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RESEARCH ARTICLE

Seasonal changes in dehydrins composition in *Picea obovata* Ledeb. from cryolithozone of Yakutia

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Abstract

This study presents the first analysis of the composition and seasonal changes of stress proteins-dehydrins induced by low temperatures in the shoots of Siberian spruce (*Picea obovata* Ledeb.), growing in the extremely cold climate of the cryolithozone of Central Yakutia. The identification of dehydrins was carried out using specific antibodies against their conserved K-segment (Agrisera, Sweden). It is shown that most of the major dehydrins with mol. wt. of 17–57 kD are relatively uniformly represented in the annual cycle of *P. obovata*, which indicates their constitutive properties. On the contrary, low-molecular dehydrins of 13 and 15 kD in spruce shoots are seasonally-dependent, inducible proteins: they almost disappear in the summer months and reappear in autumn during the period of cold adaptation when preparing trees for long dormancy. A high level of major dehydrins persisted in the low-temperature winter period, when ultra-low negative temperatures were observed and plants reached maximum frost resistance. The revealed features of seasonal dynamics and a significant representation of dehydrins in the shoots of Siberian spruce are probably associated with the formation of a unique resistance of this species of woody plants to extreme cold in the conditions of the cryolithozone of Yakutia.

Keywords

Cold tolerance, cryolithozone, dehydrines, *Picea obovata*, seasonal changes

Introduction

Forest-forming conifer species in northern regions exhibit exceptional winter survival, a trait underpinned by sophisticated cold adaptation mechanisms.The unique natural and climatic conditions of Central Yakutia, characterized by extremely low winter temperatures and permafrost, significantly limit the distribution and species composition of woody plants, having developed an unusually high frost resistance in them. In the taiga of Eastern Siberia, the dominant forest species are the larches of Cajander and Gmelin, as summer-green species that are less demanding of soil and climatic conditions, including the close occurrence of permafrost soils. Of the coniferous woody plants of Yakutia, both species of larch occupy more than 79% of the forested area of the republic (Timofeev 2003). One of the main forest-forming dark coniferous species with a narrow range in Yakutia is the Siberian spruce (*Picea obovata* Ledeb.). Together with Gmelin's larch, to the west of the Lena River, Siberian spruce forms the northern border of forests. Within Yakutia, spruce forests are found almost throughout the middle taiga subzone; in the arid central regions of Yakutia, spruce grows in narrow ribbons along rivers and on islands, vegetating in extrazonal forest-growing conditions on moist fertile soils (Pozdnyakov 1986). Siberian spruce is a mesophyte and is demanding on soil fertility. It prefers well-moistened, drained, rich alluvial soils. Being a very shade-tolerant species, it grows better in dense growth. In the conditions of the permafrost zone, it forms narrow forests, under the canopy of which the soil warms up. This species, the most frost-resistant and winter-hardy of all representatives of the genus *Picea*, tolerates extremely low temperatures (down to –60 °C) in Central Yakutia. Fully acclimatized needles, buds, and cambium tissues of Siberian spruce can withstand immersion in liquid nitrogen at −196 °C (Strimbeck et al. 2007).

In cold adaptation processes, biochemical changes occurring in a wide range of different plant species include fatty acid desaturation and lipid composition changes, accumulation of sucrose and oligosaccharides, proline, glycine-betaine, and stress protein synthesis (Li et al. 2004). Among the polypeptides involved in the processes of cold hardening, a number of proteins with structural similarities with proteins of late embryogenesis (LEA) are of particular interest. Group II of the superfamily of LEA proteins includes dehydrins, highly hydrophilic heat-stable proteins induced by dehydration (Close 1996; Allagulova et al. 2003). They are characterized by the presence of highly conserved Y-, S- and K-segments, as well as glycine-rich sequences. Dehydrins are detected under many stress effects (low temperatures, drought, salinity), accompanied by changes in the water status of plants. They are involved in stabilizing macromolecules and membranes. Different combinations of variable Y-segments, S-segments and a conserved K-segment determine their functional properties (Hara et al. 2001; Welling, Palva 2006; Malik et al. 2017; Karas et al. 2024). Dehydrins are thought to protect biopolymers and cell membranes from denaturation caused by plant water disturbance at low temperatures, and exhibit cryoprotective, antifreeze, antioxidant, and metal-binding functions (Svensson et al. 2002; Welling, Palva 2006; Kosova et al. 2010; Hara et al. 2010). Thus, it has been shown that the seasonal accumulation of some dehydrins contributes to the acquisition of frost resistance of coniferous trees not only to osmotic, but also to low-temperature stress. To date, dehydrins have been found in the needles of Siberian spruce *Picea obovata* in the northeast of Fennoscandia (Kjellsen et al. 2013) and in southern Siberia (Korotaeva et al. 2020). The relationship between the seasonal accumulation of some dehydrins and the development of frost resistance of coniferous trees has been revealed, for example, in Siberian spruce *Picea obovata* (Kjellsen et al. 2013) and Weymouth pine *Pinus strobus* (Chang et al. 2016).

