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Research Article

Mitigation Mechanisms for Drought Stress in Trees: A Focus on *Taxus* species

Sankar Som, Beauty Rani Basumatary, Kunal Boro, Bikash Kalita

Department of Botany, Gauhati University, Guwahati 781014, Assam
Corresponding address: S. Som; Email: sankarsom@gauhati.ac.in

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Abstract

The evergreen tree *Taxus* (yew) is widely recognized as a significant medicinal plant in northern hemisphere, particularly due to its anti-cancer property. There are 14 species of *Taxus* distributed across the globe, each of which are noted for its distinct therapeutic value. However, the escalating exploitation of the plant and the changing environment has forced the genus to be categorized as threatened by IUCN. The increasing temperature and drought conditions have resulted in drying of the plant, posing a substantial threat to its survival. Drought represents a major environmental stressor that restricts plant growth and reduces productivity. It disrupts the plants biochemical and physiological processes. Additionally, drought stress enhances the production and accumulation of reactive oxygen species (ROS), which disrupts various cellular processes and leads to oxidative damage of RNA and DNA. To counteract these adverse effects, various ameliorating agents were applied, and their efficacy was evaluated to determine the optimal dose for maximum resilience. This study investigates the impact of water-deficit condition on *Taxus* species and explores the optimal dose of ameliorating agents for mitigating drought-induced damage. Additionally, the research examines the mode of target delivery for these agents, focusing on the most effective methods for ensuring proper uptake and localized action within the plant. The review highlights the importance of both the appropriate concentration of ameliorating agents and the delivery mechanisms in enhancing the drought tolerance of *Taxus*, providing valuable insights for improving plant resilience in water-limited environments.

INTRODUCTION

Taxus sp. is an evergreen tree belonging to a small gymnosperm family Taxaceae. It is one of the taxonomically important groups of plants prevalent in the temperate region of the northern hemisphere, particularly in Asia, Europe and North America. *Taxus* is a slow growing, drought sensitive plant that flourishes well in moist environment with highly acidic peat soil. It exhibits strong tolerance to shade and high humidity. The genus holds medicinal as well as ecological significance. The foliage, twigs, and bark possess an array of potent medicinal properties. The medicinal importance of the plant can be ascribed to its wide array of bioactive constituents, such as essential oils, flavonoids, polysaccharides and terpenoids, etc. However, the genus is also known as the "tree of death" due to the presence of highly toxic alkaloids (taxines) (Wilson, 2001). The pharmacological potential of the genus was unveiled in 1971, when Wani and his colleagues isolated the anti-cancer compound, taxol from bark of *Taxus sp*. This discovery sparked a surge in the exploitation of *Taxus* species for taxol extraction, propelling them into a conservation crisis. This relentless harvesting has caused a dramatic decline in global populations, pushing these invaluable trees toward the brink of extinction (Bhuju and Guachan, 2018). Despite these challenges, *Taxus* continues to capture global attention for its diverse pharmacological attributes, which include not only its renowned anticancer properties but also an array of other therapeutic benefits.

The phytoconstituents of *Taxus* plants have demonstrated potent activities, including antibacterial, anti-aging, anti-Alzheimer's, anti-diabetic, anticancer, antidepressant, anti-leishmaniasis, anti-inflammatory, antinociceptive, anti-allergic, antiviral, antilipase, neuroprotective, respiratory system protective, and hepatoprotective effects, along with the ability to promote melanogenesis (Sarma *et al.*, 2024).

Therefore, *Taxus* stands as a botanical powerhouse, holding untapped potential for future medical breakthroughs. Inspite of its economic and medicinal value, the genus is at the risk of endangerment, as recognized by the International Union for Conservation of Nature. Moreover, rising temperature and drought condition threatens the existence of the plant, making it vulnerable to desiccation. Hence, there is utmost need for implementation of comprehensive strategies directed towards alleviating the adverse impact of drought and promoting the plant's growth under such adverse conditions.

Drought stress

Drought stress stands out as a pivotal force behind tree mortality. It serves as one of the critical abiotic stresses restricting plant's growth and development. Additionally, it has been claimed that it also has an impact on other abiotic stresses. The impact of drought stress varies significantly throughout species and even within species variants, depending on the intensity and length of the drought condition (Barandan *et al.*, 2024). The primary consequence of drought includes reduced rates of cell division and expansion, smaller leaves, stunted stem growth, restricted root expansion, and disrupted stomatal function. Moreover, drought also disrupts plant's water and nutrient relations, ultimately diminishing plant's water use efficiency (WUE). Many other abiotic stress-related plant parameters, such as leaf area index, dry matter accumulation, and net assimilation rates, are also negatively affected by drought. The reduction of plant biomass due to a decrease in turgor pressure in plant tissue is one of the major destructive effects of drought stress (Jyoti and Tanti, 2024). Sarmadi *et al.* (2020) highlighted the detrimental impact of drought stress on *Taxus baccata*. Their research demonstrated that drought conditions induced by osmotic agents in *Taxus baccata* callus cultures led to significant tissue browning, an increase in dry weight, and reductions in fresh weight, relative water content, cell growth, and viability. These effects were attributed to an oxidative response driven by heightened levels of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2).

Furthermore, studies on yew (*T. baccata*) seedlings (Barandan *et al.*, 2024) highlighted that drought stress led to a significant decrease in physiological processes, including photosynthesis and transpiration. During water deficit conditions, plants undergo a reduction in water potential and turgor pressure, resulting in stomatal closure, membrane damage, and protein degradation. These changes eventually lead to decreased rates of photosynthesis and transpiration.

Likewise, different research on *Quercus brantii* (Oak tree) seedlings subjected to dryness and charcoal canker pathogens (*Biscogniauxia mediterranea* and *Obolarina persica*) resulted in changed morphological and physiological parameters of the seedling. Morphologically, a significant decline in plant diameter and height growth was noted. Furthermore, a substantial reduction in photosynthetic rate, photochemical effectiveness of photosystem II, transpiration, and stomatal conductance was also observed (Ghanbary *et al.*, 2017). Therefore, drought stress compromised the physiological functions of oak trees and markedly diminished their ability to defend against pathogenic threats.

