

Research Insight

Open Access

Role of Reactive Oxygen Species in Potato's Stress Response

Zhang Qian, Wenzhong Huang ✉

Biomass Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China

✉ Corresponding email: wenzhong.huang@hitar.orgJournal of Energy Bioscience, 2025, Vol.16, No.2 doi: [10.5376/jeb.2025.16.0007](https://doi.org/10.5376/jeb.2025.16.0007)

Received: 29 Jan., 2025

Accepted: 28 Feb., 2025

Published: 14 Mar., 2025

Copyright © 2025 Qian and Huang, This is an open access article published under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

Preferred citation for this article:Qian Z., and Huang W.Z., 2025, Role of reactive oxygen species in potato's stress response, Journal of Energy Bioscience, 16(2): 64-74 (doi: [10.5376/jeb.2025.16.0007](https://doi.org/10.5376/jeb.2025.16.0007))

Abstract This study focuses on the role of reactive oxygen species (ROS) when potatoes encounter stress. ROS is a signaling molecule present in plants. When plants face external stress (such as environmental changes or pests and diseases), ROS plays an important role. However, it also has certain counter-effects. If the content of ROS in plants is too high, it will cause oxidative stress and damage cells. In order to control the amount of ROS, potatoes will activate some antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (PRXs), which can remove excess ROS and protect cells from damage, while also making plants more resistant to stress. ROS will participate in regulating responses under stress such as drought, high salt, high or low temperature environments, as well as pathogens and leaf-eating insects. It not only helps to transmit stress signals, but also cooperates with some plant hormones (such as ABA, SA and JA) to regulate the plant's defense mechanism. Through this study, we also found that there are interactions between ROS signals and other signaling pathways (such as calcium signals). The study also discusses how to use this knowledge to improve potato's stress resistance.

Keywords Reactive oxygen species (ROS); Potatoes (*Solanum tuberosum* L.); Stress tolerance; Oxidative damage; Antioxidant enzymes

1 Introduction

Potato (*Solanum tuberosum* L.) is one of the most important food crops in the world. It is a staple food in many countries and contributes greatly to global food security. It is not only rich in nutrients, but also adaptable to a variety of climates and soil conditions, so it plays an important role in global agriculture (Ma et al., 2021a). Potatoes are also of high economic value. People not only eat it directly, but it is also an important raw material for the food processing industry (Koubaa et al., 2021).

Potatoes often encounter a lot of stress during the planting process, which will affect its yield. Abiotic factors such as drought, salinity, and hypoxia will cause a lot of reactive oxygen species (ROS) in plants, causing oxidative stress (Fan, 2014; Sahoo et al., 2020; Zhang et al., 2021). In addition, pathogens such as *Phytophthora infestans* and *Erwinia carotovora* can also cause potatoes to produce ROS, which can damage cells and make the plants unhealthy (Hua et al., 2020; Luo et al., 2021). To ensure stable potato yields, we need to breed varieties with strong stress resistance (Ma et al., 2021a).

This study focuses on the specific role of reactive oxygen species (ROS) in potato response to stress. ROS is an important signaling molecule in many plant activities, including the response to stress. However, if there are too many ROS, it will also damage plant cells, so plants need to remove excess ROS. What we want to find out is how potatoes regulate and remove excess ROS when faced with stress, and try to find ways to improve potatoes' ability to resist stress. We will also study the regulation of ROS in cells and how it helps potatoes resist external stress.

2 Overview of reactive oxygen species (ROS) in potatoes

Reactive oxygen species (ROS) are a class of molecules that are particularly reactive and play an important role in the life activities of potatoes, especially when faced with external stress. Common ROS include superoxide anions (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals ($\bullet OH$). These molecules are usually generated as a byproduct of plant metabolism. In potatoes, ROS participate in signal transmission and also help plants cope with

stress. They are like signal "couriers" and play a role in many physiological activities (Fan, 2014; Zhang et al., 2021; Ma et al., 2021b). The amount of ROS needs to be balanced. Too many can harm cells, such as destroying fats, proteins, and DNA, but if the amount is right, they are important for the normal functioning of cells, such as helping growth, development, and resisting pathogens (Luo et al., 2021; Ma et al., 2021a; Sahoo et al., 2021).

2.1 Types of ROS relevant to potato physiology

The common types of ROS in potatoes are mainly superoxide anions (O_2^-) and hydrogen peroxide (H_2O_2). Superoxide anions are mostly generated during electron transfer in mitochondria and chloroplasts during photosynthesis or respiration. It is not very stable and is quickly converted into hydrogen peroxide by an enzyme called superoxide dismutase (SOD) (Fan, 2014; Koubaa et al., 2021). Hydrogen peroxide is more stable than superoxide anions. It can also pass through cell membranes and regulate plant development and response to stress like a signal (Ma et al., 2021b; Sahoo et al., 2021). There is also a type of ROS called hydroxyl radical ($\bullet OH$), which is generated from hydrogen peroxide through a process called Fenton reaction. This molecule is particularly reactive and can cause great damage to cells. But cells control its production very strictly to prevent it from causing serious damage (Hua et al., 2020; Ma et al., 2021a).

2.2 Cellular sources of ROS in potatoes

In potato cells, ROS mainly come from three places: chloroplasts, mitochondria and plasma membrane. Chloroplasts are where plants carry out photosynthesis, and in this process, electrons accidentally run to oxygen to form superoxide anions (Fan, 2014; Koubaa et al., 2021). Mitochondria are also a source of ROS, especially when they are under stress and the respiratory chain is affected, ROS are more likely to appear (Huang et al., 2016). There is also the plasma membrane, where NADPH oxidase can directly generate superoxide anions. These enzymes are important for plants because the ROS they produce can be used as signals to activate a series of defense responses (Luo et al., 2021; Ma et al., 2021b).

