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Oxidative stress and antioxidant defense in Brassicaceae plants under abiotic stresses

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Research

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ABSTRACT

Brassicaceae plants, as an important source of primary and secondary metabolites, are becoming a research model in plant science. Plants have developed different ways to ward off environmental stress factors. This is lead to the activation of various defense mechanisms resulting in a qualitative and/or quantitative change in plant metabolite production. Reactive oxygen species (ROS) is being continuously produced in cell during normal cellular processes. Under stress conditions, there are excessive production of ROS causing progressive oxidative damage and ultimately cell death. Despite their destructive activity, ROS are considered as important secondary messengers of signaling pathway that control metabolic fluxes and a variety of cellular processes. Plant response to environmental stress depends on the delicate equilibrium between ROS production, and their scavenging. This balance of ROS level is required for performing its dual role of acting as a defensive molecule in signaling pathway or a destructive molecule. Efficient scavenging of ROS produced during various environmental stresses requires the action of several non-enzymatic as well as enzymatic antioxidants present in the tissues. In this review, we describe the ROS production and its turnover and the role of ROS as messenger molecules as well as inducers of oxidative damage in Brassicaceae plants. Further, the antioxidant defense mechanisms comprising of enzymatic and non-enzymatic antioxidants have been discussed.

Keywords: Abiotic stress, Antioxidant defence, Brassicaceae, Oxidative stress, ROS

1. INTRODUCTION

One of the most damage effects of the abiotic stress in plants is the production of toxic ROS in different cellular and sub-cellular compartments [1]. Some ROS are considered to be the most potent reactive ions known. They are generated due to the decreased content of intracellular CO_2, this results in the transfer to O_2 of one, two or three electrons, to form superoxide (O_2^-), hydrogen peroxide (H_2O_2) or the hydroxyl radical (HO^-), respectively [2]. Due to their reactivity with various key cellular components, their excess can lead to irreparable metabolic dysfunction and cell death [3,4]. At normal conditions, the small amounts of ROS are by-products of normal cell metabolism, formed in vital processes such as respiration, photorespiration and photosynthesis [5,6]. Abiotic stress increases their production resulting of oxidative damage [7,8]. The presence of high concentrations of ROS in the cell leads to major disturbance of ionic homeostasis by depressing cytosolic K^+ concentrations followed by activation of proteases and endonucleases [9,10], alteration of the cell membrane integrity, inhibition of enzyme activities and the function of the photosynthetic apparatus and of DNA lesions. The collective effect can lead to cell death [11,12]. Under non-stressful conditions, ROS at low cellular concentrations play a key role as signaling molecules involved in plant growth, development, hormonal action and many other physiological processes [5,8,13-16]. Such low-level ROS functions include triggering of antioxidant defense mechanisms for adapting to abiotic stress [12,16-18]. In fact, ROS at concentrations much lower than those causing cellular damage, can activate different Na^+- and K^+-permeable ion channels [19-21] that help maintain the cytosolic K^+/Na^+ ratios needed for salinity tolerance [22]. The production of ROS is the outcome of a plant metabolism that needs to be controlled to safeguard its cellular components [23]. Under stress condition, plants activate enzymatic and non-enzymatic antioxidant systems. The latter include antioxidant compounds such as ascorbic acid, glutathione, flavonoids, β-carotenes or other phenolic compounds. Among enzymatic antioxidant systems are superoxide dismutases (SOD), catalase (CAT), ascorbate peroxidase (APX) or redox regulatory enzymes such as glutathione reductase (GR), among many others [24]. Under stress conditions, the biosynthesis and the activities of these antioxidant molecules are altered [14,25-27].

The genus Brassica includes economically important oilseed and vegetable plants. This group comprising about 100 species, including mustard (*Brassica juncea* L.), rapeseed (*B. napus* L.), turnip rape (*B. rapa* L.) and cabbage (*B. oleracea* L.) that are grown mainly for oil and vegetables [28]. Brassicaceae is grown in both arid and semiarid regions and is severely affected by both biotic stresses, including bacteria, viruses and fungi, and abiotic stresses, including cold, heat, salinity and drought. Brassica is a good source of antioxidants due to the presence of high phenolics and glucosinolate content [29].

