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Silicon by modulating the antioxidant defense system reduces the need for water and potassium: a review

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Potassium (K) deficiency in soils is common across various regions of the world, a problem exacerbated by the progression of drought due to climate change. A sustainable strategy to increase plant tolerance to drought involves the use of silicon (Si) and/or K; however, the biochemical mechanisms underlying this relationship require further elucidation. The objective of this review is to discuss the relevance of drought and nutritional deficiency to oxidative damage in crops, as well as the role of Si and K in the antioxidant defense system to enhance water use efficiency, including future research perspectives on this topic. This article examines the biochemical mechanisms involved in the interaction between Si, K, and the plant antioxidant system, emphasizing their potential to improve productivity with reduced water consumption and to mitigate challenges posed by climate change. The application of Si via fertigation has proven effective in increasing water use efficiency and modulating physiological processes, thereby promoting nutritional balance and antioxidant protection in different crops. The antioxidant effects of Si observed in field trials further reinforce its importance in enhancing physiological and nutritional responses to stress conditions in crops. Efficient Si fertigation may reduce the optimal Si rates compared to bulk applications in rainfed systems; however, it may also increase the risk of Si leaching, underscoring the need for additional research. The synergy between Si and K enhances water use efficiency by stabilizing metabolism and increasing plant resilience under adverse conditions. Future perspectives point to the optimization of Si and K fertigation as a promising strategy for sustainable agriculture, particularly in regions with water scarcity and nutrient deficiencies. The use of Si may also reduce the optimal irrigation requirements for crops without compromising yield, representing a viable alternative for irrigated agriculture that warrants further investigation in different cropping systems.

KEYWORDS

irrigated cultivation, oxidative stress, beneficial element, biochemical mechanisms, antioxidant metabolism

1 Introduction

Freshwater scarcity represents a growing and serious threat to global sustainability, especially in regions that already face water-limited conditions (Aqaei et al., 2020; Hejazi et al., 2023). This problem has worsened alarmingly due to climate change, and consequently we have seen longer, more intense and more frequent periods of water scarcity (Fang et al., 2023; Ingrao et al., 2023; Zahra et al., 2023). This drought problem harms crop productivity and quality by decreasing the water content in plant tissues, limiting metabolic functions and physiological and biochemical aspects in plants (Aqaei et al., 2020; Seleiman et al., 2021).

Water deficit is considered a multidimensional abiotic stress of extreme relevance to agriculture, limiting not only energy production but also global food security (Abbas et al., 2023). This scenario is becoming particularly critical because of accelerated population growth, which is progressively intensifying the demand for food (O'Connell, 2017; Chieb and Gachomo, 2023).

The effects of water deficit stress on plants are severe due to the decrease in water content in the plant (Teixeira et al., 2020), water potential (de Oliveira Filho et al., 2021) and the imbalance in osmotic adjustment (Pei et al., 2009), mainly due to the increase in leaf transpiration (Verma et al., 2021). Under controlled conditions, water deficit generally causes damage to the antioxidant system, decreasing the action of enzymatic and non-enzymatic antioxidant compounds (Seleiman et al., 2021; Weisany et al., 2023; Younes et al., 2024). This impairment promotes oxidative stress, mediated by the excessive production of reactive oxygen species (ROS), such as singlet oxygen ($^1O_2$), superoxide (O_2^{-}), hydrogen peroxide (H_2O_2) or hydroxyl radical (OH^-) in cells (Gratão et al., 2005). In contrast, maize plants grown in the field under water deficit show an increase in the activity of antioxidant enzymes (superoxide dismutase (SOD), ascorbate peroxidase (APX), guaiacol peroxidase (GPOX), catalase (CAT) and glutathione reductase (GR)), and in the content of proline (Yousaf et al., 2022; Al-Mokadem et al., 2023). This increase in antioxidant activity occurred despite an increase in oxidative stress indicators (H_2O, OH^- and Malondialdehyde (MDA) content), and a decrease in water use efficiency (WUE) and photosynthetic activity. Curiously, this activation of the antioxidant defense system was not enough to mitigate the negative effects of water deficit, reflected in the decrease in grain yield and quality. Additionally, in cowpea plants it was observed that water stress under field conditions decreased leaf water potential and increased enzyme activity, reaching 85% in APX and 231% in CAT, as well as the content of proline and soluble sugars (Cavalcante et al., 2024).

The increase in ROS induces the oxidation of proteins, DNA and lipids (Hussain et al., 2020a; Shemi et al., 2021; Yousaf et al., 2022). This occurs due to the transfer of energy to O_2, originating singlet oxygen ($^1O_2$), from the transfer of up to three electrons to O_2, forming superoxide (O_2^-), hydrogen peroxide (H_2O_2) (H and hydroxyl radical (OH^-) leading to lipid peroxidation of cell membranes and other compounds (Gill and Tuteja, 2010). Therefore, cellular detoxification of ROS is an extremely important defense mechanism in plants for resilience to water deficit (Shehzad and Mustafa, 2023).

