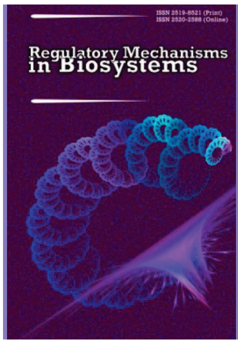

Regulatory Mechanisms in Biosystems

ISSN 2519-8521 (Print)
ISSN 2520-2588 (Online)
Regul. Mech. Biosyst.,
2021, 12(4), 628–634
doi: 10.15421/022186

Influence of soil moisture level on metabolism of non-structural carbohydrates in *Quercus robur* leaves

V. P. Bessonova, A. S. Chonhova

Dnipro State Agrarian and Economic University, Dnipro, Ukraine

Article info

Received 20.09.2021
Received in revised form 11.10.2021
Accepted 13.10.2021

Dnipro State Agrarian and Economic University, Sergey Ephremov st., 25, Dnipro, 49600, Ukraine. Tel.: +38-066-399-44-47. E-mail: a-chongova@ukr.net

Bessonova, V. P., & Chonhova, A. S. (2021). Influence of soil moisture level on metabolism of non-structural carbohydrates in Quercus robur leaves. Regulatory Mechanisms in Biosystems, 12(4), 628–634. doi:10.15421/022186

The long-term increases in average temperature and intensification of droughts which characterise the current state of the Earth's climate system have a negative impact on forest ecosystems and can lead to a decrease in their area and deterioration of the living conditions of their components. In the conditions of the Ukrainian Steppe an important environmental, antierosion, water-protective and soil-protective role belongs to the ravine forests. The most valuable component of the ravine forests is presented by natural populations of common oak (*Quercus robur* L.), which are able to tolerate the arid climate typical of the steppe region. But with global warming, the endurance of this species is changing. It is believed that a significant role in plant adaptation to drought and high temperatures may belong to non-structural carbohydrates. Therefore, it is important to study changes in the concentration of these substances in the leaves of this leading species under the action of adverse hydrothermal conditions. The article analyzes the content and dynamics of soluble sugars (glucose, fructose, sucrose) and starch in the leaves of *Quercus robur* L. under different forest growth conditions of the ravine forest (hygromesophilic ($CL_{2–3}$), mesoxerophilic (CL_1) and xerophilic (CL_0)). The research was conducted in the forest in the Viyskove area (steppe zone of Ukraine) in the thalweg and at different levels of slope of southern exposure. Content of glucose, fructose, sugar and starch in *Quercus robur* leaves was determined. It was found that when exposed to high temperatures and increasing water stress during the vegetation period in xerophilic ($CL_{0–1}$) and mesoxerophilic (CL_1) forest growth conditions, the concentration of both glucose and sucrose in the leaves of *Q. robur* increases and it becomes much higher than in conditions of more optimal water supply. At the same time, the disaccharide content increases more significantly than that of monosaccharide. The greatest amount of these sugars is observed in the driest months (July, August), when conditions for providing plants with water are the most stressful. When water stress grows the increase in concentration of glucose and sucrose is correlated with reduction of starch content. It has been found that the concentration of fructose in *Q. robur* leaves in droughty conditions of growing was comparable to more favourable conditions of moisture. In September, there is a decline in the content of all forms of non-structural carbohydrates in the leaves of plants of all variants compared to the previous month, especially in conditions of adverse water supply. Therefore, forest growth conditions do not affect the nature of the dynamics of soluble sugars and starch in the leaves of *Q. robur*, although they change their quantitative indicators. Based on the protective function of sugars under the action of stressors on plants, we can assume that in conditions of significant lack of moisture in the soil their accumulation in the leaves in areas with mesoxerophilic and xerophilic hygrotopes plays an important role in increasing *Q. robur* drought resistance.

Keywords: ravine forests; oak; forest growth conditions; unfavourable hydrothermal conditions; non-structural carbohydrates.

Introduction

Global warming is changing forest ecosystems around the world (Vieira et al., 2018), especially in steppe landscapes where tree communities are in unfavourable hydrothermal conditions (Netsvetova et al., 2021). Forests are important ecosystems that have a positive impact on the environment, and thus on the quality of human life (Barana et al., 2020). In the steppe of Ukraine, the tasks of improving the environment are especially topical for ravine forests.

Ravine forests are unique natural communities that are characterized by structural complexity, biological and ecological stability and belong to the introzonal type of vegetation (Belgard, 1971; Gensiruk, 2002; Hrivnák et al., 2019). Groves represented by natural populations of common oak (*Quercus robur* L.) are an important component of many of them. It is the most valuable forest species in steppe forest science. The value of *Q. robur* stands is due to their high marketability and ability to tolerate arid climates (Wallraf & Wagner, 2019). Turchin (2007) notes that among tree species oak groves have no equal especially in the steppe zone where their anti-erosion, water protection, environmental and soil protective role is extremely important. The recreational value of oak groves is also great. The necessity of regional researches is noted,which is caused by specificity of manifestation of biological features of *Q. robur* in specific ecological conditions.

Ravine forests have quite diverse microclimatic conditions (Netsvetova et al., 2021). Ravines are places where atmospheric water flows from the surrounding watershed areas. It is the thalweg that receives significant moisture due to rain and snow water. Bottoms of ravines have more favourable conditions of humidification also because here the groundwater is close to the surface. Up the slope deterioration of forest growth conditions is observed due to increasing dryness and greater soil erosion (Belgard, 1971; Tsvetkova, 2013). This is especially true for slopes of southern exposure, which is characterized by sharply expressed continentality. This significantly changes plant growth conditions. The deterioration of hydrothermal conditions has been particularly noticeable in recent years due to climate warming (Morgun et al., 2010).

Researching effects caused by adverse factors (first of all drought and high temperatures) on plants is one of the priority directions of ecology and physiology of plant organisms (Sauter & Kloth, 1987; Vierling & Kimpelb, 1992; Sauter & Cleve, 1995; Wang et al., 2003). The leading role in the processes of growth and survival of woody plants in their adaptation to unfavourable influences of the surrounding environment belongs to non-structural carbohydrates (NSC – soluble sugars and starch) (Kramer et al., 1983; Furze et al., 2019). Study of changes in their content and dynamics in plant organs is necessary for predicting survival of plant organisms in adverse hydrothermal conditions (Sala et al., 2012; Kaplina & Kulakov, 2015), as well as their productivity. Storage of NSC reserves also allows plants to survive seasonal periods of photosynthetic inactivity (dormancy) (Davidson et al., 2021).

Analysis of changes in the quantitative indicators of non-structural carbohydrates in the organs of *Q. robur* under various growth conditions is given considerable attention. Thus, during drought their content was determined in branches (Sala et al., 2012), in sapwood, wood of thin branches and roots in an alkaline oak grove (Kaplina & Kulakova, 2015), in conditions of traffic pollution in branches and leaves (Kulakova et al., 2017), in conditions of deteriorating living conditions (Martinez-Trinidad, 2010).

