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Original article

FEATURES OF THE PIGMENT APPARATUS OF THE PHOTOSYNTHETIC SYSTEM OF ELMS AND GLEDICHIAS IN FOREST AMELIORATION AND PROTECTIVE AFFORESTATION

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Background. Woody plants within southern Russia are impacted by drought, which leads to changes in their living conditions. The living condition depends on the work of the pigment apparatus of the photosynthetic system and leaf mesostructure. The purpose of this work was to reveal the functioning features of the pigment apparatus of the photosynthetic system and the structural organization in *Ulmus laevis*, *Ulmus parvifolia*, and *Gleditsia triacanthos* leaves.

Result. The study revealed new species-specific features of the leaf pigment apparatus of the photosynthetic system and the structural organization in “healthy and weakened” plants under stress conditions.

Methods. The vital condition of trees was evaluated by visual analysis of crown parameters according to the V.A. Alekseeva’s method. Quantitative data were processed using the Statistica 12.0 program.

Conclusion. During the analysis of genes and their products, the effect on the work of the pigment apparatus of the photosynthetic system was shown in normal and under stress. In this regard, it is necessary to further search for DNA markers of these genes and their degree of expression involved in the mechanisms of adaptation to adverse environmental factors. The study of the leaf pigment apparatus of the photosynthetic system and the structural organization in woody plants can be used to obtain new genotypes with economically valuable features, bioindication, and selection of optimal regimes for their cultivation.

Keywords: *pigment apparatus of photosynthetic system; nitrogen balance index (NBI); morphology; Ulmus parvifolia; Ulmus laevis Pall.; Gleditsia triacanthos L.*

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Научная статья

ОСОБЕННОСТИ ПИГМЕНТНОГО АППАРАТА ФОТОСИНТЕТИЧЕСКОЙ СИСТЕМЫ ВЯЗОВ И ГЛЕДИЧИИ, ИСПОЛЬЗУЕМЫХ В АГРОЛЕСОМЕЛИОРАЦИИ И ЗАЩИТНОМ ЛЕСОРАЗВЕДЕНИИ

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Обоснование. *Древесные растения, произрастающие на территории Юга России, подвержены воздействию засухи, которые приводит к изменению их жизненного состояния. Жизненное состояние зависит от работы пигментного аппарата фотосинтетической системы и мезоструктуры листа.*

Цель исследования. *Цель работы заключалась в выявлении особенностей функционирования пигментного аппарата фотосинтетической системы и структурной организации листа вяза гладкого и мелколистного и гледичии трехлопучековой.*

Материалы и методы. *Оценку жизненного состояния деревьев проводили путем визуального анализа параметров кроны по методике В.А. Алексева. Количественные данные обрабатывались с помощью программы Statistica 12.0.*

Результаты. *В результате исследования были выявлены новые видовые особенности пигментного аппарата фотосинтетической системы и структурной организации листа у «здоровых и ослабленных» растений в стрессовых условиях.*

Заключение. *В ходе анализа генов и их продуктов было показано влияние на работу пигментного аппарата фотосинтетической системы в норме и при стрессе. В связи с этим, необходимо в дальнейшем провести поиск ДНК-маркеров указанных генов и их степень экспрессии, вовлеченных в ме-*

ханизмы адаптации к неблагоприятным факторам внешней среды. Изучение пигментного аппарата фотосинтетической системы и структурной организации листа древесных растений может применяться для получения новых генотипов с хозяйственно-ценными признаками, биоиндикации и подбору оптимальных режимов для их выращивания.

Ключевые слова: пигментный аппарат фотосинтетической системы; индекс азотного баланса (NBI); морфология; *Ulmus parvifolia*; *Ulmus laevis* Pall.; *Gleditsia triacanthos* L.

