REVIEW ARTICLE

Silicon: a duo synergy for regulating crop growth and hormonal signaling under abiotic stress conditions

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Abstract

Abiotic stresses, such as salinity, heavy metals and drought, are some of the most devastating factors hindering sustainable crop production today. Plants use their own defensive strategies to cope with the adverse effects of these stresses, via the regulation of the expression of essential phytohormones, such as gibberellins (GA), salicylic acid (SA), jasmonates (JA), abscisic acid (ABA) and ethylene (ET). However, the efficacy of the endogenous defensive arsenals of plants often falls short if the stress persists over an extended period. Various strategies are developed to improve stress tolerance in plants. For example, silicon (Si) is widely considered to possess significant potential as a substance which ameliorate the negative effects of abiotic stresses, and improves plant growth and biomass accumulation. This review aims to explain how Si application influences the signaling of the endogenous hormones GA, SA, ABA, JA and ET during salinity, wounding, drought and metal stresses in crop plants. Phytohormonal cross talk plays an important role in the regulation of induced defences against stress. However, detailed molecular and proteomic research into these interactions is needed in order to identify the underlying mechanisms of stress tolerance that is imparted by Si application and uptake.

Keywords

Crop plant growth, drought, heavy metal, phytohormonal signaling, salinity, silicon wounding

Silicon occurrence, uptake and transportation in crops

Silicon (Si) is the second most abundant (approximately 31%) element in soil after oxygen. However, despite its abundance, it is not currently considered to be an essential element in the crop production strategies (Cooke & Leishman, 2001; Epstein, 1999). Si, having a strong affinity for oxygen, exists as silica, silicic acid and silicates in the soil. These forms are found in combination with various metals (Ma & Takahashi, 2002). In soil, primary silicates and silica complexes containing secondary minerals are weathered by percolating water into orthosilicic acid (Chen et al., 2011; Currie & Perry, 2007; He et al., 2013). Silicic acid (H₄SiO₄) is the most common precursor of Si in soil, where its concentration (approximately 0.1–0.6 mM) depends upon the type and properties of the soil (Cooke & Leishman, 2001; Epstein, 1994; Farmer, 2005; Jones & Handreck, 1967).

Plants take up aqueous silicic acid through the rhizosphere (Raven, 1983). In higher plants, the concentration of endogenous plant Si can be less than or equal to the concentration of Si in the soil. This is why plants carry out either passive or active uptake of Si (Cooke & Leishman, 2001; Mitani et al., 2005). Si is transported into the xylem using symplastic pathways (Raven, 1983), as the permeability of the plasma membrane allows its efficient movement across cells (Liang et al., 2007). Within individual cells, silicon is transported into the vacuole via endocytosis (Romero-Aranda et al., 2006).

After being transported into plant cells, silicic acid becomes saturated, polymerized and deposited as solid, amorphous, hydrated silica [SiO₂.nH₂O; (Cooke & Leishman, 2001; Ma & Yamaji, 2008)]. This deposition of Si can either be cell-specific, such as in silica body and motor cells, or it can be moved to become part of the cell wall, in what is known as phytoliths (Cooke & Leishman, 2001). Plant senescence redeposits Si in the soil (Twiss, 1986). The deposited Si in the form of phytoliths can occur in many shapes and sizes depending on soil properties and location. However, while all plants contain Si, not all produce phytoliths (Ma et al., 2001). In the case of monocotyledonous plants such as grasses, the role of Si has been intensively studied. However, a clear difference between the deposition of Si as phytoliths in C3 and C4 plants has not yet been fully described. The overall shape and size of phytoliths can vary from silicified microhairs or prickles to fan-shaped phytoliths in the leaves, which normally develop because of the silification of motor cells (Twiss, 1986). The phytoliths found in dicotyledonous leaves (Cooke & Leishman, 2001) are fragile crusts on cell walls. Other phytolith shapes vary among different plant families (Bremond et al., 2005).
Generally, it has been estimated that the level of Si deposition within plant tissues ranges from 0.1 to 10% of the dry weight (Epstein, 1994). This suggests that unlike elements such as calcium (0.1–0.6%) or sulfur (0.1–1.5%), Si exists in concentrations equivalent to that of several macronutrient elements (Epstein, 1999).

