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Review

Effects of silicon on plant resistance to environmental stresses: review

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Abstract. The role of exogenous silicon in enhancing plant resistance to various abiotic stressors: salinity, drought, metal toxicities and ultraviolet radiation are presented. The data on possible involvement of silicon in reducing the reactive oxygen species generation, intensity of lipid peroxidation, and in some cases, increasing the activity of enzymes of the reactive oxygen species detoxificators: superoxide dismutase, ascorbate peroxidase, glutathione reductase, guaiacol peroxidase and catalase are analyzed.

Keywords: plant resistance, stress conditions, silicon, antioxidant enzymes

EFFECT OF SOIL STRESSES ON PLANTS

Plant growth and development is closely related to soil physical processes and properties (Gliński, 2011; Gliński *et al*., 2011). These are mass transport (water, vapour, air, and chemical flow, capillary flow, molecular diffusion, osmosis), mass absorption/desorption, energy transport (heat conduction, convection, radiation), energy adsorption/emission, phase transition (evaporation, condensation, crystallization, melting), mechanical processes (impact, compression, crushing, shearing, tension). Soil conditions based on the enumerated physical factors may create stresses for plant growth and development.

Suitability of the environment for normal plant development is determined by the pool of oxygen stored in the soil and by the ability of its continuous supply from the atmosphere. After exhausting of the soil oxygen pool, and without further oxygen supply, plants start to suffer from oxygen stress; the root system perishes, and finally, the whole plant dies (Gliński *et al*., 2004). Soil oxygen is one of the most important factors, which even during a short period can severely limit plant development and nutrient uptake, thereby resulting in a significant reduction of yields (Gliński and Stępniewski, 1985). Soil aeration is closely connected with the relations of air-water conditions in soils. Imbalance in these relations, for example, by flooding the soil, changes the chemical and physical soil properties, affects the biological activity of soil microorganisms and, consequently, leads to oxygen stress (Gliński and Stępniewski, 1985). These relations affect the biological activity of soil organisms, mainly microorganisms which are very sensitive to oxidation or reduction processes (Gliński and Stępniewski, 1985). It is expected that oxygen stress depends on various abiotic (soil flooding, drought, soil compaction, salinity, high temperature or a combination of these stresses) and biotic factors. Oxygen deficiency affects the intensity and the direction of a number of physiological and biochemical reactions and induces oxidative stress in the plant cells (Balakhnina *et al*., 2004). Salt stress is one of the major environmental factors that restrict plant growth and productivity worldwide. Salt causes both ionic as well as osmotic stress on plants (Hejazi Mehrizi *et al*., 2011; Parvaiz and Satyawati, 2008). A high concentration of Na^+ causes deficiency in other nutrients in the soil and interacts with other environmental factors, such as drought, which exacerbate the problem (Parvaiz and Satyawati, 2008). The decline in growth observed in many plants subjected to excessive salinity is often associated with a decrease in their photosynthetic capacity (Yang *et al*., 2008). Conventional selection and breeding techniques have been used to improve salinity tolerance in crop plants (Parvaiz and Satyawati, 2008). Soil flooding is known as one of the abiotic stresses which influences the growth and development of plants and is recognized as an important yield-limiting factor for many crops (Balakhnina *et al*., 2010b). The most important effects are a reduction in water and nutrient uptake and disturbances

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in the plant respiratory metabolism. Excess water in the soil leads to inefficient supply of oxygen to the cells, which is one of the fundamental requirements for plant life (Chen *et al*., 2005; Pociecha *et al*., 2008). Drought stress, just like flooding, is also an important environmental factor inhibiting photosynthesis and growth (Epron and Dreyer, 1993). Plant drought stress basically originates from water shortage, which could be caused by extreme weather conditions and (or) by an insufficient amount of soil water within the rooting zone (Farkas, 2011). Drought stress is one of the major causes for crop loss worldwide, reducing average yields by 50% and over (Wang *et al*., 2003). Increasingly erratic weather patterns in the future are likely to enhance this situation more seriously. Water availability mostly affects growth of leaves and roots, photosynthesis and dry mater accumulation. In turn, a plant growing in a wet soil is able to take up soil water corresponding to the transpiration demand as soil dries until the soil water content falls below some threshold value. Then the transpiration rate begins to decrease as the roots have difficulty extracting water (Shein and Pachepsky, 1995).

