

# Regulatory Mechanisms in Biosystems

ISSN 2519-8521 (Print)  
ISSN 2520-2588 (Online)  
Regul. Mech. Biosyst.,  
2024, 15(3), 490–495  
doi: 10.15421/022469

## Peculiarities of water exchange of *Quercus robur* and *Acer campestre* in an oak-field maple forest

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### Article info

Received 04.06.2024

Received in revised form

01.07.2024

Accepted 21.07.2024

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**Bessonova, V. P., & Yakovlieva-Nosar, S. O. (2024). Peculiarities of water exchange of *Quercus robur* and *Acer campestre* in an oak-field maple forest. *Regulatory Mechanisms in Biosystems*, 15(3), 490–495. doi:10.15421/022469**

We studied the physiological and biochemical parameters of water exchange of two broadleaf forest species, *Quercus robur* L. and *Acer campestre* L., which grow under different levels of water supply. The study was conducted in the lower third of the northern slope and the middle third of the southern exposure slope in the “Viyskovyi” ravine. It was established that the content of total water in the leaves of *Q. robur* is higher than that of *A. campestre* under both mesophilic and xerophilic conditions. In *A. campestre*, the gradual dehydration of leaves during the growing season is more pronounced. The water-holding capacity of the leaves increases in both species, especially in July and August on the southern exposure slope, which is consistent with changes in the content of hydrophilic colloids. This can be considered as an adaptation of plants against rigorous hydrothermal conditions. The leaves of *A. campestre* retain water better and are characterized by a greater number of hydrophilic colloids compared to the leaves of *Q. robur* at different levels of water supply. Under xerophilic growth conditions, the suction power of the cellular junctions of leaves is more significant than under mesophilic conditions. At both experimental sites, this indicator is always higher in case of *A. campestre*, while the difference is greater only under xerophilic conditions. The increase in suction force in leaf cells occurs in parallel with the increase in soil dryness. The leaves of *A. campestre* have a greater water deficit and suction power, better water-holding capacity due to a greater content of hydrophilic colloids, and a lower intensity of transpiration. The leaves of *Q. robur* have a lower water deficit and a lower water-holding capacity, which is based on the ability to resist the lack of moisture by the development of a deep root system that allows water to be absorbed from its deep horizons. The obtained data make it possible to clarify the peculiarities of the water regime of tree species during their simultaneous growth in forest phytocoenoses and adaptation to different levels of soil moisture.

**Keywords:** ravine forest; common oak; field maple; water content; water saturation deficit; water-holding capacity; sucking power of the leaves; hygrotopes.

### Introduction

The productivity of woody plants within genetically determined limits largely depends on maintaining the water balance (McDowell et al., 2022). Knowledge of the indicators of the water regime of plants is a necessary condition for their effective cultivation (Lyr et al., 1967; Levinsh, 2023). This is especially important for the Steppe zone of Ukraine, where the amount of precipitation is 350–540 mm, the hydrothermal coefficient ranges from 0.5 to 0.9 (Adamenko, 2014), and plants often suffer from high summer temperatures and lack of water. Under the conditions of global warming (Ciscar et al., 2018; Stojko, 2020; Pörtner et al., 2022), further deterioration of forest growth conditions is predicted both in Europe (Dyderski et al., 2018; Enriquez-de-Salamanca, 2022; Li et al., 2023), as well as in Ukraine (Kramarets & Krynytskyy, 2009; Kramarets et al., 2023), along with the change in the species composition of forests (Buksha, 2009; Stoyko, 2011; Faly & Brygadyrenko, 2014; Brygadyrenko, 2015; Shparyk et al., 2020). Under such conditions, the water regime of plants can play a decisive role.

A long-term disturbance of the water balance resulting from both dry soil and air disrupts normal metabolism (Kiriziy & Stasik, 2022). A decrease in the water content in cells during a water deficit causes all kinds of negative changes in the structure and functions of biopolymers, leads to protein denaturation, inhibition of enzymatic activity, changes in the structure of the membrane lipid layer and violation of its integrity is (Shao et al., 2008; Shao et al., 2016; Aliyeva et al., 2023). A lack of water during a

water deficit in the leaves causes them to overheat due to insufficient transpiration, induces changes in the colloidal properties of the cytoplasm, which reduces the metabolism and inhibits the processes of photosynthesis (Lawlor & Cornic, 2002; Bota et al., 2004). Drought suppresses growth processes and plant development (Tschaplinski et al., 1998; Tahir et al., 2003; Thakur & Sood, 2005).

