Л.Н. Гумилев атындағы Еуразия ұлттық университетінің ХАБАРШЫСЫ.
ISSN: 2616-7034. eISSN: 2663-130X

БИОЛОГИЯЛЫҚ ҒЫЛЫМДАР СЕРИЯСЫ/
BIOSCIENCE SERIES / СЕРИЯ БИОЛОГИЧЕСКИЕ НАУКИ

IRSTI 34.31.01
Review article

DOI: https://doi.org//10.32523/2616-7034-2024-147-2-137-148

The Crucial Role of Sulfite in Enhancing Plant Stress Response

A. Bekturova*, M. Sagi

The Albert Katz International School for Desert Studies, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, Negev, Israel

**Corresponding author: aizatbekt@gmail.com*

Abstract. Sulfite, a sulfur-containing compound, has traditionally been viewed as a toxic byproduct of sulfur metabolism in plants. Recent research, however, highlights its emerging role as a signaling molecule influencing a wide range of physiological processes. This review delves into the dualistic nature of sulfite, examining its involvement in plant stress responses, developmental pathways, and metabolic regulation. Sulfite signaling is intricately linked with reactive oxygen species (ROS) and hormonal networks, particularly abscisic acid (ABA), facilitating plants' adaptive responses to environmental stresses such as drought. Moreover, the regulatory mechanisms of sulfite homeostasis, including sulfite reductase activity and sulfite transporters, underscore its significance in maintaining cellular function and redox balance. The insights into sulfite's role as a signaling molecule open new avenues for enhancing crop resilience and productivity through targeted metabolic engineering. Understanding sulfite dynamics thus represents a promising frontier in plant biology, with potential applications in sustainable agriculture and stress management.

Keywords. Sulfite, stress response, drought, reactive oxygen species, abscisic acid, adenosine 5′-phosphosulfate reductase.

Received: 13.05.2023; Accepted: 03.06.2024; Available online: 28.06.2024

Sulfite production

Sulfite is an intermediate of the assimilatory sulfur reduction pathway used by plants, algae, fungi, and bacteria to form cysteine and methionine. Above a certain threshold specific for each plant species, sulfite may cause damage to cell components such as DNA, proteins and lipids (Leustek et al., 2000; Tanaka et al., 1982; Yang and Purchase, 1985; Ziegler, 1974). Production of sulfite from sulfate anions, taken up by the sulfate transporters from the soil, occurs through the adenylation of sulfate by ATP sulfurylase [ATPS, EC 2.7.7.4] and further reduction to sulfite by adenosine 5'-phosphosulphate reductase [APR, EC 1.8.4.9] (Fig1). Sulfite also exists as atmospheric sulfur gas sulfur dioxide (SO2), which is taken up by the foliage and dissociates in the apoplastic water of the mesophyll to bisulfite (HSO3-) and sulfite (SO32-). Sulfur dioxide inhibits plant growth, affects bio-productivity (Ashenden and Williams, 1980), leads to increased susceptibility to plant diseases, leaf chlorosis and necrosis, decreases the rate of CO2 exchange in whole leaves, results in disorganization of cellular components such as endo-membranes of plastids and consequently affect photosynthesis (Hallgren and Gezelius, 1982). However, at low doses sulfur dioxide is utilized as a nutrient that may contribute significantly to the plant's sulfur, especially if the sulfur supply in the soil is in shortage (Leustek and Saito, 1999; Rennenberg, 1984).

