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PAPER REVIEW

ROLE OF SILICON IN PLANT RESISTANCE TO WATER STRESS

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Abstract:

Agricultural productivity is strongly affected by different abiotic stresses, among which water stress is the major environmental constraint limiting plants growth. The primary reason for water stress is drought or high salt concentration in soil (salinity). Because both of these stress factors lead to numerous physiological and biochemical changes in plants and result in serious loss in yields, there is a pressing need for finding the effective ways for increasing crops' resistance to stress factors. One of the alternative methods involving alleviation of negative stress effects might be application of silicon as a fertiliser (root or foliar supply).

Many plants, particularly monocotyledonous species, contain large amounts of Si (up to 10% of dry mass). In spite of the high Si accumulation in plants (its amount may equal concentration of macronutrients), until now it has not been considered as an essential element for higher plants. Many reports have shown that silicon may play a very important role in increasing plant resistance to noxious environmental factors. Hence, Si is recognised as a beneficial element for plants growing under biotic and abiotic stresses. The main form of Si which is available and easily taken up by plants is monosilicic acid (H_4SiO_4). Plants take up Si from soil solution both passively and actively. Some dicotyledonous plants such as legumes tend to exclude Si from tissues – rejective uptake. These plants are unable to accumulate Si and they do not benefit from silicon. Under water stress conditions, silicon might enhance plants' resistance to stress and ameliorate growth of plants. These beneficial effects may result from better and more efficient osomoregulation, improved plant water status, reduction in water loss by transpiration, maintenance of adequate supply of essential nutrients, restriction in toxic ions uptake and efficient functioning of antioxidative mechanisms.

Based on the current knowledge and presented data, it can be concluded that the

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role of Si in plants is not restricted to formation of physical or mechanical barrier (as precipitated amorphous silica) in cell walls, lumens and intercellular voids. Silicon can also modulate plants' metabolism and alter physiological activities, particularly in plants subjected to stress conditions. However, in some plants, increased silicon supply does not improve plant growth. Hence, a better understanding of the interactions between silicon application and plant responses will contribute to more efficient fertiliser practices, especially under stress conditions.

Key words: silicic acid, Si uptake, water stress, drought, salinity, resistance.

ROLA KRZEMU W ODPORNOŚCI ROŚLIN NA STRES WODNY

Abstrakt

Produktywność roślin uprawnych jest w znacznym stopniu ograniczana przez różne abiotyczne czynniki stresowe, wśród których stres wodny jest jednym z głównych problemów, na który narażone są rośliny. Stres wodny najczęściej jest spowodowany suszą glebową lub nadmiernym zasoleniem gleb. Ponieważ te czynniki powodują liczne fizjologiczne i biochemiczne zmiany w roślinach oraz prowadzą do poważnych strat plonów, konieczne jest znalezienie skutecznych sposobów zwiększenia odporności roślin na stresy. Jednym ze sposobów pozwalających na złagodzenie ujemnych skutków stresu wodnego może być zasilanie roślin krzemem (w formie oprysku lub dodatku do podłoża).

Wiele roślin, szczególnie jednoliściennych, zawiera duże ilości krzemu (do 10% s.m.). Pomimo że procentowa zawartość krzemu w roślinach może dorównywać zawartości makroelementów, to nie jest on uznawany za pierwiastek niezbędny do prawidłowego wzrostu i rozwoju roślin. Wyniki wielu badań wskazują jednak na ważną rolę krzemu w podnoszeniu odporności roślin na różne niekorzystne czynniki środowiska. Dlatego krzem jest uważany za pierwiastek wpływający korzystnie na rośliny, szczególnie poddane działaniu abiotycznych i biotycznych czynników stresowych. Główną formą krzemu dostępną dla roślin i łatwo przez nie pobieraną jest kwas ortokrzemowy (H_4SiO_4). Może on być pobierany z roztworu glebowego w sposób pasywny lub aktywny. Niektóre rośliny (głównie motylkowate) wykluczają krzem ze swoich tkanek (ang. *rejective uptake*). Rośliny te nie mają zdolności akumulowania tego pierwiastka, i w związku z tym nie mogą doświadczać jego korzystnego działania. W warunkach stresu wodnego krzem może zwiększać odporność roślin oraz poprawiać ich wzrost. Ten pozytywny wpływ może wynikać z: lepszej i bardziej sprawnej osmoregulacji, lepszego statusu wodnego, ograniczenia strat wody w procesie transpiracji, odpowiedniego zaopatrzenia w składniki mineralne, ograniczenia pobierania toksycznych jonów oraz sprawnego funkcjonowania mechanizmów antyoksydacyjnych.

