable and complex (Notov & Spirina, 2002), with occasional developing additional dendroid shoots from rhizomatous parts or otherwise immediately from orthotropic parts of plants, *etc*. (Fig. 2). Therefore the comparison of differences between orthotropic and plagiotropic shoots of these two species is interesting and it was the aim of the present study that involves both structural and functional characters of the orthotropic (assimilating) and the plagiotropic (heterotrophic) shoots of *Polytrichum commune* and *Climacium dendroides*.

Data on structure and functional features of plagiotropic rhizomatous shoots of bryophytes are limited (Collins & Oechel, 1974; Sveinbjörnsson & Oechel, 1981). They obviously have distinct metabolic activity related to their storage function and underground growth, and possibly the shoot structure is also different as compared to orthotropic assimilating shoots.

The existing studies on bryophytes are devoted generally to biology and systematics, partially to anatomy and morphology. Information on physiology is quite limited and restricted to only a few species (Schofield, 1985; Longton, 1988; Tenhunen *et al.*, 1992; Proctor, 2000, 2009; Shpak, 2008; Goffinet *et al.*, 2009; Bansal *et al.,* 2012), which precludes understanding of various aspects of bryophyte biology. Bryophytes are known for a low photosynthetic activity, slow growth rate and low productivity. Functional parameters of bryophytes are usually estimated per weight unit of shoots or per occupied surface area (Bansal *et al.,* 2012).

This is because of their small sizes and complicated identification of assimilating surface area. Parameters of CO$_2$ exchange and assimilating surface structure are important for assessing bryophytes productivity in different ecological conditions. Dependence of functional properties on growth form and life strategy of bryophytes is an important study topic. Its results can be used for forecasting bryophytes response to the changing environmental conditions.

MATERIALS AND METHODS

Experiments were performed in June-July 2011-2013 in the middle taiga subzone near Syktyvkar (60°40´N, 50°49´E) in a bilberry-moss spruce forest. *Polytrichum commune* and *Climacium dendroides* with plagiotropic rhizomatous shoots were studied. Sample plots were selected in similar microclimatic conditions. Light was 200 μmol / m^2 s photosynthetically active radiation (PAR) that makes 7-10% of a full sunlight under crown cover. Air temperature in a ground layer was about 15-20 °C and relative humidity of air was about 80%.

Anatomical characteristics of the orthotropic and the plagiotropic shoots were studied. Samples from 5 plants were fixed in 70% ethanol and used for temporary preparations. A middle part of stems was cut on the vibration microtome; these sections were stained with methyl green pironin and enclosed in glycerin. Slides were photographed by means of Axiovert 200 M microscope with Nikon COOLPIX 4500 digital camera. Cell and tissue sizes in 40-300 replications for each plant were measured with ocular micrometer with Amplival microscope.

The projective cover of *P. commune* or *C. dendroides* was 90-100%. To measure biomass accumulation of bryophytes, 10 plots (50×50 cm^2) for each species within a single site were studied. Dry weight of the structural parts (orthotropic and plagiotropic shoots) was represented in calculation per m^2 of tuft surface area.

Samples were sorted, weighed and scanned in the laboratory. Bryophyte samples (branches, shoots) were scanned at 600 x 1200 *PPI* using the Canon i-SENSYS MF4018 scanner (Canon Inc., USA). The fresh assimilating surface area of branches and branch length was calculated using the UTHSCSA ImageTool V.3.0 software (http://compdent.uthscsa.edu/dig/itdesc.html) (n = 33 for *P. commune*, n = 156 for *C. dendroides*). All sam-

