Response Mechanism of Plants to Drought Stress

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Abstract Drought stress is an important factor affecting plant growth and development. It will provide a theoretical basis for cultivating new stress-resistant varieties and improving water utilization rate of plants by studying the regulation mechanism of osmotic adjustment and water transportation under drought stress, and understanding the physiological and biochemical characteristics and stress resistance mechanism.

Key words Plant gene; Drought stress; Regulation mechanism; Osmotic adjustment substance; Water transportation

1 Introduction

The growth and development of plants are affected by biotic and abiotic stresses in an ecological environment. In recent years, due to the intensification of global warming, shortage of water resources, rise of temperature in various regions, and uneven distribution of precipitation, the range of arid and semi-arid areas in China has gradually expanded, and plants are increasingly stressed by drought. Plant structural characteristics and physiological and biochemical reactions will be inhibited under drought stress, which will weaken the growth and development rate and even lead to plant death. It will provide a theoretical support for genetic engineering of plant drought resistance and offer a theoretical basis for screening target genes, breeding new varieties of drought resistance and improving plant water utilization rate by studying the expression and regulation mechanism of plant related genes under drought stress, and further understanding the adaptation and resistance mechanism of plants to drought stress. Therefore, this paper describes the expression and regulation of plant genes under drought stress, and systematically introduces the expression of genes related to osmotic adjustment substances and water transportation in plants, as well as the regulation mechanism of these genes.

2 Plant response to drought stress at physiological level

2.1 Osmotic adjustment of plants Osmotic adjustment is an important physiological mechanism for plants to adapt to drought stress. It can induce solute accumulation and reduce osmotic potential to maintain normal cell oncotic pressure under drought stress. Osmotic regulators in plants mainly include proline, soluble protein, soluble sugar, betaine, *etc.* [1].

2.1.1 Proline. When plants endure drought adversity, they will quickly synthesize and accumulate a large amount of proline to improve their osmotic adjustment ability to cope with drought adversity. Among them, proline is highly soluble, highly hydrophilic and non-toxic[2]. The accumulation and synthesis of proline in plants does not interfere with physiological and biochemical reactions in cells, but interacts with proteins to protect and maintain cell membrane function when plants are injured[3], slow down cell damage, and transport proline to cytoplasm when cells are under osmotic stress to maintain the osmotic pressure balance between cell protoplasm and external environment[4]. The synthesis of proline can be divided into two ways due to different initial substrates: one is glutamic acid (Glu) pathway, and the initial substrate is L-Glu; the other is ornithine (Orn) pathway, and the initial substrate is L-Orn. Studies have shown that both Orn and Glu can be used as precursors for proline synthesis, but proline is mainly synthesized from Glu[5]. Glu is the main pathway under nitrogen deficiency and osmotic stress, while Orn is the main pathway when nitrogen is abundant[6].

Under drought conditions, the induced expression of coding genes is usually related to the increase of proline synthesis, and the introduction of exogenous *P5CS* gene into plants can improve the proline level of plants under drought stress, thus improving their drought resistance. The synthesis and accumulation ways of proline often vary with plants, physiological conditions, tissues and organs. According to the size of plants, Orn pathway is dominant in seedlings and Glu pathway is dominant in adult plants. However, both pathways play equally important roles under osmotic pressure conditions[7].

At the same time, studies have shown that the proline content in plants is not high, but it will change along with the external environment[8]. Different degrees of drought stress also have adverse impacts on proline content in plants. With the extension of drought stress, proline content in plants tends to gradually increase, and a higher content of proline helps plants to adjust and adapt to drought and water shortage[9]. The content of proline increases significantly with the degree of stress, that is, plants with strong drought tolerance have higher content of proline[10 – 11].

2.1.2 Soluble protein. When plants endure drought adversity, soluble protein is also an important osmotic adjustment substance, which can regulate and increase water absorption of plants under drought conditions, promote water absorption of plants, and further maintain physiological processes such as cell growth, photosynthesis and respiration[12]. Under mild drought, plants can resist drought stress damage by increasing protein content in cells,

Received: July 12, 2023 Accepted: September 28, 2023

Supported by Thousand Talents Program for High-end Innovative Talents of Qinghai Province (2020, 2022).

