



Physiological characteristics of fruit and berry plants *ex situ* under arid conditions of Mangystau, Kazakhstan

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ABSTRACT

The article presents the results of a comprehensive physiological study on the fruit and berry plants introduced *ex situ* under the arid conditions of Mangystau, Kazakhstan. The research focused on species belonging to the genera *Crataegus*, *Hippophae*, *Lonicera*, *Ribes*, and *Rosa* grown at the Mangyshlak Experimental Botanical Garden. During the 2024–2025 growing seasons. Key indicators of plant water regime (transpiration rate, leaf water content, and water retention capacity) and photosynthetic performance (chlorophyll *a*, chlorophyll *b*, and carotenoids) were analysed in relation to temperature and hydrothermal conditions. The results revealed that, compared to 2024, most species in 2025 exhibited a 30–35% decrease in transpiration rate, accompanied by a 1.4–2.3-fold increase in leaf water content and elevated chlorophyll *a* and *b* concentrations. These shifts indicate a transition from an intensive to a water-saving water-use strategy under more favourable hydrothermal conditions. Correlation analysis demonstrated a significant negative relationship between leaf water content and air temperature, while a positive association with photosynthetic pigments. At the same time, carotenoids served as key indicators of photoprotective responses to thermal stress. Principal component analysis (PCA) and hierarchical clustering distinguished three major physiological adaptation strategies: hydration-stable, stress-adaptive, and plastic. Integrated physiological stability indices (PSI and WBI) identified *Hippophae rhamnoides* and *Rosa canina* as the most physiologically resilient species, whereas *Lonicera* species showed pronounced physiological plasticity. The findings provide a scientific basis for selecting drought- and heat-tolerant fruit and berry plants for introduction, landscaping, and phytomelioration in the arid regions of Mangystau and Western Kazakhstan.

Keywords: Arid environment, Mangystau, Fruit and berry plants, Transpiration, Leaf water content, Photosynthetic pigments, Physiological stability, PCA.

Article type: Research Article.

INTRODUCTION

Under conditions of global climate change, arid territories are among the most vulnerable ecosystems, where the combination of high air temperatures, low relative humidity, and a deficit of atmospheric precipitation substantially limits plant growth, development, and productivity (IPCC Climate Change 2021). The primary limiting factor for plant introduction under the arid conditions of Mangyshlak is the sharply continental climate, characterized by a short, low-snow but relatively cold winter and a prolonged hot summer, high summer air temperatures (up to 43–45 °C), a severe deficit of atmospheric moisture (107–180 mm of precipitation per year), soil salinity, and frequent strong winds (Nasiyev *et al.* 2022). In such regions, the stability of plant organisms is primarily determined by their physiological ability to maintain water balance, regulate transpiration flux, and preserve the functional integrity of the photosynthetic apparatus under water and thermal stress (Chaves *et al.* 2003). The relevance of this study is due to the need for a scientifically grounded assessment of the current physiological state of fruit and berry plants to ensure food security, the rational use of plant resources, and the conservation of biological diversity (Bélanger & Pilling 2019). At present, non-native species, cultivars, and forms of fruit and berry crops are widely used across the country. However, they often exhibit limited ecological



plasticity and insufficient resistance to local soil and climatic conditions. This significantly reduces the effectiveness of their introduction and limits the possibilities for large-scale propagation, establishment of sustainable nurseries, and practical implementation in economic activities. These issues are particularly significant in the Mangystau Desert, located in western Kazakhstan and characterised by an extremely arid climate. High summer temperatures typify this territory, along with extremely low annual precipitation, frequent dry winds and dust storms, and widespread saline, shallow soils with low organic matter content and low water availability. Under conditions of the almost complete absence of natural woody and shrub communities, all cultivated plants in the region are grown exclusively under regular irrigation, the effectiveness of which is primarily determined by the level of drought and heat tolerance of the plants (Blum 2010). Physiological responses of plants to water and thermal stress include changes in transpiration intensity, redistribution of water among organs and tissues, maintenance or reduction of leaf water content, and restructuring of the pigment system. Transpiration intensity is an integrated indicator of plant water exchange and of the plant's response to atmospheric evaporative demand (Lawlor & Tezara 2009). In contrast, leaf water content reflects a plant's ability to maintain turgor, metabolic activity, and resistance to dehydration under conditions of moisture deficit. The state of the pigment system, particularly the ratio of chlorophylls *a* and *b* and the content of carotenoids, reflects the balance between photosynthetic productivity and photoprotective mechanisms that protect the photosynthetic apparatus from photooxidative damage under stress conditions (Lichtenthaler 1987). For a comprehensive assessment of the stability of introduced plants and the adaptive potential of individual species under arid conditions, quantitative statistical analysis methods are widely applied. This study employs descriptive statistics (mean, standard deviation, minimum, and maximum) to characterise seasonal and interspecific variability in transpiration intensity, leaf water content, and pigment system parameters. To identify statistically significant differences among species, analysis of variance (ANOVA) and the Kruskal–Wallis test are used with evaluation of statistical significance levels (*p*-value). Relationships between plant physiological parameters and abiotic factors are analysed using Spearman correlation analysis, with results visualised in the form of correlation matrices and heat maps (*heatmap*). In addition, regression models are applied to quantitatively assess the contribution of individual environmental factors to changes in plant physiological parameters and to identify key determinants of plant stability (Jatobá *et al.* 2019). Based on the combined set of physiological indicators, integrated indices of physiological stability are calculated, reflecting the ability of plants to maintain water regime and the functional integrity of the photosynthetic apparatus under extreme conditions. The application of correlation analysis, principal component analysis (PCA), and hierarchical clustering enables the identification of relationships among climatic factors, plant physiological responses, and plant community structure, as well as the classification of species groups with similar adaptation mechanisms to arid environments (Koblanova *et al.* 2024). Despite the existence of individual studies addressing the ecological and biological characteristics of plants in arid territories, comprehensive investigations integrating analyses of water regime, pigment system status, and multivariate statistical methods for fruit and berry plants in Mangystau remain limited. In particular, interspecific differences in physiological adaptation strategies among genera and species used in plant introduction and landscaping of the region have not been sufficiently studied. The scientific novelty of this research lies in the comprehensive assessment of the physiological characteristics of fruit and berry plants grown *ex situ* under the arid conditions of Mangystau using correlation analysis, principal component analysis (PCA), and hierarchical clustering. The results obtained enable identification of stable adaptive strategies and substantiation of practical recommendations for plant introduction and conservation in arid regions (Legendre & Legendre 2012).

MATERIALS AND METHODS

Study objects

The study was conducted during the 2024–2025 growing seasons on cultivated (*ex situ*) fruit and berry plants introduced and grown under the arid conditions of Western Kazakhstan (Trofimov *et al.* 2021). The investigated taxa belonged to five genera widely used in plant introduction, landscaping, and agroecological practices in arid and semi-arid regions: *Crataegus*, *Hippophae*, *Lonicera*, *Ribes*, and *Rosa* (Chaves *et al.* 2003; Blum 2010). Plant sampling was carried out in experimental plots of the Mangyshlak Experimental Botanical Garden, which serves as a key centre for the introduction and long-term cultivation of woody and shrub species under desert and semi-desert conditions (Akzhunis *et al.* 2025). Laboratory analyses of physiological and biochemical parameters were performed at the Laboratory of Plant Physiology and Biochemistry using standardised and widely accepted analytical protocols commonly applied in studies of plant responses to drought and thermal stress (Taiz *et al.*

2015). The study objects included nine species of fruit and berry plants: *Crataegus sanguinea* Pall., *C. ambigua* C.A. Mey., *Hippophae rhamnoides* L., *Lonicera altaica* Pall., *L. tatarica* L., *Ribes aureum* Pursh, and *Rosa canina* L. These species differ in their ecological origins, life forms, and adaptive strategies, making them suitable model organisms for assessing interspecific variability in physiological responses to drought and heat stress under arid conditions.

