

Review

Micronutrient fertilization enhances ROS scavenging system for alleviation of abiotic stresses in plants

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ABSTRACT

Reactive oxygen species (ROS) such as hydrogen peroxide at low concentrations act as signaling of several abiotic stresses. Overproduction of hydrogen peroxide causes the oxidation of plant cell lipid phosphate layer promoting senescence and cell death. To mitigate the effect of ROS, plants develop antioxidant defense mechanisms (superoxide dismutase, catalase, guaiacol peroxidase), ascorbate-glutathione cycle enzymes (ASA-GSH) (ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase and glutathione reductase), which have the function of removing and transforming ROS into non-toxic substances to maintain cellular homeostasis. Foliar or soil application of fertilizers containing B, Cu, Fe, Mn, Mo, Ni, Se and Zn at low concentrations has the ability to elicit and activate antioxidative enzymes, non-oxidizing metabolism, as well as sugar metabolism to mitigate damage by oxidative stress. Plants treated with micronutrients show higher tolerance to abiotic stress and better nutritional status. In this review, we summarized results indicating micronutrient actions in order to reduce ROS resulting the increase of photosynthetic capacity of plants for greater crop yield. This meta-analysis provides information on the mechanism of action of micronutrients in combating ROS, which can make plants more tolerant to several types of abiotic stress such as extreme temperatures, salinity, heavy metals and excess light.

1. Introduction

Reactive oxygen species (ROS) have different roles in the plant cell, acting as signalers at low concentrations or as a pro-oxidant agent at high concentrations (Foyer, 2020). Plant cells can generate various types of ROS, through the photosynthetic process in chloroplasts or during the respiratory process in the mitochondria (Sies et al., 2017). Superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^-) are among the types of ROS generated in plant cells (Foyer, 2018). ROS are highly reactive forms of oxygen that have at least one unpaired electron in their arrangement. They can interact with various cellular constituents, such as proteins, DNA, RNA and lipids, and oxidize them. The transfer of one, two or three electrons to an O_2 molecule leads to the formation of O_2^- , H_2O_2 or OH^- , respectively (Foyer, 2018).

The accumulation of ROS in cells promotes chain reactions in plant cells and cause damage to proper physiological functioning. These

effects are observed due to the vulnerability of the bonds between unsaturated fatty acids present in membranes attacked by ROS, promoting extensive damage to the cytoplasmic membrane and organelles (O'Byrne-Navia et al., 2018). The inactivation of enzymes by the oxidation of their thiol groups is the physiological and biochemical response of cells to exposure to ROS (Barbosa et al., 2014).

ROS can be mitigated from plant cells through an efficient enzyme antioxidant mechanism (Pandy et al., 2016; Silva et al., 2020). This protective mechanism includes several enzymes, especially superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD). SOD is the first enzyme in the line of defense against ROS in the antioxidant system, and is located in several cellular compartments. It is responsible for eliminating O_2^- and converting into H_2O_2 (Foyer, 2018). H_2O_2 in turn is converted into water by the antioxidant enzyme CAT and POD (Ighodaro et al., 2018). Ascorbate peroxidase (APX) is known to be one of the antioxidant enzymes widely distributed in plant cells. Due to the greater

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affinity of this enzyme for the peroxide substrate, it is considered an efficient hijacker of this reactive species under stress conditions (Soares et al., 2019).

Micronutrient applied at low concentration has the ability to increase the defense systems of plants in response to abiotic stresses. The increase in the activity of important antioxidant enzymes, such as SOD, CAT and POD with the application of copper (Cu) in peaches (*Prunus cerasifera*) (Lombardi and Sebastiani, 2005), zinc (Zn) in *Spirodela polyrhiza* L. (Upadhyay et al., 2010) and iron (Fe) in rice (*Oryza sativa*) (Li et al., 2018a) inhibited the exacerbated formation of lipid peroxidation in the cell membrane. Boron (B) applied in chickpeas (*Cicer aritimum* L.) and rice (Ardic et al., 2009; Zhu et al., 2019), manganese (Mn) in cotton (Tavanti et al., 2019), nickel (Ni) in tomato (Kumar et al., 2015) and selenium (Se) in rice plants (Reis et al., 2017) also increased the activity of antioxidative metabolism. This allows plants to avoid accelerated senescence, leaving the plants green for longer. Delayed senescence stimulate plants to activate the photosynthetic machinery for longer, producing more sugar and translocating the sugars via the phloem to the sink organs (Hui et al., 2012).

The purpose of this review is to provide the physiological roles of Cu, B, Fe, Mn, Mo, Ni, Se and Zn on the biochemical mechanisms of plant enzymatic antioxidant defense on ROS. We emphasize recent advances and discuss data on the content of these elements in plant tissues and efficient antioxidant action as strategies to combat abiotic stress in different plant species (Fig. 1).

2. Formation of ROS in chloroplasts and mitochondria

Plants require sunlight, water, nutrients and CO₂ to boost important physiological processes and fulfill their life cycle. Photosynthesis and respiration are important physiological processes. However, they can produce large amounts of ROS, as they involve the generation of energy and the production of adenosine triphosphate (ATP) (Silva et al., 2020).

For the photosynthetic process, sunlight is an unlimited energy source. Simultaneously, it is a potentially dangerous substrate and its use must be carefully managed. Under the inhibition of photosynthesis (in response to environmental fluctuations) there is a severe limitation in the use of light energy and its conversion into sugars, resulting in a large increase in the production of ROS. By inhibiting the transfer of energy (or electrons) from PSII to PSI, chloroplasts are exposed to excess energy excitation (Marutani et al., 2012).

