

## Review Article

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# Antioxidant defense in plants during RNA virus infection: the role of key enzymes

In recent decades, the issue of crop resistance to biotic stressors has gained particular relevance in the context of global food security. Among biotic factors, viral infections occupy a special position, causing significant yield losses and disrupting physiological processes in plants. RNA viruses are characterized by high adaptability and the ability to effectively reprogram host cellular metabolism, a process accompanied by disruption of redox homeostasis. The generation of reactive oxygen species (ROS) constitutes one of the key events in this process and is characterized by functional duality: ROS act as signaling molecules that initiate defense responses, whereas their excessive accumulation leads to damage to cellular components. Alterations in redox homeostasis are accompanied by activation of the plant antioxidant system, which encompasses both enzymatic and non-enzymatic defense mechanisms. Despite considerable advances in the study of redox processes in plants, the interplay between redox regulation mechanisms and antioxidant system functioning under viral infection remains insufficiently characterized and requires further investigation. In this regard, the aim of the present review is to systematize and analyze current knowledge of the roles of reactive oxygen species and key antioxidant enzymes in the regulation of immune responses in plants infected with RNA viruses.

**Keywords:** oxidative stress, plant antioxidant system, viral infection, plant immunity.

## Introduction

In recent decades, the issue of crop resistance to biotic stressors has become particularly relevant in the context of ensuring global food security. Among biotic factors, viral infections occupy a special place, causing significant yield losses and disrupting plant physiological processes. RNA viruses are characterised by high adaptability and the ability to effectively modify the host's cellular metabolism, which is accompanied by a disruption of redox homeostasis. The generation of reactive oxygen species (ROS) represents one of the key stages of this process, characterised by functional duality: on the one hand, ROS act as signalling molecules that initiate defence responses; on the other, their excessive accumulation leads to damage to cellular components. Changes in redox homeostasis are accompanied by the activation of the plant antioxidant system, which includes both enzymatic and non-enzymatic defence mechanisms. Despite significant progress in the study of redox processes in plants, the integration of redox regulation mechanisms and the functioning of the antioxidant system under conditions of viral infection remains insufficiently described to date and requires further analysis. In this regard, the aim of this review is to systematise and analyse current understanding of the role of ROS and key enzymes of the antioxidant system in the regulation of the plant immune response during RNA virus infection.

### 1. Generation of Reactive Oxygen Species during RNA Virus Infection.

Reactive oxygen species (ROS) are highly reactive oxygen-containing molecules, including free radicals such as the superoxide anion ( $O_2^{\cdot-}$ ), the hydroxyl radical ( $\cdot OH$ ), and hydrogen peroxide ( $H_2O_2$ ). The compounds listed above are natural products of cellular metabolism and are formed predominantly in the mitochondria during the functioning of the electron transport chain [1]. Under physiological conditions, ROS act as signalling molecules performing regulatory functions in the control of cell proliferation and differentiation, as well as in the activation of the immune response via redox-dependent signalling pathways [2].

However, excessive accumulation of ROS within the cell leads to the development of oxidative stress, accompanied by a disruption of redox homeostasis. Under these conditions, ROS actively interact with major

cellular macromolecules—lipids, proteins and nucleic acids—causing lipid peroxidation, oxidative modification of proteins and damage to genetic material, ultimately leading to the destabilisation of cell membranes, disruption of organelle functions and cell death [3].

Oxidative stress can be induced both by abiotic factors, including extreme temperatures, ultraviolet radiation and exposure to toxic compounds, and by biotic factors, such as bacterial, fungal or viral infections [4, 5]. In viral infections, changes in redox homeostasis are caused not only by the damaging effect but also by the functional reorganisation of cellular processes aimed at ensuring viral replication. In particular, RNA viruses actively interact with the cell's membrane structures, forming replication complexes on the surface of mitochondria, the endoplasmic reticulum and other organelles, which is accompanied by an increase in ROS production. These replication complexes are virus-induced membrane structures formed by the recruitment of intracellular organelles and serving as a platform for viral RNA synthesis [6, 7]. In plant RNA viruses, their organisation has specific features: in *Tobacco mosaic virus* (TMV), replication is associated with the membranes of the endoplasmic reticulum, in *Tomato bushy stunt virus* (TBSV)—with the membranes of peroxisomes and mitochondria, where invaginations form, creating isolated microcompartments, whereas in *Cucumber mosaic virus* (CMV) intracellular membrane structures and chloroplasts are involved in the process. Such a spatial organisation of replication is inevitably accompanied by disruption of the function of the relevant organelles and alterations in electron transport, leading to oxidative stress [8, 9].

An additional contribution to the excessive accumulation of ROS is made by the activation of NADPH oxidases and changes in the functioning of mitochondria and chloroplasts, which enhance the formation of  $O_2^-$ . In this context, ROS act not only as a by-product but also as a regulatory factor involved in the activation of signalling pathways that contribute to the maintenance of viral replication. RNA viruses are characterised by their ability to maintain ROS levels within a functionally significant range, as a moderate increase in their concentration facilitates the viral life cycle, whereas excessive accumulation is accompanied by the development of oxidative damage to the cell and a limitation of the infectious process.

The balance between ROS formation and neutralisation under conditions of viral infection is determined by the functional state of the cell's antioxidant system—an evolutionarily conserved defence mechanism capable of counteracting oxidative stress [6, 10].

## 2. Plant antioxidant defense system.

Under stress conditions such as viral infection, the maintenance of redox homeostasis in plants is ensured by the coordinated functioning of the antioxidant defence system (Fig. 1). Antioxidants are molecules capable of inhibiting free radical reactions, thereby preventing the development of cellular damage [11].

This system consists of enzymatic and non-enzymatic components (Fig. 2), which are localised in various cellular structures and regulated in response to the physiological state of the cell. In this context, antioxidant defence is formed as an integrated system that functions in a coordinated manner and mutually enhances the effectiveness of ROS detoxification during viral infections.

The enzymatic components of the plant antioxidant system (including superoxide dismutase, catalases, ascorbate peroxidase and glutathione reductase) are regarded as the main component of primary antioxidant defence, ensuring rapid enzymatic detoxification of ROS induced by viral infection.

