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An overview of molecular regulation of plant responses to temperature stress: Insights into the role of ncRNAs

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Abstract

In plants, temperature stress triggers complex responses crucial for survival and adaptation. Understanding these responses at molecular levels is essential. High temperatures lead to the production of heat shock proteins (HSPs) and phytochromes, which help in protein folding and temperature sensing. Cold stress activates signaling pathways involving OST1 and COLD1, which regulate gene expression and calcium influx. Heat stress disrupts photosynthesis, membrane stability, and causes oxidative stress. Plants counter these effects with antioxidant enzymes and osmotic regulation. Understanding these mechanisms is vital for developing stress-tolerant crops to ensure sustainable agriculture. Non-coding RNAs (ncRNAs) like microRNAs (miRNAs), long non-coding RNAs (lncRNAs), and circular RNAs (circRNAs) play key roles in regulating gene expression under temperature stress. miRNAs adjust stress-responsive genes by targeting them directly. circRNAs act as molecular sponges, sequestering miRNAs and thus controlling their activity. lncRNAs are involved in chromatin remodelling and transcriptional regulation, affecting the expression of stress-responsive genes. Together, these ncRNAs create a complex regulatory network that enhances plant resilience to temperature changes, ensuring optimal growth and development under adverse conditions.

Keywords: Temperature stress, ncRNAs, miRNAs, lncRNAs, circRNAs

Introduction

Plants, being sessile organisms, lack the ability to relocate to more favorable environments when faced with abiotic or biotic stresses. As a consequence, their growth, development, and productivity are significantly impacted. Abiotic factors, such as unfavorable environmental conditions, can negatively impact plants and significantly affect crop yields. Abiotic stresses encompass a range of challenging conditions such as drought, heat, cold, nutrient deficiency, and excessive levels of salt or toxic metals like aluminum, arsenate, and cadmium in the soil. Among these stress factors, temperature stress plays a particularly influential role in limiting agricultural productivity and posing risks to global food security. Understanding and mitigating temperature stresses have become crucial areas of research and focus in the agricultural community. Researchers are actively involved in developing stress-tolerant crops through genetic engineering and traditional breeding methods, encompassing various domains of plant science and reflecting the broad scope of research dedicated to this endeavor. Throughout the past two decades, significant progress has been made in identifying various canonical environmental signaling pathways. These pathways are vital for transmitting environmental signals, which lead to alterations in transcriptional and phenotypic responses. Nevertheless, it is becoming increasingly evident that many of these signaling pathways are context-dependent. This means that environmental signals often activate overlapping molecular components, resulting in highly specific responses that are contingent on the particular context. Despite agronomical and crop science studies extensively investigating the natural combinations of environmental stress factors, the exact molecular mechanisms governing these interactions remain unclear.