Plant materials

The research material consisted of introduced fruit and berry plants cultivated *ex situ* on the experimental plots of the Mangyshlak Experimental Botanical Garden. The study included representatives of five genera—*Crataegus*, *Lonicera*, *Rosa*, *Hippophae*, and *Ribes* — differing in ecological and biological origins, life forms, and degrees of adaptation to the arid conditions of Mangystau. The introduction of these taxa was carried out in different years over a period exceeding 50 years of the garden's existence.

Genus *Crataegus* L.

Crataegus ambigua C.A. Mey. (Ambiguous hawthorn) is a rare and endangered species in Kazakhstan and an endemic of Mangyshlak. Under natural conditions, it grows at the bottoms of ravines, in chalk and gypsum gorges, and in the region's relatively moist microhabitats. The species was introduced into cultivation by seed in 1982 from the natural flora of Mangystau. Under garden conditions, it forms a shrub or a small tree 3–4 m high with a broad, spherical crown. The species is characterised by leathery lobed leaves, regular flowering in May, and fruiting in August–September, indicating successful adaptation under cultivation. *Crataegus sanguinea* Pall. (Blood-red hawthorn) is a species with a wide distribution range, occurring in forest and forest-steppe zones of Eurasia. It was introduced to the Mangyshlak Experimental Botanical Garden by seed in 2016 from Karaganda. Under arid climatic conditions, it forms a shrub or small tree up to 2.0–2.5 m high. The species is highly light-demanding and belongs to xeromesophytes. It is characterised by stable flowering and fruiting, making it a promising introduction species for the region.

Genus *Lonicera* L.

Lonicera altaica Pall. is a shrub up to 1.8–2.0 m tall, native to mountainous regions of Siberia and Mongolia. It was introduced by seed from the Main Botanical Garden (Almaty) in 2001. Under Mangystau conditions, it forms a rounded, spreading crown and is distinguished by early flowering (late March–April) and fruit ripening in June. The species exhibits high physiological plasticity and resistance to contrasting temperature conditions.

Lonicera tatarica L. is a deciduous ornamental shrub 2.5–3.0 m high, introduced by seed from the Tashkent Botanical Garden in 1980. Under garden conditions, it is characterised by regular flowering and fruiting, high ornamental value, and the ability to form stable plantings. It belongs to xeromesophytes and is well adapted to arid conditions.

Genus *Rosa* L.

Rosa canina L. is a widely distributed species introduced by seeds of local reproduction in 1985. It is a light-demanding xeromesophyte forming a shrub up to 2.5 m high. Under Mangystau conditions, it is characterised by stable growth, regular flowering, and fruiting.

Genus *Hippophae* L.

Hippophae rhamnoides L. is a dioecious shrub up to 2.0–2.5 m high, widely distributed in the temperate zone of Eurasia. It was introduced to the Mangyshlak Experimental Botanical Garden in 2015 from the Altai Botanical Garden, in several breeding forms. The species is characterised by high drought and frost resistance, low soil requirements, and stable fruiting, making it one of the key objects of introduction research.

Genus *Ribes* L.

Ribes nigrum L. is a deciduous shrub introduced to the Mangyshlak Experimental Botanical Garden in 2011 from the Altai Botanical Garden. A powerful root system characterises it, with a pronounced leaf aroma and stable fruiting. Despite its mesophytic origin, it adapts satisfactorily to the arid climate under regular irrigation.

Physiological Parameters

To assess the physiological condition and drought resistance of introduced fruit and berry plants, parameters of the leaf water regime, transpiration intensity, and photosynthetic pigment content were analysed using classical and widely accepted methods. The leaf water regime was evaluated by determining total leaf water content, water-holding capacity, and mobile water content using the gravimetric method of Eryomin and Gasanova (Zalibekov

et al. 2024), which is commonly used in studies of plant water balance under arid and semi-arid conditions. Total leaf water content (W, %) was calculated as $W = 100 \times (M - M_2) / M$ where M is the fresh mass of the sample, M_1 is the mass of the sample after 3 h from the beginning of the experiment, and M_2 is the mass of the sample after drying to constant weight. Leaf water-holding capacity (R, %) was calculated using the formula $R = 100 \times (M_1 - M_2) / M$, while mobile water content in leaves (L, %) was determined as the difference between total water content and water-holding capacity ($L = W - R$). These indicators characterise the ability of plants to retain water in leaf tissues and maintain turgor and metabolic activity under moisture-deficient conditions. Transpiration intensity was determined using the rapid weighing method developed by Ivanov (Ivanov *et al.* 2004), which measures leaf mass loss over short time intervals and allows estimation of transpiration rate as an integrated indicator of plant water exchange and physiological response to atmospheric evaporative demand. This method is widely used in ecological and physiological studies of plant responses to drought and high temperature stress. The content of photosynthetic pigments, including chlorophyll *a*, chlorophyll *b*, and carotenoids, was determined spectrophotometrically. Pigments were extracted from fresh leaf material using 96% ethyl alcohol according to the method proposed by Godnev (Godnev *et al.* 1957). The optical density of the extracts was measured at wavelengths of 470, 644, and 663 nm, and pigment concentrations were calculated using standard equations: chlorophyll *a* = $12.25 \times A_{663} - 2.79 \times A_{644}$, chlorophyll *b* = $21.50 \times A_{644} - 5.10 \times A_{663}$, and carotenoids = $(1000 \times A_{470} - 1.82 \times \text{Chl } a - 85.02 \times \text{Chl } b) / 198$. The pigment system parameters reflect the functional state of the photosynthetic apparatus and the balance between photosynthetic activity and photoprotective mechanisms under drought and thermal stress conditions (Ashraf & Harris 2013). Air temperature and relative humidity during the measurements were recorded using a digital thermo-hygrometer to characterise microclimatic conditions at the time of sampling and to ensure correct interpretation of physiological responses.

Statistical data analysis

Statistical analysis of the obtained data was performed using descriptive statistics, including calculation of the mean, standard deviation, minimum, and maximum values, which allowed assessment of seasonal, interannual, and interspecific variability in plant physiological parameters. Prior to statistical analyses, the dataset was examined for outliers, and all quantitative variables were standardised to eliminate scale effects and ensure comparability. The normality of data distribution was assessed using the Shapiro–Wilk test, which is considered one of the most reliable tests for small and medium sample sizes (Shapiro & Wilk 1965). To identify statistically significant interspecific differences in physiological traits, both parametric and nonparametric methods were applied, depending on the data distribution. Analysis of variance (ANOVA) was used for normally distributed data, whereas the Kruskal–Wallis test was applied when normality was violated, with a significance level of $p < 0.05$ (Jatobá *et al.* 2019). Relationships between plant physiological parameters were evaluated using Pearson or Spearman correlation analysis, depending on whether the data met parametric assumptions (Conover 1999). The structure and strength of correlations were visualised using correlation matrices and heat maps, which facilitated the interpretation of complex multivariate relationships. Physiological parameters of plants, including transpiration intensity, leaf water content, chlorophyll *a* and *b*, and carotenoid content, as well as climatic variables such as air temperature and precipitation, were recorded during the 2024–2025 growing seasons. To identify the main gradients of variability and reduce data dimensionality, principal component analysis (PCA) was applied to the standardised dataset. In addition, hierarchical cluster analysis was used to classify plant species based on similarities in their physiological responses and adaptive strategies under arid environmental conditions, enabling identification of groups with comparable levels of drought and heat tolerance (Legendre & Legendre 2012).