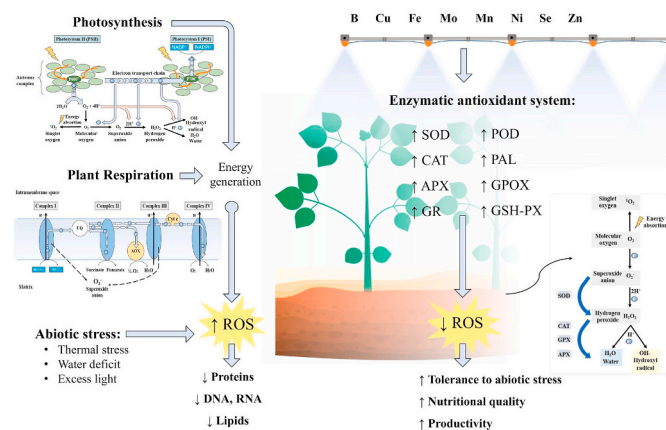


Fig. 1. Photosynthesis and respiration are important physiological processes and can produce large amounts of ROS as they are involved in the energy generation. Abiotic stresses can potentiate the generation of ROS, which can interact with several cellular constituents and oxidize them, such as proteins, DNA, RNA and lipids. Micronutrient when applied in low concentrations have the ability to increase the enzymatic antioxidant defense systems of plants in response to the increase of ROS, making plants more tolerant to abiotic stresses, in addition to increasing nutritional quality and productivity.

Molecular oxygen is a potential acceptor of unused electrons in the photochemical step of photosynthesis (Foyer, 2018). The transfer of these electrons to oxygen is inevitable. In this process, oxygen becomes an alternative dissipator of these electrons and is reduced to O₂⁻ (Foyer and Noctor, 2016). Photoactivated chlorophylls (excited state) can also produce O₂⁻ when electron transfer is limited to NADP⁺ (Krieger-Liszskay, 2005). In this situation, the undissipated photochemical energy is transformed into fluorescence, or transferred to acceptor molecules such as oxygen. As a way of extinguishing this energy, carotenoids act as effective antioxidants (Foyer, 2018). The O₂⁻ radical can be quickly converted to H₂O₂ by the action of the SOD enzymes (Sharma et al., 2012). The high abundance of ascorbic acid inside the chloroplasts also contributes to this process (Foyer et al., 2018).

Rubisco (Ribulose-1,5-bisphosphate carboxylase/oxygenase) is the main enzyme responsible for the assimilation of carbon during the photosynthetic process (Bhat et al., 2019). Rubisco activity in the form of oxygenase does not directly generate ROS in chloroplasts, since it supports the photorespiration process (Betti et al., 2016). At this point, the addition of oxygen forms phosphoglycolate and phosphoglycerate. The subsequent glyoxylate metabolism in the peroxisome is also an H₂O₂ generator (Ledford and Niyogi, 2005).

The large quantity of oxidative signals arising from photosynthesis provide cells with mechanisms to monitor the flow of photosynthetic electrons and prevent over-oxidation. Among ROS, H₂O₂ is more stable, which makes it the most likely way to act as a mobile signal at the cellular level (Foyer and Noctor, 2016). This process is undoubtedly an important source of oxidative signals for the cell nucleus (Noctor and Foyer, 2016). Such signals probably explain the wide variety of enzyme systems such as CAT, APX and GPX capable of using H₂O₂ as a substrate (Fig. 2) (Feng et al., 2013).

Enzymes of Calvin cycle such as fructose-1,6-bisphosphatase, sedoheptulose-1,7-bisphosphatase and phosphoribulokinase lose 50% of their activity when cellular H₂O₂ accumulates at levels close to 10 μM (Leegood and Walker, 1982). Under high concentrations, programmed cell death occurs (Dat et al., 2000). In general, two electrons are needed to metabolize H₂O₂ to water, decreasing the dissipation of excess energy and electron excitation (Foyer et al., 1991). It is noted that even the hydroxyl radical has high cellular reactivity; it also plays important roles in plants, such as in the metabolism and structure of cell wall (Miller et al., 2009).

The carbon organic compounds produced during the photochemical stages are mobilized and oxidized in a controlled manner during the plant respiration process. As a product, energy-rich molecules such as ATP are generated. Plant respiration process includes glycolysis, oxidative pathway of pentose phosphate, tricarboxylic acid cycle (TCA) and the mitochondrial electron transport chain (mETC) (O'Leary et al., 2019).

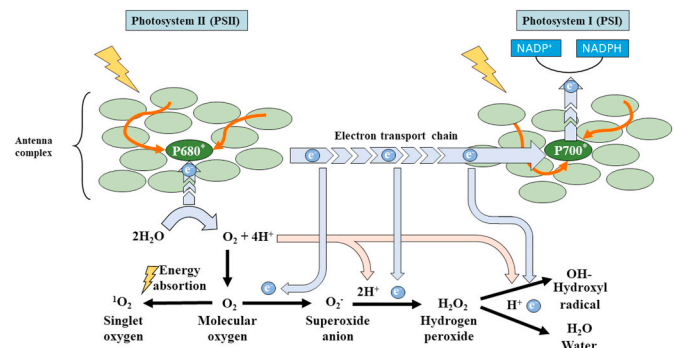


Fig. 2. Schematic representation of the generation of ROS in the photosynthetic process. With the inhibition of electron transfer between photosystems II and I, O₂ becomes an important acceptor of these electrons. The gradual reduction of O₂ leads to the formation of H₂O₂.

The inner membrane of plant mitochondria contains the mETC. In mETC, a proton gradient is formed, boosting ATP synthesis. The mETC houses electrons with sufficient free energy to directly reduce molecular oxygen and produces some types of ROS under normal conditions (Czarnocka and Karpiński, 2018). Nevertheless, its production can be significantly improved in response to biotic and abiotic stress (Gupta et al., 2016).

In general, O_2^- is generated by the plants mETC, occurring mainly in complex I and complex III (Fig. 3) (Navrot et al., 2007). The regulation of mETC is complex, due to the presence of alternative oxidases (AOX) in the mitochondria. AOX can reduce O_2^- ROS in H_2O_2 , in addition to providing a constant flow of electrons, disregarding their pumping to complexes III and IV and cytochrome (cyt) (Czarnocka and Karpiński, 2018). The increase or decrease in AOX expression has an influence on the cell death process, reducing or increasing, respectively (Van Aken et al., 2015).

3. ROS formation in response to abiotic stress (drought, heat, cold)

Plants can experience oxidative stress when exposed to conditions of thermal stress, water deficit, excess light and other types of abiotic stresses (Balfagón et al., 2020). Plants have limited control over the intensity and temperature of light, which fluctuate widely in nature. Plant metabolism is influenced by temperature to consume light-dependent photosynthetic electron transport products. Therefore, powerful and flexible regulatory mechanisms are necessary for the use of photosynthetic light in the predominant regimes of irradiance and temperature (Foyer et al., 2017). The predominance of indeterminate plant growth means that the development of new organs can be adapted more flexibly to external conditions than in many animals. These factors probably explain the particularly influential role of ROS and related redox changes in plants as an interface between internal physiology and the environment (Foyer and Noctor, 2016).

