## Mechanisms behind the Guar Drought Tolerance

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Guar is an unpretentious plant and grows on both sandy and well-drained clay soils. Guar is self-pollinating with a negligible level of cross-pollination. The plants considerably vary in height (from 50 cm to 1.5 m). The stem is sturdy, becoming woody by the plant maturation. The main root is thick and tapering in its distal parts, deeply penetrating into the soil. Due to this, guar can perfectly sustain short-term drought.

Keywords: guar ; drought stress ; drought tolerance ; photosynthesis ; carbohydrate metabolism ; nitrogen metabolism ; tricarboxylic acid ; antioxidant defense ; phytohormones

### 1. Introduction

Guar (*Cyamopsis tetragonoloba* (L.) Taub.) is an annual grain legume crop. Due to its strategic significance, it is recognized as one of the most sought-after and promising crop plants in the world. To date, the main rationale for the cultivation of guar is the high abundance of galactomannans (also known as guar gum or guarana) accumulated in the endosperm of its mature seeds <sup>[1]</sup>. As a plant polymer built from individual monosaccharides (galactose), guar gum behaves as a hydrocolloid, i.e., when dissolved in water and other liquids, it is capable of forming gelatinous mixtures resistant to freezing. This property has a high demand in the food, medical, textile, paper, cosmetics and explosives industries. However, the most important aspects of its application are the oil production and mining industries <sup>[2]</sup>. As a drilling fluid additive, guar gum has unrivaled properties <sup>[3]</sup>. When used during oil drilling, guar gum prevents the loss of water from viscous drilling fluid and effectively suspends bentonite clay. Guar gum is also cheaper than most other drilling fluid thickeners. The high worldwide demand for guar in recent decades has been the impetus for closer study and breeding of this crop in the countries of its predominant cultivation: India, the USA, Pakistan, Australia and several southern European countries. The Russian Federation, along with Germany, the Netherlands, Italy, France, Spain and the UK, is the largest importer of guar gum in Europe <sup>[4]</sup>.

Dependence on the guar import motivated European and Russian scientists and agrarians to initiate the work on the introduction of this tropical crop in the industrial cultivation in their countries. Over the last decade, significant successes in guar cultivation have been achieved in several regions of the Southern Federal District and the Lower Volga region in Russia <sup>[5]</sup>. Moreover, the State Register of Breeding Achievements was extended with ten cultivars of guar, nine of which are of domestic breeding <sup>[6]</sup>. This fact is expected to impact the development of domestic gum production. Guar can also be used for animal feed and as green manure <sup>[7]</sup>. Similarly to other legumes, it forms symbiotic interactions with nitrogenfixing rhizobia and arbuscular mycorrhiza fungi <sup>[8][9]</sup>. Therefore, the introduction of this legume crop in agricultural production in Russia will contribute to the development of green agriculture and the technological independence of the national oil production industry. Obviously, a proper soil type and climate zone need to be selected for the successful cultivation of guar in Russia <sup>[5]</sup>. For this, the mechanisms behind the adaptation of guar plants to soil and environmental conditions need to be comprehensively addressed, in addition to the diversity of their gene pool with respect to limiting environmental factors.

In particular, it is important in the context of drought, which is typical in the southern regions of the Russian Federation. Drought is known as the main factor affecting crop productivity worldwide  $^{[10]}$  and requires, therefore, the special attention of agricultural biologists. In respect of this factor, guar is generally considered a moderate drought- and heat-tolerant crop  $^{[11][12]}$ . However, the intensive studies of the recent decade  $^{[13][14][15]}$  clearly indicated that individual guar genotypes are featured with a pronounced diversity in responsivity to different irrigation modes: cultivation without irrigation, with variable water supply, as by quantity, during different stages of plant development.

Therefore, guar breeding might potentially rely on a differentiated (multitarget) approach. In terms of this approach, drought-tolerant cultivars can be cultured under water deficit conditions, whereas drought-sensitive ones can be adjusted to a specific water supply regimen.