RESULTS

General analysis of physiological parameters

Arid ecosystems of Mangystau are characterised by high air temperatures and low relative humidity, creating extreme conditions for plant growth and function. In this context, the present study aimed to assess the physiological adaptive responses of fruit and berry plants in the arid climate of Mangystau using indicators of the water regime and the pigment apparatus. During the growing season, transpiration intensity, leaf water content, and the contents of chlorophylls *a* and *b* as well as carotenoids were examined in representatives of the genera *Crataegus*, *Hippophae*, *Rosa*, *Lonicera*, and *Ribes*. Table 1 presents summarised data on physiological and climatic parameters of the studied plant species over two growing seasons (2024–2025). For each species and year of observation, mean values of transpiration activity, leaf water supply, and photosynthetic pigment content

(chlorophylls *a* and *b*, carotenoids), as well as the main environmental parameters—air temperature and relative precipitation availability—were provided. Soil moisture was maintained through artificial irrigation. Drip irrigation was used, with up to 25 irrigation events per growing season from May to September, at an irrigation rate of 325 m³ ha⁻¹ and a seasonal irrigation norm of 8125 m³ ha⁻¹. The two-year (2024–2025) observations of plant physiological status were provided under changing temperature and hydrothermal regimes. For all studied species, a wide range of variability in transpiration rate, leaf water content, and photosynthetic pigment levels was recorded, reflecting both species-specific characteristics and interannual climatic dynamics (Table 1). The parameters were calculated from repeated field measurements across different phenological stages, thereby accounting for seasonal variability in physiological processes. The data were presented as mean values ± standard deviation, with minimum and maximum values indicated, reflecting both the typical physiological status of plants and the range of their adaptive responses to changing climatic conditions. The comparison of physiological and climatic parameters in a single table allows identification of species-specific features of water exchange and pigment system status, as well as assessment of plant resistance to temperature and hydrothermal fluctuations under arid conditions. The obtained results can be used for comparative analysis of species adaptation strategies and for substantiating their suitability for introduction and utilisation in arid regions. A comparative analysis of 2024 and 2025 data revealed pronounced interannual differences in the main physiological parameters across all studied plant species. In 2024, mean transpiration rates were higher across most species than in 2025. For example, in *C. ambigua*, transpiration intensity decreased from 277.5 ± 15.2 to 183.3 ± 49.4 conventional units, corresponding to approximately a 34% reduction. A similar trend was observed in *C. sanguinea*, where transpiration decreased by about 30%. In 2025, compared to 2024, most species exhibited a 30–35% decrease in transpiration intensity accompanied by a 1.4–2.3-fold increase in leaf water content. These changes were associated with increased concentrations of chlorophylls *a* and *b*, a decrease in background temperature, and improved availability of atmospheric precipitation. The observed quantitative differences indicate a shift in adaptive strategy from an intensive to a water-saving type of water exchange, reflecting enhanced hydraulic stabilisation of leaf hydration under favourable hydrothermal conditions. At the same time, an increase in leaf water supply was observed in 2025. For instance, in *C. ambigua*, leaf water content increased from 38.0 ± 11.5% in 2024 to 55.5 ± 5.6% in 2025, while in *L. tatarica* it increased from 28.6 ± 3.9% to 66.8 ± 3.0%, i.e., more than 2.3-fold. These changes indicate a transition from an intensive to a water-saving water-use strategy. Interannual differences also affected the pigment apparatus. In 2025, most species showed increased chlorophyll *a* content. In particular, in *H. rhamnoides*, the mean chlorophyll *a* content increased from 9.4 ± 3.1 to 20.5 ± 5.5 mg g⁻¹, and in *R. canina* from 15.7 ± 4.6 to 17.6 ± 6.6 mg g⁻¹. An increase in photosynthetic pigment concentration against the background of reduced transpiration activity can be regarded as a compensatory mechanism aimed at maintaining photosynthetic efficiency under conditions of restricted water loss. The carotenoid complex also exhibited pronounced interannual variability. In species with a xeromorphic orientation (*L. altaica*, and *L. tatarica*), carotenoid content was higher in 2024 (up to 10.7–12.0 mg g⁻¹) than in 2025 (3.8–4.9 mg g⁻¹), indicating a more active photoprotective response under increased thermal stress. Climatic differences between the years support the observed physiological shifts. In 2024, the mean air temperature during the observation period was 30.7 ± 4.2 °C, whereas in 2025 it decreased to 27.2 ± 4.9 °C, accompanied by an elevation in relative precipitation availability from 36.9 ± 11.3% to 41.9 ± 13.1%. More favourable hydrothermal conditions in 2025 promoted moisture accumulation in plant tissues, thereby reducing transpiration. Overall, transpiration intensity varied widely (≈125–315 conventional units), with maximum values in *H. rhamnoides* and *R. canina* during the summer. Leaf water content in mesophytic species (*C. sanguinea*, and *R. canina*) was consistently higher than in the more xerophytic *C. ambigua*. The contents of chlorophylls *a* and *b* exhibited pronounced seasonal dynamics, whereas carotenoids performed a photoprotective function under high temperatures and reduced moisture availability. Air temperatures ranged from about 18 to 37 °C, with precipitation levels varying from 20% to 88%. This resulted in contrasting hydrothermal conditions across different seasons and years of observation.

Seasonal dynamics of the water regime and photosynthetic pigment content

The plant water regime is a key factor in determining plant viability and productivity under variable hydrothermal conditions, especially in arid ecosystems. Analysis of interspecific differences in water use requires an integrated consideration of physiological parameters and climatic factors. In this context, the application of multivariate statistical methods (correlation analysis, principal component analysis, and cluster analysis) enables identification of the main ecological gradients and adaptive physiological responses.

Table 1. Mean values (\pm SD, min–max) of physiological and climatic parameters of the studied species (2024–2025)

