



Silicon enhancement of estimated plant biomass carbon accumulation under abiotic and biotic stresses. A meta-analysis

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Abstract

Abiotic and biotic stresses are the major factors limiting plant growth worldwide. Plants exposed to abiotic and biotic stresses often cause reduction in plant biomass as well as crop yield, resulting in plant biomass carbon loss. As a beneficial and quasi-essential element, silicon accumulation in rhizosphere and plants can alleviate the unfavorable effects of the major forms of abiotic and biotic stress through several resistance mechanisms and thus increases plant biomass accumulation and crop yield. The beneficial effects of silicon on plant growth and crop yield have been widely reviewed over the last years. However, carbon accumulation of silicon-associated plant biomass under abiotic and biotic stresses has not yet been systematically addressed. This review article focuses on both the main mechanisms of silicon-mediated alleviation of abiotic and biotic stresses and their effects on plant biomass carbon accumulation in terrestrial ecosystems. The major points are the following: (1) the recovery of plant biomass via silicon mediation usually exhibits a bell-shaped response curve to abiotic stress severity and an S-shaped response curve to biotic stress severity; (2) although carbon concentration of plant biomass decreases with silicon accumulation, more than 96% of the recovered plant biomass contributes to plant biomass carbon accumulation; (3) silicon-mediated recovery generally increases plant biomass carbon by 35% and crop yield by 24%. In conclusion, silicon can improve plant growth and enhance plant biomass carbon accumulation under abiotic and biotic stresses in terrestrial ecosystems.

Keywords Abiotic stresses · Biotic stresses · Carbon accumulation · Plant biomass restoration · Silicon

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1 Introduction

Abiotic and biotic stresses are the important factors limiting plant growth and crop yield worldwide. The drought and salt stresses are the two major abiotic stress factors that restrict plant growth and productivity (Cramer et al. 2011; Zhu 2016), while pathogen infection and animal grazing are the two major biotic stress factors that cause plant injuries and biomass losses (Massey et al. 2007; Dow et al. 2017). The area subject to meteorological drought constitutes about 21% of the earth's land area, with nearly 13% under moderate to severe conditions (Prudhomme et al. 2014; Damberg and AghaKouchak 2014), whereas the area suffering from soil salinization accounts for approximately 7% of the global land area and 20% of the total cropland area (Rasool et al. 2013). Other forms of abiotic stress, such as soil acidification (Sumner and Noble 2003), heavy metal contamination (Adrees et al. 2015), UV radiation (Jansen and van den Noort 2000), extreme temperature (Levitt 1980), and nutrient imbalance (Huber et al. 2012), also have negative effects on plant growth. Among the biotic stresses, fungal pathogen contributes to 70–80% of plant diseases (Ray et al. 2017), while bacterial or viral pathogens usually have a long latent period and cause fatal plant injuries (García and Pallás 2015; Kim et al. 2016). Insect infestation and herbivore grazing often lead to tissue losses, which are more costly to renovate for slow-growing plant species (Massey et al. 2007). The negative effects of abiotic and biotic stresses have been reported to reduce crop yield and plant biomass carbon through restraining plant photosynthesis and biomass accumulation (Eneji et al. 2008; Nicol et al. 2011). Additionally, climatic and environmental changes may cause more severe and frequent occurrences of abiotic and biotic stresses in the future.

Traditional measures to alleviate abiotic and biotic stresses may have some negative environmental and ecological effects (e.g., pesticide residues). Alternatively, many studies have demonstrated that silicon (Si) accumulation in plants can increase the adaptive capacity of plants under abiotic and biotic stresses (Tuna et al. 2008; Kim et al. 2014; Kang et al. 2016; Song et al. 2016) (Fig. 1). Silicon that is tightly bound to the cell walls is naturally present as a structural material in relation to enhancement of cell wall rigidity and elasticity (Weiss and Herzog 1978; He et al. 2013). When monosilicic acid concentration is high in the xylem sap, it becomes an important osmolyte improving plant osmotic and water potentials

(Casey et al. 2004; Mitani et al. 2005; Yin et al. 2013). In addition, Si requires relatively less energy than the biomolecules such as lignin and proline with regard to structural material and osmolyte (Raven 2001; Broadley et al. 2012). Therefore, Si can improve the homeostasis of plant resistance to multiple abiotic and biotic stresses in terrestrial ecosystems at a low cost.

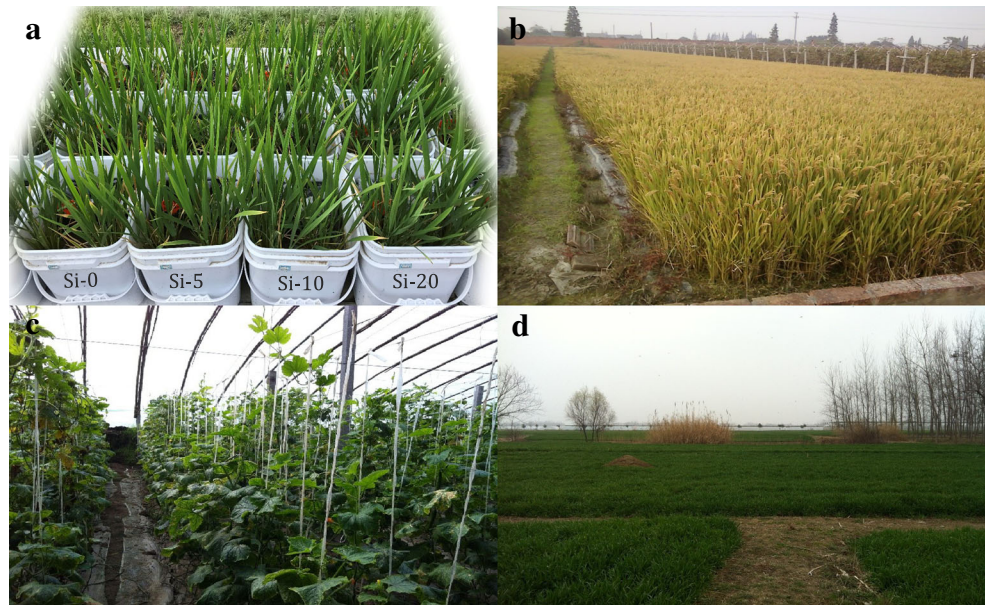
Important literature has reported that Si application can promote plant growth, biomass accumulation, and crop yield under various abiotic (Liang et al. 2007; Cooke and Leishman 2016; Rios et al. 2017) and biotic (Hartley and DeGabriel 2016; Luyckx et al. 2017; Wang et al. 2017) stresses. Recently, researches on molecular mechanisms of Si uptake, transport, and accumulation in plants have achieved a critical milestone in molecular evolution of aquaporins (Deshmukh et al. 2015; Yamaji et al. 2015; Vivancos et al. 2016). However, the linkage between the mechanism of Si-mediated alleviation and the effect of Si on plant biomass carbon accumulation in terrestrial ecosystems has not yet been clarified accurately. Different from other reviews focusing on the mechanisms of Si-mediated resistance to various stresses (Guntzer et al. 2012; Zhu and Gong 2014; Rizwan et al. 2015; Imtiaz et al. 2016), this review summarizes and discusses the mechanisms on how Si improves plant biomass carbon accumulation under abiotic and biotic stresses. First, we introduce the negative effects of various stresses on plant biomass carbon accumulation as abiotic and biotic stresses severely suppress plant growth. Second, we make the connection between the physiological mechanisms of Si-mediated alleviation under different stresses and the factors controlling Si enhancement of plant biomass carbon accumulation. Third, we discuss the role of Si in enhancing aboveground net primary productivity (ANPP) and plant biomass carbon accumulation in terrestrial ecosystems. Finally, we discuss the potential of Si in enhancing plant biomass carbon accumulation for future investigation at the ecosystem scale.

