Mitigation of climate change and environmental hazards in plants: potential role of beneficial metalloid silicon

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Abstract

In the last decades, the concentration of atmospheric CO_2 and the average temperature have been increasing and this trend is expected to become more severe in the near future. Additionally, environmental stresses including drought, salinity, UV-radiation, heavy metals, and toxic elements exposure represent a threat for ecosystems and agriculture. Climate and environmental changes negatively affect plant growth, biomass and yield production, and also enhance plant susceptibility to pests and diseases. Silicon (Si), as a beneficial element for plants, is involved in plant tolerance and/or resistance to various abiotic and biotic stresses. The beneficial role of Si has been proved in various plant species and its accumulation rely on roots uptake capacity. However, Si uptake in plants depends on many biogeochemical factors that may be substantially altered in the future affecting its functional role in plant protection. At present, it is not clear whether Si accumulation in plants will be positively or negatively affected by changing climate and environmental conditions. In this review, we focused on Si interaction with the most important factors of global change and environmental hazards in plants, discussing the potential role of its application as an alleviation strategy for climate and environmental hazards based on current knowledge.

Introduction

Climate change represents a serious problem at a global level, affecting the whole spectra of living organisms, including plants. Climate determines the rate of organism's growth and distribution, what seems to be altered due to the pressure of global warming in tandem with elevated CO_2 (eCO_2) concentration as was predicted by climate models (Newman 2011; Pugnaire *et al.* 2019). The concentration of CO_2 is currently 400 µmol CO_2 mol^{-1} air and is predicted to increase two-fold by the end of this century (Vaughan *et al.* 2018), whereas the estimation of average temperature shows an increase of 0.1 – 0.4 °C per decade (Jump and Peñuelas 2005). The other impacts of climate change include an unequal distribution of precipitation (that leads to long drought periods often followed by intensive rains) or exposure of plants to temperature stress combined with increased ultraviolet (UV) radiation (Ban *et al.* 2015; Bloeschl *et al.* 2019). The increased average temperature is also responsible for spreading of various plant pathogens. Biotic stresses induced by pests and diseases have been also a threat to agriculture, causing considerable losses in crop yield and imposing the application of large amounts of phytosanitary products (Bajwa *et al.* 2020). In a global scenario of food shortage and pressing need for environmental conservation, these aspects pose a major global concern to sustainable agricultural practices, further aggravated by the expansion of endemic pests and pathogens to areas outside their native regions due to climate change phenomena (Bebber *et al.* 2013; Timmusk *et al.* 2020). However, there is limited information available about the interaction between global changes and plant diseases. Climate change might be responsible for the positive, neutral or negative relation between hosts and pathogens because of the specificity of each pathosystem. This in turn might alter crop yield and quality (Ahanger *et al.* 2013).

Agriculture is an important sector of the world's economy and is highly dependent on climate, which ultimately constitutes an essential input to agricultural production. Assuring optimal crop yield in the context of climate change while safeguarding natural resources is deemed to be one of the biggest challenges in the current century (Le Gouis *et al.* 2020). In times where environmental pressures are compounded by nutrient-depleted soils and eminent biodiversity losses, sudden shocks to food production and supply chains pose severe threats to global sustainability (Sattar *et al.* 2017; Scherer *et al.* 2020). Amongst the different food commodity types (crops, livestock, fisheries and aquaculture) crops are by far the most affected by climate change, with losses of up to 50% (Cottrell *et al.* 2019). The latest prediction model for crop growth and water productivity suggested a yield reduction of 3.4% - 8.6% during the period of 2018 – 2027 in seed corn crops (Liu *et al.* 2020). Changes in climate will inevitably have a direct impact not only on agricultural productivity but also on farm incomes and prices (Hertel 2018).

Only in Europe, more than 650,000 sites are considered as polluted due to various inorganic and organic contaminants presented in the soil (Pérez and Rodríguez Eugenio 2018). High demand for natural sources, fast speed of industrialisation and intensification of agriculture lead to the release of heavy metals and other potentially toxic elements, like cadmium (Cd), lead (Pb), copper (Cu), zinc (Zn), chromium (Cr), aluminium (Al), arsenic (As) or antimony (Sb), as well as various organic pollutants, like polyaromated hydrocarbons (PAH), polychlorinated biphenyls (PCB), various pesticides and antibiotics into the natural or man-managed ecosystems (Huang *et al.* 2019; Kumar *et al.* 2019; Kopittke *et al.* 2019). Several agriculturally important regions of the world are seriously threatened, and therefore, marginal polluted land might play a key role in the future for food and feed production after proper remediation (Rutkowska *et al.* 2020).

Silicon (Si), the second most predominant element in the earth crust (Liu *et al.* 2019), has a beneficial effect on plants playing a functional role in the alleviation of several abiotic and biotic stresses, which have been studied for more than two decades (Líška *et al.* 2017; Lux, Lukačová, *et al.* 2020). So far there is little information about Si uptake and accumulation in plants in response to climate changes and especially to global warming. As the positive effect of Si on plants is restricted to its uptake and accumulation, the efficient transport of Si is an essential criterion. The essentiality of Si for plants has never been proved, because there is no evidence that Si is involved in cell metabolism or is component in organic compounds (Tubana *et al.* 2016). Despite this fact, Si has been used widely in agriculture due to improved productivity of several crop species and, also, Si serves as a valued element to humans (Tubana *et al.* 2016). Important to note, crop plants may extract ca. 210 – 224 million tons of silicon annually, depending on plant species (Tubana *et al.* 2016). Deposition of Si in the form of silica is predominant in above-ground plant parts, however, there are some crop species with high accumulation of silica in roots (Lux *et al.* 2020). The accumulation of Si in plants rely on root capacity to take up silicon and other mineral nutrients dissolved in water. The water content in soils will become probably less abundant in the future, so Si deposition in plants might be altered.

This study aims to perform a comprehensive literature analysis and discussion on the possible applications of Si on plants exposed to climate and environmental hazards including eCO_2, increased UV and temperature exposure that relates to drought, salinity effect, also metal and metalloid contamination involved in environmental hazard, as well as the effect of Si to biotic stresses. The review is mainly focused on crops with agronomic importance, however other model plants are also included.

General effects of climate change and environmental hazards on plant growth

Plant development generally increases linearly with temperature across a wide spectrum, with the exact range being crop dependent. Outside specific temperature ranges, crops tend to be severely impacted in terms of growth, quality and productivity. The reasons for these impacts are linked to alterations in standard biochemical and metabolic processes, phenological development stages (Piao *et al.* 2019), but also to alterations in basic processes of cell wall reorganization and remodelling (Ezquer *et al.* 2020), or root elongation (Ding *et al.* 2019). Elevated CO_2 commonly leads to an increase in internal leaf CO_2 levels and a reduction in stomatal conductance, stimulating photosynthesis in C3 plants. This may lead to higher biomass accumulation until acclimation takes place, but also may lead to nutritional losses in edible plant parts (Soares *et al.* 2019). The classical view is still that carbon (photosynthetic CO_2 uptake), ranks above any other drivers of plant growth (Körner 2015), however, carbon does not act alone. To realize increases in crop yields, soil nutrient levels, soil moisture, water availability, and other conditions must also be met. Moreover, oftentimes crops face a series of challenges at any given moment. For example, changes in the frequency and severity of droughts and floods are often associated with periods of extreme temperatures (Masson-Delmotte et al. 2018 2012). On another example, boron (B) toxicity and salinity stress are well recognized as severe stress conditions for plants. However, their coexistence in arid and semi-arid agricultural regions has shown ambiguous effects on plant growth and development (Pandey *et al.* 2019).

Worsen environmental conditions, as the results of human activities, negatively affect plant biology, especially when speaking about an agricultural point of view. One of the most important factors of environmental pollution is excessive soil contamination by metals and metalloids, typically present in wastewater used for crop irrigation serving as an environmental hazard to plants (Papaioannou *et al.* 2019). These elements are toxic when its concentration exceeds the threshold level, however, plants have evolved mechanisms to cope with metal and metalloid stress (DalCorso *et al.* 2019). The most prevalent symptom of metal and metalloid toxicity is decreased growth and biomass with subsequent alteration of yield production.

Taken together, climate and environmental variables defy several keystone aspects of plant growth and development tightly connected with crop performance, such as: 1. plant development (root and shoot); 2. photosynthesis and respiration; 3. water stress adaptations; 4. extreme temperature damage; 5. pest and disease susceptibilities.

Silicon transport in plants in response to altered climate and environmental conditions

For plants, silicic acid, $Si(OH)_4$, represents a bioavailable form of silicon that is absorbed by the root system and irreversibly polymerised into amorphous silica (SiO2–nH2O) at the final location in the plant (Richmond and Sussman 2003; Currie and Perry 2007). Plant species differ in their ability to accumulate Si in the shoots and this feature is mainly assigned to the uptake ability of the root system (Takahashi *et al.* 1990; Ma and Takahashi 2002; Hodson *et al.* 2005). The shoot concentration varies greatly between the plant species from 1% up to 10% of the dry mass (Epstein 1999). Based on the molecular and genetic studies with low silicon mutant plants, two silicon transporters in roots were discovered, i.e. channel protein Lsi1 responsible for uptake of Si from the soil environment and active transporter Lsi2 involved in translocation of Si from the root to the shoot (Ma *et al.* 2006, 2007). Subsequently, channel protein Lsi6 homologous to the Lsi1 plays a role in shoot Si distribution (Yamaji *et al.* 2008). However, besides the molecular mechanism of Si transport and accumulation, shoot Si accumulation is to a lesser content also related to transpiration process (Mitani and Ma 2005).

The concentration of silicic acid ranges from 0.1 to 0.6 mM in soil. So far there is little information about Si uptake and accumulation in plants in response to climate changes and especially to global warming. As the beneficial function of Si is restricted to uptake ability of plants, high temperature may decrease plant Si uptake and accumulation due to lower level of soil water as indicated by a recent study (Johnson *et al.* 2019). In this study, foliar Si concentration (% of dry mass) decreased in plants of pasture grass without Si addition in warmed conditions, however, it was not affected in plants supplied with Si grown upon warming. Interestingly, warming had no impact on root Si concentration in plants of pasture grass (Johnson *et al.* 2019). Other study showed that shoot Si concentration of several grass species was not generally affected by elevated temperature, except species with natural lower ability to accumulate Si (less than 1% of dry mass) (Johnson and Hartley 2018). In the case of eCO_2, Si accumulation of shoots was strongly decreased in grasses (Johnson and Hartley 2018). This study showed evidence that eCO_2 is a stronger driver of silicon accumulation in comparison to increased temperature in grasses. Thus, decreased accumulation of Si might be responsible for higher susceptibility to herbivores or abiotic stresses (Johnson and Hartley 2018). On the other hand, Si concentration was not decreased in various tree species upon eCO_2 (Fulweiler *et al.* 2014). However, the analysis of overall forest Si accumulation, based on net primary production and above-ground Si concentration of trees, showed increased Si accumulation under eCO_2 treatment. Elevated CO_2 might, thus, enhance terrestrial Si pumping in forests and contribute to Si transfer from terrestrial systems to downstream ecosystems (Fulweiler *et al.* 2014). Altered precipitations are also related to climate changes and may affect Si uptake and accumulation in above-ground parts of the plants. The negative correlation between Si and carbon (C) was found in arid conditions showing precipitation and soil nutrient status as a key driver for silicification in leaves (Quigley *et al.* 2020). This recent paper revealed that plants accumulate more Si when the level of soil water and nutrients is limiting. The cost of Si for structural support is lower in comparison to investment in C-based leaf construction. Except Si-based structural support, Si may be also involved in stress tolerance during water deficient conditions, however, general beneficial role of Si is lost, when the water level is restored (Quigley *et al.* 2020). Considering UV radiation, Si uptake and accumulation in shoots might be lowered. In the study with wheat plants, UV-B exposure in ambient or enhanced intensity caused decreased Si concentration in both below- and under-ground plant parts (Tripathi *et al.* 2017b). However, exposure of UV does not seem to affect Si concentration in leaves of millet, but together with decreased water availability Si concentration is slightly lowered (Grašič *et al.* 2019). Up to date, the number of experimental studies showing the dynamics of Si uptake or pattern of Si accumulation in plants during altered climate conditions is insufficient even if several stresses act simultaneously. At this point, it is not clear, whether Si uptake and accumulation might be positively or negatively regulated by future environmental changes and climate alterations.

Silicon in the fight against drought and salinity stress

Drought

Water stress is one of the major's environmental constraints limiting plant growth and agricultural productivity. Drought induces a range of physiological and biochemical processes in plants that can reduce crop yields up to 70 %, resulting in serious economic losses (Osakabe *et al.* 2014; Siracusa *et al.* 2018). Although plants have evolved different morpho-physiological and biochemical strategies to cope with drought stress (Lamaoui *et al.* 2018), increasing evidence suggests that the detrimental effects of drought can be mitigated by the adequate and balanced supply of mineral nutrients (Waraich *et al.* 2011). One of the methods involving the alleviation of negative water stress is the application of Si. The beneficial effect of Si on plant water status has been extensively studied in various plant species subjected to drought stress (Table 1). The improvements of relative water content and/or water potential by Si application occurred under both polyethylene glycol-induced osmotic stress (Hattori *et al.* 2007; Sonobe *et al.* 2011; Ming *et al.* 2012) and potted soil drought conditions (Gong *et al.* 2003; Amin *et al.* 2018). Different compounds of Si, including Na_2SiO_3, K_2SiO_3 or H_2SiO_3 (Table 1), have been applied either in the soil or the nutrient solution, being the first two the most studied compounds. Although in most of the studies, Si application took place after seedlings emergence, the priming of seeds with Si has been suggested as an alternative method to improve the drought stress tolerance in plants. Some studies have shown that Si-seed priming enhances plant resistance against future stress events and propose it as a promising and cost-effective procedure in circumstances, where water scarcity might be a problem (Hameed et al. 2013; Ahmed *et al.* 2014; Biju *et al.* 2017).

Table 1 - Summary of different crops in which silicon (Si) application has shown beneficial effects for drought stress mitigation

Plant species	**Family**	**Si Source**	**Si Concentrations**	**Main Results**	**Reference**
***Brassica napus* L.** Rapeseed/ Canola	Brassicaceae	Na_2SiO_3	0.35, 2.73 mmol/kg soil	↑ growth parameters, net assimilation rate, CO2 absorbance, relative water content, root amino acid content, antioxidant enzymes activity ↓ intracellular CO2 concentration, oxidative damage	(Habibi 2014)
		SiO_2	1 mM	↑ photosynthetic pigments, ROS scavenging capacity, leaf relative water content and proline content ↓ oxidative stress	(Hasanuzzaman *et al.* 2018)
***Cicer arietinum* L.** Chickpea	Fabaceae	$Na_2Si_3O_7$	100 ppm	↑ growth, relative water content, non-enzymatic antioxidant activity ↓ oxidative damage, proline content, enzymatic antioxidant activity	(Gunes *et al.* 2007)
***Cucumis sativus* L.** Cucumber	Cucurbitaceae	K_2SiO_3	120, 240 ppm	↑ biomass, net photosynthetic rate, leaf water content, chlorophyll content, antioxidant enzymes activity ↓ stomatal conductance, oxidative damage, plasma membrane permeability	(Ma *et al.* 2004)

Glycine max **L. Merrill** Soybean	Fabaceae	$Na_2SiO_3 \cdot 9H_2O$	1.70 mM	↑ growth, photosynthetic enzymes, chlorophyll and anthocyanin content, relative leaf water content ↓ oxidative damage, proline and antioxidant enzymes	(Shen *et al.* 2010)
Helianthus annuus **L.** Sunflower	Asteraceae	$Na_2Si_3O_7$	100 ppm	↓ stomatal resistance, oxidative damage, proline content, SOD and APX activity ↑ leaf relative water content, CAT activity	(Gunes *et al.* 2008)
Lens culinaris **Medik.** Lentil	Fabaceae	$Na_2Si_3O_3$	2 mM	↑ germination and seedling vigour, Si content, antioxidants, hydrolytic enzymes activity ↓ concentration of osmolytes and ROS	(Biju *et al.* 2017)
Mangifera indica **L.** Mango	Anacardiaceae	K_2SiO_3	1.5 mM	↑ growth, net assimilation rate, relative water content, photosynthetic pigments, N, P, K and protein content, IAA, GA, and CK (promoters) endogenous levels, yield and fruit quality ↓ ABA, accumulation of several osmolytes and antioxidant enzyme activity	(Helaly *et al.* 2017)
Medicago sativa L. Alfafa	Fabaceae	K_2SiO_3	4 kg/pot	↑ forage biomass, number of branches, water use efficiency ↓ transpiration rate and stomatal conductance No effect on leaf area and photosynthetic rate	(Liu and Guo 2013)
Oryza sativa L. Rice	Poaceae	K_2SiO_3	0.5, 1.0, 1.5, 2.0 mM	↑ dry weight, root traits, chlorophyll content, water potential, photosynthetic rate, transpiration rate, basal quantum yield, and maximum quantum efficiency of PSII photochemistry ↓ K, Na, Ca, Mg, Fe content	(Chen *et al.* 2011)
		Na_2SiO_3	2.5 mM	↑ growth parameters, total, free, and bound water contents, water and osmotic potential, turgor pressure, active accumulation of several osmolytes, net photosynthetic rate, transpiration, and water-use efficiency	(Ming *et al.* 2012)

***Poa pratensis* L.** Kentucky Bluegrass	Poaceae	$Na_2SiO_3 \cdot 9H_2O$	200, 400, 800 mg/L	↑ net photosynthesis, leaf water contents, relative growth rate, root/shoot ratio, instantaneous water use efficiency, leaf green color and turf quality. ↓ Stomatal conductance, C:N ratio	(Saud *et al.* 2014)
***Saccharum spp.* L.** Sugarcane	Poaceae	CaO-SiO_2	20, 40, 60, 80, 100 g/pot	↑ photosynthetic CO_2 assimilation, stomatal conductance, transpiration, chlorophyll fluorescence, plant growth, leaf relative water content, biomass-yield, photosynthetic pigments, antioxidant enzymes activity (CAT, POD, SOD), phytohormones content (ABA, IAA, GA_3)	(Verma *et al.* 2019)
***Solanum lycopersicum* L.** Tomato	Solanaceae	Na_2SiO_3	0.6, 1.2, 1.8 mM	↑ growth parameters, photosynthetic efficiency of PSII, electron transport rate, net photosynthetic rate, antioxidant enzymatic system ↓ oxidative damage, chlorophyll degradation	(Cao *et al.* 2015)
		K_2SiO_3	2.5 mM	↑ tomato growth, photosynthetic and transpiration rate, water status, root hydraulic conductance, enzymatic and non-enzymatic antioxidant system, ↓ oxidative damage and ROS levels No effect on the transcription of plasma membrane aquaporin genes or proline levels	(Shi *et al.* 2016)
		Na_2SiO_3	50 ppm	↑ K, Ca and Mg accumulation, plant growth, RWC, fruit yield ↓ Na+ uptake, electrolyte leakage, proline content	(Ullah *et al.* 2016)
		$Si(OH)_4$	1.5 mM	↑ growth parameters, chlorophyll content, uptake of sulfur and ammonium, production of amino acids (arginine, methionine, serine, proline, alanine, threonine, glutamic acid, GABA and glycine), production of free polyamines (putrescine and spermidine ↓ GSSG to GSH ratio	(Ali *et al.* 2018)