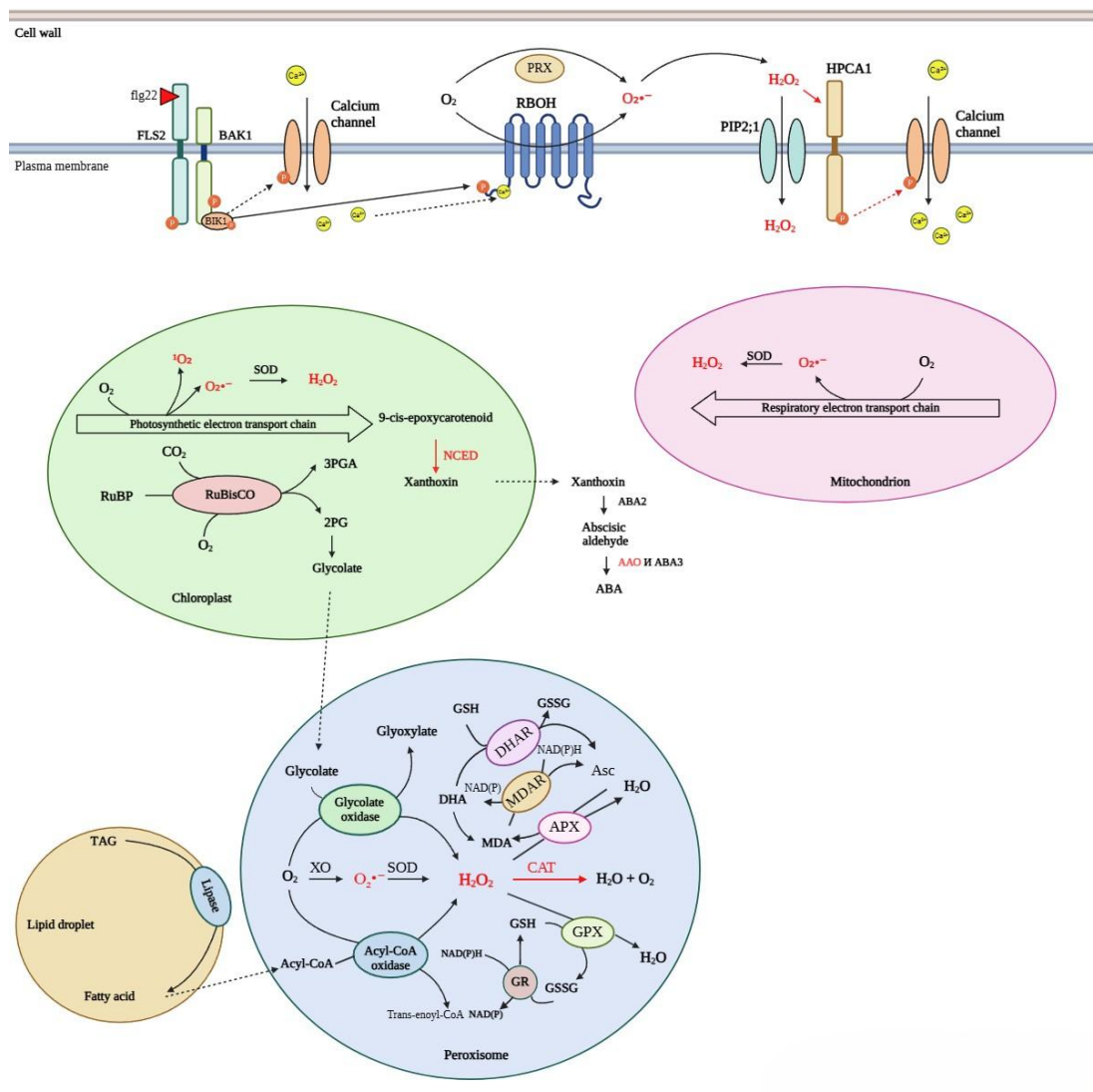


Figure 1. Plant antioxidant system.

*Note.* Compiled by the authors.

Non-enzymatic antioxidants (ascorbate, glutathione, tocopherols, carotenoids and phenolic compounds) constitute a pool of low-molecular-weight redox-active compounds that primarily perform buffering, reducing and stabilising functions in maintaining cellular redox [12–14].

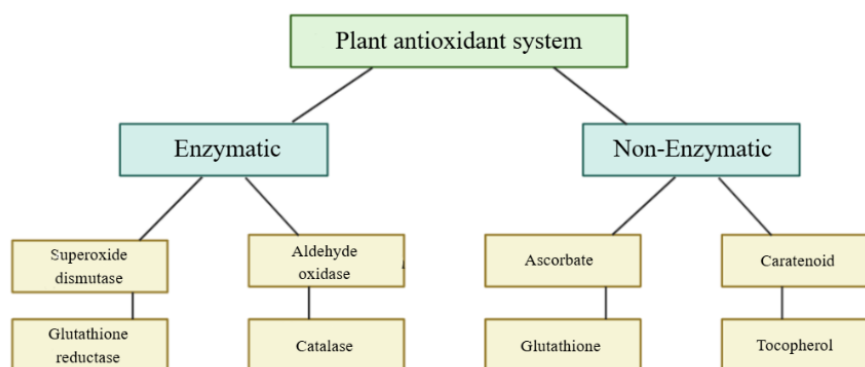


Figure 2. Enzymatic and non-enzymatic components of the antioxidant system

## 2.1 Non-enzymatic Antioxidants

Non-enzymatic antioxidants are low-molecular-weight compounds that play an important role in neutralising free radicals by donating electrons or hydrogen atoms. These compounds are divided into two categories: hydrophilic antioxidants, such as glutathione, ascorbate and phenolic compounds, and lipophilic membrane antioxidants, which include carotenoids. Among hydrophilic antioxidants, ascorbate (AsA) occupies a special place—one of the key water-soluble antioxidants in plants, playing an important role in maintaining the redox balance during viral infection. The redox state of ascorbate, regulated by the activity of ascorbate oxidase (AO), determines the apoplast's ability to participate in signal transduction associated with the activation of the plant's defence responses during a viral attack. In this context, AsA is involved not only in the neutralisation of ROS but also in the signalling regulation of the immune response. The biosynthesis of ascorbate is predominantly carried out via the Smirnov–Wheeler pathway, where the final step is the oxidation of L- galactono-1,4-lactone in the mitochondria. Due to its structure, AsA is capable of directly neutralising ROS, including  $O_2^{\cdot-}$  and  $\cdot OH$ , and also acts as an electron donor for ascorbate peroxidase (APX) during the reduction of  $H_2O_2$  [15, 16]. AsA functions as a redox buffer, coordinating antioxidant defence and immune signalling in infected cells [17]. Alongside ascorbate, glutathione (GSH)—a low-molecular-weight tripeptide—is one of the main antioxidants in plant cells during viral infection. Upon viral entry, there is enhanced ROS generation, accompanied by the accumulation of GSH in the cytosol, chloroplasts and mitochondria [18]. It is important to note that GSH participates in the ascorbate–glutathione cycle, ensuring the reduction of dehydroascorbate to ascorbate via the enzyme dehydroascorbate reductase (DHAR) [19, 20]. In this context, the GSH/GSSG ratio serves as an indicator of the cell's redox status and regulates the activation of defence response genes. Consequently, glutathione plays a dual role—as an antioxidant and a signalling molecule—ensuring thiol redox homeostasis during viral [21–23]. Regarding lipid lipophilic antioxidants, carotenoids belong to the group of isoprenoid compounds, characterized by significant structural diversity [24]. They consist of eight isoprene units, with most carotenoids deriving from the linear tetraterpene phytoene. These low-molecular-weight metabolites protect the photosynthetic apparatus by preventing the formation of reactive oxygen species through the quenching of excited chlorophyll and triplet sensitizers, whilst simultaneously reducing the level of lipid peroxidation [25].

Non-enzymatic antioxidants include functionally diverse redox-active compounds involved in maintaining cellular homeostasis. Individual representatives differ in their localisation, mechanisms of action and degree of involvement in redox regulation. A comparative characterisation of the main components of the plant antioxidant system and their roles in viral infection is presented in Table 1.

Table 1

**The importance of non-enzymatic antioxidants in antiviral response**

| Antioxidant           | Localization                                                     | Role in Antiviral Response (RNA Viruses)                                                                                                                | Sources |
|-----------------------|------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|---------|
| Ascorbate (Vitamin C) | Cytosol, chloroplasts, mitochondria; apoplast                    | Maintains redox homeostasis, participates in ROS detoxification, and enhances resistance to Turnip mosaic virus (TuMV) and Cucumber mosaic virus (CMV). | [26]    |
| Glutathione (GSH)     | Cytosol, nucleus, mitochondria, chloroplasts; apoplast/cell wall | Supports the ascorbate-glutathione cycle and influences HR and resistance to Potato virus Y (PVY) and TuMV.                                             | [27]    |
| Carotenoids           | Chloroplast thylakoid membranes; plastoglobules                  | During virus-induced chloroplast dysfunction and chlorosis, carotenoids are expected to play a crucial role in controlling $^1O_2$ .                    | [28]    |

## 2.2 Enzymatic antioxidants

SOD acts as a key enzyme in the first line of antioxidant defence; however, its reaction product,  $H_2O_2$ , is itself a toxic compound capable of converting into highly reactive OH in the presence of  $Fe^{2+}$  via the Fenton reaction. The detoxification of  $H_2O_2$  is the next essential stage in cellular antioxidant defence. This func-

tion is performed by two other first-line defence enzymes, CAT and GR, which, together with SOD, form a coordinated enzymatic system for the neutralisation of ROS [29].