Obviously, under the climate conditions of Russian Federation availability of elevated temperatures (25 °C and more) appears to be the principal limiting factor for guar field culturing. Indeed, for this crop, the sum of efficient air temperatures above 10 °C must be at least 3400–3500 °C. In terms of rainfall, 350–500 mm per growing season was reported to be sufficient <sup>[16]</sup>. Expectedly, only a few Russian regions meet these criteria. Thus, the plain parts of the Stavropol and Krasnodar regions have a natural water supply, which can be judged as sufficient for guar culturing, whereas supplementary irrigation is recommended in Crimea and in the Rostov region <sup>[16][17]</sup>. Thus, discovery of drought-tolerant genotypes among the available guar gene pool is strongly mandatory for successful culturing this plant in arid regions of southern Russia <sup>[5]</sup>. Taking into account the role of oil industry in the national economy of Russia, this aspect remains highly relevant.

However, to accomplish this task successfully, the physiological and biochemical mechanisms behind the drought tolerance in guar need to be well understood, and the underlying molecular genetic aspects of this trait need to be disclosed. Despite the high importance of water regimen in culturing of legumes, for guar this aspect still remains mostly unstudied, that might be explained by limited genome and transcript information, available for this species <sup>[18]</sup>.

### 2. Effects of Drought on Photosynthesis and Carbohydrate Metabolism

Photosynthesis is a vulnerable physiological process, usually dramatically affected by drought. These effects are typically manifested with the degradation and denaturation of chloroplast membrane systems [19]. Drought-induced suppression of photosynthetic activity is typically associated either with a restriction of the stomatal uptake of carbon dioxide and its transport to mesophyll cells, with enhancement of oxidative stress, or with inhibition of photosynthetic enzymes [20][21]. Moreover, drought results in disruption of respiration and associated oxidative phosphorylation that results in inhibition of ATP synthesis [22][23]. To understand these metabolic changes, adequate assessment of the drought-induced alterations in the structure and function of photosynthetic apparatus is required. The most adequate (although indirect) approach to address these changes in drought-sensitive guar plants is the assessment of the leaf water status and gas exchange efficiency. In particular, besides the evaluation of their gas exchange parameters, the determination of spectral characteristics (e.g., photochemical reflectance index (PRI) and normalized difference vegetation index (NDVI) are advantageous [24]. On the other hand, the optical properties of leaves need to be considered. Indeed, the ability for dynamic modification of their optical properties (i.e., reflection, absorption and transmission of light by the leaf lamina) represents one of the most important leaf adaptations [25]. Dynamic characterization of the drought-induced shifts in these properties in parallel to the analysis of gas exchange parameters and leaf pigment contents showed that the decrease in leaf photosynthetic activity was mostly associated with such markers as leaf relative water content (LRWC), stomatal conductance and drop in chlorophyll contents [26][27]. In contrast, a drought-induced increase in the contents of carotenoids and anthocyanins, which was most distinctly observed in the drought-tolerant guar line RGC-1002, impacted the improvement of membrane integrity and inhibition of formation. These biochemical shifts ensured the protection of the photosynthetic apparatus from light stress by absorbance of high-energy light. Moreover, the line RGC-1002 demonstrated a stress-induced increase in the NDVI index, which might indicate an increase in the maximal absorption of red light by chlorophyll molecules [24]. Upreti et al. found that by characterizing various chlorophyll fluorescence parameters, variety RGC-1002 has a better ability to dissipate excess light energy harmlessly compared to the droughtsensitive cultivar RGC-936 and thereby attenuate photoinhibition of both photosystems and protect the photosynthetic apparatus under drought conditions. The decrease in photosynthesis under drought conditions was smaller in the RGC-1002 cultivar compared to RGC-936, and the discrimination of stable carbon isotopes decreased more strongly in RGC-1002 [28]

To ensure the availability of energy resources (which are actually restricted under drought conditions) for essential biochemical reactions of cell primary metabolism involved in stress adaptation, plants employ the storage-mobilization strategy <sup>[29][30]</sup>. In this context, the processes of photosynthesis and different branches of carbohydrate metabolism need to be tightly coordinated. A study of carbohydrate metabolism and photosynthesis in drought-tolerant guar cultivars RGC-986 and HG-563 compared to the sensitive ones, RGC-471 and Varsha, revealed a drought-induced decrease in photosynthetic rates in all the cultivars studied, resulting in an apparent decrease in the contents of nicotinamide adenine dinucleotide phosphate (NADPH), which is required for CO<sub>2</sub> assimilation in the Calvin cycle <sup>[31]</sup>. Drought tolerant cultivars RGC-986 and HG-563 were found to exhibit more efficient coordination at the level of the photosystem II (PS II) and Calvin cycle gene regulation compared to drought tolerant cultivars RGC-471 and Varsha; higher efficiency of ROS detoxification; and enhanced biosynthesis of glucose, fructose and fructones associated with drought-protective guar metabolic rearrangement <sup>[31]</sup>.