At the same time, the physiological and biochemical mechanisms of resistance of woody plants to extremely low temperatures, in which dehydrin proteins take part, are almost not studied. In this regard, it seems very relevant to study the mechanisms responsible for the formation of the unique ability of woody plants to tolerate extremely low winter temperatures characteristic of the permafrost zone, as well as adaptive changes in the composition of stress proteins-dehydrins in wintering above-ground organs – shoots, which experience prolonged low-temperature stress in extremely cold climates. Studies of this kind in the cold regions of Northeast Eurasia, which includes the Republic of Sakha (Yakutia), have not yet been conducted.

The purpose of this work was to study the composition and seasonal changes of dehydrins in the annual cycle of coniferous plants on the example of shoots of Siberian spruce (*Picea obovata* Ledeb.), growing in the cold climate and permafrost conditions of Central Yakutia.

Materials and methods

Study Species and Site

The study object was Siberian spruce (*Picea obovata* Ledeb.), a boreal East Asian species, one of the forest-forming species of the North-East of Siberia, which has a narrow ecological range in Yakutia (Fig. 1). Plants growing in the natural and climatic conditions of Central Yakutia, which are characterized by ultra-low winter temperatures and the presence of permafrost (cryolithozone), are subject to the greatest impact of stress factors.

The sharply continental climate of Central Yakutia is characterized by large amplitudes of fluctuations in absolute maximum and minimum temperatures, which reach 99–104 °C, while winter temperatures can reach –64 °C (Fig. 2). Permafrost (cryolithozon) is ubiquitous. At the same time, the woody plant species growing in these conditions are characterized by early periods of entering a state of deep dormancy, as well as a very long period of forced dormancy at extremely low winter temperatures. As a result, low-temperature stress acts as the main selection factor in the adaptation of plants to the conditions of the North. For example, in the conditions of Central Yakutia, the average daily temperature in January is about

–40 °C (without recurrent warming in winter), while in July it is about 20 °C. The frost-free period takes about 78 to 126 days, which determines the duration of the short growing season in Yakutia up to 3.5 months. The summer-autumn months, which are optimal in terms of precipitation, contribute to the creation of favorable conditions for storing water in the soil, with an average annual precipitation in the range of 173–293 mm.

Figure 1. Siberian spruce (*Picea obovata* Ledeb.), which grows naturally in Central Yakutia. Photo courtesy of A.P. Efimova (February 2025).

The climatic indicators of the average monthly air temperature during the period of sample collection did not differ from the long-term average, when negative values close to the norm were noted. So, the average monthly air temperature in January was –38.6 °C, in July 19.9 °C, the average precipitation was 237 mm. Temperature records in the region were taken from http://meteo.ru/data.

Plant Material and Sampling

The material of the study was the shoots (annual growth) of Siberian spruce (*Picea obovata*), which grows in the natural conditions of the cryolithozone. The age of the trees was about 45–50 years. Plant samples were collected in 2014–2015 in the forest park area of the Botanical Garden of IBPC SB RAS, located in the vicinity of Yakutsk (62 °N, 129 °E). To study the seasonal dynamics of proteins, samples were taken all year round, the material was collected at least once a month throughout the year, 3–5 shoot samples from three Siberian spruce trees. Sampling was carried out in the first half of the day morning (9:00–11:00). The samples were immediately fixed in liquid nitrogen and stored in a freezer at –80 °C (Panasonic, Japan) until protein extraction.