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Introduction

It is known that stressful conditions, including moisture deficit and elevated air temperatures, contribute to reactive oxygen intermediates which have a negative effect on the plant photosynthetic apparatus damaging nucleic acids and oxidizing lipids [10; 11; 19]. The plant cell tries to protect itself from the effects of reactive oxygen intermediates by using an antioxidant system. This system includes low molecular weight, non-enzymatic substances with antioxidant properties such as carotenoids, flavonoids, vitamins, phenolic compounds, etc. The main antioxidant function is to neutralize reactive oxygen intermediates. Knowledge of the features of photosynthetic pigments and antioxidant substances can help to understand the mechanisms of plant resistance to environmental factors [10; 14; 20].

The plant pigment system is extremely sensitive to external environmental factors, including elevated atmospheric temperatures and moisture deficit. Chlorophyll in the leaf changes during the vegetation period. This is due to various abiotic, biotic, and anthropogenic environmental factors. Carotenoids and chlorophyll *b* are accessory pigments. They stabilize the work of chlorophyll *a* protecting it from photo-oxidation. Many studies note a higher carotenoid content in the leaves of plants growing in extreme forest site conditions. Carotenoids are highly reactive and protect cells from destruction by acting as antioxidants. Indicators of the plant stress level can be considered the content of chlorophyll, carotenoids, and the ratio of chlorophylls *a* and *b* [1; 9; 16].

The climatic conditions limit the spread of woody plants within the Volgograd Region. Easterly and south-easterly dry wind directions are observed with-

in the study area. The long-time average annual air temperature is 5.2–8.3°C; the mean annual rainfall is 320 mm. The average annual humidity of the atmospheric air is 70% and decreases to 15% in summer.

Under arid environmental conditions, plants rearrange the organization of photosynthetic tissues and cells, which leads to changes in the leaf mesostructure. The mesostructure includes such indicators as the lamina area, the number of mesophyll cells, the number of chloroplasts in the cell, chloroplast volume, the cross-sectional area of the chloroplast, and its surface [4; 12].

Under arid stress, changes in leaf mesostructure, photosynthetic intensity, and photosynthetic cell function are observed. In arid steppe conditions, plants form clearly expressed features of xerophytization; small leaves with high density and high content of mechanical tissues are formed, with a large number of small mesophyll cells and chloroplasts per unit leaf area [18].

Given the increasing rate of warming and increasing degradation processes of natural landscapes, the issues related to the study of plant responses at the physiological level as a reaction to environmental stressors are relevant. The nitrogen balance index (NBI) indicates the ratio of chlorophylls and flavonoids, on the basis of which it is possible to identify the adaptation peculiarities of “healthy” and “weakened” plants to growing conditions in arid climates.

The research purpose is to estimate the state of the leaf pigment apparatus of the photosynthetic system and the mesostructure features of *Ulmus laevis*, *Ulmus parvifolia*, and *Gleditsia triacanthos* used in forest amelioration in the south of Russia at the end of the vegetative period.

Materials and methods

The objects of research were “healthy” and “weakened” trees of 10 individuals in each group: *Ulmus laevis* Pall., *Ulmus parvifolia*, and *Gleditsia triacanthos* L., growing on the territory of the Federal Research Center of Agroecology of the Russian Academy of Sciences in Volgograd (48°64 N., 44°43 E). The selected species of woody plants differ in their genetic status. *Gleditsia triacanthos* is an introducer and the rest of the species are aborigines.

The vital condition of trees was evaluated by visual analysis of crown parameters according to the V.A. Alekseeva’s method [2] (Table 1).

The pigment content was determined in the leaves of “healthy” and “weakened” trees in growing season 2022. From each “healthy” and “weakened” free-standing tree, 10 leaf samples of the same tier were collected from the southern exposure. For a registration plant, analyses were performed in three biological replicates and the mean value was indicated for use in statistical pro-

cessing. Amounts of chlorophylls ($\mu\text{g}/\text{cm}^2$ of green weight), flavonoids ($\mu\text{g}/\text{cm}^2$ of green weight), anthocyanins ($\mu\text{g}/\text{cm}^2$ of green weight), and NBI in the epidermis of woody plants leaves were measured using the plant analyzer Dualex Scientific+ (Force-A, France). The ratio of chlorophylls to flavonoids (nitrogen/carbon) in conventional units (c.u.) is shown with NBI.