Opierając się na obecnym stanie wiedzy i przedstawionych danych, można stwierdzić, że rola krzemu nie ogranicza się jedynie do tworzenia mechanicznej lub fizycznej bariery (w postaci amorficznej krzemionki) w ścianach komórkowych, przestrzeniach międzykomórkowych oraz wewnątrz komórek. Pierwiastek ten może wpływać na metaboliczną i fizjologiczną aktywność roślin, szczególnie tych, które narażone są na niekorzystne wpływy środowiskowa. Jednakże w przypadku niektórych roślin nie stwierdzono pozytywnego wpływu krzemu na ich wzrost. Dlatego zrozumienie interakcji między zastosowaniem krzemu a reakcją roślin na ten pierwiastek przyczyni się do bardziej efektywnego nawożenia roślin, szczególnie w warunkach stresowych.

Słowa kluczowe: kwas ortokrzemowy, pobieranie Si, stres wodny, susza, zasolenie, odporność.

INTRODUCTION

All terrestrial plants contain silicon (Si). In spite of the high Si accumulation in plants (its amount may equal concentration of macronutrients), until now it has not been considered as an essential element for higher plants. Many reports have shown that silicon may play a very important role in increasing plants' resistance to noxious environmental factors. Hence, Si is recognised as a beneficial element for plants growing under biotic and abiotic stresses, for example heavy metals, drought, salinity, pathogens (GRENDA and SKOWROŃSKA 2004, FAUTEX et al. 2005, GAO et al. 2006, LIANG et al. 2007, TUNA et al. 2008, DONCHEVA et al. 2009, SAVVAS et al. 2009). It is worth noting that Si is an essential trace element in animal and human nutrition. Silicon plays an important role in synthesis of glucosaminoglycans and collagen, consequently in bone formation (TANAKA 1985). High levels of soluble Si (silicic acid) may reduce bioavailability and neurotoxicity of aluminium through the formation of hydroxyaluminiosilicate, which prevents binding of aluminium to the gut (BIRCHALL 1990, EDWARDSON et al. 1993).

Plants growing in natural conditions are constantly subjected to noxious environmental factors. One of the major constraints of plants' growth and productivity is water stress. Water stress may result from water deficit in soil (drought) or excessive amount of salt (salinity), most commonly NaCl. Drought occurs in many parts of the world every year, whereas increasing salinity of soil is a growing problem, particularly in irrigated areas. Hence, our understanding of crop responses to water stress is very important, but finding effective ways for increasing crop stress tolerance seems to be crucial. One of the alternative methods involving alleviation of negative stress effects might be application of silicon as a fertiliser (root or foliar supply).

The present paper describes the results of numerous investigations conducted during last two decades on the mechanism of silicon uptake and transport in higher plants as well as its possible role in enhancing plants tolerance to salt stress and drought.

