The combined use of silicon and arbuscular mycorrhizas to mitigate salinity and drought stress in rice

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Abstract

Rice (*Oryza sativa* L.), being a high silicon (Si)-accumulator, is a major global food crop for more than half of the world's population. However, both salinity and drought, two of the most challenging abiotic stresses in rice-growing areas globally, threaten world food security. Both symbiosis with arbuscular mycorrhizal fungi (AMF) and supplementing paddy soils with Si have been shown to improve rice growth during drought and salinity-stress. However, their combined impact is poorly understood. AMF may absorb Si through their spores and hyphae and thus help accumulate root Si. In turn, Si can affect mycorrhizal responsiveness but the underlying mechanisms remain largely unknown. This review explores (i) how Si and AMF act to mitigate salinity and drought stress in rice plants and (ii) how they can be applied together. We also identify areas for future study and discuss how the combined presence of arbuscular mycorrhizas (AMs) and Si in paddy soils can generate more sustainable rice productivity.

Keywords: Arbuscular mycorrhiza; silicon; rice; salinity and drought stress; stress responses; synergistic effects

1. Introduction

Agriculture is essential to achieve food security (Pawlak and Kołodziejczak, 2020). Rice (*Oryza Satvia* L.) is a major contributor to food security as it provides more than half of the world's population with calorific input and is cultivated in more than 100 countries (Bandumula, 2018). To feed the growing world population, it is estimated that rice production must increase to 800 million tons by 2025 (Bandumula, 2018). However, rice production, like that of any other crop, is directly affected by environmental factors (Zhao et al., 2016) that cause abiotic stresses (Datta et al., 2017).

Water scarcity or drought stress has serious effects on plants: It hampers plant growth and development, plant morphological characteristics, water-plant relationships, photosynthesis,
respiration, mineral nutrition and many other essential processes (Salehi-Lisar and Bakhshayeshan-Agdam, 2016).

Salinity stress affects about 20% of irrigated lands and significantly reduces agricultural production. It is estimated that half of the agricultural lands will be salinized by 2050 (Etesami and Noori, 2019). Salinity stress hinders plant growth in several ways (Fig. 1), including (i) a decrease in ambient osmotic potential which decreases the availability of water to roots and (ii) an increase in ion toxicity (mainly Na\(^+\) and Cl\(^-\)) in plant tissues. Ion toxicity can disrupt many biochemical processes such as respiration, photosynthesis, and the synthesis of proteins, and in particular the activity of enzymes. Furthermore, it reduces membrane integrity and causes nutritional imbalance. Thus, during salinity, plants are exposed to the negative effects of both excess ions and water-deficits (Kumar et al., 2019b; Shrivastava and Kumar, 2015). In addition, both salinity and drought stress induce oxidative stress in plant cells (Etesami and Noori, 2019).

Rice is a very salt sensitive crop (salinity threshold level of around 3.0 dS m\(^{-1}\)) although this does depend growth stage and cultivar (Razzaq et al., 2020). As a semi-aquatic species, it is also highly sensitive to water shortage conditions and thus is very sensitive to drought stress (Kamoshita et al., 2008). About half of the rice-growing lands around the world are short of water, reducing its yield (Ruiz-Sánchez et al., 2010). For instance, drought can reduce rice yield by more than 60% when it occurs during the panicle development stage (Boonjung and Fukai, 1996; Venuprasad et al., 2007). Different remedial approaches are available to mitigate the drought and salinity stresses in paddy fields. These generally include cultivation of salinity and drought-tolerant rice genotypes, using rice growth-regulators, applying plant growth-promoting microorganisms associated with rice roots (Etesami, 2019), removing deposited salt, and adjusting fertilizer management (Djaman et al., 2020). Among these approaches, the use of microorganisms that associate with rice plant roots has been shown to improve rice productivity via inducing rhizosphere fertility (Etesami, 2019), ultimately increasing rice yield.

Arbuscular mycorrhizal-fungi (AMF) stimulate plant growth by improving water relations, providing protection against soil-borne pathogens, and enhancing mineral uptake, particularly of
The role of AMF in improving rice growth and yield by ameliorating salt and drought stress has been confirmed in many research studies (Chareesri et al., 2020; Mboj et al., 2018; Parvin et al., 2020; Porcel et al., 2015; Tisarum et al., 2019; Tisarum et al., 2020).

Mineral nutrition is also known as an effective strategy in alleviating salt and water-deficit stress in plants (Nawaz et al., 2020; Waraich et al., 2011). A prime example is the use of silicon (Si). Though not essential, Si is a beneficial element that helps crops mitigate various stresses, including salinity and drought (Bityutskii et al., 2017; Cooke and Leishman, 2016; Coskun et al., 2016; Etesami and Jeong, 2018; Etesami et al., 2020a; Liang et al., 2007; Van Bockhaven et al., 2013; Thorne et al., 2020).

Silicon is the second most common constituent of soils after oxygen. It has a strong affinity with oxygen and thus mostly exists as silica (SiO₂) or silicate (SiO₄²⁻). It is found as a compound of many minerals (Epstein, 1999). Despite its abundance, most Si in soils is not readily available for plants to absorb (Epstein, 1999) and plants take up Si in the form of monosilicic acid or orthosilicic acid (H₄SiO₄). Plants have highly varying capacities to accumulate Si and tissue contents vary between 0.1 to 10.0% dry weight (Epstein, 1994; Epstein, 2009; Hodson et al., 2005; Ma and Takahashi, 2002). This difference is attributed to Si uptake capacity in the roots (Takahashi et al., 1990), and it has been argued that a limited capacity to absorb Si may limit the beneficial effects of this element (Anda et al., 2016; Coskun et al., 2019; Thorne et al., 2020).

To benefit from Si, plants must transport it from the soil solution to various tissues (Coskun et al., 2019). It is unknown to what extent Si must be accumulated to cause maximum benefits; in accumulators like rice, this may depend on many factors including plant species and cultivar (Thorne et al., 2022). The mechanism of plant Si uptake differs from one plant to another (Pavlovic et al., 2021) but a multitude of studies has shown an important role for several aquaporin type transporters. Data from rice, cucumber, tomato and a range of other species show Si uptake is mainly mediated by Lsi1 (‘low silicon 1), an aquaporin type protein that provides a passive mechanism for Si uptake (Ma et al., 2006) whereas carrier type anion transporters such as Lsi2 are
mainly responsible for Si release (Ma et al., 2007; Thorne et al., 2020). Other Lsi isoforms such as Lsi6 in rice (Yamaji et al., 2008) may be involved in processes such as Si translocation from root to shoot (Ma et al., 2006; Ma et al., 2007). Species dependent difference in Si accumulation may to some extent originate from differences in the densities of these various transporters (Mitani and Ma, 2005) (Fig. 2).

Rice can accumulate silica in tissues to more than 10% of its dry weight (Ma, 2002), a level that is considerably higher than that observed for major nutrients such as N, P, and K. In agricultural settings these high Si values are less often seen, moreover since Si offtake in paddy fields is substantial, thus often creating Si deficiencies (Vandevenne et al., 2015). Fertilization with Si is therefore a common practice in many rice growing countries (Li and Delvaux, 2019).

The limited provision of Si in the soil solution (typically 0.1 to 0.6 mM; Epstein 1994) can lower the capacity of crops to absorb this nutrient. However, studies have shown that AMF present an alternative route for Si uptake that can augment Si accumulation in roots of the AMF host (Etasami et al., 2021; Frew et al., 2017; Frew et al., 2018). The efficacy of this mechanism will be sensitive to many factors that include mycorrhizal colonization, soil pH and CO2 (Basu et al., 2018). *Vice versa*, Si impacts on the AM establishment (Etasami et al. 2021) and recently the interaction between Si and AMF was proposed as a novel research field to improve crop cultivation (Etasami et al. 2021). Indeed, it has been observed that Si and AMs can synergistically improve the growth and yield of plants under salinity and drought stress (Garg and Bhandari, 2016a, b; Moradtalab et al., 2019). For example, Das et al. (2021a) verified that the application of monosilicic acid (300 kg ha\(^{-1}\)) along with mycorrhizal fungal spores (*Glomus* spp.) significantly increased grain rice yield under drought stress. However, such studies are still very rare and this review aims to highlight the importance of combined treatments with AMF and Si, in particular to alleviate salinity and drought stress in rice.

2. Silicon in paddy soils and rice
Silicon present in soil comes in three main forms: (i) liquid (as mono- and polysilicic acids); (ii) adsorbed (in the form of oxides and hydroxides of iron and aluminum); and (iii) solid forms (i.e., poorly crystalline, microcrystalline, amorphous, and crystalline silica) (Sauer et al., 2006) (Fig. 3). During the process of chemical weathering of rocks, silicic acid is released into the soil solution. In addition, Si taken up by plants (biogenic silica; phytoliths) and its recycling play a significant role in generating bioavailable silicic acid (Li and Delvaux, 2019). At a pH value below 9 (pKa=9.8), Si is taken up by roots as the neutral silicic acid (Deshmukh et al., 2013). As a result, all plants grown on such soils have some Si deposits in their tissues (Haynes, 2014; Hodson et al., 2005). Intensive cultivation can lead to large Si offtake which, in combination with the excessive use of chemical fertilizers like N, P, and K, can rapidly cause Si deficient soils (Haynes, 2014; Ma et al., 2008). In general, soils are deemed deficient when accessible Si is less than 50 mg kg⁻¹ soil (Ma and Takahashi, 2002).

