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REVIEW PAPER

The impact of light and temperature on chromatin organization and plant adaptation

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Abstract

Light and temperature shape the developmental trajectory and morphology of plants. Changes in chromatin organization and nuclear architecture can modulate gene expression and lead to short- and long-term plant adaptation to the environment. Here, we review recent reports investigating how changes in chromatin composition, structure, and topology modulate gene expression in response to fluctuating light and temperature conditions resulting in developmental and physiological responses. Furthermore, the potential application of novel revolutionary techniques, such Hi-C, RNA fluorescence *in situ* hybridization (FISH) and padlock-FISH, to study the impact of environmental stimuli such as light and temperature on nuclear compartmentalization in plants is discussed.

Keywords: Chromatin regulation, flowering, gene expression, light signalling, nuclear organization, photomorphogenesis, thermomorphogenesis.

Introduction

To ensure successful growth and reproduction, plants have to adapt to the prevailing abiotic and biotic conditions in their environment, anticipate possible future changes, and yet maintain the flexibility to react to short-term fluctuations. For light in particular this is extremely important, as photoautotroph plants are acutely sensitive to changes in the quantity and quality of light available. For example, a plant may have to adapt to shade [reduced light levels, shifts in red:far red (R:FR) and blue:green light ratios, and absence of UV-B], use the duration of light perceived (daylength) to predict when best to flower, and react at a local level to short-term fluctuations in light associated with breaks in the canopy (sunflecks).

In addition to light, temperature is a key regulator of growth and can confer similar information about the environment: temperature typically rises/falls on a diurnal basis, changes over the course of a season, and also fluctuates according to the weather. Integrating these systems can add a layer of robustness and fine-tuning plant responses to changing conditions (Franklin *et al.*, 2014). Furthermore, the downstream effects of light and temperature also overlap; the phenotypes and developmental changes associated with the shade avoidance response and high temperatures have similar features (elongated hypocotyls, petioles and stems, leaf serration, and reduced vegetative phase) (Casal, 2012).

Many of these long-term adaptations and short-term reactions to light and temperature are underpinned by changes in gene expression (Franklin *et al.*, 2014; Wu, 2014). It is therefore no surprise that along with changes associated with transcription, splicing, and mRNA stability, alterations in chromatin organization driven by histone modifications and

nuclear compartmentalization of gene loci are also vital for plant responses. This review focuses primarily on recent reports investigating how external stimuli such as light and temperature drive specific histone modifications, gene relocation, as well as nuclear morphology, and how such changes trigger transcriptional regulation of plant development and architecture.

Light regulators shape plant adaptation

Light transmits key information about the environment which is crucial to plant adaptation and fitness as photoautotrophs. Photon absorbance occurs through the action of specialized proteins called photoreceptors [UV-RESISTANCE LOCUS 8 (UVR8) for UV-B; ZEITLUPE (ZTL), FLAVIN-BINDING KELCH REPEAT F-BOX 1 (FKF1), LOV KELCH PROTEIN 2 (LKP2), cryptochromes (cry), and phototropins for blue light; phytochromes (phy) for R/FR light)] which are localized throughout the plant and modulate all different aspects of light responses, thereby ensuring that the developmental transitions are set in a timely manner (Fiorucci and Fankhauser, 2017).

At the centre of environmental signal integration and regulation of plant growth, we often find a group of transcription factors called the PHYTOCHROME-INTERACTING FACTORs (PIFs) (Leivar and Monte, 2014). PIFs have the ability to integrate external signals such as light and temperature, and integral signals as well, in order to ultimately control various downstream morphogenic factors (Leivar and Monte, 2014). There are eight PIFs (PIF1–PIF8) in Arabidopsis (Pham *et al.*, 2018). These basic helix–loop–helix transcription factors can interact with the red and far-red light phytochrome photoreceptors (Leivar and Monte, 2014). PIF4 and PIF5 can also interact with CRY1 and CRY2 (Pedmale *et al.*, 2016). In response to elevated temperatures, PIF4 is essential for triggering some of the thermomorphogenic phenotypes, such as inducing the expression of genes which promote auxin biosynthesis and signalling, resulting in hypocotyl elongation (Fiorucci *et al.*, 2020). Recently the role of PIF7 in thermomorphogenesis has also been elucidated (Fiorucci *et al.*, 2020). More specifically, it has been demonstrated that both *pif4* and *pif7* mutants were not responsive to changes from ambient to elevated temperatures (Fiorucci *et al.*, 2020). Additionally there was an accumulation of PIF7 protein under higher temperatures combined with a reduction in *PIF7* transcripts, suggesting that elevated temperatures control PIF7 protein and gene transcripts in opposite manners (Fiorucci *et al.*, 2020). Thus it is believed that both PIF4 and PIF7 depend on each other and possibly are able to form heterodimers, an action which can lead to the regulation of the expression of genes such as *YUCCA8* and *INDOLE-3-ACETIC ACID INDUCIBLE* (*IAA29*), the latter being another auxin-responsive protein (Fiorucci *et al.*, 2020).

Ultimately, upon light perception, photoreceptors activate a series of transcriptional responses and clustering of key components. Nuclear organization therefore becomes crucial to initiate massive reprogramming to ensure that growth occurs uniformly throughout the plant (Fiorucci and Fankhauser, 2017).