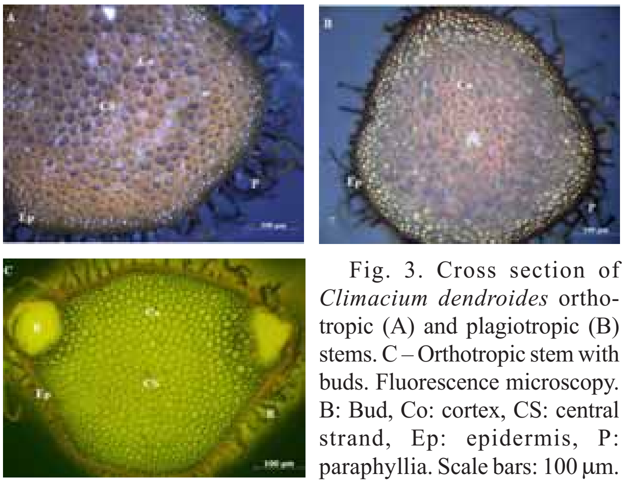


Fig. 3. Cross section of *Climacium dendroides* orthotropic (A) and plagiotropic (B) stems. C – Orthotropic stem with buds. Fluorescence microscopy. B: Bud, Co: cortex, CS: central strand, Ep: epidermis, P: paraphyllia. Scale bars: 100 µm.

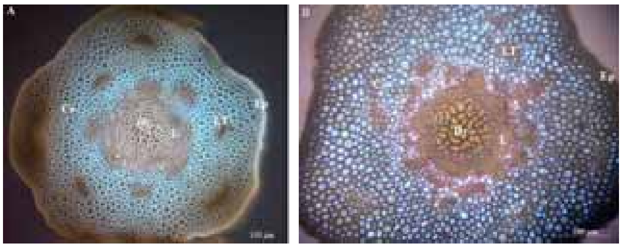


Fig. 4. Cross section of *Polytrichum commune* orthotropic (A) and plagiotropic (B) stems. Fluorescence microscopy. Co – cortex, Ep – epidermis, Hy – hydroids, L – leptoids, LT – leaf trace. Scale bars: 100 µm.

ples were dried to a constant weight at 70 °C and weighed.

Specific leaf area (SLA, cm^2 / g DW) was calculated as the ratio of the fresh assimilating surface area to the dry assimilating weight unit. Leaf area index (LAI) was computed as SLA (expressed in m^2 / g DW) multiplication by dry weight of orthotropic assimilating shoots of bryophyte per unit ground area (g DW / m^2). Dry weight per length unit (DML, mg DW / cm) of assimilating shoots was calculated by dividing dry weight of branches by their length. Water content of assimilating shoots was expressed as percent of shoot dry weight (Water Content, % DW).

The CO$_2$-exchange and evaporation rates of 10 shoots were measured on intact moss with LCPro+ (ADC BioScientific Ltd., UK). Determination was carried out at +20°C and saturating light of 500 µmol / m^2 photosynthetically active radiation (PAR). Parts of assimilating shoots about 2 cm were placed in the leaf chamber. CO$_2$ gas exchange within 15-20 minutes was measured. The respiration rate was measured in shoots 4-6 times a biological sample replicates at +20 °C in an open system, the infrared gas analyzer Li-7000 (LI-COR, Inc., USA). Two-channel analyzer was connected by an open differential circuit (Sivkov & Nazarov, 1987). Samples were placed in a chamber with an internal volume of 30 cm^3. Parts of shoots were exposed for 10-15 minutes. Ambient air with natural CO$_2$ concentration (about 350-400 ppm) was pumped through the chamber and flowmeters MMA-21 (Dwyer Instruments, Inc., USA). Air flow rate was 30 l / h. The temperature in the chamber was maintained by a thermostat LT-308a (LOIP, Russia). Respiration of the aboveground (assimilating) parts of current year shoots and the plagiotropic (heterotrophic) parts of shoots growing in a litter were measured.

Content and quality of low molecular weight carbohydrates (mono-, di- and oligosaccharides) was determined by HPLC (Heftman, 1986). Measurements were carried out in multiple analytical replicates on 3 independent samples of 3-5 plants of mosses in each.