Table 1.

Selection criteria according to the living condition of the studied trees

«Healthy»	«Weakened»
1. Absence of external crown and trunk damage	1. External crown and trunk damage
2. Crown density	2. 30% reduction in crown density due to premature falling or thinning of the crown skeletal part
3. Dead and dying branch woods are concentrated in the crown lower part and absent in its upper half	3. The presence of 30% of dead and/or dying branch woods in the crown upper half
4. The finished growing leaves are green to dark green in color, and their lifespan is typical for the region	4. Damage (overeating, burn, chlorosis, necrosis, etc.)
5. Leaf damage is insignificant (<10%) and does not affect the tree state	5. Turning off 30% of the leaf surface from assimilation activity

The contour-weight method was used to determine the lamina area. Leaf thickness was determined in slices of 10 leaves from each test tree, then 10 measurements in each leaf were performed using a light microscope Micromed 3 var. 2-20M (Micromed, Russia). Recalculation of the obtained readings (in micrometers) was performed according to the proportion after determining the ocular micrometer scale division by the stage micrometer.

To reveal the mesostructural organization features of the studied woody plant leaves, the research team cut portions from the middle part of leaves, which were fixed in 70% ethyl alcohol and stored at $-20\text{ }^{\circ}\text{C}$. The mesostructure of the woody plant photosynthetic apparatus was studied by Mokronosov's method [11]. The cell number was counted in the suspension after plant tissue maceration. For maceration, 0.5–1.0 N HCl at 60–100 $^{\circ}\text{C}$ was used. The cells were counted in the Goryaev chamber ($V = 0.9\text{ mm}^3$). To recalculate cells in thousand/ cm^2 , the average number of cells in the full volume of the Goryaev chamber was multiplied by the coefficient $K=1462$. These coefficients are valid when the leaf sample has an area of 3.8 cm^2 and the volume of suspension is 5 ml.

Chloroplasts in the cells were calculated on a prepared squash preparation. To do this, a drop of the suspension was placed on a slide and covered with a

cover slip. A small pressure was made on the cover slip so that the chloroplasts in the cell were distributed over the area.

Quantitative data were processed using the Statistica 12.0 program (StatSoft Inc., USA), the indicators used to evaluate nonparametric samples in biological studies were calculated: the normal distribution of values, median [1st quartile, 3rd quartile], and the statistical significance of sample was analyzed. To determine the differences between two independent samples, the Mann–Whitney criterion was used with confidence $p < 0.05$.

Results and discussion

Definition of the living condition

As a result of the survey, the following common defects in “weakened” woody plants were identified: dry branch woods, mechanical damage to the trunk, and lamina damage by various pests and diseases. In “weakened” elms compared to “healthy” ones, the following damages were revealed: flanking of bark, presence of foreign objects, dry branch woods in the crown, and marginal lamina necrosis. The living condition of the “weakened” *Gleditsia triacanthos* showed the presence of such defects as earlier leaf coloration, lamina necrosis, dry prune, and mechanical damage to the trunk. After describing the living condition of the studied trees for each of the objects (“Healthy” and “Weakened”), a pigment apparatus analysis of the plant photosynthetic system and the lamina structural organization was carried out.

Study of the pigment content of the photosynthetic system

In the tree leaves, the amounts of chlorophylls differed between “healthy” and “weakened” individuals ($p < 0.05$). In the leaves of “healthy” individuals of *Ulmus laevis* and *Ulmus parvifolia*, chlorophylls were 1.2 times higher than in “weakened” plants. A similar trend was observed for *Gleditsia triacanthos*.

