Leaf characteristics and morphophysiological features of selected vascular plants in goltsy deserts of the Khibiny Mountains (Kola Peninsula)

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Abstract

The stability of biota in the extreme conditions of the goltsy deserts during ongoing climate change is determined by the adaptive characteristics of individual species. This study aimed to assess the characteristics of vascular plants (*Salix polaris*, *Salix hastata*, *Saxifraga oppositifolia*, *Carex bigelowii*, and *Luzula arcuata*) to the conditions of existence in the Khibiny goltsy deserts. The assessment was based on the morphological and anatomical leaf structures, pigment content and the intensity of photosynthesis. Biomorphological adaptations of high-altitude plants include miniaturization, plagiotropy, and compactization. The leaves of the studied plant species in the goltsy deserts exhibit features characteristic of mesophytes and xerophytes. For deciduous shrubs, a dorsoventral leaf structure with a high palisade coefficient was observed. For herbaceous perennials, a homogeneous type of mesophyll structure with a uniform distribution of chloroplasts and a thick cuticle was observed. The chlorophyll and carotenoid content ranges were comparable to those of the same species in the Khibiny mountain tundra belt and the Arctic tundra of Western Svalbard, indicating genetic determinism in the chlorophyll content of these species. The highest values of photosynthetic activity were found in graminoids (*Carex bigelowii* and *Luzula arcuata*) and *Salix polaris*. The characteristics of these species provide greater stability in the extreme conditions of the goltsy deserts and under climate change. *Saxifraga oppositifolia* exhibited the lowest values of photosynthetic activity.

Key words: goltsy deserts, vascular plants, leaf anatomy, pigments content, photosynthesis, Khibiny Mountains

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Introduction

The current attitude towards the Arctic is shaped by its resource wealth and the adaptive potential of its flora and fauna in response to projected climate change and increasing anthropogenic pressures (Krutikov et al. 2020). Climate change will likely lead to a decline in the populations of many species and a loss of genetic diversity, which is crucial for their long-term survival (Hughes et al. 2008). Biodiversity is a key factor that determines the sustainability of ecosystems and the biosphere (Volkov et al. 2013).

The goltsy desert ecosystem functions in extreme conditions, including low temperatures, strong winds, uneven snow distribution, excessive exposure to solar ultraviolet radiation during the growing season, and substrate weathering. In such climatic conditions, sparse, open vegetation is formed – predominantly mosses and lichens, followed by shrubs and subshrubs (Kuvaev 1985). The sparsity of the vegetation cover is largely attributed to the uneven distribution of snow, since only few species of vascular plants can withstand snowless winter conditions (Danilova and Koroleva 2020). Therefore, the primary mechanism for plants coping with adverse conditions in high-altitude environments is the acquisition of endurance (Volkov et al. 2018). The soils of the goltsy deserts, their chemical and physicochemical properties, respectively, are similar to dry peat soils formed in the underlying mountain-tundra belt under shrub vegetation. Despite their shallow profile and low biological productivity, they are practically no different in organic carbon content compared to the soils of the mountain tundra belt (Maslov et al. 2021).

Reduction of growth function is one of the ways to increase resistance to Arctic conditions (Markovskaya and Shmakova 2017). Plagiotropy becomes evident through the development of plagiotropic shoots that lie horizontally along the soil surface. Compactization is evident in the creation of cushion-shaped, dense, hummock-like life forms, which have relatively small contact surfaces with the surrounding aboveground environment (Volkov et al. 2013).

In the goltsy deserts, plants are characterized by a cushion-like shape, inside which dead parts of plants that form the substrate accumulate. Owing to humification processes, the temperature inside the cushion is several degrees higher than that of the adjacent air layer (Danilova and Koroleva 2020). Thus, the difference between the maximum and minimum temperature inside the cushion during the day does not exceed 2.2°C (Volkov 2012). Shrubs exhibit prostrate or trailing life forms, as seen in species such as *Loiseleuria procumbens* and *Saxifraga oppositifolia*. Grasses, sedges, and wood rushes, growing as dense tussocks are primarily composed of dead leaves and densely branching shoots. Various vascular plants, mosses, and lichens grow inside and around these tussocks, giving rise to a diverse multispecies plant community (Danilova and Koroleva 2020).