### 2.2.1 Superoxide dismutase

Superoxide dismutase (SOD) is a metal-containing enzyme and one of the most effective components of the antioxidant defence system of plant cells against ROS. SOD catalyses the dismutation of  $O_2^{\cdot-}$  to form  $H_2O_2$  and  $O_2$  (Fig. 1) [30].

Depending on the metal cofactor, SOD exists in several isoforms: Cu/Zn-SOD, Mn-SOD and Fe-SOD. The Cu/Zn-SOD isoform is localised in the cytoplasm, peroxisomes, chloroplasts and apoplast, whilst Fe-SOD is found in plant chloroplasts, and Mn-SOD is localised in the mitochondrial matrix and in peroxisomes [31].

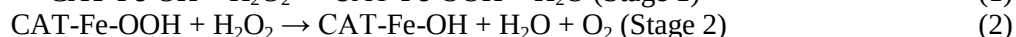
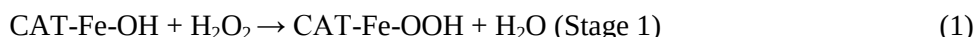
Sequence alignment, as well as structural and evolutionary studies, have revealed homology between Mn-SOD and Fe-SOD, whereas Cu/Zn-SOD has been found to be distinctly related to either Mn- or Fe-SOD [32]. Cu/Zn-SOD is activated either via a CCS-dependent pathway, which requires the covalent binding of a Cu chaperone to the  $Cu^{2+}$  ion, or via a CCS-independent mechanism [33]. The presence of two activation pathways is of significant physiological importance, as it ensures the preservation of the enzyme's catalytic activity even if one of the mechanisms is disrupted, thereby maintaining the functionality of the antioxidant system and the cell's resistance to oxidative stress.

The regulation of SOD under conditions of viral infection is characterised by multi-level modification, affecting both post-translational processes and the subcellular localisation of the enzyme. It has been established that infection with the bamboo mosaic virus (BaMV) in *Brachypodium distachyon* and *Nicotiana benthamiana* is accompanied by the accumulation of the full-length Cu/Zn-SOD precursor protein (PrNbCSD2) in the cytoplasm. This effect is attributed to the virus disrupting the processing of the PrNbCSD2 transit peptide, which impedes its normal function. The consequence is an excessive accumulation of  $H_2O_2$  in infected cells, associated with the development of chlorotic mosaic symptoms [34].

However, the neutralisation of ROS is not limited to the action of a single enzyme: the product of the reaction catalysed by SOD, hydrogen peroxide, is itself a toxic compound and requires further decomposition. This function is performed by catalase, which catalyses the dismutation of  $H_2O_2$  into water and molecular oxygen, thereby ensuring the cell's antioxidant response [35].

### 2.2.2 Catalase

Catalase (CAT) catalyses a two-step reaction for the decomposition of hydrogen peroxide and is localised in peroxisomes. In the first step,  $H_2O_2$  oxidises the iron ( $Fe^{2+}$ ) ion in the active site of CAT to form iron peroxide. It is known that at low concentrations of  $H_2O_2$ , the enzyme can remain in this intermediate state (compound I). However, at higher concentrations of  $H_2O_2$ , it acts as a reducing agent for compound I, thereby regenerating the enzyme and releasing water and oxygen [36].



The sources of  $H_2O_2$  in plant cells are chloroplasts, mitochondria and peroxisomes. In all these compartments,  $H_2O_2$  is synthesised following the dismutation of  $O_2^{\cdot-}$  by SOD. Furthermore,  $H_2O_2$  is generated by glycolate oxidase in peroxisomes [37] (Fig. 1).

Three distinct classes I, II and III have been identified based on *Nicotiana tabacum* genes. Class I CATs play a role in photosynthetic tissues and are involved in neutralising  $H_2O_2$ , which is produced during photosynthesis. Class II predominates in vascular tissues and lignification in response to ABA and during ageing, whereas class III is expressed in seeds and reproductive tissues, and its activity is high during fatty acid catabolism in the glyoxylate cycle in glyoxysomes. Three CAT isoforms (CAT1, CAT2, CAT3) have been identified in *Zea mays*. These isoforms are identical in their coding region and differ only in variable intron segments. Furthermore, the promoter sequence also differs in these different isoforms. The *Arabidopsis* genome also contains three CAT genes [38]. Recently, seven CAT genes were identified in *Gossypium* using genome-wide association studies (GWAS) [39]. The number of CAT genes varies among different plants; for example, there are three in *O. sativa*, *C. pepo* and *Cucumis sativus*, two in *Hordeum spp.* and one in *Ipomoea batatas*, *Ricinus communis* and *S. lycopersicum* [40].

Viral infections have mixed effects on catalase activity; however, in most cases, a functional suppression is observed. For example, in *Arabidopsis thaliana*, upon infection, the 2b protein interacts with the

CAT3 isoenzyme, inhibiting its activity and causing the development of necrosis [41]. A similar effect is observed during infection with maize chlorotic mottle virus (MCMV) in *Zea mays*, where the P31 protein binds to ZmCAT1, suppressing its activity, which is accompanied by the accumulation of H<sub>2</sub>O<sub>2</sub>, suppression of PR genes (ZmPR3, ZmPR4, ZmPR5) and enhanced viral replication; additional suppression of catalase isoform expression further enhances this effect [42]. Furthermore, the involvement of the PVX viral protein HC-Pro triggers a more intensive generation of H<sub>2</sub>O<sub>2</sub> compared to mutant forms. This suggests that viral factors play a direct role in regulating the cellular oxidative status.

CAT ensures the effective decomposition of H<sub>2</sub>O<sub>2</sub> predominantly in peroxisomes however, in mitochondria, where CAT is virtually absent, the detoxification of H<sub>2</sub>O<sub>2</sub> and lipid hydroperoxides is carried out by other enzymes. Maintaining redox homeostasis in these compartments requires the involvement of glutathione-dependent enzymes, the key one being GR.

### 2.2.3 Glutathione Reductase

Glutathione reductase (GR) is one of the main enzymes of the plant antioxidant system, involved in maintaining the balance between reduced (GSH) and oxidised (GSSG) glutathione. Maintaining this ratio is a critical condition for the effective neutralisation of ROS accumulating during viral infections. GR functions in close cooperation with other enzymes, in particular glutathione-S-transferases (GST), glutathione peroxidases (GPX) and  $\gamma$ -glutamyltransferases (GGT), providing comprehensive protection of cells against oxidative stress [43].

A review of the literature indicates that viral infections have a varied effect on GR activity depending on the host plant's resistance: *Turnip mosaic virus* (TuMV) and *Arabidopsis thaliana*: in resistant mutants (rbohF and rbohD/F), an increase in GR activity was observed, whereas in susceptible plants (Col-0 and rbohD), GR activity decreased 7 days post-infection [44]. *Cucumber mosaic virus* (CMV) and *Cucumis sativus*: treatment of plants with glycine betaine and chitosan led to a significant increase in GR activity, accompanied by a reduction in disease severity and viral accumulation [45]. Alongside changes in enzymatic activity, viral infections modulate the expression of glutathione system genes: TuMV and *A. thaliana*: resistant mutants demonstrated increased expression of the GSTU13 and GSTU19 genes, which correlated with a restriction of viral spread. In susceptible plants, the expression of these genes decreased 7 days post-infection [46].