Statistical analyses were conducted using XLSTAT V.7.5.2 (Addinsoft, USA). The test for normally distributed data was performed using the Shapiro-Wilk test. For independent samples, the Student's t-test was used. Linear correlation between two variables was assessed by the Pearson correlation coefficient. The p-value was used for testing a statistical hypothesis at significance level of a = 0.05.

RESULTS AND DISCUSSION

The anatomical structure of the orthotropic and the plagiotropic shoots. Stems of bryophytes have a simple anatomical structure, being composed of epidermis, the main tissue of the stem, or cortex, and conducting tissues (Goffinet *et al.*, 2009).

Orthotropic and plagiotropic shoots of *C. dendroides* have the same structure. Its surface is covered by the uni- to bistratose epidermis composed of small thick-walled cells. Cortex is subdivided into outer one, consisted of smaller cells, and inner one, or larger cells (Fig. 3). The central strand is made of uniform cells. The epidermis and the peripheral part of the cortex perform a mechanical function in stems of Bryophyta (Pog-

Table 1. Anatomical characteristics of *Climacium dendroides* stem (cross section)

Parameter	Orthotropic	Plagiotropic
Diameter, µm	700 ± 37	707 ± 37
Epidermis thickness, µm	11.3 ± 0.1	23.7 ± 1.9*
Outer cortex thickness, in µm	115 ± 8	89 ± 1.4*
in cell rows	7.3 ± 0.5	5.9 ± 0.1*
Inner cortex thickness, in µm	179 ± 9	200 ± 15
in cell rows	7.2 ± 0.5	8.2 ± 0.4
Central strand diameter, in µm	27 ± 1.3	25 ± 0.1
in cells	8.3 ± 0.4	8.9 ± 0.4

* Differences are significant at $\alpha < 0.05$.

Table 2. Anatomical characteristics of *Polytrichum commune* stem (from cross sections)

Parameter	Orthotropic	Plagiotropic
Diameter, µm	716 ± 34	715 ± 34
Epidermis thickness, µm	10.1 ± 0.7	14.3 ± 0.7
Cortex thickness, in µm	242 ± 12	252 ± 11
in cell rows	17.1 ± 0.6	18.6 ± 0.8
Hydrome diameter, in µm	104 ± 5	106 ± 2
in cell rows	4.4 ± 0.2	4.8 ± 0.3
Leptome thickness, in µm	25.5 ± 1.1	24.9 ± 0.9
in cell rows	4.1 ± 0.1	4.1 ± 0.1

Table 3. Biomass of *Climacium dendroides* and *Polytrichum commune*, g DW / m^2

Shoots	*Climacium*	*Polytrichum*
Orthotropic assimilating	6.8 ± 1.1	46.1 ± 3.1
Orthotropic brown	8.6 ± 1.7	-
Plagiotropic	8.6 ± 1.7	48.6 ± 4.0
Dry mass of whole plant	24.5 ± 3.6	94.6 ± 6.4

osyan, 1999), they are rich in cellular contents, including plastids.

Our study revealed quantitative differences in the structure of *C. dendroides* orthotropic and plagiotropic shoots (Table 1). The latter has thicker epidermis, fewer numbers of outer cortex cell layers and increased inner cortex in contrast to orthotropic shoots. These differences perform correlation with physiological parameters, which will be discussed later, and are interpreted as possibly related to the storage function of rhizomatous shoots.

Polytrichum commune stems have a similar structure (Fig. 4). The epidermis is composed of 1-2 layers of small, tightly abutting cells with thick walls. The cortex is composed of 14-19 rows of cells. Parenchyma cells of the aboveground shoot cortex have chloroplasts with starch. Chloroplasts transform into amyloplasts in the underground stem and also accumulate starch. Outer cortex cells of the *P. commune* stem have thickened walls. There are 6-7 leaf traces in the transverse sections within the cortex (Fig.4). The central cylinder of *P. commune* stem consists of hydroids and leptoids, which is considered as more primitive (Grandall-Stotler & Bartholomew-Began, 2007). The differences in anatomical structure of the *P. commune* orthotropic and plagiotropic stems were found less significant as compared to *C. dendroides* (Table 2). In basal part of *P. commune,* overground orthotropic shoots turn into plagiotropic rhizomatous shoots that branch and form new plants (Ignatov & Ignatova, 2003).