2 Materials and methods

2.1 Data compilation

Data on Si-mediated recovery of plant biomass and crop yield under abiotic and biotic stresses were collected from peer-reviewed publications. In order to avoid publication bias, the following keywords were employed to search the Web of Science: silicon, abiotic stresses (i.e., drought stress, salt stress, UV-B radiation, nutritional imbalance, and heavy metal toxicities), and biotic stresses (i.e., bacterial blight, brown

Fig. 1. Beneficial effect of Si application to rice growth under salt stress (a) and common Si-accumulating crops: rice (b), cucumber (c), and wheat (d). In sub-figure (a), Si-0, Si-5, Si-10, and Si-20 denote 0, 5, 10, and 20 g Si fertilizer per pot, respectively



spot, stalk borer, and neck blast). In addition, the following two criteria were used to select literatures for analysis:

1. Plant biomass was provided or could be calculated based on dry weight of leaf, grain, stalk, and root;
2. Crop yields were provided.

Plant biomass included aboveground biomass only or was comprised of below- and aboveground biomass. In total, 41 papers dealing with plant biomass and 12 papers dealing with crop yield were selected in our synthesis. The original data of plant growth with and without Si application under various stress conditions were extracted from reported tables or graphs using GetData Graph Digitizer (Version 2.22, Russian Federation).

2.2 Data calculation

Because the control treatment of Si application usually displays enhancement of plant biomass accumulation as well, in order to preclude the Si fertilization effect, plant biomass increment (PBI) mediated by Si application under both abiotic and biotic stresses was calculated using Eq. (1).

$$\text{PBI} (\%) = \frac{\text{BS}_{+\text{Si}}/\text{BS}_{-\text{Si}} - \text{BC}_{+\text{Si}}/\text{BC}_{-\text{Si}}}{\text{BC}_{+\text{Si}}/\text{BC}_{-\text{Si}}} \times 100 \quad (1)$$

where BS is the plant biomass under stressful condition, BC is the plant biomass of the control, and the subscripts of “-Si” and “+Si” are experimental treatment without and with Si application, respectively. For the

studies without Si application to the control, the plant biomass increment was calculated using Eq. (2).

$$\text{PBI} (\%) = \frac{\text{BS}_{+\text{Si}} - \text{BS}_{-\text{Si}}}{\text{BS}_{-\text{Si}}} \times 100 \quad (2)$$

Besides, Si-mediated plant recovery from stressful conditions usually accompanies with increasing Si concentration and decreasing carbon concentration in plant biomass. Hence, plant biomass carbon increment (BCI) was calculated using Eq. (3).

$$\text{BCI} (\%) = \text{PBI} \times \text{DC}_f \quad (3)$$

where DC_f is the coefficient of biomass carbon decreasing with Si accumulation in plant biomass. Until now, the largest Si content increase, which was induced by Si addition, was 3.96% by weight in rice leaf (Detmann et al. 2012). Thus, we concluded that Si application to alleviate multiple abiotic and biotic stresses increases no more than 4% of Si in plant biomass by weight. Besides, 1% of Si increase in plant biomass generally induces less than 1% plant biomass carbon reduction (Klotzbücher et al. 2018; Neu et al. 2017). Therefore, 0.96 was set as the coefficient in this study for estimating plant biomass carbon increment that is mediated by Si application under stressful conditions.

Similar to data calculation of plant biomass increment, crop yield increment (CYI) was calculated using Eq. (4) to exclude the Si fertilization effect.

$$\text{CYI} (\%) = \frac{\text{YS}_{+\text{Si}}/\text{YS}_{-\text{Si}} - \text{YC}_{+\text{Si}}/\text{YC}_{-\text{Si}}}{\text{YC}_{+\text{Si}}/\text{YC}_{-\text{Si}}} \times 100 \quad (4)$$

where YS is the crop yield under stressful condition, BC is the crop yield of the control, and the subscripts of “-Si” and “+Si” are experimental treatment without and with Si application, respectively. For the studies without Si application to the control, the crop yield increment was calculated using Eq. (5).

$$CYI (\%) = \frac{YS_{+Si} - YS_{-Si}}{YS_{-Si}} \times 100 \quad (5)$$

2.3 Data analysis

All statistical analyses were performed using SPSS software (IBM, version 23.0). Graph was drawn using Origin Software (OriginLab Corp., Version 9.0).

3 Plant biomass carbon accumulation under abiotic and biotic stresses

3.1 Abiotic stresses

Plants suffer from physiological stresses when exposed to abnormal environments such as extreme temperatures, drought, high salinity, heavy metals, and nutrient imbalance (Genga et al. 2011; Savvides et al. 2016). Hyperosmotic stress, cell dehydration, reactive oxygen species (ROS) overproduction, and leaf chlorosis are the main responses to such stresses (Table 1). In addition, plants endure secondary stresses when several abiotic stresses interplay. For example, interconnections between drought stress and salt stress may lead to nutritional deficiency and hyperosmotic stress, while Ca, B, Zn, and K deficiencies often increase the incidences of plant disease and insect attack (Huber et al. 2012; Zhu and Gong 2014). By contrast, low N availability caused by drought and salt stresses may enhance plant resistance to pest attacks (Huber et al. 2012). Plants have developed highly complicated strategies to efficiently acclimatize themselves to the adverse conditions (Zhu 2016). Network relationships between biological damages and abiotic stresses indicate that systemic acquired resistance of plants can alleviate most abiotic and biotic stresses.

Although plants can mediate the intrinsic defense networks to mitigate the damages caused by adverse habitats, most of them have to pay a tradeoff between extra-consumption of resources for homeostasis and plant growth. Equal proportions of plant biomass and biomass carbon are lost from abiotic stresses compared with non-stressful conditions due to almost the same carbon concentration of the harvested dry matter under stressful and non-stressful conditions. Pot experiments show that the biomass of maize (*Zea mays*) and broomcorn (*Sorghum bicolor*) decreased by 49 and 79% under

drought stress, respectively (Hattori et al. 2005; Kaya et al. 2006). The biomass of pea (*Pisum sativum*) decreased by 38% under 100 μ M chromium (VI) stresses, as compared to biomass reduction of 5 and 64% in wheat (*Triticum aestivum*) seedling exposed to 5 and 25 μ M cadmium stress, respectively, and that of 33% under UV-B stress (Tripathi et al. 2015, 2017; Wu et al. 2016a). Additionally, abiotic stresses caused by extreme weather and climate may result in plant growth arrest and even death, resulting in inefficient carbon assimilation and ANPP in terrestrial ecosystems (Kogan et al. 2004; Craine et al. 2012). In summary, plant exposure to abiotic stresses usually reduces plant biomass and crop yield, resulting in plant biomass carbon loss.

3.2 Biotic stresses

Herbivory, pathogen, and pest attacks are the main biotic stresses that plants need to cope with during their lifecycles (Table 1). The major determinants of plant disease and pest incidences include plant species (Massey et al. 2007), habitat (Massey et al. 2007), nutrient status, and the degree of overlap between the susceptible growth stages of the host plants and the reactive pathogens and pests (Walters and Bingham 2007; Huber et al. 2012). The renovation of injured tissues of slow-growing plant species is more costly in resource-limited environments than that of fast-growing plant species in resource-rich environments (Massey et al. 2007). Furthermore, the complexity of these responses is significantly affected by the extent and duration of biotic stresses (both acute and chronic) (Cramer et al. 2011), which leads to different impacts on plant growth and biomass carbon accumulation. In summary, the investment in defensive strategies among plant species to resist or tolerate these biotic stresses is usually associated with plant growth rates and their habitats.