In plants, different mechanisms have been discovered to understand the high temperatures perception: heat shock proteins (HSPs) respond to intense heat, while phytochromes are responsible for sensing milder changes in ambient temperature. Elevated temperatures disrupt the proper folding of proteins, leading to the formation of protein aggregates within cells. HSPs play a critical role in detecting misfolded and denatured proteins, and they are highly conserved across all living organisms. During high temperatures, water-soluble proteins may denature, exposing their hydrophobic core. Consequently, these hydrophobic regions from multiple proteins aggregate, causing protein precipitation. HSPs themselves possess a hydrophobic region, allowing them to interact with these unfolded proteins. Once bound to the aggregated proteins, Heat Shock Factor (HSF) are released and attach to Heat Shock Elements (HSEs), thereby regulating transcription (Lamers *et al*. 2020) [22]. Plants utilize their ability to sense ambient temperature to control crucial processes like germination and flowering time. Interestingly, the signaling pathways used by plants to transduce ambient temperature information partially overlap with those involved in responding to light signals. The convergence between light and temperature signals lays the transcription factor Phytochrome Interacting Factor4 (PIF4). PIF4 plays a key role in promoting hypocotyl elongation in response to both shade and warm temperatures, and its function is downregulated by phytochrome B (phyB). The phyB has two states: an active Pfr (far-red absorbing) state and an inactive Pr (red absorbing) state. When exposed to red light, Pr converts to the active Pfr state, while exposure to far-red light promotes the reversion of Pfr back to Pr, leading to reduced phyB activity in shaded conditions where far-red light dominates. Additionally, phyB undergoes spontaneous conversion from Pr to Pfr, known as thermal reversion. The rate of thermal reversion is influenced by temperature, with higher temperatures accelerating the process and consequently reducing phyB activity. This effect allows the accumulation of PIF4, which promotes cell elongation in response to warm temperatures (Lamers *et al*. 2020) [22]. Plants experience delays in various developmental processes when exposed to low-temperature stresses, leading to an impact on their vegetative growth. Freezing temperatures, in particular, cause the formation of ice crystals that can inflict permanent damage to cells if not properly managed. In *Arabidopsis*, the key controller of cold signaling is the Open Stomata 1 (OST1), belonging to the family of SNF1-related protein kinases 2 (SnRK2) (Ding *et al*. 2015). Upon exposure to cold treatment, Arabidopsis plants exhibit increased myristoylation of clade-E Growth-Regulating2 (EGR2) by N-myristoyltransferase1 (NMT1). This increased myristoylation triggers the phosphorylation activity of OST1. In response to the cold, OST1 phosphorylates the transcription factor Inducer of CBF expression1 (ICE1) and Basic Transcription Factor3 (BTF3). This activation of OST1 leads to the expression of Cold-Regulated (COR) genes, which are crucial for coping with cold stress (Ding *et al*. 2019) [5]. While EGR2 or NMT1 may be involved in the initial sensing of cold, OST1 serves as a downstream target in this signaling cascade. However, it is still uncertain whether the activity of NMT1 or EGR2 is directly regulated by cold temperatures and whether these proteins can be considered as cold sensors. Further investigations are needed to clarify these aspects. In rice, it has been reported that Chilling-Tolerance Divergence1 (COLD1) plays a crucial role in promoting Ca^{2+} influx within minutes after exposure to cold temperatures. This is achieved through the interaction of COLD1 with an unidentified Ca^{2+} channel or, alternatively, COLD1 itself may function as a Ca^{2+} channel (Ma *et al*. 2015) [26]. COLD1 encodes a transmembrane protein that interacts with the G-protein α-subunit1 (RGA1). This interaction results in increased GTPase activity and a subsequent influx of Ca^{2+} into the cell. As a result, the cold tolerance response is activated, enabling the plant to cope with cold stress more effectively.

The increase in global temperatures has led to a rise in the frequency of extreme temperature events, imposing both high and low temperature stresses on plants and significantly impeding their growth and productivity. To withstand such challenging circumstances, plants have developed intricate mechanisms to cope with temperature stress. Essential physiological processes in plants, including photosynthesis, respiration, and water metabolism, undergo specific responses to temperature stress. Notably, substantial progress has been made in unravelling the genes, non-coding RNAs, DNA methylation, and histone modifications involved in the response to temperature stress.

Responses of plants under high temperature stress

Elevated temperatures have impacts on physiological processes like photosynthesis, respiration, transpiration, membrane thermostability, and osmotic regulation. Heat stress disrupts photosynthesis efficiency, reducing plant lifespan and productivity. Photosynthesis is particularly sensitive to heat, with photochemical reactions and carbon metabolism in the chloroplast being vulnerable to damage. The disruption of thylakoid membranes inhibits electron carriers and enzymes, lowering the photosynthesis rate. Heat stress notably impairs the activity of photosystem II (PSII) complex, which is highly heat-sensitive. Additionally, high temperature stress affects chloroplast structure, thermal stability of photosynthetic components, and reduces ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) activity and photosynthetic pigments. These combined factors significantly contribute to decreased photosynthetic efficiency during heat stress (Zhao *et al*. 2020) [48].