Sulfite can be also generated endogenously upon degradation of S-containing metabolites such as cysteine and methionine (Brychkova et al., 2013; Hänsch and Mendel, 2005). This pathway involves production of H2S from L-cysteine by an L-cysteine desulfhydrase [DES1, EC 4.4.1.1] or O-acetylserine-(thiol) lyase [OASTL; EC 2.5.1.47] (Kurmanbayeva et al., 2017; Rennenberg et al., 1987; Riemenschneider et al., 2005). H2S is oxidized to GSSH either nonenzymatically in the presence of GSSG or catalyzed by a currently unknown cytosolic enzyme. Mitochondrial sulfurdioxygenase [ETHE, EC 1.13.11.18] oxidizes GSSH to sulfite (Krussel et al., 2014), which is either converted to thiosulfate (S2O3) via the addition of a persulfide group by sulfurtransferases [STR1, EC 2.8.1.2] or transported to the peroxisomes for oxidation to sulfate (SO4) by sulfite oxidase (SO, EC. 1.8.3.1.; (Brychkova et al., 2013; Lang et al., 2007).

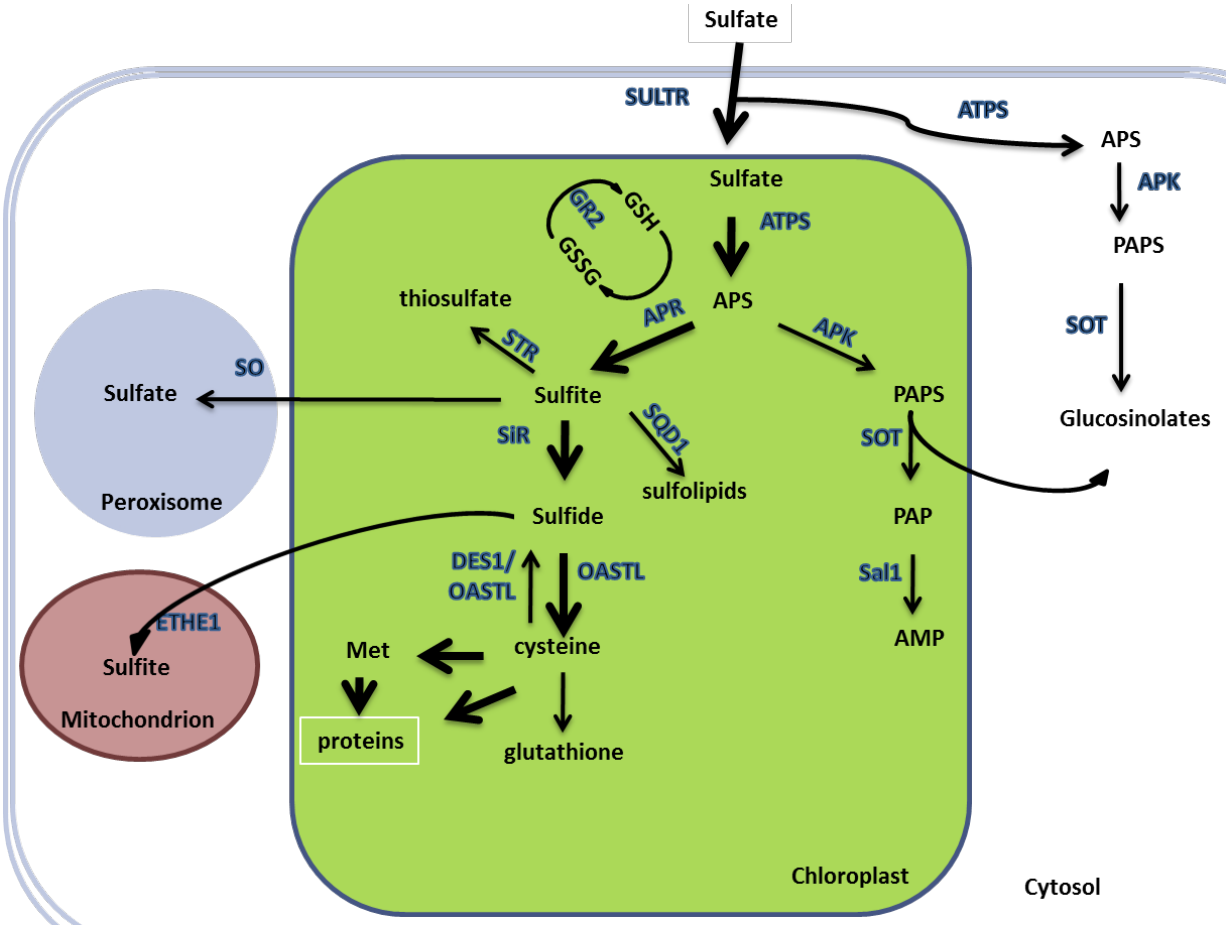

Figure 1.

