Thermomorphogenesis: Opportunities and challenges in posttranscriptional regulation

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ABSTRACT

Plants exposed to mildly elevated temperatures display morphological and developmental changes collectively termed thermomorphogenesis. This adaptative process has several undesirable consequences to food production, including yield reduction and increased vulnerability to pathogens. Understanding thermomorphogenesis is, thus, critical for understanding how plants will respond to increasingly warmer temperature conditions, such as those caused by climate change. Recently, we have made major advances in that direction, and it has become apparent that plants resource to a broad range of molecules and molecular mechanisms to perceive and respond to increases in environmental temperature. However, most of our efforts have been focused on regulation of transcription and protein abundance and activity, with an important gap encompassing nearly all processes involving RNA (i.e., posttranscriptional regulation). Here, I summarized our current knowledge of thermomorphogenesis involving transcriptional, posttranscriptional, and posttranslational regulation, focused on opportunities and challenges in understanding posttranscriptional regulation—a fertile field for exciting new discoveries.

HIGHLIGHT

There is an important knowledge gap, encompassing nearly all processes involving RNA, in our understanding thermomorphogenesis regulation, offering many opportunities for exciting new discoveries in posttranscriptional regulation, with manageable challenges.

KEYWORDS gene regulation; posttranscription; response to temperature; RNA decay; thermomorphogenesis; translation

INTRODUCTION

Climate change is an increasing threat to biodiversity and food security. Rises in global average temperature is a major consequence of climate change, with significant impact on plant development, growth, and defence (Porter and Semenov, 2005; Hatfield and Prueger, 2015; Velásquez *et al.*, 2018; Gil and Park, 2019; Lippmann *et al.*, 2019; Exposito-Alonso *et al.*, 2019). In response to elevated temperatures that are still within the physiological range (~24-30^{0}C for the plant model Arabidopsis), plants undergo a process known as thermomorphogenesis that is characterized by morphological and developmental changes (e.g., elongation of hypocotyl, leaf, leaf petiole and primary root, and hyponasty) (Delker *et al.*, 2014*b*; Quint *et al.*, 2016). These growth responses to relatively low increases in temperature are particularly important in the context of climate change, because plants are now growing in environments that are becoming slowly and steadily warmer than in the past. Importantly, plant response to elevated temperatures above the physiological range (i.e., heat stress) is phenotypically unrelated to thermomorphogenesis, can be lethal, and better models the effect of heat waves, instead of continuous warmer conditions (Box 1).

Here, I present an overview of our current understanding of how plants regulate their response to elevated temperatures and discuss opportunities and challenges in posttranscriptional regulation—a fertile field for exciting new discoveries in thermomorphogenesis.

CURRENT UNDERSTANDING OF THERMOMORPHOGENESIS REGULATION

What we know about thermomorphogenesis regulation

In the past few years, we have gained substantial understanding on how plants perceive and adapt to elevated temperatures (see key recent developments in Box 2). However, we clearly still don't know the scope of perception mechanisms, possibly because of substantial challenges associated with the identification of sensing molecules (e.g., protein, RNA, lipid, DNA, and cofactor) that directly and specifically respond to increases in temperatures with regulatory consequence. The better characterized example is phyB, a photoreceptor sensitive to red/far-red (R/FR) ratio that exists in two interconvertible forms. Red light absorption induces conformational changes that shifts the inactive (Pr) to active (Pfr) form, while far-red promotes its reversion from Pfr to Pr, inactive form (Quail *et al.*, 1995; Burgie and Vierstra, 2014). Elevated temperatures also promote phyB reversion to its inactive form Pr, a process called thermal reversion (Jung *et al.*, 2016; Legris *et al.*, 2016). Red light-activated phyB promotes degradation of the transcription factor family PYTOCHROME INTERACTING FACTORs (PIFs) (Lorrain *et al.*, 2007) and, therefore, when phyB is inactive (high R/FR ratio or elevated temperatures), PIFs accumulate and promote increased levels of the growth-stimulating hormone auxin (Koini *et al.*, 2009; Franklin *et al.*, 2011). Hence, phyB thermal reversion is a bona fide thermosensing mechanism in Arabidopsis, albeit its conservation is unknown. Another bona fide thermosensor is ELF3, a protein containing polyglutamine (polyQ) repeat embedded within a prion-like domain that undergoes temperature-dependent phase transition, rapidly and reversibly shifting from active (soluble) to inactive (droplets) in response to higher temperatures (Jung *et al.*, 2020). Natural variation in the ELF3

prion-like domain is associated with adaptation to native temperature conditions in plants (Jung *et al.*, 2020), suggesting that ELF3 thermosensing via phase transition might be a conserved mechanism. Elevated temperatures can also be sensed via conformational changes in *PIF7* mRNA, leading to increased translation efficiency at warm temperatures that is required for proper thermomorphogenic phenotype in Arabidopsis (Chung *et al.*, 2020).

