МРНТИ 34.31.15.

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Biochemical Mechanisms of the Improvement of Plant Tolerance to the Salinity and Frought by the Diatomite

Abstract: The present review describes the benefical effects of diatomite (siliceous skeletons of archaic microscopic algae – diatomei) application for improving the plant tolerance to drought and salinity. There are numerous publications on the role of diatomite in mechanical and chemical protection of plants against unfavorable environmental conditions, however, the mechanisms of such a protective effect of diatomite are poorly understood. Diatomite application improved photosynthesis, biosynthesis of soluble proteins, abscisic acid and proline, antioxidant-enzymes, superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and polyphenol oxidase (PPO) as compared to both control and stressed plants maintained at bothlevels of water regime.

Keywords: Diatomite, silica, reactive oxygen species (ROS), proline, abscisic acid (ABA), superoxide dismutase (SOD), catalase (CAT), peroxidase (POD).

Soil salinity and drought are among the most critical threats to crop productivity and food security worldwide. Approximately $700 \times 10^{\mathbf{6}}$ million hectares (ha) of land is salt affected worldwide and about 20% of the total arable area is affected by salinity with annual increase of 1–2 %[1]. In Kazakhstan, about 6.3 million ha of land is affected by salinity. Drought is another unfavorable condition for many regions of Kazakhstan. At present, from the 182 million hectares of pasture land in Kazakhstan 14 million hectares are not being used and degradation of total soil area has exceeded 50 million hectares.

Nevertheless, these lands are actively being used in agricultural production although their productivity is rather low. Due to the fact that agricultural products of the Kazakhstan are produced in such regions, the unfavorable conditions of these regions endanger the state's food security.

In agricultural production the main method of combating salinization is the melioration of saline soils and the creation of reliable drainage and watering of the soil after harvest. These processes are both extremely expensive and of little efficacy. Therefore, using natural fertilizers to increase plants' tolerance to salinity and drought is of great interesting to the agriculture. Among such natural fertilizers a particularly promising one is the diatomite - a sedimentary rock consisting of shells of diatom algae [2]. Presently, diatomite is widely used in many countries. Diatomite, being a formation of the marine and lake genesis of the Paleogene-Neogene period, is over 70% siliceous skeletons of microscopic algae – diatomei [3]. It should be noted that large reserves of diatomaceous rocks are located in the Mugolzhar district of the Aktobe region of Kazakhstan.This is, undoubtedly, of great practical importance. The typical chemical composition of oven-dried diatomaceous earth is 80 to 90% silica, with 2 to 4% alumina (attributed mostly to clay minerals) and 0.5 to 2% iron oxide. Silicon is deposited in the form of SiO_2 in diatomites. In living organisms, silica occurs in the form of amorphous silica ($SiO_2.H_2O$) and soluble silicic acid ($Si(OH)_4$).

It has been established that soluble silica has enhanced the growth, development and final yield of many plant species. The content of silica in plants is equivalent to two or more times than the major nutrients nitrogen, phosphorus and potassium supplied through fertilizers [4].Thus, the main function of silicon in the plants is the increase their resistance to unfavorable conditions, i.e.manifested in the thickening of the epidermal tissues (mechanical protection),binding toxic compounds (chemical protection) and increasing biochemical resistance to stresses (biochemical protection).The diversity of plants demonstrating a positive response to the introduction of silicon compounds proves that all these mechanisms are typical for both silicon silicates and non-silicophiles [5].

In practice, the most effective mean of plant protection against diseases and pests is the joint use of silicon preparations and pesticides [6]. It is considered that the main protective role belongs to silica which accumulate in the epidermal tissues [7] and external hairs on leaf plates [8]. It is assumed that orthosilicic acid (and oligosilicic acids) in the cell wall form orthosilicic ethers with proteins and with polysaccharides (pectins) which determine the strenthen? Don't understand the word) thermal insulation of the cell.

