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Role of Cytokinin in Modulating Plant Physiology and Biochemistry under Combined Drought and Heat Stress

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Abstract

Drought and high-temperature stress increasingly co-occur under climate change scenarios, posing severe threats to crop productivity globally, with particular concern for rainfed cereal systems such as wheat. The combined impact of these stresses on plant growth, development, biomass accumulation, and yield can differ substantially from their individual effects, yet evidence from diverse plant species shows that cytokinin (CK) signaling plays a pivotal role in mediating tolerance to both individual and combined stresses. Drought stress disrupts CK homeostasis by inhibiting its synthesis and accelerating its degradation, resulting in reduced CK levels in both roots and shoots. Enhancing endogenous CK levels either through exogenous application or genetic modification, such as overexpression of the isopentenyl transferase (*ipt*) gene involved in cytokinin biosynthesis, has shown promising results in improving plant stress tolerance and land-use efficiency. This review summarizes recent advances in cytokinin research related to plant stress responses and discusses prospects for its application in improving crop resilience.

Keywords

Cytokinin, BAP, High Temperature, Drought, Antioxidant, Combined Stress

1. Introduction

Anthropogenic climate change, driven by the sustained increase in atmospheric carbon dioxide (CO_2) concentrations, is imposing unprecedented constraints on global agricultural systems, further compounded by the progressive decline in arable land availability and soil quality. Recent assessments by the Intergovernmen-

tal Panel on Climate Change [1]-[3] conclude that human influence has unequivocally warmed the climate system, resulting in widespread and rapid changes across the atmosphere, oceans, and terrestrial ecosystems. These changes include a marked increase in the frequency and intensity of extreme temperature events, such as heatwaves, which are projected to intensify further with continued warming.

Relative to the 1850-1900 baseline, global surface temperatures have already increased by approximately 1.1˚C and are likely to exceed 1.5˚C or even 2˚C during the 21st century under high-emission scenarios [3]. Concurrently, the global hydrological cycle is intensifying, leading to increased precipitation and flooding in high-latitude regions, alongside more severe droughts in many subtropical and mid-latitude regions [1].

Ocean warming is also projected to continue, with pronounced increases in tropical and subtropical regions, further influencing climate systems and weather variability. These climatic changes are expected to significantly affect agricultural productivity by altering crop growth cycles, reducing yields, and increasing the frequency of abiotic stresses such as heat, drought, and salinity [2].

Collectively, these interconnected impacts pose substantial risks to global food security, particularly in vulnerable regions, underscoring the urgent need for climate-resilient agricultural strategies and sustainable land management practices.

These climatic perturbations are anticipated to expose crops to complex, often concurrent, abiotic stress regimes with substantial implications for agricultural productivity. Indeed, reductions in crop yield and quality, primarily driven by heat and drought stress, are identified as critical risks to global food security [2]-[4]. Abiotic stress, including thermal extremes, water deficit, salinity, oxidative stress, and nutrient imbalances, collectively represent the predominant constraints on crop performance, significantly limiting both yield potential and product quality [5]-[7].

At the organismal and cellular levels, plants exhibit highly dynamic and integrated responses to abiotic stress, encompassing morphological, physiological, biochemical, and molecular reprogramming. This response is now understood as a hierarchically organized system where stress perception is mediated by multisensor complexes and thermosensory systems that detect environmental fluctuations and internal pressure shifts. These sensors activate complex signaling networks involving secondary messengers (e.g., Ca^{2+}, reactive oxygen species), metabolic cues, and organellar retrograde signaling [8]. These cascades converge to modulate the expression of stress-responsive genes and epigenetic priming, encoding functional proteins and enzymes essential for cellular protection, metabolic adjustment, and long-term stress acclimation [8].

A central feature of abiotic stress responses is the perturbation of cellular redox homeostasis, often leading to the overaccumulation of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2). While ROS serve as critical signaling intermediates in stress-responsive pathways, acting as secondary messengers that modulate epigenetic modifications and post-translational modifications, their ex-

cessive accumulation induces oxidative damage to lipids, proteins, and nucleic acids, ultimately impairing photosynthetic efficiency and cellular integrity [8]. Under optimal conditions, ROS levels are tightly regulated by a synergistic network of enzymatic and non-enzymatic antioxidant systems; however, these detoxification mechanisms can be compromised under severe or prolonged stress exposure, shifting the cellular state from adaptive signaling to a pathological oxidative burst [8].

Phytohormonal crosstalk constitutes another pivotal regulatory layer in plant adaptation to abiotic stress. Among these, cytokinins traditionally associated with cell division and developmental processes have emerged as key modulators of stress responses, influencing source-sink relationships, antioxidant capacity, and gene expression networks [9]. Notably, the role of cytokinin in stress mitigation appears to be highly context dependent, varying with stress type, intensity, and duration. This raises critical questions regarding the extent to which cytokinin-mediated responses to individual stresses can be extrapolated to combined stress scenarios, such as the frequently co-occurring drought and heat stresses [10]. Furthermore, the potential for interpreting these responses within a cross-adaptation framework remains insufficiently explored.

