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REVIEW ARTICLE

Enhancing plant resilience: mechanisms and genetic strategies for detoxification of Reactive oxygen species

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Abstract
Plant cells are frequently exposed to oxidative cellular environments, leading to the production of harmful reactive oxygen species (ROS). Plants have developed a number of techniques, including their scavenging and antioxidant machinery, to detoxify the toxic ROS. Numerous enzymatic and non-enzymatic antioxidants are found in plant cells, which help remove harmful oxygen molecules. This mechanism, which involves both maintaining redox homeostasis and facilitating redox signaling, depends on a variety of antioxidant molecules that are located in various cellular compartments. Additionally, the significance of various antioxidant enzymes functioning in a coordinated and synergistic manner within the cell to protect it from stress-induced damage has been emphasized. It also presents the recent biotechnological approaches aimed at improving plant resilience in model and crop species to improve stress tolerance by engineering one or more than one of these components of the ROS scavenging machinery.

Keywords ROS · Antioxidants · Redox signaling · ROS homeostasis

Introduction

ATP production in plant mitochondria, similar to that in animals, relies on the presence of oxygen. However, unlike animals, plants continuously generate oxygen during photosynthesis, allowing them to tolerate even higher oxygen concentrations. In plants, the oxygen concentration is 2.5 times higher in the green leaves than in the non-green sections, such as the roots. The oxygen levels in both green and non-green parts of plants are significantly higher than those typically found in animal cells (Vanderkooi et al. 1991). However, during abiotic stress, plant tissues often experience considerable changes in oxygen availability, leading to highly hypoxic conditions in their environment (Bailey-Serres and Voesenek 2008). Plant seeds also experience huge oxygen variations. In green, photosynthetically active young seeds of *Brassica napus*, the transition between light and dark phases causes rapid and significant changes in internal oxygen levels. These fluctuations can range from extreme hyperoxia (over 700 µM during the day) to intense hypoxia (below 1 µM at night). Similar situations have also been observed in many other species (Borisjuk and Rolletschesk 2009). Plants naturally produce reactive oxygen species (ROS), such as superoxide and peroxides, as a byproduct of their oxygen metabolism Fig. 1a. Although significant levels of these ROS are harmful to plants, some ROS concentrations are essential for cell signaling. Continuous exposure to ROS induces an oxidative environment that alters the cell's redox balance. Due to the sensitivity of many cellular signaling pathways controlling cell division and stress reaction systems to redox balance, intracellular regional redox status changes have a significant impact on cell functioning (Chiu and Dawes 2012). Senescence and cell death as well as the eventual demise of the organism are frequently caused by severe redox conditions. Low molecular weight antioxidants like ascorbate, tocopherol, and glutathione are redox buffers that function as enzyme cofactors and are essential for defense, cell proliferation, and resistance to ageing and death (Tokunaga et al. 2005). In order to boost stress defense, antioxidants furnish the building blocks for the cell's redox state and regulate the expression of the genes connected to biotic and abiotic challenges. To maintain ROS homeostasis, plants have evolved intricate cellular