In paddy soils, plant available Si can also be low due to (i) biogeochemical immobility; (ii) loss of Si when paddies are drained; (iii) adsorption of Si to surfaces of Fe-hydroxides when the soil conditions become aerobic (Haynes, 2014; Cornelis and Delvaux 2016); and (iv) Si offtake, i.e. removal of Si in harvested tissues. The latter can be considerable and amounts to ~0.5-1.0 tonne of SiO₂ per hectare relative to a total rice harvest of ~5 tonnes (Klotzbücher et al., 2016). In combination, the factors listed above have ensured that Si deficiency is now a restraining factor in crop production in many areas, in particular for Si-accumulating crops like rice (Klotzbücher et al., 2016; Ma et al., 2008). Consequently, application of Si-fertilizers is required to produce better yields.

In rice and most other grasses, the shoot is the tissue where more than 90% of Si is deposited (Ma and Takahashi, 2002). Most of this stored Si is in the form of polymerized amorphous silica, as illustrated by Li et al. (2014). These authors reported that the amorphous silica is deposited mainly in cell walls of epidermal cells of leaves, sheath, roots and hulls of grains. The deposited silica in the cell walls forms two double layers with cuticle and cellulose in rice sheaths and leaves. Thus Si deposition improves defence against various pests and diseases (Ma and Takahashi, 2002; Ma and Takahashi, 2002).
and Yamaji, 2006) while increased rigidity helps to avoid lodging (Epstein, 1994; Ma and Yamaji, 2006).

3. Arbuscular mycorrhizas and rice

Arbuscular mycorrhizal symbiosis is one of the most common ways by which plants mitigate biotic and abiotic stresses. The symbiosis has traditionally been associated with an improved acquisition of nutrients and water, but recent research suggests a more complex picture. For example, not only are AMs involved in the absorption, translocation, use efficiency, and cycling of various nutrients (e.g., Cu, Fe, K, N, P, Zn, etc.), they also impact on general physiological processes such as enzymatic activity, photosynthesis, respiration, and plant metabolism. Not surprisingly then, AMs affect the plant’s capacity to fend off diseases and pathogenic organisms and abiotic stresses (Fay et al., 1996; Hashem et al., 2018; Kumar and Verma, 2018; Latef et al., 2016; Malhi et al., 2021; Ortas et al., 2011; Romero-Munar et al., 2017; Smith and Read, 2010). Rice, which is mainly cultivated in waterlogged conditions that are presumably less favorable for AM development, has received relatively little attention in this respect (Mbodj et al., 2018). However, under waterlogged soil conditions, AMs can survive by carrying out gas exchange via the rice root aerenchyma (Mbodj et al., 2018). In addition, climate change and increased water scarcity are more and more forcing rice cultivation towards non-flooded conditions, therefore giving renewed impetus to study rice-AM symbioses (Nakagawa and Imaizumi-Anraku, 2015). AMF have been reported to associate with both upland and lowland rice (Chareesri et al., 2020; Lumini et al., 2011; Parvin et al., 2019; Vallino et al., 2014; Watanarojanaporn et al., 2013) with the most common species being *Glomus mosseae, G. geosporum, G. intraradices, Acaulospora* sp., and *Scutellospora* sp. (Gosling et al., 2006; Maiti et al., 2013; Tisarum et al., 2019; Zhang et al., 2015).

4. The roles of Si and AMs in alleviating drought and salinity stress in rice
The use of either Si or AMs on their own has been proposed to stimulate plant growth during salinity and drought stresses (Bakhat et al., 2018; Etesami and Jeong, 2018, 2020; Etesami et al., 2020a; Etesami and Shafiei, 2020; Evelin et al., 2019; Hameed et al., 2014; Porcel et al., 2012; Ranjan et al., 2021). As illustrated in Table 1, the potential of Si and AMs to improve productivity of rice during periods of salinity and drought has been widely reported and some of the main underlying mechanisms (Fig. 4) are briefly discussed below.

4.1. **Alleviation of osmotic stress**

Drought and salinity cause osmotic stress in plants, leading to inhibition of water and nutrient uptake, and subsequent reduction of cell growth and leaf development (Horie et al., 2012). Osmotic stress is one of the first symptoms of increased salinity but this is further exacerbated in the longer term by ionic stress (mainly Na⁺ and Cl⁻), and leads to early senescence of older leaves (Amirjani, 2011). One of the ameliorative effects of Si and AMs on drought and salinity stress has been related to osmotic stress alleviation, by augmented water uptake and reduced water loss which are further discussed below (Evelin et al., 2009; Latef et al., 2016; Yan et al., 2020).

4.1.1. **The accumulation of compatible organic solutes**

Rebalancing of osmotic relations critically depends on synthesis and accumulation of compatible solutes such as proline, glycine betaine, trehalose and polyols (Ashraf and Foolad, 2007; Blum, 2017; Chen and Murata, 2002; Javot and Maurel, 2002). An increasing number of studies indicates that applying Si promotes the accumulation of osmolytes in rice when plants are exposed to salinity and/or drought (Abdel-Haliem et al., 2017; Chen et al., 2018a; Kuhla et al., 2021; Ming et al., 2012; Sonobe et al., 2010). The accumulation of osmolytes involves not only osmotic adjustment but also detoxification of reactive oxygen species (ROS), maintenance of membrane integrity, and stabilization of proteins/enzymes, contributing to drought and salinity tolerance (Abbas et al., 2015; Wang et al., 2021). Silicon also benefits the activities of enzymes involved in oxidative stress signaling and those that control vital plant activities like starch and sucrose metabolism. For example, the activities of enzymes such as sucrose synthase, sucrose phosphate
synthase, sucrose invertase, and sucrose synthase are affected by Si in both leaves and roots of salinity-stressed seedlings (Zhu et al., 2016).

Arbuscular mycorrhizas are also known to impact on osmotic balance in the host plants via increased accumulation of compatible osmolytes (Evelin et al., 2009; Latef et al., 2016; Ren et al., 2019; Santander et al., 2017). For example, proline is a widely occurring osmoprotectant in response to water constraints (Hare et al., 1998; Shirmohammadi et al., 2020) and salinity stress (Munns, 2005). Arbuscular mycorrhizas have been shown to stimulate proline production during stresses (Evelin et al., 2013; Garg and Manchanda, 2009; Mo et al., 2016; Yooyongwech et al., 2013), significantly improving rice plant resistance to drought stress (Kavitha Mary et al., 2018; Tisarum et al., 2019). In another study, plants colonized by *Funneliformis mosseae* exposed to salinity produced higher proline levels than non-colonized plants (Sheng et al., 2011). These findings suggest that mycorrhizal plants have a higher capacity for osmotic adjustments.

Sugars are another group of compounds that function as osmoprotectants (Abdel Latef and Chaoxing, 2014; Sheng et al., 2011). Osmotically stressed mycorrhizal plants increase the accumulation of total soluble sugars as a defense mechanism (Porcel and Ruiz-Lozano, 2004; Talaat and Shawky, 2011). The increased sugar accumulation in the mycorrhizal plants under osmotic stress was due to the increased photosynthetic capacity (Sheng et al., 2008; Wu et al., 2010). Organic acids also play an indispensable role as osmotically active metabolites in unfavorable conditions and are implicated in the osmotic adjustment of the plant’s vacuole (Hasegawa et al., 2000; Yang et al., 2007). At several tested salinity levels, the total organic acid concentration was found to be significantly raised in mycorrhizal plants when compared to non-mycorrhizal plants (Sheng et al., 2011). Mycorrhizal plants showed increases in acetic, citric, fumaric malic, oxalic, propionic, and valeric acids (Rozpâdek et al., 2016; Sheng et al., 2011).

In all, the above findings indicate that both Si application and AM establishment benefit plants during drought and salinity by improving osmotic adjustments and that this occurs via increased
biosynthesis of compatible solutes. However, it remains to be discovered how such different processes (Si nutrition and AM formation) can resemble each other in their outcomes.

4.1.2. Retention of plant water balance

Under drought-stressed conditions or low humidity, Si increases the water retention (Ma and Takahashi, 2002) (Fig. 5). In part, this is achieved by reducing cuticular water loss by forming silica-cuticle double layers under the leaf epidermis. In addition, some studies have shown reduced stomatal conductance after Si treatment, and increased root water uptake, further limiting water loss (Gong et al., 2003; Gong et al., 2006b). Silicon can also induce changes in lignin and suberin deposition which reduces the rates of water loss but in other cases the opposite was observed and Si was shown to increase transpiration (Hattori et al., 2005; Sonobe et al., 2010).

Reduction of both water uptake and transport will depend on aquaporins (AQPs), ubiquitous water channel proteins that conduct transport of water and small solutes across membranes (Maurel et al., 2008; Rios et al., 2017). Water moves within roots both radially from the root surface into xylem vessels, and axially along the xylem (Steudle and Peterson, 1998). AQPs mainly function in symplastic radial water movement (Chaumont and Tyerman, 2014). Over 30 AQP genes have been identified in the rice genome, however, only a few of them respond to stresses such as salinity. For instance, several rice tonoplast AQPs were significantly up-regulated by high salinity in both shoots and roots (Li et al., 2008). The expression of OsPIP 1–3 (a plasma membrane located AQP) was induced by salt treatment in leaves and roots of two-month-old rice seedlings (Abdelkader et al., 2012). Moderate expression of OsPIP1;1 improved rice salt tolerance and water conductance (Liu et al., 2013). Some studies suggest that Si can affect root water uptake via increasing the expression of AQPs, especially under drought stress conditions (Kaldenhoff et al., 2008; Liu et al., 2015; Zhu et al., 2015). In drought stressed plants, Si application markedly enhanced AQP expression via the upregulation of the SbPIP1;6, SbPIP2;2, and SbPIP2;6 genes, which encode plasma membrane AQPs (Chen et al., 2018a; Liu et al., 2014; Liu et al., 2015). Such transcriptional upregulation would raise the root hydraulic conductance and hence water influx. In addition,
water uptake through AQPs in rice was also improved by foliar Si application, possibly via reducing production of the reactive oxygen species $\text{H}_2\text{O}_2$ (Abdel-Haliem et al., 2017).

