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Physiological characteristics of a promising black locust (*Robinia pseudoacacia* L.) clone under marginal site conditions

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SUMMARY

This paper studies the physiological characteristics of a promising black locust (Robinia pseudoacacia L.) clone, Farkasszigeti, compared to common black locust (control), under marginal site conditions in Eastern Hungary. A clone trial was established in 2022 near Debrecen to test new black locust clones, with measurements of photosynthesis (net assimilation, efficiency of photosystem II, intercellular CO_2 level) and water-use characteristics (transpiration, stomatal conductance, water use efficiency etc.), using LI-6800 (LI-COR) portable photosynthesis system. However, the measured values were very low, indicating drought and heat stress. The results revealed that Farkasszigeti exhibited better net assimilation (2.13±0.75 µmol CO_2 m^{-2} s^{-1}), transpiration (1.41±0.20 mmol H_2O m^{-2} s^{-1}) and stomatal conductance (0.017±0.002 mol m^{-2} s^{-1}) than the control, with significant differences (p=0.05). Furthermore, its photosystem II was more efficient, thus it has better heat tolerance. Although the clone Farkasszigeti was proved to be better in terms of water use efficiency values, no significant difference was observed in comparison with the control common black locust. Today, under changing climatic conditions, the study of physiological adaptation of tree species and clones has a crucial role.

Keywords: *black locust improvement; photosynthesis; water-use characteristics*

INTRODUCTION

Climate change has a great impact on the ecosystem, especially on the forest sector (forests, tree plantations). According to the IPCC (2023) report the global surface temperature in 2011–2020 was 1.1 °C higher than temperatures in the period of 1850–1900. Nowadays, the atmospheric CO_2 is higher with 50% than it was before the 1800s (climate.gov). However, rising temperatures and elevated CO_2 concentrations in the atmosphere could enhance forest growth, provided there is adequate water and nitrogen. By contrast, climate change is also expected to increase the frequency, intensity, extent, and duration of disturbances like wildfires, pests, storms, and droughts, which could result in substantial losses of harvestable biomass (Messier et al., 2022). These factors contribute to tree mortality now and in the future, threating forests, as well as their ecosystem services (carbon sequestration, climate regulation, future wood supply) (Allen et al., 2015; McDowell et al., 2020; FAO, 2024).

Trees have developed various strategies to survive under changing environmental conditions (McDowell et al., 2008; Choat et al., 2012; Pivovaroff et al., 2016). In general, they are categorized by their hydraulic regulatory strategies into anisohydry and isohydry (Tardieu and Simonneau, 1998; Klein, 2014; Martinez-Vilalta et al., 2014). Isohydric tree species, such as pine species (e.g. *Pinus sylvestris* L.), maintain a relatively stable water potential in their leaves, duo to their strict stomatal regulation, throughout changes in environmental conditions. However, these tree species close their stomata in response to even mild drought stress, thus their photosynthesis decreases. Conversely, anisohydric tree species, such as sessile oak (*Quercus petraea* (Matt.) Liebl.), have higher stomatal conductance, so they sustain relatively high net assimilation. While the anisohydric strategy allows trees to maintain photosynthesis and growth during milder water stress, the risk is that this flexibility comes with a greater vulnerability to severe water stress and heat-induced damage. On sites where droughts are prolonged or extreme, anisohydric species are at higher risk of mortality compared to isohydric ones, which tend to regulate their water more conservatively. Hence, isohydric tree species can adapt quickly to arid conditions (Choat et al., 2012; Pretzsch et al., 2012; Martinez-Vilalta and Garcia-Forner, 2017). Black locust (*Robinia pseudoacacia* L.) employs a water regulation strategy that strikes a balance between isohydry and anisohydry to manage drought stress (Liu et al., 2024).

In the recent years, many studies have focused on the physiological investigation of black locust. Yan et al. (2024) have found that it has flexible stomatal regulation and water use strategies in response to drought. Moreover, stomatal conductance and transpiration of black locust vary with climate and soil moisture conditions. Duo to these characteristics, this North American tree species has adapted sites with semi-arid and arid conditions. Based on Mantovani et al. (2014), *Robinia* can tolerate extended drought by minimizing water loss through lower transpiration rates and smaller leaf size. However, in well-watered conditions, the tree does not regulate its transpiration, meaning it cannot be classified as a water-efficient species. Lange et al. (2022) studied the physiological performance and biomass growth of different black locust clones planted on a post-mining reclamation site in Eastern Germany. The study found significant differences in physiological traits between clones, with some demonstrating better water use efficiency (WUE) and higher chlorophyll content, which contributed to improved growth under the challenging

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conditions of the reclamation site. Overall, the research highlights that specific origins of black locust may be more suited to thrive in post-mining sites and their conditions due to their superior physiological adaptations. Some studies (Ruehr et al., 2016; Bamberger et al., 2017) show the negative impacts of drought and heat stress on the photosynthesis (net assimilation) and water-use characteristics (e.g. transpiration, stomatal conductance) of black locust. The combined effects of heat and drought are larger than the sum of each stress individually (Ruehr et al., 2016).