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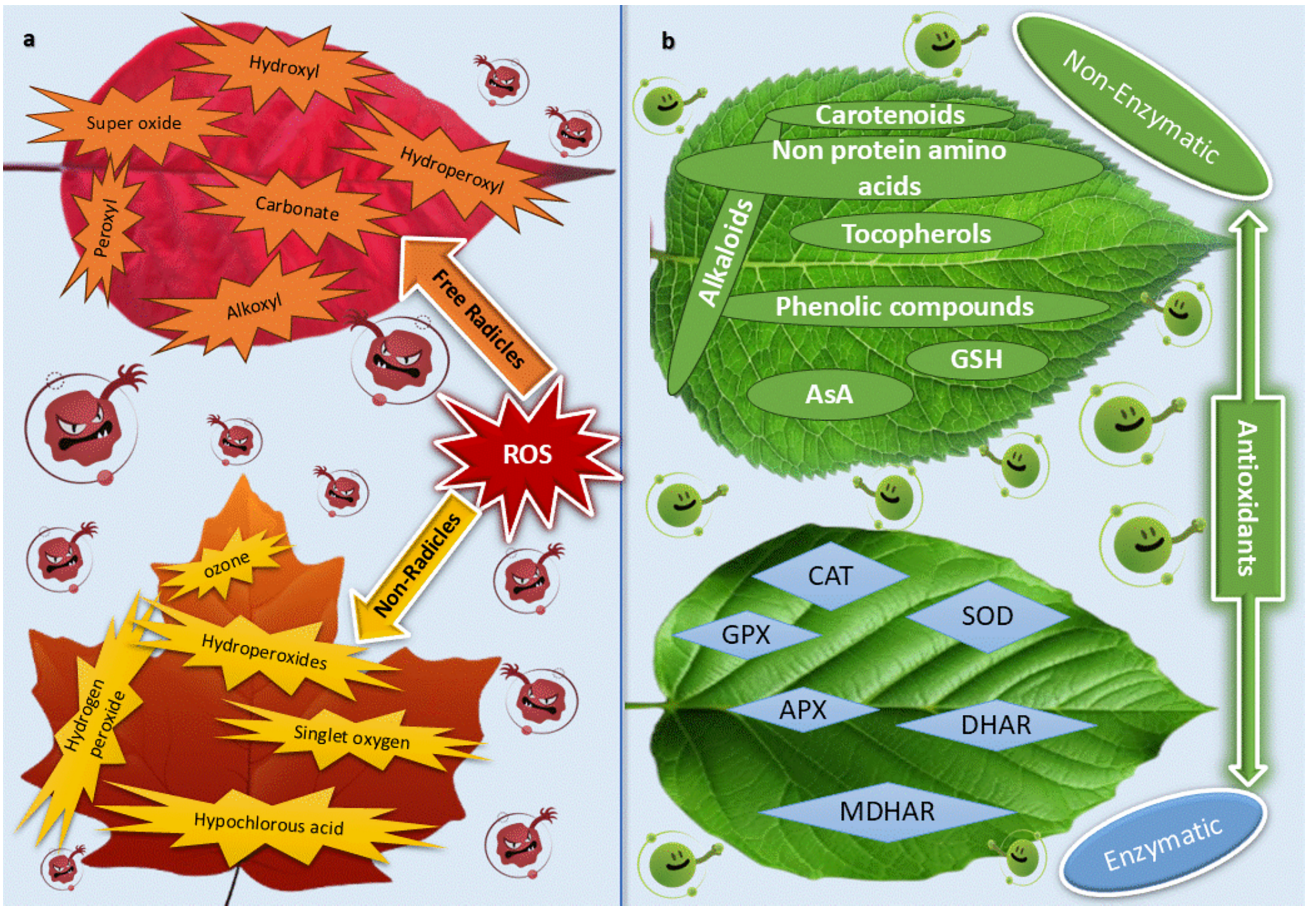

Fig. 1 **a** Different reactive oxygen species found in plants, **b** Types of antioxidants

mechanisms. A growing body of evidence points to redox homeostasis models in which antioxidant-ROS communications serve as a metabolic interface for signals originating from both metabolism and the environment.

Oxidative environment, antioxidant interactions and redox signaling in plant cell