It is remarkable the fast pace at which the thermomorphogenesis field has progressed in the past few years (Figure 1). To my knowledge, the first work to report null mutant with disrupted response to warm temperature was in 1998, describing the dependency of warm temperature response on auxin, where the authors show impaired thermomorphogenic phenotype in *AUXIN RESISTANT 1* (*AXR1*) and *TRANSPORT INHIBITOR RESPONSE 1* (*TIR1*) null mutants (Gray *et al.*, 1998). However, over half of the described thermomorphogenic mutants were published in the last three years, evidencing a strong momentum in recent years. Table 1 lists all currently known genes reported to result in thermomorphogenic phenotype in null Arabidopsis mutant plants. Except for *phyB*, *ELF3*, and *PIF7*, the listed genes have been described for their role in regulatory mechanisms downstream temperature perception. Strikingly, less than a handful of genes have been implicated in posttranscriptional regulation, while transcriptional and posttranslational regulation have yielded most known genes required for thermomorphogenic phenotype.

Gene expression, defined as a gene or combination of genes required for a phenotype, typically involves transcription, translation, and protein activity of given gene(s) in a defined condition. In thermomorphogenesis, regulation of transcription and protein activity have been extensively studied, as evidenced in Table 1, while mRNA fate after transcription (i.e., posttranscriptional regulation) in response to elevated temperatures is largely unknown. However, fine-tuning of protein abundance is a common theme in thermomorphogenesis, as well as in photomorphogenesis and clock-regulated processes. For instance, CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) and DE-ETIOLATED 1 (DET1) regulate protein abundance via proteasomal degradation of specific targets and are central players in both thermomorphogenesis and photomorphogenesis (Lau and Deng, 2012; Delker *et al.*, 2014*b*). Posttranscriptional regulation is a fundamental process in the modulation of protein abundance and, hence, likely a major regulatory step in gene expression in thermomorphogenesis.

What we (mostly) don't know about thermomorphogenesis

Many aspects of thermomorphogenesis regulation are still poorly understood and perhaps one of the most underappreciated is RNA regulation. A transcript undergoes numerous processes that offer important regulatory checkpoints. During transcription, precise definition of the transcription start site and termination, as well as splicing events, define the transcript primary sequence. RNA, however, is rarely a linear string of nucleotides in a cell; instead, RNA fold co-transcriptionally forming structures that can regulate splicing and all other downstream processes (Bushhouse *et al.*, 2022). Transcribed and folded RNA, bond to various proteins and potentially other molecules such as other RNAs, is then transported

to a subcellular space (cytoplasm, for mRNAs). An mRNA in the cytoplasm can be recruited for translation and will eventually be degraded via an RNA decay pathway. Therefore, transcriptional processes determining mRNA sequence identity and posttranscriptional modulating localization, translation, and stability are key in gene expression and offer major opportunities for phenotypical regulation in any biological context. Except for *PIF7* mRNA, the steps described above have not been characterized for their regulatory role in plant response to elevated temperatures.

OPPORTUNITIES IN POSTTRANSCRIPTIONAL REGULATION OF THERMOMORPHOGENESIS

Alternative splicing regulation

Although splicing occurs co-transcriptionally, it is typically considered a posttranscriptional process, providing a key regulatory step in gene expression. Environmental temperature has long been known to alter alternative splicing, particularly temperature extremes (reviewed in John et al., 2021). Elevated temperatures within physiological range (~27-30^{0}C for Arabidopsis) decreases the expression level of a particular splicing isoform of FLOWERING LOCUS M (FLM), namely FLM-β, involved in flowering repression, with consequent promotion of early flowering (Posé *et al.*, 2013; Lee *et al.*, 2013). At mildly warmer temperatures (i.e., 25^{0}C), most alternative splicing has been associated with epigenetic regulation involving histone H3 lysine 36 tri-methylation (H3K36me3), including in flowering time regulators (e.g., FLM, MAF2, and FCA) and circadian clock components (e.g., PRR3 and PRR7) (Pajoro *et al.*, 2017). There is also evidence that alternative splicing in response to

warmer temperatures involves PIF4, likely requiring HOOKLESS1 (HSL1) (Jin *et al.*, 2020), suggesting that control of transcript isoform is a core regulatory process in thermomorphogenesis.