Functional properties of the orthotropic and the plagiotropic shoots. *P. commune* accumulated four times more biomass than *C. dendroides* per square meter which obviously relates to the growth of the latter species by loose individual shoots (Table 3). The plagiotropic shoots in these species constitute ca. 50% and 35% of the total biomass correspondingly. A similar result for plagiotropic parts of *Polytrichum* in tundra communities, 30-40% of the total biomass, where found by Collins & Oechel (1974) and Sveinbjörnsson & Oechel (1981).

Only parts of the current and previous years have green leaves in *P. commune*. In *C. dendroides* about 36% of biomass occurs in brown parts of orthotropic shoots.

The respiration provides metabolites and energy for growth and its rate reflects the level of metabolic activity of plant organs. The respiration rates of *C. dendroides* and *P. commune* orthotropic shoots at 20 °C were found to be 0.5 and 0.3 mg of CO_2 / g DW h, respectively (Fig. 5). The respiration rates of the plagiotropic shoots were lower as compared to the assimilating orthotropic shoots. However the difference between plagiotropic and orthotropic shoots in *C. dendroides* and *P. commune* were contrastingly distinct. The respiration rate of *C. dendroides* plagiotropic shoots was by four times less than that of the orthotropic shoots, whereas in *P. commune* it was lower, less than by 1/3. In *Polytrichastrum alpinum* (Hedw.) G.L. Smith, the respiration rates of the plagiotropic rhizomes were found to be much lower as compared to the aboveground assimilating shoots (Sveinbjörnsson & Oechel, 1981). However this might be caused by the fact that this study has been done in tundra, where the respiration rate was about 1.2 mg CO_2 / g DW h that exceeds the values, shown for *P. commune* and *C. dendroides* in the middle taiga zone by several times (Fig. 5). In forest and mountain tundra communities of the North, bryophytes, including *P. commune*, taken from under snow in June had high respiration rates (1-3 mg CO_2 / g DW h) due to a sudden temperature change at that period (Shpak, 2008).

Carbohydrates are very important for the growth and development of plants. It was found that the content of nonstructural carbohydrates of *C. dendroides* and *P. commune* organs was high and constituted about 12-23% of dry weight (Tab. 4). Among them, monosaccharides (glucose, fructose), disaccharides (sucrose, maltose), and oligosaccharides (raffinose, stachyose) were found. Disaccharides being a transport form of carbohydrates made a great portion among carbohydrates (40-50%). Plagiotropic shoots of *C. dendroides* were characterized by a low portion of monosaccharides and a large portion of oligosaccharides in form of raffinose. Plagiotropic shoots of *P. commune* accumulated a large amount of monosaccharides (up to 60%). They were identified for stachyose, about 50% of all oligosaccharides.

Concerning the metabolic activity of the orthotropic and the plagiotropic shoots, there are considerable differences in respiration rate and content of nonstructural carbohydrates between them. The respiration rate of the plagiotropic (geterotrophic) shoots was lower than that of assimilating orthotropic shoots, especially for the plagiotropic rhizomatous shoots of *C. dendroides* which are primary by origin (Fig. 6). It is related with a lower functional activity of the heterotrophic organs which responds for vegetative reproduction and undergoes a storage function.