When a specific stress or a mixture of different stresses results in the production of ROS, an oxidative environment is created (Thorpe et al. 2004). Several researchers have explored the mechanisms of oxygen production in cells. (Kumar et al. 2012; Ghosh et al. 2014). Superoxide is a primary byproduct of oxidase-catalyzed reactions involved in water formation, and from superoxide, additional ROS are subsequently created. While light is being captured and the photochemical process is underway, oxygen is also generated in discrete amounts. Superoxide (O_2^-) or hydrogen peroxide (H_2O_2) is produced by a variety of enzymatic activities. Multiple cellular compartments, including chloroplasts, mitochondria, peroxisomes, and the cytoplasm, contribute to ROS generation in plant cells (Fig. 2). Drought, salinity, low or high temperatures, and other abiotic stressors frequently restrict CO_2 fixation and lessen $NADP^+$ synthesis during the Calvin cycle. As a result, the photosynthetic electron transport chain (ETC) underwent over-reduction, which caused the chloroplasts to produce superoxide radicals and singlet oxygen (Li and Jin 2007). To prevent ETC over-reduction under stress, higher plants modify the photorespiration pathway to regenerate $NADP^+$. (Hong-bo, Shao 2006). H_2O_2 is generated in peroxisomes as a by-product of the photorespiratory pathway. (Foyer and Noctor 2005). Higher plants have enzymatic and non-enzymatic antioxidant defense systems that aid in scavenging ROS and protecting the plant from oxidative damage (Fig. 1b) (Foyer and Noctor 2005). The antioxidant system effectively controls ROS accumulation through multiple mechanisms. It relies on high levels of non-enzymatic scavengers and diverse biochemical properties. Additionally, the system's flexibility comes from the varied localization of antioxidant enzymes and their differential inducibility at the transcriptional and protein levels. This allows precise spatial and temporal regulation of ROS (Foyer and Noctor 2005; Hong-bo, Shao 2006). The antioxidant