It is through changes in chromatin composition, structure, and location described in this review that plants are able to modulate transcription both dynamically in response to fluctuating conditions and persistently for the regulation of longer term developmental and physiological changes. For example, on first emerging from soil and perceiving light, rapid and large-scale changes in histone modifications (reviewed in Barneche *et al.*, 2014) and gene expression (Ma *et al.*, 2001) trigger a drastic change in seedling morphology: hypocotyl growth ceases, the apical hook and cotyledons open, and chloroplasts develop. Crucially, this developmental change, known as photomorphogenesis, is entirely dependent on a light input, and without it etiolated phenotypes persist. Once seedlings have acclimatized to life in the light, they then have to contend with a heterogeneous light environment. The presence of competitors results in changes in the R:FR of light reaching nearby or shaded plants. This triggers a suite of morphological changes to increase the chances of some part of the plant escaping the cover, and in development to accelerate seed production (Fiorucci and Fankhauser, 2017). The duration and quality of light can also be used to inform plants about the time of day or season, allowing them to adjust physiology (e.g. photosynthesis), morphology (e.g. solar tracking), and development (e.g. flowering) accordingly. By integrating the signalling associated with different light qualities and quantities, along with input from the circadian clock and other endogenous systems, plants are able to tailor their morphology and developmental trajectories accordingly.

Light-regulated chromatin organization in plant nuclei

In higher organisms, the nucleus represents the centre of life, due to the enormous amount of information that is tightly organized within it and its ability to perceive and integrate environmental cues (Liu and Weigel, 2015).

The nucleus is organized in different compartments and is separated from the cytoplasm by a two-layer membrane called the nuclear envelope (NE). The NE is formed by the outer nuclear membrane (ONM) and the inner nuclear membrane (INM). The nuclear pore complex (NPC), embedded within the two membranes, is responsible for the transport of macromolecules between the nucleus and the cytoplasm (Groves *et al.*, 2018) (Fig. 1).

The primary information on light-regulated chromatin events comes from studies based on photomorphogenesis responses (Barneche *et al.*, 2014). Early studies have shown that in Arabidopsis cotyledons, the shift from dark to light correlates with an increase in nuclear size and number of chromocentres, punctate structures that include 'pericentromeric regions' of DNA that are mainly comprised of highly repetitive, non-coding 'satellite' DNA sequences. Such structures reach a maximum size after 24 h of light exposure (Bourbousse *et al.*, 2015) (Fig. 1). Whether the cotyledon specificity of such nuclear changes during de-etiolation can be attributed to the increased photosynthetic capacity and a possible retrograde signal produced in this tissue remains to be further investigated.

