In Vitro Cell.Dev.Biol.—Plant (2016) 52:226–232
DOI 10.1007/s11627-016-9757-6

INVITED REVIEW

Application of silicon in plant tissue culture

Mahbod Sahebi [1,2] · **Mohamed M. Hanafi** [1,2] · **Parisa Azizi** [3]

Received: 17 December 2015 / Accepted: 9 March 2016 / Published online: 16 March 2016 / Editor: Prakash Lakshmanan

Abstract Silicon (Si) is one of the most plentiful mineral elements in soil. It is a macroelement involved in the responses of plants to a variety of abiotic stresses. The culture medium composition, particularly the mineral nutrients, greatly impacts the growth as well as the morphogenesis of *in vitro* plant cultures. Numerous morphological and physiological disorders including hyperhydricity, upwardly curled leaves, shoot tip necrosis, and fasciation are often related to inorganic nutrient imbalances of the tissue culture medium. Silicon has been reported to improve many growth parameters including embryogenesis and organogenesis, as well as leaf morphology, physiology, and anatomy. Silicon decreases the susceptibility of plants to salinity and low temperature, alleviates metal toxicity, lessens the incidence of hyperhydricity, and avoids oxidative phenolic browning in various plants. Overall, the evidence indicates a positive role for Si in improving various aspects of plant tissue culture, including micro-propagation, organogenesis, cryopreservation, somatic embryogenesis, and secondary metabolite production.

Keywords Disorders · Epicuticular wax · Hyperhydricity · Organogenesis · Silicon

✉ Mahbod Sahebi
mahbod_sahebi@yahoo.com

✉ Mohamed M. Hanafi
mmhanafi@agri.upm.edu.my

1 Laboratory of Plantation Crops, Institute of Tropical Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

2 Department of Land Management, Faculty of Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

3 Laboratory of Food Crops, Institute of Tropical Agriculture, Universiti Putra Malaysia, 43400 Serdang, Selangor, Malaysia

Introduction

Plant tissue culture is a well-established technology used for the culture and production of plant cells, plant tissues, and whole plants under defined and controlled nutrient and environmental conditions. Plant tissue culture media contain both inorganic and organic nutrients that sustain plant growth. To improve growth and to produce the desired morphogenesis *in vitro*, the culture medium is often optimized and the extent of culture medium modification is largely determined by the species used (Asmar *et al.* 2013a, b; Reed *et al.* 2013). Inappropriate nutrient composition may cause physiological disorders, such as hyperhydricity, shoot tip necrosis, and upwardly curled leaves, which usually result from inappropriate inorganic nutrient concentrations in the culture medium (Reed *et al.* 2013). Silicon (Si) is found in the soil and is one of the most dominant mineral nutrients in plants (Epstein 1999). Silicon helps plants tolerate different environmental stresses that are present in field conditions, such as high temperature, drought, loading, UV, freezing, nutrient imbalance, salinity, and metal toxicity (Sahebi *et al.* 2015). A number of studies have shown that Si treatment improves crop growth and yield under abiotic and biotic stress conditions (Ahmad *et al.* 2013a, b; Esfahani *et al.* 2014; Schurt *et al.* 2014; Artyszak *et al.* 2015; Chen *et al.* 2015; D'Imperio *et al.* 2015; Hartley 2015; Hussain *et al.* 2015; Muneer and Jeong 2015; Noor *et al.* 2015; Saudy and Mubarak 2015; Wang *et al.* 2015; Xu *et al.* 2015; Yin *et al.* 2015).

The photosynthetic activity and nutrient uptake of plants were remarkably be enhanced by Si fertilization. The *in vitro* morphogenic potential of plant cells and tissues has been improved with Si (Personal communication). Silicon is shown to enhance stress tolerance by altering antioxidant enzyme activity; altering endogenous hormone levels; enhancing the production of lignin, chitinase, phenolics, phytoalexins, and glucanase; increasing nutrient uptake by plants; altering the cation binding capacity in the plant cell wall; improving plant cell strength; maintaining the stomata structure and relative water content; and reducing heavy metal uptake (Vaculík *et al.* 2009; Sahebi *et al.* 2015). In this regard, Si deposited in the plant leaf epidermis has been reported to modulate transpiration that leads to decreased water loss (Mitani and Ma 2005). This review highlights the roles of Si in the tissue culture of plants.