When plants are exposed to high temperatures, their primary physiological challenge is dealing with membrane dysfunction. The extreme heat stress causes an increase in kinetic energy and biomolecular movement, leading to the weakening of chemical bonds and disintegration of membrane lipids, resulting in higher membrane fluidity. This disruption of the membranes causes an increase in cellular permeability and loss of cellular electrolytes, ultimately impairing cellular function and reducing the plant's ability to withstand heat (Xalxo *et al*. 2020) [42]. Moreover, heat stress triggers the accumulation of reactive oxygen species, which damages the membranes further, exacerbating the problem and compromising the plant's ability to tolerate the heat. Therefore, maintaining membrane thermostability is critical for plants to withstand heat stress and develop tolerance to such challenging conditions. Heat stressed plants experience an accumulation of reactive oxygen species (ROS), including superoxide radical (O_{2-}), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$), and hydroxyl radical (OH^-), leading to oxidative stress (Nosaka and Nosaka 2017) [29]. The excess energy generated in Photosystem I (PSI) and Photosystem II (PSII) causes chlorophylls to enter a triplet state, and when this excitation energy is transferred to oxygen (O_2), it produces singlet oxygen. Additionally, over-reduction of PSI contributes to the production of the superoxide anion, promoting H_2O_2 production. These ROS, such as O_2 and H_2O_2, impose oxidative stress on the plant by affecting membrane properties, degrading proteins, and inactivating enzymes, ultimately reducing the viability of plant cells (Wang *et al*. 2016) [39]. Heat stress also induces lipid peroxidation, which damages the cell membrane through free radical attacks. This can be observed, for example, in plants like sorghum, where the content of malondialdehyde (MAD), an indicator of lipid peroxidation, significantly increases under heat stress (Djanaguiraman *et al*. 2010) [6]. Furthermore, ROS can trigger programmed cell death in response to heat stress. However, plants have developed defense mechanisms to counteract the harmful effects of ROS and enhance their heat tolerance. They do this by synthesizing antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), and peroxidase (POX) (Hasanuzzaman *et al*. 2020) [15].

Fluctuating temperatures often lead to unpredictable changes in the water status of plants. When exposed to heat stress, plants experience dehydration, which significantly impacts their growth and development. This is evident as both water potential and relative water content decrease substantially, resulting in reduced photosynthetic productivity (Liu *et al*. 2020) [25]. However, when plants are exposed to transient or mild heat stress, they have mechanisms to regulate the rate of respiration and transpiration. This helps to strike a balance between water loss and heat dissipation, ensuring their survival during challenging conditions. Additionally, plants adjust the levels of soluble sugars and proteins during heat stress to maintain appropriate osmotic pressure within the cells, aiding in their adaptation to the changing environment. Despite these adaptive responses, heat stress still showed adverse effect on cereals, legumes and other crops like tea plants, leading to reduced yields. The detrimental impact of heat stress on agricultural production highlights the importance of understanding and addressing this challenge to ensure food security and sustainable crop cultivation. Throughout the process of evolution, plants have navigated intricate and varied interactions among numerous environmental factors. Consequently, plants have developed distinct mechanisms that enable them to adapt and endure challenging environmental circumstances.

Responses of plants under low temperature stress

Low temperatures have damaging effects on the growth and development of plants. The impact of cold stress is observed in various aspects, including enzyme activity, cell membrane functionality, and cell dehydration, which can lead to metabolic instability or autophagy. Reports indicate that cold stress disrupts the fluidity of cell membranes, disassociates protein complexes, increases the abundance of reactive oxygen species (ROS), reduces enzyme activity, lowers photosynthetic rates, and affects RNA helicase activity. This, in turn, reduces the stability of RNA secondary structures, leading to decreased transcriptional and translational rates (Guan *et al*. 2023) [12]. However, plants have evolved cold acclimation mechanisms through genetic variation and natural selection. To cope with cold stress, plant cells make necessary adjustments in the cytoplasm, plasma membrane, photosynthesis rates. Under conditions of low temperatures, the fluidity of protoplasts decreases, resulting in imbalanced ion exchange. This leads to observable symptoms such as wilting and yellowing (Tang *et al*. 2020) [35]. Cold stress can also negatively impact various aspects of plant growth, including germination, chlorophyll production, growth rate, flower retention, pollen viability, and fruit development (Rajametov *et al*. 2021) [33]. Higher proline content and soluble sugar levels improve plant cold stress resilience by enhancing osmotic regulation, water retention, and protein synthesis. Elevated soluble protein content also boosts cold tolerance by maintaining cell expansion and preventing ice formation (Guan *et al*. 2023) [12]. During the early phases of low-temperature stress, there is a reported occurrence of excessive accumulation of ROS and a substantial rise in peroxide levels within the membrane lipids. These conditions have been linked to disturbances in plant metabolism (Wang *et al*. 2020) [38]. To counteract oxidative damage resulting from the excessive accumulation of ROS, plant cells have developed antioxidant mechanisms comprising both enzymatic and non-enzymatic systems. These evolved mechanisms effectively neutralize the toxic effects caused by ROS accumulation. Enzymatic systems in plants involve various enzymes that help to neutralize ROS, which can cause damage to cells. These enzymes include SOD, POD, CAT and others. They work by breaking down harmful ROS molecules into less harmful forms, thus protecting the plant cells from oxidative stress. Additionally, plants have non-enzymatic antioxidants that also contribute to cell protection. These include compounds like anthocyanin, carotenoids, glutathione, tocopherol, and ascorbic acid. These antioxidants help to directly neutralize ROS and prevent them from causing damage to cellular structures. ROS accumulation in the photosynthetic system leads to the poisoning of the photosystem I (PSI) reaction center, resulting in a reduction of the overall photosynthetic capacity (Vosnjak *et al*. 2021) [37]. Additionally, during low-temperature stress, a decrease in stomatal conductance (Gs) and an increase in intercellular carbon dioxide concentration contribute to a decline in the net photosynthetic rate (Ehonen *et al*. 2019) [8]. Also, low-temperature stress impacts carbon assimilation by reducing transpiration rate, stomatal conductance, and translocation of photosynthetic substrates, CO_2 absorption, and photosynthetic capacity (Guan *et al*. 2023) [12].