The Si uptake of rice, tomato and cucumber differs only in the Si content in the shoots (Mitani et al., 2005). The Si content of rice root cells is higher (~3–5-fold) than that of the external soil solution as compared to cucumber and tomato. Studies of Si kinetics show that the radial transport of Si is modulated by a transporter, maintaining its concentration around 0.15 mM in most plant species (Epstein, 1994; Ma & Yamaji, 2008). The presence of metabolic inhibitors such as 2,4-dinitrophenol and changes in environmental conditions such as periods of low temperature can reduce the Si uptake in symplastic transport pathways of root cells in comparison to the concentrations found in apoplastic routes (Ma et al., 2001, 2006). Experimental results suggest that both channel-mediated transport and passive diffusion are involved in radial uptake, which uses essential ATP (Ma & Yamaji, 2008). The Si concentration in rice xylem sap is normally 20–100 times higher than that in cucumber or tomato (Ma & Yamaji, 2008; Ma et al., 2006). A kinetic study previously showed that the xylem loading of Si is also mediated by different types of transporters in rice, while it is mediated by passive diffusion in cucumber and tomato plants (Mitani et al., 2005). Considering the importance of Si transport system, several silicon transporter genes, that is, low silicon genes (OsLsi1, OsLsi2, OsLsi6, HvLsi1, HvLsi2, HvLsi6, ZmLsi1, ZmLsi2, and ZnLsi6) have been characterized in the roots and shoots of rice, barley and maize plants (Bremond et al., 2005; Cooke & Leishman, 2001; Ma & Yamaji, 2006; Mitani et al., 2009; Yamaji et al., 2012; Yamaji & Ma, 2014). However, it is unknown whether their rate of expression changes in response to different environmental factors.

Silicon in crop plants

It has been extensively reported that a lack or deficiency of Si causes growth abnormalities in a wide variety of crop plants (Ma & Takahashi, 2002; Ma & Yamaji, 2006). Si is “quasi-essential” for the growth of higher plants. The low Si plants are Lycoris radiata and Sansevieria trifasciata, in which Si range between 0.01 and 0.02% of total dry weight. Highest Si concentrations have been recorded in the leaves of rice plants, at 6.3% of total dry weight (Nishimura et al., 1989). The findings of Ernst et al. (2006) show that different parts of Schoenus nigricans fruits, the pericarp contained the highest levels of Si (34%) as compared to other parts. Jones and Handreck (1967) suggested that plants could be classified into the following three groups: (i) paddy-grown rice, which has the highest Si content (10–15%); (ii) dry land grasses with moderate Si (1–3%); and (iii) dicots with low Si (~1%).

There is variation in the composition of Si within a species also. For example, in 400 varieties of barley, the Si concentration in the grain varied widely, ranging from 1.24 to 3.80 mg/g (Twiss, 1986). In sugarcane, the Si concentration of shoot depends on the variety but can range from 6.4 to 10.2 mg/g. In rice, Oryza japonica has a higher Si concentration than Oryza indica (Epstein, 1999; Winslow et al., 1997). This is why the concentration of exogenous Si application still mimics the farmers from its use. However, the benefits of exogenous Si application to crops are enormous. Besides increased plant biomass and yield, it can increase light interception causing carbon assimilation through keeping the leaves erect. This phenotypic change also induces an increase in photosynthesis and hardness of the stem which reduces physical damage to the plant (Ando et al., 2002; Kvedaras et al., 2007). Other benefits such as high Si in the roots of Distichlis spicata improve the ability to penetrate heavy clay soils (Ando et al., 2002). Silica deposition also prevents the mechanical destruction of cells (Twiss, 1986). In addition, increased silicification of bulliform cells in rice plants and cell walls translate to greater mechanical strength (Ando et al., 2002). Various studies have shown a significant relationship between Si content and plant’s ameliorative strategies under different environmental conditions (Bremond et al., 2005; Ma et al., 2001, 2006; Schoelync et al., 2010; Twiss, 1986).