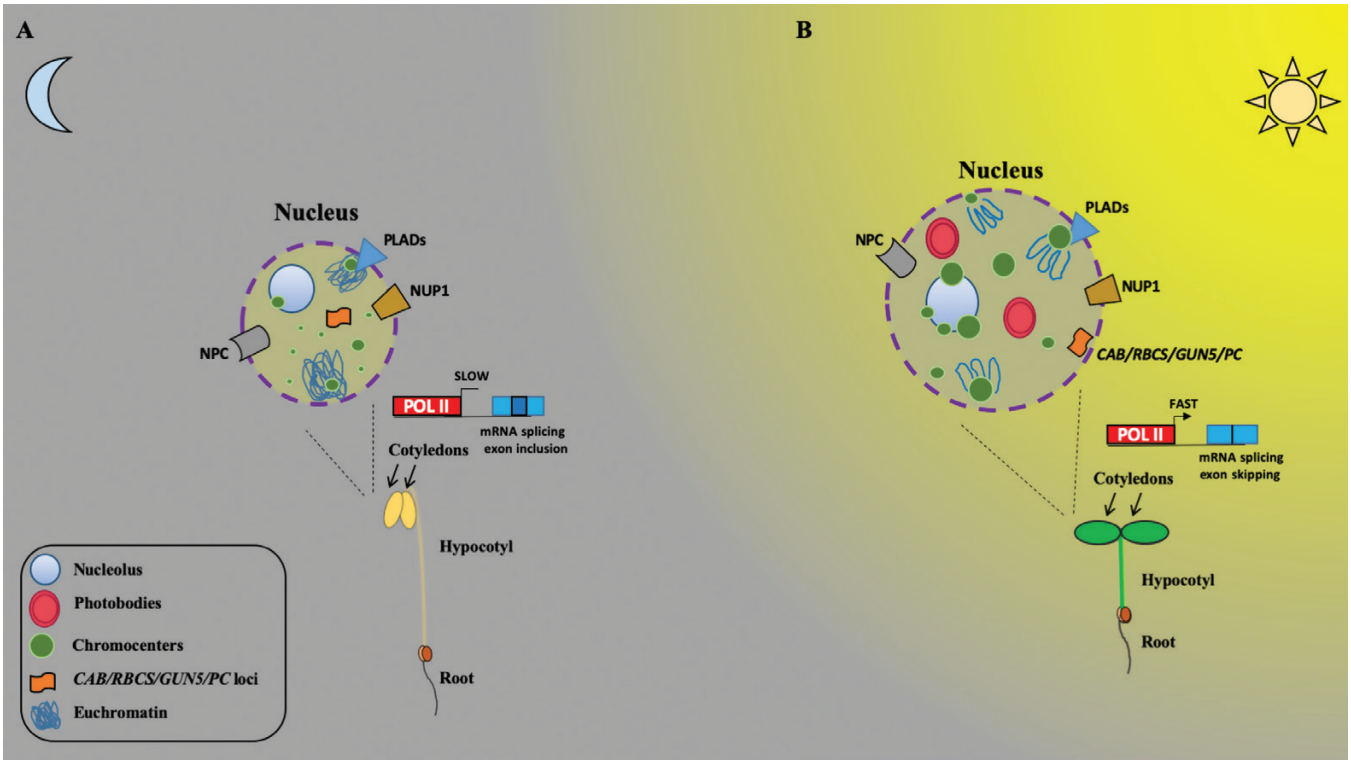

Fig. 1. Light affects plant nuclear events. (A) In the dark during skotomorphogenesis, the nucleus contains small chromocentres, the chromatin appears in a de-condensed state, and loci are located in the nuclear interior. The RNA polymerase II (Pol II) activity is slower and its elongation is decreased, precluding certain events of alternative splicing. (B) Upon light irradiation during de-etiolation, in the cotyledons the chromocentres and the nucleus increase in size, the chromatin is arranged in loops, and *CHLOROPHYLL A/B-BINDING* (*CAB*), *RUBISCO SMALL SUBUNIT* (*RBCS*), *GENOMES UNCOUPLED 5 (GUN5), and PLASTOCYANIN (PC)* loci are re-positioned to the nuclear periphery. Photoreceptors and light components are organized in photobodies. Pol II promotes fast elongation, thereby regulating mRNA splicing events. Other chromocentre dynamic events in response to low light and temperature are reported in the text. The subnuclear components are illustrated in the square box. NPC, nuclear pore complex; NUP1, nucleoporin 1; PLADs, plant lamin-associated domains.

Chromocentre organization is instead abolished in the absence of the blue light photoreceptors cry1 and cry2, suggesting that nuclear structures are mostly promoted by blue light (van Zanten *et al.*, 2012). Exposure of *cry1cry2* plants to low light showed a significant increase of the heterochromatin index compared with the wild type, indicating a stronger chromatin compaction (van Zanten *et al.*, 2010). Events of chromatin de-condensation have also been shown during flowering initiation, and biotic and abiotic stresses (Pavet *et al.*, 2006; Tessadori *et al.*, 2009; Pecinka *et al.*, 2010). In particular fluorescence *in situ* hybridization (FISH) displayed a dispersion of heterochromatin in Arabidopsis leaves subjected to long heat stress treatments (Pecinka *et al.*, 2010).

CONSTITUTIVE PHOTOMORPHOGENIC 1 and DE-ETIOLATED 1 are light signalling integrators responsible for de-condensed heterochromatin in etiolated cotyledons (Bourbousse *et al.*, 2015). COP1 is a RING E3 ubiquitin ligase that targets key regulators for degradation, including ELONGATED HYPOCOTYL 5 (HY5), LONG AFTER FAR-RED LIGHT 1 (LAF1), and LONG HYPOCOTYL IN FAR RED (HFR1). DET1 can form a complex with COP10 and DAMAGED DNA BINDING PROTEIN 1 (DDB1), aiding COP1-mediated degradation (Lau and Deng, 2012). *Cop1* and *det1* mutants displayed de-etiolation phenotypes under dark conditions, with small nuclei and increased numbers of conspicuous chromocentres, hence mirroring light-exposed wild-type plants. This observation suggests that either DET1 or COP1 is required to maintain chromatin in a de-condensed state during darkness. Bisulfite sequencing analysis and pharmacological treatments suggested no involvement of DNA methylation, whilst an increased level of Pol II activity was determined (Bourbousse *et al.*, 2015). Earlier work has also investigated these mechanisms, showing that the dark to light transition initiates a chloroplast retrograde signalling event responsible for alternative splicing for genes encoding proteins involved in RNA processing (Petrillo *et al.*, 2014). Furthermore, light promotes RNA polymerase II (Pol II) elongation, whilst such an event is mitigated by darkness (Godoy Herz *et al.*, 2019) (Fig. 1).

Taken together, this work has shown interesting examples of light-induced genetic events. DET1 and COP1 complexes operate to determine the right time and conditions for plants to develop. Coordination by the blue light signalling pathway further strengthens the importance of cryptochromes in these early developmental events. Developmental transitions as well as stress responses are inducers of loosening of chromatin compaction.

Histone modifications and light-regulated chromatin events

Histone acetylation

Nucleosome structure allows DNA packaging inside the nucleus. Histone acetylation mostly enhances transcriptional activity as it facilitates transcription factor binding through chromatin conformation changes leading to a permissive open state (Berger, 2007). The addition/removal of acetyl groups on histone tails is modulated by histone acetyltransferases (HATs) and deacetylases (HDACs), respectively. Histone acetylation may reduce the interaction between DNA and histones, allowing transcription factors to bind to specific DNA sequences, thereby initiating gene expression. Conversely, HDACs promote a tighter compaction between nucleic acids and histones leading to gene silencing (Perrella and Kaiserli, 2016). Early studies have shown a positive correlation between the acetylation state of histones and light perception. The antagonistic function between GENERAL CONTROL NON-DEREPRESSIBLE 5 (GCN5) and HISTONE DEACETYLASE19/HISTONE DEACETYLASE1 (HDA19/HD1) has been shown to modulate hypocotyl elongation under far-red light conditions (Benhamed *et al.*, 2006). Furthermore, polymorphisms in the DNA sequence of the *HISTONE DEACETYLASE 6* (*HDA6*) and the photoreceptor *PHYB* loci have been found in Arabidopsis accession Cape Verde Islands-0 (Cvi-0), which possesses low chromatin compaction (Tessadori *et al.*, 2009). HISTONE DEACETYLASE 15 has recently been shown to interact with the transcription factor HY5 to repress the transcription of hypocotyl growth-related genes, involved in cell wall organization and auxin signalling (such as *XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE PROTEIN 15*, *EXPANSIN 2*, and *INDOLE-3-ACETIC ACID INDUCIBLE19*), and therefore to promote photomorphogenesis (Shen *et al.*, 2019; Zhao *et al.*, 2019)). In detail, HDA15 can reduce the acetylation levels of such gene targets and therefore acts as a negative regulator of hypocotyl elongation.