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and with the intensification of drought stress, it shows a trend of first increasing and then decreasing. Severe drought stress often inhibits normal protein synthesis and induces protein degradation of plants, and the leaves can not carry out normal metabolism, so the protein content decreases accordingly[13-14]. Among the soluble proteins in plant cells, many enzymes have specific metabolic regulation functions. Others may act as dehydration protectors, providing binding pads for intracellular bound water, increasing the amount of bound water in plant tissues so that the cell structure does not suffer more damage when dehydrated. In addition, plants also synthesize some new or increased proteins under drought stress, such as drought-induced proteins, LEA proteins and osmotins. Osmotin is a natural component of plants, which is formed and accumulated in large quantities with the adaptation of plants to various stresses, and is rich in roots, stems, crowns and peripheral tissues of immature flower buds. Stress-inducing proteins play a protective role in plant adaptation to stress and may improve plant stress tolerance[15].

Moreover, with the intensification of drought stress, the soluble protein in plants increases first and then decreases, which is the osmotic adjustment mechanism of plants to cope with drought. Soluble protein content does not change significantly in the early stage of drought stress, but will increase significantly in the later stage. The rise of soluble protein is due to a protective mechanism by which plants self-regulate in response to adversity, and the decline of soluble protein is due to the obstruction of protein synthesis in plants, resulting in a large amount of soluble protein degradation.

2.1.3 Soluble sugar. Under drought stress, soluble sugar can reduce the damage caused by osmotic water loss by maintaining cell water content and regulating cell osmotic pressure, so as to adapt to adversity[16]. With the increase in soluble sugar content, the concentration in the cytoplasm increases, the permeability of cell membrane decreases, and the integrity of cell membrane increases, which ensures the normal activity and physiological function of cells, enhances the resistance of cells to the adverse external environment, and provides a good physiological basis for the normal activity and physiological function of cells.

Meanwhile, drought stress significantly induces the accumulation of soluble sugar content in plant leaves. After drought stress, the soluble sugar content in plant leaves increases, and the accumulation is the most obvious under severe drought stress, but there is a significant decrease in the late stage of drought. When plants are in the early stage of drought, the increase of soluble sugar content in leaves plays an important role in plant osmotic adjustment, which may be because the protective enzyme system in plants adapts them to stress, thus increasing the soluble sugar content[17]. However, with the intensification of drought stress, the synthesis of sugar may be hindered, coupled with the fibrosis of sugar, the soluble sugar content of leaves begin to decline. In the relevant studies of plants such as *Capsicum annuum*, *Lycium ruthenicum*, *Dasiphora fruticosa* and *Hedysarum scoparium*, the change in soluble sugar content also shows the same trend[18-19]. The accumulation of soluble sugar in plants not only plays a vital role in improving drought resistance and osmotic adjustment of plants, but also plays an important role in maintaining the stability of plant proteins[20]. In addition to osmotic adjustment, it also plays a role in maintaining the stability of plant proteins[21]. At the same time, the plants with strong resistance always maintain a higher content of soluble sugar, and the drought resistance index is positively correlated with soluble sugar content.

2.1.4 Betaine. Betaine exists widely in plants and is the main organic osmotic regulator of plants. It is synthesized in the following steps: choline→betaine aldehyde chloride→betaine, and is catalyzed by two enzymes. The enzymes required for the first step of the synthetic pathway vary with organisms. In higher plants, choline monooxygenase (CMO) catalyzes the first reaction. In marine invertebrates and *Escherichia coli*, the first reaction is catalyzed by choline dehydrogenase (CDH) to produce betaine aldehyde chloride[22]. The synthesis of betaine in plants to resist the damage of stress is affected by two factors, namely, cumulative concentration and localization. The cumulative concentration of betaine is not static in different plants or varying parts of the same plant, but with the degree of stress, different changes occur in different parts, thus improving plant stress tolerance. Studies have found that the content of betaine exists in leaves or chloroplasts of tobacco, maize and rice[23-25], and the content is different, giving the plants different tolerance. Betaine is synthesized not only in leaves or chloroplasts, but also in roots, and is also induced by light and ABA[26].