It is important to note that glucose is not the only drought-inducible osmoprotective compound reported in guar so far. As was shown recently, guar plants synthesize fructans, which act as osmotically active compounds also involved in the

protection of cellular membranes from damage and impact on maintaining the turgor pressure [32]. The main factor affecting the efficiency of fructan biosynthesis in guar leaf cells is the availability of sucrose, the substrate of the enzyme sucrose: sucrose fructosyltransferase (SST), which irreversibly catalyzes the transfer of fructosyl between two sucrose molecules to form 1-kestose and glucose [33]. The ketose intermediate can serve as an acceptor for fructosyl residues, which can be transferred from another fructan chain, serving as a donor in the chain elongation reaction catalyzed by fructan: fructan fructosyltransferase (FFT) [33][34]. Stress-induced enhancement of photosynthetic reactions results in enhancement of sucrose biosynthesis [35][36]. Further, the enhanced rates of 1-kestose formation and subsequent chain elongation in transfructosylation reactions support the intensive synthesis of fructose-containing oligosaccharides, leading to their accumulation in the vacuole [37]. However, the molecular mechanisms underlying carbohydrate transport in response to drought stress remain unclear. In particular, it was found that the active response to drought is the activation of the trehalose-6-phosphate/SNF1-linked protein kinase (SnRK1) signaling pathway by suppressing class I Trehalose Phosphate Synthase (*TPS*) and the expression of class II *TPS* genes. The expression of *SnRK1a* and  $\beta$ -subunits, as well as Sucrose Synthase 6, contributed to the accumulation of soluble sugars in the leaves, the accumulation of which in vacuoles supports osmoregulation in the leaves. The increased expression of sucrose synthesis genes and the reduced expression of sucrose degradation genes in the roots did not coincide with sucrose levels, which implies local sucrose production for energy [38].

The cellular fructose and sucrose pools are closely related metabolically, as they are in a continuous equilibrium state. This equilibrium is manifested by the intensive exchange of fructosyl residues, which accompanies both the accumulation and depletion of fructan storages <sup>[39]</sup>. Moreover, the pools of reserve fructans and starch are also dynamically interconnected via sucrose. Indeed, this metabolite serves as a substrate in the biosynthesis of both polymers <sup>[40]</sup>. Thus, concerted regulation of carbohydrate metabolism and photosynthesis in guar impacts the efficient survival strategy under abiotic stress <sup>[31]</sup>.

Recently, Ansari and co-workers accomplished a comparative transcriptome analysis of guar cultivars characterized by different drought tolerance. This study revealed an increased level of transcripts related to starch and sucrose metabolism in the drought-tolerant guar genotype RGC-1002 <sup>[41]</sup>. This fact can be considered as further support for the drought-induced redirection of carbon flux to carbohydrate metabolism in guar leaves. Another drought-tolerant guar variety, BWP-5595, also demonstrated increased expression levels of three genes of the SWEET (Sugars Will Eventually Be Exported Transporter) family of sugar transporters <sup>[42][43]</sup>. This fact is also in line with the proposed concept.

### 3. Effects of Drought on the Nitrogen Metabolism

Along with carbon metabolism, nitrogen metabolism is an important factor in plant growth, development and reproduction. Nitrogen assimilation is an energy-consuming process (especially when nitrate acts as the main nitrogen source) and is associated with high consumption of ATP <sup>[44]</sup>. Moreover, it is necessary to take into account the significant role of nitrogen consumption in photosynthesis <sup>[45]</sup>. Thus, in comparison to carbon assimilation, nitrogen assimilation appears to be a more critical factor for plant survival <sup>[46][47]</sup>. This becomes even more obvious under drought conditions when multiple enzymes of the nitrogen metabolism are inhibited, and carbohydrate accumulation in plant tissues is observed <sup>[48][49]</sup>.