Under unfavorable conditions, plants close their stomata, limiting CO_2 uptake and fixation. This situation causes changes in cell metabolism, especially the photosynthetic process, increasing the production of ROS (Ali et al., 2020). Under water stress conditions, the production of ROS in plant cells increases dramatically (Gupta et al., 2020).

High and low temperature limit plant growth and yield and inevitably governed by ROS overproduction. Several authors have observed an increase in ROS for several crops exposed to high temperatures, such as rice, weed rice (*Oryza* spp.), rice grass (*Echinochloa* spp.) (Oliveira et al., 2019), potato (*Solanum tuberosum* L.) (Kim et al., 2011) and soybean (*Glycine max*) (Djanaguiraman et al., 2011), as well as under low temperatures, as in tomatoes (*Solanum lycopersicum*) (Liu et al., 2019). Despite the responses of important antioxidant enzymes to be favorable when plants are subjected to such situations, the antioxidant system may not be able to remove the overproduction of ROS if the duration of stress is prolonged (Kundu et al., 2018).

In addition to the abiotic and biotic factors that motivate and affect

the yield, xenobiotic factors caused by anthropic actions can also cause major losses in crop yield. These are losses caused mainly by the use of herbicides, fungicides, atmospheric contaminants and heavy metals (Mishra et al., 2019).

Herbicides can increase the content of H_2O_2 and malondialdehyde (MDA), indicating the occurrence of lipid peroxidation and oxidative stress in plants (Kumar et al., 2020). When there is a hormonal balance, these damages are reduced. For example, salicylic acid applied at low concentrations, reduced these damage in peanuts (*Arachis hypogaea* cv. Gizé 5 and Gizé 6) (Radwan et al., 2019).

4. Enzymatic antioxidative metabolism

ROS are eliminated from plant cells through efficient enzymatic and non-enzymatic antioxidant systems. These systems play an important role in protecting against the toxicity of these molecules (Pandy et al., 2016). The enzymes that comprise the antioxidant enzyme system are SOD, CAT, guaiacol peroxidase (GPOX) and enzymes in the ascorbate-glutathione cycle (ASA-GSH), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) (Foyer and Noctor, 2011). These act synchronously, converting ROS into non-toxic forms.

SOD is the first enzyme in the line of defense against ROS, performing the dismutation of O_2^- into H_2O_2 (Guo et al., 2018) (Fig. 4). SOD can be classified according to its metal cofactor: copper/zinc (Cu/Zn-SOD), manganese (Mn-SOD) and iron (Fe-SOD), each located in different cell compartments (Mosa et al., 2018; Berwal et al., 2018). Fe or Mn-SOD are found in chloroplasts, peroxisomes and mitochondria. Eukaryotic Cu/Zn-SOD are found in several compartments, including the chloroplast and apoplast. Like superoxide generation, H_2O_2 can be produced by reducing O_2 in two electrons through various oxidases, such as glycolate oxidase (GOX), located in peroxisomes (Noctor et al., 2018).

CAT acts by catalyzing the dismutation of H_2O_2 into H_2O . Its affinity with the substrate is weaker than that of other antioxidant enzymes (Feng et al., 2013). There are reports of CAT presence in the cytosol, chloroplast and mitochondria (Mhamdi et al., 2010). The ability of CAT to effectively limit H_2O_2 concentration in cells underlines its importance in the physiological processes mentioned above, as well as being an enzyme of the first line of antioxidant defense (Ighodaro et al., 2018).

The activity of GPX most often depends on a Se cofactor (Ighodaro et al., 2018). APX is one of the most widely distributed antioxidant enzymes in plant cells. Due to its greater affinity for the H_2O_2 substrate, APX is considered an efficient sequester of this reactive species under stress conditions (Sharma et al., 2012).

GR is an enzyme highly dependent on the availability of NAD(P)H. The ROS detoxification system through the action of antioxidant enzymes is highly complex. However, the simultaneous expression of multiple antioxidant enzymes has been shown to be more effective than the expression of a single or two enzymes in the development of plant stress tolerance (Aono et al., 1995). In general, these enzymes reduce the damage caused by ROS. The detection of these enzymes activity is high indicates that possibly the plants are under stress.

5. Mode of action of micronutrient as elicitors and activators of antioxidative enzymes to reduce ROS formation

Micronutrient plays an important role in plant physiology, and the dose is an essential factor for its functionality. Application of fertilizer containing micronutrient or benefit element can favor the defense systems of plants subjected to some type of stress, or lead plants to toxicity and death (Silva et al., 2020).

The effect of micronutrient application on the antioxidative metabolism of various plant species is compiled in Table 1. The data compilation includes the action of Cu, B, Fe, Mn, Zn, Mo, Ni and Se on the activity of important enzymes that compose enzymatic antioxidant

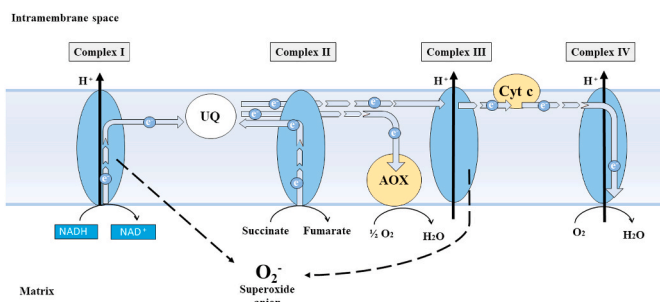


Fig. 3. Schematic representation of the generation of ROS in the plant respiration process.

