Ion-exchange properties and swelling capacity of leaf cell wall of Arctic plants

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Abstract

Ion-exchange (number of functional group) properties and swelling capacity of leaf cell walls of plant species *Betula nana*, *Salix polaris*, *Dryas octopetala* and *Cassiope tetragona* from Western Spitsbergen Island were investigated. It was found out that cell wall of Arctic plants is cation exchanger which has similar functional groups (amine groups, carboxyl groups and phenolic OH-groups) with cell wall of boreal plants. In all investigated species, the highest percentage in the structure of the cell wall was recorded for the carboxyl groups of hydroxycinnamic acids and phenolic OH-groups, which are part of phenolic compounds. In comparison with species from other climatic zones leaf cell wall of arctic plants has in 2–3 times higher amount of ion exchange groups of all types as well as the higher values of swelling coefficients. It was proposed that the high values of the ion-exchange capacity and swelling coefficient of the cell wall of all studied species contribute to greater water flow system by the apoplast and enhance the metabolic processes in the cell wall of plants at high latitudes.

Key words: plant cell wall, ion exchange capacity, swelling coefficient, Arctic plants

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Introduction

The cell wall is one of the most important structures of the plant cell, being the first involved in the adaptive processes by responding to the growth conditions. Its complex composition and functional activity (Gorshkova 2007) indicate the restructuring depending on environmental conditions. The plant cell wall is a complex multicomponent system whose composition varies during the cell cycle, growth, and development. Ion-exchange processes in cell walls have long been a matter of interest. In some

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studies devoted to acid–base properties of cell walls in herbaceous plants (Meychik et al. 1999), the cell walls were considered as weakly basic cation exchangers with a low crosslinking degree. It was established, that in the structure of leaf cell wall four types of ion-exchange groups, three of which were cationexchanging groups (carboxylic groups of two types, with one attributed to α-D-galacturonic acid, and a phenolic group), and the fourth was the anion-exchanging group (Meychik 2007). A number of publications were dedicated to impact of various stress factors (pollutants, temperature, salinity) on properties of plant cell walls (Wierzbicka 1998, Vázquez et al. 2000, Galibina et Terebova 2008, Krzeslowska 2011). The predominance of cryophilicity in Arctic species is related to adaptation to low temperatures, which includes the increased role of the apoplastic transport of assimilates. According to Gamalei (2013), the compensatory substitution of the transport channel of the symplast by the apoplast is associated with development of the apoplastic labyrinths of cell wall in the companion cells of the terminal phloem. This process leads to increase in the volume of cell wall and contributes to increase in the surface of the sugars transfer from the mesophyll to the phloem through the apoplast and correspondingly the increase in the significance of the cell wall structures in this adaptation (Gamalei et al. 1994, Gamalei et al. 2000). In fact, cell wall features of plants growing in high latitudes have still been scarcely studied. In the present study we aimed to investigate the role of ion-exchange capacity of the leaf cell walls in developing plant adaptation to Arctic conditions.

Material and Methods

The study was carried out in the tundra zone of the inland fjord of Western Spitsbergen in 2009–2010. Climatic features of study area are characterized by short growing season (40–70 days), the duration of which is determined by the time of snow cover melting in local habitats. Average daily temperature is less than 8°C and polar day lasts from April, 19 to August, 24 (Koroleva et al. 2008).

The objects of the study were species of the native flora of the Spitsbergen archipelago – *Betula nana* L. (*Betulaceae*), *Salix polaris* Walenb. (*Salicaceae*), *Dryas octopetala* L. (*Rosaceae*) and *Cassiope tetragona* (L.) D. Don. (*Ericaceae*). All species were collected in the area of Colesdalen (N 78° 07.998′, E 14° 59.363′).