The goltsy deserts (Fig. 1) represent a vegetation belt found in circumpolar and boreal mountains, located above the tundra belt and reaching the boundary of perpetual snow at altitudes of 900–1200 m. In the vegetation map of the Khibiny Mts., the goltsy deserts cover approximately 20% of the total area of the massif (Alekseenko et al. 2017). In this belt, three distinct plant groupings have been identified (moss, dwarf shrub–moss–lichen, and moss–shrub–sedge groupings), each occupying different locations and experiencing different climatic conditions (Maslov et al. 2021). Among the vascular plants, *Juncus trifidus*, *Carex bigelowii*, *Salix polaris*, *Luzula arcuata*, *Saxifraga oppositifolia*, *Phyllodoce coerulea* are often found (Danilova and Koroleva 2020).

The successful adaptation of a plant organism to climatic conditions depends on the ability of its assimilation apparatus to adjust structural parameters in order to sustain production (Plyusnina and Zagirova 2016). The most informative indicators that characterize the functional state of plants are the leaf mesostructure (Golovko et al. 2008, Ivanova 2014, Yudina et al. 2017) and photosynthetic apparatus, including the composition, content and ratio of pigments (Golovko et al. 2010, Dymova et Golovko 2019). The aim of this study was to estimate morphological and anatomical characteristics as well as photosynthetic parameters of five species of vascular plants found in the goltsy desert of the Khibiny Mts.

Fig. 1. Vegetation of the goltsy deserts (plateau of Aikuaivenchorr Mt.). Sparse curtains of mosses and lichens with inclusions of graminoids and other vascular plants: 1 – *Salix polaris*; 2 – *Salix hastata*; 3 – *Luzula arcuata*.

Material and Methods

Study site description. The study was performed at the Aikuaivenchorr Plateau (67°36'N, 33°44'E, 1070 m a.s.l.), located in the southern part of the Khibiny Mountains, Russia. Meteorological data for this area were obtained from the «Phosagro» weather station, located on Aikuaivenchorr Mount at 1075 m a.s.l. The average annual temperature in this area is -3.3°C, while the average temperature during the months with positive temperatures (May–September) is 5.1°C. The annual amount of precipitation is 1 624 mm, and the average wind speed is 6–7 m s^{-1}. Snow melts in May–June and falls in October (Danilova et al. 2023).

Studied species. The study focused on five species of vascular plants commonly encountered in the plant groupings of the Khibiny goltsy deserts: *Salix polaris* Wahlenb., *Salix hastata* L., *Saxifraga oppositifolia* L., *Carex bigelowii* Torr.ex Schwein, and *Luzula arcuata* (Wahlenb.) Sw.

Anatomical parameters were studied on leaves that had completed their growth according to Mokronosov and Borzenkova (1978). Sections from the middle part of leaf blade (n – at least 10 leaves) were analyzed using a MIKMED-6 light microscope (LOMO, Russia). The parameters (leaf thickness, stomata size, and tissue cell size) were measured using a WF10X/22mm ocular micrometer. Longitudinal paradermal sections were used to determine the type of stomatal apparatus and number of stomates in the field of view. The number of chloroplasts in one cell and mesophyll cells in the Goryaev chamber was counted in suspension after preliminary maceration of the cells in a 1 N solution of hydrochloric acid at a temperature of 80°C (Borzenkova and Khramtsova 2006). The number of stomata, chloroplasts and mesophyll cells is calculated per leaf area unit.

The content of photosynthetic pigments of leaves was determined in ethanol extracts (96%) by the measurements of the absorption maxima of chlorophylls *a* and *b* and carotenoids (Lichtenthaler and Wellburn 1983, Maslova and Popova 1993) using a UV-1800 spectrophotometer (Shimadzu, Japan). The contents of photosynthetic pigments were as means using 5 biological and 3 analytical replicates. The chlorophylls proportion allocated in the light-harvesting complexes (LHC) was estimated using the formula: [Chl *b* + 1.2 Chl *b*)/(Chl *a* + Chl *b*)], based on the fact that all Chl *b* is in the LHC, and the ratio Chl *a*/Chl *b* in this complex is 1.2 (Maslova and Popova 1993).