2.3 Dual role of ROS: essential signaling molecules vs. oxidative stress agents

ROS has two different roles in potatoes. On the one hand, it is an essential signaling molecule that can regulate many important processes, such as plant growth, development, and response to various stresses. It can also affect the expression of some genes, allowing plants to better fight pathogens (Ma et al., 2021a; Zhang et al., 2021; Otulak-Kozieł et al., 2022). On the other hand, if too much ROS accumulates, it will cause oxidative stress, damage various cell structures, and make cells malfunction. If the plant's antioxidant system is not strong, for example, the enzymes that remove ROS (such as catalase and peroxidase) are not active enough, then the cells are easily damaged or even die (Hua et al., 2020; Koubaa et al., 2021; Sahoo et al., 2021) (Figure 1).

3 ROS Production in Potatoes Under Stress

3.1 Abiotic stress

3.1.1 Drought-induced ROS production and effects on photosynthesis in potatoes

When potatoes encounter drought, more reactive oxygen species (ROS) are produced in their bodies. Most of these ROS are produced in chloroplasts during photosynthesis. Once ROS increases, it may interfere with photosynthesis, reduce efficiency, and may also damage cells (You and Chan, 2015; Miller et al., 2021). However, the accumulation of ROS under drought also has benefits. It can serve as a signal to initiate some responses to stress and help potatoes adapt to the environment. But if there are too many ROS and they are not removed in time, it is easy to cause cell damage (Czarnocka and Karpiński, 2018; Panda et al., 2024).

In order to reduce the damage caused by ROS, potatoes will activate some protective mechanisms. These include enzymes such as superoxide dismutase (SOD) and catalase (CAT), as well as some non-enzymatic antioxidants (ascorbic acid and glutathione), which work together to remove excess ROS and protect cells from damage (Das and Roychoudhury, 2014; Hasanuzzaman et al., 2020). Whether the generation and removal of ROS can be balanced is important for cell health and plant drought resistance (Mahalingam and Fedoroff, 2003; Jajić et al., 2015).

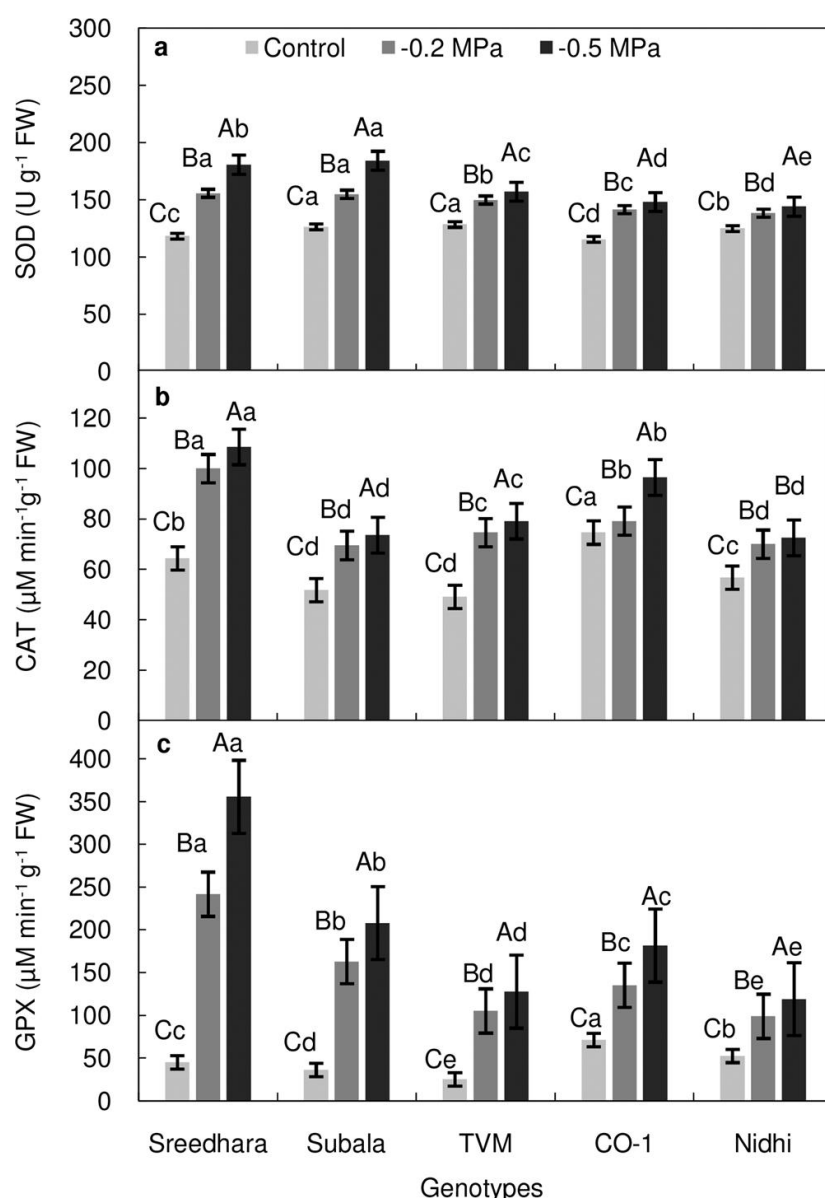


Figure 1 Effect of in vitro PEG mediated osmotic stress on antioxidative enzyme activities of leaf tissues of Chinese potato genotypes (Adopted from Sahoo et al., 2021)

Image caption: (a) superoxide dismutase (SOD, U g⁻¹ FW), (b) catalase (CAT, μM min⁻¹ g⁻¹ FW) and (c) guaiacol peroxidase (GPX, μM min⁻¹ g⁻¹ FW), Values are the mean of three replicates and bars represent standard error of means. Different letters in upper case represent significant differences between the treatments (control, -0.2 MPa and -0.5 MPa) in the genotypes and lower case represents significant difference among the genotypes under each treatment according to Tukey's test (Adopted from Sahoo et al., 2021)

3.1.2 Salinity stress: ionic imbalance and ROS generation in potato cells

Under saline-alkali stress, potatoes absorb excessive sodium and chloride, which disrupts the ion balance in cells, easily causing cell dehydration, and leading to more ROS generation. These excessive ROS attack key molecules such as fats, proteins, and nucleic acids, affecting cell function, and in severe cases, causing cell death (Miller et al., 2021; Zhang et al., 2021). Ion imbalance prevents plants from maintaining a normal state in cells and aggravates stress responses (Czarnocka and Karpiński, 2018; Panda et al., 2024). To combat the above situation, potatoes activate some special signaling pathways to activate genes related to ROS removal. At the same time, they synthesize a substance called "compatible solutes" to help maintain water balance in cells and reduce the damage caused by ROS (You and Chan, 2015; Hasanuzzaman et al., 2020). The interaction between these ROS and ion regulation is key to potato's response to salinity stress (Alscher et al., 1997; Mahalingam and Fedoroff, 2003).