Black locust is a fast-growing, light demanding, relatively drought tolerant, N-fixing, deciduous tree species. Its wood is highly durable, ideal for posts due to its longevity. It has a crucial role in apiculture. Furthermore, *Robina* has many ecosystem services, such as carbon sequestration, erosion control and landscape reclamation. It tolerates various soil conditions, but it grows best on deep, nutrient-rich, uncompacted, well-aerated, well-drained silt loams, sandy loams and sandy soils with slightly acidic pH and moderately high or high humous content (Keresztesi, 1988; Nicolescu et al., 2018, 2020). Despite its many uses, black locust has negative ecological and practical impacts, particularly in non-native regions where it becomes invasive. Managing its spread requires careful planning and control (Vítková et al., 2017).

In Hungary, where *Robinia* is one of the most commonly planted tree species, research work was launched in the 1960s, aiming to improve its stem quality and increase its yield (Ábri et al., 2023a). Recently, five new candidate cultivars are being tested in several clone trials throughout the country, mainly in the Nyírség region. Growth and physiological characteristics (photosynthesis, transpiration, water use efficiency, etc.) of these clones are studied (Ábri et al., 2022, 2024). In this study, a promising black locust candidate cultivar, called Farkasszigeti (PL040) was compared with the common (seed-originated) one by their physiological traits (e.g. net assimilation, transpiration, stomatal conductance, intercellular CO_2 level, VPD_{leaf}, WUE and the efficiency of photosystem II), under marginal site conditions.

MATERIALS AND METHODS

The clone trial was established in 2022. In this experiment five newly-bred – vegetatively propagated – black locust clones are tested and compared with the seed-originated common black locust. Farkasszigeti is one of these clones which has excellent propagating ability. The seedlings (90 per clone) were planted by machine, with a row spacing of 2.5 m and a 1.5 m plant-to-plant distance.

The experimental stand grows in the Nyírség forest region (UTM-34N: 562194, 5267604) near the city of Debrecen at an altitude of 150 m below sea level. According to the 6.768 FAI value (FAI, Forest Aridity Index, Führer, 2018) of the site, it is characterized by a Turkey oak-sessile oak climate (FAI: 6.001–7.250) with a 30-year (1991–2020) average precipitation of 578 mm and an annual average temperature of 10.8 °C. The meteorological data are from the Hungarian Meteorological Data Base (HMS, 2024) and analysed in detail in the results section.

The soil is Arenosol, according to IUSS Working Group WRB (2022). Its conditions are as follows. A sandy soil with low humous content (Hu<1%), shallow soil depth (40-60 cm) and coarse sand (k_A<25) texture. Our detailed soil analysis results indicate that the humous content is low (Hu%: 0.659 and 0.513) in the topsoil (layers of 0–10 and 0–60 cm); moreover, the soil is very humus deficient in the depth (Hu%: 0.180 in 60–100 cm and 0.053 in 100 cm). Soil pH_{KCl} was 5.6–7.3, slightly acidic in the topsoil (0–60 cm), and the pH increased with soil depth (60– cm). Its nutrient status is low, the nitrate, phosphorus (P_2O_5) and potassium (K_2O) content decreased with soil depth. The NO_3^- content in the upper layer was 9 mg kg^{-1}, decreasing drastically from 60 cm (4.7 mg kg^{-1} at 60–100 cm; 2.4 mg kg^{-1} below 100 cm). The P_2O_5 contents are 69.1 mg kg^{-1} (0–10 cm), 50.70 mg kg^{-1} (10–60 cm), 45.3 mg kg^{-1} (60–100 cm) and 32.0 mg kg^{-1} (100– cm). The K_2O content by layers as follows. 48.4 mg kg^{-1} (0–10 cm), 33.7 mg kg^{-1} (10–60 cm), 29.6 mg kg^{-1} (60–100 cm), 22.3 mg kg^{-1} (100– cm). At the time of the measurement, the stand was in its 2nd growing season, with an average height of 4.3–4.4 m and a root collar diameter of 48–49 mm. The most important site and tree characteristics are summarized in *Table 1*.

Table 1. **Site and tree characteristics**

Site characteristics							Tree characteristics	
Forestry Aridity Index	**Hydrology**	**Soil type**	**Soil depth**	**Soil texture**	**Soil humous content**	**Soil pH_{KCl}**	**H (m)**	**RCD (mm)**
6.768 (Forest-steppe climate)	Free-draining site	Humous sandy soil	shallow	coarse sand	low (1%>)	5.55–7.26	[1]4.3	[1]48.25
							[2]4.4	[2]49.46

[1] Farkasszigeti. [2] Common black locust. H = average height of 30 trees, RCD = average root collar diameter of 30 trees

On July 10th, 2024, the photosynthetic and water use characteristics of the Farkasszigeti black locust clone and common black locust were measured with LI-6800 portable photosynthesis system (LI-COR,

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Lincoln, NE, USA). The instrument recorded net assimilation (A_N), transpiration (Tr), stomatal conductance (g_{tc}), intercellular CO_2 concentration (C_i), vapor pressure deficit at leaf (VPD_{leaf}), leaf temperature (T_{leaf}), air temperature (T_{air}) and photosystem II (PSII) efficiency. Light in the sample chamber was set to 1500 µmol photons m^{-2} s^{-1} PAR, with a light ratio of 90% red (625 nm) and 10% blue (475 nm). The LI-6800-01A multiphase flash fluorometer head was used as the light source, with a 2 cm² aperture. CO_2 concentration in the chamber was maintained at 400 µmol mol^{-1} using an injector and CO_2 standards. Measurements were taken from light-adapted leaves, with five readings per leaf across three plants per plot, after at least 120 seconds once the parameters stabilized (Ábri et al., 2022).