		Na_2SiO_3	1.2 mM	↑ growth parameters, hydraulic conductivity in radial direction, water uptake, solute accumulation (proline, soluble sugar and soluble protein) osmotic adjustment ability of root, water absorption and antioxidant activity, ↓ oxidative damage	(Cao *et al.* 2017)
***Solanum tuberosum* L.** Potato	Solanaceae	$CaMgSiO_4$	284.4 mg/dm^3	↑ Si concentration in potato leaves, mean tuber weight, tuber yield and proline content. ↓ total sugars and soluble proteins, stalk lodging	Crusciol et al. 2009
***Sorghum bicolor* (L.) Moench** Sorghum	Poaceae	Not specified	1.78 mM	↑ dry weight, root water uptake, root amino acid and sugar content ↓ osmotic potential No effect on root anatomical traits related to water transport	(Sonobe *et al.* 2010)
		Na_2SiO_3	1.67 mM	↑ plant biomass, Si concentration, photosynthetic rate, stomatal conductance, leaf and whole-plant transpiration, relative water content, whole-plant hydraulic conductance and expression of root aquaporin genes ↓ root hydraulic conductance, No effect on osmotic potential of root xylem sap, on leaf-specific conductivity of stem and on root surface area, vessel diameter and number.	(Liu *et al.* 2014)
		H_2SiO_3	0.83 mM	↑ growth parameters, chlorophyll concentration, photosynthetic rate, leaf RWC, transpiration rate, soluble sugar contents, levels of both free and conjugated polyamines (putrescine, spermidine and spermine) and of several key polyamines (synthesis genes ↓ proline and 1-aminocyclopropane- 1-carboxylic acid (ACC) content and osmotic potential	(Yin *et al.* 2016)
		Na_2SiO_3	7.14 mmol	↑ biomass, leaf weight ratio, RWC, water potential and leaf area ↓ specific leaf area	(Gong *et al.* 2003)

Triticum aestivum *L.* Wheat	Poaceae	Na_2SiO_3	1, 2 mM	↑ growth parameters, chlorophyll content, RWC, Si, K and Ca concentration ↓ proline accumulation and oxidative damage	(Kaya *et al.* 2006)
Zea mays **L.** Maize	Poaceae	Ca_2SiO_4	100 ppm	↑ growth parameters, photosynthetic rate, yield and yield attributes, ↓ transpiration rate	(Amin *et al.* 2018)
		Na_2SiO_3	4, 6 mM	↑ plant growth parameters, photosynthetic pigments, antioxidant enzymatic activity ↓ oxidative damage, proline levels, accumulation of glycine betaine and total soluble sugars	(Parveen *et al.* 2019)

↑ (increase) or ↓ (decrease) in relation to water stress treatments without Si application

Although the mechanisms behind the beneficial effects of Si are still largely unknown, Si-drought improved plants' resistance seems to be primarily related with its role in increasing non-enzymatic antioxidant capacities, by activating antioxidant enzymes and decreasing $O2^{\bullet-}$ production rate, H_2O_2 content and malondialdehyde concentrations (Gong *et al.* 2003; Gunes *et al.* 2007, 2008; Shi *et al.* 2014; Cao *et al.* 2017); maintaining photosynthetic machinery, through the promotion of photosynthetic rate and increased activity of photosynthetic enzymes (Shen *et al.* 2010) and delaying leaf senescence (Hosseini *et al.* 2017). Wang *et al.* (2019) observed that Si treatment might play roles in absorption, transformation and transfer of light energy by optimizing the thylakoid membrane protein components in rice seedlings under drought stress. The impact of Si on chlorophyll fluorescence and the ultrastructure of chloroplasts of drought-stressed tomato was also reported (Cao *et al.* 2015). Silicon played an important role in suppressing the decline of the activities of ROS scavenging enzymes in the chloroplast, therefore, protecting it from severe oxidative damage, such as the distortion of the grana lamellae and stroma lamellae. Zhang *et al.* (2018) also demonstrated the positive beneficial effects of exogenous Si on the chlorophyll fluorescence and expression of photosynthesis-related genes in tomato seedlings under water stress. Increased concentrations of chlorophyll and carotenoids were also observed, thus promoting photosynthesis. Silicon is also believed to be important in reducing evaporation or controlling stomata conductance when taken up and deposited in leaf cuticle, thereby reducing transpiration (Matoh *et al.*; Gao *et al.* 2006) and consequently improving drought tolerance. It has also been shown to enhance radial hydraulic conductivity and mediate stress tolerance in sorghum seedlings and tomato plants exposed to drought (Liu *et al.* 2014; Cao *et al.* 2017). In sorghum seedlings, the increased root hydraulic conductance after Si addition was attributed to Si-mediated transcriptional up-regulation of some aquaporin genes (Liu *et al.* 2014).

Several key conjugated polyamines synthesis genes were shown to be up-regulated by Si under sorghum drought-stressed plants (Yin et al. 2014). It is suggested that Si improves sorghum drought resistance by mediating the balance of conjugated polyamines and ethylene levels. In leaves, the increased conjugated polyamines and decreased 1-aminocyclopropane-1-carboxylic acid (ACC, the precursor of ethylene) help to retard leaf senescence. In roots, the balance between conjugated polyamines and ACC participates in the modulation of root plasticity, increasing the root/shoot ratio thus contributing to an increase in water uptake (Yin et al. 2014).

Additionally, Si is pointed as responsible for maintenance of nutrient balance (Kaya et al. 2006), stimulation of osmolyte accumulation (Ming et al. 2012; Cao et al. 2017), regulation of growth substance levels (Zhu and Gong 2014) and sequestration of toxic ions (Rizwan et al. 2015) when plants are under drought stress.

Since water availability is a limited resource in many regions of the world and taking into account the increased demand for water and food production, to fulfil the need of an increased world population, sustainable approaches to promote water use efficiency (WUE) in agriculture are highly required. Therefore, the application of Si may be an important strategy to improve crop yield in arid or semi-arid areas under water-stress conditions. However, the pathways by which Si regulates the plant water status still need further investigation, especially regarding the molecular and biochemical. The proper way of Si application (i.e. doses, silicon source and plant stage) and its performance under field conditions, as most of the studies were conducted in lab trails or in hydroponic conditions, is another topic that still needs extensive investigation.

Salinity

Like for drought stress, salinity is one of the major severe abiotic factors affecting crop growth and productivity. Salt’s negative effects on plant growth have initially been associated with the osmotic stress component caused by decreases in soil water potential and, consequently, restriction of water uptake by roots (Munns and Tester 2008). High salt deposition in the soil results in osmotic as well as specific ion effects, which further lead to secondary oxidative stress in plants, thus causing a decrease on plant growth, biomass, yield, photosynthesis, WUE, and nutrient uptake but also leads to physiological drought and ion toxicity in plants, thus reducing agricultural productivity and yields (Chinnusamy *et al.* 2005; Shahid *et al.* 2018; Rehman *et al.* 2019). In addition, it increases the uptake of toxic elements such as sodium (Na+) and chlorine (Cl-), which have negative effects on plant growth and productivity (Ahanger *et al.* 2013). Various mitigation and adaptation approaches have been proposed to overcome these negative impacts (W Wang *et al.* 2019) and as for drought, Si application was shown to be involved in the alleviation of salt stress, with several studies reporting the significant regulatory role of Si in numerous plant physiological processes under these stress (Table 2). The exogenous application of Si is believed to improve plant growth either directly, by blocking the transport of Na+ ions into the plant, or indirectly, by activating different physiological processes to ameliorate the effect of salinity stress (Khan *et al.* 2019). Briefly, the mechanisms by which silicon mediates alleviation of salt stress include: (a) maintenance of optimal water content; (b) enhancement of photosynthesis and restrained transpiration rate; (c) limiting oxidative stress by alleviating ion toxicity; and (d) biosynthetic regulation of solutes and plant hormones (reviewed by Zhu and Gong 2014; Coskun *et al.* 2016; Khan *et al.* 2019). However, following the same pattern as for drought, the many different complex biological functions of Si reported by different studies suggests that the mechanisms by which Si improves the salt tolerance of plants are not yet fully understood (Khan *et al.* 2019). Nevertheless, Rios *et al.* (2017) proposed a model where it is suggested that Si absorption alleviates stress in plants grown under saline conditions through the conjugated action of different aquaporins. Moreover, recently, Soleimannejad *et al.* (2019) reported that Si improves plasma membrane activity by lowering electrolyte leakage, possibly via greater H + -ATPase activity, which could assist in Na+ exclusion from sensitive tissues. However, whether Si directly regulates the transport activity or expression of the Na+/H+ antiporter under salt stress remains unclear. Thus, the effect of Si on Na+ dynamics across membranes and through extracellular spaces in plants needs to be further explored (Khan *et al.* 2019).

Although in most of the studies, Si application took place after seedlings emergence, some studies are available regarding Si-mediated seed germination under salt stress. For example, the application of Si increased germination percentage in salt-stressed wheat (Ahmad 2014), tomato (Haghighi and Mozafarian 2012) and in momordica (Xiao-dong *et al.* 2010). However, detailed mechanisms behind Si benefits on seed germination still need to be explored for better understanding of the role of Si in plants under salt stress at early stages, especially in field conditions (Rizwan *et al.* 2015). Also, recently seed priming with Si was shown to be an efficient management technique that can be used to alleviate deleterious effects of salt-stressful conditions on germination of lettuce seeds (Alves *et al.* 2020).

The abovementioned studies (table 2) demonstrate that Si application could be a helpful tool to enhance salt stress tolerance in various crop plants and to overcome salinity stress in the future. However, many determinants and regulatory mechanisms have not been studied in detail, thus needing further elucidation. Moreover, Si-associated molecular and transcriptional changes at the plant level are yet to be elucidated, including the various metabolomic and proteomic changes in different plant organs. To this end, more focus is needed on the effects of Si under field conditions rather than greenhouse or laboratory studies.

Table 2 - Summary of different crops in which silicon (Si) application has shown beneficial effects for salinity stress mitigation

Plant species	**Family**	**Si Source**	**Si Concentrations /doses**	**Main Results**	**Reference**
***Brassica napus* L.** Rapeseed/ Canola	Brassicaceae	Na_2SiO_3	2 mmol/L	↑ plant growth parameters, levels of chlorophyll, ROS scavenging capacity ↓ lignification and the Na^+ accumulation in shoots, oxidative damage	(HASHEMI *et al.* 2010)
		Na_2SiO_3	1.7 mM	↑ fresh weight and length, leaf thickness, chlorophyll content, antioxidant enzyme activity, K, P, Si and Fe concentration ↓ oxidative damage, Na^+ and Cl^- uptake	(Farshidi *et al.* 2012)
***Capsicum annuum* L.** Sweet Pepper	Solanaceae	K_2SiO_3	1.8 mM	↑ growth, photosynthesis, integral nutrient management, antioxidant enzyme metabolism, expression of proteins involved in photosynthesis, cellular metabolism, and stress resistance. ↓ oxidative damage	(Manivannan *et al.* 2016)
***Cicer arietinum* L.** Chickpea	Fabaceae	K_2SiO_3	4 mM	↑ endogenous nutrients profile, growth characteristics, yield, leaf relative water content, K^+:Na^+ ratio, chlorophyll and RUBISCO content	(Garg and Bhandari 2016)

***Cucumis sativus* L.** Cucumber		Na_2SiO_3	1 mM	↑ growth, activity of antioxidant enzymes, Ca^{2+} and K^+ uptake and concentration, K^+:Na^+ ratio ↓ oxidative damage, Na^+ uptake and concentration	(Khoshgoftar manesh *et al.* 2014)
***Cucurbita pepo* L.** Zucchini squash		K_2SiO_3	0.1, 1 mM	↑ growth and yield, photosynthesis ↓Na^+ and Cl^- translocation, expansion of a powdery mildew (*Podosphaera xanthii*)	(Savvas *et al.* 2009)
***Glycine max* (L.) Merr.** Soybean		Na_2SiO_3	2.5 mM	↑ growth, endogenous gibberellins and chlorophyll content ↓ ABA and proline content	(Lee *et al.* 2010)
***Hordeum vulgare* L.** Barley		H_2SiO_3	1 mmol/L	↑ antioxidant enzymes ↓ oxidative damage	(Liang *et al.* 2003)
***Medicago sativa*. L.** Alfafa		K_2SiO_3	1 mmol/L	↑ growth parameters, K^+, Ca^{2+}, Mg^{2+} and Zn shoot content ↓ Na^+ content	(Wang and Han 2007)
***Saccharum officinarum* L.** Sugarcane		Ca_2SiO_3	1.4, 2.1, 2.8 mM	↑ K^+ concentrations, yield and yield attributes and juice quality ↓ uptake and translocation of Na^+	(Ashraf *et al.* 2010)
***Solanum lycopersicum* L.,** Tomato	Solanaceae	K_2SiO_3	2 mmol/L	↑ yield and healthier fruit (lower blossom end rot incidence), several fruit quality-related traits (e,g. shelf-life)	(Costan *et al.* 2020)
		K_2SiO_3	2.5 mM	↑ total chlorophyll and carotenoid content, net-photosynthesis, transpiration and stomatal conductance ↓ N^{a+} concentration and oxidative damage	(Muneer *et al.* 2014)

		Na_2SiO_3	2 mM	↑ growth, photosynthetic pigments, soluble protein content, net photosynthetic rate, leaf transpiration stomatal conductance, root morphological traits, leaf water status, root hydraulic conductance and antioxidant ability. ↓ Na^+ and Cl^- concentration and oxidative damage	(Li *et al.* 2015)
Sorghum bicolor **(L.) Moench** Sorghum	Poaceae	Not specified	1.44, 1.92 g.kg/soil	↑ dry matter accumulation, antioxidant enzyme metabolism, total antioxidant and phenol contents, membrane stability index and soluble sugar content.	(Kafi *et al.* 2011)
Spinacia oleracea **L. cv. Matador** Spinach		Na_2SiO_3	2 mmol/kg	↑ fresh weight, chlorophyll concentration and antioxidant enzymes ↓ oxidative damage	(Eraslan *et al.* 2008)
Triticum aestivum **L.** Wheat	Poaceae	$Na_2SiO_3 \cdot 9H_2O$	0.78 mM	↑ growth attributes, antioxidant enzymes, K^+ content, K^+:Na^+ ratio, chlorophyll and carotenoids content ↓ oxidative damage and Na+ content	(Daoud *et al.* 2018)
		K_2SiO_3	2.1, 4.2, 6.3, and 8.4 mg Si/10 plants	↑ biomass, grain yield, nutrient grain concentration (N, P, and K) and uptake, chlorophyll and carotenoids content ↓ Na^+ and proline concentrations	(Ibrahim, M *et al.* 2016)
		Ca_2SiO_3	50, 130 µg/g	↑ dry matter and yield, K concentration and K^+:Na^+ shoot ratio ↓ Na^+ uptake	(Tahir *et al.* 2006)
		K_2SiO_3	75, 150 µg/g	↑ growth, K uptake and K^+/Na^+ shoot ratio ↓ Na+ uptake	(Tahir *et al.* 2011)

Triticum durum* and *Triticum aestivum	Poaceae	Na_2SiO_3	0.25, 0.50 mM	↑ plant dry matter and chlorophyll content, Ca^{2+} and K^+ content ↓ Membrane permeability,	(Tuna *et al.* 2008)
***Vicia faba* L.** Faba bean		$SiO_2.nH_2O$	250, 500, 1000 ppm	↑ growth, chlorophyll and carotene, pod yield and seed number, K^+ concentration, K^+:Na^+ ratio ↓ Na^+ content	(Hellal *et al.* 2012)
***Vigna radiata* (L.) Wilczek** Mung bean		Na_2SiO_3		↑ growth, biomass, chlorophyll and carotene content, leaf relative water content, chlorophyll fluorescence, gas exchange parameters, K^+ and Ca2+ accumulation, K^+:Na^+ ratio, enzymes, and proline, glycine and betaine content ↓ oxidative damage and Na^+ accumulation	(Ahmad *et al.* 2019)
***Zea mays* L.** Maize		Na_2SiO_3	3 mM	↑ dry weight, antioxidant enzymes, photosynthetic activity, total proteins, and chlorophyll a content ↓ oxidative damage and proline concentration	(Moussa 2006)

↑ (increase) or ↓ (decrease) in relation to salinity stress treatments without Si application

Role of Si in mitigation of elevated CO_2 stress

One of the main contributors to climate change is the rise in atmospheric CO_2. Just 150 years ago atmospheric CO_2 levels were at 280 ppm and, given the registered trend for an increase in the past years, it is predicted to rise to 550 ppm by 2050 (Long *et al.* 2006). As a consequence, it has also been estimated that, by 2050, the nutrition status of 1.4 billion people will be negatively impacted, particularly in sub-Saharan Africa, India, Asia, Central Latin America and the Caribbean (Medek *et al.* 2017).

Elevated atmospheric CO_2 severely impacts plant physiology. Early studies have shown that eCO_2 results in increased plant growth and biomass, that are a consequence of higher photosynthetic rates reached after acclimation. These effects are associated with a putative positive effect in agriculture (referred to as the "CO_2 fertilization effect"). However, recent studies found a significant negative effect of eCO_2 levels in the concentration of zinc, iron and protein in certain grasses and legumes (as recently reviewed in Soares *et al.* 2019). This effect can be explained by the alteration of important physiological processes, such as photosynthesis stimulation (Long *et al.* 2006), improved water use efficiency (Owensby *et al.* 1993; Guo *et al.* 2015; Han *et al.* 2015; Li *et al.* 2018), decreased stomatal conductance and altered transpiration efficiency (Drake *et al.* 1997; Christy *et al.* 2018). Elevated CO_2 is also reported to positively impact root nodulation and biological nitrogen fixation (Fischinger *et al.* 2010; Guo *et al.* 2013).