Drought and other environmental stresses results in the excessive production of reactive oxygen species (ROS) such as superoxide (O_2^-), singlet oxygen ($^1O_2$), hydroxyl radicals (OH), and hydrogen peroxide (H_2O_2) which ultimately lead to oxidative stress. This oxidative stress activates signaling molecules that stimulate the production of secondary metabolites (SMs) (Roy *et al.*, 2024). Numerous studies have reported an increase in SMs as a response to drought-induced oxidative stress, including in species such as *Scrophularia ningpoensis* (Wang *et al.*, 2010), *Taxus baccata* (Sarmadi *et al.*, 2020*)*, and *Plantago major* (Ghorbanpour *et al.*, 2018). When avoidance strategies are insufficient, plants resort to drought tolerance mechanisms aimed at safeguarding tissues from damage. These involved inducing protective components for cellular dehydration, facilitating osmotic adjustment, and detoxifying reactive oxygen species (ROS). Notably, while both gymnosperms and angiosperms share general principles in responding to drought stress, gymnosperms are typically more drought-resistant due to differences in xylem structure and stomatal behaviour. Conversely, angiosperms exhibit more intricate anatomical adaptations in response to drought (Moran *et al.*, 2017).

The Genesis, Scavenging mechanism and Essential Roles of Reactive Oxygen Species in Drought stress

The survival and biological functions of aerobic organisms depend heavily on oxygen. During its metabolic reduction, if oxygen is not fully reduced, a range of substances with high reactivity derivatives known as reactive oxygen species (ROS) are produced. These species include hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), hydroxyl radicals (·OH), singlet oxygen ($^1O_2$), and various organic oxygen radicals (ROO·, RO·) (Mignolet *et al.*, 2016). Normally, ROS production in plants is counterbalanced

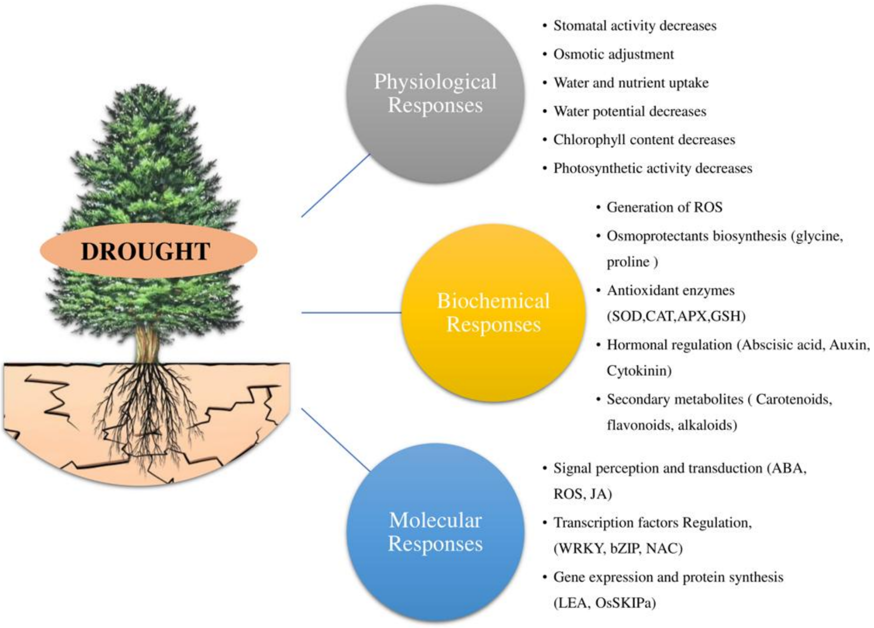

Fig. 1. Different types of physiological, biochemical, and molecular responses of *Taxus* under drought stress conditions.

by their scavenging systems. However, drought conditions disrupt this equilibrium, increasing ROS production and resulting in oxidative stress. When the ROS levels surpass the system's scavenging capacity, plants experience oxidative damage, which can manifest in DNA damage, protein denaturation, lipid peroxidation of cell membranes and inhibited photosynthesis.

In order to properly regulate ROS levels, plants have developed both enzymatic and non-enzymatic defense mechanisms. ROS are generated in plants through various metabolic processes, especially within mitochondria, chloroplasts, and peroxisomes, which are the key areas known for significant oxidative activity and strong electron transfer. Chloroplasts are recognized as the primary sites for ROS generation in plants. Under drought, the proficiency of light energy assimilation and carbon dioxide fixation decreases, reducing the distribution of $NADP^+$ and increasing the rate of electron transfer to oxygen, thus forming O_2^-. This initiates a series of outcomes producing a larger quantity of ROS. When electrons leak during electron transport in the respiratory chain, mitochondria also play a role in the generation of ROS (Roy *et al.*, 2024). Additionally, the plasma membrane and plasmids, featuring enzymes like NADPH oxidase, amine oxidases, oxalate oxidases and cell wall peroxidases, are significant ROS sources. Furthermore, enzymes in the endoplasmic reticulum, such as cyclooxygenases, peroxidases, and lipoxygenases, generate ROS through a variety of chemical reactions.

According to Sarmadi *et al.* (2020) research, applying osmotic agents to simulate water-deficit stress in *T. baccata* callus cultures led to increased levels of MDA and H_2O_2, indicating the induction of oxidative stress. The rise in ROS and free radicals, such as H_2O_2, is linked to tissue and cell damage, which resulted in browning of the calli and cell death at higher treatment concentrations. Furthermore, the detrimental effects of H_2O_2 were attributed to its capacity to oxidize biochemical macromolecules due to its rapid generation and its involvement in cell wall hardening. This suggested that H_2O_2 played a crucial role in inhibiting cell growth. Additionally, they found a strong positive association between the production of H_2O_2, MDA levels, and callus browning, alongside a notable negative correlation between H_2O_2 concentrations, relative growth rate (RGR), and callus viability during stress treatments.

Strategies for Plant Protection against Oxidative Stress

To safeguard plants from the damaging impacts of ROS, they possess intrinsic antioxidant protection systems composed of enzymatic and non-enzymatic antioxidants. This dual system functions synergistically to maintain a dynamic equilibrium between ROS production and reduction, consequently stress damage is decreased and plants are better equipped to withstand drought conditions. Non-enzymatic scavengers in plants predominantly include reduced glutathione (GSH), ascorbate, vitamin E, carotenoids, flavonoids and mannitol, that either clearly neutralize ROS or act as substrates for enzymes in the process of scavenging ROS. Additionally, small molecules like vitamins also play a crucial role in preventing lipid peroxidation and scavenging oxygen radicals, constituting a crucial part of the plant's defense against oxidative stress (Jyoti and Tanti, 2024). The enzymes glutathione reductase (GR), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) comprise the enzymatic portion of the antioxidant defense in plants. SOD is essential for the plant's main defense against ROS because it catalyses the transformation of superoxide radicals (O^{2-}) into H_2O_2. CAT and POD primarily facilitate the ejection of H_2O_2 within the cells. MDHAR, DHAR, GR and APX are vital for further reducing H_2O_2 levels, representing a secondary defense line against ROS. As a tertiary line of defense in the ROS scavenging mechanism, GPX targets the oxidative degradation of lipids and alkyl peroxides (Sarmadi *et al.*, 2020)

