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Dynamics of non-structural carbohydrates in *Pinus pallasiana* D. Don needles under different forest growth conditions of ravine anti-erosion plantations

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Abstract

The research was aimed at analysing the peculiarities of non-structural carbohydrate metabolism in the needles of *Pinus pallasiana* D. Don in anti-erosion plantations on the slope and in the thalweg of the Viyskovyi ravine under different forest growth conditions. The ravine is located in the Dnipropetrovsk region and belongs to the southern geographical variant of ravine forests. The studied plants grew at three experimental sites of man-made plantation: in the thalweg (forest growth conditions – mesophilic, fresh, CL_2), in the middle part of the slope of the southern exposure (mesoxerophilic, somewhat dry, or semi-arid, CL_1) and on the upper part of this slope (xerophilic, arid, CL_{0-1}). Changes in glucose, fructose, reducing sugars, sucrose and starch during the period from May to October were studied.

The concentration of osmotically active substances (glucose, sucrose) increases in the months with the most unfavourable hydrothermal parameters, especially in plants of mesoxerophilic and xerophilic forest growth conditions. The dynamics of fructose content revealed two maxima (July and October), when the concentration of glucose tends to increase steadily, with the highest values found in October. During the study period, the level of fructose in the needles under the arid conditions of the upper and middle parts of the slope was much lower than under the fresh conditions of the thalweg. The dynamics curve of the starch content tends to decrease from the maximum values in May to the first minimum in August. It is followed by some increase in the concentration of this polysaccharide that does not reach the previous values. The second minimum is registered in October. Such changes in the level of starch in the needles of plants are observed under all forest growth conditions. The decrease in polysaccharide content is consistent with the increase in glucose and sucrose, especially in August. A more significant increase in the concentration of soluble osmoprotective sugars (glucose, sucrose) in *P. pallasiana* needles under unfavourable hydrothermal conditions compared to normal moisture conditions indicates the ability of plants to adapt to mesoxerophilic and xerophilic conditions.

Key words

ravine, man-made plantation, Crimean pine, forest growth conditions, sugars, starch

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Introduction

Over the last century, changes in the Earth's surface temperatures have had an upward trend over time (Summary 2014; Kotlikoff et al. 2017). Global warming, according to modern models, will lead to negative consequences, namely, an increase in the frequency and duration of droughts (Chaves et al. 2009). The strategic way to solve this problem is to rehabilitate the biosphere and restore the climate-forming functions of the global biota, including the greening of our planet. Restoration of forest ecosystems is extremely necessary for Ukraine (Matsevityi et al. 2016).

In the southeast of Ukraine, an important role is played not only by the preservation of natural ravine forests, but also by the creation of artificial phytocenoses that will perform an anti-erosion function on the slopes of ravines. Introduced species of North American (*Acer negundo* L., *Elaeagnus argentea* Pursh, *Robinia pseudoacacia* L., *Gleditsia triacanthos* L., *Fraxinus pennsylvanica* Marshall) and Asian (*Juglans regia* L., *Morus alba* L., *Ailanthus altissima* Mill., etc.) origin are traditionally widely used in artificial afforestation of Ukraine (Bessonova et al. 2017). At the same time, not enough attention is paid to other non-indigenous species that are characterised by valuable reclamation, biological and decorative qualities, in particular, *Pinus pallasiana* D. Don. This species has sufficient resilience and adaptive potential to unfavourable abiotic conditions (Korshikov and Lapteva 2014; Voron and Ivashinyuta 2004), low rates of Heterobasidion root disease, high landscaping and decorative qualities, as well as high resin productivity (Levin et al. 2019) and slow growth in height at the initial stage of ontogenesis, compared with the aboriginal species *Pinus sylvestris* L. (Kruchkov and Kireeva 2015). This allows the use of *P. pallasiana* as an admixed and buffer species in the introduction of valuable deciduous species in the mixing scheme (Levin et al. 2019). In contrast to some rather aggressive introduced species (*Ac. negundo* L., *Ai. altissima* Mill., etc.) (Abduloyeva and Karpenko 2012), the natural regeneration of *P. pallasiana* in forests is localised within the canopy of parent plantations (Saltykov et al. 2018).

