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CHANGES IN THE CONTENT OF WATER-SOLUBLE SUGARS IN NEEDLES OF SCOTS PINE AND SIBERIAN SPRUCE GROWING IN THE SOUTH OF EASTERN SIBERIA

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Scots pine (Pinus sylvestris L.) and Siberian spruce (Picea obovata Ledeb.), which are common for the south of Eastern Siberia, differ from each other in their ecophysiological characteristics. Scots pine is more thermophilic and drought-resistant, while Siberian spruce is more hydrophilic and tolerates cooling better. In different seasons, both species accumulate water-soluble sugars (WSS) in their needles, which are one of the factors of cold and drought resistance of needles. The level of WSS accumulation in needles can be influenced by both factors determined by the tree species and territorial ones, associated with the climate of the growing region. For the first time, this study introduces a comparison of changes in WSS content in Scots pine and Siberian spruce growing in the south of Eastern Siberia during two annual cycles. During the observation period, winter 2015-2016 was colder than winter 2016-2017, and the growth period 2015 was warmer and wetter than the same period in 2016. WSS content in Scots pine needles was found to be less subject to fluctuations and, according to the results of most of the observations made, to be higher than in Siberian spruce needles both in more favorable and less favorable conditions for the physiological activity. The exception was the period of November-February 2015-2016 (when WSS content in the needles of both species was the same) and March-April 2016 (when it was higher in Siberian spruce needles). The ability of Scots pine to maintain higher WSS reserve in its needles is possibly one of the mechanisms that allow trees of this species to successfully compete with Siberian spruce and occupy larger territories under the extreme conditions of the south of Eastern Siberia.

Keywords: *Pinus sylvestris L.; Picea obovata Ledeb.; south of Eastern Siberia; needle; water-soluble sugars; seasonal changes*

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ИЗМЕНЕНИЯ В СОДЕРЖАНИИ ВОДОРАСТВОРИМЫХ САХАРОВ В ХВОЕ СОСНЫ ОБЫКНОВЕННОЙ И ЕЛИ СИБИРСКОЙ, ПРОИЗРАСТАЮЩИХ НА ЮГЕ ВОСТОЧНОЙ СИБИРИ

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Распространенные на юге Восточной Сибири виды сосна обыкновенная Pinus sylvestris L. и ель сибирская Picea obovata Ledeb. отличаются друг от друга по своим экофизиологическим характеристикам. Сосна более теплолюбива и засухоустойчива, ель более влаголюбива и лучше переносит охлаждение. В различные периоды года оба вида накапливают в хвое водорастворимые сахара (ВРС), которые являются одним из факторов холодо- и засухоустойчивости хвои. На уровень накопления ВРС в хвое могут влиять как видовые, так и территориальные факторы, связанные с особенностями климата региона произрастания. В исследовании впервые на протяжении двух годичных циклов сравнивали изменение содержания ВРС у сосны обыкновенной и ели сибирской, произрастающих на юге Восточной Сибири. В период наблюдения зима 2015-2016 была морознее, чем зима 2016-2017, а период роста в 2015 был более теплым и влажным, чем аналогичный период в 2016. Установлено, что и в более благоприятных, и в менее благоприятных для физиологической активности условиях содержание ВРС в хвое сосны меньше подвергалось колебаниям и было почти всегда выше, чем в хвое ели, за исключением ноября-февраля 2015-2016 (когда содержание ВРС в хвое деревьев двух видов было одинаковым) и марта-апреля 2016 (когда оно было выше в хвое ели). Возможно, способность сосны обыкновенной поддерживать более высокий запас ВРС в хвое является одним из механизмов, который позволяет деревьям этого вида в экстремальных условиях юга Восточной Сибири успешно конкурировать с елью и занимать более обширные территории.