The plant's antioxidant defense mechanism is primarily based on the action of enzymes such as superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (APX, EC 1.11.1.11) and guaiacol peroxidase (GPOX, EC1.11.1.7), as well as non-enzymatic antioxidants such as proline and phenolic compounds (Hua et al., 2020; Al-Mokadem et al., 2023). SOD acts in the dismutation of O_2^{-} into H_2O_2 while APX and GPX in the detoxification of H_2O_2 transforming it into H_2O (Gratão et al., 2005; Hua et al., 2020). In addition, the contribution of non-enzymatic defense agents, such as proline, which is an essential osmotic agent, play an important role in metabolic signaling, while phenolic compounds which are crucial in detoxifying excess hydrogen peroxide in plant cells (Ahammed et al., 2020; Bashir et al., 2021).

Water deficiency can trigger secondary effects on plant metabolism, limiting the absorption and transport of nutrients, and potassium (K^+) stands out (Hu and Schmidhalter, 2005; Qi et al., 2019). This cation plays a fundamental role in various physiological and biochemical processes in plants, including the regulation of stomatal opening and closing, cell osmotic adjustment, maintenance of water potential and stability of cell turgor pressure (de Mello Prado, 2021; Johnson et al., 2022a), improving water relations and increasing water use efficiency (WUE) in drought-stressed plants (Egilla et al., 2005). However, K deficiency aggravated by water scarcity greatly impairs plant metabolism and resistance by triggering worsening oxidative stress (Johnson et al., 2022a). This effect occurs due to the impairment of stomatal regulation and photosynthetic CO_2 fixation, limiting the conversion of light energy into chemical energy. As a result, there is a reduction in the transportation of photoassimilates through the phloem to the drainage organs (Cakmak, 2005; Sardans and Peñuelas, 2021).

Actions to mitigate the effects of drought on crops and guarantee food and water security in the current and future global scenario are urgent. It is therefore important to seek ways to intensify the rational use of water in agricultural crops (Besharat et al., 2020) and at the same time strategies to increase crop resilience.

Despite the different mechanisms that plants develop to ensure survival in drought conditions (Shehzad and Mustafa, 2023), an additional promising strategy is the use of silicon (Rakesh, 2024). The supply of Si is a beneficial strategy for plants under stress conditions, because it reduces oxidative damage caused by ROS by decreasing the content of H_2O_2, and lipid peroxidation (Rakesh, 2024; Younes et al., 2024). This is due to the multiple benefits provided by Si, including an increase in the plant's enzymatic and non-enzymatic defense system, which work together to protect cell membranes, minimizing oxidative damage resulting from lipid peroxidation (Zargar et al., 2019).

Si can improve different aspects of plant physiology, such as nutrient absorption, photosynthesis, hormone regulation (Pereira et al., 2024) and decrease oxidative damage (Moldes et al., 2013), by inducing the transcription of genes involved in defense responses (Liang et al., 2007; Khandekar and Leisner, 2011; Alberto Moldes et al., 2013). Si can also stimulate K absorption in soybean (Miao et al., 2010), maize plants (dos Santos Sarah et al., 2021), consequently increase chlorophyll content and photosynthetic rates in sorghum (Chen et al., 2016), bean plants (Gonzalez-Porras et al., 2024), and improve water use efficiency and nutritional balance in bean plants grown under field conditions (Teixeira et al., 2024). In this situation, Si is relevant in reducing oxidative stress (Teixeira et al., 2021) as it decreases H_2O_2 concentrations in plant cells (Irfan et al., 2023) due to the regulation of the expression of some genes such as *TaSOD, TaCAT and* TaAPX (Ma et al., 2016). This induces the activation of enzymes responsible for neutralizing and eliminating excess ROS in plant cells (Mahmoud et al., 2023; Sharf-Eldin et al., 2023; Li et al., 2024).

This review is structured into three main sections. The first addresses advances in irrigation for crops, highlighting current challenges, the impacts on both irrigated and non-irrigated systems, and emphasizing the importance of efficient water management in the current context of climate change. The second section discusses the impacts of water deficit on the plant antioxidant system, focusing on the main physiological mechanisms involved in the stress response. Finally, the third section explores the role of Si and K in modulating the antioxidant system to enhance plant tolerance to water deficit, with emphasis on agronomic strategies such as Si fertigation.