In this review, the effect of oxidative stress on Brassicaceae and the role played by ROS as signaling molecule in the mechanism of response of Brassicaceae to abiotic stress are discussed in detail.

2. Family Brassicaceae

The Brassicaceae (or cruciferae/mustard family) is considerably a large angiosperm family of dicots belonging to order brassicales with 10–19 tribes comprising of 338–360 genera and 3709 species [30]. The largest genera are Draba (365 species) followed by Lepidium (230 species), Erysimum (225 species), Cardamine (200 species) and Alysum (195 species) [31]. The family comprises of several plant species with agronomic and economic significance including model species (e.g. *Arabidopsis* and *Brassica*), developing model systems (e.g. *Brassica* and *Cradamine*) as well as various cultivated plant species (e.g. cauliflower, horseradish, cabbage, turnip, etc.) [32]. In 1934, Morinaga [33], using cytological work demonstrated the relationships among the cultivated *Brassica* species. According to his hypothesis, the high chromosome number of species *B. napus* (2n = 38, AACC), *B. juncea* (2n = 36, AABB), and *B. carinata* (2n = 34, BBCC) are amphidiploids combining in pairs the chromosome sets of the low chromosome number species *B. nigra* (2n = 16, BB), *B. oleracea* (2n = 18, CC), and *B. rapa* (2n = 20, AA) (Figure 1).

The family Brassicaceae serves as a good source of oils, vegetables, weeds, and ornamentals of huge economic importance. For example, locally known as shagsoo, Christolea is used as vegetable in combination with milk in addition to the edible Meeacarpea species. Mustards (*B. nigra* and *B. juncea*) are used as condiments. Seeds of *B. campestris*, *B. juncea*, *B. nigra* and *B. pekinensis* are crushed in preparation of edible oils. In different regions, *Camelina sativa*, *Eruca sativa* and *Sinapis alba* which are odiferous are also cultivated as oil plants along with the seeds of Capsella which contain about 15–20% oil. The seeds of *Conringia orientalis* contain fatty oil and its young sprouts are also comestible. Fresh leaves of *Lepidium sativum* are used as salad, and its seeds contain 5% fatty oil, making it worthy for illumination. Some species like Arabis are cultivated as ornamentals in rock gardens. *Parrya exscapa* grows at high altitudes laced with beautiful flowers. Different pigments from *Isatis tinctoria* serve as a dying agent besides being a honey-producing plant. *Erysimum Perofskianum* seeds serve as crude material for the formulation of cardiac drugs in pharmaceutical industry.

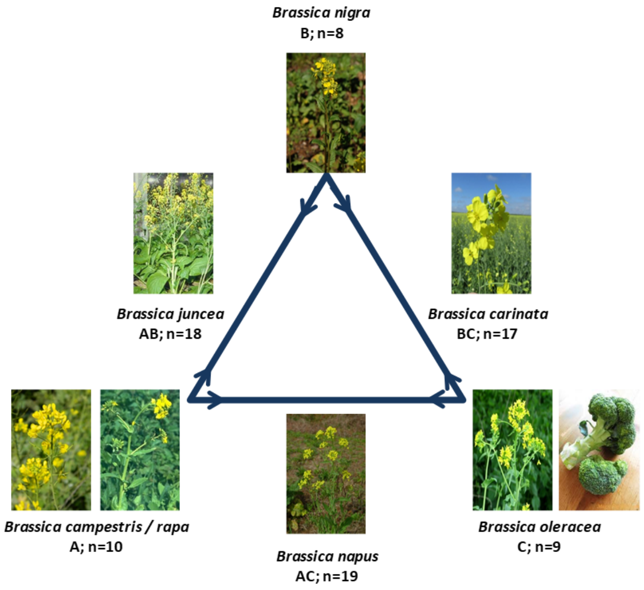

Figure 1. The U-triangle showing derivation of the high chromosome Brassica species from low chromosome species