A widely recognized cold stress response pathway is the ICE1-CBF-COR transcriptional cascade, which remains consistent across flowering plants, including tea. Tea plants, among others, have duplicated ICE genes, with ICE1 protein notably concentrated at MYC-binding sites (CANNTG) in the CBF promoter region. Several studies have proven that mutations in the ICE1 gene impede CBF3 expression, while the introduction of extra ICE1 copies into plants substantially amplifies CBF3 expression in genetically modified varieties (Tang *et al*. 2020) [35]. ICE2 functions as a redundant counterpart to ICE1, exhibiting comparable cold-responsive activities in plants. Within plant systems, ICE proteins play a pivotal role, orchestrating the regulation of numerous downstream genes in response to cold stress. Plants have evolved intricate mechanisms to counteract cold stress, with the ICE1-CBF-COR cascade emerging as a prominent pathway. Within this cascade, ICE1 and ICE2 assume control over CBF gene expression, subsequently overseeing the regulation of numerous downstream COR genes to effectively manage the plant's response to cold stress.

Involvement of non-coding RNAs during temperature stress response

The ncRNAs stands out as a significant group of molecular entities, receiving attention as an interesting group of molecules with promising prospects. ncRNAs regulate diverse cellular mechanisms encompassing chromatin remodelling, epigenetic retention, transcription, RNA processing, modification, and translation. They hold indispensable functions in upholding genomic stability, fostering plant growth, governing development, senescence, and managing plant reactions to both biological and environmental stresses. This category encompasses a wide array of non-coding RNA entities, including small RNAs (such as miRNAs and various types of siRNAs), circRNAs and lncRNAs. Despite the variations in the biogenesis of these ncRNAs, their regulatory pathways are interconnected (Zhang *et al*. 2022) [46].