Ключевые слова: *Pinus sylvestris L.; Picea obovata Ledeb.; юг Восточной Сибири; хвоя; водорастворимые сахара; сезонные изменения*

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Introduction

Siberian spruce and Scots pine are one of the main forest-forming species in Eastern Siberia. Scots pine occupies more than a third of the forest area of Eastern Siberia, and Siberian spruce – no more than 10% of the area [5].The studying of the the ecophysiological features of these species is important for understanding their contribution to the carbon sink and reforestation possibilities, their significance for forest biocenoses, and for obtaining economically useful metabolites under the given climatic conditions. Siberian spruce belongs to cold-resistant and hydrophilic species. The habitat of Siberian spruce (compared to that of Scots pine) lies to the north; it enters the Primorye Territory with a more humid climate [6]. Scots pine is drought-resistant and potentially less resistant to cold, the southern border of its habitat lies to the south and enters the Mediterranean [6]. Scots pine production processes are mostly limited by the root system cooling, while Siberian spruce production processes are limited by the lack of moisture; moisture deficiency is not the main limiting factor for Scots pine productivity [2, 36]. However physiological capabilities for cold adaptation and protection against water deficiency are widely represented in both tree species [21, 31, 33, 34, 35].

An extensive group of mono- and polymers, which are based on a cyclic hydrocarbon and are easily soluble in water, refers to water-soluble sugars (WSS). The level of WSS content in plants is determined by the balance between production and growth processes. In addition, WSS content is influenced by the environmental conditions [8, 14, 25, 26, 28]. At the beginning of the active growth period in spring and in the middle of this period in summer, WSS content in perennial plants depends not only on the current level of photosynthesis, but also on WSS reserves from the previous year growth period [14]. The consumption of carbohydrates occurs differently. It depends on their origin and on the season. Prior to the start of active summer photosynthesis, WSS reserves are spent mainly on the formation, growth processes, and respiration of buds and young shoots [14, 20]. When young shoots begin to actively photosynthesize and grow owing to their own photosynthates, WSS reserves are directed to the growth of needles, second-year branches, and the main axial organs (stem, root) [14]. During the transition of perennial plants to the dormant period, WSS accumulates in their tissues [15, 32] both as the result of the decrease in metabolic sinks [16], and as the result of the seasonal cold adaptation reaction [13]. Episodically, photosynthesis sometimes occurs in temperate evergreens in winter during periods of rising air temperature. That is why little photosynthetic activity contributes to the accumulation of carbohydrates during the cold season [14]. WSS that contribute to the emergence of cold and frost resistance in woody plants are basically oligosaccharides (raffinose, stachyose) and, to a lesser extent, monosaccharides (glucase, fructose) [9, 15, 29, 35]. Drawing out water from cells is one of the stages of cold hardening. In this respect, soluble sugars can act as cryoprotectants, protecting cell membranes by interacting with lipid molecules and protecting specific enzymes during cold-induced dehydration [7]. Accumulation of soluble carbohydrates in living tissues of stem and buds leads to a decrease in the freezing point, enhancing the probability of extracellular ice formation [19, 30]. WSS bind ROS, thus protecting intracellular structures from toxic oxidation, the probability of which is high during a sharp drop in temperature [10, 13, 23, 31]. Thus, WSS accumulation promotes an increase in the cold resistance of tissues in overwintering plants at the onset of the cold season. In addition, during the period of active growth, oligo- and monosaccharides, which contribute to the development of cold resistance, have a protective effect and contribute to the origin of drought resistance [9, 21, 22]. Cold- and drought-resistant plants were noted to be capable of increased formation of protective WSS [21, 26].

Since Siberian spruce is somewhat more cold-adapted than Scots pine, its needles can be assumed to accumulate more WSS during winter dormancy compared to Scots pine needles. Since Scots pine is better adapted to water deficiency, its needles can accumulate more WSS during drought. This assumption is supported by some research [24, 34]. However, the level of WSS accumulation in needles is quite probable to be influenced by both species and population characteristics, as well as territorial ones associated with the climate in the given macroregion. Such studies have been previously carried out for conifers growing in Eastern Siberia, but they included 4 months of one year of growth period [1]. According to our information, in this study, species growing in the south of Eastern Siberia were used for the first time for continuous comparison during two years of observations of WSS accumulation in two species of coniferous trees different in the strategy of adaptation to environmental conditions. Comparison of the dynamics of WSS content over a two-year period was carried out with simultaneous monitoring of changes in the environmental conditions.