small RNA regulation

Plant small RNAs (sRNAs), including small interfering RNA (siRNAs) and microRNAs (miRNAs), can modulate their target mRNAs stability or translation, both resulting in reduced protein levels (Bologna and Voinnet, 2014) and, although sRNAs play key role in development, growth, and plant adaptation, little attention has been given to their activity in thermomorphogenesis. Warm temperature reduces gene silencing, with less production of siRNAs likely caused by lowered SGS3 protein levels, exhibiting transgenerational epigenetic inheritance, evidencing a memory mechanism that might also influence plant defence in warm environments (Zhong *et al.*, 2013). However, another study showed that less than 1% of sRNA loci are differentially expressed in response to warmth, suggesting a rather specific role for sRNAs (Gyula *et al.*, 2018). In the same work, miRNAs such as miR169, which targets NF-YA transcription factors that regulated flowering, were shown to be regulated by warm temperature. Indeed, early flowering induction by warm temperatures has been shown to involve miRNA regulation in Arabidopsis (May *et al.*, 2013) and, possibly, tomato (Zhou *et al.*, 2016). It is possible that miRNAs also regulate root, hypocotyl, and leaf growth, fertility, yield, among others that are impacted by warm temperatures. Such knowledge can be valuable for crop improvement, because plant miRNAs and their targets are often conserved, and gene editing of target sites can be implemented for most crops. Hence, characterization of miRNA-target pairs involved in thermomorphogenesis might enable

genetic manipulation for increased protein levels of key players, without interfering with transcription.

Transcript stability regulation

RNA levels depend on transcription rate and RNA stability. RNA decay regulation modulates plant development (Xu and Chua, 2009), adaptation (Chantarachot *et al.*, 2020), and defence (Yu *et al.*, 2019), evidencing a critical role played by posttranscriptional regulation of RNA levels. Transcript stability is primarily determined by the 5′ 7-methylguanosine triphosphate (m^7G) cap and 3′ poly-(A) tail, and RNA decay usually initiates via 3′ poly-(A) tail removal (i.e., deadenylation) with consequent transcript degradation via either 5′-3′ exoribonuclease (i.e., decapping) or 3′-5′ exonuclease activity (Sorenson *et al.*, 2018). Importantly, RNA stability is specific, selective, and dynamic process (Gerstberger *et al.*, 2014; Perea-Resa *et al.*, 2016; Yu *et al.*, 2019). For instance, rice exposed to heat stress showed decrease in transcript stability that correlated with unfolding of RNA structure in response to the high temperature treatment, with no evidence for translational regulation (Su *et al.*, 2018). Also, RNA decay via the 5′-3′ exonuclease activity of XRN4 is required for proper circadian rhythm and *xrn4* mutants display long period phenotype for clock gene expression and leaf movement (Careno *et al.*, 2022), while light regulates mRNA stability of the clock gene CCA1 via RNA modification (Wang *et al.*, 2021). Although clock and light response interplay with warm temperature response, little is still known about RNA stability in thermomorphogenesis, albeit it is likely that tight control of RNA clearance is also an important process in the response to warm temperature.

Translational regulation

Transcript and protein abundance often don't correlate, particularly for tightly regulated genes, as a consequence of translational and posttranslational regulation. Translation itself is complex and can be modulated by a myriad of processes such as differential expression and protein modification of ribosomal subunits (Malik Ghulam *et al.*, 2022; Zhang *et al.*, 2022), ribosomal stalling and collision (Wan *et al.*, 2021), and stress granule formation (Kosmacz *et al.*, 2019). In turn, these processes are usually regulated by information in the mRNA sequence and structure, beyond the instructions for protein synthesis. In stress granule formation—a hallmark of heat stress—, translation is inhibited via subcellular arrest of mRNA to distinct loci formed by specific proteins that respond to stresses such as heat (Kosmacz *et al.*, 2019) and, importantly, this is a selective process that inhibit translation of specific subset of transcripts, as shown for heat stress response in wheat (Tian *et al.*, 2022*b*). However, little is known about the determinant features within specific transcripts for selective arrest in stress granules. Identification of sequence and RNA structural determinant features required for specific transport to stress granules might enable less disruptive genetic manipulation for crop improvement, with less risk for pleiotropic effect by avoiding manipulation of proteins involved in stress granules formation itself. The role of stress granules is, however, still speculative for plants exposed to warm physiological temperatures. In fact, translational regulation in response to warm temperature, with phenotypical consequence, has only been shown for *PIF7* mRNA so far. Hypocotyl elongation at elevated temperatures, an important thermomorphogenic trait, is primarily driven by PIF4, PIF7 and, to a lesser extent, PIF5 (Koini *et al.*, 2009; Fiorucci *et al.*, 2020*a*; Chung *et al.*, 2020). *PIF7* mRNA has been shown to form a temperature-dependent inhibitory