In this review, we synthesize current knowledge on cytokinin biosynthesis, metabolism, and signal transduction, with particular emphasis on their roles in modulating plant responses to combined drought and heat stress. We also highlight recent advances and emerging perspectives on leveraging cytokinin-mediated regulatory networks to enhance crop resilience under multifactorial stress conditions.

2. Influence of Cytokinin under Combined Drought and High Temperature

Stress on Plant Physiological and Biochemical Attributes

Climate change projections indicate that plants will increasingly experience simultaneous abiotic stresses, particularly drought and high temperature, which often impose more severe effects on plant growth and productivity than individual stresses [11]-[13]. Although numerous studies have investigated plant responses to single stress factors such as drought or heat, these responses cannot always predict the outcomes under combined stress conditions because plants exhibit unique physiological, biochemical, and molecular responses when exposed to multiple stresses simultaneously [12] [13].

Several studies have demonstrated that the combined effects of drought and heat stress significantly reduce plant productivity. For instance, Pradhan *et al.* [14] reported that leaf chlorophyll content, individual grain weight, and grain yield in wheat declined progressively with increasing stress severity, in the order of drought < high temperature < combined stress. Similarly, Prasad *et al.* [15] observed that the simultaneous occurrence of drought and heat stress significantly decreased leaf chlorophyll content, grain number, and harvest index in spring wheat cultivars. Furthermore, Wang *et al.* [16] dissected the differential effects of

each stress: under heat stress alone, chlorophyll content, net photosynthetic rate (PN), carboxylation efficiency (CE), and apparent quantum yield (AQY), were primarily reduced; when under drought stress alone, transpiration rate (E), stomatal conductance (g_s), and intercellular CO_2 concentration (Ci) were significantly reduced, while enhancing antioxidant activity. When both stresses were applied simultaneously, photosynthesis was more severely inhibited than under individual stress treatment.

Studies in *Arabidopsis thaliana* have demonstrated that combined drought and heat stress trigger specific metabolic and transcriptional responses distinct from those induced by individual stresses [11]. Under such conditions, plants accumulate metabolites such as sucrose that contribute to osmotic adjustment and stress tolerance. Moreover, plant growth reduction is generally more severe under combined stress than under individual stress treatments [11] [17]. Similar responses have been reported in crops such as wheat and barley, where combined drought and heat stress significantly reduce grain yield, spikelet fertility, chlorophyll content, and harvest index [15] [18].

Physiologically, abiotic stresses frequently impair photosynthesis by destabilizing the enzyme Rubisco and causing damage to photosystem II (PSII) [19]. High temperature stress also disrupts membrane stability by increasing the kinetic energy of membrane lipids, which enhances membrane fluidity and leads to protein denaturation and increased electrolyte leakage [20]. Such membrane damage is commonly evaluated using cell membrane thermostability (CMT), which has been used as an indicator of heat tolerance in crops such as soybean, potato, tomato, wheat, cotton, sorghum, cowpea, and barley [21]-[26].

At the cellular level, combined drought and heat stress can alter mesophyll cell ultrastructure and damage organelles such as chloroplasts and mitochondria. Grigorova *et al*. [27] reported that drought-tolerant wheat cultivars maintained better structural integrity of cellular organelles compared with sensitive cultivars under combined stress conditions. Water relations are also strongly affected. Machado *et al*. [28] showed that high temperature intensified the effects of drought by reducing soil water content, relative water content, and leaf water potential in wheat and sorghum. Similarly, Perdomo *et al*. [29] demonstrated that combined drought and heat stress significantly reduced plant biomass and altered gas exchange parameters in rice, wheat, and maize, with wheat being the most sensitive species.

In addition to these physiological and structural changes, phytohormones play a crucial role in regulating plant responses to combined abiotic stresses. Among them, cytokinins are key regulators of plant growth, cell division, and stress responses. Cytokinin has been reported to delay leaf senescence, maintain chlorophyll content, and enhance photosynthetic activity under abiotic stress conditions [30] [31]. Under drought and heat stress, endogenous cytokinin levels often decline, which contributes to accelerated leaf senescence and reduced photosynthetic efficiency [32]. However, exogenous application or genetic manipulation that increases cytokinin levels has been shown to improve plant tolerance to stress.