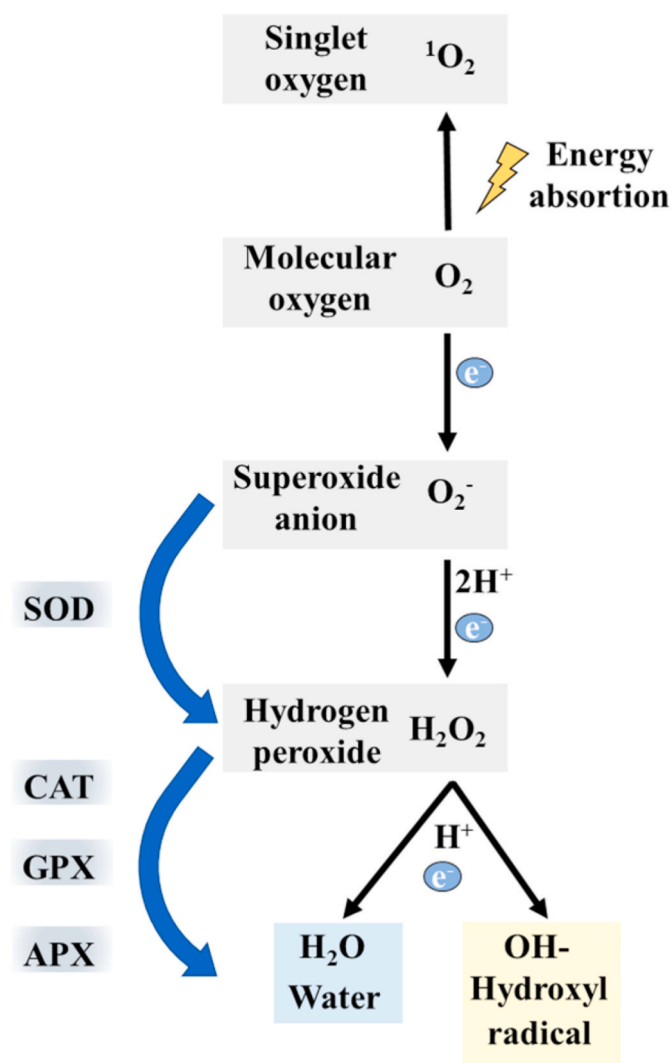


Fig. 4. Schematic representation of ROS dismutation by the enzymatic antioxidant mechanism SOD, CAT, GPX and APX. SOD is the first enzyme in the line of defense against ROS, performing the dismutation of O_2^- into H_2O_2 . CAT, GPX and APX enzymes act by catalyzing the dismutation of H_2O_2 into H_2O .

metabolism, such as SOD, CAT, APX, GR, POD, GPOX and GSH-Px. The activity of these enzymes (decreased, did not change or increased) are the result of the application of different doses of these elements in relation to a control treatment in different species and parts of plants.

5.1. Boron

Boron is essential for plant growth and development (Hänsch et al., 2009). Boron participates in numerous physiological processes in plants. This includes the construction of cell walls, structure and function of the cell membrane and cell division (Lewis, 2019). Boron has essential functions in respiration, RNA metabolism, ascorbate metabolism, indole-acetic acid (Gondim et al., 2014), nitrogen metabolism, carbohydrate metabolism and in the photosynthesis process (Shireen et al., 2018).

Regarding the enzymatic antioxidant metabolism, B application can favor the increase of important enzymes, such as SOD, CAT and APX in chickpea genotypes (Ardic et al., 2009). An increase in the activity SOD, CAT and APX corresponded with the application of B in 89, 80 and 75% of the studies analyzed in this review (Table 1). These results indicate that B application can positively influence the enzymatic antioxidant metabolism of plants.

Ardic et al. (2009) observed an increase in SOD activity in two cultivars of chickpeas at doses of 1.6 and 6.4 mM of B. On the other hand, only one cultivar increased CAT and APX. Michael et al. (2012) reported an increase in SOD activity in cowpea under stress conditions caused by B and high irradiation. Keleş et al. (2011) observed that doses of 40 and 60 g B kg⁻¹ increased the SOD in sunflower and tomato plants. Zhu et al. (2019) in pretreatment of 3 μM of B in rice showed an increase in the enzymatic activity of APX, POD and CAT.

Boron application at high concentrations can affect different plant processes including growth, root cell division, photosynthesis, leaf chlorophyll content and biochemical processes (Reid, 2013). This situation creates a stress condition for plants, leading to biochemical and physiological limitations. Typical symptoms such as yellowing, mottled chlorosis or dryness, followed by necrosis in the leaf tissues are observed (Fitzpatrick and Reid, 2009). Kelleş et al. (2011) studying B toxicity in tomato and sunflower (*Helicunthus annuus*), concluded that in tomato leaves, GR and SOD activity increased, but CAT activity decreased with higher concentrations of B. In leaves of sunflower, the activities of three enzymes increased, but the activity of CAT and GR began to decrease in higher applications. Other similar results for B toxicity were obtained in rice (Wang et al., 2016) and in tomato plants (Cervilla et al., 2007).

Inal et al. (2009) concluded that silicon relieves B toxicity, possibly preventing damage to the oxidative membrane, both by decreasing B uptake and by increasing tolerance to excess B in plant tissues.

5.2. Copper

Copper (Cu) plays an important role in ROS homeostasis (Balyan, 2017). Flow through major metabolic pathways critically depends on Cu-containing metalloproteins. For example, in electron transport chains photosynthesis and respiration, cell wall biosynthesis and secondary metabolism (Schulten et al., 2017).

Babu et al. (2003) investigating aquatic plant (*Lemna gibba*) exposed to Cu stress (0–10 μM of CuSO₄), concluded that there was a significant increase in SOD and GR activities. Similar results were observed by Liu et al. (2018) in corn (*Zea mays*) (0.156 μM Cu²⁺), and in duckweed (*Spirodela polyrrhiza* L.) up to 100 μM of CuSO₄ (Upadhyay et al., 2010).

Sarkar et al. (2020) studying the action of Cu oxide nanoparticles (CuONPs) in the cultivation of duckweed (*Lens culinaris*) found an increase in the enzymatic defense action as POD, polyphenol oxidase, phenylalanine ammonia lyase and β-1,3 glucanase activities in response to 0.025 mg mL⁻¹ of CuONPs supply. On the other hand, the levels of phenol and flavonoids were induced, also the antioxidant enzymes such as CAT, APX and SOD.