Cell walls were isolated from the leaves by the method described in (Meychik et al. 1999). Fixed and dried plant material was put into a glass ion-exchanging column ($V \approx 0.25$ l) and washed successively by the following solutions: 10 mM KOH ($V \approx 0.5$ l), distilled water ($V \approx 2$ l), and 10 mM HCl ($V \approx 0.5$ l). The samples obtained were washed with distilled water until chloride ions were eliminated and then dried to a constant weight at 55–60°C. The absence of chloride ions in the leaf cell wall was determined by negative reaction of the wash water with 10 mM AgNO3 solution (white curd like precipitate of AgCl was not formed). This procedure converted all cation-exchange groups of cell walls into the H^+-form, which allows comparative study of sorption properties for ionexchanging materials with different structure of functional groups.

The weight coefficient of cell wall swelling was determined by the gravimetric method (Helfferich 1959). The fragments of water-swollen standardized cell walls were blotted with a filter paper, and their fresh weight (G_{Fcw}) was measured.

Then the cell walls were dried at 50°C to a constant weight and weighed to obtain their dry weight (G_{Dcw}). The weight coefficient of swelling for standardized cell walls (K_{cw}) was determined from the formula (Helfferich 1959):

$$K_{CW} = (G_{F_{CW}} - G_{D_{CW}})/G_{F_{CW}} \qquad \textit{Eqn.}\ 1$$

where G_F and G_D are fresh and dry weight of the samples, expressed in grams; index cw denotes standardized cell walls.

The composition and content of ionogenic groups in cell walls was measured by potentiometric titration technique (Meychik et al. 1999). Dry samples of 40 ± 0.1 mg were placed into 50–ml conical flasks with ground glass stoppers and covered with 12.5 ml of KOH or HCl solution at various concentrations. In all cases the ionic strength was kept constant (10 mM) by adding appropriate amounts of KCl. The pH of stock solutions was measured with a pH-meter (Model pH 214, Hanna, Germany); the concentrations of acid or alkale were determined by titration with an indicator bromothymol blue. After 48–h incubation, the samples were removed from the solution, and pH of the medium (pH_i) and remaining concentrations of acid or alkal were measured. Sorption capacities of cell walls at each pH_i value were calculated from changes in concentrations of H^+ and OH^- according to the equation:

$$S_i = (C - C_i)\,V/g \qquad \textit{Eqn.}\ 2$$

where S_i is the cation-sorption capacity of samples at each pH_i value, expressed in μmol / gram dry weight of cell walls; C and C_i are the initial and equilibrium concentrations of KOH or HCl in the solution, respectively (mM); V is the solution volume (ml); g is the sample weight expressed in grams.

The obtained experimental curves $pH_i = f(S_i)$ were deconvoluted into monosigmoid regions according to the differential curves $(dS_i/dpH_i) = f(pH_i)$, which show a series of minima, corresponding to the beginning (α=0) and the end (α=1) of ionization of functional groups of each type (*see* Fig. 1).

By performing numeric differentiation of experimental curves, we determined the number of ionogenic groups of each type (ΔS_j) and the degree of dissociation α_i at each pH_i value according to the formula:

$$\alpha = (S_i - S_{j\,min})\Delta S_i \qquad \textit{Eqn.}\ 3$$

where S_i is a sorption capacity at corresponding pH_i (μmol / gram dry wet of cell walls), $\Delta S_j = S_{j\,max} - S_{j\,min}$, $S_{j\,min}$ and $S_{j\,max}$ are minimal and maximal values of the sorption capacity, obtained from extremums on differential curves and corresponding to the beginning and the end of ionization of a jth type group (μmol/gram dry weight of cell walls). In order to calculate dissociation constants, we used Henderson–Hasselbalch equation, modified by Gregor et al. (1954):

$$pH = pK_a + n\log\left\{\frac{\alpha}{1-\alpha}\right\} \qquad \textit{Eqn.}\ 4$$

where pK_a is an apparent dissociation constant of the polymer ionogenic group, α is the degree of dissociation, n is a constant that depends on the structure of polymer matrix and on the nature of counterion.