MECHANISMS OF SILICON UPTAKE

Silicon (Si) is the second, after oxygen, most abundant element in earth crust and its percentage value reaches 26%. In nature, Si does not occur as an elemental form but it is a compound of many minerals which form rocks. Silicon occurs mainly in the form of silicon dioxide (silica) and silicates that contain Si, oxygen and metals (BROGOWSKI 2000, ŘEZANKA and SIGLER 2008). Minerals containing Si are resistant to weathering processes and decomposition, hence the amount of silicon in soil solution is low (BROGOWSKI 2000). Monosilicic acid (H_4SiO_4 = $Si(OH)_4$) is amobile and soluble form of Si which is available to plants. Concentration of Si in soil solution ranges from 0.0004 to 2.0 mmol dm^{-3} but most values lie between 0.1 and 0.6 mmol dm^{-3} (EPSTEIN 1994, 1999, SOMMER et al. 2006). Uptake of Si from external solution and its transport through roots might be an active or a passive (diffusion) process (TAMAI and MA 2003, MITANI and MA 2005, MA and YAMAJI 2006). Functioning and activity of silicon transporters require energy supply. MA and YAMAJI (2006) described Si transport process in three species that evidently differ in the ability of Si accumulation: rice (high accumulation), cucumber (medium) and tomato (low Si level). These authors stated that in all the three species transport of Si is mediated by a similar transporter with K_m value of 0.15 mmol dm^{-3} but there are differences in the V_{max} values (i.e. rice > cucumber > tomato). This may suggest that among plants species there are differences in density of Si transporters. Results of investigations conducted on four different species of mono- and dicotyledonous plants (*Oryza sativa*, *Zea mays*, *Helianthus annuus*, *Benincasa hispida*) showed that both active and passive components of Si uptake system co-exist in plants (LIANG et al. 2006a). Relative contribution of these components depends on plant species and external Si concentrations. In the case of rice and maize (both gramineous species), the active component is the major mechanism responsible for Si uptake (LIANG et al. 2006a). A very important step in Si translocation is its transport from cortical cells to the xylem (xylem loading). In rice, a typical silicon accumulator, its concentration in xylem sap is high (2 mM) and process of xylem loading of Si is mediated by specific transporters (MITANI and MA 2005). Whereas in cucumber and tomato, xylem loading is a passive process, hence transport efficiency is very limited. The determined Si concentration of xylem sap in rice was 20- and 100-fold higher than that in cucumber and tomato respectively. Moreover, Si concentration in xylem of both plants was lower than in the external solution (MITANI and MA 2005). However LIANG and his colleagues (2005a) presented a contrary conclusion. They demonstrated that in *Cucumis sativus* L. silicon uptake and xylem loading are also active processes, such as in rice. Such distinct discrepancy in the results obtained might be caused by the different experimental conditions and further investigations are needed to solvethe controversy. Some dicotyledonous plants such as legumes do not accumulate Si in tissues and tend to exclude this element – rejective uptake (VAN DER VORM 1980, LIANG et al. 2005a). These plants take up Si more slowly than water and they contain less silicon than would be expected from nonselective passive uptake of silicic acid during plant growth.

Concluding, silicon is taken up in the form of uncharged molecule – silicic acid – and in plants three different modes of its uptake (active, passive, rejective) may function.

Silicon distribution in aerial parts of plants is dependent on intensity of transpiration. In the transpiration stream in xylem, silicic acid is transported to leaves and it is accumulated in older tissues (it is not mobile within the plant). In the shoot, owing to the loss of water (transpiration), silicic acid is concentrated and polymerised (Ma and Yamaji 2006). In consequence, Si forms colloidal silicic acid and finally silica gel. Silicon in the form of silica gel may amount to 90% of total Si concentration in shoots (Ma and Yamaji 2006).

SILICON ACCUMULATION AMONG PLANT SPECIES

There are substantial differences in silicon concentration in plant kingdom. The range of its concentration is 0.1-10% Si on a dry matter basis (Epstein 1994, 1999). Plant species older in the evolutionary sense (diatoms, cyanosis, horsetails, ferns) contain more Si than plants that emerged later. Among higher plants, species from *Gramineae* i *Cyperaceae* families accumulate Si in large amounts and are considered as Si accumulators (higher than 1% Si on dry weight). Rice and other wetland grasses are an example of Si accumulators. Most dicotyledenous plants contain less than 1% of Si on dry matter (non-acumulators). A third distinguishable group of plants has an intermediate level of Si at about 1-3%. Among these intermediate plants, Jones and Handreck (1967) listed dryland grasses such as rye and oats. However, recent studies indicate that a high Si concentration is not a general feature of monocotyleonous species (Hodson et al. 2005). Within dicotyledenous plants there are considerable differences in silicon concentration. Plants from *Cucurbitaceae* and *Urticaeae* families accumulate high amounts of Si and may be classified as intermediate category. Such differences in Si concentration resulted from different abilities of plant roots to uptake and transport silicic acid (as mentioned in the previous section). The plants that take up Si only by the passive process do not accumulate this element and its concentration in plant tissues is very low. Epstein (1994) published data concerning Si distribution in plant kingdom. Analyses of 175 species grown in the same soil showed that among nine examined elements (Si, Ca, Mg, K, P, Fe, Mn, B, Al) silicon was the most variable. Most analysed plants (81%) did not accumulate silicon and the mean concentration of Si was only 0.25% Si in dry weight. This information indicates that most plants, especially dicotyledonous, are unable to accumulate a large amount of Si and hence they do not benefit from silicon.