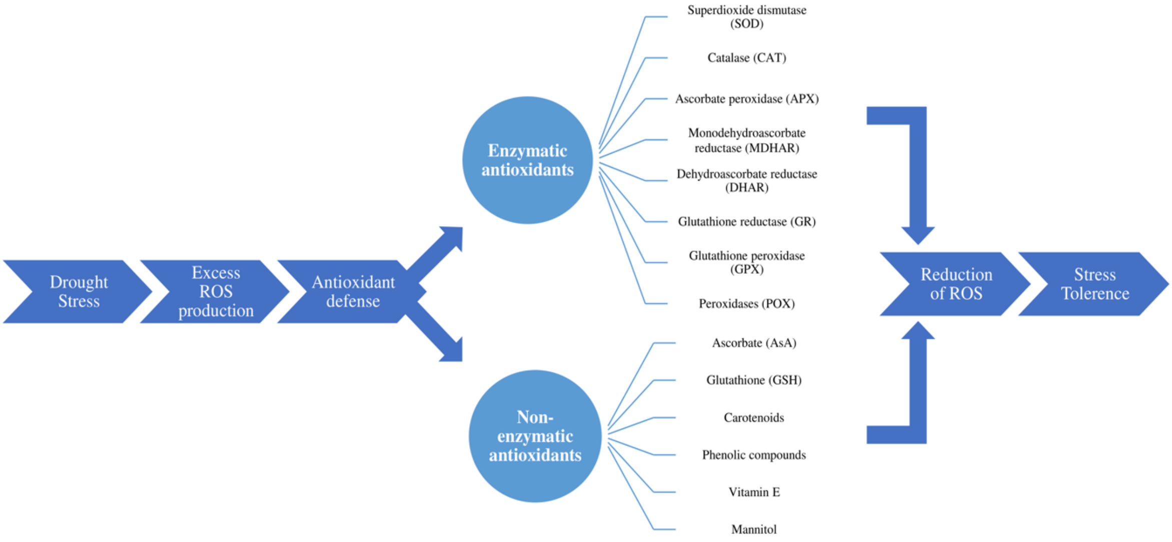

Fig. 2. Antioxidant Defense Mechanism Under Drought Stress. Excess ROS generation under drought stress causes the antioxidant defense systems to be triggered in order to counteract the ROS produced. It emphasizes the functions of enzymatic antioxidants (SOD, CAT, and APX) and non-enzymatic antioxidants (including glutathione, ascorbate and carotenoids) in mitigating ROS levels, thereby enhancing stress tolerance in plants.

Non-enzymatic antioxidants

Ascorbic acid

Ascorbic acid, commonly referred to as vitamin C, is a well-researched antioxidant found abundantly across various organelles and plant cell types. Ascorbate is usually found mostly in its reduced form (AsA), making upto 90% of its total pool, with intracellular concentrations that range from 20–300 mM in the chloroplast stroma to 20 mM in the cytoplasm. The mitochondria create ascorbate, which is then transferred to other parts of the cell either via facilitated diffusion or a proton-electrochemical gradient (Horemans *et al.*, 2000). AsA is essential for several physiological processes, including plant growth, metabolic regulation and differentiation. It is essential to a plant's defense mechanism by primarily protecting it against oxidative damage from H_2O_2 and other reactive oxygen derivatives, acting as a reductant and neutralizing various free radicals. AsA is utilized by APX in the ascorbate-glutathione cycle, to convert H_2O_2 into water, simultaneously producing MDA, a short-lived radical.

The application of AsA in a study revealed its significant role in regulating oxidative stress and taxol production in *Taxus*. Pretreatment with AsA effectively reduced oxidative stress, leading to enhanced taxol production compared to the control. This suggested that AsA not only mitigates oxidative stress but also plays a crucial role in promoting taxol synthesis (Yu *et al.*, 2002). The findings imply that AsA may influence the regulatory mechanisms involved in secondary metabolite production, potentially involving hydrogen peroxide (H_2O_2) as an intermediate signaling molecule in the synthesis of taxol.

Glutathione

Glutathione, a tripeptide made of γ-glutamylcysteinylglycine, is found in many cellular organelles, including the chloroplasts, cytosol, endoplasmic reticulum, mitochondria and vacuoles. In the majority of plant cells, it is the main source of non-protein thiols. Because glutathione's thiol group is so reactive, it is necessary for a number of metabolic functions in all life forms. This reactivity is essential for interacting with particular electrophiles and creating mercaptide bonds with metals because of the thiol group's nucleophilic characteristics. As an antioxidant, glutathione participates in multiple ways.

In the ascorbate-glutathione cycle, it is essential, where it enzymatically and non-enzymatically produces the reduced form of dehydroascorbate (DHA), while being oxidized to glutathione disulfide (GSSG). Glutathione reductase utilizes NADPH as a reducing agent to aid in the conversion back from GSSG to GSH. The cysteine residue in glutathione is essential for its potent reductive action, which allows it to react with other reactive oxygen species such as singlet oxygen, superoxide radicals, and hydroxyl radicals as well as neutralise harmful hydrogen peroxide. Its ability to regenerate ascorbic acid, which sustains the ascorbate-glutathione cycle, which is essential for preserving cellular redox equilibrium, highlights its basic function in antioxidative defence (Millar *et al.*, 2003).

In *Taxus chinensis*, glutathione (GSH) deficiency is essential for the stress-induced activation of glucose-6-phosphate dehydrogenase (G6PDH). Fungal elicitors from *Aspergillus niger* led to a significant reduction in GSH levels, which in turn activated G6PDH. Interestingly, this activation was independent of catalase, as evidenced by the ineffectiveness of catalase inhibitors, suggesting that G6PDH initiation is specifically linked to GSH depletion. Additionally, the GSH precursor N-acetylcysteine (NAC) suppresses G6PDH activity, underscores the inverse relationship between GSH levels and G6PDH activation. This highlighted the critical task of GSH in regulating the oxidative stress response in *Taxus chinensis* (Yu *et al.*, 2004).

Carotenoids

Carotenoids are pigments found naturally in plants and microbes, with over 600 kinds known. The antioxidative capabilities of carotenoids are largely attributed to their capacity to stabilize unpaired electrons, facilitated by their conjugated double-bonded structures. This structural feature is key to β-carotene's effectiveness in quenching singlet oxygen without breaking down and in reacting with various free radicals like ($^{\bullet}OH$, $ROO^{\bullet}$), and superoxide radicals ($O_2^{\bullet-}$). When found in large quantities, carotenoids are also capable of shielding lipids from oxidative damage. It was seen that in cultivated species of *Taxus cuspidate*, the downregulation of carotenoids contributed to the lighter and uneven coloration of leaves and fruits. This reduction contrasted with the wild species, which maintain higher carotenoid levels that contribute to their dark green leaves, increasing photosynthetic efficiency and enhancing their adaptability to colder environments (Wang and Zhang, 2024).