Importance of Silicon in Plant Tissue Culture

Mature seeds of three varieties of rice (*Oryza sativa*), Pajam, Kalizira, and Lucky, have been cultured to evaluate the effects of calcium silicate ($CaSiO_3$) on callus induction and plant regeneration (Islam *et al.* 2005). It has been reported that MS medium containing $CaSiO_3$ increases the frequency of callus induction. Another study examining the development of *Phragmites australis* also showed that the effect of Si on plant growth and root formation is dependent on the genotype used for callus induction (Mathe *et al.* 2012). Callus growth from the root and stem nodes of *P. australis* was enhanced by Si supplied as sodium silicate (Na_2SiO_3) to the MS medium. However, it was observed that the Si effect on somatic embryogenesis depends on explants because it is able to stimulate embryogenesis in the root callus but not in the stem nodal callus. For *Cattleya loddigesii* shoot multiplication, potassium metasilicate (K_2SiO_3) was found to be more effective than sodium silicate (Na_2SiO_3) (Soares *et al.* 2011). The molecular and biochemical bases of Si action on organogenesis and somatic embryogenesis remain unknown. It has been reported that Si accumulation in plant leaves cultured on MS medium supplemented with Si would be more increased compared to the leaves of plants cultured on MS medium without Si inclusion (Sivanesan and Jeong 2014).

Role of Silicon as a Protective Element Against Abiotic Stresses

It has been extensively reported that Si can suppress both physical and chemical stresses. For instance, it was reported that Si treatment increases cold tolerance in *Dendrobium moniliforme* by increasing free proline, soluble protein, and soluble sugar contents and by reducing MDA content (XiaoYu *et al.* 2013). Silicon enhanced grape (*Vitis vinifera* × *Vitis labrusca*) callus survival rate at low temperature by avoiding browning (Moriguchi *et al.* 1988). *In vitro* studies on the storage of *Solanum tuberosum* var. *gersa* and *Coleus hybridus* indicated that silicone oil helps maintain the regenerative potential and reduces plant growth (Radovet *et al.* 2008; Radovet-Salinschi and Cachita-Cosma 2012). These results highlight the cryoprotective role of Si, which can be incorporated into cryoprotective mixtures. The ameliorating effect of Si on salt stress has been reported in *in vitro* culture of *Ajuga multiflora* (Sivanesan and Jeong 2014), *Salvia splendens* (Soundararajan *et al.* 2013), and *S. tuberosum* (Qing *et al.* 2005). There are reports that show Si-induced salinity tolerance as a result of reducing NaCl uptake by plants and the consequent preservation of stomatal ultrastructure, photosynthetic activity, antioxidant enzyme production, and modulation of free proline content (Qing *et al.* 2005; Soundararajan *et al.* 2013; Sivanesan and Jeong 2014). The results of another study investigating the effects of Si on aluminum (Al) tolerance of *Picea abies* cells indicated that Si is able to reduce the free Al concentration in the cell wall and Si is able to reduce Al toxicity (Prabagar *et al.* 2011). Silicon is also reported to minimize heavy metal toxicity (*Cucumis sativus* and *Triticum* spp.), improve drought tolerance (*S. tuberosum* L., *Piperaceae*, and *Zea mays*), improve salt stress (*Glycine max*, *Hordeum vulgare* L., *O. sativa* L., *Brassica napus* L., and *Ziziphus jujuba* cv.), and enhance resistance to temperature as well as radiation stresses (*Z. mays* and *G. max*) (Balakhnina and Borkowska 2013; Zhu and Gong 2014). Si is also able to induce some regulatory mechanisms in plants that may account for wide-spectrum disease resistance (Van Bockhaven *et al.* 2013).

In Vitro Application of Silicon

Role of silicon in plantlets grown and developed *in vitro* The anatomical as well as the morphological characteristics of field-grown seedlings are different from *in vitro*-grown plantlets. It has been reported that the growth and development of plants are affected by Si application. For instance, *Phalaenopsis* hybrid plantlets cultured in Went and Vacin medium containing $CaSiO_3$ showed increased leaf growth (Zhuo 1995). The modified Linsmaier and Skoog liquid medium used for cell suspension culture of *Perilla frutescens* with silicon A inclusion enhanced cell growth and anthocyanins content (Zhong *et al.* 1992).

It has been shown that both the root number and the growth of *C. loddigesii* seedlings grown in modified Knudson medium supplemented by Na_2SiO_3 (20.0 mgL^{-1}) and K_2SiO_3 (5.0 mgL^{-1}) were significantly increased (Soares *et al.* 2011). It was also reported that Si was able to increase the rooting of the *Phalaenopsis* hybrid (Zhuo 1995). The Na_2SiO_3 and GA_3 in combination increased the growth, leaf number, and root number of *C. loddigesii* more than GA_3 alone (Soares *et al.* 2013). The optimal concentration of Si needed for plant growth and development varies among different genotypes within the same species and between plant species (Lim *et al.* 2012).