Most Si is deposited in cell walls of roots, leaves, stems and hulls, where it may form a thin layer consisting of silica gel ($SiO_2 \cdot nH_2O$). Investigations conducted by Ma et al. (2003) on grains of 401 barley varieties showed that the variation in Si concentration in grains is controlled genetically. More than 80% of total Si was localised in the hull and its amount ranged between 15.343 and 27.089 mg kg^{-1} in tested varieties.

WATER STRESS

Water availability in soil is one of the major environmental factors that limit the growth of plants and the production of crops. Water deficiency may result from shortage of water in soil (drought) or problem with its uptake (physiological drought). In the latter case, water is in soil solution but plants cannot take it up because there are some physiological reasons, for example high salt concentrations (salinity), excess of water (flooding), low temperatures. All these factors consequently cause water stress and changes in cell water relations. Water potential is reduced and turgor of plant cells lowered. These changes result in disruption of most important processes and reduction in growth rates. When plants are exposed to salinity, they suffer additionally from a toxic level of salts in cells. Water deficit affects adversely photosynthesis, uptake and transport of essential nutrients and causes overproduction of ROS – reactive oxygen species ($O_2^{\cdot -}$, $^1O_2$, $OH^{\cdot}$, H_2O_2). These very reactive molecules lead to serious disorder in plant metabolism and damage in membranes (Hasegawa et al. 2000, Reddy et al. 2004).

ROLE OF SILICON IN INCREASING PLANTS RESISTANCE TO WATER STRESS

Plants growing under natural conditions are subjected to a multitude of different stress factors through their life cycle. Cellular water deficiency may result not only from drought, salinity and low temperature but can be a secondary effect caused for example by heavy metals or high radiation. Hence, it is very important to determine mechanisms of plant resistance to water stress and also to find the ways for increasing this resistance. For overcoming the negative impact of water stress, addition of Si to the growth medium may have a beneficial effect on plants. It is worth noticing that the beneficial function of silicon does not reveal itself under optimal circumstances but mainly under stress conditions (Henriet et al. 2006, Kaya et al. 2006, Hattori et al. 2007). Ma and Yamaji (2006) point at the fact that silicon exerts positive effects when its concentration in plant tissues is high.

Mechanisms which are important in plant resistance to water stress and a possible role of Si in these processes may be considered at different levels (molecular, cellular, whole-plant). Essential features of plants' response to water stress are following: i) maintenance of homeostasis, including ionic balance and osmotic adjustment, ii) counteraction to damages and their prompt repair, e.g. elimination of ROS and prevention of oxidative stress, iii) detoxification of excess salts under salinity, iv) regulation and recovery of growth.

Results of experiments conducted by Kaya et al. (2006) on maize growing under water stress indicated that silicon (1 and 2 mmol dm^{-3} Na_2SiO_3) significantly improve shoot growth although it did not affect root growth. It is worthy of note that higher Si dose was more efficient than lower one, although in the case of leaf relative water content (RWC) both Si concentrations caused similar increase of this parameter in comparison to plants growing without Si. Improved plant water status (higher RWC index) may result from reduced water loss by transpiration due to deposition of Si (forming silica gel layer) on epidermal cell walls. It was surprising that both Si treatments lowered proline concentration in maize plants grown under water stress (Kaya et al. 2006). Similar response was observed in wheat growing under salinity (Tuna et al. 2008). Amino acid proline occurs widely in proteins but it may also accumulate in the cytosol in response to environmental stresses, especially under osmotic stress. Accumulated free proline contributes substantially to osmotic adjustment and may protect and stabilise sub-cellular structures (e.g. proteins and membranes).