For the selection of information, a systematic literature review was conducted using relevant scientific databases (e.g., Scopus, Web of Science, PubMed) with specific search queries combining keywords such as irrigation, fertigation, water stress, silicon, silicates, potassium, plant antioxidant defense, and antioxidant enzymes. Studies published within the last 10 years were selected, with emphasis on experimental research under both field and controlled conditions, aiming for a comprehensive and up-to-date analysis of the topics addressed.

A strategy that is still little discussed is the interaction of Si and K, as these two elements are involved in water use efficiency by modulating the antioxidant defense system - an aspect that becomes even more critical in view of the physiological and biochemical effects triggered by water deficit in plants which is the biggest challenge facing agriculture as climate change advances.

The aim of this review is to discuss the relevance of drought and nutritional deficiency to oxidative damage in crops and the role of silicon and potassium in the antioxidant defense system to enhance water use efficiency, including future research perspectives on this topic. The structure of the review is illustrated in Figure 1.

2 Advances in crop irrigation

The advance of climate change has increased the frequency of drought in different crops, and this has increased the need for irrigation.

Irrigation is an essential agricultural practice to guarantee productivity and food security, especially in regions where rainfall distribution is irregular or insufficient (Darko et al., 2016). With technological advances and increased demand for food, irrigation systems combined with new water-saving strategies have been widely studied and implemented to optimize the efficient use of this resource. In this context, sustainable and innovative technologies are increasingly being developed with the aim of reducing waste and increasing crop yields, especially in bean and maize crops (Darko et al., 2016; Al-Mokadem et al., 2023; Awad et al., 2024).

However, despite its importance, irrigated agriculture is responsible for approximately 40% of global food production, while demanding a significant volume of fresh water - which corresponds to more than 70% of the total available (Elshamly, 2023; Awad et al., 2024). This scenario is even more critical due to the intensification of droughts, which have become the biggest challenge for agricultural production worldwide, especially in arid and semi-arid regions (Ingrao et al., 2023; Awad et al., 2024). In this context, irrigation has become an indispensable tool for guaranteeing the stability of crop production under climate change (Darko et al., 2016), making it essential to develop more efficient and sustainable methods for using irrigation water, thus guaranteeing the maintenance of crop productivity.

The adoption of more efficient irrigation technologies makes it possible to expand the irrigated area and optimize the use of water resources and can increase crop yields by between 10% and 30% compared to non-irrigated systems (Darko et al., 2016), which represents great potential for boosting agricultural production globally, especially of annual maize-bean crops. Research carried out under conditions of water deficiency in common beans indicates that water shortages during critical stages of development, such as flowering and grain filling, can decrease yields by up to 36% (Rivera, 2024), due to interference in pod

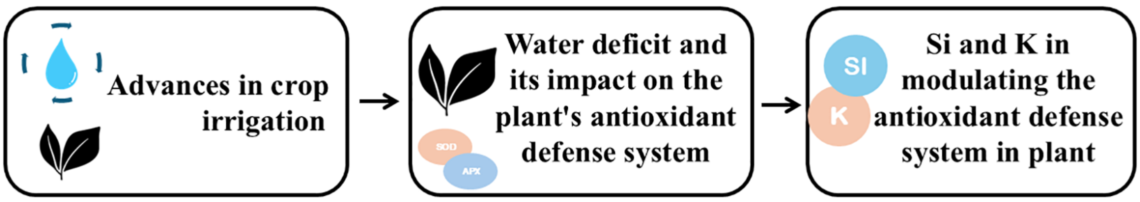

FIGURE 1
Schematic representation of the thematic structure of the review: The figure illustrates the sequential approach about advances in crop irrigation, impacts of water deficit on the antioxidant defense system, and the role of silicon (Si) and potassium (K) in enhancing plant resilience.

formation and grain development (Heshmat et al., 2021). In addition, recent studies have shown that nutrient absorption, photosynthetic rate, relative water content (RWC), shoot biomass and grain yield in bean plants are significantly reduced under conditions of water stress when compared to optimal irrigation (Heshmat et al., 2021; Gonzalez-Porras et al., 2024; Teixeira et al., 2024). Another relevant aspect to consider is the efficiency of water use in the bean crop (Webber et al., 2006; Darko et al., 2016), a fundamental parameter for the sustainability of irrigation. These authors observed that the common bean has lower water use efficiency under water deficit, which suggests that this crop is not as adapted to conditions of water scarcity as other cultivars.

Poaceae are highly sensitive to water stress, especially during the vegetative and reproductive stages (Ge et al., 2012; Al-Mokadem et al., 2023). Water restriction impairs plant development, as it does not meet the water consumption of between 390 and 575 mm of water per year of the crop in drought conditions (Çakir, 2004). There are reports in controlled environment crops that moderate and severe water deficit conditions (60% and 40% of field capacity) cause oxidative stress, increasing the production of reactive oxygen species (ROS) and decreasing growth and yield in different maize hybrids (Anjum et al., 2017; Parveen et al., 2019), and also increase the activity of antioxidant enzymes (SOD, POD, CAT, APX, GR) and the content of proline and phenolic compounds, compared to the optimal irrigation condition (Anjum et al., 2017).