Silicon improves the morphological traits of crops

In various plants, Si has been reported to promote growth and biomass increases (Ma & Yamaji, 2008; Epstein, 1999). This growth promotion is devoted to the protection of Si in treated plants under environmental stresses. However, the interaction between exogenous Si and soil phosphorus may produce dual beneficial effects that are not directly attributable to Si (Ma & Takahashi, 1991). Si application (0.17 mM) to cucumber (Cucumis sativus) plants exhibited higher concentrations of chlorophyll pigments, increased light interception and rougher petioles than plants not treated with Si (Adatia & Besford, 1986). Examples of increased plant growth and development due to Si application have been demonstrated in rice [Oryza sativa (Bremond, 2005; Wang, 2007; Ma & Yamaji, 2008; Kim, 2012)], loblolly pine, [Pinus taeda (Emadian & Newton, 1989)], cotton, [Gossypium hirsutum (Li et al., 1989)], annual brome, [Bromus secalinus (Gali & Smith, 1992)], Poinsettia, [Euphorbia pulcherrima (McAvoy & Bible, 1996)], soybean [Glycine max; (Hamayun et al., 2010)], wheat [Triticum aestivum; (Gong et al., 2005)], sorghum [Sorghum bicolor; (Hattori et al., 2005)], cucumber [Cucumis sativus; (Feng et al., 2009)], barley [ Hordeum vulgare; (Savant et al., 1999)], sugar cane beans [ Phaseolus vulgaris; (Zaccarinii, 2008)], tomato [ Solanum lycopersicum; (Al-aghabary et al., 2005; Liang et al., 2007)], spinach [Spinacia oleracea; (Eraslan et al., 2008)], and maize [ Zea mays (Liang et al., 2005)] (Supplementary Tables 1 and 2). Si is used as a fertilizer for sugarcane production in Australia, Brazil and South Africa (Datnoff et al., 1991). For example, the application of silicate rock from western Australia promoted the growth of wheat (Hinsinger et al., 1996) clover, [Trifolium subterraneum] and ryegrass [Lolium rigidum] (Hinsinger et al., 1996). Due to unprecedented improvements in the growth dynamics, Si is applied as a fertilizer to nonsiliceous crops but is still under development and needs more extensive studies.
Crop growth dynamics during abiotic stresses

Increases in human population have raised the demand for food over the last three decades. Though the green revolution has increased per acre grain yields, but advances in industrialization have also added intangible side effects. Most of the environmental stresses experienced by crops are caused by the results of anthropogenic activity, such as global warming and pollution. Such changing environmental conditions pose a threat to agricultural sustainability, as they introduce new problems such as high salinity, drought, heat and heavy metal exposure. Some studies have shown that Si application can play a pivotal role in crop production under conditions of environmental stress; however, these interactions still mimic our understanding (Supplementary Table 2).

Salinity stress

Globally, about 800 million hectare (ha) of land (almost 6% of the world’s total area) has been affected by salinity. With a changing global climate, this can be expected to increase further, resulting in 50% loss in crop production by the year 2050 (Munns & Tester, 2008). Salinity stress hampers plant growth by the following: (i) reducing osmosis, (ii) increasing the toxicity of various ions (Na+, Cl− and SO2−4) inside the plant cell and (iii) influencing nutritional imbalances (Hasegawa et al., 2000). High salt concentrations in turn increase the cytosolic Ca2+ concentration and the subsequent activation of plasma membrane-localized anion channels (Lee & Luan, 2012), guard cell depolarization, potassium efflux, and loss of guard cell turgor and volume, finally resulting in stomatal closure (Hasegawa et al., 2000).

The accumulation of toxic sodium ions results in the production of an unprecedented level of reactive oxygen species (ROS), which can damage the cellular apparatus, including the lipid membrane, chloroplasts, mitochondria, peroxisomes, and nucleic acids via the alteration of the normal cellular plant metabolism (Imlay, 2003; Munns & Tester, 2008). Antioxidants can be either enzymatic or non-enzymatic and include superoxide dismutase (SOD), catalase (CAT), peroxidase (PO) and polyphenol oxidase (PPO) (Ahmad et al., 2010; Choudhury et al., 2013; Inlay, 2003; Mittler et al., 2004). CAT, PO and PPO, which are recruited to cope with ROS stress, help the plants eliminate H2O2 from the mitochondria, cytosol, and chloroplasts, and can regulate plant stress responses. ROS induce lipid peroxidation and stimulate H+-ATPase in the cellular membranes (Liang et al., 2003). The desaturation of membrane-based fatty acids can adversely affect the phytohormonal biosynthesis of jasmonic acid (JA), thus weakening the plant’s ability to respond defensively to herbivore and pathogen attack.

However, it has been widely observed that the negative effects of salinity stress are efficiently mitigated by the application of exogenous Si to crops (Supplementary Table 2). Treatment with approximately 0.89 mM Si reduced the transport of sodium ions into the shoots and increased biomass production compared to the controls (Matoh et al., 1986). Si application in wheat (Munns et al., 2006) and barley (Lumsdon & Farmer, 1995) led to the suppression of sodium chloride transport in plants. Salinity reduces the ability of plants to take up water and nutrients such as K+ and Ca2+ from the soil (Munns et al., 2006). Chlorophyll content is sensitive to salinity stress. However, in several plants, such as pea (Ahmad & Jhon, 2005), cucumber (Hamayun et al., 2010), rice (Gong et al., 2006) and tomato (Al-aghabary et al., 2005), the chlorophyll content was significantly increased by the application of exogenous Si to the foliar or root zones (Figure 1; Supplementary Table 2).