Great attention is also paid to studying dynamics of content of non-structural carbohydrates in organs of other species of oak. Analysis of seasonal changes of these compounds was carried out in the sapwood of branches and leaves *Q. petraea* in Switzerland (Hock et al., 2003). Distribution of nonstructural carbohydrates in durmast oak organs was studied in four key phenological stages (Barthes et al., 2013). In France, the carbohydrate reserve in the thin branches and roots of mature trees of two contrasting widespread species – of beech (*Fagus sylvatica*) and durmast oak (*Q. sessiliiflora*) (Barboroux et al., 2003) and the sapwood of the latter (El Zein, 2011) has been investigated. Phenological and temperature regulation of the dynamics of nonstructural carbohydrates in *Q. rubra* was considered by Gough et al. (2010). Influence of groundwater availability on the dynamics of radial growth and NSC fluctuations in *Q. pubescens* in the sub-Mediterranean region was analyzed (Gricar et al., 2019). In this species, the role of NSC in the regrowth of trees after pruning was established, and the NSC pool was restored to a greater extent than growth (Palacio et al., 2020).

The purpose of this research is to analyze contents and dynamics of the NSC in *Q. robur* leaves in various ravine forest growth conditions differing in the soil moisture.

Materials and methods

The research areas are located in the ravine forest of the Viyskove area (the length along the narrower part is 48º11′08″ N, 35º07′45″ E: 48º10′41″ N, 35º10′12″ E) in Dnepropetrovsk region (the Steppe zone of Ukraine) in various forest growth conditions (Fig. 1). The first area is located in the thalweg (hygromesophilic growth conditions, $CL_{2–3}$). The second area is located in the middle part and the third – in the upper part of the slope of the southern exposure. Their forest growth conditions are mesoxerophilic, dry, CL_1 and dry xerophilic $CL_{0–1}$, respectively. Humidification in the thalweg is soil-based and atmospheric-based humidification, and on the slopes of the ravine – it is atmospheric transit (Belgard, 1971; Tsvetkova, 2013).

Fig. 1. Map of the Viyskove area, Ukraine, Dnipropetrovsk region

Samples of leaves were selected from 5 model trees (25-30 year-old trees) from the south-eastern side at the height of 2.5 m, from 10 branches of the same branching order on each tree. The second and third leaves from the base of annual shoots were used. Determination of soluble sugars was carried out by the iodometric method, and starch was determined colometrically (Pochinok, 1971) in four repetitions.

Humidity and temperature were determined using an electronic thermometer hygrometer Flus ET-951 (China). Average agrometeorological indicators on the territory of the research areas are presented for 2019. (Table1).

Table 1
Average agrometeorological indicators during the period of research

Agrometeorological indicators	May	June	July	August	September
Average air temperature, °C	+23.5	+30.8	+27.6	+27.1	+22.1
Maximum air temperature, °C	+30	+35	+33	+34	+32
Temperature on the day of sampling, °C	+29	+35	+32	+31	+21
Precipitation, mm	23	57	30	20	23
Minimum humidity of air, %	51	38	25	44	60
Maximum soil surface temperature, °C	37.2	50.8	61.0	58.4	55.1

Note: the data were partially obtained from the archives of the meteorological station near Viyskove village (https://rp5.ua).

Soil samples were selected at depth of 10 and 40 cm, soil moisture was determined by thermogravimetric method (DSTU ISO 11465: 2001) and measurements were made in triplicate (Kucerik et al., 2013).

Table 2
Soil moisture in the research areas of the ravine forest in the Viyskove area (% of absolutely dry mass)

Month	Depth, cm	Thalweg CL_{2-3}	Middle part of the slope CL_1	Upper part of the slope CL_{0-1}
May	10	20.11 ± 0.18^a	17.13 ± 0.15^b	17.05 ± 0.16^b
	40	25.39 ± 0.21^a	20.38 ± 0.23^b	21.12 ± 0.23^b
June	10	22.42 ± 0.29^a	15.31 ± 0.17^b	12.08 ± 0.14^b
	40	23.50 ± 0.33^a	18.79 ± 0.19^b	17.14 ± 0.20^c
July	10	18.36 ± 0.12^a	10.13 ± 0.16^b	9.26 ± 0.13^b
	40	21.63 ± 0.28^a	13.77 ± 0.18^b	11.51 ± 0.15^c
August	10	13.43 ± 0.13^a	7.28 ± 0.15^b	5.72 ± 0.12^c
	40	19.65 ± 0.17^a	12.69 ± 0.17^b	8.31 ± 0.16^c
September	10	14.71 ± 0.18^a	8.18 ± 0.16^b	6.10 ± 0.11^c
	40	18.74 ± 0.21^a	10.22 ± 0.11^b	9.85 ± 0.17^b

Note: significant difference between groups is indicated in lines with different letters; statistical analysis was performed by one-way ANOVA with several comparisons using Tukey testing.

As can be seen from Table 2, in June the moisture content in the soil of the upper part of the slope ($CL_{0–1}$) at the depth of 10 cm was much lower than in areas in the middle and lower parts of the slope. At the depth of 40 cm the soil remains more moisturized just like the soil of the middle part of the slope. In July, the quantitative indicators of water content in the soil of all areas were reduced, especially in mesoxeromorphic and xeromorphic forest growth conditions. In August, soil moisture at the depth of 10 cm became even lower in all research areas, but the lowest level was registered on the top of the slope. During the first autumn month water content in the soil in the research areas remained almost the same as in August. Thus, plants in the middle part and especially the upper parts of the slope are influenced by a significant soil drought combined with air drought and action of high temperatures (Tables 1, 2).

The standard IBM SPSS Statistics 22 (IBM, USA, 2013) software package was used for data analysis. Data are presented as the mean value with standard error (x ± SE). The value of $P < 0.05$ was considered statistically significant. The Tukey criterion of honestly significant difference of group mean values was applied (with Bonferroni correction).

Results

Dynamics of changes in glucose content in the leaves of *Q. robur* during the vegetation period in various forest growth conditions are similar (Fig. 2a). In May and June, the figure for this monosugar was the lowest. This may be due to its use for the growth of shoots. Slowed growth during the vegetation period and changes in the hydrothermal regime (Table 2) led to an increase in glucose content in the leaves of *Q. robur* in all research areas in July, its maximum level was observed in August. In September, a drop in concentration of this form of sugar was observed in leaves of plants of all variants. This is probably due to the autumn outflow of the monosaccharide into the shoots which is typical or the first phase of hardening of woody plants. Thus, the dynamics of changes in the amount of glucose in the leaves of *Q. robur*, which grows in different forest growth conditions ($CL_{2–3}$, CL_1 and $CL_{0–1}$), are similar. However, the plant growing conditions affect the amount of this reducing sugar.