3. Oxidative Stress and Generation of ROS

During abiotic stresses, plants undergo several mechanisms to combat increased ROS production. The balance between production and scavenging of ROS may be disturbed by a number of biotic and abiotic factors, which may increase the intracellular levels of ROS [13]. When the level of ROS exceeds the defense mechanisms, the cell is in a state of oxidative stress [4,13]. Oxidative stress leads to the loss of physiological capacity and eventual cell death. Therefore, defense mechanisms against oxidative damage are activated during stress to regulate toxic levels of ROS [34]. ROS are a group of free radicals, reactive molecules, and ions derived from oxygen. The most common ROS include singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\square -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\square}$). These substances are highly reactive and toxic and can lead to oxidative destruction of the cell [13,14,27]. ROS are generated mainly by mitochondrion via electron transport. However, it can found in others various subcellular compartments such as chloroplasts via the Mehler reaction, and peroxisomes via photorespiration [14]. The oxidative stress usually results from excessive ROS production, mitochondrial dysfunction, impaired antioxidant system, or a combination of these factors. Abiotic and biotic stresses can severely disturbed the balance between production and elimination of ROS [5]. These disturbances in the ROS equilibrium (redox homeostasis) can lead to a rapid increase in intracellular ROS levels, which can cause significant damage to cell structures [35]. However, when ROS production overcomes the cellular scavenging capacity, there occurs an unbalancing of the cellular redox homeostasis resulting in a rapid and transient excess of ROS, known as oxidative stress [4,34]. Thus, the antioxidant defense imbalance disrupts metabolic activities [36], causing severe oxidative damages to cellular constituents, which can lead to loss of function and even cell death (Figure 2) [34].

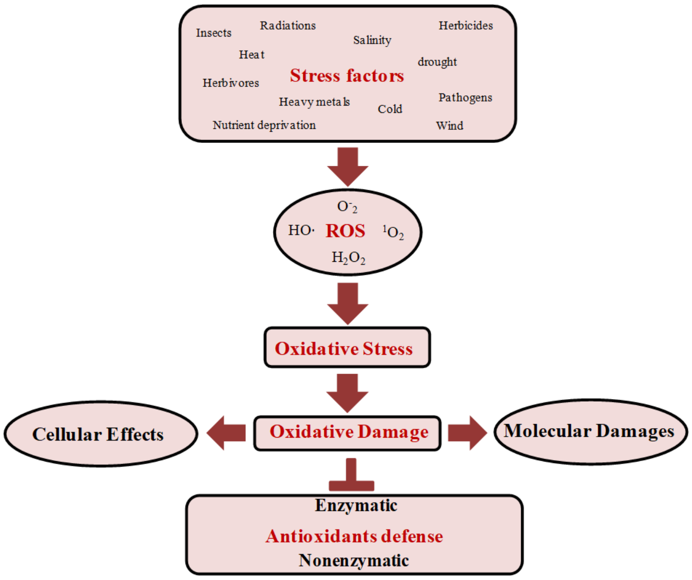

Figure 2. Stress factors, ROS generation, oxidative damage, and antioxidant defense. Several stress factors increased the ROS production, such as $HO^{\cdot}$, O^{-}_2, $^1O_2$, and H_2O_2. The increased ROS levels lead to oxidative stress. Consequently, oxidative damage at the molecular and cellular levels occurs. Defense mechanisms against oxidative stress are activated to neutralize toxic levels of ROS. Singlet oxygen ($^1O_2$), superoxide radical ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\cdot}$).

