

UDC 633.72:581.1:58.056

doi: 10.15389/agrobiology.2019.3.458eng

doi: 10.15389/agrobiology.2019.3.458rus

**PHYSIOLOGICAL MECHANISMS AND GENETIC FACTORS  
OF THE TEA PLANT *Camellia sinensis* (L.) Kuntze RESPONSE  
TO DROUGHT  
(review)**

**L.S. SAMARINA, A.V. RYNDIN, L.S. MALYUKOVA, M.V. GVASALIYA,  
V.I. MALYAROVSKAYA**

*All-Russian Research Institute of Floriculture and Subtropical Crops*, 2/28, ul. Yana Fabritsiusa, Sochi, 354002 Russia, e-mail samarinalidia@gmail.com, ryndin@vniisubtrop.ru, malukovals@mail.ru (✉ corresponding author), m.v.gvasaliya@mail.ru, malyarovskaya@yandex.ru

ORCID:

Samarina L.S. orcid.org/0000-0002-0500-1198

Gvasaliya M.V. orcid.org/0000-0001-7394-4377

Ryndin A.V. orcid.org/000-0001-9640-4840

Malyarovskaya V.I. orcid.org/0000-0003-4213-8705

Malyukova L.S. orcid.org/0000-0003-1531-5745

Authors declare no conflict of interests

Acknowledgements:

Supported financially by the Russian Science Foundation, project No. 18-76-10001

Received February 9, 2019

**Abstract**

The main constraint in the tea plants growth in the world is drought, which reduces the productivity of plantations by 15-45 % (R.M. Bhagat et al., 2010; R.D. Baruah et al., 2012). In this regard, physiological (M. Mukhopadhyay et al., 2014; T.K. Maritim et al., 2015) and molecular mechanisms (W.D. Wang et al., 2016; Y. Guo et al., 2017) drought tolerance of tea plants are a matter of great interest. The purpose of this review is to summarize the international experience of phenotyping and genotyping of tea drought response to create a comprehensive picture of the plant response to osmotic stress and to understand the reproducibility of response mechanisms in different climatic regions. During drought stress the main signaling role is played by abscisic, jasmonic and salicylic acids, as well as ethylene (S.C. Liu et al., 2016), the metabolic pathway of which includes cascades of physiological changes and involves response genes (T. Umezawa et al., 2010). It was reported that tea plants had increased expression of genes encoding cytokinin biosynthesis enzymes (trans-zeatin and cis-zeatin and isopentenyladine) under drought, and during recovery its expression decreased. It is assumed that an increase in cytokinin content may partially mitigate the negative effect of stress on photosynthetic apparatus and slow down leaf senescence induced by stress. An important adaptive response of tea plant to drought is an increase in the concentration of proline, glycine-betaine, mannitol and other osmolytes which neutralize reactive oxygen species, protect macromolecules from damage by free radicals, and maintain the osmotic potential of the cell (W.D. Wang et al., 2016). Under the drought in tea plant starch decomposes to glucose, and mannitol, trehalose, and sucrose contents increase. The accumulation of reactive oxygen species (ROS) directly correlates with the accumulation of glucose, to prevent the negative effects of stress. In addition, it has been shown that many genes involved in the metabolism and signaling of phytohormones, osmolytes, antioxidants and carbohydrates are also involved in tolerance to osmotic stress (S. Gupta et al., 2013; Y. Guo et al., 2017). Several families of transcription factors play a crucial role in the regulation of tea response to drought in tea. In particular, 39 *CsbHLH* genes were identified with increased expression in drought conditions (X. Cui et al., 2018). From the NAC family, the *CsNAC17* and *CsNAC30* genes have been identified that can be used in the breeding for drought tolerance of tea (Y.-X. Wang et al., 2016). From the WRKY family, the *CsWRKY2* gene has been identified which is involved in the mechanisms of protection from drought and can act as an activator or repressor of abscisic acid (ABA). From the DREB gene family, 29 *CsDREB* have been identified, which increase drought tolerance of tea through ABA-dependent and ABA-independent pathways and can act as a link between different biochemical networks in response to drought (M. Wang et al., 2017). From the HD-Zip family, *Cshdz* genes have been identified which are divided into 4 groups according to their functions, of which HD-Zip I and HD-Zip IV play the major role in drought response in tea (W. Shen et al., 2018). Of the HSP (HSF) family, 47 transcription factors were identified in tea, including 7 *CsHSP90*, 18 *CsHSP70*, and 22 *CsHSP* genes the expression of which increases resistance to oxidative stress, protection of photosystem II and stabilizes photosynthesis during drought (J. Chen et al., 2018). The transcription factors of the bZIP family also play

the important role in ABA-mediated drought response. From the Dof family, 29 transcription factors were revealed in tea plants and their increased expression was shown in the resistant cultivars under drought. The important role of CsDof-22 in ABA biosynthesis has been revealed (H. Li et al., 2016). An increased expression of the SBP family CsSBP genes in tea plants led to assumption of its participation in signaling pathways involving ABA, gibberellic acid, and methyl jasmonate (P. Wang et al., 2018). The genes of the CsLOX1, CsLOX6 and CsLOX7 family of lipoxygenases in tea can also play an important role in drought response (J. Zhu et al., 2018). In addition, miRNA play an important role in gene regulation at transcription and translation level in tea plants (Y. Guo et al., 2017). Despite the great progress in the functional genomics of tea plant further research is needed to identify the location of various genes in regulatory networks and their impact in drought tolerance.