When plants are subjected to drought stress, they will maintain water balance in the body, promote plant growth and development, and reduce the damage of drought stress on plants by adjusting the betaine content in the body, so as to adapt to the stressed environment and improve drought resistance. Gao Xiuping *et al.*[27] found that the betaine content in plants under drought stress was significantly higher than that under normal water supply conditions. Similarly, spraying exogenous betaine also leads to the same result. For plants growing under drought stress, the application of exogenous betaine can improve the stress resistance of plants, increase the water content of seedlings, and enhance the yield and leaf area growth rate[28]. In addition, the optimum concentration of betaine obtained by seed soaking, root soaking and hydroponics can also play a good role in drought resistance[29].

Therefore, betaine plays an important regulatory role under drought stress. Betaine, as an important osmotic adjustment substance of plant cells, can improve plant resistance through external application. In addition to promoting plant growth and improving plant resistance, it can also improve plant yield, which is very important for the development and utilization of crops. The development and utilization of this aspect can be increased in the future to cultivate more resistant and high-quality plants.

2.2 Stomatal regulation of plants Stomata play a regulatory role in photosynthesis and transpiration, and become an important channel for water transportation and gas exchange, making plants better adapt to the ecological environment. Stomata are located on the surface of plant leaves and consist of many small holes, each surrounded by two guard cells. Stomatal protective cells are very sensitive to changes in plant growth environment and adjust the size of stomatal aperture through inlet and outlet water flow[30]. The regulation of stomatal size is a defense mechanism for plants to cope with adversity stress.

Under drought stress, the stomatal opening of plants will decrease or close to reduce the intensity of transpiration, reduce the water loss of plants, and form a protective mechanism to adapt to the arid environment. Previously, scientists thought stomata opening was due to less water being taken up by plant roots under dry conditions, resulting in less water in the leaves. Therefore, the degree of opening and closing is regulated by inducing stomata in plant leaves, which is called "hydraulic control theory"[31]. Subsequent studies have also demonstrated that stomatal regulation is the regulation of chemical signals transmitted from roots to leaves, and one of which is ABA. When ABA is released into guard cells, it causes water loss, thereby reducing or even closing stomatal opening[32].

Meantime, drought stress increases stomatal density, and decreases stomatal conductance, length, width, opening and opening rate[33]. Yu Haiqiu[34] also obtained the decreasing trend of stomatal opening and tension when subjecting maize to drought stress. Therefore, plants reduce water loss by minishing stomatal opening and tension to cope with drought stress. Other studies found that stomatal opening and stomatal size decreases significantly with the intensification of drought stress[35]. With the intensification of drought stress, leaf stomatal density presents a trend of first increasing and then decreasing, that is, moderate drought can increase leaf stomatal density, whereas excessive drought can decrease leaf stomatal density[36].

This may be due to the fact that mild and moderate drought stress can inhibit the growth of cells, resulting in decreased leaf area, increased unit cell area, and increased stomatal density. This conclusion has been confirmed in the studies of Chinese wildrye, ginger and jujube[37]. The stomatal conductance of plant leaves decreases significantly with the increase of drought stress. In addition, plants with strong drought resistance will adjust leaf structure according to soil moisture to maintain their growth and development.

In summary, stomatal tension, opening and density are important indexes to measure drought resistance of plants. Plants with strong drought resistance have small stomata and high density, and sensitive stomatal conductance to soil water change, so they have better adjustment ability.

3 Plant response to drought stress at molecular level

3.1 Aquaporin gene Aquaporins regulate the water balance of plants by controlling the flow of water molecules into and out of cells. Compared with animals and microorganisms, plant aquaporins are particularly abundant in species. More than 100 kinds of aquaporins have been discovered so far. According to the sequence homology, subcellular localization and structural characteristics of AQPs, they can be classified into 7 categories. Studies have found that different AQPs have diverse localization[38]. For example, it resembles AQP but has completely different subcellular localization; different subtypes of vacuolar membrane embedding protein also have different localization; different subtypes of vacuolar imbedding proteins are also co-expressed in vacuoles, and different subtypes of vacuolar membrane embedding proteins of the same type are found in plant vacuoles. This suggests that the subcellular patterns of AQP localization in plants are diverse and specific[39].