The MS medium supplemented with 0.5 and 2.0 mgL^{-1} of $CaSiO_3$ promotes the growth of both native "*Brassavola perrinii*" as well as hybrid orchid plants, respectively

(Soares *et al.* 2012). The results of another study investigating the effects of diverse Si sources, such as Na_2SiO_3, K_2SiO_3, and $CaSiO_3$, on the anatomical characteristics and growth of strawberry (*Fragaria* × *ananassa)* seedlings showed that the seedling's fresh and dry weight were increased in MS medium supplemented with 1.0 g L^{-1} Na_2SiO_3 (Braga *et al.* 2009). Moreover, another study of banana (*Maca'banana*) seedlings cultured in medium containing $CaSiO_3$ showed an increase in chlorophyll content; however, those grown in MS medium supplemented with Na_2SiO_3 showed an increase in the fresh, dry weight, and length of shoots (Asmar *et al.* 2011). It has been reported that the inclusion of Si in the rooting medium causes an increase in the thickness of the leaf tissue and a deposition of epicuticular wax in strawberry (Braga *et al.* 2009) and banana (*Grande Naine*) (Asmar *et al.* 2013a, b) plantlets. The modified rooting medium supplemented with K_2SiO_3, Na_2SiO_3, and $CaSiO_3$ improved the leaf tissue anatomy of banana plantlets (*Maca'banana*) (Magno Queiroz Luz *et al.* 2012). Moreover, the inclusion of $CaSiO_3$ in the culture medium enhanced the photosynthetic rate and, consequently, the chlorophyll content in banana (*Maca'banana*) plantlets (Asmar *et al.* 2013a, b). In contrast, the electron and light microscopic analysis of the *in vitro*-cultured strawberry that was cultured without Si showed deformation of the leaf epidermis and chlorenchyma of plantlets (Soares *et al.* 2012). Another study has reported Si deposition within the cell walls of rice (*O. sativa*) obtained from *in vitro*-cultured plantlets (He *et al.* 2013). This study indicated the role of Si in improving the stability of the cell wall structure. Silicon is able to enhance the stability of cell walls through elongation and subsequent division, leading to the maintenance of the shape of cells that may be vital for the function and survival of the cells. The investigation of the effects of Si on hyperhydricity in *in vitro*-cultured *Ornithogalum dubium* revealed that modified MS liquid medium supplemented with NAA, BA, and 6% sucrose using a bioreactor considerably decreases the hyperhydric shoot induction and enhances the mechanical strength and firmness of plants (Ziv 2010). It has been shown that Si treatment of the regenerated *O. dubium* shoots significantly decreased the hydrogen peroxide content and oxidative activity of some reductive enzymes including ascorbate oxidase, GPX, and APX in the leaves obtained from regenerated shoots compared with control plants.

Role of silicon in regeneration of adventitious shoots and suppression of NaCl stress It has been shown in various studies that Si can be effective in lightening salt stress in different plants. Silicon supplementation to the culture medium increases the shoot induction frequency and average number of shoots per explant (Sivanesan and Jeong 2014). It has been shown that Si can be effective for shoot regeneration in rice (Islam *et al.* 2005) and reed (Máthé *et al.* 2012). The results of another experiment showed that, while the shoot generation of *A. multiflora* on the culture medium containing 100 mM NaCl is completely inhibited, supplementing this medium with Si improves the shoot generation of leaf and petiole explants (Sivanesan and Jeong 2014). They showed that the percentage of shoot induction is increased linearly by enhancing Si supplementation to the medium containing NaCl. The ion imbalance resulting from high concentrations of Na^+ and Cl^- ions in the culture medium reduces the number of regenerated shoots per explant, while additional Si can play key roles under nutrient imbalance (Ma 2004). It has been reported that MS media containing NaCl caused a decrease in SOD activity in the leaves and roots of *A. multiflora* (Sivanesan and Jeong 2014) and *H. vulgare* L. (Liang 1997), while both of these studies indicated that Si treatment of the culture medium containing NaCl considerably increased the SOD activity in both organs.