Net CO_2 exchange **(Pn)** was measured in the field using open-flow infrared gas analysis Li-850 (LI-COR, USA). An originally developed chamber made of clear acryl was used for the measurements (chamber area – 36 cm^2, height – 6 cm). Net CO_2 exchange rate (Pn) measurements were carried out during the growing season: on a sunny day (air temperature was 17°C, illumination – 70-90 klx) and with clouds (air temperature was 14°C, illumination –13-35 klx). Calculations of Pn were made in mg CO_2 m^{-2} h^{-1}.

The leaf area (mean of at least 10 fully developed leaves) was determined by computer scanning in the ImageJ program (LOCI, University of Wisconsin, USA). The dry matter content in the leaves was determined by oven drying at 105°C to dry weight (DW).

Statistical analysis. Data processing was performed using the standard software package in Microsoft Excel 7.

Results

Morphological and anatomical studies

Table 1 presents the morphological and anatomical characteristics of the assimilating organs. Deciduous dwarf shrubs and *Carex bigelowii* have the largest leaf blades (1–1.3 cm^2) and the smallest thickness (215–276 µm). The smallest leaves, but the thickest ones, were in *Saxifraga oppositifolia* (0.05 cm^2 and 440 µm, respectively).

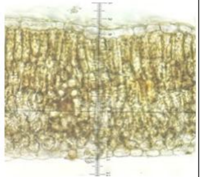
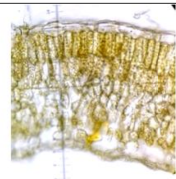
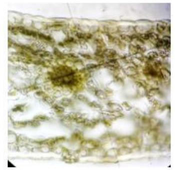
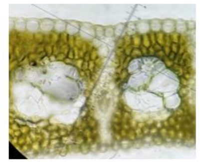
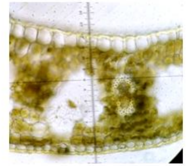
Species	Deciduous dwarf shrubs		Herbaceous perennials		
	Salix polaris	*Salix hastata*	*Saxifraga oppositifolia*	*Carex bigelowii*	*Luzula arcuata*
Fragment of leaf cross-section (photo taken at 40x magnification)					
Indices					
Leaf area, cm^2	1.07±0.04	1.13±0.08	0.05±0.01	1.26±0.06	0.85±0.03
Thickness leaf, µm	215.5±2.1	276.4±1.2	439.7±15.6	246.4±3.6	305.2±8.8
Stomata, UE/LE: number, pieces mm^{-2} area, µm^2	 92±5 / 177±4 493±16 / 516±24	 * / 295±10 * / 455±11	 121±5 / 215±18 808±29 / 754±22	 * / 312±9 * / 560±13	 * / 78±6 * / 574±15
PM cells: volume, thousand µm^3 number, thousand cm^{-2}	 3.6±0.2 289±2	 5.1±0.5 180±1.6	**	**	**
SM cells: volume, thousand µm^3 number, thousand cm^{-2}	 3.3±0.4 265±2.7	 3.8±0.5 149±1.1	 13.9±1.4 393±3.3	 – 677±4.4	 6.1±0.5 861±4.5
Chloroplast number PM/SM: per cell, pieces per 1 cm^2 leaf, million	 21±1 / 17±1 6.1±1.7 / 4.5±1.1	 24±1 / 16±1 4.3±0.8 / 2.4±0.5	–	–	 * / 22±1 * / 18.9±2.4
Cell volume corresponding to 1 chloroplast, µm^3, PM/SM	169±9 / 192±22	229±18 / 259±33	–	–	* / 297±22

Table 1. Indices of leaf mesostructure of vascular plants (goltsy deserts of Aikuaivenchorr Mt., Khibiny). *Note:* Epidermis (E): U – upper, L – lower; Mesophyll (M): P – palisade, S – spongy. * – stomata are absent; ** – PM is not expressed. Dash – no data.