3.1.3 Effects of extreme temperatures on ROS production in potato tissues

The level of ROS in potatoes increases when exposed to high or low temperatures. High temperatures accelerate the metabolic activity of cells, causing a rapid increase in ROS. Low temperatures may cause problems in the photosynthesis system and also lead to ROS accumulation (Hasanuzzaman et al., 2020; Panda et al., 2024). ROS triggered by these temperatures can cause oxidative stress, damage cells, and affect the normal development of plants (Jajić et al., 2015; Czarnocka and Karpiński, 2018). Potatoes will activate some protective mechanisms to cope with it, such as producing heat shock proteins or low temperature response genes, which can help stabilize proteins and cell membrane structures. At the same time, the antioxidant system will also increase its efforts to remove excess ROS (Das and Roychoudhury, 2014; You and Chan, 2015). Whether or not ROS levels can be regulated in time and these protective responses can be initiated is the key to potato's ability to withstand extreme temperatures (Alscher et al., 1997; Mahalingam and Fedoroff, 2003).

3.2 Biotic stress

3.2.1 ROS bursts during pathogen attacks on potatoes

When pathogens invade, potatoes will produce a large amount of ROS in a short period of time. This phenomenon is called "oxygen burst". Oxygen burst is a reaction used by plants to prevent the spread of pathogens and is part of the early defense response. ROS will cause some cells to die, thereby controlling the pathogens in a local area (Mahalingam and Fedoroff, 2003; Czarnocka and Karpiński, 2018). These ROS will also serve as signals to activate the expression of defense genes and improve the immunity of the entire plant (Alscher et al., 1997; Das and Roychoudhury, 2014). However, this process must be strictly controlled, otherwise it is easy to damage the plant's own tissues. In this process, the antioxidant system of potatoes will intervene to adjust the level of ROS to ensure that they only work when needed and do not cause excessive damage (Jajić et al., 2015; Hasanuzzaman et al., 2020). This balance is very important for disease resistance (Czarnocka and Karpiński, 2018 ; Panda et al., 2024).

3.2.2 Role of ROS in potato herbivore defense mechanisms

When insects eat potatoes, potatoes also use ROS as a defense. On the one hand, these ROS can directly damage the cell tissues in the insect body, playing a deterrent role; on the other hand, ROS can also act as a signal, allowing the plant to produce some toxic or insect-unpleasant compounds, thereby playing a repellent role (Alscher et al., 1997; Mahalingam and Fedoroff, 2003). This ROS-induced reaction is an important part of potato's defense against insects (Das and Roychoudhury, 2014; Czarnocka and Karpiński, 2018). In this process, ROS usually also activates signaling pathways, prompting the plant to synthesize defense compounds such as phenols and alkaloids, increasing potato's resistance to insects and strengthening the overall defense effect (Jajić et al., 2015; Panda et al., 2024). The coordination between ROS and these defense substances is the key to the success of the defense system (Czarnocka and Karpiński, 2018 ; Hasanuzzaman et al., 2020).

3.2.3 General oxidative stress responses in potatoes to biotic factors

Whether it is pathogens or insects, potatoes usually respond by producing ROS when encountering biotic stress. These ROS can not only directly participate in defense, but also send out signals to activate more defense mechanisms (Alscher et al., 1997; Mahalingam and Fedoroff, 2003). The potato response process is a complex system, including the generation of ROS, signal transduction, and the process of clearing ROS. The antioxidant system will also be strengthened here to maintain ROS within a reasonable range (Jajić et al., 2015; Hasanuzzaman et al., 2020). In this way, ROS can play a role without causing too much damage to the plant itself. This flexible regulatory ability is the key to potato's "resistance" in the face of biological stress (Czarnocka and Karpiński, 2018; Panda et al., 2024).

4 ROS as Signaling Molecules in Potato Stress Responses

4.1 ROS-triggered activation of stress-responsive genes in potatoes

Reactive oxygen species (ROS) play a critical "signaling" role when potatoes respond to stress. Once a plant is stressed, ROS are often one of the first molecules produced. They act like switches to turn on the expression of

some defense-related genes. When certain enzymes called RBOH in potatoes become active, the number of ROS increases, which then activates antioxidant-related genes such as CPRX1, PRX2, and CAT1. These changes allow potatoes to better defend against pathogens such as late blight. Studies have shown that after adding a gene called StRbohA to potatoes, the plants' disease resistance has become stronger (Soliman et al., 2021) (Figure 2). ROS signals are also related to many gene networks that regulate abiotic stresses such as drought or high salt. There are some regulatory proteins in these networks, such as WRKY or zinc finger proteins. They act like "coordinators" that can integrate signals from different parts so that potatoes can respond to stress in a unified manner (Miller et al., 2008).