In the present study, interspecific differences within the genus Elm were noted, which manifested themselves in a greater difference (1.3–1.4 times) in chlorophylls in the leaves of the *Ulmus laevis* than in the *Ulmus parvifolia* in both living condition groups. *Ulmus parvifolia* and *Ulmus laevis*, regardless of the living condition, synthesized chlorophylls more by 1.2–1.7 times compared with *Gleditsia triacanthos* ($p < 0.05$) (Fig. 1A).

The difference in flavonoids in two elm species between “healthy” and “weakened” was revealed which differed by 1.3 times ($p < 0.05$). No significant differences between “healthy” and “weakened” trees were found in *Gleditsia triacanthos* (Fig. 1B). *Gleditsia triacanthos* of different living conditions synthesized 1.3 times more flavonoids than *Ulmus parvifolia*. Compared with

Gleditsia triacanthos, *Ulmus laevis* of a healthy living condition had a higher flavonoid in the leaves.

Ulmus parvifolia had a significant difference in anthocyanins. More anthocyanins were detected in “weakened” individuals of this species under stressful conditions and amounted to 0.08 which was 0.012 higher than in “healthy” plants ($p < 0.05$). In the content of anthocyanins in the leaves of *Ulmus laevis* and *Gleditsia triacanthos*, no statistically significant differences were found between “healthy” and “weakened” individuals ($p > 0.05$). The maximum of anthocyanins was observed in “healthy” and “weakened” individuals of *Gleditsia triacanthos* compared to other plants. Significant differences in the number of anthocyanins were revealed between the studied species of different living conditions ($p < 0.05$) (Fig. 1C).

In “healthy” individuals of *Ulmus parvifolia*, the NBI was 1.5 times higher than in weakened individuals. Similar trends were observed in individuals of *Ulmus parvifolia* ($p < 0.05$). NBI of the introduced species, *Gleditsia triacanthos*, had minimal values compared to representatives of the genus Elm (Fig. 1D).

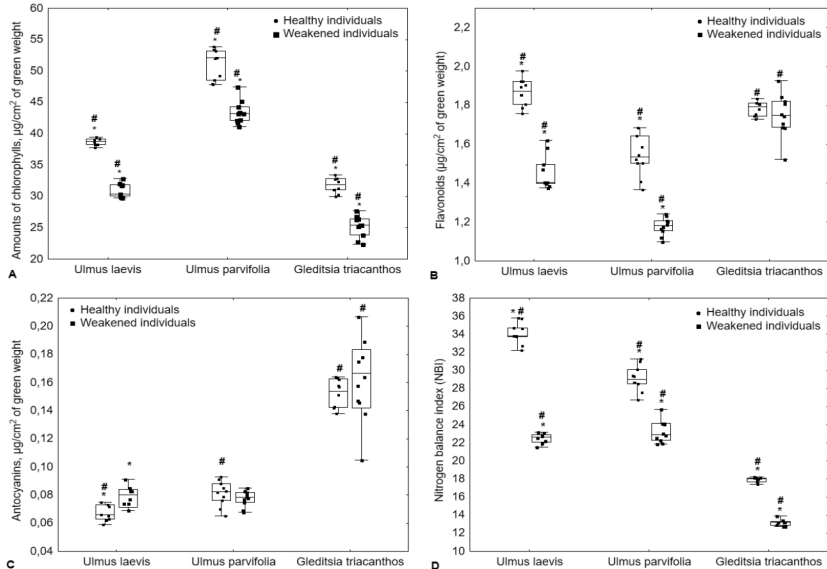


Fig. 1. The content in the plant leaves: A – amount of chlorophylls, B – flavonoids, C – anthocyanins, and D – NBI. Statistically significant differences between * – “healthy” and “weakened” plants, # – between species with different living conditions. The Mann-Whitney criterion at $p < 0.05$.