Plant physiological responses often have double-edged effects when they are used to counteract various biotic stresses. For example, the bilateral functions of ROS induced by various environmental stresses not only cause damage to plants but also act as signaling transducer and cause programmed cell death in response to fungal attack (Schieber and Chandel 2014; Demidchik 2015; Lehmann et al. 2015). Furthermore, Si coupling with Mn accumulation in the infected region may lead to increased biosynthesis of phenolics and phytoalexins, which are catalyzed by Mn-containing enzymes (Huber et al. 2012). In addition, many facultative and obligate parasites may increase the risk of disease outbreak, especially when the concentrations of sugars and amino acids in the apoplasts of the leaves increase due to nutrient imbalances such as insufficient Ca, B, Zn, and K and excess N (Walters and Bingham 2007; Huber et al. 2012). These results indicate that plant nutrient status plays an important role in counteracting the negative effects of biotic stresses on plant growth and biomass accumulation.

Table 1 Effects of various abiotic and biotic stresses on plant growth

Environmental factor	Secondary stress	Damage	References
Abiotic stress			
Drought	Nutrient deficiency, oxidative and osmotic stresses	Nutrient uptake limit, ROS damage, cell dehydration, and photosynthetic decline	Farooq et al. (2009); Zhu and Gong (2014)
Salinity	Nutrient deficiency, oxidative, drought and osmotic stresses	Disturbance of nutrient uptake, ROS damage, ion toxicity, water deficit, hyperosmotic potential, cell dehydration, and photosynthetic decline	Zhu and Gong (2014); Zhu (2016)
Toxic metals	Nutrient deficiency, oxidative and osmotic stresses	Disturbance of nutrient uptake, ROS damage, cell membrane dysfunction, leaf chlorosis, and abnormal root morphology	Nagajyoti et al. (2010); Imtiaz et al. (2016)
Nutrient imbalance			
A. Nutrient deficiency	Pathogen infection and oxidative stress	A: increased membrane permeability, impair polymer synthesis, ROS damage, and leaf chlorosis	Pham et al. (2004); Ma and Yamaji (2006); Huber et al. (2012)
B. Nutrient excess	Oxidative and osmotic stresses, heat and drought stresses	B: over-luxuriant growth and poor haulm stability	Jansen and van den Noort (2000); Cramer et al. (2011); Shen et al. (2010a)
Radiation			
A. UV-radiation	Oxidative and osmotic stresses, and/or drought stress	A: ROS damage, stomatal closure, leaf bronzing and curling, impair photosynthesis	Levitt (1980); Hasanuzzaman et al. (2013); Savvides et al. (2016); Zhu (2016)
B. Excessive light		B: midday depression and wilting	
Extreme temperature			
A. Heat		A: ROS damage, water deficit, photosynthetic decline, protein denaturation and aggregation	
B. Chilling		B: cell dehydration, extracellular ice crystals, membrane damages and hyperosmotic potential	
Crop lodging	Blocked photosynthesis	Harvest difficulty and productivity reduction	Pham et al. (2004); Wu et al. (2012)
Biotic stress			
Fungal disease	Oxidative and wilting stresses	Localized necrosis, eyespot lesions, leaf spot, plugging of the vessels, dieback, and root rot	Gostinčar et al. (2011); Goyal and Manoharachary (2014); Lehmann et al. (2015); Ray et al. (2017)
Bacterial disease	Oxidative and drought stresses	Leaf and stem blight, bacterial canker, vascular wilt, soft rot, bacterial scabs and galls	Diogo and Wydra (2007); Kim et al. (2016); Dow et al. (2017)
Viral disease	Oxidative stress	Leaf chlorosis, wrinkling or curling of leaf margin	Narayananamy (2011); Garcia and Pallás (2015); Pearson (2017)
Pest damage	Oxidative and drought stresses	Insect grazing, wilting induced by root-knot and cyst, root, stems or foliar lesions and plant death	Gilioli et al. (2014); Douma et al. (2016); Johnson et al. (2016)
Herbivore injury	Wound-induced stress	Herbivore grazing and leaf lesion	Massey et al. (2007); Gong and Zhang (2014); Katz (2015)

The effects of biotic stresses have two different patterns, i.e., pathogen infection and grazing, on suppression of plant growth and biomass accumulation (Table 1). Plants suffering from pathogen infection often undergo lower photosynthetic capacity and carbon assimilation due to leaf necrosis and vascular wilt. A pot experiment shows that rice (*Oryza sativa*) infected with leaf blight decreased by 55% of biomass on average (Song et al. 2016). In contrast, insect and herbivore grazing has an immediate biomass loss and the ANPP is regulated by the grazing intensity (Schönbach et al. 2010; Irisarri et al. 2016). In addition, extra-consumption of resources for systemic acquired resistance and homeostasis has negative effects on plant photosynthesis and carbon assimilation as well. In conclusion, plant biomass reduction caused by pathogen infection and herbivore damage usually generates potential loss of biomass carbon in terrestrial ecosystems.

4 Silicon distribution in plants and its alleviation of stresses

4.1 Silicon distribution and accumulation in plants

Silicon is the second most abundant element and constitutes 28.8% of the Earth's crust (Epstein 1999). The Si content in soils ranges widely from less than 1% in histosols to 45% in the very old podzols (Skjemstad et al. 1992; Sommer et al. 2006). In the soil matrix, primary silicate mineral, secondary clay mineral, and amorphous silica account for most of the total Si pool, but they are relatively insoluble and biogeochemically inert (Savant et al. 1997; Sommer et al. 2006). Plant-available Si is primarily released from the recycling of biogenic Si pools and partly derived from the geochemical cycling of mineral Si pools (Bartoli 1985; Alexandre et al. 1997; Tubaña and Heckman 2015; Cornelis and Delvaux 2016). In the plant–soil system, successive Si influx and efflux transporters in plants regulate Si uptake and transport from the solution in vitro to the terminals of the transpiration stream (Ma and Yamaji 2006). Monosilicic acid movement from soil solution to the exodermis and endodermis root cells passes through an influx channel-type transporter (*Lsi1*) via the passive transport (Ma and Yamaji 2015). Then, an active Si efflux transporter (*Lsi2*) facilitates Si loading from the endodermis root cells to the xylem (Yamaji et al. 2015). In rice xylem sap, the concentration of monosilicic acid can reach up to 20 mM, while silicic acid in vitro polymerizes into silica gel when its concentration exceeds 2 mM (Mitani et al. 2005). Monosilicic acid unloads from the xylem into leaf cells via another Si influx transporter (*Lsi6*) as similar to *Lsi1*, but its localization is in the xylem transfer cell layer (Ma and Yamaji 2015). In addition, another Si efflux transporter (*Lsi3*) localized at rice node in cooperation with *Lsi2* and *Lsi6* reloads Si to the xylem of diffuse vascular bundle and

facilitates Si unloading to the panicle (Yamaji et al. 2015). Finally, more than 90% of Si in plants is distributed in the shoots and most of it is deposited in the leaf sheaths and leaf blades (Broadley et al. 2012). In summary, the ability of plants to absorb Si is regulated by the cooperative system of Si influx and efflux transporters in plant.

Increasing evidence suggested that the ability of Si accumulation in different plant species demonstrates a direct correlation between Si transporter genes (*NIP2s*) and *Lsi2s* (Deshmukh et al. 2015; Deshmukh and Bélanger 2016; Vivancos et al. 2016). However, homologous genes of Si transporters in different plant species do not show the same Si uptake and transport patterns due to diverse root and shoot architectures (Deshmukh and Bélanger 2016). In principle, all monocots (e.g., sugarcane, rice, and most cereals) and a few dicots (e.g., sunflower, soybean, and cucumber) are defined as high Si-accumulating plants (> 1% dry weight) and acquire positive effects from Si application (Ma et al. 2001; Liang et al. 2005a; Deshmukh and Bélanger 2016). By contrast, most dicots (e.g., tomato) taking up small amounts of Si (< 0.1% dry weight) are defined as low Si-accumulating plants. The dicots accumulating Si ranging from 0.1 to 1% of Si belong to the intermediate Si accumulator category (Guntzer et al. 2012; Deshmukh and Bélanger 2016). In addition, systematical benefits of Si conferred to plants depend on the ability of Si adsorption among different plant species (Ma and Yamaji 2006; Deshmukh and Bélanger 2016). Hence, Si-accumulating plants are more sensitive to Si feeding than intermediate and low Si-accumulating plants.