Enzymatic Antioxidants

Superoxide dismutase

Superoxide dismutase is a metalloenzyme that transforms superoxide radicals ($O_2^{-\bullet}$) into hydrogen peroxide (H_2O_2). Initially, its presence was identified in maize, where six distinct genetic and biochemical isoforms were observed. The metal ion in the active site of SODs determines their classification: iron (FeSOD), manganese (MnSOD), or copper and zinc (Cu/Zn SOD). Additionally, a form comprising nickel (NiSOD) was identified in *Streptomyces*. MnSOD is present in the peroxisomes and mitochondrial matrix, while Cu/Zn SOD is usually found in the chloroplast and cytosol of plant cells. The plant's reaction to oxidative stress brought on by external stimuli is closely linked to the stimulation of SOD activity. For instance, Yang *et al.* (2008) demonstrated that in dragon spruce (*Picea asperata*) seedlings, the activity of SOD dramatically enhanced when drought and strong light were coupled. Sarmadi *et al.* (2020) investigated the activity of superoxide dismutase (SOD) in *Taxus baccata* under drought conditions, where they used agents like mannitol and sorbitol to induce drought stress. Their findings revealed that under moderate drought stress, SOD activity rose, indicating an adaptive mechanism to enhance oxidative defense. However, at higher osmotic concentrations, SOD activity exhibited a significant decrease. This decline suggests that the antioxidant capacity of *T. baccata* may become limited under severe stress conditions, highlighting the complex dynamics of antioxidant responses in this species.

Catalases

Catalases are enzymes that include tetrameric heme, primarily located in peroxisomes, that catalyse the transformation of two H_2O_2 molecules into water and O_2. Catalases can oxidise substrates such as ethanol, methanol, formic acid and formaldehyde, or they can dismutate H_2O_2 directly. It was shown that drought stress has a major impact on *Taxus baccata* calli's CAT activity. CAT activity was increased under moderate osmotic stress, reflecting the plant's adaptive response to enhance hydrogen peroxide (H_2O_2) detoxification. However, they found that at higher osmotic concentrations, CAT activity decreased, indicating a limitation in the antioxidant defense mechanism. This decline correlated with reduced cell viability and increased oxidative damage, suggesting that CAT was less effective in mitigating ROS in severe stress situations (Sarmadi *et al.*, 2020).

Glutathione peroxidases

Glutathione peroxidase is a class of isozymes that catalyse the conversion of hazardous hydroperoxides and hydrogen peroxide (H_2O_2) to their respective alcohols. In addition to neutralizing H_2O_2, GPXs also play a role in detoxifying lipid peroxidation by-products that are generated by ROS activity. Nonselenium-dependent phospholipid hydroperoxide GPX (PHGPX), selenium-dependent GPX and glutathione transferases displaying GPX activity (GST-GPX) are the three forms of GPXs found in plants.

Due to the kind of selenium bonding at their active sites and their catalytic processes, GPX and GST have different subunit compositions. It has been demonstrated that *E. coli*'s resistance to singlet oxygen is enhanced by the overexpression of the glutathione peroxidase or glutathione S-transferase genes (Ledford *et al.,* 2007). In *Taxus baccata* calli, glutathione peroxidase (GPX) activity increased with rising glucose concentrations, reaching its peak at 2%. This activity was further enhanced by pretreatment with salicylic acid (SA) across all glucose levels. At 2% glucose, GPX activity was 1.6 times higher compared to the control. However, at 3% glucose, GPX activity was shown to decrease, likely indicating a reduced ability of the calli to manage oxidative stress at higher glucose levels. Despite this decline, the cells compensated with an increase in catalase (CAT) activity, suggesting an adaptive response to mitigate oxidative damage under higher stress conditions (Sarmadi *et al.,* 2018).

Ascorbate peroxidase

Ascorbate peroxidase (APX) plays a key role in eliminating hydrogen peroxide (H_2O_2) through both the water–water and ascorbate–glutathione cycles, utilizing ascorbic acid (AsA) as the electron donor. By converting H_2O_2 into water, APXs are crucial components of the plant antioxidant system. APX displays a higher affinity for H_2O_2 compared to catalase (CAT) and peroxidase (POD), suggesting it plays a critical role in regulating ROS stress and signaling. APX1 is particularly sensitive to light and oxidative stress.

The study by Sarmadi *et al.* (2020) found that APX activity in *Taxus baccata* calli increased under moderate drought stress, indicating an enhanced antioxidative response. However, at higher levels of osmotic stress (e.g., 4% sorbitol and mannitol, 8% sucrose), APX activity declined, suggesting that the enzyme becomes less effective under severe stress conditions, leading to reduced cell viability and increased oxidative damage.

Glutathione reductase

Glutathione reductase has been extensively purified from various plant tissues and is a highly conserved enzyme. It plays a crucial role in catalyzing the NADPH-dependent reduction of the disulfide bond in glutathione disulfide (GSSG), thereby maintaining the reduced form of glutathione (GSH). GR is predominantly localized in the chloroplast stroma but can also be found in mitochondria, the cytosol, and peroxisomes. The role of glutathione and GR in hydrogen peroxide (H_2O_2) scavenging is well established through the Halliwell–Asada enzyme cycle. GR catalyzes the rate-limiting final step in the ascorbate–glutathione pathway. Enhanced GR activity may increase the NADP+/NADPH ratio, ensuring a sufficient supply of NADP+ to accept electrons from the photosynthetic electron transport chain. This electron flow regulation could reduce electron leakage to oxygen, thereby minimizing the formation of superoxide radicals. GR plays a critical role in maintaining a high GSH/GSSG ratio, which is essential for the regeneration of ascorbate and the activation of several chloroplastic enzymes involved in CO_2 fixation (Sudhakar *et al.,* 2001). Increased GR activity in plants has been associated with elevated GSH levels, which enhances plant’s tolerance to stress. The activity of glutathione reductase (GR) plays a crucial role in the antioxidant defense mechanisms of *Taxus x media* during winter. Increased levels of GR, along with glutathione and the lipid-soluble antioxidant α-tocopherol, indicate a robust response to drought stress in cold conditions. Despite the lack of upregulation of the water-water cycle in winter, these components are essential for managing reactive oxygen species (ROS). This suggests that while the superoxide-scavenging water-water cycle may not be operational during winter months, GR and other antioxidants are critical for maintaining plant health under drought stress (Verhoeven *et al.,* 2005).