The expression of plant aquaporins is influenced by environmental factors and hormones. It is found that aquaporins can improve plant tolerance under drought stress. The expression of hydrotonin gene significantly improves the drought resistance of plants, such as rice, wheat, banana, tomato, apple and tobacco. When Ta-AQP7 is overexpressed in tobacco, the drought resistance of tobacco is significantly improved. Overexpression of MaPIP2-7 in bananas can significantly improve the drought tolerance of bananas. Under stress conditions, the expression of most AQPs is reduced at the transcriptional and protein levels, and the activity of AQP channels is reduced or even disappears. AQP shutdown can reduce the environmental conditions in the early phase of drought, which can stimulate the synthesis and expression of aquaporins. However, under long-term drought stress, soil water shortage will inhibit the activity of aquaporins in roots. The expression analysis of 35 aquaporin genes in *Arabidopsis thaliana* showed that most *PIP* and *TIP* genes had higher expression levels under drought conditions, while *NIP* had lower expression levels[40]. In addition, AQP gene is also regulated by the expression of plant hormones such as abscisic acid (ABA), gibberellin (GA) and brassinosteroid (BR). Brassinolide controls the activity of AQP on *A. thaliana* cell membrane and can alter the water permeability of cell membrane[41-43].

In summary, plant aquaporins are abundant in species, numerous in family and complex in expression. The expression of AQPs, is affected by environment and hormones. Under stress conditions, the general expression is to increase AQPs, content. Overexpression of AQPs can improve drought resistance of plants, and plant hormone leaves can also induce the expression of aquaporins. At present, although some achievements have been made in molecular structure and expression regulation mechanism of plant AQPs, the signal transduction related to *AQPs* gene expression regulation, the isolation of *AQPs* gene promoter, and the analysis of expression types are not very clear, and all need further research.

3.2 Antioxidant metabolism gene The expression of *ABP9*, *GbMPK3* and *ZFP245* genes can promote the removal of reactive oxygen species and enhance the drought resistance of plants. Li Jing *et al.*[44] showed that the expression of *ABP9* gene in

A. thaliana can reduce plant oxidative damage, thus playing an important role in plant drought resistance. Under drought conditions, the expression of *GbMPK3* gene can significantly improve the antioxidant enzyme activity of tobacco, and cope with drought by enhancing plant reactive oxygen scavenging capacity[45]. Yuan Xi *et al.* [46] found that the expression of *ZFP214* gene could promote the synthesis of antioxidant enzymes in rice to inhibit the accumulation of reactive oxygen species and enhance the drought tolerance of plants.

4 Response of plant hormones to drought stress

4.1 ABA ABA controls plant responses to biotic and abiotic environmental stresses by affecting transcriptional and post-transcriptional modifications of downstream regulatory factors in its signaling pathway, thereby enhancing plant resistance[47]. Its synthesis begins with a series of reactions of acetyl-coenzyme formed by the metabolism of sugars, fats and proteins to synthesize farnesyl pyrophosphate (FPP). The process of FPP forming ABA can be divided into two ways: One is terpenoid pathway, also known as C_{15} direct pathway, which directly forms C_{15} ABA from FPP through cyclization and oxidation; the other is carotenoid pathway, also known as C_{40} intermediate pathway, where FPP is converted to β-carotene in the plastid, and then to retinaldehyde, which is finally converted to ABA in the cytoplasm. Under normal circumstances, the content of ABA is relatively low, but when the plant is short of water, the content of ABA in the body will increase greatly. With the increase of drought stress, the ABA content of *Pinus massoniana* from different germplasm sources shows different upward trends, which may be due to the difference in plant resistance, and the increase amplitude and trend vary with germplasm sources. At present, more than 150 plant genes are known to be induced by exogenous ABA, and 245 ABA-inducing genes and nearly 300 drought-inducing genes have been identified in *A. thaliana* related experiments. Among the 245 ABA-inducing genes, drought can induce more than 150 genes. These results may indicate that ABA is involved in the regulation of a large number of genes during drought stress[48].

In summary, ABA, as an important plant hormone, plays an important role in plant growth and development, response to drought stress, agricultural production, disaster reduction and yield protection, and ecological environment restoration, and its regulatory mechanism is mainly manifested in an increasing trend, while the increasing trend and amplitude vary among plants. The synthesis and decomposition of ABA are manifested in both leaves and roots of plants. Some key mechanisms of ABA signal transduction have been studied, but there are still some key regulatory mechanisms that have not been fully explained and need further study.