4.2 Silicon alleviation of abiotic stresses

Silicon in the soil solution is transported to the rhizosphere as monosilicic acid (H_4SiO_4) by belowground transpiration streams. Soluble Fe/Al–O–Si complexes may also be transferred to the root zones and activated by root exudates (Pokrovski et al. 2003; Hobara et al. 2016; Wu et al. 2016b). The accumulation of monosilicic acid in the rhizosphere and the formation of iron plaques on the root absorbency area play important roles in preventing the entrance of heavy metals into plant roots (Liang et al. 2005b; Wu et al. 2016b). Coprecipitation of toxic cationic metals with plant-available Si and adsorption of toxic anionic metals on the iron plaques are the major mechanisms for Si to mediate the alleviation of heavy metal toxicity in soils (Liang et al. 2005b; Gu et al. 2011; Adrees et al. 2015; Wu et al. 2016b). In addition, Si deposition in the roots is the primary inhibitory effect on apolasmic transport of Na^+ across the roots (Gong et al. 2006), while monosilicic acid competition with arsenite can reduce plant arsenic uptake under anaerobic conditions (Ma et al. 2008; Tripathi et al. 2013; Marmioli et al. 2014; Tripathi et al. 2016a). Furthermore, Si-mediated alleviation of heavy metal toxicity also occurs in root cells and xylem vessels

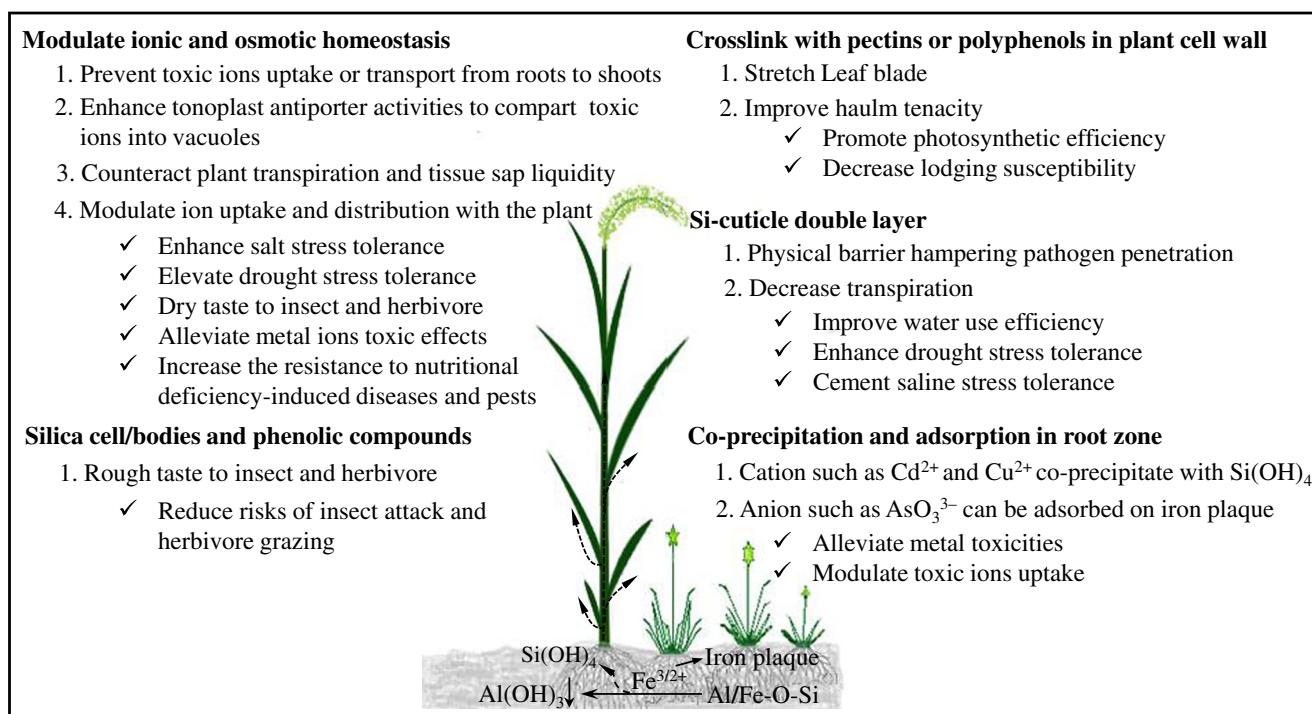


Fig. 2. Principal mechanisms of silicon-mediated alleviation of abiotic and biotic stresses on plant growth and development

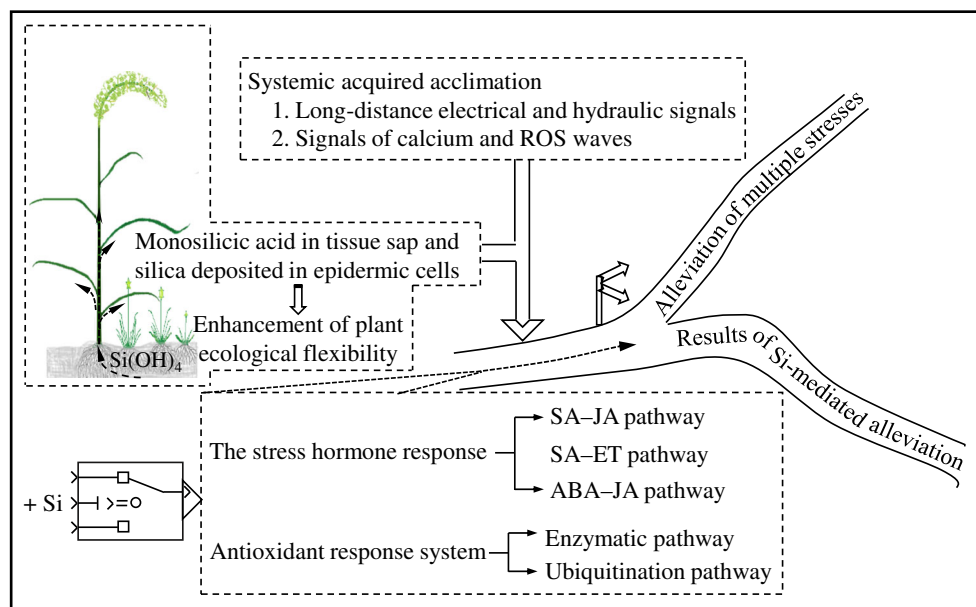
(Liang et al. 2007; Lukačová et al. 2013; Ma et al. 2014). The activated Si in the rhizosphere, root systems, and xylem vessels inactivates the detrimental substances in vitro and in vivo (Fig. 2) and prevents them from entering plant shoots. For nutrient uptake, Si application elevates the harvest index and nitrogen use efficiency (Detmann et al. 2012; Song et al. 2017). More plant-available Si can suppress excessive phosphorus uptake in rice (Ma and Takahashi 1990) but promote phosphorus uptake under phosphorus deficiency stress (Ma et al. 2001; Pontigo et al. 2015; Kostic et al. 2017). Increasing Si application can mediate potassium accumulation in shoots when plants are subject to salt stress and potassium deficiency (Wang and Han 2007; Chen et al. 2015). In addition, Si can alleviate iron deficiency in cucumber (*Cucumis sativus*) and soybean (*Glycine max*), although this effect is plant-specific and dose-dependent (Gonzalo et al. 2013; Pavlovic et al. 2013). However, the effects of Si on manganese and zinc are not clear (Hernandez-Apaolaza 2014). In general, Si imposes positive effects on regulation of plant nutrition uptake.