Calculating water use efficiency, the data from the leaf measurements (A_N and Tr) were used, following the formula proposed by Tanner and Sinclair (1983).

Before the comparison, the normal distributions in the groups were tested with the Shapiro-Wilk tests. As the measured data did not meet the parametric test conditions, Mann-Whitney test was used for pairwise comparison. Statistical analyses were performed with IBM SPSS 25.0 statistical software.

RESULTS AND DISCUSSION

Weather conditions in the period of 2022–2024

Meteorological data from 2022 to 2024 presented in *Table 2* help to characterize the physiological traits of the studied clone and common black locust. The total annual precipitation in the year of the planting (2022) was 468.6 mm, 109.5 mm less than the 30-year (1991–2020) average. In the vegetation period (from April to October) the sum of precipitation was also below the 30-year average. The May-August period, which is the most important with regarding tree growth, was extremely dry with 89.8 mm. The monthly rainfalls were less than in the period from 1991 to 2020 with values of 51.6 (May), 49 (June), 37.8 (July), and 21.6 mm (August), respectively. 27% of the annual precipitation fell in September. In this year the drought was accompanied by high temperatures. The annual average temperature was 1.7 °C higher than the 30-year average. In the summer months, the temperature was 2.4 °C (June), 1.9 °C (July), and 2.2 °C (August) higher than the long-term averages. The temperature in the vegetation period was 0.8 °C higher than in the period of 1991–2020. In 2023, the precipitation was 112.5 mm more than the 30-year average, but in the vegetation period, it was 17.4 mm below the average. However, the annual rainfall was above the 30-year average, this year is very warm. The average temperatures were 12.3 °C (annual) and 17.3 °C (vegetation period), higher than the averages with 1.5 °C and 1 °C, respectively. It is worth mentioning the unusually warm January (4.3 °C) of this year, which was 5.2 °C higher than the multi-year average. The year of the measurement (2024) was also very warm. The annual average temperature was 12.8 °C, 2.0 °C higher than the 30-year average. The temperature of the vegetation period was 18.7 °C, which was 1.8 °C higher than the long-term average. The summer of this year was full of heat periods. The average temperature of the summer months (June, July, August) was 23.6 °C, which was 2.6 °C higher than the 30-year average. February was extremely mild in this year (7.9 °C), as the monthly average temperature was 7.1 °C higher than the multi-year average. The precipitation in 2024 was not only below the multi-year average but also lower than the amounts in the previous two years, respectively. The amount of rainfall was 384.2 mm in the year, and 274.1 mm in the vegetation period. From January to June, the precipitation was 201.5 mm, which was 76.3 mm below the 30-year average.

Table 2. **Monthly sum of rainfall (mm) and average air temperature (°C) throughout the years 2022–2024. Data recorded at HMS (2024) meteorological station Debrecen, Hungary**

	Precipitation (mm)				Air temperature (°C)			
	2022	2023	2024	Avg. of 1991–2020	2022	2023	2024	Avg. of 1991–2020
January	12.5	59.6	37.5	30.1	-0.6	4.3	0.9	-0.9
February	14.9	16.9	9.7	37.2	3.7	2.3	7.9	0.8
March	10.6	41.8	10.1	32.8	4.9	7.1	9.5	5.7
April	55.4	40.4	40.4	44.9	9.3	9.7	13.7	11.7
May	9.5	55.3	46.3	61.1	17.4	16.6	17.5	16.5
June	22.7	89.9	57.5	71.7	22.4	19.8	21.6	20.0
July	30.4	56.5	12.2	68.2	23.5	22.8	24.7	21.6
August	27.2	61.9	16.4	48.8	23.6	22.8	24.3	21.4
September	133.7	23.4	60.2	49.8	15.5	19.7	18.3	16.1
October	6.5	42.9	41.3	43.2	12.0	13.8	10.8	10.6
November	51.7	133.6	39.8	43.3	6.5	5.8	2.8	5.2
December	93.5	68.3	13.0	47.1	2.5	2.8	1.9	0.3
Year (Jan–Dec)	468.6	690.6	384.2	578.1	11.7	12.3	12.8	10.8
Veg. (Apr–Oct)	285.3	370.3	274.1	387.7	17.7	17.9	18.7	16.9

Veg. means vegetation period (from April to October)

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Overall, the precipitation measured during the growing seasons (from April to October) was below the 30-year average in all three years. Furthermore, the temperature was above the multi-year average and increased year by year during the 2022–2024 period. The monthly average temperatures during the summer, as well as the winter period, were higher than the multi-year averages in each year. In 2024, the lowest precipitation and highest average temperature were measured, both for the whole year and for vegetation period.

Results of physiological measurements

Based on the results of the Mann-Whitney test, significant differences (p=0.05) were found between most of the studied physiological traits (A_N, Tr, g_{tc} and the efficiency of PS II). No statistically observable differences were shown for intercellular CO_2 concentration, WUE values and leaf temperature values.

Due to the extreme weather conditions (*Table 2*), stomatal conductance values of clone Farkasszigeti and common black locust are very low 0.017±0.002 mol m^2 s^{-1} and 0.013±0.001 mol m^{-2} s^{-1}, respectively (*Figure 1*). Farkasszigeti has higher g_{tc} value. Low g_{tc} values indicate the combined heat-drought stress. If g_{tc} values decrease below 0.05 mol·m^{-2}·s^{-1}, irreversible damage to the photosystem may occur (Flexas and Medrano, 2002; Ruehr et al., 2016). There are strong correlations between stomatal conductance and net assimilation, as well as transpiration and stomatal conductance values (Kutasy et al., 2022; Ábri et al., 2023b).