Plants grown in the field under water deficit showed greater oxidative stress due to an increase in MDA, H_2O_2 and OH^-content (Yousaf et al., 2022), a decrease in water use efficiency (WUE) and delayed grain maturation under severe water stress (35% of field capacity) (Ge et al., 2012). In addition, decreasing available soil water (AW) to 80% and 60% decreased plant height by 23% and 42%, ear length and diameter by 43% and 62%; 44% and 70%, the number of grains per year by 14% and 36.08%, and yield by up to 10% and 22%, respectively, compared to 100% AW. In addition, water deficit also decreases chlorophyll content, photosynthetic activity and nutrient content such as N, P, K and Si in grains (Al-Mokadem et al., 2023).

In this context, it is necessary to adopt practices that promote the efficient use of water and the sustainability of production systems, such as investments in research and development of irrigation technologies, combined with proper crop management, which are crucial to guaranteeing food security and the resilience of crop production in the context of climate change.

Techniques such as supplementary irrigation and proper water management are essential to mitigate these effects, such as the adoption of controlled deficit irrigation, precision irrigation systems such as drip irrigation (Sezen et al., 2005, 2008) and the use of cultivars that are more tolerant to water stress (Anjum et al., 2017; Papathanasiou et al., 2022; Mladenov et al., 2023). Other promising strategies to mitigate water deficit include Si fertigation. Studies conducted in different locations indicate that maximum yield was associated with Si application rates of 5.7 to 8.2 kg ha^{-1} in common bean crops (Gonzalez-Porras et al., 2024), 3 mM (SiO_2 nanoparticles) in maize crops (Al-Mokadem et al., 2023),and 6 kg ha^{-1}, 7 kg ha^{-1}, and 8 kg ha^{-1} in common bean crops under different water conditions—namely, 80% (no water deficit) and 60% and 40% (water deficit) of soil water-holding capacity, respectively (Teixeira et al., 2024). However, the number of studies indicating the optimal Si dose for fertigation is still limited to a few soil types, highlighting the need to establish critical levels or sufficiency ranges of available Si in irrigated cropping systems.

One advantage of Si application in irrigated systems compared with rainfed cultivation is the reduction in the optimal Si dose, as more soluble sources are generally used, such as potassium silicate and/or a combination with sodium silicate. Another promising Si source for application in fertigation systems is nanoparticulate silicon dioxide in colloidal suspension. A potential drawback of Si fertigation, which requires further investigation, is the risk of Si leaching, especially in soils with clay content below 35%. Research in this area needs to advance to optimize Si fertigation management without losses in cropping systems. Another concern when using Si in fertigation is the application of solutions with high Si concentrations (>3 mM), as they may present a risk of polymerization, which reduces its availability and plant uptake. Overall, Si fertigation is a promising strategy, but careful management of this beneficial element is essential to prevent losses.

The beneficial effect of nutrient application, such as potassium, is further studied, with many reported results, such as those of Heshmat et al. (2021) in common bean plants and Weisany et al. (2023) in maize plants.

Prospects include the adoption of sustainable technologies combined with more effective irrigation methods, which improve the use of water and fertilizers, contributing to increased agricultural productivity (Yan et al., 2021; Elshamly, 2023; Elshamly and Abaza, 2024). The combination of precision irrigation with fertilizers and biostimulants such as Si is a promising strategy to revolutionize water management in crops by reducing water consumption without compromising growth and production. This is essential to meet the current and future challenges facing agriculture, given the growing need to optimize the use of water resources and ensure environmental sustainability.

3 Water deficit and its impact on the plant's antioxidant defense system

Water deficit is characterized by insufficient fresh water to meet the demands of human activities and ecosystems, resulting in low soil moisture content, which is a consequence of natural climatic events such as droughts (Balint et al., 2013). Droughts represent one of the greatest challenges for agriculture today, being characterized as multidimensional stress due to its recurring nature that is difficult to predict and is not restricted to a specific region or period (Salehi-Lisar and Bakhshayeshan-Agdam, 2016). It is a climatic phenomenon associated with prolonged periods of drought and low rainfall, directly compromising water availability, especially for agricultural activities - a scenario that is intensifying in the face of global climate change (Fang et al., 2023; Ingrao et al., 2023; Zahra et al., 2023).

