DOI: 10.12731/2658-6649-2025-17-3-1118 **EDN: ZFIWHO**
UDC 577.2:630

Scientific Reviews

GENES OF WOODY PLANTS INVOLVED IN THE FORMATION OF DROUGHT AND SALT TOLERANCE

A.V. Tretaykova, V.O. Malov, P.A. Krylov

Abstract

Background. The study of the molecular mechanisms regulating gene expression in response to various types of stress in woody plants, particularly drought and high soil salinity, is becoming a necessary condition for breeding or creating new resistant cultivars, forms, and hybrids with specific economically valuable traits. Currently, the extent and depth of studying the genes involved in drought and high soil salinity tolerance in woody plants is extremely low compared to agricultural crops, which significantly complicates and slows down the breeding process that should be based on achievements in molecular biology and genetics.

Purpose. To summarize, describe, and select potential genes involved in the formation of drought and salt tolerance in a range of woody plants used in agroforestry and protective afforestation, growing in areas with arid and semi-arid climates.

Materials and methods. To achieve the research objectives, more than 250 scientific sources were reviewed and a search in open gene databases was conducted to identify genes and their homologues databases using the BLAST program associated with drought and salt tolerance in woody plants used in agroforestry and protective afforestation.

Results. This study summarizes and describes 28 genes associated with drought tolerance and 14 genes associated with salt tolerance in the genera *Quercus* and *Populus*, and the families *Fabaceae*, *Rosaceae*, and *Oleaceae*.

Conclusion. Thus, as a result of the analysis of genes associated with drought and salt tolerance in woody plants, key targets have been identified that can serve as a basis for molecular selection, followed by the identification of potential markers and their possible association with economically valuable traits.

Keywords: drought tolerance genes; salt tolerance genes; woody plants, marker-assisted selection; agroforestry; review

For citation. Tretaykova, A. V., Malov, V. O., & Krylov, P. A. (2025). Genes of woody plants involved in the formation of drought and salt tolerance. *Siberian Journal of Life Sciences and Agriculture*, *17*(3), 614-633. https://doi.org/10.12731/2658-6649-2025-17-3-1118

Научные обзоры

ГЕНЫ ДРЕВЕСНО-КУСТАРНИКОВЫХ РАСТЕНИЙ, ВОВЛЕЧЕННЫЕ В ФОМИРОВАНИЕ УСТОЙЧИВОСТИ К ЗАСУХЕ И ЗАСОЛЕННОСТИ ПОЧВ

А.В. Третьякова, В.О. Малов, П.А. Крылов

Аннотация

Обоснование. Изучение молекулярных механизмов регуляции генов в ответ на различие типы стрессов у древесно-кустарниковых растений, в частности засухи и высокой засоленности почв, становятся обязательным условием для выведения или создания новых устойчивых сортов, форм и гибридов с заданными хозяйственно-ценными признаками. В настоящий момент степень и глубина изучения генов, вовлеченных в формирование устойчивости к засухе и высокой засоленности почв у древесно-кустарниковых растений крайне низка по сравнению с сельскохозяйственными растениями, что значительно затрудняет и замедляет селекционный процесс, который должен базироваться на достижениях молекулярной биологии и генетики.

Цель. Обобщить, описать и отобрать потенциальные гены, вовлеченные в формирование засухо- и солеустойчивости у ряда древесно-кустарниковых растений, используемых в агролесомелиорации и защитном лесоразведении, произрастающий на территориях с аридным и субаридным климатом.

Материалы и методы. Для достижения поставленной цели исследования был произведён обзор свыше 250 научных источников, поиск в открытых базах данных генов и их гомологов с помощью программы BLAST, связанных с формированием засухо- и солеустойчивости у древесно-кустарниковых растений, используемых в агролесомелиорации и защитном лесоразведении.

Результаты. В данной работе обобщены и описаны 28 генов, вовлеченных в формирование засухоустойчивости, и 14 генов с солеустойчивостью у родов *Quercus, Populus* и семейств *Fabaceae, Rosaceae, Oleaceae*.

Заключение. Таким образом, в результате анализа генов, связанных с формированием засухо- и солеустойчивости у древесно-кустарниковых растений, обозначены основные мишени, которые могут быть взяты за основу для молекулярной селекции с последующим выявлением возможных маркеров и их возможной связи с хозяйственно-ценными признаками.

Ключевые слова: гены засухоустойчивости; гены солеустойчивости; древесно-кустарниковые растения; маркерная селекция; агролесомелиорация; обзор

Для цитирования. Третьякова, А. В., Малов, В. О., & Крылов, П. А. (2025). Гены древесно-кустарниковых растений, вовлеченные в формирование устойчивости к засухе и засоленности почв. *Siberian Journal of Life Sciences and Agriculture*, *17*(3), 614-633. https://doi.org/10.12731/2658-6649-2025-17-3-1118

Introduction

Woody plants play a crucial role in agroforestry, protecting crops from various negative impacts and fighting against desertification [3; 14; 38; 49]. Studying the molecular mechanisms that regulate gene expression in response to different types of stress, such as drought and high soil salinity, is extremely important for plants, including woody plants [15; 17; 53; 57; 63]. Open database resources such as Genome (NCBI) and Phytozome13 (Department of Energy's Joint Genome Institute) provide complete genomic sequences, but there is a lack of information on the genomes of woody plants, while information on agricultural plant genomes prevails. At the same time, the limited knowledge of genomes and genes in woody plants, especially genes involved in responding to adverse environmental factors, makes the selection process more complex and protracted, as the success in creating new varieties with economically valuable traits depends on the development of molecular techniques and genetic knowledge [1; 25].

Based on the above, there is currently a need to identify genes responsible for stress tolerance in woody plants widely used in agroforestry practices, and to create new varieties with desired agronomic traits.

Purpose. To summarize, describe, and select potential genes involved in the formation of drought and salt tolerance in a range of woody plants used in agroforestry and protective afforestation, growing in areas with arid and semi-arid climates.