Under stress conditions, the reactive oxygen species (ROS) are generated in plants which can exceed the antioxidant potential of the cell and cause an oxidative damage (Ali and Alqurainy, 2006). Generation of ROS such as superoxide radicals (O_2^-), hydroxyl radicals ($OH\cdot$) and hydrogen peroxide (H_2O_2) is a normal metabolic process, which inevitably occurs in the cells of all aerobic organisms (Alsher, 1997). One of the sites where ROS may be formed is the electron transport chain, due to $NADP^+$ content limitation. This is the way oxygen becomes an alternative electron acceptor (Egneus *et al*., 1975). Induction of ROS initiates lipid peroxidation (LPO), as well as degradation of proteins, pigments, and other cell compounds (Allen 1995; Balakhnina *et al*., 2009, 2010a; Halliwell, 1984). Plants possess an evolutionary formed defence system against oxidative destruction. This system consists of low molecular antioxidants (ascorbic acid, reduced glutathione, tocopherols, and others) and antioxidant enzymes decomposing ROS (Larson, 1988). The enzymatic antioxidant system includes several functionally interrelated enzymes such as superoxide dismutase - SOD (EC 1.15.1.1), catalase – CAT (EC 1.11.1.6), guaiacol peroxidase – GPX (EC 1.11.1.7), ascorbate peroxidise – APX (EC 1.11.1.11) and glutathione reductase – GR (EC 1.6.4.2) (Asada, 1992, 2006; Gunes *et al*., 2007a). The primary scavenger in detoxification of active oxygen species in plants is SOD, which converts superoxide to H_2O_2 and O_2, protecting cells against superoxide-induced oxidative stress. However, H_2O_2 is also toxic to cells, and must be further detoxified by CAT to water and oxygen (Zhu *et al*., 2010).

At the optimal metabolic conditions in the plant cells, there is dynamic equilibrium between the activity of the antioxidant system and intensity of lipid peroxidation processes (Alsher *et al*., 1997). Changes in the activity level of one or more antioxidant enzymes are connected with plant resistance to stressor action (Allen, 1995). Because of excessive formation of ROS under abiotic stresses, the dynamic equilibrium between the activity of the antioxidant system and intensity of LPO processes is displaced to intensification of LPO processes that may lead to oxidative degradation and death of plant cells (Mittler, 2002; Molassiotis *et al*., 2005).

The plant capability to activate the defence system against oxidative destruction may be a key link in the mechanism of plant tolerance to unfavourable conditions. Changes in the activity level of one or more antioxidant enzymes are connected with plant resistance to stressor action (Bennicelli *et al*., 2005).

ENZYME ANTIOXIDANT SYSTEMS IN PLANT DEFENCE

Superoxide dismutase

SODs are a family of metalloenzymes known to accelerate spontaneous transformation of free superoxide radicals (O_2^-) formed by univalent reduction of molecular oxygen to hydrogen peroxide (H_2O_2) and dioxygen (O_2) in the cytoplasm, chloroplasts and mitochondria (Beyer *et al*., 1991; Bowler *et al*.,1992). SODs play a central role in protection of aerobic organisms against oxygen-activated toxicity. There are three types of SODs containing Mn, Fe, or Cu/Zn as metal cofactors. These SODs are located in different cell compartments: Fe-SOD in the chloroplast and peroxisomes, Mn-SOD in the mitochondria and peroxisomes, and Cu/Zn-SOD in the chloroplast, peroxisomes, glyoxysomes, the cytosol, and possibly in extracellular spaces (Beyer *et al*., 1991; Bowler *et al*., 1992; Kubiś, 2005). Introduction of the SOD transgene into plants has been shown to produce desired phenotypes such as increased resistance to physical (chilling, drought, salinity and high light intensity) and chemical (O_3, metal ions, O_2 – generating herbicides) stress, and improved biomass production with larger shoot, crown and root systems (Bafana *et al*., 2011; Balakhnina *et al*., 2005). An increased level of SOD can also protect plants against cold stress at high altitude and O_3 injury (Bafana *et al*., 2011).