Concomitantly, as Si acts in several of these physiological processes (Xie *et al.* 2014; Kaushik and Saini 2019), there are evidence that its external application could act synergistically with eCO_2 (Johnson *et al.* 2018), probably due to the fact that Si cycling helps to control atmospheric CO_2 concentrations (Song *et al.* 2012). However, the publications on this matter are few. Increasing concentration of atmospheric CO_2 might have a severe impact on the regulation of plant Si homeostasis. For example, in *Pinus* species, it was reported that while Si concentrations in plant tissues might decrease under eCO_2, the total amount of Si uptake is increased by this condition (Fulweiler *et al.* 2015). This response was also found in grasses, which are Si-accumulators. It was demonstrated that, under eCO_2 conditions, Si accumulation in plant tissue is decreased with a consequent increase in Si uptake, although genotypic variation in the vulnerability to eCO_2 was found among species (Johnson and Hartley 2018). Recently, Hall *et al.* (2020) using *Brachypodium distachyon* as a model object found that eCO_2 reduced the natural Si concentration in plant tissues, and dramatically decreased the endogenous JA content. Plants supplemented with extra Si had higher baseline JA levels compared to control plants under control non-stressed conditions. Therefore, Hall *et al.* (2020) suggest that predicted increases in CO_2 levels within this century may significantly reduce Si-based mechanical defences against herbivory via a reduction of endogenous JA.

Foliar Si concentration decreases under eCO_2 conditions (Takahashi *et al.* 2008) also in rice, that belong to Si-accumulator species (Alvarez and Datnoff 2001) highly impacted by the changing atmospheric CO_2 concentration (Kimball 2016; Zhu *et al.* 2018). It was further demonstrated that under eCO_2 conditions, Si content significantly decreases in all tissues of fully developed plants due to decreased translocation of this element, similarly to the pattern of essential nutrients such as calcium, manganese and copper (Ujiie *et al.* 2019). This is putatively related to the fact that eCO_2 suppresses transpiration, altering Si flow rates and yield.

While studies looking at increasing atmospheric CO_2 concentration describe a general scenario of increased yield and decreased mineral, amino acid and protein concentrations (Zhu *et al.* 2018), the combination with other environmental challenges, such as drought and temperature, can offset these expected outcomes (Osborne 2016). Given Si beneficial role in plant biological mechanisms, its supplementation is a potential alternative to maintain plants productivity under climatic alterations, as recently demonstrated in legumes (Johnson *et al.* 2018).

Beneficial effects of Si against increased UV-light exposure and temperature stress

The solar UV-B radiation (280–315 nm) that reaches the Earth surface is able to damage plants and also other organisms. Although this type of radiation is effectively absorbed by the ozone layer, due to its depletion during the last decades as a result of increased air pollution, UV-B intensity seems to become a more important issue in the future (Watanabe *et al.* 2011; Líška *et al.* 2017). The prediction for the latter half of the 21st century is likely to be 15–20% increase of UV-B in comparison to current levels (Watanabe *et al.* 2011). The UV radiation is also indirectly responsible for global warming due to the stimulation of release of volatile molecules from plant tissues (Bornman *et al.* 2015). The negative effect of increased UV-B exposure in plants is well documented and is involved in decreased biomass and yield production, generation of reactive oxygen species (ROS) affecting cell processes, membrane damage caused by lipid peroxidation and electrolyte leakage, damage to photosynthetic pigments, etc. (Shen *et al.* 2010; Líška *et al.* 2017).

Generally, silicon application to plants suffering from increased UV-B radiation showed an ameliorative effect. Plants exposed to UV-B increase content of UV-absorbing molecules such as anthocyanins and soluble phenols to protect various UV-sensitive cell targets. Interaction of Si with UV-B exposure alleviates or decreases the content of UV-absorbing compounds (Shen *et al.* 2010). It seems that Si is associated with phenolic biosynthesis under UV radiation (Goto *et al.* 2003). It was also found that Si decreases H_2O_2 concentration and content of TBARSs that represents the products of ROS-mediated oxidation of polyunsaturated membrane lipids under increased UV radiation in maize plants (Mihaličová Malčovská *et al.* 2014). Reduction of photosynthetic performance in wheat plants exposed to UV-B was alleviated by Si application; however, when Si was used in the form of nanoparticles, the mitigation effect was even more effective (Tripathi *et al.* 2017a). This protective role of Si may be based on NO-mediating triggering of antioxidant defence, because under UV-B exposure without Si, level of NO may not be sufficient (Tripathi *et al.* 2017a). The other mechanism behind the positive effect of Si on UV-B exposure toxicity may be due to screening of UV radiation by silica double-layer acting as a glass layer in leaf epidermis (Schaller *et al.* 2013). In addition, the silica layer and also increased phytolith production in leaves contributes to plant tolerance in the presence of UV radiation and thus may affect the leaf reflectance and transmittance in the UV region (Golob *et al.* 2017). Taking together, the application of Si as a beneficial nutrient may be useful to protect plants and/or plant yield against the harmful effect of increased UV-B radiation in the near future.

For the 2006–2015 period the mean land surface air temperature was 1.53 °C higher than the average temperature in the preindustrial period 1850–1900, and 0.66 °C higher when considered the global mean temperature (Shukla, P.R. *et al.* 2019). This has resulted in a higher frequency of extreme weather events related to climate change. In the next decades, it will lead to alternations in the arrangement of climate zones, precipitation patterns and regional crop yield scarcity as a consequence of exposing plants to suboptimal conditions (Cogato *et al.* 2019; Shukla, P.R. *et al.* 2019). Heat stress as a major climate change inducing factor may have severe impacts on agriculture including the level of seed filling, yield and nutritional quality (Lamaoui *et al.* 2018; Sehgal *et al.* 2018; Larmure and Munier-Jolain 2019). In this case of the negative impact of heat stress in plants, Si seems to be promising in mitigation these effects in several ways of action (Prasad *et al.* 2008; Líška *et al.* 2017; Artyszak 2018; Chiluwal *et al.* 2020).

According to Wang *et al.* (2005) biosilicified structures present in the leaf epidermis of creeping bentgrass (*Agrostis palustris)* contribute to decreasing of leaf temperature about 3–4.14 °C in plants exposed to 35–40 °C. This mechanism is based on the physical ability of Si to disperse the radiation by mid-infrared emission. In this case, a higher efficiency was observed in treatment with foliar-applicated Si nanoparticles compared to treatment with substrate-added Si in Na_2SiO_3 form. Furthermore, Si remaining in the cultivation substrate (not taken up by the plants) resulted in cooling pots and consequently the plant root system. The application of another form of Si ($CaSiO_3$) to soil during reproductive phase extensively improved performance of two late sown wheat varieties (Sehar and Faislabad) under heat stress. These plants treated with Si showed more than 20% increased net photosynthesis and stomatal conductance and relative water content higher about 34% in comparison to Si-untreated plants subjected to high temperatures (Sattar *et al.* 2017). Liu *et al.* (2019) proved the beneficial effect of Si fertilizer on rice plant in the heading stage exposed to high daylight temperatures. In this experiment, foliar application increased translocation rates of N, P and K and reduced grain yield loss. Subirrigational application of K_2SiO_3 to medium promoted growth and photosynthetic rate of strawberries (*Fragaria* × *ananassa*) (Muneer *et al.* 2017; Park *et al.* 2018). Tomato plants are known as low Si accumulators (lack of functional root silicon efflux transporter) significantly increased Si concentration in xylem sap and leaves after expressing cucumber transporter CsLsi2 in tomato roots. Elevated Si accumulation leads to a decrease in electrolyte leakage rate from leaf discs exposed to 38 °C for 6 and 12 hours (Sun *et al.* 2019).

Moreover, the efficiency of Si supplementation resulting in inhibition of electrolyte leakage in rice was proven by Agarie *et al.* (1998) more than two decades before. Agarie *et al.* (1998) also suggested that decreased electrolyte leakage could be due to Si-improved thermal stability of membrane lipids under heat stress. These findings are in agreement with Carneiro-Carvalho *et al.* (2019) who found that when fertilizing chestnut (*Castanea sativa*) plants with Si at 32 °C enhanced the ratio between saturated and unsaturated fatty acids, and thus increased thermostability of membranes through maintaining their integrity and functions. The oxidative membrane disruption might be also prevented by enhanced activity of antioxidative enzymes of Si-treated plants. For late sown wheat (up to 36 °C during heading stage), Si addition increased about 35 % of superoxide dismutase (SOD) and about 38 % of catalase (CAT) activity when compared to untreated plants (Sattar *et al.* 2017). Muneer *et al.* (2017) documented increased expression of SOD, CAT and ascorbate peroxidase (APX) at 33 °C and 41 °C in strawberries with Si supplementation. In *Salvia splendens,* Si treatment (K_2SiO_3 form) during heat stress changed total protein content, protein pattern and enhanced activity of guaiacol peroxidase (GPX), SOD and APX (Soundararajan *et al.* 2014). Silicon mitigated extreme heat stress (43 °C) in *Solanum lycopersicum* plants via upregulation of Si transporter genes and heat transcription factors (Khan, Khan, *et al.* 2020). Finally, according to (Wu *et al.* 2014) exogenous application of sodium silicate on rice effectively improved fertility parameters of pollen grains that are generally decreased under heat stress conditions.

From the previous records, it might be concluded that silicon application may enhance plant tolerance to increased temperature stress. As the prediction models suggest warming of the atmosphere, application of Si for the agriculture crops seems to be a very promising way.

Silicon as a tool for remediation of metal or metalloid contaminated soil

Since the global industrial revolution in 18th century, and, especially intensive exploitation of natural resources in 19th and 20th century, relatively large part of active or possible agricultural land became contaminated by mining activity, ore processing, and different kinds of industrial activities, and, especially in the last century also by the intensification of traffic and various agricultural practices (Kopittke *et al.* 2019). Therefore, a relatively large percentage of the soils are nowadays considered as not suitable for agricultural/horticultural use due to high concentration of various dangerous heavy metals, other toxic metals or metalloids (Hanfi *et al.* 2019). Such areas are often considered as marginal lands and many years no attention has been paid for their restoration or remediation. Especially now, when the area of usable land is decreasing every year, such areas may represent great importance after their remediation. Therefore, in the last years the research about the finding the solutions and mechanisms allowing soil restoration is gaining high importance (Gong *et al.* 2018; Song *et al.* 2019; Rutkowska et al., 2020).

Heavy metals and other toxic metals and metalloids represent a serious threat for living organisms, including plants. Although some of them are essential for the plants, when in excess these may be very dangerous and together with non-essential ones may retard the growth and greatly affect the physiological and metabolic processes. Silicon has been shown to positively influence the growth of the whole spectra of plants exposed to metals and metalloids (Imtiaz *et al.* 2016; Emamverdian *et al.* 2018; Bhat *et al.* 2019). Increment in the length of root and shoot as well as the increase in root and shoot biomass after Si addition have been observed in agricultural crops that were exposed to toxic doses of metals and metalloids, e.g. in rice (Song *et al.* 2011; Tripathi *et al.* 2013), maize (Da Cunha *et al.* 2008; Vaculík *et al.* 2009; Lukačová *et al.* 2013), barley (Ali *et al.* 2013), wheat (Keller *et al.* 2015; Tripathi *et al.* 2015), cucumber (Feng *et al.* 2009, 2010); however also in many other important plant species, like cotton (Farooq *et al.* 2013; Anwaar *et al.* 2015), peanut (Shi *et al.* 2010; Shen *et al.* 2014) or even mangroves (Zhang *et al.* 2013, 2015). Several mechanisms behind the alleviative effect of Si have been proposed (Vaculík *et al.* 2020). For example, restriction of root uptake and immobilization of metals in the rhizosphere through root exudation (Huang *et al.* 2016; Wu *et al.* 2016) or binding to root cap mucilage (Kopittke *et al.* 2017). Other Si-based mechanisms attributed the lower toxicity of metals and metalloids to restriction in uptake and root to shoot transfer by modification of apoplasmic movement (Vaculík *et al.* 2009, 2012; Vatehová *et al.* 2012; Lukačová *et al.* 2013), or restriction of toxic metals availability through binding to the polymers of the cell walls (Cocker *et al.* 1997; Wang *et al.* 2004; Ma *et al.* 2015, 2017). Within shoots, heavy metals may be encapsulated by silica phytoliths protecting aerial parts of the plant (Delplace *et al.* 2020). Silicon was also shown to improve the permeability of cell membranes that were damaged by heavy metals (Vaculíková *et al.* 2014; Bosnić *et al.* 2019; Chen *et al.* 2019), and influence the synthesis of various osmoprotectants (Howladar *et al.* 2018). The antioxidant system, that plays a key role in homeostasis of the whole organism, has been shown to react to Si presence, although the data vary from species to species, time and dose of Si, and therefore should be considered in a whole context (Líška *et al.* 2017; Vaculík and Vaculíková 2017). Additionally, the positive effect of Si on the functioning of photosynthetic apparatus can also support the better performance of Si affected plants (Ali *et al.* 2013; Vaculik *et al.* 2015; Guo *et al.* 2018). Silicon has been also shown to affect the phytohormone signalling pathways in response to metal(loid) stress (Kim *et al.* 2016), although our knowledge within this field is very limited. Kim *et al.* (2016) reported that the reduced uptake of metals in the roots modulated the signalling of phytohormones involved in responses to stress and host defence, such as abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA). It was recently observed (Khan, Bilal, *et al.* 2020) that although Si showed varying accumulation of SA, JA, and ABA in plants stressed by Cd, Si markedly downregulated these phytohormones under combined NaCl-Cd stress.

In the light of these findings, there is no doubt that exogenously applied Si might help to overcome the stress caused by toxicity of various metals, metalloids and other toxic elements and could be considered as one possibility for remediation and restoration of contaminated soils and substrates. This is necessary as the growing demand for arable land might result to re-use of slightly contaminated sites again for agricultural purposes in the future. Additionally, the application of Si to metal contaminated soils and substrates would allow to grow various sensitive species and obtain more yield and biomass. This might be one of the key aspects of re-greening the marginal land and would allow increase the percentage of forests, help to keep the moisture in urban and industrial land and support the biodiversity in changing global environment.

Role of Si in increased tolerance to biotic stress

Great efforts have been made in the past decades to understand how Si could improve plant tolerance to biotic stressors while maintaining their productivity. Several works have demonstrated that Si application has a suppressive effect of various plant diseases in a vast diversity of crops, including rice blast, brown spot and leaf scald (Van Bockhaven *et al.* 2015; Domiciano *et al.* 2015; Tatagiba *et al.* 2016), barley and wheat powdery mildew (Wiese *et al.* 2005; Moldes *et al.* 2016), tomato and banana root rot (Huang *et al.* 2011; Vermeire *et al.* 2011), and banana, cotton and lettuce Fusarium wilt (Fortunato *et al.* 2012; Chitarra *et al.* 2013; Whan *et al.* 2016) (Fig. 1).

Figure 1 – Summary of (A) plants/crops that positively responded to Si application under biotic stress, and of (B) pest/pathogens that were negatively affected by Si treatment of their host plants. For a more detailed description see Wang *et al.* (2017), Majumdar and Prakash (2020), Souri *et al.* (2020) *and references therein.*

Silicon application in has also proved to be beneficial in the control of leaf blast, caused by *Pyricularia grisea*, in several finger millet genotypes, with specific genotypes showing higher Si accumulation with enhanced plant resistance (Jadhao and Rout 2020). These authors propose that Si-accumulating genotypes could be used for selective breeding programs, further increasing the potential of this element in mitigating biotic stresses. Additionally, silica nano-particles produced using rice husk have been recently proposed as a green and eco-friendly alternative to chemical fertilisers in the treatment of *Fusarium fujikuroi* in rice plants (Elamawi *et al.* 2020). Seed priming with Si nanoparticles also resulted in increased resistance of beetroots against *Meloidogyne incognita*, *Pectobacterium betavasculorum* and *Rhizoctonia solani* (Khan and Siddiqui 2020). These pieces of evidence open the possibility for the further development of Si-based methodologies that allow a more sustainable and effective control of plant pests and diseases.

Although the importance of Si in plant protection against pests and pathogens has been reported from as early as 1917 (Onodera 1917), only more recently special focus on the defence-related mechanisms activated by this element in plant tissues have been made. It is now recognized that Si enhances plant tolerance to pests and diseases through the activation and/or upregulation of both constitutive and induced resistance mechanisms (Fortunato *et al.* 2012; Whan *et al.* 2016), which include plant cell-wall modifications, increased synthesis of defence-related molecules and compounds, and broad genome reprogramming (Fig.2).

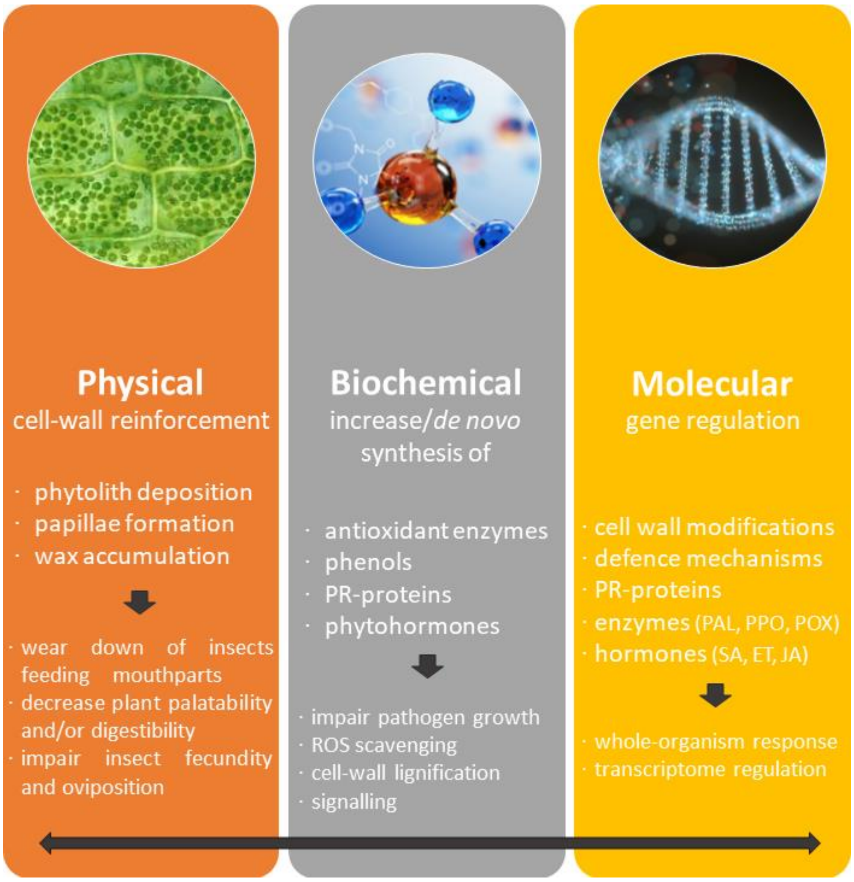

Figure 2 – Si-mediated physical, biochemical and molecular plant defence responses. Abbreviations: pathogenesis related proteins (PR-proteins), reactive oxygen species (ROS), phenylalanine ammonia-lyase (PAL), polyphenoloxidase (PPO), salicylic acid (SA), ethylene (ET) and jasmonic acid (JA).