Thus, there was a specificity of species in the indicators characterizing the functioning of the pigment system of the studied species. The “weakened” *Ulmus parvifolia* showed lower chlorophylls and flavonoids and a balance index compared to “healthy” plants which is consistent with the living condition. At the same time, anthocyanins in “weakened” plants were significantly higher. It can be assumed that in this species, they are involved in the formation of adaptation to unfavorable environmental factors. A similar pattern was observed in *Ulmus laevis*, only the anthocyanins did not have any significant differences between different living conditions.

Features of the lamina structural organization

In “healthy” individuals of *Ulmus parvifolia*, the lamina area was 1.1 times larger compared to the “weakened” individual. This index in *Ulmus laevis* had no statistically significant differences between living conditions ($p > 0.05$). A similar situation was observed in *Gleditsia triacanthos*, as in *Ulmus parvifolia* (Fig. 5A). Maximum leaf thickness was in “healthy” individuals of *Ulmus parvifolia*, but there were no statistically significant differences with “weakened” individuals. In *Ulmus laevis*, significant differences were found between individuals of different living conditions ($p < 0.05$). Since *Gleditsia triacanthos* had species features of the lamina size and structure, the lamina area and thickness were smaller compared to representatives of the genus Elm, with significant differences between the living conditions ($p < 0.05$) (Fig. 5B).

Counting mesophyll cells per unit leaf surface area showed that the number of mesophyll cells was 1.4 and 1.6 times higher in “healthy” *Ulmus laevis* and *Ulmus parvifolia* individuals compared to “weakened” ones. The number of mesophyll cells in the “weakened” plants of *Gleditsia triacanthos* was higher than in the “healthy” plants of this species (Fig. 5C). According to the number of chloroplasts in mesophyll cells in the studied plant species, a general trend was noted. “Healthy” plants had 1.6 times more chloroplasts in their cells compared to “weakened” plants, but no significant interspecific differences were revealed ($p < 0.05$) (Fig. 5D).

The living conditions of woody plants, the content of photosynthetic system pigments, and the lamina structural organization depend on the implementation of molecular genetic mechanisms of response to negative abiotic factors. In this regard, a meta-analysis of genes and molecules associated with the work of the photosynthetic apparatus, which could lead to a “weakened” state of the studied trees in response to various environmental stressors inherent in the southern regions of Russia, was carried out.

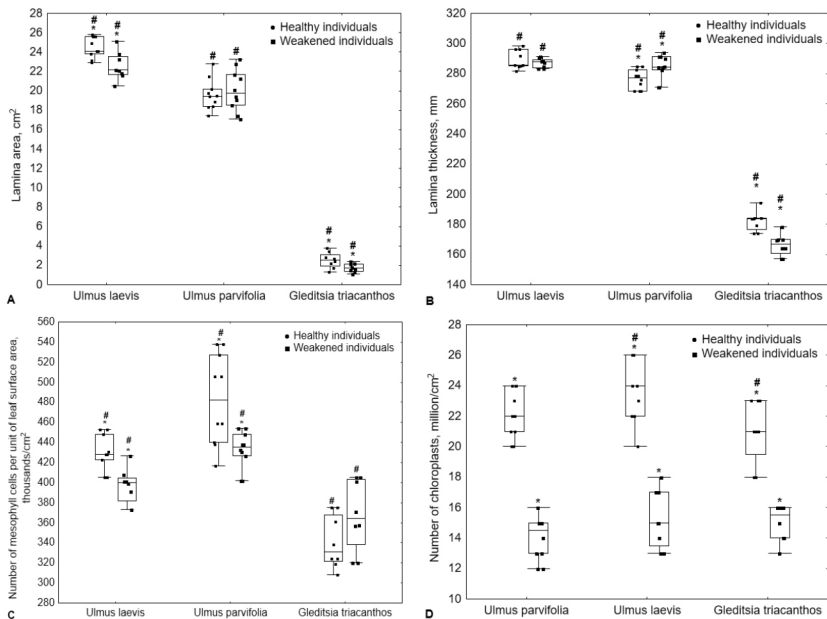


Fig. 2. The structure and morphology of plant leaves: A – lamina area, B – lamina thickness, C – the number of mesophyll cells per unit leaf surface area and D – the number of chloroplasts in the palisade mesophyll cells. Statistically significant differences between * – “healthy” and “weakened” plants, # – between species with different living conditions. The Mann-Whitney criterion at $p < 0.05$.