Histone acetylation plays an additional role in the regulation of light-induced alternative splicing. Pharmacological treatment of Arabidopsis seedlings with trichostatin A (an inhibitor of HDACs) was shown to promote alternative splicing by determining Pol II elongation status during the dark to white light exposure (Godoy Herz *et al.*, 2019). ChIP-seq experiments indicated that the histone acetylation status of alternatively spliced genes *ARGININE/SERINE-RICH SPLICING FACTOR 31* (*At-RS31*) and *U2 SNRNP AUXILLIARY FACTOR 65* (*At-U2AF65*) does not change with light, suggesting that rather than being induced by light, histone acetylation only mimics the effect of light as global acetylation levels are also not affected by light conditions. Interestingly, a genetic approach suggested that other chromatin modifications, including histone and DNA methylation, were not involved in this process, revealing a unique function for this specific type of histone modification (Godoy Herz *et al.*, 2019).

Histone ubiquitination

Histone ubiquitination (HUB) is a reversible post-translational modification characterized by the addition and removal of ubiquitin moieties. In Arabidopsis, H2B proteins are monoubiquitinated on Lys143 or Lys145 by the HUB1/HUB2 E3 ubiquitin ligase, a homologue of the budding yeast Bre1 protein (Bourbousse *et al.*, 2012). Upon light perception, the levels of histone H2B ubiquitination (H2Bub) change dynamically and often correlate with an induction of the expression of light components such as *TANDEM ZINC KNUCKLE PLUS3* (*TZP*) (Bourbousse *et al.*, 2012). Recent studies have shown that DET1 is essential for the regulation of H2Bub in Arabidopsis (Nassrallah *et al.*, 2018). Mass spectrometry and immuno-blot analysis of histone modifications revealed a drastic reduction of H2Bub in the *det1-1* mutant compared with the wild type. Interaction studies postulated the presence of a trimeric complex, termed the de-ubiquitination module (DUBm), that mediates H2Bub deubiquitination in Arabidopsis and whose abundance is reduced in the dark in a DET1-dependent manner (Nassrallah *et al.*, 2018). More specifically, double mutant seedlings of *det1-1* and *ubiquitin protease* (*ubp*) *22-1* rescued the partial loss of ubiquitination observed in the *det1-1* single mutant, suggesting that DET1 counteracts the DUBm in H2Buq removal (Nassrallah *et al.*, 2018). Taken together, the data unveil a novel mechanism by which protein turnover modulates histone ubiquitination in a light-dependent manner.

Temperature-induced chromatin changes and their effect on plant development

Chromatin remodellers

The different temperatures which plants can be subjected to (ranging from low, to ambient and high temperatures) can significantly affect all stages of plant growth (Balasubramanian *et al.*, 2006; Quint *et al.*, 2016) and have a significant impact on crop yield as well (Peng *et al.*, 2004). At the molecular level, chromatin remodelling is implicated in temperature sensing (Tasset *et al.*, 2018). In the first instance, histone deacetylation plays a major role for plants to perceive, respond, and adapt to temperature changes (Tasset *et al.*, 2018). For example, it has been shown that repression of histone deacetylation prevents hypocotyl elongation under elevated temperatures (Tasset *et al.*, 2018). Another chromatin remodelling category is the exclusion or integration of H2A.Z nucleosomes (Quint *et al.*, 2016). The exclusion of the histone variant H2A.Z from nucleosomes is important for the increase in chromatin accessibility which leads to differences in gene expression under elevated temperatures (Kumar *et al.*, 2010; Coleman-Derr and Zilberman, 2012; Quint *et al.*, 2016; Cortijo *et al.*, 2017; Dai *et al.*, 2017). The integration of H2A.Z-containing nucleosomes in chromatin is controlled by ACTIN RELATED PROTEIN 6 (ARP6) (Quint *et al.*, 2016). Since *arp6* mutants show misregulation of several genes associated with responses to general environmental signals, it is speculated that H2A.Z

nucleosome dynamics are most likely also involved in the response to more general environmental cues (Quint *et al.*, 2016; Sura *et al.*, 2017). Very recently, a possible connection between histone deacetylation and H2A.Z nucleosome dynamics has been described (Tasset *et al.*, 2018). At the centre of this connection is the protein POWERDRESS (PWR), which can interact with HDA9, with this interaction being essential for the mediation of thermomorphogenic responses in Arabidopsis (Tasset *et al.*, 2018). PWR is known for having a putative role in mRNA splicing and it also contains a SANT domain (Yang *et al.*, 2019). SANT domains are protein domains which allow the interaction between chromatin-remodelling proteins and histones (Horton *et al.*, 2007). Specifically, increased temperatures induce H3K9 deacetylation of the +1 nucleosome of *PIF4* and *YUCCA8* loci (Tasset *et al.*, 2018; van der Woude *et al.*, 2019) which are both involved in temperature responses (Koini *et al.*, 2009; Franklin *et al.*, 2011; Sun *et al.*, 2012; Quint *et al.*, 2016), and *PWR* is required for this process (Tasset *et al.*, 2018). Furthermore meta-analysis of genes which are controlled by H2A.Z nucleosome dynamics and genes which are affected by a *pwr* mutation suggested an overlap, hinting at a link between these two chromatin-remodelling processes (Tasset *et al.*, 2018).