Figure 1. **Stomatal conductance of Farkasszigeti black locust clone and common black locust (control). Mean±standard deviation. Letters indicate the significant difference (*p*=0.05)**

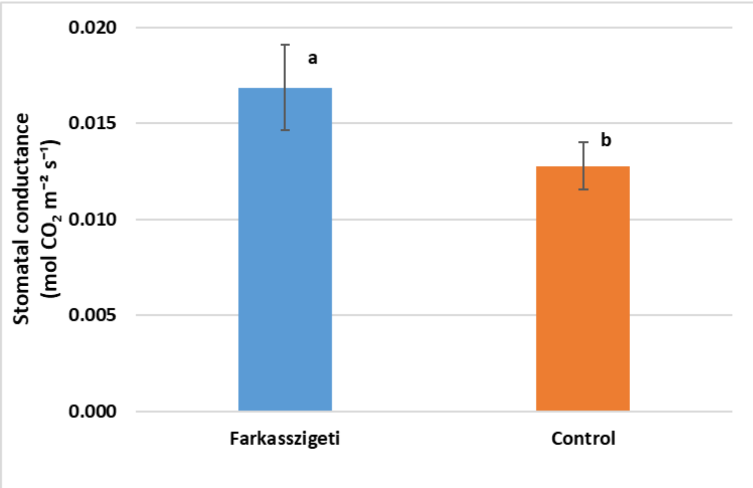
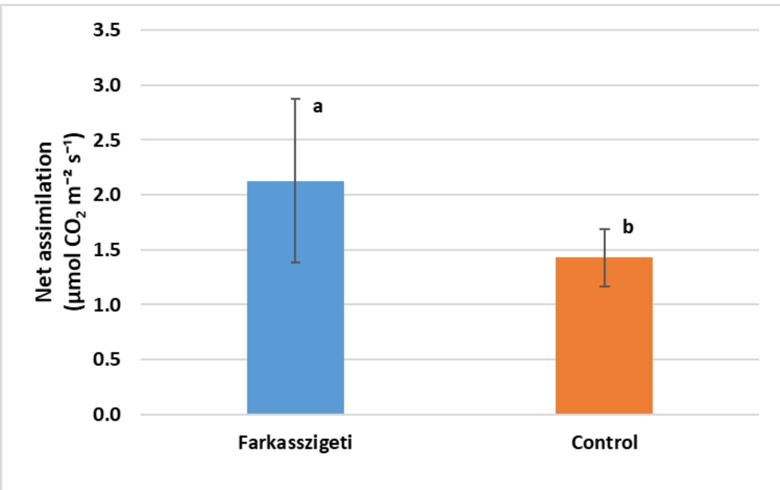


Figure 2. **Net assimilation of Farkasszigeti black locust clone and common black locust (control). Mean±standard deviation. Letters indicate the significant difference (*p*=0.05)**



As a consequence of low g_{tc} values, the A_N and Tr were very low for both tested black locusts. The A_N for Farkasszigeti was 2.13 (±0.75) µmol m^{-2} s^{-1}, and 1.43 (±0.26) µmol m^{-2} s^{-1} for the control (*Figure 2*). The

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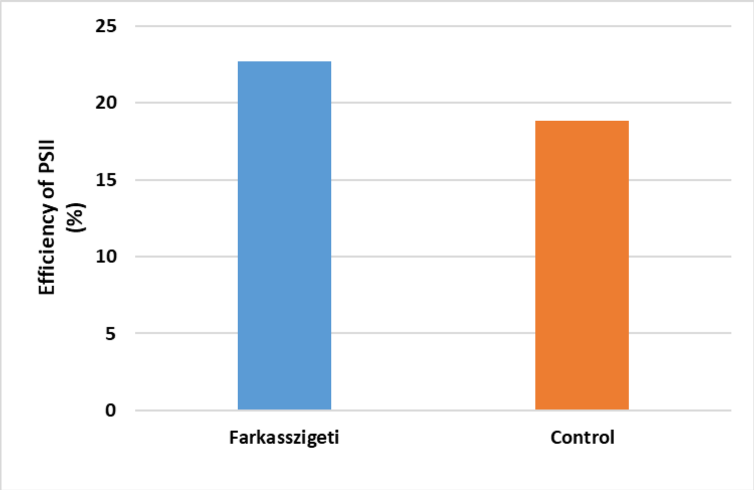
clone Farkasszigeti proved to be better in this parameter. The difference was significant at p=0.05 level. Regarding the results, it is worth noting that the net assimilation is affected by many factors (e.g. temperature, light intensity, precipitation, soil moisture, nutrient supply etc.) (Farquhar and Sharkey, 1982; Pethő, 1998; Meng et al., 2014; Ábri et al., 2022, 2024).