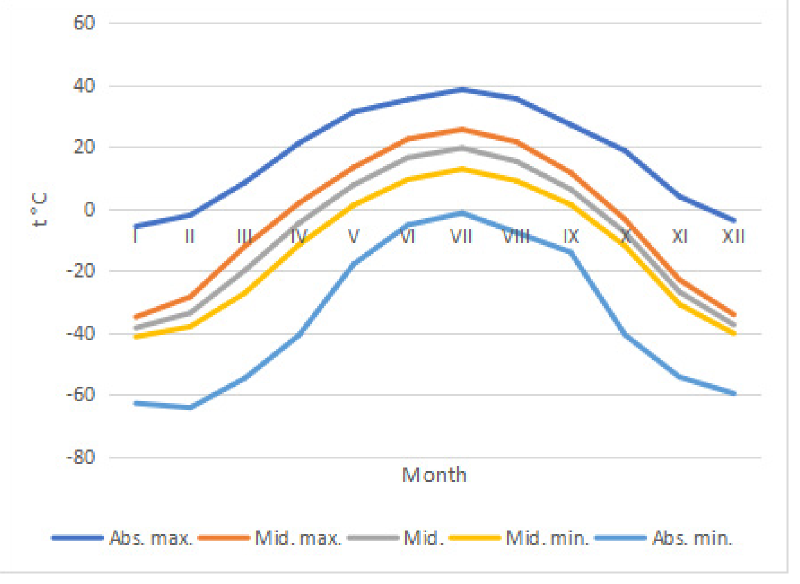

Figure 2. Dynamics of the average monthly temperature in Central Yakutia. The average long-term indicators of absolute maximum and minimum, average values, maximum and minimum temperature are given (according to http://pogodaiklimat.ru/climate/24959.htm).

Protein Extraction and Quantification

Total proteins were extracted from the annual shoots of Siberian spruce according to Korotaeva (2012). A sample amount (1.5–2.0 g) was ground in a mortar in liquid nitrogen in the presence of insoluble polyvinylpyrrolidone (Serva, Germany, 2.5% by volume of buffer). All procedures were performed at a temperature of +4 °C. Proteins were extracted with a buffer containing 0.1 M Tris-HCl, pH 7.5, 12 mM β-mercaptoethanol, 1% DDS-Na, 10 mM EDTA, 3 mM PMSF (phenylmethylsulfonyl fluoride). The homogenate was centrifuged at 50000 g for 40 min. Polyvinylpyrrolidone (2.5%) was added to the supernatant filtered through a nylon cloth and centrifuged at 50000 g for 35 min. The total proteins were precipitated with five volumes of acetone at -20 °C for 1 h. Protein precipitate was homogenized in an electrophoretic buffer containing 1 M Tris-HCl, pH 7.5, 10% DDS-Na, 5% β-mercaptoethanol, 10% glycerol. The protein solution was clarified by centrifugation at 17000 g (20 min, +4 °C) and used for electrophoresis. Protein content was determined by the Bradford method (Bradford 1976).

Electrophoresis and Immunoblotting

Electrophoretic separation of proteins was carried out in 13.5% PAAG in the presence of DDS-Na according to the Laemmli method (Laemmli 1970) using molecular weight markers (ThermoScientific, USA) and subsequent staining with Coumassi G-250 (Serva, Germany). An equal amount of protein (10–15 μg) was applied to the tracks. Protein alignment in PAAG tracks was carried out experimentally according to the intensity of color of protein bands in comparison with the known amount of the control sample (10–15 μg). Protein transfer from PAAG to PVDF (polyvinylidene difluoride) membrane (Bio-Rad, USA) was carried out according to the Timmons and Dunbar method (Timmons, Dunbar 1990). Identification of dehydrins was performed using polyclonal antibodies against their K-segment (EKKGIME/DKIKEKLPG) at a dilution of 1:500 (Agrisera, Sweden). Dehydrins were visualized using anti-rabbit antibodies conjugated with alkaline phosphatase at a dilution of 1:2500 (Sigma, USA). 5-bromo-4-chloro-3-indolyl phosphate and nitrotetrazolium blue were used as chromogenic substrates (AppliChem, Germany).