Indicators of water exchange in woody plants are studied mainly under urbogenic growth conditions (Hnatyshyn, 2015; Kovalevskyy & Kryvokhatko, 2018; Tymoshenko, 2018; Yukhymenko et al., 2021). Yet there are few studies characterizing the water exchange of woody plants in natural (Gracani et al., 1970; Kotsiubynska, 1977; Olijnyk & Rak, 2018) and artificial forest phytocoenoses (Bessonova et al., 2016), although they are very important for effective planning and implementation of forestry work. However, even in these cases only a handful of indicators were taken into consideration.

Analysis of the water balance of individual plants as well as entire plantations, especially under conditions of constant water supply, is considered a more important task for ecologists and plant physiologists. Increasing productivity of woody plants depends heavily on its assessment (Lyr et al., 1967). The obtained results will help to better understand the peculiarities of water exchange of various tree species during their simultaneous growth in forest phytocoenoses and adaptive reactions to forest plant conditions with a varying level of soil moisture.

The aim of this work is to analyze the indicators of water exchange in leaves of *Q. robur* and *A. campestre* from natural oak groves under meso-

philic and xerophilic growth conditions in the Viyskovyi ravine of Dnipropetrovsk region.

## Materials and methods

The objects of the study are oak (*Quercus robur* L.) and field maple (*Acer campestre* L.), which grow in the thickets of the Viyskovyi ravine at different levels of water supply (Fig. 1). The study of their water regime was carried out in 2023 on two trial areas. Trial area 1 (TA1) is located in the lower third of the northern exposure slope. Hygrotope – CL2 (clay-

loam soil), mesophilic (fresh). Trial area 2 (TA2) is located in the middle third of the southern exposure slope. Hygrotope – CL1, xerophilic, dry. Atmospheric transit humidification is inherent to both areas.

Samples for analysis were taken using garden loppers from the south-east side of the middle part of the crown of the studied species during the growing season (May 15, June 21, July 14, August 16, September 13) under the same lighting conditions. In parallel with sampling, air temperature and humidity were measured with a TA-308 electronic thermohygrometer (Tcom, Chongqing, China).



Fig. 1. Map of the research area: coordinates of extreme points (48°11'08'' N 35°07'45'' E; 48°10'41'' N 35°10'12'' E)

The amount of total water in the leaves was determined by drying the plant material to a constant weight at a temperature of 105 °C, calculated as a percentage of the raw weight. The water-holding capacity was determined by the wilting method according to A.A. Arland. It was characterized by water loss after 30, 60 and 120 minutes, expressed as a percentage of the initial moisture content in the samples. The afternoon water deficit in the leaves was determined by increasing the weight of cuttings after their saturation with water. The osmotic pressure of cells was determined by the refractometric method (Bessonova, 2006). Hydrophilic colloids were determined according to the method described by Kushnirenko et al. (1970).

Soil samples were taken at a depth of 10–20 and 30–40 cm, soil moisture was determined by the thermogravimetric method (DSTU ISO 11465:2001).

Table 1

The amount of total water in the leaves of *Q. robur* and *A. campestre* in the oak groves under different growth conditions (% of the raw weight,  $\bar{x} \pm SE$ ,  $n = 5$ )

Ecosystems	Species	Months				
		May	June	July	August	September
TA1	<i>Q. robur</i>	68.71 ± 0.27 <sup>a</sup>	66.43 ± 0.21 <sup>a</sup>	63.44 ± 0.32 <sup>a</sup>	58.61 ± 0.32 <sup>a</sup>	56.41 ± 0.27 <sup>a</sup>
	<i>A. campestre</i>	68.27 ± 0.46 <sup>a</sup>	64.23 ± 0.18 <sup>b</sup>	60.53 ± 0.34 <sup>b</sup>	55.56 ± 0.34 <sup>b</sup>	54.27 ± 0.41 <sup>b</sup>
TA2	<i>Q. robur</i>	67.92 ± 0.24 <sup>a</sup>	64.27 ± 0.33 <sup>b</sup>	59.43 ± 0.23 <sup>c</sup>	56.54 ± 0.40 <sup>b</sup>	54.32 ± 0.19 <sup>b</sup>
	<i>A. campestre</i>	66.34 ± 0.32 <sup>b</sup>	61.12 ± 0.28 <sup>c</sup>	56.41 ± 0.44 <sup>d</sup>	52.40 ± 0.31 <sup>c</sup>	51.21 ± 0.21 <sup>c</sup>