Cytokinin plays an important role in maintaining photosynthetic machinery under stress conditions. They promote chloroplast development, stabilize photosynthetic proteins, and prevent chlorophyll degradation, thereby sustaining photosynthetic efficiency during drought and heat stress [30] [33]. Moreover, cytokinin signaling interacts with other hormonal pathways such as abscisic acid (ABA) to regulate stomatal behavior and water balance under drought conditions [34]. Increased cytokinin levels can also enhance antioxidant defense systems by stimulating the activity of enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidases, which help detoxify reactive oxygen species generated during stress [35].

Furthermore, cytokinins improved root-shoot communication and nutrient transport under adverse environmental conditions. By regulating source-sink relationships and delaying senescence, cytokinin helps maintain metabolic activity and biomass accumulation during stress [32] [33]. Genetic studies have also demonstrated that transgenic plants with elevated cytokinin biosynthesis exhibit improved drought tolerance, enhanced water-use efficiency, and better maintenance of photosynthetic capacity compared with wild-type plants [30].

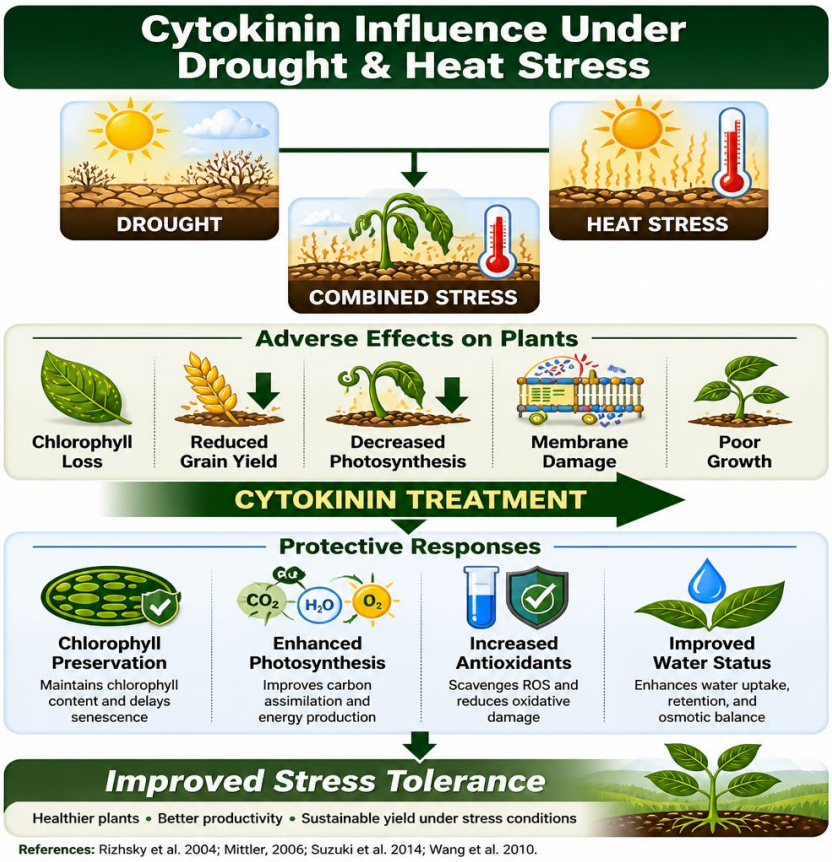

Figure 1. This infographic illustrates how cytokinin, a type of plant hormone, helps plants survive and adapt to environmental challenges like drought and extreme heat. The diagram breaks down the process into three main stages: the damage caused by stress, the intervention (treatment), and the resulting protective benefits.

Overall, combined drought and high temperature stress impose complex physiological and biochemical constraints on plants, leading to reduced photosynthesis, impaired water relations, oxidative damage, and decreased productivity. However, cytokinins play a crucial regulatory role in mitigating these effects by maintaining chlorophyll content, enhancing antioxidant defense systems, stabilizing photosynthetic processes, and delaying stress-induced senescence. Therefore, manipulation of cytokinin metabolism and signaling represents a promising strategy for improving plant resilience to combined abiotic stresses under changing climatic conditions (**Figure 1**).

3. Role of Cytokinin on Physiological, Biochemical, and Growth Parameters in Plants

Cytokinins (CKs) are an important class of phytohormones that regulate numerous physiological and developmental processes in plants. They are primarily known for their role in promoting cell division in both roots and shoots. Several cytokinin biosynthetic pathways are in plastids, indicating their crucial role in chloroplast development and biogenesis [36]. Beyond cell division, cytokinin regulates diverse plant processes including cell differentiation, stem cell maintenance, chloroplast biogenesis, seed development, branching of roots and shoots, leaf senescence, nutrient allocation, and adaptation to environmental stresses [37].