Silicon and cell culture in bioreactors/suspension Correspondingly, the modified MS medium supplemented with Si as K_2SiO_3 led to decreased hyperhydricity in *Cotoneaster wilsonii* by reducing the MDA content within the regenerated shoot parts compared with the control plants (Sivanesan *et al.* 2011). Based on the dispersive X-ray results of one study of *C. wilsonii*, no trace of Si was observed in the hyperhydric leaf samples, while the presence of Si was shown in non-hyperhydric plants. Therefore, the hyperhydricity problem can be decreased through Si supplementation to the liquid as well as the solid medium (Sivanesan *et al.* 2011).

Tissue culture of woody plants usually includes many disorders, such as tissue browning (a bottleneck) that results from phenolic oxidative activity. It has been shown that Si is able to prevent tissue browning completely in guava (*Psidium guajava*) by sealing the cut ends of nodal explants with a silicon mixture (Youssef *et al.* 2010) without any subsequent effects for the rest of the *in vitro* propagation steps. Based on this result, it was suggested that Si may be utilized during the preparation of other explants to avoid phenolic tissue browning. It can be concluded that the anatomical, morphological, and physiological uniqueness of different plantlets can be improved *in vitro* by modifying the culture medium by supplementation with Si. Nevertheless, the precise evaluation of the effects of different Si concentrations and sources on the growth and development of various plants is necessary.

Role of Silicon on Metabolomics, Growth Traits, and Rooting Ability

The addition of the proper amount of Si to the culture medium results in an increase in *A. multiflora* height. For example, the inclusion of 3.6 mM Si to the MS media enhanced plant height, while 7.2 mM of Si supplementation led to shorter plants (Sivanesan and Jeong 2014). This study also showed that an increase in the Si concentration in the MS media leads to a decrease in the number of leaves grown per shoot. It has been reported that Si treatment of the culture medium causes an increase in the growth traits of plants under salinity stress (Ma 2004; Liang *et al.* 2007).

The maximum amount of Si supplementation to the culture media of *A. multiflora* is limited to 3.6 mM, which leads to an increase in the number of leaves per shoot and an increase in the fresh and dry weights of the root and shoot; however, an increase in the Si concentration to 7.2 mM leads to the greatest root length per explant (Sivanesan and Jeong 2014). This study also indicated that Si treatment of up to 3.6 mM resulted in the maximum chlorophyll level, whereas an increase in the Si concentration negatively affected the chlorophyll content. *In vitro* studies investigating the effects of potassium silicate on the growth characteristics of *Begonia semperflorens* and Pansy (*Viola* × *wittrockiana*) have indicated that Si significantly increased the fresh weight, chlorophyll content, and leaf area of *Begonia* and Pansy (Lim *et al.* 2012). Leaf anatomy studies of *B. perrinii* using different Si concentrations showed that treatments with silicate prevent the deformation of the chlorenchyma and the epidermis compared with non-Si treatments and can affect plant growth conditions directly or indirectly (Soares *et al.* 2012).

Antioxidant enzymes increase the morphogenesis and growth traits in many plants. For instance, it was shown that the antioxidant enzyme activities in *Caladium bicolor* (Isah and Mujib 2011), *Brassica rapa* var. *turnip* (Abbasi *et al.* 2011), *Crocus sativus* (Vatankhah *et al.* 2010), plum (Faize *et al.* 2013), and *Piper nigrum* (Ahmad *et al.* 2013a, b) are increased during organogenesis. It was reported that the antioxidant enzyme activities in many plants are affected by Si treatment (Ma 2004; Liang *et al.* 2007). The results of one study of *A. multiflora* indicated that the addition of Si to MS medium containing IAA and 2iP improves adventitious shoot regeneration by enhancing the activity of some antioxidant enzymes such as APX, CAT, SOD, and SOD (Sivanesan and Jeong 2014).

Gibberellins (Gas) are plant growth hormones that play critical roles in diverse developmental processes, such as dormancy, germination, stem elongation, flowering, enzyme induction, sex expression, leaf senescence, and fruit senescence. It has been reported that Si inclusion can increase the levels of both GA_1 and GA_{20} in rice cultivars (Hwang *et al.* 2007). It has been indicated that shoot induction in citrus (Pérez-Tornero *et al.* 2010), apple (Isogai *et al.* 2008), and *Cephaelis ipecacuanha* (Kaushal *et al.* 2005) is affected by GA_3. On the other hand, Si positively affects shoot induction; therefore, this effective role of Si may result from altering endogenous levels of Gas.