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

Hydration of leaves in both types of trees under mesophilic growth conditions (TA1) was higher than under xerophilic ones (TA2), except for May. The biggest difference in water content between the two variants of water supply was found in July. In *Q. robur*, it is 4.0%, in *A. campestre* – 4.1%, that is, in both types of plants, these values are practically the same.

A comparison of the total water content in the leaves of the studied tree species shows that it was higher in *Q. robur* compared to *A. campestre* in almost all periods of determination both on TA1 and TA2, with the

exception of May, when the difference was unreliable. Consequently, the leaves of *Q. robur* had a higher humidity than *A. campestre* in the summer months, and it fell somewhat less during the growing season with increasing soil dryness, which is especially noticeable under xerophilic growing conditions.

## Results

It was established that the amount of moisture in the leaves of both species decreased during the growing season (from May to September): on TA1 (fresh oak grove, mesophilic conditions) by 12.3% in *Q. robur* and by 14.0% in *A. campestre*. On TA2 (dry oak grove, xerophilic conditions), the values of these indicators are 13.6% and 15.1%, respectively (Table 1).

The next indicator studied by us, which characterizes the state of the water balance of plants, is water deficit. As can be seen from Table 2, the afternoon water deficit in the leaves of *Q. robur* at TA1 (mesophilic con-

ditions) ranges from 4.8% in May to 20.9% in August. In September, the value of this indicator slightly decreases compared to the August values. On TA2 (xerophilic conditions), as well as on TA1 (mesophilic conditions), the smallest amount of water deficit is observed in May, the largest

in August. Its values in *Q. robur* leaves are greater under xerophilic growth conditions (CL1) compared to mesophilic ones (CL2). This increase is most significant in July (5.4%) and August (4.5%).

**Table 2**

Water deficiency in leaves of *Q. robur* and *A. campestre* in oak groves under different forest vegetation conditions (% of water content with a complete tissue saturation,  $\bar{x} \pm SE$ ,  $n = 5$ )

Ecosystems	Species	Months				
		May	June	July	August	September
TA1	<i>Q. robur</i>	4.81 ± 0.25 <sup>a</sup>	8.11 ± 0.20 <sup>a</sup>	16.34 ± 0.42 <sup>a</sup>	20.86 ± 0.61 <sup>a</sup>	18.30 ± 0.26 <sup>a</sup>
	<i>A. campestre</i>	5.62 ± 0.31 <sup>a</sup>	10.65 ± 0.24 <sup>b</sup>	20.02 ± 0.50 <sup>b</sup>	26.54 ± 0.43 <sup>b</sup>	22.16 ± 0.51 <sup>b</sup>
TA2	<i>Q. robur</i>	7.35 ± 0.47 <sup>b</sup>	10.27 ± 0.18 <sup>b</sup>	21.76 ± 0.33 <sup>c</sup>	25.32 ± 0.36 <sup>b</sup>	20.38 ± 0.34 <sup>c</sup>
	<i>A. campestre</i>	6.14 ± 0.62 <sup>ab</sup>	15.58 ± 0.33 <sup>c</sup>	26.31 ± 0.24 <sup>d</sup>	30.34 ± 0.27 <sup>c</sup>	28.42 ± 0.40 <sup>d</sup>

Note: the same as in Table 1.

Changes in the moisture supply of *A. campestre* leaves during the growing season show the same regularity as in the case of *Q. robur*. For trees of this species, higher values of water deficiency of leaves were established also under xerophilic growth conditions. The maximum excess was found in July. A comparison of the values of the water deficit of the two studied species shows that for May the differences between their values are unreliable. In all subsequent months of the experiments, higher values of differences were established in the leaves of *A. campestre* both on TA1 and TA2.