To meet the plant demand for both amino acid and carbohydrate biosynthesis <sup>[50]</sup>, the assimilation of carbon and nitrogen in irradiated leaves needs to occur simultaneously and in a well-coordinated way, i.e., the relevant metabolic pathways need to be tightly regulated. Thereby, the tissue levels of reduced nicotinamide adenine dinucleotide (NADH) are critical for successful nitrate and ammonia assimilation <sup>[51]</sup>. Thus, the carbohydrate metabolism (including glycolysis and tricarbon acid cycle, TCA) yields appropriate amounts of ATP and provides a pool of reduced NAD(P)H nucleotides necessary for the reactions of nitrogen assimilation. It is important to note that besides the contribution to the ATP/NADH pool, TCA serves as the precursor of some amino acids (e.g., glutamate), which rely on the carbon skeleton of 2-oxoglutarate, a metabolite of the tricarboxylic acid (TCA) cycle <sup>[49]</sup>.

Generally, regulation of the carbon-to-nitrogen ratio in plant tissues typically relies on the ammonium and nitrate ions, as well as several key nitrogen-containing metabolites such as glutamate, glutamine and aspartate <sup>[44]</sup>. These metabolic regulators interfere with cytokinin signaling, which, in turn, is involved in the regulation of plant growth responses to alterations in nitrogen supply availability <sup>[52]</sup>. Nitrate enhances the expression of the key enzyme of cytokinin biosynthesis —isopentenyltransferase IPT3. Cytokinin is perceived by receptors, and the signal is transmitted by phosphorylation of the two-component His-Asp system and subsequent cytokinin-mediated signaling associated with development control, protein synthesis and macronutrient assimilation <sup>[52]</sup>. In addition, experiments in conditions of water scarcity on transgenic IPT plants under the control of P(SARK), a promoter induced by maturation and stress, *Oryza sativa* japonica "Kitaake" demonstrated that stress-induced cytokinin synthesis contributed to increased uptake through cytokinin-dependent

coordinated regulation of carbon and nitrogen metabolism, which contributes to increased tolerance in transgenic plants exposed to water deficit [53].

The short-term effects of drought on carbohydrate and nitrogen metabolism were addressed with the four contrasting guar cultivars described above, i.e., two drought-tolerant accessions (HG-563 and RGC-986) and two sensitive ones (RGC-471 and Varsha). The guar plants were subjected to 15 days of drought by watering interruption, after which such parameters as respiration, gas exchange efficiency, water potential, changes in activities of the enzymes involved in carbon and nitrogen metabolism along with expression of genes encoding the principal actors of oxidative phosphorylation, TCA cycle and nitrogen metabolism, were evaluated by an array of physiological, biochemical and molecular approaches [49]. Thus, nitrogen and carbon contents, assessed by the isotope-ratio mass spectrometry (IRMS)-based elemental analysis in the leaves, stems and roots of the four differentially drought-tolerant guar accessions, demonstrated a strong decrease and increase, respectively, in response to experimental drought in comparison to corresponding controls [49]. Thus, the nitrogen concentration decreased significantly (p < 0.05) at all stages of drought in all studied varieties of guar plants, while the carbon concentration significantly increased in all guar varieties exposed to water stress than in control plants. Roots decreasing in nitrogen concentration were observed, with 72% in Varsha variety, 68% in RGC-471, 45% in RGC-986 and 22% in HG-563 compared to control plants. The trend of decreasing nitrogen concentration continued in the stems and leaves of the analyzed varieties. In the roots and stems of the four varieties, HG-563 showed a higher concentration of carbon, followed by RGC-986, RGC-471 and Varsha, while in the leaves, at the stage of severe drought, the carbon concentration increased by 36% in HG-563, 31% in RGC-986, 21% in RGC-471 and 16% in Varsha varieties, respectively [49].

To date, analysis of the stress-induced patterns of differential gene expression represents one of the major approaches to addressing the mechanisms behind drought tolerance in plants. Recently, such patterns were reported for guar. Thus, the transcript levels of the genes related to nitrogen metabolism in *C. tetragonoloba* (nitrate reductase, nitrite reductase, glutamine synthetase and glutamate synthetase) demonstrated significant changes in response to drought. Specifically, the decrease in expression levels was more pronounced in the drought-sensitive guar varieties RGC-471 and Varsha, which hindered the growth and development of those plants [54].