Materials and methods

The search for genes of interest associated with drought and salt tolerance was conducted in the open database PubMedCentral (NCBI, USA). Ar-

ticles were searched using synonymous constructs [(“gene”) AND (“plants” OR “organism”) AND “salt”[All Fields]) AND resistant [All Fields] OR “droughts”[All Fields] AND resistance [All Fields] AND arid [All Fields] AND zone [All Fields])]. The “organism” section specified the studied plant in English/Latin.

Further investigation of information on each potential gene of interest was conducted, including functions according to the Gen RIF section and articles in the PubMed database. *Arabidopsis thaliana* L., a well-studied model plant at the molecular-genetic level, was used as the model organism. Subsequently, homologs of these genes were searched among taxa of interest in the open database Gene (NCBI, USA) using the synonymous construct (Gene name) AND Taxon of interest name [Organism]. Homologues of genes were searched using the BLAST program. Genera and families of woody shrubs and trees were taken from the forest seed base organization program for protective forest management in the Southern region of Russia [2]. The taxa of interest included the oak genus (*Quercus*), poplar genus (*Populus*), legume family (*Fabaceae*), rose family (*Rosaceae*), and olive family (*Oleaceae*).

Results of the research and discussion

As a result of the conducted search, 28 genes associated with drought tolerance and 14 genes associated with salt tolerance were identified. Figure 1 presents a histogram showing the identified genes and their homologs in the studied taxa. Since *A. taliana* is a model organism, it had the highest number of genes related to drought and salt tolerance. Genes and their homologs associated with drought tolerance were most commonly found in the *Fabaceae* family, and least commonly were found in the genus *Quercus* and in the *Oleaceae* family.

The genus *Populus* and the *Fabaceae* family had slightly more potential genes identified compared to the genus Quercus, the *Rosaceae* family, and the *Oleaceae* family. The Fabaceae family is one of the largest and most diverse plant families, which includes many species adapted to arid conditions [21], which may explain the number of identified genes and homologs. Other families and species are presumably less studied in this regard.

Tables 1 and 2 present the identified potential genes and homologs in the woody plants. Table 1 shows genes associated with drought tolerance, and table 2 shows genes associated with salt tolerance.

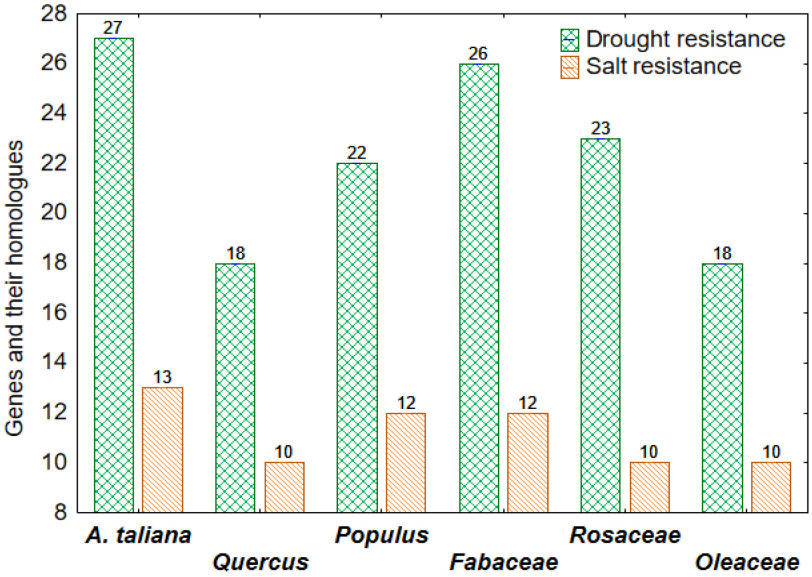

Figure 1. The number of identified genes and their homologs in the genus *Quercus*, genus *Populus*, *Fabaceae* family, *Rosaceae* family, and *Oleaceae* family.

Table 1.

Potential genes associated with drought tolerance

Gene name	Physiological processes	Taxa
	Enzymes	
ABA3	Sulfur metabolism, abscisic acid biosynthesis, drought tolerance [18]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
ABI1	Negative regulator of stomatal closure, negative regulator of drought response [32], growth, stomatal function [4]	*Arabidopsis taliana, Populus, Fabaceae, Rosaceae, Oleaceae*
COP1	Suppression of growth in light, drought tolerance, control of flowering, photoperiodism [26, 37]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
EDS1	Drought tolerance, response to pathogen invasion, growth regulation [51]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
HA1	Proton transport across the cytoplasmic membrane, ATPase, stomatal closure in response to drought [29]	*Arabidopsis taliana, Populus, Fabaceae, Rosaceae, Oleaceae*
KIN11 (SNRK1.2)	Sucrose metabolism, hypocotyl growth, drought tolerance [36]	*Arabidopsis taliana, Quercus robur, Populus, Fabaceae, Rosaceae, Oleaceae*

MPK6	Drought tolerance [60], response to oxidative stress [56], response to osmotic stress [30]	*Arabidopsis taliana, Fabaceae*
NCED3	Drought tolerance, abscisic acid biosynthesis [20].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae*
PAD4	Drought tolerance, response to pathogen invasion, growth regulation [51].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
PLDAL-PHA1	Drought tolerance, stomatal movement [33], negative regulator of cold response [40]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
PLDDEL-TA	Negative regulator of drought tolerance, recovery after freezing, reactive oxygen species metabolism [13]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
RbohD	Regulation of reactive oxygen species, response to various stress types, drought tolerance, salt tolerance [31]	*Arabidopsis taliana, Quercus robur, Populus, Fabaceae, Rosaceae*
SAL1	Negative regulator of drought tolerance [59], sulfur assimilation, response to cold, degradation of small RNAs [18]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
SIZ1	Plant immunity, drought tolerance, response to low temperatures, growth regulation [35]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
YUC6	Drought tolerance, regulation of reactive oxygen species [9]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
Transcription factors		
ABF3	Response to various stress types, drought tolerance, salt tolerance, chlorophyll degradation [16]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
ABI4	Drought tolerance, response to various stress types, regulation of lateral root formation [26, 46], regulation of flowering [47]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
ABI5	Drought tolerance [34], regulation of flowering [58]	*Arabidopsis taliana, Fabaceae*
AGL20	Flowering under drought conditions, drought tolerance [42]	*Arabidopsis taliana, Rosaceae*
AREB1	Activation of genes related to drought response, response to salt stress [61]	*Quercus robur, Populus, Fabaceae*
DREB2A	Transcription factor activating drought response genes, response to high temperature [44].	*Arabidopsis taliana, Fabaceae, Rosaceae*
LSD1	Drought tolerance, response to pathogen invasion, growth regulation [51]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
MYB96	Drought tolerance, response to cold, response to various stress types, seed germination [26]	*Arabidopsis taliana*

