



Deciphering the role of enzymatic and non-enzymatic antioxidants in bhut jolokia under abiotic stresses

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Abstract

Bhut Jolokia, commonly known as the ghost pepper (*Capsicum chinense* Jacq.), is one of the hottest chillies in the world, boasting the highest content of capsaicinoids. Due to increasing climate anomalies such as global warming, irregular precipitation and seasonal shifts, *C. chinense* is particularly susceptible to environmental stressors. When exposed to abiotic stresses like extreme heat, cold, drought and heavy metals, the plant suffers from oxidative stress due to the overproduction of reactive oxygen species (ROS). To counteract this, Bhut Jolokia has developed various antioxidant systems, encompassing both enzymatic and non-enzymatic defense mechanisms. Enzymatic antioxidants in Bhut Jolokia include superoxide dismutase (SOD), which converts O_2^- into H_2O_2 and O_2 and catalase (CAT), which breaks down H_2O_2 into H_2O and O_2 . Additionally, glutathione peroxidase (GPX) reduces H_2O_2 and organic peroxides using glutathione as a cofactor, while ascorbate peroxidase utilizes ascorbate to reduce H_2O_2 to H_2O . Peroxiredoxins also play a role by reducing hydrogen peroxide, alkyl hydroperoxides and peroxynitrite. Non-enzymatic antioxidants include ascorbate (vitamin C), a potent water-soluble antioxidant that scavenges ROS and glutathione, a tripeptide that neutralizes ROS and regenerates other antioxidants. Carotenoids, which are lipid-soluble antioxidants, quench singlet oxygen and scavenge peroxy radicals and the abundant capsaicinoids in Bhut Jolokia also exhibit antioxidant properties. The balance and interaction between these enzymatic and non-enzymatic antioxidants are crucial for Bhut Jolokia to maintain cellular redox homeostasis and survive under various abiotic stresses. This review focuses on understanding the antioxidant defense system of Bhut Jolokia, which can aid in improving the cultivation and medicinal applications of this plant species.

Keywords: Ghost pepper, capsaicin, pungency, antioxidants, abiotic stress, Capsicum

Introduction

In recent decades, climate change has posed a serious threat to living organisms, with its impact particularly evident in diverse plant species (Rehman and Tanti, 2020^[40]; Lepcha, 2024^[26]). Plants, being stationary, are especially vulnerable to various abiotic stresses arising from climatic anomalies, such as temperature fluctuations, irregular precipitation patterns and soil degradation. These stresses adversely affect the morphological, physiological, biochemical and molecular foundations of plants (Kumar, 2020)^[24]. Due to their immovable nature, plants have developed various stress tolerance mechanisms and metabolic processes in order to adapt under unfavourable environments (Pradhan *et al.*, 2020)^[38]. During abiotic stress conditions, the generation of harmful reactive oxygen species (ROS) disrupts cellular homeostasis, adversely affecting plant growth and productivity. These ROS molecules include superoxide anion radicals (O_2^-), singlet oxygen (1O_2), hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH). ROS are highly reactive compounds produced as natural byproducts during various metabolic pathways in the presence of oxygen (Juan *et al.*, 2021)^[18]. At the early stages of stress exposure, ROS production serves as a stress signal, initiating a series of molecular responses to mitigate the stress. These molecules function as secondary messengers in numerous signalling and metabolic pathways, activating stress-responsive genes and pathways that underpin plant adaptation and survival mechanisms. However, during extreme temperatures, severe drought and water logging, the balance is disrupted as the plant cannot efficiently scavenge the increased ROS accumulation (Hasanuzzaman *et al.*, 2020a^[15]; 2020b). The extent of ROS generation and the

ability to scavenge them varies among plant species, depending on the severity and duration of the stress (Hasanuzzaman *et al.*, 2020b)^[16]. To balance the effects of ROS, plants possess various antioxidant defense systems, including enzymatic antioxidants (SOD, CAT, GR, GPX and APX) and non-enzymatic antioxidants (ascorbate, glutathione, polyphenols, carotenoids and proline) (Saikia and Tanti, 2023)^[42].