In agriculture, water deficit can be classified into different stages of stress, mild, moderate and severe, based on the relative water content (RWC) of the plants (Laxa et al., 2019). The authors add that, for example, under conditions of mild stress, the RWC varies between 60-70%, moderate stress between 40-60%, while in severe stress it can drop to less than 40%, compared to the control which is ≥90%. These stages reflect the progression of water deficit severity, which can be reached quickly in soils with low water retention capacity.

Water deficit worsens when water loss through transpiration exceeds absorption by the roots, decreasing leaf water potential (Ψ_{md}), stomatal conductance and carbon assimilation, thus compromising crop growth and yield (Avila et al., 2021). Low water content also affects the activity of saccharolytic enzymes, such as cell wall acid invertases, which reflect in lower carbon partitioning from the leaves to the drain organs (Chen et al., 2019; Du et al., 2020). Under these conditions, the availability of carbohydrates to the reproductive organs decreases due to the greater accumulation of reducing sugars, soluble sugars, and starch in the leaves, which intensifies the generation of reactive oxygen species, leading to oxidative damage (Avila et al., 2021).

Aerobic metabolism naturally results in the formation of highly reactive and toxic molecules in plant cells, called reactive oxygen species (ROS). Under normal conditions, they are produced at low levels in organelles such as chloroplasts, mitochondria and peroxisomes, with photosystems II (PSII) and I (PSI) in the thylakoids of chloroplasts being the main sources of these compounds (Gill and Tuteja, 2010; Sharma et al., 2012).

ROS is a collective term that includes oxygen radicals such as superoxide anion ($O_2^{\cdot-}$), hydroxyl radical ($OH^{\cdot-}$), peroxyl ($ROO^{\cdot-}$), etc., as well as other non-radicals such as singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2) and ozone (O_3), etc (Gratão et al., 2005; Gill and Tuteja, 2010; Sharma et al., 2012; Del Río, 2015). Under conditions of water deficit, the overproduction of these compounds leads to what is known as "oxidative stress", which occurs when the antioxidant defense mechanisms are unable to control the levels of ROS produced (Sharma et al., 2012), indicating that there is an imbalance between production and the ability of the antioxidant defense system to eliminate them efficiently. In high concentrations, these molecules are extremely cytotoxic, causing serious oxidative damage to cells by damaging essential macromolecules, causing lipid peroxidation, protein oxidation, DNA damage, enzyme inhibition, and ultimately programmed cell death (Hussain et al., 2020a; Shemi et al., 2021; Yousaf et al., 2022).

During conditions of water deficit stress, plants tend to present immediate mechanisms to deal with such conditions, the first reaction being the closure of stomata, which is an efficient strategy to reduce water loss through transpiration (Sharma et al., 2012; Ahluwalia et al., 2021). However, this action becomes harmful, because although stomatal closure mitigates transpiration, it limits the entry of CO_2 into the leaves, negatively affecting photosynthesis (Chiappero et al., 2019; Laxa et al., 2019; Abbas et al., 2023). When the light energy absorbed exceeds the capacity to assimilate CO_2 under conditions of water deficit, there is an overproduction of ROS, and this occurs because when CO_2 is in low concentration, there is a process of oxygenation of the enzyme Rubisco (ribulose-1,5-bisphosphate), known as photorespiration, which causes an increase in the production of H_2O_2 in the peroxisomes (Laxa et al., 2019). In addition, the decrease in CO_2 affects the reactions of the Calvin-Benson cycle by decreasing the oxidation of NADPH and the consumption of ATP, leading to the accumulation of electrons and an excessive reduction in the electron transport chain (Chiappero et al., 2019). This results in the reduction of oxygen as an alternative electron acceptor in photosystem I (PSI), generating superoxide anion ($O_2^{\cdot-}$) and H_2O_2, decreasing the regeneration of electron acceptors ($NADP^+$, NAD^+, FAD), which facilitates the transfer of electrons from the electron transport chain to oxygen, leading to greater production of ROS (Robinson and Bunce, 2000; Laxa et al., 2019).

Excessive reactive oxygen species (ROS) in plants cause irreversible damage, including lipid peroxidation, protein damage, and DNA impairment (Gill and Tuteja, 2010; Sharma et al., 2012). The excess of ROS causes considerable damage to proteins, leading to the inactivation of enzymes and increasing their susceptibility to degradation through processes such as nitrosylation, carbonylation, disulfide bond formation and glutathionylation, and proteins can also undergo indirect modifications by conjugating with products resulting from fatty acid peroxidation (Yamauchi et al., 2008). DNA is also compromised by deoxyribose oxidation and chain breaks, which can result in mutations and genomic instability, as well as triggering processes such as apoptosis (programmed cell death), necrosis, accelerated dehydration and, in extreme situations, plant death (Sharma et al., 2012).