The first layer of protection against invading organisms relies on the deposition of SiO_2 in the form of biogenic opal, mainly in the epidermal cells of plant stems and leaves (Liang *et al.* 2015). In rice, for example, Si is deposited beneath the cuticle layer (with 0.1 µm of thickness), forming a cuticle-silica double layer in leaf blades (of 2.5 µm thickness) (Yoshida *et al.* 1962). Phytolith deposition increases cell-wall rigidity and physical toughness, thus: i) acting as a physical barrier against pathogen penetration (Kim *et al.* 2002), ii) wearing down the feeding mouthparts of insects (Massey and Hartley 2009), iii) decreasing plant digestibility (Massey and Hartley 2006), or iv) impairing insect oviposition and fecundity activities (Handley *et al.* 2005). Silicon application to wheat infected with the fungus *P. oryzae* has been shown to prevent hyphael entry in leaves, whereas in non-treated plants hyphae easily invaded several neighbouring leaf cells (Sousa *et al.* 2013). A similar result was observed for the insect *E. saccharina*, which showed reduced larval stalk penetration in sugarcane with increased Si accumulation in plant tissues (Kvedaras and Keeping 2007).

In addition to the reinforcement of cell walls by phytoliths deposition, during pathogen infection Si is also known to induce the formation of papillae, i.e. plant cell wall modifications enriched with the (1,3)-β-glucan cell wall polymer callose. In fact, in rose plants, Si supplementation increased the number of papillae in leaf cells in response to infection by the fungus *P. pannosa* (Shetty *et al.* 2011). On the other hand, insect mouthpart wear due to Si treatment was demonstrated for *S. exempta* larvae, for example, which showed increased mandible wear when feeding in silica-rich diets (Massey and Hartley 2009). Moreover, high Si concentrations in plant tissues may reduce their digestibility and palatability, thus slowing the growth rate of insects such as *S. exempta* and *E. saccharina* (Kvedaras and Keeping 2007; Massey and Hartley 2009). Silicon could also aid plant defence by reducing the mechanical breakdown of the leaf, thus protecting the resources in the chlorenchyma cells and reducing chlorophyll released after grinding (Keeping *et al.* 2009). Wax deposition on the abaxial surface of coffee seedlings and formation of ladder-like structures in *Arabidopsis thaliana* trichomes were also found to occur after Si supplementation, impairing the feeding ability of the desert locust *Schistocerca gregaria* and the diamondback moth *P. xylostella*, respectively (Pozza *et al.* 2004; Handley *et al.* 2005).

Si supplementation has also shown to enhance the yield, net photosynthesis rate and water use efficiency, of rice plants infested with the Asiatic pink stem borer *Sesamia inferens* (Jeer *et al.* 2020). Silicon-enhanced resistance against pests and pathogens has been associated not only with the formation of mechanical barriers, but also with the reprogramming of plant primary and secondary metabolism, including increased or *de novo* synthesis of several enzymes, metabolites and proteins such as: (i) defence-related enzymes, such as superoxide dismutase (SOD), catalase (CAT), polyphenoloxidase (PPO), glucanase, peroxidase, and phenylalanine ammonia-lyase (PAL), (ii) antimicrobial compounds, including phenolics, flavonoids and phytoalexins, iii) pathogenesis-related (PR) proteins, and (iv) phytohormones, such as SA, JA and ethylene (ET) (Fauteux *et al.* 2005; Datnoff *et al.* 2007; Fortunato *et al.* 2012; Khan and Siddiqui 2020)

Silicon has been reported to stimulate the activity of defence-related enzymes in several pathosystems, including rice blast (Domiciano *et al.* 2015), soybean target spot (Fortunato *et al.* 2015), and melon powdery mildew (Dallagnol *et al.* 2015). These enzymes include chitinases, peroxidases, polyphenoloxidases, β-1,3-glucanase, PAL, superoxide dismutase, ascorbate peroxidase, glutathione reductase, catalase, lipoxygenases, and glucanases (Fauteux *et al.* 2005; Datnoff *et al.* 2007; Dallagnol *et al.* 2015; Fortunato *et al.* 2015; Domiciano *et al.* 2015), which are involved not only in direct ROS scavenging (Han *et al.* 2016), but also in degrading the cell wall of pathogenic fungi (Dallagnol *et al.* 2011), plant cell wall lignification (Song *et al.* 2016) and regulation of secondary metabolites (Rahman *et al.* 2015). Silicon has been described to stimulate the activity of several antimicrobial compounds, such as phenols, flavonoids, and phytoalexins, during pathogen infection (Hao *et al.* 2011; Rahman *et al.* 2015), which can impair the growth of the invading pathogen and increase plant resistance (Dallagnol *et al.* 2011; Fortunato *et al.* 2015). Fast accumulation of phenols following Si application was found in wheat plants infected with *B. graminis* f. sp. *tritici* (Rémus-Borel *et al.* 2005) and in banana plants infected with *F. oxysporum* f. sp. *cubense* (Fortunato *et al.* 2014). Additionally, leaf extracts from Si-supplemented chestnut plants showed higher inhibitory activity against *Phytophthora cinnamomi* and *Cryphonectria parasitica*, possibly due to increased activity of PAL and polyphenol oxidase (Carneiro-Carvalho *et al.* 2020).

Several studies have also suggested that Si may modulate plant defence strategies through phytohormone homeostasis and signalling (Ghareeb *et al.* 2011; Chen *et al*. 2015; Reynolds *et al.* 2016). Both JA and ET have been shown to accumulate in Si-treated plants rice plants and increase their resistance against herbivory or pathogen invasion (Ye *et al.* 2013) and in tomato plants infected with *R. solanacearum* (Ghareeb *et al.* 2011). However, Si deposition was found to decrease when the JA signalling pathway was compromised, indicating not only a promotion of Si accumulation by JA, but also a strong interaction between the JA-pathway and Si in plant defence against biotic stress (Ye *et al.* 2013). On its turn, it has been recently demonstrated that Si supplementation reduces JA concentrations in *B. distachyon* plants subjected to treatment with methyl jasmonate or herbivory (*H. armigera*) and increases plant macrohairs density (Hall *et al.* 2019). Therefore, Hall *et al.* (2020) proposed a model showing that Si acts as a physical stimulus in the plant, which causes a small, transient increase in JA. Although +Si plants potentially show a faster induction of JA due to this Si-priming after herbivore attack, they have less utility for JA-induced defences and show lower levels of JA induction overall (Hall *et al.* 2020). The relationship between Si and phytohormones in biotic stress scenarios is not very straightforward, needing to be further elucidated. Besides, knowledge of how pathogenesis-related (PR) proteins interfere in plant tolerance against pests and pathogen under Si supplementation is also very scarce. A single study using two-dimensional electrophoresis maps demonstrated that 26 proteins were altered (16 of them increased and 10 decreased) in the roots of tomato plants supplied with Si and infected with *R. solanacearum*. Most of these proteins were associated with plant metabolism and defence-related mechanisms, giving a cue that PR-proteins may have important roles in increasing plant resistance against biotic stressors under Si-supply (Chen *et al.* 2015).

Several genomic studies conducted during the last two decades have tried to elucidate the genetic machinery involved in plant responses against pests and pathogens when under Si supplementation. In general, this reported increased expression of genes related with: (i) structural modifications of cell walls, (ii) general plant defence mechanisms, (iii) PR-proteins, (iv) enzymes related with the production of phenylpropanoids, such as PAL, and (v) regulation of systemic signals, including SA, ET and JA (Kauss *et al.* 2003; Shetty *et al.* 2011; Van Bockhaven *et al.* 2015; Tatagiba *et al.* 2016).

In *A. thaliana*, infection with the powdery mildew fungus *E. cichoracearum* led to the down-regulation of primary metabolism genes, but following Si-treatment downregulated genes were found to be not as severely impacted (Fauteux *et al.* 2006). Similarly, in wheat plants, infection with *B. graminis* f. sp. *tritici* up-regulated the expression of 900 genes related with pathogen infection in non-supplemented plants, whereas in Si-supplied plants only a few genes were significantly impacted by the pathogen (Chain *et al.* 2009). These findings were also supported by another study (Brunings *et al.* 2009), which showed little transcriptomic alterations in Si-supplemented rice plants inoculated with *M. oryzae*. Several genes related with pathogen perception, such as *CHI-II*, *GLU*, *PGIP*, *POD*, were observed to be down-regulated in Si-supplemented tomato plants infected with *R. solanacearum*, whereas genes related with defence and response to stress, such as the late embryogenesis rich protein, trehalose phosphatase, and *WRKY1* transcription factor, were found to be upregulated (Ghareeb *et al.* 2011). Similar observations were reported in tomato plants under Si-treatment inoculated with *R. solanacearum*, in which most of the upregulated genes were involved in signal transduction, defence, protein synthesis and metabolism, and downregulated genes mostly related with photosynthesis and lipid metabolism (Kurabachew *et al.* 2013). More recently, Jadhao *et al.* (2020) have demonstrated that Si amendment induces a synergistic response in plant defence mechanisms by increasing the transcript level of not only silicon transporter genes (such as *EcLsi1*, *EcLsi2* and *EcLsi6*) but also defence-related hormone regulating genes (*EcSAM*, *EcPAL* and *EcLOX*) in finger millet plants infested with *S. inferens*. It is clear that the genetic responses against pest and pathogen invasion is extremely specific to each pathosystem and should be more thoroughly explored to achieve the full potential of Si-supplementation in plant protection.

Conclusion and future perspectives

To help mitigate climate change effects on plant growth and guarantee enough food production for the growing population, innovative strategies need to be tested, including the application of novel compounds that help plants cope with environmental hazards. In this study, we have clearly shown that various chemical forms of Si have been proved to mitigate the negative effects of many different abiotic stresses simulating global and environmental changes (summarised in Fig. 3). Silicon plays a role in the induction of resistance to plants suffering from drought, salinity, UV-radiation, temperature stress, eCO_2 and heavy metal and toxic element exposure. The effect of climate changes is also linked with biotic stresses in plants. Interestingly, silicon application was also found to increase plant resistance to various biotic stressors including bacterial, fungal, insect and other biological attacks. However, the fusion of negative effects of several stresses on plants at the same time and also in interaction with Si application have been poorly studied. Additionally, the mechanisms underlying plant responses to Si application in response to the aforementioned stresses are not yet well explored, however, some of them already described are summarised in Fig. 4. The uptake, translocation and accumulation of Si by plants in response to climate change are not clear enough and need to be studied more deeply in the future. Since climate change will threat several important agricultural regions over the world, which will lose its significance, mankind should be ready to utilise the so-called “marginal lands”. Therefore, the application of Si with its beneficial effects on growth and improvement of plant resistance might play a key role in these processes in the future.

Finally, whenever possible, strategies suggesting Si application should also help meet three main global goals (Masson-Delmotte et al. 2018; Griscom *et al.* 2017; Ripple *et al.* 2019): to reduce 45% of the emissions by 2030, to achieve climate neutrality by 2050 (net zero carbon footprint), and to stabilize global temperature rise at 1.5 °C by the end of the century.

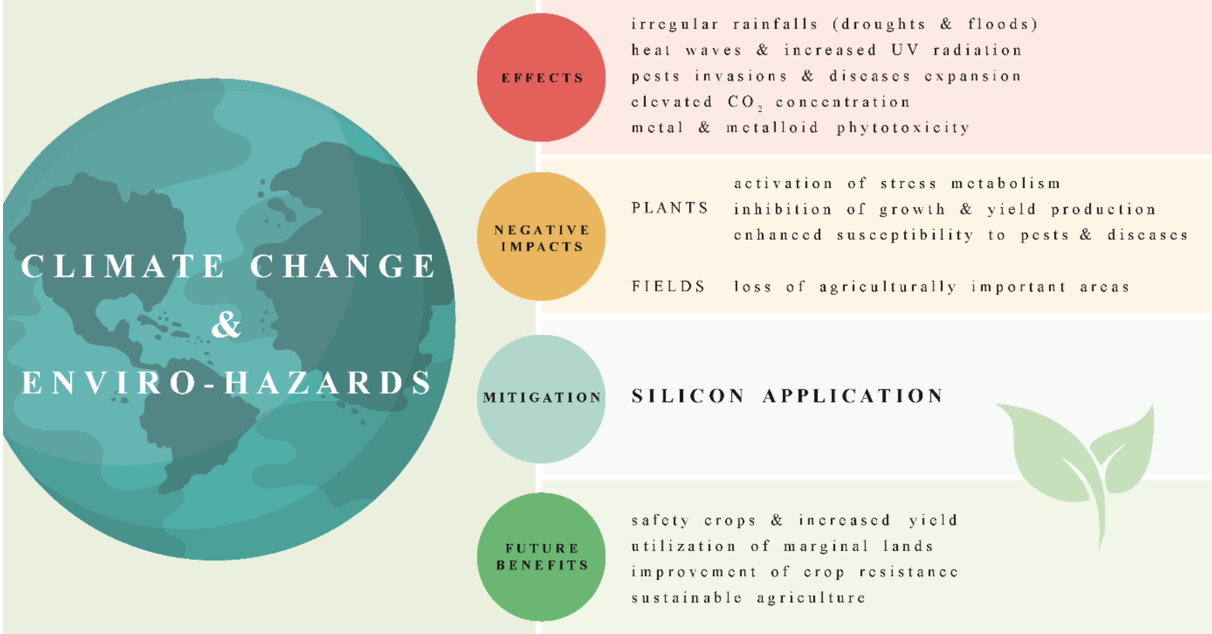

Figure 3. The Summary of climate change and environmental hazards effect on plant production and possibility of Si application.

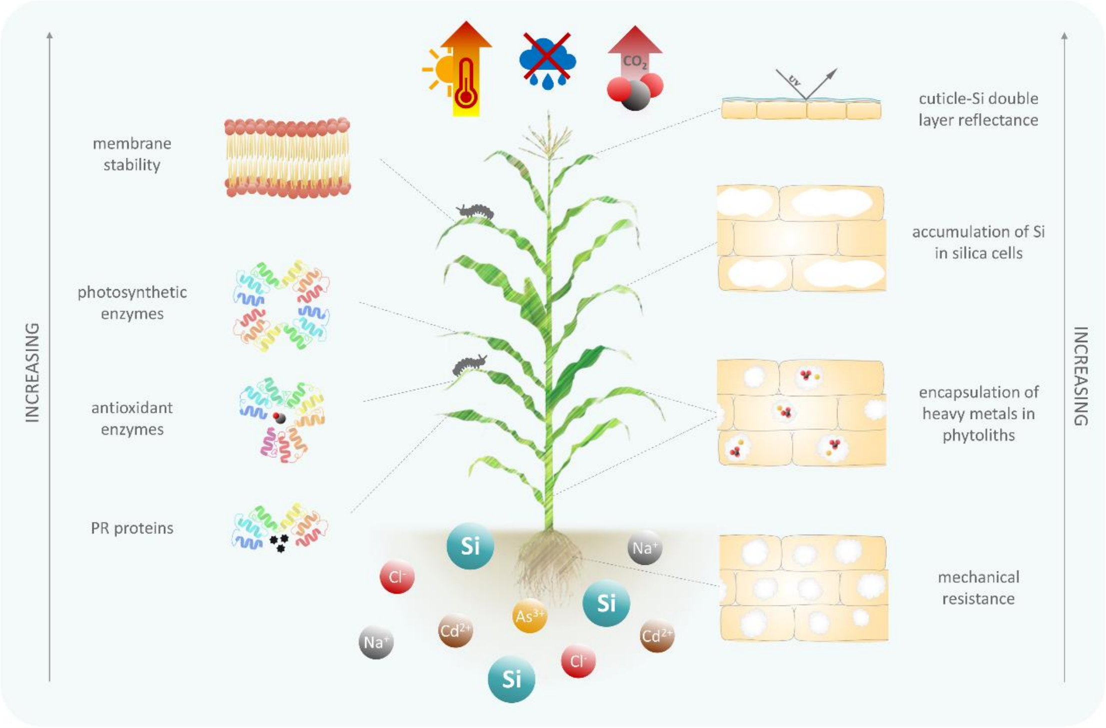

Figure 4. Schematic representation of the processes involved in increased plant tolerance to wide spectrum of chemical hazards (heavy metals, salinity, eCO_2), physical hazards (UV, heat, drought) and biohazards (pathogens & herbivores) in response to Si application. Within root Si deposition in form of phytoliths increased mechanical resistance of central cylinder. In above-ground parts, Si deposition in form of specialized silica cells contribute to mitigation of stress caused by heavy metals by their encapsulation. Formation of Si-cuticle layer in epidermis is involved in increased protection against biotic stress. This double layer also increases leaf reflectance, thus contribute to reducing leaf temperature. Furthermore, Si application increases stability of cell membranes. At protein level, Si application enhances activity of pathogenesis related proteins (PR proteins), antioxidant enzymes and photosynthetic enzymes.