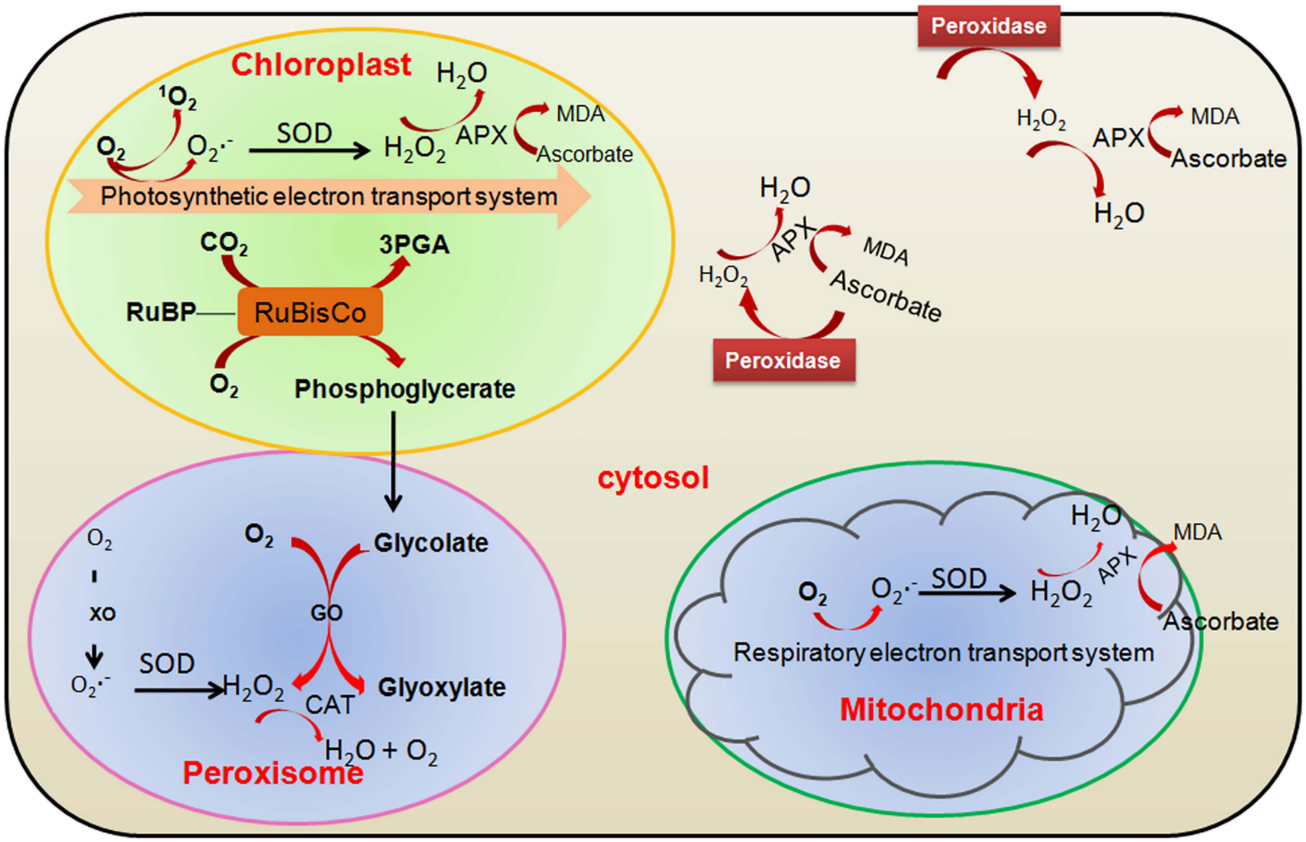

Fig. 2 Major sites of reactive oxygen species (ROS) production in photosynthetic cells and involvement of major antioxidative enzymes (Das et al. 2015)

enzymes such as catalase (CAT), superoxide dismutase (SOD), glutathione reductase (GR), ascorbate peroxidase (APX) and monodehydroascorbate reductase (MDHAR) play a major role in scavenging the toxic ROS inside the plant cell along with the non-enzymatic ROS scavengers like ascorbic acids and reduced glutathione.

Redox homeostasis in plants

For competent transit across electron transport cascades in plants, both reduced and oxidised versions of electron transporters must exist simultaneously. Redox poising is the term for this situation, which is characterised by a continuous conversion of electrons from various locations in the respiratory and photosynthetic electron transport chains to oxygen molecules. Since these ROS are reactive, not only should their rising concentration be managed, but they can also function as signalling molecules. The antioxidative system, which helps cells to maintain the biological components in an active state for metabolism, controls the level of ROS accumulation. Similar to many other aerobic animals, plants maintain the majority of their cytoplasmic thiols in their reduced (2SH) state due to the thiol buffering effect of millimolar glutathione concentrations. However, ascorbate, an additional hydrophilic redox buffer that provides excellent resistance against oxidative stress, is produced in high amounts by plant cells. The huge pools of these antioxidants control redox homeostasis by keeping the levels of reductants and oxidants in a balanced condition. Important lipid soluble redox buffers made by plants are tocopherols (Vitamin E). Tocopherol is a well-known singlet oxygen scavenger, although it may also effectively scavenge other ROS (Foyer and Noctor 2005). Additionally, the tocopherol redox pair expands the spectrum of effective superoxide scavenging since it has a higher constructive midpoint potential than the ascorbate pool. One of their key traits is the ability of the glutathione, ascorbate, and tocopherol pools to operate as redox buffers in plant cells. The homeostatic regulation carried out by antioxidant redox buffering enables ROS signaling pathways. Antioxidants control the duration and the specificity of the ROS signal as they process it continuously. Plant cells typically handle the high rate of ROS formation carefully. Although cellular oxidation plays a crucial role in all biotic and abiotic stress events, there is debate over the severity and physiological effects of oxidative injury. For

example, plants with low levels of cytosolic APX and CAT activity exhibit less severe signs of stress than plants that need one or both of these enzymes (Rizhsky et al. 2002).