Schematic overview of primary and secondary sulfur metabolism in *Arabidopsis thaliana.* Primary sulfate assimilation is represented by bold arrows, since it represents a major sink for sulfate assimilation. Enzymes are indicated in blue, metabolites in black. Abbreviations: SULTR, sulfate transporter; AMP, adenosine monophosphate; ATPS, ATP sulfurylase; APR, APS reductase; APK, APS kinase; DES1, L-cysteine desulfhydrase; ETHE1, sulfurdioxygenase; GR2, glutathione reductase 2; GSH, reduced glutathione, GSSG, oxidized glutathione; OASTL, O-acetylserine-(thiol) lyase; PAP, 3′-phosphoadenosine 5′-phosphate; PAPS, 5'-phosphoadenosine 3'-phosphosulfate; SAL1, 3'-phosphoadenosine 5'-phosphate phosphatase, SiR, sulfite reductase; SO, sulfite oxidase; SOT, sulfotransferase, STR, sulfurtransferase.

Sulfite consumption

Due to its toxicity, sulfite levels are tightly regulated by the sulfite network enzymes through the interplay between sulfite production and consumption. Sulfite utilizing enzymes such as sulfite reductase [SiR, EC 1.8.7.1] and sulfite oxidase (SO) have been considered as a defensive team, protecting plant cells from sulfite damage, likely by increasing SiR and SO

activities as reported in Arabidopsis and tomato plants (Brychkova et al., 2007; Lang et al., 2007; Yarmolinsky et al., 2013). The exact molecular mechanisms involved in sulfite signaling are still largely unknown, yet studies with SiR and SO mutants have demonstrated the existence of a tight coregulatory mechanism of the sulfite network components. Suppression of SiR or SO genes resulted in the compensation by other components of the network that consume sulfite (Brychkova et al., 2013; Yarmolinsky et al., 2013).

SiR is the bottleneck enzyme for the sulfite reduction pathway, whose activity affects nitrogen and carbon metabolism and which is essential for growth and development in Arabidopsis (Khan et al., 2010). Plant SiR is encoded by a single-copy gene, that contains one iron-sulfur cluster and one siroheme as prosthetic groups (Nakayama et al., 2000). Sulfite reduction to hydrogen sulfide (H2S) by plant SiR is processed in a ferredoxin (Fd)-dependent manner in which a relatively high proportion of NADPH is needed to drive the electron transfer from Fd by Fd-NADP+ reductase (FNR) (Yonekura-Sakakibara et al., 2000). SiR appears to be an important enzyme which protects plant tissue against sulfite toxicity, specifically in the chloroplast (Yarmolinsky et al., 2013). Leaves of SIR Ri tomato plants contained significantly higher sulfite levels than the corresponding leaves of the wild type plants which resulted in early senescence (Yarmolinsky et al., 2014).

SO is a molybdenum cofactor (MoCo)-containing enzyme, localized in the plant peroxisomes, which catalyzes the oxidation of sulfite to sulfate. SO activity is the primary response of the sulfite network, protecting plant cells from the prolonged excessive sulfite in the mutant leaves or under sulfite/sulfur dioxide exposure (Brychkova et al., 2013; Randewig et al., 2012; Yarmolinsky et al., 2013). Representing 0.1% of all proteins, this enzyme was long considered to be constitutively expressed (Lang et al., 2007). Yet, SO deficiency in plants is not necessarily lethal, unless other sulfite network enzymes are down-regulated or there is a need for sulfite detoxification, while in mammalian cells the mitochondrion localized SO deficiency leads to severe neurological abnormalities.