Lipid peroxidation is one of the main mechanisms of oxidative damage in biological systems, characterized by the oxidative degradation of membrane lipids, mediated by excess ROS (Gill and Tuteja, 2010; Sharma et al., 2012). It is a process in which highly reactive lipid-derived radicals such as peroxylipids and hydroperoxylipids are produced (Gill and Tuteja, 2010). The effects of this peroxidation include increased fluidity and permeability of the cell membrane, resulting in membrane rupture and leakage of electrolytes and other essential components (Gill and Tuteja, 2010; Sharma et al., 2012).

It has been recognized that the oxidation of polyunsaturated lipids during lipid peroxidation produces various molecules, including small hydrocarbon fragments such as malondialdehyde (MDA). This compound is frequently used as a parameter to quantify cellular damage and to assess plant tolerance to stress caused by water scarcity (Yamauchi et al., 2008; Garg and Manchanda, 2009; Chiappero et al., 2019; Marques et al., 2019). Increased lipid peroxidation has also been reported in many plants under water restriction stress, such as bean (Mombeni and Abbasi, 2019), chickpea (Gunes et al., 2007), sunflower (Gunes et al., 2008), lentil (Biju et al., 2017), sugarcane and energy cane (Teixeira et al., 2022)) and maize (de Sousa Leite et al., 2023).

The excessive accumulation of ROS is neutralized by sophisticated and efficient antioxidant defense systems, which regulate the intracellular levels of these molecules, maintaining a balance between their production and elimination (Gill and Tuteja, 2010). These systems include a variety of enzymes, such as SOD, EC

1.15.1.1, APX, EC 1.11.1.11 and GPOX, EC1.11.1.7, as well as non-enzymatic metabolites (Hua et al., 2020; Al-Mokadem et al., 2023; Shehzad and Mustafa, 2023), such as proline and phenolic compounds. The balance between the generation of ROS and the activity of antioxidant enzymes determines whether cell signaling, or oxidative damage will occur (Sharma et al., 2012; Kaur and Asthir, 2017). According to the same authors, under conditions of water deficit, the imbalance between the accumulation of ROS and the capacity of the antioxidant system can lead to widespread oxidative damage, compromising cell survival.

These components act cooperatively to detoxify cells, neutralizing ROS and protecting them from oxidative damage, thus ensuring the maintenance of essential metabolic functions and plant development (Shehzad and Mustafa, 2023). SOD, EC 1.15.1.1 acts in the dismutation of $O_2^{\,-}$ into H_2O_2 while APX, EC 1.11.1.11 and GPOX, EC1.11.1.7 act in the detoxification of H_2O_2 transforming it into H_2O (Gratão et al., 2005; Hua et al., 2020). In addition, there is the contribution of non-enzymatic defense agents, such as phenolic compounds and proline. The increase in proline concentration is a notable response in plants exposed to water deficit and is considered a versatile plant metabolite, because in addition to being an important Osmo protectant, proline can play a crucial role as a metabolic signal (Ahammed et al., 2020), while also acting to increase the redox potential in cells, contributing to replenishing the supply of $NADP^+$ (Hassine et al., 2008), providing protection against different types of ROS, such as hydrogen peroxide, hydroxyl radicals and also singlet oxygen (Rehman et al., 2021). Phenolic compounds also contribute to the control and elimination of ROS in plant cells, because phenols are secondary metabolites produced by metabolic activities with antioxidant properties, which act by blocking different oxidative reactions, eliminating free radicals, as well as serving as a substrate for some enzymes such as peroxidases (Mukarram et al., 2022).

4 The role of Si and K in modulating the antioxidant defense system in plant tolerance to water restriction

Silicon (Si) is one of the most abundant mineral elements in the earth's crust, after oxygen (Zhu et al., 2020), accounting for up to 28% of the earth's crust, and silicon dioxide (SiO_2) comprises approximately 50-70% of the soil mass (Epstein, 1994). It occurs in many forms in the soil, mainly in the form of silicate minerals, secondary aluminosilicates and different forms of silicon dioxide (Tubaña and Heckman, 2015). In plant tissue, the Si content is between 0.1 and 10% of the dry weight, varying between plant species (Hodson et al., 2005). Based on this, plants were divided into three groups: (i) non-accumulators or excluders; (ii) intermediate accumulators; and (iii) accumulators, which must respectively present the Si content per dry mass corresponding to: <0.5%; 0.5-1% and >1% (Ma et al., 2002). In general, monocot species from the Poaceae family are known as Si accumulators, as they have higher levels of Si accumulation (10-15%) compared to other eudicot species (0.5% or less) (Hodson et al., 2005).