There are data on the use of *P. pallasiana* in protective reclamation plantations of agricultural landscapes (Dubenok et al. 2017; Kulik et al. 2019; Kulik and Semenyutina 2010), in urban plantations (Korzh et al. 2016) and in the practice of greening of industrial zones (Korshikov et al. 2005; Korshikov and Terlyga 2008; Krasnoshtan 2017, 2016).

A number of studies have dealt with the morpho-physiological parameters of *P. pallasiana* in the forest stands of southeastern Ukraine (Terlyga et al. 2002; Bessonova et al. 2015; Bessonova and Gritsay 2018; Bessonova and Jusypiva 2018), bioecological features of the introduction of this species (Levin and Pashchenko 2018; Levin et al. 2019), as well as the use of its pollen for bioindication of the environment (Lapteva 2016). At the same time, the adaptive capabilities of *P. pallasiana* under different forest growth conditions have not been studied. However, they are important when creating anti-erosion plantations on the slopes of ravines in the steppe zone of Ukraine, where specific growth conditions are formed due to frequent droughts and high temperatures in summer. These stressors pose a special threat to woody plants, as they disrupt the stability of phytocenoses and their recovery processes (Brunner et al. 2013). Due to global warming, this threat is growing.

Changes in the metabolism of non-structural carbohydrates (NSCs) are of great importance in the adaptation of plants to stressors. This may be demonstrated by the fact that the NSC level in the bark of *Pinus contorta* trees attacked by bark beetles was higher when the trees were still alive for at least a year, compared to those that died shortly after the invasion (Wiley et al. 2016). There are data on the involvement of NSCs in maintaining the hydraulic integrity of the xylem of *Pinus koraiensis* Sieb. et Zucc., especially in winter (Ai-Ying Wang et al. 2018). Several authors emphasise the key role of NSCs in the protective response of woody plants not only to low temperature stress, but also to drought (Tomasella et al. 2020). These works are devoted to the study of NSC reserves in xylem. The study of the dynamics of carbohydrate content in the trunks and roots of *Pinus cembra* (L.) and *Larix decidua* (Mill.), which grow in the alpine forest zone, showed an excess of NSC concentration in the phloem by 5–7 times compared to xylem (Gruber et al. 2013). A similar pattern was also found for the three dominant species of mountain mixed forest (*P. koraiensis*, *Fraxinus mandschurica* Rupr. and *Tilia amurensis*) (Wang et al. 2019).

Sugars are osmolytes and play a leading role in ensuring the adaptation of plants to a number of natural stressors (Maevskaya and Nikolaeva 2013). These chemical compounds influence the expression of many genes involved in glycolysis, photosynthesis, nitrogen metabolism (Rolland et al. 2006) and regulation of the cell cycle (Van't Hof 1973). Reducing sugars function as signalling molecules by controlling the cell metabolism, plant growth and development, and the corresponding stress responses (Rolland et al. 2006), whereas sucrose is attributed to the regulation of growth processes. It is used as a central molecule during plant life, starting with germination and ending with the formation of seeds in annual plants (Kiriziy et al. 2014). Based on the above, determining the characteristics of quantitative transformations of NSCs in the needles of *P. pallasiana* under fresh and arid forest growth conditions of anti-erosion plantations is important for understanding its adaptive responses to drought.

The aim of the research is to analyse the peculiarities of NSC metabolism in the needles of *P. pallasiana* D. Don in the anti-erosion plantations on the slope and in the thalweg of a ravine under different forest growth conditions.

Material and methods

The studied plants of *P. pallasiana* grew in the Viyskovyi ravine in the Dnipropetrovsk region, which belongs to the southern geographical variant of ravine forests (Belgard 1971). The total length of the ravine is 3.2 km. It has three spurs (Fig. 1). The ravine forest is represented by areas of oak forests, as well as man-made anti-erosion plantations (*P. pallasiana*, *R pseudoacacia* L.) (Bessonova et al. 2015, 2017). The study area is characterised by low rainfall (420–450 mm) and low humidity (0.67) (Tsvetkova 2013).

The studied plants were growing at three test sites of man-made plantations. Test site 1 is located in the thalweg on its flat, slightly elevated part at a distance of about 35 m from the stream that flows along the bottom of the ravine in the deepened riverbed. The soil moisture is ground and atmospheric. The mechanical composition of the soil is loam. Forest growing conditions according to Belgard (1971) are CL_2 (mesophilic, fresh). Test site 2 is located in the middle part of the slope of the southern exposure, which is the steepest. The soil moisture is atmospheric, transit. Forest growing conditions are CL_1 (mesoxerophilic, somewhat dry or semi-arid). The third test site is located at the top of the slope of the southern exposure. The soil moisture is atmospheric, transit. Forest growing conditions are CL_{0-1} (xerophilic, arid).