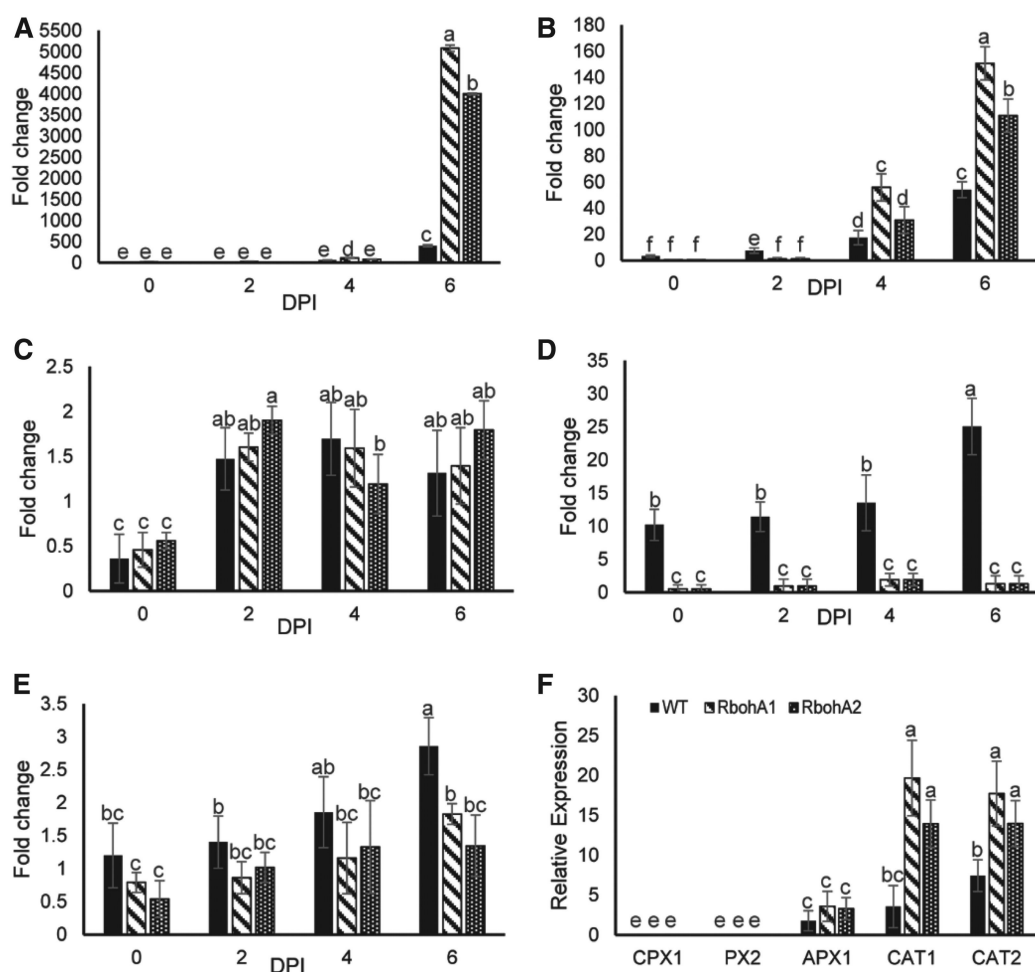


Figure 2 Expression of reactive oxygen species (ROS) detoxification genes in infected StRbohA lines and infected wild type (WT) plants (Adopted from Soliman et al., 2021)

Image caption: Five ROS detoxification genes were tested at 0, 2, 4, and 6 days postinoculation (dpi): A, CPRX1; B, PRX2; C, APRX; D, CAT1; and E, CAT2. F, Relative expression CPRX1, PRX2, APRX, CAT1, and CAT2 in noninoculated WT and StRbohA lines. The fold changes of the quantitative real-time PCR data were calculated via the $2^{-\Delta\Delta Ct}$ method (Livak and Schmittgen 2001). The noninoculated plants from each line were used as experimental controls for each corresponding inoculated line. The analysis was performed on data collected from three biological replicates for each line at each time point. The housekeeping gene elongation factor 1 alpha (EF1 α) was used as the internal normalizer. The represented mean values in the graph that were assigned the same letters are not statistically different at $P \leq 0.05$ (Adopted from Soliman et al., 2021)

4.2 Interaction of ROS with potato hormones like ABA, SA, and JA

The interaction between ROS and several other plant hormones is very important in the stress response of potato. Hormones such as ABA (water stress related), SA (disease prevention related) and JA (insect resistance related) all interact with ROS. During drought, ABA increases ROS production, causing the stomata of plant cells to close, thereby reducing water loss. This process involves the production of ROS at different cell locations, helping to

regulate the response of cells around the stomata while maintaining a balance in ROS levels (Postiglione and Muday, 2020; Li et al., 2022). SA and JA have opposite effects on ROS. SA enhances the signal of ROS, while JA inhibits it. They have a bit of "opposite" effects on each other. It is this balance that allows plants to respond appropriately to different stresses (Lukan and Coll, 2022; Myers et al., 2022).

4.3 Cross-talk between ROS and other signaling pathways in potato stress responses

When facing stress, ROS is not only a signaling molecule, it also interacts with other signaling pathways in the potato body to jointly regulate the plant's response. It affects a signaling pathway called TOR. TOR was originally a key system for regulating cell growth and autophagy, but when there is stress, ROS will participate in regulating this pathway to help potatoes improve their disease resistance, such as fighting late blight (Luo et al., 2021). ROS also often works in conjunction with calcium signals. These two signaling systems form a network that together transmit "stress information" in the environment to different parts of the plant. Certain key proteins can connect ROS and calcium signals, allowing plants to quickly sense stress and respond (Ravi et al., 2023). This "cooperative combat" approach is an important guarantee for potatoes to adapt to external changes.

5 Antioxidant Defense Mechanisms in Potatoes

5.1 Enzymatic antioxidants in potatoes

Potatoes rely on some enzymes to remove excess reactive oxygen species (ROS) in the body, which can reduce oxidative damage. These enzymes mainly include superoxide dismutase (SOD), catalase (CAT) and peroxidase (PRXs). SOD converts superoxide radicals into hydrogen peroxide, and then CAT and PRXs decompose hydrogen peroxide into water and oxygen to help cells avoid injury (Fan, 2014; Koubaa et al., 2021). The activity of these enzymes will also change under different stress conditions. For example, under hypoxia or when oxygen is just restored, the activity of SOD, CAT and APX enzymes in the mitochondria of potato tubers will decrease at first, and then increase again. This shows that they will adjust according to the amount of ROS (Fan, 2014). In particular, class III peroxidases are also important in removing ROS. For example, a gene called IbPRX17 functions under the regulation of a transcription factor called IbBBX24. It can enhance the activity of peroxidase and reduce the accumulation of hydrogen peroxide, thereby improving the tolerance of potatoes to salinity and drought (Zhang et al., 2021). This also shows that transcriptional regulation is also critical in the potato antioxidant system.