Nineteen studies analyzed indicated an increase in antioxidant enzymes. Among the most studied enzymes, SOD increased in 75%, and CAT in 85% of the cases (Table 1). The enzymatic activity through the interaction of Cu in the physiological processes of the plant are reported in several studies in different crops such as blackberry (*Morus alba* L.) (Tewari et al., 2006), rice (Thounaojam et al., 2013; Azooz et al., 2012; Thounaojam et al., 2014; Nisha et al., 2016), *Arabidopsis thaliana* (Drażkiewicz et al., 2004), *Pisum sativum* (Malecka et al., 2012) and coffee (*Coffea arabica* L.) (Santos et al., 2017b). In all studies, it was possible to observe the increased CAT, SOD and APX activities.

Lombardi and Sebastiani (2005) observed the enzymatic and antioxidant behavior in peach plants in response from 10 to 100 μM of CuSO₄. The reduction of ROS was more active at concentrations below 50 μM CuSO₄ due to increased CAT and SOD activities. On the other hand, Wang et al. (2004) studied the stress induced by Cu due to the antioxidant responses in mustard roots (*Brassica juncea* L.) and concluded that the moderate concentration of Cu (8 μM) might be able to activate defensive mechanisms against oxidative stress inducing CAT, SOD and APX in roots. However, high concentrations of Cu caused low enzymatic activities promoting the increase of cellular oxidation. A similar result was obtained in *Lemna minor* L. by Panda (2008), where the concentration of 100 μM CuSO₄ decreased SOD activity.

Table 1
Overview of analyzed studies in this meta-analysis in response to micronutrient boron (B), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni), selenium (Se) and zinc (Zn) effect on the antioxidant metabolism.

Element	Number of analyzed studies																		Total	References						
	SOD			CAT			APX			GR			POD			PAL					GPOX			GSH-Px		
	↓	=	↑	↓	=	↑	↓	=	↑	↓	=	↑	↓	=	↑	↓	=	↑			↓	=	↑	↓	=	↑
B	1		8	1	1	8	1	1	6	–	1	3	–	–	2	–	–	1	2	1	–	–	–	–	37	Inal et al. (2009); Eraslan et al. (2007); Cervilla et al. (2007); Ardic et al. (2009); Michael et al. (2012); Sahin et al. (2017); Sarabandi et al. (2019); Wang et al. (2016); Keleş et al. (2011); Keleş et al. (2004); Zhu et al. (2019).
Cu	2	2	12	1	1	11	2	–	7	–	1	4	–	–	5	–	–	–	1					1	51	Li et al. (2006); Babu et al. (2003); Tewari et al. (2006); Z Lombardi and Sebastiani (2005); Liu et al. (2018); Wang, et al. (2004); Upadhyay et al. (2010); Panda (2008); Contreras et al. (2018); Maleva et al. (2018); Azooz et al. (2012); Drażkiewicz et al. (2004); Malecka et al. (2012); Zhao et al. (2010); Nisha et al. (2016); Santos et al. (2017b); Thounaojam et al. (2014); Pan et al. (2017).
Fe	–	1	4	3	1	5	1	–	1	–	–	–	1	–	2	–	–	–	1	–	1	1	–	1	23	Jucoski et al. (2013); Li et al. (2018a); Msilini et al. (2012); Rout et al. (2015); Dangola et al. (2019); Sun et al. (2016); Tewari et al. (2013); Tombuloglu et al. (2019).
Mn	2	1	5	1	1	1	2	–	3	–	2	3	1	–	–	–	–	–	–	–	2	–	–	–	24	Gonzalez et al. (1998); Li et al. (2012); Rahman et al. (2016); Sieprawska et al. (2016); Silber et al. (2009); Tavanti et al. (2019).
Mo	–	–	5	–	–	5	–	–	4	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	16	Al-Issawia et al. (2016); Babenko et al. (2015); Datta et al. (2011); Li et al. (2018b); Taran et al. (2016); Wu et al. (2017); Xu et al. (2018).
Ni	2	–	11	5	1	9	–	–	9	–	–	2	–	–	2	–	–	1	1	–	8	–	–	1	52	Awasthi et al. (2013); Barcelos et al. (2018); Duman et al. (2010); Eriyamremu et al. (2010); Gajewska et al. (2006); Gajewska et al. (2007); Kumar et al. (2012); Kumar et al. (2015); Maleva et al. (2018); Mohamed (2013); Nasibi et al. (2013); Nazir et al. (2019); Singh et al. (2011); Tammam et al. (2019); Tombuloglu et al. (2019).
Se	–	3	11	3	3	12	–	3	7	–	1	5	1	–	7	–	–	–	–	–	2	–	3	5	66	Alves et al. (2019); Andrade et al. (2018); Castillo-Godina et al. (2016); Chan et al. (2010); Dai et al. (2019a); Dai et al. (2019b); Elkelish et al. (2019); Hawrylak-Nowak et al. (2018); Kong et al. (2005); Lara et al. (2019); Mroczek-Zdyrska et al. (2012); Oliveira et al. (2019); Rady et al. (2020); Ramos et al. (2010); Sharma et al. (2014); Yin et al. (2019); Wu et al. (2020).
Zn		1	8	–	2	7	–	–	4	–	–	1	1	–	–	–	–	–	–	–	1	–	–	3	28	Li et al. (2006); Zoufan et al. (2018); Michael et al. (2011); Ramakrishna et al. (2012); Malecka et al. (2012); Sida-Arreola et al. (2017); Thounaojam et al. (2014); Upadhyay et al. (2010); Wu et al. (2015).

↑: increased; = : did not change; ↓: decreased.

Santos et al. (2017b) also reported that both the deficiency and the excess Cu in the plant metabolism cause changes in the activities of CAT, SOD and APX causing a nutritional imbalance and, consequently, physiological stress increasing ROS formation in the plant cell.

Contreras et al. (2018), studying the effect of Cu supplementation (50 and 300 μM of CuSO_4) on the antioxidant metabolism in *Colobanthus quitensis* (Kunth) Bartl.) observed an increase in SOD and CAT and a decrease in APX activity. Maleva et al. (2018) concluded that the addition of urea (2 mM) and Cu (10 mM) promoted a decreased APX and increased in CAT activity. Zhao et al. (2010) concluded that there is an increase in SOD and POD up to 120 mg L^{-1} of CuCl_2 in *Festuca arundinacea* L. and *Lolium perenne* L. plants. In lettuce (*Lactuca sativa*) an increase of APX was observed at a concentration of 0.16 mg L^{-1} of CuSO_4 (Pan et al., 2017).