Role of Hormones in Mediating Abiotic Stress Responses

Plant hormones are pivotal biological molecules that govern plant growth and development from seed germination to fruit formation and dispersion of seed. These compounds therefore regulates plants adaptive response to environmental conditions. The hormonal regulation of development during abiotic stress entails a complicated signaling cascade, where stress perception is intricately linked to subsequent gene expression. Extensive research has demonstrated that ROS mediated signaling network and hormonal responses interact, enabling plants to adapt their performance to both biotic and abiotic challenges (Tognetti *et al.,* 2012). Consequently, significant insights into how these plant hormones influence drought-induced oxidative stress have been discussed below.

Abscisic acid-mediated signalling during abiotic stress

Osmotic stress signal transduction is regulated through both ABA-dependent and ABA-independent pathways (Agarwal and Jha, 2010). Additionally, secondary messengers such as calcium ions (Ca^{2+}), reactive oxygen species (ROS), and nitric oxide (NO) are key contributors to these signaling pathways, playing critical role in physiological responses like stomatal closure. Abiotic stress triggers an accumulation of ROS, including singlet oxygen ($^1O_2$), superoxide anion (O_2^-), hydroxyl radical ($HO\cdot$), and hydrogen peroxide (H_2O_2), which act as immediate signaling molecules (Roychoudhury *et al.,* 2013).

The ABA-independent signaling pathway is regulated by various transcription factor (TF) families, including the dehydration-responsive element-binding (DREB) proteins and C-repeat binding factors (CBFs).Osmotic stress activates DREB1/CBF proteins, which bind to DRE/CRT motifs, triggering the expression of stress-responsive genes without ABA involvement. DREB2 also plays a key role in osmotic stress signaling, engaging DRE/CRT elements to control gene expression without ABA influence, as detailed by Maruyama *et al.* (2004). In addition to DREB proteins, NAC domain proteins regulate stress-induced genes in an ABA-independent manner. Zinc finger homeodomain (ZFHD) proteins also mediate stress responses independently of ABA, except ZFHD1, which is ABA-responsive (Tran *et al*., 2007).

ABA-mediated signalling is initiated when ABA interacts with the PYR/PYL/RCAR receptors, forming a ternary complex with PP2C This interaction leads to the activation of SnRK2 proteins through phosphorylation, which further phosphorylates AREB/ARFs. Protein kinases play a pivotal role in the phosphorylation of downstream targets in ABA-dependent pathways, triggering a series of transcriptional events (Ma *et al.*, 2009).While the role of SnRKs is well-characterized in *Arabidopsis*, recent studies in wheat have identified additional SnRK2 homologs involved in ABA-mediated responses to abiotic stress. The discovery and analysis of TaSnRK2.3, TaSnRK2.4, and TaSnRK2.8 indicated that these proteins are crucial components in stress signaling pathways. The overexpression of TaSnRK2.3 and TaSnRK2.8 in *Arabidopsis* led to enhanced tolerance to drought, salinity, and cold stress, which was associated with an increased accumulation of stress-related metabolites like proline, as well as higher expression levels of both ABA-dependent and independent stress-responsive genes. In TaSnRK2.8 overexpression lines, an upregulation of ABA biosynthetic genes (ABA1, ABA2) and key signaling components (ABI3, ABI4, ABI5), alongside ABA-independent genes (CBF1, CBF2, CBF3), were observed, suggesting that stress tolerance involves a complex interplay of genetic and physiological responses (Zhang *et al.*, 2010).

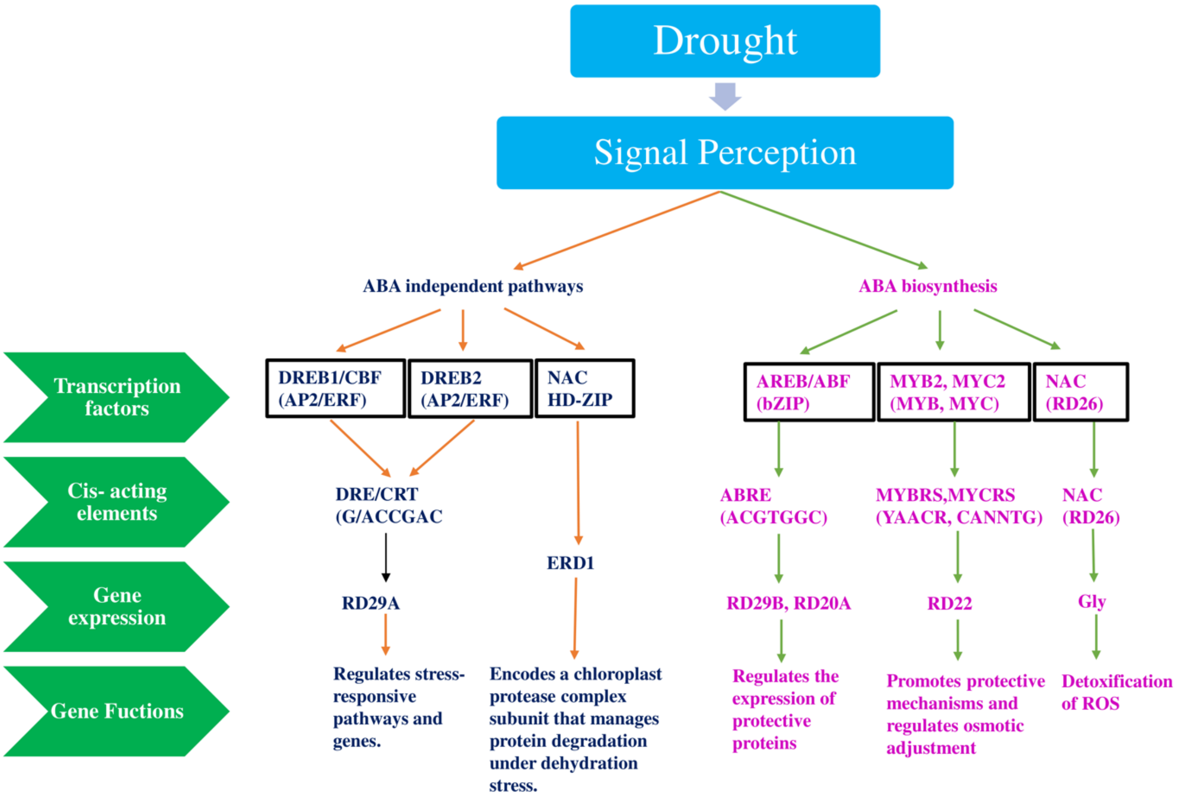

Fig. 3. Transcriptional Regulatory Networks in Drought Stress Responses. It involves at least six key signal transduction pathways: three ABA-independent and three ABA-dependent. In ABA-independent pathways, DRE regulates genes under drought and other abiotic stress, with DREB1/CBFs and DREB2 acting as its transcription factors. A separate pathway is also involved that includes NAC and HD-ZIP transcription factors controlling ERD1 expression. In ABA-dependent pathways, ABRE regulates gene expression via AREB/ABFs transcription factors. MYC2 and NAC transcription factors participate in cross-talk between abiotic and wound stress. MYB2 and MYC2 control ABA-induced RD22 expression, while RD26 (NAC family) responds to the excess ROS produced.