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Mitigation of climate change and environmental hazards in plants: potential role of beneficial metalloid silicon

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Abstract

In the last decades, the concentration of atmospheric CO_2 and the average temperature have been increasing and this trend is expected to become more severe in the near future. Additionally, environmental stresses including drought, salinity, UV-radiation, heavy metals, and toxic elements exposure represent a threat for ecosystems and agriculture. Climate and environmental changes negatively affect plant growth, biomass and yield production, and also enhance plant susceptibility to pests and diseases. Silicon (Si), as a beneficial element for plants, is involved in plant tolerance and/or resistance to various abiotic and biotic stresses. The beneficial role of Si has been proved in various plant species and its accumulation rely on roots uptake capacity. However, Si uptake in plants depends on many biogeochemical factors that may be substantially altered in the future affecting its functional role in plant protection. At present, it is not clear whether Si accumulation in plants will be positively or negatively affected by changing climate and environmental conditions. In this review, we focused on Si interaction with the most important factors of global change and environmental hazards in plants, discussing the potential role of its application as an alleviation strategy for climate and environmental hazards based on current knowledge.

Introduction

Climate change represents a serious problem at a global level, affecting the whole spectra of living organisms, including plants. Climate determines the rate of organism's growth and distribution, what seems to be altered due to the pressure of global warming in tandem with elevated CO_2 (eCO_2) concentration as was predicted by climate models (Newman 2011; Pugnaire *et al.* 2019). The concentration of CO_2 is currently 400 µmol CO_2 mol^{-1} air and is predicted to increase two-fold by the end of this century (Vaughan *et al.* 2018), whereas the estimation of average temperature shows an increase of 0.1 – 0.4 °C per decade (Jump and Peñuelas 2005). The other impacts of climate change include an unequal distribution of precipitation (that leads to long drought periods often followed by intensive rains) or exposure of plants to temperature stress combined with increased ultraviolet (UV) radiation (Ban *et al.* 2015; Bloeschl *et al.* 2019). The increased average temperature is also responsible for spreading of various plant pathogens. Biotic stresses induced by pests and diseases have been also a threat to agriculture, causing considerable losses in crop yield and imposing the application of large amounts of phytosanitary products (Bajwa *et al.* 2020). In a global scenario of food shortage and pressing need for environmental conservation, these aspects pose a major global concern to sustainable agricultural practices, further aggravated by the expansion of endemic pests and pathogens to areas outside their native regions due to climate change phenomena (Bebber *et al.* 2013; Timmusk *et al.* 2020). However, there is limited information available about the interaction between global changes and plant diseases. Climate change might be responsible for the positive, neutral or negative relation between hosts and pathogens because of the specificity of each pathosystem. This in turn might alter crop yield and quality (Ahanger *et al.* 2013).

Agriculture is an important sector of the world's economy and is highly dependent on climate, which ultimately constitutes an essential input to agricultural production. Assuring optimal crop yield in the context of climate change while safeguarding natural resources is deemed to be one of the biggest challenges in the current century (Le Gouis *et al.* 2020). In times where environmental pressures are compounded by nutrient-depleted soils and eminent biodiversity losses, sudden shocks to food production and supply chains pose severe threats to global sustainability (Sattar *et al.* 2017; Scherer *et al.* 2020). Amongst the different food commodity types (crops, livestock, fisheries and aquaculture) crops are by far the most affected by climate change, with losses of up to 50% (Cottrell *et al.* 2019). The latest prediction model for crop growth and water productivity suggested a yield reduction of 3.4% - 8.6% during the period of 2018 – 2027 in seed corn crops (Liu *et al.* 2020). Changes in climate will inevitably have a direct impact not only on agricultural productivity but also on farm incomes and prices (Hertel 2018).

Only in Europe, more than 650,000 sites are considered as polluted due to various inorganic and organic contaminants presented in the soil (Pérez and Rodríguez Eugenio 2018). High demand for natural sources, fast speed of industrialisation and intensification of agriculture lead to the release of heavy metals and other potentially toxic elements, like cadmium (Cd), lead (Pb), copper (Cu), zinc (Zn), chromium (Cr), aluminium (Al), arsenic (As) or antimony (Sb), as well as various organic pollutants, like polyaromated hydrocarbons (PAH), polychlorinated biphenyls (PCB), various pesticides and antibiotics into the natural or man-managed ecosystems (Huang *et al.* 2019; Kumar *et al.* 2019; Kopittke *et al.* 2019). Several agriculturally important regions of the world are seriously threatened, and therefore, marginal polluted land might play a key role in the future for food and feed production after proper remediation (Rutkowska *et al.* 2020).

Silicon (Si), the second most predominant element in the earth crust (Liu *et al.* 2019), has a beneficial effect on plants playing a functional role in the alleviation of several abiotic and biotic stresses, which have been studied for more than two decades (Líška *et al.* 2017; Lux, Lukačová, *et al.* 2020). So far there is little information about Si uptake and accumulation in plants in response to climate changes and especially to global warming. As the positive effect of Si on plants is restricted to its uptake and accumulation, the efficient transport of Si is an essential criterion. The essentiality of Si for plants has never been proved, because there is no evidence that Si is involved in cell metabolism or is component in organic compounds (Tubana *et al.* 2016). Despite this fact, Si has been used widely in agriculture due to improved productivity of several crop species and, also, Si serves as a valued element to humans (Tubana *et al.* 2016). Important to note, crop plants may extract ca. 210 – 224 million tons of silicon annually, depending on plant species (Tubana *et al.* 2016). Deposition of Si in the form of silica is predominant in above-ground plant parts, however, there are some crop species with high accumulation of silica in roots (Lux *et al.* 2020). The accumulation of Si in plants rely on root capacity to take up silicon and other mineral nutrients dissolved in water. The water content in soils will become probably less abundant in the future, so Si deposition in plants might be altered.

This study aims to perform a comprehensive literature analysis and discussion on the possible applications of Si on plants exposed to climate and environmental hazards including eCO_2, increased UV and temperature exposure that relates to drought, salinity effect, also metal and metalloid contamination involved in environmental hazard, as well as the effect of Si to biotic stresses. The review is mainly focused on crops with agronomic importance, however other model plants are also included.

General effects of climate change and environmental hazards on plant growth

Plant development generally increases linearly with temperature across a wide spectrum, with the exact range being crop dependent. Outside specific temperature ranges, crops tend to be severely impacted in terms of growth, quality and productivity. The reasons for these impacts are linked to alterations in standard biochemical and metabolic processes, phenological development stages (Piao *et al.* 2019), but also to alterations in basic processes of cell wall reorganization and remodelling (Ezquer *et al.* 2020), or root elongation (Ding *et al.* 2019). Elevated CO_2 commonly leads to an increase in internal leaf CO_2 levels and a reduction in stomatal conductance, stimulating photosynthesis in C3 plants. This may lead to higher biomass accumulation until acclimation takes place, but also may lead to nutritional losses in edible plant parts (Soares *et al.* 2019). The classical view is still that carbon (photosynthetic CO_2 uptake), ranks above any other drivers of plant growth (Körner 2015), however, carbon does not act alone. To realize increases in crop yields, soil nutrient levels, soil moisture, water availability, and other conditions must also be met. Moreover, oftentimes crops face a series of challenges at any given moment. For example, changes in the frequency and severity of droughts and floods are often associated with periods of extreme temperatures (Masson-Delmotte et al. 2018 2012). On another example, boron (B) toxicity and salinity stress are well recognized as severe stress conditions for plants. However, their coexistence in arid and semi-arid agricultural regions has shown ambiguous effects on plant growth and development (Pandey *et al.* 2019).

Worsen environmental conditions, as the results of human activities, negatively affect plant biology, especially when speaking about an agricultural point of view. One of the most important factors of environmental pollution is excessive soil contamination by metals and metalloids, typically present in wastewater used for crop irrigation serving as an environmental hazard to plants (Papaioannou *et al.* 2019). These elements are toxic when its concentration exceeds the threshold level, however, plants have evolved mechanisms to cope with metal and metalloid stress (DalCorso *et al.* 2019). The most prevalent symptom of metal and metalloid toxicity is decreased growth and biomass with subsequent alteration of yield production.

Taken together, climate and environmental variables defy several keystone aspects of plant growth and development tightly connected with crop performance, such as: 1. plant development (root and shoot); 2. photosynthesis and respiration; 3. water stress adaptations; 4. extreme temperature damage; 5. pest and disease susceptibilities.

Silicon transport in plants in response to altered climate and environmental conditions

For plants, silicic acid, $Si(OH)_4$, represents a bioavailable form of silicon that is absorbed by the root system and irreversibly polymerised into amorphous silica (SiO2–nH2O) at the final location in the plant (Richmond and Sussman 2003; Currie and Perry 2007). Plant species differ in their ability to accumulate Si in the shoots and this feature is mainly assigned to the uptake ability of the root system (Takahashi *et al.* 1990; Ma and Takahashi 2002; Hodson *et al.* 2005). The shoot concentration varies greatly between the plant species from 1% up to 10% of the dry mass (Epstein 1999). Based on the molecular and genetic studies with low silicon mutant plants, two silicon transporters in roots were discovered, i.e. channel protein Lsi1 responsible for uptake of Si from the soil environment and active transporter Lsi2 involved in translocation of Si from the root to the shoot (Ma *et al.* 2006, 2007). Subsequently, channel protein Lsi6 homologous to the Lsi1 plays a role in shoot Si distribution (Yamaji *et al.* 2008). However, besides the molecular mechanism of Si transport and accumulation, shoot Si accumulation is to a lesser content also related to transpiration process (Mitani and Ma 2005).

The concentration of silicic acid ranges from 0.1 to 0.6 mM in soil. So far there is little information about Si uptake and accumulation in plants in response to climate changes and especially to global warming. As the beneficial function of Si is restricted to uptake ability of plants, high temperature may decrease plant Si uptake and accumulation due to lower level of soil water as indicated by a recent study (Johnson *et al.* 2019). In this study, foliar Si concentration (% of dry mass) decreased in plants of pasture grass without Si addition in warmed conditions, however, it was not affected in plants supplied with Si grown upon warming. Interestingly, warming had no impact on root Si concentration in plants of pasture grass (Johnson *et al.* 2019). Other study showed that shoot Si concentration of several grass species was not generally affected by elevated temperature, except species with natural lower ability to accumulate Si (less than 1% of dry mass) (Johnson and Hartley 2018). In the case of eCO_2, Si accumulation of shoots was strongly decreased in grasses (Johnson and Hartley 2018). This study showed evidence that eCO_2 is a stronger driver of silicon accumulation in comparison to increased temperature in grasses. Thus, decreased accumulation of Si might be responsible for higher susceptibility to herbivores or abiotic stresses (Johnson and Hartley 2018). On the other hand, Si concentration was not decreased in various tree species upon eCO_2 (Fulweiler *et al.* 2014). However, the analysis of overall forest Si accumulation, based on net primary production and above-ground Si concentration of trees, showed increased Si accumulation under eCO_2 treatment. Elevated CO_2 might, thus, enhance terrestrial Si pumping in forests and contribute to Si transfer from terrestrial systems to downstream ecosystems (Fulweiler *et al.* 2014). Altered precipitations are also related to climate changes and may affect Si uptake and accumulation in above-ground parts of the plants. The negative correlation between Si and carbon (C) was found in arid conditions showing precipitation and soil nutrient status as a key driver for silicification in leaves (Quigley *et al.* 2020). This recent paper revealed that plants accumulate more Si when the level of soil water and nutrients is limiting. The cost of Si for structural support is lower in comparison to investment in C-based leaf construction. Except Si-based structural support, Si may be also involved in stress tolerance during water deficient conditions, however, general beneficial role of Si is lost, when the water level is restored (Quigley *et al.* 2020). Considering UV radiation, Si uptake and accumulation in shoots might be lowered. In the study with wheat plants, UV-B exposure in ambient or enhanced intensity caused decreased Si concentration in both below- and under-ground plant parts (Tripathi *et al.* 2017b). However, exposure of UV does not seem to affect Si concentration in leaves of millet, but together with decreased water availability Si concentration is slightly lowered (Grašič *et al.* 2019). Up to date, the number of experimental studies showing the dynamics of Si uptake or pattern of Si accumulation in plants during altered climate conditions is insufficient even if several stresses act simultaneously. At this point, it is not clear, whether Si uptake and accumulation might be positively or negatively regulated by future environmental changes and climate alterations.

Silicon in the fight against drought and salinity stress

Drought

Water stress is one of the major's environmental constraints limiting plant growth and agricultural productivity. Drought induces a range of physiological and biochemical processes in plants that can reduce crop yields up to 70 %, resulting in serious economic losses (Osakabe *et al.* 2014; Siracusa *et al.* 2018). Although plants have evolved different morpho-physiological and biochemical strategies to cope with drought stress (Lamaoui *et al.* 2018), increasing evidence suggests that the detrimental effects of drought can be mitigated by the adequate and balanced supply of mineral nutrients (Waraich *et al.* 2011). One of the methods involving the alleviation of negative water stress is the application of Si. The beneficial effect of Si on plant water status has been extensively studied in various plant species subjected to drought stress (Table 1). The improvements of relative water content and/or water potential by Si application occurred under both polyethylene glycol-induced osmotic stress (Hattori *et al.* 2007; Sonobe *et al.* 2011; Ming *et al.* 2012) and potted soil drought conditions (Gong *et al.* 2003; Amin *et al.* 2018). Different compounds of Si, including Na_2SiO_3, K_2SiO_3 or H_2SiO_3 (Table 1), have been applied either in the soil or the nutrient solution, being the first two the most studied compounds. Although in most of the studies, Si application took place after seedlings emergence, the priming of seeds with Si has been suggested as an alternative method to improve the drought stress tolerance in plants. Some studies have shown that Si-seed priming enhances plant resistance against future stress events and propose it as a promising and cost-effective procedure in circumstances, where water scarcity might be a problem (Hameed et al. 2013; Ahmed *et al.* 2014; Biju *et al.* 2017).

Table 1 - Summary of different crops in which silicon (Si) application has shown beneficial effects for drought stress mitigation

Plant species	**Family**	**Si Source**	**Si Concentrations**	**Main Results**	**Reference**
***Brassica napus* L.** Rapeseed/ Canola	Brassicaceae	Na_2SiO_3	0.35, 2.73 mmol/kg soil	↑ growth parameters, net assimilation rate, CO2 absorbance, relative water content, root amino acid content, antioxidant enzymes activity ↓ intracellular CO2 concentration, oxidative damage	(Habibi 2014)
		SiO_2	1 mM	↑ photosynthetic pigments, ROS scavenging capacity, leaf relative water content and proline content ↓ oxidative stress	(Hasanuzzaman *et al.* 2018)
***Cicer arietinum* L.** Chickpea	Fabaceae	$Na_2Si_3O_7$	100 ppm	↑ growth, relative water content, non-enzymatic antioxidant activity ↓ oxidative damage, proline content, enzymatic antioxidant activity	(Gunes *et al.* 2007)
***Cucumis sativus* L.** Cucumber	Cucurbitaceae	K_2SiO_3	120, 240 ppm	↑ biomass, net photosynthetic rate, leaf water content, chlorophyll content, antioxidant enzymes activity ↓ stomatal conductance, oxidative damage, plasma membrane permeability	(Ma *et al.* 2004)

***Glycine max* L. Merrill** Soybean	Fabaceae	$Na_2SiO_3 \cdot 9H_2O$	1.70 mM	↑ growth, photosynthetic enzymes, chlorophyll and anthocyanin content, relative leaf water content ↓ oxidative damage, proline and antioxidant enzymes	(Shen *et al.* 2010)
***Helianthus annuus* L.** Sunflower	Asteraceae	$Na_2Si_3O_7$	100 ppm	↓ stomatal resistance, oxidative damage, proline content, SOD and APX activity ↑ leaf relative water content, CAT activity	(Gunes *et al.* 2008)
***Lens culinaris* Medik.** Lentil	Fabaceae	$Na_2Si_3O_3$	2 mM	↑ germination and seedling vigour, Si content, antioxidants, hydrolytic enzymes activity ↓ concentration of osmolytes and ROS	(Biju *et al.* 2017)
***Mangifera indica* L.** Mango	Anacardiaceae	K_2SiO_3	1.5 mM	↑ growth, net assimilation rate, relative water content, photosynthetic pigments, N, P, K and protein content, IAA, GA, and CK (promoters) endogenous levels, yield and fruit quality ↓ ABA, accumulation of several osmolytes and antioxidant enzyme activity	(Helaly *et al.* 2017)
Medicago sativa L. Alfafa	Fabaceae	K_2SiO_3	4 kg/pot	↑ forage biomass, number of branches, water use efficiency ↓ transpiration rate and stomatal conductance No effect on leaf area and photosynthetic rate	(Liu and Guo 2013)
Oryza sativa L. Rice	Poaceae	K_2SiO_3	0.5, 1.0, 1.5, 2.0 mM	↑ dry weight, root traits, chlorophyll content, water potential, photosynthetic rate, transpiration rate, basal quantum yield, and maximum quantum efficiency of PSII photochemistry ↓ K, Na, Ca, Mg, Fe content	(Chen *et al.* 2011)
		Na_2SiO_3	2.5 mM	↑ growth parameters, total, free, and bound water contents, water and osmotic potential, turgor pressure, active accumulation of several osmolytes, net photosynthetic rate, transpiration, and water-use efficiency	(Ming *et al.* 2012)

***Poa pratensis* L.** Kentucky Bluegrass	Poaceae	$Na_2SiO_3 \cdot 9H_2O$	200, 400, 800 mg/L	↑ net photosynthesis, leaf water contents, relative growth rate, root/shoot ratio, instantaneous water use efficiency, leaf green color and turf quality. ↓ Stomatal conductance, C:N ratio	(Saud *et al.* 2014)
***Saccharum spp.* L.** Sugarcane	Poaceae	CaO-SiO_2	20, 40, 60, 80, 100 g/pot	↑ photosynthetic CO_2 assimilation, stomatal conductance, transpiration, chlorophyll fluorescence, plant growth, leaf relative water content, biomass-yield, photosynthetic pigments, antioxidant enzymes activity (CAT, POD, SOD), phytohormones content (ABA, IAA, GA_3)	(Verma *et al.* 2019)
***Solanum lycopersicum* L.** Tomato	Solanaceae	Na_2SiO_3	0.6, 1.2, 1.8 mM	↑ growth parameters, photosynthetic efficiency of PSII, electron transport rate, net photosynthetic rate, antioxidant enzymatic system ↓ oxidative damage, chlorophyll degradation	(Cao *et al.* 2015)
		K_2SiO_3	2.5 mM	↑ tomato growth, photosynthetic and transpiration rate, water status, root hydraulic conductance, enzymatic and non-enzymatic antioxidant system, ↓ oxidative damage and ROS levels No effect on the transcription of plasma membrane aquaporin genes or proline levels	(Shi *et al.* 2016)
		Na_2SiO_3	50 ppm	↑ K, Ca and Mg accumulation, plant growth, RWC, fruit yield ↓ Na+ uptake, electrolyte leakage, proline content	(Ullah *et al.* 2016)
		$Si(OH)_4$	1.5 mM	↑ growth parameters, chlorophyll content, uptake of sulfur and ammonium, production of amino acids (arginine, methionine, serine, proline, alanine, threonine, glutamic acid, GABA and glycine), production of free polyamines (putrescine and spermidine ↓ GSSG to GSH ratio	(Ali *et al.* 2018)