The Na+ concentration can be reduced by the application of Si, which can also help reduce cellular electrolytic leakage in rice plants under salinity stress (Liang et al., 2007). This might be due to the Si in silicified cells beneath the cuticle layer (0.1 mm) of leaf blades creating a physical barrier (Ma & Yamaji, 2008). The deposition of Si in leaf blades can help combat multiple abiotic and biotic stresses, including physical injury or herbivory, and accumulation of cell-degrading ions (e.g., sodium) during salinity (NaCl) stress, which are later converted to stable complexes (Gong et al., 2006; Kim et al., 2011; Zhao et al., 2013).

Si application regulates the generation of ROS during stress by making stable complexes (Rouhier & Jacquot, 2008).
Low ROS concentrations are known to trigger signaling cascades by activating defense responses, but high ROS concentrations are detrimental to the cell (Choudhury et al., 2013; Rouhier & Jacquot, 2008; Soundararajan et al., 2015). The levels of enzymatic CAT, PO and PPO are significantly lower in plants treated with Si and NaCl than in those treated only with NaCl. The significantly reduced CAT activity in Si-treated plants under stress is indicative of the decreased H$_2$O$_2$ regulation at the cellular level. However, enzymatic activities increase with salinity, drought, and heat (Muñns & Tester, 2008); thus negatively affecting plant growth (Liang et al., 2003, 2005, 2007). Despite this, some findings suggest that these enzymatic activities are reduced in Si-treated plants exposed to abiotic and biotic stress (Kim et al., 2014c). These altered levels also suggest that plants treated with Si experienced less stress.

Higher ROS concentrations, on the other hand, autocatalyze the peroxidation of the lipid membrane under high temperatures and drought stress (Choudhury et al., 2013). Lipid peroxidation decreased in rice plants treated with both Si and NaCl treatments, compared to control (Kim et al., 2014c). This is indicative of a decrease in membrane injury and reduced oxidative stress induction in Si-treated plants. Salinity causes higher electrolytic leakage where linolenic acid increases and linoleic acid decreases. However, these membrane-associated fatty acids are less damaged in Si-treated plants. Further in-depth analyses at the transcriptomic level are needed, because the mechanism responsible for Si-mediated regulation of the antioxidant enzyme system under salinity stress remains poorly understood.

### Wounding stress

In plants, wounding stress is caused by physical injury due to factors such as wind or herbivore attack. Such injuries can cause the death of plant tissues and make it vulnerable to pathogenic attacks. The plant health and yield of many C3 and C4 plants are compromised by wounding due to lodging (León et al., 2001). Similar to salinity, wounds initiate oxidative stress, thereby damaging the unsaturated lipid layers of cell membranes. The lipoxygenase activity that occurs in response to wounding leads to lipid peroxidation (Farmer, 2005; Figure 2), which increases the synthesis of jasmonic acid (JA) via lipid-derived signals from γ-linolenic acid. During wounding stress, lipid peroxidation and JA synthesis markedly increase (Gfeller et al., 2011). However, JA levels are sustained and transduced into specific responses; thus, it is important to understand in plant stress responses in JA-mediated wounding stress tolerance.

Recent reports have emphasized the use of Si to minimize the lodging of rice and wheat plants (Liang et al., 1994; Mitani-Ueno et al., 2014). Oxidant production, on the other hand, occurs in cellular masses during wounding or injury. The antioxidant activities of CAT, PO, and PPO are significantly increased in Si-treated and wounded rice plants compared to control plants (Kim et al., 2014b). A similar trend of increased antioxidant enzyme activity was also found in wheat (Gong et al., 2005), maize and barely (Liang et al., 2005). H$_2$O$_2$ causes damage where plant recruits and excessively uses CAT and PO to reduce H$_2$O$_2$ to H$_2$O during wounding stress. Thus, the accumulation of antioxidative enzymes in Si-treated plants functions as a strategy for coping with wounding stress (Figure 2).

Besides the regulation of oxidative stress, Si application has been known to modulate lipid peroxidation during wounding stress (Davey et al., 2005; Esterbauer et al., 1991). In rice plants, lipid peroxidation was significantly lower in Si-treated plants than in non-Si-treated plants under wounding (Kim et al., 2014b). Product of lipid disintegration, malondialdehyde (MDA), indicates a low degree of lipid saturation. This could be due to the silicified cells that are the result of Si accumulation (Ma & Takahashi, 2002). These cells can mechanically impede the penetration of wounds by pathogens and thereby disrupt the infection process (Ma & Yamaji, 2008). Thus, Si seems to act as a physical barrier against wounding stress; however, the underlying molecular mechanisms are still poorly understood.