TOC1	Drought tolerance, photoperiodism [27]	*Arabidopsis taliana, Fabaceae*
Other proteins		
GI regulatory co-chaperone	Photoperiodism, control of flowering, carbohydrate metabolism, drought tolerance [19]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
GRP7 RNA-binding protein	Drought tolerance [62], stomatal closure, response to cold, circadian rhythms [45]	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
NHX1 ion channel	Sodium ion transport, drought tolerance, salt tolerance [6]	*Arabidopsis taliana, Populus, Fabaceae, Rosaceae, Oleaceae*

The identified protein of the alpha-beta hydrolase family, PAD4, tightly interacts with the proteins EDS1 and LSD1, regulating physiological processes such as response to moisture deficiency, growth and biomass accumulation, as well as defense against pathogens. These functions have been well studied in Arabidopsis thaliana, and PAD4 homologs are present in plants of interest for agroforestry. Another important DNA-binding protein, ABI4, is involved in abscisic acid signaling, regulating seed germination and the expression of the NA+/K+ channel HKT1, which is important for the stress response. Its homologues are also found in plants of interest. The multidomain protein COP1 regulates photoperiodism, drought resistance, and stomatal closure. NHX1 is an ion antiporter channel, transporting protons and sodium ions, essential for salt and drought tolerance. Homologs of this protein are absent in the genome of *Q. robur*. SIZ1 attaches the small ubiquitin-like modifier SUMO to proteins, participating in signaling pathways in response to drought and cold, regulating growth. HA1 is an ATPase, transporting protons across the cytoplasmic membrane, important for stomatal closure under moisture deficiency. Mutations in this gene reduce this function. GI, a regulator of circadian rhythms and morphogenesis, also plays a role in the response to moisture deficiency. AGL20 regulates flowering in drought conditions through the gibberellin pathway, while the transcription factor TOC1 affects histone modification and chromatin organization. NCED3 catalyzes the biosynthesis stage of abscisic acid in chloroplasts and has numerous homologs in plants of interest. Phospholipase delta PLDDELTA is involved in the response to cold and drought tolerance. ABI1, an abscisic acid antagonist, also has no homologs in *Q. robur*. MPK6 is a MAP kinase involved in signaling pathways related to pathogen invasion, oxidative stress responses, and moisture deficiency with few homologs. ABI5, a critical participant in the abscisic acid response, also has few homologs. YUC6, a flavin-binding monooxygenase, regulates active oxygen species content and stress

tolerance, with numerous homologs. ABA3 sulfotransferase is involved in the final stage of abscisic acid biosynthesis. GRP7, an RNA-binding protein, regulates circadian rhythms and immunity, with many homologs. Phospholipase D alpha PLDALPHA1 is a positive regulator of abscisic acid and an antagonist of the cold response. KIN11 (SNRK1.2) phosphorylates bZIP transcription factors and has many homologs. Lastly, RbohD is a NADPH oxidase that regulates the active oxygen species content. Homologs of this protein are numerous but not found in the *Oleaceae* family.

The transcription factor SAL1has phosphatase activity and is involved in sulfur assimilation. Similar to previously studied proteins, it has numerous homologs in plant genomes of interest. Mutants of this gene are drought-resistant but sensitive to cold. DREB1A, a DNA-binding transcription factor activating drought response genes, is present in plants of interest but absent in the genome of *Q. robur*. AREB, a stress-activated bZIP transcription factor, has few homologs in the genomes of interest. Other important transcription factors include ABF3 and DREB2A, which also play a key role in stress response, activating drought and high temperature response genes. The transcription factor MYB96, activated by abscisic acid, has no homologs in the genomes of interest.

Table 2.

Potential genes associated with salt tolerance

Gene name	Physiological processes	Taxa
	Ion channels	
CLC-A	Transport of nitrates [12] and chlorides across the tonoplast [22].	*Arabidopsis taliana, Fabaceae*
CLC-B	Transport of nitrate anions across the tonoplast [55], transport of chloride anions [22].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
CLC-C	Transport of chloride anions across the tonoplast, stomatal movement [24].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
EIN2 translation regulator, ion channel	Leaf senescence, transport of metal cations, regulation of salt stress [28].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
HKT1	Salt tolerance, transport of sodium ions, potassium ions [10].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
NHX1	Transport of sodium ions, drought resistance, salt tolerance [50].	*Arabidopsis taliana, Populus, Fabaceae, Rosaceae, Oleaceae*
SOS1	Salt tolerance, extrusion of sodium cations from the cell [5, 64].	*Arabidopsis taliana, Populus*

Enzymes		
CDPK	Salt tolerance, resistance to excess light [29].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
PCS1	Chelation of metal cations [11].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
RbohF	Salt tolerance, degradation of H_2O_2, regulation of reactive oxygen species [7].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
Transcription factors		
AREB1	Response to abiotic stress factors, initiation of transcription [23].	*Quercus, Populus, Fabaceae*
STZ	Salt tolerance, initiation of transcription, response to various types of stress [43].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*
Other proteins		
AZI1 protein-binding protein	Negative regulator of salt tolerance, mutants with overexpression are hypersensitive to salt stress [39].	*Arabidopsis taliana*
MT2A metallothionein	Binding and immobilization of metal ions in metal-protein clusters [15].	*Arabidopsis taliana, Quercus, Populus, Fabaceae, Rosaceae, Oleaceae*

HKT1 is a transmembrane transporter of sodium and potassium cations, expressed in the parenchyma surrounding vessels in *A. thaliana*. Homologs of this protein have been found in all sequenced taxa, indicating its importance for plant survival. Ion transport across the cell membrane is also facilitated by NHX1, an ion channel transporting sodium cations. This channel is widespread in the plant kingdom, with homologs even found in *Q. robur*. CLC-A, CLC-B, and CLC-C - anion channels located in the vacuole membrane - play an important role in ion balance regulation. CLC-A and CLC-B transport chloride and nitrate anions, while CLC-C transports only chloride anions and is also involved in stomatal movement regulation. Both channels are present in many plants, with the exception of CLC-A in *Q. robur*. SOS1, an ion channel that extrudes sodium cations from the cell, is critically important for salt tolerance. Mutants with impaired SOS1 function are hypersensitive to salt stress. A SOS1 homolog has only been found in the genus *Populus*, indicating its evolutionary novelty or specialization.

