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The role of small RNAs under abiotic stress in plants

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Abstract. Small RNAs (sRNA) play an essential role in the epigenetic modulation of the genome. They are implicated in numerous processes, encompassing factors that mitigate both abiotic and biotic stressors. Notable among these are heat shock proteins (HSP), enzymes involved in reactive oxygen species (ROS) scavenging, and nuclear factor Y (NF-Y). Molecularly, sRNAs are characterized by sequences of approximately 21–23 nucleotides in length. Based on contemporary understandings in plant science, numerous abiotic constraints have the potential to curtail crop yield, growth, and reproductive potential in plants. These constraints exert their deleterious effects by undermining cellular homeostasis, perturbing ionic equilibrium, and impinging upon essential physiological processes. However, evolution has endowed certain plant species with the ability to adapt to elevated thermal conditions through the nuanced regulation of genes and proteins, notably heat shock factors (HSF) and HSP. While there has been an incremental growth in literature concerning microRNA (miRNA) functionality in plants, the emergent targets of miRNA and their intricate relationship with the HSF-HSP complex remain underexplored. In this scholarly review, we delve into the thermal responses of HSF-HSP in both *Hordeum vulgare* and *Arabidopsis thaliana,* emphasizing their regulation by miRNA under conditions of heat stress.

Keywords: small RNAs (sRNA), heat shock proteins (HSP), microrna (miRNA), abiotic stress, heat shock factors (HSF), gene regulation

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Introduction

Small RNAs (sRNA) represent a specific subset of non-coding RNAs, typically spanning 21–24 nucleotides in length. They play a pivotal role in modulating gene expression through two primary mechanisms: transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTSG) [1-3]. The biogenesis of sRNA commences with the endonuclease action of Dicer-like proteins (DCL) acting upon the helical regions of RNA precursors composed of an array of molecular structures. Subsequent to this, one strand of the generated duplex associates with an Argonaute protein (AGO). This particular sRNA strand possesses the capability to hybridize with its complementary target RNAs. The AGO protein, in turn, can either directly catalyze or indirectly suppress the activities of these target genes. This repression is evidenced at various stages such as the downregulation of translational processes, increased instability of RNA, and the imposition of repressive chromatin modifications [4].

MicroRNAs (miRNAs), which are encoded by MIR genes, undergo transcription by RNA polymerase II. These primary miRNAs subsequently experience modifications, especially at their 5'–3' terminal regions [5]. Recent scientific investigations have underscored the crucial regulatory functions of miRNA and short interfering RNA (siRNA) in plant cells subjected to extreme thermal conditions. Under standard conditions, miRNAs bind to a set of target genes leading to their repression. Furthermore, they can modulate the expression of genes, some of which code for vital entities like transcription factors. This emerging body of knowledge solidly positions miRNAs as integral players in orchestrating plant development and fortifying resistance against various stressors [2].

The aim of this review is to elucidate the multifaceted roles of small RNAs, with a particular focus on miRNAs, in orchestrating plant responses to abiotic stressors. By synthesizing recent findings, we aim to provide a comprehensive understanding of the molecular mechanisms and regulatory pathways underpinning these responses, thereby highlighting potential avenues for enhancing plant resilience in a changing environment.

Roles of small RNAs in plant under abiotic stress

In recent times, there has been an upsurge in the identification of miRNAs, especially those interacting with genes integral for thermos-tolerance. With increasing temperatures, a distinct pattern emerges where three specific miRNAs are discerned across seven diverse plant species. Intriguingly, these miRNAs, when induced by thermal extremes, are implicated in various facets of plant growth and developmental stages [6].

Cold and heat stress mechanisms in plants are intricately regulated by miRNAs. Despite many miRNAs maintaining a consistent presence across various plant species, certain miRNAs display specific regulatory patterns, acting in a more selective manner. As an illustrative example, miR172 exhibits differential regulation; it gets activated under cold conditions in species like *Brachypodium* and *Prunus persica* but is found to be suppressed in wheat and grapevine [7].

