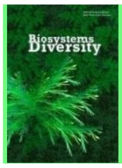

Biosystems
Diversity

ISSN 2519-8513 (Print)
ISSN 2520-2529 (Online)
Biosyst. Divers.

Ecological differentiation of *Viburnum* species according to their resistance to hydrothermal stress using water regime indicators

M. I. Hudimov*, **, I. O. Zaitseva*

**Oles Honchar Dnipro National University, Dnipro, Ukraine*
***South-Eastern Interregional Centre of the State Institution 'Institute of Soil Protection of Ukraine', Dnipro Region, Ukraine*

Article info

Received 11.01.2026
Received in revised form 06.02.2026
Accepted 09.03.2026

Oles Honchar Dnipro National University,
Nauky Av., 72, Dnipro,
49045,Ukraine.
Tel.: +38-067-437-02-76.
E-mail:
irinza.ldfr@gmail.com

South-Eastern Interregional Centre of the State Institution 'Institute of Soil Protection of Ukraine',
Naukova st., 65A,
Doslidne Settlement,
Dnipro Region, 52071,
Ukraine.
Tel.: +38-098-562-98-46.
E-mail:
ngudimov99@gmail.com

Hudimov, M. I., & Zaitseva, I. O. (2026). Ecological differentiation of Viburnum species according to their resistance to hydrothermal stress using water regime indicators. Biosystems Diversity, 34(1), e2605. doi:10.15421/012605

Intensified aridization of climate and increase in the frequency of extreme weather events actualize the problem of studying the adaptive strategies of introduced woody plants to ensure stability of the cultivated phytocenoses. The paper presents a comparative analysis of the physiological stability of 12 taxa of the *Viburnum* L. genus in the conditions of the Steppe Dnipro region during the growing season with the contrast moisture regime. We established the main directions of phenotypic modifications contributing to realization of the adaptive potential of species in the drought conditions – increased signs of xeromorphism of the leaf morphostructure (*V. lantana*, *V. carlesii*, *V. rhytidophyllum*, *V. ×juddii*), physiological mechanisms of increase in water-holding capacity of the tissues (*V. trilobum*, *V. ×bodnantense*, *V. prunifolium*, *V. opulus*), and complex effect of these reactions (*V. plicatum*, *V. lentago*, *V. farreri*, *V. farreri* 'fragrans'). Dynamics of the physiological state of plants was assessed based on the monitoring of the set of water regime parameters using the multivariate statistical analysis (hierarchical clustering with the Ward's method). Results of the study demonstrate a clear differentiation of species according to strategies of their adaptation to hydrothermal stress. Analysis of dendrograms allowed us to identify four stable cluster groups maintaining structural integrity under conditions of moderate moisture and to find "free elements" characterized by chaotic physiological response. The peak drought load in July was observed to destabilize the cluster structure, resulting in the separation of moderately resistant species (in particular, *V. lantana*) from the formed groups. Based on the assessment of the stability of interspecific relationships, the taxa under study are differentiated into three categories: resistant, moderately resistant, and nonresistant. Regarding the formation of resistance, the determining role of ecological and geographical origin in this process was revealed: Taxa of North American (*V. prunifolium*, *V. lentago*) and European origin, evolutionarily adapted to the continental climate, demonstrated the highest adaptive potential. By contrast, the representatives of the East Asian flora (*V. carlesii*, *V. farreri*), being the typical mesophytes of the monsoon climate, showed the lowest drought tolerance. Partial regrouping of the studied taxa under the influence of peak loads is a consequence of sufficiently long period of introduction of these species in the conditions of steppe zone, in the area with unstable moisture. As a result, morphophysiological features of the plants under study are transformed. The proposed methodological approach and established ecological differentiation of mesophytic species in the xerothermic conditions allow us to predict the success of introduction and scientifically justify the selection of a sustainable assortment of ornamental shrubs for regions with risky hydrothermal regime.

Keywords: hydrothermal stress; drought tolerance; *Viburnum*; adaptive strategies; plant introduction, hierarchical clustering.

Introduction

Hydrothermal stress (combined effect of moisture deficit and high temperatures) is recognized as one of the key abiotic factors limiting the growth, development and productivity of plants worldwide (Ortiz et al., 2021; Vale et al., 2021). It is important to emphasize the synergic effect of these two stressors: Their combined negative effect on the plant physiology is often much stronger than a sum of individual effects (Zandalinas et al., 2018). In the conditions of global climate change, characterized by increase in average annual temperatures, as well as frequency and intensity of extreme weather events, such as prolonged droughts and heat waves, study of the impact of this phenomenon on the biosystems becomes especially relevant (Seneviratne, 2021; IPCC, 2023). Forecasts of climatologists indicate the further expansion of arid and semiarid zones, where climatic accidents weaken the soil structure, damage the nutrient cycling and alter plant growth, posing a threat to stability of both natural ecosystems and artificial biocenoses (Weed et al., 2013; Didukh et al., 2016; Zia et al., 2021). Today there is an urgent need for development of the integrated strategies aimed at mitigation of and adaptation to climate change, including implementation of climate-resilient crop practices and technologies of the urban green infrastructure (Abbass et al., 2022; Wang et al., 2023; Oishy et al., 2025).

In the soil and climatic conditions of areas with unstable moisture, tree and shrub vegetation is found only in the local intrazonal ecotopes, and it has a limited species composition. Meanwhile, in the warming conditions, the risks of loss of local species biodiversity increase (Manes et al., 2021; Pokhrel et al., 2025). In this regard, the species introduced from different botanical and geographical regions are taken for the creation of various plantations (for decorative, protective, reclamation purposes, etc.). In particular, according to Ivanko et al. (2025), taxonomic diversity of trees and shrubs in a university campus located in the steppe zone of Ukraine included 75.2% of introduced species. Enrichment of species diversity in areas of unstable moisture can be considered as a strategy for adapting green infrastructure to climate change (De la Sota et al., 2019). However, it faces certain difficulties, including the problem of ecological stability of plants and their adaptation to a set of xerothermic factors of the growing season (Rana & Varshney, 2023).

At the physiological level, the plant response to hydrothermal stress is a complex process involving a cascade of rapid and long-term adaptive responses (Yang et al., 2021). The primary and fastest response to moisture deficit is the closure of stomata, which is a critical mechanism for reducing transpirational water loss. Unfortunately, this protective action has negative consequences: It limits the diffusion of CO_2 to photosynthetic centers in the leaf, which inevitably leads to a decrease in the intensity of photosynthesis and carbon assimilation (Chaves et al., 2009). For maintaining the cell turgor and protecting macromolecules under conditions of dehydration, plants also accumulate compatible osmolytes, in particular, proline amino acid, which acts as an osmoprotector (Szabados & Savouré, 2010). Higher temperatures, in turn, cause direct damage to the cell structures. The protein apparatus of photosystem II is particularly sensitive to heat stress, which can lead to its degradation and disruption of the electron transport chain, increasing the overall inhibition of the processes of growth and biomass accumulation (Allakhverdiev et al., 2008). At the molecular level, plants respond to heat by synthesis of heat shock proteins (HSPs), which prevent denaturation of proteins and promote their restoration (Wang et al., 2004). The most of studied HSP genes of the cultivated plants take part in the protective response to drought, changing the expression level depending on the growing conditions (Slishchuk, 2025). Despite these protective mechanisms, synergic effect of stressors often provokes an imbalance, resulting in excessive accumulation of the reactive oxygen species and development of large-scale oxidative stress, which damages the cellular components (Apel & Hirt, 2004). Therefore, understanding of the complex mechanisms of drought tolerance is a fundamental task of modern biology and ecology.

Drought tolerance of plants is determined by the peculiarities of their physiological and biochemical reactions aimed at maintaining the cell viability under conditions of dehydration, or enhancing water-retaining properties of cells. Water loss is also minimized through morphoanatomical adaptations that enhance the xerophytic features of the leaf morphostructure (Bai et al., 2019), associated with an increase in the relative number of mechanical elements of conductive and parenchymal tissues, the number of stomata and the network of veins per unit area of the leaf (Hughes et al., 2017), development of integumentary tissue and its surface formations, and mesophyll cells' densification (Picotte et al., 2008; Leshcheniuk & Chipilyak, 2020), which leads to increase in the specific weight of a leaf and changes in the relationships between the quantitative water content and structural elements of the plant tissues (Zaitseva, 2018). These characteristics allow assessing the general functional state of plant assimilation organs under xerothermic conditions. For this purpose, they were used in our study.

Despite a significant number of studies addressing the response of individual plant species to abiotic stresses, including the plants of the cultivated dendroflora under drought conditions (Chartzoulakis et al., 2002; Zhang et al., 2017; Yang et al., 2018; Jafari et al., 2019; Khalegh et al., 2019; Bhusal et al., 2020), comparative analysis of resistance within a large genus remains a priority. The studies above are critical for understanding the evolution of adaptive traits and for predicting the responses of related species to future climate change (Valladares et al., 2014).

Increase in the polymorphism of morphophysiological characteristics of plants under stressful conditions results in the appearance of a large variety of phenotypic forms as different variants of the genotype realization (Crispo et al., 2009; Kordyum & Dubyna, 2019). Phenotypic polymorphism of the related species, which has a genetic nature, is manifested in the parallel signs of genotypic variability (Ghalambor et al., 2007). In this regard, studies of the functional state of phylogenetically related species of introduced species (representatives of generic complexes or taxa of a higher rank) are particularly relevant and practically valuable. Based on the biogenetic law, it allows to determine the degree of resistance and directions of the adaptive restructuring, which are conditioned by the similar genotypic basis of species involved in the introduction process (Rueda et al., 2017). This approach is feasible primarily for the taxonomic ranks at the genus level, which constitute a compound phylogenetic complex of a large number of species, differing in their botanical and geographical origin and ecological properties, for example, tree species of the *Acer* L., *Syringa* L., *Juniperus* L., *Salix* L., *Quercus* L. genera (Holikova & Zaitseva, 2009, 2017; Kolodiazhenska, 2013; Horielov, 2016; Kosakivska et al., 2023). In view of this, a promising model system used in our study is *Viburnum* L. genus set, which is characterized by a complex phylogenetic structure and significant species diversity, represented in three centers of speciation (East Asian, Mediterranean and Atlantic-North American centers) in the temperate and subtropical climatic zones (Demchenko, 2005). *Viburnum* species introduced to Ukraine are characterized by a wide amplitude of ecological properties in relation to hydrothermal conditions of the natural growth areas, with a predominance of mesophilic forms (Kokhno et al., 2005).