Sulfite utilization also refers to other components such as the sulfurtransferases (STR) that generate thiosulfate from sulfite and thiocyanate as well as the UDP-sulfoquinovose synthase [SQD1, EC 3.13.1.1] that initiates the biosynthesis of sulfolipids from UDP-glucose and sulfite (Brychkova et al., 2013; Sanda et al., 2001). In the Arabidopsis genome 20 putative STRs were identified as proteins containing an Rhd domain (Mao et al., 2011; Papenbrock et al., 2011). STRs perform a wide variety of functions, including cyanide detoxification (Ito and Minami, 1999), hydrogen sulfide detoxification (Ramasamy et al., 2006), involvement in sulfate metabolism (Nandi and Westley, 1998), management of the cytotoxicity of reactive oxygen species in aerobic tissues (Nandi et al., 2000), mobilization of sulfur for iron-sulfur cluster biosynthesis or repair of iron-sulfur proteins (Mao et al., 2011; Pagani et al., 1984), and interaction with thioredoxin (Ray et al., 2000). The affinity of STRs to sulfite was demonstrated (Tsakraklides et al., 2002), as well as induction of sulfite consuming activity towards thiosulfate production by sulfite application (Brychkova et al., 2013). SQD1 transcripts and proteins appeared to be also highly sensitive to sulfite application, responding already 30 min after sulfite application, yet the role of STRs as well as SQD1 in sulfite detoxification need to be further studied.

Sulfite and reactive oxygen species

ROS play an important signaling role in plants controlling processes such as growth, development, response to biotic and abiotic environmental stimuli, and programmed cell death. Plants produce reactive oxygen species (ROS) at a very low level under normal growth conditions in chloroplasts, mitochondria and peroxisomes. However abiotic and biotic stresses can increase the rate of ROS production which may cause oxidative damage. ROS mediated signaling is controlled by a delicate balance between production and scavenging. Changes in the balance of reduced vs. oxidized forms of certain antioxidants such as glutathione may be used as a sensor for changes in the environment, and changes in ROS levels may directly affect the redox situation in the cell (Tripathi et al., 2009).

High sulfite may cause elevated ROS accumulation and might be one of the causes for sulfite-induced damage (Yarmolinsky et al., 2014). On the other hand ROS were shown to initiate sulfite oxidation in a non-enzymatic way (Hänsch et al., 2006; Ziegler, 1974). At low sulfite concentrations, H2O2 as a reaction product of SO is degraded by catalase. At higher sulfite concentrations accumulating H2O2 derived from the SO reaction oxidizes non-enzymatically a second sulfite molecule. An additional defense system was recently proposed (Hansch et al., 2006). Plant specific class III peroxidases, also called guaiacol peroxidases [EC 1.11.1.7, (Tognolli et al., 2002)], may act as a back-up mechanism for survival upon sulfite exposure in so-ko mutant (Baillie et al., 2019).

Relation of sulfite to drought

Stomata regulate gas exchange between plants and the atmosphere and allow CO2 provision for photosynthesis. Control of the size of the stomatal aperture optimizes the efficiency of water use through dynamic changes in the turgor of the guard cells. Many environmental factors such as CO2 concentration, biotic and abiotic stresses, and additionally different plant hormones, can modulate stomatal reaction. For plants that encounter dehydration stress, the most essential factor is the ability of stomatal closure to prevent excess water loss. Opening and closing is achieved by the swelling and shrinking of the guard cells, which is driven by ion exchange; cytoskeleton reorganization and metabolite production; the modulation of gene expression and the posttranslational modification of proteins (Kim et al., 2010). Recently, a role of sulfur and sulfur-containing compounds in abiotic stress defenses has also been postulated (Chan et al., 2013).