Last year's needles were sampled at a height of 2 m from the southeastern side of the crown under the same lighting conditions from five trees. According to

Figure 1. Map of the studied area (https://www.google.com/maps/). Coordinates of extreme points (48°11′08″N, 35°07′45″E; 48°10′41″N, 35°10′12″E)

the Mykilski forestry, the age of anti-erosion plantations of *P. pallasiana* is 28–30 years.

Determination of sugars in the needles was carried out by iodometric method and starch by colorimetric methods (Pochinok 1976). The analyses were performed in quadruplicate.

Determination of sugars was carried out after inactivation of enzymes, their extraction with distilled water and precipitation of proteins with 1 N sodium hydroxide solution and 10% zinc sulphate. Sugars (glucose, fructose) and the amount of mono and disaccharides were determined in the filtrate by the iodometric method. The amount of sucrose was defined as the difference between the total amount of sugars and the amount of reducing sugars.

The method of colorimetric determination of starch is based on its dissolution when heated in an 80% solution of calcium nitrate followed by precipitation of the obtained solution with iodine. In the presence of potassium iodide and calcium nitrate, iodine completely precipitates starch as a dark blue compound. After centrifugation and washing of the precipitate, starch was determined by the colorimetric method. The precipitate of iodine starch was dissolved in sodium hydroxide, diluted with distilled water and reacted with iodine in an acidic environment.

The optical density of the solution was measured at 580–610 nm in a 10-ml cuvette on a KFK-3-01-ZOMZ photometer. The obtained results were compared with the calibration curve and the starch content was calculated. Soluble starch was used to construct the calibration curve.

The tables and graphs show the average values and their standard errors. Statistical analysis of the data was performed using Statistica 6.0 software with the help of one-way analysis of variance (ANOVA) and applying Tukey's criterion of significant difference of group average ($P < 0.05$).

Results

Glucose content in the needles of *P. pallasiana*, which grows both in the thalweg (CL_2 – mesophilic, fresh moisture conditions) and under arid forest growth conditions (CL_1 – mesoxerophilic, semi-arid and CL_{0-1} – xerophilic, arid), is the lowest in May and June (Tab. 1).

Table 1. Glucose content in the needles of *Pinus pallasiana* under different forest growth conditions, % absolute dry weight

Month	Thalweg	Middle part of the slope	Upper part of the slope
May	0.50 ± 0.03	0.31 ± 0.02^{a}	0.30 ± 0.03^{a}
June	0.62 ± 0.03	0.39 ± 0.04^{a}	0.33 ± 0.03^{a}
July	0.84 ± 0.04	1.10 ± 0.03^{a}	1.32 ± 0.05$^{a.b}$
August	0.89 ± 0.09	1.54 ± 0.05^{a}	1.65 ± 0.07^{a}
September	0.99 ± 0.05	1.65 ± 0.06^{a}	1.72 ± 0.05^{a}
October	2.50 ± 0.07	2.25 ± 0.08^{a}	2.05 ± 0.04^{a}

Note: a. The difference between the „Thalweg" variant and the „Middle part of the slope", „Upper part of the slope" variants is statistically significant ($P < 0.05$); b. The difference between the „Middle part of the slope" and „Upper part of the slope" variants is statistically significant ($P < 0.05$).

In July, the glucose content increases significantly, especially in plants of the middle and upper part of the slope. The amount of monosaccharide in the needles from the test sites 1, 2, 3 increases by 1.35, 2.82 and 4.0 times, respectively, compared to the previous month. In August, there is a further increase in the concentration of glucose in the needles of *P. pallasiana* under semi-arid and arid forest growth conditions. It does not change under fresh forest growth conditions. In the following month, the glucose content level is almost the same as in August, but in October, there is an increase in all studied cases, especially under fresh forest growth conditions (CL_2).