For any plant species or population, the study of responses to the environmental changes requires an understanding of the phenotypic variations in individual plants caused by external factors (Nicotra et al., 2010), which represent species of the cultivated dendroflora in the points of introduction, in particular, in the botanical collections, and are involved in the introduction studies. In this study of plant responses to the arid conditions, we used plant specimens representing the *Viburnum* L. genus from the dendrological collection of the botanical garden.

Given the large variety and wide distribution of representatives of the *Viburnum* L. genus in the areas with different conditions, their physiological response to hydrothermal stress cannot be considered universal. On the contrary, it will demonstrate a clear interspecific differentiation, which can be formalized by multivariate statistical methods. Studying the variations in the physiological responses allows us to identify the subtle evolutionary strategies and mechanisms, determining different degrees of resistance even in closely related species, which may demonstrate unexpectedly different adaptive capabilities (Ackerly, 2004). The adaptive potential of introduced species should be determined by the climatic conditions of their natural range, where species from the continental regions have an advantage over species growing in the climate of monsoon type. In this context, representatives of the *Viburnum* L. genus are considered a convenient model group. This genus includes numerous species originating from different climatic zones, but introduced and grown under the same conditions of the botanical collection. This approach, using the "common garden" concept is a powerful tool, which provides a valid comparison of genetically determined adaptive responses of species, minimizing the influence of microclimatic and soil differences (Clausen, Keck & Hiesey, 1940; Donoghue et al., 2004). For a comprehensive assessment of the related species' adaptive potential, it is appropriate to use statistical processing methods that allow considering the indicators of a number of physiological characteristics at once and making interspecific comparison. One of such methods is cluster analysis, which takes into account unlimited number of physiological indicators and presents the results in a graphical form of dendrograms, thus allowing us to compare the degree of similarity of objects according to the given indicators. Based on cluster analysis of the phenotypic variations, changes in the relationship between the traits are determined and the best genotypes resistant to water stress and salinity are selected (Leonov, 2013; Pereira et al., 2015; Nejat & Sadeghi, 2016).

Thus, to test the presented hypotheses, this paper aims to provide a comprehensive assessment of the resistance of viburnum shrubs (*Viburnum* L.) to moisture deficit. This objective was achieved through solving the problems related to analysis of the dynamics of key indicators of the plant water exchange, taking into account the temperature and moisture regimes, the determination of the specificity of the most characteristic reactions of sensitive and resistant species, their ecological differentiation by the degree of similarity of physiological reactions using cluster analysis and the development of a hierarchical structure of the studied complex of related species by the level of their resistance to hydrothermal stress.

Materials and methods

The research was conducted on the basis of the dendrological collection of the botanical garden of Oles Honchar Dnipro National University (DNU), located in Dnipro city, Ukraine (48°26′ N, 35°03′ E) in the temperate continental climate zone. The research area is characterized by hot dry summers, creating a natural background for studying plant responses to hydrothermal stress.

The collection of species of the *Viburnum* genus is located in the sector of flowering shrub plants, which are not widely cultivated. The objects of research were 12 species, including two hybrid species, represented in the collection by 1-3 model specimens. The plants of generative age, without any visible signs of diseases and damage, were grown in open soil conditions in the same site with good sunlight. This approach allowed us to correctly compare the genetically determined adaptive responses of the different plant species, minimizing the influence of microclimatic and soil differences.

According to modern concepts (The Angiosperm Phylogeny Group, 2016), *Viburnum* L. genus belongs to the Adoxaceae Raf.

family of the order Dipsacales Juss. ex Bercht. & J. Presl. Studied species represent five of nine sections of the genus:

– section 1 *Thyrsosma* (Raf.) Rehd. – *V. farreri* Stearn and *V. farreri* 'fragrans' Bunge (two phenotypically distinct specimens in the habit and leaf morphology), *V.* ×*bodnantense* Aberc ex Stearn;

– section 2 *Lantana* Spach – V. carlesii Hemsl., V. lantana L., V. rhytidophyllum Hemsl., V. ×juddii Rehd.;

– section 4 *Pseudotinus* Clarke – *V. plicatum* Thunb.;

– section 5 *Lentago* DC. – *V. lentago* L. and *V. prunifolium* L.;

– section 9 *Opulus* DC. – *V. trilobum* Marsh. and *V. opulus* L.

Species of sections 1, 2, and 4 are of East Asian origin (Northeast China, Korea, Japan), species of section 5 and *V. trilobum* Marsh. (section 9) grow naturally in the Atlantic region of the North America. Species *V. lantana* L. (section 2) and *V. opulus* L. (section 9) are of the European origin, being a part of the aboriginal woody plants of the study area, i.e. the Northern Steppe of Ukraine. The taxa nomenclature is given according to the POWO international database https://powo.science.kew.org. The range of the ecological valence of the studied species complex is determined by the climatic conditions of natural ranges from the continental to monsoon climatic regions of the temperate and subtropical zones of Europe, Asia, and North America. By cenomorphic characteristics, the genus mostly comprises forest dwellers, adapted to varying degrees of mesophytic conditions. According to the types of hygromorphs, Tarasov (2012) characterizes the aboriginal species *V. lantana* L. and *V. opulus* L. as xeromesophytes.

The research was conducted during the growing season of 2025, with contrasting moisture conditions. Plant samples (leaves) were collected twice a month during the period of active growth of the vegetative organs (in the 1st and 3rd decades of May and June), and during the period of secondary growth, lignification of shoots and vegetation of mature leaves (in the 1st and 2nd decades of July and the 1st decade of September). This research design allowed covering a wide range of climatic conditions and assessing the state of model plants during their seasonal development. Simultaneously with the plant sampling, the moisture content in one-meter layer of soil of the collection site was measured.

The soil of the collection site belongs to the group of low-humic, easily washed-out chernozems, and by its granulometric composition it belongs to heavy loams, as evidenced by the content of physical clay (sum of fractions 0.005–0.010, 0.001–0.005, and <0.001 mm are 51.80% and 52.13% in soil layers). According to the grading scale, the soil of the site corresponds to soils of average quality. It is characterized by the neutral reaction of the soil solution (pH 7.4) and relatively high content of organic matter (3.24%) in the upper horizon (0–30 cm), which indicates high potential fertility (Method for agrochemical certification, 2019). According to the WRB classification (World Reference Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps), the soils of the site belong to the Calcic Chernozem (Siltic) group.

To characterize the climatic conditions, we used the meteorological data presented in Figure 1 in the form of a climatogram according to H. Walter (Zepner et al., 2021). Meteorological data for the current year (average monthly temperature and precipitation) were obtained from the archive of synoptic observations at the Dnipro station (WMO code: 34504) using the Ogimet online service, 2025 www.ogimet.com/gsynres.phtml.en, and the data of the climatic norm (1991–2020) are retrieved from the climatological archive of the Dnipro city, Climate-Data.org, 2025 https://en.climate-data.org/europe/ukraine/dnipropetrovsk-oblast/dnipropetrovsk-4039.

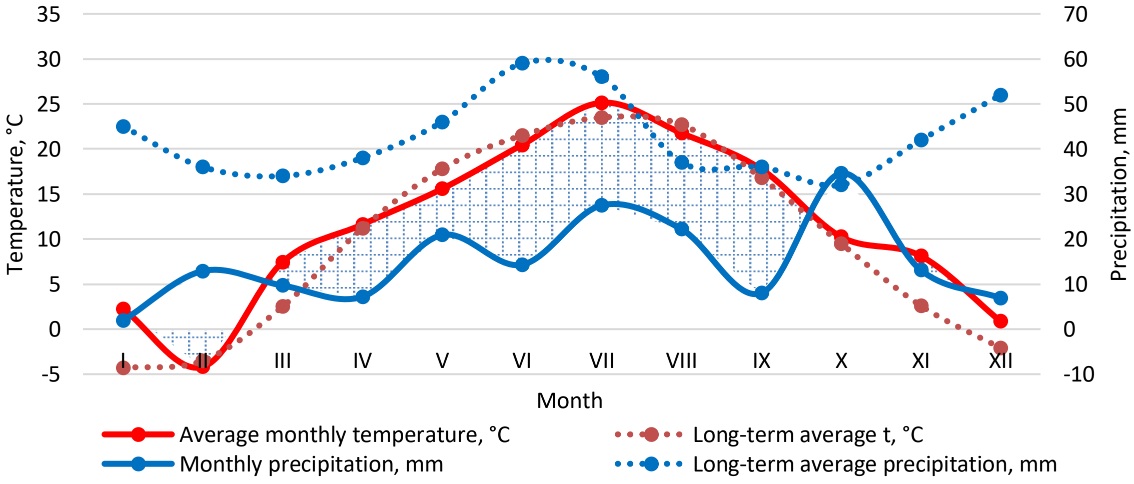

Fig. 1. Walter-Lieth climatic diagrams for Dnipro (2025), according to the Ogimet online service, 2025 www.ogimet.com/gsynres.phtml.en : the shaded area where the temperature line is above the precipitation line (in the ratio 1:2 of temperature to precipitation values on the graph) indicates the period of drought

Table 1 presents a description of the water supply status of the territory based on the coefficients calculated from the ratio of temperatures and precipitation during the research period – the hydrothermal coefficient (HTC) according to Selianinov (Method for agrochemical certification, 2019) and the climate humidity coefficient (CHC) according to Vorobyov (Kokhno & Kurdiuk, 1994) which is used to assess the prospects for the introduction of woody plants in a certain natural and climatic region. The coefficients reflect the balance between precipitation and water evaporation against the background of the temperature regime (sum of active temperatures – HTC, sum of positive temperatures – CHC), which affects the indicator of productive moisture in one-meter layer of soil (Table 1). It is one of the key indicators in crop production regarding the potential ability of soils to provide water supply in the current conditions of the growing season.