5.2 Non-enzymatic antioxidants in potatoes

In addition to enzymes, there are some non-enzymatic substances in potatoes that fight ROS, mainly including ascorbic acid, glutathione and flavonoids, which can directly remove ROS and play a role in supplementing defense in cells. Among them, ascorbic acid and glutathione are an important part of the ascorbic acid-glutathione cycle. They help detoxify hydrogen peroxide and maintain the balance of redox in cells. The content of these substances usually increases when facing environmental stress. Some potato varieties with stronger resistance have higher levels of these antioxidants in their bodies (Sahoo et al., 2021; Li and Huang, 2024), especially glutathione, which plays a vital role in potato's response to biological stress such as viruses. Glutathione can reduce oxidative damage and regulate defense responses. When potatoes interact with viruses, glutathione levels will increase, and its content will increase more in resistance reactions. This change is also related to the reduction of viruses and the decrease of ROS (Otulak-Kozieł et al., 2022).

5.3 Dynamic balance between ROS production and scavenging in potatoes under stress

Under stress, the generation and removal of ROS in potatoes must maintain a dynamic balance. ROS is a byproduct of plant metabolism and a stress signal molecule. If there are too many ROS, it may damage cells. Therefore, the scavenging system in plants must be strong enough to control the dynamic balance of ROS (Fan, 2014; Sahoo et al., 2021). This balance is mainly achieved by the two sets of enzymatic and non-enzymatic antioxidant systems. Together, they can reduce the damage caused by ROS to the plant itself. Under the osmotic stress caused by polyethylene glycol, the ability of potatoes to remove ROS will increase. This includes both the enhanced activity of scavenging enzymes and the increased content of non-enzymatic antioxidants, which work

together to maintain the stability of ROS levels (Sahoo et al., 2021). This balance process is also regulated by some signaling pathways, such as the calcium-dependent protein kinase pathway. These pathways enable plants to cope with stress more effectively by regulating the generation and removal of ROS (Ma et al., 2021b).

6 ROS and Potato Stress Tolerance Mechanisms

6.1 ROS-mediated systemic acquired resistance (SAR) in potatoes

Reactive oxygen species (ROS) play an important role in systemic acquired resistance (SAR) in potato. They act like a signal that triggers the plant's defense response. When pathogens (such as *Phytophthora infestans*) invade potato, ROS are often one of the first responses. If the potato can express more RBOH-like genes (such as *StRbohA*), it can produce more ROS at the site of infection. These ROS activate some defense genes and increase defense hormones such as salicylic acid, thereby limiting the spread of the pathogen (Soliman et al., 2021). ROS can also cooperate with other signaling systems. For example, ROS interact with plant hormones (such as salicylic acid SA and jasmonic acid JA) to further regulate defense responses, allowing the potato immune system to be activated quickly and accurately without damaging its own tissues (Xia et al., 2015; Czarnocka and Karpiński, 2018).

6.2 ROS involvement in potato drought and salinity tolerance

In drought or high-salt environments, the level of ROS in potatoes will increase. If there are too many ROS and they cannot be removed, they will damage the cells. However, if properly regulated, ROS can also serve as a signal to initiate various protective responses. In sweet potatoes, there is a module called *IbBBX24-IbTOE3-IbPRX17*, which can help improve the ability to remove ROS, reduce the accumulation of ROS in the body, protect cells from damage, and improve the resistance of plants to drought and salinity (Zhang et al., 2021). The ascorbic acid-glutathione cycle is also important in drought and salt stress. In this cycle, enzymes and non-enzymatic antioxidants work together to help remove excess ROS and maintain balance. Some Chinese potato varieties (such as *Sreedhara* and *Subala*) show stronger ability to remove ROS and are more resistant to drought and salt stress (Sahoo et al., 2020). These examples show that if you want potatoes to adapt to harsh environments, you have to control ROS.

6.3 ROS interaction with epigenetic changes during stress adaptation in potatoes

In addition to being a signaling molecule, ROS can also regulate the epigenetic regulation of potatoes. Simply put, ROS can "indirectly" control which genes should be turned on and which genes should be turned off, which is also important for the plant's ability to resist stress. ROS can regulate the activity of some regulatory proteins related to DNA methylation and histone modification. These modifications can change the way genes are expressed, thereby helping plants better cope with stress (Hu et al., 2024; Li et al., 2024). What's more interesting is that this regulation caused by ROS is sometimes long-term, that is, the plant will "remember" the stress. When the same stress comes again, it can react faster and stronger than before. This "memory" ability is particularly useful for crops such as potatoes that are often affected by environmental changes. (Das and Roychoudhury, 2014; You and Chan, 2015).

7 Advances in ROS Research for Potato Improvement

7.1 Techniques for detecting and measuring ROS in potatoes

In recent years, scientists have made a lot of progress in the detection of reactive oxygen species (ROS) in potatoes. Now many technologies can more clearly see the changes in ROS, especially under different stresses. A common method is to use chloroplast-targeted redox-sensitive green fluorescent protein (roGFP2) for whole-plant imaging. This technology can record the redox state in potato chloroplasts in real time, allowing researchers to understand how ROS changes under conditions such as light and drought (Hipschi et al., 2020). Many people also use quantitative methods to measure ROS, such as measuring the content of hydrogen peroxide (H_2O_2) or superoxide anion (O_2^-). These methods can help analyze how ROS accumulates in key processes such as tuber formation (Lei et al., 2023). Molecular techniques can also be used to look at the expression of related genes, such as qPCR or RNA sequencing. Researchers have analyzed the expression of some ROS-related genes in potato,

such as StCDPKs and StRbohA, to understand their role in ROS generation and stress resistance (Ma et al., 2021b; Soliman et al., 2021). These technologies have given us a more comprehensive understanding of the dynamic changes of ROS and its impact on potato stress response.