Modifying root characteristics such as hydraulic conductivity can improve the osmotic stress tolerance levels (Evelin et al., 2009). The above findings point to Si dependent improvement in root hydraulic conductance in rice plants under water-deficit and salt stress (Wang et al., 2021). For example, Hattori et al. (2008) reported that Si application enhanced root hydraulic conductance. Sonobe et al. (2010) further suggested that the improvement of this parameter could occur in a radial direction in roots rather than axially. Nevertheless, the influence of Si on transpiration and its role in stomatal function are controversial (Agarie et al., 1998; Gao et al., 2006). It is clear that, under water deficiency, if Si reduced transpiration, an increase in water use efficiency followed by protection against wilting would occur (Gao et al., 2005). However, if transpiration is increased, accompanied by higher root hydraulic conductance (Sonobe et al., 2010), water use efficiency (WUE) may increase since elevated photosynthetic rates can be achieved. Furthermore, the impact of Si on AQP activity needs explaining as no mechanism has yet been forwarded that explains how Si can influence gene transcription.

Arbuscular mycorrhiza formation is also known to affect water absorption by the host via transfer through the AM hyphal system (Duan et al., 2021; Evelin et al., 2009; Ren et al., 2019). For example, in a study by Duan et al. (2021), the inoculation of *Funneliformis mosseae* significantly improved the WUE of drought-stressed plants. However, the effect of this AMF on the WUE of well-irrigated plants was moisture-dependent. The enhanced water status of mycorrhizal plants may be due to the ability of the fungi to take up water from a wider rhizosphere and via access to smaller soil pores (Augé, 2001; Bárzana et al., 2012; Ruiz-Lozano, 2003). AM plants inoculated with *Glomus claroideum*, *G. mosseae* *G. coronatum*, and *G. intraradices* all showed a considerable raise in water uptake (Marulanda et al., 2003).

AQPs may be important for the AM benefits that have been observed described; Colonization by AMF differentially affected expression of plasma membrane and tonoplast aquaporins, consequently improving plant water status (Evelin et al., 2019). The first aquaporin from an
Arbuscular mycorrhizal fungus (*GintAQP1*) was cloned by Aroca et al. (2009) and they found evidence that the fungal AQP could compensate for the drought-induced down-regulation of host plant AQPs. These authors also observed that osmotically unstressed parts of the mycelium saw an upregulation of *GintAQP1* expression compared to parts of the mycelium that were stressed. This implies that unstressed and stressed mycelium may communicate with each other. *GintAQPF1* and *GintAQPF2* are two AQPs present in the AMF *Rh. intraradices* (Li et al., 2013b) whose expression is upregulated during osmotic stresses (Li et al., 2013a).

Arbuscular mycorrhizal fungi may also improve soil characteristics in a way that indirectly reduces osmotic stress for plants (Martin et al., 2012). Soil physical improvements occur through the interaction between soil particles and extraradical mycelium to form stable aggregates that contribute to water retention (Mardhiah et al., 2016). AMF release hydrophobic organic products like glomalin (‘glomalin-related soil protein’ GRSP), mucilage, and polysaccharides into soils (Singh et al., 2013). Such compounds take part in carbon sequestration and the formation of stable-aggregates (Tisdall and Oades, 1982). The stable aggregates boost water penetration and maintenance, slowing down the rhizospheric water deficit (Manoharan et al., 2010; Rillig and Mummey, 2006). In a recent investigation, Zhang et al. (2017) observed that in the rhizosphere soil of *Poncirus trifoliata* plants growing in saline conditions, inoculation with *Diversispora versiformis* resulted in a higher GRSP amount than that of non-colonized plants, which was also connected with a greater amount of water-stable aggregates. Zou et al. (2014) additionally discovered a high correlation either between the amounts of GSRP and water stable aggregates, or between the amounts of GRSP and soil available water. These findings highlight that GSRP is important for plants to cope with osmotic stresses in soil. They also suggest that some of the processes by which Si and AMs increase drought and salinity tolerance are complementary and their combined application may even result in synergistic effects.
4.2. Reduction in ion toxicity

Salinity stress is usually associated with an excessive amount of NaCl which has the potential to cause “ion toxicity” or “ionic stress” (Munns and Tester, 2008). Ion toxicity can be directly related to deleterious effects of high Na⁺ and Cl⁻ concentrations. However, Na⁺ and Cl⁻ accumulation also interferes with the acquisition and physiological roles of essential ions like K⁺, Ca²⁺ and NO₃⁻ an aspect of salt stress that is often termed “nutritional stress”. Recently, Zhao et al. (2020) therefore proposed that the term “ionic imbalance” is more appropriate as it covers both direct and indirect manifestations.

Key factors that impact on ion toxicity are the ion influx at the root-soil boundary, removal mechanisms to protect the cytoplasm (e.g., Na⁺ efflux from root symplast into the soil solution), compartmentation of Na⁺ and Cl⁻ in the vacuole and partitioning between organs such as preferential storage in roots rather than shoots, or in older leaves (Maathuis, 2013). Two major mechanisms for Na⁺ entering roots are nonselective cation channels (NSCCs) and high-affinity K⁺ transporters (HKTs) (Kronzucker and Britto, 2011; Maathuis, 2013).

Si has been shown to reduce Na⁺ and Cl⁻ translocation from roots to shoots (Gong et al., 2006b; Krishnamurthy et al., 2011; Saqib et al., 2008). In rice, the inhibition of Na⁺ and Cl⁻ accumulation by Si may be the result of increased suberization of the root endodermis and exodermis. The subsequent formation of a physical barrier in the endodermal and exodermal Casparian bands reduces apoplastic (“bypass”) flow of ions, thereby preventing the accumulation of Na⁺ and Cl⁻ ions in the shoot (Krishnamurthy et al., 2011).

It has also been suggested that Si stimulates H⁺-ATPase activity in the root plasma membrane (Liang et al., 2005). Such increased H⁺-ATPase activity may accelerate K⁺ import into the root. This helps to maintain a high K⁺:Na ratio, a parameter that promotes ion and nutritional balance.

Arbuscular mycorrhiza formation can help reduce Na⁺ uptake of the host plant and increase K⁺ uptake under saline conditions (Estrada et al., 2013; Evelin et al., 2019; Mbodj et al., 2018). This feat is linked to the ability of AMF to selectively take up and translocate K⁺ to the host plant while
avoiding Na\(^+\) uptake (Evelin et al., 2009; Hammer et al., 2011; Porcel et al., 2012). In addition, expression analyses of Na\(^+\) transporters suggested that AM symbiosis can limit toxic Na\(^+\) effects in shoots by favoring Na\(^+\) sequestration in root vacuoles (Porcel et al., 2016). In some cases AM formation has also been shown to induce the expression of genes involved in Na\(^+\) extrusion to the soil solution, K\(^+\) acquisition (by phloem loading and unloading) and K\(^+\) release into the xylem. Combined, these transcriptional changes promote maintenance of a favorable Na:K ratio (Evelin et al., 2019). In rice, AMs decreased the toxicity of Na\(^+\) and Cl\(^-\) by increasing plant biomass (Porcel et al., 2015) and subsequent dilution of Na\(^+\) and Cl\(^-\) (Talaat and Shawky, 2011). Furthermore, AMs stimulate host plants to retrieve Na\(^+\) from the xylem, and divert it away from photosynthetic tissues (Evelin et al., 2013). For example, mycorrhizal rice plants can compartmentalize Na\(^+\) into vacuoles via up regulation of OsNHX3 (sodium/hydrogen exchanger), and mediate efflux of Na\(^+\) from cytosol to the apoplast via increased activity of OsSOS1 (salt overly sensitive) and OsHKT2;1 (high affinity potassium transporter) (Porcel et al., 2016).

4.3. Alleviation of oxidative stress

Oxidative stress is a phenomenon caused by an imbalance between production and detoxification of ROS. This balance is readily disturbed during abiotic stresses such as drought and salinity. Oxidative stress reduces membrane integrity (causing ion leakage), leads to protein and lipid peroxidation and generally damages macromolecules that are essential for plant growth and development (Egert and Tevini, 2002). The antioxidative processes that reduce ROS in plant cells include both enzymes like superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), and non-enzymatic compounds such as ascorbate (AsA), glutathione (GSH), tocopherols, and carotenoids (Gong et al., 2005; Shi et al., 2014). Many studies provide evidence that Si alleviates oxidative damage under salinity and drought stress via modulating plant antioxidant defense systems based on enzymatic or non-enzymatic constituents (Etesami et al., 2020a; Kim et al., 2017). Silicon also helps plants maintain membrane function such as selective permeability and reduces the malondialdehyde (MDA) levels, the end product of lipid-peroxidation (Gong et al.,
Despite this multitude of sources attesting to the beneficial effects of Si with regard to amelioration of drought and salt-induced oxidative stress (Cassol et al., 2020; Kumar et al., 2019a; Ming et al., 2012; Rachmawati et al., 2020; Yan et al., 2020), the mechanisms remain largely unknown. It has been suggested that Si is involved in regulating the expression of genes that encode antioxidant enzymes, such as TaSOD, TaCAT, and TaAPX (Gong et al., 2008). Moreover, exogenous application of Si during drought stress was found to affect transcription of enzymes involved in the ascorbate-glutathione cycle and in flavonoid secondary metabolism (Gong et al., 2008). Silicon induced biosynthesis of compatible solutes (see section 4.1.1) is another strategy by which plants can reduce oxidative stress.