These patterns are consistent with data obtained in other model systems and reflect the context-dependent nature of glutathione system regulation during viral infection. Thus, in *Solanum lycopersicum* infected with ToLCNDV, the SIGR3 isoform is significantly induced at the transcript and protein levels, whereas its suppression via virus-induced gene silencing (VIGS) leads to increased viral DNA accumulation and loss of resistance [47]. At the same time, during TuMV infection in *Arabidopsis thaliana*, the activity of the glutathione peroxidase-like enzyme (GPXL) decreases in susceptible genotypes and increases in resistant ones, accompanied by a change in the GSH/GSSG ratio, which reflects the redox state of the cell and determines the outcome of the infection [48].

GR plays a central role in ensuring the regeneration of reduced glutathione and thereby maintaining the functionality of the entire glutathione-dependent antioxidant system. However, under conditions of viral stress, not only ROS but also highly reactive aldehydes accumulate in the cell—by-products of the oxidative degradation of lipids and carbohydrates, which are themselves capable of damaging proteins, nucleic acids and membranes. The neutralisation of these compounds requires the involvement of specialised enzymes, one of which is AO.

### 2.2.4 Aldehyde oxidase

Aldehyde oxidase (AO) is a common molybdenum-iron-flavoprotein that oxidises various aldehydes to carboxylic acids [49]. The mechanism of action of AO is characteristic of molybdeno-flavoproteins: in the active site, molybdenum binds the aldehyde and transfers the oxygen group, reducing it, after which electrons are sequentially transported through two iron-sulphur clusters and FAD to an O<sub>2</sub> molecule. In the process, superoxide and, predominantly, hydrogen peroxide are formed [50]. Collectively, AO performs key regulatory functions in plant metabolism, catalysing the final stages of phytohormone biosynthesis by oxidising their aldehyde precursors. Four AO genes (AAO1–AAO4) have been identified in the *Arabidopsis thaliana* genome, exhibiting different substrate affinities and tissue localisation (Tab. 2) [51].

Major isoforms of AO and their biochemical properties

| Isoform | Structure                                                                  | Localization                            | Biochemical function                                                                                          | Source |
|---------|----------------------------------------------------------------------------|-----------------------------------------|---------------------------------------------------------------------------------------------------------------|--------|
| AAO1    | Homodimer (denoted as AO $\alpha$ )                                        | Seeds, roots, seedlings                 | IAAld $\rightarrow$ IAA. Participates in the alternative auxin biosynthesis pathway and oxidizes benzaldehyde | [52]   |
| AAO2    | Forms homo- and heterodimers, often in combination with AAO1 (AO $\beta$ ) | Seedlings, roots, and senescing leaves  | Participates in the alternative auxin biosynthesis pathway and oxidizes benzaldehyde                          |        |
| AAO3    | Homodimer                                                                  | Leaves (vascular tissues), seeds, roots | ABAld $\rightarrow$ ABA. Key enzyme of the final stage of abscisic acid biosynthesis                          |        |
| AAO4    | Homodimer                                                                  | Developing fruits (siliques), pollen    | Benzaldehyde $\rightarrow$ Benzoic acid. Participates in the metabolism of secondary compounds in seeds       |        |

The data obtained reflect the functional specialisation of isoforms: AAO1–AAO2 are involved in growth and development processes (biogenesis of secondary metabolites, oxidation of aldehydes), AAO3—in the synthesis of ABA under stress conditions, AAO4—in the detoxification of aldehydes and the utilisation of O<sub>2</sub> metabolites in fruits [52].

Since the effectiveness of antioxidant defence is determined by the preservation of functionally significant molecular mechanisms, it seemed appropriate to assess the degree of evolutionary conservation of the enzymes under investigation. Analysis of amino acid sequences and the construction of phylogenetic trees allow us to identify the level of conservation of functionally important domains, as well as to establish phylogenetic relationships between the proteins under investigation in different plant species. A high degree of conservatism in antioxidant enzymes may indirectly indicate the fundamental role of these proteins in maintaining redox homeostasis and plant adaptation to stressors, including viral infection. In this regard, key enzymes of the antioxidant system were examined and a comparative phylogenetic analysis was conducted.

#### Phylogenetic analysis

A search for the amino acid sequences of enzymes in the antioxidant system—SOD, CAT, GR and AO—was conducted in the NCBI Protein database. For the analysis, representatives of dicotyledonous plants (Eudicots) belonging to various families were selected: Solanaceae (*Solanum tuberosum*, *Solanum lycopersicum*, *Nicotiana tabacum*), Fabaceae (*Glycine max*, *Cicer arietinum*), Cucurbitaceae (*Cucumis sativus*), Rosaceae (*Malus domestica*) and Brassicaceae (*Arabidopsis thaliana*). Comparing representatives of phylogenetically distant families within a single class enabled the identification of both conserved and variable regions of protein sequences and also allowed the evaluation of the evolutionary relationships of the enzymes under investigation at the level of eudicots as a whole.

The criteria for sequence selection were the presence of full-length, experimentally validated records without fragmentary regions, a high degree of genomic annotation for each of the included species, and comparability of the species composition of the sample for all four enzymes, which ensured the validity of the comparative analysis. The exception was the analysis of AO, which included seven species instead of eight due to the absence of a full-length validated sequence for *Cucumis sativus* in the NCBI database.

Multiple alignment of amino acid sequences was performed using the MUSCLE method in MEGA 11.

To assess the evolutionary conservatism of the enzymes under study, phylogenetic trees were constructed based on the alignment of SOD, CAT, GR and AO amino acid sequences from selected dicotyledonous plant species (Figs. 3–6).

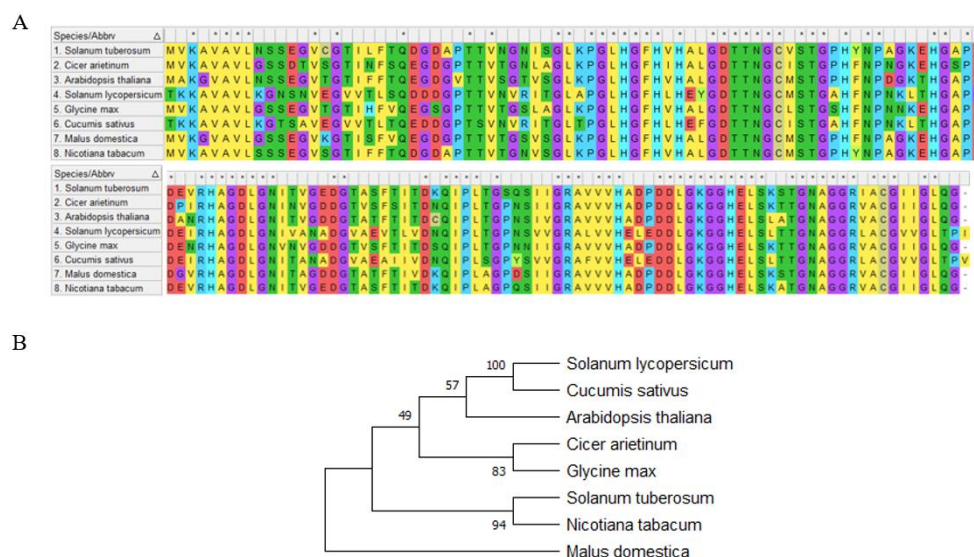


Figure 3. SOD phylogenetic tree and alignment of amino acid residues from different plant species:

A — MUSCLE alignment (MEGA 11); colors reflect the physicochemical properties of amino acids.