Based on equation (4) with α_i values obtained from equation (3) at various pH_i, we used regression analysis to calculate pK_a and n_j for each stage of dissociation. Having found the parameter values, we calculated $S_{i\ calc}$ for all pH_i values obtained in our experiments using the formula:

$$S_{i\ calc} = S - \sum_{\substack{j=1 \\ i=1}}^{k,m} S_j \Big/ \{1 + \exp 10\ (pK_{aj} - pH_i) n_j\} \qquad \textit{Eqn.}\ 5$$

where S is the total ion-exchange capacity of cell walls, μmol/gram dry weight; S_j is the total content of ionogenic groups of the jth type, μmol/gram dry weight; $S_{i\ calc}$ is the calculated ion-exchange capacity of cell walls at corresponding pH_i, μmol/gram dry weight; pK_{aj} is the apparent dissociation constant of jth type ionogenic groups; n_j is a constant from equation (4) for jth type ionogenic groups; k is the number of points on experimental potentiometric curve, and m is the number of types of ionogenic groups.

The adequacy of the applied approach to the description of acid–base equilibrium was estimated with regression analysis by calculating the parameters of the equation:

$$S_{calc} = bS_{exp} + a \qquad \textit{Eqn.}\ 6$$

where S_{exp} and S_{calc} are experimental and calculated values of ion-exchange capacity of cell walls at corresponding pH, μmol/gram dry weight.

Statistical analysis was performed using SAS software (version 9.2, SAS Institute, Cary, NC). The MIXED procedure for analysis of variance was used to determine statistical differences ($p < 0.05$) from Arctic plants. Initially, the data were tested for homogeneity of variance and normality, however, violations were found. Average values are reported with transformed lettering according to Fisher's LSD at $p \leq 0.05$.

Results

According to the obtained results, four types of ion-exchange or functional groups were included in the structure of the leaf cell walls of the studied Arctic plants (*see* Table 1).

There was one anion-exchange amine group with ionization constant (pK_a ~ 3–4) and three cation-exchange groups: carboxyl groups of ά-D polygalacturonic acid (COOH PGUA) (pK_a ~ 5–6), carboxyl groups of hydroxycinnamic acids (COOH HCA) (pKa ~ 7–8) and phenolic OH-groups (pK_a ~ 9–10). The total number of ion-exchange groups in the structure of the leaf cell walls of plants determines the maximum values of the cell wall sorption capacity. These groups perform transport function and take part in the exchange reactions.

Analysis of the amino-groups amount in leaf cell walls of studied plants showed that the highest values (up to 1200 μmol / gram dry weight of cell walls) were obtained for *Betula nana*, a rare species for

Western Spitsbergen. For other studied species this index was much lower and for *Cassiope tetragona,* which is a widespread species, especially on calcareous soil, the number of groups was 400 μmol / g of dry cell weight. (*see* Table 1).

In fact, the cation exchanger group includes the carboxyl group of ά-D-polygalacturonic acid (COOH PGUA). The maximum values of this acid were found in the leaf cell walls of *Betula nana* (1900 μmol / gram dry weight of cell walls), high values – in *Dryas octopetala* (1100 μmol / gram dry weight of cell walls) and low values – in *Salix polaris* (450 μmol / gram dry weight of cell walls) and *Cassiope tetragona* (600 μmol / gram dry weight of cell walls) (*see* Table 1).

The second cation-exchange group is the carboxyl group of hydroxycinnamic acids (COOH HCA). The studied plant species were grouped according to the amount of COOH HCA in the leaf cell wall: the first group of plants with the highest values included *Betula nana* (2500 μmol / gram dry weight of cell walls), *Dryas octopetala* (3000 μmol / gram dry weight of cell walls), and the second group with lower values consisted of *Salix polyaris* (1700 μmol / gram dry weight of cell walls) and *Cassiope tetragona* (750 μmol / gram dry weight of cell walls) (*see* Table 1).

The third cation-exchange group is presented by phenolic OH-groups that comprise in the components of the secondary cell wall such as lignin and suberin. The high amount of these groups in the cell wall was registered for such species as *Betula nana* and *Dryas octopetala* (2700 and 2600 μmol / gram dry weight of cell walls, respectively). Species *Cassiope tetragona* had half as manly of phenolic OH-groups in cell walls – 950 (μmol / gram dry weight of cell walls) and *Salix polaris* had even less groups – 550 (μmol / gram dry weight of cell walls) (*see* Table 1).