Silicon Absorption and Transportation

It has been reported that Si absorption and transportation in different plant species are dependent on both species as well as on the outer Si concentration (Sahebi *et al.* 2015). The role of plant species in Si absorption and transportation depends on their passive or active ability to uptake Si (Liang *et al.* 2007). Personal communication comparing Si accumulation between three Malaysian rice varieties indicated that calluses of the MR276 variety, with a high potential of Si absorption, were more embryogenic (Fig. 1), and the plant regeneration percentage obtained from calluses was higher than that of the other two varieties, MR219 and MR220, with less ability to accumulate Si.

It was shown that silicification occurs in the endodermis of gramineae roots during maturation. However, the cell walls of other tissues, including epidermal, vascular, and cortical tissues, may be silicified within older roots. Moreover, silicification also occurs in different parts of grasses, including roots and shoots (Sangster *et al.* 2001). It was shown that a layer of deposited Si of approximately 2.5 μm is formed immediately under the cuticle in rice leaf blades. It has been shown that the silicification of cells, such as "dumb-bell-shaped cells" in silica cells, vascular bundles, and silica bodies of bulliform cells, is not restricted to the leaf blades of rice because silicified cells

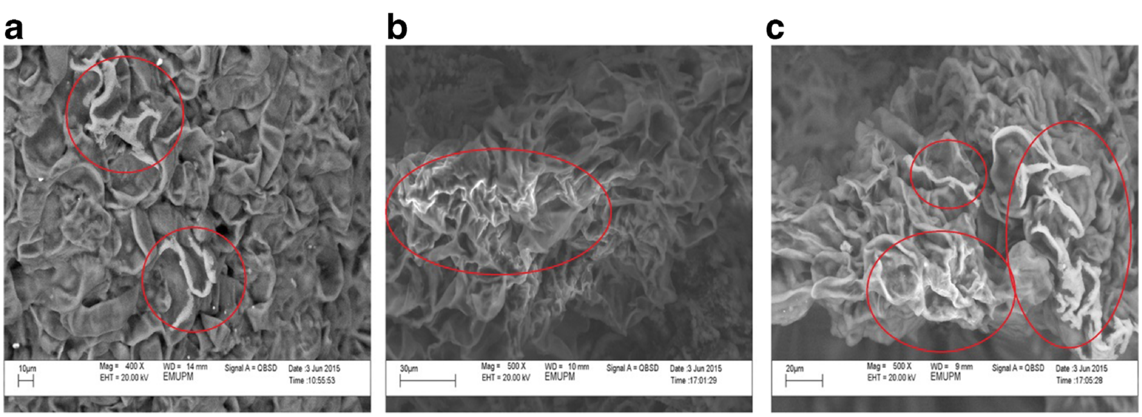

Figure 1 Scanning electron microscopy (SEM) image of the calluses of different rice varieties. (*a*–*c*) Three Malaysian rice varieties MR219, MR220, and MR276, respectively. *White traces highlighted with red circle* are accumulated silicon.

may be found inside the epidermal layer as well as in the vascular tissues of the stem, hull, and leaf sheath (Prychid *et al.* 2003). Another study on *Equisetum* indicated that the silicified structures can be found on the epidermal surface of the cell wall (Holzhüter *et al.* 2003). The silicified cells produced in the different tissues including vascular tissue, leaf blade, epidermis stem, hull, and leaf sheath cooperate to protect against a wide range of stresses in plants (Hodson *et al.* 2005). The mechanism of bio-silica formation in plants has been reviewed in a previous study (Sahebi *et al.* 2015). The silica concentration in the environment is affected by many factors such as silica condensation, temperature, pH, and presence of other polymers, different ions, and small molecules. Distances of Si–O bond and the angle of Si–O–Si bond play the essential role through different silica species polymerization. Environmental reactions and OH groups may differ in diverse species due to the composition, solubility, hardness, density, and viscosity. Functional groups of amino acid residues in the structure of proteins are accessible to silica and play an important role in determining the nature and physical structure of substances which are formed during different maturing stages. Amino acids and peptides are effective in the formation of polysilicic species through interactions with different silicate species in the solution (Sahebi *et al.* 2015).

Future Directions

Biochemical and physiological functions of silicon at different molecular levels as well as at a single cell level should be more illustrated through utilizing two systems of the plant tissue culture and *in vitro* cell suspension culture. Although the beneficial role of silicon to prompt the secondary metabolites in all parts of plants has been shown recently, but there is still a big gap to understand its involved mechanisms. Hence, much work is needed to find an excel formulation of tissue culture medium not only to settle numerous micro-propagation problems but also to increase plant tissue culture success.