Sulfate is the only macronutrient that increases in the xylem sap during drought stress treatments (Ernst et al., 2010). Sulfate accumulates at early stages of drought preceding drought-related hydraulic signaling and ABA accumulation. A sulfate feeding experiment demonstrated a stimulating effect of sulfate on ABA synthesis and QUAC1/ALMT12 channels activation that subsequently leads to stomatal turgor loss and stomatal closure (Malcheska et al., 2017).

Hydrogen sulfide (H_2S) participates in stress responses, development, and stomatal movement in plants. H_2S is enzymatically produced by SiR through sulfite reduction and also during catabolic pathway of conversion of cysteine to pyruvate, H_2S, and NH_3+ catalyzed by DES1(Alvarez et

al., 2010). It was shown that H2S participates in ABA- or ethylene-induced stomatal closure in different plant species. ABA treatment did not lead to stomata closure in isolated epidermal strips of des1 mutants, indicating that DES1 is required for ABA-dependent stomatal closure (Scuffi et al., 2014). Also it was shown that H_2S may act independently or upstream of ABA by inactivation of current carried by inward-rectifying K+ channels (Papanatsiou et al., 2015).

Detoxification of increasing ROS levels during drought may necessitate increased glutathione production. Thus the importance of GSH during drought seems to be apparent. Yet, glutathione has been shown to negatively regulate ABA-induced guard cell movement (Akter et al., 2012; Okuma et al., 2011). The Arabidopsis cad2 - 1 mutant that is deficient in γ-GCS enzyme and the application of 1-chloro-2,4- dinitrobenzene (CDNB), a chemical that decreases GSH content, to wild type Arabidopsis enhanced the ABA-induced stomatal closure. Restoring levels of GSH by external application of glutathione monoethyl ether restored the phenotype of wild type Arabidopsis. The level of glutathione under drought stress was shown to be decreased at early stages when drought was not yet measurable in leaves, and increased in correlation with ROS level at later stages of drought (Koffler et al., 2014).

3′-phosphoadenosine 5′-phosphate (PAP), produced in secondary sulfur assimilation as a byproduct of sulfotransferase [EC 2.8.2.-] catalyzed sulfation reactions, is suggested to function as a retrograde drought signal from the chloroplast to the nucleus. In A. thaliana, a 30-fold increase of PAP was observed under drought conditions (Estavillo et al., 2011). The PAP content is regulated in the chloroplasts by the 3' (2'),5'-bisphosphate nucleotidase (SAL1, EC 3.1.3.7), which dephosphorylates PAP to adenosine monophosphate (Quintero et al. 1996). Consequently, a loss of function mutation of SAL1 led to an increase of PAP, but also to a 50 % higher drought tolerance. The targeting of SAL1 to the nucleus of sal1 knockout mutants led to the complete complementation of PAP and drought tolerance to wild type levels (Estavillo et al., 2011).

The effects of sulfur dioxide and sulfite on transpiration, stomatal aperture, and water loss in plants remain inconclusive. Various studies have reported decreases, no changes, or even increases in stomatal aperture size in response to these compounds (Majernik and Mansfield, 1970; Biscoe et al., 1973; Black et al., 1979; Taylor et al., 1981). Both reductions and a lack of effect on stomatal conductance and aperture have been observed in Arabidopsis. Recently, the impact of short-term exposure to sulfur dioxide and sulfite on the sulfite network – particularly involving APR and SO, the major sulfite-producing and consuming enzymes – and its implications for stomatal aperture was demonstrated (Bekturova et al., 2021). Arabidopsis wild type, SO RNA-interference (SO Ri), and SO overexpression (SO OE) transgenic lines infiltrated with sulfite showed distinct responses due to physiological differences in stomatal aperture size. Sulfite counteracted the effect of sulfate and abscisic acid-induced stomatal closure in both wild-type and SO Ri plants. The increase in APR activity in response to sulfite infiltration in wild-type and SO Ri leaves resulted in elevated endogenous sulfite levels, highlighting the crucial role of APR in sulfite-induced increases in stomatal aperture.