Environmental stresses strongly influence cytokinin metabolism and signaling in plants. Unfavorable conditions often reduce endogenous cytokinin levels, thereby affecting plant growth and stress responses [19]. Multiple studies have shown that cytokinin levels decline in plants under drought stress, particularly in the xylem sap, indicating a direct link between water availability and cytokinin transport [38]. Reduced cytokinin synthesis under water deficit can lead to accelerated senescence and decreased photosynthetic activity.

However, maintenance or enhancement of cytokinin levels has been shown to improve plant tolerance to abiotic stresses. For example, genetic transformation with the isopentenyl transferase (IPT) gene, which regulates cytokinin biosynthesis, has been used to maintain endogenous cytokinin levels under stress conditions. In creeping bent grass, IPT expression improved tolerance to water stress by enhancing osmotic adjustment, improving water-use efficiency, maintaining higher photosynthetic rates in mature leaves, and increasing root viability [39]. Similarly, transgenic cassava plants expressing the SAG12::IPT construct delayed senescence and enhanced drought tolerance [40].

Exogenous application of cytokinins has also been shown to enhance plant stress tolerance and accelerate recovery after stress exposure. Early studies reported that external cytokinin application improves tolerance to mild stress conditions and promotes recovery after rehydration by stimulating stomatal conductance and photosynthetic activity [41] [42]. Cytokinin also regulates the expression of numerous stress-responsive genes. Within a few hours of application, cytokinin can

induce the transcription of genes encoding transcription factors, signaling proteins, and regulators of developmental and hormonal pathways, thereby modulating primary and secondary metabolism and enhancing cellular energy generation [43] [44].

Furthermore, cytokinin-mediated genetic modification has been shown to enhance tolerance to high temperature stress. For instance, SAG::IPT-transformed creeping bent grass plants exhibited improved heat tolerance characterized by increased tiller formation, better chlorophyll retention, and enhanced root growth compared with non-transformed plants [45]. Understanding the role of cytokinin in plant stress responses and recovery mechanisms is therefore essential for developing strategies to enhance crop resilience under rapidly changing climatic conditions (**Figure 2**).

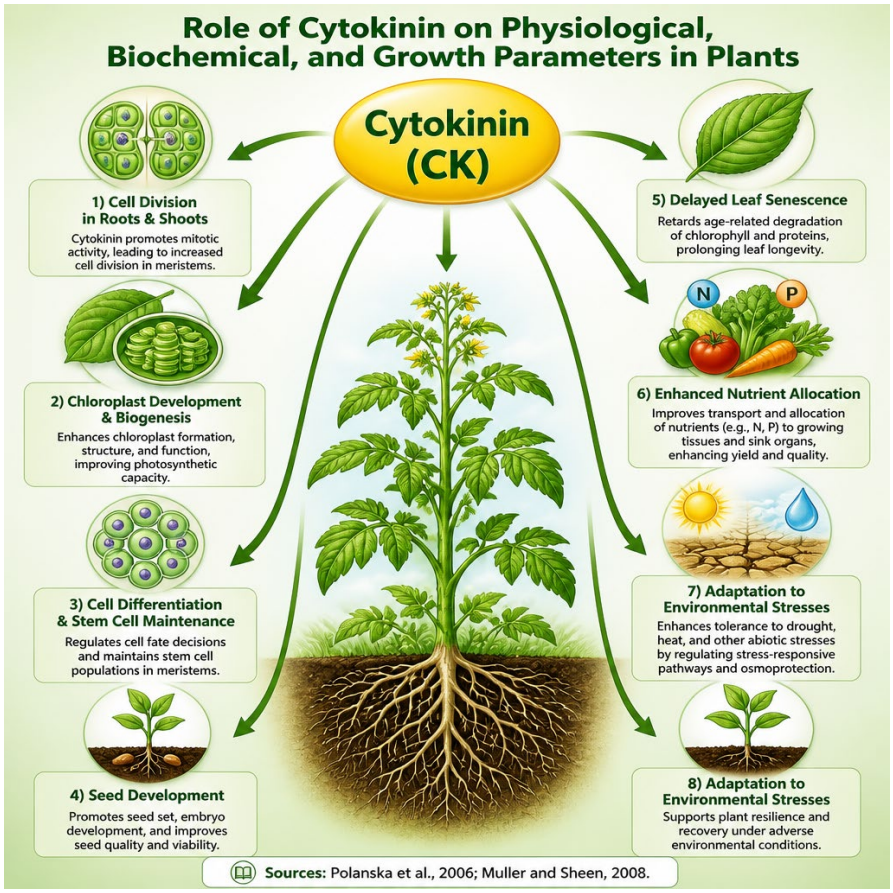

Figure 2. Role of cytokinin (CK) in regulating plant physiological, biochemical, and growth parameters. Cytokinins promote cell division in roots and shoots, regulate chloroplast development and biogenesis, maintain stem cell differentiation, enhance nutrient allocation, delay leaf senescence, and facilitate adaptation to environmental stresses. They also influence seed development and branching of roots and shoots, highlighting their central role in plant growth and development.