Data Analysis

Gel and membrane scanning data were processed using ImageJ 1.46r (USA). Quantitative indicators of the content of dehydrins were estimated by the intensity of membrane color in relative units of densitometric density (D, relative units). The value of the densitometric density of dehydrin with mol. wt. of 13 kD in July is taken as a zero level. The figures show typical membranes reflecting stably reproducible results of immunodetection of dehydrins using specific antibodies against the K-segment. Measurements were carried out in a threefold biological repeat using the statistical package of Microsoft Office Excel, the results show arithmetic averages and their standard deviations, the differences are significant at $P < 0.05$. The differences are significant at $P < 0.05$ (Student's t-test) when comparing the content of individual dehydrins between the winter (December-February) and summer (June-August) months in their seasonal cycle (some insignificant differences are discussed in the Results).

Results

An important role in the adaptation of plants to abiotic stressors is played by protective proteins-dehydrins, the features of the structure and physicochemical properties of which determine their participation in the protection of biopolymers and cell membranes from dehydration under stress. This study showed that in annual shoots of *P. obovata*, growing in the natural and climatic conditions of the cryolithozone of Central Yakutia, stress proteins-dehydrins were found, mainly in a range of mol. wt. of 13–57 kD. In the shoots of Siberian spruce, the protein spectra in the seasonal cycle of plants were characterized by a wide variety of dehydrins. Using specific antibodies to the conserved K-segment in *P. obovata* shoots, major dehydrins with mol. wt. of 13, 15, 17, 24, 29, 35, 37, 45 and 57 kD were identified in *P. obovata* shoots (Fig. 3).

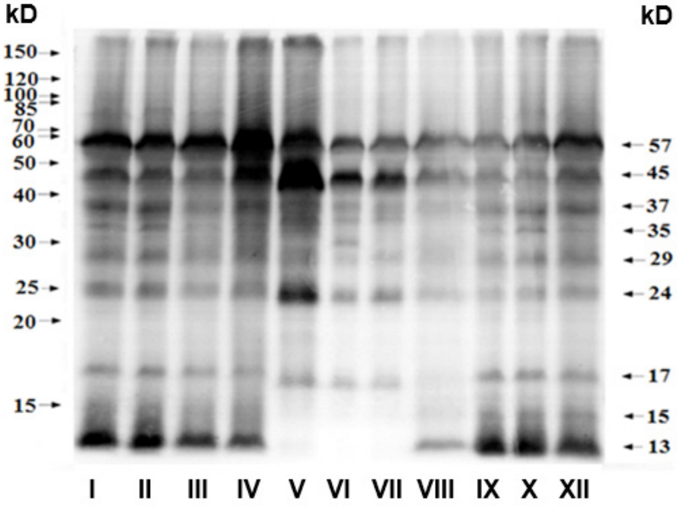

Figure 3. Seasonal changes in dehydrins in shoots of Siberian spruce (*Picea obovata* Ledeb.) in Central Yakutia. Typical membranes of immunodetection of dehydrins are presented. Molecular weights are indicated: markers (M) on the left, dehydrins on the right.

We have found that during the annual cycle, most of the major dehydrins in spruce shoots in the autumn-winter periods are evenly represented, but undergo significant changes in the summer months. Quantitative characteristics of dehydrins in annual shoots of Siberian spruce are shown in Figs 4–6. The detected changes in the composition of individual dehydrins are clearly traced on histograms, from which it follows that a consistently high level of almost all dehydrins in spruce shoots was observed in the winter months (December–February) during the period of prolonged dormancy of trees, when ultra-low negative temperatures were observed.

On the histograms (Figs 4–6) the data are presented in the form of arithmetic averages and their standard deviations, the differences are significant at $P < 0.05$ when comparing their contents between winter (December-February) and summer (June-August) months in the seasonal cycle. Only 45 kD dehydrin showed the opposite trend – a slight increase in summer with insignificant differences compared to the winter period.