The values of the total amount of all the studied functional groups of the leaf cell walls varied from the maximum in *Betula nana* (8300 μmol / gram dry weight of cell walls) to the minimum in *Cassiope tetragona* (2700 μmol / gram dry weight of cell walls) (*see* Table 1). Among the studied species *Betula nana* and *Dryas octopetala* had higher and similar values. The total amount of all functional groups in cell wall of species *Salix polaris* and *Cassiope tetragona* was almost 2–2.5 times less.

Analysis of group ratios in the leaf cell walls of the studied species revealed that among all species the carboxyl groups of hydroxycinnamic acids (from 28% in *Cassiope tetragona* to 54% in *Salix polaris*) and phenolic OH groups (from 18% in *Salix polaris* to 35% in *Dryas octopetala*) had highest percentage. The lowest values of percentage of amino groups were obtained for *Dryas octopetala* (7%) while the highest values of carboxyl groups of hydroxycinnamic acids were found in the cell wall of *Salix polaris* (54%) (*see* Table 2)

One of the indicators of the functional state of the cell wall is the ionization constant of ion-exchange groups, which depends on the qualitative composition of polymers and their polymerization degree.

The highest values of the ionization constant (pK_a) were registered for phenolic OH groups (9.03–9.73) and COOH HCA (7.79–8.07) as element of the phenolic compounds. The lower values of pK_a were characteristic of COOH PGUA (5.87–7.04) and the minimum values were obtained for the amino groups (3.38–4.50). However, the differences between plant species according to the range of pK_a variation were less significant for COOH HCA (0.49%) and phenolic OH groups (0.88%) (*see* Table 3). This might be indicate a significant role of phenolic compounds in the developing of plants adaptation to high latitude conditions.

Type of group	Amount of groups, S μmol / gram of dry cell weight			
	Betula nana	*Dryas octopetala*	*Salix polaris*	*Cassiope tetragona*
Amino groups	1200±50[a]	500±50[b]	450±30[b]	400±20[b]
COOH PGUA	1900±30[a]	1100±50[b]	450±20[c]	600±40[c]
COOH HCA	2500±90[a]	3000±60[a]	1700±90[b]	750±30[c]
Phenolic OH-group	2700±80[a]	2600±60[a]	550±25[b]	950±70[c]
Total number of cation exchange groups	7100±100[a]	6700±80[a]	2700±50[b]	2300±50[b]
Total number of functional groups	**8300±100[a]**	**7200±90[a]**	**3150±50[b]**	**2700±50[c]**

Table 1. The content of ion-exchange groups in leaf cell wall of Arctic plants.
Data presented with different letters in the same line indicate a significant difference at $p \leq 0.05$ from Arctic plants to Fisher's LSD test. Data were determined in 5 replications, standart deviation values are given after ±. *Abbreviations*: COOH PGUA - carboxyl group of ά-D-polygalacturonic acid, COOH HCA - carboxyl group of hydroxycinnamic acids.

Type of group	*Betula nana*	*Dryas octopetala*	*Salix polaris*	*Cassiope tetragona*
Amino groups	15±2[a]	**7**±2[a]	14±2[a]	15±2[a]
COOH PGUA	23±3[b]	15±1[b]	14±1[a]	22±1[b]
COOH HCA	30±2[c]	43±2[c]	**54**±5[b]	28±4[b]
Phenolic OH-group	32±5[c]	35±3[c]	18±3[a]	35±2[c]

Table 2. Group ratios in the leaf cell walls of Arctic plants (%).
Data presented with different letters in the same column indicate a significant difference at $p \leq 0.05$ from % type of group to Fisher's LSD test. Data were determined in 5 replications, standart deviation values are given after ±. *Abbreviations*: COOH PGUA - carboxyl group of ά-D-polygalacturonic acid, COOH HCA - carboxyl group of hydroxycinnamic acids.