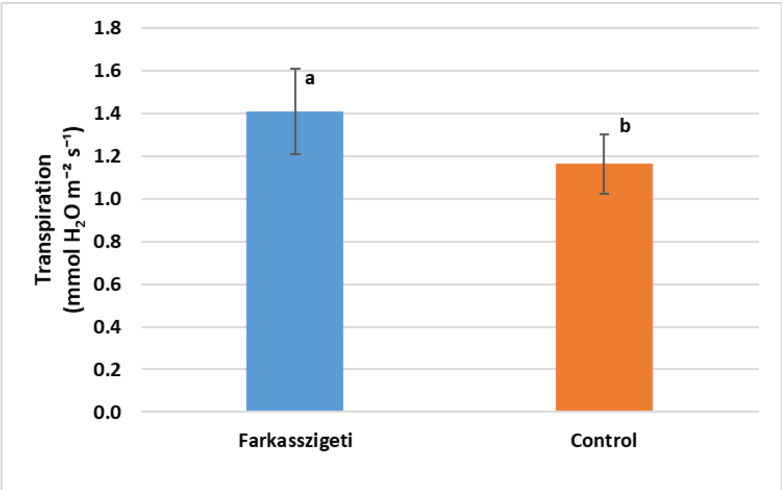
Heat stress inhibits photosynthesis, the primary target of high temperature is PSII (Mathur et al., 2014). I found significant differences (p=0.05) between the two black locusts in the efficiency of PSII. Farkasszigeti was found to be better in this parameter too. The values were 23% (Farkasszigeti) and 19% (Control) (*Figure 3*). Higher PSII value indicates better heat-tolerance ability and there is a close link between PSII efficiency and illumination (PPFD) level: as the illumination level increases, the efficiency of PSII decreases (Ábri et al., 2024). In terms of C_i the mean of the measured data was higher in the case of common black locust (255.01±26.42), so the clone Farkasszigeti (245.42±34.02) was better in this parameter.

Figure 3. **Efficiency of PSII of Farkasszigeti black locust clone and common black locust (control). Mean (%).**



As shown in *Figure 4,* a significant difference (p=0.05) was found also in the transpiration rate Farkasszigeti was proved to be better in this trait with 1.41±0.20 mmol H_2O m^{-2} s^{-1}. The transpiration value of the control is 1.16±0.14 mmol H_2O m^{-2} s^{-1}. This result suggests that both studied black locusts have low transpiration. Farkasszigeti has better cooling ability. Some studies (Kutasy et al., 2022; Ábri and Csajbók, 2023; Ábri et al., 2023) found a strong relationship between transpiration and net assimilation.

Figure 4. **Transpiration rate of Farkasszigeti black locust clone and common black locust (control). Mean±standard deviation. Letters indicate the significant difference (p=0.05)**



Water use efficiency (WUE) can be used to quantify changes in the balance between net assimilation and transpiration. Farkasszigeti proved to be higher WUE value by 0.56 kg m^{-3} (3.64±0.90 kg m^{-3}). There was no significant difference. An acclimation in WUE was not

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observed during or after water limitation (Mantovani et al., 2014; Ruehr et al., 2016).

In case of VPD_{leaf}, very high values were measured: 4.97±0.34 kPa for Farkasszigeti and 5.39±0.25 kPa for common black locust. 3 kPa VPD value is a threshold; VPD above 4 kPa is very high, which can affect the tree growth (Shirke and Pathre, 2004; Williams et al., 2013; Sancho-Knapik et al., 2022). Mann-Whitney test showed significant differences between the two studied black locusts. The lower VPD_{leaf} values mean better cooling ability, which may have an effect on the plant productivity.

The physiological traits of clone Farkasszigeti were also studied in a clone trial near the settlement of Napkor (Ábri et al., 2022, 2023b, 2024). Similar measurements were carried out in 2022, when the tested clone was in its second vegetation period. The summer of 2022 was drought and warm (Ábri and Csajbók, 2023). So, the weather conditions were almost the same as at the time of the Debrecen measurement (2024). The nutrient supply and soil moisture of the soil – humous and NO_3^-, P_2O_5 and K_2O content – is better and the soil pH is lower in Napkor (Ábri et al., 2022), than Debrecen.

As shown in *Table 3*, in Napkor, clone Farkasszigeti was proved to be better in almost all studied physiological traits. The g_{tc} values was 0.207 mol m^{-2} s^{-1} for Farkasszigeti in Napkor and it was 0.017 mol m^{-2} s^{-1} in Debrecen. Thus, the higher A_N and Tr values were measured in Napkor. The efficiency of PSII was also better. The VPD_{leaf} value was lower in Napkor than Debrecen, hence the tested clone was proved to be better in Napkor in this trait, too. However, the WUE values are almost the same (Ábri et al., 2023b; Ábri and Csajbók, 2023). This confirms the findings published by Ruehr et al. (2016) and Mantovani et al. (2014), which state that no acclimation in WUE values is observed during periods of water limitation. These results confirmed that black locusts adopt a balanced water regulatory strategy between isohydric and anisohydric to cope with drought stress. This isohydrodynamic regulatory behavior allows them to maintain a relatively stable water potential gradient. This helps mitigate the impact of severe droughts caused by rainfall variations. Furthermore, this water regulation strategy may facilitate an optimal balance between transpiration, carbon sequestration, and hydraulic control (Sanchez-Martinez et al., 2023; Liu et al., 2024).