Materials and methods

The climate of the south of Eastern Siberia is sharply continental. It is characterized by a large range of daily and annual temperatures, a high level of insolation, predominance of evaporation over precipitation (especially in the warm season), and deep soil freezing in winter. Due to the remoteness of the studied territory and its enclosure by mountain ranges, humid air masses from the Atlantic and the Pacific Oceans can enter there only in summer, as the air warms up. In spring, the study territory is characterized by low relative air humidity (up to 10%) and low average annual precipitation (359 mm). The frost-free period is about 100 days. In Eastern Siberia, during the period of active growth, late spring (until June 15) and early autumn (after August 25) light frosts are possible [5]. Thus, the climatic conditions of Eastern Siberia can be classified as extreme for growth.

The study was carried out in 2015-2017, according to a multi-year research plan. Scots pine and Siberian spruce trees, planted from one-year-old seedlings in 1985 and growing on the experimental plot of Siberian Institute of Plant Physiology and Biochemistry of the Siberian Branch of the Russian Academy of Sciences, were used for the study. At the beginning of 2015, the age of the trees was 30 years. The plot is located on the outskirts of Irkutsk (52°01′40″ N, 104°01′60″ E) on a gentle slope of eastern exposure (2-3° of steepness). The plot soil is gray forest non-podzolic loamy on Jurassic coaly loams underlain by sand. Groundwater occurs at a considerable depth (11–50 m) and does not significantly affect the soil moisture regime. To characterize the hydrothermal conditions of tree growth, the temperature and humidity of the air were measured, as described earlier [17, 18]. Additionally, data from the Internet resource of All-Russian Research Institute of Hydrometeorological Information (http://meteo.ru/) were used for the year-round characterization of the average monthly air temperature. The years 2015-2017 turned out to be contrasting both in terms of temperature and humidity conditions, which are important for detecting physiological reactions in both types of trees.

The measurements of the total water content and WSS content were carried out in second-year needles, collected from the branches of the middle part of the crown on the 20th of each month. To determine WSS content, a sample of 0.01 g was used, to determine the water content – 0.1 g. WSS content was determined spectrophotometrically using the anthrone reagent (Merck) by the Dreywood method [11]. The measurement was carried out against the reaction medium at 620 nm by using the Specord – S100 spectrophotometer (Analytik Jena, Germany). Sucrose was used to construct a calibration curve. WSS content was determined relative to dry weight of needles. Dry weight and total water content were determined by the weight method after drying the needles to constant weight at 80°C. All the measurements were carried out in at least three biological replicates. The significance of differences was estimated using the nonparametric Mann-Whitney test by the Statistica software program.

Results

While observing the climatic conditions, the following characteristics were revealed: summer 2015 was warmer and wetter compared to summer 2016 (high humidity was noted in the first half of summer 2015, Fig. 1A, B); frosts were stronger in winter 2015-2016 compared to winter 2016–2017 (Fig. 1C).