5.3. Iron

Iron (Fe) is an essential micronutrient for plants, involved in several cellular processes and functions such as photosynthesis and respiration (Gao et al., 2019). Broadley et al. (2012) highlighted the importance of Fe as a common transition metal, a cofactor in many proteins involved in plant physiological processes. The main antioxidant enzymes require Fe for their metabolism, acting as an important catalyst for electron transfer reactions. The main potential targets include ROS, such as H_2O_2 and OH^- that are reduced to H_2O (antioxidant activity) or oxidized as O_2 with concomitant reduction of Fe^{3+} to Fe^{2+} . In addition, the reduction of molecular oxygen to O_2 is also possible, as ferrous iron; Fe^{2+} catalyzes the reduction of H_2O_2 to OH^- , one of the most efficient oxidants in nature (Halliwell, 2006).

Evaluating the physiological effect of Fe in plants, 80% of the analyzed studies show increased SOD and 55% increased CAT activities (Table 1). Considering the great importance of CAT and APX enzymes in the germination of rice cultivation, Li et al. (2018a) evaluated the effect of Fe biofortification on crop germination using ferrous sulfate, concluding that the concentration of 0.25 g L^{-1} of FeSO_4 significantly increased CAT activities, increasing the ability to develop antioxidant defense mechanisms. Msilini et al. (2012) analyzed the variability of the phenolic and antioxidant metabolism in lettuce (*Lactuca sativa*) plants evaluating the consequences of Fe deficiency. They found that the control treatment showed decreased CAT, GPX and APX activity. There was a significant induction in the reduction of antioxidant capacity in lettuce leaves.

Tewari et al. (2013) observed that canola (*Brassica napus*) Fe-deficient plants showed increased SOD activity. Fe deficiency negatively affects the biosynthesis of chloroplast pigments, affecting photosynthetic activity. Jucoski et al. (2013) observed Fe toxicity (2.0 mM Fe as FeEDTA) in the cherry (*Eugenia uniflora*) increased the activities of SOD, GR, CAT, POX and APX.

Application of Fe concentrations (0, 25, 50, 100 and 200 μM of FeSO_4) in *Withania somnifera* L. increased SOD and CAT activities to mitigate oxidative damage caused by ROS (Rout et al., 2015). CAT activity has also increased in barley (*Hordeum vulgare* L.) plants in response to Fe application (Tombuloglu et al., 2019). Fe is a constituent of enzymes associated with the cellular antioxidant system, such as ascorbate peroxidase (APX), CAT, POD and Fe-SOD. Plants exposed to Fe deficiency would be more sensitive to oxidative stress (Sun et al., 2016).

5.4. Manganese (Mn)

Mn acts as a modulator of photosynthesis and antioxidant metabolism in plants (Santos et al., 2017a). Mn plays a major role in the enzymatic activation of SOD, an enzyme with an important role in combating oxidative stress caused by ROS. It is involved in numerous redox reactions and is a cofactor of polyphenol oxidase systems, indole-3-acetic acid (AIA). Mn is one of the main enzymatic activators of decarboxylases and dehydrogenases involved in the citric acid cycle

(Logan, 2018). The most well-known function of Mn in plants is its participation in the Hill reaction, whereby oxygen is produced from water (Takashima et al., 2012).

From results summarized in Table 1, 62% of analyzed studies showed increased SOD, 60% increased APX and 60% increased GR activity (Table 1). Tavanti et al. (2019) concluded that cotton genotypes increased the activities of SOD, APX and GR in response of 200 μM of Mn. In pepper fruits (*Capsicum annuum* L.) fertilized with Mn, attenuated H_2O_2 concentration and the activity of ascorbate oxidase was suppressed, resulting in an increase in the concentration of apoplastic ascorbic acid (Silber et al., 2009).

Li et al. (2012) observed that tomato plants exposed to 10 and 200 μM of Mn^{2+} significant increased SOD, POD, APX, GR activity and AsA concentration in leaves and roots. Rahman et al. (2016) observed rice plants treated with 0.3 mM MnSO_4 reduced oxidative damage and lipid peroxidation in response to cadmium-induced stress.

5.5. Molybdenum

Mo has been widely reported to enhance tolerance to abiotic stress against salinity, low temperature and water stress in plants (Sun et al., 2009, 2014; Zhang et al., 2012; Wu et al., 2014). Among the results analyzed in this study, Mo was the nutrient that most increased antioxidant enzymes. All the studies evaluated showed an increase in the activity of SOD, CAT, APX and POD (Table 1). These enzymes act as a defense mechanism of plants to face toxicity in plant cell (Xu et al., 2018).

Application of nanomolybdenum resulted in increased SOD and CAT activities in chickpea plants (Taran et al., 2016). In addition, results with increased SOD and CAT were also obtained in rice (Li et al., 2018b), forage (*Agropyron cristatum*) (Babenko et al., 2015) and wheat (Al-Issawi et al., 2016) in response to Mo fertilization.

It was demonstrated in wheat plants under drought stress that SOD, CAT, POD and APX activities were significantly increased in the leaves due to Mo fertilization (Wu et al., 2017). These results suggest that antioxidant defense capacity was improved due to the activation of the activities of antioxidant enzymes by Mo. SOD activity increased dramatically in the plants treated with Mo from both wheat cultivars, but it was higher in the winter wheat cultivar compared to the spring cultivar. CAT and GPX also increased dramatically in response to the application of Mo (Al-Issawi et al., 2016).

5.6. Nickel

Nickel (Ni) is essential at low concentration for plant growth and development (Awasthi et al., 2013). Nickel is cofactor of urease, an enzyme responsible for breaking down urea into ammonia and carbon dioxide (Barcelos et al., 2018; Maleva et al., 2018). Antioxidant metabolism in plants is elicited by Ni application. According to Table 1, there was an increase in the activity of the enzymes: SOD, CAT, APX, GR, POD, PAL, GPOX and GSH-PX by 85%, 60%, 100%, 100%, 100%, 100%, 89% and 100% of the analyzed studies, respectively. These data support that Ni stimulates the antioxidant metabolism of plants, which protect plant cells against ROS.