Development of transgenic plants tolerant to abiotic stress by enhancing ROS defense mechanisms

Researchers have engineered multiple transgenic plant varieties by altering genes linked to enzymatic and non-enzymatic mechanisms for scavenging reactive oxygen species (ROS). These modifications have resulted in improved resistance to various abiotic stresses (Table 1). A notable strategy includes increasing the expression of genes responsible for producing ROS-detoxifying enzymes like superoxide dismutase (SOD), (Prashanth et al. 2008), CAT (Al-Taweel et al. 2007), APX (Kim et al. 2008), MDHAR (Etrayeb et al. 2007), DHAR (Ushimaru et al. 2006), GR (Kornyeyev et al. 2003) and GPX (Gaber et al. 2006) in various plant species, isolates derived from the same or different organisms have been shown to confer enhanced tolerance to one or more abiotic stresses by reducing oxidative damage. Complete neutralization of ROS molecules involves more than one enzyme localized in the same or different sub cellular compartments of the cell as depicted in Fig. 3. Transgenic cassava (*Manihot esculenta* Crantz) has demonstrated elevated levels of several key reactive oxygen species (ROS) scavenging enzymes, including MDHR, DHAR, and GR. Likewise, the overexpression of essential enzymes involved in the antioxidant biosynthetic pathways plays a pivotal role in enhancing tolerance to various abiotic stresses. For instance, transgenic plants exhibit increased drought tolerance when the gene encoding P5CS, a critical enzyme in proline biosynthesis, is overexpressed (Yamada et al. 2005; Vendruscolo et al. 2007). Similarly, overexpression of the VTE1 gene, which encodes tocopherol cyclase, a key enzyme in tocopherol biosynthesis, contributes to improved stress resilience. They have demonstrated that plants that overexpress VTE1 are more drought-tolerant. Transgenic Arabidopsis that was overexpressing the antioxidant AtERF98 TF showed higher ascorbic acid buildup and increased salt tolerance (Zhang et al. 2012). In addition to ROS-scavenging enzymes and non-enzymatic antioxidants, plant's ability to tolerate stress is also influenced by the overexpression of ROS-responsive signaling and regulatory genes. The regulatory genes have been beneficial in promoting tolerance to abiotic stresses such as drought, salt, oxidative, cold, and heavy metal stress. These regulatory genes modulate a wide range of acclimation-related pathways, including ROS detoxification. Enhanced abiotic stress tolerance in Arabidopsis has been attributed to the overexpression of mitogen-activated protein kinase kinase 1 (MKK1), which amplifies the activity of the MAPK cascade, a signaling pathway also activated by reactive oxygen species (ROS) (Xing et al. 2008). Additionally, increased tolerance to salt, drought, or osmotic stressors was seen in the presence of over-expression of transcription factors (Zat12 or JERF3, Zat10, etc.) that govern the expression of several ROS-scavenging genes encoding enzymes (Rizhsky et al. 2004). According to Rai et al. (2013), tomato (cv. Kashi Vishesh) plants overexpressing AtDREB1A/CBF3 from Arabidopsis under the control of the stress-inducible promoter rd29A exhibited increased accumulation of antioxidants and ROS-scavenging enzymes, along with enhanced tolerance to drought-induced oxidative stress. Transgenic plants developed through gene pyramiding or co-expression of multiple antioxidant genes have demonstrated superior stress tolerance compared to those overexpressing a single antioxidant gene (Table 1). For example, the co-expression of Mn-SOD and APX in *Nicotiana tabacum* has been reported to enhance tolerance to multiple abiotic stresses. Similarly, the co-expression of MeAPX2 and MeCu/ZnSOD in cassava (*Manihot esculenta* Crantz) resulted in improved resistance to methyl viologen (MV)-induced H_2O_2 stress and a two-fold increase in tolerance to chilling stress compared to wild-type plants (Xu et al. 2014).