Another important detoxification mechanism is the binding and immobilization of metals. PCS1, phytochelatin synthase 1, synthesizes short peptides called phytochelatins, which bind to metal cations and convert them into a less

dangerous form. MT2A, metallothionein, also plays a role in detoxification by binding to metal cations and immobilizing them in metal-protein clusters. Homologs of both PCS1 and MT2A have been found in all sequenced taxa, which highlights their role in adaptation to adverse factors.

Equally important is the regulation of gene activity in response to stress. AREB1, a transcription factor characterized in the tomato genome (*Solanum lycopersicum* L.), is involved in the response to various types of stress. However, homologs of this gene have been found in only a small number of genomes, which may indicate its specialized role. Another transcription factor, STZ, which contains a zinc finger domain, is involved in the response to salt stress and other abiotic stress types, and has many homologs in genomes of interest.

Regulation of reactive oxygen species levels is another crucial mechanism of stress adaptation. RbohF, an NADPH oxidase, regulates reactive oxygen species content and is involved in degradation of hydrogen peroxide. Homologs of this protein have been found in many genomes, highlighting its significance in plant defense mechanisms.

CDPK, calcium-dependent protein kinase, is involved in signal transduction in response to various abiotic stress types. It has numerous homologs in plant genomes, indicating its central role in adaptive processes. EIN2, a metal cation transporter, influences salt tolerance, leaf senescence, and participates in the ethylene signaling pathway. It is also found in the genomes of many plants. Another protein, AZI1, is involved in signaling pathways in response to cold, pathogen invasion, and other stress types. Overexpression mutants of AZI1 are hypersensitive to salt stress. Homologs of this protein have not been found in many genomes, suggesting a specific role.

Genes involved in the regulation of the abscisic acid signaling pathway are critically important for plant adaptation to stress, and therefore represent a promising target for breeding and genetic engineering [8; 54]. In this case, the following genes are of interest: *ABI1*, *ABI4*, *ABI5*, *AREB1*, *NCED3*, *ABA3*. Additionally, genes involved in regulating stress responses, such as *DREB1A*, *DREB2A*, *MPK6*, *KIN11*, *RbohD*, and *YUC6*, are also significant [48]. Among the genes involved in salt tolerance, the most important role is played by genes involved in ion transfer, for example, *HKT1, SOS1, CLC-A, CLC-B, CLC-C, a*nd *NHX1*. The transcription factor AREB1, activated during stress and regulating the expression of genes related to salt tolerance, is also of interest. However, the role of each gene in drought and salt stress may vary depending on the plant species, environmental conditions, and other factors [52]. Some genes may interact with each other, creating complex regulatory networks [41]. Further

research is important to fully understand the role of these genes in combating drought and soil salinity.

Conclusion

Thus, the study summarized and described 28 genes involved in drought tolerance and 14 genes involved in salt tolerance in genera *Quercus*, *Populus*, and families *Fabaceae*, *Rosaceae*, *Oleaceae*. Analysis of genes associated with drought and salt tolerance in woody plants identified key potential target genes that can be used as a basis for molecular selection with the subsequent identification of potential markers and their possible link to economically valuable traits. Further research will deepen the understanding of the molecular mechanisms underlying salt and drought tolerance in woody plants.

Conflict of interest information. The authors declare that there is no conflict of interest.

Sponsorship information. The research was carried out within the framework of the state task of the Ministry of Science and Higher Education of the Russian Federation No. FNFE-2022-0022 “Search and management of patterns of expression of forest and cultural plant genes responsible for adaptation to environmental hazards and productivity”.

References / Список литературы

1. Belyaev, A. I., Krylov, P. A., Pugacheva, A. M., & Derevshchikova, L. V. (2023). Analysis of genomes of tree and shrub plants used in agroforestry reclamation in southern regions of Russia. *Proceedings of the Nizhnevolzhsky Agro-University Complex: Science and Higher Professional Education*, *70*(*2*), 30-42 (Беляев, А. И., Крылов, П. А., Пугачева, А. М., & Деревщикова, Л. В. (2023). Анализ наличия геномов древесно-кустарниковых растений, используемых в агролесомелиорации южных регионов России. *Известия Нижневолжского агроуниверситетского комплекса: Наука и высшее профессиональное образование, 70*(2), 30-42). https://doi.org/10.32786/2071-9485-2023-02-03. EDN: https://elibrary.ru/ttkjca
2. Kryuchkov, S. N., & Matiss, G. Ya. (2014). *Forest planting in arid conditions*. Volgograd: VNIALMI. 300 p. (Крючков, С. Н., & Матисс, Г. Я. (2014). *Лесоразведение в засушливых условиях*. Волгоград: ВНИАЛМИ. 300 с.) ISBN: 5-900761-29-0. EDN: https://elibrary.ru/ysbxrb
3. Kulik, K. N., Belyaev, A. I., & Pugacheva, A. M. (2023). Role of protective forest planting in combating drought and desertification of agrolandscapes. *Arid Eco-*

systems, *94*(*1*), 4-14 (Кулик, К. Н., Беляев, А. И., & Пугачёва, А. М. (2023). Роль защитного лесоразведения в борьбе с засухой и опустыниванием агроландшафтов. *Аридные экосистемы, 94*(1), 4-14). https://doi.org/10.24412/1993-3916-2023-1-4-14. EDN: https://elibrary.ru/cszxwa