At the beginning of the vegetation period the highest content of monosaccharide was found in the leaves of thalweg plants (hygromesophilic conditions $CL_{2–3}$, Fig. 2a). But in July glucose concentration in these organs in mesoxerophilic (CL_1) and, especially, xerophilic ($CL_{0–1}$) conditions of the ravine forest became higher than in hygromesophilic conditions ($CL_{2–3}$) by 30.7% and 47.5%, respectively. At a later stage, as the air and soil drought intensified, there was an increase in the concentration of monosaccharide in the leaves compared to plants that grew under conditions of better water supply. Thus, in August the difference in its content in CL_1 and $CL_{0–1}$ areas was 42.1% and 61.8% respectively compared to the $CL_{2–3}$ variant. However, in September, against the background of the ongoing drought, the concentration of glucose in the leaves of *Q. robur* in arid growth conditions (CL_1 and $CL_{0–1}$) became slightly lower than in plants growing in more favourable conditions of water supply, – the strongest decrease was typical for plants of the upper slope ($CL_{0–1}$). This may be due to the negative effect of prolonged drought on photosynthesis, and thus – on synthesis of sugars.

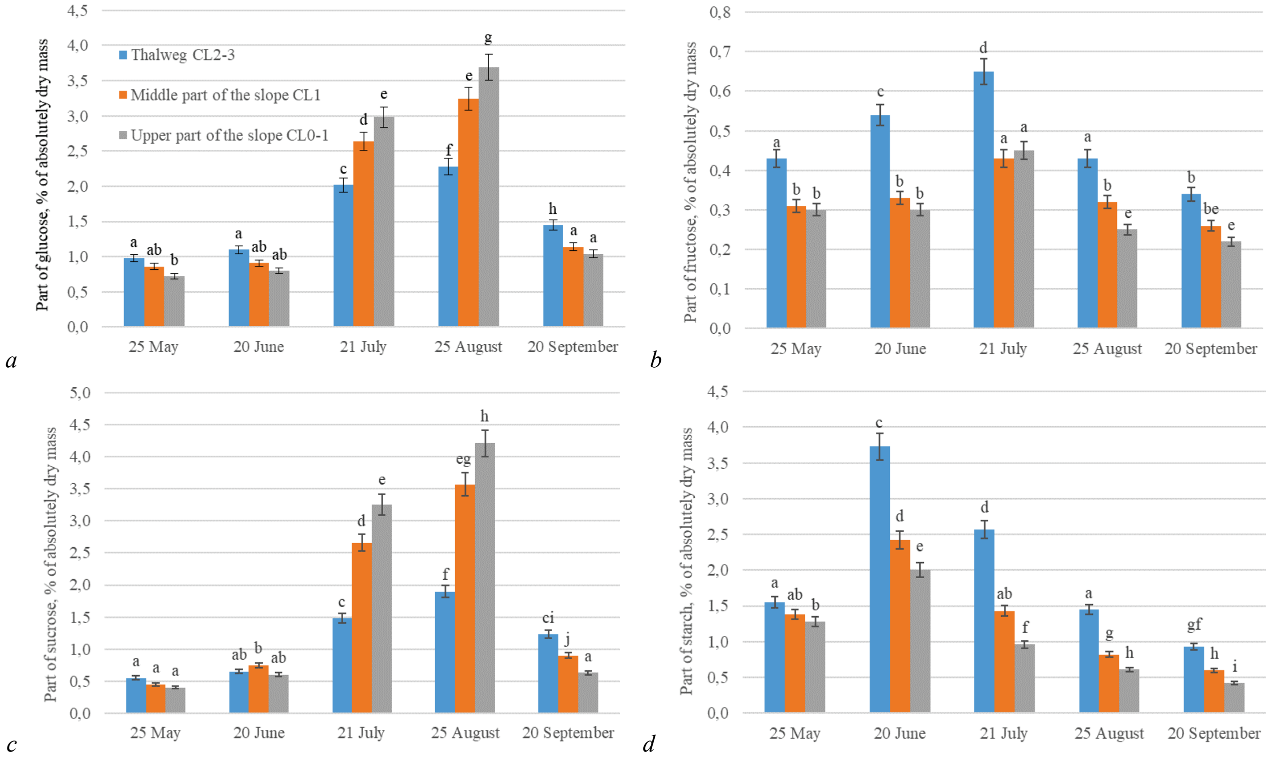

Fig. 2. Influence of forest growth conditions on the content of the following elements in *Q. robur* leaves: *a* – glucose, *b* – fructose, *c* – sucrose, *d* – starch; % per absolutely dry mass (x ± SE, n = 5); statistical analysis was performed by Tukey testing

Quantitative changes in fructose in *Q. robur* leaves during the vegetation period are presented in Figure 2b. Comparison of concentration of this monosaccharide during the research months indicates that it was maximum in the leaves of plants of all researched variants in July, further on a decrease was observed with a minimum in September. It should be noted that changes in fructose levels in mesoxerophilic and xerophilic conditions during the vegetation period are smaller than in thalweg plants (hygromesophilic conditions). In contrast to glucose, the fructose content of tree leaves growing in the middle (CL_1) and upper ($CL_{0–1}$) parts of the slope remains lower throughout the vegetation period compared to the conditions of better water supply.

The amount of reducing sugars in the leaves of *Q. robur* in hygromesophilic forest growth conditions was the highest in July and August, and the indicators in these sampling periods do not differ statistically (Table 3). In mesoxerophilic and xerophilic conditions plant growth was the highest in August. In September concentration of reducing sugars dropped significantly in the leaves of thalweg plants by 1.51 times, and in the middle and upper part of the slope the reduction was by 2.54 and 3.42 times respectively compared to the previous month. Since content of glucose in plant leaves is much higher than that of fructose, the dynamics of reducing sugars and the direction of their quantitative changes in plant leaves both in arid growth conditions and relatively wet hygromesophilic ($CL_{2–3}$) conditions is determined mainly by glucose concentration.

As can be seen from Table 3, in May and June the amount of reducing sugars in the leaves of plants under favourable conditions of soil moisture was greater than under mesoxerophilic and xerophilic conditions (with the lowest level under the latter). With increasing drought in July and August, their concentration grew and became higher in arid forest growth conditions. However, in September, despite the drought and high temperatures, content of these sugars in the leaves was lower than under conditions of better water supply. The amount of sucrose in the leaves of *Q. robur* trees growing in the thalweg was less than that of glucose during all months of research. This is not typical for plants that grow under lack of moisture in the soil. Under mesoxerophilic CL_1 conditions in July–August the content of sucrose was almost the same as that of glucose, and in xerophilic $CL_{0–1}$ conditions it was higher (Fig. 2c). In the process of vegetation, content of disaccharide increased with the maximum in August, and in September it dropped significantly. Such dynamics of quantitative changes are typical for all researched variants.