Similar to other crops, *Capsicum* species experience significant yield reductions and decreased growth due to adverse abiotic conditions such as drought, salinity and extreme temperatures and humidity. These environmental stresses limit productivity and impact the morphological and physiological growth of *Capsicum* species, especially Bhut Jolokia (*C. chinense* Jacq.), by disrupting osmotic balance, affecting growth, reproduction, fruit ripening and quality. Therefore, it is critical for researchers to focus on mitigating the impacts of these environmental challenges (Momo *et al.*, 2022)^[31]. Deviations from the optimal temperature range affect various physiological processes in *Capsicum* species, including germination, fruit setting, fruit maturity and the accumulation of metabolites, particularly capsaicinoids. These temperature fluctuations also impact the reproductive stage and overall productivity of the plant. Additionally, salinity negatively affects *Capsicum* species at multiple stages of productivity, including germination, flowering, fruit development and nutrient concentration (Kpinkoun *et al.*, 2019)^[22]. This review focuses on elucidating the impact of enzymatic and non-enzymatic antioxidants in Bhut Jolokia (*C. chinense* Jacq.) under different environmental conditions and understanding the tolerance mechanisms provided by these antioxidants.

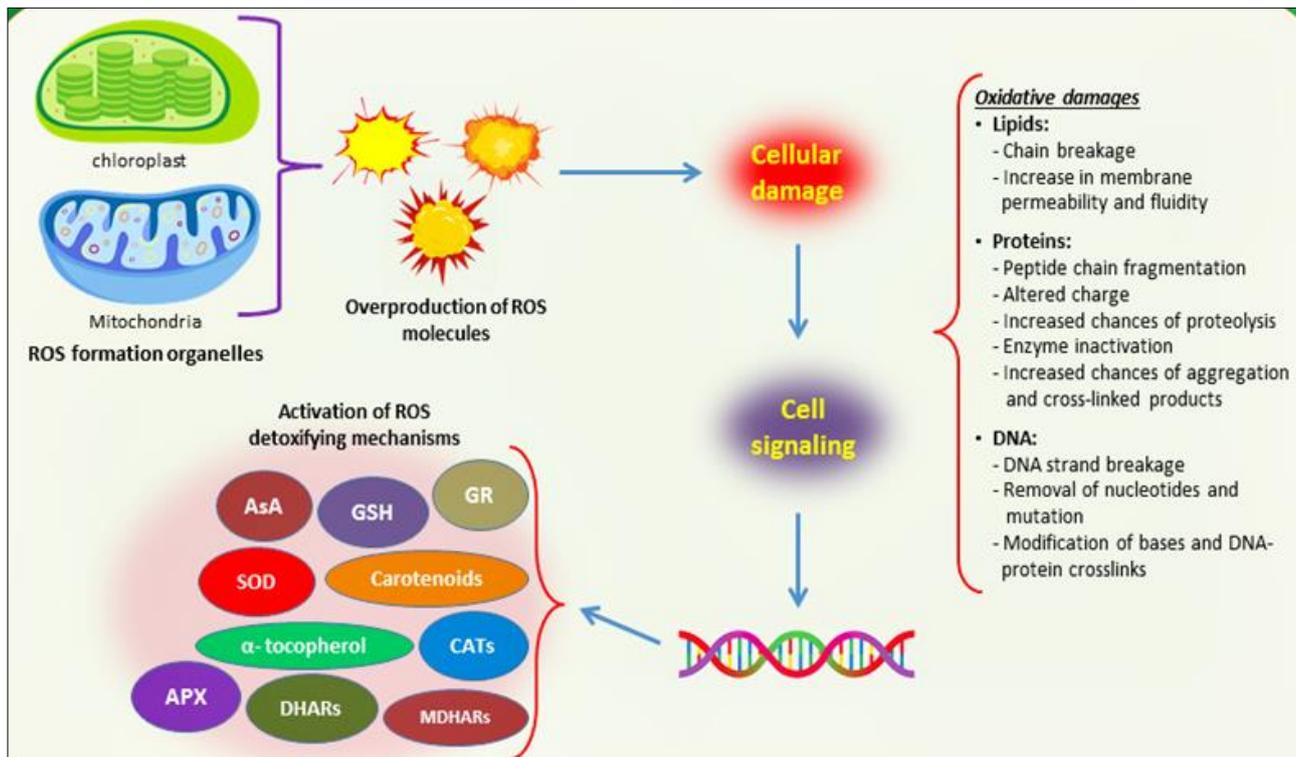


Fig 1: Overproduction of ROS leads to various oxidative damages affecting the cellular machinery (Mishra *et al.*, 2023) ^[30]