Excess ROS may also negatively regulate the activities of plasma membrane AQPs (Shi et al., 2016). AQPs phosphorylation status and intracellular trafficking are regulated by ROS-dependent signaling mechanisms (Boursiac et al., 2008). Therefore, the regulation of water movement by Si is directly affected by the ROS-mediated process. In addition, root hydraulic conductance can be inhibited by high exogenous hydrogen peroxide (H₂O₂) levels, which are correlated with membrane electrolyte leakage and ROS levels (Benabdellah et al., 2009). Interestingly, hydrogen peroxide is also involved in the formation of suberin lamellae, which form a hydrophobic barrier in the endodermis and exodermis of roots (Razem and Bernards, 2002). Under stress conditions, Si application reduces H₂O₂ production and suberin lamella formation and further raises water permeability (Shi et al., 2016).

Arbuscular mycorrhizas are known to stimulate the activities of antioxidant enzymes (Ait-El-Mokhtar et al., 2020; Evelin et al., 2019; Talaat and Shawky, 2014). This includes antioxidant enzyme such as SOD, CAT, POD, and APX (Hajiboland et al., 2010; Hegazi et al., 2017; Latef and Chaoxing, 2011; Porcel et al., 2012; Wu et al., 2013). In previous studies (Ruíz-Sánchez et al., 2011; Ruiz-Sánchez et al., 2015), rice plants were exposed to drought stress and the results showed that AMs diminished the accumulation of H₂O₂ in the plant and diminished oxidative damage to lipids due to increased accumulation of the antioxidant glutathione. In fenugreek, colonization by
AMF also increased the concentrations of antioxidant molecules such as α-tocopherols, AsA, GSH, and carotenoids (Evelin and Kapoor, 2014).

4.4. Root morphology adaptations

Roots form the plant’s structure responsible for uptake of water and nutrients and hence are crucial for enhancing plant resistance to salt and drought stress. Salinity causes soil compactness and hardness upon which plants cannot establish an effective root system (Machado and Serralheiro, 2017). In addition, salinity and drought stress result in a decline in primary root growth due to salt and drought stress-induced inhibition of cell division and elongation, while lateral root development gets initiated (Jung and McCouch, 2013; Rahnama et al., 2011). In many plants, Si is important for root development and water uptake under drought stress conditions (Hattori et al., 2003; Hattori et al., 2008). For instance, Si application affects polyamine (PA) and 1-aminocyclopropane-1-carboxylic acid (ACC) levels under drought stress conditions to increase root growth and thus a higher root:shoot ratio (Yin et al., 2014). Silicon-mediated changes in rice root development also increase its endodermal silicification and suberization (Fleck et al., 2011; Lux et al., 2002), therefore enhancing the capability of water retention to overcome the effects of drought stress.

Establishment of AMs can also improve a plant’s adaptive ability by modifying the root architecture (e.g., an increase in the length, surface area, and projected area of the root) (Harris-Valle et al., 2018; Kapoor et al., 2008; Kumar et al., 2010). Such adapted root systems enable the plant to forage for water and minerals in relatively non-saline areas until exploitation of high salt areas becomes inescapable (Alqarawi et al., 2014; Campanelli et al., 2013). Arbuscular mycorrhizal symbiosis increased rice root branching, producing large lateral roots via mechanisms that possibly involved AMF signaling molecules and/or changes in plant nutrient status (Paszkowski and Gutjahr, 2013; Vallino et al., 2014). This AM-associated root system architecture may be particularly benefiting drought stressed rice since lateral roots typically form...
the predominant sites for water absorption (Ahmed et al., 2018; Henry et al., 2012; Ruiz-Sánchez et al., 2011; Ruiz-Sánchez et al., 2010; Ruiz-Sánchez et al., 2015).

4.5. Regulation of phytohormone biosynthesis

Plant hormones are essential components of plant responses to abiotic stress (Ryu and Cho, 2015). Plant growth regulators (PGRs) such as methyl jasmonate (MeJ), abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), gibberellins (GAs), ethylene (ET), and indole-3-acetic acid (IAA), can affect plant tolerance to salinity and drought via a multitude of pathways, tissues and interactions (Etézami and Jeong, 2018; Fahad et al., 2015; Wani et al., 2016). For example, in response to salinity, GA levels in soybean plants were down (Lee et al., 2010) and in general, salinity and drought stresses adversely affect plant hormonal balance (Fahad et al., 2015). Salinity and drought typically lead to production of higher ACC levels, resulting in higher ET concentrations that ultimately reduce the growth and yield of plants (Etézami et al., 2020b). Silicon application can also affect the endogenous phytohormone balance by impacting on GA, JA, SA, and ET (Kim et al., 2014c; Yin et al., 2014). The mechanism of how Si interacts with hormone biosynthesis is not known but, in some cases, may entail modulation of the transcription of genes that are involved in stress-responsive pathways (e.g., JA, ABA, and phenylpropanoid) (Kim et al., 2014b; Manivannan and Ahn, 2017; Shetty et al., 2011; Song et al., 2016). For example, in rice, Si treatment may alter expression of the transcription factors OsNAC5 and OsDREB2A, which triggers the expression of stress-responsive genes that impart tolerance to osmotic stress via ABA-dependent and ABA-independent pathways, respectively (Dubouzet et al., 2003; Hussain et al., 2011). The Si-dependent upregulation of transcription factors could function via cis-elements located in the promoter regions (Manivannan and Ahn, 2017). In other rice studies, SA and MeJ biosynthesis were reduced after Si plus salt application compared to salt treatment on its own, while the reverse was observed for ABA (Kim et al., 2014a; Kim et al., 2014c). Silicon addition also enhanced the drought tolerance of sorghum, at least in part, by regulating the synthesis of polyamines (PAs), as well as ACC (Yin et al., 2014). Furthermore, Si decreased JA contents in
soybean under drought (Hamayun et al., 2010), which suggested Si inhibited an early signaling event required for JA production. In barley plants, Si application affected ABA levels in leaves but the direction of change depended on the presence of potassium (Hosseini et al., 2017). Despite the large amount of literature available on the role of phytohormones in salinity and drought tolerance, this aspect has received little interest in the context of AMs. However, AM formation itself may include ABA, auxin, JA, and SA as signaling molecules (Gutjahr and Paszkowski, 2009; Miransari, 2012). Therefore, it can be postulated that these hormones play significant roles in improving plant tolerance to salinity stress via AMs. In one study, AM colonization significantly altered ABA catabolism and the resulting high ABA, AM plants were more resilient to salt stress (Ren et al., 2018). Arbuscular mycorrhizas also impart positive influence on the endogenous concentrations of GAs (Shaul-Keinan et al., 2002). Based on these studies, there is enough evidence to suggest that Si and AMs could alleviate salinity and drought stress via their effects on phytohormone balance and associated signaling events.

4.6. Improvement in carbon assimilation and photosynthesis

Carbon assimilation and photosynthesis are responsible for a large part of the growth and biomass accumulation of plants (Hussain et al., 2017). Salt and drought stress can decrease the physiological cell activities involved in photosynthesis, mostly due to osmotic stress, nutritional imbalance, and/or nutritional toxicity combined with later oxidative stress (Garg and Bhandari, 2016a). Furthermore, salinity and drought decrease gas exchange, WUE, pigment concentrations (Chla and Chlb), and PSII efficiency thus limiting net CO₂ assimilation (Amirjani, 2011; Hussain et al., 2017). In rice, salinity was shown to cause early leaf senescence and reduced photosynthetic leaf area (Shereen et al., 2005). Silicon application can significantly improve WUE, photosynthetic pigment contents, and photosystem activity. It can increase stomatal conductance and hence gas exchange and net photosynthetic rate (Abbas et al., 2015; Detmann et al., 2012; Gong et al., 2006b; Harizanova et al., 2014; Mateos-Naranjo et al., 2013; Ouzounidou et al., 2016; Pilon et al., 2013;
Rios et al., 2017). Some studies indicate that Si might increase the expression of vital photosynthesis-related genes (Ashfaque et al., 2017; Song et al., 2014) though, as argued above, no known mechanism for this exists. Alternatively, the feedforward stimulation by Si of net assimilation rate of CO₂ may stem from enhanced mesophyll and epidermal conductance which augment chloroplastic CO₂ levels (Detmann et al., 2012). In addition, recent evidence indicates that Si influences photosynthesis via impacting water uptake and transport (Rios et al., 2017).

Silicon application also improves shoot and root remobilization of amino acids and carbohydrates (Detmann et al., 2012; Zhu et al., 2016). For example, the soluble carbohydrate content in stressed-plant leaves decreased drought and salinity after Si application (Silva et al., 2012; Zhu et al., 2016). Detmann et al. (2012) found that with increasing Si application, the contents of glucose, fructose, and sucrose in flag leaf of low-Si mutant rice diminished in response to Si use. Increasing Si accumulation in crops, thus stimulates a high translocation rate of photo-assimilates, resulting in a strengthened carbon sink (Li et al., 2018). From a bigger perspective, applying Si in agriculture helps immobilize the atmospheric CO₂ as photo assimilates.