Species	Year	Transpiration rate	Water content of leaves (%)	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Carotenoids	Temperature (°C)	Precipitation (%)
<i>Crataegus ambigua</i>	2024	277.5 \pm 15.2 (257.4–306.1)	38.0 \pm 11.5 (25.4–56.1)	11.4 \pm 3.7 (7.0–17.7)	6.7 \pm 2.6 (2.4–9.8)	3.7 \pm 1.2 (1.9–5.2)	30.6 \pm 4.0 (24.5–37.8)	33.7 \pm 8.1 (24.0–46.7)
<i>Crataegus ambigua</i>	2025	183.3 \pm 49.4 (127.7–278.8)	55.5 \pm 5.6 (47.3–63.3)	14.4 \pm 6.0 (6.0–22.3)	7.0 \pm 2.8 (0.6–9.5)	4.6 \pm 2.1 (1.9–8.2)	27.2 \pm 4.9 (21.7–36.5)	41.9 \pm 13.1 (26.6–62.0)
<i>Crataegus sanguinea</i>	2024	233.4 \pm 10.9 (217.8–248.6)	56.3 \pm 3.0 (51.4–60.4)	16.2 \pm 4.8 (10.9–25.2)	7.8 \pm 3.0 (2.6–12.1)	6.9 \pm 5.1 (3.4–19.8)	30.7 \pm 4.2 (24.5–37.8)	36.9 \pm 11.3 (23.7–53.9)
<i>Crataegus sanguinea</i>	2025	162.8 \pm 27.7 (129.2–216.3)	57.8 \pm 2.1 (54.6–59.9)	16.5 \pm 6.8 (7.2–25.6)	9.0 \pm 2.2 (5.9–12.2)	5.0 \pm 1.8 (2.4–7.6)	27.2 \pm 4.9 (21.7–36.5)	41.9 \pm 13.1 (26.6–62.0)
<i>Hippophae rhamnoides</i>	2024	226.6 \pm 25.6 (174.0–253.5)	61.8 \pm 3.7 (58.7–68.8)	9.4 \pm 3.1 (6.6–14.4)	5.3 \pm 2.1 (0.2–7.1)	3.2 \pm 1.4 (1.9–5.2)	30.7 \pm 4.2 (24.5–37.8)	36.9 \pm 11.3 (23.7–53.9)
<i>Hippophae rhamnoides</i>	2025	215.5 \pm 60.4 (150.5–314.5)	62.9 \pm 6.3 (48.2–68.1)	20.5 \pm 5.5 (11.9–27.4)	10.5 \pm 4.5 (7.1–20.1)	5.8 \pm 1.5 (3.7–7.4)	27.2 \pm 4.9 (21.7–36.5)	41.9 \pm 13.1 (26.6–62.0)
<i>Lonicera tatarica</i>	2024	198.1 \pm 16.6 (174.1–221.6)	28.6 \pm 3.9 (23.2–33.7)	6.8 \pm 1.6 (3.3–8.4)	3.2 \pm 0.6 (2.4–4.2)	10.7 \pm 3.1 (5.9–14.4)	44.8 \pm 16.5 (24.2–73.9)	59.2 \pm 3.0 (55.3–65.3)
<i>Lonicera tatarica</i>	2025	185.2 \pm 30.6 (152.8–235.2)	66.8 \pm 3.0 (61.5–70.6)	13.9 \pm 5.6 (7.1–26.1)	7.8 \pm 1.2 (6.6–9.7)	4.9 \pm 2.0 (2.2–8.2)	27.1 \pm 6.6 (18.6–37.4)	52.1 \pm 18.5 (25.6–88.8)
<i>Lonicera altaica</i>	2024	212.2 \pm 44.1 (168.3–310.2)	58.8 \pm 3.8 (53.8–65.3)	7.6 \pm 2.2 (2.7–8.9)	3.9 \pm 1.0 (2.9–6.0)	12.0 \pm 3.6 (7.3–19.6)	28.6 \pm 3.7 (23.2–33.7)	44.7 \pm 17.5 (24.2–73.9)
<i>Lonicera altaica</i>	2025	186.0 \pm 35.7 (127.1–231.3)	60.6 \pm 1.6 (57.3–62.4)	13.7 \pm 4.7 (7.3–18.3)	7.8 \pm 1.3 (6.4–9.4)	3.8 \pm 1.4 (2.0–5.8)	27.0 \pm 6.6 (18.6–37.4)	52.1 \pm 18.5 (25.6–88.8)
<i>Ribes aureum</i>	2024	183.1 \pm 13.6 (171.1–214.2)	39.2 \pm 14.6 (19.0–55.4)	5.4 \pm 1.0 (3.7–7.0)	5.9 \pm 0.6 (5.0–6.6)	2.0 \pm 0.4 (1.5–2.5)	30.3 \pm 4.1 (24.3–36.2)	41.5 \pm 15.5 (21.8–60.4)
<i>Ribes aureum</i>	2025	204.5 \pm 29.7 (152.8–235.4)	62.0 \pm 1.9 (59.4–64.6)	6.9 \pm 3.3 (3.7–12.9)	6.3 \pm 1.0 (5.2–8.1)	2.4 \pm 1.2 (1.1–4.7)	27.0 \pm 6.6 (18.6–37.4)	52.1 \pm 18.5 (25.6–88.8)
<i>Rosa canina</i>	2024	233.0 \pm 22.3 (194.5–267.6)	61.9 \pm 3.3 (58.7–68.8)	15.7 \pm 4.6 (8.9–21.3)	8.1 \pm 2.7 (3.2–10.5)	4.2 \pm 1.2 (2.4–5.7)	30.7 \pm 4.2 (24.5–37.8)	36.9 \pm 11.3 (23.7–53.9)
<i>Rosa canina</i>	2025	223.9 \pm 41.2 (183.5–301.4)	56.3 \pm 4.2 (48.9–60.2)	17.6 \pm 6.6 (8.4–26.7)	10.3 \pm 3.3 (6.7–17.0)	4.2 \pm 1.1 (2.2–5.8)	27.2 \pm 4.9 (21.7–36.5)	41.9 \pm 13.1 (26.6–62.0)

During the growing season, all studied species exhibited pronounced seasonal dynamics of transpiration. Maximum values were recorded during the summer months. They coincided with periods of elevated air temperatures and reduced relative humidity, whereas in the autumn, transpiration intensity decreased due to reduced atmospheric evaporative demand. Leaf water content in most species remained relatively stable at the

beginning of the growing season; however, a decline was observed during periods of maximum thermal stress. *Hippophae rhamnoides* and species of the genus *Crataegus* were the most stable with respect to this parameter. Leaf water content, which reflects plant water status and their ability to maintain turgor and functional activity of tissues, showed pronounced interspecific and seasonal variability based on the combined analysis of data from 2024–2025.

Table 2. Interspecific variability of leaf water content (2024–2025).

Adaptive species group	Characteristics of leaf hydration	Biological assessment
Hydration-stable (<i>H. rhamnoides</i> , <i>C. sanguinea</i> , <i>L. tatarica</i>)	High and weakly variable values	Effective maintenance of water balance and turgor
Intermediate (plastic) (<i>R. canina</i> , <i>R. aureum</i>)	Moderate values with pronounced variability	Flexible regulation of the water regime depending on conditions
Stress-adaptive (<i>C. ambigua</i> , <i>L. altaica</i>)	Reduced and highly variable values	High sensitivity of water status to thermal stress

Based on leaf hydration patterns, the studied species were clearly differentiated into three adaptive groups. Species with a hydration-stable strategy (*H. rhamnoides*, *C. sanguinea*, and *L. tatarica*) were characterised by high and weakly variable leaf water content, indicating effective maintenance of water balance and turgor regardless of hydrothermal fluctuations. The plastic (intermediate) group (*R. canina*, and *R. aureum*) showed moderate hydration levels with pronounced interannual variability, reflecting flexible regulation of water regime depending on temperature background and moisture availability. Species of the stress-adaptive group (*C. ambigua*, and *L. altaica*) exhibited reduced and highly variable leaf water content, indicating increased sensitivity of their water status to thermal and hydrothermal stress (Table 2). Correlation analysis revealed strong relationships among leaf water content, photosynthetic, and climatic parameters. A significant positive correlation was found between leaf hydration and chlorophyll *a* ($r = 0.48$; $p < 0.05$) and chlorophyll *b* ($r = 0.50$; $p < 0.05$), indicating that the stability and activity of the photosynthetic apparatus depend on tissue water supply. At the same time, a significant negative correlation with air temperature was established ($r = -0.68$; $p < 0.05$), reflecting intensification of water deficit under elevated temperature regimes. The relationship between leaf water content and transpiration intensity was negative but weak and statistically insignificant ($r = -0.23$), suggesting the presence of regulatory mechanisms that limit excessive water loss. Correlation with precipitation amount was weakly positive ($r = 0.25$), reflecting the indirect influence of atmospheric moisture on plant water status under arid conditions. Overall, the results confirm the key role of leaf water content in maintaining plant physiological stability and shaping adaptive responses to thermal and water stress. The content of photosynthetic pigments (chlorophylls *a* and *b* and carotenoids) showed pronounced seasonal, interannual, and interspecific variability, reflecting plant adaptive responses to fluctuations in hydrothermal conditions throughout the growing season. At the beginning of the growing season (June), most species exhibited elevated chlorophyll *a* value, indicating active photosynthetic function under favourable water availability. As the season progressed into summer (July–August), accompanied by increasing air temperatures and reduced moisture availability, a decrease in chlorophyll content—particularly chlorophyll *b*—was observed in several species, indicating a restructuring of pigment composition and partial limitation of photosynthetic activity under hydrothermal stress. In contrast, carotenoids tended to increase during periods of maximum thermal load. Elevated carotenoid levels recorded in mid- and late summer reflect the activation of photoprotective mechanisms that mitigate the adverse effects of excessive light and high temperatures. Seasonal differences were evident in the patterns of pigment shifts. Stress-adaptive species showed pronounced fluctuations in chlorophyll content, accompanied by an increased proportion of carotenoids during unfavourable periods. Species with a stable water regime maintained relatively constant levels of chlorophylls *a* and *b* throughout the season. In contrast, species with a plastic type of regulation exhibited intermediate patterns of change. Under the arid conditions of Mangystau, most fruit and berry plants exhibited a 30–35% reduction in transpiration, accompanied by increases in leaf water content and chlorophyll concentration under more favourable temperature and moisture conditions, indicating a shift toward a water-saving water-use strategy. *H. rhamnoides*, *C. sanguinea*, and *L. tatarica* were characterised by the most stable water regime and pigment system. In contrast, *C. ambigua* and *L. altaica* demonstrated increased sensitivity to thermal and water stress.