Despite the similar nature of the dynamics of changes in glucose content in the needles of *P. pallasiana* during the growing season at all the test sites, it is significantly affected by forest growth conditions. Comparison of the data obtained from plants growing in different growth conditions shows that in May and June, the concentration of this monosaccharide in the needles of trees from the thalweg area is the highest (CL_2), while under arid conditions (CL_1 and CL_{0-1}), it is lower. The glucose content in the needles of plants of the middle and upper parts of the ravine is almost the same. With increasing temperature and decreasing soil moisture in July, there is a more significant increase in glucose content in the needles of plants under semi-arid and arid forest growth conditions compared with those under more favourable moisture conditions (thalweg). As a result, the concentration of reducing sugars becomes higher than that of the thalweg plants.

The driest months are August and September. During this period, the glucose content in the needles of *P. pallasiana* in the middle and upper parts of the slope is higher than in the thalweg area: in August, 1.73 and 1.85 times and in September, 1.67 and 1.73 times. Thus, the concentration of glucose does not change significantly in September compared to August.

In the second autumn month (October), the level of this reducing sugar in the needles of *P. pallasiana* increases in all variations of the experiment compared to the previous month, especially in plants under more favourable moisture conditions (CL_2) (by 152.5%). Compared to the previous values, under arid (CL_{0-1}) conditions, this increase is 19.2% and under semi-arid (CL_1) conditions, it is 36.4%.

The concentration of fructose in the needles of *P. pallasiana* is lower compared to other water-soluble sugars. In seasonal changes of the amount of this monosaccharide under all forest growth conditions, two maxima are found: in July and October. The lowest level is observed in May (Tab. 2). After the concentration rises in July, it decreases in the next 2 months, which are the driest and are characterised by the highest temperatures. Soil moisture regime affects the fructose content in the needles. The fructose content is more lower under arid conditions compared to the thalweg (CL_2).

The difference in the concentration of this reducing sugar in the needles under the semi-arid and arid conditions is statistically significant only in August and October.

Table 2. Fructose content in the needles of *Pinus pallasiana* under different forest growth conditions, % absolute dry weight

Month	Thalweg	Middle part of the slope	Upper part of the slope
May	0.29 ± 0.01	0.22 ± 0.02[a]	0.20 ± 0.02[a]
June	0.52 ± 0.03	0.37 ± 0.02[a]	0.34 ± 0.02[a]
July	0.93 ± 0.02	0.65 ± 0.03[a]	0.55 ± 0.04[a]
August	0.61 ± 0.03	0.40 ± 0.03[a]	0.30 ± 0.01[a.b]
September	0.41 ± 0.02	0.25 ± 0.01[a]	0.21 ± 0.02[a]
October	0.87 ± 0.04	0.60 ± 0.03[a]	0.41 ± 0.02[a.b]

Note: a. The difference between the „Thalweg" variant and the „Middle part of the slope", „Upper part of the slope" variants is statistically significant ($P < 0.05$); b. The difference between the „Middle part of the slope" and „Upper part of the slope" variants is statistically significant ($P < 0.05$).

The dynamics curve of the amount of reducing sugars in the needles of *P. pallasiana* in all variations of the experiment is generally similar to the direction of changes in glucose levels, which predominate quantitatively. At the beginning of the growing season, the concentration of reducing sugars is the lowest; then it increases in July and remains high in August and September. A new significant increase occurs in October.

In May and June, the level of reducing sugars in the needles of *P. pallasiana* is lower under arid (CL_{0-1}) and semi-arid (CL_1) forest growth conditions compared to fresh ones (CL_2) (Fig. 2). The difference in their content at sites 2 and 3 is statistically insignificant. In July, the content of reducing sugars in the needles of trees at sites 1 (CL_2) and 2 (CL_1) is almost the same, but at site 3 (CL_{0-1}), it is higher (1.77% ± 0.10%, 1.75% ± 0.11% and 1.87% ± 0.08% of absolute dry weight, respectively). During the next 2 months, which are characterised by the most unfavourable hydrothermal conditions, the concentration of reducing sugars in the needles becomes higher in both cases with insufficient moisture, compared to the favourable conditions. In October, the content of reducing sugars increases: 2.57 times in thalweg plants (CL_2) and in plants of the middle (CL_1) and upper (CL_{0-1}) parts of the slope – 1.58 and 1.27 times, respectively. As a result, the concentration of reducing sugars becomes