Table 3. **Ecophysiological traits of 3-year-old Farkasszigeti black locust clones in Napkor (2022) and Debrecen (2024)**

	A_N µmol CO_2 m^{-2} s^{-1}	Tr mmol H_2O m^{-2} s^{-1}	g_{tc} mol m^{-2} s^{-1}	C_i µmol mol^{-1}	VPD_{leaf} (kPA)	WUE (kg m^{-3})	T_{air}-T_{leaf} (°C)	PSII eff. (%)
Napkor (2022)	15.02 ±1.42	10.01 ±1.13	0.207 ±0.060	287.38 ±16.93	3.08 ±0.55	3.68 ±0.15	1.03 ±1.30	30
Debrecen (2024)	2.13 ±0.75	1.41 ±0.20	0.017 ±0.002	245.42 ±34.02	4.97 ±0.34	3.64 ±0.90	-1.18 ±0.58	19

Projections of the recent FAO report on the state of the world's forests indicate large increases in wood demand by 2050. The area of forest plantations could increase by 20–40 million hectares in the near future. To achieve this goal innovative biotechnologies will be needed. Research works are being applied to genetic research and tree improvement to increase yields, resistance to disease and adaptation to negative effects of the changing climate conditions (FAO, 2024). Thus, studying the physiological performance (carbon sequestration, water-use characteristics) of tree species, such as black locust is pivotal, because this multi-purpose tree species will play a crucial role in future forest management, primarily in tree plantations.

Due to its many advantages (adaptability to many sites and climates, durable wood, key role in apiculture), black locust is the most commonly planted tree species in Hungary, covering 24% of the forested area (Nicolescu et al., 2018; National Forest Data Base, 2023). Research aimed at improving its stem quality, enhancing its drought tolerance, and increasing its yield is still ongoing today, continuing the research efforts of the past decades (Keresztesi, 1988; Ábri et al., 2023a). Even more so, as the drier site conditions are expected to expand (Mátyás et al., 2018). Thus, in the selection of suitable tree species, the ability of physiological adaptation and acclimatation is becoming more significant.

CONCLUSIONS

In conclusion, both tested black locusts showed low values for net assimilation, transpiration, stomatal conductance, and water use efficiency. However, clone Farkasszigeti demonstrated better physiological traits compared to the common black locust, particularly in stomatal conductance, net assimilation, efficiency of photosystem II, and transpiration rate. These differences indicate the clone's better tolerance to combined heat and drought stress compared to a control. There is no significant difference found in water use efficiency (WUE) values. Both clones showed high VPD_{leaf} values, which could affect the growth negatively. The lower VPD_{leaf} values observed in Farkasszigeti suggest better cooling ability. The current physiological results measured in Debrecen were compared with those from a similar trial in Napkor. It was determined that, at the same age, the values for most of the studied parameters were significantly higher in the Napkor trial. However, the WUE results were almost the same. Overall, clone Farkasszigeti's performance under extreme weather

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conditions highlights its potential for adaptation to climate change, making it a promising candidate for forestry applications.

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REFERENCES

Ábri, T.; Borovics, A.; Csajbók, J.; Kovács, E.; Koltay, A.; Keserű, Z.; Rédei, K. (2023b): Differences in the Growth and the Ecophysiology of Newly Bred, Drought-Tolerant Black Locust Clones. *Forests*, *14*, https://doi.org/10.3390/f14091802

Ábri, T.; Csajbók, J. (2023): Comparative study of newly-bred black locust clones with regard to photosynthetic rate and water use efficiency: early evaluation. *AAD*, *1*, 5–10. https://doi.org/10.34101/actaagrar/1/12256

Ábri, T.; Cseke, K.; Keserű, Z.; Porcsin, A.; Szabó, F.M.; Rédei, K. (2023a): Breeding and improvement of black locust (*Robinia pseudoacacia* L.) with a special focus on Hungary: a review. *iForest*, *16*, 290–298. https://doi.org/10.3832/ifor4254-016

Ábri, T.; Gaganetz, D.Z.; Csajbók, J. (2024): Light response curve analysis of juvenile black locust clones: A case study from eastern Hungary. *J. For. Sci.*, *70*, 202–207. https://doi.org/10.17221/120/2023-JFS

Ábri, T.; Keserű, Z.; Borovics, A.; Rédei, K.; Csajbók, J. (2022): Comparison of Juvenile, Drought Tolerant Black Locust (*Robinia pseudoacacia* L.) Clones with Regard to Plant Physiology and Growth Characteristics in Eastern Hungary: Early Evaluation. *Forests*, *13*, https://doi.org/10.3390/f13020292

Allen, C.D.; Breshears, D.D.; McDowell, N.G. (2015): On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, *6*, 1–55. https://doi.org/10.1890/ES15-00203.1

Bamberger, I.; Ruehr, N.K.; Schmitt, M.; Gast, A.; Wohlfahrt, G.; Arneth, A. (2017): Isoprene emission and photosynthesis during heatwaves and drought in black locust. *Biogeosciences*, *14*, 3649–3667. https://doi.org/10.5194/bg-14-3649-2017

Choat, B.; Jansen, S.; Brodribb, T.J.; Cochard, H.; Delzon, S.; Bhaskar, R.; Bucci, S.J.; Feild, T.S.; Gleason, S.M.; Hacke, U.G.; Jacobsen, A.L.; Lens, F.; Maherali, H.; Martinez-Vilalta, J.; Mayr, S.; Mencuccini, M.; Mitchell, P.J.; Nardini, A.; Pittermann, J.; Pratt, R.B.; Sperry, J.S.; Westoby, M.; Wright, I.J.; Zanne, A.E. (2012): Global convergence in the vulnerability of forests to drought. *Nature*, *491*, 752–755. https://doi.org/10.1038/nature11688

Climate.gov. Available online: https://www.climate.gov/news-features/understanding-climate/climate-change-atmospheric-carbon-dioxide, (accessed on 30 January 2025).