Duman et al. (2010) observed that Ni application at low concentration increased SOD activity and biomass of *Nasturtium officinale* plants. Barcelos et al. (2018), observed that application of 40 g ha^{-1} of Ni increased the activity of the urease, SOD, CAT and APX in soybean plants. These authors also observed that combination of Ni with 300 mL ha^{-1} of pyraclostrobin fungicide reduced the severity of powdery mildew up to 99% in soybeans, suggesting that urease is a key enzyme regulated by Ni, and has an important role in the defense of the host against powdery mildew by stimulating antioxidant metabolism. Other studies have also observed Ni effect on SOD (Nazir et al., 2019; Pavlovkin et al., 2016; Tammam et al., 2019), CAT and PAL activity (Nazir et al., 2019).

Nickel toxicity is a limiting factor for plant growth and yield losses of crops (Kumar et al., 2012; Reis et al., 2017). Nickel toxicity in plants is characterized as chlorosis in young leaves and reduced growth according to studies carried out in *Luffa cylindrica* (Awasthi et al., 2013), beans (*Vigna unguiculata*), corn (*Zea mays*) (Eriyamremu et al., 2010) and wheat (*Triticum aestivum*) (Gajewska et al., 2006). Nickel toxicity also cause oxidative damage in plants cells due to overproduction of hydrogen peroxide. Nickel application at the concentrations 50 and 100 μM in *Hyoscyamus niger* plants (Nasibi et al., 2013), 65 μM in cowpea plants, 130 μM in corn plants (Eriyamremu et al., 2010), 50 mM in tomato plants (Kumar et al., 2015) caused an increased activity of antioxidant enzymes SOD, CAT, GPOX and APX.

Gajewska et al. (2006) observed that application of 200 μM Ni to wheat plants caused inhibition of stem growth, decreased in CAT and SOD activity, chlorophyll oxidation, proline accumulation and occurrence of visible symptoms of Ni toxicity. Similarly, studies by Gajewska et al. (2007) observed that application of 100 μM of Ni in wheat leaves also reduced plant growth parameters and increased H_2O_2 concentration promoting lipid peroxidation in plant cell. These authors also observed that SOD and CAT activity decreased with Ni. Other studies using similar doses of Ni in wheat plants, observed an increase in the activity of SOD, CAT, APX and GPOX (Mohamed, 2013).

Kumar et al. (2012) studied the effects of Ni toxicity by the application of 200 μM and 400 μM of Ni in barley plants. These authors observed a decreased root and shoot fresh weight. Visible symptoms of Ni toxicity were characterized as chlorosis and leaf necrosis. There was an increase in H_2O_2 concentration in both roots and leaves. Regarding the enzymatic antioxidant metabolism, GPX, APX, SOD and GR activities increased in leaves and roots in response to 200 μM and 400 μM of Ni supply. Similarly, Tombuloglu et al. (2019) investigating the effects of Ni magnetic ferrite nanoparticles (NiFe_2O_4) in barley plants, observed that 1000 mg L^{-1} of Ni reduced the plant growth. However, these authors observed that CAT activity was suppressed in the leaves and induced in the roots.

5.7. Selenium

Se application at low concentrations is considered a beneficial element for plants (Terry et al., 2000). Selenium applied as selenate form has physico-chemical properties highly similar to sulfur, and plays a very important role in antioxidant reactions and in hormonal balance of plant cells including increased GPX activity (Cartes et al., 2010; Silva et al., 2018). Table 1 shows that Se is responsible to enhance antioxidant metabolism by the increasing the enzymes activity such as SOD, CAT, APX, GR, POD and GSH-Px in 78%, 66%, 70%, 83%, 87% and 62% of the analyzed studies, respectively. In this scenario, promising reports were observed for Se biofortification in rice (Reis et al., 2018; Yin et al., 2019; Dai et al., 2019b), corn (Chilimba et al., 2012), wheat (Broadley et al., 2009), lettuce (Ramos et al., 2010) and tomato plants (Castillo-Godina et al., 2016; Alves et al., 2019; Rady et al., 2020).

Selenium application at low concentration plays an important role in the antioxidant protection of plants, positively modulating enzymes such as SOD and CAT, allowing to reduce lipid peroxidation governed by ROS formation in plant cells (Saidi et al., 2014; Alves et al., 2019). Oliveira et al. (2019) observed an increased SOD and APX activity in response to 1.5, 3 or 5 mg kg^{-1} of Se supply, while CAT was greater with 1.5 and 3 mg kg^{-1} of Se in tubers of *Solanum tuberosum*. Similar results were observed by Castillo-Godina et al. (2016) that application of 5 mg L^{-1} of Se increased SOD, CAT and GSH-Px activities in tomato plants.

Foliar Se application at the concentration of 50 g ha^{-1} increases photosynthetic pigments, photosynthesis and cowpea yield (Silva et al., 2020; Lanza et al., 2021). In addition, the activities of SOD, CAT, APX and GR increased dramatically in response to foliar application of 50 g ha^{-1} decreasing the formation of ROS in the plant cell. Similarly, Lara et al. (2019) also observed that the application of Se at 21 g ha^{-1} promoted an increase in the photosynthetic rate of wheat plants, positively

influencing carbohydrate metabolism and resulting in higher grain yield.

The application of Se mixed with other nutrients also has beneficial effects on plants. Wu et al. (2020) found that foliar application of Se and Zn increased SOD, POD, CAT and APX activity in wheat plants. Similarly, Dai et al. (2019a) observed an increased SOD, POD, CAT, APX and GR activity in response to application of 1 mg kg^{-1} of Se in Chinese cabbage.

Considering the Se effect on the antioxidant system, there are reports that Se can relieve several types of abiotic stresses in plants, such as those caused by heavy metals. The oxidative stress caused by lead toxicity (Pb) in *Vicia faba* was relieved when 3 μM of Se was applied, by increasing GPOX and GSH-Px activity (Mroczek-Zdyrska et al., 2012). Alves et al. (2019), evaluating the application of Se at low concentration (1 μM selenate or selenite) in *Solanum lycopersicum*, observed an enhanced antioxidant metabolism governed by the increasing of SOD, CAT, APX and GSH-Px activity under cadmium stress (Cd).