Recent reports showed that at ambient temperature HDA15 is a direct repressor of genes related to warmer temperature responses (Shen *et al.*, 2019). Specifically, HDA15 directly interacts with the transcription factor HFR1 in order to collectively repress thermomorphogenic responses (Shen *et al.*, 2019). On the other hand, HDA19 has a positive role in the expression of stress-responsive genes under elevated ambient temperatures (Shen *et al.*, 2019), whereas HDA9, which as mentioned before interacts with PWR (Tasset *et al.*, 2018), can promote thermomorphogenic gene expression via the action of other positive regulators and is required for their expression at higher temperatures (Shen *et al.*, 2019). It is even possible that at higher temperatures PWR might recruit HDA9 in order to mediate the deacetylation of histones at specific target genes (Shen *et al.*, 2019). Consequently through a HDA9-dependent network, H2A.Z is excluded from nucleosomes associated with genes required for plant growth such as *YUCCA8* (van der Woude *et al.*, 2019). The above observation leads to the conclusion that the histone deacetylation properties of HDA9 can facilitate the exclusion of H2A.Z without being the primary cause (van der Woude *et al.*, 2019).

One more important chromatin modification for providing functional diversity is histone methylation. Histone methylation can act as an activation mark, as shown for H3K4me3 and H3K36me3 marks (Greer and Shi, 2012). Recently a novel transcriptional regulator was reported to be a common integrator of light and temperature stimuli with an effect on the H3K4me3 methylation of the growth-stimulating genes *IAA6* and *IAA19* (Huai *et al.*, 2018). This transcriptional regulator, SEUSS (SEU), can also physically interact with PIF4, which as previously mentioned is implicated in light and high

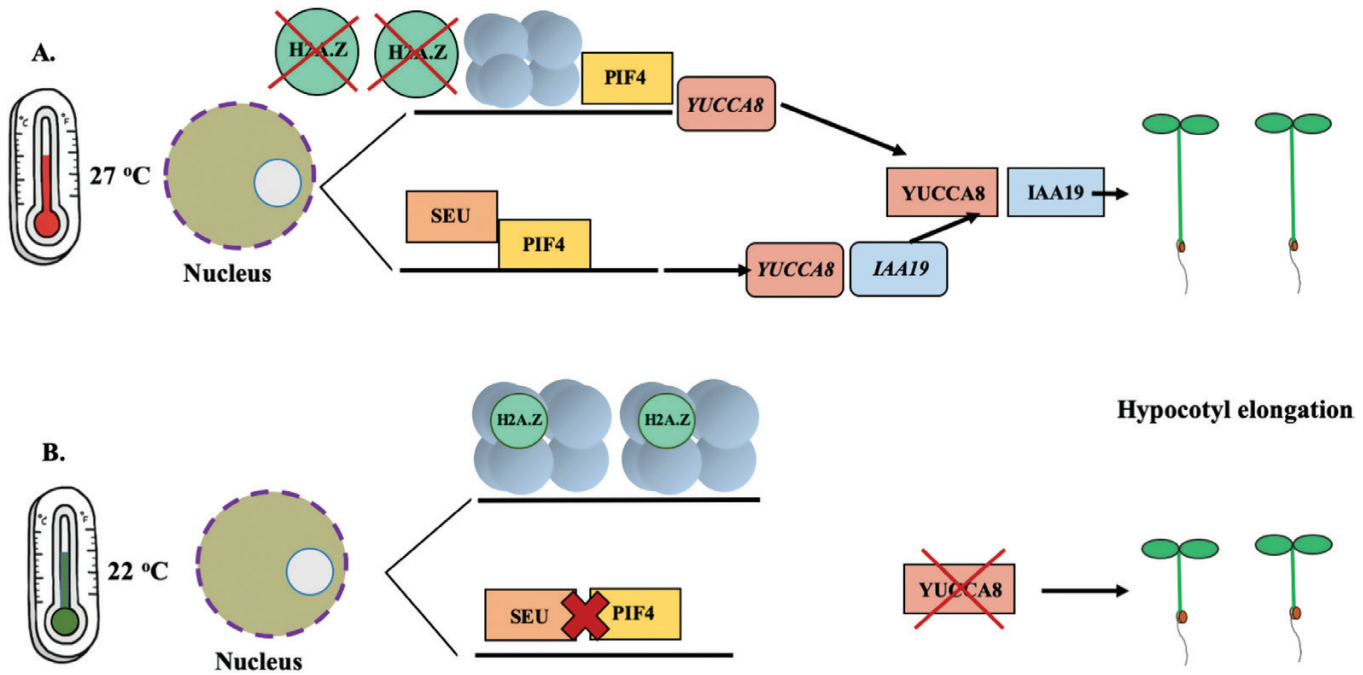

Fig. 2. Warm temperatures induce hypocotyl elongation in Arabidopsis. (A) Under elevated temperatures, several mechanisms ultimately lead to hypocotyl elongation. Specifically, H2A.Z exclusion from nucleosomes, which are associated with genes such as *YUCCA8*, permits the binding of PIF4 to the promoter of *YUCCA8* leading to the expression of the YUCCA8 protein that regulates auxin biosynthesis in response to warm temperatures and can induce hypocotyl elongation growth. Additionally, the interaction of transcription regulator SEUSS (SEU) with PHYTOCHROME INTERACTING FACTOR 4 (PIF4) also induces the activation of the *YUCCA8* gene and of the growth-stimulating gene *INDOLE-3-ACETIC ACID INDUCIBLE19* (*IAA19*), promoting hypocotyl elongation. (B) Under ambient temperatures, the repressive H2A.Z variant is incorporated in the nucleosomes and PIF4 cannot bind to the promoter of *YUCCA8*, therefore preventing gene activation. Similarly at 22 °C, the SEU–PIF4 complex is not formed, hence *YUCCA8* is not induced. As a consequence, there is no increase in hypocotyl elongation. Proteins are represented in square boxes and H2A.Z, a histone variant, in circles. Genes are represented in italics and boxes with rounded edges.

temperature responses (Huai *et al.*, 2018) (Fig. 2). This interaction is permitted under elevated temperatures, since warmer temperatures have the ability to repress the active form of the photoreceptor phyB, which in turn regulates both SEU and PIF4 (Huai *et al.*, 2018) (Fig. 2). More specifically, in the *seu* mutant, the levels of H3K4me3 methylated chromatin are reduced in *IAA19* and *YUCCA8* genes, compared with wild-type Arabidopsis (Huai *et al.*, 2018).