Conservatism: “\*” — identity, “:”/ “.” — similarity, B — The Maximum Likelihood tree (500 bootstrap replications).

The length of the branches is proportional to the number of amino acid substitutions per site

The SOD phylogenetic tree is characterised by clear clustering, reflecting the systematic position of the species. The genus *Solanum* is grouped with high support (94 %), the family Solanaceae forms a single, connected cluster, whilst *Glycine max* and *Cicer arietinum* are grouped separately in accordance with their membership of the Fabaceae. *Malus domestica* occupies an independent position on the tree. Sequence alignment shows 90 % identity within *Solanum* and 70–80 % between families, indicating the conservation of functionally significant domains of the catalytic centre. At the level of deep branches, bootstrap support drops to 40–50 %, reflecting the limited resolution of a single gene for reconstructing ancient phylogenetic relationships.

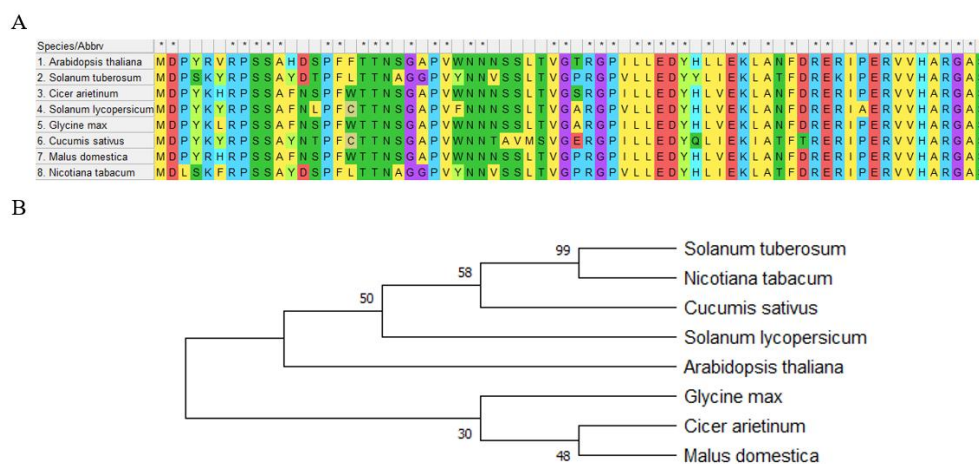


Figure 4. Comparative analysis of the amino acid sequences of catalase (CAT) in eight plant species:

A — MUSCLE alignment (MEGA 11); colors reflect the physicochemical properties of amino acids.

Conservatism: “\*” — identity, “:”/ “.” — similarity, B — The Maximum Likelihood tree (500 bootstrap replications).

The length of the branches is proportional to the number of amino acid substitutions per site

The topology of the CAT tree generally agrees with that of SOD, but differs in having higher bootstrap support values within key clusters. The *Solanum tuberosum*–*Nicotiana tabacum* pair is grouped with maximum support of 99 %, indicating exceptional conservatism of CAT within the Solanaceae family. Fabaceae are grouped with 80–85 % support, whilst *Arabidopsis thaliana* and *Malus domestica* again occupy isolated

positions. The consistency of the SOD and CAT tree topologies may indicate their co-evolution, driven by functional interdependence: SOD generates  $H_2O_2$ , the immediate detoxification of which is provided by CAT.

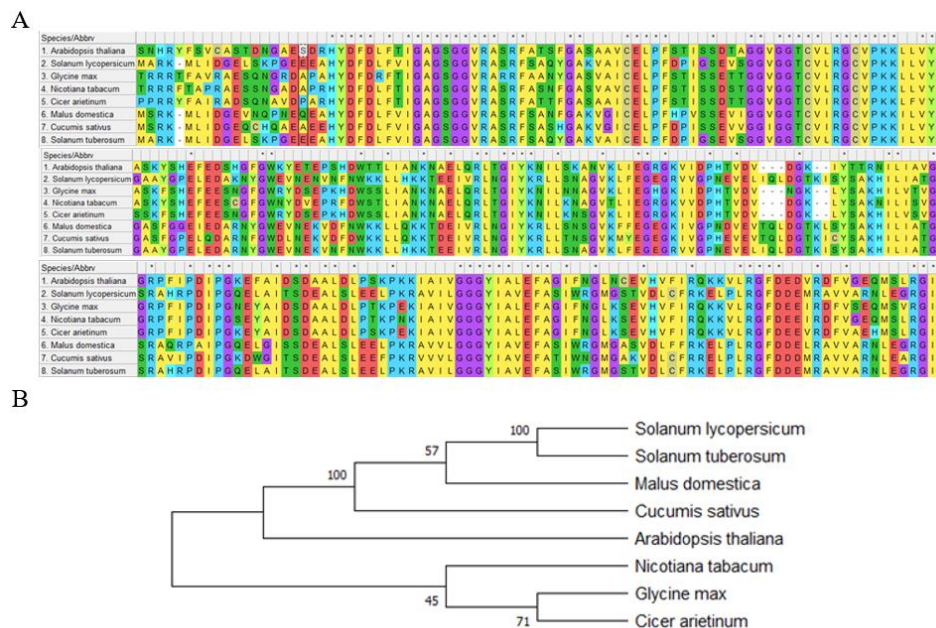


Figure 5. Comparative analysis of amino acid sequences of glutathione reductase (GR) in eight plant species: A — MUSCLE alignment (MEGA 11); colors reflect the physicochemical properties of amino acids.

Conservatism: “\*” — identity, “:/” — similarity, B — The Maximum Likelihood tree (500 bootstrap replications). The length of the branches is proportional to the number of amino acid substitutions per site

Phylogenetic analysis of GR revealed a number of topological features that distinguish this enzyme from SOD and CAT. *Solanum lycopersicum* and *Solanum tuberosum* are grouped together with maximum bootstrap support, confirming the high conservation of GR within the genus. Notably, *Malus domestica*, which occupied an isolated position on the SOD and CAT trees, is grouped together with representatives of the genus *Solanum* in this analysis with 100 % support. *Glycine max* and *Cicer arietinum* are grouped together with 71 % support. The partial divergence of the GR tree topology from the SOD and CAT trees may reflect differences in the intensity of evolutionary pressure on this enzyme in dicotyledonous plants, which is associated with its broader functional role in maintaining cellular redox balance.

Among all the enzymes considered, AO exhibits the most structured phylogenetic topology with two distinct monophyletic groups: Solanaceae (100 % support) and Fabaceae (100 % support), whilst *Malus domestica* occupies a sister position (75 %), and *Arabidopsis thaliana* occupies a basal position. High support values for deep nodes (75–85 %) and identity of functionally important domains exceeding 92 % within dicots indicate a slower evolutionary rate of the AO gene and pronounced purifying selection aimed at preserving the enzyme’s catalytic structure.

Phylogenetic analysis of the amino acid sequences of SOD, CAT, GR and AO in dicotyledonous plants revealed a high degree of conservatism of the enzymes under study within closely related taxa. The highest bootstrap support values were recorded within the genus *Solanum* and amounted to 94 %, 99 %, 100 % and 100 % for SOD, CAT, GR and AO, respectively. Representatives of the Fabaceae family were consistently grouped together in all four analyses, reflecting the conservation of the amino acid sequences of these enzymes within the family. The topologies of the resulting trees are generally consistent with the systematic position of the taxa under study, confirming the validity of the analysis. The results obtained indicate the evolutionary conservatism of the enzymes of the antioxidant system in dicotyledonous plants and their functional significance in the mechanisms of cellular defence against oxidative stress during viral infection.