# 4. The Role of Tricarboxylic Acid (TCA) Cycle Metabolites in the Drought Tolerance of Guar

The impressing numbers and diversity of the individual metabolites and even metabolic pathways involved in the plant response to drought might indicate the high capacity of plants to adapt to environmental changes <sup>[55][56]</sup>. Thus, the pathways of the primary and secondary metabolism, such as glycolysis, TCA cycle, urea cycle, amino acid metabolism, glutamate-mediated proline biosynthesis, synthesis of phytohormones and unsaturated fatty acids, as well as the biosynthetic pathways of phenolic compounds, are critical for the plant response to drought. Among these, the TCA cycle represents a crucial aerobic pathway involved in the final steps of carbohydrate oxidation and plays a key role in establishing drought tolerance in plants <sup>[56]</sup>. To obtain a complete picture of the accompanying physiological changes, the expression levels of the genes encoding the key enzymes of oxidative phosphorylation and tricarboxylic acid cycle (which are assumed to be indicative of the effect of drought on the respiratory metabolism) were analyzed in guar plants <sup>[49][54]</sup>.

In the most efficient way, this aspect can be considered in the context of nitrogen metabolism. Thus, recently, a comparative study of the guar carbon (oxidative phosphorylation and tricarboxylic acid cycle) and nitrogen metabolism revealed increased expression levels of the genes involved in respiration-related metabolic pathways and decreased expression levels of the genes encoding enzymes of nitrogen metabolism pathways involved at all stages of the plant response to drought <sup>[51]</sup>. The expression levels of pyruvate dehydrogenase (PDH), which is involved in the oxidative decarboxylation of pyruvate, gradually increased in guar tissues as drought response developed in the stressed plants in comparison to the controls. The transcript levels of the gene encoding phosphoenolpyruvate carboxylase (PEPC), which catalyzes the interaction between bicarbonate and phosphoenolpyruvate to yield oxaloacetate and inorganic phosphate, were increased under drought conditions in all four guar varieties. Thereby, the most pronounced stress-induced increase in the levels of the PEPC gene expression was observed in the drought-tolerant cultivar HG-563, whereas the droughtsensitive cultivar Varsha showed the least expressional response. The maximal expression level of dihydrolipoamide dehydrogenase (DLD), a mitochondrial enzyme that plays a vital role in energy metabolism in plants, was also observed in drought-tolerant guar variety HG-563 [49][54]. The upregulation of DLD was maximum in HG-563 by about 4.2 times in comparison to control plants at severe stages of drought [49]. DLD converts dihydrolipoic acid and NAD+ into lipoic acid and NADH. Lipoic acid is an antioxidant that also stimulates photosystem II activity and the gene expressions of carbon fixation and chlorophyll metabolism enzymes [57].

Also, in the study by Pandey and co-workers <sup>[49]</sup>, it was found that the leaf tissue levels of aspartate aminotransferase (*AspAT*) and isocitrate dehydrogenase (*ICDH*) activities were decreased under drought stress. On the other hand, a pronounced stress-induced increase in the aminase and glutamate deaminase (*NADH-GDH/NAD-GDH*) activities in all the varieties analyzed. Other important genes involved in mitochondrial respiration—NADH dehydrogenase (*NADH DEHYDROGENASE*), cytochrome C oxidase (*CYT C OXIDASE*), cytochrome C reductase (*CYT C REDUCTASE*) and pyrophosphorylase (*PPP*), showed increased transcript levels in all four guar cultivars exposed to drought: HG-563, RGC-986, Varsha and RGC471. Thereby, the levels of all transcripts were higher in the drought-tolerant cultivars HG-563 and RGC-986 in comparison to the drought-sensitive ones RGC-471 and Varsha <sup>[49][54]</sup>.

Generally, the enhancement of cellular respiration is thought to be utilized by the plant as a short-term drought adaptation mechanism to cope with the demand for increased energy consumption <sup>[58]</sup>. In agreement with this, under the drought conditions, all studied guar cultivars showed pronounced changes in the transcript levels of the key TCA components, which likely serve as the targets in the biochemical rearrangement behind the stress-induced metabolic adjustments. Specifically, a decrease in the 2-oxoglutarate dehydrogenase (*OGDH*) gene expression level, along with up-regulation of succinate dehydrogenase (*SDH*) and mitochondrial malate dehydrogenase (*MDH*) transcripts, were observed. It was also found that the expression levels of the fumarate dehydrogenase (*FDH*) gene were increased in the guar varieties HG-563 and RGC-986 and decreased in Varsha and RGC471  $^{[49][54]}$ .