Table 1
Hydrothermal conditions of the growing season in the research area

Indicators	Months						
	IV	V	VI	VII	VIII	IX	X
Moisture content in one-meter layer of soil, mm (n = 7)	159.1 ± 6.4	141.4 ± 4.5	106.9 ± 4.6	65.2 ± 1.4	85.6 ± 2.4	90,6±2.7	not determined
Climate humidity coefficient, CHC	0.29	0.89	0.11	0.34	0.40	0.06	3.08
Hydrothermal coefficient, HTC	0.09	0.39	0.22	0.35	0.33	0.14	1.33

Note. The CHC and HTC coefficients were calculated based on the meteorological data of www.ogimet.com/gsynres.phtml.en for 2025.

The negative balance of moisture available in the soil is estimated by negative CHC values and positive values of <1. The HTC values of <0.4 are interpreted ae complying with the conditions of extremely severe drought, 0.4–0.5 – severe drought, 0.6–0.7 – moderate drought, 0.8–0.9 – mild drought. According to the coefficient values, the hydrothermal conditions during the research period are characterized as highly arid. For the research area and this type of soil, the optimal value of moisture content in one-meter layer of soil at the beginning of the growing season is 190 mm (Method for agrochemical certification, 2019), while in our studies it is 159 mm, and subsequently, the soil moisture availability decreased.

In general, the growing season was marked by increasing moisture deficit, which turned into severe drought in early July, lasting until September. It was accompanied by a decrease in the reserves of available soil moisture to critical values of hydrological constants – the breakage of capillary bonds and wilting of plants. High temperatures (exceeding the long-run annual average rate in summer months by 1.3–2.2 °C) contributed to the development of xerothermic conditions; however, the main reason for the prolonged severe drought was a significant decrease in precipitation (by 40–81%) from April to September, compared with the climatic norm.

We determined the following physiological parameters of the water regime that reflect respective features: the state of leaf tissue water saturation under current temperature and moisture conditions – total water content (WC, %); and the difference between WC and the hydration level required for the most efficient functioning of plant tissues of a given species under specific conditions – water deficit (WD, %). In addition, we determined the indicators reflecting the structural and morphological features of leaves, which allow comparing species by the degree of leaf structure xeromorphy: The area occupied by 1 g of leaf in its hydrated state at the time of sampling – surface development (SD, cm²/g); the mass of a 1 cm² leaf blade at full water saturation – degree of succulence (DS, mg/cm²), and after drying – specific leaf weight (SW, mg/cm²). Measurements were performed in six biological replicates.

To adjust the water regime indicators to a single scale, the input data for each sampling date were standardized using the z-score method. The further statistical analysis and classification of the studied species were performed using the hierarchical cluster analysis in Statistica 12 software package. Based on the standardized data, we calculated the Euclidean distance matrix, which served as a measure of difference between species. Further clustering was carried out using the agglomerative technique (the Ward's method), which minimized the variance within clusters at each step of the integration (Ward, 1963). Results of the cluster analysis were visualized in the form of dendrograms.

Results

The results of studies showed a significant variation in the morphophysiological indicators in the phases of development of the plants' vegetative organs against the background of increasing drought. In a generalized form for the season, they can be considered as species-specific ranges of the norm of reaction to water-temperature stress (Fig. 2).

However, in response to changes in the temperature and humidity, the studied species within the norm of reaction demonstrate different directions of morphophysiological responses; their degree of adaptability can be determined based on the analysis of the dynamics of the indicator values and consistency of their changes in the growing season. For example, from the beginning of the growing season (1st decade of May) to the final period of observations (1st decade of September), stress phenomena intensify in most species. It manifests in the lower total leaf water content and increased water deficit, as well as in the changes in morphophysiological indicators, expressing the weight and plane ratios of the structural component of the leaf tissues that are in the state of initial (current at the time of recording) tissue hydration (SD – surface development), maximum hydration capacity (DS – degree of succulence), or in a dehydrated state (SW – specific weight) (Fig. 3).

Total water content of the leaf tissues during the period of formation and growth of the leaf blades at the beginning of vegetation (Fig. 3b) under relatively favorable environmental conditions can serve as an indicator of the plant demand for the degree of hydration, which is sufficient to ensure the physiological processes of photosynthetic tissues. The low water content in the tissues at the initial stage of vegetation observed in *V. lentago*, *V. prunifolium*, *V. farreri*, *V. ×bodnantense*, combined with low values of water (Fig. 3a), is typical for drought-resistant species; however, only *V. lentago* and *V. prunifolium* from this group retained these features at the end of vegetation, while *V. opulus*, *V. trilobum*, *V. plicatum* developed similar features. At the end of vegetation, the indicators of relationship between the tissue hydration and water deficit changed toward critical in *V. farreri*, *V. lantana*, *V. carlesii*, and *V. ×juddii*. A decrease in water content and an increase in water deficit occured in the species with significant water deficit at the beginning of vegetation (*V. rhytidophyllum*, *V. carlesii*, *V. farreri* 'fragrans', *V. × juddii*). The critical values were exhibited by *V. carlesii* and *V. × juddii*, indicating insufficient physiological resistance of these species to drought.

Generally, all species experienced water loss and decrease in the total water content of the leaf tissues to a greater or lesser extent during the growing season. According to the dynamics of dehydration, we can distinguish high-resistant (*V. trilobum*, *V. plicatum*, *V. farreri*, *V. ×bodnantense*), moderately resistant (*V. opulus*, *V. lentago*, *V. prunifolium*, *V. rhytidophyllum*), and low-resistant (*V. lantana*, *V. carlesii*, *V. farreri* 'fragrans', *V. ×juddii*) species.

At the same time, differentiation of species by water deficit occured in the other way – during the vegetation, low water deficit was presented by *V. opulus*, *V. trilobum*, *V. prunifolium* and *V. plicatum*; and the most stressful state with high water deficit in the leaves was observed for *V. lantana*, *V. carlesii*, *V. rhytidophyllum* and *V. ×juddii*. Peculiarities of the seasonal dynamics of water loss in the leaves and water deficit are shown in Figure 4 on the example of the most typical representatives featuring high and low resistance according to these indicators.

Peculiarities of the seasonal dynamics of the indicators of surface development, degree of succulence, and specific weight of leaves are given in Figure 5 on the example of the most typical representatives of species featuring high and low resistance according to these indicators.

The highest values of development of the surface, i.e. the area of leaf surface of 1 g in a hydrated state on the current sampling date, were exhibited by the leaves of *V. lantana*, *V. plicatum*, *V. rhytidophyllum* and *V. ×juddii*, which may characterize their mesophilic structure or be a consequence of significant tissue dehydration. The opposite features of xerophytism of the leaf morphostructure may be indicated by low SD values, which are most pronounced in *V. opulus*, *V. trilobum*, *V. prunifolium* and *V. farreri* 'fragrans' (Fig. 5a). Low SD values were also characteristic of the succulent plants, with a specific path of xerothermic adaptations.

It should be noted that the values of the surface development during the vegetation were characterized by a fairly high resistance, in particular, in species showing an adaptive nature of the surface development. For example, the coefficients of variation (CV, %) of SD indicator in *V. rhytidophyllum* and *V. ×juddii* (CVSD 7.47 ± 1.98; CVSD 4.82 ± 1.98) indicate the low level of variability, whereas physiological indicators of the state of tissue hydration are characterized by significant level of variability in species, demonstrating an adaptive nature of changes in the total water content of the leaves (*V. ×bodnantense* CVWC 77.09 ± 9.66; *V. trilobum* CVWC 55.82 ± 9.89) and water deficit (*V. trilobum* CVWD 44.65 ± 9.25; *V. prunifolium* CVWD 33.38 ± 7.86). The same patterns were observed in species classified as low-resistant ones, with the characteristic manifestations of mesophilic morphophysiological signs in the dynamics of increase in the drought phenomena – insignificant variation in the surface development (*V. opulus* CVSD 10.21 ± 2.69; *V. trilobum* CVSD 11.81 ± 3.11) and medium and high levels of variation of changes in the total water content (*V. lantana* CVWC 72.38 ± 4.46; *V. ×juddii* CVWC 17.70 ± 4.95) and leaf water deficit (*V. carlesii* CVWD 25.29 ± 6.31; *V. lantana* CVWD 26.94 ± 6.65). The differentiation of species based on the degree of leaf succulence (Fig. 5b) is consistent with the peculiarities of the species distribution according to the surface development. Species characterized by low SD values have increased DS values, i.e. larger weight per unit area of a leaf in the state of maximum water saturation (*V. lantana*, *V. carlesii*, *V. rhytidophyllum*, *V.* ×*juddii*), and vice versa (*V. opulus*, *V. trilobum*, *V. prunifolium*, *V. farreri* 'fragrans'). Intermediate values are typical for *V. lentago*, *V. plicatum*, *V. farreri*, *V.* ×*bodnantense*. To identify the significance of water content in the formation of this indicator, we isolated the contribution of the leaf morphostructural components, i.e. dry weight per unit area of the leaf. In this case, the ratio of species has almost not changed, except for *V. carlesii*, in which the weight of the maximum possible water content corresponded more to the average level of DS values than to the values of the first group. Therefore, the species differentiation by the degree of succulence really reflects the water saturation ability of the leaf tissues under favorable moisture conditions.