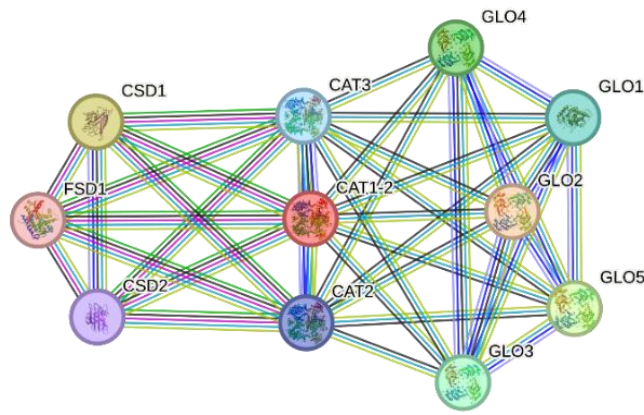


Figure 7. Functional interaction network of catalase (CAT1-2)

The network was constructed in STRING for *A. thaliana*. Colored nodes represent primary interaction partners.

Edge types: teal lines—curated database evidence, pink lines—experimental data, black lines—co-expression.

### Results and Discussion

The analysis identified ten high-confidence interaction partners of CAT1-2 (Tab. 3), predominantly represented by glycolate oxidases (GLO1–GLO5), superoxide dismutases (CSD1, CSD2, FSD1), as well as catalase isoforms CAT2 and CAT3.

Table 3

Functional interaction partners of CAT1-2 identified via STRING database analysis

| Protein | Description                                   | Score |
|---------|-----------------------------------------------|-------|
| GLO2    | (S)-2-hydroxy-acid oxidase GLO2               | 0.950 |
| CSD1    | Superoxide dismutase [Cu-Zn] 1                | 0.942 |
| GLO5    | Peroxisomal oxidase GLO5                      | 0.932 |
| GLO4    | Peroxisomal oxidase GLO4                      | 0.931 |
| GLO3    | Peroxisomal oxidase GLO3                      | 0.930 |
| GLO1    | (S)-2-hydroxy-acid oxidase GLO1               | 0.930 |
| CAT3    | Catalase-3                                    | 0.906 |
| CAT2    | Catalase-2                                    | 0.902 |
| CSD2    | Superoxide dismutase [Cu-Zn] 2, chloroplastic | 0.878 |
| FSD1    | Superoxide dismutase [Fe] 1, chloroplastic    | 0.823 |

The most robust interactions were detected between CAT1-2 and glycolate oxidase family proteins, including GLO2 (0.950), GLO5 (0.932), GLO4 (0.931), and GLO1/GLO3 (0.930), indicating tight functional integration between catalase-dependent peroxide detoxification and photorespiratory metabolism and confirming the existence of a well-coordinated peroxisomal redox regulation module.

Strong associations with cytosolic CSD1 (0.942), chloroplastic CSD2 (0.878), and iron-containing FSD1 (0.823) demonstrate that antioxidant regulation during viral infection operates through coordinated multi-compartmental ROS buffering rather than isolated enzymatic reactions, linking chloroplasts, cytosol, and peroxisomes into a unified system. This organization is particularly critical under viral infection, where oxidative stress develops simultaneously across multiple intracellular compartments, necessitating rapid redistribution of redox-buffering capacity throughout the cell (Fig. 8).

A further characteristic feature of the CAT1-2 interactome is strong connectivity among catalase isoforms CAT2 (0.902) and CAT3 (0.906), suggesting functional redundancy and the presence of compensatory mechanisms that maintain network stability under pathogen-induced oxidative damage and reduce the likelihood of complete disruption of hydrogen peroxide detoxification pathways.

Analysis of the CSD1 interaction network revealed a similarly high level of structural integration across multiple cellular compartments (Fig. 8).

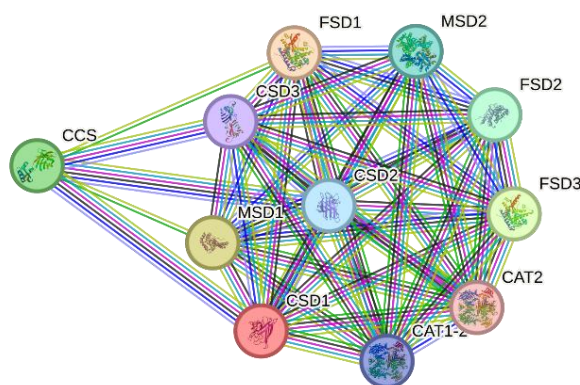


Figure 8. Network analysis of superoxide dismutase CSD1 interactions  
Visualization was performed using the STRING database (*A. thaliana*). Nodes represent different SOD types (CSD, FSD, MSD), the chaperone CCS, and catalases (CAT). The combined confidence score for primary interaction partners exceeds 0.900.

Edge types: teal lines—curated database evidence, pink lines—experimental data, black lines—co-expression.

The reconstructed interactome comprised a broad set of functional partners identified via STRING analysis (Tab. 4), including Cu/Zn-containing superoxide dismutases, chloroplastic Fe-SOD isoforms (FSD1–FSD3), mitochondrial Mn-SOD proteins (MSD1–MSD2), catalases CAT1-2 (score = 0.942) and CAT2 (score = 0.893), as well as the copper chaperone CCS (score = 0.991). Thus, the interaction profile of CSD1 reflects the formation of a highly interconnected cross-compartmental antioxidant network that integrates ROS regulatory systems across chloroplasts, mitochondria, cytosol, and peroxisomes.

Table 4

**Functional interaction partners of CSD1 identified via STRING database analysis (*A. thaliana*)**

| Protein | Description                    | Localization        |
|---------|--------------------------------|---------------------|
| FSD1    | Superoxide dismutase [Fe] 1    | Chloroplast         |
| MSD1    | Superoxide dismutase [Mn] 1    | Mitochondria        |
| FSD3    | Superoxide dismutase [Fe] 3    | Chloroplast         |
| CCS     | Copper chaperone for SOD       | Chloroplast/cytosol |
| FSD2    | Superoxide dismutase [Fe] 2    | Chloroplast         |
| MSD2    | Superoxide dismutase [Mn] 2    | Mitochondria        |
| CSD2    | Superoxide dismutase [Cu-Zn] 2 | Chloroplast         |
| CAT1-2  | Catalase-1                     | Peroxisome          |
| CSD3    | Superoxide dismutase [Cu-Zn] 3 | -                   |
| CAT2    | Catalase-2                     | Peroxisome          |

Partners are ranked by combined confidence score in descending order. The network encompasses all major SOD isoforms across chloroplastic (FSD1–3, CSD2), mitochondrial (MSD1–2), and cytosolic compartments, the copper chaperone CCS, and peroxisomal catalases (CAT1-2, CAT2), reflecting the broad integration of CSD1 into the plant antioxidant defense network.

Particularly strong interactions were observed between CSD1 and chloroplast-localized FSD isoforms, supporting the existence of coordinated ROS regulation between the cytosolic and chloroplastic compartments during oxidative stress. At the same time, the inclusion of mitochondrial MSD proteins within the same interaction cluster suggests that mitochondrial ROS-associated pathways are also structurally integrated into the global antioxidant network. This multi-compartmental organization implies that oxidative stress induced by viral infection is regulated at the level of the entire cell through synchronized interactions among multiple organelle-associated antioxidant defense systems (Fig. 9).