3.1. Effect of Cytokinin on Plant Growth

Cytokinin plays a critical role in regulating plant growth and development by con-

trolling cell division and differentiation. Studies involving plants overexpressing cytokinin oxidase (CKX) genes or ipt loss-of-function mutants, which possess reduced cytokinin levels, have demonstrated that cytokinins are essential for cell division during embryogenesis, in the shoot apical meristem, young leaves, cambium, and cultured plant cells. However, higher cytokinin concentrations may negatively regulate root elongation and branching by controlling the transition of dividing cells from the meristematic zone to the elongation zone. Nevertheless, a basal level of cytokinin signaling is necessary for normal root development, as mutants lacking cytokinin receptors exhibit severe inhibition of both root and shoot growth [46].

3.2. Effect of Cytokinin on Photosynthetic Pigments, Proline Content, and Relative Water Content

Leaf senescence represents the final developmental stage of leaf growth and involves the degradation of cellular macromolecules and the mobilization of nutrients to other plant parts. This process includes the cessation of photosynthesis, disintegration of chloroplasts, degradation of proteins, chlorophyll loss, and redistribution of amino acids [47]. Cytokinnins are well known for their ability to delay leaf senescence and maintain photosynthetic activity in plants [48].

Gan and Amasino [49] demonstrated that elevated cytokinin levels can delay or even reverse leaf senescence, resulting in tissue re-greening. Transgenic tobacco plants expressing the ipt gene under the control of the senescence-specific SAG12 promoter exhibited delayed senescence. Similarly, treatment with N6-benzyladenine (BA) delayed senescence of rosette leaves in Arabidopsis thaliana, and heat shock pre-treatment further enhanced the cytokinin-induced delay of senescence [50].

Cytokinin also promotes chlorophyll synthesis and protects the photosynthetic apparatus. For example, BA treatment stimulated cotyledon greening in Cucurbita pepo by activating chlorophyll biosynthesis [50]. In etiolated leaf tissues, inhibition of photosynthetic activity, chlorophyll accumulation, and chloroplast development can be reversed by cytokinin application [45]. Cytokinin, therefore, enhances plant productivity by protecting photosynthetic machinery against abiotic stress damage [51].

Heat stress often induces premature leaf senescence in plants. Cytokinin acts as a potent inhibitor of senescence and promotes recovery following heat stress. Applications of kinetin and benzyl adenine have been shown to accelerate recovery from heat stress and improve grain development by enhancing sink strength and thermo-stability [43]. Kinetin application reversed heat shock injury in wheat [52], while benzyl adenine treatment in Phaseolus vulgaris delayed leaf senescence and maintained chlorophyll content [53].

Cytokinin also helps maintain carotenoid levels and protects cellular structures under stress conditions. Benzyl adenine treatment inhibited stress-induced degradation of chlorophyll and carotenoids while increasing xanthophyll content and

de-epoxidation, thereby enhancing photoprotection [54]. Carotenoids play an important role in protecting plant cells from oxidative damage caused by abiotic stress [55].

Further evidence indicates that cytokinin treatments preserve chloroplast ultrastructure and protein stability. Zavaleta-Mancera *et al.* [56] reported that benzyl aminopurine (BAP) treatment retained up to 60% of initial chlorophyll content and 77% of total protein content in leaves. BAP also reduced the degradation of key photosynthetic proteins such as the light-harvesting chlorophyll-binding protein (LHCP-2) and the large and small subunits of Rubisco. Moreover, BAP-treated leaves maintained well-organized chloroplast structures with intact grana thylakoids for longer periods compared with untreated plants.

Application of cytokinin has also been shown to improve physiological parameters under drought stress. It was demonstrated that foliar application of putrescine and benzyl adenine significantly improved photosynthetic efficiency, water status, and chlorophyll content in wheat subjected to water stress. These treatments also enhanced the accumulation of osmolytes such as proline, soluble sugars, and amino acids while reducing membrane injury, resulting in improved yield and yield attributes [54] [57] [58].

Similarly, Shivani *et al.* [58] reported that cytokinin analogues such as thidiazuron (TDZ) and benzyl aminopurine (BAP) improved osmotic stress tolerance in wheat seedlings. Cytokinin treatments increased endogenous cytokinin levels by regulating IPT gene expression and downregulating cytokinin oxidase (CKX) expression. As a result, relative water content increased by approximately 30%, membrane stability improved by 15%, nitrogen assimilation increased, and leaf senescence was delayed. It was also observed that BA application improved relative water content, chlorophyll content, and proline accumulation in chickpea plants exposed to high temperature stress [59].