Keywords: tea plant, *Camellia sinensis*, drought, phytohormones, osmolytes, antioxidant system, transcription factors

Tea *Camellia sinensis* (L.) Kuntze is the most important industrial crop cultivated in more than 50 countries of the world, including in the humid subtropical zone of Russia. This perennial plant, growing in one place for up to 70 years or more, periodically encounters prolonged drought (1-2 months) in the summer period, which leads to oxidative stress and the formation of mineral deficiency. According to various authors, these abiotic factors become one of the main reasons for the decrease in tea plantation yields (on average by 15-45%) [1-3] and even partial death of plants (up to 19%) [4]. The predicted global climate changes towards aridization [5] will further aggravate the existing problems of tea cultivation and actualize the tasks to increase its endurance to extreme environmental conditions [6-9]. In this regard, the physiological, biochemical, and molecular mechanisms of tea plant resistance to drought and the effectiveness of using various exogenous inducers are studied, and the selection search for more drought-tolerant varieties is performed [10]. Over the years of research in foreign countries, significant experimental material has been accumulated concerning the physiological, biochemical, and molecular mechanisms of the resistance of tea and other crops to drought [11-14], which can be used as a scientific basis for the development of selection research in Russia.

The purpose of this report is to summarize the international experience of phenotyping and genotyping of tea plants on the basis of resistance to stress factors in order to create a holistic picture of the plant's response to osmotic stress and to understand the reproducibility of response mechanisms in different climatic zones.

The most effective strategies for plant adaptation to drought, including tea, include the so-called mechanisms of stress avoidance by shortening the life cycle, growing season and flowering, which are aimed at reducing water loss by the organism [15, 16]. The most important morphological symptoms of plant adaptation are the characteristics of the root system (biomass, length, depth, and density of roots) [17-19], the ratio of root/shoot biomass, the number and size of leaves, the area and nature of the leaf surface, the ratio of leaf mass to surface, the structure of the photosynthetic apparatus, the structure and form of chloroplasts [20-24]. The main physiological mechanisms of avoidance are the reduction of water loss through stomatal control of transpiration [25-27], a decrease in the number and size of stomata [28], an increase in the viscosity of the cytoplasm, and maintenance of the osmotic potential of the cell. All these processes are based on cascades of biochemical reactions involving three groups of metabolites — phytohormones, osmolytes, and antioxidant components.

Phytohormones. According to modern research, among phytohormones, abscisic (ABA), salicylic and jasmonic acids, as well as ethylene, play an important role in responding to drought. A comparative study of two tea varieties, which are contrasting in terms of resistance, revealed an increase in the content of abscisic and salicylic acids 4 days after the onset of drought [25].

Other phytohormones, such as indoleacetic acid (IAA) and cytokinins, were involved in plant recovery after drought. In the case of the tea plant, the ABA-dependent response path to drought has been studied quite fully, although some links have not yet been identified. ABA-dependent signaling primarily affects constitutively expressed transcription factors, which then induce direct effector stress resistance genes [29]. A key regulatory link in ABA biosynthesis in both roots and leaves is probably catalyzed by 9-cis-epoxycarotenoid deoxygenase, which is an enzyme that converts the epoxycarotenoid precursor into xanthoxin in plastids. ABA initiates the formation of reactive oxygen species, which in a chain activate superoxide dismutase (SOD), which is the first line of defense against free radicals [12, 25]. The increasing activity of SOD leads to an increase in the amount of H<sub>2</sub>O<sub>2</sub>, activation of Ca<sup>2</sup> channels, and calcium-dependent protein kinases that regulate stomata closure [26, 30-32]. When recovering from drought, the amount of ABA decreases, as a result of which the calcium concentration in the cytosol supposedly reduces, the influx of potassium and anions into the stomata trailing cells decreases and, as a result, stomata open [26, 33-35].

Under the influence of drought, the expression of the jasmonic acid synthesis gene increases, which turns into a more active compound (–)-jasmonoyl-L-isoleucine (JA-Ile) [26]. Genes encoding the main components of ethylene signaling are also activated. After the onset of stress, the expression of the 1-aminocyclopropane-1-carboxylic acid (ACC) gene is increased, which indicates the accumulation of ethylene, and it is suppressed during the recovery period after drought [26].

Salicylic acid is a phenolic compound involved in the regulation of photosynthesis, nitrogen metabolism, proline, glycine-beta-in synthesis, an antioxidant defense system, and water potential under stress conditions [36]. The main regulator of salicylic acid metabolism is the *NPR1* gene, a decrease in the expression of which under conditions of drought led to a weakening of tea resistance to disease [26].

Indoleacetic acid (IAA) regulates many physiological processes. In a tea plant, the expression of genes associated with the synthesis of IAA decreased in response to drought [26]. However, to maintain the activity of physiological processes under these conditions, alternative routes for the synthesis of IAA from indole via tryptophan were activated.

It was reported that during a drought period, the expression of genes encoding cytokinin biosynthesis enzymes (trans- and cis-zeatin and isopentenyladenine) increased in a tea plant, and during the recovery after stress, it decreased. Apparently, an increase in the content of cytokinins can partially mitigate the negative effect of stress on photosynthetic activity and slow down accelerated leaf aging [36].