4. Arend, M., Schnitzler, J. P., Ehlting, B., Hänsch, R., Lange, T., Rennenberg, H., Himmelbach, A., Grill, E., & Fromm, J. (2009). Expression of the Arabidopsis mutant ABI1 gene alters abscisic acid sensitivity, stomatal development, and growth morphology in gray poplars. *Plant Physiol., 151*(4), 2110-2119. https://doi.org/10.1104/pp.109.144956
5. Ariga, H., Katori, T., Yoshihara, R., Hase, Y., Nozawa, S., Narumi, I., Iuchi, S., Kobayashi, M., Tezuka, K., Sakata, Y., Hayashi, T., & Taji, T. (2013). Arabidopsis sos1 mutant in a salt-tolerant accession revealed an importance of salt acclimation ability in plant salt tolerance. *Plant Signal Behav., 8*(7), e24779. https://doi.org/10.4161/psb.24779
6. Asif, M. A., Zafar, Y., Iqbal, J., et al. (2011). Enhanced Expression of AtNHX1, in Transgenic Groundnut (Arachis hypogaea L.) Improves Salt and Drought Tolerence. *Mol Biotechnol., 49*, 250-256. https://doi.org/10.1007/s12033-011-9399-1. EDN: https://elibrary.ru/ozmfnn
7. Ben Rejeb, K., Benzarti, M., Debez, A., Bailly, C., Savouré, A., & Abdelly, C. (2015). NADPH oxidase-dependent H2O2 production is required for salt-induced antioxidant defense in Arabidopsis thaliana. *J Plant Physiol, 174*, 5-15. https://doi.org/10.1016/j.jplph.2014.08.022
8. Chen, K., Li, G. J., Bressan, R. A., Song, C. P., Zhu, J. K., & Zhao, Y. (2020). Abscisic acid dynamics, signaling, and functions in plants. *J Integr Plant Biol., 62*(1), 25-54. https://doi.org/10.1111/jipb.12899. EDN: https://elibrary.ru/yxwwtp
9. Cheol Park, H., Cha, J. Y., & Yun, D. J. (2013). Roles of YUCCAs in auxin biosynthesis and drought stress responses in plants. *Plant Signal Behav., 8*(6), e24495. https://doi.org/10.4161/psb.24495
10. Chu, M., Chen, P., Meng, S., Xu, P., & Lan, W. (2021). The Arabidopsis phosphatase PP2C49 negatively regulates salt tolerance through inhibition of AtHKT1;1. *J Integr Plant Biol., 63*(3), 528-542. https://doi.org/10.1111/jipb.13008. EDN: https://elibrary.ru/voblyu
11. Clemens, S. (2001). Molecular mechanisms of plant metal tolerance and homeostasis. *Planta, 212*(4), 475-486. https://doi.org/10.1007/s004250000458. EDN: https://elibrary.ru/atgnqz
12. De Angeli, A., Monachello, D., Ephritikhine, G., Frachisse, J. M., Thomine, S., Gambale, F., & Barbier-Brygoo, H. (2006). The nitrate/proton antiporter

AtCLCa mediates nitrate accumulation in plant vacuoles. *Nature, 442*(7105), 939-942. https://doi.org/10.1038/nature05013

13. Distéfano, A. M., Valiñas, M. A., Scuffi, D., Lamattina, L., Ten Have, A., García-Mata, C., & Laxalt, A. M. (2015). Phospholipase D δ knock-out mutants are tolerant to severe drought stress. *Plant Signal Behav., 10*(11), e1089371. https://doi.org/10.1080/15592324.2015.1089371
14. Eldridge, D. J., Ding, J., Dorrough, J., et al. (2024). Hotspots of biogeochemical activity linked to aridity and plant traits across global drylands. *Nat. Plants, 10*, 760-770. https://doi.org/10.1038/s41477-024-01670-7. EDN: https://elibrary.ru/vpfehm
15. Elliott, K. J., & Swank, W. T. (1994). Impacts of drought on tree mortality and growth in a mixed hardwood forest. *Journal of vegetation science, 5*(2), 229-236. https://doi.org/10.2307/3236155
16. Gao, S., Gao, J., Zhu, X., Song, Y., Li, Z., Ren, G., Zhou, X., & Kuai, B. (2016). ABF2, ABF3, and ABF4 Promote ABA-Mediated Chlorophyll Degradation and Leaf Senescence by Transcriptional Activation of Chlorophyll Catabolic Genes and Senescence-Associated Genes in Arabidopsis. *Mol Plant, 9*(9), 1272-1285. https://doi.org/10.1016/j.molp.2016.06.006
17. Martins, G. de F., Antonio, L. de O., Freire, C. F., Bakke, I. A., & França, D. F. (2023). Gas exchange and initial growth of Mimosa tenuiflora (Willd.) Poir. plants under salinity conditions. *Concilium, 23*(2), 555-569. https://doi.org/10.53660/clm-792-23a47
18. Gy, I., Gasciolli, V., Lauressergues, D., Morel, J. B., Gombert, J., Proux, F., Proux, C., Vaucheret, H., & Mallory, A. C. (2007). Arabidopsis FIERY1, XRN2, and XRN3 are endogenous RNA silencing suppressors. *Plant Cell, 19*(11), 3451-3461. https://doi.org/10.1105/tpc.107.055319
19. Han, Y., Zhang, X., Wang, W., Wang, Y., & Ming, F. (2013). The suppression of WRKY44 by GIGANTEA-miR172 pathway is involved in drought response of Arabidopsis thaliana. *PLoS One, 8*(11), e73541. https://doi.org/10.1371/journal.pone.0073541
20. Hao, G. P., Zhang, X. H., Wang, Y. Q., Wu, Z. Y., & Huang, C. L. (2009). Nucleotide variation in the NCED3 region of Arabidopsis thaliana and its association study with abscisic acid content under drought stress. *J Integr Plant Biol, 51*(2), 175-183. https://doi.org/10.1111/j.1744-7909.2008.00786.x
21. Hasanuzzaman, M., Araújo, S., & Gill, S. S. (2020). The plant family fabaceae. https://doi.org/10.1007/978-981-15-4752-2
22. Hechenberger, M., Schwappach, B., Fischer, W. N., Frommer, W. B., Jentsch, T. J., & Steinmeyer, K. (1996). A family of putative chloride channels from

