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Review

Biostimulant activity of silicon in horticulture

Dimitrios Savvas*, Georgia Ntatsi

Agricultural University of Athens, Department of Crop Science, Laboratory of Vegetable Crops, Iera Odos 75, 11855 Athens, Greece

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ABSTRACT

Although silicon (Si) is the second most abundant element in the earth's crust, it is not considered an essential element for plant nutrition. However, both research results and practical experience advocate for a beneficial impact of Si on growth and development of many plant species, especially when exposed to abiotic or biotic stress. In this review, only the biostimulating effects of Si on plants exposed to abiotic stress are considered. In the soil solution, Si occurs mainly as monomeric silicic acid (H_4SiO_4) at concentrations ranging from 0.01 to 2.0 mM. H_4SiO_4 does not dissociate at pH lower than 9 and thus plants take up Si in this non-ionic form, actively or passively, depending on the external Si concentration and their inherent requirements. The latter vary considerably as indicated by the large variation in tissue Si concentrations between species, which range from 0.1% to 10% in dry weight. After uptake, Si accumulates in various tissues mainly as a polymer of hydrated amorphous silica. Currently, Si is applied in some commercial crops aiming at inducing resistance to abiotic stresses, diseases, and pathogens but the use of this element as a biostimulant in horticulture can be further extended. Si alleviates salt, drought, and nutrient stress, as well as stress associated with climatic conditions, minimizes metal and metalloid toxicities, and may delay plant senescence processes. However, the mechanisms underlying Si-mediated alleviation of abiotic stresses remain poorly understood. The key mechanisms involved in Si-mediated alleviation of abiotic stresses in higher plants include: (1) silica deposition inside the plant tissues which provides mechanical strength and erectness to leaves and modulates nutrient and water mobility inside the plants, (2) stimulation of antioxidant systems in plants, (3) complexation or co-precipitation of toxic metals with Si both in plant tissues and in soil, (4) modulation of gene expression and signaling through phytohormones, although evidence for a direct Si involvement in plant metabolic functions is currently lacking.

Contents

* Corresponding author. Fax: +30 210 5294504.
E-mail address: dsavvas@aua.gr (D. Savvas).

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1. Introduction

Silicon (Si) is the second most abundant element in the earth's crust following oxygen, when considered either on the basis of mass or number of atoms (Ma, 2005). As reported by Kovda (1973), the Si content amounts to 200–350 g kg^{-1} in clay soils and 450–480 g kg^{-1} in sandy soils. Although most of Si is present in the form of insoluble oxides or silicates in the soil, some water-soluble Si also occurs. Silicon is a non-essential element for plant nutrition in the sense of the classical criteria postulated by Arnon and Stout (Epstein, 1994); however, biostimulatory Si effects on growth and development of higher plants have been well established (Epstein, 1999; Ma and Yamaji, 2006). Chemical elements which are non-essential for plant nutrition but have the capacity to modify physiological processes of plants in a way that provides benefits to growth, development and/or stress responses constitute a distinct category of biostimulants. Many investigations have shown that monocotyledons and especially Poaceae species such as rice respond positively to an enhanced supply of Si (Epstein, 1999; Ma et al., 2007). However, beneficial effects associated with Si application have been reported also for many dicotyledons, especially when the plants are exposed to abiotic or biotic stress (Ma, 2004; Fauteux et al., 2005). Therefore, many authors characterize Si a 'quasi-essential' element for higher plants, in the sense that plant growth may be stimulated by enhanced Si supply of, while Si-starved plants may exhibit physical abnormalities (Rafi and Epstein, 1997; Ma and Yamaji, 2008).

In non-stressed crops, Si may sometimes enhance plant growth by improving leaf erectness, thereby increasing light interception and concomitantly canopy photosynthesis (Adatia and Besford, 1986; Savvas et al., 2007). However, in most cases, the effects of Si on plant growth become obvious under stress conditions, while, in the absence of a stress factor, the crop usually does not benefit from Si application (Ma and Yamaji, 2008; Guntzer et al., 2012). Many laboratory, greenhouse and field experiments have shown that silicon is capable of mitigating both biotic stresses caused by plant diseases and pest damage and abiotic stresses such as salinity, drought, manganese and aluminum toxicity, heavy metal toxicity, nutrient imbalance, waterlogging, high radiation, high temperature, wounding, and freezing (Van Bockhaven et al., 2013; Zhu and Gong, 2014).