Osmolytes. Another strategy for adapting to drought is to increase the synthesis of osmolytes – substances with a low molecular weight dissolved in the cytosol, which are not toxic to the plant even in high concentrations [37-39]. Osmolytes increase the viscosity of the cytoplasm, absorb reactive oxygen species and protect macromolecules from free radicals, thereby maintaining the integrity of the membranes and the metabolic activity of tissues, which ensures the resumption of growth after improving the water regime [40-42]. These substances belong to three main classes: amino acids (glutamine, proline, glycine-betaine, carnitine), sugars (starch, di- and monosaccharides) and polyols (mannitol, sorbitol) [43]. Proline [44], which is synthesized from glutamate (with the participation of the pyrroline-5-carboxylate synthase enzyme) or ornithine [26, 43] is especially important among amino acids. The accumulation of proline is accompanied by the prevention of protein denaturation, the preservation of the struc-

ture and activity of enzymes, as well as the protection of membranes from ROS damage during moisture deficiency and high solar activity. The most studied components of osmotic regulation include glycine-betaine [45], which has a positive effect on enzyme stability and membrane integrity, acting as an osmoprotector and also indirectly participating in transduction signals [46]. In the paper by Maritim et al. [19], accumulation of proline and glycine-betaine under simulated water deficiency stress in the leaves of 8 varieties of tea was shown, which is more pronounced in drought-tolerant varieties. Based on this, it was concluded that proline can be used as a biochemical marker for screening genetic material for drought tolerance.

A significant contribution of carbohydrates to cell resistance under osmotic stress has also been shown [25, 26, 47]. So, under drought conditions in tea plants, starch was decomposed to glucose, and the synthesis of mannitol, trehalose, and sucrose increased. The accumulation of reactive oxygen species (ROS) was directly correlated with the accumulation of glucose, which is involved in the closure of stomata and increases the adaptability of the plant, prevents the decomposing of chlorophyll and transpiration of water under osmotic stress. In addition, soluble sugars play a dual function, as they are associated with both anabolism and catabolism of ROS, such as the oxidative pentose phosphate pathway and NADPH production [48–51]. Physiological and molecular genetic studies conducted by Liu et al. [25, 26] showed that the concentration of soluble sugars in the tea plant increased significantly as the drought intensified, and then rapidly decreased after rehydration. These results suggested that photoassimilated carbon was mainly used for the synthesis of osmolytes, and starch was mainly decomposed to glucose.

**Antioxidant components.** Antioxidant defense systems include both enzyme (SOD, catalase, peroxidase, ascorbate peroxidase, glutathione reductase) and non-enzymatic (cysteine, reduced glutathione, and ascorbic acid) components [27, 37, 52]. It has been established that in addition to catalase, various peroxidases and peroxiredoxins [25, 53, 46], several more enzymes are involved in the process of liquidation of hydrogen peroxide and free radicals: dehydroascorbate reductase, monodehydroascorbate reductase, and glutathione reductase [31, 54]. Transcriptomic studies by Liu et al. [26] have shown that under drought conditions in a tea plant, the expression of the gene of ribulose biphosphate carboxylase (RuBisCO), the key enzyme of the Calvin cycle, decreased, indicating inhibition of carbon dioxide fixation. Moreover, the synthesis of regulatory enzymes of glycolysis of hexokinase under drought conditions did not stop. Researchers have suggested that the tea plant maintains ATP supply by maintaining glycolytic metabolism [26]. The role of  $\beta$ -carotene in protecting against oxidative stress and maintaining photochemical processes was identified [55, 56], which presumably involves the direct quenching of triplet chlorophyll, which prevents the formation of reactive oxygen species [37].

**Other signaling paths.** The group of molecular messengers that regulate the work of response genes is very numerous. Thus, aquaporins, the family of the main membrane (plasma and vacuolar) proteins, regulate the passive exchange of water through membranes [57]. Dehydrins and heat shock proteins (chaperones) stabilize the structure of other proteins and macromolecules, which prevents their denaturation under stress [58].

Protein kinases and protein phosphatases often act together to phosphorylate and dephosphorylate their targets. Protein kinases in a tea plant play a positive role, and protein phosphatases play a negative regulatory role in the response to drought, ensuring the maintenance of homeostasis and signal transduction in the tea plant. According to Wan et al. [59–62], all 29 calcium-dependent

protein kinases found in tea contain cis-elements of the multiple stress response in the promoter region of the gene.

Genetic factors. Among all the mechanisms, transcription factors are the main regulators of the plant's response to abiotic stress. Tea is supposed to have 12 families of transcription factors involved in response to drought: AP2/EREBP, bHLH, bZIP, HD-ZIP, HSF (HSP), MYB, NAC, WRKY, zinc-finger protein TFs, SCL, ARR, SPL [63-66].

One of the largest families of bHLH transcription factors (basic helix-loop-helix) is widespread in eukaryotes. These factors determine signal transmission and secondary metabolism of brassinosteroids, jasmonic acid, anthocyanin synthesis, modulation of plant growth and development, control of embryo development, branching of shoots, flower and fruit development. In addition, bHLHs are involved in ABA signaling and plant response to abiotic stresses. 39 *CsbHLH* genes were identified in tea, the expression of which is enhanced under drought conditions [67].

The NAC family of transcription factors (NAM-ATAF1/2-CUC) regulates the formation of the apical meristem, lateral roots, secondary cell wall, leaf aging, seed development, flavonoid biosynthesis. Many genes of the NAC family are involved in stress response and hormonal signaling. An analysis of these genes expression in tea plant during drought revealed the candidate genes *CsNAC17* and *CsNAC30*, which can be used in breeding tea for drought tolerance [68].

The WRKY transcription factor group is involved in responses to abiotic stress. The *CsWRKY2* gene was identified in tea, which is involved in protection against drought. Its greatest expression was observed in leaves, the smallest – in flowers and shoots. A high degree of expression of *CsWRKY2* was noted under the conditions of drought and cold. It has been shown that WRKY proteins can act as ABA activators or repressors [69].