As previously described, H2A.Z plays a key role in regulating gene networks in response to environmental cues (Willige *et al.*, 2019, Preprint). H2A.Z, amongst other actions, has the ability to prevent any unwanted or unnecessary gene expression, thereby offering an additional checkpoint and plasticity in transcription (Willige *et al.*, 2019, Preprint). Temperature signals can also be mediated by H2A.Z nucleosomes (Kumar *et al.*, 2010, 2012). Even though the functional relationship between PIFs and H2A.Z in not well understood, it was recently reported that PIFs are involved in shaping the landscape of H2A.Z action (Willige *et al.*, 2019, Preprint). Specifically, it was observed that certain light signals, such as low R:FR, which are able to induce the binding of PIF7 to its DNA targets, as well as the eviction of H2A.Z at PIF7 target genes, display similar kinetics (Willige *et al.*, 2019, Preprint). It was further determined that the H2A.Z eviction required the DNA binding of PIF (Willige *et al.*, 2019, Preprint). Previously the role of H2A.Z as a mediator of temperature signals has been studied with regards to its role in affecting the accessibility of PIF4 binding to the flowering promoter *FT* (Kumar *et al.*, 2012). More specifically it was demonstrated that high temperatures reduce the levels of H2A.Z-containing nucleosomes at the *FT* locus, thus facilitating PIF4 binding to *FT* (Kumar *et al.*, 2012). Furthermore, it has been suggested that not all information from temperature signals is transmitted via H2A.Z nucleosomes, since *arp6* mutants, which control the chromatin integration of H2A.Z-containing nucleosomes, still show a level of thermomorphogenic response (Quint *et al.*, 2016).

Chromatin regulation of FLOWERING LOCUS C *(*FLC*)*

One of the most studied mechanisms of chromatin silencing occurs through the autonomous pathway and the silencing of the MADS-box transcriptional repressor of flowering, *FLOWERING LOCUS C* (*FLC*) (Michaels and Amasino, 2001; Wu *et al.*, 2019). This happens when plants are exposed to prolonged cold temperatures during the winter (Fornara *et al.*, 2010). When the temperature rises in spring, *FLC* is silenced to allow flowering-promoting genes to be activated and ultimately for flowering to occur (Fornara *et al.*, 2010). Another important protein for flowering regulation, FLOWERING LOCUS D (FLD), is a histone Lys4 demethylase and has the ability to associate with the chromatin on *FLC* and can lead to the demethylation of H3K4me2 in the main body of *FLC* (Wu *et al.*, 2016). The above demethylation happens with a simultaneous decrease in H3K36me3 and additional increase of H3K27me3 on the *FLC* locus (Wu *et al.*, 2019). The exact mechanism of the deposition of the H3K27me3 repressive mark is not yet fully deciphered (Wu *et al.*, 2019). It is known though, that H3K27me3 covers the entire locus of the *FLC* gene, from the transcriptional start site, up to the 3'-untranslated region (Wu *et al.*, 2019). The above is speculated to be a result of repressed transcription (Berry *et al.*, 2017; Laugesen *et al.*, 2019). FLD can also associate with HDA6 when bound to *FLC* chromatin, indicating a link between histone demethylation and histone deacetylation in the regulation of transcription (Yu *et al.*, 2011). Other proteins which have an H3K27me3 activity are CURLY LEAF (CLF) and SWINGER (SWN) (Lopez-Vernaza *et al.*, 2012), and mediate *FLC* repression during the vegetative phase of plant development (Chanvivattana *et al.*, 2004; Bouyer *et al.*, 2011). *Clf* mutants show a reduction in the H3K27me3 repressive mark and an up-regulation of *FLC* transcript levels (Lopez-Vernaza *et al.*, 2012). The Polycomb Repressive complex 2, members of which constitute the aforementioned proteins CLF and SWN, is also required for the silencing of *FLC* (Berry *et al.*, 2017; Portoso *et al.*, 2017; Laugesen *et al.*, 2019), since it is responsible for setting the H3K27me3 repressive mark (Schubert *et al.*, 2005). On the other hand, when *FLC* chromatin is active, it has low levels of H3K27me3 and high levels of H3K4me3, H3Ac, and also H3K36me3, which are histone marks associated with transcriptionally active chromatin (Wu *et al.*, 2019). The H3K36me3 methyltransferase *EARLY FLOWERING IN SHORT DAYS* is also required for the active expression of *FLC* (Hyun *et al.*, 2017).

Relocation of gene loci in response to light and temperature

In recent years, enormous progress has been made in understanding the impact of environmental stimuli on nuclear organization. Compared with yeast and metazoan models, little is known about the positioning of individual genes in plants. In that regard, the Chen lab has been a pioneer by applying the padlock-FISH technique on Arabidopsis nuclei. Using the aforementioned approach, the authors were able to monitor the position of photosynthetic gene loci such as *CHLOROPHYLL A/B-BINDING* (*CAB*), *RUBISCO SMALL SUBUNIT* (*RBCS*), *GENOMES UNCOUPLED 5 (GUN5),* and *PLASTOCYANIN (PC),* and, most importantly, their re-location from the nuclear interior to the nuclear periphery upon light activation (Feng *et al.*, 2014) (Fig. 1).