Interannual dynamics of the water regime and photosynthetic activity of plants

Interannual variations in climatic factors in the arid zone of Mangystau lead to pronounced changes in the water regime and the photosynthetic activity of plants, which are key criteria for plant introduction and for assessing

their adaptive potential. In 2025, compared to 2024, most of the studied woody and shrub species exhibited a 30–35% drop in transpiration activity accompanied by a 1.4–2.3-fold elevation in leaf water content. These changes were associated with higher concentrations of chlorophylls *a* and *b*, which were related to lower air temperatures and improved atmospheric moisture availability. The obtained data reflect a shift from intensive to water-saving transpiration and indicate stabilisation of the plant water regime (Table 5).

Table 3. Relationships between leaf water content and photosynthetic and climatic parameters (2024–2025).

Parameter	Relationship relative to leaf water content	r	p	Type of relationship	Biological interpretation
Leaf water content	Central indicator of plant water status	1.00	—	—	Reflects the ability to maintain turgor and functional tissue activity
Transpiration intensity	With increasing transpiration	–0.23	>0.05	Weak, not significant	Regulation of water exchange and limitation of water loss
Air temperature	With increasing temperature	–0.68	<0.05	Negative, significant	Intensification of water deficit under thermal stress
Precipitation amount	With increasing precipitation	0.25	>0.05	Weak positive	Indirect influence of atmospheric moisture
Chlorophyll <i>a</i>	With increased hydration	0.48	<0.05	Positive, significant	Stability and activity of the photosynthetic apparatus
Chlorophyll <i>b</i>	With increased hydration	0.50	<0.05	Positive, significant	Functioning of light-harvesting complexes

Note: *r* — Pearson correlation coefficient; *p* — level of statistical significance. The analysis was performed using pooled data from 2024–2025.

Table 4. Seasonal dynamics of photosynthetic pigments in the studied species.

Period / Year	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Carotenoids	Main trend
June	high	moderate	low	Active photosynthesis
July–August	decrease	pronounced decrease	increase	Photoprotective adjustment
Autumn	stabilization	stabilization	moderate	Balance recovery

Table 5. Interannual changes in plant water regime and photosynthetic activity (2024–2025).

Variable	2024	2025	Trend
Transpiration rate	100% (baseline)	65–70% of 2024	↓ 30–35%
Leaf water content	1.0	1.4–2.3× higher	Increase
Chlorophyll <i>a</i>	≈6–12 (low–moderate)	≈13–21 (elevated)	Increase
Chlorophyll <i>b</i>	≈3–7 (low–moderate)	≈7–12 (elevated)	Increase
Air temperature	Higher	Lower	Decrease
Precipitation availability	Lower	Higher	Increase
Water-use strategy	Intensive	Water-saving	Regime stabilization

Analysis of Table 5 shows that in 2025 transpiration intensity in all species dropped to 65–70% of the 2024 baseline level, while leaf water content increased by 1.4–2.3 times. This indicates the formation of a more economical water-use regime and improved tissue water status. At the same time, an elevation in chlorophyll *a* and *b* content was observed, reflecting the optimisation of photosynthetic apparatus functioning and an increase in the photosynthetic potential of plants. The scatter plot (X-axis — transpiration intensity; Y-axis — leaf water content, %) demonstrates apparent interannual differences in plant water exchange. In 2024, higher transpiration values, combined with relatively low leaf water content, predominated, reflecting increased hydrothermal stress. In 2025, the data points shifted toward moderate transpiration and higher leaf water content, indicating stabilisation of the water regime under milder climatic conditions. Contour ellipses highlight grouping of the data by year: the ellipse for 2024 is characterised by high transpiration and reduced leaf water supply, whereas the ellipse for 2025 reflects a shift of the physiological “centre” toward a water-saving water-use strategy. In 2024, a

wide range of transpiration values (≈ 180 – 280 relative units) and high variability in leaf water content (≈ 28 – 62%) were observed, typical of stressful growing conditions. *C. ambigua* and *L. tatarica* exhibited high transpiration rates and relatively low leaf water content, suggesting a less efficient water-use strategy. In contrast, *H. rhamnoides* and *R. canina* exhibited a more balanced ratio of these parameters. In 2025, the distribution of data shifted toward moderate transpiration (≈ 160 – 225 relative units) and higher, more clustered leaf water content values (≈ 55 – 67%), indicating more favourable hydrothermal conditions and increased stability of water exchange.

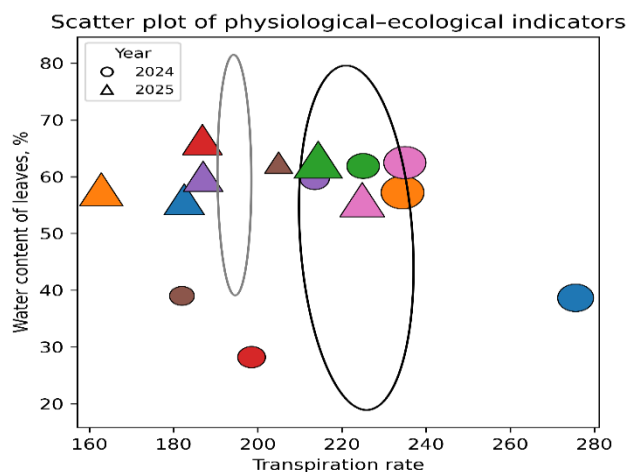


Fig. 1. Interannual dynamics of the water regime of woody and shrub species (2024–2025). Marker shape indicates the year (circle — 2024; triangle — 2025), while colour denotes species identity (blue — *Crataegus ambigua*; orange — *C. sanguinea*; green — *Hippophae rhamnoides*; red — *Lonicera tatarica*; purple — *L. altaica*; brown — *Ribes aureum*; pink — *R. canina*). Grouping ellipses illustrates the transition from an intensive to a water-saving water-use strategy.

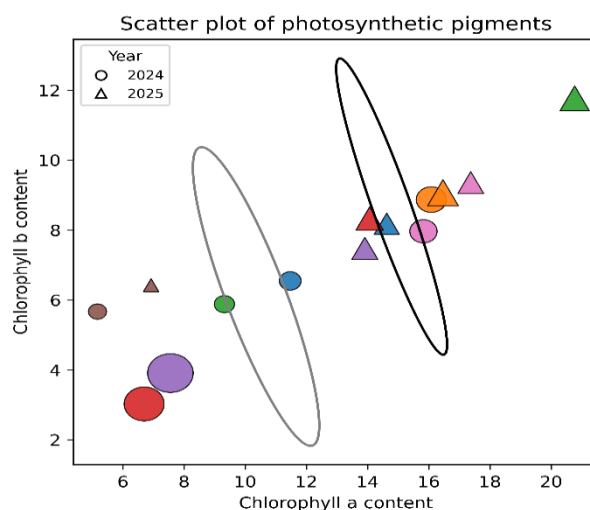


Fig. 2. Interannual dynamics of the pigment complex (2024–2025). Marker shape indicates the year of observation (circle — 2024; triangle — 2025), while marker colour denotes species identity (blue — *Crataegus ambigua*; orange — *Crataegus sanguinea*; green — *Hippophae rhamnoides*; red — *Lonicera tatarica*; purple — *Lonicera altaica*; brown — *Ribes aureum*; pink — *Rosa canina*). Ellipses represent interannual variability of the pigment composition and depict the dispersion of observations for each year; marker size is proportional to carotenoid content.