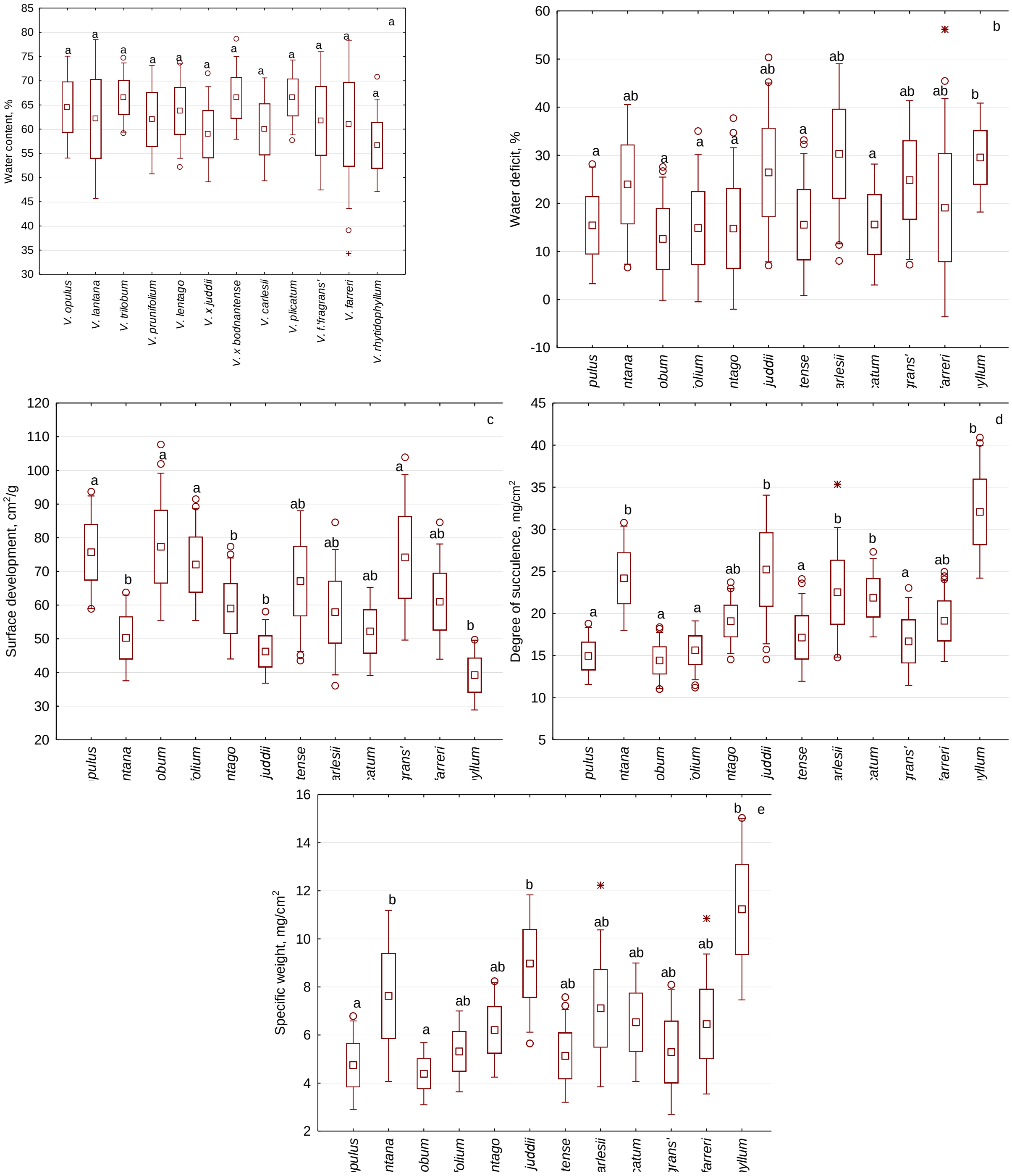

Fig. 2. Ranges of variation of indicators of total leaf water content (*a*), water deficit (*b*), leaf surface development (*c*), degree of succulence (*d*), and leaf specific weight (*e*) of the studied species during the growing season (n = 6)

The leaf specific weight as an indicator, reflecting the weight of a unit area of the leaf in the absolutely dry state, can be formed due to the features of the morphoanatomical structure, in particular, the density and size of epidermal cells, density of stomata and elements of conductive tissues, thickness of the cell walls of the xylem and phloem mechanical elements, development of collenchyma and sclerenchyma, the layer of derived deposits of epicuticular waxes on the surface of the primary integumentary tissue of the leaf, etc. (Picotte et al., 2008; Jafari et al., 2019; Leshcheniuk & Chipilyak, 2020). Comparison of the nature and direction of the dynamics of the leaf specific weight under the impact of hydrothermal stress with other indicators does not always indicate the adaptability of changes associated with the increase in this indicator in the studied *Viburnum* species, while for true xerophytes it is undoubtedly a sign of the xeromorphic structure of leaf blades and their adaptation to xerothermic conditions. Nevertheless, based on the formal sign of the leaf specific weight, the species are divided into groups with high (*V. lantana*, *V. carlesii*, *V. rhytidophyllum*, *V.* ×*juddii*), medium (*V. lentago*, *V. prunifolium*, *V. plicatum*, *V. farreri*), and low (*V. opulus*, *V. trilobum*, *V. farreri* 'fragrans', *V.* ×*bodnantense*) SW values (Fig. 5c).

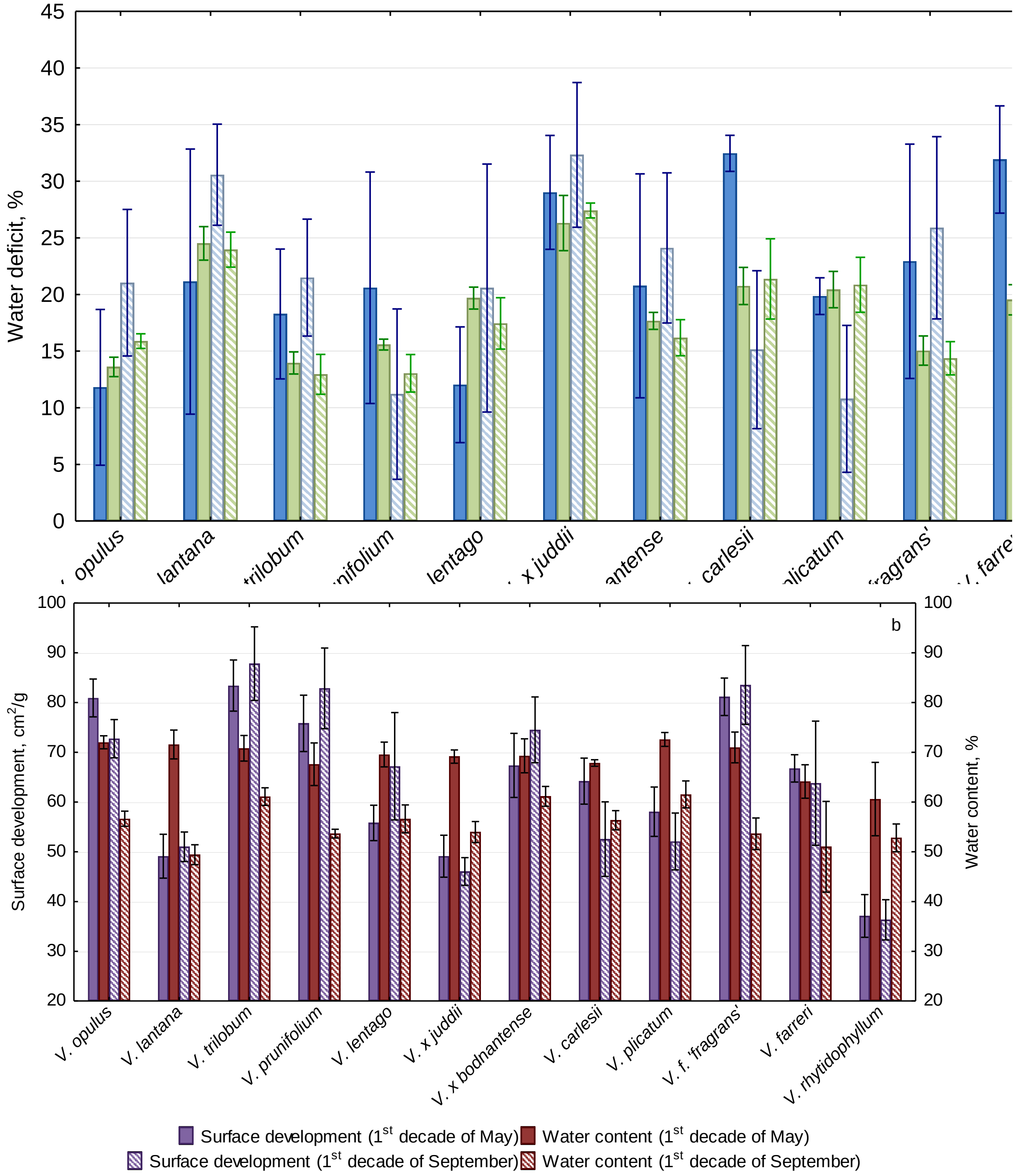

Fig. 3. Values of water deficit and degree of succulence (*a*) and surface development and total water content (*b*) at the beginning and at the end of vegetation (n = 6)

Discussion

Experimentally determined indicators of the morphophysiological state of *Viburnum* species, which provide the grounds for dividing them into groups by the ranges of variation and adaptability, differ within each group in magnitude and correspondence to the degree of adaptability, characterizing each group. To visualize the degree of adaptability of changes in the studied morphophysiological indicators, a correlation-based heat map was constructed (Fig. 6).

The heat map shows significant ecological differentiation of species and allows establishing the main directions of phenotypic modifications, due to which the adaptive potential of species is realized in response to the long-term effects of stress factors.

One of the ways of adaptive strategy is implemented in the *V. lantana*, *V. carlesii*, *V. rhytidophyllum*, *V.* ×*juddii* species through strengthening of the signs of xeromorphic morphostructure – development of the leaf surface and its specific weight (from 0 to 1.3 points) with a minor role of physiological mechanisms of water-retaining forces in the reduction of water deficit and water loss by cells (from 2.0 to 3.0 points). It should be noted that these species taxonomically belong to *Lantana* Spach. section, characterized by thickened leaves with wrinkled or felty surface covered with stellate trichomes (Nicotra et al., 2010). Morphostructural features of these species also determine high degree of succulence of the leaf tissues; however, in combination with low water-retaining capacity, this possibility is practically not realized in their phenotypic responses to stress.