With regards to flowering initiation triggered by vernalization, Rosa and collaborators used single-molecule RNA FISH to monitor the *FLC* locus in Arabidopsis root nuclei through the combination of intronic and exonic RNA probes fused to fluorescent dyes (Rosa *et al.*, 2016). Interestingly, both *FLC* mRNA and the unspliced version showed a decrease in fluorescence correlated with longer exposure of plants to cold (Rosa *et al.*, 2016). Conversely, the levels of the antisense transcript *COOLAIR*, a cold-induced long antisense intragenic RNA that covers the entire *FLC* locus, were induced in response to low temperatures (Swiezewski *et al.*, 2009). In particular, *COOLAIR* pre-mRNAs were displayed as 'cloudy' signals, suggesting that the transcripts were induced and accumulated in a short time. Co-localization of both *FLC* and *COOLAIR* showed that both transcripts are mutually exclusive, suggesting that *COOLAIR* clouds block the accumulation or the

recruitment of the active histone mark H3K36me3, thereby facilitating *FLC* sense transcript repression (Wu *et al.*, 2016).

These findings have uncovered and linked transcriptional events with movements and re-location in the nucleus in response to light or temperature changes. Further work is required to expand the monitoring to other loci, light components, and their relationship with environmental cues.

Chromatin organization and chromosomal interactions

In eukaryotes, chromatin is enclosed and packaged in the nucleus following a specific hierarchy (Gibcus and Dekker, 2013). Altogether, chromatin architecture and conformation, including intra- and interchromosomal interactions, have a functional relevance to ensure genome integrity, DNA replication, and gene expression (Liu *et al.*, 2016). The use of advanced technologies such as the genome-wide high-resolution interaction map (Hi-C) combined with chromosome conformation capture (3C) has allowed the identification of chromosomal regions associated with lamin proteins named lamin-associated domains (LADs) in animals (Grob, 2019). LADs are known to be transcriptionally repressed chromatin regions depleted of active histone marks (van Steensel and Belmont, 2017; Leemans *et al.*, 2019). In plants, the lack of LADs is compensated by the presence of an association between the chromocentres and the nuclear periphery. Nucleoporins such as NUP1 which is a component of the nuclear basket of the NPC, are localized within the nuclear periphery (Bi *et al.*, 2017). ChIP experiments using mild sonication combined with enzyme digestions revealed that NUP1 regions are predominantly enriched with transposable elements and non-coding regions. Furthermore, unlike LADs, such regions are not AT rich; a typical feature of LADs (Bi *et al.*, 2017).

Lamin-like proteins have been identified in plants such as CROWDED NUCLEI proteins (CRWNs) that are also localized to the nuclear periphery, and are required for chromatin compartmentalization and positioning. ChIP-seq experiments showed a strong association between CRWNs and tightly packed chromatin domains that were therefore named plant LADs (PLADs) (Hu *et al.*, 2019) (Fig. 1). PLADs are enriched with intergenic regions and repressive chromatin marks that largely overlap with NUP1-dependent domains (Hu *et al.*, 2019).

Hi-C experiments have revealed the presence of topologically associating domains named TADs in animals and yeast. TADs are absent in Arabidopsis but they are found in more complex plant crop genomes including rice (Liu *et al.*, 2017). Further studies have shown that TADs can be associated with histone marks, including H3K27me3, and chromatin loops. Integration of results from both Hi-C maps and ChIP-seq data demonstrated a correlation between heterochromatin and histone repressive marks, with an enrichment primarily in the pericentrometric regions (Dong *et al.*, 2018). Plant TADs, however, do not contain CCCTC-binding factors, key regulators of animal TADs, calling into question the need for specific proteins to delineate the 3D chromosome structures. To answer this question, studies from the Barneche and Laloi labs have identified specific plant proteins that might act as insulators that ensure the distinction between transcriptionally active and inactive genomes (A/B compartments) (Grob *et al.*, 2014; Méteignier *et al.*, 2019, Preprint). Ongoing experiments using Hi-C approaches in multiple labs employing different genetic mutant backgrounds, light quality, quantity, and temperature parameters will cast light on how nuclear architecture and chromatin topology are organized at a genome-wide level in response to a changing environment.

Recent reports revealed that DNA topoisomerase VI plays a role in heterochromatin formation as *Topo VI* mutants lack chromocentres. Topo VI is also required for allowing H3K9me2 repressive marks to spread into euchromatin regions (Méteignier *et al.*, 2019, Preprint). Similarly, studies from the Baroux lab have also shown that depletion of H1 in plants affects heterochromatin formation and nucleosome density (Rutowicz *et al.*, 2019). However, these drastic changes only affect gene expression and plant development moderately, indicating a more structural function for the histone linker.

Extending the aforementioned revolutionary studies to investigate the impact of environmental stimuli such as light and temperature on nuclear compartmentalization and chromatin organization is key for understanding the molecular principles of plant adaptation at the nuclear level.