### Heavy metal stress

The crop fields are contaminated by heavy metal such as cadmium (Cd), copper (Cu) and aluminum (Al) via irrigation often influence soil chemistry and become available to plants via their roots (Shimo et al., 2011). Si application has been...
found to play a dynamic role in rehabilitating this type of altered soil chemistry. Si treatment reduced the total manganese (Mn) content in leaves (Shimo et al., 2011). Studies have shown that Si often protects plants against the toxicity of Mn and other hazardous metals such as Al, high levels of which in the soil are also highly toxic to crops. However, the mechanisms by which Si ameliorates the adverse effects of metal toxicity are not well understood (Barceló et al., 1993). In addition, the kinetics of Si solubility and mobility in a medium contaminated with metal is another area that is poorly understood, and thus requires special attention from soil chemists.

More concentrated Si solutions increase the polymerization and precipitation rates of Si with metals. In case of Al contamination, the ameliorative effects on crop plants may be due to the precipitation of subcolloidal, inert hydroxyl-alumino-silicate (Baylis et al., 1994; Li et al., 1989; Liang et al., 2005). It was found that the growth of plants exposed to excess Al (60–120 μM) was less inhibited when Si (4 μM) was applied (Barceló et al., 1993). The combined application of Si and Al affected the synthesis of organic acids, with the most significant changes occurring in the synthesis of malic and formic acids. Similarly, when the Al-sensitive variety of corn (Zea mays var. BR201F) was treated with Si and exposed to Al stress, root elongation was observed. Thus, Si pretreatment was an effective means of counteracting the inhibition of root elongation by Al (Barceló et al., 1993). In wheat, the mitigation of Al toxicity was also shown to be due to changes in physiological processes (Cocker et al., 1998). The protection against Al toxicity that Si provides is a lively topic of study, not just in plant physiology but also in research on biota in general, with studies also being carried out in fish (Lumsdon & Farmer, 1995; Figure 3; Supplementary Information 1 & 2).

The relationship between Cu and Cd exposure and Si-treatment is less well known. Previous research in rice plants showed that Cd and Cu are readily absorbed by rice roots and are then transported to the shoot via the symplastic pathway (Liu et al., 2003). An increased concentration of Cd or Cu inhibits essential plant metabolic processes such as photosynthesis, electron transport, and lipid peroxidation because these metals bind to sulfhydryl groups (Sudo et al., 2008).

Si application significantly improves the growth of rice plants under Cd or Cu stress (Figure 4; Kim et al., 2014a). Cd and Cu applied to rice plants caused weak root growth, while Si application to rice plant prevented (Liu et al., 2009). In Brassica napus, Cd (5 μM) application reduced plant growth, chlorophyll content and photosynthesis; however, these adverse effects were rescued by exogenous Si treatment (Baryla et al., 2001). The accumulation of Cd and Cu inside root tissues significantly lowered plant growth while Si minimized the negative effects of Cd and Cu by maintaining root morphology intact (Kim et al., 2014a). The cellular structure of the root epidermis, exodermis, and cortex were seriously damaged by increasing durations of Cu or Cd stress, but the root structure was less affected when treated with Si (Kim et al., 2014a). The possible mechanisms behind the Si inhibition of metal transport in plants may be due to the thickening of the casparian strips in the endodermis and cell wall of the xylem, leading to the deposition of lignin and Si in the cell walls of the dermal regions (Chen et al., 2000; da Cunha & do Nascimento, 2009).

Excessive metal exposure induces leaf chlorosis and necrosis by affecting chlorophyll synthesis and breaking down the lipid membrane (Liu et al., 2003; Sharma & Dietz, 2009; Takahashi et al., 2011). The findings revealed that in rice plants subjected to metal stress, Si mediated both leaf chlorosis and lipid peroxidation. The application of Si to the root zone reduces lipid peroxidation under metal stress, while under normal circumstances any stress causes increased oxidation of the lipid layer (Morelli & Scarano, 2004). Metal stress significantly reduced the percentage of α-linolenic acid, suggesting that there was greater ROS damage to the lipid membrane compared to that in plants treated with Si (Dresler et al., 2015; Tripathi et al., 2015). Kim et al. (2014b) recently concluded that high concentrations of α-linolenic acid in chloroplasts and mitochondria result in the production of small oxygenated compounds, such as MDA, and subsequently signal and absorb the ROS generated in these organelles.