miRNAs are a group of naturally occurring small RNAs, typically around 20–22 nucleotides in length. They play a role in reducing the expression of genes by interacting with mRNAs, which results in either the cleavage of the mRNA or the inhibition of its translation. miRNAs hold distinct roles in developmental processes as well as responses to stress, particularly demonstrating significant involvement in plant temperature stress responses. Arabidopsis miR398 stands out as a regulator of heat stress. It becomes active in response to two heat shock transcription factors, and its elevated activity results in the silencing of genes like COPPER/ZINC SUPEROXIDE DISMUTASE 1 (CSD1), CSD2, and COPPER CHAPERONE OF CSD. This gene silencing, in turn, promotes the expression of HSPs, consequently enhancing plant heat tolerance. Intriguingly, experiments involving transgenic plants that carry miR398-resistant versions of CSD1, CSD2, and COPPER CHAPERONE OF CSD displayed better heat sensitivity and reduced heat tolerance (Guan *et al*. 2013) [11]. Li *et al*. (2022) [23] demonstrated that elevating the expression of miR9748 enhanced the capacity of *Arabidopsis thaliana* to withstand high temperatures. Their analysis of the transcriptome suggests that miR9748 might facilitate high-temperature resilience by influencing the phytohormone signaling pathway. The intended target of miR9748 is CsNPF4.4, a gene that exerts a negative influence on high-temperature stress tolerance by inhibiting the jasmonate signaling pathway (Li *et al*. 2022) [23]. In a separate study, Ahmed *et al*. (2019) [1] identify novel and conserved miRNAs responsive to heat in Chinese cabbage. This analysis unveiled 41 conserved miRNAs belonging to 19 families, with miRNA156, miRNA159, miRNA168, miRNA171, and miRNA1885 being the highly expressed among them (Ahmed *et al*. 2019) [1]. Elevating the levels of miR156 through overexpression resulted in increased cell viability and growth rates when plants encountered cold stress. This phenomenon was observed in Arabidopsis, pine, and rice. In Arabidopsis, pine, and rice, miR156 overexpression strengthened cold tolerance by targeting OsSPL3, a gene known to have a positive effect on the expression of OsWRKY71. The latter, in turn, operates as a negative regulator for the transcription factor genes OsMYB2 and OsMYB3R-2 (Zhou and Tang 2019) [49]. SlNAM3 contributes to enhance cold resilience, whereas Sl-miR164a/b-5p exerts a counteractive role by restriction the expression of SlNAM3's upstream factors. The SlmiR164a-SlNAM3 unit prompts the synthesis of ethylene by directly influencing the expression of SlACS1A, SlACS1B, SlACO1, and SlACO4; this, in turn, increasing cold tolerance in tomato (Dong *et al*. 2022) [7]. The miR1320-OsERF096 module impacts cold stress tolerance. Specifically, the APETALA2/ethylene response factor (ERF) transcription factor OsERF096 serves as a target for miR1320. Downregulating miR1320 diminishes cold tolerance, while upregulating it enhances cold resilience. The miR1320-OsERF096 duo orchestrates these effects by inhibiting the jasmonate-mediated cold signaling pathway (Sun *et al*. 2022) [34]. In a study by Zhang *et al*. (2014) [47] investigated the response to cold stress in tea cultivars 'Yingshuang' (YS – cold-tolerant) and 'Baiye 1' (BY – cold-responsive). They identified miRNAs from conserved families - miR156, miR159, and miR396 - known for regulating defense mechanisms, yet these miRNAs displayed inconsistent regulatory patterns under cold stress in tea. Additionally, csn-miR171 and csn-miR474 were predicted to target a bHLH transcription factor and NADP-ME (Nicotinamide adenine dinucleotide phosphate dependent malic enzyme) gene, respectively, with differential expression correlating to cold tolerance differences between YS and BY (Zhang *et al*. 2014) [47]. Also, csn-miR164 targeted a LEA protein, vital for organismal viability under metabolic low water states, suggesting potential crosstalk between cold and drought signaling pathways in tea plant (Zhang *et al*. 2014) [47].