Plant description

Capsicum chinense Jacq., commonly known as Bhut Jolokia, is a herbaceous plant belonging to the Solanaceae family. Native to Central and South America (Mosquera and Mendez, 1994), this self-pollinated plant can also experience up to 10% cross-pollination in the presence of increased insect activity. Bhut Jolokia is highly valued both commercially and economically as a spice and vegetable crop (do Rego *et al.*, 2012) ^[9]. It grows extensively in various regions, particularly in Assam, Northeast India. Bhut Jolokia holds the Guinness World Record (2006) for being the hottest chili in the world, with a pungency level of 1,001,304 Scoville Heat Units (SHU) due to its high capsaicin content (Roy *et al.*, 2024) ^[41]. The plant is semi-perennial, reaching a height of 50-100 cm, with nodes displaying anthocyanin pigmentation. Its leaves are ovate and have a characteristic crinkled morphology. At maturity, each node can produce 2-3 flowers and fruits. The plant exhibits a bunching and overhanging flowering habit, with flowers featuring white corollas, blue and purple anthers and filaments. The fruits of *C. chinense* are 5-7 cm long and 2.5-3.0 cm in diameter, displaying a range of colors such as light green, dark red and bright orange and typically have 4-5 hollow locules. The plant yields 15-20 mature fruits and 10-14 immature fruits per season (Sarwa, 2012; Anupam, 2016 ^[1]; Gogoi, 2017) ^[12]. Capsaicin and dihydrocapsaicin are the primary compounds responsible for the chili's pungency, with higher pungency levels linked to increased capsaicin content. Bhut Jolokia also possesses various medicinal properties, including pain relief, weight loss aid,

antioxidant properties, antimicrobial effects and potent anticancer activity (Yamamoto and Nawata, 2009 ^[48]; Gogoi, 2017) ^[12].

Enzymatic and antioxidant enzymes

The antioxidant defense system in plants is crucial for mitigating the damaging effects of reactive oxygen species (ROS) generated during abiotic stress conditions. Under stress conditions such as extreme temperatures, drought and salinity, plants produce elevated levels of ROS as natural by-products of various metabolic processes (Zandi and Schnug, 2022) ^[49]. If left unchecked, these ROS molecules can disrupt cellular functions and structures, leading to oxidative stress. The antioxidant defense system consists of a network of molecules and enzymes that collectively scavenge ROS and reduce their detrimental impact on plant growth and productivity. Enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), glutathione peroxidase (GPX) and ascorbate peroxidase (APX), work holistically to detoxify these harmful molecules. In addition to enzymatic antioxidants, non-enzymatic antioxidants are low molecular weight molecules that fall into two categories: water-soluble (ascorbic acid and glutathione) and lipophilic (tocopherols and β-carotene) (Mishra *et al.*, 2023) ^[30]. This defense system also includes antioxidants such as flavonoids, isoprenoids, tocopherols and carotenoids. These molecules directly interact with ROS to neutralize them, thereby protecting cellular structures from oxidative damage (Fig. 1).