The leaves of the studied species belonging to the genus *Salix* has a typical dorsoventral structure. The assimilatory tissue of leaf blade was clearly differentiated into a palisade and spongy mesophyll (Table 1). The palisade mesophyll was developed on the adaxial side and consisted of two rows of densely arranged elongated cells (the average shape index is 3.9 in *Salix polaris* and 3.7 in *S. hastata*). In *S. polaris*, the palisade mesophyll cells are smaller, with their number being 1.6 times greater than in *S. hastata* (cell volume 3.6 and 5.1 thousand μm^3, quantity is 289 and 180 thousand cm^{-2}, respectively). Spongy mesophyll on the abaxial side is represented in *S. polaris* by 4-5 layers of densely packed cells (shape index – 1.4, volume – 3.3 thousand μm^3, quantity – 265 thousand cm^{-2}) with small intercellular gaps. Compared to *S. polaris*, *S. hastata* possesses larger spongy mesophyll cells, (volume – 3.8 thousand μm^3), their number is 1.8 times less (149 thousand cm^{-2}). Furthermore, these cells are located more loosely. The palisade coefficient (Fig. 2) in these species (*i.e.* the ratio of palisade parenchyma thickness to spongy tissue thickness) was quite high (1.2 in *S. polaris* and 1.1 in *S. hastata*).

The upper epidermis in both species is thicker than the lower (in *S. polaris* – 1.3 times, in *S. hastata* – 1.5 times). Additionally, *S. hastata* has larger epidermal cells compared to *S. polaris* (Fig. 2). The leaves of *S. hastata* exhibit pubescence, with a matte green upper side and a bluish or pale green lower side, distinguishing them from the dark green, glossy, and glabrous leaves of *S. polaris*. *S. polaris* features an amphistomatic leaf blade, with stomata present on both sides of the leaf. The number of stomata on the lower epidermis is almost 2 times greater than on the upper (Table 1). In S. *hastata*, stomata are located only on the lower epidermis (hypostomatic type of leaf blade). The number of stomata on the lower epidermis of *S. hastata* is 1.7 times greater than in *S. polaris*. However, their size is smaller, with a stomatal area of 455 and 516 μm, respectively. These species possess an anomocyte type of stomatal apparatus (the stomata were surrounded by an indeterminate number of cells, which did not differ in shape or size from the main cells of the cover tissue).

In both *S. polaris* and *S. hastata*, the number of plastids per cell was found similar, ranging from 16 to 24. The number of chloroplasts in the palisade mesophyll was higher than in the spongy mesophyll for both species. Species specific difference in the number of leaf cells was apparent (Table 1). Therefore, in *S. polaris*, the number of chloroplasts in the palisade mesophyll is 1.4 times greater, and in the spongy mesophyll, it is 1.9 times greater than in the leaves of *S. hastata*.

In herbaceous perennials, there was no differentiation of mesophyll into palisade and spongy tissue. The leaves of *Saxifraga oppositifolia* are loosely homogeneous, featuring marginal cilia. The average thickness of the leaf blade was 440 μm. The stomata, oriented in one direction, are located on both sides of the leaf, indicating an amphistomatic leaf blade type. The number of stomata on the lower epidermis was 1.8 times higher than on the upper epidermis, while their area was larger on the upper epidermis (Table 1). The stomatal apparatus type is anomocyte. The mesophyll was formed by large cells, with a volume of 13.9 thousand μm^3, and intercellular gaps. The number of cells per unit leaf area is 393 thousand cm^2.

The leaves of two graminoids (*Carex bigelowii* and *Luzula arcuate*) exhibited a similar anatomical structure (Table 1) characterized by a densely homogeneous mesophyll composed of numerous densely packed cells (680–860 thousand cm^2). Stomata were located on the lower epidermis in longitudinal strands along the entire length of a leaf blade. *L. arcuata* had a smaller number of stomata (an average 78 pieces mm^{-2}) that the other studied species, and a higher number of chloroplasts per unit leaf area (19 million cm^{-2}). However, the number of plastids per cell remained similar to that of deciduous dwarf shrubs (Table 1).