Water stress very often leads to impairment of mineral nutrition and disruptions in ion homeostasis. Kaya et al. (2006) reported that under drought stress maize leaves contained approx. 50% less calcium than control plants while in roots its amount was higher comparing to the control. Decrease in Ca concentration in plant cells is harmful because this element plays an essential role in maintaining the structural and functional integrity of plant membranes and regulation of their permeability and selectivity. The ability of plants to maintain membrane stability is a crucial trait of stress resistance. Some investigations indicate that addition of Si may increase concentrations of Ca in plant tissues and hence restore membrane integrity in water-stressed plants (Kaya et al. 2006). Disruption of ion homeostasis may result from reduced K^+ concentrations in water-stressed plants. Potassium plays an important role in processes involving osmotic adjustment and its adequate level in plants may improve water stress tolerance. Under water-stress conditions, the presence of Si may result in better supply of K^+ (Kaya et al. 2006). This beneficial effect may be attributed to the stimulating action of Si on H^+-ATP-ase (Liang 1999).

In plants growing under salt-stress conditions, added silicon helps in maintaining an adequate supply of essential nutrients and reduces sodium uptake and its transport to shoots (Liang 1999, Tuna et al. 2008). In experiments with salt-stressed barley, Liang (1999) indicated that Si (1 mmol dm^{-3} K_2SiO_3) decreases sodium but increases potassium concentrations both in roots and shoots. Selective uptake of mineral ions is associated with the activity of H^+-ATP-ase. This membrane-located enzyme generates proton motive force that is used for ion transport inside the cell. Liang (1999) reported that under salinity (120 mmol dm^{-3} NaCl) there was a dramatic decrease in ATP-ase activity. In a salt-tolerant barley cultivar, this decline reached nearly 66% whereas in a salt-sensitive one it was 75% comparing to the control plants. In both cases, supplemental silicon resulted in a 2-fold increase in enzyme activity in comparison to plants growing without this element. It is interesting to note that salt stress caused substantial fall in potassium and calcium concentrations and added silicon led to a nearly 2-fold increase in K^+ level but had little effect on calcium content in shoots (LIANG 1999).

As mentioned above, one of the most important mechanisms of plant resistance to salinity is to control Na^+ uptake and prevent its excessive accumulation in plant tissues. LIANG (1999) and several other authors reported that addition of silicon considerably lowers concentration of potentially toxic ions in aerial parts of plants (AHMAD et al. 1992, YEO et al. 1999, GUNES et al. 2007a,b, TUNA et al. 2008, ZUCCARINI 2008). It is possible that silicon present in plant cells limits uptake of toxic ions and prevents their translocation to shoots. The beneficial effect of silicon may be related to the depression of water loss by transpiration and consequently reduced rate of passive uptake and transport of minerals (YEO et al. 1999, GAO et al. 2006, ROMERO-ARANDA et al. 2006). On the other hand, silicon deposited in the form of polymerised SiO_2 in the apoplast of roots considerably restricts ionic translocation from roots to shoots (EPSTAIN 1999, WANG 2004). However, some reports indicate that added silicon does not lower concentration of Na^+ and Cl^- (ROMERO-ARANDA et al. 2006). Maintenance of low concentration of saline ions in plant tissues is a very important mechanism of salt stress tolerance, although more crucial is the capability of plants to take up and retain water in tissues despite its low potential in external medium. This may be related to a decrease in water loss, high water use efficiency and very efficient osmotic adjustment. ROMERO-ARANDA et al. (2006) stated that silicon evidently improves water status in tomato growing under salt stress (80 mmol dm^{-3} NaCl). When salinised plants were treated with Si, their water content increased by 40% and value of water use efficiency (estimated as the ratio between net CO_2 assimilation and transpiration rate) was 17% higher than in salinised plants without silicon. Increased water content in plants growing under osmotic stress shows that processes contributed to osmotic adjustment are very effective. On the other hand, improved ability to retain water by plants treated with Si may result from a lowered transpiration rate and higher values of water use efficiency (GAO et al. 2004, 2006, ROMERO-ARANDA et al. 2006). ROMERO-ARANDA et al. (2006) maintain that beneficial effect of Si might be related to hydrophilic nature of silicon. SiO_2 nH_2O deposited in plant cells permits plants to keep water, dilute salts and protect tissues from physiological drought. In experiments with water-stressed sorghum, HATTORI et al. (2007) showed that silicon application could affect stomatal conductance through the modification of plant water status but not through any physical changes. It could be concluded that silicon facilitates water uptake and its transportation into leaves.