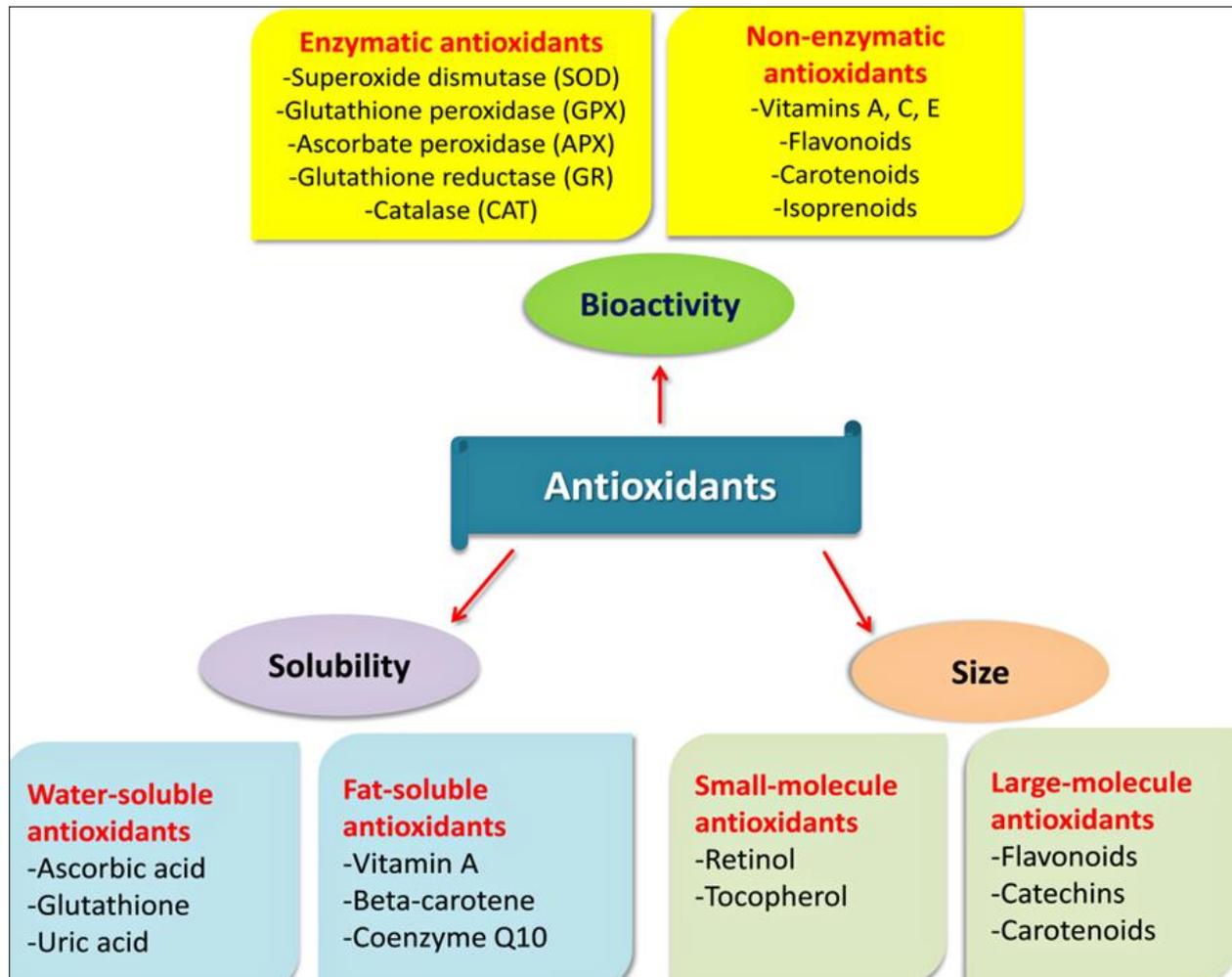


Fig 2: Different classes of antioxidants (Ayoka *et al.*, 2022) ^[30]

Enzymatic antioxidant enzymes

Sod (Superoxide dismutase)

Under the antioxidant defense system, one of the most significant cellular enzymes is superoxide dismutase (SOD; EC 1.15.1.1), which is critical for eliminating superoxide radicals (O_2^-) generated during various abiotic stress conditions. This class of enzymes acts as the frontline defense against injuries caused by reactive oxygen species. Superoxide dismutase works by scavenging superoxide radicals (O_2^-) and converting them into molecular oxygen (O_2) and hydrogen peroxide (H_2O_2). It is the only antioxidant enzyme that catalyzes superoxide anions and reactive nitrogen species, inhibiting the production of peroxynitrite and further damage caused by these anionic molecules.

In mammals, SOD is present in three isoforms: cytoplasmic Cu/ZnSOD (SOD1), mitochondrial MnSOD (SOD2) and extracellular Cu/ZnSOD (SOD3), each requiring a catalytic metal (Cu or Mn) for activation. Butt *et al.* (2022) investigated the response of antioxidant enzymes in various chili varieties exposed to different salinity levels. Their study showed that the activity levels of enzymes such as SOD, CAT and POD increased in relation to the salinity concentration, especially at 70 mM. Under normal conditions, SOD levels are optimal, but the enzyme is upregulated under different abiotic stress conditions.