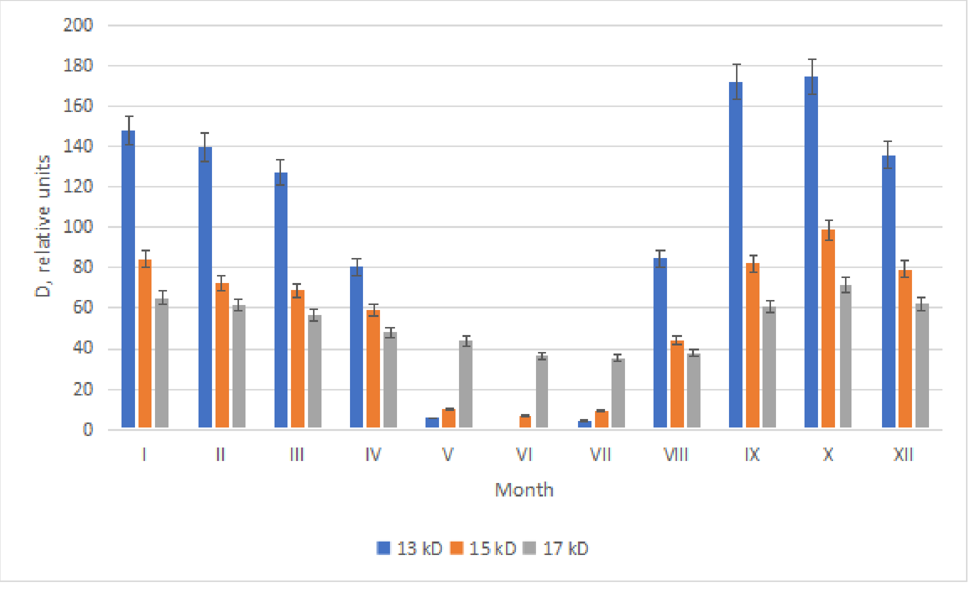

Figure 4. Seasonal changes in the content of dehydrins of 13, 15 and 17 kD in the shoots of Siberian spruce (*Picea obovata* Ledeb.) in the conditions of Central Yakutia. Densitometric density (D, relative units) of 13 kD of dehydrin in June was taken as zero.

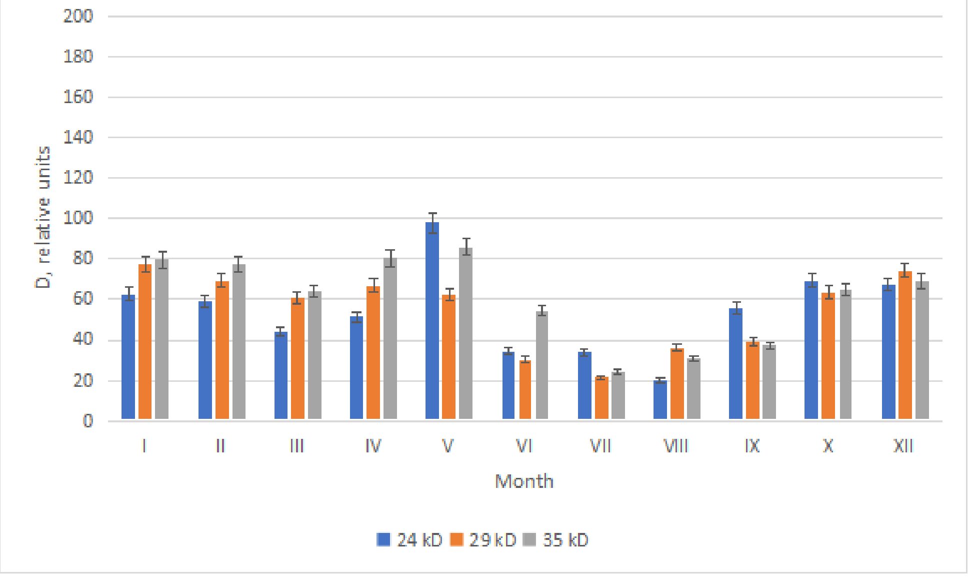

Figure 5. Seasonal changes in the content of dehydrins of 24, 29 and 35 kD in the shoots of Siberian spruce (*Picea obovata* Ledeb.) in the conditions of Central Yakutia.