structure at its 5′ untranslated region (Chung *et al.*, 2020). At lower ambient temperatures, the inhibitory structure is formed, while elevated temperatures disrupt it, leading to increased *PIF7* translational efficiency at warm temperatures and consequent thermomorphogenic response. Only few studies in plant science incorporate translation analysis, as compared to the large majority that analyses transcript steady-state levels, and it is, thus, possible that translational regulation will remain relatively overlooked in thermomorphogenesis for longer than most regulations that require changes in transcript levels.

Regulation via RNA modification

Study of RNA modification is a hot field, with continuous technical advances and new evidence for biological relevance. N^6-methyladenosine (m^6A), the most abundant and well-characterized mRNA modification in plants and animals, has been shown to regulate the circadian clock via photoreceptor cryptochromes (Wang *et al.*, 2021). Further, disruption of the methyltransferase FIONA1 leads to phytochrome signalling-dependent hypocotyl elongation and photoperiod-independent early flowering (Sun *et al.*, 2022; Wang *et al.*, 2022), and FIONA1-dependent m^6A modification of *FLOWERING LOCUS C* (*FLC*) transcript is important for *FLC* mRNA stability (Sun *et al.*, 2022). In human, it has been recently shown that m^6A modification can guide DNA demethylation, leading to reprogrammed chromatin accessibility and gene transcription (Deng *et al.*, 2022). In addition to m^6A, several other modifications play major role in gene expression regulation, including pseudouridylation (Ψ) and 5-methylcytosine (m^5C) (Anreiter *et al.*, 2021). Currently, however, the role of RNA

modification in thermomorphogenesis is still speculative and likely represents an interesting research opportunity.

CHALLENGES IN THERMOMORPHOGENESIS REGULATION

Our understanding of thermomorphogenesis regulation is advancing at very fast pace (Figure 1) and it is apparent that previous knowledge in photobiology, chronobiology, and plant development have been the main drivers until now. Indeed, plant response to elevated temperatures closely resembles shade avoidance (photobiology), carbon allocation for growth is tightly regulated by biological rhythms (chronobiology), and plant architecture and developmental transitions are regulated by environmental temperature. Thermomorphogenesis regulation, however, has its own particularities. For instance, elevated temperature triggers different molecular response in root, hypocotyl, and shoot (Bellstaedt *et al.*, 2019; Borniego *et al.*, 2022; Costigliolo Rojas *et al.*, 2022), implicating that studies should avoid combining different plant tissues in given samples (e.g., whole seedling analysis) to minimize confounding variables that can bias the results. It is possible that initial perception of environmental temperature further displays tissue or cell type specificity, e.g., more pronounced in epidermis because of its close contact with air (aboveground organs) and soil (root), in which case the discovery and characterization of thermosensors will likely benefit from approaches involving single cell analysis and others that increase signal-to-noise ratio for cell-specific molecular responses. It can be speculated that a main challenge

in thermomorphogenesis regulation will soon be our ability to shift from whole plant or tissue to single cell studies.

Posttranscriptional regulation

Posttranscriptional regulation of mRNAs primarily involves translation and transcript stability. Factors such as mRNA transport, subcellular localization, partnering proteins, modification, and structure are usually the mechanisms underlying posttranscriptional regulation. Compared to healthcare, research in plant biology is limited by a narrow range of commercially available antibodies, difficulting analyses of protein levels and leading to gaps in our knowledge of how much of a given transcript results in protein accumulation. This is further constraint by the reduced number of research groups that produce data on translation and transcript stability. Consequently, most works on thermomorphogenesis present data on transgenic plants expressing tagged proteins that likely lack some of the native regulatory elements, as well as are focused mostly on steady-state transcript levels (RT-qPCR and RNA-seq). Therefore, a main challenge in studying posttranscriptional regulation in response to warmth is the availability of data that accurately describes the native state of mRNAs, including all endogenous regulatory elements without biases introduced with typical transgenic expression (e.g., lack of untranslated regions, UTRs, and incomplete sequence because of poor gene annotation).