Table 1 Representative reports for raising transgenic plants by overexpressing enzymes involved in ROS scavenging, which show improved tolerance to various abiotic stresses

S.no	Gene	Transgenic plant	Gene source	Stress tolerance	References
1	Cu/Zn SOD	*Nicotiana tabacum*	*Oryza sativa*	Salinity, drought	Badawi et al. (2004)
2	MDHAR1	*Nicotiana tabacum*	*Arabidopsis thaliana*	Salinity,ozone,drought	Etrayeb et al.(2007)
3	GPX	*Nicotiana tabacum*	*Chlamydomonas*	Salinity,cold,oxidative	Yoshimura et al. (2004)
4	GR	*Gossypium hirsutum*	*Arabidopsisthaliana*	Cold, photo-oxidative	Kornyeyev et al. (2003)
5	DHAR	*Arabidopsis thaliana*	*Oryzasativ*	Salinity	Chen and Gallie (2005)
6	*OsAPXa*	*Oryzasativa*	*Oryzasativa* L	Cold	Sato et al. (2011)
7	MeAPX2 + MeCu/	ZnSOD *Manihot esculenta* Crantz	*Manihot esculenta* Crantz	Chilling, oxidative	Xu et al. (2014)
8	cytAPX + cytSOD	*Prunus domestica*	cytsod from spinach and cytapx from pea	Salinity,oxidative	Diaz-Vivancos et al. (2013)