By the carbohydrate analysis of bryophytes, content of total nonstructural carbohydrates is high in the orthotropic shoots as compared with plagiotropic ones (Tab. 3). The main portion of carbohydrates in tissues of the orthotropic shoots was sucrose which is the main transport form of sugars in mosses (Sveinbjörnsson & Oechel, 1981). The plagiotropic shoots, especially for *C. dendroides*, accumulate disaccharides and oligosaccharides and thus can be assumed as having both transport and storage functions. These data are in concordance with published results on *Polytrichum commune*, where starch

Table 4. Content of carbohydrates in shoots of bryophytes, mg / g DW

Shoots	Monosaccharides		Disaccharides		Oligosaccharides	
	Fructose	Glucose	Sucrose	Maltose	Raffinose	Stachyose
			Climacium dendroides			
Orthotropic	23.9 ± 2.5	36.7 ± 3.6	94.8 ± 9.4	3.7 ± 0.6	67.5 ± 6.8	-
Plagiotropic	4.3 ± 0.8	8.3 ± 1.3	46.4 ± 0.5	5.0 ± 0.2	52.0 ± 0.7	-
			Polytrichum commune			
Orthotropic	9.5 ± 3.0	17.6 ± 4.2	45.8 ± 0.7	7.5 ± 1.2	19.4 ± 1.3	-
Plagiotropic	10.7 ± 1.1	16.0 ± 1.7	3.5 ± 0.3	4.3 ± 0.5	5.7 ± 0.4	5.6 ± 0.8

content in the *Polytrichum commune* plagiotropic rhizomes was 3-4% in average which is three times higher than that in the orthotropic assimilating shoots (Sveinbjörnsson & Oechel, 1981). The fact that photoassimilates are transported from aboveground plant part to plagiotropic underground rhizomes where they can be converted to starch was shown by Sveinbjörnsson & Oechel (1981) and Hobbs & Pritchard (1987).

Apparently a relatively low content of soluble carbohydrates in the organs of faster growing *P. commune* can be explained by their efficient usage for growth in its shoots as compared to *C. dendroides*, which agrees with our data on a greater biomass per m^2 for *P. commune* than *C. dendroides* (Tabl.3).

Physiological characteristics of bryophyte assimilation apparatus. The orthotropic assimilating shoots of *P. commune* were taller than those of *C. dendroides* (Table 5). The average values of assimilating shoot's length and area of *P. commune* were 3.5 and 16 times greater than those of the *C. dendroides* branching shoots, respectively. The length of shoots and assimilating surface area were positively correlated for C. *dendroides,* R = 0.66 (p-value <0.0001) and *P. commune* R = 0.65 (p-value <0.0001).

Specific leaf area (SLA) and dry mass per unit length (DML) of assimilating shoots are closely related to the growth rate, accumulation of biomass, and CO$_2$-exchange (Migalina, 2008). *P. commune* assimilating shoots per area and length units contained significantly more dry matter than *C. dendroides* shoots (Table 5). The SLA value of *P. commune* was 4 times less than that of *C. dendroides*. The DML index for *P. commune* exceeded that of *C. dendroides* by more than 20 times.

The intensity of net photosynthesis for the studied bryophytes was low, averaging 1-3 µmol / m^2 s (Table 5). Bryophytes differed in the intensity of net photosynthesis in the same light and temperature conditions. *P. commune* shoots assimilated about 3 µmol CO$_2$ / m^2 s which was three times more than that of *C. dendroides*.

Leaf area index (LAI) is the ratio of assimilating surface area to ground area. Leaf area indices of *C. dendroides* and *P. commune* were relatively low, about 0.2-0.3 (Table 5).

Growth, metabolism, and intensity of gas exchange depend on the water regime. Endohydric and ectohydric bryophytes have different resistance to drought and its duration (Proctor, 2009). *C. dendroides* and *P. commune* had relatively low water content in shoots. Water content in assimilating shoots constituted 210-260% DW (Table 5).