Arabidopsis and functional complementation of a yeast strain with a CLC gene disruption. *J Biol Chem, 271*(52), 33632-33638. https://doi.org/10.1074/jbc.271.52.33632. EDN: https://elibrary.ru/yciqrm

23. Hsieh, T. H., Li, C. W., Su, R. C., Cheng, C. P., Sanjaya, Tsai, Y. C., & Chan, M. T. (2010). A tomato bZIP transcription factor, SlAREB, is involved in water deficit and salt stress response. *Planta, 231*(6), 1459-1473. https://doi.org/10.1007/s00425-010-1147-4. EDN: https://elibrary.ru/nzitmr
24. Jossier, M., Kroniewicz, L., Dalmas, F., Le Thiec, D., Ephritikhine, G., Thomine, S., Barbier-Brygoo, H., Vavasseur, A., Filleur, S., & Leonhardt, N. (2010). The Arabidopsis vacuolar anion transporter, AtCLCc, is involved in the regulation of stomatal movements and contributes to salt tolerance. *Plant J, 64*(4), 563-576. https://doi.org/10.1111/j.1365-313x.2010.04352.x. EDN: https://elibrary.ru/pmabmj
25. Kang, K. K., & Cho, Y. G. (2022). Genetic Research and Plant Breeding. *Genes (Basel), 14*(1), 51. https://doi.org/10.3390/genes14010051. EDN: https://elibrary.ru/flfiim
26. Lee, K., & Seo, P. J. (2015). Coordination of seed dormancy and germination processes by MYB96. *Plant Signal Behav, 10*(9), e1056423. https://doi.org/10.1104/pp.15.00162
27. Legnaioli, T., Cuevas, J., & Mas, P. (2009). TOC1 functions as a molecular switch connecting the circadian clock with plant responses to drought. *EMBO J, 28*(23), 3745-3757. https://doi.org/10.1038/emboj.2009.297
28. Lei, G., Shen, M., Li, Z. G., Zhang, B., Duan, K. X., Wang, N., Cao, Y. R., Zhang, W. K., Ma, B., Ling, H. Q., Chen, S. Y., & Zhang, J. S. (2011). EIN2 regulates salt stress response and interacts with a MA3 domain-containing protein ECIP1 in Arabidopsis. *Plant Cell Environ, 34*(10), 1678-1692. https://doi.org/10.1111/j.1365-3040.2011.02363.x
29. Liu, J., Elmore, J. M., Fuglsang, A. T., Palmgren, M. G., Staskawicz, B. J., & Coaker, G. (2009). RIN4 functions with plasma membrane H±ATPases to regulate stomatal apertures during pathogen attack. *PLoS Biol, 7*(6), e1000139. https://doi.org/10.1371/journal.pbio.1000139
30. Liu, X. M., Nguyen, X. C., Kim, K. E., Han, H. J., Yoo, J., Lee, K., Kim, M. C., Yun, D. J., & Chung, W. S. (2013). Phosphorylation of the zinc finger transcriptional regulator ZAT6 by MPK6 regulates Arabidopsis seed germination under salt and osmotic stress. *Biochem Biophys Res Commun, 430*(3), 1054-1059. https://doi.org/10.1016/j.bbrc.2012.12.039
31. Liu, Z., Guo, C., Wu, R., Hu, Y., Zhou, Y., Wang, J., Yu, X., Zhang, Y., Bawa, G., & Sun, X. (2022). FLS2-RBOHD-PIF4 Module Regulates Plant Response

to Drought and Salt Stress. *Int J Mol Sci, 23*(3), 1080. https://doi.org/10.3390/ijms23031080. EDN: https://elibrary.ru/rzcxnp

32. Luo, X., Li, C., He, X., Zhang, X., & Zhu, L. (2020). ABA signaling is negatively regulated by GbWRKY1 through JAZ1 and ABI1 to affect salt and drought tolerance. *Plant Cell Rep, 39*(2), 181-194. https://doi.org/10.1007/s00299-019-02480-4. EDN: https://elibrary.ru/fpjfhg
33. Mane, S. P., Vasquez-Robinet, C., Sioson, A. A., Heath, L. S., & Grene, R. (2007). Early PLDalpha-mediated events in response to progressive drought stress in Arabidopsis: a transcriptome analysis. *J Exp Bot, 58*(2), 241-252. https://doi.org/10.1093/jxb/erl262
34. Mittal, A., Gampala, S. S., Ritchie, G. L., Payton, P., Burke, J. J., & Rock, C. D. (2014). Related to ABA-Insensitive3(ABI3)/Viviparous1 and AtABI5 transcription factor coexpression in cotton enhances drought stress adaptation. *Plant Biotechnol J, 12*(5), 578-589. https://doi.org/10.1111/pbi.12162
35. Miura, K., Okamoto, H., Okuma, E., Shiba, H., Kamada, H., Hasegawa, P. M., & Murata, Y. (2013). SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in Arabidopsis. *Plant J, 73*(1), 91-104. https://doi.org/10.1111/tpj.12014
36. Mizoguchi, M., Umezawa, T., Nakashima, K., Kidokoro, S., Takasaki, H., Fujita, Y., Yamaguchi-Shinozaki, K., & Shinozaki, K. (2010). Two closely related subclass II SnRK2 protein kinases cooperatively regulate drought-inducible gene expression. *Plant Cell Physiol, 51*(5), 842-847. https://doi.org/10.1093/pcp/pcq041. EDN: https://elibrary.ru/nyxkdb
37. Moazzam-Jazi, M., Ghasemi, S., Seyedi, S. M., & Niknam, V. (2018). COP1 plays a prominent role in drought stress tolerance in Arabidopsis and Pea. *Plant Physiol Biochem, 130*, 678-691. https://doi.org/10.1016/j.plaphy.2018.08.015. EDN: https://elibrary.ru/yixptv
38. Moreno-Calles, A., Casas, A., Blancas, J., et al. (2010). Agroforestry systems and biodiversity conservation in arid zones: the case of the Tehuacán Valley, Central México. *Agroforest Syst, 80*, 315-331. https://doi.org/10.1007/s10457-010-9349-0. EDN: https://elibrary.ru/gknatu
39. Pitzschke, A., Datta, S., & Persak, H. (2014). Salt stress in Arabidopsis: lipid transfer protein AZI1 and its control by mitogen-activated protein kinase MPK3. *Mol Plant, 7*(4), 722-738. https://doi.org/10.1093/mp/sst157
40. Rajashekar, C. B., Zhou, H. E., Zhang, Y., Li, W., & Wang, X. (2006). Suppression of phospholipase Dalpha1 induces freezing tolerance in Arabidopsis: response of cold-responsive genes and osmolyte accumulation. *J Plant Physiol, 163*(9), 916-926. https://doi.org/10.1016/j.jplph.2005.08.006