Silica binds to the proteins either through free OH groups of hydroxy amino acids (serine, tyrosine and threonine) or through N-Si bonds with amino groups of N-terminal amino acids [9]. Silica is deposited beneath the cuticle to form a double layer of cuticle-silicon. This layer can mechanically prevent fungi penetration, thereby avoiding the infection process. The protective effects of silicon in pest damage could also be related to the mechanical barrier provided by silica deposition in the cell wall which would make it difficult to penetrate into plant tissues [10].

Haijon Gong et al. (2012) demonstrated that silicon treated plants could maintain better water status than those without silicon. In his opinion, water status has been linked to its effects on accumulation of polar monosilicic acid or polymerized silicic acid in epidermal cell walls which may form hydrogen bonds between H_2O and $SiO_2.nH_2O$ making water less likely to escape from leaf surface [11].

Matichenkov and Bocharnikova (2010) reported that diatomites have chemical ability to bind toxic metals such as Cu, Pb, Cr, Ni and Co. Several mechanisms were responsible for neutralizing the heavy metals: a weak physical or strong chemical adsorption heavy metals by the diatomite and reaction between monosilicic acid and heavy metals [12].

The silica was found to have positive chemical interaction with nitrogenous (N),phosphoric (P) and potassium (K) fertilizers and secondary micronutrients. Tavakkoli *et al.* (2011) observed beneficial effects of silica application on phosphoric nutrition in rice crop. Silicon significantly increased P uptake by 120 percent. Although silica application improved P uptake, crop increase was more likely associated with the reduced manganese (Mn) toxicity, particularly with the increase of P/Mn and P/Fe ratios following silica application [13]. Hydroponic experiments conducted by Yang *et al.* (2008) showed that silica application to low P nutrient solution enhances P content in maize seedling roots. Silica application also increased dry matter production and content of silica and P in different parts of plants [14].

In some studies have shown that silica plays an important role in preventing different environmental stresses in plants [15]. Environmental stresses cause the damage in plant metabolism and also oxidative injures by enhancing the production of reactive oxygen species (ROS). Plant resistance to stress factors is associated with their antioxidant capacity and increased levels of the antioxidants may prevent stress damage. One effect of ROS accumulation in plant cells under stress is lipid peroxidation via oxidation of unsaturated fatty acids leading to membrane damage and electrolyte leakage.

Recently, two genes (*Lsi1* and *Lsi2*) encoding silica transporters have been identified in rice. *Lsi1* (low silicon 1) belongs to a *Nod26*-like major intrinsic protein subfamily in aquaporin, while *Lsi2* encodes a putative anion transporter. *Lsi1* is localized on the distal side of both exodermis and endodermis in rice roots, while *Lsi2* is localized on the proximal side of the same cells. *Lsi1* shows influx transport activity for Si, while *Lsi2* shows efflux transport activity[16].

According to Arnon and Stout (1939) silica is not considered to be an essential element for the higher plants, however, numerous studies in last decades show that it is a beneficial element for the healthy growth and development of many higher plant species such as rice and wheat. Application of silica improved the activity of photosynthetic pigments and dry matter content [17].Photosynthesis is one of the first physiological processes affected by drought. Benefitial effects of silicon on photosynthetic activity under drought and salinity have been studied in many plants. Hattori et al (2005) reported that photosynthetic rate in sorghum plants treated by silicon was higher compared with those of control plants under drought[18].

Jafari *et al.* (2013) reported that increased fresh and dry weight, the content of chlorophyll *a* and *b*, carotenoids and N, P, K in wheat plants at 70 days after planting with increased levels of N with diatomite and K_2SiO_3 as foliar application. It was observed that the application of 150 kg N + 5 per cent diatomite increased the biological yield, crop and harvest index compared to addition of 50 or 100 kg N + 5 percent K_2SiO_4. Addition of 100 kg N with 5 per cent K_2SiO_4 as foliar application had a remarkable effect on total and uptake of NPK and protein as compared with 50 or 150 kg N with K_2SiO_4 as foliar application [19]. Indeed, diatomite-treated plants displayed better morphological increments and physiological activity measured in terms of shoot and root length, number of leaves, fresh and dry weights of shoots, chlorophyll *a* and *b* content as well as total pigments, total soluble sugars, photosynthetic rate, leaf stomatal conductance, leaf relative humidity and all nutrients' concentrations as opposed to non-treated faba bean plants [19].