Considerable amounts of Si that are deposited in the cell walls of plant roots and xylem vessels can withstand crop lodging through strengthening the mechanical property of plant roots and the haulms (Balasta et al. 1989; Hattori et al. 2003; Ma and Yamaji 2006). More than 90% Si absorbed by plant roots is transferred into shoots via the xylem (Ma and Takahashi 2002). High concentrations of monosilicic acid in the xylem and leaves can improve the osmotic potential of epidermis cells and increase the leaf water potential against plant evapotranspiration (Mitani et al. 2005; Pei et al. 2010;

Chen et al. 2011; Ming et al. 2012). Silicon deposition beneath the cuticle of the epidermal cells and the inflorescence bracts reduces the leaf and panicle transpiration, stretches the leaf blade, and promotes photosynthetic efficiency (Hattori et al. 2008; Ma and Yamaji 2006, 2008; Tripathi et al. 2016b). Overall, these beneficial effects of Si on plant water retention have been shown to improve plant tolerance to drought, salt, extreme temperature, and excessive light stresses (Kaya et al. 2006; Liang et al. 2008; Ming et al. 2012; Tuna et al. 2008; Soundararajan et al. 2014; Shen et al. 2010a; Guntzer et al. 2012; Zhu and Gong 2014) (Fig. 2). In addition, Si application can improve plant water use efficiency and increase photosynthesis pigment as well as net assimilation rate under multiple abiotic stresses (Shen et al. 2010b; Chen et al. 2011; Shi et al. 2013). In summary, Si-mediated changes to osmotic potential and the physical barrier can help regulate plant transpiration and improve water use efficiency.

The alleviation of oxidative stress caused by silicon accumulation in plants (Shen et al. 2010a; Zhu et al. 2016) may decrease the activity of ROS-scavenging enzymes that are involved in lignin, phenolics, and phytoalexin biosynthesis (Ortega et al. 2006; Huber et al. 2012; Schaller et al. 2012). For example, lignin content in canola decreases when Si is applied as a fertilizer and increases as Si is deficient (Hashemi et al. 2010; Suzuki et al. 2012; Zhang et al. 2013s). Application of Si can decrease the concentrations of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) without complete relation to goal-oriented ROS-scavenging enzyme activities (Shen et al. 2010a; Zhang et al. 2013;

Fig. 3. Possible pathways of Si-mediated alleviation of phytohormone defense systems and antioxidant defense systems. SA, salicylic acid; JA, jasmonic acid; ET, ethylene; ABA, abscisic acid. The figure depicts that the stress hormone response and antioxidant system may be regulated by post-feedback of Si-mediated alleviation rather than forward feedback of Si-associated signaling pathway



Coskun et al. 2016), indicating indirect effects of Si on biosynthesis of antioxidant enzyme (Fig. 3). Hence, we speculate that Si accumulation in plants promotes tolerance of plants to the adverse effect of various abiotic stresses, which decreases the effects of oxidative stress as well as ROS production and reduces ROS-dependent signal transduction as well as biosynthesis of antioxidant enzyme (Schieber and Chandel 2014; Zhu et al. 2016). Furthermore, based on systemic-acquired acclimation, we also suggest that the effects of Si-mediated alleviation of the archetypal defense hormones can be derived from the improvement of physiological conditions rather than from the regulation of Si on the pathways of plant hormones (Kim et al. 2014; Rizwan et al. 2015) (Fig. 3). Until now, no direct evidence has shown the existence of Si-involved signaling pathway in plants. Therefore, antioxidant enzyme activities and phytohormone levels independent of Si concentration are probably the result of Si-mediated alleviation instead of Si itself. In conclusion, the down-regulated responses of antioxidant defenses and hormone immunity are probably attributed to Si-mediated improvements in plant homeostasis.

4.3 Silicon regulation of biotic stresses

The deposition of Si in the cell walls of roots improves the biomechanical properties of plants (Hansen et al. 1976) and thus increases root resistance to soil-borne diseases and pests (Johnson et al. 2010). The appearance of root-specific phytoliths in the roots and tubers shows that Si also participates in protecting belowground tissues from soil-borne pests (Lux et al. 2003; Chandler-Ezell et al. 2006). Plant transpiration leads to the accumulation of over 90% Si in the shoots where the Si is used as the structural materials for the cuticle-silica double layer and silicified cells (Hodson and Sangster

1989; Ma and Takahashi 2002; Huber et al. 2012). The cuticle-silica double layer often serves as a physical barrier that impedes the penetration of fungus and pest (Ma and Yamaji 2006). Silica cell/bodies in grasses can result in rough taste to insect pests and herbivores (Hartley and DeGabriel 2016) (Fig. 2). Furthermore, it is the symplastic Si, rather than the apoplastic Si, that seems to inhibit the spread of *Pythium aphanidermatum* in tomato plant roots (Heine et al. 2007). The osmotic effect of soluble Si (Liang et al. 2005c; Liang et al. 2015) and the Si-associated biosynthesis of phytoalexins (Ghanmi et al. 2004) enhance the resistance of host plants to pathogen infection. This may be related to the symplastic Si (Fig. 3), which may act as a modulator that influences the timing and extension of the systemic acquired resistance (Liang et al. 2015) through the long-distance electrical and hydraulic signals. However, the interaction between the symplastic Si and systemic acquired resistance is not clear. The effects of Si-mediated plant osmotic and water potential on electrical and hydraulic signals under biotic stresses need to be further investigated.

Silicon accumulated around the attempted infection sites is three to four times higher than that around the successful penetration sites (Heath and Stumpf 1986; Carver et al. 1987). Manganese accumulation that accompanies Si at the infection sites may be related to Si-mediated biosynthesis of phenolics and phytoalexins to resist pathogen infection (Menzies et al. 1991; Huber et al. 2012). Furthermore, plant diseases and pests induced by nutrient deficiencies and ion imbalances would be alleviated by Si-mediated nutrient uptake and distribution (Pavlovic et al. 2013; Gonzalo et al. 2013; Hernandez-Apaolaza 2014; Chen et al. 2015). Therefore, Si accumulation in plant tissues may increase the resistance to nutrient deficiency-induced diseases and pests by alleviating

m micronutrient deficiencies in plants. Besides, the cuticle–silica double layer and silica cell/bodies do not account for all the preventive effects because soluble Si in plant tissues is also involved in prophylactic alleviation of the detrimental impact of many biotic stresses (Liang et al. 2015). These studies show that Si deposition in leaves and silica cell/bodies postpones protection from pathogen and insect pest attack, while soluble Si in plant tissues plays a real-time role in plant resistance.

Classic hormone defense pathways have little correlation with Si-mediated plant resistance to various biotic stresses (Van Bockhaven et al. 2015; Vivancos et al. 2015). The down-regulated archetypal defense hormones such as abscisic acid, jasmonic acid, and salicylic acid are not derived from the Si-mediated mechanism related to plant disease resistance (Van Bockhaven et al. 2015; Vivancos et al. 2015). At present, only the ethylene pathway of rice against the brown spot fungus has been testified (Van Bockhaven et al. 2015). Silicon-induced changes in plant enzymatic or non-enzymatic defense systems that counteract ROS overproduction (Debona et al. 2014; Nascimento et al. 2016) may also result from Si-mediated alleviation of various biotic stresses (Fig. 3). In summary, increasing Si in plant tissues could reduce the metabolic costs of systemic acquired acclimation for adapting to multiple biotic stresses.

5 Silicon enhancement of plant biomass carbon accumulation under stresses

5.1 Silicon enhancement of carbon accumulation under abiotic stresses

Silicon supply has beneficial effects on plant biomass carbon accumulation under multiple abiotic stresses (Hattori et al. 2005; Liang et al. 2005b; Fu et al. 2012; Mateos-Naranjo et al. 2015). Compared with plant biomass carbon loss caused by multiple abiotic stresses, Si-mediated plant biomass carbon recovery rarely reaches the biomass carbon accumulation under non-stress condition. Compared to the control, wheat plants lose their biomass carbon by 32 and 44% under salinity stress and 25 and 16% in salt-tolerant and salt-sensitive Si-fed plants, respectively (Tuna et al. 2008). The stress-sensitive plants would receive more biomass carbon accumulation than the stress-tolerant ones as well as when Si is added under drought stress and heavy metal toxicity (Kaya et al. 2006; Farooq et al. 2013; Wu et al. 2016a). In addition, increasing Si application (monosilicic acid in soil solution at pH below 9.0 is less than 2 mM) can improve the performance of plant biomass carbon accumulation (Kaya et al. 2006; Tuna et al. 2008; Pei et al. 2010). However, the performance of Si application to alleviate cadmium toxicity in wheat increases with stress severity in moderate stress conditions but decreases in both mild stress and severe stress conditions (Farooq et al.