The cuticle thickness of herbaceous perennials was: in *Saxifraga oppositifolia* – 9-13 µm; in *Carex bigelowii* – 2.5-5 µm; in *Luzula arcuata* – 5-7.5 µm. The cuticle above the upper epidermis was thicker than above the lower epidermis in all species. The cells of epidermis were found round–square or rectangular, elongated along the leaf. Additionally, across all species, the cells of the upper epidermis were nearly twice as thick as those of the lower epidermis (Fig. 2).

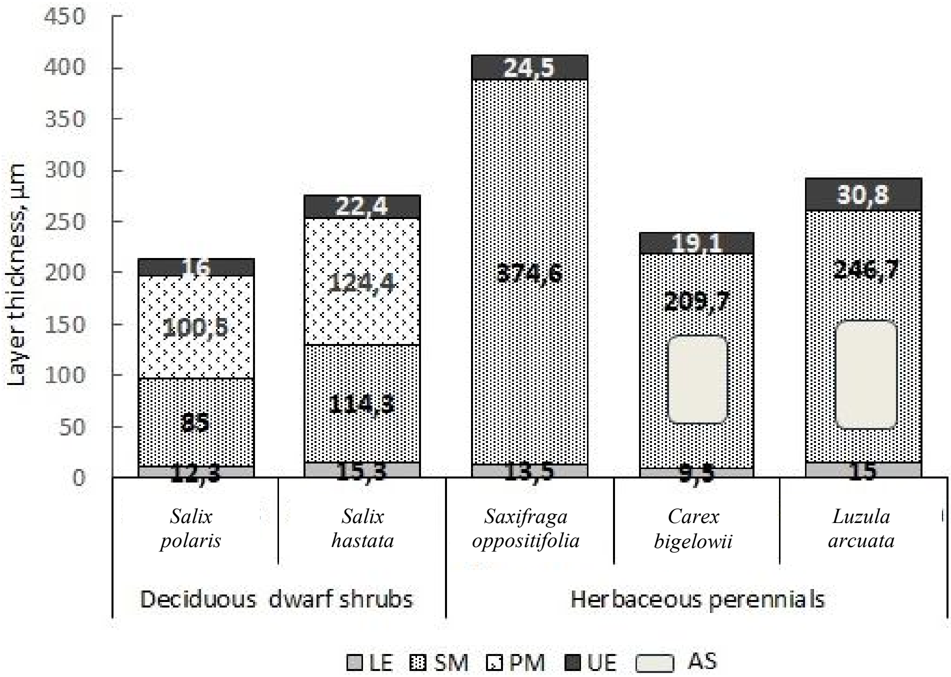


Fig. 2. The thickness of the structural layers of leaves of vascular plants (goltsy deserts of Aikuaivenchorr Mt., Khibiny). LE – lower epidermis; SM – spongy mesophyll; PM – palisade mesophyll; UE – upper epidermis; AS – large space filled with chlorophyll-free parenchyma cells.

Content of photosynthetic pigments

In the studied vascular plant species of goltsy deserts, the green pigment content in the leaves is 3.4–6.8 mg g^{-1} DW, the carotenoids (Car) — 0.8–1.6 mg g^{-1} DW. The highest chlorophyll (Chl) content was observed in graminoids (*Carex bigelowii* and *Luzula arcuata*) and *Salix polaris*. The chlorophyll content of *Salix hastata* and *Saxifraga oppositifolia* was the lowest. The Chl *a*/*b* ratio was 2.6–3.0, and the Chl/Car ratio was 3.8–4.4. A low Chl *a*/*b* ratio in *Saxifraga oppositifolia* indicates a higher proportion of the light-collecting pigment Chl *b* in the pigment apparatus. The value of the light-harvesting complex was 61%. In other species, LHC fluctuates in a narrow range (51–56%).