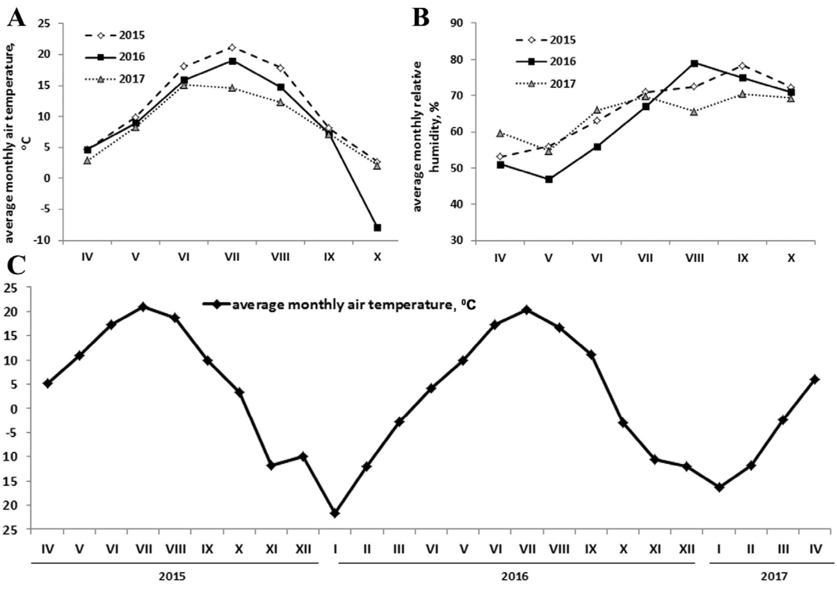

Fig. 1. Hydrothermal conditions during the period of observation from April 2015 to April 2017. A, B – the results of own measurements; C – data of the internet portal meteo.ru. Months are shown in Roman numerals. C – years are shown under the lines.

During the dormant period 2015-2016 (from November to March), WSS content had similar values in needles of both species. During the dormant period 2016-2017, WSS content in Siberian spruce needles turned out to be lower compared to that in Scots pine needles and underwent more significant changes (Fig. 2B). Such changes in WSS content are possibly associated with a warmer winter 2016–2017 compared to winter 2015–2016 (Fig. 1C). There is a high probability of episodic activation of respiration and the attendant WSS consumption in Siberian spruce needles with an increase in air temperature in the cold season [24, 34]. A sharp decrease in air temperature, which did not occur in October-November 2016, was noted between October and November 2015 (Fig. 1C). This decrease coincided with a pronounced increase in WSS content in Siberian spruce in November 2015, which was not noted for Scots pine. However, WSS content in Scots pine and Siberian spruce needles after that turned out to be almost the same (Fig. 2B).

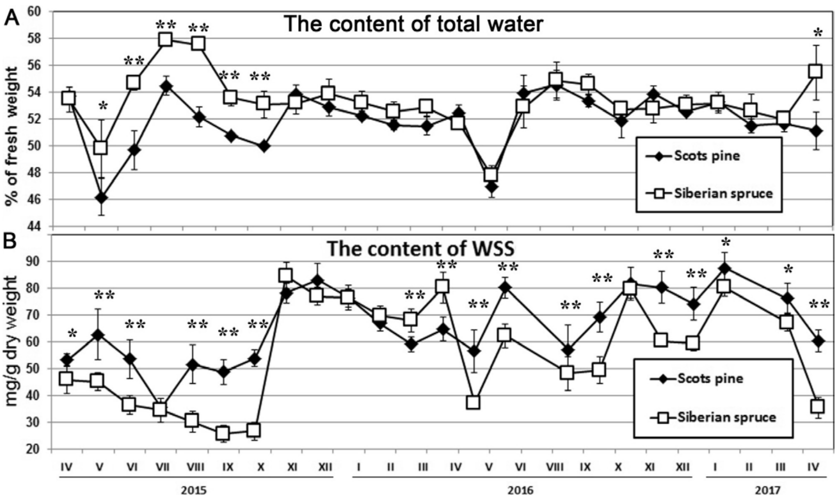

Fig. 2. Variations of the content of total water and WSS in the needles of Scots pine and Siberian spruce. Average means and confidence intervals are presented.* – the differences are significant at $p<0.05$; ** – the differences are significant at $p<0.01$. Non-parametric Mann-Whitney U test was used for the assessment of the reliability of the differences. Months are shown in Roman numerals. Years are shown under the lines.