The expression of Si transporter genes OsLsi1 and OsLsi2 were significantly increased in plants treated with Si during Cd and Cu stress (Kim et al., 2014a; Zhang et al., 2014). Heavy metal transport was lower in the Si-treated plants than

Figure 3. Effects of silicon application to rice root in hydroponic system under heavy metal stress (copper and cadmium; Cu and Cd). The figure shows how Si helps in mitigating leaf necrosis and cell death. The response against Cu is significant. In the figures, 1, 5 and 10 DAT indicated duration of stress treatment and numbers from 1 to 5 showed each treatment (1: Control; 2: 100 μM Cu; 3: 100 μM Cd; 4: 100 μM Cu + 1.0 mM Si; 5: 100 μM Cd + 1.0 mM Si). Each white bar in figures indicated 5 cm.
in the non-Si-treated plants. The mRNA expression analysis of the metal transport genes *OsHMA2* and *OsHMA3* in rice revealed similar results. The results also showed that during Cd and Cu stress, the *OsLsi* genes were not expressed as strongly as *OsHMA3*. However, after the application of Si in combination with the Cd and Cu treatments, both *OsHMA3* and *OsLsi* genes were expressed at significant levels, in order to counteract the negative impacts of the metal stress (Kim et al., 2014a).

**Plant hormonal signaling during Si treatment and abiotic stress**

Phytohormones, such as GA, SA, JA, ABA and ET, can influence various plant physiological processes at very low concentrations, either in distant tissues via cellular transportation or via direct synthesis (Colebrook et al., 2014). The role(s) of these essential metabolites have been studied extensively under various stressful conditions; however, their regulation under both Si application and stress conditions have been poorly understood.

**Gibberellins**

Gibberellins (GA) regulate all aspects of plant life, from seed germination to vegetative growth and fruiting (Colebrook et al., 2014; Peleg & Blumwald, 2011). Increased GA regulation can be an ameliorative strategy that not only counteracts abiotic stress, but also maintains host plant growth and development. Endogenous bioactive GA$_1$ and GA$_4$ content increased when higher doses of Si were applied to cucumber plants under salinity and drought stress (Hamayun et al., 2010). This clearly suggests that GAs play significant roles in salt and drought stress alleviation. This suggests an intensive reprogramming in the metabolic activities of Si-treated plants under stress. On the other hand, a combination of Si and nitrogen increased the growth of two different rice cultivars, whilst also significantly upregulated the production of endogenous GA$_1$ and its immediate precursor, GA$_{20}$, at the vegetative and anthesis stages of the rice plants (Lee et al., 2010). Similarly, application of 2.5 mM Si to *Glycine max* significantly increased the production of endogenous gibberellins during salinity stress (Hwang, 2007). Si is known to increase plant growth, which can also be associated with the effects of exogenous gibberellins application to crop plants. This also suggests that the Si application activates GA biosynthesis in order to maintain growth and impart stress tolerance. However, the underlying mechanisms have yet to be elucidated at the omics level.

**Jasmonic acid**

Jasmonic acid (JA) triggers the activation of inducible immune responses in crops, which are regulated in response to attacks by pathogenic microbes and herbivorous insects (Caarls et al., 2015). In response to such attacks, the plant signals the accumulation JA and its derivatives, which play major roles in the activation of downstream defense responses (Pieterse et al., 2012). JA synthesis begins with the 13-lipoxygenase (13-LOX)-catalyzing oxygenation of α-linolenic acid, followed by the metabolism of the LOX product 13-hydroperoxy linolenic acid by an allene oxide synthase (AOS). Subsequently, 12-oxophytodienoic acid (OPDA) is formed by allene oxide cyclase (AOC). Finally, a reductase and three β-oxidation steps form JA (Wasternack et al., 2006). This compound can act either synergistically or antagonistically with other hormones like SA and ET during stress responses. Studies demonstrated that exogenous Si treatments under the conditions of salinity stress could result in significantly lower JA production compared to that observed in control plants. This altered level of JA might be correlated with the lower level of stress experienced by Si-treated plants than by control plants (Epstein, 2009; Liang et al., 2005). Ollas et al. (2013) recently observed that stimulated endogenous JA production could also enhance the accumulation of ABA during osmotic stress.
There is an indirect relationship between the functional membrane and JA synthesis in plants. Si can provide additional strength to the plant membrane, demonstrating its role in protecting membranes from injury during stress (Liang et al., 2007; Ma & Yamaji, 2008; Zhao et al., 2013). This is in relation with reduced electrolytic leakage and lipid peroxidation as mentioned in earlier sections. Si accumulation modulates this interactive signaling in order to reduce levels of JA synthesis compared to non-Si plants under salinity stress (Kramell et al., 1995). Since small subsets of genes are affected by ET and JA signaling, the interaction between these two pathways is likely to be downstream. Increased levels of JA are observed in various crop plants that have experienced waves of stresses such as salinity, drought (Hamayun et al., 2010) and herbivory (Agrawal et al., 2003). Endogenous JA levels decreased in barley leaf tissues after abiotic stress (Kramell et al., 1995). This indicated that during Si treatments and salinity stress, JA synthesis levels were altered. The application of Si to the root zones of rice plants can ameliorate the adverse effects of salinity stress by increasing plant growth and accumulating higher Si, as well as lower MDA, electrolytes and Na⁺ levels.