4.2 IAA IAA is a plant hormone that improves water absorption by promoting plant root growth, thereby increasing drought resistance in plants. The content of IAA in plants does not change regularly. For example, under drought stress, the IAA content in *Tamarix chinensis* was significantly higher than that in the control group, while that in *Picea koraiensis* and *Dalbergia odorifera* gradually decreased with the aggravation of drought[49].

4.3 GA GA mainly involves in plant growth and development and seed germination, and can quickly break organ dormancy. It is found that the GA content of some plants increases under drought stress, which promotes the synthesis of IAA and increases the IAA content of plants, thus improving the drought resistance of plants[47].

5 Conclusions

Drought stress seriously affects the growth and development of plants, so it is particularly important to study the drought resistance mechanism of plants under drought stress. In this paper, the definition, classification structure and synthetic expression of related genes such as proline, soluble sugar, soluble protein, aquaporin, stomata, betaine and ABA are reviewed, and their regulatory mechanism under drought stress is further expounded. Currently, with the rapid development of molecular biology and related disciplines, people can understand the physiological functions of osmotic adjustment substances and the mechanism of binding physiological functions, and study the genes of osmotic adjustment substance synthase. However, the synthesis and regulation of osmotic adjustment substances, especially the accumulation under environmental stress, are still unclear. The transformation and expression of osmotic adjustment synthase genes in plants and stress-resistant varieties need more research on how plants respond to drought stress under random stress conditions, which signal transduction factors stimulate the expression of genes related to proline synthesis and degradation under stress conditions, and transcription factors regulate the transcription and expression of these genes, *etc.*

References

[1] FU ZX, FAN XM, SHI DY. Comparison of osmotic substance contents in leaves of two varieties of kale under low temperature stress[J]. Modern Agricultural Science and Technology, 2019(24): 33–34, 38. (in Chinese).

[2] XIE Q, CHEN L. Role of proline accumulation in bryophytes under resistant conditions[J]. Contemporary Horticulture, 2020, 43(15): 51–52, 130. (in Chinese).

[3] PENG ZH, PENG KQ, HU JJ, *et al.* Research progress on accumulation of proline under osmotic stress in plants[J]. Chinese Agricultural Science Bulletin, 2002, 18(4): 80–83. (in Chinese).

[4] TANG ZC. Accumulation of proline in plants under adverse conditions and its possible significance[J]. Plant Physiology Communications, 1984 (1): 15–21. (in Chinese).

[5] QIAN DW, ZHOU HK, JIANG DK, *et al.* Pathways of proline synthesis and accumulation in *Sesuvium portulacastrum* under the stress of NaCl [J]. Chinese Wild Plant Resources, 2013, 32(3): 35–39. (in Chinese).

[6] HUANG CM, BI LM, YANG LT, *et al.* Effects of polyethylene glycol stress on proline accumulation and the activities of the key enzymes in leaves of sugarcane (*Saccharum officinarum* L.) at the elongation Stage [J]. Plant Physiology Communications, 2007, 43(1): 77–80. (in Chinese).

[7] YANG S, YANG JW, YE CH, *et al.* Analysis of drought to lerance physiological effect based on proline biosynthesis and accumulation at the

tillering stage in sugarcane[J]. Journal of Guangdong Ocean University, 2015, 35(6): 87 –93. (in Chinese).

[8] LI Y, WEI HD, CHEN F, *et al.* Proline and chlorophyll content in leaves of typical sand plants in the Hexi Region of Gansu Province[J]. Journal of Northwest Forestry University, 2018, 33(3): 27 –32, 73. (in Chinese).

[9] YANG QY, LUO YZ, YANG Y, *et al.* Effects of drought stress on physiological and biochemical indexes of *Dendrobium officinale* 'Jinhu No. 1' [J]. Chinese Wild Plant Resources, 2023, 42(2): 69 –75. (in Chinese).

[10] ZHOU L, WANG NJ. Physiological responses of *Xanthoceras sorbifolia* seedling leaves under soil drought stress[J]. Journal of Northwest Forestry University, 2012, 27(3): 7 –11, 16. (in Chinese).

[11] CUI Y, LI QX, LIU B, *et al.* Effects of drought stress on morphology and physiological characteristics of *Ficus tikoua* seedlings[J]. Journal of Northwest Forestry University, 2020, 35(6): 82 –88, 227. (in Chinese).