The maximum water deficit of *Q. robur* leaves was observed in August at TA2 – 25.3%. In *A. campestre*, it was 30.3%, which led to partial loss of leaves.

To diagnose the adaptation of plants to drought, it is necessary to have data on the water-holding capacity of the leaves. Let's consider how the water-holding capacity of leaves changed during the growing season. In May, after 30 min of exposure at both TA1 and TA2, there was no difference between the indicators of water loss by the leaves of the two types of trees – *Q. robur* and *A. campestre*. It increased slightly after 60 and 120 min of the experiment. In the other months of the study, the leaves of *A. campestre* were characterized by lower moisture losses than the leaves of *Q. robur* at exposures of 30, 60, and 120 min. The difference in the value of this indicator between tree species ranges from 25.5% to 42.1% (Table 3).

**Table 3**

Changes in the water-holding capacity of the leaves of *Q. robur* and *A. campestre* under different forest vegetation conditions (% water loss from the initial mass,  $\bar{x} \pm SE$ ,  $n = 5$ )

Months	Ecosystems	Species	Water expenditure after		
			30 min	60 min	120 min
May	TA1	<i>Q. robur</i>	7.51 ± 0.75 <sup>a</sup>	21.26 ± 0.21 <sup>a</sup>	30.17 ± 0.44 <sup>a</sup>
		<i>A. campestre</i>	5.93 ± 0.40 <sup>a</sup>	17.88 ± 0.45 <sup>b</sup>	25.14 ± 0.73 <sup>b</sup>
	TA2	<i>Q. robur</i>	5.21 ± 0.46 <sup>ab</sup>	15.39 ± 0.54 <sup>c</sup>	22.71 ± 0.46 <sup>c</sup>
		<i>A. campestre</i>	4.24 ± 0.33 <sup>ab</sup>	12.11 ± 0.91 <sup>d</sup>	18.32 ± 0.74 <sup>d</sup>
June	TA1	<i>Q. robur</i>	8.30 ± 0.72 <sup>a</sup>	15.41 ± 0.71 <sup>a</sup>	27.31 ± 0.68 <sup>a</sup>
		<i>A. campestre</i>	5.10 ± 0.56 <sup>b</sup>	12.27 ± 0.43 <sup>b</sup>	20.11 ± 0.81 <sup>b</sup>
	TA2	<i>Q. robur</i>	6.34 ± 0.34 <sup>bc</sup>	12.42 ± 0.70 <sup>bc</sup>	20.32 ± 0.97 <sup>bc</sup>
		<i>A. campestre</i>	3.72 ± 0.40 <sup>d</sup>	9.11 ± 0.45 <sup>d</sup>	15.07 ± 1.20 <sup>d</sup>
July	TA1	<i>Q. robur</i>	7.21 ± 0.43 <sup>a</sup>	13.20 ± 0.42 <sup>a</sup>	24.42 ± 0.31 <sup>a</sup>
		<i>A. campestre</i>	4.31 ± 0.37 <sup>b</sup>	8.31 ± 0.37 <sup>b</sup>	17.18 ± 0.42 <sup>b</sup>
	TA2	<i>Q. robur</i>	5.27 ± 0.36 <sup>bc</sup>	10.20 ± 0.60 <sup>c</sup>	18.27 ± 1.42 <sup>bc</sup>
		<i>A. campestre</i>	3.72 ± 0.39 <sup>d</sup>	7.13 ± 0.37 <sup>d</sup>	13.56 ± 0.35 <sup>d</sup>
August	TA1	<i>Q. robur</i>	8.30 ± 0.41 <sup>a</sup>	15.24 ± 0.34 <sup>a</sup>	25.76 ± 0.70 <sup>a</sup>
		<i>A. campestre</i>	5.24 ± 0.27 <sup>b</sup>	10.30 ± 0.56 <sup>b</sup>	19.43 ± 0.62 <sup>b</sup>
	TA2	<i>Q. robur</i>	6.72 ± 0.24 <sup>c</sup>	11.18 ± 0.21 <sup>bc</sup>	18.94 ± 0.42 <sup>b</sup>
		<i>A. campestre</i>	4.15 ± 0.18 <sup>d</sup>	8.10 ± 0.32 <sup>d</sup>	13.10 ± 0.54 <sup>c</sup>
September	TA1	<i>Q. robur</i>	11.36 ± 0.58 <sup>a</sup>	27.50 ± 0.81 <sup>a</sup>	39.21 ± 1.22 <sup>a</sup>
		<i>A. campestre</i>	7.62 ± 0.71 <sup>b</sup>	20.11 ± 0.84 <sup>b</sup>	32.14 ± 0.94 <sup>b</sup>
	TA2	<i>Q. robur</i>	8.42 ± 0.46 <sup>bc</sup>	22.23 ± 0.65 <sup>bc</sup>	30.29 ± 0.75 <sup>bc</sup>
		<i>A. campestre</i>	7.22 ± 0.75 <sup>b</sup>	16.31 ± 0.80 <sup>d</sup>	25.84 ± 0.81 <sup>d</sup>