Anatomical changes in plant tissues imposed by silica deposition in cell walls may be the causal factors for some beneficial effects of Si (Raven, 2001; Piperno et al., 2002; Ma, 2004). Other investigators state that the beneficial effects of Si on higher plants are mainly due to its direct or indirect involvement in plant metabolism (Epstein, 1999; Liang et al., 2003; Zhu et al., 2004). Nevertheless, the impact of Si on many metabolic processes conferring stress tolerance and growth benefits to plants is still not well understood (Liang et al., 2007; Guntzer et al., 2012; Gonzalo et al., 2013). Despite our insufficient knowledge regarding the physiological implication of Si in plant metabolism, silicon application as fertilizer is currently a common practice in rice (*Oryza sativa* L.) and sugarcane (*Saccharum officinarum* L.) crops (Savant et al., 1999; Ma et al., 2007). Application of silicon fertilizers in rice and sugarcane cultivated in soils with low levels of water-soluble Si is not only beneficial but rather necessary to avoid yield losses, because low tissue Si levels in these plants are associated with considerable yield losses (Tavakkoli et al., 2011; Zhu and Gong, 2014).

Although currently the most prevalent use of Si in agriculture is its application as a fertilizer in rice and some other field crops belonging to the Poaceae family, the aim of the present paper is to review the use of Si as a biostimulant in horticultural crops. Many investigations have shown that exogenous Si supply to several horticultural plants, such as cucumber, zucchini squash, bean, tomato, roses, may result in increased growth and productivity (Miyake and Takahashi, 1983; Savvas et al., 2007, 2009; Zuccarini, 2008; Toresano-Sánchez et al., 2012). When these plants are cultivated in the soil, the stimulatory effects of Si on plant growth and development may be evident only when the level of water soluble Si in the soil solution is low, depending on the soil type. Despite the abundance of Si in the soil, low Si levels in the soil solution constitute a common problem in many areas of the world, especially in highly weathered Oxisols and Ultisols as well as in organic soils such as Histosols (Haynes, 2014). In China for instance, soils that are deficient in water-soluble Si account for more than 40 % of the total agricultural land (Ma et al., 2009). Furthermore, Si application may be beneficial also to some soilless-cultivated greenhouse plants, due to the absence of soil in the root environment, which is a source of Si to crops (Savvas et al., 2009).

The benefits of silicon application on crop growth, and the potential uses of Si as fertilizer (especially in Monocots), biostimulant (especially in Dicots) or plant protectant (in both Monocots and Dicots) have been reported in several recent reviews (Liang et al., 2007; Ma and Yamaji, 2008; Epstein, 2009; Guntzer et al., 2012; Zhu and Gong, 2014;). However, none of them has focused on the practical applications of Si as a biostimulant in horticultural crops while also attempting to highlight the underlying mechanisms. Hence, in the present paper, recent advances on silicon uptake, transport, and accumulation in horticultural plants are reported, while attempting to elucidate mechanisms implicated in the ability of silicon to act as a biostimulant on these plants. In this review, only the biostimulant effects of Si on plants exposed to abiotic stress will be considered.

2. Silicon forms

Because of its strong affinity with oxygen, in nature Si always exists as silica (SiO_2) or silicates that are chemically bound with various metals. About 60% of the mass of the earth's crust, and more than 50% of the soil mass is SiO_2 (Ma, 2005). Si in soil solution is mainly present in the form of monosilicic acid (H_4SiO_4, also denoted as $Si(OH)_4$ in scientific texts), an uncharged monomeric molecule when the solution pH is below 9 (Ma and Yamaji, 2006). At pH levels higher than 9, silicic acid dissociates into silicate ion, i.e., $(OH)_3SiO^-$. The solubility of H_4SiO_4 in water at 25 °C is about 2 mM (equivalent to a SiO_2 concentration of 120 mg L^{-1}), while at concentrations exceeding 2 mM, polymerization of silicic acid into amorphous silica ($SiO_2 \cdot nH_2O$) occurs. According to Epstein (2001) and Sommer et al. (2006), the Si concentration in the soil solution ranges commonly from 0.1 to 0.5–0.6 mM, while according to Karathanasis (2002) the general range of Si in soil solutions is from 0.01 to 2.0 mM. Several factors may affect the amount of dissolved silicon in the soil solution, including parent material, soil develop-