The central role of adenosine 5'-phosphosulfate reductase in sulfur assimilation

APS reductase (APR) is one of the most important enzymes of the sulfate assimilation pathway that reduces APS to sulfite through GSH-dependent electron transfer. APR is exclusively

localized in the plastids and is encoded by a small gene family. In Arabidopsis, genes encoding three isoforms of APR are regulated in the same way but their response timing and strength are different (Kopriva, 2004). APR2 response towards various hormone treatments was found to be different from APR1 and APR3 (Koprivova et al., 2008), indicating a specific function of each isoform. APR2 is the major form, as knockout of APR2 reduced total APR activity by approx. 80%. APR is highly regulated by various conditions: the expression level of APR2 is down regulated upon exposure to reduced sulfur compounds such as sulfide, cysteine, and GSH. Stresses such as heavy metals, salinity, high light or cold caused up-regulation in the APR expression level. An increase in APR activity was reported upon addition of sugars to the plant media. It was also found that APR shows a diurnal rhythm where a higher activity rate was observed during the day compared with the night. Under nitrogen starved condition, APR activity was decreased whereas the addition of amino acids or ammonium resulted in an increase in APR activity, highlighting the possible connection between sulfate and nitrogen assimilation. Reduced APS kinase activity in apk1 apk2 mutants led to an increased flux through the pathway to cysteine and GSH by upregulating APR activity. A QTL analysis of sulfate content in leaves of recombinant inbred lines from Bay-0 and Shahdara ecotypes revealed a non-synonymous single nucleotide polymorphism (SNP) in the gene encoding for the APR2 isoform of APS reductase, resulting in almost complete inactivation of the corresponding enzyme (Loudet et al., 2007). Loss of Sha APR2 resulted in diminishing of total enzyme activity by 75%. Thus, naturally occurring variation at one of the main sulfate assimilation enzymes directly affects sulfate homeostasis in the plant.

Conclusion

Sulfur-containing metabolites, particularly sulfite and sulfur dioxide, play crucial and multifaceted roles in plant physiology. Traditionally viewed primarily as byproducts of sulfur metabolism, recent research has illuminated their significant functions as signaling molecules in various plant processes. These compounds are integral to managing oxidative stress, modulating hormonal pathways, and regulating stomatal behavior, especially under environmental stress conditions such as drought. The interaction of sulfite with key enzymes and its influence on reactive oxygen species (ROS) and abscisic acid (ABA) signaling underscores its importance in maintaining cellular homeostasis and enhancing stress resilience. Understanding the dual role of sulfite—as both a potentially toxic metabolite and a vital signaling molecule—opens new avenues for agricultural innovation. By leveraging the regulatory mechanisms of sulfite and its impact on plant stress responses, it is possible to develop crops with enhanced tolerance to adverse conditions, thereby contributing to sustainable agriculture and food security. Continued research into sulfur metabolism and the specific roles of sulfite and sulfur dioxide will further elucidate their contributions to plant health and stress adaptation, offering potential strategies for optimizing crop performance in a changing climate.

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А. Бектурова, М. Саги

Альберт Кац халықаралық шөлді зерттеу мектебі, Джейкоб Блаустейн шөлді зерттеу институты, Негевтегі Бен-Гурион университеті, Седе Бокер кампусы, Негев, Израиль