Catalase, peroxidases and glutathione reductase

CAT is a principal enzyme that scavenges active oxygen species and prevents lipid peroxidation, cell membrane damage and chlorophyll degradation. CAT controls the H_2O_2 level in plant cells, reduces the seed germination rate, and participates in the photosynthetic process (Khelifa *et al*., 2011). Plants contain monofunctional, tetrameric and heme-containing catalases that are mostly localized in peroxisomes or glyoxysomes. The CAT scavenging system has a decisive role in salt tolerance in rice cultivars. However, a decrease in CAT activity is frequently observed under some stress conditions, while other enzymes of the active oxygen species scavenging system, such as SOD, APX, and GR are usually induced by stress treatments (Shim *et al*., 2003).

GPXs are located in the cytosol, vacuole, cell wall, apoplast and extracellular medium, and are assumed to be involved in a range of processes related to plant growth and development (Ghamsari *et al*., 2007). GPX is considered an important ROS scavenger because of its broader substrate specifications and stronger affinity for H_2O_2 than those of CAT (Brigelius-Flohe and Flohe, 2003).

APX belongs to a group of plant peroxidases which are localized in the chloroplast, microbody, and cytosol and their main function is to scavenge H_2O_2 and defend plant cells against oxidative stress using ascorbate as a specific electron donor (Ghamsari *et al*., 2007; Rosa *et al*., 2010; Shigeoka *et al*., 2002). Expression of APX genes can be activated by specific factors such as pathogen attack, mechanical pressure, injury, ultraviolet-B (UV-B) radiation, water deficiency, salt stress, excess excitation energy, too low or too high temperature, excess oxygen after a period of anoxia, atmospheric pollution, excess metal ions, deficiency in some mineral salts *eg*. phosphates, and herbicides. APX activities generally increase along with activities of other antioxidant enzymes like CAT, SOD, and GR in response to various environmental stress factors (Shigeoka *et al*., 2002). The function of APXs does not have to be limited to antioxidative protection, but may be more extensive; there may be some connection between APX induction and regulation of metabolism.

GR is a flavoprotein that catalyzes the NADPH-dependent reduction of oxidized glutathione (GSSG) to reduced glutathione (GSH). A high GSH/GSSG ratio is essential for protection against oxidative stress to neutralize H_2O_2 (Asada, 1992). GR, together with APX, is involved in the ascorbate-glutathione cycle, which is an important and efficient enzymatic defence system for decomposing H_2O_2 and maintaining the balance of antioxidants (Asada, 2006; Gunes *et al*., 2007a). APX is the first enzyme in this pathway, and its major function is catalyzing the reaction of H_2O_2 to H_2O conversion. GR is the last step in the pathway, playing a crucial role in protection against oxidative stress by maintaining a reduced glutathione level.

Role of silicon in improvement of plant resistance

Silicon in soil

Silicon is the second most prevalent element in the soil. Soils generally contain from 50 to 400 g Si kg^{-1} (Kovda, 1973). The silicon content in the soil depends on the soil type and varies from 200 to 350 g of Si kg^{-1} of soil in clay soils while in the sandy soil – from 450 to 480 g Si kg^{-1} of soil (Kovda, 1973). The inert quartz or crystalline silicates are the main Si-rich compounds forming the skeleton of the soil. The physically and chemically active Si substances in the soil are represented by soluble monosilicic acids, polysilicic acids, and organosilicon compounds (Matichenkov and Ammosova, 1996). The soluble monosilicic acids are absorbed by plants and microorganisms (Yoshida, 1975). They also control chemical and biological properties of the soil P, Al, Fe, Mn and heavy metal mobility, microbial activity, stability of soil organic matter and formation of polysilicic acids and secondary minerals in the soil (Matichenkov *et al*., 2000; Sokolova, 1985). Plants and microorganisms can absorb only monosilicic acid (Yoshida, 1975). Polysilicic acid has a significant effect on soil texture, water holding capacity, adsorption capacity, and stability of soil erosion (Matichenkov *et al*., 2000). Plants can absorb enough Si (Savant *et al*., 1997), which can determine silicon effect on the soil fertility and plants.