Table 3
Influence of forest growth conditions on the content of reducing sugars in *Q. robur* leaves (% per absolutely dry mass, x ± SE, n = 5)

Date	Thalweg $CL_{2–3}$	Middle part of the slope CL_1	Upper part of the slope $CL_{0–1}$
25 May	1.41 ± 0.04^a	1.17 ± 0.02^b	1.02 ± 0.07^b
20 June	1.64 ± 0.09^a	1.27 ± 0.03^b	1.10 ± 0.04^b
21 Jule	2.67 ± 0.03^a	3.07 ± 0.04^b	3.43 ± 0.05^c
25 August	2.71 ± 0.06^a	3.58 ± 0.05^b	3.94 ± 0.10^c
20 September	1.79 ± 0.04^a	1.40 ± 0.02^b	1.26 ± 0.03^b

Note: the same as in Table 2.

Comparison of sucrose concentration in the leaves of trees in various forest growth conditions shows that in the first two months of vegetation the difference between the variants is statistically unreliable, but later on it increases. Under mesoxerophilic conditions in July the amount of sucrose was much higher than under favourable water supply, and in August the difference became even greater. In the xerophilic conditions ($CL_{0–1}$) differences of indicators were even greater in comparison with thalweg plants (mesohygrophilic hygrotope). In September, the sucrose content in *Q. robur* leaves in all researched variants decreased significantly; this decrease was greater in drier forest conditions, which may be due to the inhibition of sucrose synthesis caused by long-term lack of moisture in the soil, as well as outflow into shoots.

Figure 2d shows the dynamics of changes in the starch content in leaves of *Q. robur* growing in various forest growth conditions. Graphically, the curves of quantitative changes in polysaccharide in various researched variants are similar; they are single-humped with a maximum in June. In July, a sharp decline in starch content in the leaves was observed: Under hygromesophilic conditions ($CL_{2–3}$) this decline was 45.7%, in mesoxerophilic conditions (CL_1) – it is 69.2% and in xerophilic conditions ($CL_{0–1}$) starch content declined by 108.2%. That is, a larger deficit of moisture caused the most significant drop in the amount of polysaccharide. At later stages its content in the leaves continued to decline and in September it reached the lowest values.

Forest growth conditions significantly affect the amount of starch in leaves of *Q. robur*. The highest starch content was found in hygromesophilic forest growth conditions ($CL_{2–3}$). At the beginning of vegetation in May, the difference in the size of these indicators in leaves of trees growing on the middle (CL_1) and upper ($CL_{0–1}$) part of the slope was statistically unreliable. In June and July difference between these two variants became significant. In the most unfavourable conditions of moisture supply the content of starch was the lowest. Thus, in July in leaves of plants in the middle part of the slope the starch content was 1.79 times less, and (and in the upper part of the slope it was 2.67 times less) compared to the trees in the thalweg. In August, these values were 1.78 and 2.38, and in September they were 1.55 and 2.21, respectively.

During the vegetation period the ratio of sucrose content to the content of starch changed in leaves of all variants of *Q. robur* (Fig. 3a). It was especially high in July–August. The greatest values of this indicator are found in leaves of plants growing in xerophilic conditions It is typical that a similar pattern of changes is established for the ratio of glucose / starch (Fig. 3b).

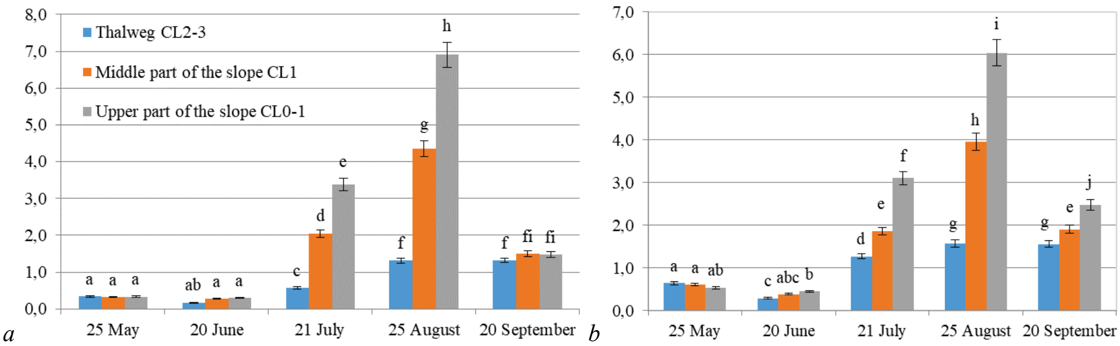

Fig. 3. Sucrose to starch ratio (*a*) and glucose to starch ratio (*b*): x ± SE, n = 5; the same as in Figure 2

Thus, forest growth conditions do not affect the nature of the dynamics of soluble sugars and starch in the leaves of *Q. robur*, however, these conditions change their quantitative indicators.

Discussion

When plants are exposed to high temperatures and increasing water stress during the vegetation season in xerophilous and mesoxerophilous forest growth conditions, the concentration of both glucose and sucrose in the leaves of *Q. robur* becomes much higher compared to plants growing in conditions of more optimal water supply (Fig. 2a–d).

It should be noted that in our research increase of sucrose content in leaves of *Q. robur* under conditions of soil and air drought is more significant than increase of glucose level. Similar results were obtained for some other species of tree plants. In the work by Obraztsova (1973) it is indicated that in hot dry weather in August sucrose content in the leaves of drought-resistant plants increases several times – in *Acer campestre* L. – 3.56 times, in *Gleditsia triacanthos* L. – 3.52, in leaves of the non-drought-resistant species of *Salix alba* L. the sucrose content does not actually change, and in *Alnus glutinosa* L. it even decreases compared to the previous month. Bessonova et al. (1976) note that disaccharide content in leaves of *Robinia pseudoacacia* L. in dry forest growth conditions is higher than in fresh moisturized conditions. With increasing water and temperature stress in the leaves of drought-resistant genotypes of apple trees, the sucrose content increases (Ulyanovskaya et al., 2010). It was also found that in the leaves of *Q. robur* in an alkaline oak grove the amount of this sugar is almost twice higher than in a sedge oak grove, which is due to poorer water supply under these conditions and the need to maintain osmotic pressure in cells (Kaplina & Kulakova, 2015). All the above data confirm the role of sucrose in adaptation of tree plants to drought.

According to our data, concentration of fructose in *Q. robur* leaves in drought conditions of growth (unlike glucose and sucrose) decreases compared to more favourable conditions of moisture (Fig. 2b). Some researchers observed the opposite pattern in a number of plants. Thus, in the leaves of more drought-resistant varieties of wheat in relation to less resistant ones fructose content increases (Maevskaya et al., 2013). A similar pattern was obtained by Kameli & Lozei (1993). The inconsistency of our results with the given literature data can be explained by the species specificity of plant reaction to drought.

When water stress grows the increase in concentration of glucose and sucrose in our research is correlated with reduction of starch content (Fig. 4, 5). Interconversion of glucose, sucrose and starch is an integral part of carbohydrate metabolism in both vegetative and reproductive organs (Kramer et al., 1983; Nazonha et al., 2018). Synthesis of sugar and starch are competitive processes. UDPGlucose is the substrate for the synthesis of the both substances. Thus, slowing down of starch synthesis leads to the presence of free substrates for sucrose synthesis (Heldt, 2011). Hydrolysis of starch can also cause an increase in the amount of sucrose (Kursanov, 1976) and hexoses (Lawlor & Cornis, 2019).