Salt-induced osmotic stress in plants precipitates ion toxicity, adversely impacting various physiological attributes, notably affecting organ growth and development. Plants, through evolutionary processes, have devised protective mechanisms such as ion exclusion to combat such stresses. Complementing these intrinsic mechanisms, a multitude of genes and transcription factors get expressed to counteract the deleterious effects of stress. Within this complex regulatory framework, miRNAs emerge as key post-transcriptional regulators. Depending on the stress context, miRNAs can either upregulate or downregulate target genes that are pivotal for stress tolerance [8-9].

Drought, as an abiotic stressor, poses profound challenges, imperiling vital plant processes from development and reproduction to overall growth and crop yield. Plants have evolved multifaceted strategies to mitigate drought stress. These strategies span from temporal adjustments in reproductive cycles to physiological alterations like maintaining a high-water potential and optimizing water use by modulating root depth and reducing transpiration. These adaptive mechanisms encompass a host of processes such as turgor maintenance via osmotic adjustments, cellular plasticity enhancements, and reduction in cell size, all governed by an extensive gene network [9].

Drought conditions invariably induce alterations in the expression profiles of a myriad of genes crucial for plant survival. Examples include genes like glutathione S-transferase (GST) and those induced by abscisic acid (ABA) such as Late embryogenesis abundant protein (LEA), Ras-related protein RABG (RAB), Cold-regulated protein (COR), RuBisCo, helicase, proline, and various carbohydrates. In this dynamic interplay, miRNAs serve as pivotal regulators, orchestrating the expression of genes that confer drought tolerance [10].

Table 1

Changes of essential miRNA expression in A. thaliana under abiotic stress [24]

miRNA	Type of regulation	Source [24]
miR156, miR159, miR167, miR168, miR171, miR172, miR319, miR393, miR394a, miR395c, miR395e, miR396 miR397	Up-regulated	*A. thaliana*
miR161, miR168a, miR168b, miR169, miR171a miR319c	Downregulated	*A. thaliana*

Recent research insights suggest that plant responses to drought stress, mediated by miRNA regulation, vary according to developmental stages and are also species-dependent. The intricate relationship between miRNA-guided regulation of drought tolerance mechanisms and developmental processes appears to be deeply intertwined, potentially representing facets of a unified adaptive response. For instance, some of miRNAs in plants like *Arabidopsis* (table 1), *Prunus persica*, and *Hordeum vulgare* exhibit repression in rice. In contrast, while miR169 is found to be downregulated in certain species, it is upregulated in others, underscoring the complex regulatory landscape [11-13].

A case in point is miR169c, a significant miRNA that targets entities like the nuclear factor Y (NF-Y) transcription factor (TF), the heme-activated protein (HAP), and the CCAAT-binding factor (CBF). This miRNA modulates its targets, primarily by diminishing the levels of NF-Y RNA.

The expression patterns of miR169c, especially under drought conditions, are influenced by degradation-responsive elements present in its promoter region. This expression, however, is contingent upon various external factors including, but not limited to, the onset, duration, and severity of the stress exposure [14-15].

Regulation of NF-Y by sRNA and its effect on plants under stress

The nuclear factor, often termed as the CCAAT Binding Factor (CBF) or Heme Activator Protein (HAP), comprises three subunits: NF-YA (CBF-B/HAP2), NF-YB (CBF-A/HAP3), and NF-YC (CBF-C/HAP5). This complex is pivotal for recognizing and binding the CCAAT box in DNA. While these subunits collaboratively function as heterodimers or heterotrimers, their individual modulation is independent [16-17].

Unlike animals and yeast, where all subunits of NF-Y are encoded by a single gene but have multiple splicing forms, plants have multiple genes encoding subunits of NF-Y. Several of these subunits, notably NF-YA, NF-YB, and NF-YC, have defined roles under drought stress conditions. Specifically, NF-YA5 overexpression correlates with decreased water loss from leaves and heightened drought tolerance. Furthermore, drought stress conditions induce increased expression of many NF-Y subunits, with NF-YB1 exhibiting the capability to modulate drought tolerance without the involvement of ABA signaling [18].

In a broader genomic perspective, miR169 predominantly targets the genes encoding the NF-Y subunit A. The NFYB and NF-YC subunits, characterized by their inherent histone fold domains, synergize to form heterodimers. These heterodimers play a critical role in ensuring a robust and stable interaction with NF-YA. An inverse correlation is observed between the down-regulation of miR169 and the elevated expression of NF-YA5, suggesting a potential regulatory mechanism wherein miR169 modulates drought stress tolerance through NF-YA5. Further accentuating this hypothesis is the observation that the transgenic upregulation of NF-YA5 bolsters drought resistance in plants [19-20].