Note: the same as in Table 1.

An increase in the water retention capacity of the leaves of *Q. robur* and *A. campestre* was revealed in June compared to May. In July, this indicator after 30 min of exposure almost did not change compared to the previous month, but water losses at exposure durations of 60 and 120 min

were smaller than in June, which indicates an increase in the water-holding capacity of the leaves of both types of trees against the background of a decrease in soil moisture content (Fig. 2). In August, there were no significant changes in the value of this indicator compared to July. However, in September, there was a significant drop in the water-holding capacity in both *Q. robur* and *A. campestre* in both test plots. In *A. campestre*, the decrease in water-holding capacity in September compared to August was more significant than in *Q. robur*. Thus, water loss in September by *Q. robur* leaves on TA1 (mesophilic conditions) for 120 min of exposure was greater by 52.2% compared to the previous month, on TA2 (xerophilic conditions) by 59.9%, and in *A. campestre* by 65.5% and 97.3%, respectively, although the greater ability of *A. campestre* to hold water remained the same as in previous months.

Therefore, when growing under both mesophilic and xerophilic conditions, the leaves of *A. campestre* had higher a water retention capacity than the leaves of *Q. robur*. This pattern persisted throughout the growing season.

The suction power of a cell is considered as a measure of water activity in a plant and one of the most reliable indicators of water availability. We found that the suction power of the cells of *A. campestre* leaves increased in both experimental areas from May to September, and in the leaves of *Q. robur* – from May to August, the difference between the indicators recorded for this species in August and September is not statistically reliable (Table 4). The suction power of the cells of the leaves of both species in oak groves under xerophilic growth conditions (TA2) was greater than in mesophilic ones (TA1), starting from June. In May, there is no difference between these options, since there was no significant difference in the water content of soil during this period. The increase in suction power is correlated with the decrease in soil moisture (Table 5).

**Table 4**

Suction power of plant cells of leaves of *Q. robur* and *A. campestre* in oak groves (measured in atmospheres,  $\bar{x} \pm SE$ ,  $n = 5$ )

Ecosystems	Species	Months				
		May	June	July	August	September
TA1	<i>Q. robur</i>	8.21 ± 0.31 <sup>a</sup>	10.96 ± 0.22 <sup>a</sup>	13.46 ± 0.32 <sup>a</sup>	16.52 ± 0.28 <sup>a</sup>	16.40 ± 0.24 <sup>a</sup>
		7.62 ± 0.24 <sup>a</sup>	13.22 ± 0.27 <sup>b</sup>	16.15 ± 0.25 <sup>b</sup>	19.70 ± 0.30 <sup>b</sup>	21.82 ± 0.21 <sup>b</sup>
	<i>A. campestre</i>	9.34 ± 0.34 <sup>b</sup>	14.57 ± 0.28 <sup>c</sup>	17.21 ± 0.22 <sup>c</sup>	19.61 ± 0.21 <sup>bc</sup>	19.68 ± 0.42 <sup>c</sup>
		8.53 ± 0.41 <sup>b</sup>	17.72 ± 0.41 <sup>d</sup>	20.64 ± 0.30 <sup>d</sup>	25.41 ± 0.42 <sup>d</sup>	27.72 ± 0.30 <sup>d</sup>

Note: the same as in Table 1.