RNA structure has been shown to modulate virtually all processes involving RNAs, from transcription initiation (Wu *et al.*, 2020) and termination (Wanrooij *et al.*, 2010; Breaker, 2012),

to splicing (Cheah *et al.*, 2007; Warf *et al.*, 2009; Oikawa *et al.*, 2010; Yang *et al.*, 2011; Kar *et al.*, 2011), localization (Gonsalvez *et al.*, 2005; Mayer *et al.*, 2008; Aragón *et al.*, 2009; Chao *et al.*, 2010; Bullock *et al.*, 2010; Subramanian *et al.*, 2011), translation control (Mortimer *et al.*, 2014; Reis *et al.*, 2021), and RNA decay (Winkler *et al.*, 2004; Badis *et al.*, 2004; Prouteau *et al.*, 2008; Fukuchi and Tsuda, 2010). In addition to be a fundamental property of RNAs, RNA structure is formed co-transcriptionally (Bushhouse *et al.*, 2022) and, hence, blurs the line between transcriptional and posttranscriptional regulation, given that structure regulates processes that are typically thought as transcriptional, such as transcription initial and termination, and splicing. Because RNA structure formation and stability are highly dependent on temperature (Wan *et al.*, 2012; Becskei and Rahaman, 2022), it is possibly that changes in structure conformation plays a broad, yet largely unexplored regulatory role in thermomorphogenesis. Although there have been major technical advances enabling transcriptome-wide interrogation of RNA structures (Ding *et al.*, 2014), the incorporation of *in vivo* RNA structural analysis to understand posttranscriptional regulation is still challenging and demands specific experimental setup and data analysis.

CONCLUSIONS

Each 1^0C increase in global average temperature is consequential for crop yield and can lead to serious food security problems (Zhao *et al.*, 2017). Thermomorphogenesis describes a collection of phenotypical changes common to most plants grown in mildly warmer environments that, to a great extent, is similar to observed consequences of global warming

on crop plants (Parent and Tardieu, 2012). Understanding the molecular mechanisms that regulate thermomorphogenesis is critical and timely. The plant community has been active on this topic, as evidenced by a strong upwards momentum in newly discovered players in plant response to elevated temperatures. However, there are still important gaps that have not been given proper attention yet, including the role of posttranscriptional regulation (Box 2).

Effective understanding of thermomorphogenesis regulation requires the inclusion of multiple expertise, but also the adoption of various technical approaches by the broader community, such as analysis of translation and transcript stability, as well as *in vivo* RNA structure. Detailed mechanistic understanding when involving posttranscriptional regulation will likely require collaborative effort in most cases, because of the need to study mRNA features (e.g., RNA modification, structure, and binding sites) that often requires specialised expertise. Because there has still been little advance in the identification and characterization of posttranscriptional regulation in thermomorphogenesis, the study of regulatory processes involving RNA is a fertile field for exciting new discoveries.

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CONFLICT OF INTEREST

The author declares no conflict of interest.

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BOXES

Box 1. Thermomorphogenesis and global warming: what's the link?

Global warming leads to two main changes in environmental temperature: increases in heat wave frequency and mild increases in global average temperature. Heat waves can be lethal for plants and have been extensively studied (Ohama *et al.*, 2017), while mild temperature increases are not lethal and are much less understood. Modelling plant response to heat waves in the laboratory is not experimentally complex because precise control of temperature is usually not relevant, and phenotype typically involve growth arrest that is straightforward to be scored. Modelling response to mild temperature increases, however, requires certain temperature precision (usually 27-30^{0}C vs 20-23^{0}C, for Arabidopsis), and phenotype is characterized by specific morphological and developmental changes, termed thermomorphogenesis (Casal and Balasubramanian, 2019; Delker *et al.*, 2022). Therefore, the study of thermomorphogenesis is associated with global warming effect on average temperatures and is unrelated to heat stress and response to heat waves. Indeed, it is apparent that our extensive knowledge in plant heat stress provides limited help in the understanding of how plants adapt to warmth. Furthermore, it can be argued that crop plants improved for heat wave response will not solve the yield problem—typically reduced with warmth. For effective measures towards global warming-resilient plants, it is essential that we tackle both heat stress response and thermomorphogenesis.

Box 2: Key developments in understanding posttranscriptional regulation in thermomorphogenesis

(A) Chung et al. (2020) identified a hairpin structure in the *PIF7* 5′ UTR, near the translation initiation site, that functions as an RNA thermometer by shifting its conformation in warmer temperature, thereby enhancing *PIF7* translation, that is necessary for thermomorphogenic phenotype. Currently, this is the only direct evidence for translational regulation in thermomorphogenesis.

(B) Zhong et al. (2013) identified SGS3, required for the amplification of small interfering RNAs (siRNA)s, as involved in the response to warm temperature. This work points towards a largely untapped role for siRNAs in thermomorphogenesis.