Abdalla (2011) conducted an experiment using a series of diatomite concentrations of 0, 1,5, 3 and 4,5 10 g kg^{-1}. Results indicated that diatomite was most effective at 3g/kg and 4,5g/kg. Application of diatomite significantly offset the negative effects of salinity and increased tolerance of clovers to salinity stress, the growth parameters, photosynthesis rate and total pigments [20].

Supplementation of silica increased the transcript levels of *PsbY*, a vital polypeptide involved in photosystem II, however, at high silica concentrations *PsbY* expression was reduced. *PsaH*-is a subunit of *PSI* located in the center of *PS I* dimer. The addition of silica to the control or the treated plants increased the level of PsaH expression [21]. Chlorophyll content and photosynthetic activity were significantly improved despite the unfavorable effects of salinity by the silicon addition. In the absence of silicon application, the leaf ultrastructural organelles were badly damaged by salinity. It can be explained by the damage to double membrane of the organelles [22].

Lobato et al (2009) indicated that the silicon increased the tolerance to water deficit, in which the leaf relative water content, transpiration, stomatal conductance, chlorophylls *a* and *b*, as well as carotenoids were maintained in higher levels, as compared to stress plants[23].

Haijon Gong et al (2012) investigated the photosynthetic carboxylation activity in wheat leaves.The ratio of RUBPC/PEPC was decreased under drought, whereas it was increased in silicon–applied plants [11]. Adatia and Besford also reported that chlorophyl content and RUBPC activity in cucumber were increased after silicon application [24].

In a few studies the quantitative real-time PCR (qRT-PCR) was used to analyze gene expression for key antioxidant enzymes including ascorbate peroxidase, catalase, superoxid dismutase and enzymes of flavonoid biosynthesis.

The silicon-dependent expression of genes was first investigated by Watanabe et al. (2004) in rice using microarray approach. According to their results silica addition up-regulated the abundance of a zinc finger protein homolog. In general, the zinc finger proteins act as the major transcription factors for stress response genes and the enhancement of their expression[25].

Dongyun Ma (2015) studied the level of expression of stress related genes after the treatment with silicon. The contents of malondialdehyde and hydrogen peroxide (H_2O_2) in well watered plants without silicon treatment increased, but silicon application decreased both malondialdehyde and H_2O_2 content in wheat leaves exposed to drought. Ascorbate levels increased by 5,7%. They also noted that silicon application significantly decreased H_2O_2 content in plants. The glutathione content of wheat leaves in the moderate drought with silicon is increased by 3,2% compared with the moderate drought without silicon.

The effects of silicon on relative expression levels of genes encoding antioxidant enzymes and ASC-GSH were also studied. The relative expression level of the *TaSOD* gene in wheat leaves in the moderate drought with silicon increased two fold compared to the control, and expression of the *TaCAT*gene increased 1.5-fold compared to the moderate drought without silicon treatment. Silicon treatment can improve *TaSOD* and *TaCAT* gene expression levels, and the effect was more significant as the drought stress progressed. In the absence of silicon application the expression levels of the *TaGR, TaDHAR* and *TaGS* genes in stressed plants are decreased. The relative gene expression levels in plants treated with silicon were significantly higher, which indicates that application of silicon can improve the expression of genes involved in the ASC-GSH cycle [26].

Yongchao Liang et al.(1999) investigated the effects of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. Similarly, in this study superoxide dismutase activity is increased by silicon addition, but the concentration of malondialdehyde in leaves is decreased [27]. Xuefeng Shen (2010) observed that catalase and peroxidase activities are stimulated, whilst superoxide dismutase activity is inhibited under drought stress. Also, the ultrastructure of chloroplasts which were damaged by the added NaCl significantly improved [28].