One of the most extensive families of plant transcription factors is DREBs (dehydration-responsive element-binding proteins). Twenty-nine *CsDREB* genes were identified in tea; their localization in the cell nucleus was shown. The expression of these genes was enhanced by various abiotic stresses, including drought. Overexpression of *CsDREB* genes increases resistance to stress through both ABA-dependent and ABA-independent path. An analysis of the expression of *CsDREB* genes showed that they can act as a link between different response chains in the response of tea to stress [70].

The HD-Zip family of proteins (homeodomain-leucine zipper) is an important group of transcription factors, which is divided into four subgroups (HD-Zip I, HD-Zip II, HD-Zip III, and HD-Zip IV). Thirty-three transcription factors belonging to these subgroups were found in tea. Among them, HD-Zip I and HD-Zip IV are most involved in response to drought. HD-Zip I proteins mainly respond to external signals, such as extreme temperatures, drought, and other abiotic stresses, while regulating the processes of growth and adaptation of plants to environmental factors. The HD-Zip IV subgroup is involved in root formation, cell differentiation, trichome formation, and anthocyanin accumulation. The results of the analysis of tea *Cshdz* genes expression confirmed their participation in various stress responses, including drought [71].

Heat shock proteins (HSPs) play an important role in the growth and development of plants and protect cell structures under stress. Forty-seven *CsHSP* genes, including 7 *CsHSP90*, 18 *CsHSP70*, and 22 *CssHSP* genes, were identified in tea, the expression of which increases resistance to oxidative stress, protecting the photosystem II and supporting the photosynthetic apparatus [72].

The transcription factors of the bZIP family (basic region/leucine zipper)

are divided into 13 groups (AL and S). The most studied group A includes the so-called ABRE-binding factors (ABFs) responsible for the work of ABA. These and other bZIP family genes are involved in the response and mechanisms of tea plant resistance to drought, act as positive regulators of resistance to oxidative stress, and play a central role in biochemical cascades involving glucose and ABA [73].

The Dof family of transcription factors (DNA-binding with one finger) regulates the expression of genes involved in seed maturation and germination, flowering periods, accumulation of secondary metabolites, and also in protective processes. Twenty-nine transcriptional Dof factors were identified in tea and the participation of *CsDof-22* in ABA biosynthesis was shown. An increase in the expression of *CsDof* genes was observed in resistant tea varieties under stress [74].

SBPs (SQUAMOSA promoter binding protein) encode transcription factors, are involved in sporogenesis, shoot and leaf development, flowering, fertilization, fruit ripening, hormonal signaling, and responses to abiotic and biotic stresses in many plant species. Overexpression of these genes was observed in response to an increase in the content of jasmonic acid and led to an increase in the content of superoxide dismutase and peroxidase. Tea plant shows increased expression of *CsSBP* genes in the buds and leaves; these reactions can be associated with signaling pathways involving ABA, gibberellic acid, and methyl jasmonate [75].

Oxylipins are oxidized derivatives of fatty acids, including jasmonic acid, hydroxy-, oxo- or keto- fatty acids, volatile aldehydes, and are important signaling molecules in higher plants. Lipoxygenases (LOXs) are a family of iron-containing enzymes that catalyze the oxidation of polyunsaturated fatty acids, which initiates the biosynthesis of oxylipins. In a tea plant, the lipoxygenase family genes *CsLOX1*, *CsLOX6*, and *CsLOX7* are involved in response to stresses (cold, drought, biotic stress) via an ABA-independent pathway [76].

MicroRNAs regulate the expression of transcription factors at the translation stage. Sixty-two microRNAs were identified in tea; they are involved in the response to drought through the regulation of transcription and suppression of translation. It was found that microRNAs expression varies depending on the strength of the stress factor and manifests itself in the form of morphological, physiological, and biochemical changes [77].

Thus, many biochemical and genetic signals have been established and described for tea plants; they activate genetic matrices in response to osmotic stress, which leads to physiological and metabolic changes that ensure plant resistance. This process involves many genes involved in the metabolism and signaling of phytohormones, the metabolism of osmolytes, the regulation of antioxidant activity, and the regulation of stomatal apparatus functions. However, the role of all genetic factors in the response to drought still requires further study to fully understand their place in cascades of biochemical reactions. Therefore, despite significant progress in the functional genomics of plants, including tea, further studies are required to identify the place of various genes in regulatory networks and the response to drought.

## REFERENCES

1. Bhagat R.M., Baruah R.D., Safique S. Climate and tea [*Camellia sinensis* (L.) O. Kuntze] production with special reference to north eastern India: a review. *Journal of Environmental Research and Development*, 2010, 4(4): 1017-1028.
2. Baruah R.D., Bhagat R.M. Climate trends of Northeastern India: a longterm pragmatic analysis for tea production. *Two and a Bud*, 2012, 59(2): 46-49.
3. Malyukova L.S. *Plodovodstvo i yagodovodstvo Rossii*, 2014, 38(1): 255-261 (in Russ.).