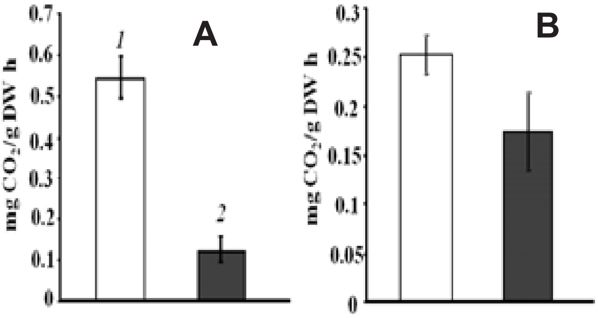
The water evaporation rate from assimilating shoots of *P. commune* exceeded 3.0 µmol H$_2$O / m^2 s and was significantly higher than that of *C. dendroides* (Table 5). The ratio of net photosynthesis to water evaporation is considered as water use efficiency (WUE). WUE of *P. commune* was 2.5 times higher as compared to *C. dendroides* WUE (Table 5).

Thus, *P. commune* has higher rates of net photosynthesis, water use efficiency, dry mass accumulation and a higher leaf area index as compared to *C. dendroides*

Table 5. Physiological parameters of the assimilating shoots of *Climacium dendroides* and *Polytrichum commune*: WC – water content, SLA – specific leaf area, DML – dry mass per unit length, LAI – leaf area index, Pn – net photosynthesis, E – evaporation. The length and assimilating shoots area of branching shoots of *C. dendroides* were measured (Fig. 2). * Differences are significant at α <0.05.

Parameters	*Climacium*	*Polytrichum*
Length, sm	1.5 ± 0.02	5.0 ± 0.2
Area, cm^2	0.4 ± 0.1	6.5 ± 0.3
WC, % of dry weight	236 ± 25	232 ± 11
SLA, cm^2 / g DW	327 ± 18	74 ± 4
DML, mg DW / cm	0.8 ± 0.1	17.0 ± 0.5
LAI	0.2	0.3
Pn, ìmol / m^2 s	1.05 ± 0.35*	2.92 ± 0.42
E, ìmol / m^2 s	3.32 ± 0.05*	3.80 ± 0.03
Pn/E, ìmol CO$_2$ / mol H$_2$O	0.3 ± 0.1*	0.8 ± 0.1

Fig. 5. Respiration rates of orthotropic (*1*) and plagiotropic (*2*) shoots of *Climacium dendroides* (A) and *Polytrichum commune* (B) at 20 °C.



(Table 5). The relatively high physiological activity of *P. commune* may be due to its growth form, life strategy, and high growth rate. *P. commune* colonies form parallel vertical shoots and tend to form a spreading carpet. Due to formation of creeping shoots, bryophytes are capable for horizontal sprawl and moving in space. It increases the competitiveness of *P. commune*. *C. dendroides* plants have a tree-like growth form when sympodial shoots develop into plagiotropic stolons which transform into assimilating dendroid orthotropic shoots.

P. commune and *C. dendroides* grow in similar light and water conditions and take equal assimilating surface areas. Low LAI values of bryophytes are related to their position in low and shaded floor of bilberry-green moss spruce forest. Bryophytes are adapted to grow under canopy of coniferous forests with low illumination. The study on CO_2-exchange of bryophytes and the analysis of photosynthesis light curves highlights the efficiency of assimilation apparatus of the studied mosses, which is a characteristic for the shade-tolerant plants (Shpak et al., 2009).

The water regime of bryophytes is closely related to their size and life form – a joint growth of individuals (Proctor, 2000). The study of *C. dendroides* and *P. commune* water regime has revealed relatively low water content in shoots, due to their endohydric type of water storage.

The studied mosses had a relatively high rate of water evaporation. This feature is typical for bryophytes growing in habitats with good water supply (Wllliams & Flanagan, 1996). Evaporation of water per surface unit of *P. commune* assimilating shoots was significantly higher than that of *C. dendroides* (Table 5). Calculated for turf area, the difference in water evaporation rate between species is 1.6 times. This can be explained by a more active growth and metabolism of *P. commune*.

The CO_2 assimilation rate of bryophytes depended on water content in assimilating shoots. Our data are consistent with the results obtained on other bryophytes in similar micro-climatic conditions in forest communities (Kubasek *et al.*, 2014).

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