During the growth period 2015 (from April to September), WSS content in Siberian spruce needles turned out to be lower than that in Scots pine needles; it was also the lowest over the observation period (Fig. 2B). Summer 2015 was favorable in terms of air temperature and humidity (Fig. 1). The increased water content in Siberian spruce needles corresponded to favorable environmental conditions (Fig. 2A). Favorable environmental conditions and increased moisture content in needles contribute to the development of high-intensity growth processes and the pronounced demand for photosynthates [8] that could cause a high level of WSS consumption. Probably, due to these reasons, WSS content in Siberian spruce needles during that period was low. During the subsequent period of winter 2015-2016, WSS content in Siberian spruce needles was the highest over the observation period. Perhaps, the reason for the large reserve of WSS in winter 2015-2016 was the highly productive summer 2015.

During the growth period 2016 (from April to September), WSS content in Siberian spruce needles was higher compared to that period of the previous year. The air temperature and humidity in summer 2016 were lower than in summer 2015 (humidity was lower in the first half of the summer, Fig. 1A, B), which was well within the low water content in Siberian spruce needles (Fig. 2A). The above factors of environmental conditions possibly contributed to a decrease in metabolic activity and growth rate of needles. That is why there was a low demand for photosynthates. Thus, WSS consumption during the growth period 2016 was lower, and WSS content turned out to be higher than in 2015. It is important to emphasize that during the growth period 2016, WSS content in Scots pine needles was higher than in Siberian spruce needles, while the moisture content during that period was the same for both species (Fig. 2).

In March and April 2016, WSS content in Siberian spruce needles was higher than in Scots pine needles. During all the other months of the observation period, WSS ratio in Siberian spruce and Scots pine was opposite (Fig. 2B). Perhaps, in March and April 2016, favorable conditions for the early photosynthesis activation developed in Siberian spruce needles resulting in the accumulation of carbohydrates.

The lowest air humidity during the observation growth period was noted in May 2016 (Fig. 1B). In the same month, the lowest over the observation period water and WSS contents in Siberian spruce needles were recorded (Fig. 2). In that month, the intensive WSS consumption was most likely associated with the costs of photosynthates for adaptation and overcoming the harmful effects of water deficiency. One of the necessary processes to fight against the consequences of water deficiency is the adaptive respiratory activation [12]. WSS were possibly used for this process.

During the active vegetation period (May-September), WSS content in Scots pine needles turned out to be significantly reduced only in July 2015 when it was the lowest over the observation period (Fig. 2B). In July 2015, a high level of temperature and humidity was recorded (Fig. 1). In the same month, Scots pine needles contained the largest amount of water over the observation period (Fig. 2A). Perhaps, exceptionally favorable conditions for the growth of Scots pine created due to the combination of external factors in July 2015 were the reason for the increased sinks of WSS to ensure metabolic activity and growth.

Discussion

Well within the literature data, WSS content in needles of Scots pine and Siberian spruce increased with the onset of the cold season [33, 34, 35]. In winter 2015-2016, WSS content in needles of Scots pine and Siberian spruce had similar values; in winter 2016-2017, it was lower in Siberian spruce needles. These data contradict those obtained by Strimbeck et al. [34] for Scots pine and Siberian spruce growing in Norway and those obtained by O¨gren et al. [25] for these species growing in Sweden. Throughout the entire period of winter dormancy, WSS content in Siberian spruce needles was higher compared to Scots pine needles [25, 34]. Perhaps, differences in the climate of tree growth are the reason for the contradictions in the data. Unlike the climate of Eastern Siberia, the climate of Norway and Sweden is characterized by high air humidity. The humid climate contributes to a more complete realization of the potential production capacity of Siberian spruce resulting in the creation of a larger reserve of photosynthates compared to Scots pine. Additionally, differences in climatic conditions can explain why WSS values for Siberian spruce needles in the present study turned out to be lower than those obtained by Robakidze et al. for trees growing in the Komi Republic [27]. Mean annual rainfall in the Komi Republic is almost twice as high as in Eastern Siberia. A higher level of soil moisture apparently contributes to a high realization degree of the metabolic potential and a higher level of WSS accumulation in Siberian spruce needles [5]. Thus, Siberian spruce growing in Eastern Siberia does not accumulate more WSS in needles than Scots pine, despite the fact that Siberian spruce is potentially more resistant to cold. The influence of the climate of the growing area turned out to be no less important factor for WSS accumulation in Scots pine and Siberian spruce needles than the metabolic potential of the species. However, the growth of Siberian spruce in Eastern Siberia on more moist soils near water bodies can positively affect WSS content in needles and contribute to a more successful spread of trees of this species.