Discussion

An important indicator of standing timbers is their sanitary state. In some individuals, the formation of dead branch woods, various lamina necroses, and the total area of the affected leaves can reach 70%. This may be due to local growing conditions and the impact of biotopic factors of the arid zone.

Chlorophyll assessment in leaves of “healthy” and “impaired” plants agrees with the generally accepted patterns of the pigment apparatus of the photosynthetic system [14; 20; 16].

The authors found that the studied species contained an increased flavonoid in the leaves. This may be due to the fact that these plants live in drought conditions and flavonoids provide their protection [12]. Many authors confirm their role in protecting against unfavorable environmental factors (bacterial, viral, fungal infections, and oxidative stress) [4].

The authors identified features in *Ulmus laevis*, which had higher anthocyanins in “weakened” individuals compared to “healthy” plants. This may be due to the fact that plants compensate for the decrease in chlorophyll by increasing anthocyanins. This is consistent with the literature that anthocyanins are non-plastid pigments, localizing in cell vacuoles, and can protect leaves during photosynthesis by absorbing excessive photons. It has previously been shown that anthocyanins in many plant species reduce the photoinhibition frequency and also accelerate the photosynthetic apparatus recovery [15].

In “weakened” plants, the active state of the photosynthetic apparatus decreases due to a decrease in chlorophyll and an increase in flavonoids in the lamina. The assessment of the NBI of “weakened” plants confirmed these patterns [4; 15].

Changes in the leaf mesostructure of “weakened” trees that were identified in the study suggest that the lamina area, the number of mesophyll cells, and the number of chloroplasts in them are reduced compared to “healthy” individuals. This indicates structural rearrangements of the photosynthetic apparatus at the cell and chloroplast level [1]. This is a manifestation of one of the mechanisms of plant adaptation to water deficit in an arid climate [11]. When plants are exposed to an arid climate, a response is manifested as a decrease in photosynthetic tissue in the leaf.

During the study, interesting features of the thickness of the *Ulmus parvifolia* lamina were revealed. The thickness of the *Ulmus parvifolia* lamina in “weakened” individuals was higher than in “healthy” plants. This may be due to the fact that under arid stress, the proportion of photosynthetic tissue decreases by increasing the thickness of the cover tissues [22] and changing the structural organization of the leaf of this species.

The disruption or remodeling of physiological processes at the molecular genetic level may be one of the reasons for the appearance of “weakened” states of woody plants [13]. Stressful conditions lead to a decrease in the living condition of plants by increasing the intensity of oxidative processes spatially oriented in the plant organism tissues. A multi-level antioxidant system protects against oxidative stress, including drought and high temperatures. Along with other antioxidant system components, flavonoids protect plants from negative environmental factors [3]. Recent studies have shown that an increased concentration of certain flavonoids (kaempferol, naringenin) is associated with better plant resistance to moisture deficit and UV [6]. There is evidence that the accumulation of anthocyanins occurs both in photosynthetic and individual cells, where this process is not implemented, provides protection from sunlight, and

reduces the photosynthesis activity [25]. Synthesis of anthocyanins occurs in individual cells where photosynthesis is not taking place. Other authors note that anthocyanins are involved in the utilization of reactive oxygen intermediates. Reactive oxygen intermediates stimulate the synthesis of anthocyanins [23].