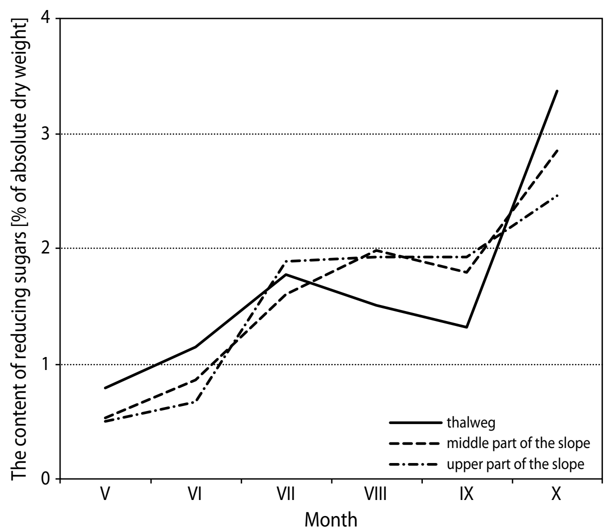

Figure 2. The content of reducing sugars in the needles of *Pinus pallasiana* under different forest growth conditions, % of absolute dry weight

much lower under conditions of poor moisture supply, especially at site 3 ($CL_{0–1}$).

The concentration of sucrose is higher than glucose and fructose in the needles of *P. pallasiana*. During the growing season, the amount of disaccharide increases from May to August. In September, it hardly changes. Such dynamics of changes in the content of this disaccharide is observed in all variations of the experiment (Fig. 3).

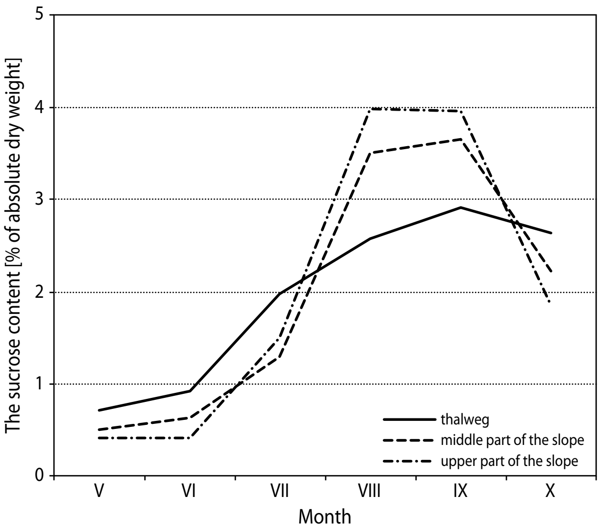

Figure 3. The sucrose content in the needles of *Pinus pallasiana* under different forest growth conditions, % of absolute dry weight

Analysis of the influence of growth conditions on the sucrose content shows that in May, July and June, it is lower in plants growing at sites 2 (CL_1) and 3 ($CL_{0–1}$) compared to those from more favourable moisture conditions (mesophilic, CL_2). In May and July, the concentration of disaccharides in the needles of trees growing in the upper and middle parts of the slope is not statistically different. In June, it is lower in plants of the upper part of the slope ($CL_{0–1}$, xerophilic conditions). During the aridest and hot periods, the sites with insufficient water supply (CL_1 and $CL_{0–1}$) are characterised by a higher sucrose content compared to the site with a more favourable water supply (CL_2). Thus, in August, it is 1.36 and 1.54 times and in September, 1.25 and 1.36 times, respectively, relative to the concentration of sucrose in the needles of plants of mesophilic growth characteristics (CL_2).

In October, the amount of this form of sugar decreases in *P. pallasiana* trees, which grow at all test sites, but more significantly under arid ($CL_{0–1}$) and semi-arid (CL_1) forest growth conditions compared to fresh ones (CL_2).

The starch content in the needles of *P. pallasiana* in all variants is quite variable. The highest amount of this polysaccharide in pine needles is found in May (Fig. 4). Later, in the summer months, the level of the compound gradually decreases, with the first minimum observed in August. In September, the amount of starch increases, but does not rise to the level preceding this decline. The second minimum amount of the polysaccharide is found in October. Similar dynamics of changes in the starch content are observed in all variations of the experiment.