Helal R.M. (2006) determined the content and activity of catalase, superoxide dismutase, malondialdehyde, prolinein maize after silicon treatment. These results are in accordance with those of Liang (1999) and Al-aghabary et al.(2004). Addition of NaCl significantly increased the malondialdehyde content under absence of silica application, however, its content was less increased by NaCl addition in the presence of silica in nutrient solution. This study indicated that lipid peroxidation induced by NaCl was significantly lower in the silica treated maize seedlings under salt stress than that under salt stress without silica treatment. Thus, it is proposed that silica protects the lipid membranes against ROS. Production of superoxide dismutase and catalase enzymes was significantly higher with the addition of silica. Proline content in plants showed no remarkable increase with silica application. Salt stress sharply increased the free proline content. However, silica treatment caused a significant decrease in free proline content. The content of free proline and H_2O_2 concentrations were significantly lowered with the supplemental silica than in silica untreated plants. It seems to be that silica shows protective role in the preventing negative effects of environmental stresses in maize [29].

In the absence of NaCl between barley roots treated with silica and without there of no significant differences in ATPase activity were observed. This result supports the previous findings that under salt stress, silica decresed the permeability of plasma membrane of leaf cells. Dramatic reduction of ATPase activity was found in simultaneously salt-stressed and silica-treated barley roots. Whilst NaCl decreased ATPase activity by 65.8% in the absence of silica, in the presence of silica this reduction was equal to 33,1%[30].

In interesting experiments conducted on rice (Ma and Takahashi,1993), silica supplementation decreased shoot Ca^{2+} content by about 20% compared to rice without silicon. As a result the transpiration rate was decreased. Galves and Clark (1991) reported that addition of Si significantly reduced Ca^{2+} content of sorghum exposed to Al but had no effect on accumulation of Ca^{2+} [31].

Application of metasilicic acid (0, 0,04,0,08, 0,20, 0,40 or 0,80 g L^{-1}) to hydroponically-grown *Bradyrhizobium cowpea* showed increased accumulation of silicon in roots and shoots, which triggered a significant ($p < 0{,}05$) increase of root growth, but not shoot growth[32]. Stressful environment can induce the expression of stress related genes. Among the stress related genes transcription factors play important role in defense against biotic and abiotic stresses. TF are able bind the *cis*-elements or regulons of genes located in promoter region [33]. Plants contain diverse number of transcription factors responding to environment stress, for example dehydration responsive element binding protein (*DREB 2)* triggered by temperature and drought stress. According Khattab et al (2014) adding Si resulted in up-regulation of TFs involved in *DREB2* expression in rice. *DREB2* can stimulate a wide range of signal transduction pathways during the stress. The gene *osDREB* in rice plays an important role in biosynthesis of abscisic acid. Radioimmunoassay of lateral roots showed that abscisic acid stimulates hormonal signal and root growth is remarkably increased. The concentration of abscisic acid in roots is increased as a result of silicon application. It is suggested that this element might be an inducer of abscisic biosynthesis. In contrast, the concentration of a cytokinine zeatin ribose, is deacreased with the increasing metasilicate supply [34].

Hassan Gh. (2011) reported that silica influences the expression of defense-related genes. Twelve defense marker genes were investigated by qRT-PCR in response to silica application in plants inoculated or not inoculated with *R. solanasearum.* In response to silica treatment and inoculation with *R. solanasearum,*the expression of ethylene marker genes *JERF3* and FD-1 were significantly up-regulated relative to the inoculated and the only silica-treated plants [35].

Silicon may be involved in metabolic and physiological activity in higher plants exposed to abiotic and biotic stresses. This has not yet been determined due to the absence of direct evidence that it is part of the molecule of an essential plant constituent or metabolite [36]. But there is evidence that silicon can form bonds with organic substances. Such possible forms of compounds of silicon with organic substances of vegetation are:

1) Silicon membrane of the protein layer of the cell membrane of the orthosilicic and oligosilicic acids bond between silica with hydroxy groups of amino acids);

2) Silica forms a bond with amino group of amino acids;

3) Silica serves as a cross-linking bridge in polysaccharides (Si-O-C with sugar residues). The binding energy of silicon atoms with carbon atoms (57.6 kcal / mole) is approximately equal to the binding energy of carbon atoms with each other. The Si-C bond seems to be practically covalent [37].