Conclusion

Although many beneficial effects of Si on the tissue culture of several species plants have been demonstrated recently, they need to be verified in different plant species to prove its usefulness at the field level. Plant tissue and cell suspension culture can be used as tools to study the physiological and biochemical functions of Si at single cell and plant levels. Silicon may also be used to increase the production of secondary metabolites within *in vitro* cultures of plant cells and tissues. It can be concluded that Si be included in the tissue culture medium as a constructive nutrient to improve micropropagation including plant quality.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interests.

References

Abbasi BH, Khan M, Guo B, Bokhari SA and Khan MA (2011) Efficient regeneration and antioxidative enzyme activities in *Brassica rapa* var. turnip. Plant Cell, Tissue and Organ Culture (PCTOC) 105: 337-344

Ahmad A, Afzal M, Ahmad A, Tahir M (2013a) Effect of foliar application of silicon on yield and quality of rice (Oryza Sativa L). Cercet Agro Mold 46:21–28

Ahmad N, Abbasi BH, ur Rahman I, Fazal H (2013b) *Piper nigrum*: micropropagation, antioxidative enzyme activities, and chromatographic fingerprint analysis for quality control. Appl Biochem Biotechnol 169:2004–2015

Artyszak A, Gozdowski D and Kucińska K (2015) The effect of calcium and silicon foliar fertilization in sugar beet. Sugar Tech: 1-6

Asmar S, Castro E, Pasqual M, Pereira F, Soares J (2013a) Changes in leaf anatomy and photosynthesis of micropropagated banana plantlets under different silicon sources. Sci Hortic 161:328–332

Asmar SA, Pasqual M, de Araujo AG, Silva R, Rodrigues FA, Pio L (2013b) Morphophysiological characteristics of acclimatized 'Grande Naine' banana plants in response to in vitro use of silicon. Semina Cienc Agrar 34:73–81

Asmar SA, Pasqual M, Rodrigues FA, Araujo AGD, Pio LAS, Silva SDO (2011) Sources of silicon in the development of micropropagated seedlings of banana 'Maçã'. Cienc Rural 41: 1127–1131

Balakhnina T, Borkowska A (2013) Effects of silicon on plant resistance to environmental stresses: review. Int Agrophys 27:225–232

Braga FT, Nunes CF, Favero AC, Pasqual M, Carvalho JGD, Castro EMD (2009) Anatomical characteristics of the strawberry seedlings micropropagated using different sources of silicon. Pesq Agrop Brasileira 44:128–132

Chen Y, Liu M, Wang L, Lin W, Fan X, Cai K (2015) Proteomic characterization of silicon-mediated resistance against *Ralstonia solanacearum* in tomato. Plant Soil 387:1–16

D'Imperio M, Renna M, Cardinali A, Buttaro D, Santamaria P, Serio F (2015) Silicon biofortification of leafy vegetables and its bioaccessibility in the edible parts. J Sci Food Agric. doi:10.1002/jsfa.7142

Epstein E (1999) Silicon. Annu Rev Plant Biol 50:641–664

Esfahani AA, Pirdashti H, Niknejhad Y (2014) Effect of iron, zinc and silicon application on quantitative parameters of Rice (*Oryza Sativa* L. CV. Tarom Mahalli). Intl JFarm Alli Sci 3:529–533

Faize M, Faize L, Petri C, Barba-Espin G, Diaz-Vivancos P, Clemente-Moreno MJ, Koussa T, Rifai LA, Burgos L, Hernandez JA (2013) Cu/Zn superoxide dismutase and ascorbate peroxidase enhance in vitro shoot multiplication in transgenic plum. J Plant Physiol 170: 625–632

Hartley SE (2015) Round and round in cycles? Silicon-based plant defences and vole population dynamics. Funct Ecol 29:151–153

He C, Wang L, Liu J, Liu X, Li X, Ma J, Lin Y, Xu F (2013) Evidence for 'silicon' within the cell walls of suspension-cultured rice cells. New Phytol 200:700–709

Hodson MJ, White PJ, Mead A, Broadley MR (2005) Phylogenetic variation in the silicon composition of plants. Ann Bot-London 96: 1027–1046

Holzhüter G, Narayanan K, Gerber T (2003) Structure of silica in *Equisetum arvense*. Anal Bioanal Chem 376:512–517

Hussain I, Ashraf MA, Rasheed R, Asghar A, Sajid MA, Iqbal M (2015) Exogenous application of silicon at the boot stage decreases accumulation of cadmium in wheat (*Triticum aestivum* L.) grains. Braz J Bot 38:1–12