Although it is not considered essential for normal plant development, Si is recognized as a beneficial element, acting significantly in increasing plant resistance to water and oxidative stress in various crops (Weisany et al., 2024), playing a similar role to nutrients such as nitrogen, phosphorus and potassium in strengthening the plant's defense mechanisms, contributing to the stabilization of cell membranes, helping with osmotic regulation and modulating antioxidant compounds (Li et al., 2024; Rakesh, 2024; Weisany et al., 2024). In addition, Si regulates the expression of genes associated with antioxidant defense, helping to maintain the redox balance in stressful situations (Singh et al., 2023; Chen et al., 2024). This is because Si acts to modulate enzymes that fight oxidative stress, inducing the expression of defense genes in various plant species (Liang et al., 2007; Khandekar and Leisner, 2011; Alberto Moldes et al., 2013). Other benefits of Si include the ability to reduce the effects of K deficiency by stimulating its absorption in soybean (Miao et al., 2010) and corn (dos Santos Sarah et al., 2021) plants, increase photosynthetic rates and chlorophyll levels in sorghum (Chen et al., 2016), and modulate the accumulation of polyphenols and their antioxidant action in barley (Benslima et al., 2022) grown in pots.

In legumes grown in field conditions, the supply of Si via fertigation was effective in increasing the efficiency of water use in plants, promoting photosynthetic adjustment (Gonzalez-Porras et al., 2024) and nutritional balance (Teixeira et al., 2024). This effect has also been observed in other plants of the same family, such as in field-grown canola plants, where the application of Si nanoparticles (PSN) increased the activities of antioxidant enzymes (peroxidase (POD) and catalase (CAT)), reduced oxidative damage, improved stomatal conductance, relative leaf water content and fatty acid composition, resulting in better grain oil quality (Alghanem et al., 2025). Similar results were observed in plants of the Poaceae family, such as wheat, suggesting that Si improved water use and grain yield (Johnson et al., 2022b), while in maize plants, Si improved antioxidant enzyme activities (SOD, POD, CAT, APX, GR), non-enzymatic substances and photosynthetic activity (Xu et al., 2022). In addition, the beneficial role of Si has been shown to be effective in different pot-grown species such as sugar cane and energy cane (Teixeira et al., 2022), cucumber (Ma et al., 2004), chickpea (Gunes et al., 2007), sunflower (Gunes et al., 2008), soybean (Shen et al., 2010); tomato (Shi et al., 2016), lentil (Biju et al., 2017) and cowpea (de Sousa Leite et al., 2023).

The interest in Si fertilization is because soils have low available concentrations of the element (Gascho, 2001), and its relevance in mitigating the deleterious effects of water deficit on plants. However, most studies have been carried out in controlled environments growing in containers, and there is still limited research carried out in field conditions (Barão, 2023). Among the sources of Si available for use in agriculture, calcium silicates from a rock (wollastonite) or steel waste have limited solubility, requiring application with incorporation to increase the solubilization process. Field studies have shown evidence of the potential of Si to mitigate the effects of water deficit in wheat plants (Johnson et al., 2022b). The authors observed that the application of amorphous silica significantly reduced the negative effects of water deficit on plant growth and grain yield, attributed to the benefits mediated by Si in improving water use efficiency. Similarly, the exogenous application of Si and SA to plants increased the activities of antioxidant enzymes and the accumulation of osmolytes, decreasing the levels of H_2O_2 and MDA in stressed wheat plants (Maghsoudi et al., 2019).

One strategy to improve the efficiency of Si absorption by the plant would be to use soluble sources in fluid form such as soluble silicates (potassium silicate and sodium silicate) (Liang et al., 2015). And the appropriate use of these sources in solution with concentrations that avoid polymerization has been useful for enhancing absorption and the effects on plant physiology even under conditions of water deficit (Gonzalez-Porras et al., 2024; Teixeira et al., 2024). To this end, the use of fertigation can improve the use of water and fertilizers, contributing to increased agricultural productivity (Yan et al., 2021; Elshamly, 2023; Elshamly and Abaza, 2024). However, inadequate management of this practice can result in losses in soil quality and productivity associated with environmental impacts due to nutrient leaching and aquifer contamination (Yan et al., 2021).

The use of Si is known to optimize gas exchange by forming a physical barrier, reducing transpiration without affecting CO_2 assimilation, favoring stomatal conductance and minimizing oxidative stress by increasing antioxidant enzymes, ensuring cellular integrity and optimal cellular and plant metabolism.

Another important element in increasing water use efficiency is potassium. Potassium (K^+) is a nutrient for plant metabolism, acting as a key regulator in various physiological and biochemical processes (Wang et al., 2013; Johnson et al., 2022a). Its functions include controlling stomatal opening, cell osmotic balance, maintaining water potential and preserving turgor pressure, which are critical factors for the structural and functional integrity of plants (de Mello Prado, 2021; Johnson et al., 2022a). K^+ also contributes to the survival of plants exposed to various biotic and abiotic stresses, such as water deficit (Wang et al., 2013), playing a vital role in activating antioxidant mechanisms and helping to neutralize ROS. This protective action is directly associated with its participation in the transport of solutes across cell membranes and in the synthesis of proteins, fundamental processes for plant growth and development (Sardans and Peñuelas, 2021; Johnson et al., 2022a).