(C) Pajoro et al. (2017) and Jin et al. (2020) showed that H3K36me3 and PIF4, respectively, are involved in alternative splicing regulation in response to warm temperature. Hence, it is possible that splicing is a major regulatory checkpoint in thermomorphogenesis.

Box 3: Outstanding questions in posttranscriptional regulation in thermomorphogenesis

- miRNAs are key regulators of development and adaptation. Which miRNAs and regulatory networks are involved in plant response to elevated temperatures?
- Transcript level (steady state) is a snapshot of transcription rate and RNA stability integrated outcome. What is the role of RNA decay pathways in plant response to warmth? How do elevated temperatures modulate mRNA stability?
- Protein abundance often does not correlate with transcript level, in part because of translational regulation. How is translation regulated by warmth? Are changes in RNA structure a common feature of translational control by warmth? What are the proteins involved in translational control by warmth?
- mRNA can be chemically modified to acquire specific protein binding partners. What are the relevant RNA modifications in thermomorphogenesis? How does RNA modification modulate plant response to elevated temperatures?
- Alternative splicing can modulate mRNA regulation and protein composition, including protein localization and activity. How does mRNA isoform diversity contribute to thermomorphogenesis? What are the specific alternative splicing isoforms involved in plant response to elevated temperatures?

FIGURES

Figure 1. The recent surge of thermomorphogenesis. Number of publications describing mutants with thermomorphogenic phenotype across the years (see Table 1), and number of articles mentioning the term “thermomorphogenesis” (Scholar Google).

Figure 2. Depiction of critical regulations in thermomorphogenesis. Illustration of processes involved in transcriptional, posttranscriptional, and posttranslational regulation, listing known factors required in thermomorphogenesis (blue; see Table 1).

TABLE

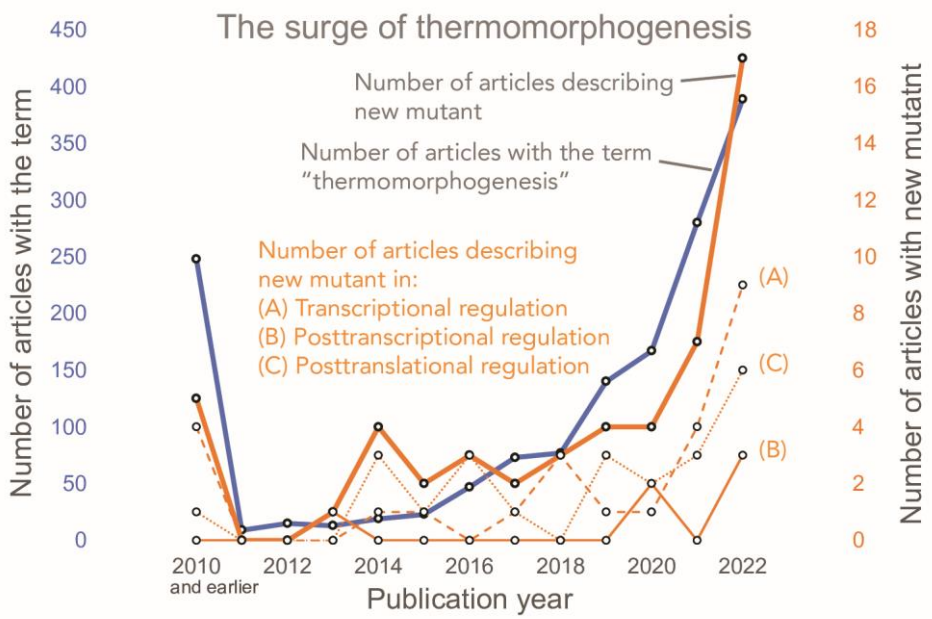
Table 1. Genes associated with thermomorphogenic phenotype in Arabidopsis.