Silicon uptake and accumulation in plants

Although abundant, silicon is never found in a plant available form and is always combined with other elements, usually forming oxides or silicates (Gunes *et al*., 2007b). Silicon is absorbed by plants in the form of uncharged silicic acid, $Si(OH)_4$, and is ultimately irreversibly precipitated throughout the plant as amorphous silica (Ranganathan *et al*., 2006). Therefore, although silicon is plentiful, most sources of silicon are insoluble and in a plant-unavailable form. Typical concentrations of silicic acid in soil solution range from 0.1 to 0.6 mM. Plant silicon concentrations vary greatly in the aboveground parts, ranging from 1.0 to 100.0 g Si kg^{-1} of dry weight. In a study of more than 500 plant species, divisions were formed to group the high-, intermediate-, and nonsilicon accumulators. The groupings were based upon measurements (on a dry weight basis) of silicon and the silicon-to-calcium ratio in plant tissues (Ma *et al*., 2001a). The wide variation in Si concentration in plant species is attributed mainly to differences in the characteristics of Si-uptake and transport. Active Si-uptake has been demonstrated in Graminaceous species such as rice (Ma *et al*., 2001b), wheat (Rains *et al*., 2006), ryegrass (Jarvis, 1987), and barley (Barber and Shone, 1966). However, some Gramineae plants such as oats take up Si passively (Jones and Handreck, 1967). Passive Si-uptake has been demonstrated in some dicots such as cucumber, melon, strawberry and soyabean (Liang *et al*., 2005). Unfortunately, molecular mechanisms underlying Si uptake in these plants are unknown (Ma and Yamaji, 2006).

Investigations of the mechanisms by which silicon is absorbed into the plants conducted by Parry and Kelso (1975) showed that silicon interacted with polyphenols in xylem cell walls and affected lignin deposition and biosynthesis. In rice, under water deficit induced by polyethylene glycerol, addition of silicon decreased the transpiration rate and membrane permeability (Agarie *et al*., 1998). In sorghum (*Sorghum bicolor* Moench), application of silicon increased the relative water content and dry mass of plants. It was suggested that the improvement of drought tolerance in sorghum achieved by adding silicon might be associated with enhancement of water uptake ability (Hattori *et al*., 2005, 2007). Addition of silicon also improved water status and increased dry mass of wheat plants in pots under drought (Gong *et al*,. 2005, 2008). Lux *et al*. (2002, 2003) demonstrated that Si was deposited in the cell walls of roots, leaves, stems, and hulls. Richmond and Sussman (2003) and Ma and Yamaji (2006) have reported that this might be a beneficial result of Si on plant growth during stress conditions, because it is unlikely that Si affects the activity of antioxidant enzymes. Hossain *et al*. (2007) have reported that silicon applied modifies the cell wall architecture, which may be responsible for the increase in the cell wall extensibility.

Protective role of silicon

Although silicon is not traditionally considered as an essential element in plants, numerous studies have shown that it can influence positively plant growth and yield (Ahmed *et al*., 2011; Balakhnina *et al*., 2012; Gunes *et al*., 2007a; Ma *et al*., 2004; Savant *et al*., 1997). Silicon is applied to improve plant growth and yield, in particular, under stress conditions (Hattori *et al*., 2005). Several functions have been attributed to silicon: improvement of nutrient imbalance, reduction of mineral toxicities, improvement of mechanical properties of plant tissues and enhancement of resistance to other various abiotic (salt, metal toxicity, nutrient imbalance, lodging, drought, radiation, high temperature, freezing, UV) and biotic stresses (Epstein, 1999; Ma and Yamaji, 2006). Biel *et al*. (2008) suggest that the protective role of silicon in plants may be connected with accumulation of polysilicic acids inside cells. This opinion found indirect support in the fact of increased stress-tolerance accompanying an increase in the concentration of polysilicic acid in plant tissues (Matichenkov *et al*., 2000).