Enhanced level of ROS can cause damage to biomolecules such as lipids (lipid peroxidation), proteins (fragmentation of the peptide chain) and DNA (deoxyribose oxidation, strand breakage, removal of nucleotides, variety of modifications in the organic bases of the nucleotides, and DNA-protein crosslinks), and so forth ultimately resulting in cell death [4]. To avoid potential damage caused by ROS and to maintain growth, development and metabolism, the balance between production and elimination of ROS must be regulated. Plants possess complex antioxidative defense system comprising of non-enzymatic and enzymatic components to scavenge ROS [5,14]. Nonenzymic components of the antioxidative defense system include the major cellular redox buffers ascorbate (AsA) and glutathione (*γ*-glutamyl-cysteinyl-glycine, GSH) as well as tocopherol, carotenoids, and phenolic compounds [5,14,36]. The enzymatic components of the antioxidative defense system comprise of several antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (GPX), enzymes of ascorbate glutathione (AsA-GSH) cycle ascorbate peroxidase (APX), monodehydro ascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and glutathione reductase (GR) [5,36]. Various components of antioxidative defense system involved in ROS scavenging have been already well characterized into plant models, and disturbances or alterations in this system are an excellent strategy to understand the different signaling pathways involving ROS.

3.1. Nonenzymatic antioxidants

Nonenzymatic antioxidants interact with numerous cellular components and play key roles in defense and as enzyme cofactors. Moreover, these antioxidants influence plant growth and development, cell elongation and cell death [37].

Ascorbate (AsA) is found in organelles of most plant cell types and in the apoplast. AsA has a key role in defense against oxidative stress caused by enhanced level of ROS because of its ability to donate electrons in a number of enzymatic and nonenzymatic reactions. AsA can directly eliminate $O_2^{\square -}$, $OH^{\square}$, and $^1O_2$, and thus reduce H_2O_2 to water via the ascorbate peroxidase reaction [38]. AsA is generally maintained in its reduced state by a set of NAD(P)H-dependent enzymes, including monodehydroascorbate reductase, dehydroascorbate reductase, and glutathione reductase [14,27]. Moreover, AsA is involved in the regulation of cell division, cell elongation and it participates in multiple functions in photosynthesis [39].

Glutathione (*γ*-glutamylcysteinyl- glycine, GSH) is one of the crucial thiol that plays an important role in intracellular defense against ROS-induced oxidative damage. GSH is oxidized by ROS to form oxidized glutathione (GSSG), which is present in all cellular compartments. The balance between the GSH and glutathione disulfide (GSSG) is a central component in maintaining cellular redox state [5,40,41]. Due to its reducing power, GSH plays an important role in diverse biological processes, including cell growth/division, enzymatic regulation, regulation of sulfate transport, conjugation of metabolites, synthesis of proteins and nucleic acids, signal transduction and the expression of the stress responsive genes [42].

Tocopherols (α, β, γ, and δ) is a group of lipophilic antioxidants involved in scavenging of oxygen free radicals, lipid peroxyradicals, and $^1O_2$ [4]. The α-tocopherol with its three methyl substituents has the highest antioxidant activity of tocopherols [43]. The α -tocopherol present in the membrane of chloroplasts protects them against photooxidative damage [38,44]. Accumulation of *α*-tocopherol has been shown to induce tolerance to water deficit, salinity and chilling, in different plant species [45,46]. Chemical investigation of Brassicaceae has revealed the presence of tocopherols, of which α-tocopherol is the most abundant [47].

Phenolic compounds are abundantly found in plant tissues, such as flavonoids, lignin, tannins, hydroxycinnamate esters, and possess antioxidant properties [48]. They have been shown to outperform well -known antioxidants, AsA and *α*-tocopherol, in *in vitro* antioxidant assays because of their strong capacity to donate electrons or hydrogen atoms. They also modify lipid packing order and decrease fluidity of the membranes [49]. Species within the Brassicaceae family are also rich in phenolics, including simple phenolic acids, flavonoids, anthocyanins and lignans as the major chemical classes [50,51].

3.2. Enzymatic antioxidants

Enzymatic components of the antioxidative defense system comprise several antioxidant enzymes such as catalase (CAT, EC 1.11.1.6), superoxide dismutase (SOD, EC 1.15.1.1), glutathione peroxidase (GPX, EC 1.11.1.9), guaiacol peroxidase (POX, EC 1.11.1.7), peroxiredoxins (Prxs, EC 1.11.1.15), enzymes of ascorbateglutathione (AsA-GSH) cycle ascorbate peroxidase (APX, EC 1.1.11.1), monodehydroascorbate reductase (MDHAR, EC 1.6.5.4), dehydroascorbate reductase (DHAR, EC 1.8.5.1), and glutathione reductase (GR, EC 1.8.1.7) [5,14,36,27]. This antioxidant system plays an important role in the maintenance of cell homeostasis and in the antioxidant response in plants.