2013; Wu et al. 2016a). The results suggest that Si-mediated biomass carbon accumulation probably displays progressive increase from mild to moderate stress but turns into decline under severe stress conditions. In summary, the recovery performances of plant biomass carbon induced by Si-modulated mitigation have different responses to plant cultivars, Si application dosage, and abiotic stress intensity. Therefore, we propose that the efficiency of Si-mediated alleviation responses to the severity gradients of abiotic stresses will probably display a bell-shaped curve (Fig. 4(a)). Accordingly, the input–output ratio between Si fertilization and the restoration performance of plant biomass carbon should be fully scrutinized.

In addition, most studies have reported that Si application to alleviate many abiotic stresses can enhance the expression of key genes related to photosynthesis, increase photosynthetic pigments, and promote plant photosynthesis as well as net assimilation rate (Shen et al. 2010b; Chen et al. 2011; Shi et al. 2013; Song et al. 2014; Li et al. 2015a; Kang et al. 2016). As a result, Si-mediated recovery from multiple abiotic stresses can stimulate CO₂ assimilation in plants and biomass carbon accumulation in terrestrial ecosystems. Furthermore, Si application to grassland can enhance ANPP and maintain biodiversity of grassland under high nitrogen fertilizer (Xu et al. 2015). Specifically, the mass proportion of the increased Si ranges from 0.02 to 3.96% of the recovered plant biomass (Detmann et al. 2012; Kurabachew and Wydra 2014), while 1% of Si increase in rice and wheat reduces plant biomass carbon by 0.87 and 0.57%, respectively (Klotzbücher et al. 2018; Neu et al. 2017). It suggests that an increase in the Si content of plant by 1% may reduce the plant biomass carbon by less than 1%. Therefore, although carbon concentration of plant biomass decreases with silicon accumulation, more than 96% of the recovered plant biomass contributes to plant biomass carbon accumulation. In conclusion, Si cycling improves carbon accumulation through abiotic stress mitigation in terrestrial ecosystems.

5.2 Silicon enhancement of carbon accumulation under biotic stresses

Plant growth and biomass accumulation often respond differently to herbivores, insect pests, and diseases due to multifarious attack patterns (Table 1). Therefore, the response mechanisms of Si-modulated alleviation may depend on the biotic stresses the plant is subject to (Etesami and Jeong 2018). Silicon-modulated prevention of biotic stresses is the major effect of Si-associated ecological functions (Soininen et al. 2013; Hartley and DeGabriel 2016). The effect of Si-mediated alleviation on various biotic stresses, especially on the diseases induced by fungi and bacteria, often depends on their active periods and the susceptible stages of the host plants (Huber et al. 2012).

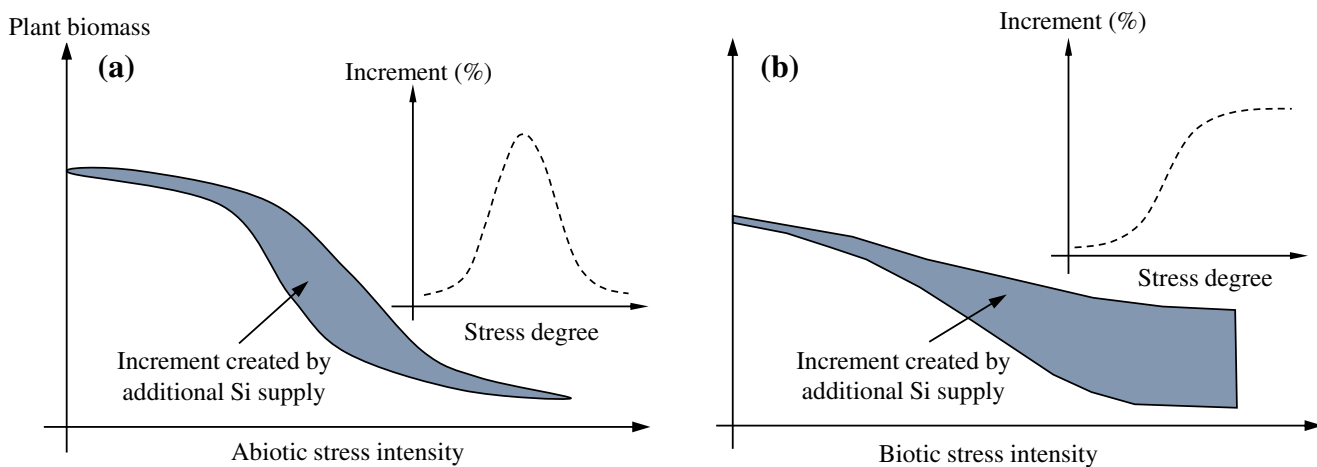


Fig. 4. Potential of plant biomass enhanced by additional silicon supply under different abiotic (a) and biotic (b) stress degrees. The hypotheses we proposed illustrate that the performances of plant biomass recovery

from Si-mediated alleviation are stress degree-dependent for abiotic stress and stress degree-independent for biotic stress

Compared to the control, Song et al. (2016) reported that rice biomass decreased by 59 and 72% under bacterial blight infection (*Xanthomonas oryzae* pv. *oryzae*) without Si addition in hydroponic and pot experiments, respectively, but decreased by 55 and 47% due to Si application. In addition, Si-mediated plant biomass carbon recovery from biotic stresses demonstrated a positive correlation with the application amount of Si (Ferreira et al. 2015). Similar to abiotic stresses, more than 96% of the Si-mediated plant biomass recovery under biotic stresses contributes to plant biomass carbon. However, the

mutability of biomass carbon loss which is caused by different biotic stresses often gives rise to difficulties in evaluating Si-mediated alleviation efficiency.

Plant species with different survival strategies and habitats also have a decisive influence on the efficiency of Si-mediated alleviation of plant biomass losses (Massey et al. 2007; Kurabachew and Wydra 2014). For example, chewing insects and herbivores have few adverse effects on inherently fast-growing plant species that live in resource-rich environments, whereas they have considerable negative impacts on slow-growing plant species that

Fig. 5. Frequency distributions of Si-mediated plant biomass carbon restoration from abiotic and biotic stresses. Data were collected from peer-reviewed publications. Plant biomass carbon increment was calculated from Si-mediated plant biomass increment coupling with the coefficient of 0.96, which was estimated from the tradeoff of Si-mediated plant Si accumulation and biomass carbon loss in plant biomass

