Hydrogen Peroxide

Signaling Mechanisms and Crosstalk in Plant Development and Stress Responses

Edited by Mohd Tanveer Alam Khan, Taiba Saeed, Aqeel Ahmad, Qazi Fariduddin, and Mohammad Yusuf

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Mohammad Yusuf, Mohd Tanveer Alam Khan, Taiba Saeed, Mohammad Faizan, and Mayank Anand Gururani

INTRODUCTION

A century ago, Louis Jacques Thenard made the discovery of hydrogen peroxide (H_2O_2), a chemical compound with characteristics that could warrant its classification as a phytohormone (Cerny et al. 2018). Today, H_2O_2 is recognized as a type of reactive oxygen species and is regarded as a ubiquitous cellular metabolite. Plants produce this molecule through multiple sources, encompassing both enzymatic and non-enzymatic routes, involving NADPH oxidases and peroxidases, as well as metabolic processes like photorespiration (Niu and Liao 2016). Moreover, its production is elevated during stress conditions and is also a crucial component in various growth and developmental processes. However, H_2O_2 has the potential to cause oxidative damage in excess, its controlled production and regulated levels serve important functions in plant physiology, helping plants adapt to environmental challenges and maintain their overall health. On the other hand, when present in minute nanomolar concentrations, H_2O_2 acts as a signaling molecule, garnering increased attention for its influence on plant growth and development (Htet et al. 2019). Studies have unveiled that H_2O_2 plays a pivotal role in regulating stress defenses and secondary metabolic functions in plants (Ellouzi et al. 2017). By modulating the proteome model, H_2O_2 also holds the potential to significantly modulate the morpho-physiological and biochemical responses in plants (Khan et al. 2019). H_2O_2 exhibits the potential to alter the activation state of RuBisCO (Jamaludin et al. 2020). In a recent study by Jamaludin et al. (2020), foliar application of H_2O_2 was found to enhance the expression of the plastid DNA-origin rbcL gene, associated with the RuBisCO component, in *F. deltoideae*, thereby boosting photosynthesis. H_2O_2 has firmly established its significant contributions to plant responses to various environmental factors, including heavy metals (Hasanuzzaman et al. 2017; Nazir et al. 2019), waterlogging (Andrade et al. 2018), salinity (Bagheri et al. 2019), and low-temperature stress (Khan et al. 2019). The researchers propose that H_2O_2 influences gene expression through protein oxidation, kinase activation, and modulation of transduction cascades. Moreover, H_2O_2 foliar application increased both electron transport (J) and triose phosphate (TPU) in water-deficient plants, which positively impacted the photosynthetic dynamics and resulted in improved growth compared to well-watered plants. Stomatal closure, a primary limiting factor for photosynthesis in moderately water-deficient plants, reduces CO_2 concentration available for the process (Barzotto et al. 2023). As assimilation decreases with declining CO_2 concentration, there is a subsequent reduction in sucrose-phosphate synthase enzyme activity (Barzotto et al. 2023), potentially leading to decreased TPU. Sharkey (2007 suggested that restricting TPU capacity by

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eliminating the reproductive component causes sucrose accumulation and negative feedback for photosynthesis. The condition of water deficiency and the need for osmotic adjustment likely constrain drainage strength, consequently diminishing growth capacity. Higher TPU is correlated with increased sucrose-phosphate synthase enzyme activity, as demonstrated by Ozaki et al. (2009) following H_2O_2 administration to *Cucumis melo* plants. It is widely acknowledged that H_2O_2 exerts a substantial influence on plant stress responses, primarily by serving as a mediator that orchestrates the metabolically or ecologically monitored activation of specific tolerance genes (Phukan et al. 2016; Pornsiriwong et al. 2017; Qi et al. 2018). Research on protein kinases indicates that mitogen-activated protein kinases (MAPKs) undergo activation in response to H_2O_2 in both animal and plant systems, potentially influencing gene expression (Torres and Forman, 2003). The role of H_2O_2 in plant signaling during abiotic stress suggests its potential exogenous use to induce metabolic shifts and facilitate acclimation (Barzotto et al. 2023). This process, akin to defense priming, enhances the capacity for improved stress response following initial signaling (Torres and Forman 2023). H_2O_2 induces the oxidation of cysteine residues, serving as a recognized molecular switch implicated in numerous signaling pathways. This leads to the formation of disulfides in conjunction with glutathione, believed to protect proteins from further oxidation and modulate interactions with DNA. Through control of gene expression, this signaling mechanism enables swift responses without the need for de novo mRNA synthesis and nuclear export (Lennicke et al. 2015). Crucial to these responses within the plant innate immune system is a signaling pathway wherein NADPH oxidase serves as a key mediator, regulating H_2O_2 production and influencing the intensity of defensive responses (Rohman et al. 2024). In the upcoming sections, this chapter will examine the origin, prevalence, and dispersion of H_2O_2 in plants. It will delve into the physiological responses of plants, with particular attention to how the photosynthetic machinery responds to H_2O_2 in stressful environmental conditions. Additionally, it will analyze the signaling pathways triggered by H_2O_2 in plant cells under abiotic stress. Lastly, it will investigate the interactions between H_2O_2 and other phytohormones during periods of abiotic stress.

ORIGIN, OCCURRENCE, AND DISTRIBUTION OF H_2O_2

Origin: H_2O_2 is a common molecule found in plant cells. It plays a crucial role in various physiological processes such as growth, development, and stress responses. The origin of hydrogen peroxide in plants can be traced back to both enzymatic and non-enzymatic processes. Enzymatic production of hydrogen peroxide occurs via the activity of various enzymes such as NADPH oxidases, peroxidases, and amine oxidases. NADPH oxidases are responsible for generating H_2O_2 during growth and development in different areas of the plant such as the root, shoot, leaf, and flower (Cerny et al. 2018). Peroxidases, on the other hand, play a vital role in stress responses such as pathogen attack, wounding, and exposure to abiotic stress. They catalyze the oxidation of different macromolecules such as lignin and phenolics, which leads to the formation of H_2O_2 (Quan et al. 2008). Additionally, amine oxidases contribute to H_2O_2 generation during cell wall maturation and ripening of fruits. Non-enzymatic processes are also involved in the production of H_2O_2 in plants. This includes the auto-oxidation of various molecules such as flavonoids and polyphenols. These molecules can undergo oxidation in the presence of atmospheric oxygen, which results in the formation of H_2O_2 (Quan et al. 2008). Moreover, the photochemical reactions that take place during photosynthesis can also lead to the formation of H_2O_2. Once produced, H_2O_2 is involved in various physiological processes in plants such as programmed cell death, pathogen defense, and cell signaling. It is also involved in redox signaling, which is the process of regulating cellular processes through the transfer of electrons between different molecules. H_2O_2 functions as a signaling molecule in plants, regulating various processes such as growth, development, and stress responses.

Occurrence: In plants, flavin-containing proteins have the potential to catalyze the reduction of oxygen in a manner dependent on blue light. H_2O_2 production stemming from cryptochrome, a blue