Catalases catalyze the dismutation of two molecules of H_2O_2 into water and oxygen. CATs are largely, but not exclusively, localized to peroxisomes. Plants possess multiple CATs encoded by specific genes, which respond differentially to various stresses that are known to generate ROS [52,53]. Overexpression of a CAT gene from *Brassica juncea* introduced into tobacco, enhanced its tolerance to Cd induced oxidative stress [54].

Superoxide dismutases catalyze the dismutation of $O_2^{\square}$ to H_2O_2. These enzymes may be attached to a metal ion (Mn, Fe, Cu/Zn, and Ni); thus, they are classified according to their subcellular location and metal cofactor. SOD activity has been reported to increase in plants exposed to various environmental stresses, including drought and metal toxicity [53].

Ascorbate peroxidases are enzymes that play a key role in catalyzing the conversion of H_2O_2 in to H_2O and use ascorbate as a specific electron donor. Plants have different APX isoforms that are distributed in distinct subcellular compartments, such as mitochondria, chloroplasts, peroxisomes, and the cytosol. The APX genes are differentially modulated by several abiotic stresses in plants [55-57]. Overexpression of the tApx gene in either tobacco or in *Arabidopsis* increased tolerance to oxidative stress [58]. The balance between SODs, CATs, and APXs is crucial for determining the effective intracellular level of $O_2^{\square}$ and H_2O_2, and changes in the balance of these appear to enhance compensatory mechanisms [13,52,53].

Glutathione peroxidases are nonheme thiol peroxidases that catalyze the reduction of H_2O_2 or organic hydroperoxides to water. The GPX proteins have been identified in many life species [59]. In plants, the GPX proteins are localized to mitochondria, chloroplasts, and cytosol.

Peroxiredoxins are a family of thiol-specific antioxidant enzymes that are involved in cell defense and protection from oxidative damage. The peroxiredoxins are a group of peroxidases that have reducing activity in their active sites via cysteine residues. They do not possess a prosthetic group and catalyze the reduction of H_2O_2, peroxynitrite, and a wide variety of organic hydroperoxides to their corresponding alcohols [60]. The peroxiredoxins are widely distributed in plant cells and are important proteins in chloroplast ROS detoxification [61].

Guaiacol peroxidases are involved in H_2O_2 detoxification. The POX proteins are hemecontaining enzymes that belong to class III or the "secreted plant peroxidases". Theses enzymes are able to undertake a second cyclic reaction, called the hydroxylic reaction, which is distinct from the peroxidative reaction. Due to the use of both cycles, class III peroxidases are known to participate in many different plant processes, from germination to senescence, cell wall elongation, auxin metabolism, and protection against pathogens [62].

Monodehydroascorbate reductase is a flavin adenine dinucleotide enzyme that catalyzes the regeneration of AsA from the monodehydroascorbate radical using NAD(P)H as an electron donor. Thereby, MDAR plays an important role in the plant antioxidant system by maintaining the AsA pool [63]. Isoforms of MDAR have been reported to be present in the cytosol, chloroplasts, peroxisomes, and mitochondria [64]. Overexpression of *Arabidopsis* MDHAR gene in tobacco confers enhanced tolerance to salt stress [65]. Tomato chloroplastic MDHAR overexpressed in transgenic *Arabidopsis* enhanced its tolerance to temperature and methyl viologen-mediated oxidative stresses [66].

Dehydroascorbate reductase is a thiol enzyme that maintains AsA in its reduced form. DHAR catalyzes the reduction of dehydroascorbate to AsA using GSH as a reducing substrate [36,63]. It is present in various plant tissues, and its modulation activity has been reported in various plant species [67]. Transgenic potato overexpressing *Arabidopsis* cytosolic AtDHAR1 showed higher tolerance to salt, drought and herbicide stresses [68].