Karimova (2008) proposes to use the ratio of starch and soluble sugars as a test to assess the degree of resistance of cotton plant species to soil drought. Sakalo (2009) indicates that increase in sugar/starch ratio may be an additional criterion in assessing the potential drought. As can be seen from Figure 3, the value of the sucrose/starch ratio in the leaves of *Q. robur* greatly increases in mesoxerophilic and xerophilic growing conditions relative to hygromesophilic, especially in the variant with the lowest amount of water in the soil. This indicates that in extreme conditions of moisture supply *Q. robur* plants are characterized by adaptive changes in carbohydrate metabolism, which, along with other means of adaptation, can ensure implementation of relatively normal functioning in adverse hydrothermal conditions. We found that under conditions of hydrothermal stress an increase in glucose occurs in leaves of *Q. robur*, alongside an increase of sucrose (although the increase of glucose is expressed to a lesser extent). It is shown that glucose is an important component necessary for the formation of resistance to abiotic stress, as far as a large number of stress response genes are induced namely by this molecule (Castrillo, 1992; Seki et al., 2002). And sucrose affects the work of the proton-sugar importer involved in loading the phloem. The predominant participation in the regulation of growth processes is attributed to sucrose (Kiriziy et al., 2015). It is in adverse hydrothermal vegetation conditions that these processes are very important for survival of plants. It is characteristic that the highest content of these sugars is observed in July and August, when the most stressful conditions for providing plants with water are formed due to a significant reduction of water in the soil (Table 2). As is shown, such conditions result the maximum water deficiency in leaves of *Q. robur* (Bessonova et al., 2016).

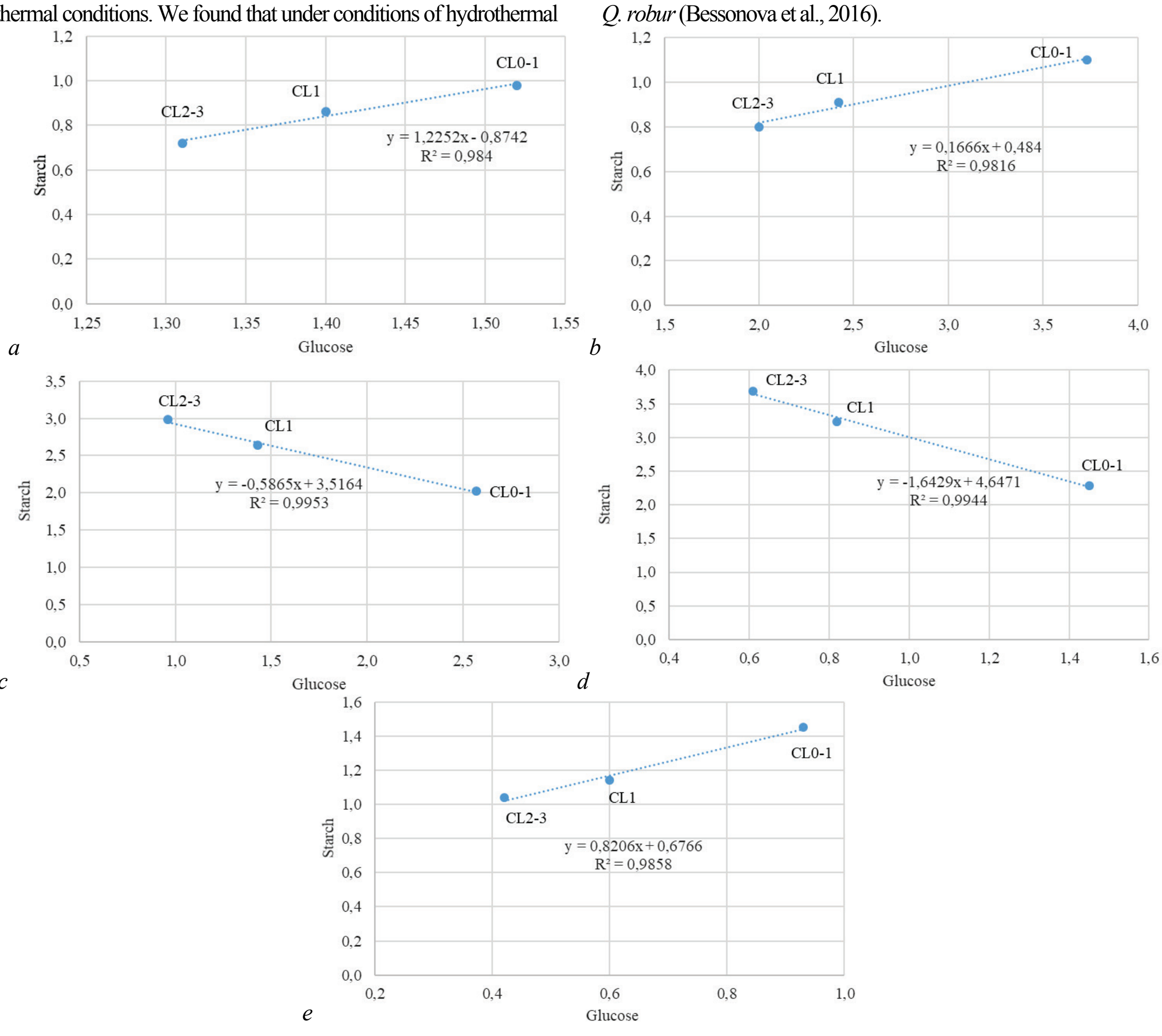

Fig. 4. Correlation between starch and glucose concentration (% per absolutely dry mass) by months depending on forest growth conditions: *a* – May; *b* – June; *c* – July; *d* – August; *e* – September

In conditions of water deficiency, the protective role of these sugars in plant cells is that they play the role of osmolytes. Therefore, increased concentration of these soluble sugars contributes to water retention and maintenance of turgor (Rolland et al., 2006). They are also osmoprotectors preventing damage of cell membranes and inactivation of enzymes (Hare et al., 1998). It is known that water deficiency alters certain physiological and biochemical processes in cells, which leads to formation of active oxygen forms, causes oxidative stress (Blochina et al., 2003; Reddy et al., 2004; Sudachkova et al., 2015). The action of these strong oxidants can be neutralized by metabolites involved in the process of controlling free radicals (Sudachkova et al., 2015). It has been established that sugars, along with other compounds, protect cells from free radical oxidation (Averyanov & Lapikova, 1989; Pharr, 1995; Couee et al., 2006; Kolupaev & Karpets, 2010). Therefore, given all these protective functions of sugars, increase in their level in leaves of *Q. robur* in conditions of significant lack of moisture in the soil (in mesoxerophilic and xerophilic forest growth conditions) plays an important role in adapting plants to these growing conditions, increasing their resistance to drought. However, with prolonged exposure to adverse hydrothermal conditions on plants there is a decrease in the content in leaves of both soluble sugars and starch (September) relative to hygromesophilic conditions (Fig. 1), which can be explained by a decrease in the adaptive potential of *Q. robur* at the end of the vegetation period as well as by outflow of sugars into shoots due to the beginning of the first phase of plant hardening after starch hydrolysis. However, in general, despite the fact that the growth of common oak decreases in arid conditions and indicators of water metabolism change (Bessonova et al., 2016), we can note a satisfactory adaptation of *Q. robur* to such adverse growth conditions.