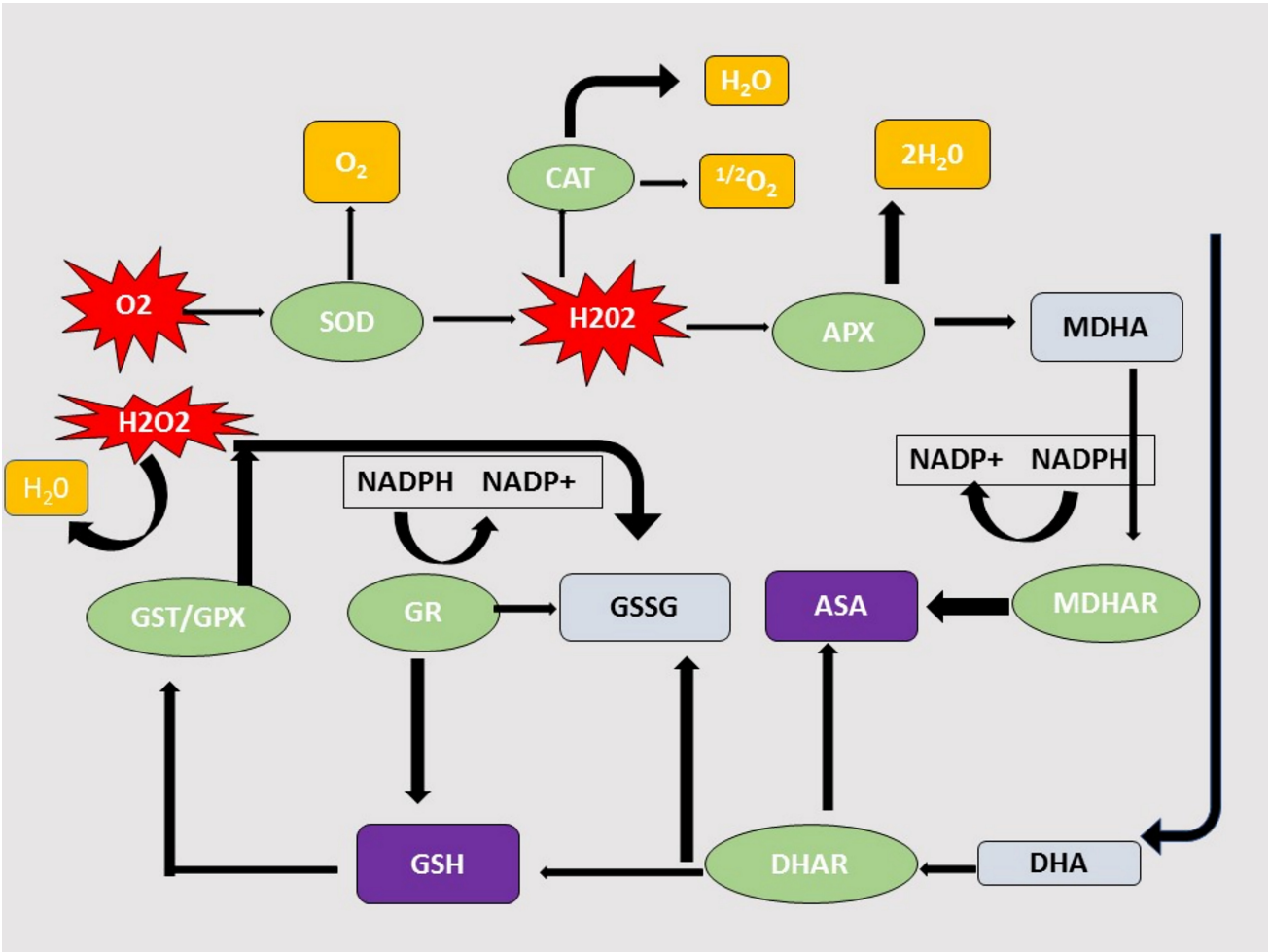

Fig. 3 Mechanism of antioxidant enzymes and low molecular weight antioxidants to detoxify ROS

Potential limitations of transgenic approaches and their applicability under field conditions

Transgenic strategies aimed at enhancing reactive oxygen species (ROS) detoxification mechanisms have demonstrated promise in controlled environments; however, their effectiveness under field conditions is influenced by multiple factors. Environmental variability poses a significant challenge, as field conditions expose plants to diverse abiotic stresses such as drought, salinity, and extreme temperatures, which can impact the expression and stability of introduced transgenes, leading to inconsistent performance outside controlled settings (Lawlor 2013). Additionally, the complexity of plant stress responses further complicates transgenic approaches, as stress tolerance involves intricate signaling networks, and the overexpression of specific antioxidant enzymes may inadvertently disrupt these pathways, causing unintended physiological effects (Hasanuzzaman et al. 2020). Another critical concern is gene flow and its ecological impact, as transgenes may spread to wild relatives or non-transgenic crops, potentially leading to the emergence of invasive species or disturbances in local ecosystems (Anwar and Kim 2020). Moreover, regulatory challenges and public skepticism continue to hinder the widespread adoption of transgenic crops, with concerns over food safety, environmental impact, and ethical considerations restricting their acceptance in various regions (Ahanger et al. 2017). Finally, economic and agronomic factors play a crucial role, as the successful implementation of transgenic technologies requires substantial investment in infrastructure, making access difficult for small-scale farmers. Furthermore, the performance of transgenic plants in real-world agricultural settings is often influenced by interactions with diverse biotic and abiotic factors, which may limit their anticipated benefits (Sharma et al. 2012).

Conclusion and future prospects

Normally, ROS are produced by a plant's metabolic process and function as assigning molecules to activate a plant metabolic pathway. The production of ROS does, however, rise during environmental stress in various cell compartments, including the mitochondria, peroxisomes, and chloroplasts. A higher concentration of ROS causes oxidative stress in plants, which damages macromolecules like nucleic acids, proteins, and lipids through oxidative degradation as well as cell membranes (lipid peroxidation). Plants have powerful ROS scavenging mechanisms to protect them from the negative effects of excessive ROS accumulation. To maintain the correct balance between diverse cellular metabolic pathways, which become disturbed in unfavorable circumstances, ROS are essential signaling molecules that interact with one another and with other cellular antioxidant systems. Thus, the ROS themselves do not determine whether they have a positive or negative impact on plants; rather, it is their concentration within cells. There is a wealth of knowledge available on the production of ROS, the function of free radicals in intracellular communication, and their efficient scavenging, but our grasp of the entire ROS scavenging and signalling route is incomplete. Future studies in this field will be beneficial for developing a plan of action to maximise yield even in unfavorable conditions. Although transgenic technology targeting ROS scavenging components has enhanced abiotic and biotic stress tolerance in various crop plants to some extent, further improvements are needed through gene pyramiding to achieve the near-potential yield of crops under rapidly changing climatic conditions. However, for practical application under field conditions, careful consideration of environmental, ecological, and socio-economic factors remains essential.

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Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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