FAO (2024): The State of the World's Forests 2024 – Forest-sector innovations towards a more sustainable future; FAO: Rome, Italy, https://doi.org/10.4060/cd1211en, 122.

Farquhar, G.D.; Sharkey, T.D. (1982): Stomatal conductance and photosynthesis. *Annu. Rev. Plant Physiol.*, *33*, 317–345.

Flexas, J.; Medrano, H. (2002): Drought-inhibition of photosynthesis in C3 plants: stomatal and non-stomatal limitations revisited. *Ann. Bot.*, *89*, 183–189. https://doi.org/10.1093/aob/mcf027

Führer, E. (2018): A klímaértékelés erdészeti vonatkozásai. *Erdészettud. Közl.*, *8*, 27–42. (in Hungarian) https://doi.org/10.17164/EK.2018.002

Hungarian Meteorological Service (HMS). Available online: https://odp.met.hu/climate/homogenized_data/gridded_data_series/daily_data_series/from_1971/, (accessed on 16 April 2025)

IPCC (2023): Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]; IPCC: Geneva, Switzerland, 184. https://doi.org/10.59327/IPCC/AR6-9789291691647

IUSS Working Group WRB (2022): World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps. 4th edition; International Union of Soil Sciences (IUSS): Vienna, Austria.

Keresztesi, B. (1988): The Black Locust; Akadémiai Kiadó: Budapest, Hungary, 196.

Klein, T. (2014): The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct. Ecol.*, *28*, 1313–1320.https://doi.org/10.1111/1365-2435.12289

Kutasy, E.; Buday-Bódi, E.; Virág, I.C.; Forgács, F.; Melash, A.A.; Zsombik, L.; Nagy, A.; Csajbók, J. (2022): Mitigating the Negative Effect of Drought Stress in Oat (*Avena sativa* L.) with Silicon and Sulphur Foliar Fertilization. *Plants*, *11*, https://doi.org/10.3390/plants11010030

Lange, C.A.; Knoche, D.; Hanschke, R.; Löffler, S.; Schneck, V. (2022): Physiological Performance and Biomass Growth of Different Black Locust Origins Growing on a Post-Mining Reclamation Site in Eastern Germany. *Forests*, *13*, https://doi.org/10.3390/f13020315

Liu, B.; Tang, X.; Wang, L.; Zhang, P.; He, J.; Yue, C. (2024): Physiological responses of a black locust plantation to drought stress based on a throughfall exclusion experiment in semi-arid northwestern China. *Forestry*, https://doi.org/10.1093/forestry/cpae027.

Mantovani, D.; Veste, M.; Freese, D. (2014): Black locust (*Robinia pseudoacacia* L.) ecophysiological and morphological adaptations to drought and their consequence on biomass production and water-use efficiency. *N.Z.J. For. Sci.*, *44*, https://doi.org/10.1186/s40490-014-0029-0.

Martínez-Vilalta, J.; Garcia-Forner, N. (2017): Water potential regulation, stomatal behaviour and hydraulic transport under drought: deconstructing the iso/anisohydric concept. *Plant Cell Environ.*, *40*, 962–976. https://doi.org/10.1111/pce.12846

Martínez-Vilalta, J.; Poyatos, R.; Aguadé, D.; Retana, J.; Mencuccini, M. (2014): A new look at water transport regulation

DOI: 10.34101/ACTAAGRAR/1/15473

in plants. *New Phytol.*, *204*, 105–115. https://doi.org/10.1111/nph.12912

Mathur, S.; Agrawal, D.; Jajoo, A. (2014): Photosynthesis: response to high temperature stress. *J. Photochem. Photobiol. B*, *137*, 116–126. https://doi.org/10.1016/j.jphotobiol.2014.01.010

Mátyás, C.; Berki, I.; Bidló, A.; Csóka, G.; Czimber, K.; Führer, E.; Gálos, B.; Gribovszki, Z.; Illés, G.; Hirka, A.; Somogyi, Z. (2018): Sustainability of forest cover under climate change on the temperate-continental xeric limits. *Forests*, *9*, https://doi.org/10.3390/f9080489.

McDowell, N.; Pockman, W.T.; Allen, C.D.; Breshears, D.D.; Cobb, N.; Kolb, T.; Plaut, J.; Sperry, J.; West, A.; Williams, D.G.; Yepez, E.A. (2008): Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.*, *178*, 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

McDowell, N.G.; Allen, C.D.; Anderson-Teixeira, K.; Aukema, B.H.; Bond-Lamberty, B.; Chini, L.; Clark, J.S.; Dietze, M.; Grossiord, C.; Hanbury-Brown, A.; Hurtt, G.C.; Jackson, R.B.; Johnson, D.J.; Kueppers, L.; Lichstein, J.W.; Ogle, K.; Poulter, B.; Pugh, T.A.M.; Seidl, R.; Turner, M.G.; Uriarte, M.; Walker, A.P.; Xu, C. (2020): Pervasive shifts in forest dynamics in a changing world. *Science*, *368*, https://doi.org/10.1126/science.aaz9463

Meng, F.; Peng, M.; Pang, H.; Huang, F. (2014): Comparison of photosynthesis and leaf ultrastructure on two black locust (*Robinia pseudoacacia* L.). *Biochem. Syst. Ecol.*, *55*, 170–175. https://doi.org/10.1016/j.bse.2014.03.025

Messier, C.; Baker, C.; Carreiras, J.M.B.; Pearson, T.R.H.; Vasconcelos, M.J. (2022): Warning: Natural and Managed Forests are Losing their Capacity to Mitigate Climate Change. *For. Chron.*, *98*, 2–8. https://doi.org/10.5558/tfc2022-007

National Forest Data Base (2023): Available online: https://foldalap.am.gov.hu/Magyarorszag_erdeivel_kapcsolatos_adatok_news_513, (accessed on 27 January 2025).