4. Cheruiyot E.K., Mumera L.M., Ng'etich W.K., Hassanali A., Wachira F.N. High fertilizer rates increase susceptibility of tea to water stress. *Journal of Plant Nutrition*, 2009, 33(1): 115-129 (doi: 10.1080/01904160903392659).
5. Reynolds M.P., Ortiz R. Adapting crops to climate change: a summary. In: *Climate change and crop production*. M.P. Reynolds (ed.). CAB International, 2010: 1-8 (doi: 10.1079/9781845936334.0001).
6. Sinclair T.R. Challenges in breeding for yield increase for drought. *Trends in Plant Science*, 2011, 16(6): 289-293 (doi: 10.1016/j.tplants.2011.02.008).
7. Ashraf M. Inducing drought tolerance in plants: recent advances. *Biotechnology Advances*, 2010, 28(1): 169-183 (doi: 10.1016/j.biotechadv.2009.11.005).
8. Varshney R.K., Bansal K.C., Aggarwal P.K., Datta S.K., Craufurd P.Q. Agricultural biotechnology for crop improvement in a variable climate: hope or hype? *Trends in Plant Science*, 2011; 16(7): 363-371 (doi: 10.1016/j.tplants.2011.03.004).
9. Tsonev S., Todorovska E., Avramova V., Kolev S., Abu-Mhadi N., Christov N.K. Genomics assisted improvement of drought tolerance in maize: QTL approaches. *Biotechnology & Biotechnological Equipment*, 2009, 23(4): 1410-1413 (doi: 10.2478/V10133-009-0004-8).
10. Mukhopadhyay M., Mondal T.K. The physio-chemical responses of *Camellia* plants to abiotic stresses. *J. Plant Sci. Res.*, 2014, 1(1): 1-12.
11. Bernier J., Atlin G.N., Serraj R., Kumar A., Spaner D. Breeding upland rice for drought resistance. *Journal of the Science of Food and Agriculture*, 2008, 88(6): 927-939 (doi: 10.1002/jsfa.3153).
12. Fleury D., Jefferies S., Kuchel H., Langridge P. Genetic and genomic tools to improve drought tolerance in wheat. *Journal of Experimental Botany*, 2010, 61(12): 3211-3222 (doi: 10.1093/jxb/erq152).
13. Manavalan L.P., Guttikonda S.K., Tran L.S., Nguyen H.T. Physiological and molecular approaches to improve drought resistance in soybean. *Plant and Cell Physiology*, 2009, 50(7): 1260-1276 (doi: 10.1093/pcp/pcp082).
14. Yadav R.S., Sehgal D., Vadez V. Using genetic mapping and genomics approaches in understanding and improving drought tolerance in pearl millet. *Journal of Experimental Botany*, 2011, 62(2): 397-408 (doi: 10.1093/jxb/erq265).
15. Araus J.L., Slafer G.A., Reynolds M.P., Royo C. Plant breeding and water relations in C<sub>3</sub> cereals: what should we breed for? *Annals of Botany*, 2002, 89 (7): 925-940 (doi: 10.1093/aob/mcf049).
16. Pchikhachev E.K., Korzun B.V. *Subtropicheskie kul'tury*, 2010, 1(4): 219-220 (in Russ.).
17. Duov M.T. *Nauchnye osnovy povysheniya kachestva i produktivnosti chaynykh plantatsii Rossii. Doktor'skaya dissertatsiya* [Scientific basis for improving quality and productivity of tea plantations in Russia. DSc Thesis]. Sochi, 1997 (in Russ.).
18. Das A., Das S., Mondal T.K. Identification of differentially expressed gene profiles in young roots of tea (*Camellia sinensis* (L.) O. Kuntze) subjected to drought stress using suppression subtractive hybridization. *Plant Mol. Biol. Rep.*, 2012, 30(5): 1088-1101 (doi: 10.1007/s11105-012-0422-x).
19. Maritim T.K., Kamunya S.M., Mireji P., Mwendia C.M., Muoki R.C., Cheruiyot E.K., Wachira F.N. Physiological and biochemical response of tea (*Camellia sinensis* (L.) O. Kuntze) to water-deficit stress. *The Journal of Horticultural Science and Biotechnology*, 2015, 90(4): 395-400 (doi: 10.1080/14620316.2015.11513200).
20. Jaleel C.A., Manivannan P., Wahid A., Farooq M., Somasundaram R., Panneerselvam R. Drought stress in plants: a review on morphological characteristics and pigments composition. *Int. J. Agric. Biol.*, 2009, 11(1): 100-105.
21. Waheed A., Hamid F.S., Shan A.H., Ahmad H., Khalid A., Abbasi F.M., Ahmad N., Aslam S., Sarwar S. Response of different tea (*Camellia sinensis* L.) clones against drought stress. *J. Mater. Environ. Sci.*, 2012, 3(2): 395-410.
22. Gvasaliya M.V. *Spontannye i induktsirovannyye sorta i formy chaya (Samellia sinensis (L.) Kuntze) vo vlazhnykh subtropikakh Rossii i Abkhazii, perspektivy ikh razmnozheniya i sokhraneniya v kul'ture in vitro. Kandidatskaya dissertatsiya* [Spontaneous and induced varieties and forms of tea (*Camellia sinensis* (L.) Kuntze) in the humid subtropics of Russia and Abkhazia, the prospects for their reproduction and preservation in culture in vitro. PhD Thesis]. Krasnodar, 2015 (in Russ.).
23. Nyabundi K.W., Owuor P.O., Netondo G.W., Bore J.K. Genotype and environment interactions of yields and yield components of tea (*Camellia sinensis*) cultivars in Kenya. *American Journal of Plant Sciences*, 2016, 7(6): 855-869 (doi: 10.4236/ajps.2016.76081).
24. Vavilova L.V., Korzun B.V. *Novye tekhnologii*, 2016, 4: 114-120 (in Russ.).
25. Liu S.C., Yao M.Z., Ma C.L., Jin J.Q., Ma J.Q., Li C.F. Physiological changes and differential gene expression of tea plant under dehydration and rehydration conditions. *Scientia Horticulturae*, 2015, 184(5): 129-141 (doi: 10.1016/j.scienta.2014.12.036).
26. Liu S.C., Jin J.Q., Ma J.Q., Yao M.Z., Ma C.L., Li C.F., Ding Z.T., Chen L. Transcriptomic analysis of tea plant responding to drought stress and recovery. *PLoS ONE*, 2016, 11(1): e0147306 (doi: 10.1371/journal.pone.0147306).
27. Li X., Liu F. Drought stress memory and drought stress tolerance in plants: biochemical and