Plant species	Ionization constant of ion-exchange groups, pK_a			
	Amino group	COOH PGUA	COOH HCA	Phenolic OH- group
Betula nana	4.50±0.62	7.04±0.22	7.95±0.15	9.40±0.08
Dryas octopetala	3.38±0.58	5.87±0.35	7.79±0.18	9.03±0.09
Salix polaris	4.05±0.45	6.42±0.41	8.07±0.10	9.73±0.10
Cassiope tetragona	3.39±0.32	6.22±0.12	7.62±0.10	9.35±0.11
CV, %	7.78	3.77	0.49	0.88

Table 3. The ionization constants of ion-exchange groups (pK_a) and their coefficient of variation of leaf cell wall of Arctic plants. Data were determined in 5 replications, standart deviation values are given after ±. *Abbreviations*: COOH PGUA - carboxyl group of ά-D-polygalacturonic acid, COOH HCA - carboxyl group of hydroxycinnamic acids.

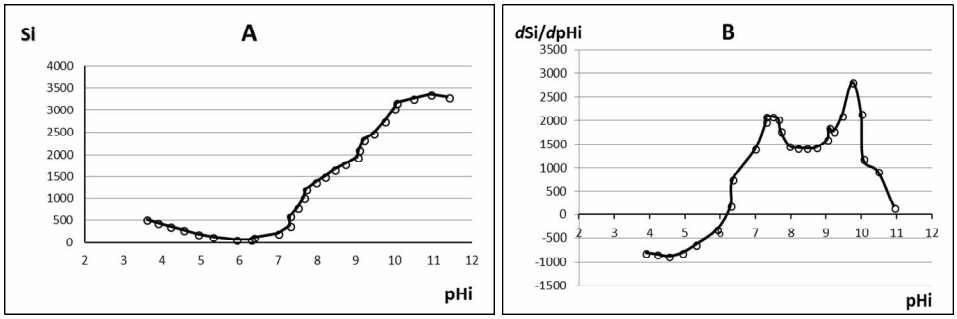

Fig. 1. The potentiometric curve (**A**) and the differential curve (**B**) obtained from the experimental data of titration of the *Salix polaris* leaf cell wall.

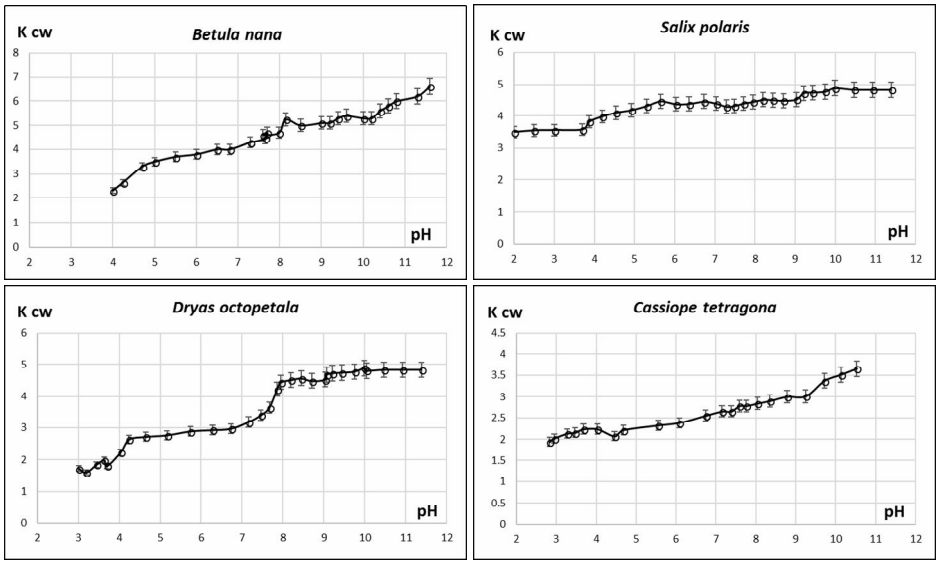

Fig. 2. Dependence of the swelling constant K_{cw} (g H_2O / g of dry cell weight) of the cell wall in leaves of the Arctic plants on the pH of the solution.

The measurements showed that the highest values of K_{cw} *in water* were registered for the cell wall of *Salix polaris* (2.6 g H_2O / g dry cell wall weight). The lower values of K_{cw} were obtained for *Betula nana* and *Dryas octopetala* (1.93 and 1.45 g H_2O / g dry cell wall weight, respectively) and the lowest one (0.83 g H_2O / g dry cell wall weight) was recorded for *Cassiope tetragona*.