Table 2 presents data for the pigment complex of the same species of vascular plants in different regions of the Arctic and Subarctic. In all plant species within the goltsy deserts, the chlorophyll content was found higher than in plants from the mountain tundra of Khibiny and the Arctic tundra of Western Svalbard. In *Carex bigelowii*, however, chlorophyll content was the same. Although the limits of variation in the content of green and yellow pigments in the studied species in all regions were close. In the goltsy deserts, the limits of variation in chlorophyll contents were 3.4–6.8, in the Arctic tundra – 2.5–6.5, in the mountain tundra belt – 2.8–6.8 mg g^{-1} DW. The carotenoid content varied in the range of 0.8–1.6, 0.7–1.7 and 0.6–1.8 mg g^{-1} DW, respectively.

Net CO_2 exchange rate on sunny day in July was 580 mg CO_2 m^{-2} h^{-1} for *S. polaris*, 524 for *S. hastata*, 1074 for *Luzula arcuata*, 1388 for *Carex bigelowii* and 105 for *Saxifraga oppositifolia.* Net CO_2 exchange rate was estimated for some plants on cloudy day in August: for *S. polaris* it was 681 mg CO_2 m^{-2} h^{-1}, 236 for *S. hastata* and 603 for *Luzula arcuata*.

Dry matter content, %	Pigment content, mg g^{-1} dry weight		Chl *a*/*b*	Chl/Car	Light-harvesting complex, %	Region
	Chl (*a*+*b*)	Car				
Salix polaris						
37	5.9	1.1	2.9	5.5	56	GD
32	5.2	1.2	3.3	4.2	51	MT
29	5.0	1.2	3.3	4.3	51	AT
Salix hastata						
31	3.4	0.9	3.0	3.8	55	GD
Saxifraga oppositifolia						
27	3.4	0.8	2.6	4.4	61	GD
24	2.8	0.6	3.9	4.8	45	MT
26	2.5	0.7	2.7	3.5	60	AT
Carex bigelowii						
37	6.8	1.2	3.3	5.7	51	GD
36	6.8	1.8	3.6	3.8	48	MT
24	6.5	1.7	3.1	3.9	54	AT
Luzula arcuata						
29	6.7	1.6	3.1	4.2	54	GD
29	5.8	1.2	2.6	4.6	61	AT

Table 2. Photosynthetic pigments content of the same species of vascular plants in different regions of the Arctic and Subarctic. *Note*: GD – goltsy deserts, Khibiny (own data); MT – mountain tundra, Khibiny (Shmakova et al. 1996); AT – arctic tundra, West Svalbard (Markovskaya and Shmakova 2017); Chl – chlorophylls; Car – carotenoids.

Discussion

The leaves of the studied vascular plant species from the goltsy deserts are small, ranging from 0.05 to 1.3 cm^2 in leaf area. This small size of individual plants and their organs is attributed to limited energy and resources. Owing to their small size and prostrate growth form, these plants tend to grow close to the heated soil surface, where the temperature conditions are more conducive to their vital activities compared to the cooler air and deeper soil layers (Volkov et al. 2018). The reduction in leaf area results in increased thermal dissipation and reduced transpiration losses (Ivanova 2014), which are crucial adaptations for survival on stony substrates.

The analysis of leaf mesostructure reveals the presence of species exhibiting both dorsoventral (deciduous dwarf shrubs) and homogeneous mesophyll structures (herbaceous perennials). The dorsoventral type of mesophyll structure in Arctic species is weakly expressed and occurs less frequently than the homogeneous one (Gamaley 2004, Vasilevskaya 2010). Nevertheless, some researchers (Goryshina 1989, Pyankov 1993) argue that plants with a dorsoventral mesophyll structure exhibit significant ecological plasticity, enabling them to thrive in diverse habitat conditions. The dorsoventral mesophyll type is often associated with plant adaptation to moisture deficiency and intense lighting (Popova 2013).

Salix polaris exhibits plagiotropic shoots, often concealed beneath a layer of litter and fine-grained soil, with only their leaf-bearing tips emerging to the surface. *S. hastata* features orthotropic shoots without indications of lodging (Fig. 1). The proximity to the soil surface provides more favorable conditions for creeping willows, allowing them to enter the active phase of vegetation earlier, presenting an advantage over *S. hastata* with its orthotropic shoots (Volkov 2006). Significant differences in shoot arrangement between the studied deciduous dwarf shrubs, *S. polaris* and *S. hastata*, might be considered as devices to goltsy desert conditions. In the Arctic tundra of Wrangel Island, the trellis growth pattern and the prevalence of underground growth in *Salix polaris* have been observed (Nedoseko and Viktorov 2018).