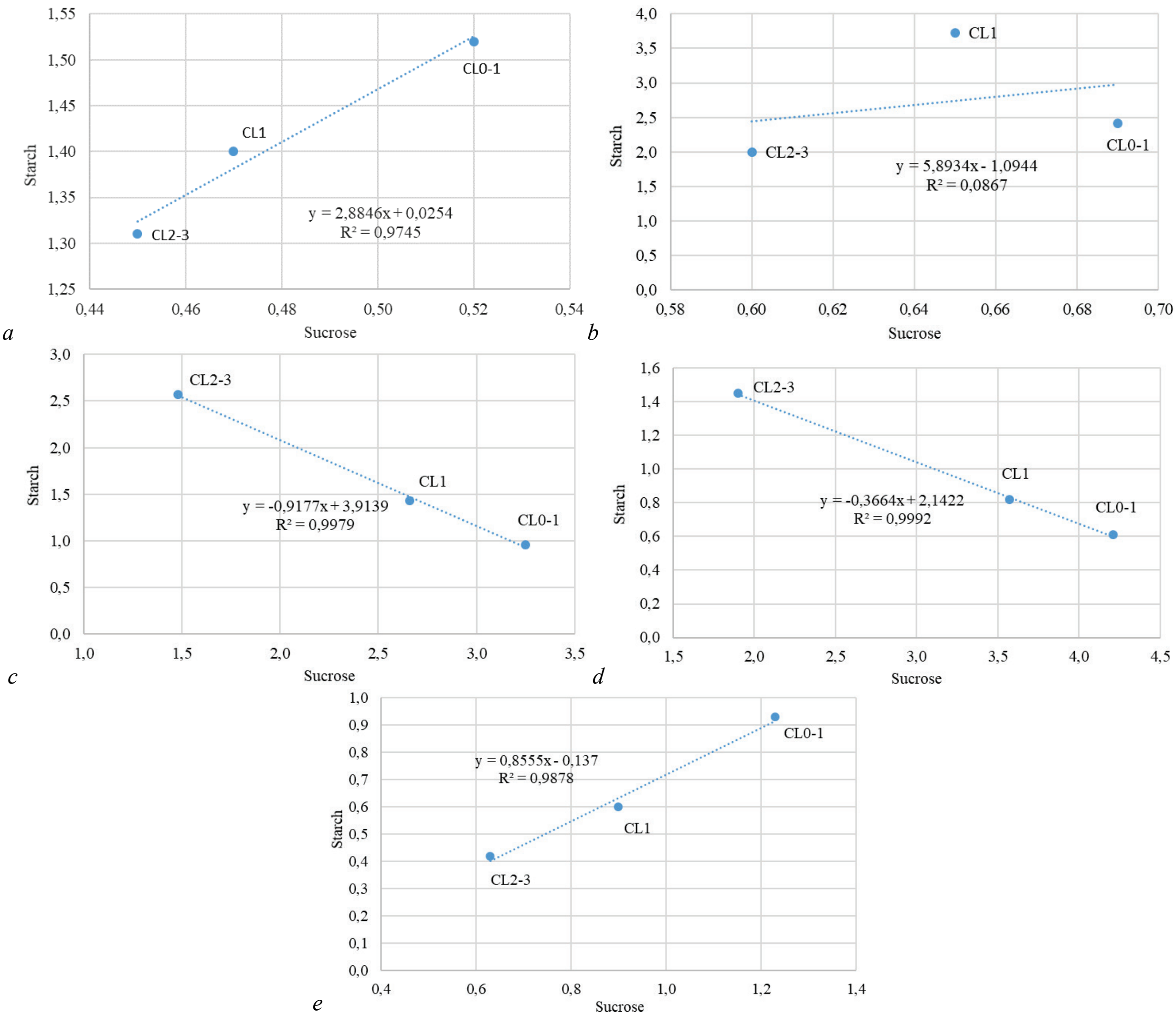

Fig. 5. Correlation between starch and sucrose concentration (% per absolutely dry mass) by months depending on forest growth conditions: *a* – May; *b* – June; *c* – July; *d* – August; *e* – September

Conclusions

In different soil moisture forest conditions (hygromesophilic, xeromesophilic and xerophilic) during the process of vegetation the dynamics of non-structural carbohydrates in leaves of *Q. robur* are similar. Soil and air drought (areas with hygrotope $CL_{1–2}$, CL_1) leads to changes in the quantitative indicators of sugars and starch in leaves during the driest months (July and August). Under influence of increasing water stress during the process of vegetation concentration of sugars, both glucose and sucrose in leaves of *Q. robur* increases in all variants of the research, but the most significant increase is typical for mesoxerophilic and especially for xerophilic conditions. Increase in the level of these soluble sugars in leaves of *Q. robur* under adverse moisture conditions correlates with a decrease in the level of starch. These metabolic changes can be considered as an adaptive response of plants to arid growing conditions.

In September, despite drought and high temperatures, there was a drop in the content of all forms of non-structural carbohydrates in leaves of plants of all variants compared to the previous month. Decrease in the content of sugars and starch in the leaves in mesoxerophilic and xerophilic conditions during this period of vegetation in relation to these indicators in plants growing under normal water supply can be considered a decrease in the adaptive potential of plants under prolonged stress. In general, changes in carbohydrate metabolism in the leaves of *Q. robur* in the ravine forest in arid forest growth conditions are one of the mechanisms of adaptation of *Q. robur* to these conditions.

The research was performed within the research project No. 0117U003964 "Comprehensive assessment of green areas of urban man-made territories of the Dnipro economic region".

References

Averyanov, A. A., & Lapikova, V. P. (1989). Vzaimodeystvie saharov s gidroksilnyim radikalom v svyazi s fungitoksichnostyu vyideleniy listev [Interaction of sugars with hydroxyl radicals due to fungitoxicity of leaf excretions]. Biochemistry, 54(10), 1646–1651 (in Russian).

Barana, J., Pielecha, R., Kauzalb, P., Kuklac, W., & Bodziarczyk, J. (2020). Influence of forest management on stand structure in ravine forests. Forest Ecology and Management, 463(1), 118018.

Barbaroux, C., Breda, N., & Dufrene, E. (2003). Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (*Quercus petraea* and *Fagus sylvatica*). New Phytologist, 157, 605–615.

Barthes, L., Blanot, D., & Fresneau, C. (2013). Distribution of non-structural nitrogen and carbohydrate compounds in mature oak trees in a temperate forest at four key phenological stages. Trees, 27, 1023–1034.