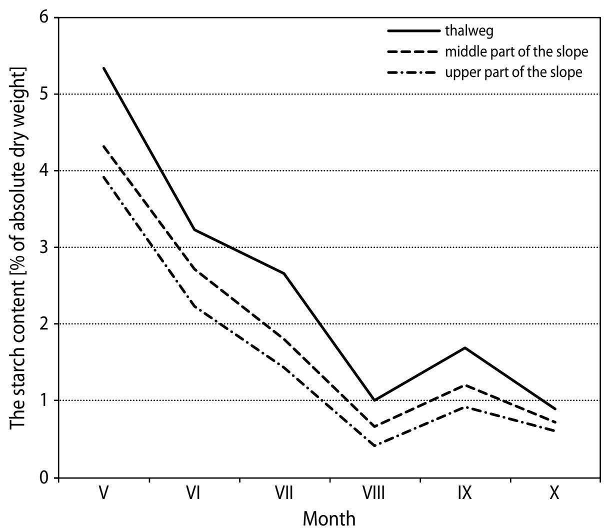

Figure 4. The starch content in the needles of *Pinus pallasiana* under different forest growth conditions, % of absolute dry weight

Under unfavourable growth conditions, namely, semi-arid (CL_1) and arid ($CL_{0–1}$) conditions, the amount of polysaccharide in pine needles is lower than in fresh forest growth conditions (CL_2) during all months of the research period, especially in plants at site 3 ($CL_{0–1}$, arid forest growth conditions). The most significant difference between the variants $CL_{0–1}$ and CL_2 is found during the period of the greatest decline in starch content – in August (2.43 times).

Discussion

The analysis of research results shows the influence of forest growth conditions on quantitative changes in the content of NSC in the needles of *P. pallasiana*. As can be seen from Table 1, the intensification of soil and air drought in July compared to June leads to a rise in glucose levels in the needles of plants at all the sites. During the next driest months (August and September), the amount of the monosaccharide increases significantly. In plants growing in the middle and upper parts of the slope, that is, under semi-arid (CL_1) and arid (CL_{0-1}) forest growth conditions, the concentration of glucose in the needles increases more significantly than in the needles from the trees in the thalweg area (CL_2, fresh conditions). As a result, the content of this form of sugar in the needles of plants under arid and semi-arid conditions becomes higher compared to plants growing at the site with favourable moisture conditions (thalweg – CL_2). The increasing amount of this reducing sugar due to water deficiency can be considered as an adaptive response to drought. The increase in the amount of glucose in the leaves of plants under insufficient moisture conditions is indicated in a number of works (Lawlor and Cornic 2002; Lawlor and Teraza 2009; Karimova et al. 2008; Povorotnia 2015). Hexoses effectively regulate the osmotic adaptation to drought (Kameli and Lösel 1993). According to some researchers, the reason for the increase in their content under hydrothermal stress may be the hydrolysis of starch (Hare et al. 1998; Mohammadkhani and Heidari 2008).

In October, with a decrease in air temperature, especially at night, there is another increase in the amount of glucose in the needles of *P. pallasiana* in all variations of the experiment, more significantly under fresh conditions (CL_2). It is known that the hydrolysis of starch is enhanced when the temperature drops to −3°C or −5°C. This leads to the accumulation of sugars, which is an adaptation to hypothermia in winter (Tumanov 1976; Kolupaev and Trunova 1992; Kolupaev et al. 2015; Zeng et al. 2011).

In contrast to glucose, the fructose content in the needles of *P. pallasiana*, which grows under arid conditions (CL_1 and CL_{0-1}), is lower compared to plants in the thalweg (fresh forest growth conditions, CL_2). It should be noted that some researchers have observed an increase in fructose in the leaves of plants due to the lack of water (Kameli and Lösel 1993; Maevskaya and Nikolaeva 2013). This discrepancy of results is explained by the specifics of the reaction of different plant species to drought and different growth conditions.

As follows from our results, in the month with the most unfavourable hydrothermal conditions, the concentration of reducing sugars is higher in the needles of plants growing under arid (CL_{0-1}) and semi-arid (CL_1) forest growth conditions compared to the needles from the area with mesophilic CL_2 conditions. A number of researchers point to the accumulation of reducing sugars under the action of water stress on plants (Tarchevsky 2001; Kameli and Lösel 1993; Nikolaeva et al. 2017).