CAT (Catalase)

The second important enzyme in the antioxidant defense system is catalase (CAT, EC 1.11.1.6). Catalase is a major defensive enzyme against ROS-generated injury, catalyzing the breakdown of hydrogen peroxide (H_2O_2) into water (H_2O) and molecular oxygen (O_2). Typically, catalase exists in a tetrameric, heme-containing form, with each subunit bearing a heme group that aids in the breakdown of hydrogen peroxide. The enzyme's rapid turnover allows it to scavenge H_2O_2 molecules more efficiently, thereby protecting cells from oxidative damage and preserving redox equilibrium within the cellular environment. This class of enzyme is usually found in peroxisomes (Mishra *et al.*, 2023) ^[30].

Under various abiotic stress conditions such as drought, high salinity, extreme temperatures and heavy metal toxicity, the increase in ROS production can lead to the formation of hydrogen peroxide due to a defective antioxidant defense system (Liu *et al.*, 2022) ^[28]. Kopta *et al.* (2020) noted a significant increase in catalase and APX content in chili cultivars under drought stress compared to untreated plants.

GPX (Glutathione peroxidase)

Glutathione peroxidase (GPX, EC 1.11.1.9) plays a crucial role in *Capsicum chinense* Jacq. by protecting against the

damaging effects of abiotic stresses. This enzyme reduces hydrogen peroxide (H_2O_2) and organic hydroperoxides to water (H_2O) and corresponding alcohols using glutathione (GSH) as a substrate (Pei *et al.*, 2023) ^[36]. During abiotic stress, the accumulation of reactive oxygen species (ROS) in chili plants can lead to oxidative damage, affecting cellular structures and metabolic processes. GPX mitigates this oxidative stress by efficiently scavenging ROS, thus preventing lipid peroxidation, protein oxidation and DNA damage (Saikia *et al.*, 2021) ^[21]. In chili plants, abiotic stress often triggers an upregulation of GPX activity and expression, enhancing the plant's defensive response. This adaptive mechanism is critical for maintaining cellular redox homeostasis, which is essential for the plant's survival and productivity. The enzymatic activity of GPX is closely linked to the regeneration of GSH from its oxidized form (GSSG), a process facilitated by glutathione reductase (GR), ensuring a continuous supply of GSH for ROS detoxification (Lou, 2022) ^[29].

Additionally, GPX plays a role in signalling pathways that regulate the expression of stress-responsive genes, thereby modulating the plant's overall stress response. An effective GPX response in chili plants helps maintain photosynthetic efficiency, cellular integrity and metabolic balance under adverse conditions (Kopta *et al.*, 2020) ^[21]. GPX significantly contributes to the resilience and adaptive capacity of chili plants, ensuring better growth, yield and quality even in the face of challenging environmental conditions.

APX (Ascorbate peroxidase)

Ascorbate peroxidase (APX, EC 1.11.1.11) plays a crucial role in detoxifying reactive oxygen species (ROS) under abiotic stress conditions in chili peppers. APX catalyzes the conversion of hydrogen peroxide (H_2O_2) into water (H_2O) using ascorbic acid (vitamin C) as an electron donor, thereby protecting plant cells from oxidative damage (Kaur *et al.*, 2021) ^[19]. This enzyme is vital for maintaining cellular redox homeostasis, especially during various abiotic stress events that lead to increased ROS production. Studies indicate that APX activity is significantly upregulated in chili pepper plants subjected to drought stress, reflecting the plant's adaptive response to mitigate oxidative stress. Various cultivars of chili peppers exhibit different levels of APX activity, suggesting that some genotypes possess enhanced mechanisms for ROS scavenging compared to others (Hareem *et al.*, 2024a) ^[14]. APX operates in conjunction with other components of the ascorbate-glutathione cycle, including monohydro-ascorbate reductase, dehydro-ascorbate reductase and glutathione reductase, to regenerate ascorbate and sustain a robust antioxidative defense system. This cyclic mechanism ensures the continuous removal of H_2O_2 and maintains a pool of reduced ascorbate, crucial for the sustained activity of APX. Thus, APX not only directly detoxifies H_2O_2 but also contributes to the broader network of antioxidant defenses. Hareem *et al.* (2024b) ^[13] studied the mitigation of drought stress in chili plants (*Capsicum annuum* L.) using mango fruit waste biochar, fulvic acid and cobalt. They reported a reduction in the activity of various antioxidants, including APX, POD, CAT and SOD enzymes when treated with these mitigating agents.