The diagram showing the relationship between chlorophylls *a* and *b* (marker size proportional to carotenoid content) reflects restructuring of the photosynthetic apparatus in response to changes in hydrothermal conditions. In 2024, chlorophyll *a* content ranged mainly between ≈ 6 – 12 relative units, while chlorophyll *b* ranged between ≈ 3 – 7 relative units; for several species, reduced chlorophyll concentrations combined with relatively high carotenoid levels indicated activation of photoprotective mechanisms under physiological stress. In 2025, the distribution shifted toward higher chlorophyll concentrations ($a \approx 13$ – 21 relative units; $b \approx 7$ – 12 relative units) with a simultaneous decrease in the relative proportion of carotenoids, reflecting optimisation and stabilisation of the photosynthetic apparatus under more favourable hydrothermal conditions. Species-specific differences highlight the diversity of adaptive strategies: *C. sanguinea*, *H. rhamnoides*, and *R. canina* are characterised by high

photosynthetic potential; *L. tatarica* and *R. aureum* exhibit more stress-oriented responses; whereas *C. ambigua* and *L. altaica* demonstrate pronounced plasticity of the pigment apparatus. Marker size, proportional to chlorophyll *a* content, indicates differences in photosynthetic intensity: larger markers correspond to species with higher photosynthetic activity. In contrast, smaller ones reflect a more conservative, adaptive mode of photosynthesis. Overall, comparisons of 2024 and 2025 data revealed marked differences in plant physiological status, driven by contrasting hydrothermal conditions during the growing seasons. In 2024, characterised by higher temperatures and moisture deficit, plants showed increased transpiration, reduced leaf water content, elevated carotenoid levels, and relatively lower chlorophyll concentrations. In contrast, under the more favourable moisture conditions of 2025, a decrease in transpiration activity, restoration of water balance, an increase in chlorophyll *a* and *b* contents, and a reduction in the proportion of carotenoids were observed, indicating stabilisation of plant physiological functioning.

Correlation and cluster analysis

Under the arid conditions of Mangystau, the plant water regime is a key factor determining viability, productivity, and adaptive potential under a variable hydrothermal background. Identifying interspecific differences in water-use strategies requires a comprehensive statistical analysis of plant physiological traits in combination with environmental climatic parameters. The application of multivariate statistical approaches—including correlation analysis, principal component analysis (PCA), and cluster analysis—permits identification of the main ecological gradients and types of adaptive physiological responses, as well as assessment of plant physiological stability under arid climate conditions.

Correlation analysis

The correlation analysis revealed stable and statistically significant relationships between physiological and climatic variables (Table 6), reflecting key mechanisms of plant adaptation to arid environments.

Table 6. Pearson correlation matrix (*r*, *p*) between physiological and climatic variables (*n* — pooled data for 2024–2025).

Variables	Transpiration	Leaf water content	Chlorophyll <i>a</i>	Chlorophyll <i>b</i>	Carotenoids	Air temperature	Air humidity
Transpiration	1.00	−0.23 (<i>p</i> <0.05)	−0.02 (<i>p</i> >0.05)	−0.66 (<i>p</i> <0.01)	−0.10 (<i>p</i> >0.05)	0.42 (<i>p</i> <0.01)	0.42 (<i>p</i> <0.05)
Leaf water content		1.00	0.48 (<i>p</i> <0.01)	0.50 (<i>p</i> <0.01)	−0.14 (<i>p</i> >0.05)	−0.68 (<i>p</i> <0.01)	−0.68 (<i>p</i> <0.01)
Chlorophyll <i>a</i>			1.00	0.40 (<i>p</i> <0.01)	0.11 (<i>p</i> >0.05)	−0.03 (<i>p</i> >0.05)	0.25 (<i>p</i> >0.05)
Chlorophyll <i>b</i>				1.00	−0.33 (<i>p</i> <0.05)	−0.65 (<i>p</i> <0.01)	−0.03 (<i>p</i> >0.05)
Carotenoids					1.00	0.62 (<i>p</i> <0.01)	−0.65 (<i>p</i> <0.01)
Air temperature						1.00	0.62 (<i>p</i> <0.01)
Air humidity							1.00

Note: *r* — Pearson correlation coefficient; *p* — significance level.

Relationships between transpiration, water status, and climate. Transpiration rate showed a moderate positive correlation with air temperature ($r \approx 0.40$ – 0.60), indicating enhanced evaporative processes under increased thermal load. At the same time, transpiration was negatively correlated with leaf water content ($r \approx -0.20$ to -0.35), reflecting increasing water losses as internal tissue water reserves decline. The relationship between transpiration and precipitation was weak to moderate and generally manifested with a temporal lag.

Photosynthetic pigments and water regime. Chlorophyll *a* and *b* contents were characterised by a stable positive correlation ($r \approx 0.40$ – 0.55), indicating coordinated regulation of the pigment apparatus. A significant positive relationship was found between chlorophyll content and leaf water content ($r \approx 0.45$ – 0.60), most pronounced in *C. sanguinea* and *R. canina*, suggesting that photosynthetic activity depends on tissue water availability. In contrast, chlorophyll content, especially chlorophyll *b*, showed a predominantly negative correlation with air temperature (up to $r = -0.65$), reflecting high sensitivity to thermal stress.

Carotenoids as indicators of stress adaptation. Carotenoid content exhibited a pronounced positive correlation with air temperature ($r \approx 0.55$ – 0.65), confirming their key role in photoprotection under elevated temperatures.

Relationships between carotenoids and chlorophylls were weak or negative, indicating a redistribution of the pigment pool toward protective components under stress conditions.

Overall, these correlations underscore the decisive roles of temperature and water availability in shaping plants' physiological and biochemical states and reflect species-specific mechanisms of adaptation to aridity.

Qualitative interpretation of interspecific differences

A qualitative assessment of correlation patterns (Table 7) revealed marked interspecific differences in the regulation of water exchange and photosynthetic activity.

Table 7. Correlation relationships between plant physiological traits and climatic factors (qualitative assessment)

Plant species	Temperature ↔ chlorophylls (a, b)	Temperature ↔ carotenoids	Temperature ↔ transpiration	Leaf water content ↔ pigments	Ecological interpretation
<i>Crataegus ambigua</i>	Negative (—)	Weak / not pronounced	Positive (+)	Weak	High sensitivity of the photosynthetic apparatus to thermal stress
<i>Crataegus sanguinea</i>	Weak/stable	Weak	Moderate (+)	Positive (++)	Mesophytic strategy: optimal coupling of water regime and photosynthesis
<i>Hippophae rhamnoides</i>	Weak	Positive (++)	Positive (++)	Moderate (+)	High ecological plasticity; enhanced activation of photoprotective mechanisms
<i>Lonicera tatarica</i>	Variable	Moderate (+)	Variable	Variable	Flexible adaptation to temperature and moisture fluctuations
<i>Lonicera altaica</i>	Variable	Moderate (+)	Variable	Variable	High physiological plasticity
<i>Ribes aureum</i>	Weak/negative (—)	Low	Moderate	Weak	Water-saving strategy; reduced pigment activity
<i>Rosa canina</i>	Stable	Moderate (+)	Moderate (+)	Positive (++)	Stable mesophytic strategy

Legend:
 ++ — strong positive correlation;
 + — moderate positive correlation;
 — — moderate negative correlation;
 — — strong negative correlation;
 Variable — high interannual and intraspecific variability.