The pubescence on the lower surface of the leaves in *S. hastata* serves as protection against excessive transpiration through the stomata, while the upper part of the leaf benefits from radiation protection provided by integumentary tissues, cuticles, and wax layer. It is believed that plants with amphistomatic leaves have increased photosynthesis efficiency (Rotondi et al. 2003). According to our data, *S. polaris* (amphistomatic type) has a higher of net CO_2 exchange rate (Pn) than *S. hastata*. It was found that Pn in *S. polaris* was higher on a cloudy day than on a sunny day. In *S. hastata*, Pn was 2.2 times lower on a cloudy day. For *S. polaris* on Spitsbergen (Barták et al. 2012), absolute maxima of photosynthetic electron transport rate were reached during a partly cloudy day, when a few clouds acted as additional sources of reflected radiation. However, *S. polaris* exhibits a high photosynthetic rate only when well supplied with water. In the goltsy deserts, *S. polaris* forms various forms of cohabitation with mosses that help retain water. Gornall et al. (2011) demonstrated that *S. polaris* from shallow moss mats had a greater biomass than that from bare soil.

Our leaf mesophyll data for the studied willows were comparable to previous study (Ivanova 2014), and revealed that both species exhibited characteristics of mesophytes and xeromesophytes. Light-loving mesophytes typically display a dorsoventral leaf structure and a predominance of stomata on the lower epidermis (Gorlacheva 2010), a trait observed in both species. The leaf thickness of 200–250 μm aligned with the characteristics of xeromesophytes and mesoxerophytes. Regarding the number of cells per unit leaf area (554 thousand cm^{-2}), *S. polaris* falls within the range typical for xeromesophytes (400–700 thousand cm^{-2} according to Ivanova 2014).

A thick cuticle distinguished a group of species exhibiting a homogeneous type of mesophyll structure. A leaf with a thick cuticle can reflect up to 40% of the incident radiation, with the upper mesophyll cells shielding the underlying cells, thereby changing the optical properties of the leaf (Golovko et al. 2008). Among the studied herbaceous perennials from the goltsy deserts, the upper epidermis cells were nearly twice as thick as those of the lower epidermis, similarly to the observation in mountainous *Luzula sylvatica* (Barták et al. 2020), in which the upper epidermis was found 1.8 times thicker than the lower epidermis.

The succulent leaves of *Saxifraga oppositifolia* is considered an adaptation to the dry and rocky habitats, aiding in the regulation of water metabolism during periods of intermittent moisture deficiency (Volkov et al. 2018). *S. oppositifolia* typically adopts a prostrate or trellis-like life form within the goltsy deserts (Danilova and Koroleva 2020). High-altitude plants with trellis-like life forms spread across the substrate, forming various cohabitations with bryophytes (Volkov and Volkova 2001). These formations typically exhibit a two-tiered structure, with bryophytes comprising the ground layer and the photosynthetic and generative organs of the flowering plant densely arranged on top. Thus, bryophytes enhance the adaptive properties of the entire structure when residing in extreme high-altitude conditions (Volkov et al. 2018). Mosses may prevent frost damage to roots. Their growth form both aids moisture retention and enhances boundary layer resistance, reducing the desiccating impacts of strong arctic winds (Gornal et al. 2011). Because of their low thermal conductivity, mosses have a high insulating capacity, especially when they are dry and their tissue contains a large volumetric air fraction (O'Donnell et al. 2009). Saxifrages are lithophiles adapted to rocky environments. They get the necessary nutrients from the remains of mosses, the atmosphere (rainwater) or from their own dead tissues and parts. The number of cells per unit area of the *Saxifraga oppositifolia* leaf (393 thousand cm^{-2}) closely resembles the characteristics of xeromesophytes (400–700 thousand cm^{-2} according to Ivanova 2014).