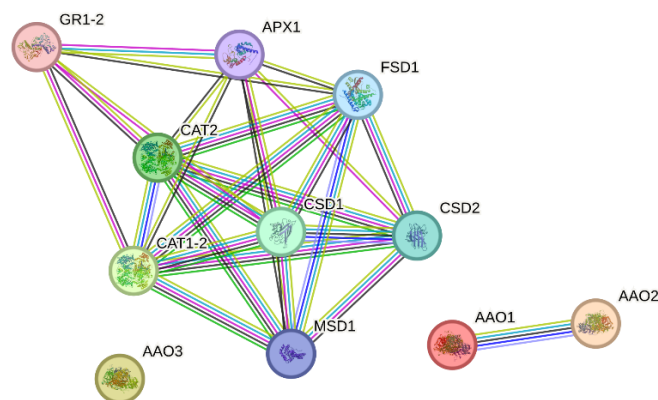


Figure 9. Comprehensive protein-protein interaction network of antioxidant defense and aldehyde metabolism systems. Analysis was performed in STRING (*A. thaliana*). Network nodes correspond to proteins (SOD, CAT, APX, GR, and AAO isoforms). Pronounced clustering is observed: the core direct ROS detoxification system (SOD–CAT–APX–GR) operates distinctly from the aldehyde oxidase module (AAO1–3).

Edge types: teal lines—curated database evidence, pink lines—experimental data, black lines—co-expression

The interaction between CSD1 and the copper chaperone CCS (score = 0.991) highlights the importance of post-translational regulation in antioxidant defense architecture, indicating that adaptation during infection depends not only on transcriptional responses but also on mechanisms controlling enzyme assembly and cofactor delivery.

Reconstruction of the combined antioxidant interactome revealed two major functional modules (Fig. 9). The first comprised core ROS detoxification enzymes, including SOD isoforms, catalases, ascorbate peroxidase, and glutathione reductase, forming a densely connected central redox-buffering scaffold. GLO-like peroxisomal glycolate oxidases (GLO1–GLO5; scores 0.930–0.950) constituted a tightly integrated peroxisomal submodule directly linked to CAT1-2 as the primary  $\text{H}_2\text{O}_2$ -scavenging component. In contrast, aldehyde oxidase proteins AAO1–AAO3 formed a relatively segregated cluster with limited direct connectivity to the core network, indicating that aldehyde oxidase-associated metabolic routes operate as a coordinated but structurally distinct regulatory system.

#### Conclusion on PPI Analysis of the *Arabidopsis thaliana* Antioxidant System

PPI network reconstruction of key antioxidant enzymes in *Arabidopsis thaliana* using STRING revealed a modular topology reflecting the functional architecture of the redox regulatory system under pathogen-induced stress. The analyzed network, comprising 11 protein nodes represented by SOD isoforms (CSD1, CSD2, FSD1, MSD1), catalases (CAT1-2, CAT2), ascorbate peroxidase (APX1), glutathione reductase (GR1-2), and aldehyde oxidases (AAO1–AAO3), demonstrated high-confidence associations (combined score  $\geq 0.823$ ) verified by experimental data, curated databases, and co-expression analysis.

The network separates into two functionally distinct modules. The core antioxidant module (SOD–CAT–APX–GR) is characterized by high inter-node connectivity spanning cytosolic, chloroplastic, mitochondrial, and peroxisomal compartments, implementing sequential ROS detoxification: dismutation of superoxide ( $\text{O}_2^{\cdot -}$  to  $\text{H}_2\text{O}_2$  by SOD isoforms), followed by  $\text{H}_2\text{O}_2$  degradation via catalases and APX1, and regeneration of reduced ascorbate through the ascorbate-glutathione cycle involving GR1-2, thereby forming a closed metabolic circuit maintaining redox homeostasis during oxidative burst. The aldehyde oxidase cluster (AAO1–AAO3) functions as a relatively autonomous unit mediating auxin and abscisic acid biosynthesis. The absence of direct protein contacts between AAO proteins and the SOD–CAT core indicates that crosstalk between hormonal signaling and antioxidant defense operates predominantly at the transcriptional level rather than through physical protein complex formation.

The obtained data indicate that reactive oxygen species during RNA viral infection perform a dual function determined by their concentration, subcellular localization, and temporal characteristics of generation. A moderate increase in  $\text{H}_2\text{O}_2$  and superoxide anion levels is necessary to trigger the host plant's defensive signaling cascades, whereas their excessive accumulation activates cell death mechanisms that limit the spread of infection [53]. The localization specificity of viral replication complexes is also of considerable importance: in TMV they are associated with endoplasmic reticulum membranes, in TBSV with peroxisomes

and mitochondria, and in CMV with elements of the endomembrane system. This indicates that viruses specifically form organelle-specific redox microenvironments and exploit ROS as a tool for regulating their own life cycle, rather than merely as a byproduct of cellular stress [54, 55].

Viral proteins can interfere with the plant antioxidant system through various mechanisms. The CMV 2b protein interacts with catalase CAT3 of *Arabidopsis* and suppresses its activity, leading to H<sub>2</sub>O<sub>2</sub> accumulation and the development of necrotic processes. The MCMV P31 protein inhibits ZmCAT1 in maize, simultaneously reducing PR gene expression and enhancing viral replication. A different mechanism is observed in Bamboo mosaic virus, where processing of the transit peptide of Cu/Zn-SOD PrNbCSD2 is disrupted, preventing the enzyme from being transported to the chloroplast and causing loss of functional activity without direct suppression of synthesis. Tomato chlorosis virus (ToCV) acts even more indirectly: its p22 protein disrupts  $\alpha$ -tocopherol biosynthesis through interaction with the FBN1.1-VTE1 complex, creating heightened vulnerability in the cellular compartment where singlet oxygen production is most intense. Despite the mechanistic differences, the common thread among all these strategies is not the complete suppression of the antioxidant system, but rather its targeted modulation in specific cellular structures [56, 57].

Reconstruction of the PPI network of key antioxidant enzymes of *Arabidopsis thaliana* using the STRING platform revealed pronounced modular organization playing an important role in the systemic redox response. The core direct ROS detoxification system—comprising SOD, CAT, APX, and GR—is characterized by high inter-protein interaction density and multi-compartmental organization. The isoforms CSD1, CSD2, FSD1, FSD2, FSD3, MSD1, and MSD2 function in concert, providing compartment-specific neutralization of superoxide anion with subsequent degradation of H<sub>2</sub>O<sub>2</sub> by catalases and ascorbate peroxidase. The particularly high combined scores for the CSD1-FSD1 and CSD1-MSD1 pairs reflect evolutionarily established functional redundancy of the system. The aldehyde oxidase cluster—AAO1, AAO2, and AAO3—operates relatively autonomously and does not form direct protein contacts with the SOD-CAT core, indicating that the link between the antioxidant response and hormonal reprogramming during infection is predominantly regulatory in nature.

The glutathione system demonstrates a pronounced context-dependence of response. Increased GR activity and changes in the GSH/GSSG ratio correlate with resistance in *rbohF* *Arabidopsis* mutants during TuMV infection, whereas in susceptible genotypes enzyme activity decreases. Identification of tomato SIGR3 as a causative resistance component against Tomato leaf curl New Delhi virus (ToLCNDV) via VIGS verification demonstrates that cellular redox status can serve as a kind of epigenetic switch determining the outcome of viral infection. Nevertheless, certain limitations of this study must be acknowledged. All PPI analyses were conducted using *Arabidopsis thaliana* as a model, so extrapolation to crop plants with different multigene family compositions requires caution. Furthermore, the static nature of network analysis does not reflect the dynamic post-translational modifications occurring during infection. Data on non-enzymatic antioxidants, including carotenoids and tocopherols, also remain predominantly indirect. Despite this, the findings provide an important conceptual framework for developing biotechnological approaches to enhance plant resistance. Promising directions include marker-assisted selection based on ascorbate and glutathione loci, as well as the application of exogenous biostimulants capable of enhancing GR-mediated protection during viral infection.