C. ambigua showed the strongest negative relationship between air temperature and chlorophyll content, indicating high sensitivity of the photosynthetic apparatus to thermal stress. *C. sanguinea* and *R. canina* demonstrated stable positive relationships between leaf water content and pigment levels, consistent with a mesophytic adaptive strategy. *H. rhamnoides* showed higher transpiration activity and increased carotenoid accumulation with rising temperature, indicating high ecological plasticity and an enhanced capacity to activate photoprotective mechanisms. Species of the genus *Lonicera* (*L. tatarica*, *L. altaica*) exhibited high variability of physiological traits, suggesting flexible adaptation to fluctuations in temperature and moisture. *R. aureum* displayed a more conservative, water-saving strategy with relatively low pigment activity. Correlation analysis demonstrated that air humidity substantially modulates plant water status and pigment composition under arid conditions. A moderate positive relationship with transpiration ($r = 0.42$) and a strong negative relationship with leaf water content ($r = -0.68$) indicate internal water redistribution associated with increased evaporative flux. Concurrently, a decrease in carotenoid content under higher humidity reflects a reduction in photoprotective demand and a shift toward more efficient photosynthetic function.

Multivariate statistical analysis of plant physiological resilience

Principal component analysis (PCA)

Principal component analysis identified two major components that together explained 65.9% of the total variance in physiological and climatic variables. The contribution of the first principal component (PC1) was 35.3%, while the second component (PC2) accounted for 30.6% of the variance (Fig. 3).

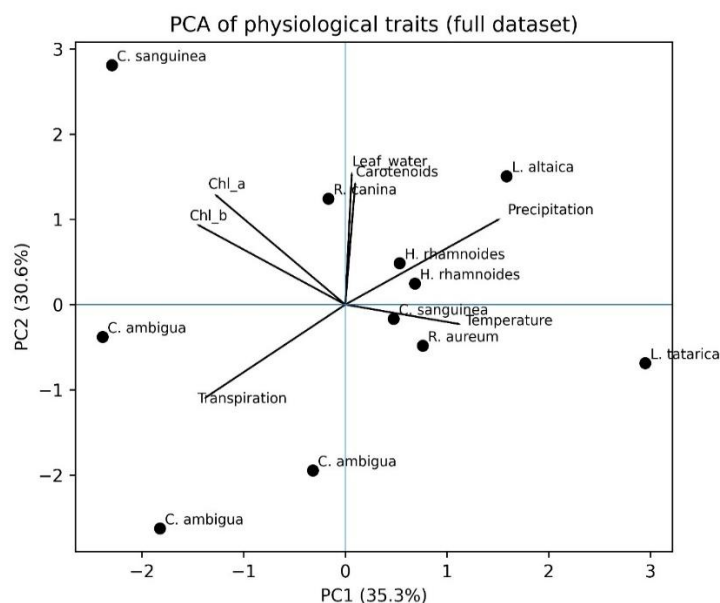


Fig. 3. Principal component analysis (PCA) of physiological traits of fruit and berry plants cultivated *ex situ* under arid conditions of Mangystau.

Table 8. Presenting the factor loadings of physiological and climatic variables on the first two principal components.

Variable	PC1	PC2	Functional meaning
Transpiration rate	0.72	-0.18	Evaporative response to thermal stress
Leaf water content	-0.81	0.22	Plant hydration status
Chlorophyll a	-0.48	0.67	Photosynthetic efficiency
Chlorophyll b	-0.65	0.58	Photosystem II functioning
Carotenoids	0.69	-0.31	Photoprotective mechanisms
Air temperature	0.78	-0.12	Climatic stress factor
Precipitation	-0.36	0.19	Moisture availability

Note: Variables with loadings $\geq |0.6|$ were considered to have a substantial contribution to the corresponding principal component.

The first principal component (PC1) represents a hydrothermal gradient associated with thermal and evaporative stress. The most substantial positive loadings were observed for air temperature (0.78), transpiration rate (0.72), and carotenoid content (0.69), while leaf water content showed a strong negative loading (-0.81). Thus, positive PC1 scores indicate species functioning under elevated temperatures with enhanced photoprotective activity, whereas negative scores indicate a more favourable water regime and reduced stress intensity. Pigment-related physiological traits mainly determine the second principal component (PC2). High positive loadings of chlorophyll *a* (0.67) and chlorophyll *b* (0.58) reflect the functional state and efficiency of the photosynthetic apparatus. Positive PC2 values characterise species with stable leaf hydration and high photosynthetic performance. Species ordination in the PCA space revealed clear differentiation of physiological strategies. *L. tatarica* and *L. altaica* were positioned in the positive PC1 region, indicating active involvement of photoprotective mechanisms. *H. rhamnoides* occupied a central position, reflecting a balanced water-use strategy and high ecological plasticity. Representatives of the genus *Crataegus*, especially *C. ambigua*, showed greater dispersion in scores, indicating high variability in physiological responses across environmental conditions. Species of the genera *Ribes* and *Rosa* occupied intermediate positions, combining moderate transpiration activity with adaptive restructuring of the pigment system. Analysis of variable vectors confirmed these patterns: the transpiration vector was oriented in the opposite direction to the leaf water content vector, indicating a negative relationship between evaporative intensity and tissue hydration. Vectors of chlorophyll *a* and *b* were co-directed, reflecting coordinated regulation of the photosynthetic apparatus. In contrast, carotenoids were aligned with the temperature gradient, highlighting their key role in photoprotection under thermal stress.

Cluster analysis and ranking of species by physiological resilience

Hierarchical clustering identified three stable clusters reflecting different levels and types of adaptive capacity (Fig. 4).

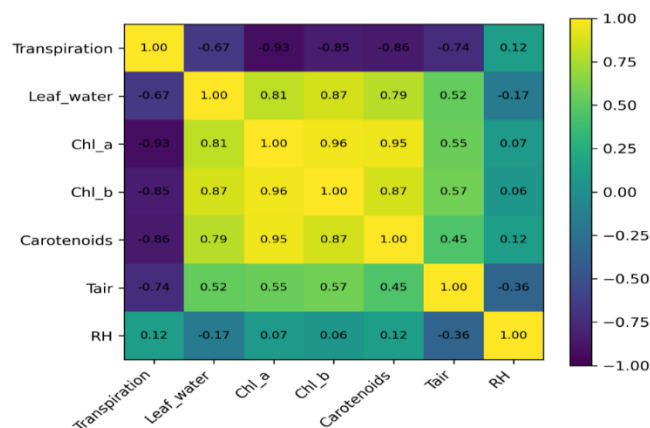


Fig. 4. Dendrogram of physiological resilience of fruit and berry plants under arid conditions of Mangystau.

The identified clusters correspond to: Stress-adaptive cluster — species with high transpiration rates and active accumulation of carotenoids; Hydration-stable cluster — species maintaining stable leaf water content and relatively constant chlorophyll levels; Intermediate (plastic) cluster — species with high physiological plasticity. The resulting cluster structure closely agrees with the PCA results and confirms the existence of contrasting physiological water-use strategies.

Integral indices of physiological resilience

Calculation of the integral indices PSI and WBI enabled quantitative assessment of interspecific and interannual differences in physiological resilience. In 2025, most species showed higher values of both indices, indicating improved leaf water retention and optimised photosynthetic apparatus under more favourable hydrothermal conditions (Table 9).

Table 9. Physiological resilience indices (PSI and WBI) of fruit and berry plants cultivated *ex situ* under arid conditions of Mangystau (2024–2025).

Species	Year	PSI	WBI
<i>Crataegus ambigua</i>	2024	4.87	0.14
	2025	4.67	0.30
<i>Crataegus sanguinea</i>	2024	3.48	0.24
	2025	5.05	0.36
<i>Hippophae rhamnoides</i>	(2024)	4.66	0.27
	2025	5.34	0.29
<i>Lonicera altaica</i>	2024	0.89	0.28
	2025	5.34	0.33
<i>Lonicera tatarica</i>	2024	0.93	0.14
	2025	4.93	0.36
<i>Ribes aureum</i>	2024	5.69	0.22
	2025	5.55	0.30
<i>Rosa canina</i>	2024	5.40	0.26
	2025	6.37	0.25

Definitions: $PSI = (Chl\ a + Chl\ b) / Car$ — photosynthetic stability index; $WBI = Leaf\ water\ content / Transpiration\ rate$ — water balance index.