Belgard, A. L. (1971). Stepnoe lesorazvedenie [Steppe afforestation]. Lesnaya Promyishlennost, Moscow (in Russian).

Bessonova, V. P., Mihaylov, O. R., & Koryitova, A. I. (1976). Dinamika pigmentov i uglevodov v listyah akacii beloy proizrostayuschey v razlichnyiy lesorastitelnyih usloviyah [Dynamics of pigments and carbohydrates in the leaves of *Robinia pseudoacacia* growing in different forest conditions]. Voprosyi Stepnogo Lesovedenija i Ohrany Prirody, 5(2), 100–105 (in Russian).

Bessonova, V. P., Tkach, V. V., & Kryvoruchko, A. P. (2016). Vodnyj obmin lystia *Quercus robur* u protyerozijnomu nasadzhenni na pivdni arealu vydu [Water exchange of *Quercus robur* leaves in a proterosian plantation in the southern part of the species areal]. Visnyk Dnipropetrovskoho Universytetu, Series Biology, Ecology, 24(2), 444–450 (in Ukrainian).

Blochina, O., Virolainen, E., & Fagerstedt, K. V. (2003). Antioxidants oxidative damage and xygen deprivation stress: A review. Annals of Botany, 91(2), 179–194.

Castrillo, M. (1992). Sucrose metabolism in bean plants under water deficit. Journal of Experimental Botany, 43(12), 1557–1561.
Couee, I., Sulmon, C., Gouesbet, G., & El Amrani, A. (2006). Involvement of soluble sugars in reactive oxygen species balance and responses to oxidative stress in plants. Journal of Experimental Botany, 57(3), 449–459.
Cvetkova, N. N. (2013). Osobennosti migracii organo-mineral'nyh veshchestv i mikroelementov v lesnyh biogeocenozah Stepnoj zony Ukrainy [Features of migration of organo-mineral substances and microelements in forest biogeocenoses of the Steppe zone of Ukraine]. Stanley, Dnepropetrovsk (in Russian).
Davidson, A., Le, S. T., Cooper, K. B., Lange, E., & Zwieniecki, M. (2021). No time to rest: Seasonal dynamics of non-structural carbohydrates in twigs of three Mediterranean tree species suggest year-round activity. Scientific Reports, 11, 5181.
El Zein, R., Maillard, P., Brida, N., Marchand, J., Montpied, P., & Gerant, D. (2011). Seasonal changes of C and N non-structural compounds in the stem sapwood of adult sessile oak and beech trees. Tree Physiology, 31(8), 843–854.
Furze, M. E., Huggett, B. A., Aubrecht, D. M., Stolz, C. D., Carbone, M. S., & Richardson, A. D. (2019). Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. The New Phytologist, 221(3), 1466–1477.
Gough, C. M., Flower, C. F., Vogel, C. S., & Curtis, P. S. (2010). Phenological and temperature controls on the temporal non-structural carbohydrate dynamics of *Populus grandidentata* and *Quercus rubra*. Forests, 1(1), 65–81.
Gričar, J., Zavadlav, S., Jyske, T., Lavrič, M., Laakso, T., Hafner, P., Eler, K., & Vodnik, D. (2019). Effect of soil water availability on intra-annual xylem and phloem formation and non-structural carbohydrate pools in stem of *Quercus pubescens*. Tree Physiology, 39(2), 222–233.
Hare, P. D., Cress, W. A., & Van Staden, J. (1998). Dissecting the roles of osmolyte accumulation during stress. Plant, Cell and Environment, 21, 535–553.
Heldt, G. V. (2011). Biohimiya rastenij [Plant biochemistry]. Binom, Laboratoriya Znanij, Moscow (in Russian).
Hensiruk, S. A. (2002). Lisy Ukrainy [Forests of Ukraine]. Vydavnytstvo Naukovoho Tovarystva imeni Shevchenka, Lviv (in Ukrainian).
Hock, G., Richter, A., & Korner, C. (2003). Non-structural carbon compounds in temperate forest trees. Plant, Cell and Environment, 26(7), 1067–1081.
Hrivnák, R., Slezák, M., Ujházy, K., Máliš, F., Blanár, D., Ujházyová, M., & Kliment, J. (2019). Phytosociological approach to scree and ravine forest vegetation in Slovakia. Annals of Forest Research, 62(2), 183–200.
Hrytsaienko, Z. M., Hrytsaienko, A. O., & Karpenko, V. P. (2003). Metody biolohichnykh ta ahronomichnykh doslidzhen roslyn i hruntiv [Methods of biological and agronomic research on plants and soils]. Nichlava, Kyiv (in Ukrainian).
Kameli, A., & Losel, D. M. (1993). Carbohydrate and water status in wheat plants under water stress. New Phytology, 125, 609–614.
Kaplina, N. F., & Kulakova, N. Y. (2015). Soderzhanie nestrukturnyh uglevodov v organah duba chereshchatogo v usloviyah yuzhnoy lesostepi Evropeyskoj chasti Rossii [The content of non-structural carbohydrates in the organs of the pedunculate oak in the conditions of the southern forest-steppe of the European part of Russia]. Vestnik Privolzhskogo Gosudarstvennogo Tehnologicheskogo Universiteta, Forest Ecology, Nature Management, 28, 84–97 (in Russian).
Karimova, I. S., Ergashev, A., & Abdullaev, A. (2008). Vlijanie pochvennoj zasuhi na soderzhanie uglevodov razlichnyh sortov i linij srednevoloknistogo hlopchatnika [Influence of soil draught on the content of carbohydrate in varieties and lines of *Gossypium hirsutum*]. Izvestiya Akademiya Nauk Respubliki Tatarstan, Otdelenie Biologicheskih i Meditsinskih Nauk, 163, 31–36 (in Russian).
Kirizij, D. A., Frantijchuk, V. V., & Stasik, O. O. (2005). Soderzhanie rastvorimyh uglevodov i starenie flagovogo lista pshenicy pri eksperimental'nom blokirovanii ottoka assimiliatov [The content of soluble carbohydrates and aging of the flag leaf of wheat during experimental blocking of the outflow of assimilates]. Plant Physiology and Genetics, 47(2), 136–146 (in Russian).
Kolupaev, Y. E., & Karpec, Y. V. (2010). Uchastie rastvorimyh uglevodov i nizkomolekulyarnyh soedinenij azota v adaptivnyh reakcijah rastenij [Participation of soluble carbohydrates and low molecular nitrogen compounds in adaptive plant responses]. Visnyk of Kharkiv National Agrarian University, Series Biology, 2, 36–53 (in Russian).
Kramer, P. D., & Kozlovskij, T. T. (2013). Fiziologiya drevesnyh rastenij [Physiology of woody plants]. Kniga po Trebovaniju, Moscow (in Russian).
Kucerik, J., Ctvrtnickova, A., & Siewert, C. (2013). Practical application of thermogravimetry in soil science. Part 1: Thermal and biological stability of soils from contrasting regions. Journal of Thermal Analysis and Calorimetry, 113(3), 1103–1111.