### Conclusion

The present review systematically analyzes the role of reactive oxygen species and the antioxidant defense system in plant-RNA virus interactions. The data collectively demonstrate that ROS occupy a central position in this relationship, functioning simultaneously as triggers of host immune responses and as regulatory factors exploited by viruses to facilitate their own replication cycle. The dual nature of ROS signaling—protective at moderate concentrations and cytotoxic upon excessive accumulation—determines the outcome of infection and reflects the evolutionary arms race between plant hosts and RNA viruses.

The enzymatic components of the antioxidant system—superoxide dismutase, catalase, glutathione reductase, and aldehyde oxidase—do not function as isolated units but form a highly integrated, multi-compartmental network. Protein-protein interaction analysis of key *Arabidopsis thaliana* antioxidant enzymes via the STRING platform confirmed this architecture, revealing two functionally distinct modules: a densely interconnected core ROS detoxification system (SOD-CAT-APX-GR) spanning cytosolic, chloroplastic, mitochondrial, and peroxisomal compartments, and a relatively autonomous aldehyde oxidase cluster (AAO1-AAO3) linked to phytohormone biosynthesis. The absence of direct protein contacts between

these modules suggests that crosstalk between antioxidant defense and hormonal signaling operates predominantly at the transcriptional level.

Phylogenetic analysis of SOD, CAT, AO, and GR across eight dicotyledonous species confirmed the high evolutionary conservation of these enzymes, particularly within closely related taxa, underscoring their fundamental and indispensable role in cellular redox homeostasis. The functional redundancy observed within multigene families—multiple SOD isoforms across compartments, multiple CAT isoenzymes—provides a buffering capacity that prevents complete antioxidant collapse even when individual components are suppressed by viral effector proteins.

The reviewed literature demonstrates that RNA viruses have evolved diverse and precise strategies to manipulate the host antioxidant system: direct inhibition of catalase activity by CMV 2b and MCMV P31, disruption of SOD transit peptide processing by Bamboo mosaic virus, and impairment of tocopherol biosynthesis by ToCV p22. Crucially, these mechanisms share a common logic—not wholesale destruction of antioxidant capacity, but fine-tuned modulation that maintains ROS within a range permissive for viral replication while avoiding irreversible cellular damage.

Taken together, these findings establish redox regulation as a central battlefield in plant-virus interactions and provide a conceptual basis for the development of novel resistance strategies. Biotechnological approaches targeting the enhancement of GR-mediated glutathione regeneration, marker-assisted selection at ascorbate and glutathione biosynthesis loci, and the application of exogenous antioxidant biostimulants represent promising directions for improving crop resistance to RNA viral pathogens.

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#### Conflict of Interest

The authors declare no conflicts of interest.

#### Author contribution

The manuscript was written through contributions of all authors. All authors have given approval to the final version of the manuscript. CRediT: **Iksat N.N.** — conceptualization, supervision, writing original draft preparation, writing review and editing; **Yertayeva T.G.** — writing original draft preparation, writing review and editing; **Belgibay S.D.** — writing original draft preparation, writing review and editing; **Artykbayeva D.E.** — writing original draft preparation, writing review and editing; **Baikarayev Z.M.** — writing original draft preparation, writing review and editing.

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## Өсімдіктердің РНҚ вирустарымен инфекциялануы кезіндегі антиоксиданттық қорғанысы: негізгі ферменттердің рөлі

Соңғы онжылдықтарда ауылшаруашылық дақылдарының биотикалық стрессорларға төзімділігі мәселесі жаһандық азық-түлік қауіпсіздігін қамтамасыз ету тұрғысынан ерекше өзектілікке ие болды. Биотикалық факторлардың ішінде өнімділіктің айтарлықтай төмендеуіне және өсімдіктердің физиологиялық процестерінің бұзылуына әкелетін вирустық инфекциялар ерекше орын алады. РНҚ вирустары жоғары бейімделгіштікпен және иесінің жасушалық метаболизмін тиімді түрде өзгерту қабілетімен сипатталады, бұл процесс редокс-гомеостаздың бұзылуымен қатар жүреді. Белсенді оттегі түрлерінің (БОТ) түзілуі бұл процестің негізгі кезеңдерінің бірі және функционалдық екіұдайлықпен сипатталады: БОТ қорғаныс реакцияларын қоздыратын сигналдық молекулалар ретінде әрекет етеді, ал олардың шамадан тыс жиналуы жасушалық компоненттердің зақымдалуына әкеледі. Редокс-гомеостаздағы өзгерістер ферментативті және ферментативті емес қорғаныс механизмдерін қамтитын

өсімдіктердің антиоксиданттық жүйесінің белсендірілуімен жалғасады. Редокс-процестерді зерттеудегі айтарлықтай жетістіктерге карамастан, вирустық инфекция жағдайында редокс-реттелу механизмдерінің интеграциясы және антиоксиданттық жүйенің жұмыс істеуі бүгінгі күнге дейін жеткілікті түрде сипатталмаған және әрі қарай талдауды қажет етеді. Осыған байланысты, бұл шолудың мақсаты — РНК вирустарымен инфекцияланған өсімдіктердегі иммундық жауапты реттеудегі белсенді оттегі түрлері мен антиоксиданттық жүйенің негізгі ферменттерінің рөлі туралы қазіргі түсініктерді жүйелеу және талдау.

*Кілт сөздер:* оксидативтік стресс, өсімдіктің антиоксиданттық құрылымы, вирустық инфекция, өсімдік иммунитеті.

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## **Антиоксидантная защита растений при инфицировании РНК-вирусами: роль ключевых ферментов**

В последние десятилетия проблема устойчивости сельскохозяйственных культур к биотическим стрессорам приобрела особую актуальность в контексте обеспечения глобальной продовольственной безопасности. Среди биотических факторов особое место занимают вирусные инфекции, вызывающие значительные потери урожая и нарушающие физиологические процессы растений. РНК-вирусы характеризуются высокой адаптивностью и способностью эффективно модифицировать клеточный метаболизм хозяина, что сопровождается нарушением редокс-гомеостаза. Генерация активных форм кислорода (АФК) является одним из ключевых этапов этого процесса и характеризуется функциональной двойственностью: АФК выступают в роли сигнальных молекул, инициирующих защитные реакции, в то время как их избыточное накопление приводит к повреждению клеточных компонентов. Изменения редокс-гомеостаза сопровождаются активацией антиоксидантной системы растений, включающей как ферментативные, так и неферментативные механизмы защиты. Несмотря на значительные успехи в изучении редокс-процессов, интеграция механизмов редокс-регуляции и функционирование антиоксидантной системы в условиях вирусной инфекции к настоящему времени остаются недостаточно описанными и требуют дальнейшего анализа. В связи с этим целью настоящего обзора является систематизация и анализ современных представлений о роли активных форм кислорода и ключевых ферментов антиоксидантной системы в регуляции иммунного ответа у растений, инфицированных РНК-вирусами.

*Ключевые слова:* окислительный стресс, антиоксидантная система растений, вирусная инфекция, иммунитет растений.

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