In fact the process of swelling in the roots cell walls is related to the pH of the external solution (Meychik et Ermakov 2001). Little is known about these processes in the leaves. When changing the pH of the external solution from 2–3 to 5-7, the K_{cw} of the cell wall varies as follows: *Betula nana* from 1.8 to 6.5, in *Salix polaris* –from 3.5 to 5, in *Dryas octopetala* – from 1.8 to 5, and *Cassiope tetragona* - from 2 to 3.7 (g H_2O / g dry weight of the cell walls) (*see* Fig. 2).

Discussion

The transport function of the plant cell wall includes the transportation of substances through the apoplast and it is associated with the formation of special structures of the cell wall. These structures are deposited in the period of cell wall formation and they regulate and direct transport flows (Gorshkova 2007) that emerge during the growth and development of plants. Being a weak cation exchanger, cell wall enhances the transportation of water-soluble molecules including water, gases and various low-molecular substances. All of them are slightly affected by the counteraction on the part of the cell wall structures (up to 10–15%). According to Gorshkova (2007), the number of functional groups is species-specific and depends on the species origin, features of the cell wall structure, physiological features as well as geographical range. Using the method of potentiometric titration Meychik et al. (1999) four types of ion-exchange groups were found, three of which were cationexchanging groups (carboxylic groups of two types, with one attributed to α-D-galacturonic acid, and a phenolic group), and the fourth was the anion-exchanging group. The ion-exchange amino groups of the cell wall are a part of structural proteins and enzymes and their amount can reach 15% of the cell mass. As Gorshkova (2007) reported, they represent continuous series from alkaline, minimally glycosylated proteins (proline–rich) to acidic, highly glycosylated proteoglycans (arabinogalactan proteins). The main amino-acid in the hydrolyzate of the cell wall is hydroxyproline, that can comprise up to 40% (Lamport 1970). The enzyme system of the cell wall is represented by hydrolases that hydrolyse the polysaccharides and lead to the changes in the physical properties of the cell wall and ion exchange changes. In the formation of the surface layers of the epidermis (cutin and suberin), that can be found in almost all leaves of the Arctic plants, transacylases take a part.

The main polymer of pectic substances is polygalacturonic acid, with its polymers in the pyranose form. Pectic substances are natural ion exchangers and their main function is to regulate the action of enzymes through the creation of a mobile system of local changes in pH and electric charge. Thus, polygalacturonic acid is particularly responsible for the negative charge of the cell wall (Gorshkova 2007). COOH HCA is a metabolic constituent of suberin, kutin and pectin polysaccharides. Moreover, such oxycinnamic acids as n-coumaric, ferulic and synapic are regarded as to the labile metabolic constituent of the cell wall (Gorshkova 2007). Due to the formation of diferulates, ferulic acid can serve a structural function in the cell walls by means of binding the polysaccharides and reducing the extensibility of the cell walls (Sharova 2004, Iiyama et al. 1994). Phenolic acids of cell walls can participate in oxidation-reduction processes as reducing agents, contributing to the recycling of active forms of oxygen. They can also act as growth regulators and play a signaling role in the interaction of plants and microorganisms (Wallace et Fry 1994).

In fact, lignin as a structural stable component of the cell wall comprise up to 40% of its dry mass. Phenolic compounds, the products of secondary metabolism, play several functions in the plant, including defense, both from biogenic and from abiogenic factors.

It is reported that the number of ionogenic groups in the structure of the plant cell wall of different organs can be affected by heavy metals (Krzeslowska 2011) and salinization (Meychik et al. 2006, Meychik et al. 2010).

Thus, the results of the study showed that the leaf cell wall of plants in the Arctic region is a cation exchanger, which is represented by a similar composition of

ion-exchange groups with the leaf cell walls of other tree species (Terebova et Galibina 2010) and roots of herbaceous plants (Meychik et Yermakov 2001). However, the Arctic plants are characterized by increasing (2–3 fold) the amount of ion-exchange groups of each type in the structure of the leaf cell wall compared with species of other climatic zones (Galibina et Terebova 2014). This is mainly related to the increase in phenolic OH groups in leaf cell wall. This fact corresponds to the previous by obtained data on the increased (almost 5–fold) content of flavonoids in Arctic plants (Markovskaya et Shmakova 2012).