Glutathione reductase a NAD(P)H-dependent enzyme catalyzes the reduction of GSSG to GSH and, thus, maintains high cellular GSH/GSSG ratio. It is a key enzyme of the AsA-GSH cycle; it protects cells against oxidative damage; and it maintains adequate levels of reduced GSH. A high GSH/GSSG ratio is essential for protection against oxidative stress [15].

4. Effect of Environmental Stress on Family Brassicaceae

The plant families Brassicaceae, also known as Cruciferae, contain high phenolics and glucosinates levels thereby considered them a good source of antioxidants [69,70]. These compounds are known to have a preventive role against different types of diseases [69]. However, presence of some polyphenols, tannins, glucosinolates, erucic acid and S-methylcysteine sulfoxide, in Brassicaceae vegetables, reflected its anti-nutritional effects [71]. Under abiotic and biotic stress, plants respond through activation of their defense system to ensure their growth and development [72,73]. In *Brassica* plants, these stress factors affect the primary and secondary metabolism, increasing the metabolite level production, e.g. amino acids, sugars and indoles [69,74]. Abiotic and biotic stresses enhance some specific secondary metabolite production which activate a number of signal pathways like abscisic acid (ABA), salicylic acid (SA), ethylene (ET) or jasmonic acid (JA) pathways [75]. These pathways are known to have a well-defined role in the plant defense responses [72,75].

4.1. Effect of Stress on Primary Metabolites

Abiotic stress affects plant metabolite production [76]. In *B. napus* leaves drought stress lead to a distinctive increase of amino acids, followed by a reduction in concentration upon rehydration of the plants [77]. The same stress has been proved to increase sugar contents in cabbage seedlings as compared to their control ones [78]. Similarly, metal exposure caused rapid increase in the levels of photosynthetic pigments, free amino acids, proteins and sugar content compared to the unstressed plants [79]. In *Arabidopsis* plants, ROS production were caused by cadmium stresses and this generate oxidative damage resulting in a significant decrease of chlorophyll content [80]. In *B. pekinensis* plants, increased total free amino acid content was noticed after exposure to copper stress, where free amino acids are reported to play a role in the detoxification of the copper stress [81]. Metal stress is also known to accumulate low-molecular compounds with chelating properties in *Brassica* [82]. Also, the ascorbic acid content was reported to be largely decreased after boiling of brussels sprouts, broccoli kale, and white cauliflower [83], whereas UV light exposure of broccoli (*B. oleracea* var. italica) caused an increased levels of ascorbic acid [84,85].

4.2. Effect of Stress on Secondary Metabolites

Brassicaceae family is known for some metabolites like glucosinolates, which are derived from amino acid biosynthesis (e.g. tryptophan, methionine, phenylalanine, etc.) [76]. These compounds are benefic for human health including anti-carcinogenic, cholesterol-reducing and other pharmacological effects [69,86,87] with some known anti-nutritional effects as well [88]. In addition, these secondary metabolites play a key role in plant defense after exposure to salt stress [89], wounding and/or pathogen attack [90], insect herbivory [91,92], other environmental stresses [93] or by plant signaling molecules [94], viz. SA, JA and MeJA [95].

Brassicaceae is attributed also for a group of naturally occurring plant steroidal compounds, brassinosteroids (BRs), with a broad range of biological activities and the capacity to make these *Brassica* plants to confer resistance against a wide range of both abiotic and biotic stresses [96], viz. salt stress, water stress, low and high temperatures, pathogen attack [96,97] and heavy metal stress [98]. These steroid compounds not only function as the precursors of brassinosteroids and membrane constituents but are known to have an essential role in plant growth and development [99]. For example, in radish seedlings, brassinosteroids were able to keep the membrane intact during Cd stress, thus checking ROS production by increasing levels of antioxidant enzyme activities [100].