41. Rehman, S., & Mahmood, T. (2015). Functional role of DREB and ERF transcription factors: regulating stress-responsive network in plants. *Acta Physiol Plant, 37*, 178. https://doi.org/10.1007/s11738-015-1929-1. EDN: https://elibrary.ru/frqxzj
42. Riboni, M., Galbiati, M., Tonelli, C., & Conti, L. (2013). Gigantea enables drought escape response via abscisic acid-dependent activation of the florigens and suppressor of overexpression of constans. *Plant Physiol., 162*(3), 1706-1719. https://doi.org/10.1104/pp.113.217729
43. Sakamoto, H., Maruyama, K., Sakuma, Y., Meshi, T., Iwabuchi, M., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2004). Arabidopsis Cys2/His2-type zinc-finger proteins function as transcription repressors under drought, cold, and high-salinity stress conditions. *Plant Physiol., 136*(1), 2734-2746. https://doi.org/10.1104/pp.104.046599. EDN: https://elibrary.ru/xnyjqt
44. Sakuma, Y., Maruyama, K., Osakabe, Y., Qin, F., Seki, M., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2006). Functional analysis of an Arabidopsis transcription factor, DREB2A, involved in drought-responsive gene expression. *Plant Cell, 18*(5), 1292-1309. https://doi.org/10.1105/tpc.105.035881
45. Schöning, J. C., Streitner, C., Meyer, I. M., Gao, Y., & Staiger, D. (2008). Reciprocal regulation of glycine-rich RNA-binding proteins via an interlocked feedback loop coupling alternative splicing to nonsense-mediated decay in Arabidopsis. *Nucleic Acids Res., 36*(22), 6977-6987. https://doi.org/10.1093/nar/gkn847
46. Shkolnik-Inbar, D., & Bar-Zvi, D. (2010). ABI4 mediates abscisic acid and cytokinin inhibition of lateral root formation by reducing polar auxin transport in Arabidopsis. *Plant Cell, 22*(11), 3560-3573. https://doi.org/10.1105/tpc.110.074641. EDN: https://elibrary.ru/nyxgux
47. Shu, K., Chen, Q., Wu, Y., Liu, R., Zhang, H., Wang, S., Tang, S., Yang, W., & Xie, Q. (2016). Abscisic acid-insensitive 4 negatively regulates flowering through directly promoting Arabidopsis flowering locus C transcription. *J Exp Bot., 67*(1), 195-205. https://doi.org/10.1093/jxb/erv459
48. Singh, K., & Chandra, A. (2021). DREBs-potential transcription factors involve in combating abiotic stress tolerance in plants. *Biologia, 76*, 3043-3055. https://doi.org/10.1007/s11756-021-00840-8. EDN: https://elibrary.ru/igqkgv
49. Sobola, O. O., Amadi, D. C., & Jamala, G. Y. (2015). The role of agroforestry in environmental sustainability. *IOSR Journal of Agriculture and Veterinary Science, 8*(5), 20-25. https://doi.org/10.9790/2380-08512025
50. Sottosanto, J. B., Saranga, Y., & Blumwald, E. (2007). Impact of AtNHX1, a vacuolar Na+/H+ antiporter, upon gene expression during short- and long-

term salt stress in Arabidopsis thaliana. *BMC Plant Biology, 7*, 18. https://doi.org/10.1186/1471-2229-7-18. EDN: https://elibrary.ru/tjqilz

51. Szechyńska-Hebda, M., Czarnocka, W., Hebda, M., Bernacki, M. J., & Karpiński, S. (2016). PAD4, LSD1 and EDS1 regulate drought tolerance, plant biomass production, and cell wall properties. *Plant Cell Reports, 35*(3), 527-539. https://doi.org/10.1007/s00299-016-1955-5. EDN: https://elibrary.ru/nrsvca
52. Tikhomirova, T. S., Krutovsky, K. V., & Shestibratov, K. A. (2022). Molecular Traits for Adaptation to Drought and Salt Stress in Birch, Oak and Poplar Species. *Forests, 14*(1), 7. https://doi.org/10.3390/f14010007. EDN: https://elibrary.ru/uukoib
53. Trejo-Téllez, L. I. (2023). Salinity Stress Tolerance in Plants. *Plants, 12*, 3520. https://doi.org/10.3390/plants12203520. EDN: https://elibrary.ru/xmkys
54. Trivedi, D. K., Gill, S. S., & Tuteja, N. (2016). Abscisic Acid (ABA): Biosynthesis, Regulation, and Role in Abiotic Stress Tolerance. In *Abiotic Stress Response in Plants* (pp. 315-326). https://doi.org/10.1002/9783527694570.ch15
55. von der Fecht-Bartenbach, J., Bogner, M., Dynowski, M., & Ludewig, U. (2010). CLC-b-mediated NO-3/H+ exchange across the tonoplast of Arabidopsis vacuoles. *Plant Cell Physiology, 51*(6), 960-968. https://doi.org/10.1093/pcp/pcq062. EDN: https://elibrary.ru/nyymvf
56. Wang, P., Du, Y., Zhao, X., Miao, Y., & Song, C. P. (2013). The MPK6-ERF6-ROS-responsive cis-acting Element7/GCC box complex modulates oxidative gene transcription and the oxidative response in Arabidopsis. *Plant Physiology, 161*(3), 1392-1408. https://doi.org/10.1104/pp.112.210724
57. Wang, W., Peng, C., Kneeshaw, D. D., Larocque, G. R., & Luo, Z. (2012). Drought-induced tree mortality: ecological consequences, causes, and modeling. *Environmental Reviews, 20*(2), 109-121. https://doi.org/10.1139/a2012-004. EDN: https://elibrary.ru/poxqip
58. Wang, Y., Li, L., Ye, T., Lu, Y., Chen, X., & Wu, Y. (2013). The inhibitory effect of ABA on floral transition is mediated by ABI5 in Arabidopsis. *Journal of Experimental Botany, 64*(2), 675-684. https://doi.org/10.1093/jxb/ers361
59. Wilson, P. B., Estavillo, G. M., Field, K. J., Pornsiriwong, W., Carroll, A. J., Howell, K. A., Woo, N. S., Lake, J. A., Smith, S. M., Harvey Millar, A., von Caemmerer, S., & Pogson, B. J. (2009). The nucleotidase/phosphatase SAL1 is a negative regulator of drought tolerance in Arabidopsis. *Plant J., 58*(2), 299-317. https://doi.org/10.1111/j.1365-313x.2008.03780.x
60. Xu, D. B., Chen, M., Ma, Y. N., Xu, Z. S., Li, L. C., Chen, Y. F., & Ma, Y. Z. (2015). A G-protein β subunit, AGB1, negatively regulates the ABA response and drought tolerance by down-regulating AtMPK6-related pathway