		Na_2SiO_3	1.2 mM	↑ growth parameters, hydraulic conductivity in radial direction, water uptake, solute accumulation (proline, soluble sugar and soluble protein) osmotic adjustment ability of root, water absorption and antioxidant activity, ↓ oxidative damage	(Cao *et al.* 2017)
***Solanum tuberosum* L.** Potato	Solanaceae	$CaMgSiO_4$	284.4 mg/dm^3	↑ Si concentration in potato leaves, mean tuber weight, tuber yield and proline content. ↓ total sugars and soluble proteins, stalk lodging	Crusciol et al. 2009
***Sorghum bicolor* (L.) Moench** Sorghum	Poaceae	Not specified	1.78 mM	↑ dry weight, root water uptake, root amino acid and sugar content ↓ osmotic potential No effect on root anatomical traits related to water transport	(Sonobe *et al.* 2010)
		Na_2SiO_3	1.67 mM	↑ plant biomass, Si concentration, photosynthetic rate, stomatal conductance, leaf and whole-plant transpiration, relative water content, whole-plant hydraulic conductance and expression of root aquaporin genes ↓ root hydraulic conductance, No effect on osmotic potential of root xylem sap, on leaf-specific conductivity of stem and on root surface area, vessel diameter and number.	(Liu *et al.* 2014)
		H_2SiO_3	0.83 mM	↑ growth parameters, chlorophyll concentration, photosynthetic rate, leaf RWC, transpiration rate, soluble sugar contents, levels of both free and conjugated polyamines (putrescine, spermidine and spermine) and of several key polyamines (synthesis genes ↓ proline and 1-aminocyclopropane- 1-carboxylic acid (ACC) content and osmotic potential	(Yin *et al.* 2016)
		Na_2SiO_3	7.14 mmol	↑ biomass, leaf weight ratio, RWC, water potential and leaf area ↓ specific leaf area	(Gong *et al.* 2003)

Triticum aestivum L. Wheat	Poaceae	Na_2SiO_3	1, 2 mM	↑ growth parameters, chlorophyll content, RWC, Si, K and Ca concentration ↓ proline accumulation and oxidative damage	(Kaya *et al.* 2006)
Zea mays **L.** Maize	Poaceae	Ca_2SiO_4	100 ppm	↑ growth parameters, photosynthetic rate, yield and yield attributes, ↓ transpiration rate	(Amin *et al.* 2018)
		Na_2SiO_3	4, 6 mM	↑ plant growth parameters, photosynthetic pigments, antioxidant enzymatic activity ↓ oxidative damage, proline levels, accumulation of glycine betaine and total soluble sugars	(Parveen *et al.* 2019)

↑ (increase) or ↓ (decrease) in relation to water stress treatments without Si application

Although the mechanisms behind the beneficial effects of Si are still largely unknown, Si-drought improved plants' resistance seems to be primarily related with its role in increasing non-enzymatic antioxidant capacities, by activating antioxidant enzymes and decreasing $O2^{\bullet -}$ production rate, H_2O_2 content and malondialdehyde concentrations (Gong *et al.* 2003; Gunes *et al.* 2007, 2008; Shi *et al.* 2014; Cao *et al.* 2017); maintaining photosynthetic machinery, through the promotion of photosynthetic rate and increased activity of photosynthetic enzymes (Shen *et al.* 2010) and delaying leaf senescence (Hosseini *et al.* 2017). Wang *et al.* (2019) observed that Si treatment might play roles in absorption, transformation and transfer of light energy by optimizing the thylakoid membrane protein components in rice seedlings under drought stress. The impact of Si on chlorophyll fluorescence and the ultrastructure of chloroplasts of drought-stressed tomato was also reported (Cao *et al.* 2015). Silicon played an important role in suppressing the decline of the activities of ROS scavenging enzymes in the chloroplast, therefore, protecting it from severe oxidative damage, such as the distortion of the grana lamellae and stroma lamellae. Zhang *et al.* (2018) also demonstrated the positive beneficial effects of exogenous Si on the chlorophyll fluorescence and expression of photosynthesis-related genes in tomato seedlings under water stress. Increased concentrations of chlorophyll and carotenoids were also observed, thus promoting photosynthesis. Silicon is also believed to be important in reducing evaporation or controlling stomata conductance when taken up and deposited in leaf cuticle, thereby reducing transpiration (Matoh *et al.*; Gao *et al.* 2006) and consequently improving drought tolerance. It has also been shown to enhance radial hydraulic conductivity and mediate stress tolerance in sorghum seedlings and tomato plants exposed to drought (Liu *et al.* 2014; Cao *et al.* 2017). In sorghum seedlings, the increased root hydraulic conductance after Si addition was attributed to Si-mediated transcriptional up-regulation of some aquaporin genes (Liu *et al.* 2014).

Several key conjugated polyamines synthesis genes were shown to be up-regulated by Si under sorghum drought-stressed plants (Yin et al. 2014). It is suggested that Si improves sorghum drought resistance by mediating the balance of conjugated polyamines and ethylene levels. In leaves, the increased conjugated polyamines and decreased 1-aminocyclopropane-1-carboxylic acid (ACC, the precursor of ethylene) help to retard leaf senescence. In roots, the balance between conjugated polyamines and ACC participates in the modulation of root plasticity, increasing the root/shoot ratio thus contributing to an increase in water uptake (Yin et al. 2014).

Additionally, Si is pointed as responsible for maintenance of nutrient balance (Kaya et al. 2006), stimulation of osmolyte accumulation (Ming et al. 2012; Cao et al. 2017), regulation of growth substance levels (Zhu and Gong 2014) and sequestration of toxic ions (Rizwan et al. 2015) when plants are under drought stress.

Since water availability is a limited resource in many regions of the world and taking into account the increased demand for water and food production, to fulfil the need of an increased world population, sustainable approaches to promote water use efficiency (WUE) in agriculture are highly required. Therefore, the application of Si may be an important strategy to improve crop yield in arid or semi-arid areas under water-stress conditions. However, the pathways by which Si regulates the plant water status still need further investigation, especially regarding the molecular and biochemical. The proper way of Si application (i.e. doses, silicon source and plant stage) and its performance under field conditions, as most of the studies were conducted in lab trails or in hydroponic conditions, is another topic that still needs extensive investigation.

Salinity

Like for drought stress, salinity is one of the major severe abiotic factors affecting crop growth and productivity. Salt's negative effects on plant growth have initially been associated with the osmotic stress component caused by decreases in soil water potential and, consequently, restriction of water uptake by roots (Munns and Tester 2008). High salt deposition in the soil results in osmotic as well as specific ion effects, which further lead to secondary oxidative stress in plants, thus causing a decrease on plant growth, biomass, yield, photosynthesis, WUE, and nutrient uptake but also leads to physiological drought and ion toxicity in plants, thus reducing agricultural productivity and yields (Chinnusamy *et al.* 2005; Shahid *et al.* 2018; Rehman *et al.* 2019). In addition, it increases the uptake of toxic elements such as sodium (Na+) and chlorine (Cl-), which have negative effects on plant growth and productivity (Ahanger *et al.* 2013). Various mitigation and adaptation approaches have been proposed to overcome these negative impacts (W Wang *et al.* 2019) and as for drought, Si application was shown to be involved in the alleviation of salt stress, with several studies reporting the significant regulatory role of Si in numerous plant physiological processes under these stress (Table 2). The exogenous application of Si is believed to improve plant growth either directly, by blocking the transport of Na+ ions into the plant, or indirectly, by activating different physiological processes to ameliorate the effect of salinity stress (Khan *et al.* 2019). Briefly, the mechanisms by which silicon mediates alleviation of salt stress include: (a) maintenance of optimal water content; (b) enhancement of photosynthesis and restrained transpiration rate; (c) limiting oxidative stress by alleviating ion toxicity; and (d) biosynthetic regulation of solutes and plant hormones (reviewed by Zhu and Gong 2014; Coskun *et al.* 2016; Khan *et al.* 2019). However, following the same pattern as for drought, the many different complex biological functions of Si reported by different studies suggests that the mechanisms by which Si improves the salt tolerance of plants are not yet fully understood (Khan *et al.* 2019). Nevertheless, Rios *et al.* (2017) proposed a model where it is suggested that Si absorption alleviates stress in plants grown under saline conditions through the conjugated action of different aquaporins. Moreover, recently, Soleimannejad *et al.* (2019) reported that Si improves plasma membrane activity by lowering electrolyte leakage, possibly via greater H + -ATPase activity, which could assist in Na+ exclusion from sensitive tissues. However, whether Si directly regulates the transport activity or expression of the Na+/H+ antiporter under salt stress remains unclear. Thus, the effect of Si on Na+ dynamics across membranes and through extracellular spaces in plants needs to be further explored (Khan *et al.* 2019).

Although in most of the studies, Si application took place after seedlings emergence, some studies are available regarding Si-mediated seed germination under salt stress. For example, the application of Si increased germination percentage in salt-stressed wheat (Ahmad 2014), tomato (Haghighi and Mozafarian 2012) and in momordica (Xiao-dong *et al.* 2010). However, detailed mechanisms behind Si benefits on seed germination still need to be explored for better understanding of the role of Si in plants under salt stress at early stages, especially in field conditions (Rizwan *et al.* 2015). Also, recently seed priming with Si was shown to be an efficient management technique that can be used to alleviate deleterious effects of salt-stressful conditions on germination of lettuce seeds (Alves *et al.* 2020).

The abovementioned studies (table 2) demonstrate that Si application could be a helpful tool to enhance salt stress tolerance in various crop plants and to overcome salinity stress in the future. However, many determinants and regulatory mechanisms have not been studied in detail, thus needing further elucidation. Moreover, Si-associated molecular and transcriptional changes at the plant level are yet to be elucidated, including the various metabolomic and proteomic changes in different plant organs. To this end, more focus is needed on the effects of Si under field conditions rather than greenhouse or laboratory studies.

Table 2 - Summary of different crops in which silicon (Si) application has shown beneficial effects for salinity stress mitigation

Plant species	**Family**	**Si Source**	**Si Concentrations /doses**	**Main Results**	**Reference**
***Brassica napus* L.** Rapeseed/ Canola	Brassicaceae	Na_2SiO_3	2 mmol/L	↑ plant growth parameters, levels of chlorophyll, ROS scavenging capacity ↓ lignification and the Na^+ accumulation in shoots, oxidative damage	(HASHEMI *et al.* 2010)
		Na_2SiO_3	1.7 mM	↑ fresh weight and length, leaf thickness, chlorophyll content, antioxidant enzyme activity, K, P, Si and Fe concentration ↓ oxidative damage, Na^+ and Cl^- uptake	(Farshidi *et al.* 2012)
***Capsicum annuum* L.** Sweet Pepper	Solanaceae	K_2SiO_3	1.8 mM	↑ growth, photosynthesis, integral nutrient management, antioxidant enzyme metabolism, expression of proteins involved in photosynthesis, cellular metabolism, and stress resistance. ↓ oxidative damage	(Manivannan *et al.* 2016)
***Cicer arietinum* L.** Chickpea	Fabaceae	K_2SiO_3	4 mM	↑ endogenous nutrients profile, growth characteristics, yield, leaf relative water content, K^+:Na^+ ratio, chlorophyll and RUBISCO content	(Garg and Bhandari 2016)

***Cucumis sativus* L.** Cucumber		Na_2SiO_3	1 mM	↑ growth, activity of antioxidant enzymes, Ca^{2+} and K^+ uptake and concentration, K^+:Na^+ ratio ↓ oxidative damage, Na^+ uptake and concentration	(Khoshgoftar manesh *et al.* 2014)
***Cucurbita pepo* L.** Zucchini squash		K_2SiO_3	0.1, 1 mM	↑ growth and yield, photosynthesis ↓Na^+ and Cl^- translocation, expansion of a powdery mildew (*Podosphaera xanthii*)	(Savvas *et al.* 2009)
***Glycine max* (L.) Merr.** Soybean		Na_2SiO_3	2.5 mM	↑ growth, endogenous gibberellins and chlorophyll content ↓ ABA and proline content	(Lee *et al.* 2010)
***Hordeum vulgare* L.** Barley		H_2SiO_3	1 mmol/L	↑ antioxidant enzymes ↓ oxidative damage	(Liang *et al.* 2003)
***Medicago sativa*. L.** Alfafa		K_2SiO_3	1 mmol/L	↑ growth parameters, K^+, Ca^{2+}, Mg^{2+} and Zn shoot content ↓ Na^+ content	(Wang and Han 2007)
***Saccharum officinarum* L.** Sugarcane		Ca_2SiO_3	1.4, 2.1, 2.8 mM	↑ K^+ concentrations, yield and yield attributes and juice quality ↓ uptake and translocation of Na^+	(Ashraf *et al.* 2010)
***Solanum lycopersicum* L.,** Tomato	Solanaceae	K_2SiO_3	2 mmol/L	↑ yield and healthier fruit (lower blossom end rot incidence), several fruit quality-related traits (e,g. shelf-life)	(Costan *et al.* 2020)
		K_2SiO_3	2.5 mM	↑ total chlorophyll and carotenoid content, net-photosynthesis, transpiration and stomatal conductance ↓ N^{a+} concentration and oxidative damage	(Muneer *et al.* 2014)

		Na_2SiO_3	2 mM	↑ growth, photosynthetic pigments, soluble protein content, net photosynthetic rate, leaf transpiration stomatal conductance, root morphological traits, leaf water status, root hydraulic conductance and antioxidant ability. ↓ Na^+ and Cl^- concentration and oxidative damage	(Li *et al.* 2015)
Sorghum bicolor **(L.) Moench** Sorghum	Poaceae	Not specified	1.44, 1.92 g.kg/soil	↑ dry matter accumulation, antioxidant enzyme metabolism, total antioxidant and phenol contents, membrane stability index and soluble sugar content.	(Kafi *et al.* 2011)
Spinacia oleracea **L. cv. Matador** Spinach		Na_2SiO_3	2 mmol/kg	↑ fresh weight, chlorophyl concentration and antioxidant enzymes ↓ oxidative damage	(Eraslan *et al.* 2008)
Triticum aestivum **L.** Wheat	Poaceae	$Na_2SiO_3 \cdot 9H_2O$	0.78 mM	↑ growth attributes, antioxidant enzymes, K^+ content, $K^+:Na^+$ ratio, chlorophyll and carotenoids content ↓ oxidative damage and Na+ content	(Daoud *et al.* 2018)
		K_2SiO_3	2.1, 4.2, 6.3, and 8.4 mg Si/10 plants	↑ biomass, grain yield, nutrient grain concentration (N, P, and K) and uptake, chlorophyll and carotenoids content ↓ Na^+ and proline concentrations	(Ibrahim, M *et al.* 2016)
		Ca_2SiO_3	50, 130 µg/g	↑ dry matter and yield, K concentration and $K^+:Na^+$ shoot ratio ↓ Na^+ uptake	(Tahir *et al.* 2006)
		K_2SiO_3	75, 150 µg/g	↑ growth, K uptake and K^+/Na^+ shoot ratio ↓ Na+ uptake	(Tahir *et al.* 2011)

Triticum durum* and *Triticum aestivum	Poaceae	Na_2SiO_3	0.25, 0.50 mM	↑ plant dry matter and chlorophyll content, Ca^{2+} and K^+ content ↓ Membrane permeability,	(Tuna *et al.* 2008)
***Vicia faba* L.** Faba bean		$SiO_2.nH_2O$	250, 500, 1000 ppm	↑ growth, chlorophyll and carotene, pod yield and seed number, K^+ concentration, K^+:Na^+ ratio ↓ Na^+ content	(Hellal *et al.* 2012)
***Vigna radiata* (L.) Wilczek** Mung bean		Na_2SiO_3		↑ growth, biomass, chlorophyll and carotene content, leaf relative water content, chlorophyll fluorescence, gas exchange parameters, K^+ and Ca2+ accumulation, K^+:Na^+ ratio, enzymes, and proline, glycine and betaine content ↓ oxidative damage and Na^+ accumulation	(Ahmad *et al.* 2019)
***Zea mays* L.** Maize		Na_2SiO_3	3 mM	↑ dry weight, antioxidant enzymes, photosynthetic activity, total proteins, and chlorophyll a content ↓ oxidative damage and proline concentration	(Moussa 2006)

↑ (increase) or ↓ (decrease) in relation to salinity stress treatments without Si application

Role of Si in mitigation of elevated CO_2 stress

One of the main contributors to climate change is the rise in atmospheric CO_2. Just 150 years ago atmospheric CO_2 levels were at 280 ppm and, given the registered trend for an increase in the past years, it is predicted to rise to 550 ppm by 2050 (Long *et al.* 2006). As a consequence, it has also been estimated that, by 2050, the nutrition status of 1.4 billion people will be negatively impacted, particularly in sub-Saharan Africa, India, Asia, Central Latin America and the Caribbean (Medek *et al.* 2017).

Elevated atmospheric CO_2 severely impacts plant physiology. Early studies have shown that eCO_2 results in increased plant growth and biomass, that are a consequence of higher photosynthetic rates reached after acclimation. These effects are associated with a putative positive effect in agriculture (referred to as the "CO_2 fertilization effect"). However, recent studies found a significant negative effect of eCO_2 levels in the concentration of zinc, iron and protein in certain grasses and legumes (as recently reviewed in Soares *et al.* 2019). This effect can be explained by the alteration of important physiological processes, such as photosynthesis stimulation (Long *et al.* 2006), improved water use efficiency (Owensby *et al.* 1993; Guo *et al.* 2015; Han *et al.* 2015; Li *et al.* 2018), decreased stomatal conductance and altered transpiration efficiency (Drake *et al.* 1997; Christy *et al.* 2018). Elevated CO_2 is also reported to positively impact root nodulation and biological nitrogen fixation (Fischinger *et al.* 2010; Guo *et al.* 2013).