7.2 Genetic engineering approaches to modify ROS pathways in potatoes

Now, scientists are also using genetic engineering methods to modify the ROS regulatory system in potatoes to make them more resistant to stress. For example, studies have found that by allowing potatoes to express more of a gene called StRbohA, ROS production can be increased, further triggering defense responses and making plants more resistant to late blight (Soliman et al., 2021). Another popular technology is CRISPR-Cas9. Researchers used it to knock out the gene StSP6A, which is related to H₂O₂-induced tuber formation. In this way, scientists can better understand the genetic mechanism of ROS in stress response (Lei et al., 2023). In sweet potato, researchers have also conducted similar experiments, such as increasing the expression of IbBBX24 and IbPRX17 genes. The results showed that this can increase the activity of peroxidase, reduce the accumulation of hydrogen peroxide in the body, and make the plant more resistant to drought and salt (Zhang et al., 2021). These methods also have great potential in potato improvement. The goal is to regulate the level of ROS and improve yield and stress resistance.

7.3 Insights from potato genomics and transcriptomics in ROS-related stress responses

Using genomic and transcriptomic technologies, scientists can better understand the molecular mechanism of ROS in potato stress response. Transcriptome analysis shows that ROS regulates many genes related to stress resistance, including those involved in plant hormone synthesis and signal transduction (Terrón-Camero et al., 2022). The study also found some key "transcriptional imprints" that are related to peroxisome signaling, indicating that ROS can regulate the expression of a large number of genes under stress (Terrón-Camero et al., 2022). Scientists also combined a variety of "omics" technologies to study the relationship between ROS and other signaling systems. For example, some studies have explored the cross-talk between ROS and TOR signaling pathways. TOR is a signaling system that regulates cell growth. The results showed that when infected with late blight, if the PiTOR gene is inactivated, the resistance of potatoes to pathogens will be enhanced (Luo et al., 2021).

8 Challenges and Future Directions in Potato ROS Research

8.1 Challenges in understanding ROS signaling dynamics in potatoes

It is quite difficult to understand the changing patterns of reactive oxygen species (ROS) signals in potatoes. One of the biggest difficulties is that this signaling system is too complicated. ROS are not just something produced by the way during cell metabolism, they also act as signaling molecules to regulate many physiological processes, such as plant growth and development, and responses to drought or disease (Baxter et al., 2014; Myers et al., 2024). What is more difficult to understand now is: how does ROS affect gene expression step by step? There are many regulatory factors and signaling pathways involved, and each step is quite detailed (Dvořák et al., 2021; Mishra et al., 2023). Another difficulty is that the production and removal of ROS must not only be appropriate in quantity, but also occur at the right time and in the right place. ROS cannot be too much, otherwise it will damage cells; but too little will not start the reaction. This "just right" balance will be affected by the environment and the state of the plant itself (You and Chan, 2015; Dvořák et al., 2021). ROS signals do not have a clear transmission order like some hormone pathways, so it is more difficult to figure out how they coordinate with each other in the cell (Myers et al., 2024; Zhu and Shen, 2024).

8.2 Potential of ROS-based biomarkers for potato stress tolerance

Now many people have begun to study whether ROS can be used as a "marker" to judge the stress resistance of potatoes. Simply put, the level of ROS can reflect the stress state of the plant (You and Chan, 2015; Dvořák et al., 2021). If the expression level of some enzymes that remove ROS is very high, it means that the plant may be more drought-resistant and salt-resistant. These enzymes may be used as "biomarkers" to help us determine which varieties are more stress-resistant (Soliman et al., 2021; Zhang et al., 2021). If these ROS-related markers can be used in breeding, it will be possible to select varieties with strong "natural" ROS regulation ability more quickly.

Potatoes bred in this way will also be more resilient to extreme weather or soil problems. It will take a lot of research to find truly reliable ROS markers. We have to understand the performance and specific role of these markers in various stress responses before we can use them in breeding with confidence.

8.3 Integrating ROS knowledge into potato breeding and field applications

Using ROS research results in actual breeding and field planting is a promising development direction. As long as we understand how ROS affects stress responses, breeders can select genes that perform better in ROS control, thereby improving potato resistance (Soliman et al., 2021; Zhang et al., 2021). In addition to selecting seeds in the laboratory, ROS research can also guide actual planting methods. For example, we can develop some "biostimulants" that can regulate ROS levels, or through the proper management of fertilizers and water, let the plants balance ROS better and reduce the losses caused by drought, salt damage, diseases and insect pests (You and Chan, 2015; Dvořák et al., 2021). It is not easy to move from research to practical application. This requires the combination of molecular biology, breeding genetics and agricultural management. Only in this way can we truly develop an effective ROS regulation strategy to improve potatoes and increase yield and adaptability.

9 Conclusion

Reactive oxygen species (ROS) play a key role when potatoes encounter stress. It acts as a signal that allows plants to initiate defense responses. For example, in the case of drought, salinity or pathogen attack, the level of ROS in potatoes will increase, which may cause oxidative stress and damage cells. To deal with this problem, potatoes have their own way. They will activate some antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (PRXs). These enzymes can remove excess ROS, help cells avoid damage, and make plants more resistant to stress.

For potatoes to stay healthy, the production and removal of ROS must be maintained at a balance. The right amount of ROS is useful, it can help transmit signals and trigger defense responses; but if there are too many ROS, it will damage cells and cause problems with the physiological functions of plants. In the process of regulating ROS, two types of molecules, calcium-dependent protein kinases (CDPKs) and Rbohs, interact with each other and can regulate the production of ROS together. In addition, systems such as the ascorbic acid-glutathione cycle can also help remove ROS, indicating that both enzymatic and non-enzymatic antioxidant methods are important. These mechanisms allow potatoes to cope with external stress while continuing to grow and develop normally.