in Arabidopsis. *PLoS One, 10*(1), e0116385. https://doi.org/10.1371/journal.pone.0116385

61. Yáñez, M., Cáceres, S., Orellana, S., Bastías, A., Verdugo, I., Ruiz-Lara, S., & Casaretto, J. A. (2009). An abiotic stress-responsive bZIP transcription factor from wild and cultivated tomatoes regulates stress-related genes. *Plant Cell Rep., 28*(10), 1497-1507. https://doi.org/10.1007/s00299-009-0749-4. EDN: https://elibrary.ru/jaczur
62. Yang, D. H., Kwak, K. J., Kim, M. K., Park, S. J., Yang, K. Y., & Kang, H. (2014). Expression of Arabidopsis glycine-rich RNA-binding protein AtGRP2 or AtGRP7 improves grain yield of rice (Oryza sativa) under drought stress conditions. *Plant Sci., 214*, 106-112. https://doi.org/10.1016/j.plantsci.2013.10.006
63. Yuan, Lu., F., J., Zeng., Xiaoda, Li., & Bo, Zhang. (2021). Physiological changes of three woody plants exposed to progressive salt stress. *Photosynthetica, 59*(1), 171-184. https://doi.org/10.32615/PS.2021.007. EDN: https://elibrary.ru/pnbgdy
64. Yue, Y., Zhang, M., Zhang, J., Duan, L., & Li, Z. (2011). Arabidopsis LOS5/ABA3 overexpression in transgenic tobacco (Nicotiana tabacum cv. Xanthi-nc) results in enhanced drought tolerance. *Plant Sci., 181*(4), 405-411. https://doi.org/10.1016/j.plantsci.2011.06.010

AUTHOR CONTRIBUTIONS

The authors contributed equally to this article.

ВКЛАД АВТОРОВ

Все авторы сделали эквивалентный вклад в подготовку статьи для публикации.

DATA ABOUT THE AUTHORS

Anna V. Tretyakova, Research Engineer at the Laboratory of Genomic and Postgenomic Technologies
Federal Scientific Center of Agroecology, Complex Melioration, and Protective Afforestation RAS
97, Universitetsky pr., Volgograd, 400062, Russian Federation
tretaykova@vfanc.ru
SPIN-code: 8498-4535
ORCID: https://orcid.org/0009-0001-4478-4711
ResearcherID: JAN-9574-2023

Vsevolod O. Malov, Research Engineer at the Laboratory of Genomic and Postgenomic Technologies
Federal Scientific Center of Agroecology, Complex Melioration, and Protective Afforestation RAS
97, Universitetsky pr., Volgograd, 400062, Russian Federation
malov-v@vfanc.ru
SPIN-code: 7408-8285
ORCID: https://orcid.org/0000-0003-2766-0124
ResearcherID: HHR-9077-2022

Pavel A. Krylov, Cand. Sc. (Biology), Leading Researcher, Head of the Laboratory of Genomic and Postgenomic Technologies
Federal Scientific Center of Agroecology, Complex Melioration, and Protective Afforestation RAS
97, Universitetsky pr., Volgograd, 400062, Russian Federation
krylov-p@vfanc.ru
SPIN-code: 9652-7459
ORCID: https://orcid.org/0000-0001-9587-5886
ResearcherID: V-6884-2017
Scopus Author ID: 57213164834

ДАННЫЕ ОБ АВТОРАХ

Третьякова Анна Вадимовна, инженер-исследователь лаборатории геномных и постгеномных технологий
Федеральное государственное бюджетное научное учреждение «Федеральный научный центр агроэкологии, комплексных мелиораций и защитного лесоразведения Российской академии наук»
пр-т Университетский, 97, г. Волгоград, 400062, Российская Федерация
tretaykova@vfanc.ru

Малов Всеволод Олегович, инженер-исследователь лаборатории геномных и постгеномных технологий
Федеральное государственное бюджетное научное учреждение «Федеральный научный центр агроэкологии, комплексных мелиораций и защитного лесоразведения Российской академии наук»
пр-т Университетский, 97, г. Волгоград, 400062, Российская Федерация
malov-v@vfanc.ru

Крылов Павел Андреевич, кандидат биологических наук, ведущий научный сотрудник с и.о. заведующего лабораторией геномных и постгеномных технологий

Федеральное государственное бюджетное научное учреждение «Федеральный научный центр агроэкологии, комплексных мелиораций и защитного лесоразведения Российской академии наук»

пр-т Университетский, 97, г. Волгоград, 400062, Российская Федерация

krylov-p@vfanc.ru

Поступила 26.07.2024
После рецензирования 01.09.2024
Принята 28.10.2024

Received 26.07.2024
Revised 01.09.2024
Accepted 28.10.2024