Biological silicon has been found in a variety of biological organic molecules, such as peptides, proteins, carbohydrates and amines. Metabolic stages that are crucial to biosilica formation include Si uptake, storage and transportation. Biological silicification *in vivo* is the biomineralization of inorganic silica into organisms [38].

Serine-rich proteins play an important regulatory role during gene expression in all plants, first of all pre-mRNA splicing. Serine-rich proteins by the excision of introns generate multiple mature messenger-RNAs which lead to encoding of proteins with different functions and structures [39].

Mahbod Sahebi(2014) investigated serine-rich proteins for silicon accumulation in mangrove. Real-time qRT-PCR detected high expression level of the serine-rich protein gene in the root tissues of transgenic plants in response to treatment with silicon (1,5mM SiO_2 , 7 days) in comparison to the wild type plants. Due to the role of serine-rich protein genes in pre-mRNA splicing the expression of this gene in different parts of plants may lead to different characteristics. It was clear that the high adaptability of mangrove plants to salinity, drought and moisture stresses is strongly related to the amount of accumulated Si which is controlled by the expression level of the serine-rich protein gene [40].

Thus, Si in diatomite has enormous benefits to plants to overcome biotic and abiotic stresses by enhancing levels of the antioxidants which may prevent oxidative stress damage. Even if molecular and biochemical influence of diatomite and Si is at rudimentary stage, based on the current publications it is evident that silicon possess the ability to regulate genes involved in photosynthesis and stress related genes. In future, it is promising to investigate the influence of diatomite in Kazakhstan as a source of Si for plants and it is also very important to define biochemical mechanisms of its effects on plant growth, development and stress-tolerance.

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Өсімдіктердің құрғақшылыққа және тұздылыққа төзімділігіне диатомиттің биохимиялық әсері

Аннотация: Әдеби талдау нәтижесі бойынша, диатомит (ежелгі диатомды балдырлардың қаңқасы) өсімдіктердің құрғақшылыққа, тұздылыққа төзімділігін арттырады. Қазіргі таңда диатомиттің механикалық және химиялық әсері жақсы зерттелген, алайда өсімдіктерге әсер ету механизмі толықтай зерттелмеген. Диатомитті қолдану фотосинтетикалық ырғақты, белоктардың синтезделу деңгейін сонымен қатар, абсциз қышқылы, пролин, супероксид дисмутаза, каталаза, пероксидаза және полифенол оксидаза мөлшерін өзгертеді және бақылаудағы өсімдіктермен салыстырғанда жоғары деңгейде болады. Бұл әдеби шолуда стресстік жағдайда диатомит өсімдіктердің өсіп өнуіне ықпал ететіндігі жайында ақпараттар берілген.

Түйін сөздер: диатомит, кремний, оттегінің белсенді формалары, пролин, абсциз қышқылы, супероксид дисмутаза, каталаза, пероксидаза.

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Биохимический механизм воздействия диатомита на засухоустойчивость и солеустойчивость растений

Аннотация: Анализ литературных данных показывает что, диатомит (останки древних диатомовых водорослей) благоприятно воздействует на устойчивость растений к засухе и к солевому стрессу. На сегодняшний день существуют публикации, которые раскрывают механическое и химическое влияние диатомита на растения в неблагоприятных условиях окружающей среды, но механизм воздействия изучен мало. Применение диатомита улучшает фотосинтетический ритм, уровень синтеза белков, абсцизовой кислоты, пролина, супероксид дисмутазы, каталазы, пероксидазы и полифенол оксидазы по сравнению с контрольными растениями. В обзоре приведена информация о роли диатомита на рост и развитие растений в стрессовых условиях.

Ключевые слова: диатомит, кремний, активные формы кислорода, пролин, абсцизовая кислота, супероксид дисмутаза, каталаза, пероксидаза.

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Поступила в редакцию 12.04.2018