In future studies, scientists can focus on how to further improve the stress resistance of potatoes through breeding or biotechnology. For example, key genes that can remove ROS can be found and "amplified", which may make potatoes perform better in the face of drought or disease. Continuing to study the interaction between ROS and other signaling molecules will also help find new stress resistance strategies. If we can understand how ROS transmits signals in cell structures such as mitochondria, we may be able to discover more new ways to make potatoes stronger.

Acknowledgments

We would like to thank Ms. Kris Jin continuous support throughout the development of this study.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Alscher R., Donahue J., and Cramer C., 1997, Reactive oxygen species and antioxidants: Relationships in green cells, *Physiologia Plantarum*, 100: 224-233.
<https://doi.org/10.1111/J.1399-3054.1997.TB04778.X>
- Baxter A., Mittler R., and Suzuki N., 2014, ROS as key players in plant stress signalling, *Journal of Experimental Botany*, 65(5): 1229-1240.
<https://doi.org/10.1093/jxb/ert375>
- Czarnocka W., and Karpiński S., 2018, Friend or foe? Reactive oxygen species production, scavenging and signaling in plant response to environmental stresses, *Free Radical Biology and Medicine*, 122: 4-20.
<https://doi.org/10.1016/j.freeradbiomed.2018.01.011>

- Das K., and Roychoudhury A., 2014, Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants, *Frontiers in Environmental Science*, 2: 53.
<https://doi.org/10.3389/fenvs.2014.00053>
- Dvořák P., Krasylenko Y., Zeiner A., Šamaj J., and Takáč T., 2021, Signaling toward reactive oxygen species-scavenging enzymes in plants, *Frontiers in Plant Science*, 11: 618835.
<https://doi.org/10.3389/fpls.2020.618835>
- Fan W., 2014, Effects of anoxia and post-anoxia on reactive oxygen species(ROS) and antioxidant enzymes in tuber mitochondria of potato(*Solanum tuberosum* L.), *Plant Physiology*, 50(3): 283-289.
- Hasanuzzaman M., Bhuyan M., Zulfikar F., Raza A., Mohsin S., Mahmud J., Fujita M., and Fotopoulos V., 2020, Reactive oxygen species and antioxidant defense in plants under abiotic stress: revisiting the crucial role of a universal defense regulator, *Antioxidants*, 9(8): 681.
<https://doi.org/10.3390/antiox9080681>
- Hipsch M., Lampl N., Zelinger E., Barda O., and Rosenwasser S., 2020, Sensing stress responses in potato with whole-plant redox imaging, *bioRxiv*.
<https://doi.org/10.1101/2020.11.26.386573>
- Hu Y., Zhao H., Xue L., Nie N., Zhang H., Zhao N., He S., Liu Q., Gao S., and Zhai H., 2024, IbMYC2 contributes to salt and drought stress tolerance via modulating anthocyanin accumulation and ROS-scavenging system in sweet potato, *International Journal of Molecular Sciences*, 25(4): 2096.
<https://doi.org/10.3390/ijms25042096>
- Hua, D., Duan, J., Li, Z., and Li, H., 2020, Reactive oxygen species induce cyanide-resistant respiration in potato infected by *Erwinia carotovora* subsp. *Carotovora*, *Journal of Plant Physiology*, 246-247: 153132.
<https://doi.org/10.1016/j.jplph.2020.153132>
- Huang S., Van Aken O., Schwarzländer M., Belt K., and Millar A., 2016, The roles of mitochondrial reactive oxygen species in cellular signaling and stress response in plants, *Plant Physiology*, 171: 1551-1559.
<https://doi.org/10.1104/pp.16.00166>
- Jajić I., Sarna T., and Strzałka K., 2015, Senescence, stress, and reactive oxygen species, *Plants*, 4: 393-411.
<https://doi.org/10.3390/plants4030393>
- Koubaa R., Ayadi M., Saidi M., Charfeddine S., Gargouri-Bouزيد R., and Nouri-Ellouz O., 2021, Comprehensive genome-wide analysis of the catalase enzyme toolbox in potato (*Solanum tuberosum* L.), *Potato Research*, 66: 23-49.
<https://doi.org/10.1007/s11540-022-09554-z>
- Lei C., Ye M., Li C., and Gong M., 2023, H2O2 participates in the induction and formation of potato tubers by activating tuberization-related signal transduction pathways, *Agronomy*, 13(5): 1398.
<https://doi.org/10.3390/agronomy13051398>
- Li S., Liu S., Zhang Q., Cui M., Zhao M., Li N., Wang S., Wu R., Zhang L., Cao Y., and Wang L., 2022, The interaction of ABA and ROS in plant growth and stress resistances, *Frontiers in Plant Science*, 13: 1050132.
<https://doi.org/10.3389/fpls.2022.1050132>
- Li X., Wang Z., Sun S., Dai Z., Zhang J., Wang W., Peng K., Geng W., Xia S., Liu Q., Zhai H., Gao S., Zhao N., Tian F., Zhang H., and He S., 2024, IbNIEL-mediated degradation of IbNAC087 regulates jasmonic acid-dependent salt and drought tolerance in sweet potato, *Journal of Integrative Plant Biology*, 66(2): 176-195.
<https://doi.org/10.1111/jipb.13612>
- Li C.Y., and Huang Y.M., 2024, Metabolic engineering of tea: enhancing bioactive compound production, *Bioscience Methods*, 15(3): 114-123.
- Lukan T., and Coll A., 2022, Intertwined roles of reactive oxygen species and salicylic acid signaling are crucial for the plant response to biotic stress, *International Journal of Molecular Sciences*, 23(10): 5568.
<https://doi.org/10.3390/ijms23105568>
- Luo X., Tian T., Bonnaville M., Tan X., Huang X., Li Z., and Ren M., 2021, The molecular mechanisms of Phytophthora infestans in response to reactive oxygen species (ROS) stress, *Phytopathology*, 111(11): 2067-2079.
<https://doi.org/10.1094/PHYTO-08-20-0321-R>
- Ma L., Jiang H., Bi Y., Li Y., Yang J., Si H., Ren Y., and Prusky D., 2021b, The interaction between StCDPK14 and StRbohB contributes to Benzo-(1, 2, 3)-Thiadiazole-7-Carbothioic acid S-Methyl Ester-induced wound healing of potato tubers by regulating reactive oxygen species generation, *Frontiers in Plant Science*, 12: 737524.
<https://doi.org/10.3389/fpls.2021.737524>
- Ma R., Liu W., Li S., Zhu X., Yang J., Zhang N., and Si H., 2021a, Genome-wide identification, characterization and expression analysis of the CIPK gene family in potato (*Solanum tuberosum* L.) and the role of StCIPK10 in response to drought and osmotic stress, *International Journal of Molecular Sciences*, 22(24): 13535.
<https://doi.org/10.3390/ijms222413535>
- Mahalingam R., and Fedoroff N., 2003, Stress response, cell death and signalling: the many faces of reactive oxygen species. *Physiologia Plantarum*, 119: 56-68.
<https://doi.org/10.1034/J.1399-3054.2003.00156.X>
- Miller G., Shulaev V., and Mittler R., 2008, Reactive oxygen signaling and abiotic stress, *Physiologia Plantarum*, 133(3): 481-489.
<https://doi.org/10.1111/j.1399-3054.2008.01090.x>