A comparison of the magnitude of the suction force in the leaves of *Q. robur* and *A. campestre* shows that the digestive parameters are not statistically different for both TA1 and TA2. In the following months, the suction force was higher in the leaves of *A. campestre* under both xerophilic and mesophilic growth conditions. The difference between the indicators of the studied species was more significant under conditions of worsened water supply (TA2), while it was most significant in September.

Therefore, under xerophilic growth conditions, the suction power in the cells of the leaves of the experimental plants was more significant than in the mesophilic ones, which is consistent with the greater dryness of the

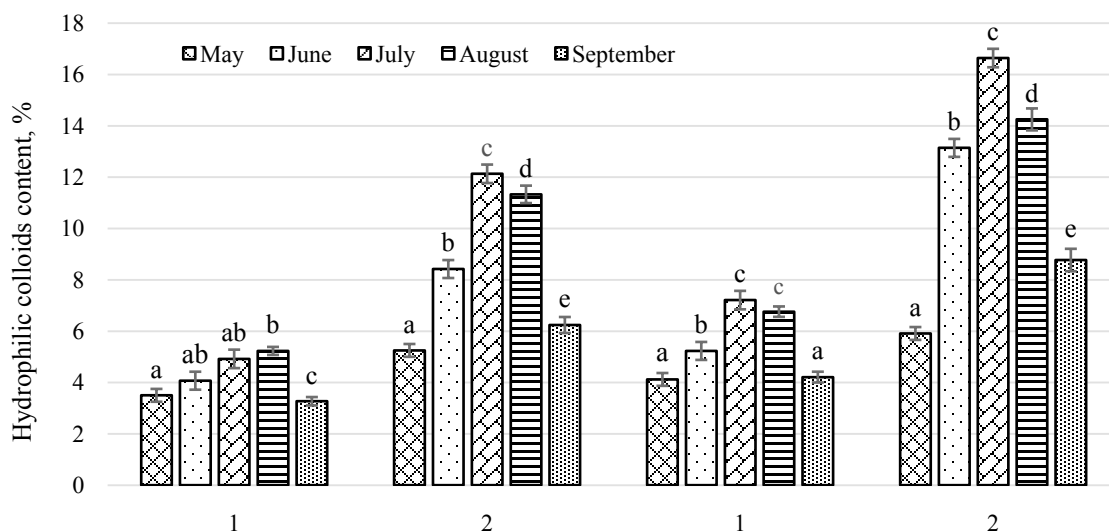
soil. In both areas, this indicator was higher in *A. campestre*, while its difference was greater under xerophilic conditions (TA2).

**Table 5**

Soil moisture in the studied areas of ravine forest in Viyskovyi (% of absolutely dry weight,  $\bar{x} \pm SE$ ,  $n = 5$ )

Ecosys-tems	Depth, cm	Months				
		May	June	July	August	September
TA1	10–20	22.3 ± 0.71 <sup>a</sup>	20.2 ± 0.47 <sup>b</sup>	12.7 ± 0.53 <sup>c</sup>	10.6 ± 0.49 <sup>d</sup>	12.1 ± 0.31 <sup>c</sup>
	30–40	25.1 ± 0.36 <sup>a</sup>	22.4 ± 0.24 <sup>b</sup>	16.4 ± 0.21 <sup>c</sup>	14.4 ± 0.29 <sup>d</sup>	15.3 ± 0.22 <sup>c</sup>
TA2	10–20	20.5 ± 0.58 <sup>a</sup>	16.4 ± 0.39 <sup>b</sup>	8.2 ± 0.41 <sup>c</sup>	7.1 ± 0.33 <sup>d</sup>	8.7 ± 0.29 <sup>c</sup>
	30–40	23.7 ± 0.32 <sup>a</sup>	18.6 ± 0.28 <sup>b</sup>	13.3 ± 0.23 <sup>c</sup>	10.2 ± 0.27 <sup>d</sup>	11.3 ± 0.18 <sup>c</sup>