3.3. Role of Cytokinin in Lipid Peroxidation and Membrane Stability

Lipid peroxidation is widely recognized as an indicator of oxidative stress in plants because it reflects damage to cellular membranes caused by ROS. Elevated levels of lipid peroxidation have been reported in plants exposed to heat stress, including chickpea, cotton, and lilies [60] [61].

Cytokinin plays an important role in reducing oxidative damage by limiting lipid peroxidation and enhancing membrane stability under stress conditions. For instance, cytokinin treatment significantly reduced lipid peroxidation in creeping bent grass subjected to heat stress [62]. Similar results were observed in wheat, where cytokinin application improved membrane stability and reduced oxidative damage during osmotic stress [58].

Furthermore, exogenous application of benzyl adenine (BA; 40 μM) improved physiological parameters, including relative water content, membrane stability index, and photosynthetic efficiency, in both drought-tolerant and drought-sensi-

tive wheat cultivars under water-deficit conditions [58]. In addition, BA application enhanced high-temperature tolerance by restricting lipid peroxidation and improving membrane stability [59].

3.4. Cytokinin-Mediated Signaling Network under Combined Drought and Heat Stress

When plants are subjected to the simultaneous occurrence of drought and heat stress, CK signaling functions as a central integrator of the environmental perception and adaptive response. Stress perception is initiated at the plasma membrane, where sensors detect reduced water availability and elevated temperature, triggering the rapid accumulation of secondary messengers, including cytosolic Ca^{2+} fluxes and reactive oxygen species (ROS) [2] [63].

Within this signaling context, CK biosynthesis is catalyzed by isopentenyl transferase (IPT) enzymes, which carry out the rate-limiting step in the isoprenoid CK pathway. The resulting inactive CK precursors are then converted to bioactive forms through the action of LONELY GUY (LOG) phosphoribohydrolase enzymes. Concurrently, CK degradation is mediated by cytokinin oxidase/dehydrogenase (CKX), which irreversibly cleaves the side chain of CKs [64] [65].

CK perception is mediated by histidine kinase receptors (AHKs) localized at the plasma membrane and endoplasmic reticulum. Ligand binding to AHKs triggers autophosphorylation and initiates a multistep phosphorelay signaling cascade: Phosphate groups are transferred sequentially from AHKs to histidine phosphotransfer proteins (AHPs) and ultimately to response regulators (ARRs). Type-B ARRs act as transcriptional activators that induce the expression of stress-responsive genes, including those encoding heat shock proteins (HSPs), osmolyte biosynthesis enzymes, and antioxidant defense components. Type-A ARRs provide negative feedback to fine-tune signaling amplitude and prevent runaway activation [64] [66].

At the level of downstream stress responses, CK signaling engages in extensive crosstalk with abscisic acid (ABA), the primary drought hormone. Under combined stress, CK-ABA antagonistism regulates stomatal aperture, transpiration rate, and water-use efficiency, with the relative dominance of each hormone depending on stress severity and timing [34] [67]. CK also interacts with ethylene, auxin, and salicylic acid pathways to coordinate growth modulation, senescence delay, and pathogen defense under multifactorial stress conditions [68]. Additionally, CK enhances the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX), thereby reducing ROS-induced oxidative damage [69]. Collectively, these integrated actions position CK signaling as an essential hub through which plants coordinate physiological, biomedical, and molecular reprogramming in the response to combined abiotic stresses [65].

Importantly, **Figure 3** emphasizes that plant responses to combined drought and heat stress are not merely additive but involve unique transcriptional and

metabolic reprogramming. This includes the induction of heat shock proteins (HSPs), accumulation of osmoprotectants such as proline, and activation of stress-responsive transcription factors, including DREB, NAC, and HSF families [63] [68]. Arrows in the diagram indicate activation or positive regulation, whereas blunt-ended lines represent inhibition or negative feedback. Dashed lines denote indirect or context-dependent interactions. Collectively, this network highlights cytokinin as a central regulatory hub that integrates environmental signals with hormonal and redox pathways to enhance plant resilience under combined abiotic stress conditions.