The dehydration-responsive element-binding factors (DBFs) are categorized within the AP2/ERF family. Enhanced expression of TaAIDFa in *Arabidopsis* was shown to elevate the transcript levels of RD29A, COR15A, and ERD10, thereby improving osmotic tolerance. WDREB2, a member of the AP2/ERF transcription factor family and a homolog to DREB2, is primarily triggered by drought stress and to some extent by the application of exogenous ABA. This induction of WDREB2 results in the upregulation of WRAB19 transcript levels, implying that it might directly influence COR/LEA genes. Moreover, the alternative splicing of WDREB2 varies according to the stress encountered, indicating a potential ABA-dependent regulatory pathway for drought stress (Egawa *et al.*, 2006).

Salicylic acid

Salicylic acid (SA) is a versatile phytohormone that influences how plant responses to wide ranges of biotic and abiotic stresses, including drought. It is an essential signaling molecule that is known to play a critical role in modulating physiological and biochemical pathways that enhance drought tolerance through regulation of gene expression, antioxidant defense, osmotic balance, and stomatal conductance. SA's defense mechanisms include tightening the stomatal aperture to limit water loss, and reprogramming the expression of drought-responsive genes (Damalas and Koutroubas, 2021). Furthermore, it promotes the accumulation of osmolytes, such as total soluble sugars and proline, which helps maintain plant water status. It also enhances the activity of antioxidant enzymes, including peroxidase, superoxide dismutase, and catalase. This boost in antioxidant enzyme activity reduces lipid peroxidation due to ROS activity, decreases lipoxygenase activity, and lowers H_2O_2 production. Additionally, it preserves chlorophyll content, thereby protecting the photosynthetic machinery. Consequently, plants treated with SA showed less oxidative damage, indicated by lower levels of MDA content and relative electrolyte conductivity (REC) (Sarmadi *et al.*, 2018). Although low concentrations of SA are generally effective in enhancing drought tolerance, higher concentrations may have little to no effect or could even be harmful. Numerous studies have demonstrated that foliar application of SA could alleviate the negative impact of drought stress in variety of plants, such as rice, maize, wheat, sunflower, beans, cucumber, basil, cumin etc. and several other plants (Damalas and Koutroubas, 2021). Recent advances in understanding SA-mediated drought tolerance and its underlying metabolic pathways are reviewed to shed light on its potential for enhancing crop tolerance to drought.

Furthermore, Chini *et al.* (2004) emphasized that salicylic acid (SA) is essential in conferring drought tolerance by modulating the expression of drought-responsive genes, such as ADR1, which is involved in enhanced disease and drought tolerance. SA's influence is further amplified through its crosstalk with other plant hormones, especially abscisic acid (ABA), to coordinate complex responses under water-deficit conditions. This hormonal interaction enables plants to fine-tune osmotic balance and activate a suite of stress-responsive proteins, ultimately boosting resilience against drought stress.

Melatonin

Melatonin (N-acetyl-5-methoxytryptamine) is a multifunctional indoleamine compound found in plants. It was primarily identified in the pineal gland of animals and later found in a variety of plants, where it has a role as a complex signaling molecule that modulates growth, development, and responses to environmental stressors. These molecules significantly influence a variety of physiological processes and play a critical role in enhancing resilience against diverse abiotic stresses, particularly drought (Arnao and Hernández-Ruiz, 2019). In the context of drought, melatonin acts as an intrinsic regulator, attenuating the adverse effects of stress and promoting plant survival.

Melatonin has shown to counteract oxidative stress by enhancing the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). Melatonin's direct ROS scavenging ability, along with its upregulation of antioxidant enzymes, results in a reduction of malondialdehyde (MDA) levels-a common indicator of lipid peroxidation under stress conditions (Imran *et al.*, 2021). Transcriptomic studies in plants treated with melatonin have revealed differential expression of antioxidant genes such as *APX1* (ascorbate peroxidase 1), *CAT2* (catalase 2), and *SOD1* (superoxide dismutase 1) (Munir *et al.*, 2024). This antioxidant defense is crucial for maintaining membrane stability and preventing cellular damage during drought.

Melatonin also interacts with several plant hormones, including abscisic acid (ABA), a vital regulator of drought stress responses. During drought, ABA triggers stomatal closure to reduce water loss through transpiration. Additionally, melatonin enhances the accumulation of important osmoprotectants like proline, soluble sugars, and polyamines. These substances are essential for stabilizing proteins and cellular membranes, reducing osmotic stress, and maintaining cell turgor, thus protecting physiological functions and supporting plant survival under drought stress (Arnao and Hernández-Ruiz, 2019).

Spermidine

Spermidine, a class of polycationic polyamine plays significant role in plant growth, development, and defense mechanism against various stress conditions. It is involved in various physiological and biochemical processes that enable plants to mitigate the detrimental effects of abiotic stresses, such as drought. Studies have revealed that spermidine (spd) treatment reduced oxidative damage by decreasing malondialdehyde content, electrolyte leakage, and hydrogen peroxide levels, while preserving photosynthetic performance and relative water content. Additionally, spermidine upregulated polyamine biosynthetic genes (VfADC, VfSAMDC, and VfSPDS) and several drought-responsive genes involved in antioxidant defense, stress signaling, and osmotic regulation. Furthermore, spd pretreatment altered the accumulation of growth-related hormones, resulting in reduced indole-3-acetic acid (IAA) and gibberellin A3 (GA3) levels after prolonged drought exposure (Li *et al.*, 2015). These findings suggest that spermidine is a promising agent for enhancing drought resilience in plants.

Notably, studies have revealed that pre-treatment of wheat seeds in spermidine can alleviate the inhibition of seed germination caused by drought stress (Liu *et al.*, 2016). Moreover, exogenous spermidine application helped to maintain antioxidant enzyme activities in Welsh onion (*Allium fistulosum*), thereby enhancing the radical scavenging system and curbing oxidative damage (Yiu *et al.*, 2009).