[12] WAN W. Establishiment of tissue culture regeneration system and salt-tolerance of *Broussonetia papyrifera* (L.) Vent[D]. Beijing: Beijing Forestry University, 2010. (in Chinese).

[13] ZHANG LS, ZHAO WM. LEA protein functions to tolerance drought of the plant[J]. Plant Physiology Communications, 2003, 39(1): 61 –66. (in Chinese).

[14] YEO A. Molecular biology of salt tolerance in the whole plant physiology [J]. Journal of Experiment Botnny, 1999(49): 915 –920 . (in Chinese).

[15] YU LL, PEI ZP, KONG J, *et al.* Drought resistance of four plant species in ecological regeneration on Mining Area under drought stress[J]. Northern Horticulture, 2013(12): 61 –64. (in Chinese).

[16] XIAO ZH, LI XH, PAN G, *et al.* Effects of manganese stress on seed germination, and seedling physiological and biochemical characteristics of *Cleome viscosa*[J]. Acta Prataculturae Sinica, 2019, 28(12): 75 –84. (in Chinese).

[17] LIU RJ, TANG YW, YUAN HJ. Study of changes of soluble sugar content of barley blades in conditions of drought situation[J]. Tibet Journal of Agricultural Sciences, 2013, 35(4): 9 –11, 5. (in Chinese).

[18] MA ZL, ZHOU HF, XIE XY. Effect of betaine(GB) and salicylic acid (SA) on phytosynthetic characters of hot pepper under drought stress during blossom and fruit period[J]. Northern Horticulture, 2019(11): 18 –23. (in Chinese).

[19] DING L, ZHAO HM, ZENG WJ, *et al.* Physiological responses of five plants in northwest China arid area under drought stress[J]. The Journal of Applied Ecology, 2017, 28(5): 1455 –1463.

[20] SUN P, DUAN XH. Effects of drought stress on soluble sugars and photosynthetic characteristics of *Catharanthus roseus* seedlings[J]. Journal of Northeast Forestry University, 2010, 38(8): 54 –56. (in Chinese).

[21] DU JY, CHEN XY, LI W, *et al.* Expression and regulation of genes induced by drought stress in plant[J]. Biotechnology Information, 2004 (2): 10 –14. (in Chinese).

[22] CHEN TH, MURATA N. Enhancement of tolerance to abiotic stress by metabolic engineering of betaines and other compatible solutes[J]. Current Opinion in Plant Biology, 2002, 5(3): 250 –257.

[23] YANG XH, LU CM . Photosynthesis is improved by exogenous glycinebetaine in salt-stressed maize plants[J]. Physiol Plantarum, 2005, 124 (3): 343 –352.

[24] SAKAMOTO A, ALIA, MURATA N. Metabolic engineering of rice leading to biosynthesis of glycinebetaine and tolerance to salt and cold [J]. Plant Molecular Biology, 1998, 38(6): 1011 –1019.

[25] QUAN R, SHANG M, ZHANG H, *et al.* Improved chilling tolerance by transformation with betA gene for the enhancement of glycinebetaine synthesis in maize[J]. Plant Science, 2004, 166(1): 141 –149.

[26] ZHENG GQ, XU X, DENG XP, *et al.* Effects of salt and water stresses on osmotic adjustment of *Lycium barbarum* seedlings[J]. Agricultural Reseach in The Arid Areas, 2002, 20(2): 56 –59 . (in Chinese).

[27] GAO XP, RUN JY, LIU EK, *et al.* Changes in betaine level in pear, jujube and grapevine leaves under water stress[J] . Acta Horticulturae Sinica, 2002, 29(3): 268 –270. (in Chinese).

[28] ZENG LM, ZENG J. Research progress on the function and regulation of aquaporin in plant response to stress[J]. Chinese Journal of Tropical Agriculture, 2020, 40(7): 59 –65. (in Chinese).

[29] JIANG LJ, CHEN CH, YAN X, *et al.* Research progress on responsive mechanism of aquaporins to drought stress in plants[J]. Guihaia, 2018, 38(5): 672 –680. (in Chinese).

[30] MENG FX, ZHANG SQ, LOU CH. The structural foundation of stomatal function[J]. Chinese Bulletin of Botany, 2000, 17(1): 27 –33. (in Chinese).