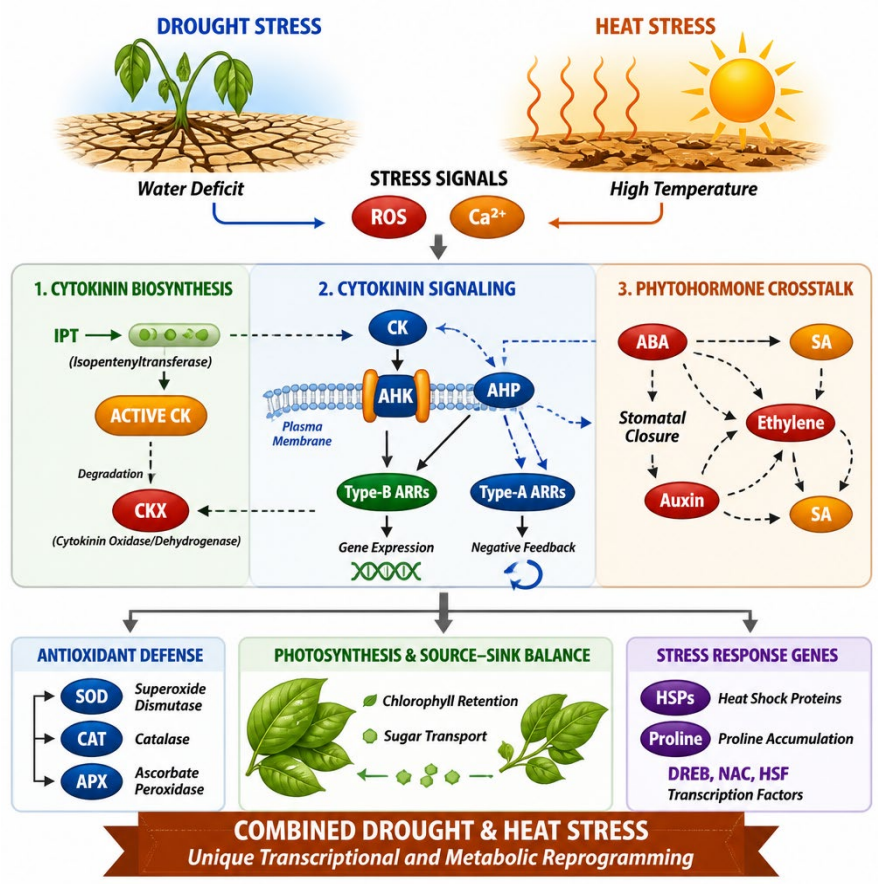

Figure 3. Cytokinin-mediated signaling network under combined drought and heat stress. The schematic illustrates cytokinin biosynthesis (IPT), activation, and degradation (CKX), along with signal transduction via AHK receptors, AHP phosphotransferase proteins, and ARR response regulators. It highlights crosstalk with phytohormones such as ABA, auxin, ethylene, and salicylic acid, as well as downstream regulation of antioxidant defense systems, photosynthesis, and stress-responsive gene expression under combined stress conditions.

4. Cytokinin and Accumulation of Compatible Osmolytes

Under environmental stress conditions, plants accumulate various compatible osmolytes such as soluble sugars, sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds, and tertiary sulphonium compounds to maintain

cellular osmotic balance [70]. Among these osmolytes, proline is one of the most widely distributed amino acids in higher plants and accumulates significantly in response to abiotic stresses, including drought, salinity, and high temperature [71]. Proline plays a crucial role in stress tolerance by stabilizing cellular structures, protecting proteins and membranes, maintaining osmotic balance, and scavenging reactive oxygen species. In particular, proline accumulation has been reported to mitigate heat stress by preventing protein denaturation and membrane damage [72].

Cytokinins play an important role in regulating osmotic adjustment during stress conditions. The application of natural or synthetic cytokinins has been reported to partially alleviate the detrimental effects of water deficit by promoting the accumulation of compatible osmolytes, improving cellular hydration, and maintaining metabolic activity. In addition, cytokinins delay stress-induced leaf senescence and reduce premature leaf and fruit abscission, thereby sustaining photosynthetic activity and plant productivity under unfavorable environmental conditions (**Figure 4**).