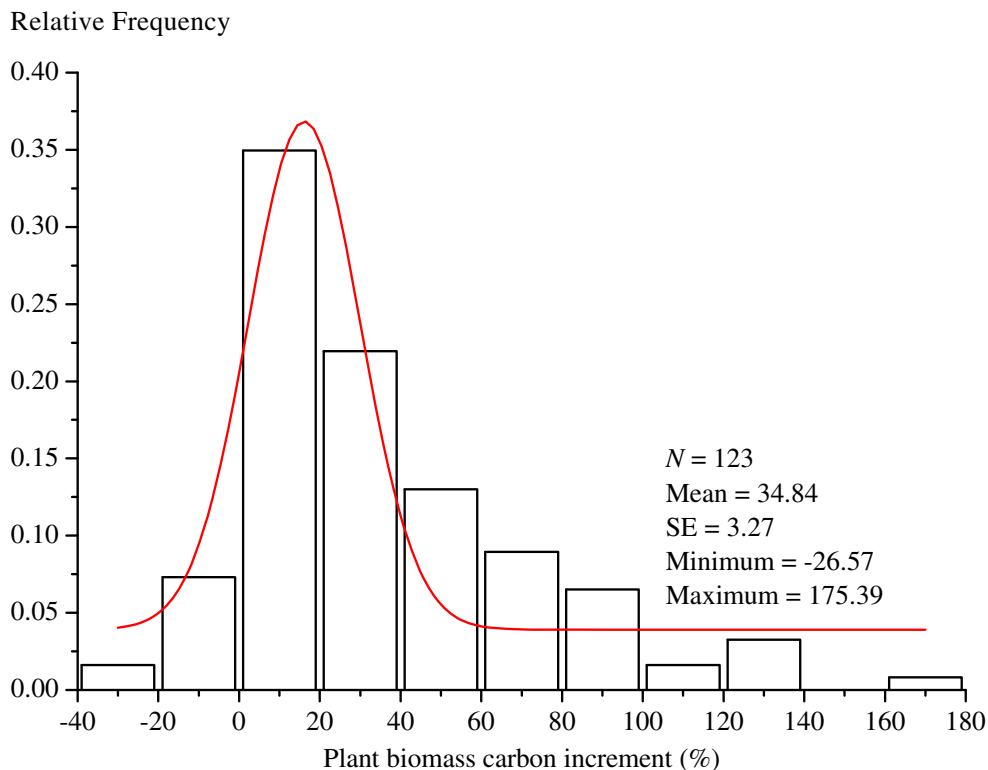


Table 2 Silicon enhancement of the estimated plant biomass carbon accumulation under abiotic and biotic stresses

Stress type	Plant species	Estimated biomass carbon increment (%)	References	
Drought	<i>Sorghum bicolor</i>	98–123	Hattori et al. (2005)	
	<i>Zea mays</i>	26–43	Kaya et al. (2006)	
	<i>Triticum aestivum</i>	–1 to 12	Ahmad et al. (2007)	
	<i>Chloris gayana</i>	88	Eneji et al. (2008)	
	<i>Sorghum sudanense</i>	18		
	<i>Festuca arundinacea</i>	28		
	<i>Phleum pratense</i>	44		
	<i>Triticum aestivum</i>	48	Pei et al. (2010)	
	<i>Lupinus albus</i>	37–63	Abdalla (2011)	
	<i>Sorghum bicolor</i>	26	Ahmed et al. (2011)	
	<i>Oryza sativa</i>	57–60	Chen et al. (2011)	
	<i>Oryza sativa</i>	17	Ming et al. (2012)	
	Salt	<i>Solanum lycopersicum</i>	21	Al-Aghabary et al. (2005)
		<i>Triticum aestivum</i>	5–49	Tuna et al. (2008)
		<i>Triticum aestivum</i>	26–116	Ali et al. (2009)
<i>Cucurbita pepo</i>		–2 to 35	Savvas et al. (2009)	
<i>Saccharum officinarum</i>		5–83	Ashraf et al. (2010)	
<i>Oryza sativa</i>		16–39	Shi et al. (2013)	
<i>Abelmoschus Medicus</i>		4–15	Abbas et al. (2015)	
<i>Solanum lycopersicum</i>		75	Li et al. (2015b)	
<i>Cicer arietinum</i>		6–29	Garg and Bhandari (2016)	
UV-B radiation		<i>Saccharum officinarum</i>	6–12	Elawad et al. (1985)
	<i>Glycine max</i>	4–10	Shen et al. (2010b)	
	<i>Triticum aestivum</i>	53	Pavlovic et al. (2013)	
	<i>Triticum aestivum</i>	–13 to –1	Tripathi et al. (2017)	
P deficiency	<i>Oryza sativa</i>	4–16	Ma et al. (2001)	
Fe deficiency	<i>Glycine max</i>	–3 to 45	Gonzalo et al. (2013)	
Fe ²⁺ toxicity	<i>Oryza sativa</i>	8–17	Fu et al. (2012)	
Cu toxicity	<i>Spartina densiflora</i>	42	Mateos-Naranjo et al. (2015)	
Zn toxicity	<i>Glycine max</i>	26–40	Pascual et al. (2016)	
As toxicity	<i>Oryza sativa</i>	–21 to 33	Wu et al. (2016b)	
	<i>Oryza sativa</i>	–27 to 9	Zia et al. (2017)	
Cd toxicity	<i>Zea mays</i>	60–123	Liang et al. (2005b)	
	<i>Gossypium hirsutum</i>	25–44	Farooq et al. (2013)	
	<i>Avicennia marina</i>	4–11	Zhang et al. (2014)	
	<i>Triticum aestivum</i>	8–40	Wu et al. (2016a)	
	<i>Solanum nigrum</i>	5	Liu et al. (2013)	
Cr toxicity	<i>Hordeum vulgare</i>	39–59	Ali et al. (2013)	
	<i>Pisum sativum</i>	9	Tripathi et al. (2015)	
Mn toxicity	<i>Cucurbita moschata</i>	81–137	Ma et al. (2001)	
Bacterial blight	<i>Oryza sativa</i>	5–87	Song et al. (2016)	
Bacterial fruit blotch	<i>Cucumis melo</i>	29–175	Ferreira et al. (2015)	
Bacterial wilt	<i>Solanum lycopersicum</i>	42	Diogo and Wydra (2007)	
	<i>Solanum lycopersicum</i>	15–66	Kurabachew and Wydra (2014)	
Brown spot	<i>Oryza sativa</i>	70–100	Ning et al. (2014)	

live in resource-poor environments (Massey et al. 2007). Therefore, the Si-mediated alleviation of different plant species living in different habitats could lead to variations in recovery performances. Nevertheless, positive impacts have been demonstrated in crops and grasses, especially for high Si-accumulating crops (Datnoff et al. 1997; Ma and Takahashi 2002) and grasses grown in poor-resource habitats (Massey et al. 2007; Soininen et al. 2013; Hartley and DeGabriel 2016). Accordingly, we propose a hypothesis that the efficiency of Si-mediated alleviation against

the severity of a certain biotic stress follows an S-shaped curve (Fig. 4(b)). The beneficial effects of the Si-modulated restoration would increase with Si supply and the severity of the biotic stresses. The relatively earlier formation of the cuticle–silica double layer and silica cells/bodies will improve resistance to biotic stresses during the highest active period of pathogens and pests. As a result, the beneficial effects of Si on plant biomass recovery from multiple biotic stresses will enhance plant biomass carbon accumulation in terrestrial ecosystems.