Өсімдіктердің стреске реакциясын арттырудағы сульфиттің шешуші рөлі

Аңдатпа. Күкірті бар қосылыс сульфит дәстүрлі түрде өсімдіктердегі күкірт алмасуының улы жанама өнімі ретінде қарастырылады. Алайда соңғы зерттеулер оның физиологиялық процестердің кең ауқымына әсер ететін сигналдық молекула ретінде пайда болатын рөлін көрсетеді. Бұл шолу сульфиттің дуалистік табиғатын зерттейді, оның өсімдіктердің стресстік реакцияларына, даму жолдарына және метаболизмді реттеуге қатысуын талдайды. Сульфит сигналы реактивті оттегі түрлерімен (ROS) және гормондық желілермен, әсіресе абсциз қышқылымен (ABA) тығыз байланысты, бұл өсімдіктердің құрғақшылық сияқты қоршаған ортаның стресстеріне бейімделу реакциясын жеңілдетеді. Сонымен қатар, сульфиттік редуктаза белсенділігі мен сульфитті тасымалдаушыларды қоса алғанда, сульфит гомеостазының реттеуші механизмдері оның жасушалық функциясы мен тотығу-тотықсыздану тепе-теңдігін сақтаудағы маңыздылығын көрсетеді. Сульфиттің сигналдық молекула ретіндегі рөлін түсіну мақсатты метаболикалық инженерия арқылы дақылдардың төзімділігі мен өнімділігін арттырудың жаңа жолдарын ашады. Осылайша, сульфит динамикасын түсіну тұрақты ауыл шаруашылығында және стрессті басқаруда әлеуетті қолданбалары бар өсімдіктер биологиясындағы перспективалы шекара болып табылады.

Түйін сөздер: сульфит, стресске жауап беру, құрғақшылық, реактивті оттегі түрлері, абсциз қышқылы, аденозин 5'-фосфосульфатредуктаза.

А. Бектурова, М. Саги

Международная школа исследований пустынь Альберта Каца, Институт исследования пустынь Якоба Блаустейна, Университет Бен-Гуриона в Негеве, кампус Седе Бокер, Негев, Израиль

Решающая роль сульфита в усилении реакции растений на стресс

Аннотация. Сульфит, серосодержащее соединение, традиционно рассматривается как токсичный побочный продукт метаболизма серы в растениях. Однако недавние исследования подчеркивают его растущую роль в качестве сигнальной молекулы, влияющей на широкий спектр физиологических процессов. Этот обзор углубляется в двойственную природу сульфита, изучая его участие в реакциях растений на стресс, путях развития и метаболической регуляции. Передача сигналов сульфита неразрывно связана с активными формами кислорода (АФК) и гормональными сетями, особенно абсцизовой кислотой (АБК), облегчая адаптивные реакции растений на стрессы окружающей среды, такие, как засуха. Более того, регуляторные механизмы сульфитного гомеостаза, включая активность сульфитредуктазы и сульфитные переносчики, подчеркивают его значение в поддержании клеточной функции и окислительно-восстановительного баланса. Понимание роли сульфита как сигнальной молекулы открывает новые возможности для повышения устойчивости и продуктивности сельскохозяйственных культур посредством целенаправленной метаболической инженерии. Таким образом, понимание динамики сульфитов представляет собой многообещающую область в биологии растений с потенциальным применением в устойчивом сельском хозяйстве и управлении стрессом.

Ключевые слова: сульфит, реакция на стресс, засуха, активные формы кислорода, абсцизовая кислота, аденозин-5’-фосфосульфатредуктаза.

Information about authors:

Bekturova A. **–** PhD, The Albert Katz International School for Desert Studies, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 8499000, Negev, Israel.

Sagi M. **–** professor, The Albert Katz International School for Desert Studies, The Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 8499000, Negev, Israel.

Бектурова А. **–** PhD, Альберт Кац халықаралық шөлді зерттеу мектебі, Джейкоб Блаштейн шөлді зерттеу институты, Бен-Гурион университеті, Седе Бокер кампусы, 8499000, Негев, Израиль.

Саги М. **–** профессор, Альберт Кац халықаралық шөлді зерттеу мектебі, Джейкоб Блаштейн шөлді зерттеу институттары, Бен-Гурион университеті, Седе Бокер кампусы, 8499000, Негев, Израиль.