Based on the integrated results of PCA, cluster analysis, and integral indices, the species were conditionally ranked according to their level of physiological resilience as follows: high resilience — *H. rhamnoides*, *R. canina*; moderate resilience — *C. ambigua*, *C. sanguinea*, *L. tatarica*; relatively low resilience.

DISCUSSION

Under the arid conditions of Mangystau, the water regime and the functional state of the photosynthetic apparatus represent key indicators of the physiological resilience of fruit and berry plants and largely determine their adaptive potential under *ex situ* cultivation. Numerous studies have demonstrated that under conditions of high temperature and limited water availability, the ability of plants to regulate transpiration, maintain leaf hydration, and preserve photosynthetic functionality becomes a critical factor for survival and productivity (Chaves *et al.*

2003). The results obtained in the present study confirm this concept and indicate that the resilience of introduced species in Mangystau is shaped by coordinated regulation of transpiration intensity, leaf water content, and the pigment apparatus, all of which exhibit pronounced seasonal and interannual variability in response to fluctuations in temperature and moisture availability. A key outcome of this study is the identification of a directed shift in physiological adaptive responses from an intensive evaporative mode to a water-saving mode of functioning under improved temperature–moisture conditions. The reduction in transpiration activity accompanied by an increase in leaf water content observed in 2025 in most of the studied species reflects not a decline in physiological activity, but rather an elevation in hydraulic efficiency and optimisation of water exchange. Similar responses have been described for drought-tolerant woody plants and xeromesophytes, in which reduced transpiration is associated with enhanced water-use efficiency and maintenance of photosynthetic capacity (Lambers *et al.* 2008). In contrast to previously reported mainly qualitative observations, the present study provides quantitative confirmation of this adaptive mechanism in introduced fruit and berry plants in Mangystau using correlation analysis, PCA, and clustering. The pigment apparatus was closely linked to tissue water status. The positive correlations between chlorophyll *a* and *b* contents and leaf water content, together with their negative relationships with air temperature, confirm that the stability of the photosynthetic system directly depends on the hydration state of leaf tissues. This relationship is well documented in studies showing that dehydration and thermal stress lead to chlorophyll degradation and impairment of photosystem II activity (Demmig-Adams & Adams 2006). Chlorophyll *b* proved to be the most sensitive pigment to thermal stress, which is consistent with its functional role in light-harvesting complexes and its vulnerability under conditions of excessive radiation and high temperature. At the same time, the increase in chlorophyll concentrations in 2025, observed against the background of reduced transpiration, indicates a compensatory reorganisation of the photosynthetic apparatus aimed at maintaining carbon assimilation under water-saving conditions, a strategy typical of stress-resilient plants (Taiz *et al.* 2015). Carotenoids emerged as reliable indicators of stress-adaptive responses. Their positive correlation with air temperature and negative relationships with air humidity and leaf water content reflect the activation of photoprotective mechanisms under thermal and water stress. Elevated carotenoid levels in xeromorphic and stress-tolerant species during the hotter year confirm their crucial role in dissipating excess excitation energy and protecting photosystems from photooxidative damage (Salmurzauly *et al.* 2024). Conversely, a reduction in the relative contribution of carotenoids under more favourable conditions suggests a reallocation of metabolic resources toward enhanced photosynthetic productivity rather than stress defence. Multivariate analysis revealed two fundamental physiological gradients of adaptation: a hydrothermal stress gradient and a pigment–photosynthetic gradient. Their relative orthogonality highlights the partial independence of water-regulation and photosynthetic-regulation mechanisms, which together ensure high plasticity of adaptive responses in arid environments. Species clustering based on integrated physiological traits identified three stable adaptive types—stress-adaptive, hydration-stable, and plastic—supporting the concept of a continuum of water-use strategies rather than discrete adaptive categories, as previously proposed for woody plants in arid and semi-arid ecosystems (Legendre & Legendre 2012). The study's practical relevance is underscored by its integrated assessment of physiological resilience using the PSI and WBI indices. Their concordant dynamics demonstrate that plant resilience under arid conditions is determined not by absolute values of individual physiological traits, but by the balance between water-retention capacity and photosynthetic efficiency. The revealed interspecific and interannual differences indicate that in 2025, most species adopted stronger water-saving strategies, as reflected by higher WBI values. The highest PSI values observed in *Rosa canina*, *Ribes aureum*, and *Hippophae rhamnoides* indicate a high stability of their photosynthetic apparatus under arid conditions, whereas species of the genus *Lonicera* exhibited a more pronounced photoprotective strategy characterised by increased carotenoid content. Overall, the results expand the current understanding of the physiological mechanisms underlying the adaptation of fruit and berry plants to *ex situ* cultivation in extremely arid environments. The integration of classical physiological measurements with modern multivariate statistical approaches proved effective for identifying adaptive strategies and resilience patterns. The revealed regularities can be applied to predict the performance of introduced species, optimise species selection for introduction and landscaping, and develop scientifically grounded programs for urban greening, horticulture, and sustainable plant production in the arid regions of Kazakhstan.

CONCLUSION

The present study provides a comprehensive physiological assessment of fruit and berry plants cultivated *ex situ* under the extremely arid conditions of Mangystau. Based on integrated analyses of the plant water regime,

transpiration intensity, photosynthetic pigment composition, and multivariate statistical approaches, clear patterns of physiological adaptation and resilience were identified across species and growing seasons. The results demonstrate that the physiological stability of introduced plants in Mangystau is primarily determined by coordinated regulation of transpiration, maintenance of leaf water content, and restructuring of the photosynthetic pigment apparatus. Interannual comparisons revealed a pronounced shift from an intensive to a water-saving water-use strategy in 2025, characterised by a 30–35% reduction in transpiration intensity, a 1.4–2.3-fold increase in leaf water content, and elevated concentrations of chlorophylls *a* and *b*. These changes reflect enhanced hydraulic stabilisation and optimisation of photosynthetic functioning under more favourable hydrothermal conditions. Correlation analysis confirmed the key role of leaf water content as a central indicator of physiological resilience, showing significant positive relationships with chlorophyll content and negative relationships with air temperature. Carotenoids were identified as reliable markers of stress adaptation, increasing under thermal and water stress and decreasing under improved moisture conditions, thereby reflecting the balance between photoprotective mechanisms and photosynthetic productivity. Multivariate analyses (PCA and hierarchical clustering) revealed two principal physiological gradients—hydrothermal stress and pigment–photosynthetic regulation—and enabled the classification of species into three adaptive types: hydration-stable, stress-adaptive, and physiologically plastic. This classification supports the concept of a continuum of water-use strategies rather than discrete adaptive categories in woody and shrub plants under arid conditions. Integrated physiological resilience indices (PSI and WBI) provided a quantitative evaluation of adaptive capacity and confirmed pronounced interspecific differences. *Hippophae rhamnoides* and *Rosa canina* exhibited the highest overall physiological resilience, combining stable water balance with high photosynthetic stability. *Crataegus sanguinea* and *Lonicera tatarica* showed moderate resilience, while *Crataegus ambigua* and *Lonicera altaica* were characterised by greater sensitivity to thermal and hydrothermal stress, as evidenced by greater variability in water regime and pigment parameters. Overall, the study expands current understanding of the physiological mechanisms underlying the adaptation of fruit and berry plants under *ex situ* cultivation in extremely arid environments. The integration of classical physiological methods with modern statistical analyses proved effective for identifying adaptive strategies and predicting plant resilience. The obtained results provide a scientific basis for optimising species selection for plant introduction, landscaping, phytomelioration, and sustainable horticulture in the arid regions of Mangystau and Western Kazakhstan.

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Conflict of Interest

There is no conflict of interest.

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