In the case of wounding stress, rice plants are exposed to physical injury, during which Si application improves the systemic signaling of defense-related JA (Hamayun et al., 2010). Previously, studies on rice defense responses had indicated that JA plays a central role in self-defense against feeding attacks (Kim et al., 2011, 2014b; Lee et al., 2001). The relative expression levels of mRNA associated with the regulation of JA biosynthesis genes during Si treatment and wounding stress is not fully understood. Kim et al. (2014b) demonstrated that the JA synthesis-related genes also respond to wounding stress during Si application. LOX is expressed in response to wounding and drought (Kim et al., 2011). Its signaling-related gene converts the linolenic acid to JA via the octadecanoid pathway (Dombrowski, 2003). The JA may activate LOX, which in turn increases JA synthesis via feed-forward activation (Lee et al., 2004) under drought and wounding stress (Sato et al., 2011). The downregulation of LOX may correspond to decreased JA signaling, and a subsequent decrease in the amount of linolenic acid participated during wounding stress and Si application. The reduction in linolenic acid further indicates the low level of damage to the cellular membranes of Si-treated plants. This also corresponds to the reduced lipid peroxidation observed in Si treatments under wounding stress (Kim et al., 2014b).

Similarly, mechanical wounding is known to trigger AOS transcription, which in turn increases JA production levels (Mei et al., 2006). OPR3 is upregulated after wounding, while OsAOC catalyzes the stereospecific cyclization of an unstable allene oxide to octadecadienoic acid, which is the ultimate precursor to JA (Agrawal et al., 2003). Only one AOC gene from tomato has been characterized upon wounding (Agrawal et al., 2003). Interestingly, OsLOX, OsAOS1, OsAOS2 and OsOPR3 mRNA levels were significantly downregulated after Si was applied during wounding stress. These results indicate that the transcription rates of these mRNAs were altered, and thus JA biosynthesis was also found downregulated. The wound-induced mRNA expression of LOX, AOS, AOC, and OPR3 in tomato occurred early during stress response (Agrawal et al., 2003; Kramell et al., 1995), and the downregulation of either of these genes by antisense expression led to a decrease in JA formation in both tomato and tobacco plants (Kramell et al., 1995). These results reveal the regulatory role played by Si during wounding stress. The release of α-linolenic acid from plant lipid membrane by stress-activated lipases is thought to provide a substrate for lipoxygenase and the subsequent synthesis of JA (Upchurch, 2008). Because the Si-treated plants are less affected by metal stress, the rice plant may require less α-linolenic acid for JA synthesis. However, the true nature of these dynamics is still unclear, and extensive studies examining Si and JA modulation under stress conditions are required. Kramell et al. (2000) found an abrupt increase in the endogenous JA content of barley leaves subjected to osmotic stress using sorbitol or mannitol. A decrease in JA levels in response to Si would support that Si as an efficient element for use in the improvement of plant resistance to abiotic stresses.

Salicylic acid

Salicylic acid (SA) is known to cause systemic acquired resistance to pathogenic attack and ROS generation, but recently its role in the tolerance of abiotic stresses such as drought and salinity has also been emphasized (Hara et al., 2012). Under heavy metal stress, a higher level of SA was observed, which suggests that ROS production might have been mitigated. Interestingly, Si treatment significantly lowers SA regulation during metal stress. The exogenous application of SA results in the increased tolerance of plants to many biotic stresses such as fungi, bacteria, and viruses and abiotic stresses such as chilling, drought and heat (Bandurska & Stroinski, 2005; Senaratna et al., 2000, 2003). However, when a mutant Arabidopsis variety, which exhibits high SA accumulation, was subjected to ozone stress, programmed cell death was significantly induced in the mutant Arabidopsis. In addition, hypertolerance to salt and drought stress conditions was exhibited by SA-deficient Arabidopsis plants (Borsani et al., 2001; Rao & Davis, 1999). Thus, the role of exogenous SA application during abiotic stress is still ambiguous, but it is clear that the application of a suitable concentration of SA can mitigate the effects of various stresses via the regulation of a variety of biochemical pathways (Kidokoro et al., 2009).