The amount of sucrose, as well as glucose, in the needles of *P. pallasiana* increases from July and is highest in September under all forest growth conditions. During this period, the drought is the most severe, as during August–September, there is no precipitation in the form of rain. However, the level of increase in the disaccharide content in different variations of the experiment is not the same. There is a slight increase in sucrose content in the needles of plants growing under more favourable moisture conditions (CL_2). The most significant increase in its concentration occurs under arid conditions (CL_{0-1}). There is evidence that under conditions of moisture deficiency, the increase in sucrose levels in the leaves of plants can be due to its synthesis (Hare et al. 1998) and due to transformation of starch (Ulyanovskaya et al. 2010). It is known that assimilation starch can very quickly turn into sucrose in plant cells (Kursanov 1976). The accumulation of sucrose in the leaves of plants can occur due to reduction in its outflow into the young leaves, as indicated by Nikolaeva et al. (2017).

Sucrose, like hexoses, is an active osmolyte, a regulator that provides high water potential and osmotic regulation in pine cells.

A number of authors (Nikolaeva et al. 2015; Povorotnia 2015; Maevskaya and Nikolaeva 2013) note an increase in sucrose concentration in the leaves of plants during a drought.

The maximum amount of starch is found in May in the needles of *P. pallasiana*. The decrease in its content in the summer months occurs in all variations of the experiment. However, under arid conditions, it is more significant, especially in CL_{0-1} forest growth conditions. A greater decrease in the starch content in pine needles coincides with an increase in the concentration of glucose and sucrose, which may indicate its conversion to these forms of sugars during droughts.

Starch is considered to be a good indicator of changes in environmental conditions, as its transformation is reversible and is closely related to the physiological state of plants and their growing conditions (Novitskaya 1971; Karimova et al. 2008).

During the entire growing season, the starch content in pine needles is lower under arid conditions (CL_1 and CL_{0-1}) and higher in the thalweg area (CL_2). This may be due to the negative effects of droughts on starch synthesis.

Thus, during the driest months, there is an increase in osmotically active substances – glucose and sucrose – in the needles of *P. pallasiana* in all variations of the experiment. Under arid forest growth conditions of CL_{0-1} and CL_1, the accumulation of these sugars is more significant than under fresh ones (CL_2).

It should be noted that Korytova et al. (1976) stated that during the summer months, the needles of *P. sylvestris* L., which grow in the arid pine barrens, are characterised by a higher content of mono- and disaccharides in comparison with those growing in subor forests (natural pine (with a mix of other species) forest that grows on sandy soils). Under unfavourable hydrothermal conditions, sugars and osmoregulators play an important role in preserving cells' turgor, thus making it possible to maintain high activity of physiological processes. Osmolytes are also involved in protecting cells from oxidative stress due to adverse abiotic factors (high temperature and low temperature, drought) (Reddy et al. 2004; Couee et al. 2006; Kaur and Asthir 2015; Kolupaev and Trunova 1992; Sin'kevich et al. 2011). Sugars act as osmoprotectors. They prevent damage to organelles and cell membranes (Hare et al. 1998).

The obtained data on the active accumulation of glucose and sucrose in the needles of *P. pallasiana* under arid forest growth conditions in contrast to favourable moisture conditions indicate the adaptation of this plant to unfavourable hydrothermal conditions.

Conclusion

The study conducted in anti-erosion plantations of the Viyskovyi ravine showed that the needles of *P. pallasiana* are characterised by an increased content of osmotically active substances – glucose and sucrose – in the month with the highest temperatures and increasing drought. The increase in these soluble sugars is more significant under mesoxerophilic and xerophilic forest growth conditions on the slopes of the ravine (in comparison with the mesophilic [thalweg] conditions). Soluble sugars play an important role in adapting to droughts and high temperatures. Quantitative changes in fructose are slightly different from glucose. The dynamics of its content revealed two peaks (July and October), while the concentration of glucose tends to increase steadily, with the highest values found in October. Under arid conditions of the upper and middle parts of the slope of the ravine, the level of fructose in the needles is much lower than under fresh conditions (thalweg). The dynamics of changes in the starch content tends to decline from the highest in May to the first lowest in August, after which there is some increase in the concentration of this polysaccharide. The second minimum amount of starch in pine needles is found in October. Under unfavourable forest growth conditions, especially dry ones, the starch level is lower throughout the study compared to plants in the thalweg area. There is a correspondence between changes in starch content and the accumulation of soluble sugars: a decrease in polysaccharide content is consistent with an increase in glucose and sucrose, especially in August. A more significant increase in the concentration of soluble osmoprotective sugars in *P. pallasiana* needles under unfavourable hydrothermal conditions compared to normal humidification conditions indicates the ability of plants to adapt to mesoxerophilic and xerophilic conditions.

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