- molecular basis. In: *Drought stress tolerance in plants*. M. Hossain, S. Wani, S. Bhattacharjee, D. Burritt, L.S. Tran (eds.). Springer, Cham, 2016, Vol. 1: 17-44 (doi: 10.1007/978-3-319-28899-4).
28. Daszkowska-Golec A.D., Szarejko I. Open or close the gate-stomata action under the control of phytohormones in drought stress conditions. *Front. Plant Sci.*, 2013, 4: 138 (doi: 10.3389/fpls.2013.00138).
  29. Umezawa T., Nakashima K., Miyakawa T., Kuromori T., Tanokura M., Shinozaki K., Yamaguchi-Shinozaki K. Molecular basis of the core regulatory network in ABA responses: sensing, signaling and transport. *Plant Cell Physiol.*, 2010, 51(11): 1821-1839 (doi: 10.1093/pcp/pcq156).
  30. Miller G., Schlauch K., Tam R., Cortes D., Torres M.A., Shulaev V., Jeffery L. Dang, Mittler R. The plant NADPH oxidase RBOHD mediates rapid systemic signaling in response to diverse stimuli. *Science Signaling*, 2009, 2(84): 1-10 (doi: 10.1126/scisignal.2000448).
  31. Upadhyaya H., Dutta B.K., Sahoo L., Panda S.K. Comparative effect of Ca, K, Mn and B on post-drought stress recovery in tea [*Camellia sinensis* (L.) O. Kuntze]. *American Journal of Plant Sciences*, 2012, 3(4): 443-460 (doi: 10.4236/ajps.2012.34054).
  32. Meyer S., Mumm P., Imes D., Endler A., Weder B., Al-Rasheid K.A.S., Geiger D., Marten I., Martinoia E., Hedrich R. AtALMT12 represents an R-type anion channel required for stomatal movement in Arabidopsis guard cells. *The Plant Journal*, 2010, 63(6): 1054-1062 (doi: 10.1111/j.1365-313X.2010.04302.x).
  33. Upadhyaya H., Panda S.K., Dutta B.K. CaCl<sub>2</sub> improves post-drought recovery potential in *Camellia sinensis* (L.) O. Kuntze. *Plant Cell Rep.*, 2011, 30(4): 495-503 (doi: 10.1007/s00299-010-0958-x).
  34. Gao X.Y., Yang G.P., Xu Z.Q. Xu F.C. Effect of calcium on antioxidant enzymes of lipid peroxidation of soy-bean leaves under water stress. *J. South China Agric. Univ.*, 1999, 2: 58-62.
  35. Bowler C., Fluhr B. The role of calcium and activated oxygen as signals for controlling cross-tolerance. *Trends Plant Sci.*, 2000, 5(6): 241-243 (doi: 10.1016/S1360-1385(00)01628-9).
  36. Miura K., Tada Y. Regulation of water, salinity, and cold stress responses by salicylic acid. *Front. Plant Sci.*, 2014, 5: 4 (doi: 10.3389/fpls.2014.00004).
  37. Defez R., Andreozzi A., Dickinson M., Charlton A., Tadini L., Pesaresi P., Bianco C. Improved drought stress response in alfalfa plants nodulated by an IAA over-producing *Rhizobium* strain. *Front Microbiol.*, 2017, 14(8): 2466 (doi: 10.3389/fmicb.2017.02466).
  38. Farooq M., Wahid A., Kobayashi N., Fujita D., Basra S.M.A. Plant drought stress: effects, mechanisms and management. *Agron. Sustain. Dev.*, 2009, 29(1): 185-212 (doi: 10.1051/agro:2008021).
  39. Damayanthi M.M.N., Mohotti A.J., Nissanka S.P. Comparison of tolerant ability of nature field grown tea (*Camellia sinensis* L.) cultivars exposed to a drought stress in Passara Area. *Tropical Agricultural Research*, 2010, 22(1): 66-75 (doi: 10.4038/tar.v22i1.2671).
  40. Mukhopadhyay M., Ghosh P.D., Mondal T.K. Effect of boron deficiency on photosynthesis and antioxidant responses of young tea (*Camellia sinensis* (L.) O. Kuntze) plantlets. *Russ. J. Plant Physiol.*, 2013, 60(5): 633-639 (doi: 10.1134/S1021443713030096).
  41. Pritula Z.V., Malyukova L.S. *Problemy agrokhimii i ekologii*, 2017, 3: 31-34 (in Russ.).
  42. Tholalakabavi A., Zwiazek, J.J., Thorpe, T.A. Effect of mannitol and glucose-induced osmotic stress on growth, water relations, and solute composition of cell suspension cultures of poplar (*Populus deltoids* var. *Occidentalis*) in relation to anthocyanin accumulation. *In Vitro Cell Dev. Biol. — Plant*, 1994, 30(3): 164-170 (doi: 10.1007/BF02632208).
  43. Serraj R., Sinclair T.R. Osmolyte accumulation: can it really help increase crop yield under drought conditions? *Plant, Cell Environ.*, 2002, 25(2): 333-341 (doi: 10.1046/j.1365-3040.2002.00754.x).
  44. Guo Y., Zhao S., Zhu C.H., Chang X., Yue C.H., Wang Z.H., Lin Y., Lai Z.H. Identification of drought-responsive miRNAs and physiological characterization of tea plant (*Camellia sinensis* L.) under drought stress. *BMC Plant Biol.*, 2017, 17(1): 211 (doi: 10.1186/s12870-017-1172-6).
  45. Szabados L., Savoure A. Proline: a multifunctional amino acid. *Trends Plant Sci.*, 2010, 15(2): 89-97 (doi: 10.1016/j.tplants.2009.11.009).
  46. Farooq M., Basra S.M.A., Wahid A., Cheema Z.A., Cheema M.A., Khaliq A. Physiological role of exogenously applied glycinebetaine in improving drought tolerance of fine grain aromatic rice (*Oryza sativa* L.). *J. Agron. Crop Sci.*, 2008, 194(5): 325-333 (doi: 10.1111/j.1439-037X.2008.00323.x).
  47. Upadhyaya H., Panda S.K. Abiotic stress responses in tea [*Camellia sinensis* (L.) O. Kuntze]: an overview. *Reviews in Agricultural Science*, 2013, 1: 1-10 (doi: 10.7831/ras.1.1).
  48. Ciereszko I. Sucrose metabolism in plant tissues under stress conditions: key enzymes, localization and function In: *Compartmentation of responses to stresses in higher plants, true or false*. W. Maksymiec (ed.). Transworld Research Network, Trivandrum, 2009: 193-218 (ISBN: 978-81-7895-422-6).
  49. ElSayed A.I., Rafudeen M.S., Gollack D. Physiological aspects of raffinose family oligosaccharides in plants: protection against abiotic stress. *Plant Biology*, 2014, 16(1): 1-8 (doi: 10.1111/plb.12053).