Non-enzymatic antioxidant enzymes

Ascorbate

Ascorbate, also known as vitamin C, is a crucial non-enzymatic antioxidant in plant defense against abiotic stresses such as drought, salinity, extreme temperatures and heavy metals, which lead to the overproduction of reactive oxygen species (ROS) within plant cells (Venkatesh and Park, 2014) ^[47]. These ROS molecules, including superoxide radicals, hydrogen peroxide and hydroxyl radicals, can cause significant oxidative damage to cellular components like lipids, proteins and nucleic acids, thereby inhibiting plant growth and productivity. Ascorbate alleviates these harmful effects by directly scavenging ROS, preventing oxidative damage. A primary function of ascorbate is its ability to donate electrons in redox reactions, neutralizing ROS and converting them into less harmful molecules. In the ascorbate-glutathione cycle, ascorbate acts as a reducing agent, transforming H_2O_2 into H_2O with the help of ascorbate peroxidase (Foyer and Kunert, 2024) ^[11]. During this process, ascorbate is oxidized to monodehydroascorbate, which can be reverted to ascorbate by monodehydroascorbate reductase or can disproportionate into ascorbate and dehydroascorbate. Dehydroascorbate can then be reduced back to ascorbate by dehydroascorbate reductase using glutathione as an electron donor, thus maintaining a pool of reduced ascorbate. Under abiotic stress, the synthesis and recycling of ascorbate are upregulated to enhance the plant's antioxidative capacity. This involves increased expression of genes encoding enzymes such as L-galactono-1,4-lactone dehydrogenase, which catalyzes the final step of ascorbate biosynthesis. Additionally, various transporters responsible for ascorbate distribution within plant cells are upregulated, ensuring sufficient ascorbate levels in different cellular compartments where ROS are generated.

Glutathione

Glutathione (GSH) is a critical non-enzymatic antioxidant that plays a vital role in protecting plants from the adverse effects of abiotic stresses. It is a tripeptide composed of glutamine, cysteine and glycine and exists in two forms: reduced (GSH) and oxidized (GSSG) (Dorion *et al.*, 2021) ^[10]; Rai *et al.*, 2023) ^[39]. Under normal conditions, GSH is predominantly in its reduced form, actively participating in detoxifying reactive oxygen species (ROS) generated during abiotic stress (Rai *et al.*, 2023) ^[39]. This detoxification occurs through the direct scavenging of ROS or as a substrate in enzymatic reactions catalyzed by glutathione peroxidase and glutathione S-transferase. These enzymes use GSH to reduce peroxides and conjugate GSH to xenobiotic substrates, respectively, thereby preventing cellular damage. Additionally, GSH is involved in regenerating other antioxidants, such as ascorbate, through the ascorbate-glutathione cycle, further enhancing the plant's defense mechanisms. The GSH/GSSG ratio is a critical indicator of cellular redox status, with a high ratio reflecting a reduced state favorable for growth and stress resilience (Chen *et al.*, 2024) ^[7]. During abiotic stress, GSH synthesis is upregulated through the γ -glutamyl cycle, boosting the plant's capacity to counteract oxidative stress. Furthermore, GSH plays a role in signal transduction pathways that modulate stress-responsive gene expression, contributing to the plant's adaptive responses. Thus, glutathione is essential for maintaining cellular redox homeostasis and enhancing the tolerance of *C. chinense* plants to various abiotic stresses.