However, it's essential to highlight that the expression levels of various NF-Y subunits can exert dual impacts on drought tolerance. Therefore, specific miRNAs, through their modulation of genes encoding NF-Y subunits, can be pivotal in enhancing or attenuating plant drought resilience [20].

Regulation of HSFs and HSPs by sRNA and their effect on plants under stress

Heat Shock Factors (HSFs) play a pivotal role in plant thermotolerance, primarily by regulating heat shock proteins (HSPs) which serve as molecular chaperones for key proteins. Enhanced expression of certain HSF and HSP genes, namely CaHSP25.9, ZmHSF05, TaHSP23.9, and OsHSP20, augments the host cell's resilience against elevated temperatures [6]. Small heat shock proteins (sHSPs or Hsp20s) are integral in counteracting the detrimental effects of abiotic stresses in plants. Specifically, CaHsp25.9 is associated with enhanced drought and thermal stress tolerance, an observation underscored by its overexpression. Recent findings indicate that CaHsp25.9 is localized in the cell membrane and cytoplasm. Enhanced expression of CaHsp25.9 curtails malonaldehyde (MDA) accumulation, electrolytic leakage, and levels of reactive oxygen species (ROS) such as superoxide anion and hydrogen peroxide during multifaceted abiotic stress. Conversely, overall chlorophyll levels decrease [7].

HSPs, essential molecular chaperones, encompass five primary families: sHSPs (Hsp20s), Hsp60s, Hsp70s, Hsp90s, and Hsp100s. Notably, Hsp20s spearhead the plant's initial defense against stress, operating in tandem with ATP [21-22]. Hsp20s proteins are recognized for their binding capabilities, altered physicochemical attributes, and collaboration with the HSP70-SP100 bi-chaperone system in refolding and disassembling molecules [9]. Most Hsp20s have molecular weights within the 15-42 kDa range. Key functions linked to the structure of Hsp20s include:

1. The Hsp20 domain, or α-crystallin domain (ACD), characterized by its compact β-sheet architecture, aids in the dissociation of oligomers and facilitates interaction with non-native proteins.
2. C-terminal extensions contribute to the stabilization of the oligomeric assembly.
3. The variable N-terminal region orchestrates and relays cellular signals [23].

According to recent studies, Hsp20s have sub-families: cytoplasm/nuclear, mitochondria, chloroplast, peroxisome, and EPR. Each subfamily serves distinct roles within the cell. Regardless of their spatial distribution and structural attributes, they respond to various abiotic stresses, including drought, salinity, and thermal stress. In *A. thaliana*, AtHsp21 underpins heat stress tolerance and thermomemory, attesting to the positive modulation of plants by Hsp20s during stress conditions [24].

Furthermore, miRNAs enhance thermotolerance by modulating HSF/HSP genes. During thermal stress episodes, genes such as HEAT STRESS ASSOCIATED 32 (HSA32) and HSP17.6A are upregulated. However, the miR156 module downregulates their expression, a critical component in establishing plant stress memory [13].

In transgenic plants possessing miRNA-resistant genes, namely CSD1, CSD2, and CCS, there is a diminished expression of HSF genes (HSF1e, HSFA2, HSFA3, HSFA7b) and HSP genes (HSP17.6, HSP70B, HSP90.1). This reduced expression culminates in programmed cell death (PCD). Conversely, mutant plants exhibit enhanced gene expression, thereby conferring thermotolerance. Intriguingly, as a shown in table 2 the interaction between HSFA1b, HSFA7b, and the promoter region of miR398b indicates a positive regulatory feedback mechanism [27]. While research in this domain is rapidly advancing, our understanding of certain signaling pathways and the regulatory roles of miRNA remains incomplete.