Two reasons may contribute to the decrease in photosynthesis: the lower CO₂ availability due to the closure of stomata [21] and the inhibition of light phase reactions, primarily photosystem II and, as a consequence, reduced production of ATP and NADP [17]. The synthesis of photosynthesis-related proteins is usually reduced under stress conditions; for example, this occurs with LHC-II (light-harvesting complex II), the amount of which correlates with the amount of chlorophyll [3].

The signaling pathways leading to a stress response contain common elements found in most plants. For example, cyclic AMP is known as a messenger of “cellular hunger”. The SnRK kinase group (SNF-related protein kinase) is usually involved in the stress response. There are three SnRK subgroups. SnRK1 kinases transmit an energy deficit signal, which leads to the intensification of catabolic processes and retardation of anabolic ones. Despite the similarity with SNF and AMPK, SnRK1 kinases are insensitive to AMP inhibition. SnRK1 phosphorylates C/S bZIP transcription factors that activate alternative metabolic pathways under stress [8]. SnRK2 kinases are activated by hyperosmotic stress when they are phosphorylated by RAF kinases [7]. These kinases are divided into three groups, one of which is activated by abscisic acid. Plant genotypes with SnRK2 overexpression have hypersensitivity to abscisic acid, accelerated growth, and biomass accumulation suggesting that some of these kinases stimulate plant growth under normal conditions [24]. ABA (abscisic acid) is one of the main phytohormones involved in signal conducting under stress. The ABA-PYL complex binds PP2C, an inhibitor protein of several compounds, thus releasing SnRK2 and SnRK1 from its bonds. One of the main effects of abscisic acid is to retard plant growth, and ABA hypersensitivity mutations increase survival under stress and reduce growth rate under normal conditions [5]. SnRK3 kinases are involved in the response to various types of stress, especially salt stress. SnRK3 have a self-inhibitory domain normally bound to the SCaBP-SnRK3 complex. Ca₂⁺ binding releases the complex and allows the phosphorylation of various ion channels [26].

All the above-mentioned genes and molecules have a direct or indirect impact on the photosynthetic apparatus of the plant cell in normal conditions and under stress of different natures, and molecular and genetic adaptation mechanisms. An important note is that the genome of the studied plants has not been

sequenced at this time and the analysis concerns general possible mechanisms inherent in all woody and shrub plants. In this regard, it is necessary to further search for DNA markers of these genes and their degree of expression involved in the mechanisms of adaptation to unfavorable environmental factors.

Thus, in “weakened” plants of the tree plant species under study, significant changes occur in the leaf pigment apparatus of the photosynthetic system and the structural organization. The involvement of various genes and their polymorphisms in the cell photosynthetic apparatus and adaptation to unfavorable environmental factors remains an understudied area and requires further experimental research.

Conclusion

The study revealed new regularities in the work of the pigment apparatus of the photosynthetic system and leaf structure organization in “healthy and weakened” plants under arid climate conditions.

The adaptation of the pigment apparatus of the synthetic system of “weakened” individuals of the genus Elm was manifested in an increase in leaf anthocyanins. The role of anthocyanins in the mechanism of adaptation to the arid climate remains incompletely understood. In general, the studied species of woody plants, except for *Ulmus parvifolia*, had regular changes in the structural organization of leaves. In the native *Ulmus parvifolia*, perhaps another mechanism of adaptation to unfavorable factors was found, consisting in an increase in the lamina thickness, and hence a change in the pigment apparatus of photosynthetic system functioning.

The primary analysis of genes, proteins, and metabolites has shown many unresolved issues in the photosynthetic apparatus related to the adaptation mechanisms to unfavorable environmental factors at the molecular-genetic level.

The study of the leaf pigment apparatus of the photosynthetic system and structural organization of woody plants growing in an arid climate and used in forest amelioration can be used to obtain new genotypes with economically valuable features, bioindication, and selection of optimal regimes for their cultivation.

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and cultivated plant genes responsible for adaptation to unfavorable environmental factors and productivity”.

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