Exogenous Application of Bioactive Agents for Alleviating Drought-Induced Stress in *Taxus* species

In *Taxus* species, several plant hormones play critical role in mediating responses to abiotic stress conditions such as drought, salinity, and extreme temperatures. Abscisic acid (ABA) is a primary hormone involved in regulating water use efficiency and promoting stomatal closure during drought stress, thereby reducing water loss. Additionally, salicylic acid (SA) is known to enhance stress tolerance by activating defense pathways that mitigate oxidative damage. Melatonin has also been identified as a critical player in enhancing stress resilience in *Taxus*, as it acts as an antioxidant and modulates hormone interactions (Zhang *et al.*, 2015). Furthermore, polyamines such as spermidine is also found to modulate plant responses to various abiotic stresses, including drought, osmotic stress, salinity, heat, and chilling. They achieve this by directly interacting with membrane phospholipids, neutralizing harmful radicals, balancing osmotic condition, and maintaining ionic ratios in cells (Liu *et al.*, 2016).

Evidences showed that pre-treatment of *Taxus baccata* calli with SA led to the increase in antioxidant enzyme activities, including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), which suggested that SA strengthened the plant's antioxidative defense system, effectively reducing the accumulation of malondialdehyde (MDA), a marker of lipid peroxidation and membrane damage. Consequently, SA-treated plants exhibited a lower level of oxidative damage, as evidenced by reduced MDA content and relative electrolyte conductivity (REC) (Sarmadi *et al.*, 2018). In the study performed by Shen *et al.* (2014) in *Torreya grandis*, it was observed that the application of SA alleviated the drought-induced growth inhibition in *T. grandis* seedlings by promoting root and shoot development and enhancing physiological traits such as relative water content (RWC), photosynthetic rate, and chlorophyll content. SA-treated plants exhibited a marked improvement in water retention capacity and proline accumulation, which is essential for osmotic adjustment under water deficit conditions. Additionally, SA application helped in maintaining higher levels of chlorophyll and photosynthetic pigments, suggesting its role in enhancing photosynthetic efficiency under drought stress.

The exogenous application of melatonin in *Taxus baccata* (Shahmohammadi *et al.*, 2024) elicited distinct biochemical responses in plants, leading to a marked increase in both shoot and root biomass. Under mild drought conditions, melatonin treatment significantly enhanced physiological traits such as relative water content (RWC) and chlorophyll concentration, indicating its role in maintaining cellular hydration and promoting photosynthetic efficiency. These results suggest that melatonin application not only mitigates the adverse effects of drought but also stimulates overall plant growth and productivity, even under suboptimal water availability. In *Taxus chinensis*, supplementary application of melatonin has been found to regulate ABA biosynthesis and signaling pathways, thereby effectively fine-tuning the balance between growth and stress response (Zhang *et al.*, 2015).

Further research by Wen *et al.* (2023) demonstrated that post-drought rehydration by application of spermidine could reverse the adverse effects of drought in *Taxus chinensis* var. *mairei* underscoring its potential as a post-stress therapeutic agent to restore plant vitality.

These findings highlight the potential of these agents to enhance drought resilience, paving the way for more resilient cultivation of *Taxus* under adverse environmental conditions. The results of the study also provide insights for the conservation and recovery of other species of *Taxus* against environmental challenges. Despite these promising results, research is limited, and further studies are needed to elucidate the mechanisms and optimize the use of these agents in *Taxus* species under drought conditions.

Modern Spraying Technologies for Targeted Stress Management in Trees

Extensive research to enhance pesticide application efficiency and minimize off-target drift has resulted in more accurate and efficient canopy sprayer designs to mitigate various stresses in trees. Initially centered around radial air-blast sprayers, modern alternatives such as multi-row curtain sprayers, recycling tunnel sprayers, tower sprayers, and electrostatic sprayers have been developed for specific cropping systems.These innovations align with advances in pesticide formulations, enabling targeted stress management at lower doses. Newer sprayers reduce drift by 40% - 90%, use 20% - 80% less volume, and improve spray deposition, providing more effective coverage for trees experiencing stress or nutrient deficiencies (Kasner *et al.*, 2020).

Electrostatic Sprayers for Improved Spray Accuracy

Electrostatic sprayers enhance the precision of spray applications by electrically charging the droplets through induction. This process generates a high-voltage field near the nozzle, giving the droplets a negative charge, which makes them attracted to positively charged crops. In orchards, these sprayers provide 33% - 74% better deposition with significantly lower spray volumes than radial air-blast sprayers, reducing off-target losses and improving efficiency. Lower volumes also increase the area covered per tank, minimizing refills and reducing costs. While electrostatic sprayers offer superior coverage, they produce fine droplets (30-60 µm) that can drift easily, so they are best used in calm conditions (Neto *et al.*, 2015). However, their high-voltage components require insulation, leading to higher maintenance and operational costs.

Machine-Vision Controlled Sprayers

Machine-vision controlled sprayers enhance precision by detecting plant's presence and modulating spray release, thus reducing unnecessary applications in empty spaces or gaps within plant canopies. These systems are especially advantageous in horticultural crops like orchards, nurseries, and vineyards, where plant structures vary significantly and pesticide use is high (Steward *et al.*, 2002).

Infrared Sensors

Infrared sensors emit and detect infrared radiation reflected from plant surfaces to identify plant's presence. They are cost-effective and straightforward to implement, making them suitable for basic on/off sprayers. However, these sensors struggle with accurately detecting fine plant structures and are less reliable in low-light conditions, such as during dawn or dusk when spraying is common (Zhang *et al.*, 2018). Typically, infrared sensors are used in herbicide applications, activating or deactivating the spray based on plant detection, but they do not provide precise control over spray volume.

Ultrasonic Sensors

Ultrasonic sensors function by emitting high-frequency sound waves (5-20 Hz) and measuring the time it takes for the waves to return after hitting plant surfaces. This data helps calculate the distance and volume of the plant canopy. When arranged in arrays, ultrasonic sensors can estimate canopy volumes with accuracy similar to manual measurements, making them particularly useful for larger trees and dense canopies. These sensors operate on an on/off mechanism, lacking fine modulation of spray volume, and can be affected by external noise and signals, which may lead to detection errors. Ultrasonic sensors are often integrated with radial or tower sprayers for improved efficiency (Giles *et al.*, 2011).