Table 2

Effects of gene expression of some HSFs by regulating miRNA [12, 25, 26]

Genes	miRNA	Effect of genes	Type of plants [12, 25, 26]
HSFA1, HSFA1b	sha-miR319d	Heat tolerance	*Solanum habrochaite*
AsHSP17.0, AsHSP26.7a	Osa-miR393	Heat tolerance	*Arabidopsis thaliana*

Reactive oxygen species (ROS) are unavoidable byproducts of cellular metabolism. Under many circumstances, they induce oxidative damage to proteins, lipids, and result in electrolyte leakage. Nonetheless, plants possess an antioxidant defense system categorized into enzymatic and non-enzymatic ROS scavenging pathways, ensuring a balance between ROS production and elimination [16].

The H2O2-H2O2 signaling interactions are modulated by various phytohormones and distinct signaling pathways. Salicylic acid (SA), jasmonic acid (JA), auxin, ethylene (ET), abscisic acid (ABA), and other phytohormones can negatively influence H2O2 homeostasis. These hormones can prompt alterations in gene expression, specifically targeting stress-responsive cis-regulatory promoter elements downstream of transcription factors. Additionally, they amplify signaling cascades, such as mitogen-activated kinase pathways, with ROS (Figure 1) acting as mediators [17], [18].

Under low-temperature stress, plants deploy protective strategies, including changes in gene expression, cell membrane modifications, antioxidant accumulation, and synthesis of cryoprotectants and cold-regulated proteins [19]. Prominent antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) actively participate in ROS scavenging. Oxidative stress often emerges as a secondary response to these stressors. MiRNA, when induced by temperature stress, can inhibit the expression of genes such as CSD1 and CSD2, leading to elevated ROS levels in cells. Consequently, these elevated ROS levels stimulate the overexpression of heat shock factors (HSFs) and other genes crucial for plant thermotolerance [28].

The interplay between miRNA, HSF, and ROS scavenging enzymes is intricate. For example, miR398 can be modulated by tocopherol and PAP in plants. Increased ROS accumulation or the suppression of ROS scavenging enzymes can trigger the activation of HSF1Aa and HSF1Ab in transgenic plants. However, for many miRNAs, such as miR319d, their specific targets, localization, and involvement in signaling pathways remain to be elucidated [29].

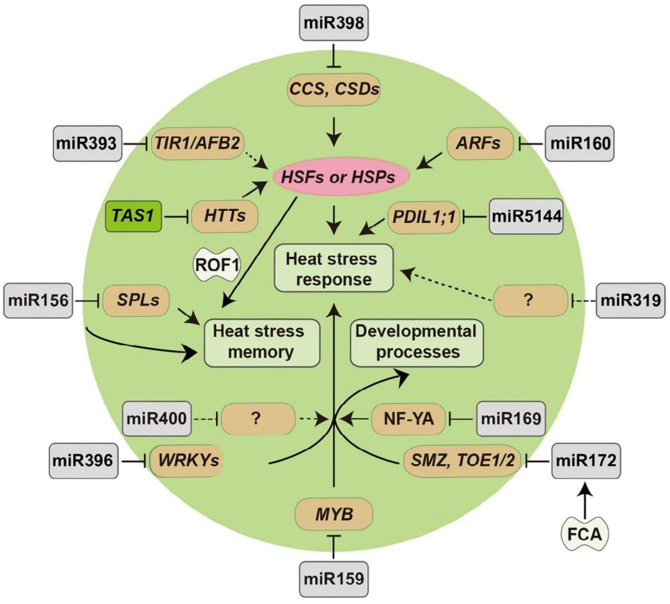

Figure 1. The effect of ROS-scavenging pathway regulating by small RNA to abiotic stress. Adapted from [28]

Conclusion

In the intricate landscape of molecular responses that Hordeum vulgare deploys against abiotic stress, small RNAs emerge as paramount modulators. Their pivotal role in orchestrating adaptive mechanisms is evidenced not only by their direct interaction with stress-responsive pathways but also by their nuanced regulation of key molecular entities. Among these entities, the Nuclear Factor Y (NF-Y) transcription factor stands out, shedding light on the profound interplay between small RNAs and gene expression dynamics in response to environmental challenges. Additionally, the interwoven relationship of small RNAs with the ROS scavenging pathway underscores their crucial function in maintaining cellular homeostasis, emphasizing their significance in managing oxidative stress.