Cell wall as a structural unit is characterized by the property of swelling, which determines its hydraulic conductivity. The swelling coefficient K_{cw} (g H_2O / g of the dry weight of the cell walls) is a quantitative characteristic of the permeability of the polymer matrix of the cell wall and it depends on the degree of cross-linking between cell wall polymers (stiffness) as well as the total number of functional groups, and their ionization constant, and external solution concentration (Meychik 2007).

For leaf cell wall of Arctic plants the higher values of swelling coefficient K_{cw} of in solutions with different pH were registered (1.8–7g H_2O / g dry weight of the cell walls) in comparison with plants from southern regions (1.5–3.5 g H_2O / g dry weight of the cell walls) (Galibina et Terebova 2014). This might be explained by the dominance of the apoplastic transport, where a higher sugar content leads to increase in the osmotic potential controlling the hydrostatic pressure (Gamalei 2013). The highest values of K_{cw} in water of leaf cell wall of *Salix polaris* are caused by the weakest degree of cross-linking between polymer chains of the cell wall and consequently more intensive water flow in the cell wall system in comparison with other species. The lowest values of K_{cw} in water of the leaf cell wall of *Cassiope tetragona* are possibly related to high degree of cutinization and resinification of epidermis, as well as parenchymal cells that contributes to the rigidity of the cell wall structure.

Comparative analysis of leaf cell wall properties of studied Arctic plants allows to determine two ways of adaptation involving the cell wall structure. These ways are expressed differently in all the studied species. First way is associated with the synthesis of protective substances (cutin, suberin) preventing the direct impact of environmental factors on the plant organism. The second way includes increasing in the functional activity of the plant apoplast, where water and carbohydrate fluxes increase including by increasing the amount of the cell wall free space due to the formation of apoplastic labyrinths (Gamalei 2013).

The first way is recorded mostly for species *Cassiope tetragona* which is characterized by the synthesis of protective substances (cutin, suberin). However this species has a lower ion-exchange capacity of leaf cell wall and lower values of swelling coefficient compared to other studied species.

The second way is expressed mainly for the cell wall of the *Betula nana*. The species is characterized by a higher ion-exchange capacity of leaf cell wall as well as higher values of the swelling coefficient, associated with a greater activity of metabolic processes in the apoplast. The first way («structural adaptation») was typical for widespread species in the territory of Western Spitsbergen while the second way («metabolic adaptation») was found for species sporadically represented in this territory, being at border of its geographical range.

The obtained data for the first time showed that there are functional differences at the level of composition of ionogenic groups of the cell wall in Arctic species, but all species are characterized by its high functional activity in comparison with plants of lower latitudes. This result corre-

sponds to the with previous studies of the high photosynthetic and respiratory activity of Arctic plants (Semichatova et al. 2007, Muraoka et al. 2008).

In the process of evolution, one of the conditions for the expansion of the plants to the conditions of the Arctic was the maintenance in the homeostasis of organisms in extreme environmental conditions. Homeostasis of the internal environment was achieved in particular due to the development of exodermises tissues and protective structures defending the body from the negative impact of factors. The evolution of Arctic plants was accompanied by the development of organs and mechanisms that ensured connection between plants and the environment. This could occur by means of introduction of additional functions in existing structures. The cell wall could also be included in this process, and in addition to perfoming function was also included in the metabolic processes, which led to the increase in the integrity of the organism (Volkov 2006). This was especially true for northern plants, with the increased role of the apoplastic flow, in which a crucial role is given to metabolic processes in the free space of the cell wall (Gamalei 2004). This conclusion is congruent with the strategy of adaptive plant evolution, which opted for increasing the overall efficiency of structures and minimizing the negative impact of external factors (Gamalei 2013, Markovskaya et Schmakova 2017).

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