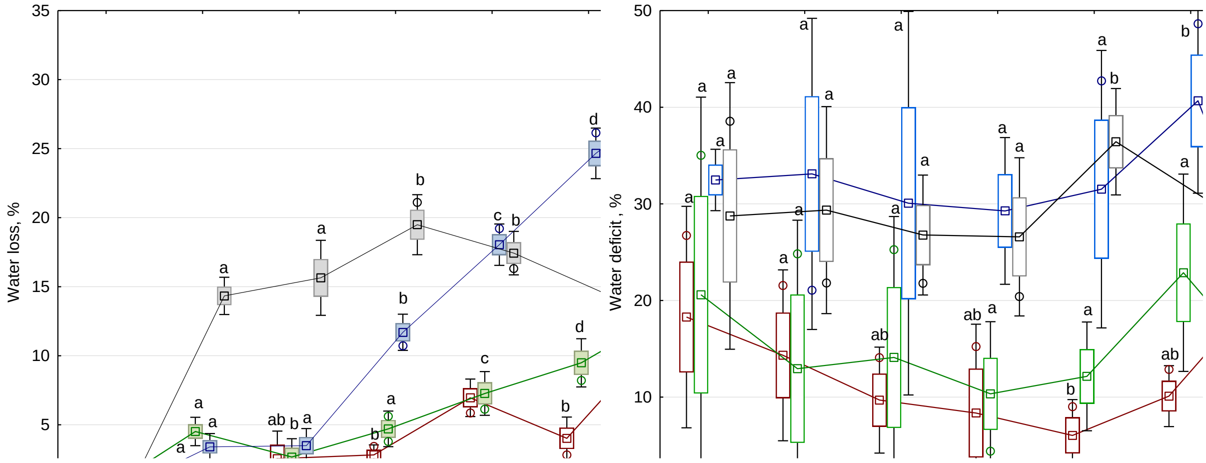

Fig. 4. Dynamics of water loss by leaves compared with the initial level of total water content in the 1st decade of May (*a*) and changes in water deficit (*b*) during the growing season; *1–7* – sampling (*1, 2* – 1st and 3rd decades of V; *3, 4* – 1st and 3rd decades of VI; *5, 6* – 1st and 3rd decades of VII; *7* – 1st decade of IX; n = 6

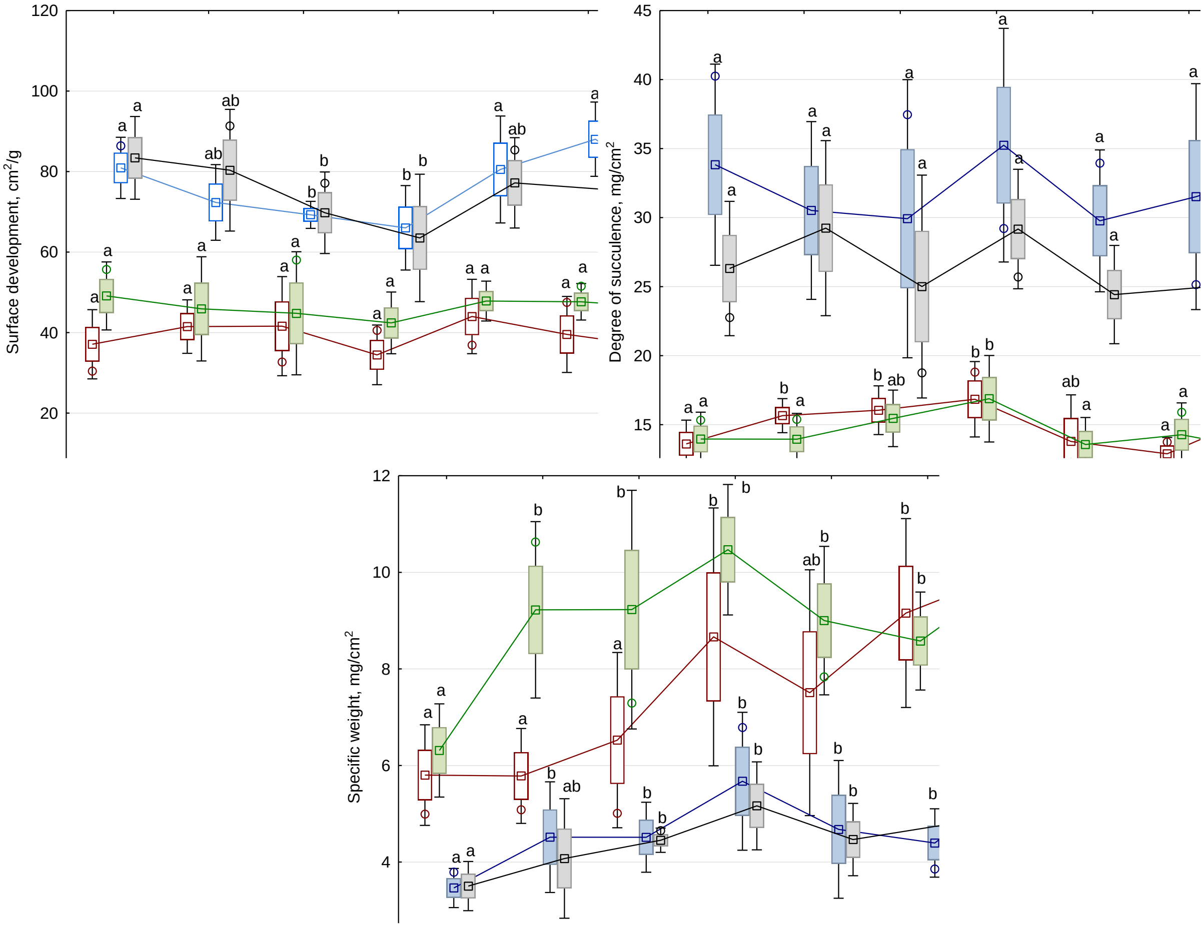

Fig. 5. Dynamics of surface development (*a*), degree of succulence (*b*), and specific weight of leaves (*c*) during the growing season: *1–7* – sampling (*1, 2* – 1st and 3rd decades of V; *3, 4* – 1st and 3rd decades of VI; *5, 6* – 1st and 3rd decades of VII; *7* – 1st decade of IX; n = 6

Regarding the degree of succulence of leaves, it may be noted that this indicator reflects absorptive capacity of the leaf tissues under conditions of unlimited water access, which were simulated in the experiment. It is a characteristic of the potential capabilities of the tissues to acquire the maximum state of hydration in the plants, which do not belong to the ecological group of succulents. In the latter, high degree of water saturation of leaves in the natural arid areas is due to a number of morphophysiological adaptations that ensure the inflow of water and limit its loss through transpiration, while in the plants of other hygromorphs such mechanisms are either absent or appear fragmentarily, in particular in mesophytes, xeromesophytes, and mesoxerophytes. Therefore, high degree of succulence in the absence or limitation of water-retaining properties rather serves as a mesophytic characteristic, i.e. adaptation of cells to functioning in the conditions of high relative water content, as established for species of this group. Their differentiation in the gradient of changes in hydrothermal factors under conditions of increased hydrothermal stress is as follows (in order of increasing adaptability of the corresponding responses to stress): *V. rhytidophyllum* < *V.* ×*juddii* < *V. carlesii* < *V. lantana*. Physiological mechanisms of high water-retaining capacity of the protoplast (Bhusal et al., 2020) represent another direction of realization of the adaptive potential of species of the genus complex, ensuring the cell resistance to the action of dehydrating factors, maintenance of a stable level of hydration and low water deficit of the leaf tissues (from 0 to 1.7 points), while the morphostructural component is characterized by low adaptability (from 2.0 to 3.0 points). Species of this group are characterized by low degree of succulence, which fully corresponds to the adaptive strategy aimed at maintaining the amount of water that is available to plants under conditions of moisture deficiency. In order of increasing pronouncement of the characteristics of this adaptive strategy, the differentiation of species is as follows: *V. opulus* < *V. prunifolium* < *V.* ×*bodnantense* < *V. trilobum*. The basis of this group are species of the *Opulus* DC. and *Lentago* DC sections.

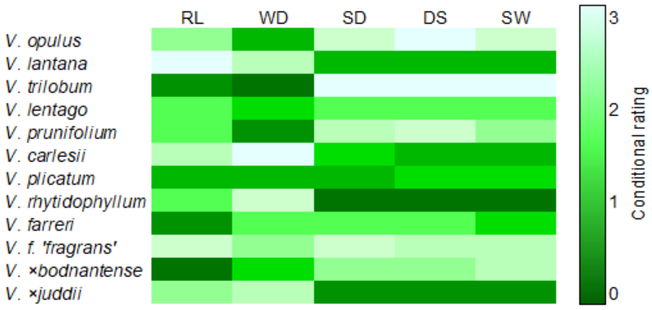

Fig. 6. Conditional rating of the degree of adaptability of changes in morphophysiological indicators of leaves during long period of drought: 0 points – hypothetical index of "absolute" adaptability; from >0 to 1.0 – high adaptability; from >1.0 to 2.0 – moderate adaptability; from >2.0 to 3.0 – low adaptability, or no adaptability; RL – relative loss of water by leaves (%); WD – water deficit (%); SD – leaf surface development (cm^2/g); DS – degree of leaf succulence (mg/cm^2); SW – leaf specific weight (mg/cm^2)

Genotypes in which all morphophysiological components of the adaptive potential are phenotypically realized in equal measure under the action of prolonged drought can be considered the most balanced ones according to the set of morphophysiological adaptations. In this group of the most resistant species, in terms of the set of indicators, three different sections are represented (*Pseudopulus* Dipp., *Lentago* DC., *Thyrsosma* Rehd.). Thus, *V. plicatum* is characterized by the highest resistance in terms of the set of morphostructural (1 point) and physiological (1.0–1.3 points) features. The same adaptive strategy is also quite successfully implemented by *V. lentago* and *V. farreri* (0.7–1.7 and 1.3–1.7 points). The taxon *V. farreri* 'fragrans' present in the collection, which is close to *V. farreri*, is characterized by low adaptability of changes in the set of morphostructural features (2.0–2.7 and 2.3–2.7 points). However, this specimen requires further clarification of its taxonomic affiliation in the genus system.