Carotenoids

Carotenoids are vital non-enzymatic antioxidants in plants, playing a crucial role in mitigating the harmful effects of various abiotic stresses. These pigments, such as beta-carotene, lutein and zeaxanthin, are integral to the photosynthetic apparatus. They absorb excess light energy and neutralize reactive oxygen species (ROS), including singlet oxygen and free radicals. During abiotic stress, elevated ROS levels can lead to oxidative damage to lipids, proteins and nucleic acids, impairing cellular function and overall plant health. In chili plants, carotenoids act as a first line of defense by dissipating excess energy as heat through non-photochemical quenching (NPQ), thereby protecting the photosynthetic machinery from photo-inhibition and photo-oxidative damage (Sun *et al.*, 2022^[45]; Ashikhmin *et al.*, 2023)^[2]. Additionally, carotenoids stabilize the structure of photosynthetic complexes, enhancing the plant's ability to maintain efficient photosynthesis under stress conditions. This protective function is especially critical during high light exposure and water deficit, where the risk of photodamage and oxidative stress is increased. Furthermore, carotenoids contribute to the plant's antioxidative defense by serving as precursors for the synthesis of abscisic acid (ABA), a hormone that plays a significant role in stress signaling and adaptive responses (Sun *et al.*, 2022). ABA mediates various physiological processes, including stomatal closure to reduce water loss during drought and activation of stress-responsive genes that enhance the plant's tolerance to adverse conditions (Ng *et al.*, 2014; Muhammad *et al.*, 2022)^[32]. The biosynthesis and accumulation of carotenoids in chili plants are often upregulated during abiotic stresses, boosting the plant's ability to mitigate oxidative damage and maintain cellular homeostasis (Pola *et al.*, 2020)^[37]. This adaptive mechanism not only preserves the integrity of the photosynthetic apparatus but also supports overall plant growth, development and productivity under challenging environmental conditions. Thus, carotenoids are essential for the resilience and adaptability of chili plants, ensuring better survival and yield in the face of abiotic stresses.

Polyphenols

Polyphenols are essential non-enzymatic antioxidants that play a multifaceted role in defending *C. chinense* against abiotic stress. This group of compounds includes flavonoids, phenolic acids, tannins and lignins, which are synthesized via the phenylpropanoid pathway. Their biosynthesis is often upregulated in response to stress stimuli (Kumar *et al.*, 2023)^[23]. Polyphenols are renowned for their potent antioxidant properties, primarily through their ability to scavenge reactive oxygen species (ROS), thus mitigating oxidative damage to cellular components such as lipids, proteins and nucleic acids. In chili plants under abiotic stress, increased production of polyphenols enhances the antioxidative defense system. For example, flavonoids effectively neutralize ROS, chelate metal ions and inhibit lipid peroxidation (Ullah *et al.*, 2020^[46]; Kejík *et al.*, 2021)^[20]. These actions are crucial for protecting cellular membranes and maintaining cellular integrity. Phenolic acids, another significant class of polyphenols, reduce oxidative stress by stabilizing free radicals and regenerating other antioxidants, such as ascorbate and tocopherol, thus sustaining the antioxidative network (Bešlo *et al.*, 2023)^[5]. Phytochemicals like phenols, quercetin, luteolin and

capsaicinoids have been reported to provide protection against oxidative stress in chili species (Bal *et al.*, 2022)^[4]. Additionally, polyphenols modulate stress-responsive signaling pathways by interacting with plant hormones like abscisic acid (ABA) and salicylic acid (SA), which are crucial for stress perception and signal transduction. This interaction helps activate stress-responsive genes and proteins that enhance the plant's ability to cope with adverse conditions. Furthermore, lignins contribute to the structural fortification of cell walls, making them more resilient to mechanical stress and pathogen invasion, which are often exacerbated under abiotic stress conditions. Overall, the role of polyphenols in chili plants underscores their importance not only in direct antioxidative protection but also in maintaining physiological and structural stability and enhancing the plant's general resilience to abiotic stresses.

Conclusion

The study on Bhut Jolokia (*Capsicum chinense* Jacq.) highlights the critical roles of both enzymatic and non-enzymatic antioxidants in the plant's defense against abiotic stresses such as heat, cold, drought, waterlogging, salinity and heavy metal exposure. Key enzymatic antioxidants, including superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), ascorbate peroxidase (APX) and peroxidase (POD), show significant increases in activity under stress conditions, underscoring their importance in mitigating oxidative damage by neutralizing reactive oxygen species (ROS). Likewise, non-enzymatic antioxidants such as ascorbic acid, glutathione, polyphenols and carotenoids are present in higher concentrations, further protecting the plant by directly scavenging ROS. The varied expression levels of these antioxidants suggest that Bhut Jolokia has developed a robust antioxidant defense system. This system not only preserves metabolic functions but also supports capsaicinoid levels essential for the chili's pungency. Furthermore, the correlation between antioxidant activity and stress tolerance underscores the potential for selecting and breeding more resilient varieties. Thus, this study emphasizes the vital role of both enzymatic and non-enzymatic antioxidants in enhancing Bhut Jolokia's resilience to abiotic stresses.

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