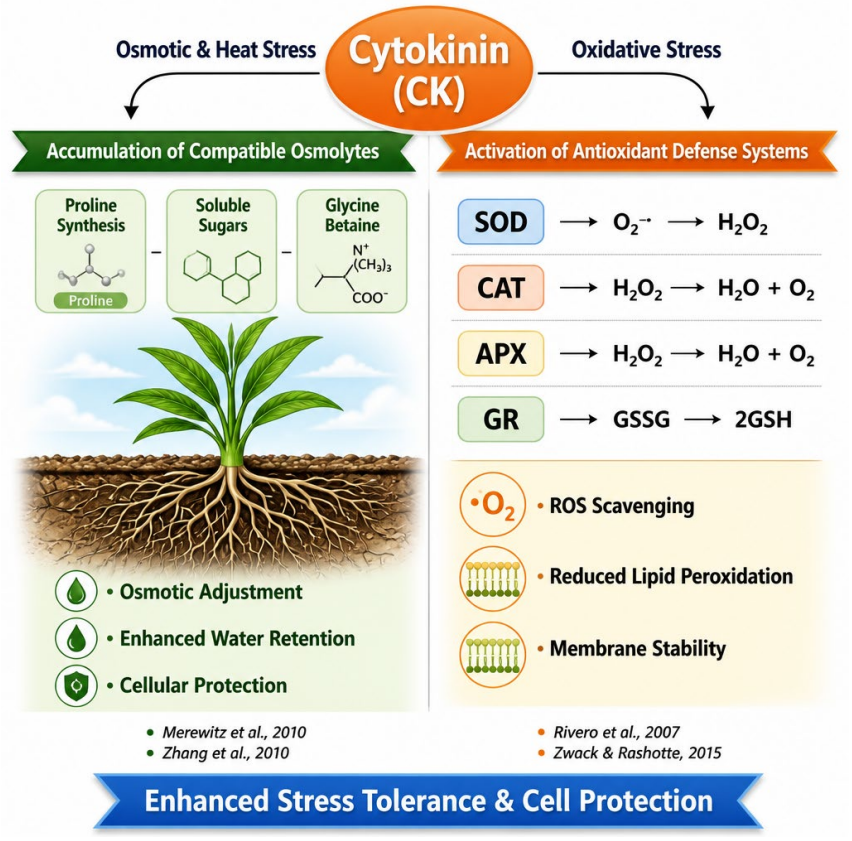

Figure 4. Cytokinin-mediated enhancement of stress tolerance through osmolyte accumulation and antioxidant defense systems. Cytokinin promotes the accumulation of compatible osmolytes such as proline, soluble sugars, and glycine betaine for osmotic adjustment, while simultaneously activating antioxidant enzymes, including SOD, CAT, APX, and GR. These mechanisms collectively reduce oxidative damage, improve membrane stability, and enhance plant resilience under drought and heat stress.

5. Cytokinin and Activation of Antioxidant Defense Systems

Abiotic stresses such as drought and high temperature often lead to excessive production of reactive oxygen species (ROS), including superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (•OH). These reactive molecules cause oxidative damage by initiating the autocatalytic peroxidation of membrane lipids and pigments, resulting in loss of membrane integrity and disruption of cellular functions [73] [74].

To counteract oxidative stress, plants activate both enzymatic and non-enzymatic antioxidant defense systems. Under heat stress, plants typically increase the activity of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), glutathione reductase (GR), and peroxidase (POX). However, in many cases, these antioxidant responses are insufficient to provide adequate protection, particularly in stress-susceptible genotypes. For instance, heat-tolerant wheat cultivars such as C306 exhibit significantly higher activities of SOD, APX, CAT, GR, and POX under heat stress compared with susceptible cultivars like PBW 343, which show reduced antioxidant enzyme activity [75]. Similarly, environmental stresses such as heat and cold have been reported to alter antioxidant defense systems in grape plants [76].

Cytokinins play a significant role in enhancing the antioxidant defense system and mitigating oxidative damage under stress conditions. Several studies have shown that cytokinins can reduce the deleterious effects of high temperature stress by scavenging free radicals and modulating the activity of antioxidant enzymes [77] [78]. Benzylaminopurine (BAP) treatment significantly increased the activities of catalase (CAT) and ascorbate peroxidase (APX) while reducing hydrogen peroxide (H_2O_2) accumulation in senescence-delayed tissues [56]. These findings indicate that cytokinins help maintain cellular redox homeostasis by enhancing antioxidant enzyme activity and reducing ROS levels. Consequently, cytokinin-mediated antioxidant regulation protects cellular membranes and the photosynthetic machinery from oxidative damage, thereby improving plant tolerance to abiotic stresses.

6. Conclusions and Prospects

Studies of endogenous cytokinin levels under diverse environmental conditions indicate that cytokinin metabolism is tightly regulated as part of the plant's response to abiotic stress. Hormone quantification analyses suggest that plants often exhibit a transient increase in cytokinin levels during the early phase of stress exposure, followed by a decline in overall cytokinin content as the stress response progresses. Such dynamic regulation highlights the complexity of hormonal adjustments in stress acclimation.

Recent research has demonstrated that exogenous application of cytokinins (CKs) can enhance plant growth, delay leaf senescence, reduce cell membrane damage and lipid peroxidation, and improve tolerance to major abiotic stresses such as drought and heat stress. For example, cytokinin treatments have been shown

to ameliorate the adverse effects of combined drought and heat stress in wheat seedlings, improving physiological markers and stress resilience compared with untreated controls. Additionally, several reviews support the role of cytokinin signaling in regulating adaptive responses to heat and water stress, offering insights into biotechnological strategies to improve crop tolerance.

Given the crucial role of cytokinin in drought and heat stress responses, future research should emphasize genetic manipulation of cytokinin biosynthesis and signaling pathways, including targeted regulation of cytokinin receptors and signaling components, to develop crop varieties with enhanced stress resilience. Advanced gene editing and regulatory network analyses may provide robust tools for enhancing abiotic stress tolerance while maintaining yield and productivity under changing climatic conditions.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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