The intercellular cells in the spongy mesophyll of *S. hastat*a and *Saxifraga oppositifolia* act as reservoirs for air essential for the respiration of plant tissues. Air is a poor conductor of heat. It provides insulation against low temperatures, thereby safeguarding the plant tissues (Volkov et al. 2018). Moreover, the abundance of extracellular space facilitates gas exchange regulation and enhances the absorption of light energy through multiple scattering within the extracellular space (Kultiasov 1982).

Leaves of *C. bigelowii* and *L. arcuata* in the goltsy deserts typically form dense tussocks (Danilova et Koroleva 2020). Such leaf arrangement provide an effective wind barrier, protecting the inner part of the tussocks. The mesophyll of these species comprises many densely packed cells (680–860 thousand cm^{-2}), a characteristic that classifies them as xerophytes based on the number of cells per unit leaf area. A vast system of cavities is formed within the plant, filled with chlorophyll-free parenchyma cells. These cells absorb heat during daytime exposure to intense sunlight, delaying heat transfer from the living parts of the plant during the cooler nighttime period. An essential aspect of the xeromorphic leaf organization is the ribbed upper surface, facilitating leaf folding during hot weather and increasing the layering of chlorophyll-bearing parenchyma (Volkov 2006). *Luzula arcuata* has a large number of plastids per unit area (19 million cm^{-2}), which contributes to an increase in the internal assimilating surface of the leaves (Chukina et al. 2017).

The light-harvesting complex (LHC) values in the studied vascular plants from the goltsy deserts fluctuate in a narrow range (51–61%). Species with lower LHC values (up to 55%), such as *C. bigelowii*, *L. arcuata*, and *S. polaris*, typically do not require protection for their assimilation apparatus against excessive sunlight (Markovskaya and Shmakova 2017). The leaves of *C. bigelowii* and *L. arcuata* are oriented vertically and during the daytime are satisfied with direct grazing and diffused light (Slemnev et al. 2008). *Saxifraga oppositifolia* exhibited the lowest pigment content (chlorophylls and carotenoids) and the highest LHC value among the examined plants (61%). Saxifraga have morphological devices that limit the excess absorption of radiant energy. The leaves have an imbricated structure and only the marginal leaves and leaf tips actually receive direct sunlight (Slemnev et al. 2008). *Saxifraga oppositifolia* had the lowest photosynthetic activity values – the net CO_2 exchange rate on sunny day was 105 mg CO_2 m^{-2} h^{-1}. A low photosynthesis rate was noted in this species near Ny-Alesund in the northwestern part of Spitsbergen (Muraoka et al. 2008). The light-saturated photosynthetic rate in *Saxifraga oppositifolia* was 5 times lower than in *S. polaris* (24.4 nmol CO_2 g^{-1} leaf s^{-1} and 124.1, respectively). It was noted that in the goltsy deserts, the net CO_2 exchange rate in *Saxifraga oppositifolia* was also 5 times lower than in *S. polaris*.

The examined goltsy deserts vascular plant species exhibit a low chlorophyll content, similar to plants in other Arctic and Subarctic regions. A decrease in the number of chlorophylls led to significant changes and optimization at all levels of leaf structure development. A decrease in the area and thickening of leaves, compaction of their tissues, an increased number of stomata per unit surface area, folding and thickening of the cuticle – show that the growth and stretching of leaf cells are suppressed. Such anatomical features of arctic plants are associated with the effect of underdevelopment of structures (Gamaley 2004). In all plant species within the goltsy deserts, the chlorophyll content was higher than in plants from the mountain tundra of Khibiny and the Arctic tundra of Western Svalbard. Perhaps, in this way, plants in the goltsy deserts may compensate for the lack of heat with a relatively consistent light regime, enabling vascular plants to function intensively during favorable periods. Comparative analysis of the pigment complex in perennial dwarf shrubs and herbaceous perennials revealed that the limits of variation in the content of green and yellow pigments in the studied species from these extreme areas were similar, indicating a genetic determination of chlorophyll content.

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