Concomitantly, as Si acts in several of these physiological processes (Xie *et al.* 2014; Kaushik and Saini 2019), there are evidence that its external application could act synergistically with eCO_2 (Johnson *et al.* 2018), probably due to the fact that Si cycling helps to control atmospheric CO_2 concentrations (Song *et al.* 2012). However, the publications on this matter are few. Increasing concentration of atmospheric CO_2 might have a severe impact on the regulation of plant Si homeostasis. For example, in *Pinus* species, it was reported that while Si concentrations in plant tissues might decrease under eCO_2, the total amount of Si uptake is increased by this condition (Fulweiler *et al.* 2015). This response was also found in grasses, which are Si-accumulators. It was demonstrated that, under eCO_2 conditions, Si accumulation in plant tissue is decreased with a consequent increase in Si uptake, although genotypic variation in the vulnerability to eCO_2 was found among species (Johnson and Hartley 2018). Recently, Hall *et al.* (2020) using *Brachypodium distachyon* as a model object found that eCO_2 reduced the natural Si concentration in plant tissues, and dramatically decreased the endogenous JA content. Plants supplemented with extra Si had higher baseline JA levels compared to control plants under control non-stressed conditions. Therefore, Hall *et al.* (2020) suggest that predicted increases in CO_2 levels within this century may significantly reduce Si-based mechanical defences against herbivory via a reduction of endogenous JA.

Foliar Si concentration decreases under eCO_2 conditions (Takahashi *et al.* 2008) also in rice, that belong to Si-accumulator species (Alvarez and Datnoff 2001) highly impacted by the changing atmospheric CO_2 concentration (Kimball 2016; Zhu *et al.* 2018). It was further demonstrated that under eCO_2 conditions, Si content significantly decreases in all tissues of fully developed plants due to decreased translocation of this element, similarly to the pattern of essential nutrients such as calcium, manganese and copper (Ujiie *et al.* 2019). This is putatively related to the fact that eCO_2 suppresses transpiration, altering Si flow rates and yield.

While studies looking at increasing atmospheric CO_2 concentration describe a general scenario of increased yield and decreased mineral, amino acid and protein concentrations (Zhu *et al.* 2018), the combination with other environmental challenges, such as drought and temperature, can offset these expected outcomes (Osborne 2016). Given Si beneficial role in plant biological mechanisms, its supplementation is a potential alternative to maintain plants productivity under climatic alterations, as recently demonstrated in legumes (Johnson *et al.* 2018).

Beneficial effects of Si against increased UV-light exposure and temperature stress

The solar UV-B radiation (280–315 nm) that reaches the Earth surface is able to damage plants and also other organisms. Although this type of radiation is effectively absorbed by the ozone layer, due to its depletion during the last decades as a result of increased air pollution, UV-B intensity seems to become a more important issue in the future (Watanabe *et al.* 2011; Líška *et al.* 2017). The prediction for the latter half of the 21st century is likely to be 15–20% increase of UV-B in comparison to current levels (Watanabe *et al.* 2011). The UV radiation is also indirectly responsible for global warming due to the stimulation of release of volatile molecules from plant tissues (Bornman *et al.* 2015). The negative effect of increased UV-B exposure in plants is well documented and is involved in decreased biomass and yield production, generation of reactive oxygen species (ROS) affecting cell processes, membrane damage caused by lipid peroxidation and electrolyte leakage, damage to photosynthetic pigments, etc. (Shen *et al.* 2010; Líška *et al.* 2017).

Generally, silicon application to plants suffering from increased UV-B radiation showed an ameliorative effect. Plants exposed to UV-B increase content of UV-absorbing molecules such as anthocyanins and soluble phenols to protect various UV-sensitive cell targets. Interaction of Si with UV-B exposure alleviates or decreases the content of UV-absorbing compounds (Shen *et al.* 2010). It seems that Si is associated with phenolic biosynthesis under UV radiation (Goto *et al.* 2003). It was also found that Si decreases H_2O_2 concentration and content of TBARSs that represents the products of ROS-mediated oxidation of polyunsaturated membrane lipids under increased UV radiation in maize plants (Mihaličová Malčovská *et al.* 2014). Reduction of photosynthetic performance in wheat plants exposed to UV-B was alleviated by Si application; however, when Si was used in the form of nanoparticles, the mitigation effect was even more effective (Tripathi *et al.* 2017a). This protective role of Si may be based on NO-mediating triggering of antioxidant defence, because under UV-B exposure without Si, level of NO may not be sufficient (Tripathi *et al.* 2017a). The other mechanism behind the positive effect of Si on UV-B exposure toxicity may be due to screening of UV radiation by silica double-layer acting as a glass layer in leaf epidermis (Schaller *et al.* 2013). In addition, the silica layer and also increased phytolith production in leaves contributes to plant tolerance in the presence of UV radiation and thus may affect the leaf reflectance and transmittance in the UV region (Golob *et al.* 2017). Taking together, the application of Si as a beneficial nutrient may be useful to protect plants and/or plant yield against the harmful effect of increased UV-B radiation in the near future.

For the 2006–2015 period the mean land surface air temperature was 1.53 °C higher than the average temperature in the preindustrial period 1850–1900, and 0.66 °C higher when considered the global mean temperature (Shukla, P.R. *et al.* 2019). This has resulted in a higher frequency of extreme weather events related to climate change. In the next decades, it will lead to alternations in the arrangement of climate zones, precipitation patterns and regional crop yield scarcity as a consequence of exposing plants to suboptimal conditions (Cogato *et al.* 2019; Shukla, P.R. *et al.* 2019). Heat stress as a major climate change inducing factor may have severe impacts on agriculture including the level of seed filling, yield and nutritional quality (Lamaoui *et al.* 2018; Sehgal *et al.* 2018; Larmure and Munier-Jolain 2019). In this case of the negative impact of heat stress in plants, Si seems to be promising in mitigation these effects in several ways of action (Prasad *et al.* 2008; Líška *et al.* 2017; Artyszak 2018; Chiluwal *et al.* 2020).

According to Wang *et al.* (2005) biosilicified structures present in the leaf epidermis of creeping bentgrass (*Agrostis palustris)* contribute to decreasing of leaf temperature about 3–4.14 °C in plants exposed to 35–40 °C. This mechanism is based on the physical ability of Si to disperse the radiation by mid-infrared emission. In this case, a higher efficiency was observed in treatment with foliar-applicated Si nanoparticles compared to treatment with substrate-added Si in Na_2SiO_3 form. Furthermore, Si remaining in the cultivation substrate (not taken up by the plants) resulted in cooling pots and consequently the plant root system. The application of another form of Si ($CaSiO_3$) to soil during reproductive phase extensively improved performance of two late sown wheat varieties (Sehar and Faislabad) under heat stress. These plants treated with Si showed more than 20% increased net photosynthesis and stomatal conductance and relative water content higher about 34% in comparison to Si-untreated plants subjected to high temperatures (Sattar *et al.* 2017). Liu *et al.* (2019) proved the beneficial effect of Si fertilizer on rice plant in the heading stage exposed to high daylight temperatures. In this experiment, foliar application increased translocation rates of N, P and K and reduced grain yield loss. Subirrigational application of K_2SiO_3 to medium promoted growth and photosynthetic rate of strawberries (*Fragaria* × *ananassa*) (Muneer *et al.* 2017; Park *et al.* 2018). Tomato plants are known as low Si accumulators (lack of functional root silicon efflux transporter) significantly increased Si concentration in xylem sap and leaves after expressing cucumber transporter CsLsi2 in tomato roots. Elevated Si accumulation leads to a decrease in electrolyte leakage rate from leaf discs exposed to 38 °C for 6 and 12 hours (Sun *et al.* 2019).

Moreover, the efficiency of Si supplementation resulting in inhibition of electrolyte leakage in rice was proven by Agarie *et al.* (1998) more than two decades before. Agarie *et al.* (1998) also suggested that decreased electrolyte leakage could be due to Si-improved thermal stability of membrane lipids under heat stress. These findings are in agreement with Carneiro-Carvalho *et al.* (2019) who found that when fertilizing chestnut (*Castanea sativa*) plants with Si at 32 °C enhanced the ratio between saturated and unsaturated fatty acids, and thus increased thermostability of membranes through maintaining their integrity and functions. The oxidative membrane disruption might be also prevented by enhanced activity of antioxidative enzymes of Si-treated plants. For late sown wheat (up to 36 °C during heading stage), Si addition increased about 35 % of superoxide dismutase (SOD) and about 38 % of catalase (CAT) activity when compared to untreated plants (Sattar *et al.* 2017). Muneer *et al.* (2017) documented increased expression of SOD, CAT and ascorbate peroxidase (APX) at 33 °C and 41 °C in strawberries with Si supplementation. In *Salvia splendens,* Si treatment (K_2SiO_3 form) during heat stress changed total protein content, protein pattern and enhanced activity of guaiacol peroxidase (GPX), SOD and APX (Soundararajan *et al.* 2014). Silicon mitigated extreme heat stress (43 °C) in *Solanum lycopersicum* plants via upregulation of Si transporter genes and heat transcription factors (Khan, Khan, *et al.* 2020). Finally, according to (Wu *et al.* 2014) exogenous application of sodium silicate on rice effectively improved fertility parameters of pollen grains that are generally decreased under heat stress conditions.

From the previous records, it might be concluded that silicon application may enhance plant tolerance to increased temperature stress. As the prediction models suggest warming of the atmosphere, application of Si for the agriculture crops seems to be a very promising way.

Silicon as a tool for remediation of metal or metalloid contaminated soil

Since the global industrial revolution in 18th century, and, especially intensive exploitation of natural resources in 19th and 20th century, relatively large part of active or possible agricultural land became contaminated by mining activity, ore processing, and different kinds of industrial activities, and, especially in the last century also by the intensification of traffic and various agricultural practices (Kopittke *et al.* 2019). Therefore, a relatively large percentage of the soils are nowadays considered as not suitable for agricultural/horticultural use due to high concentration of various dangerous heavy metals, other toxic metals or metalloids (Hanfi *et al.* 2019). Such areas are often considered as marginal lands and many years no attention has been paid for their restoration or remediation. Especially now, when the area of usable land is decreasing every year, such areas may represent great importance after their remediation. Therefore, in the last years the research about the finding the solutions and mechanisms allowing soil restoration is gaining high importance (Gong *et al.* 2018; Song *et al.* 2019; Rutkowska et al., 2020).

Heavy metals and other toxic metals and metalloids represent a serious threat for living organisms, including plants. Although some of them are essential for the plants, when in excess these may be very dangerous and together with non-essential ones may retard the growth and greatly affect the physiological and metabolic processes. Silicon has been shown to positively influence the growth of the whole spectra of plants exposed to metals and metalloids (Imtiaz *et al.* 2016; Emamverdian *et al.* 2018; Bhat *et al.* 2019). Increment in the length of root and shoot as well as the increase in root and shoot biomass after Si addition have been observed in agricultural crops that were exposed to toxic doses of metals and metalloids, e.g. in rice (Song *et al.* 2011; Tripathi *et al.* 2013), maize (Da Cunha *et al.* 2008; Vaculík *et al.* 2009; Lukačová *et al.* 2013), barley (Ali *et al.* 2013), wheat (Keller *et al.* 2015; Tripathi *et al.* 2015), cucumber (Feng *et al.* 2009, 2010); however also in many other important plant species, like cotton (Farooq *et al.* 2013; Anwaar *et al.* 2015), peanut (Shi *et al.* 2010; Shen *et al.* 2014) or even mangroves (Zhang *et al.* 2013, 2015). Several mechanisms behind the alleviative effect of Si have been proposed (Vaculík *et al.* 2020). For example, restriction of root uptake and immobilization of metals in the rhizosphere through root exudation (Huang *et al.* 2016; Wu *et al.* 2016) or binding to root cap mucilage (Kopittke *et al.* 2017). Other Si-based mechanisms attributed the lower toxicity of metals and metalloids to restriction in uptake and root to shoot transfer by modification of apoplasmic movement (Vaculík *et al.* 2009, 2012; Vatehová *et al.* 2012; Lukačová *et al.* 2013), or restriction of toxic metals availability through binding to the polymers of the cell walls (Cocker *et al.* 1997; Wang *et al.* 2004; Ma *et al.* 2015, 2017). Within shoots, heavy metals may be encapsulated by silica phytoliths protecting aerial parts of the plant (Delplace *et al.* 2020). Silicon was also shown to improve the permeability of cell membranes that were damaged by heavy metals (Vaculíková *et al.* 2014; Bosnić *et al.* 2019; Chen *et al.* 2019), and influence the synthesis of various osmoprotectants (Howladar *et al.* 2018). The antioxidant system, that plays a key role in homeostasis of the whole organism, has been shown to react to Si presence, although the data vary from species to species, time and dose of Si, and therefore should be considered in a whole context (Líška *et al.* 2017; Vaculík and Vaculíková 2017). Additionally, the positive effect of Si on the functioning of photosynthetic apparatus can also support the better performance of Si affected plants (Ali *et al.* 2013; Vaculik *et al.* 2015; Guo *et al.* 2018). Silicon has been also shown to affect the phytohormone signalling pathways in response to metal(loid) stress (Kim *et al.* 2016), although our knowledge within this field is very limited. Kim *et al.* (2016) reported that the reduced uptake of metals in the roots modulated the signalling of phytohormones involved in responses to stress and host defence, such as abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA). It was recently observed (Khan, Bilal, *et al.* 2020) that although Si showed varying accumulation of SA, JA, and ABA in plants stressed by Cd, Si markedly downregulated these phytohormones under combined NaCl-Cd stress.

In the light of these findings, there is no doubt that exogenously applied Si might help to overcome the stress caused by toxicity of various metals, metalloids and other toxic elements and could be considered as one possibility for remediation and restoration of contaminated soils and substrates. This is necessary as the growing demand for arable land might result to re-use of slightly contaminated sites again for agricultural purposes in the future. Additionally, the application of Si to metal contaminated soils and substrates would allow to grow various sensitive species and obtain more yield and biomass. This might be one of the key aspects of re-greening the marginal land and would allow increase the percentage of forests, help to keep the moisture in urban and industrial land and support the biodiversity in changing global environment.

Role of Si in increased tolerance to biotic stress

Great efforts have been made in the past decades to understand how Si could improve plant tolerance to biotic stressors while maintaining their productivity. Several works have demonstrated that Si application has a suppressive effect of various plant diseases in a vast diversity of crops, including rice blast, brown spot and leaf scald (Van Bockhaven *et al.* 2015; Domiciano *et al.* 2015; Tatagiba *et al.* 2016), barley and wheat powdery mildew (Wiese *et al.* 2005; Moldes *et al.* 2016), tomato and banana root rot (Huang *et al.* 2011; Vermeire *et al.* 2011), and banana, cotton and lettuce Fusarium wilt (Fortunato *et al.* 2012; Chitarra *et al.* 2013; Whan *et al.* 2016) (Fig. 1).

Figure 1 – Summary of (A) plants/crops that positively responded to Si application under biotic stress, and of (B) pest/pathogens that were negatively affected by Si treatment of their host plants. For a more detailed description see Wang *et al.* (2017), Majumdar and Prakash (2020), Souri *et al.* (2020) *and references therein.*

Silicon application in has also proved to be beneficial in the control of leaf blast, caused by *Pyricularia grisea*, in several finger millet genotypes, with specific genotypes showing higher Si accumulation with enhanced plant resistance (Jadhao and Rout 2020). These authors propose that Si-accumulating genotypes could be used for selective breeding programs, further increasing the potential of this element in mitigating biotic stresses. Additionally, silica nano-particles produced using rice husk have been recently proposed as a green and eco-friendly alternative to chemical fertilisers in the treatment of *Fusarium fujikuroi* in rice plants (Elamawi *et al.* 2020). Seed priming with Si nanoparticles also resulted in increased resistance of beetroots against *Meloidogyne incognita*, *Pectobacterium betavasculorum* and *Rhizoctonia solani* (Khan and Siddiqui 2020). These pieces of evidence open the possibility for the further development of Si-based methodologies that allow a more sustainable and effective control of plant pests and diseases.

Although the importance of Si in plant protection against pests and pathogens has been reported from as early as 1917 (Onodera 1917), only more recently special focus on the defence-related mechanisms activated by this element in plant tissues have been made. It is now recognized that Si enhances plant tolerance to pests and diseases through the activation and/or upregulation of both constitutive and induced resistance mechanisms (Fortunato *et al.* 2012; Whan *et al.* 2016), which include plant cell-wall modifications, increased synthesis of defence-related molecules and compounds, and broad genome reprogramming (Fig.2).

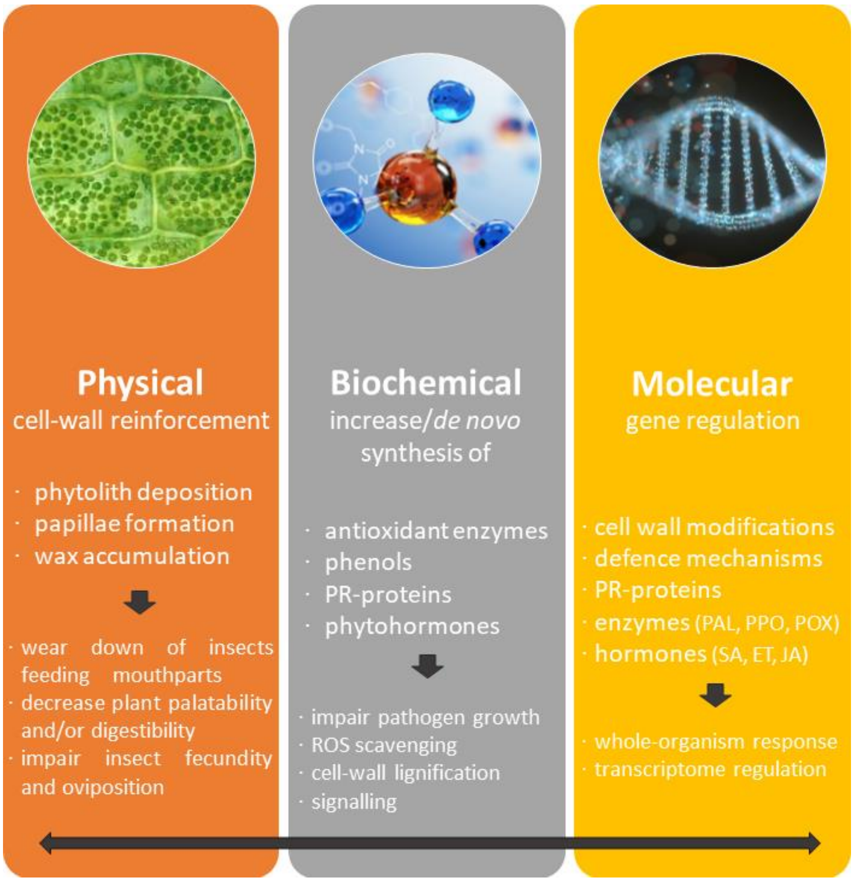

Figure 2 – Si-mediated physical, biochemical and molecular plant defence responses. Abbreviations: pathogenesis related proteins (PR-proteins), reactive oxygen species (ROS), phenylalanine ammonia-lyase (PAL), polyphenoloxidase (PPO), salicylic acid (SA), ethylene (ET) and jasmonic acid (JA).