Salinity

Height salt concentrations normally impair the cellular electron transport within the different subcellular compartments and lead to generation of ROS, which triggers phytotoxic reactions such as lipid peroxidation, protein degradation and DNA mutation (Ali and Alqurainy, 2006). Addition of Si decreased permeability of the plasma membrane of leaf cells, and significantly improved the ultrastructure of chloroplasts, which were badly damaged by NaCl addition with the double membranes disappearing and the grannae being disintegrated in the absence of Si (Liang *et al*., 2003). It was shown in *Distichlis spicata* growing under soil salinity (Biel *et al*,. 2008) that the plants accumulate bigger amounts of Si in their particular parts under stressful conditions. Al-Aghabary *et al*. (2004) results demonstrate that silicate partially offsets the negative impact of NaCl stress, which increases tolerance of tomato plants to NaCl salinity by raising superoxide dismutase and catalase activities. Liang *et al*. (2003) showed that exogenous Si significantly enhanced the activities of SOD, CAT, and GR in roots of salt-stressed plants. Molassiotis *et al*. (2005) reported increases in SOD activity under salt stress. Zhu (2001) also observed that addition of Si increased the activities of SOD, GPX, and APX of salt-stressed cucumber. In Soylemezoglu *et al*. (2009) a study on the effect of silicon on antioxidant response of two grapevine (*Vitis vinifera* L.) rootstocks grown in boron toxic, saline and boron toxic-saline soil, application of Si lowered SOD and CAT but increased APX.

Metal toxicity

Heavy metal stress negatively affects processes associated with biomass production and grain yield in almost all major field grown crops (Bednarek *et al*., 2006). Every metal and plant interact in a specific way, which depends on several factors such as the type of soil, growth conditions, and the presence of other ions (Rana and Masood, 2002). Hammond *et al*. (1995) showed that silicon treatments gave significant alleviation of the toxic effect of Al in barley plants. Aluminium uptake by roots was significantly diminished in the presence of Si. Silicon-mediated alleviation of (heavy) metal toxicity in higher plants is widely accepted. Shi *et al*. (2005) reported that the alleviation of Mn toxicity by Si in cucumber was attributed to a significant reduction in lipid peroxidation (LPO) intensity caused by excess Mn and to a significant increase in enzymatic *eg* SOD, APX, and GR, and non-enzymatic antioxidants *eg* ascorbate and glutathione). In the study conducted by Gunes *et al*. (2007a), unlike SOD and CAT activities, APX activity of barley was significantly higher, compared to plants growing without Si supplementation. It can be concluded from the APX results that APX was probably more important than CAT in H_2O_2 detoxification. Such coordinated responses of APX with H_2O_2 concentrations in tissues are believed to promote tolerance to oxidative stress (Gunes *et al*., 2007a). Soylemezoglu *et al*. (2009) showed that the activities of SOD and CAT in boron stressed plants obviously increased, whereas that of APX was decreased. The results related to antioxidant enzyme responses under B toxicity were in agreement with the findings of Molassiotis *et al*. (2005), who reported increased SOD and CAT activity under B toxicity in apple rootstocks.

Drought

Drought, one of the environmental stresses, is the most significant factor restricting plant growth and crop productivity in a majority of agricultural fields of the world (Devkota and Jha, 2011; Said-Al Ahl *et al*., 2009). Numerous studies demonstrate that the antioxidant defence system improves the relationship between enhanced or constitutive antioxidant enzyme activities and increased resistance to drought stress. Compared with the non-silicon treatment, application of silicon under drought increased the activities of some antioxidant enzymes: SOD, CAT, and GR as well as the fatty acid unsaturation of lipids and the content of photosynthetic pigments, whereas the content of H_2O_2 was decreased and the activities of GPX and AsP showed no significant difference (Gong *et al*,. 2005). Gong *et al*. (2005) suggest that the improvement of drought tolerance provided by silicon in wheat plants is associated with an increase in antioxidant defence abilities, thereby alleviating oxidative damage of cellular functional molecules induced by over production of ROS under drought and maintaining many physiological processes of stressed plants. The study by Schmidt *et al*. (1999) showed that foliar application of silicate stimulated the antioxidant activity of SOD in drought-stressed bent grass. In the studies by Ma *et al*. (2004), silicon alleviated the physiological response of peroxidase (POD) to drought stress, maintained the SOD normal adaptation, and increased the activity of CAT. Under severe stress, these physiological biochemical reactions showed positive correlations with the amount of silicon supply. Gong *et al*. (2008) showed that the intensity of oxidative destruction tested by the concentration of thiobarbituric acid reactive substances (TBARs) in the leaves of wheat was increased by drought, and there was a smaller increase upon application of silicon.