Gene name	Short name	Regulatory mechanism in response to temperature	Reference
Transcriptional regulation			
AUXIN RESISTANT 1	AXR1	Transcriptionally regulated	(Gray *et al.*, 1998)
BRASSINAZOLE RESISTANT 1	BZR1	Transcription of targets	(Ibañez *et al.*, 2018)
BRI1-EMS-SUPPRESSOR 1	BES1	Transcription of targets	(Costigliolo Rojas *et al.*, 2022)
CENTROMERIC HISTONE H3	cenH3	Haploid induction	(Ahmadli *et al.*, 2022)
CRYPTOCHROME 2	CRY2	Unknown	(Sanchez-Bermejo *et al.*, 2015)
EARLY FLOWERING 7	ELF7	Transcription elongation factor	(Zhao *et al.*, 2023)
EARLY FLOWERING 8	ELF8	Transcription elongation factor	(Zhao *et al.*, 2023)
ELONGATED HYPOCOTYL 5	HY5	Transcription of targets	(Delker *et al.*, 2014*a*)
HISTONE H3.3	H3.3	Epigenetic	(Zhao *et al.*, 2023)
HISTONE H2A PROTEIN 9	H2A.Z	Epigenetic	(Xue *et al.*, 2021)
HISTONE DEACETYLASE 6, 9, 15, and 19	HDA6, HDA9, HDA15, and HDA19	Epigenetic	(Tasset *et al.*, 2018; Shen *et al.*, 2019)
HOOKLESS1	HSL1	Transcription of targets	(Jin *et al.*, 2020)
INO80 ORTHOLOG	INO80	Epigenetic	(Xue *et al.*, 2021)
ISOCHRISMATESYNTHASE1	ICS1	Transcription of targets	(Samaradivakara *et al.*, 2022)
JASMONATE INSENSITIVE 1	JIN1/MYC2	Transcription of targets	(Agrawal *et al.*, 2022)
KINETOCHORE NULL 2	KNL2	Haploid induction	(Ahmadli *et al.*, 2022)
LATE ELONGATED HYPOCOTYL	LHY	Transcription of targets	(Gould *et al.*, 2006)
LONG HYPOCOTYL IN FAR-RED	HFR1	Transcription of targets	(Shen *et al.*, 2019)
MEDIATOR COMPONENTS 14 and 17	MED14 and	Transcription initiation	(Agrawal *et al.*, 2022; Bajracharya *et*

	MED17		*al.*, 2022)
NON RACE-SPECIFIC DISEASE RESISTANCE 1	NDR1	Transcription of targets	(Samaradivakara *et al.*, 2022)
PHYTOCHROME INTERACTING FACTOR 4	PIF4	Transcription of targets	(Koini *et al.*, 2009)
POWERDRESS	PWR	Epigenetic	(Tasset *et al.*, 2018)
REVEILLE 5 and 7	RVE5 and RVE7	Transcription of targets	(Tian *et al.*, 2022*a*; Li *et al.*, 2023)
SUPPRESSOR OF NPR1-1, CONSTITUTIVE 1	SNC1	Transcription of targets	(Gangappa *et al.*, 2017)
SUPPRESSOR OF TY'S 4	SPT4	Transcription elongation	(Xue *et al.*, 2021)
SUPPRESSOR OF TY'S 5	SPT5	Transcription elongation	(Xue *et al.*, 2021)
TRANSPORT INHIBITOR RESPONSE 1	TIR1	Transcriptionally regulated	(Gray *et al.*, 1998)
TCP FAMILY TRANSCRIPTION FACTOR 4	TCP4	Transcription of targets	(Saini *et al.*, 2022)
Posttranscriptional regulation			
LAMMER kinases (AT4G24740)	AFC2	Alternative splicing	(Lin *et al.*, 2022)
FLOWERING LOCUS M	FLM	Alternative splicing	(Jin *et al.*, 2022)
HOOKLESS1	HSL1	Alternative splicing	(Jin *et al.*, 2020)
PHYTOCHROME INTERACTING FACTOR 7	PIF7	RNA conformational changes and transcription of targets	(Fiorucci *et al.*, 2020*b*; Chung *et al.*, 2020)
SUPPRESSOR OF GENE SILENCING 3	SGS3	Gene silencing	(Zhong *et al.*, 2013)
SUPPRESSOR OF MAX2 1	SMAX1	Reduced protein levels by unknown mechanism (partially via proteasome)	(Park *et al.*, 2022)
Posttranslational regulation			
LAMMER kinases (AT4G24740)	AFC2	Protein modification (phosphorylation)	(Lin *et al.*, 2022)
CONSTITUTIVE PHOTOMORPHOGENIC 1	COP1	Protein ubiquitination (degradation)	(Delker *et al.*, 2014*a*; Park *et al.*, 2017; Nieto *et al.*, 2022)
CRYPTOCHROME 1	CRY1	Protein-protein interaction with PIF4	(Ma *et al.*, 2016)
CYCLING DOF FACTOR 2	CDF2	Protein-protein	(Gao *et al.*, 2022)