Kulakova, N. Y., Kolesnikov, A. V., Baranova, Y. A., & Golubeva, M. V. (2017). Issledovaanie adaptacionnyh vozmozhnostej duba chereshchatogo (*Quercus robur*) k avtotransportnomu zagryazneniyu [Investigation of the adaptive capabilities of the pedunculate oak (*Quercus robur*) to road traffic pollution]. Russian Journal of Agricultural and Socio-Economic Sciences, 62, 239–249 (in Russian).
Kursanov, A. L. (1976). Transport assimiliatov v rastenij [Transport of assimilates in the plants]. Nauka, Moscow (in Russian).
Maevskaya, S. N., & Nikolaeva, M. K. (2013). Reakcija antioksidantnoj i osmoprotektornoj sistem prorostkov pshenicy na zasuhu i regidrataciju [Reaction of antioxidant and osmoprotective systems of wheat seedlings to drought and rehydration]. Plant Physiology, 60(3), 351–359 (in Russian).
Martinez-Trinidad, T., Watson, W. T., Arnold, M. A., Lombardini, L., & Appel, D. N. (2010). Comparing various techniques to measure tree vitality of live oaks. Urban Forestry and Urban Greening, 9(3), 199–203.
Morgun, V. V., Kirichij, D. A., & Shadchina, T. M. (2010). Ekofiziologicheskie i geneticheskie aspekty adaptacii kul'turnyh rastenij k global'nym izmenenijam klimata [Ecophysiological and genetic aspects of adaptation of cultivated plants to global climate changes]. Physiology and Biochemistry of Cultivated Plants, 42(1), 3–22 (in Russian).
Netsvetova, M., Prokopuka, Y., Ivankob, I., Kotovychb, O., & Romenskyyc, M. (2021). *Quercus robur* survival at the rear edge in steppe: Dendrochronological evidence. Dendrochronologia, 67, 125843.
Noronha, H., Silva, A., & Gerós, H. (2018). A molecular perspective on starch metabolism in woody tissues. Planta, 248, 559–568.
Obrazcova, V. I. (1973). Dinamika uglevodov v list'jah drevesnyh rastenij v uslovijah stepnoj zony Ukrainy [Dynamics of carbohydrates in the leaves of woody plants in the steppe zone of Ukraine]. Voprosy Stepnogo Lesovedenija, 2, 84–87 (in Russian).
Palacio, S., Paterson, E., Hester, A. J., Nogués, S., Lino, G., Anadon-Rosell, A., Maestro, M., & Millard, P. (2020). No preferential carbon-allocation to storage over growth in clipped birch and oak saplings. Tree Physiology, 40(5), 621–636.
Pharr, D. M., Stoop, J. M. H., Williamson, J. D., Studer Feusi, M. E., Massel, M. O, & Conkling, M. A. (1995). The dual role of mannitol as osmoprotectant and photoassimilate in celery. Hortscience, 30(6), 1182–1188.
Pochinok, H. N. (1976). Metody biohimicheskogo analiza rastenij [Methods of biochemical analysis of plants]. Naukova Dumka, Kiev (in Russian).
Reddy, R. A., Chaitanya, K. V., & Vivekanandan, M. (2004). Drought-induced responses of photosynthesis and antioxidant metabolism in higher plants. Journal of Plant Physiology, 161(11), 1189–1202.
Rolland, F., Baena-Gonzalez, E., & Sheen, J. (2006). Sugar sensing and signaling in plants: Conserved and novel mechanisms. Annual Review of Plant Biology, 57, 675–709.
Sakalo, V. D., Larchenko, K. A., & Kurchii, V. M. (2009). Syntez i metabolizm sakharozy v lystkakh prorostkiv kukurudzy za umov vodnoho defitsytu [Synthesis and metabolism of sucrose in the leaves of corn seedlings under conditions of water deficiency]. Physiology and Biochemistry of Cultivated Plants, 41(4), 305–313 (in Russian).
Sala, A., Woodruff, D. R., & Meinzer, F. C. (2012). Carbon dynamics in trees: Feast or famine? Tree Physiology, 32(6), 764–775.
Sauter, J. J., & Kloth, S. (1987). Changes in carbohydrates and ultrastructure in xylem ray cells of *Populus* in response to chilling. Protoplasma, 137, 45–55.
Sauter, J., & Cleve, B. (1995). Storage, mobilization and interrelations of starch, sugars, protein and fat in the ray storage tissue of poplar trees. Trees, (8), 297–304.
Seki, M., Narusaka, M., Ishida, J., Nanjo, T., Fujita, M., Oono, Y., Kamiya, A., Nakajima, M., Enju, A., Sakurai, T., Satou, M., Akiyama, K., Taji, T., Yamaguchi-Shinozaki, K., Carninci, P., Kawai, J., Hayashizaki, Y., & Shinozaki, K. (2002). Monitoring the expression profiles of 7000 *Arabidopsis* genes under drought, cold and high-salinity stresses using a full-length cDNA microarray. The Plant Journal, 31(3), 279–292.
Sudachkova, N. E., Romanova, L. I., & Milyutina, I. L. (2015). Dejstvie zasuhi na formirovanie drevesiny i antioksidantnuju zashchitu kambial'noj zony sosny obyknovennoj [The effect of drought on the formation of wood and antioxidant protection of the cambial zone of Scots pine]. Siberian Forestry Journal, 5, 54–63 (in Russian).
Turchin, T. Y. (2007). Bajrachnye dubravy i vedenie hozyajstva v nih [Ravine oak forests and their management]. Forestry, 1, 21–24 (in Russian).
Ul'yanovskaya, E. V., Nen'ko, N. I., Zaharova, M. V., & Karavaevaya, A. V. (2010). Fiziologo-biohimicheskie osobennosti ustojchivosti k zasuhe genotipov yabloni raznoj ploidnosti [Physiological and biochemical characteristics of drought resistance of apple genotypes of different ploidy]. Fruit Growing and Viticulture of the South of Russia, 3(2), 29–42 (in Russian).
Vieira, J., Matos, P., Mexia, T., Silva, P., Lopes, N., Freitas, C., Correia, O., Santos-Reis, M., Branquinho, C., & Pinho, P. (2018). Green spaces are not all the same for the provision of air purification and climate regulation services: The case of urban parks. Environmental Research, 160, 306–313.
Vierling, E., & Kimpelb, J. A. (1992). Plant responses to environmental stress. Current Opinion in Biotechnology, 3(2), 164–170.
Wallraf, A., & Wagner, S. (2019). Effects of initial plant density, interspecific competition, tending and age on the survival and quality of oak (*Quercus robur* L.) in young mixed stands in European Russia. Forest Ecology and Management, 446, 272–284.
Wang, W., Vinocur, B., & Altman, A. (2003). Plant responses to drought, salinity and extreme temperatures: Towards genetic engineering for stress tolerance. Planta, 218(1), 1–14.