LiDAR Sensors

In drought Management for Specialty Crops LiDAR (Light Detection and Ranging) sensors are increasingly utilized in managing drought conditions for specialty crops. These sensors emit light beams in a two-dimensional plane around the sensor using a rotating mirror, providing detailed data on canopy structure and health. This information is vital for precision agriculture, particularly in optimizing water use during drought. For instance, LiDAR-controlled sprayers can adjust water and nutrient applications based on the actual foliage volume, ensuring that plants receive the right amount of moisture without waste. In practical applications, studies have shown that using LiDAR technology can reduce water usage significantly by 80% for crops like apples, peaches, and blueberries compared to traditional constant-rate irrigation methods (Chen *et al.*, 2019). This not only conserves water but also enhances plant health and resilience under drought stress. Additionally, LiDAR systems improve pest and disease control while minimizing water runoff and evaporation losses, which are critical during dry periods. For a typical 16.2-hectare apple orchard, the investment in a LiDAR-controlled irrigation system can be recouped quickly through water savings alone. However, the technology is still relatively new and may be limited in availability, and its high cost can complicate maintenance for users.

Trees

The advancement of precision agriculture has significantly improved the way we manage crops, including ornamental trees. One critical area where precision can be highly beneficial is the estimation of agrochemical requirements, particularly when it comes to sustainable management practices. The drone technology offers several advantages for canopy measurement, such as rapid data collection, high accuracy, and the ability to access areas that are difficult to measure manually. Drones can automate the process of collecting tree canopy data, reducing labor costs, and enhancing precision. By capturing high-resolution images of the tree canopy, the RGB sensor can generate detailed representations of tree structure, which can be analyzed to determine essential canopy attributes. These attributes are crucial for calculating

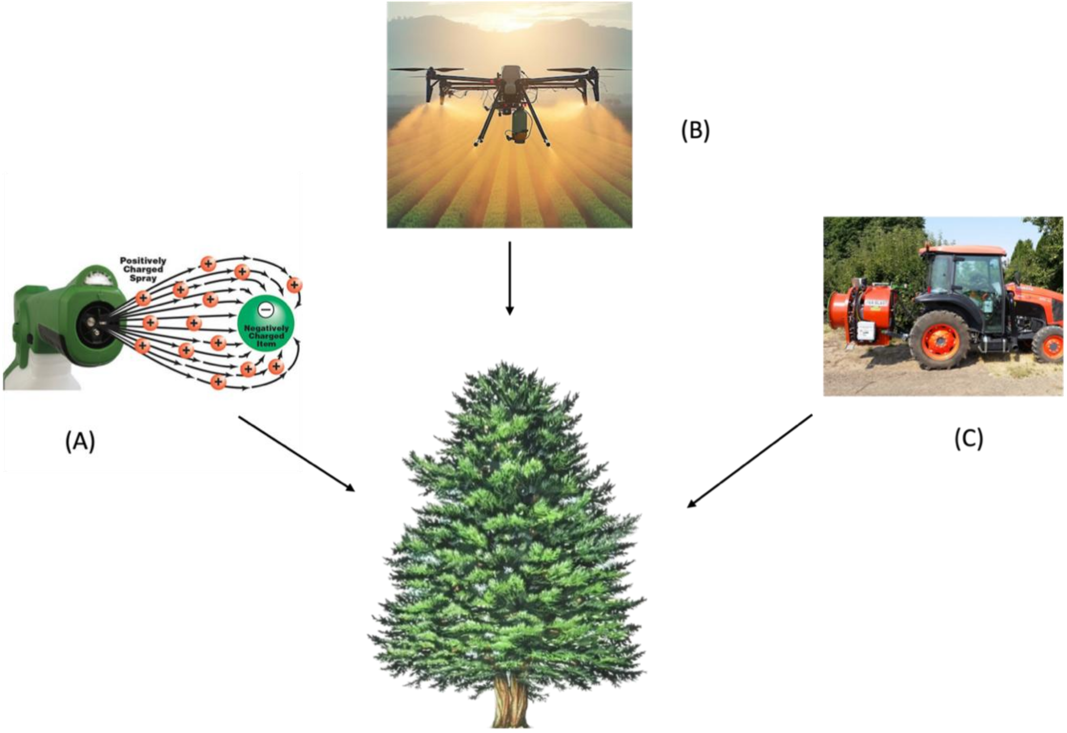

Fig. 4. Modern Spraying Technologies for Targeted Stress Management in Trees (A) Electrostatic sprayers improve spray efficiency by using charged droplets that adhere better to plant surfaces. (B) Drones offer targeted, efficient chemical spraying. (C) LiDAR sensors measure canopy dimensions, optimizing spray amounts for accurate application. Together, these technologies ensure effective use of ameliorating agents.

the correct amount of agrochemicals needed for applications like spraying pesticides or fertilizers.

Drone-Based Canopy Measurement for Precision Agrochemical Application in Ornamental

In the study, Rayamajhi *et al.* (2024) explored the accuracy of drone-derived measurements of tree heights and canopy attributes across three experimental plots, D1, D2 and D3. They achieved notable precision, particularly in plot D1 with an average absolute error of just 2.43%. Comparisons of drone data with manual measurements showed minimal discrepancies in canopy area and volume in plot D3, with an RMSE for canopy area at 0.18 m^2 and for canopy volume at 0.33 m^3. Despite encountering slight overestimations of tree heights and counts due to noise from external factors such as weather conditions and physical obstructions, the study successfully used a Self-Attention Mechanism (SAM) algorithm to address the issue of overlapping canopies. This method allowed for accurate agrochemical needs estimation, necessary for preventing over- or under- application of chemicals, crucial for environmental and crop health commercial operations within both the ornamental and fruit tree sectors. The high accuracy of the canopy measurements, combined with the potential for reducing labor costs and agrochemical waste, makes it a valuable tool for both ornamental, fruit, and other tree industries. This methodology sets a strong foundation for future research and further refinement of canopy attribute measurement techniques.

Conclusion

Taxus, a genus renowned for its valuable medicinal properties, represents a botanical reservoir of bioactive compounds with immense therapeutic potential. However, the limited regenerative capacity of these plants poses a challenge to their population density and conservation. Moreover, fluctuations in climatic conditions and exposure to various environmental stressors, such as drought, temperature extremes, and soil salinity, threaten the growth and development of *Taxus* species. These adverse conditions can hinder the production of key metabolites, further impacting their medicinal value. Therefore, it is crucial to explore the innate defense mechanisms employed by *Taxus* to cope with such environmental challenges. Understanding these mechanisms at the molecular, physiological, and biochemical levels can provide insights into their resilience and adaptive responses. Additionally, identifying and characterizing exogenous agents, such as phytohormones, osmoprotectants, and signaling molecules, that can enhance stress tolerance is essential. Such studies will not only contribute to the development of effective strategies for mitigating environmental stress in *Taxus* species but also support the sustainable conservation and utilization of this important medicinal resource.

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