		interaction with PIF4	
DE-ETIOLATED 1	DET1	Protein ubiquitination (degradation)	(Delker *et al.*, 2014*a*)
EARLY FLOWERING 3	ELF3	Phase transition	(Box *et al.*, 2015; Raschke *et al.*, 2015; Jung *et al.*, 2020)
EARLY FLOWERING 4	ELF4	Protein movement	(Chen *et al.*, 2020)
FLOWERING CONTROL LOCUS A	FCA	Protein-protein interaction with PIF4	(Lee *et al.*, 2014)
GIGANTEA	GI	Chaperone activity (protein target stabilization)	(Gould *et al.*, 2006; Park *et al.*, 2020; Kim *et al.*, 2020)
HEMERA	HMR	Protein-protein interaction with PIF4	(Qiu *et al.*, 2019; Bajracharya *et al.*, 2022)
HEAT-SHOCK PROTEIN 90	HSP90	Chaperone activity	(Zeng *et al.*, 2023)
HISTONE REGULATORY HOMOLOG A	HIRA	Chaperone activity	(Zhao *et al.*, 2023)
ANTI-SILENCING FUNCTION 1	ASF1	Chaperone activity	(Zhao *et al.*, 2023)
KIP-RELATED PROTEIN1	KRP1	Kinase inhibitor?	(Saini *et al.*, 2022)
PHOTOPERIODIC CONTROL OF HYPOCOTYL 1	PCH1	Protein-protein interaction with phyB	(Huang *et al.*, 2019; Murcia *et al.*, 2021)
PHYTOCHROME B	phyB	Protein conformational change	(Jung *et al.*, 2016; Legris *et al.*, 2016)
REGULATOR OF CHLOROPLAST BIOGENESIS	RCB	Protein-protein interaction with HMR	(Qiu *et al.*, 2021)
SHORT VEGETATIVE PHASE	SVP	Protein-protein interaction with specific FLM isoform	(Jin *et al.*, 2022)
TANDEM ZINC KNUCKLE PROTEIN	TZP	Protein localization of phyB (nuclear body)	(Fang *et al.*, 2022)
TARGET OF TEMPERATURE 3 TOT3		Protein modification (phosphorylation)	(Vu *et al.*, 2021)
TEOSINTE BRANCHED 1/CYCLOIDEA/ 132	TCP5, TCP13,	Protein-protein interaction with	(Han *et al.*, 2019; Zhou *et al.*, 2019)

PROLIFERATING CELL FACTORS 5, 13, and 17	and TCP17	PIF4 and CRY1	
TIMING OF CAB EXPRESSION 1	TOC1	Protein-protein interaction with PIF4	(Zhu *et al.*, 2016)
TOT3-INTERACTING PROTEIN 4 and 5	TOI4 and TOI5	Protein modification (phosphorylation)	(Vu *et al.*, 2021)
UVB-RESISTANCE 8	UVR8	Protein-protein interaction with COP1	(Hayes *et al.*, 2017)
WRKY DNA-BINDING PROTEIN 14, 35, 65, and 69	WRKY14, WRKY35, WRKY65, and WRKY69	Protein-protein interaction with TCP5	(Qin *et al.*, 2022)
ZEITLUPE	ZTL	Protein ubiquitination (degradation)	(Kim *et al.*, 2020)



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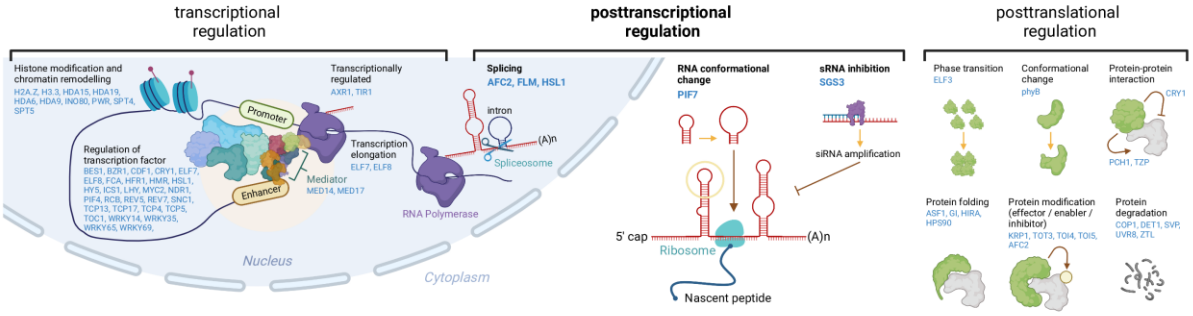

Figure 2. Depiction of critical regulations in thermomorphogenesis. Illustration of processes involved in transcriptional, posttranscriptional, and posttranslational regulation, listing known factors required in thermomorphogenesis (blue; see Table 1).