The reason for the low WSS content in Siberian spruce needles in winter 2016-2017 (compared to winter 2015-2016) could be the less productive summer 2016, which first half was characterized by lower humidity (Fig. 1B). Soil moisture is known to be the main limiting factor for the productivity of Siberian spruce [5]. In addition to low air humidity, summer 2016 was characterized by a lower average monthly air temperature (Fig. 1A), which is a limiting factor for the productivity of Scots pine [5]. However, during the subsequent dormant period 2016-2017, there was no decrease in WSS content in Scots pine needles compared to the previous year. In winter 2016-2017 (November-March), fluctuations in WSS content occurred; they were more pronounced in Siberian spruce needles (Fig. 2B). A stronger fluctuation in WSS content in Siberian spruce needles compared to Scots pine needles in winter 2016-2017 can be associated with episodic increases in air temperature, which, according to the literature data, provoke the activation of respiration in needles [25]. WSS reserves of needles can be spent on respiration that changes the overall carbohydrate balance and negatively affects the resistance of needles to cold [25, 34]. Low frost resistance can lead to negative consequences if a sudden cold snap occurs after warming. On the contrary, the preservation of WSS reserve in Scots pine needles contributes to the preservation of the state of cold adaptation and resistance to cold even during the period of winter warming and possible activation of respiration. In November 2015, a sharp decrease in air temperature caused a more powerful increase in WSS content in Siberian spruce needles compared to Scots pine needles. However, WSS content in both species after that turned out to be almost the same, since there were not observed such pronounced changes in WSS content in Scots pine needles.

Thus, during the observation period, WSS content in two species turned out to be either the same or lower in Siberian spruce needles. It was observed not only at the maximum but also at the average water saturation of needles, under more and less favorable climatic conditions, as well as under conditions of water deficiency. In contrast to WSS of Scots pine needles, those of Siberian spruce needles underwent significant changes that coincided in time with weak or pronounced fluctuations in temperature, air humidity, and water content in needles. Consequently, under the given growing conditions and in the presence of wide ranges of changes in environmental conditions and water content in needles, WSS level turned out to be more stable and often higher in Scots pine than in Siberian spruce. According to the results obtained, WSS content in Scots pine needles is more constant and often higher both during the dormant period and during the period of active vegetation. The lower content and more pronounced fluctuations in WSS content in Siberian spruce needles suggest that they are more vulnerable (compared to Scots pine needles) during periods of sudden severe cooling and moisture deficiency that negatively affects the physiological activity and survival of trees. However, it should be noted, that a larger observation with more trees, as well as longer experiment duration is required to strengthen the conclusions drawn.

Conclusion

Despite the more pronounced potential for growth in cold climates, as well as a higher mass fraction of photosynthetic mesophyll and photosynthetic pigments, which provide high carbon fixation activity and photosynthetic productivity [2, 3, 4], Siberian spruce growing in the south of Eastern Siberia is to a greater extent limited in WSS reserving compared to Scots pine. Possibly, the capability of Scots pine to maintain WSS reserve under the influence of both favorable and unfavorable environmental conditions for physiological activity is one of the mechanisms that successfully compensates for the fact that this species is slightly inferior to Siberian spruce with regard to frost resistance. This capability possibly allows Scots pine to successfully compete with Siberian spruce and occupy vast territories in Baikal region. The lack of WSS, as one of the factors of cold and drought resistance, can be one of the reasons limiting the spread of Siberian spruce over the south of Eastern Siberia.

Conflict of interest information. The authors declare that there is no conflict of interest.

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