Nicolescu, V.N.; Hernea, C.; Bakti, B.; Keserű, Z.; Antal, B.; Rédei, K. (2018): Black locust (*Robinia pseudoacacia* L.) as a multi-purpose tree species in Hungary and Romania: a review. *J. For. Res.*, *29*, 1449–1463. https://doi.org/10.1007/s11676-018-0626-5

Nicolescu, V.N.; Rédei, K.; Mason, W.L.; Vor, T.; Pöetzelsberger, E.; Bastien, J.C.; Brus, R.; Benčať, T.; Đodan, M.; Cvjetkovic, B.; Andrašev, S.; La Porta, N.; Lavnyy, V.; Mandžukovski, D.; Petkova, K.; Roženbergar, D.; Wąsik, R.; Mohren, G.M.J.; Monteverdi, M.C.; Musch, B.; Klisz, M.; Perić, S.; Keça, L.; Bartlett, D.; Hernea, C.; Pástor, M. (2020): Ecology, growth and management of black locust (*Robinia pseudoacacia* L.), a non-native species integrated into European forests. *J. For. Res.*, *31*, 1081–1101. https://doi.org/10.1007/s11676-020-01116

Pethő, M. (1998): A növényélettan alapjai; Akadémiai Kiadó: Budapest, Hungary, 176. (in Hungarian)

Pivovaroff, A.L.; Pasquini, S.C.; De Guzman, M.E.; Alstad, K.P.; Stemke, J.S.; Santiago, L.S. (2016): Multiple strategies for drought survival among woody plant species. *Funct. Ecol.*, *30*, 517–526. https://doi.org/10.1111/1365-2435.12518

Pretzsch, H.; Schütze, G.; Uhl, E. (2012): Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol.*, *15*, 483–495. https://doi.org/10.1111/j.1438-8677.2012.00670.x

Ruehr, N.K.; Gast, A.; Weber, C.; Daub, B.; Arneth, A. (2016): Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiol.*, *36*, 164–178. https://doi.org/10.1093/treephys/tpv102

Sanchez-Martinez, P.; Mencuccini, M.; García-Valdés, R.; Hammond, W.M.; Serra-Diaz, J.M.; Guo, W.Y.; Segovia, R.A.; Dexter, K.G.; Svenning, J-C.; Allen, C.; Martínez-Vilalta, J. (2023): Increased hydraulic risk in assemblages of woody plant species predicts spatial patterns of drought-induced mortality. *Nat. Ecol. Evol.*, *7*, 1620–1632. https://doi.org/10.1038/s41559-023-02180-z

Sancho-Knapik, D.; Mendoza-Herrer, O.; Alonso-Forn, D.; Saz, M.A.; Martín-Sánchez, R.; dos Santos Silva, J.V.; Ogee, J.; Peguero-Pina, J.J.; Gil-Pelegrín, E.; Ferrio, J.P. (2022): Vapor pressure deficit constrains transpiration and photosynthesis in holm oak: A comparison of three methods during summer drought. *Agric. For. Meteorol.*, *327*, https://doi.org/10.1016/j.agrformet.2022.109218

Shirke, P.A.; Pathre, U.V. (2004): Influence of leaf-to-air vapour pressure deficit (VPD) on the biochemistry and physiology of photosynthesis in *Prosopis juliflora*. *J. Exp. Bot.*, *55*, 2111–2120. https://doi.org/10.1093/jxb/erh229

Tanner, C.B.; Sinclair, T.R. (1983): Efficient water use in crop production: Research or Re-search? In: Limitations to Efficiency Water Use in Crop Production Limitations to Efficient Water Use in Crop Production; Taylor, H.M.; Jordan, W.R. and Sinclair, T.R. (Eds.); American Society of Agronomy: Madison, Wisconsin, USA, 1–27.

Tardieu, F.; Simonneau, T. (1998): Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. *J. Exp. Bot.*, *49*, 419–432.

Vítková, M.; Müllerová, J.; Sádlo, J.; Pergl, J.; Pyšek, P. (2017): Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. *For. Ecol. Manag.*, *384*, 287–302.https://doi.org/10.1016/j.foreco.2016.10.057

Williams, A.P.; Allen, C.D.; Macalady, A.K.; Griffin, D.; Woodhouse, C.A.; Meko, D.M.; Swetnam, T.W.; Rauscher, S.A.; Seager, R.; Grissino-Mayer, H.D.; Dean, J.S.; Cook, E.R.; Gangodagamage, C.; Cai, M.; McDowell, N.G. (2013): Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat. Clim. Change*, *3*, 292–297. https://doi.org/10.1038/NCLIMATE1693

Yan, X.; Zhang, Z.; Zhao, X.; Huang, M.; Wu, X.; Guo, T. (2024): Differentiated responses of plant water use regulation to drought in *Robinia pseudoacacia* plantations on the Chinese Loess Plateau. *Agric. Water Manag.*, *291*, https://doi.org/10.1016/j.agwat.2023.108659.