50. Sami F., Yusuf M., Faizan M., Faraz A., Hayat S. Role of sugars under abiotic stress. *Plant Physiology and Biochemistry*, 2016, 109: 54-61 (doi: 10.1016/j.plaphy.2016.09.005).
51. Thalmann M., Santelia D. Starch as a determinant of plant fitness under abiotic stress. *New Phytologist*, 2017, 214(3): 943-951 (doi: 10.1111/nph.14491).
52. Kamanga R.M., Mbega E., Ndakidemi P. Drought tolerance mechanisms in plants: physiological responses associated with water deficit stress in *Solanum lycopersicum* Adv. *Crop. Sci. Tech.*, 2018, 6(3): 362 (doi: 10.4172/2329-8863.1000362).
53. Das A., Mukhopadhyay M., Sarkar B., Saha D., Mondal T.K. Influence of drought stress on cellular ultrastructure and antioxidant system in tea cultivars with different drought sensitivities. *J. Environ. Biol.*, 2015, 36(4): 875-882.
54. Belous O.G. *Aktivnost' katalazy v list'yakh chaya v zone vlaznykh subtropikov Rossii*. LAP LAMBERT Academic Publishing, Saarbruchen, 2012.
55. Pedranzani H., Vigliocco A. Evaluation of jasmonic acid and salicylic acid levels in abiotic stress tolerance: Past and present. In: *Mechanisms behind phytohormonal signalling and crop abiotic stress tolerance. Chapter 15*. V.P. Singh, S. Singh, S.M. Prasad (eds.). Nova Science Publishers, 2017: 1-60.
56. Manivannan P., Jaleel C.A., Kishorekumar A., Sankar B., Somasundaram R., Sridharan R., Panneerselvam R. Drought stress induced changes in the biochemical parameters and photosynthetic pigments of cotton (*Gossypium hirsutum* L.). *Indian J. Appl. Pure Biol.*, 2007, 22: 369-372.
57. Pritula Z.V., Malyukova L.S., Velikii A.V. *Plodovodstvo i yagodovodstvo Rossii*, 2017, 51: 299-307 (in Russ.).
58. Tyerman S.D., Niemietz C.M., Bramley H. Plant aquaporins: multifunctional water and solute channels with expanding roles. *Plant, Cell & Environment*, 2002, 25(2): 173-194 (doi: 10.1046/j.0016-8025.2001.00791.x).
59. Wahid A., Gelani S., Ashraf M., Foolad M.R. Heat tolerance in plants: an overview. *Environmental and Experimental Botany*, 2007, 61(3): 199-223 (doi: 10.1016/j.envexpbot.2007.05.011).
60. Spalding E.P., Harper J.F. The ins and outs of cellular Ca<sup>2+</sup> transport. *Current Opinion in Plant Biology*, 2011, 14(6): 715-720 (doi: 10.1016/j.pbi.2011.08.001).
61. Saruhashi M., Ghosh T.K., Arai K., Ishizaki Y., Hagiwara K., Komatsu K., Shiwa Y., Izumikawa T., Yoshikawa H., Umezawa T., Sakata Y., Takezawa D. Plant Raf-like kinase integrates abscisic acid and hyperosmotic stress signaling upstream of SNF1-related protein kinase 2. *Proceedings of the National Academy of Sciences*, 2015, 112(46): E6388-6396 (doi: 10.1073/pnas.1511238112).
62. Wan X., O'Quinn R.P., Pierce H.L., Joglekar A.P., Gall W.E., DeLuca J.G., Carroll C.W., Liu S.-T., Yen T. J., McEwen B.F., Stukenberg T., Desai A., Salmon E.D. Protein architecture of the human kinetochore microtubule attachment site. *Cell*, 2009, 137(4): 672-684 (doi: 10.1016/j.cell.2009.03.035).
63. Kim T.H., Böhmer M., Hu H.H., Nishimura N., Schroeder J.I. Guard cell signal transduction network: advances in understanding abscisic acid, CO<sub>2</sub>, and Ca<sup>2+</sup> signaling. *Annual Review of Plant Biology*, 2010, 61: 561-591 (doi: 10.1146/annurev-arplant-042809-112226).
64. Gupta S., Bharalee R., Bhorali P., Das S.K., Bhagawati P., Bandyopadhyay T., B. Gohain, Agarwal N., Ahmed P., Borchetia S., Kalita M.C., Handique A.K., Das S. Molecular analysis of drought tolerance in tea by cDNA-AFLP based transcript profiling. *Mol. Biotechnol.*, 2013, 53(3): 237-248 (doi: 10.1007/s12033-012-9517-8).
65. Gelmesa D., Dechassa N., Mohammed D., Gebre E., Monneveux P., Bündig C., Winkelmann T. In vitro screening of potato genotypes for osmotic stress tolerance. *Open Agriculture*, 2017, 2(1): 308-316 (doi: 10.1515/opag-2017-0035).
66. Wang W.D., Xin H.H., Wang M.L., Ma Q.P., Wang L., Kaleri N.A., Wang Y.H., Li X.H. Transcriptomic analysis reveals the molecular mechanisms of drought-stress-induced decreases in *Camellia sinensis* leaf quality. *Front Plant Sci.*, 2016, 7(795): 385-412 (doi: 10.3389/fpls.2016.00385).
67. Cui X., Wang Y.-X., Liu Z.-W., Wang W.-L., Li H., Zhuang J. Transcriptome-wide identification and expression profile analysis of the bHLH family genes in *Camellia sinensis*. *Functional & Integrative Genomics*, 2018, 18(5): 489-503 (doi: 10.1007/s10142-018-0608-x).
68. Wang Y.-X., Liu Z.-W., Wu Z.-J., Li H., Zhuang J. Transcriptome-wide identification and expression analysis of the NAC gene family in tea plant [*Camellia sinensis* (L.) O. Kuntze]. *PLoS ONE*, 2016, 11(11): e0166727 (doi: 10.1371/journal.pone.0166727).
69. Wang Y., Shu Z., Wang W., Jiang X., Li D., Pan J., Li X. CsWRKY2, a novel WRKY gene from *Camellia sinensis*, is involved in cold and drought stress responses. *Biologia Plantarum*, 2016, 60(3): 443-451 (doi: 10.1007/s10535-016-0618-2).
70. Wang M., Zhuang J., Zou Z., Li Q., Xin H., Li X. Overexpression of a *Camellia sinensis* DREB transcription factor gene (CsDREB) increases salt and drought tolerance in transgenic *Arabidopsis thaliana*. *J. Plant Biol.*, 2017, 60: 452-461 (doi: 10.1007/s12374-016-0547-9).
71. Shen W., Li H., Teng R., Wang Y., Wang W., Zhuang J. Genomic and transcriptomic analyses of HD-Zip family transcription factors and their responses to abiotic stress in tea plant (*Camellia sinensis*). *Genomics*, 2018 (In Press, Corrected Proof) (doi: 10.1016/j.ygeno.2018.07.009).