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



**Fig. 2.** Influence of water supply conditions on the content of hydrophilic colloids in leaves (% of the absolute dry mass,  $\bar{x} \pm SE$ ,  $n = 5$ ): 1 – *Quercus robur*, 2 – *Acer campestre*

## Discussion

We determined the content of total water in the leaves of the studied tree species, since its value is used as an important indicator of the ecological and physiological features of the water regime of plants. According to the data presented in Table 1, during the growing season, a decrease in the amount of total water in the leaves of both *Q. robur* and *A. campestre* is noted, reaching minimum values in September. Some authors also observed a decrease in the hydration of the leaves of woody plants under the conditions of water shortage during the ontogenesis of these organs, assuming that the reason is their aging (Kushnirenko, 1967; Nesterova & Hryhoriuk, 2013; Bessonova et al., 2016) and a drop in soil moisture. The level of hydration of the leaves of the species we studied also depends on the hygrotome of growth (under xerophilic conditions it is lower compared to mesophilic ones) and on the species of woody plants. In *Q. robur*, the water content of leaf tissues under both mesophilic and xerophilic conditions during the summer months was higher than in *A. campestre*, especially in arid growing areas.

As an indicator of water balance disorder, Lyr et al. (1967), who directly studied the water exchange of woody plants, consider it appropriate to use the deficit of water saturation, or water deficit. The change in this indicator in the leaves depends on the environmental conditions of growth, which is shown in a number of fruit crops (Kushnirenko et al., 1967; Kushnirenko & Pecherskaya, 1991; Shackel, 2007) as well as forest-forming and decorative woody plants (Gracani et al., 1970; Ponomareva, 2011; Carley et al., 2021).

According to the data we obtained, water deficit in the leaves of both studied tree species in May and June on the test plots did not exceed 14%, with the exception of *A. campestre* in June on TA2. Also, Lyr et al. (1967) established that a water deficit from 3% to 14% is considered relatively

The analysis of the obtained results shows that the reaction of *Q. robur* and *A. campestre* in oak groves under different soil moisture conditions is slightly different. The leaves of the latter are characterized by a more significant decrease in water content under the worsening hydrothermal growth conditions. They have a greater water deficit and suction power of the cells, which indicates a greater need for water, despite a better water-holding capacity. It is known that the water-holding capacity of leaves is determined by the content of hydrophilic colloids, the amount of which is greater in *A. campestre* (Fig. 2).

As can be seen from Figure 3, the number of hydrophilic colloids in the leaves of both species increased in June compared to May. It was highest in July and August, and in September there was a significant decrease in this indicator. The leaves of *A. campestre* both on TA1 (mesophilic conditions) and TA2 (xerophilic conditions) are characterized by their higher content than the leaves of *Q. robur*, which is largely consistent with changes in the water-holding capacity of these species.

small, at which physiological processes can occur without noticeable disturbances and with open stomata. In our experiments in July under mesophilic growth conditions (TA1), the water deficit in the leaves of both *Q. robur* and *A. campestre* was already higher than the upper limit of the relative norm indicated by these authors. On TA2 (xerophilic conditions), this indicator is already significantly higher, especially in *A. campestre*. In August, the water deficit increased, and in September it fell somewhat, but still remained at a high level.

According to Celniker (1958), the maximum water deficit for *Q. robur* in tree stands of the Derkul' Steppe was equal to 26.0%. Lethal values of this indicator for many tree species reached 40–50%, when the plant is no longer able to counteract adverse factors (Celniker, 1955). We did not observe such critical values of water deficit even under extreme hydrothermal conditions (high temperatures and low water content in the soil) on the southern exposure slope of the ravine under study.

Data on the water-holding capacity of leaves are used to assess the adaptation of plants to moisture deficit. This indicator is often used to determine the degree of resistance of plants to the effects of drought (Bolotova & Shalpyikov, 2016; Kovalevskyi & Kryvokhatko, 2018). In both species studied by us, an increase in the ability of leaves to retain water was observed in June, and even more significantly – in July. This is an adaptation to reducing air humidity and increasing its temperature and increasing soil dryness. In August, the indicators remain at July levels.

The drop in the water-holding capacity of leaves in September may be related to the aging of leaf tissues, as indicated by some authors (Bessonova et al., 2016).