The results regarding the differentiation of *Viburnum* species present in the dendrological collection, according to the directions of adaptive strategies in stressful hydrothermal conditions, can be correlated to a certain extent with the studies of the evolutionary phylogeny of the *Viburnum* L. genus (Agolf, 1962). Thus, in *V. lantana*, *V. carlesii*, which belong to relatively primitive species, the morphostructural component is most pronounced in the formation of appropriate responses to stress, while in *V. rhytidophyllum* from the group of more progressive species the role of the physiological component in response to stress is enhanced. Small amplitude of the variability of morphostructural features indicates their stability and significance for the preservation of the most ancient species (Crispo et al., 2009).

The group of less primitive species, compared with *V. lantana*, *V. carlesii*, includes *V. plicatum* and *V. lentago* (Agolf, 1962), in which, according to our studies, physiological responses play a significant role within the adaptive responses, along with morphostructural features. It is the set of features that is considered the most adequate in the xerothermic conditions of the introduction area – the North-Steppe subzone of the steppe zone of Ukraine.

The species of section 9, *Opulus* DC. (*V. opulus*, *V. trilobum*), are considered the most evolutionarily progressive ones. Here, according to our data, physiological responses have an absolute advantage in forming a response to hydrothermal stress. The physiological components of the adaptive response, as shown by our data, are characterized by the highest variability, which indicates the phenotypic plasticity of the feature and its importance in forming the adaptive response to stress. Thus, it is possible to outline the direction of evolutionary development in the formation of genotypes better adapted to drought within the predominantly mesophilic *Viburnum* genus complex, which consists in strengthening of the physiological mechanisms of the protoplast water-retaining properties. In this regard, we are planning to study this component of the adaptive strategy of the *Viburnum* genus, which becomes increasingly important in the conditions of climate change.

To confirm the obtained generalizations, we used the hierarchical cluster analysis. The structure of clusters for each observation period is visualized on the dendrograms (Fig. 7). In order to monitor the group stability in time, we analyzed each species' belonging to a certain cluster for each sampling date. This analytic procedure allowed us to identify four stable groups of species retaining their uniformity in the most independent samplings: group 1 (*V. opulus*, *V. trilobum*, *V. prunifolium*); group 2 (*V.* ×*bodnantense*, *V. farreri* 'fragrans'); group 3 (*V. lantana*, *V. plicatum*, V. lentago); and group 4 (*V.* ×*juddii*, *V. rhytidophyllum*). Along with the stable groups, two "free elements" were determined (*V. carlesii* and *V. farreri*). These species did not show a stable association with any of the groups and were attached to different clusters throughout the observation period (Fig. 7).

The analysis showed that the stability of some groups was disrupted as the hydrothermal stress increased, reaching a maximum in July. In particular, the dendrogram for the first decade of July (Fig. 7e) shows that *V. lantana* and *V. farreri* 'fragrans' species were separated from their usual clusters, which was not observed under more favorable conditions.

Cluster analysis of water regime indicators allowed both recording the dynamics of the morphophysiological responses of *Viburnum* species to hydrothermal stress and conducting their substantiated ecological differentiation. The results clearly indicate that the studied species can be conditionally divided into three groups according to the level of their resistance: resistant, moderately resistant, and non-resistant ones. In our opinion, this differentiation is largely explained by the ecological and geographical origin of the species and their morphostructural and physiological adaptations to moisture conditions in the natural ranges. The dendrogram generalized for all observation periods (Fig. 8) clearly demonstrates the grouping of species into three clusters, where species are combined in accordance with the main directions of adaptive strategies, based on the results of our analysis of the phenotypic plasticity of morphophysiological features of leaves: cluster 1 (*V. opulus*, *V. prunifolium*, *V.* ×*bodnantense*, *V. trilobum*), cluster 2 (*V. lentago*, *V. farreri*, *V. plicatum*), and cluster 3 (*V. lantana*, *V. carlesii*, *V.* ×*juddii*, *V. rhytidophyllum*).

The resistant group includes species that are best adapted to the conditions of the temperate continental climate. The basis of the group is represented by North American species (*V. trilobum*, *V. lentago*, *V. prunifolium*) and Eurasian *V. opulus*, which evolved in the regions with the characteristic summer droughts. The East Asian *V. plicatum* species also joined this group; its resistance is likely explained by morphology, in particular, dense leaves that effectively regulate transpiration (Toscano et al., 2021), and, as our studies show, by the complex of physiological stress responses. *Viburnum lentago* is also characterized by the complex morphophysiological adaptive responses under conditions of introduction. Physiological responses play a leading role in the formation of the adaptive response to stress in the other two resistant species (*V. trilobum* and *V. prunifolium*). The hybrid *V.* ×*bodnantense* species demonstrated the same adaptive strategy and high resistance. One of its parents (*V. grandiflorum* Wall.) comes from the Himalayas, a region with harsh high-altitude conditions, which probably explains high resistance of the hybrid to abiotic stresses.

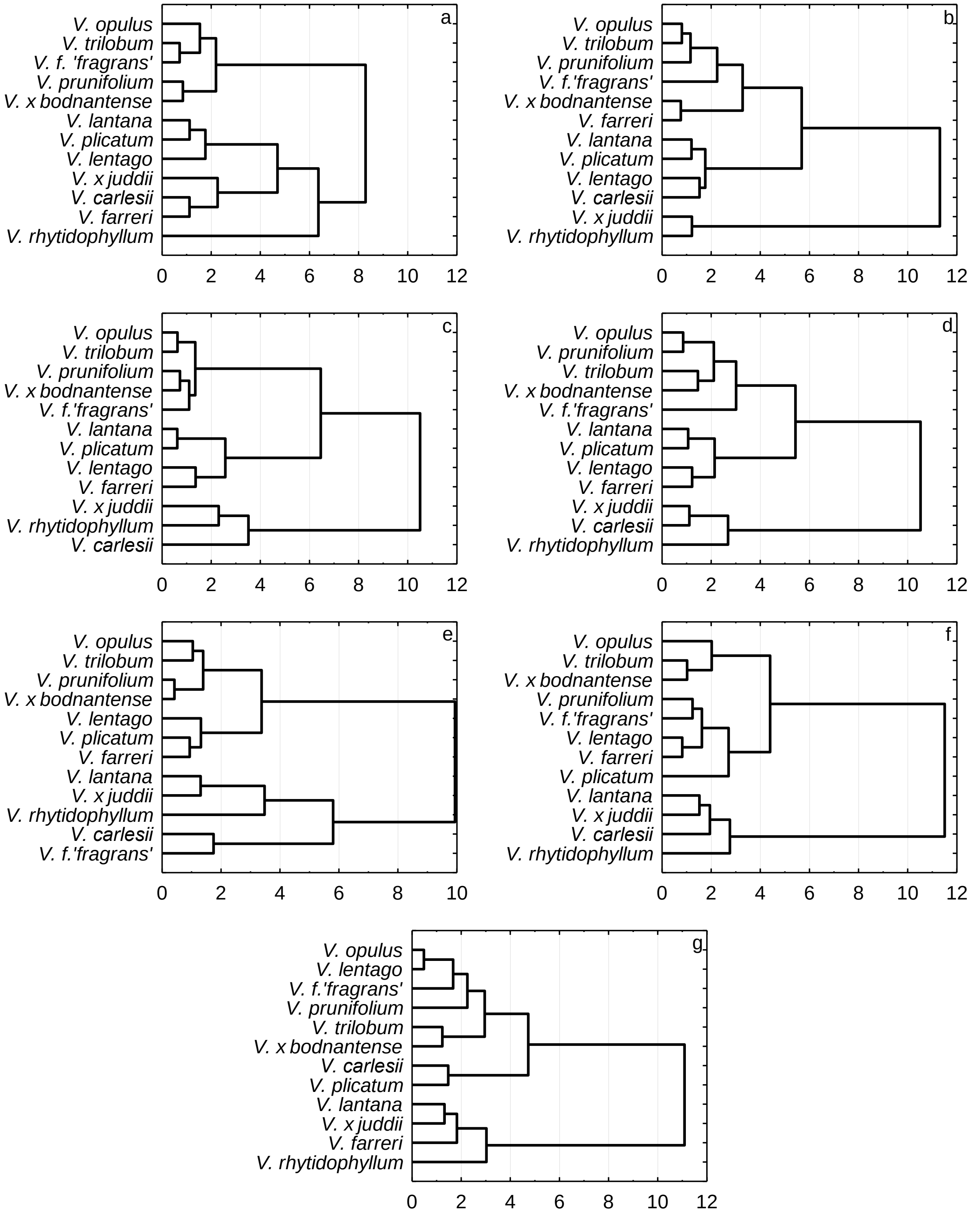

Fig. 7. Dendrograms of hierarchical clustering of species of the *Viburnum* genus based on the water regime indicators, developed using the Ward's method based on Euclidean distances. The panels correspond to different periods of observations during the growing season: *a*, *b* – 1st and 3rd decades of May; *c*, *d* – 1st and 3rd decades of June; *e*, *f* – 1st and 3rd decades of July; *g* – 1st decade of September; along the OX axis – linkage distance (Ward's method)

The moderately resistant group combined the species whose resistance is a compromise between the presence of adaptive traits and features that make them vulnerable under peak loads. For example, the Mediterranean species *V. lantana* has the dense pubescent leaves being a classic adaptation to reduce evaporation (Bai et al., 2019). However, as our data show, this mechanism is insufficient under conditions of the extreme drought. A similar situation is observed in *V. rhytidophyllum*: Its large leather-like pubescent leaves have xeromorphic features, but the significant surface area is at the same time a risk factor for the intense water loss. The same group includes *V.* ×*juddii* and the form of *V. farreri* 'fragrans'. The physiological stability of these cultivated forms, often selected for their decorative features, rather than resistance, can be lower compared with wild species, which explains the low resistance under maximum stress.

The least adapted species are *V. carlesii* and *V. farreri*. Both species originate from the regions of East Asia (Korea, China) with monsoon or temperate climates, where summer droughts are not a regular ecological factor (POWO International Database https://powo.science.kew.org). Their relatively thin, soft leaves characterize them as typical mesophytes, whose physiological mechanisms are not adapted to survive in the conditions of severe moisture deficit (Khaleghi et al., 2019). The chaotic change in their position on dendrograms (Fig. 7) is a classic manifestation of stress in the introduced species, which have been outside their climatic optimum.