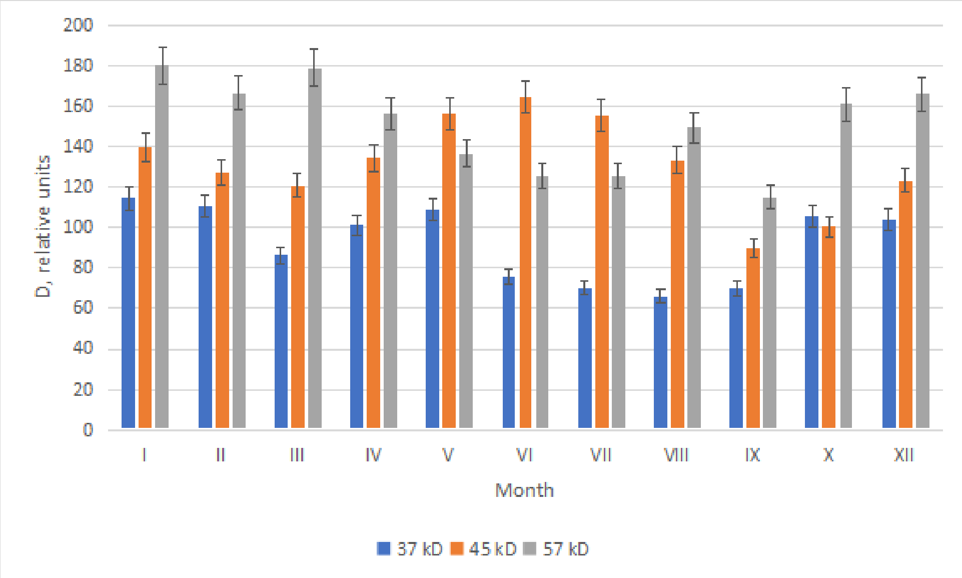

Figure 6. Seasonal changes in the content of dehydrins of 37, 45 and 57 kD in the shoots of Siberian spruce (*Picea obovata* Ledeb.) in the conditions of Central Yakutia.

Low-molecular dehydrins are subject to the most pronounced changes in the annual cycle of *P. obovata* (Fig. 4). Thus, seasonally-dependent proteins in the shoots of Siberian spruce are dehydrins with mol. wt. of 13 and 15 kD, which were found during the dormancy of trees, but were actually absent in July. With the beginning of growth processes in April–May, a significant decrease in their content was observed in spruce shoots, up to complete disappearance, and a low, but stable, level in the summer months. Resumption of the synthesis of dehydrins in spruce shoots occurred in autumn when trees went dormant (end of August–September) with the achievement of maximum values in October by the end of phenological autumn. At the same time, the dynamics of dehydrins with average molecular weights had a smoother seasonal variability (Figs 5, 6). These proteins were present in all seasons and did not disappear completely in summer, although their number, except for 45 kD dehydrin, decreased markedly during plant growth and development (June–August).

Discussion

Molecular mechanisms of adaptation of woody plants to abiotic environmental factors in the North-East of Eurasia have not been sufficiently studied at present. A significant part of the time in the natural and climatic conditions of Yakutia, the tissues of wintering plants in the autumn-winter period are in a state of deep, and then prolonged forced dormancy. Along with this, the above-ground organs of woody plants are most susceptible to long-term exposure to low temperatures, leading to osmotic stress. Protective proteins-dehydrins are also likely to take part in the formation of plant resistance to extreme conditions of the permafrost zone, preventing the cell from losing water due to high hydrophilicity and stabilizing macromolecules and membranes (Hara 2010; Hanin et al. 2011; Cuevas-Velazquez et al. 2014; Malik et al. 2017; Chang et al. 2021).

To identify the probable relationship of dehydrins with the formation of frost resistance in the specific conditions of the permafrost zone of Yakutia, a study of their seasonal dynamics in the shoots of Siberian spruce was undertaken. It was found that the features of seasonal changes in dehydrins in the annual cycle of Siberian spruce were: a decrease in the level of dehydrins after the plants come out of dormancy, their minimal content or absence during the growing season, the appearance and their accumulation at the end of summer during the autumn preparation for dormancy (August–September). At the same time, during the transition of plants to dormancy, the inducer of their autumn rise can apparently be a photoperiodic reaction, which contributes to the beginning of the synthesis of stress proteins, including dehydrins, in advance, before relatively low temperatures are reached. At that, same time, the level of individual dehydrins increased markedly and remained consistently high during the period of ultra-low negative temperatures in the winter months (October–February). Such appearance of dehydrins, especially low-molecular ones, during the autumn acclimation of plants to the cold indicates their inducible nature, caused by the processes of reducing the length of the day and increasing the cold factor.