Arbuscular mycorrhizas also increase photosynthesis (e.g., by increasing stomatal conductance and photosystem II) and regulate hormone levels in the host plant under salinity and drought stress. Formation of AM symbiosis boosts quantum efficiency of PSII under salt stress conditions by increasing antenna proteins involved in transfer of excitation energy (Evelin et al., 2019). A previous study (Porcel et al., 2015) reported that the concentration of chlorophyll a in rice plants inoculated with mycorrhizal fungi was significantly increased at a salinity of 150 mM NaCl. This increase in chlorophyll a concentration was attributed to AM mediated-increased uptake of rice P and Mg. In another salinity stress study, rice was co-inoculated with two different genera of mycorrhizal fungi, *Acaulospora laevis* (BEG13) and *Gigaspora margarita* (BEG34). The AMF increased the total chlorophyll content, K⁺/Na⁺ ratio, root biomass, and grain yield of rice plants compared to the non-inoculated rice plants. In general, rice inoculation with the AMF increased its yield at salinity levels of 75 and 120 mM NaCl by 125 and 143%, respectively, compared to the non-inoculated control treatment (Parvin et al., 2020). In the study of Porcel et al. (2015), rice
inoculated with AMF showed higher photochemical efficiency in CO₂ fixation, which increased the plant's resistance to salinity stress via preventing damage to photosystem reaction centers and permitting better use of light energy in photochemical processes. Indeed, AMF can increase rice photosynthetic efficiency by 40% under drought stress, cause the accumulation of glutathione, and diminish accumulation of ROS. In general, the above-mentioned studies highlight that AMs and Si application are potentially important, sustainable methodologies that can effectively mitigate drought and salinity by improving carbon assimilation and photosynthesis.

4.7. Maintenance of nutrient balance

Mineral nutrient uptake and homeostasis can be disrupted by salinity and drought stress (Chen et al., 2011; Hu and Schmidhalter, 2005; Razzaq et al., 2020). For example, salinity renders P less available to plants due to its precipitation with other cations, such as Ca²⁺, Mg²⁺, and Zn²⁺ (Etesami and Noori, 2019). Saline conditions (osmotic stress) interfere with uptake of NO₃⁻ and NH₄⁺ ions by immobilizing them (Hodge and Fitter, 2010). Furthermore, NO₃⁻ uptake is challenged by Cl⁻ while NH₄⁺ absorption faces competition from Na⁺ at the membrane. The acquisition of micronutrients such as Zn, Cu, and Fe by plants is also negatively affected by salinity (Grattan and Grieve, 1992).

In contrast, the uptake of many nutrients, including N, P, K, Ca, Mg, Fe, Cu, and Mn, has been reported to increase in response to Si application during salinity and drought stress (Etesami and Jeong, 2018; Etesami et al., 2020a; Thorne et al., 2020). One explanation is the Si-stimulated root growth, which increases soil area from which plants may absorb nutrients (Hernandez-Apaolaza, 2014). Silicon’s influence on micronutrient transporters is also expected to be a factor in increasing micronutrient uptake. Silicon addition also impacts on micronutrient mobility; nutrient mobilization via the phloem led to a rise in micronutrient content of seeds and fruits, suggesting a more productive use of available micronutrients (Bityutskii et al., 2014). The latter is exemplified by Si supplementation leading to increased Zn contents of stems, roots, and husks in rice (Gu et
Mechanistically, Si might alter expression of Zn transporters to cause this Zn redistribution (Pavlovic et al., 2013).

Applying Si also decreases soil P fixation and so enhances P bioavailability (Rezakhani et al., 2019, 2020, 2022). For example, Si increased P use efficiency by around 10% (Singh et al., 2005). Under P deficiency, Si also improved the accessibility of internal P by reducing the additional influx of Fe and Mn (Soratto et al., 2019). According to Kostic et al. (2017), Si can also improve plant P uptake via increasing root exudation of organic acids such as malate and citrate that mobilize the rhizospheric P.

As stated above, Si improves K+ uptake, which can in turn stimulate H+-ATPases in plasma membrane to overcome salt stress (Etesami and Jeong, 2018; Liang et al., 2005). The increased K uptake, also enables a high K+/Na+ to be retained which counters Na+ ion toxicity (Xu et al., 2015). For example, rice K content was considerably increased in response to Si application under salinity stress (Ahmed et al., 2019), with K benefitting plant growth, osmotic adjustment, and salinity tolerance. In general, the possible mechanisms by which Si affects mineral nutrient uptake include (i) increasing water uptake and transpiration (Chen et al., 2018a; Liu et al., 2014), thus enhancing mineral nutrient movement from soil into roots; (ii) enhancing ion mobilization in roots by increasing the apoplastic root micronutrient pool and enhancing micronutrient mobilization by chelator compounds (Pavlovic et al., 2013); (iii) stimulating membrane H+-ATPase activity driving mineral nutrient uptake (Liang, 1999); (iv) regulating ion transporter genes in plants (Che et al., 2016; Feng Shao et al., 2017; Kostic et al., 2017; Pavlovic et al., 2013); and (v) enhancing the translocation of metabolites (such as citrate) that contribute to root/shoot ion transport (Hernandez-Apaolaza, 2014).

Similar to Si, AMs can also increase the availability of macro- and micronutrients (Bahadur et al., 2019; Evelin et al., 2019; Porcel et al., 2012; Rapparini and Peñuelas, 2014). The structure of extraradical AMF is much finer than plant roots, so the fungi are able to absorb minerals more efficiently than the plant (Smith and Smith, 2011). It has been estimated that the extraradical
hyphae of AMF can supply up to 80, 25, 10, 25, and 60% of plant’s P, N, K, Zn, and Cu, respectively (Marschner and Dell, 1994). Tisarum et al. (2020) found that the inoculation of upland pigmented rice with *Glomus etunicatum*, *Glomus geosporum*, and *Glomus mosseae* strains improved the uptake of P, K and Ca in the plant under salinity stress. In AM-colonized plants under osmotic stresses, especially in soils where drought affects nutrient diffusion, plants take up an increased amount of mineral nutrients (Marschner et al., 1997). In addition, AMs reduce the Na\(^+\) translocation to crop tissues and thus prevent toxic Na\(^+\) levels. This is because AMF can store such ions in their vacuoles and retain them in structures like vesicles and intraradical mycelium (Augé, 2001; Mardukhi et al., 2011). In the plant host, AMs led to the removal of sodium from the cytoplasm, its accumulation in vacuoles, its retrieval from xylem, and re-circulation from photosynthetic organs to the roots (Estrada et al., 2013; Porcel et al., 2016). In the rhizosphere, AMF enhance nutrient availability by exuding organic acids and polyamines (Evelin et al., 2013; Talaat and Shawky, 2013).

Arbuscular mycorrhizal formation improves P absorption in plants growing under limiting conditions (Bowles et al., 2016; Garg and Manchanda, 2009; Smith and Read, 2008). In rice, AMF can contribute up to 80% to rice P uptake (Yang et al., 2012). Enhanced P acquisition in AM plants is attributed to – (i) increased soil P availability due to secretion of acid and alkaline phosphatases by hyphae; (ii) maintenance of intrinsic phosphate concentration by forming polyphosphates inside the hyphae; (iii) ability of AMF to take up P from lower external concentrations due to the presence of high affinity phosphate transporter genes (*GvPT*, *GiPT*, and *GmosPT*); and (iv) sustained P movement into roots as AMF are capable of accumulating large amounts of absorbed P (Etesami et al., 2021; Evelin et al., 2019).

Other examples where AMs affect nutrient uptake is in the absorption and assimilation of N (Evelin et al., 2019; Govindarajulu et al., 2005; Hodge et al., 2001; Hodge et al., 2010). As an example, Fileccia et al. (2017) demonstrated that higher N uptake in AM plants under salt stress is due to higher expression of nitrate (*NRT1.1, NAR2.2*) and ammonium transporters (*AMT1.1 and*...
AMT1.2 in mycorrhized durum wheat (colonized with a mixture of *Rhizophagus irregularis* and *Funneliformis mossea*).

In summary, increased nutrient concentration in plants induced by AMF may be credited to – (i) a widespread root-hyphal system that increases the foraging area and shortens the path of nutrients into the root (Subramanian and Tenshia, 2009); (ii) fungal mycelium serving as a substrate for nutrients to bind; (iii) AMF-induced changes in the pH of the rhizosphere (Li and Christie, 2001); (iv) increase in sink size of Cu and Zn due to higher shoot P (Liu et al., 2000); and (v) the up-regulation of the expression of transporter genes (Burleigh et al., 2003).

5. Silicon-AM interactions

As mentioned above, Si nutrition can impart significant benefits to plants, but to what extent, may be limited by the plant’s capacity to absorb Si (Anda et al., 2016; Etiesami et al., 2021; Thorne et al., 2022). On the other hand, AMs have been consistently reported to increase Si uptake (Clark and Zeto, 2000; Clark and Zeto, 1996; Garg and Bhandari, 2016a; Garg and Kashyap, 2017; Oye Anda et al., 2016; Yost and Fox, 1982). It is well established that AMF can accumulate Si within their spores and hyphae and transfer it into plant roots which in turn increases the plant's access to Si (Hammer et al., 2011). Silicon accumulation in AMF has been shown for *Glomus etunicatum*, *G. coronatum*, *G. versiform*, *Rhizophagus irregularis* (=*Glomus intraradices*), *Funneliformis mossea* (=*Glomus mossea*), and *Rhizophagus clarus* (=*Glomus clarum*) (Anda et al., 2016; Garg and Bhandari, 2016b; Hammer et al., 2011) but it remains unknown how this Si fraction is passed onto the host.

The increased Si uptake mediated by the presence and activity of mycorrhizal fungi can increase the plant's tolerance to environmental stresses (Etiesami et al., 2021; Nogueira et al., 2002). Hammer et al. (2011) found that hyphae and spores of AMF in saline soils exhibited a higher Si buildup compared to hyphae and spores of AMF in regular growth environments. Clark and Zeto (2000) also observed an elevated Si concentration in AM colonized plants growing in saline soils (Garg and Bhandari, 2016b) and in low-Si soils (Frew et al., 2017). Increased Si can promote tolerance to drought and salinity as discussed in previous sections and benefits may also accrue
since AM formation can enhance lateral root formation (Paszkowski and Gutjahr, 2013) thus adapting root architecture to stress conditions.