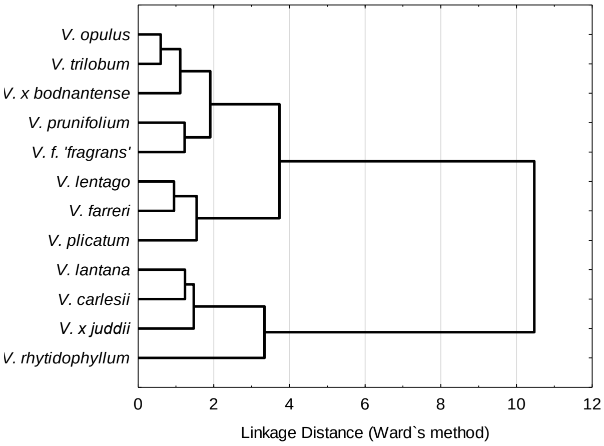

Fig. 8. Dendrogram of hierarchical clustering of species of the *Viburnum* genus according to water regime indicators, generalized for the research period

The results of analysis allow us to conclude that the key factor in stress resistance is the ecological and geographical origin of species and their formation in the phylogenesis in the soil and climatic conditions of the natural growth areas. This conclusion is consistent with the results of a number of other comparative studies of resistance of trees and shrubs. For example, the study of Gaspar et al. (2013) clearly shows that populations of pine (*Pinus pinaster*) originating from more arid areas demonstrate significantly higher resistance to drought than populations from humid regions. Similarly, Rennenberg et al. (2006) note that Mediterranean pine species (*Pinus*) adapted to summer droughts have significantly more effective mechanisms for controlling water loss compared with boreal species from the wetter and cooler regions. Thus, the pattern we identified is considered expected, and it confirms the general theory of adaptation.

We should also note certain limitations of this study. Since some species in the collection are represented by only a single specimen, the results obtained for them reflect the individual response of a particular specimen. Therefore, caution is required when generalizing the conclusions for the species as a whole, and there is a need for the further research using a larger sample of plants. Despite these limitations, the study allowed us to differentiate 12 species of the *Viburnum* genus according to their resistance to hydrothermal stress. This approach has practical significance and can be used in selection of a range of species for landscaping in the southern regions, where summer droughts represent a serious constraint.

Conclusion

Based on the analysis of the dynamics of water regime indicators of 12 *Viburnum* species, belonging to 5 sections of the genus, we identified the groups of species that are resistant, moderately resistant, and poorly resistant to hydrothermal stress. The resistance of species is determined by the phenotypic plasticity of morphostructural and physiological features of leaves and the degree of adaptability of their changes in response to hydrothermal stress.

The adaptive potential of three identified groups of species is realized mainly due to the morphostructural component in the formation of appropriate responses to stress, or the physiological component, or their combined manifestation, which is the most adequate in drought conditions. We determined the directions of adaptive strategies, which are in some way consistent with the phylogenetic development of *Viburnum* species. The results show that the key factor in stress resistance is the ecological and geographical origin of species and their formation in phylogenesis in the soil and climatic conditions of the natural growth areas. The highest resistance was demonstrated by species originating from the regions with the temperate continental climate, adapted to periodic summer droughts.

The results of cluster analysis confirm the ecological differentiation of species, which is based on the formation of various adaptive strategies of the *Viburnum* species in response to hydrothermal stress. Under conditions of stress loads associated with moisture deficiency and elevated temperatures, the resulting clustering represents, to some extent, an alternative to the existing system of phylogenetic relationships of the *Viburnum* genus. It allows us to predict the directions of introductory adaptation of mesophytic species in arid climates. The study of adaptation mechanisms inherent in different ecological groups of the introduced *Viburnum* species is a promising direction of further research. However, it should be noted that the approach to the ecological differentiation of introduced representatives of the *Viburnum* genus complex presented in this paper can be currently used in the theory and practice of the plant introduction in the areas with arid climates.

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Abbass, K., Qasim, M. Z., Song, H., Murshed, M., Mahmood, H., & Younis, I. (2022). A review of the global climate change impacts, adaptation, and sustainable mitigation measures. Environmental Science and Pollution Research International, 29(28), 42539–42559.

Ackerly, D. D. (2004). Functional traits of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs, 74(1), 25–44.

Allakhverdiev, S. I., Kreslavski, V. D., Klimov, V. V., Los, D. A., Carpentier, R., & Mohanty, P. (2008). Heat stress: An overview of molecular responses in photosynthesis. Photosynthesis Research, 98(1–3), 541–550.

Apel, K., & Hirt, H. (2004). Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. Annual Review of Plant Biology, 55(1), 373–399.

Bai, T., Li, Z., Song, C., Song, S., Jiao, J., Liu, Y., Dong, Z., & Zheng, X. (2019). Contrasting drought tolerance in two apple cultivars associated with difference in leaf morphology and anatomy. American Journal of Plant Sciences, 10, 709–722.

Bhusal, N., Lee, M., Han, R., Han, A. R, & Kim, H. S. (2020). Responses to drought stress in *Prunus sargentii* and *Larix kaempferi* seedlings using morphological and physiological parameters. Forest Ecology and Management, 465, 118099.

Chartzoulakis, K., Patakas, A., Kofidis, G., Bosabalidis, A., & Nastou, A. (2002). Water stress affects leaf anatomy, gas exchange, water relations and growth of two avocado cultivars. Scientia Horticulturae, 95, 39–50.

Chaves, M. M., Flexas, J., & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. Annals of Botany, 103(4), 551–560.

Clausen, J., Keck, D. D., & Hiesey, W. M. (1940). Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institution of Washington Publication, Washington.

Crispo, E., Dibattista, J., Correa, C., Thibert-Plante, X., McKellar, A., Schwartz, A., Berner, D., De León, L., & Hendry, A. (2009). The evolution of phenotypic plasticity in response to anthropogenic disturbance. Evolutionary Ecology Research, 12, 47–66.

De la Sota, C., Ruffato-Ferreira, V. J., Ruiz-García, L., & Alvarez, S. (2019). Urban green infrastructure as a strategy of climate change mitigation: A case study in northern Spain. Urban Forestry and Urban Greening, 40, 145–151.

Demchenko, O. O. (2005). Systematyka ta filohenetychni zviazky vydiv rodu *Viburnum* L. [Systematics and phylogenetic relationships of species of the genus *Viburnum* L.]. Plant Introduction, 2, 27–33 (in Ukrainian).

Didukh, Y. P., Chornei, I. I., Budzhak, V. V., Tokariuk, A. I., Kish, R. Y., Protopopova, V. V., Shevera, M. V., Kozak, O. M., Kontar, I. S., Rozenblit, Y. V., & Norenko, K. M. (2016). Klimatohenni zminy roslynnoho svitu Ukrainskykh Karpat [Climatogenic changes of plant life of the Ukrainian Carpathians]. Drukart, Chernivtsi (in Ukrainian).

Donoghue, M. J., Baldwin, B. G., Li, J., & Winkworth, R. C. (2004). *Viburnum* phylogeny based on chloroplast *trnK* intron and nuclear ribosomal ITS DNA sequences. Systematic Botany, 29(1), 188–198.

Egolf, D. R. (1962). A cytological study of the genus *Viburnum*. Journal of the Arnold Arboretum, 43(2), 132–172.

Gaspar, M. J., Velasco, T., Feito, I., Alía, R., & Majada, J. (2013). Genetic variation of drought tolerance in *Pinus pinaster* at three hierarchical levels: A comparison of induced osmotic stress and field testing. PLoS One, 8(11), e79094.

Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology, 21(3), 394–407.

Holikova, M., & Zaitseva, I. (2009). Ctrukturno-funktsionalni osoblyvosti adaptatsii vydiv rodu *Acer* v umovakh stepovoho Prydniprovia [Structural and functional features of adaptation of species of the genus *Acer* in the conditions of the Steppe Dnieper region]. Biosystems Diversity, 17, 30–36 (in Ukrainian).

Horielov, O. M. (2016). Porivnialna otsinka posukhostiikosti verb z kolektsii Natsionalnoho botanichnoho sadu imeni M. M. Hryshka [Comparative assessment of drought resistance of willows from the collection of the M. M. Hryshko National Botanical Garden]. Plant Introduction, 2, 25–34 (in Ukrainian).

Hughes, J., Hepworth, C., Dutton, C., Dunn, J.A., Hunt, L., Stephens, J., Waugh, R., Cameron, D.D., & Gray, J. E. (2017). Reducing stomatal density in barley improves drought tolerance without impacting on yield. Plant Physiology, 174(2), 776–787.

Ivanko, I. A., Baranovskyi, B. O., Kabar, A. M., Karmyzova, L. O., Nikolaieva, V. V., Zhykharieva, A. V., Kulik, A. F., Dovhanenko, D. O., & Karas, L. M. (2025). Dendrolohichne riznomanittia ta suchasnyi stan zelenykh nasadzhen Dniprovskoho natsionalnoho universytetu imeni Olesia Honchara [Dendrological diversity and current state of green plantings of Oles Honchar Dnipro National University]. Ecology and Noospherology, 36(1), 12–21 (in Ukrainian).

Jafari, S., Hashemi Garmdareh, S. E., & Azadegan, B. (2019). Effects of drought stress on morphological, physiological, and biochemical characteristics of stock plant (*Matthiola incana* L.). Scientia Horticulturae, 253, 128–133.

Khaleghi, A., Naderi, R., Brunetti, C., Maserti, B. E., Salami, S. A., & Babalar, M. (2019). Morphological, physiochemical and antioxidant responses of *Maclura pomifera* to drought stress. Scientific Reports, 9, 19250.

Kokhno M. A., & Kurdiuk O. M. (1994). Teoretychni osnovy ta dosvid introduktsii derevnykh roslyn v Ukrayini [Theoretical foundations and experience of introducing woody plants in Ukraine]. Naukova Dumka, Kyiv (in Ukrainian).