JA normally increases, while indole-3-acetic acid (IAA) and SA decreases, in response to salinity stress (Wang et al., 2001). The essential role played by SA in increasing plant stress tolerance is assumed to be a result of the ability to induce the expression of genes coding for pathogenesis-related proteins (PR-proteins), as well as of extension genes, as was found in Arabidopsis (Kidokoro et al., 2009). However, more in-depth studies would essentially understand the hormonal regulation of SA during Si and stress.

Abscisic acid

Abscisic acid (ABA) accumulates in plant tissues in order to prevent water loss by stomatal closure during salinity stress (Munns & Tester, 2008; Ollas et al., 2013). ABA is synthesized from a carotenoid via an indirect pathway. First, the carotenoid is converted to zeaxanthin. Zeaxanthin is
converted to all-trans-violaxanthin via two-step epoxidation catalyzed by zeaxanthin epoxidase (ZEP) in plastids (Agrawal et al., 2001). 9-Cis-epoxycarotenoid dioxygenase (NCED) catalyzes the oxidative cleavage of the 9-cis isomer of violaxanthin or neoxanthin, and produces a C_{15} product, xanthoxin, and a C_{25} metabolite (Shinozaki et al., 2003). Xanthoxin is converted into abscisic aldehyde, after which abscisic aldehyde is oxidized to ABA by abscisic aldehyde oxidase (Seo et al., 2000). The two enzymes (ZEP and NCED) play key roles as mediators of ABA biosynthesis. The function of these genes has been widely been studied under salinity stress but the manner in which it responds to the application of Si is not fully understood.

There is well-established available data on the synthesis and genetic regulation of ABA in various plants, such as maize (Zea mays), tomato (Lycopersicon esculentum), tobacco (Nicotiana tabacum), potato (Solanum tuberosum), barley (Hordeum vulgare), and Arabidopsis (Shinozaki et al., 2003). Previous studies have shown that abiotic stresses tend to upregulate ABA biosynthetic genes (ZEP and NCED3) (Shinozaki et al., 2003). In contrast, as the duration of Si treatment increases (from 6 to 24 h), the mRNA expression levels of Si-treated plants also decrease under salinity, as compared to non-Si-treated plants. This indicates that with the passage of time, the rice plants take up larger amounts of Si in order to counteract the negative impact of salinity on plant growth. As Si concentration increases, ABA activation during stress decreases. ABA production is also significantly reduced in Si-treated plants under heavy metal exposure. Some studies report that ABA content increases in plants exposed to Cu and Cd contamination (Monni et al., 2001). The adverse effects of metal toxicity are ameliorated by Si treatment, resulting in the production of less ABA.

**Ethylene**

Ethylene (ET) is also involved in several external stimuli-related signals mediating responses. It is a well-known factor in abiotic stress tolerance and is known to corroborate with other phytohormones such as JA and SA (Von Dahl & Baldwin, 2007). Besides stress tolerance, ET can regulate various physiological responses such as seed germination, flowering, and the triple response of etiolated pea seedlings (Kim et al., 2011). ET is produced via a more simple biosynthetic process than other phytohormones: only three enzymes, S-adenosyl-methionine (SAM) synthetase, 1-aminoacyclopropane-1-carboxylic acid (ACC) synthase, and ACC oxidase are involved in its biosynthesis pathway (65; Von Dahl & Baldwin, 2007). According to Kim et al. (2011), the exogenous application of Si did not affect ET production in rice plants; however, when Si was applied to rice plants subjected to mechanical wounding, ET production decreased significantly compared to that seen in plants not treated with Si. Further studies related ET and its role in Si-mediated stress tolerance are needed in various crops.

**Conclusion**

The application of Si to monocotyledonous and dicotyledonous plants can improve crop growth and production under adverse climate and soil conditions. It has been proposed that stress tolerance conferred to plants during Si-treatment is modulated via signal transduction of phytohormones. However, such responses vary in different crops as observed in rice and vegetables. SA, ABA and JA cross talk plays an important role in regulating induced defenses against stress by exerting antagonistic effects; however, these interactions require further study at the molecular level if the underlying mechanisms of stress tolerance, especially in the presence of Si treatments, are to be fully understood. Higher concentrations of Si imparted greater resistance to salinity stress by regulating the genes responsible for ABA biosynthesis, and by reducing JA synthesis. However, the responses of SA to Si treatments were irregular and thus require further elucidation both at the biochemical and at the molecular levels. In addition, the ever-present hormonal cross talk varies depending on the types of external stimuli. Such dynamic interactions act as a hurdle in improving our understanding related to Si effects under stress. However, these questions can be solved, as more advance transcriptomic and proteomic techniques are available now and could increase our knowledge of Si-plant–stress interactions.

**Declaration of interest**

The authors report no conflicts of interest. The authors alone are responsible for the content and writing of this article.

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Supplementary material available online.