One of the most reliable indicators of a plant's water supply is the suction power of cells, which determines the need of cells for water and its entry into the plant (Kushnirenko et al., 1970). Based on their own and literary data, Kondo et al. (1981) also state that the amount of suction power



is an effective criterion for water availability of plants. Kushnirenko (1970) indicates that this indicator is more sensitive to changes in soil moisture than the concentration of cell sap, since the latter changes depending on growth processes and the activity of photosynthesis. According to the obtained data, under xerophilic growth conditions, the suction force in the cells of *Q. robur* and *A. campestre* leaves is more significant than under mesophilic ones. At both experimental sites, its values are higher in *A. campestre* compared to *Q. robur*, while the difference is greater under xerophilic conditions (TA2). According to our results, the increase in the suction power of leaf cells in the studied deciduous species is correlated with the increase in soil dryness. It should be noted that according to Kondo et al. (1981), the data that express the suction power of the leaves of grapes of the Dimyat cultivar are almost a mirror image of the soil moisture in the horizons of 25 and 50 cm. Therefore, according to these authors, it is necessary to establish critical indicators of the suction power in order to understand the potential capabilities of plants to tolerate soil droughts.

As already mentioned, the species under study have developed different strategies for adapting to existence under conditions of water shortage. In the leaves of *A. campestre*, compared to *Q. robur*, there is a greater water deficit and suction power, a better water-holding capacity due to a greater content of hydrophilic colloids, and a lower intensity of transpiration.

Along with leaf adaptation mechanisms, the drought resistance of woody plants is generally determined by the features of their root systems (Kramer & Kozlovskiy, 1983). To maintain the water balance, it is necessary that the evaporation of water through the leaves is compensated by its absorption by the roots.

The root system of *A. campestre* spreads to the sides for 3–5 m, is superficial, the main mass of the roots is concentrated mainly in the upper layer of the soil 0–35 cm (Crow, 2005), which quickly loses water during the period of high summer temperatures and little precipitation. *Quercus robur* has a powerful root system, it is a deep-rooted species. The root system of *Q. robur* consists of a taproot, a long (up to 16–23 m) root, which goes deep into the soil. Lateral roots also sink deep into the soil. The oak's ability to form a deeply penetrating root system contributes to its survival during droughts by maintaining water exchange rates. It has been established that the absence of a tap root for any reason leads to dry tops and drying of trees of this species (Guz et al., 2009).

Therefore, the adaptation of *A. campestre* to drought is manifested in an increase in the water-holding capacity of the leaves due to a higher content of hydrophilic colloids in them and more economical transpiration than in *Q. robur* (Bessonova et al., 2023), and in *Q. robur* due to the deep root system, which allows for the absorption of water from lower horizons.

## Conclusions

Both in fresh (CL2) and dry (CL1) oak groves, the content of total water in the leaves of *Q. robur* was higher than that of *A. campestre* throughout the growing season, with the exception of May, when the moisture reserves in the soil were still at a sufficiently high level at both trial areas. Gradual dehydration of leaves during the growing season was more pronounced in *A. campestre*.

The water-holding capacity of the leaves of trees of both studied species increased in June relative to May, it increased even more in July, and remained at the same level in August, which is consistent with changes in the content of hydrophilic colloids. This can be seen as an adaptation to unfavourable hydrothermal conditions, which are intensified during the summer months, especially on the southern exposure slope.

*Acer campestre* leaves retain water better and are characterized by a greater number of hydrophilic colloids compared to *Q. robur* leaves under both xerophilic (CL1) and mesophilic (CL2) growth conditions.

Despite the better water-holding capacity of the tissues of the leaves of *A. campestre*, their suction power and water deficit are higher than those of the leaves of *Q. robur*. This indicates a worse supply of water for *A. campestre* plants, especially under more rigorous hydrothermal conditions of the southern exposure slope (xerophilic conditions).

The leaves of *A. campestre* tolerate drought due to their high water-holding capacity, which is consistent with the higher content of hydrophilic colloids in the cells. The ability of *Q. robur* to withstand a lack of mois-

ture is due to the deep penetration of the root system into the soil, which allows it to absorb water from its deep horizons. This explains the lower water deficit of the leaves against the background of their lower water-holding capacity.

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