- Miller G., Suzuki N., Ciftci-Yilmaz S., and Mittler R., 2010, Reactive oxygen species homeostasis and signalling during drought and salinity stresses, *Plant, Cell & Environment*, 33(4): 453-467.
<https://doi.org/10.1111/j.1365-3040.2009.02041.x>
- Mishra S., Ganapathi T., Pandey G., Foyer C., and Srivastava A., 2023, Meta-analysis of antioxidant mutants reveals common-alarm signals for shaping abiotic stress-induced transcriptome in plants, *Antioxidants & Redox Signaling*, 41(1-3): 42-55.
<https://doi.org/10.1089/ars.2023.0361>
- Myers R., Fichman Y., Zandalinas S., and Mittler R., 2022, Jasmonic acid and salicylic acid modulate systemic reactive oxygen species signaling during stress responses, *Plant Physiology*, 191(2): 862-873.
<https://doi.org/10.1093/plphys/kiac449>
- Myers R., Peláez-Vico M., and Fichman Y., 2024, Functional analysis of reactive oxygen species-driven stress systemic signalling, interplay and acclimation, *Plant, Cell & Environment*, 47(8): 2842-2851.
<https://doi.org/10.1111/pce.14894>
- Otulak-Kozieł K., Kozieł E., Przewodowski W., Ciacka K., and Przewodowska A., 2022, Glutathione modulation in PVYNTN susceptible and resistant potato plant interactions, *International Journal of Molecular Sciences*, 23(7): 3797.
<https://doi.org/10.3390/ijms23073797>
- Panda S., Gupta D., Patel M., Vyver C., and Koyama H., 2024, Functionality of reactive oxygen species (ROS) in plants: toxicity and control in poaceae crops exposed to abiotic stress, *Plants*, 13(15): 2071.
<https://doi.org/10.3390/plants13152071>
- Postiglione A., and Muday G., 2020, The role of ROS homeostasis in ABA-induced guard cell signaling, *Frontiers in Plant Science*, 11: 968.
<https://doi.org/10.3389/fpls.2020.00968>
- Ravi B., Foyer C., and Pandey G., 2023, The integration of reactive oxygen species (ROS) and calcium signalling in abiotic stress responses, *Plant, Cell & Environment*, 46(7): 1985-2006.
<https://doi.org/10.1111/pce.14596>
- Sahoo M., Devi T., Dasgupta M., Nongdam P., and Prakash N., 2020, Reactive oxygen species scavenging mechanisms associated with polyethylene glycol mediated osmotic stress tolerance in Chinese potato, *Scientific Reports*, 10: 5404.
<https://doi.org/10.1038/s41598-020-62317-z>
- Soliman A., Adam L., Rehal P., and Daayf F., 2021, Overexpression of *Solanum tuberosum* respiratory burst oxidase homolog A (StRbohA) promotes potato tolerance to *Phytophthora infestans*, *Phytopathology*, 111(8): 1410-1419.
<https://doi.org/10.1094/PHYTO-10-20-0482-R>
- Terrón-Camero L., Peláez-Vico M., Rodríguez-González A., Del Val C., Sandalio L., and Romero Puertas M., 2022, Gene network downstream plant stress response modulated by peroxisomal H₂O₂, *Frontiers in Plant Science*, 13: 930721.
<https://doi.org/10.3389/fpls.2022.930721>
- Xia X., Zhou Y., Shi K., Zhou J., Foyer C., and Yu J., 2015, Interplay between reactive oxygen species and hormones in the control of plant development and stress tolerance, *Journal of Experimental Botany*, 66(10): 2839-2856.
<https://doi.org/10.1093/jxb/erv089>
- You J., and Chan Z., 2015, ROS regulation during abiotic stress responses in crop plants, *Frontiers in Plant Science*, 6: 1092.
<https://doi.org/10.3389/fpls.2015.01092>
- Zhang H., Wang Z., Li X., Gao X., Dai Z., Cui Y., Zhi Y., Liu Q., Zhai H., Gao S., Zhao N., and He S., 2021, The IbBBX24-IbTOE3-IbPRX17 module enhances abiotic stress tolerance by scavenging reactive oxygen species in sweet potato, *The New Phytologist*, 233(3): 1133-1152.
<https://doi.org/10.1111/nph.17860>
- Zhu Y.L., and Shen Z.C., 2024, Response analysis of root and leaf physiology and metabolism under drought stress in rice, *Rice Genomics and Genetics*, 15(3): 19-27.

**Disclaimer/Publisher's Note**

The statements, opinions, and data contained in all publications are solely those of the individual authors and contributors and do not represent the views of the publishing house and/or its editors. The publisher and/or its editors disclaim all responsibility for any harm or damage to persons or property that may result from the application of ideas, methods, instructions, or products discussed in the content. Publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.