*Vice versa*, Si can increase mycorrhizal effectiveness, which is defined as the growth difference between AM and non-AM plants (Etesami et al., 2021; Janos, 2007). Various factors exert influence on mycorrhizal effectiveness, such as fungal species, soil conditions, plant species, and genotype (Tawaraya, 2003). The effect of Si on mycorrhizal effectiveness has yet to be widely explored but in two recent studies, Si applications to crops inoculated with the AMF *Glomus versiform*, *Rh. clarus*, and *Rh. intraradices* increased the mycorrhizal effectiveness compared to AM plants not treated with Si (Hajiboland et al., 2018; Moradtalab et al., 2019).

Mechanisms by which Si improves AM effectiveness have been postulated and include (Etesami et al., 2021): (i) increased photosynthetic rate that provides an increased carbon source for fungi, for example, by boosting leaf chlorophyll contents and stomatal conductance (Guntzer et al., 2012; Hajiboland, 2012) and improving the physical stability of plant leaves to optimize light perception (Botta et al., 2014). In one study Si increased the formation of arbuscules which may have resulted from enhanced plant nutrient uptake and transfer, higher photosynthetic rate, and root growth (Etesami et al., 2021; Oye Anda et al., 2016); (ii) stimulated root growth of AM plants and enhanced uptake and transfer of nutrients, which may promote AMF colonization (Hajiboland et al., 2018). Arbuscular mycorrhizal fungi and Si applications can mitigate the disturbances in nutritional status caused by salinity and drought. Pavlovic et al. (2013) and Dragišić Maksimović et al. (2012) observed that Si use boosted Fe and Zn absorption when at low concentrations in the rhizosphere. Plants with a higher root AMF colonization more efficiently took up and translocated macro-nutrients and micro-nutrients to the shoot of the host (Cakmak et al., 1989; Rouphael et al., 2015); (iii) an increased pool of soluble sugars in the host root, which is important for supporting AMF entry, is another plausible mechanism by which Si promotes AM formation (Moradtalab et al., 2019). This may be due to boosted photosynthetic allocations to roots and/or net CO₂ assimilation, and may in turn help stimulate root growth in stressed-plants. It also contributes to
lowering the osmotic potential and hence boost root water absorption (Moradtalab et al., 2019); and (iv) reduced lignin synthesis and polymerization and/or modified metabolic pathways of phenolics in AM host plant (Hajiboland et al., 2018; Mandal et al., 2010; Rodrigues et al., 2004). Silicon was reported to impact on the metabolism of flavonoid-type phenolics (Rodrigues et al., 2004) which may help facilitate AM initiation (Mandal et al., 2010).

6. Potential synergisms between AMF and Si in alleviating salinity and drought stress

There is evidence that a combined use of AMF and Si leads to better improvement of stress tolerance than either treatment itself (Etesami et al., 2021, 2022; Frew et al., 2017; Frew et al., 2018). For example, a report on rice under drought stress showed that the simultaneous use of Si and AM fungus (Glomus spp.) had the potential to diminish water deficit stress-induced damage to rice growth and yield (Das et al., 2021a). This study showed that the application of monosilicic acid (300 kg ha⁻¹) with Glomus spp. was the most successful in improving rice yield when plants were drought stressed (50% field capacity). In another study with well-watered strawberry plants, a significant increment in shoot growth was observed after Si treatment but the highest shoot biomass production was achieved when AMF (Rhizophagus clarus) and Si were applied together (Moradtalab et al., 2019). In addition, fungal colonization also increased with Si use in this study. In the study of Garg and Bhandari (2016b), it was found that the combined use of Si and mycorrhizal fungus (Funneliformis mosseae) improved soil nutrient status and plant growth and yield characteristics under salinity stress conditions. These authors reported that Si is better than AMF at improving the K⁺/Na⁺ ratio, while AMF are more efficient than Si at enhancing plant growth and productivity. Mycorrhization substantially improved Si uptake, and Si supplementation with mycorrhization significantly decreased Na⁺ levels, enhanced the nutrient uptake, improved photosynthetic rates and stimulated growth and yield.

Another study by the same researchers (Garg and Bhandari, 2016a) showed that the use of Si and mycorrhizal fungi (F. mosseae) synergistically reduced oxidative damage in chickpea plant. In this work, Si was found to diminish the accumulation of stress metabolites and the AM fungus was
involved in increasing the activity of antioxidants. Similar results were obtained after the concomitant use of Si and mycorrhizal fungi *Glomus mosseae* and *Gigaspora gigantean* on watermelon plants (Bijalwan et al., 2021).

In all, these studies suggest that, the combined use of Si and AMF is more beneficial to plant growth than their standalone applications. The findings imply that AMF inoculation can enhance plant Si uptake whereas Si can promote AM formation (Fig. 6).

### 7. Conclusions and future perspectives

Drought and salinity stresses are two of the major agricultural afflictions that reduce rice yield worldwide. The use of Si and AMF are known as two of the most effective and economical ways to enhance plant tolerance to salinity and drought. This review evaluated AM inoculation and Si fertilization alone or in combination as important, sustainable tools to effectively attenuate the damage caused by salinity and water-deficit. The strategy of combining Si and AMF application could be highly useful in boosting rice tolerance, potentially generating synergistic effects since Si may increase AM effectiveness while AMs consistently boost Si absorption. Many of the mechanistic details are as yet to be revealed and are urgently needed to better inform stress management strategies in paddy fields. Understanding how Si and AMs interact at the metabolic and molecular levels would be very helpful. Further investigations using a wider set of AMF and varying Si sources are equally required such as evaluations of AM performance in combination with (insoluble) silicate sources under different field conditions. Detailed cost-benefit analyses should be carried out to assess the economic feasibility of Si and AMF treatments.

### Conflict of interest

The authors have no conflict of interest

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Fig. 1: Effect of salt and drought stress on rice plant. Salt and drought stress cause both osmotic stress (physiological drought), imbalance in nutrients (typically a decrease in nutrient uptake), and oxidative stress, thereby leading to decrease rice growth and yield. In addition, salinity leads to ion toxicity, particularly the accumulation of Na\(^+\) and Cl\(^-\).
Fig. 2: Silicon transport in rice plant. Silicic acid, Si (OH)$_4$, from the soil is transported into the root symplast by the action of aquaporins such as Lsi1 channels. The silicic acid then diffuses across the root into the endodermis. At the endodermis, Lsi2 transports silicic acid into the stelar apoplast from where it diffuses into the xylem and is transported to the shoot in the transpiration stream. The presence of aerenchyma means that Lsi2 is localized at both the exodermis and endodermis. In the shoot, silicic acid is unloaded from the xylem by further aquaporins such as Lsi6 and deposited in the cell walls and in specific silica cells. For more details see Thorne et al. (2020).
**Fig. 3:** Various fractions of silicon (Si) in paddy soil.
Fig. 4: The mechanisms by which silicon and arbuscular mycorrhizal fungi (AMF) alleviate the negative effects of drought and salinity stress on rice plants.

<table>
<thead>
<tr>
<th>AMF &amp; Silicon</th>
<th>Salinity &amp; drought</th>
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| - Maintenance of water uptake  
  - Prevention of water loss in exposed tissues  
  - Accumulation of compatible solutes  
  - Retention of plant water balance | - Osmotic stress  
  (Decreased availability of water to plant roots and plant water uptake) |
| - Retention of nutrient balance | - Disturbance of nutrient balance |
| - Detoxification of reactive oxygen species | - Oxidative stress |
| - Maintenance of ion homeostasis | - Disturbance of intracellular ion homeostasis |
| - Improved root architecture | - Decreased root system architecture |
| - Regulation of biosynthesis of phytohormones | - Disturbance of plant hormonal balance |
| - Improvement in photosynthesis | - Decreased photosynthesis |
| - Induced drought and salinity resistance genes in plant | - Decreased expression of salt and drought stress-responsive genes |
Fig. 5: Possible mechanisms of silicon (Si) that impact on growth and yield of rice plant. Drought and salinity stress cause severe osmotic stress in rice plant, leading to decreased water uptake by the plant. The water deficiency induces the formation of reactive oxygen species (ROS) inside the cell which in turn cause protein oxidation, lipid oxidation (resulting in increased electrolyte leakage out of the cell), and activation of stress response genes. Reactive oxygen species also decrease the aquaporin activity by up-regulating the expression of Plasma membrane Intrinsic Protein (PIPs) aquaporin genes. However, Si enhances the aquaporin activity by up-regulating the expression of PIPs aquaporin genes and alleviating the ROS-induced aquaporin activity inhibition. Silicon also enhances the accumulation of soluble sugars and/or amino acids in the xylem sap by osmoregulation. Silicon activates the K⁺ translocation to the xylem by...
activating the expression of *SKOR* (*Stelar K*⁺ *Outward Rectifier*). The osmolyte accumulations in the xylem sap increase the osmotic driving force. Silicon can increase the root/shoot ratio, which together with enhanced aquaporin activity and osmotic driving force contribute to the improvement of root hydraulic conductance and hence improve plant resistance to water deficiency. Leaf transpiration can be reduced by Si via reduced cuticular conductance and by regulation of stomatal movement. Silicon induced root endodermal silicification and suberization leads to reduced Na⁺ and Cl⁻ accumulation in the shoot. For more details see the text, Chan et al. (2018a), Thorne et al. (2020), and Wang et al. (2021).