Saline stress can also be relieved by applying Se as observed by Kong et al. (2005). Selenium application at low concentrations (1–5 μM) can stimulate the growth of sorrel varieties (*Rumex spp.*) and boost antioxidant metabolism by increasing the SOD and POD activities. However, at higher concentrations (10–30 μM), the beneficial effects of Se were reduced. Similarly, Elkelish et al. (2019) observed that wheat seedlings supplemented with 5 and 10 μM of Se increased SOD, CAT, APX and GR activities under salt stress. Water deficit stress in rice plants was mitigated by the application of Se (Andrade et al., 2018). Soil application of 0.5 mg kg^{-1} of Se, these authors observed an increased SOD activity and a reduced hydrogen peroxide concentration in the leaves, indicating a lower lipid peroxidation of plant cell. Under stress caused by high temperature, Hawrylak-Nowak et al. (2018) observed and increased CAT and GPOX activity in response to application of 50 mg dm^{-3} of Se *Valerianella locusta* plants.

Soil or foliar Se application at high concentrations can be toxic to plants. Sharma et al. (2014) observed in increased hydrogen peroxide, proline concentration and CAT activity and increased APX activity in seleniferous soils (0.14 and 2.85 mg kg^{-1}) compared to non-seleniferous soil (0.14 mg kg^{-1}). The application of Se at high concentrations causes chlorosis in rice and coffee leaves (Gouveia et al., 2020; Mateus et al., 2020) and necrotic damage in cowpea leaves was observed by Lanza et al. (2021) caused by the overproduction of ROS.

5.8. Zinc

Zinc has essential roles on enzymes like dehydrogenases, isomerases, transphosphorylases, RNA and DNA polymerases (Lee et al., 2020). Zn is necessary for several physiological and biochemical processes, including photosynthesis, protein synthesis, growth regulation (Hafeez et al., 2013) and stress resistance mechanisms (Ma et al., 2017), including Cu/Zn-SOD (Broadley and White, 2007).

Among the analyzed studies (Table 1), 89% of obtained results for increased SOD and 77% of increased CAT activity were observed for several plant species fertilized with Zn. Few studies have presented not conclusive results on Zn effect on APX and GR activities. Zn interferes on oxidative stress induced in the reduction of H_2O_2 via O_2 reduction or elimination of ROS, through the stimulation of the antioxidant defense system (Taran et al., 2016).

Pepper plants (*Capsicum annum* L.) treated with high Zn concentration resulted in decreased H_2O_2 concentrations and MDA and stimulated the enzymatic antioxidants enzymes SOD, CAT and POD (Kaya et al., 2018). Foliar application of 1.5–10 ppm zinc oxide (ZnO) to seedlings of *Cicer arietinum* increased the biomass accumulation. This response was attributed to the low levels of ROS governed by lower lipid peroxidation in plant cell. Less activity of antioxidant enzymes such as SOD was also observed in untreated plants (Uday et al., 2013). This result indicates the importance of Zn fertilization to deficient soils in order to increase the antioxidant metabolism to combat ROS.

Upadhyay et al. (2010) observed that Zn enhanced duckweed (*Spirodela polyrhiza* L.) to combat oxidative stress promoted by Cu. Zoufan et al. (2018), studying the effects of different concentrations of Zn in growth and antioxidant metabolism responses in *Chenopodium murale* L., concluded that an excess of Zn led to an increase in lipid peroxidation, proline and ascorbate. In addition, high levels of Zn increased the activity of CAT, GPX and SOD in *Chenopodium murale* plants.

Wu et al. (2015) evaluating the efficiency of Zn in combating water stress in cotton (*Gossypium hirsutum*), concluded antioxidant metabolism such as SOD, CAT and APX activity, and non-enzymatic antioxidants, such as carotenoid, glutathione reductase and ascorbic acid significantly increased. This suggests that Zn improved the osmotic adjustment capacity of cotton plants and also the alleviation of ROS in plant cell. Sida-Arreola (2017), evaluating common bean (*Phaseolus vulgaris* L.) seeds after biofortification with Zn, concluded that antioxidant enzymes significantly increased the activity of SOD. Zoufan et al. (2018) performed a hydroponic system experiment and observed increased activity of SOD, CAT and GPX in plants exposed to 600 μ M of Zn. In addition, Sida-Arreola et al. (2017) observed that bean plants grown in 25 μ M of Zn significantly increased SOD activity. Michael et al. (2011) also studying beans observed increased POX, PPO activity in plants treated with 50 ppm of Zn.

6. Conclusion and future prospects

The production of ROS by plants can be generated under ideal conditions to growth, as a by-product of metabolic pathways or when subjected to environmental stresses. In this way, they act as signaling molecules at low concentrations or can cause great damage at high concentrations. Although great progress has been made in recent years on the effect of ROS on plant growth and crop yield, little is known about its formation, half-life and reactivity.

Nutrition with micronutrient and beneficial elements is essential to achieve high crop yields. Adequate supplementation with Cu, B, Fe, Mn, Mo, Ni, Se and Zn should be investigated on dose-response, sources and times of application in various plant species. Greater production of food should be aimed based on micronutrient positive effects on the enzymatic antioxidant metabolism and on the nutritional quality of the edible parts. Different edaphoclimatic conditions affect the development of plant species and influence the production of ROS, making interventions with the application of these elements necessary for the crops to achieve the expected yield.

We concluded that each element studied has a specific action, and that it can benefit plant defense mechanisms. For this to occur, it is necessary to understand the characteristics of the crops, as well as the mechanism of action and optimal doses. The toxicity and sensitivity to micronutrient deficiency varies depending on the plant species. It is necessary to redefine strategies, monitor and evaluate the methodologies for applying these elements, as well as conducting research in other crops of economic interest, in order to understand the entire mode of action.

CRedit authorship contribution statement

Tauan Rimoldi Tavanti: Conceptualization, Investigation, Methodology, Validation, Writing – original draft. **Andressa Aparecida Rodrigues de Melo:** Investigation, Methodology, Validation. **Luan Dionnes Kaiber Moreira:** Investigation, Methodology, Validation. **Douglas Enrique Juarez Sanchez:** Investigation, Methodology, Validation. **Rafael dos Santos Silva:** Investigation, Methodology, Validation. **Ricardo Messias da Silva:** Investigation, Methodology, Validation, review & editing. **André Rodrigues dos Reis:** Conceptualization, Validation, Supervision, Writing – review & editing.

Declaration of competing interest

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.

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