72. Chen J., Gao T., Wan S., Zhang Y., Yang J., Yu Y., Wang W. Genome-wide identification, classification and expression analysis of the HSP gene superfamily in tea plant (*Camellia sinensis*). *Int. J. Mol. Sci.*, 2018, 19(9): 2633 (doi: 10.3390/ijms19092633).
73. Wang L., Cao H., Qian W., Yao L., Hao X., Li N., Yang Y., Wang X. Identification of a novel bZIP transcription factor in *Camellia sinensis* as a negative regulator of freezing tolerance in transgenic arabidopsis. *Annals of Botany*, 2017, 119(7): 1195-1209 (doi: 10.1093/aob/mcx011).
74. Li H., Huang W., Liu Z.-W., Wang Y.-X., Zhuang J. Transcriptome-based analysis of Dof family transcription factors and their responses to abiotic stress in tea plant (*Camellia sinensis*). *Int J Genomics*, 2016: 5614142 (doi: 10.1155/2016/5614142).
75. Wang P., Chen D., Zheng Y., Jin S., Yang J., Ye N. Identification and expression analyses of SBP-box genes reveal their involvement in abiotic stress and hormone response in tea plant (*Camellia sinensis*). *Int. J. Mol. Sci.*, 2018, 19(11): 3404 (doi: 10.3390/ijms19113404).
76. Zhu J., Wang X., Guo L., Xu Q., Zhao S., Li F., Yan X., Liu S., Wei C. Characterization and alternative splicing profiles of the lipoxygenase gene family in tea plant (*Camellia sinensis*). *Plant and Cell Physiology*, 2018, 59(9): 1765-1781 (doi: 10.1093/pcp/pcy091).
77. Guo Y., Zhao S., Zhu C., Chang X., Yue C., Wang Z., Lin Y., Lai Z. Identification of drought-responsive miRNAs and physiological characterization of tea plant (*Camellia sinensis* L.) under drought stress. *BMC Plant Biology*, 2017, 17: 211 (doi: 10.1186/s12870-017-1172-6).