Table 3 Silicon enhancement of crop yield under abiotic and biotic stresses

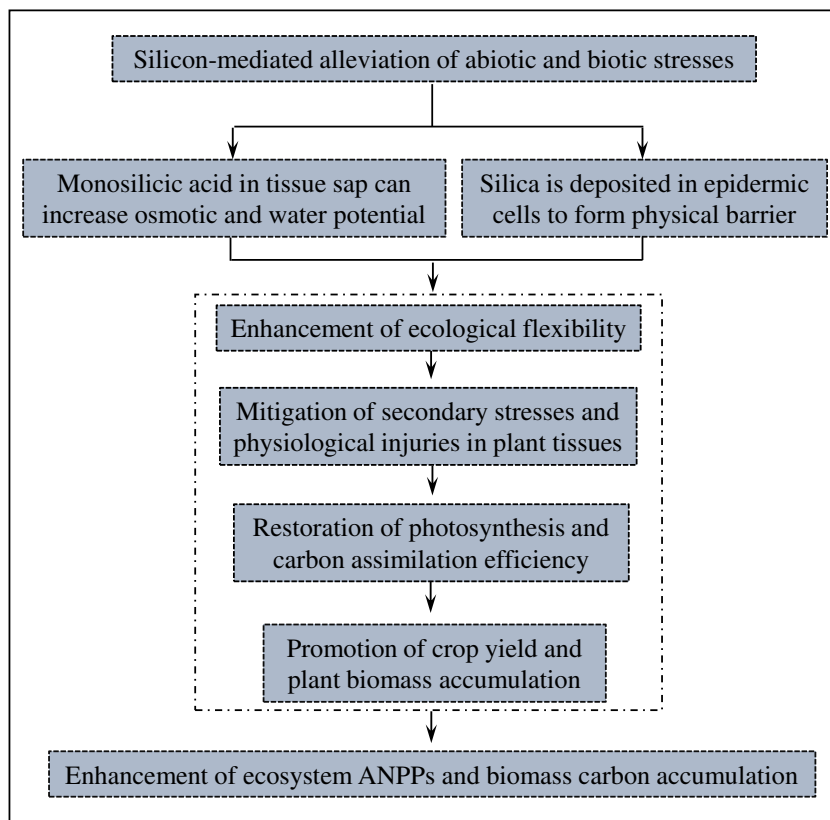
Stress type	Plant species	Range of yield increment (%)	References
Drought stress	<i>Triticum aestivum</i>	14–25	Ahmed et al. (2016)
	<i>Vitis vinifera</i>	11–17	Zhang et al. (2017)
Salt stress	<i>Cucurbita pepo</i>	1–26	Savvas et al. (2009)
	<i>Vicia faba</i>	– 6 to 48	Kardoni et al. (2013)
P deficiency	<i>Oryza sativa</i>	20–55	Ma et al. (2001)
As toxicity	<i>Oryza sativa</i>	– 17 to 60	Wu et al. (2016b)
Fungal infection	<i>Phaseolus vulgaris</i>	13	Polanco et al. (2014)
Neck blast	<i>Oryza sativa</i>	18–73	Seebold et al. (2000)
	<i>Oryza sativa</i>	33–51	Datnoff and Rodrigues (2005)
	<i>Saccharum officinarum</i>	4–23	Keeping and Meyer (2002)
Stalk borer damage	<i>Saccharum officinarum</i>	16–18	Meyer and Keeping (2005)

6 Implications for the management of terrestrial ecosystems

In terrestrial ecosystems, biogenic Si dissolution and mineral weathering are the major sources of bio-available Si pools (Tubaña and Heckman 2015; Cornelis and Delvaux 2016). The supplement rate of monosilicic acid to soil solution depends mainly on the size of bio-available Si pools, water retention time, temperature, and Si turnover rate (Sommer et al. 2006; Liang et al. 2015; Tubaña and Heckman 2015; Cornelis

and Delvaux 2016). Rapidly available Si in soils and water-soluble Si in rivers have been used to estimate the biogeochemical cycles of Si in many watersheds (Neal et al. 2005; Klotzbücher et al. 2015), while little attention has been given to the Si pool in terrestrial vegetation. However, the biogeochemical Si cycle in terrestrial ecosystems plays a considerable role in improving ANPP and ecosystem resilience (Massey et al. 2007; Tuna et al. 2008; Wu et al. 2016a). The multiple beneficial effects of Si on plant growth and biomass accumulation are more significant under various stresses (Ma

Fig. 6. Primary approaches of Si-mediated enhancement of ecosystem ANPPs and plant biomass carbon accumulation



and Takahashi 2002). In total, Si-mediated plant biomass restoration from multiple abiotic and biotic stresses contributes, on average, to 35% of biomass carbon (Fig. 5, Table 2) and 24% of crop yield increments (Table 3). By contrast, the effect of Si-mediated restoration of plant biomass is ambiguous under arsenic stress (Wu et al. 2016b; Zia et al. 2017). In addition, the Si-mediated defensive responses commonly demonstrate a systemic acquired acclimation (Zhu 2016) and result in survival cost minimization. Overall, regardless of the plant-available Si located in the rhizosphere, plant roots, xylem vessel, or leaves, the beneficial effects of Si on the alleviation of abiotic and biotic stresses play crucial roles in the performances of belowground and aboveground plant organs.

The restoration of plant biomass that is derived from Si-mediated alleviation of abiotic and biotic stresses would promote the ANPP of terrestrial vegetation and ecosystem carbon accumulation (Fig. 6). Different levels of Si application can change the contents of plant cellulose, lignin, and phenol that depend on plant tissue function (Schaller et al. 2012; Klotzbücher et al. 2018). In summary, the elevated ANPPs have positive effects on the long-term carbon sequestration in terrestrial ecosystem and soils. However, the concentration of Si in the shoots varies greatly among plant species (Ma and Takahashi 2002; Hodson et al. 2005), which suggests that Si requirement and the restoration effects will differ greatly among different plant species under the same abiotic or biotic stresses. Moreover, different defensive investment strategies among plant species against herbivore grazing (Massey et al. 2007) suggest that the efficiency of Si for different plant species to cope with various environmental stresses would also vary considerably. This means that the effects of Si on plant biomass carbon accumulation are very difficult to evaluate across many ecosystems but relatively easy for croplands and grasslands due to their fewer plant species and higher sensitivity to environmental changes. Therefore, the distribution of vegetation and the supply capacity of plant-available Si are the main determinants to evaluate the utility of Si to ecosystem resilience.

Terrestrial ecosystems in fragmented landscapes or resource-imbalanced regions constantly suffer from multiple abiotic and biotic stresses (Walters and Bingham 2007; Renton et al. 2013). The interconnection among the primary and secondary stresses greatly decreases plant biomass production and local biodiversity, which results in ecosystem degradation (Eneji et al. 2008; Cramer et al. 2011; Rasool et al. 2013). Because Si has versatile and beneficial effects on plant growth under multiple abiotic and biotic stresses (Liang et al. 2007; Ma and Yamaji 2008; Farooq and Dietz 2015; Meharg and Meharg 2015), more plant-available Si supply to these vulnerable landscapes could enhance the ecosystem health and resilience and thus promote the ecological

restoration. Overall, ecosystems that possess more bio-available Si would have a higher ANPP (Fig. 6), which could be crucial for terrestrial carbon turnover and result in more ecosystem carbon accumulation, especially under abiotic and/or biotic stresses.

7 Conclusions and perspectives

Based on the adverse impacts of multiple stresses on plant growth and the mechanisms of Si-mediated alleviation under abiotic and biotic stresses, this review highlighted the role of Si in enhancing plant biomass carbon accumulation. More plant-available Si in the ecosystem can enhance the ANPP and plant biomass carbon accumulation under various stress conditions. It is presumed that Si-mediated recovery of plant biomass usually exhibits a bell-shaped response curve to abiotic stresses and an S-shaped response curve to biotic stresses. Although more Si accumulation in plant reduces carbon concentration of plant biomass, more than 96% of the increased plant biomass contributes to plant biomass carbon accumulation. Si application to crops suffering from abiotic and biotic stresses can increase averaged plant biomass carbon and crop yield by 35 and 24%, respectively. However, the effectiveness of Si-mediated restoration significantly fluctuates with plant species and cultivars, intensity of abiotic and biotic stresses, and bio-available Si supply. Silicon-mediated alleviation usually exhibits immediate and preventive effects on plants suffering from abiotic and biotic stresses. In brief, additional Si supply and the subsequent increase in biogeochemical Si cycle could alleviate the adverse effects of abiotic and biotic stresses and thus accelerate biomass carbon accumulation in terrestrial ecosystems.

Based on this review, we suggest that researchers should investigate further the following areas:

1. Because experiments on Si application have yet mainly been conducted in hydroponics and pots, field- to ecosystem-scale studies are now urgently needed.
2. Several challenges, such as the coupling relations between Si and plant essential elements, the efficiencies of Si-mediated plant biomass carbon restoration among plant species and stress intensities, and the relationship between biogeochemical Si cycle and the resilience of terrestrial ecosystems, require further investigation especially in the fragmented landscapes.
3. Finally, it should be developed an evaluation model that predicts Si-mediated recovery contribution to plant biomass carbon accumulation in different terrestrial ecosystems.

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