Further compounding the importance of small RNAs in Hordeum vulgare's abiotic stress response is their interaction with HSF/GSP factors, illuminating yet another layer of molecular defense strategies. The cumulative insights from this review underscore the multifaceted roles of small RNAs, highlighting their potential as vital targets for future research endeavors. Delving deeper into these small RNA-mediated mechanisms not only enhances our understanding of plant stress biology but also paves the way for innovative approaches in crop improvement and sustainable agriculture.

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Authors' contribution

Samat A.: writing a text and/or critically reviewing its content.
Zhanassova K.: design of the work.
Syzdyk K.: data analysis.
Soltabayeva A.: review and editing.
Akbassova A.: collection of data.
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Кіші РНҚ-ның өсімдіктерде абиотикалық стресс жағдайындағы рөлі

Аңдатпа. Кіші РНҚ (sRNA) геномның эпигенетикалық модификациясында маңызды рөл атқарады. Олар абиотикалық және биотикалық стресстерді жеңілдететін факторлармен бірге көптеген процестерге қатысады. Олардың ішінде жылу шоктары белоктары (HSP), реактивті оттегі түрлерін (ROS) тазартуға қатысатын ферменттер және ядролық фактор Y (NF-Y) ерекшеленеді. Молекулалық деңгейде sRNA шамамен 21-23 нуклеотид ұзындықта болатын тізбектермен сипатталады. Өсімдіктер ғылымы саласындағы қазіргі түсініктерге сәйкес, көптеген абиотикалық шектеулер өсімдік өнімділігін, өсуін және репродуктивті әлеуетін айтарлықтай төмендетуі мүмкін. Бұл шектеулер жасушалық гомеостазды бұзу, иондық теңгерімді бұзу және маңызды физиологиялық процестерге әсер ету арқылы зиянды ықпалын тигізеді. Дегенмен, эволюция кейбір өсімдік түрлерін жоғары температураларға бейімделуге мүмкіндік берген, бұл гендер мен белоктарды, әсіресе жылу шок факторларын (HSF) және HSP реттеу арқылы жүзеге асады. Өсімдіктерде микрорНК (miRNA) функционалдығы туралы ғылыми деректердің өсуіне қарамастан, miRNA жаңа мишенелері мен олардың HSF-HSP кешенімен күрделі өзара әрекеттестігінің зерттелуі әлі де аз. Бұл шолу жұмысында біз Hordeum vulgare және Arabidopsis thaliana өсімдіктерінде HSF-HSP жылу реакцияларын зерттеп, олардың жылу стресі жағдайында miRNA арқылы реттелуіне ерекше назар аударамыз.

Түйін сөздер: Кіші РНҚ (sRNA), жылу шоктары белоктары (HSP), микроРНК (miRNA), абиотикалық стресс, жылу шок факторлары (HSF), ген реттелуі

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Роль малых РНК при абиотическом стрессе у растений

Аннотация. Малые РНК (sRNA) играют важную роль в эпигенетической модификации генома. Они участвуют в многочисленных процессах, включая факторы, которые помогают преодолевать как абиотические, так и биотические стрессы. Среди них можно выделить белки теплового шока (HSP), ферменты, участвующие в утилизации активных форм кислорода (ROS), и ядерный фактор Y (NF-Y). На молекулярном уровне sRNA характеризуются последовательностями, длина которых составляет примерно 21-23 нуклеотида. Согласно современным представлениям в области науки о растениях, множество абиотических факторов могут значительно снизить урожайность, рост и репродуктивный потенциал растений. Эти факторы оказывают свое разрушительное воздействие, нарушая клеточный гомеостаз, нарушая ионный баланс и воздействуя на важнейшие физиологические процессы. Однако эволюция наделила некоторые виды растений способностью адаптироваться к повышенным температурам посредством тонкой регуляции генов и белков, в частности, факторов теплового шока (HSF) и HSP. Несмотря на рост научных данных о функциональности микрорНК (miRNA) в растениях, новые мишени miRNA и их сложные взаимосвязи с комплексом HSF-HSP остаются малоизученными. В данном обзоре мы исследуем тепловые реакции HSF-HSP в Hordeum vulgare и Arabidopsis thaliana, акцентируя внимание на их регуляции miRNA в условиях теплового стресса.

Ключевые слова: малые РНК (sRNA), белки теплового шока (HSP), микрорНК (miRNA), абиотический стресс, факторы теплового шока (HSF), регуляция генов

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