lncRNAs are a distinct category of RNA molecules characterized by their extended nucleotide sequences, typically exceeding 200 nucleotides. This distinguishes them from other non-coding RNAs like miRNAs and siRNAs. Despite their structural similarity to mRNAs, lncRNAs have notably small open reading frame, usually containing fewer than 100 amino acids. This inherent feature prevents them from encoding functional proteins. These categories serve as effective regulators, both in cis and trans, capable of influencing the transcriptional dynamics of their target loci. In some instances, these lengthy non-coding RNA sequences actively participate in gene expression regulation by acting as miRNA target mimics. This unique property often leads to altered interactions in molecular binding patterns. Instead of interacting with the protein-coding genes responsible for functional gene expression, promoters or inhibitors of gene activity engage with these gene mimics. This distinctive mechanism can lead to significant changes in gene expression patterns (Mattick *et al*. 2023) [28]. lncRNAs are responded to play crucial roles in plant responses to temperature stresses in various species of plants. For instance, in Arabidopsis, the natural long non-coding antisense asHSFB2a has been identified as a regulator of the heat stress response, impacting the expression of HSFB2a, a central regulator of this process (Wunderlich *et al*. 2014) [41]. Another example is the Cold induced lncRNA 1 (CIL1) in Arabidopsis, which has been demonstrated to positively regulate the response to cold stress by influencing hormone signaling, maintaining ROS homeostasis, and modulating glucose metabolism (Huo *et al*. 2022) [19]. Cold stress triggers the expression of COOLAIR, a collection of alternatively processed antisense noncoding transcripts in Arabidopsis. These transcripts play a role in reducing the expression of FLC, a gene associated with flowering regulation. They achieve this by recruiting protein complexes that influence chromatin states or by altering the abundance and conformation of structural elements (Marquardt *et al*. 2014) [27]. Interestingly, a homolog of FLC in response to cold stress was identified in kiwifruit. An antisense lncRNA exhibiting an expression pattern opposite to AcFLCL (the FLC homolog) was found, suggesting a mechanism resembling Arabidopsis COOLAIR, even outside the Brassicaceae family (Voogd *et al*. 2022) [36]. These findings collectively underscore the involvement of lncRNAs in orchestrating plant responses to temperature-induced stresses. In cotton, the lncRNA XH123, responsive to cold stress, actively participates in enhancing cold tolerance at the molecular level during the seedling stage (Cao *et al*. 2021) [2].

circRNAs are recognized as a unique class of RNA molecules that play essential roles in various biological and developmental processes. It has also been documented to have significant involvement in plant growth, development, and stress tolerance. circRNAs are distinguished from linear RNAs by a covalent and conventional linkage that occurs through backsplicing, connecting a downstream 3′ splice site to an upstream 5′ splice site. One of the remarkable functions attributed to circRNAs is their ability to act as miRNA sponges, thereby inhibiting miRNA activity. Studies have shown that the overexpression of circRNAs functioning as miRNA sponges leads to increased expression of miRNA targets, while knockdown of these circRNAs has the opposite effect. Some circular RNAs, known as ecircRNAs, have the capability to sequester or localize RBPs, and they are assumed to modulate RBP function in a manner similar to how they regulate miRNA activity (Kalwan *et al*. 2023) [21]. Through their sponging activity, circRNAs can exert control over protein expression by sequestering mRNA translation start sites. In recent years, a substantial number of circRNAs have been predicted to participate in essential cellular and physiological responses, including cellular redox reactions, cell wall degradation, the production of heat and cold shock proteins, responses to chilling stress, salt-responsive proteins, and various low-temperature-induced transcription factors like CBP and WRKY (Yang *et al*. 2020) [43]. Research has revealed that Circ_0003418 acts as a negative regulator of heat stress and influences the expression of PtoXBAT32.5, thereby regulating membrane lipid peroxidation and ethylene production in *Populus tomentosa* (He *et al*. 2020) [17]. In the context of cold stress, a total of 475 differentially expressed circRNAs have been identified in grapevines. Notably, a grapevine circRNA called Vv-circATS1, originating from glycerol-3-P acetyltransferase, has been found to enhance cold tolerance in Arabidopsis when overexpressed (Gao *et al*. 2019) [10]. In tea plants exposed to cold stress, a crucial circRNA, known as CSS-circFAB1, has been identified. Experimental evidence suggests that CSS-circFAB1 likely functions as a positive regulator in mediating the cold tolerance of tea plants (Huang *et al*. 2023) [18]. However, a comprehensive understanding of its specific functions and regulatory mechanisms requires further investigation.

Conclusion

Climate change, driven by global warming, is causing rapid and severe changes in the global climate. These changes are expected to worsen and will have significant impacts on various sectors including agriculture. Recent research has shown that ncRNAs play important roles in helping plants respond to stress, such as extreme temperatures, both low and high temperature conditions. These ncRNAs are involved in pathways related to hormone signaling, antioxidant defenses, and the regulation of stress-related genes. Understanding temperature-responsive ncRNAs has given us important insights into how plants manage stress at the molecular level. Despite these advancements, there are still many questions about how exactly ncRNAs work to manage temperature stress. The complexity increases because different types of ncRNAs can overlap in their functions and interact with each other. Future research should aim to identify and validate the functions of these ncRNAs comprehensively. Applying this knowledge can help develop crops that are more resilient to climate change, ensuring sustainable agriculture for the future.

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