Thus, changes in the expression of the genes encoding TCA enzymes and alterations in the abundances and/or activities of the corresponding key enzymes indicate the effect of drought on respiratory metabolism. These findings support increased energy requirements of guar plants and increased rates of respiratory reactions under stress conditions.

### 5. Effect of Drought on the Guar Antioxidant Defense

It is well known that dehydration of plant tissues triggers oxidative stress, i.e., the state when the capacities of the cellular antioxidant systems are overwhelmed by enhanced generation of reactive oxygen species (ROS) <sup>[59][60]</sup>. ROS are highly reactive and cause severe damage to membranes and disruption of their functions, as well as inhibition of multiple enzyme activities, enhancement of mutagenesis and cell cycle arrest, leading to the death of individual cells or even the whole organism <sup>[19][61]</sup>. Detoxification of ROS in plants is accomplished by the antioxidant defense system, which includes both enzymes (peroxidase, catalase, ascorbate peroxidase, ascorbate peroxidase, superoxide dismutase, glutathione reductase) and small molecules (ascorbic acid, glutathione, cysteine, proline) <sup>[62]</sup>.

In agreement with this, the drought-induced oxidative stress was reported to cause an increase in the activities of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (ASP) in the drought-tolerant guar cultivar RGC-1002. Interestingly, although the activities of glutathione reductase (GR), ascorbate peroxidase (APX) and dehydroascorbate reductase (DHAR) were increased in dehydrated leaves of these plants, the corresponding activities were only minimally affected when water stress was applied to drought-sensitive cultivar RGC-936. Moreover, the RGC-1002 plants were featured with higher levels of tissue phenolics and proline in comparison to the drought-sensitive guar variety RGC-936, although the levels of the oxidative stress marker malondialdehyde and the total phenolic contents (well-known indicators of the drought-related cell damage) were increased in the tissues of all cultivars addressed in the experiment <sup>[28]</sup>.

Regarding the low molecular weight antioxidants, drought triggers a pronounced enhancement in the synthesis of small antioxidant molecules like ascorbic acid (ASC) and glutathione (GSH). Thereby, the ratios of ascorbic acid/dehydroascorbate (ASC/DHA) and reduced/oxidized glutathione (GSH/GSSG) are typically increased in response to dehydration. Thus, in another study, the maximal increases in these ratios (nine- and eight-fold, respectively) were found in the drought-tolerant guar cultivar RGC-1002. In the drought-sensitive cultivar RGC-1066, the ratio of both these antioxidants was significantly reduced <sup>[41]</sup>.

### 6. Effect of Drought on the Metabolism of Phytohormones in Guar

Plant response to abiotic stress (particularly to drought stress) relies on a complex array of physiological, biochemical and metabolic reactions in which phytohormones play an essential role  $^{[41]}$ . The early responses are at least partly associated with the cellular damage and are represented by a pattern of relatively fast and efficient adaptations. These adaptations allow for preserving cell functionality under water stress conditions and are typically manifested with metabolic adjustment and alterations in cell structure  $^{[63]}$ .

For example, the contents of abscisic acid (ABA) are well known to increase under drought stress conditions <sup>[64]</sup>. This metabolic shift protects plants from tissue dehydration by triggering stomata closure <sup>[65]</sup>. This effect is underlined by an array of ABA-induced transcriptional regulatory responses. Thus, drought-tolerant guar cultivars HG-563 and RGC-986 showed increased (in comparison to the stress-sensitive ones RGC-471 and Varsha) expression of F-box and WRKY transcription factors, which regulate ABA-mediated responses to drought <sup>[66]</sup>.

Besides ABA, several other hormones and corresponding associated signaling pathways affect the control of stomatal conductivity under water deficit conditions. While brassinosteroids, jasmonic and salicylic acids support ABA effects, auxins, cytokinins and ethylene tend to inhibit the ABA-mediated mechanism of stomatal closure <sup>[67]</sup>. Besides the ABA signaling, the WRKY transcription factor is involved in the regulatory network associated with the salicylate and jasmonate signaling induced in response to the osmotic stress <sup>[68]</sup>.

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