It is generally thought that stability and integrity of biological membranes is a crucial element of plant resistance to abiotic stress. Water stress, like other stress factors, may affect plasma membranes and cause various dysfunctions (changes in membrane permeability and fluidity, disturbance in activity of enzymes located in plasma membranes). These negative effects may result from membrane damage largely caused by membrane lipid peroxidation (oxidation of membrane bound unsaturated fatty acids). It is well known that free radicals induce peroxidation of membrane lipids and consequently increase membrane permeability to ions and electrolytes. Stability and permeability of membranes can be readily determined by measuring the electrolytes efflux from plant cells. Both drought and salinity may cause membranes damage and enhance their permeability (BAJII et al. 2001, EL-TAYEB 2005). ZHU et al. (2004) reported that moderate salinity (50 mmol dm^{-3} NaCl) leads to a rise in H_2O_2 content in cucumber leaves, membrane peroxidation as well as increase in electrolyte efflux. However, silicon added to saline nutrient solution (1 mmol dm^{-3} K_2SiO_3) significantly alleviated these negative effects. Beneficial impact of Si (1 mmol dm^{-3} H_4SiO_4) on membrane fluidity, stability and functioning was also observed in salt-stressed barley (LIANG et al. 2005b, LIANG et al. 2006b). Similarly, KAYA et al. (2006) reported that silicon might protect cell membranes from the adverse effect induced by drought.

Reactive oxygen species (ROS) react not only with membrane lipids but may also interact non-specifically with other important compounds e.g. photosynthetic pigments, proteins, nucleic acids. For this reason, ROS concentration in plant cells must be precisely controlled and regulated. Antioxidative mechanisms that participate in the regulation and scavenging of ROS include non-enzymatic compounds (ascorbic acid, glutathione, tocopherols, carotenoids) and enzymes (superoxide dismutase, catalase, peroxidases). Efficient cooperating of these protective mechanisms is a crucial feature of plant response to water stress as well as to other stress factors (ALLEN 1995, SAIRAM and SAXENA 2000). Addition of silicon can enhance activity of antioxidant enzymes and concentration of antioxidant metabolites in plants growing under water stress (LIANG 1999, AL.-AGHABARY et al. 2004, ZHU et al. 2004, LIANG et al. 2006b, QIAN et al. 2006). On the other hand, added silicon may improve concentration of chlorophyll and ultrastructure of chloroplasts preventing grannae disintegration under stress conditions (LIANG 1998, KAYA et al. 2006, QIAN et al. 2006, TUNA et al. 2008).

Numerous reports indicate that silicon improves growth parameters of plants growing under water stress (ZHU et al. 2004, KAYA et al. 2006, TUNA et al. 2008, ZUCCARINI 2008). In some cases, this beneficial effect was not observed but on the other hand added silicon may improve other processes e.g. water use efficiency (GAO et al. 2004, HATTORI at al. 2007) as well as increase plant resistance to pathogens (FAUTEUX et al. 2005).

In conclusion, it can be stated that the role of Si in plants is not restricted to formation of a physical or mechanical barrier (as precipitated amorphous silica) in cell walls, lumens and intercellular voids. Silicon modulates plants' metabolism and alters physiological activities, particularly in plants subjected to stress conditions. There is a need for further experiments that will allow us to understand better the interactions between silicon application and plant responses. This information will be used in fertilisation practice for enhancing stress tolerance in crop systems.

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