Kokhno, M. A., Trofymenko, N. M., Parkhomenko, L. I., Sobko, V. H., Horb, V. K., Klymenko, S. V., Hrevtsova, H. T., Halkin, S. I., Muzyka, H. I., Schepytska, T. S., Demchenko, O. O., Bilyk, O. V., Boniuk, Z. H., Balabushka, V. K., Halushko, R. V., Haponenko, M. B., Klymenko, Y. O., Kolesnychenko, O. M., Sydoruk, T. M., Kliuienko, O. V., Korniichuk, V. S., Strila, T. Y., Fedorovskyi, V. D., Yadrov, A. A., & Kurdiuk, O. M. (2005). Dendroflora Ukrayiny. Dykorosli i kultyvovani dereva i kuschi. Pokrytonasinni. Chastyna II. Dovidnyk [Dendroflora of Ukraine. Wild and cultivated trees and shrubs. Angiosperms. Part II. Guide]. Phytosociocenter, Kyiv (in Ukrainian).

Kolodiazhenska, T. I. (2013). Porivnialna otsinka posukhostiikosti mezofanerofitiv rodu *Juniperus* L. v umovakh Lisostepu Ukrainy [Comparative assessment of drought tolerance of mesophanerophytes of the genus *Juniperus* L. in the conditions of the forest-steppe Ukraine]. Plant Introduction, 4, 92–97 (in Ukrainian).

Kordyum, E. L., & Dubyna, D. V. (2019). Phenotypic plasticity in plant adaptation and coexistence. International Journal of Advanced Research in Science, 5(3), 8–13.

Kosakivska, I. V., Voitenko, L. V., Vasiuk, V. A., & Shcherbatiuk, M. M. (2023). Morfolohichni, fiziolohichni i molekuliarni skladovi adaptatsiynoyi vidpovidi predstavnykiv rodu *Quercus* (Fagaceae) na posukhu [Morphological, physiological, and molecular components of the adaptive response to drought in the genus *Quercus* (Fagaceae)]. Ukrainian Botanical Journal, 80(3), 251–266 (in Ukrainian).

Leonov, O. Y. (2013). Hrupuvannia zrazkiv pshenytsi miakoyi za plastychnistiu ta stabilnistiu proiavu kilkisnykh oznak [Grouping of soft wheat samples by plasticity and stability of manifestation of quantitative traits]. Henetychni Resursy Roslyn, 13, 28–39 (in Ukrainian).

Leshcheniuk, O., & Chipilyak, T. (2020). Morpho-anatomical adaptation of the leaves of certain *Veronica* species to arid conditions. Plant Introduction, 87–88, 47–53.

Manes, S., Costello, M. J., Beckett, H., Debnath, A., Devenish-Nelson, E., Grey, K.-A., Jenkins, R., Khan, T. M., Kiessling, W., Krause, C., Maharaj, S. S., Midgley, G. F., Price, J., Talukdar, G., & Vale, M. M. (2021). Endemism increases species' climate change risk in areas of global biodiversity importance. Biological Conservation, 257, 109070.

Nejat, N., & Sadeghi, H. (2016). Finding out relationships among some morpho-biochemical parameters of Christ's Thorn (*Ziziphus spina-christi*) under drought and salinity stresses. Planta Daninha, 34(4), 667–674.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U., Poot, P., Purugganan, M. D., Richards, C. L., Valladares, F., & van Kleunen, M.. (2010). Plant phenotypic plasticity in a changing climate. Trends in Plant Science, 15(12), 684–692.

Oishy, M. N., Shemonty, N. A., Fatema, S. I., Mahbub, S., Mim, E. L., Hasan Raisa, M. B., & Anik, A. H. (2025). Unravelling the effects of climate change on the soil-plant-atmosphere interactions: A critical review. Soil & Environmental Health, 3(1), 100130.

Ortiz, A. M. D., Outhwaite, C. L., Dalin, C., & Newbold, T. (2021). A review of the interactions between biodiversity, agriculture, climate change, and international trade: Research and policy priorities. One Earth, 4(1), 88–101.

Pereira, J., Cristina, E., Da Luz, L., Nogueira, R. J., Filho, P., Lima, L., & Santos, R. (2015). Cluster analysis to select peanut drought tolerance lines. Australian Journal of Crop Science, 9(11), 1095–1105.

Picotte, J. J., Rhode, J. M., & Cruzan, M. B. (2008). Leaf morphological responses to variation in water availability for plants in the *Piriqueta caroliniana* complex. Plant Ecology, 200, 267–275.

Pokhrel, S., Subedi, C., Thakuri, S., Kunwar, R., Sharma, K., Chaudhary, R., & Ghimire, S. K. (2025). Evaluating the ecological vulnerability and adaptive capacity of forest vegetation under climate stress across Nepal's mountain landscapes. Geocarto International, 40(1), 2551806.

Rana, P., & Varshney, L. R. (2023). Exploring limits to tree planting as a natural climate solution. Journal of Cleaner Production, 384, 135566.

Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R. S., & Gessler, A. (2006). Physiological responses of forest trees to heat and drought. Plant Biology, 8(5), 556–571.

Rueda, M., Godoy, O., & Hawkins, B. A. (2017). Spatial and evolutionary parallelism between shade and drought tolerance explains the distributions of conifers in the conterminous United States. Global Ecology and Biogeography, 26(1), 31–42.

Seneviratne, S. I. (2021). Chapter 11: Weather and climate extreme events in a changing climate. In: Masson-Delmotte, V., et al. (Eds.). Climate change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Slishchuk, H., & Volkova, N. (2025). Dyferentsiyna ekspresiya heniv proteyiniv teplovoho shoku u nutu (*Cicer arietinum* L.) pry vidpovidi na posukhu [Differential expression of heat shock protein genes in chickpea (*Cicer arietinum* L.) in response to drought]. Faktory Eksperymentalnoyi Evoliutsiyi Orhanizmiv Factors of Experimental Evolution of Organisms, 36, 142–147 (in Ukrainian).

Szabados, L., & Savouré, A. (2010). Proline: a multifunctional amino acid. Trends in Plant Science, 15(2), 89–97.

Tarasov, V. V. (2012). Flora Dnipropetrovskoi ta Zaporizkoi oblastei [Flora of Dnipropetrovsk and Zaporizhia regions]. Lira, Dnipro (in Ukrainian).

The Angiosperm Phylogeny Group (2016). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society, 2016, 181(1), 1–20.

Toscano, S., Ferrante, A., Romano, D., & Tribulato, A. (2021). Interactive effects of drought and saline aerosol stress on morphological and physiological characteristics of two ornamental shrub species. Horticulturae, 7(12), 517.

Vale, M. M., Arias, P. A., Ortega, G., Cardoso, M., Oliveira, B. F., Loyola, R., & Scarano, F. R. (2021). Climate change and biodiversity in the Atlantic Forest: Best climatic models, predicted changes and impacts, and adaptation options the Atlantic forest. In: Marques, M. C. M., & Grelle, C. E. V. (Eds.). The Atlantic forest. Springer, Cham. Pp. 253–267.

Valladares, F., Matesanz, S., Guilhaumon, F., Araujo, M. B., Balaguer, L., Benito-Garzon, M., Cornwell, W., Gianoli, E., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., & Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. Ecology Letters, 17(11), 1351–1364.

Wang, F., Harindintwali, J. D., Wei, K., Shan, Y., Mi, Z., Costello, M. J., Grunwald, S., Feng, Z., Wang, F., Guo, Y., Wu, X., Kumar, P., Kastner, M., Feng, X., Kang, S., Liu, Z., Fu, Y., Zhao, W., Ouyang, C., & Tiedje,

J. M. (2023). Climate change: strategies for mitigation and adaptation. Innovation Geoscience, 1(1), 100015.

Wang, W., Vinocur, B., Shoseyov, O., & Altman, A. (2004). Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends in Plant Science, 9(5), 244–252.

Ward, J. H. (1963). Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association, 58(301), 236–244.

Weed, A. S., Ayres, M. P., & Hicke, J. A. (2013). Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs, 83(4), 441–470.

Yang, X., Lu, M., Wang, Y., Wang, Y., Liu, Z., & Chen, S. (2021). Response mechanism of plants to drought stress. Horticulturae, 7(3), 50.

Yang, Z., Zhou, B., Chen, Q., Ge, X., & Shi, Y. (2018). Effects of drought on root architecture and non-structural carbohydrate of *Cunninghamia lanceolata*. Plants, 38, 6729–6740.

Zaitseva, I. O. (2017). Kilkisna otsinka posukhostiikosti introdutsentiv rodu *Syringa* L. v umovakh Stepovoho Prydniprovia [Quantitative assessment of drought tolerance of introduced species of the genus *Syringa* L. in the conditions of the Steppe Dnieper Region]. Pytannia Stepovoho Lisoznavstva ta Lisovoyi Rekultyvatsiyi Zemel’, 46, 76–81 (in Ukrainian).

Zaitseva, I. O. (2018). Vidnosna kil’kist’ prodykhiv yak pokaznyk stiykosti introdutsentiv rodu *Syringa* L. u stepoviy zoni [Relative number of stomata as an indicator of the resistance of introduced species of the genus *Syringa* L. in the steppe zone]. Naukovi Zapysky Ternopil’s’koho Natsional’noho Pedahohichnoho Universytetu, Seriya Biolohiya, 73, 17–21 (in Ukrainian).

Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V., & Gómez-Cadenas, A. (2018). Plant adaptations to the combination of drought and high temperatures. Physiologia Plantarum, 162(1), 2–12.

Zepner, L., Karrasch, P., Wiemann, F., & Bernard, L. (2021). ClimateCharts.net – an interactive climate analysis web platform. International Journal of Digital Earth, 14(3), 338–356.

Zhang, C., Yang, H., Wu, W., & Li, W. (2017). Effect of drought stress on physiological changes and leaf surface morphology in the blackberry. Brazilian Journal of Botany, 40, 625–634.

Zia, R., Nawaz, M. S., Siddique, M. J., Hakim, S., & Imran, A. (2021). Plant survival under drought stress: Implications, adaptive responses, and integrated rhizosphere management strategy for stress mitigation. Microbiological Research, 242, 126626.