The first layer of protection against invading organisms relies on the deposition of SiO_2 in the form of biogenic opal, mainly in the epidermal cells of plant stems and leaves (Liang *et al.* 2015). In rice, for example, Si is deposited beneath the cuticle layer (with 0.1 μm of thickness), forming a cuticle-silica double layer in leaf blades (of 2.5 μm thickness) (Yoshida *et al.* 1962). Phytolith deposition increases cell-wall rigidity and physical toughness, thus: i) acting as a physical barrier against pathogen penetration (Kim *et al.* 2002), ii) wearing down the feeding mouthparts of insects (Massey and Hartley 2009), iii) decreasing plant digestibility (Massey and Hartley 2006), or iv) impairing insect oviposition and fecundity activities (Handley *et al.* 2005). Silicon application to wheat infected with the fungus *P. oryzae* has been shown to prevent hyphael entry in leaves, whereas in non-treated plants hyphae easily invaded several neighbouring leaf cells (Sousa *et al.* 2013). A similar result was observed for the insect *E. saccharina*, which showed reduced larval stalk penetration in sugarcane with increased Si accumulation in plant tissues (Kvedaras and Keeping 2007).

In addition to the reinforcement of cell walls by phytoliths deposition, during pathogen infection Si is also known to induce the formation of papillae, i.e. plant cell wall modifications enriched with the (1,3)-β-glucan cell wall polymer callose. In fact, in rose plants, Si supplementation increased the number of papillae in leaf cells in response to infection by the fungus *P. pannosa* (Shetty *et al.* 2011). On the other hand, insect mouthpart wear due to Si treatment was demonstrated for *S. exempta* larvae, for example, which showed increased mandible wear when feeding in silica-rich diets (Massey and Hartley 2009). Moreover, high Si concentrations in plant tissues may reduce their digestibility and palatability, thus slowing the growth rate of insects such as *S. exempta* and *E. saccharina* (Kvedaras and Keeping 2007; Massey and Hartley 2009). Silicon could also aid plant defence by reducing the mechanical breakdown of the leaf, thus protecting the resources in the chlorenchyma cells and reducing chlorophyll released after grinding (Keeping *et al.* 2009). Wax deposition on the abaxial surface of coffee seedlings and formation of ladder-like structures in *Arabidopsis thaliana* trichomes were also found to occur after Si supplementation, impairing the feeding ability of the desert locust *Schistocerca gregaria* and the diamondback moth *P. xylostella*, respectively (Pozza *et al.* 2004; Handley *et al.* 2005).

Si supplementation has also shown to enhance the yield, net photosynthesis rate and water use efficiency, of rice plants infested with the Asiatic pink stem borer *Sesamia inferens* (Jeer *et al.* 2020). Silicon-enhanced resistance against pests and pathogens has been associated not only with the formation of mechanical barriers, but also with the reprogramming of plant primary and secondary metabolism, including increased or *de novo* synthesis of several enzymes, metabolites and proteins such as: (i) defence-related enzymes, such as superoxide dismutase (SOD), catalase (CAT), polyphenoloxidase (PPO), glucanase, peroxidase, and phenylalanine ammonia-lyase (PAL), (ii) antimicrobial compounds, including phenolics, flavonoids and phytoalexins, iii) pathogenesis-related (PR) proteins, and (iv) phytohormones, such as SA, JA and ethylene (ET) (Fauteux *et al.* 2005; Datnoff *et al.* 2007; Fortunato *et al.* 2012; Khan and Siddiqui 2020)

Silicon has been reported to stimulate the activity of defence-related enzymes in several pathosystems, including rice blast (Domiciano *et al.* 2015), soybean target spot (Fortunato *et al.* 2015), and melon powdery mildew (Dallagnol *et al.* 2015). These enzymes include chitinases, peroxidases, polyphenoloxidases, β-1,3-glucanase, PAL, superoxide dismutase, ascorbate peroxidase, glutathione reductase, catalase, lipoxygenases, and glucanases (Fauteux *et al.* 2005; Datnoff *et al.* 2007; Dallagnol *et al.* 2015; Fortunato *et al.* 2015; Domiciano *et al.* 2015), which are involved not only in direct ROS scavenging (Han *et al.* 2016), but also in degrading the cell wall of pathogenic fungi (Dallagnol *et al.* 2011), plant cell wall lignification (Song *et al.* 2016) and regulation of secondary metabolites (Rahman *et al.* 2015). Silicon has been described to stimulate the activity of several antimicrobial compounds, such as phenols, flavonoids, and phytoalexins, during pathogen infection (Hao *et al.* 2011; Rahman *et al.* 2015), which can impair the growth of the invading pathogen and increase plant resistance (Dallagnol *et al.* 2011; Fortunato *et al.* 2015). Fast accumulation of phenols following Si application was found in wheat plants infected with *B. graminis* f. sp. *tritici* (Rémus-Borel *et al.* 2005) and in banana plants infected with *F. oxysporum* f. sp. *cubense* (Fortunato *et al.* 2014). Additionally, leaf extracts from Si-supplemented chestnut plants showed higher inhibitory activity against *Phytophthora cinnamomi* and *Cryphonectria parasitica*, possibly due to increased activity of PAL and polyphenol oxidase (Carneiro-Carvalho *et al.* 2020).

Several studies have also suggested that Si may modulate plant defence strategies through phytohormone homeostasis and signalling (Ghareeb *et al.* 2011; Chen *et al*. 2015; Reynolds *et al.* 2016). Both JA and ET have been shown to accumulate in Si-treated plants rice plants and increase their resistance against herbivory or pathogen invasion (Ye *et al.* 2013) and in tomato plants infected with *R. solanacearum* (Ghareeb *et al.* 2011). However, Si deposition was found to decrease when the JA signalling pathway was compromised, indicating not only a promotion of Si accumulation by JA, but also a strong interaction between the JA-pathway and Si in plant defence against biotic stress (Ye *et al.* 2013). On its turn, it has been recently demonstrated that Si supplementation reduces JA concentrations in *B. distachyon* plants subjected to treatment with methyl jasmonate or herbivory (*H. armigera*) and increases plant macrohairs density (Hall *et al.* 2019). Therefore, Hall *et al.* (2020) proposed a model showing that Si acts as a physical stimulus in the plant, which causes a small, transient increase in JA. Although +Si plants potentially show a faster induction of JA due to this Si-priming after herbivore attack, they have less utility for JA-induced defences and show lower levels of JA induction overall (Hall *et al.* 2020). The relationship between Si and phytohormones in biotic stress scenarios is not very straightforward, needing to be further elucidated. Besides, knowledge of how pathogenesis-related (PR) proteins interfere in plant tolerance against pests and pathogen under Si supplementation is also very scarce. A single study using two-dimensional electrophoresis maps demonstrated that 26 proteins were altered (16 of them increased and 10 decreased) in the roots of tomato plants supplied with Si and infected with *R. solanacearum*. Most of these proteins were associated with plant metabolism and defence-related mechanisms, giving a cue that PR-proteins may have important roles in increasing plant resistance against biotic stressors under Si-supply (Chen *et al.* 2015).

Several genomic studies conducted during the last two decades have tried to elucidate the genetic machinery involved in plant responses against pests and pathogens when under Si supplementation. In general, this reported increased expression of genes related with: (i) structural modifications of cell walls, (ii) general plant defence mechanisms, (iii) PR-proteins, (iv) enzymes related with the production of phenylpropanoids, such as PAL, and (v) regulation of systemic signals, including SA, ET and JA (Kauss *et al.* 2003; Shetty *et al.* 2011; Van Bockhaven *et al.* 2015; Tatagiba *et al.* 2016).

In *A. thaliana*, infection with the powdery mildew fungus *E. cichoracearum* led to the down-regulation of primary metabolism genes, but following Si-treatment downregulated genes were found to be not as severely impacted (Fauteux *et al.* 2006). Similarly, in wheat plants, infection with *B. graminis* f. sp. *tritici* up-regulated the expression of 900 genes related with pathogen infection in non-supplemented plants, whereas in Si-supplied plants only a few genes were significantly impacted by the pathogen (Chain *et al.* 2009). These findings were also supported by another study (Brunings *et al.* 2009), which showed little transcriptomic alterations in Si-supplemented rice plants inoculated with *M. oryzae*. Several genes related with pathogen perception, such as *CHI-II*, *GLU*, *PGIP*, *POD*, were observed to be down-regulated in Si-supplemented tomato plants infected with *R. solanacearum*, whereas genes related with defence and response to stress, such as the late embryogenesis rich protein, trehalose phosphatase, and *WRKY1* transcription factor, were found to be upregulated (Ghareeb *et al.* 2011). Similar observations were reported in tomato plants under Si-treatment inoculated with *R. solanacearum*, in which most of the upregulated genes were involved in signal transduction, defence, protein synthesis and metabolism, and downregulated genes mostly related with photosynthesis and lipid metabolism (Kurabachew *et al.* 2013). More recently, Jadhao *et al.* (2020) have demonstrated that Si amendment induces a synergistic response in plant defence mechanisms by increasing the transcript level of not only silicon transporter genes (such as *EcLsi1*, *EcLsi2* and *EcLsi6*) but also defence-related hormone regulating genes (*EcSAM*, *EcPAL* and *EcLOX*) in finger millet plants infested with *S. inferens*. It is clear that the genetic responses against pest and pathogen invasion is extremely specific to each pathosystem and should be more thoroughly explored to achieve the full potential of Si-supplementation in plant protection.

Conclusion and future perspectives

To help mitigate climate change effects on plant growth and guarantee enough food production for the growing population, innovative strategies need to be tested, including the application of novel compounds that help plants cope with environmental hazards. In this study, we have clearly shown that various chemical forms of Si have been proved to mitigate the negative effects of many different abiotic stresses simulating global and environmental changes (summarised in Fig. 3). Silicon plays a role in the induction of resistance to plants suffering from drought, salinity, UV-radiation, temperature stress, eCO_2 and heavy metal and toxic element exposure. The effect of climate changes is also linked with biotic stresses in plants. Interestingly, silicon application was also found to increase plant resistance to various biotic stressors including bacterial, fungal, insect and other biological attacks. However, the fusion of negative effects of several stresses on plants at the same time and also in interaction with Si application have been poorly studied. Additionally, the mechanisms underlying plant responses to Si application in response to the aforementioned stresses are not yet well explored, however, some of them already described are summarised in Fig. 4. The uptake, translocation and accumulation of Si by plants in response to climate change are not clear enough and need to be studied more deeply in the future. Since climate change will threat several important agricultural regions over the world, which will lose its significance, mankind should be ready to utilise the so-called “marginal lands”. Therefore, the application of Si with its beneficial effects on growth and improvement of plant resistance might play a key role in these processes in the future.

Finally, whenever possible, strategies suggesting Si application should also help meet three main global goals (Masson-Delmotte et al. 2018; Griscom *et al.* 2017; Ripple *et al.* 2019): to reduce 45% of the emissions by 2030, to achieve climate neutrality by 2050 (net zero carbon footprint), and to stabilize global temperature rise at 1.5 °C by the end of the century.

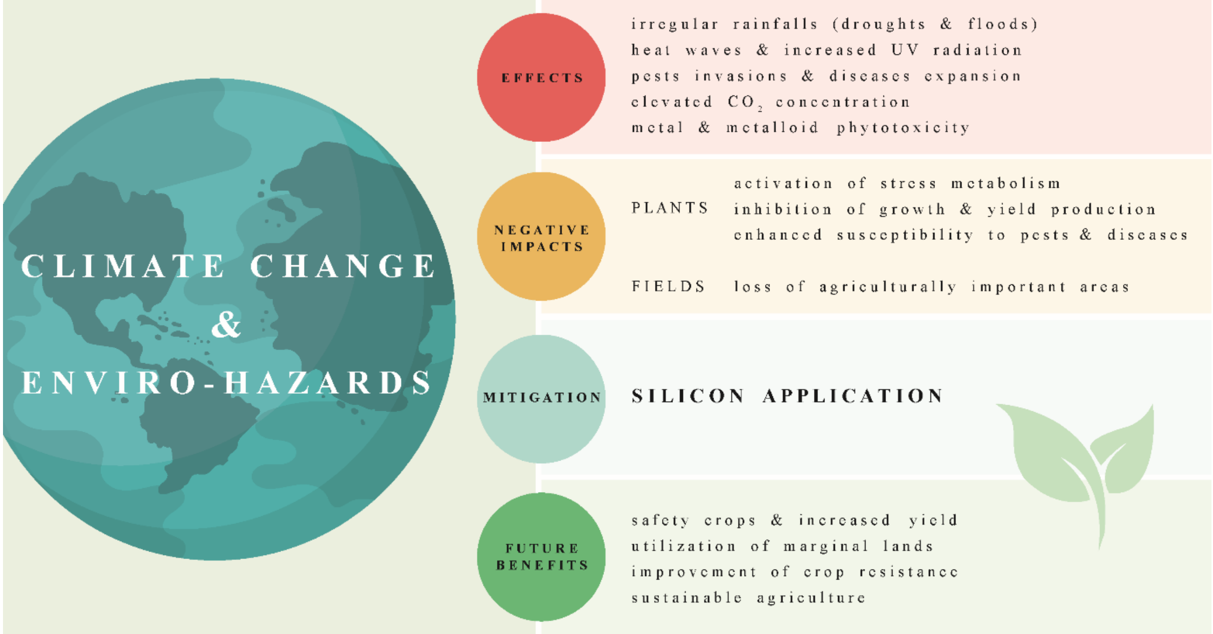

Figure 3. The Summary of climate change and environmental hazards effect on plant production and possibility of Si application.

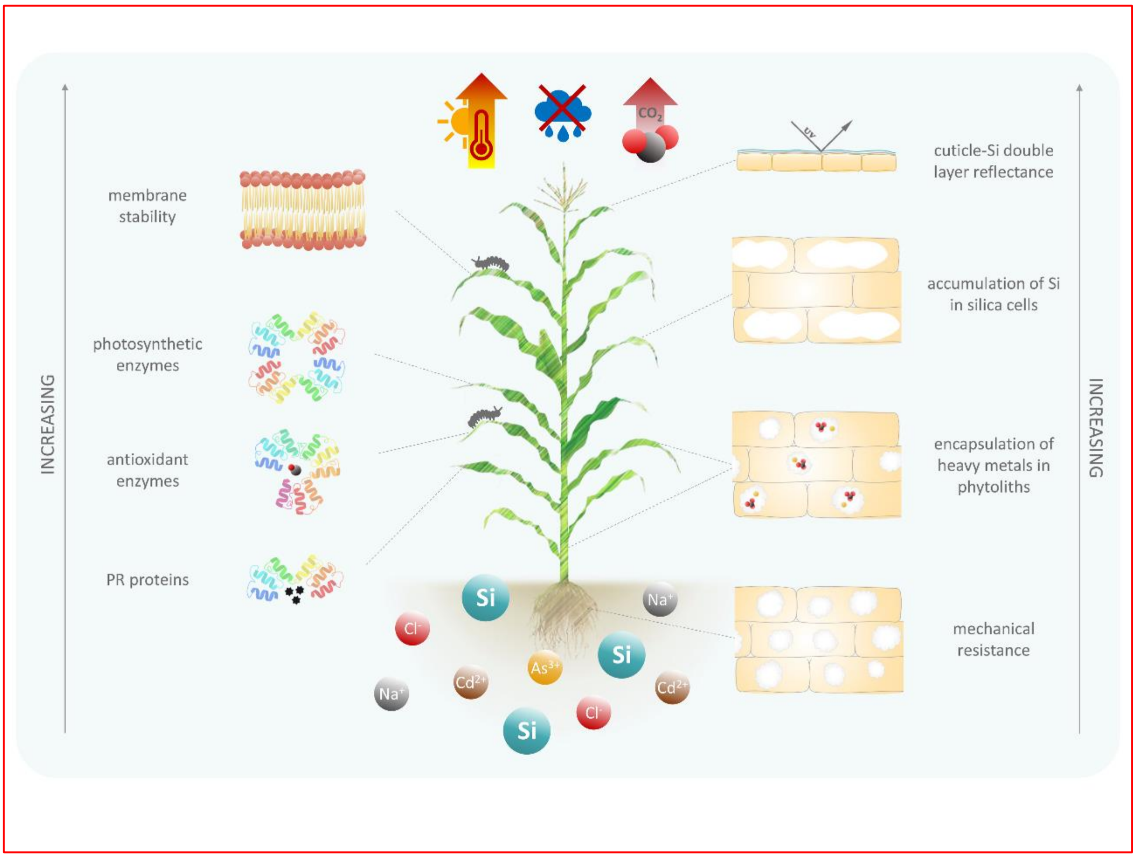

Figure 4. Schematic representation of the processes involved in increased plant tolerance to wide spectrum of chemical hazards (heavy metals, salinity, eCO_2), physical hazards (UV, heat, drought) and biohazards (pathogens & herbivores) in response to Si application. Within root Si deposition in form of phytoliths increased mechanical resistance of central cylinder. In above-ground parts, Si deposition in form of specialized silica cells contribute to mitigation of stress caused by heavy metals by their encapsulation. Formation of Si-cuticle layer in epidermis is involved in increased protection against biotic stress. This double layer also increases leaf reflectance, thus contribute to reducing leaf temperature. Furthermore, Si application increases stability of cell membranes. At protein level, Si application enhances activity of pathogenesis related proteins (PR proteins), antioxidant enzymes and photosynthetic enzymes.

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Graphical Abstract