5. Development of Plants from Family Brassicaceae Tolerant to Oxidative Stress

Understanding of the oxidative mechanism of action may contribute to the development of plants most well adapted to the environment. The increase of stress tolerance of crop plants is related to the maintenance of high antioxidant capacity to remove toxic levels of ROS. Maintaining high level of antioxidant enzymes will help a plant to protect itself against oxidative damage by rapidly scavenging the toxic levels of ROS in its cells and restoring redox homeostasis. Using transgenic approaches, several species were studied aiming at the improvement of tolerance to stress enhancing antioxidant capacity of antioxidant genes. Some examples of the successful and positive responses were obtained for Brassicaceae with increased tolerance to salt, drought, cold, heat, hydrogen peroxide, methyl viologen, and metals stresses (Table 1).

Table 1. Some examples of the transgenic Brassicaceae plants with potential stress tolerance expressing antioxidant genes.

Gene	Native specie	Target specie	Stress tolerance	Reference
Catalase	*Brassica oleracea*	*Arabidopsis thaliana*	Heat	[101]
Catalase	*B. juncea*	*Nicotiana tabacum*	Cadmium	[54]
Ascorbate peroxidase	*Hordeum vulgare*	*Arabidopsis thaliana*	Zinc, Cadmium	[102]
Ascorbate peroxidase	*B. compestris*	*Arabidopsis thaliana*	Heat	[103]
Ascorbate peroxidase	*Puccinellia tenuiflora*	*Arabidopsis thaliana*	Salinity, Hydrogen peroxide	[104]
Glutathione peroxidase	*Triticum aestivum*	*Arabidopsis thaliana*	Salinity, Hydrogen peroxide	[105]
Peroxiredoxins	*Suaeda salsa*	*Arabidopsis thaliana*	Salinity, Cold	[106]
Glutathione reductase	*B. compestris*	*Nicotiana tabacum*	Methyl viologen	[107]
Ascorbate peroxidase / Superoxide dismutase	*Rheum austral / Potentilla astrisanguinea*	*Arabidopsis thaliana*	Cold	[108]

Plants overexpressing one or more antioxidant genes have more antioxidant capacity and more efficient ROS elimination; consequently, plants can protect their cellular components against toxic effects of ROS produced during the exposure to stress. As a consequence, plants suffer less oxidative injury and can tolerate a stress condition more effectively. Recently, a numbers of transgenic plants have been developed with disposed expression of antioxidant enzymes that enhanced increased tolerance to salinity, drought, and extreme temperatures [109]. In fact, overexpression of Chinese cabbage (*B. campestris*) *BcAPX2* and *BcAPX3* in *Arabidopsis* enhanced seed germination rate and improved high temperature tolerance via efficient scavenging of cellular H_2O_2 [110]. Notably, overexpression of a single gene could increase plant tolerance to different stresses such as the overexpression of *SOD* for enhancing stress tolerance [111]. Nevertheless, the stress tolerance can develop markedly by applying the simultaneous coexpression of genes involved in metabolic pathways. For example, coexpression of *B. rapa BrMDHAR* and *BrDHAR* genes via hybridization conferred tolerance to freezing [112]. Coexpression of *PaSOD* and *RaAPX* genes from *Potentilla atrosanguinea* and *Rheum austral,* respectively, in transgenic *Arabidopsis* showed increased salt tolerance [113].

6. Conclusion and future prospects

Many research aiming to increase the tolerance of plants to environmental stresses using antioxidant genes. However, due to the complexity of the antioxidant system and plant stress tolerance, it will be difficult to state that ROS scavenging is the only pathway that determines the level of tolerance. Furthermore, stresses often occur in combination; thus, the relation between ROS signaling mechanisms in different stress responses is very complex. Additionally, since *Brassica* plants are considered to be important staple food, it is important to understand, how different environmental factors triggering mechanisms and pathways affect their metabolic profile, since these will ultimately affect its quality, functional properties, and attributes such as taste and aroma, which will influence consumer acceptability.

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Conflict of interest

The authors declare that there is no conflict of interest.

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