[31] ZHANG SQ, LI JH, SHAN L. Regulation of the plant stomatal movement under drought condition[J]. Acta Botanica Boreali-occidentalia Sinica, 2001, 21(6): 1263 –1270. (in Chinese).

[32] DAVIES WJ, ZHANG J. Root signals and the regulation of growth and developmentof plants in drying soil[J]. Annual Review of Plant Physiology and Plant Molecular Biology, 1991, 42(1): 55 –76.

[33] CHRISTMANN A, GRILLE. Peptidesignal alerts plants to drought[J]. Nature, 2018, 556(700): 178 –179.

[34] YU HQ, WANG XL, JIANG CH, *et al.* Injured process on anatomical structure of maize seedling under soil drought[J]. Agricultural Reseach in the Arid Areas, 2008, 26(5): 143 –147. (in Chinese).

[35] LI ZH, LIU JP, GU HL, *et al.* Review on the effects of drought stress on plant stomatal characteristics[J]. Subtropical Plant Science, 2016, 45(2): 195 –200. (in Chinese).

[36] XIE ZS, SONG SX, CAO HM. Comparisons of leaf anatomical structure and stoma characteristic among three different blueberry varieties[J]. Northern Horticulture, 2015(4): 5 –8. (in Chinese).

[37] MAKBUL S, GVLER NS, DURMUS N, *et al.* Changes in anatomical and physiological parameters of soybean under drought stress[J]. Turkish Journal of Botany, 2011, 35(4): 369 –377.

[38] ZHANG LL, PENG D, ZHANG J, *et al.* The function and modulation mechanism of aquaporin in plant abiotic resistance[J]. Molecular Plant Breeding, 2017, 15(11): 4441 –4450. (in Chinese).

[39] CHEN RG, ZHU WC, GONG ZH, *et al.* Cloning and sequence analysis of the aquaporins gene CaAQP in pepper[J]. Scientia Agricultura Sinica, 2010, 43(20): 4323 –4329. (in Chinese).

[40] ALEXANDERSSON E, FRAYSSE L, SJOVALL-LARSEN S, *et al.* Whole gene family expression and drought stress regulation of aquaporins [J]. Plant Molecular Biology, 2005, 59(3): 469 –484.

[41] WU XJ, WANG XM, GAO HW, *et al.* Cloning and analysis of the aquaporins gene from galega orientalis[J]. Acta Agrestia Sinica, 2011, 19(2): 331 –339. (in Chinese).

[42] KALDENHOFF R, KÖLLING A, RICHTER G. Regulation of the *Arabidopsis thaliana* aquaporin gene AthH2 (PIP1b)[J]. Journal of Photochemistry and Photobiology B: Biology, 1996, 36(3): 351 –354.

[43] PHILLIPS AL, HUTTLY AK. Cloning of two gibberellin-regulated cDNAs from Arabidopsis thaliana by subtractive hybridization: expression of the tonoplast water channel, γ-TIP, is increased by GA3[J]. Plant Molecular Biology, 1994, 24(4): 603 –615.

[44] LI J. Expression of ABP9 enhances tolerance to drought stress in transgenic alfalfa[D]. Lanzhou: Lanzhou University, 2012. (in Chinese).

[45] ISHITANI M, NAKAMURA T, HAN SY, *et al.* Expression of the betaine aldehyde dehydrogenase gene in barley in response to osmotic stress and abscisic acid[J]. Plant Molecular Biology, 1995, 27(2): 307 –315.

[46] YUAN X. Functional analysis of zinc finger proteins ZFP150 and ZFP214 in responses to abiotic stress in rice (*Oryza sativa* L.)[D]. Nanjing: Nanjing Agricultural University, 2015. (in Chinese).

[47] ZHANG Q, WANG JY, DONG DL, *et al.* The vital roles of abscisic acid signal transduction pathway in response to abiotic stress in plants [J]. Chemistry of Life, 2021, 41(6): 1160 –1170. (in Chinese).

[48] LI Y, WAN LQ, LI XL. Progress in understanding relationships between the physiological mechanisms of endogenous abscisic acid and drought resistance of alfalfa[J]. Acta Prataculturae Sinica, 2015, 24 (11): 195 –205. (in Chinese).

[49] ZENG Y. Study on drought resistance of four kinds of common vertical greening plants[D]. Ya'an: Sichuan Agricultural University, 2015. (in Chinese).