**Improved photosynthetic parameters**
- Increased leaf chlorophyll levels
- Increased photosynthetic enzyme activities
- Increased stomatal conductance
- Improved the leaf stability so that leaves are oriented more horizontally

**Mycorrhizal effectiveness**
- Increased uptake and transfer of nutrients for rice
- Stimulated rice root growth
- Regulation of biosynthesis of phytohormones
- Modified phenolic metabolic pathways (e.g., flavonoids) in rice plants
  - Increased root exudates (e.g., sugars, amino acids, carboxylates, etc.)
  - Increased the pool of soluble sugars in the roots

**Fig. 6:** Synergistic role of arbuscular mycorrhizal fungi (AMF) and silicon (Si) in alleviating drought and salinity in rice plant: Si increases the photosynthetic rate such that the fungal partner is able to
receive a greater carbon supply, for example, by increasing the leaf chlorophyll levels, photosynthetic enzyme activities, and stomatal conductance and improving the leaf stability so that leaves are oriented more horizontally. Around 4–20% of photosynthetic carbon is transferred to the AMF, and carbon supply is positively correlated with the hyphal absorption capacity and arbuscule formation. Si also enhances the uptake and transfer of nutrients which can promoted AM formation. Si-induced plant growth is in part attributed to modified plant hormone levels. For example, Si modifies biosynthesis of lignin and other phenolic compounds, such as flavonoids. The latter are known to affect AM formation. Silicon also increases the pool of soluble sugars in the roots, which is crucial for the entry and further establishment in the roots of AMs. Silicon can promote AMF extraradical hyphal growth and allow AMF to explore a greater volume of the mycorrhizosphere. AMF also play a substantial role in Si uptake and its transfer from the fungal cells to the plant root; The AMF solubilized Si is effectively absorbed by rice plants.
Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:
HE wrote the manuscript. ZL, FM, and JC edited and revised and approved the final version to be published. All the authors contributed to the article and approved the submitted version.
Drought and salinity-stressed rice plants

-AMF  -Si  +Si  +AMF  +Si  +AMF

- Facilitation of arbuscular mycorrhizal fungi (AMF) interaction with plant by modification of the phenolic metabolic pathways
- An increase in uptake and transfer of nutrients for plants (Stimulation of the root growth=more root exudates)
- An increase in the net photosynthetic rate (a greater carbon supply for AMF)
- An increase in root system and exudation of organic acids (a greater carbon supply for AMF and to supply more active sites and access for symbiotic AMF association)
- Promotion of AMF colonization

-An increase in the uptake and translocation of silicon (Si) from the external solution to the intraradical mycelium, and its transfer from the fungal cells to the root cells

+, in the presence of
-, in the absence of
### Table 1: A list of studies in which silicon (Si) and Arbuscular mycorrhizal fungi (AMF) was used to alleviate salinity and drought stress in rice plant

<table>
<thead>
<tr>
<th>Stress type</th>
<th>Si/AMF</th>
<th>The content of Si applied</th>
<th>Assay conditions</th>
<th>Observed effects</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>Silicic acid</td>
<td>1.5 mM</td>
<td>Growth chamber</td>
<td>An increase in antioxidant enzymes, transpiration and photosynthesis, and water transfer and a decrease in Na⁺ toxicity, Na⁺ to K⁺ ratio, Na transfer from root to shoot, oxidative damage, and energy cost used for adapting to salinity stress in rice plants treated with Si</td>
<td>Yan et al. (2020)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium metasilicate</td>
<td>0.5, 1.0, or 2.0 mM</td>
<td>Growth chamber</td>
<td>A decrease in sodium accumulation, lipid peroxidation and electrolytic leakage and an increase in antioxidant enzymes in rice plants treated with Si</td>
<td>Kim et al. (2014b)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate solution</td>
<td>50 mL</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in activity of enzymatic and non-enzymatic antioxidants, accumulation of osmolytes such as proline to maintain osmotic pressure inside rice plant cells, and the expression of genes (Lsi1 and Lsi2) involved in Si uptake by rice plant and prevention of sodium uptake by the rice plant</td>
<td>Abdel-Haliem et al. (2017a)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>150 mg kg⁻¹</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in shoot growth, the intensity of net photosynthesis, stomata conductance, the potassium to chloride ratio in shoot, water use efficiency, and transpiration and a decrease in chloride concentration of shoot, and transpirational bypass flow in root (a decrease in the transfer of chloride from the root to the shoot)</td>
<td>Farooq et al. (2019)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>3 mM</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in shoot growth and a decrease in shoot sodium content compared to Si non-treated rice plants</td>
<td>Shi et al. (2013)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>3 mM</td>
<td>In vitro conditions</td>
<td>A significant increase in shoot growth compared to Si non-treated rice plants</td>
<td>Mahdieh et al. (2015)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>3 mM</td>
<td>Pot experiment in greenhouse</td>
<td>A significant increase in shoot growth compared to Si non-treated rice plants</td>
<td>Gong et al. (2006a)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>1.67 and 3 mM</td>
<td>Growth chamber</td>
<td>An increase in shoot growth and a decrease in shoot sodium content</td>
<td>Flam-Shepherd et al. (2018)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Source of Si</td>
<td>Concentration</td>
<td>Experiment Conditions</td>
<td>Effects on Rice</td>
<td>References</td>
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<tr>
<td>Salinity</td>
<td>Silicic acid</td>
<td>8, 100, 200, and 300 mg kg⁻¹</td>
<td>Pot experiment in greenhouse</td>
<td>An increase plant biomass, leaf area, leaf chlorophyll concentration, Si concentration, and superoxide dismutases activity.</td>
<td>Saleh et al. (2019)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>0 and 150 mg kg⁻¹</td>
<td>Pot experiment in greenhouse</td>
<td>A decrease in the absorption of sodium by rice, the activity of antioxidant enzymes ascorbate peroxidase and guaiacol peroxidase, and the intensity of plant transpiration and an increase in leaf relative water content, photosynthetic efficiency (due to higher uptake of Si and K), and the oxidative damage to the rice plant</td>
<td>Farooq et al. (2015)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>2 mM</td>
<td>Pot experiment in greenhouse</td>
<td>A decrease in the accumulation of reactive oxygen species in both salt-sensitive and salt-resistant rice cultivars and an increase in the activity level of all ascorbate-glutathione cycle enzymes and the antioxidant defense mechanisms</td>
<td>Das et al. (2018)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Rice husk ash</td>
<td>0.4 and 8 tons ha⁻¹ (containing 55.02% of SiO₂)</td>
<td>In vitro conditions</td>
<td>An increase in the levels of carotenoids, chlorophyll, and the activity of superoxide dismutase in rice</td>
<td>Lestari and Rachmawati (2020)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>0 or 3 mM</td>
<td>Hydroponic conditions</td>
<td>A decrease in the accumulation of sodium in the shoots, the concentration of sodium in the leaf blades and leaf sheath and an increase in the stomatal conductance of rice seedlings</td>
<td>Gurmani et al. (2013)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium meta-silicate solution</td>
<td>2mM</td>
<td>In vitro conditions</td>
<td>An increase in the carbon flow in the TCA (tricarboxylic acid cycle) cycle, the activity of all enzymes involved in the TCA cycle and a decrease in reactive oxygen species.</td>
<td>Das et al. (2019)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Calcium silicate</td>
<td>0, 50, 75, and 100 mg kg⁻¹</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in the root to shoot dry weight ratio, the K to Na ratio, the number of seeds per spikelet, harvest index, the concentration of P, K, and Si in the roots, straw, leaves, and seeds of rice treated with Si</td>
<td>Ahmed et al. (2019)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Sodium silicate</td>
<td>0, 2, 5, 10, and 15 mM</td>
<td>Growth chamber</td>
<td>An increase in germination percentage, chlorophyll content, activity of superoxide dismutase and peroxidase enzymes, and</td>
<td>Liang et al. (2015)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Salinity Source</td>
<td>Treatment</td>
<td>Conditions</td>
<td>Response</td>
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<tr>
<td>Zinc silicate</td>
<td>0, 50, and 100 μg g⁻¹</td>
<td>-</td>
<td>Soluble protein content and a decrease in malondialdehyde content in Si treated rice plants. An increase in plant height (106 cm), total spikelet number per panicle, 1000-seed weight (21.76 g), shoot biomass (25.62 g), and shoot dry matter (12.86 g)</td>
<td>Tahir et al. (2021)</td>
<td></td>
</tr>
<tr>
<td>Sodium metasilicate</td>
<td>2 mM</td>
<td>In vitro conditions</td>
<td>An increase in proline level, sucrose phosphate synthase activity in shoot, invertase acid activity in root, and starch phosphorylase activity at concentrations of 50 and 100 mM sodium chloride and a decrease in hydrogen peroxide, malondialdehyde, invertase acid activity in shoot, sucrose phosphate synthase activity in root, and catalase (more in the shoot than the root)</td>
<td>Das et al. (2016)</td>
<td></td>
</tr>
<tr>
<td>Calcium silicate</td>
<td>0, 2, and 4 mM</td>
<td>In vitro conditions</td>
<td>An improvement in the anatomical properties of the root (e.g., an increase in root cortical thickness, vascular cylinder diameter (stele), and root diameter) and an increase in suberin and lignin in rice, the development of an apoplastic defense system, and prevention of sodium from entering the vascular cylinder</td>
<td>Rachmawati et al. (2021)</td>
<td></td>
</tr>
<tr>
<td>Rice husk ash</td>
<td>0, 4, and 8 tons ha⁻¹ containing (55.02% SiO₂)</td>
<td>In vitro conditions</td>
<td>A significant increase in superoxide dismutase activity in response to increased salinity tolerance</td>
<td>Rachmawati et al. (2020)</td>
<td></td>
</tr>
<tr>
<td>Sodium metasilicate</td>
<td>2 mM</td>
<td>Growth chamber</td>
<td>Increased the activity of enzymes related to the biosynthesis of polyamines and prevented the activity of enzymes degrading polyamines, which resulted in increased production and accumulation of polyamines in both salinity-sensitive and resistant cultivars</td>
<td>Das et al. (2021b)</td>
<td></td>
</tr>
<tr>
<td>Calcium silicate</td>
<td>0, 2, and 4 mM</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in the activity of superoxide dismutase and catalase enzymes, proline content and a decrease in malondialdehyde content</td>
<td>Fatikhasari and Rachmawati (2020)</td>
<td></td>
</tr>
<tr>
<td>Silicic acid</td>
<td>0.5 mM</td>
<td>In vitro conditions</td>
<td>An increase in salinity tolerance in plants by increasing the activity of ascorbate peroxidase and catalase enzymes and a decrease in hydrogen peroxidase, the accumulation of salts in</td>
<td>Lekklar et al. (2019)</td>
<td></td>
</tr>
<tr>
<td>Condition</td>
<td>Treatment</td>
<td>Amount</td>
<td>Experiment</td>
<td>Description</td>
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<tr>
<td>Salinity</td>
<td>Nano-silica, potassium silicate, and magnesium silicate</td>
<td>50, 100 and 150 mg kg(^{-1}) for nano-silica and 500, 1000, and 1500 ppm for potassium silicate and magnesium silicate</td>
<td>Field experiment</td>
<td>Significant increases in physiological characteristics (chlorophyll content and stomatal conductance), morphological characteristics (plant height, number of buds, leaf area index and dry matter production), chemical composition in leaves (e.g., the content of K, K / Na, and Si), total yield (number of spikelets, weight and length of spikelets, number of grains, and weight of 1000 grains), grain quality characteristics (% hulling, % milling, % head rice, protein, and % amylose), and a significant reduction in the sodium of the leaves, the number of empty seeds, and the whitening of the seeds</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Potassium silicate</td>
<td>0, 0.5, 1.0, 1.5, and 2.0 mM</td>
<td>In vitro conditions</td>
<td>An increase in shoot dry weight, leaf water potential, length, area, volume and root activity, root water uptake, leaf transpiration, and photosynthesis (e.g., by increasing chlorophyll level and efficiency of photosystem II)</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Calcium silicate</td>
<td>198.3 g kg(^{-1})</td>
<td>Pot experiment in greenhouse</td>
<td>An increase in leaf transpiration and photosynthesis and a decrease in the amount of proline, which had increased in drought-tolerant rice</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Sodium metasilicate</td>
<td>0, 0.2, 0.5, 0.8, 1.0, and 2.0 mM</td>
<td>Growth chamber</td>
<td>Elimination of dehydration and chlorosis of rice seedlings and reduced the accumulation of peroxide, which disrupted the photosynthetic system</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>SiO(_2)</td>
<td>0, 75, 150, 300, and 600 kg ha(^{-1})</td>
<td>Greenhouse</td>
<td>An increase in dry matter weight (1 to 6%), spikelet (0.3 to 7.3%), soil fertility (0. to 8%), and grain yield (34 to 45%) compared to rice plants without silicone fertilizer</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Ca and Mg silicate</td>
<td>0, 200, 400 or 600 kg ha(^{-1}), 0 or 350 kg ha(^{-1})</td>
<td>Greenhouse</td>
<td>An increase in plant proline content</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Calcium silicate</td>
<td>0, 2, 1, 4, 6.3, and 8.4 mg Si/10 plants</td>
<td>In vitro conditions</td>
<td>An increase in plant height, total biomass, and grain yield</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>K silicate</td>
<td>0, 2.1, 4.2, 6.3, and 8.4 mg Si/10 plants</td>
<td>Greenhouse</td>
<td>An increase in growth and grain and straw yields and saving 30 to 40% of the water source needed for rice growth</td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Sodium metasilicate and</td>
<td>0.4, 0.8, and 16 g L(^{-1})</td>
<td>Greenhouse</td>
<td>An increase in chlorophyll a and b content, the activity of superoxide dismutase and guaiacol peroxidase enzymes, and dry weight of roots and shoots in rice plant, and a decrease in lipid</td>
<td></td>
</tr>
</tbody>
</table>