Similar dynamics in the accumulation of dehydrins of different molecular weights was found in coniferous woody plants. For example, dehydrins of 32, 34 and 50 kD, characteristic of two species of spruce, *Picea glauca* and *P. obovata*, accumulated during periods of cold stress and disappeared under optimal growing conditions in the northeast of Fennoscandia (Strimbeck et al. 2015). In the conditions of the Cis-Baikal region, dehydrins with mol. wt. of 17, 26 and 32 kD (Korotaeva et al. 2012), are considered to be specific for winter dormancy of pine Pinus sylvestris; dehydrins of 14.5, 34, 38, 55 kD were detected in the needles of Siberian spruce *Picea obovata* in October (Korotaeva et al. 2020), close in mol. wt. values to those in the needles of spruce *Picea obovata* (33, 35 and 53 kD) in Norway, previously described in the work (Kjellsen et al. 2013). Accumulation of low-molecular dehydrins in wintering woody plants occurred mainly only during periods of low negative temperatures, which indicates their clear relationship with the adaptation of trees to the cold factor, observed in gymnosperms, including those resistant to extreme temperatures, such as *Pinus sylvestris* in climatic conditions of northern Finland and Central Yakutia (Kontunen-Soppela, Laine 2001; Tatarinova et al. 2017), *Larix cajander* (Tatarinova et al. 2023), *Picea glauca* in Canada (Liu et al. 2004), *Picea obovata* (Kjellsen et al. 2013). For example, increases in dehydrin levels associated with adaptation to low temperatures have been observed in gymnosperms, including those resistant to extreme temperatures, such as *Pinus sylvestris* (Kontunen-Soppela, Laine 2001; Tatarinova et al. 2017), *Larix cajander* (Tatarinova et al. 2023), *Picea glauca* (Liu et al. 2004), *Picea obovata* (Kjellsen et al. 2013). Some differences between the molecular weights of dehydrins of Siberian spruce, growing in the natural conditions of the permafrost zone, in comparison with those given in the literature, can probably be associated with the species and tissue specifics of plants, as well as the properties of the antibodies used in the work. It should be noted that at least 53 different types of dehydrins have been identified from the white spruce (*Picea glauca*) in Canada gene database alone (Rigault et al. 2011).

In some genera of conifers, such as larch, spruce and fir, the number of types of dehydrins significantly exceeds that of pine. Such a diversity of dehydrins is probably caused by specific features of adaptation that led to the divergence of phylogenetic branches (taxa) (Sena et al. 2017). In addition, the high diversity of major dehydrins in spruce shoots may be due to the ecological plasticity of Siberian spruce and the more moisture-loving nature of this species of coniferous trees. The accumulation and maintenance of high levels of dehydrins in spruce shoots during the transition to long-term dormancy suggest the participation of these proteins in the protection of cells from dehydration during the low-temperature winter period, thereby contributing to the survival and successful overwintering of *Picea obovata* when adapting to the conditions of the cryolithozone. Thus, the changes in the composition and high diversity of stress proteins-dehydrins in the seasonal cycle of Siberian spruce indicate their important role in the formation of resistance of evergreen conifers to the extremely cold climate of Yakutia.

Conclusions

This study provides the first evidence of seasonal variation in dehydrin stress proteins in shoots of Siberian spruce (*Picea obovata* Ledeb.) from Yakutia. Immunoblot analysis identified a suite of major dehydrins in a mol. wt. range of 13–57 kD, the consistently high content of which during the winter dormancy period correlates with the highest frost resistance of trees. The discovered features of seasonal changes in dehydrins in the shoots of Siberian spruce suggest their participation in the formation of frost resistance of woody plants in the extremely cold climate of Yakutia.

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