Hwang S-J, Hamayun M, Kim H-Y, Na C-I, Kim K-U, Shin D-H, Kim S-Y, Lee I-J (2007) Effect of nitrogen and silicon nutrition on bioactive gibberellin and growth of rice under field conditions. J Crop Sci Biotechnol 10:281–286

Isah T, Mujib A (2011) Studies on antioxidant enzymes activity during in vitro morphogenesis of *Caladium bicolor* Linn. Int J Mod Cell Mol Bio 1:1–9

Islam MM, Ahmed M, Mahaldar D (2005) In vitro callus induction and plant regeneration in seed explants of rice (*Oryza Sativa* L.). Res J Agric Biol Sci 1:72–75

Isogai S, Touno K, Shimomura K (2008) Gibberellic acid improved shoot multiplication in *Cephaelis ipecacuanha*. In Vitro Cell Dev Biol Plant 44:216–220

Kaushal N, Modgil M, Thakur M, Sharma D (2005) In vitro clonal multiplication of an apple rootstock by culture of shoot apices and axillary buds. Indian J Exp Biol 43:561

Liang Y (1997) Effect of silicon on leaf ultrastructure, chlorophyll content and photosynthetic activity of barley under salt stress. Pedosphere 8: 289–296

Liang Y, Sun W, Zhu Y-G, Christie P (2007) Mechanisms of silicon-mediated alleviation of abiotic stresses in higher plants: a review. Environ Pollut 147:422–428

Lim MY, Lee EJ, Jana S, Sivanesan I, Jeong BR (2012) Effect of potassium silicate on growth and leaf epidermal characteristics of begonia and pansy grown in vitro. Korean J Hortic Sci Technol 30:579–585

Ma JF (2004) Role of silicon in enhancing the resistance of plants to biotic and abiotic stresses. Soil Sci Plant Nutr 50:11–18

Magno Queiroz Luz J, Abreu Asmar S, Pasqual M, Gomes de Araujo A, Pio L, Ferreira Resende R (2012) Modifications in leaf anatomy of banana plants cultivar 'Maca' subjected to different silicon sources in vitro. Acta Hortic 961:239–243

Mathe C, Mosolygó Á, Surányi G, Beke A, Demeter Z, Tóth VR, Beyer D, Mészáros I, Márta M (2012) Genotype and explant-type dependent morphogenesis and silicon response of common reed (*Phragmites australis*) tissue cultures. Aquat Bot 97:57–63

Mitani N, Ma JF (2005) Uptake system of silicon in different plant species. J Ex B 56:1255–1261

Moriguchi T, Kozaki I, Matsuta N, Yamaki S (1988) Plant regeneration from grape callus stored under a combination of low temperature and silicone treatment. Plant Cell Tissue Organ Cult 15:67–71

Muneer S, Jeong BR (2015) Proteomic analysis of salt-stress responsive proteins in roots of tomato (*Lycopersicon esculentum* L.) plants towards silicon efficiency. J Plant Growth Regul 77: 133–146

Noor T, Batool N, Mazhar R, Ilyas N (2015) Effects of siltation, temperature and salinity on mangrove plants. Eur Aca Res 2: 14172–14179

Pérez-Tornero O, Tallon C, Porras I (2010) An efficient protocol for micropropagation of lemon (*Citrus limon*) from mature nodal segments. Plant Cell Tiss Org Cult (PCTOC) 100: 263–271

Prabagar S, Hodson MJ, Evans DE (2011) Silicon amelioration of aluminium toxicity and cell death in suspension cultures of Norway spruce (*Picea abies* L.). Environ Exp Bot 70:266–276

Prychid CJ, Rudall PJ, Gregory M (2003) Systematics and biology of silica bodies in monocotyledons. Bot Rev 69:377–440

Qing W, Huiying H, Jinwen Z (2005) Effect of exogenous silicon and proline on potato plantlet in vitro under salt stress. China Vegetables 9:16–18

Radovet D, Cachita-Cosma D and Petrus A (2008) The micropropagation of coleus hybridus *Jupiter vitrocultures* under different paraffin or silicon oil stratums. Studia Universitatis "Vasile Goldiş", Seria Ştiinte Vieții (Life Sciences) 18: 61-70

Radovet-Salinschi D, Cachita-Cosma D (2012) Testing the regenerative capacity of *Solanum tuberosum* var. Gersa explants after 24 weeks storage in living collection. Anal Univ din Oradea, Fascicula: Ecotoxicol Zootehnie Tehnologii de Industrie Alimentară 11:423–430