K^+ deficiency, especially when combined with water scarcity, can trigger serious metabolic imbalances, reduce photosynthetic efficiency and plant resistance to adverse conditions (Johnson et al., 2022a). This is because a lack of this nutrient impairs stomatal regulation, affecting the conversion of light energy into chemical energy and the transportation of photoassimilates via the phloem to the reserve organs (Cakmak, 2005; Johnson et al., 2022a). Consequently, there is a decrease in photosynthetic efficiency (Verma et al., 2021), causing serious damage to plant development, resulting in lower biomass accumulation and negatively impacting crop yields.

Studies highlight K's ability to improve water and nutrient absorption, as well as promoting greater plant resilience to limiting water conditions (Alghanem et al., 2025). For example, it has been observed that in sugar beet plants the application of K increased the RWC, decreased membrane damage due to the efficiency of the defense system during water deficit stress (Aksu and Altay, 2020). In maize plants, the application of K^+ was efficient in osmotic adjustment, contributing to higher nutritional quality and grain yield (Hussain et al., 2020b; Ul-Allah et al., 2020).

The joint application of K and Si can promote additive or synergistic effects on water use efficiency by optimizing stomatal function (Kaya et al., 2006), since by decreasing leaf transpiration (Gong et al., 2005), it increases the relative water content in the leaves (Ahmad & Haddad, 2011) without decreasing the photosynthesis rate even under water stress (Zhu & Gong, 2014; Farooq et al., 2016). It is believed that this synergy between K and Si in gas exchange only occurs due to the stability of the plant's metabolism thanks to the action of the antioxidant defense system, but this needs to be better studied. In addition, Si can improve the efficiency of potassium use by plants, favoring its transport and metabolic use (Eneji et al., 2008).

These benefits of Si can increase the leaf area index, reduce the frequency of irrigation and increase productivity per volume of water applied, even in K-deficient areas. It should also be noted that the combined use of K and Si can have a synergistic effect on physiological performance due to the efficient antioxidant defense system, resulting in gains in productivity even under conditions of water limitation and/or deficit irrigation. This Si and K synergy can increase crop tolerance to moderate water deficits and/or water-saving irrigation. The main hypothesis is that this interaction between Si and K may occur because the effect of Si is more pronounced under stress conditions—specifically K deficiency—compared to scenarios of nutrient sufficiency, thereby enhancing its physiological benefits.

5 Future prospects

It is important that silicon researchers focus their efforts on developing innovative strategies based on optimizing Si fertigation with adequate doses to ensure greater nutritional efficiency, minimizing environmental risks and increasing crop resilience and sustainable productivity. More studies are still needed on the effects of Si on enzymatic antioxidative mechanisms in field crops, as different non-nutritional factors are usually interacting with the soil-plant system and these aspects are little known.

Most studies involving Si are associated with Si accumulator species, although there are clear indications of the benefits of Si in the antioxidant defense of non-accumulator species, but more research is needed on these species to better understand the mechanisms involved. Studies on the synergy between Si and K in water use efficiency are lacking at a physiological and biochemical level, and further research is needed. It is necessary to test whether this synergy is more evident when K is less than optimal in the plant. Further research is needed to gain a better understanding of the role of Si at a transcriptomic level to identify the activated genes that promote greater crop tolerance to drought and nutritional deficiency.

6 Conclusion

The main damage caused by water limitation is nutritional, especially potassium, both of which potentiate oxidative stress and consequently limit crop growth and productivity. The use of silicon and/or potassium can reverse this damage by increasing the enzymatic antioxidant defense system, inducing an increase in drought and/or nutritional tolerance.

The use of Si in irrigated systems can reduce pressure on water resources, minimize nutrient leaking and contribute to greater resilience of the production system in the face of climate change. Therefore, silicon represents a promising agronomic tool for improving water use efficiency in irrigated systems, favoring greater productivity with lower water consumption.

The synergy between potassium and silicon represents an effective agronomic strategy to increase water use efficiency in agricultural crops. Applying these nutrients together improves the physiological performance induced by the plants' efficient antioxidant defense system, reduces the negative effects of water stress and contributes to more sustainable production systems. Adopting this approach, especially via fertigation, could be decisive in meeting the water challenges facing agriculture in the future.

Author contributions

PF: Conceptualization, Investigation, Writing – review & editing, Writing – original draft. RP: Writing – original draft, Supervision, Investigation, Resources, Conceptualization, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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