UV radiation

Ultraviolet-B (UV-B) radiation negatively affects plant cells, causing generation of ROS such as superoxide anions (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH) and singlet oxygen (O_2) (Beckmann *et al*., 2012; Lizana *et al*., 2009; Rybus-Zając and Kubiś, 2010; Zancan *et al*., 2008). Fang *et al*. (2011), Li *et al*. (2007) and have reported that Si increases plant tolerance to UV-B radiation. The experiment performed by Shen *et al*. (2010) showed that drought and UV-B radiation stresses caused intensification of LPO in soybean seedlings, but Si application significantly reduced the membrane damage. The CAT and SOD activities increased under the effect of UV-B radiation and significantly decreased at Si application. The UV-B light had more adverse effects on growth than drought, the data also showed that Si could alleviate seedling damage under these stress conditions.

SUMMARY

Environmental stress causes huge losses in agriculture productivity worldwide. Therefore, researches aimed at overcoming environmental stresses needs to be quickly and fully implemented. These reports suggest that Si has certain physiological functions in plants. Its role becomes more important under adverse environmental conditions. Increasing of the content of silicon in plant tissues enhances their resistance to various stresses. The presence of silicon in the cell walls of plants increases their strength, as silicon increases resistance to salinity, drought tolerance, and photosynthetic activity, and promotes active growth of roots and foliage. The results of these studies illustrate that the entry of silicon to plant tissues leads to inhibition of the oxidative destruction processes that is accompanied with increasing activity of some antioxidant enzymes that neutralize ROS induced by drought, salinity, toxic metals, and UV-B radiation, they also suggest that Si could be used as a potential growth regulator to improve plant growth and resistance under stress conditions. This may be a promising new strategy for improvement of soil properties in agriculture.

Future prospect

Current knowledge of silicon function in individual plant species under abiotic stress conditions (salinity, metal toxicity, drought and UV radiation) is developing, but there is also the need to better understand its function in more species, other stress conditions (high and low temperature) and more complex interactions (especially higher temperatures combined with optimal watering, drought and UV-B radiation).

High temperature represents one of the principal limitations affecting plant germination, growth, and distribution; it can also result in further reduction in crop production. When the plant is subjected to high or low temperature stress, the cell membrane is first affected by increased membrane permeability. At the same time, a variety of ROS, such as superoxide radicals (O_2^-), hydroxyl radicals (OH), and hydrogen peroxide (H_2O_2) are induced, causing loss of balance between production and scavenging in the cell or organism, which causes LPO intensification (Jaleel *et al*., 2009; Zhu *et al*., 2010). Consequently, plants protect themselves against oxidative injury by inducing osmotic adjustment and activity of antioxidant enzymes (Zhu *et al*., 2010). Taking into account the ability of silicon to influence the anatomical-morphological, physiological and biochemical reactions in plants during stress (drought, salinity, metal toxicity, UV-radiation) it can be expected that silicon will have a protective function in plants in thermal stress conditions. However, further studies are needed for understanding the mechanism of physiological or biochemical roles of Si in plants under thermal stress conditions.

An important but very poorly understood issue is the silicon effects on plants under combined stress conditions. Plants growing in natural conditions are simultaneously affected by a number of stress factors, *eg* low or high temperature, water deficiency, excessive photosynthetically active radiation, UV radiation, salinity, *etc*. Understanding these processes should be the objective of future experiments. Such studies will broaden the knowledge of plant adaptation to adverse environmental conditions and can be used in farming practice to increase crop yields.

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