Reed BM, Wada S, DeNoma J, Niedz RP (2013) Mineral nutrition influences physiological responses of pear in vitro. In Vitro Cell Dev Biol Plant 49:699–709

Sahebi M, Hanafi MM, Siti Nor Akmar A, Rafii MY, Azizi P, Tengoua F, Nurul Mayzaitul Azwa J, Shabanimofrad M (2015) Importance of silicon and mechanisms of biosilica formation in plants. BioMed Res Int 2015:16

Sangster A, Hodson M, Tubb H (2001) Silicon deposition in higher plants. St Plant Sci 8:85–113

Saudy H, Mubarak MM (2015) Mitigation the detrimental impacts of nitrogen deficit and fenoxaprop–p–ethyl herbicide on wheat using silicon. Commun Soil Sci Plant Anal 46:897–907

Schurt DA, Cruz MF, Nascimento KJ, Filippi MC, Rodrigues FA (2014) Silicon potentiates the activities of defense enzymes in the leaf sheaths of rice plants infected by *Rhizoctonia solani*. Trop Plant Pathol 39:457–463

Sivanesan I, Jeong BR (2014) Silicon promotes adventitious shoot regeneration and enhances salinity tolerance of *Ajuga multiflora* Bunge by altering activity of antioxidant enzyme. Sci World J 2014

Sivanesan I, Song JY, Hwang SJ, Jeong BR (2011) Micropropagation of *Cotoneaster wilsonii* Nakai—a rare endemic ornamental plant. Plant Cell Tissue Org Cult 105:55–63

Soares JDR, Pasqual M, de Araujo AG, de Castro EM, Pereira FJ, Braga FT (2012) Leaf anatomy of orchids micropropagated with different silicon concentrations. Acta Sci Agron 34:413–421

Soares JDR, Pasqual M, Rodrigues FA, Villa F, Araujo AG (2011) Silicon sources in the micropropagation of the *Cattleya* group orchid. Acta Sci Agron 33:503–507

Soares J, Villa F, Rodrigues F, Pasqual M (2013) Concentrations of silicon and GA3 in in vitro propagation of orchids under natural light. Sci Agrár Parana 12:286–292

Soundararajan P, Sivanesan I, Jo EH, Jeong BR (2013) Silicon promotes shoot proliferation and shoot growth of *Salvia splendens* under salt stress in vitro. Hortic Environ Biotechnol 54:311–318

Vaculík M, Lux A, Luxová M, Tanimoto E, Lichtscheidl I (2009) Silicon mitigates cadmium inhibitory effects in young maize plants. Environ Exp Bot 67:52–58

Van Bockhaven J, De Vleesschauwer D, Höfte M (2013) Towards establishing broad-spectrum disease resistance in plants: silicon leads the way. J Ex B 64:1281–1293

Vatankhah E, Niknam V, Ebrahimzadeh H (2010) Activity of antioxidant enzyme during in vitro organogenesis in *Crocus sativus*. Biol Plant 54:509–514

Wang H-S, Yu C, Fan P-P, Bao B-F, Li T, Zhu Z-J (2015) Identification of two cucumber putative silicon transporter genes in *Cucumis sativus*. J Plant Growth Regul 34:332–338

XiaoYu D, Min T, WeiShuang W (2013) Effects of silicon on physiology and biochemistry of dendrobium moniliforme plantlets under cold stress. Agric Biotechnol 2:18–21

Xu C, Ma Y, Liu Y (2015) Effects of silicon (Si) on growth, quality and ionic homeostasis of aloe under salt stress. S Afr J Bot 98:26–36

Yin L, Wang S, Tanaka K, Fujihara S, Itai A, Den X, Zhang S (2015) Silicon-mediated changes in polyamines participate in silicon-induced salt tolerance in *Sorghum bicolor* L. Plant Cell Environ. doi:10.1111/pce.12521

Youssef M, El-Helw M, Taghian A, El-Aref H (2010) Improvement of *Psidium guajava* L. using micropropagation. Acta Hortic 849:223–230

Zhong J-J, Seki T, Kinoshita S-I, Yoshida T (1992) Effects of surfactants on cell growth and pigment production in suspension cultures of *Perilla frutescens*. World J Microbiol Biotechnol 8:106–109

Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. Agron Sustain Dev 34:455–472

Zhuo T-S (1995) The detection of the accumulation of silicon in *Phalaenopsis* (Orchidaceae). Ann Bot 75:605–607

Ziv M (2010) Silicon effects on growth acclimatization and stress tolerance of bioreactor cultured *Ornithogalum dubium* plants. Acta Hortic 865:29–35