Bassiouni et al. (2020)
Chen et al. (2011)
Yang et al. (2019)
Wang et al. (2019)
Ullah et al. (2018)
Mauad et al. (2016)
Nolla et al. (2012)
Ibrahim et al. (2018)
Cassol et al. (2020)
<table>
<thead>
<tr>
<th>Condition</th>
<th>Treatment</th>
<th>Concentration</th>
<th>Location</th>
<th>Effect</th>
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<tr>
<td>Drought</td>
<td>Sodium metasilicate</td>
<td>2.5 mM</td>
<td>Greenhouse</td>
<td>An increase in water content in the roots and leaves, water potential and osmotic potential in roots and leaves, the active accumulation of some osmolytes in the roots and leaves of drought-stressed rice, intensity of photosynthesis, and water use efficiency of rice leaves under drought stress. Ming et al. (2012a)</td>
</tr>
<tr>
<td>Drought</td>
<td>SiO&lt;sub&gt;2&lt;/sub&gt;</td>
<td>200 kg ha&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>Field experiment</td>
<td>An increase in the content of proline, antioxidant enzymes, and rice grain yield by 12%. Kumar et al. (2019a)</td>
</tr>
<tr>
<td>Drought</td>
<td>SiO&lt;sub&gt;2&lt;/sub&gt;</td>
<td>0, 1, and 2 mM</td>
<td>Greenhouse</td>
<td>An increase in root volume and length, dry and fresh biomass of roots and shoots, water content of shoots, chlorophyll a and b, soluble sugars and proline in the plant and a stimulating effect on the growth and metabolism of rice plants. Ramírez-Olvera et al. (2021)</td>
</tr>
<tr>
<td>Drought</td>
<td>SiO&lt;sub&gt;2&lt;/sub&gt;</td>
<td>15 g kg&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>In vitro conditions</td>
<td>An increase in the amount of photosynthesis and stomatal conductance and an improvement in water availability for rice. Kuhla et al. (2021)</td>
</tr>
<tr>
<td>Drought</td>
<td>Funnelliformis mosseae, F. geosporus, Claroideoglomus claroideum, Glomus microaggregatum, and Rhizophagus irregularis</td>
<td></td>
<td></td>
<td>An increase grain yield, leaf P concentrations, stomatal conductance and chlorophyll fluorescence, and levels of IAA. Chareesri et al. (2020)</td>
</tr>
<tr>
<td>Drought</td>
<td>Glomus geosporum, G. etunicatum and G. mosseae</td>
<td></td>
<td>Pot experiment</td>
<td>An increase in concentration of chlorophyll b, net photosynthetic rate, total soluble sugar and free proline, shoot height and number of tillers, grain yield, panicle dry weight, cyanidin-3-glucoside and peonidin-3-glucoside concentrations in pericarp and anthocyanin fortification in rice grain. Tisarum et al. (2019)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Funnelliformis mosseae, Acaulospora laevis, and Gigaspora margarita</td>
<td></td>
<td>Pot experiment</td>
<td>An increase in total chlorophyll concentration (photosynthetic efficiency), shoot K&lt;sup&gt;+&lt;/sup&gt;/Na&lt;sup&gt;+&lt;/sup&gt; ratio, root biomass, spikelet fertility, and grain yield (125 to 143%) and a decrease in shoot Na&lt;sup&gt;+&lt;/sup&gt;/root Na&lt;sup&gt;+&lt;/sup&gt; ratio (restriction in Na&lt;sup&gt;+&lt;/sup&gt; uptake and transport from root to shoot in AMF-inoculated plants. Parvin et al. (2020)</td>
</tr>
<tr>
<td>Salinity</td>
<td>Claroideoglomus etunicatum</td>
<td></td>
<td>Pot experiment</td>
<td>An increase in the actual quantum yield of PSII photochemistry, photochemical efficiency for CO&lt;sub&gt;2&lt;/sub&gt; fixation and solar energy. Porcel et al. (2015)</td>
</tr>
<tr>
<td>Condition</td>
<td>Fungi Species (AMF)</td>
<td>Treatment</td>
<td>Experiment</td>
<td>Result</td>
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</tr>
<tr>
<td><strong>Salinity</strong></td>
<td><em>Glomus etunicatum</em>, <em>Glomus geosporum</em>, and <em>Glomus mosseae</em></td>
<td></td>
<td>Pot experiment</td>
<td>An increase in fructose and free proline, shoot height, flag leaf length, number of panicles, panicle length, panicle weight, 100-grain weight, yanidin-3-glucoside and peonidin-3-glucoside in the pericarp of rice, and anthocyanins enrichment in the pericarp of grains. Application of 300 kg Si ha(^{-1}) increased shoot dry matter by 28% compared with 0 kg Si ha(^{-1}) under limited soil moisture availability of 75% and 50% field capacity. Grain yield was increased by 37% and 39% at 300 kg Si ha(^{-1}) compared with the control in the –AMF and + AMF plants, respectively, under moderate soil moisture level of 75% field capacity. The corresponding increase at 50% field capacity was 52% and 55%, respectively. The results demonstrated a synergistic effect of exogenous application of Si at 300 kg ha(^{-1}) (60 kg ha(^{-1}) soluble Si) and AMF inoculation on rice under water-deficit stress.</td>
</tr>
<tr>
<td><strong>Drought</strong></td>
<td>Monosilicic acid (0, 75, 150 and 300 kg ha(^{-1})) and <em>Glomus spp.</em> (AMF)</td>
<td></td>
<td>Pot experiment</td>
<td></td>
</tr>
</tbody>
</table>