Future perspectives

Light and temperature can have huge impacts on the developmental trajectory and morphology of plants. With respect to long-term adaptations to the environment, changes in chromatin and nuclear architecture can lead to switches in gene expression that can be transmitted through cell division, ensuring a coordinated long-lasting response to a change in light condition. For example, developmental decisions such as photomorphogenesis and flowering are often irreversible once a critical point has been reached, with changes in chromatin providing a simple means by which genes whose expression is no longer needed can be efficiently shut down. In addition, chromatin regulation can also lead to rapid and temporary changes in gene expression. In this context, the rapid eviction of H2A.Z-containing nucleosomes under warm temperatures as well as the effect of histone modifications, modulate transcripts responsible for various plant responses including hypocotyl elongation (Bourbousse *et al.*, 2012; Cortijo *et al.*, 2017; Wu *et al.*, 2019). Indeed, even for more stable and predictable changes in the light environment, a quick response has the potential to give a plant a competitive edge.

It is key to understand how changing light and temperature regimes influence large-scale chromosomal interactions and gene topology, and how such events correlate with changes in gene expression underlying plant developmental transitions and plasticity. To achieve this, the application of novel revolutionary techniques such as advanced FISH and Hi-C on plants exposed to specific light and temperature conditions prior to and during key developmental and morphological transitions at a tissue-/organ-specific resolution is key. These studies would help us address questions such as the following. Are there wavelength- or temperature-induced TADs

in plant genomes? Does temperature also influence the position of genes from the nuclear periphery and, if so, does gene relocation correlate with changes in gene expression? What are the structural determinants that drive gene relocation and chromosomal interactions in plants in response to environmental stimuli? Is there stochasticity in higher order chromatin organization in plant species and, if so, how does it affect gene expression? Answering such questions will allow scientists to understand the molecular mechanisms of nuclear organization and genome regulation in plants and offer potential targets for crop improvement.

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References

Balasubramanian S, Sureshkumar S, Lempe J, Weigel D. 2006. Potent induction of *Arabidopsis thaliana* flowering by elevated growth temperature. PLoS Genetics **2**, 0980–0989.

Barneche F, Malapeira J, Mas P. 2014. The impact of chromatin dynamics on plant light responses and circadian clock function. Journal of Experimental Botany **65**, 2895–2913.

Benhamed M, Bertrand C, Servet C, Zhou DX. 2006. Arabidopsis GCN5, HD1, and TAF1/HAF2 interact to regulate histone acetylation required for light-responsive gene expression. The Plant Cell **18**, 2893–2903.

Berger SL. 2007. The complex language of chromatin regulation during transcription. Nature **447**, 407–412.

Berry S, Dean C, Berry S, Dean C, Howard M. 2017. Slow chromatin dynamics allow polycomb target genes to filter fluctuations in transcription factor activity. Cell Systems **4**, 445–457.e8.

Bi X, Cheng YJ, Hu B, Ma X, Wu R, Wang JW, Liu C. 2017. Nonrandom domain organization of the Arabidopsis genome at the nuclear periphery. Genome Research **27**, 1162–1173.

Bourbousse C, Ahmed I, Roudier F, Zabulon G, Blondet E, Balzergue S, Colot V, Bowler C, Barneche F. 2012. Histone H2B monoubiquitination facilitates the rapid modulation of gene expression during Arabidopsis photomorphogenesis. PLoS Genetics **8**, e1002825.

Bourbousse C, Mestiri I, Zabulon G, Bourge M, Formiggini F, Koini MA, Brown SC, Fransz P, Bowler C, Barneche F. 2015. Light signaling controls nuclear architecture reorganization during seedling establishment. Proceedings of the National Academy of Sciences, USA **112**, E2836–E2844.

Bouyer D, Roudier F, Heese M, *et al*. 2011. Polycomb repressive complex 2 controls the embryo-to-seedling phase transition. PLoS Genetics **7**, e1002014.

Casal JJ. 2012. Shade avoidance. The Arabidopsis Book **10**, e0157.

Chanvivattana Y, Bishopp A, Schubert D, Stock C, Moon YH, Sung ZR, Goodrich J. 2004. Interaction of Polycomb-group proteins controlling flowering in Arabidopsis. Development **131**, 5263–5276.

Coleman-Derr D, Zilberman D. 2012. Deposition of histone variant H2A.Z within gene bodies regulates responsive genes. PLoS Genetics **8**, e1002988.

Cortijo S, Charoensawan V, Brestovitsky A, Buning R, Ravarani C, Rhodes D, van Noort J, Jaeger KE, Wigge PA. 2017. Transcriptional regulation of the ambient temperature response by H2A.Z nucleosomes and HSF1 transcription factors in Arabidopsis. Molecular Plant **10**, 1258–1273.

Dai X, Bai Y, Zhao L, *et al*. 2017. H2A.Z represses gene expression by modulating promoter nucleosome structure and enhancer histone modifications in Arabidopsis. Molecular Plant **10**, 1274–1292.

Dong Q, Li N, Li X, *et al*. 2018. Genome-wide Hi-C analysis reveals extensive hierarchical chromatin interactions in rice. The Plant Journal **94**, 1141–1156.

Feng CM, Qiu Y, Van Buskirk EK, Yang EJ, Chen M. 2014. Light-regulated gene repositioning in Arabidopsis. Nature Communications **5**, 3027.

Fiorucci AS, Fankhauser C. 2017. Plant strategies for enhancing access to sunlight. Current Biology **27**, R931–R940.

Fiorucci AS, Galvão VC, Ince YÇ, Boccaccini A, Goyal A, Allenbach Petrolati L, Trevisan M, Fankhauser C. 2020. PHYTOCHROME INTERACTING FACTOR 7 is important for early responses to elevated temperature in Arabidopsis seedlings. New Phytologist **226**, 50–58.

Fornara F, de Montaigu A, Coupland G. 2010. SnapShot: control of flowering in Arabidopsis. Cell **141**, 3–5.

Franklin KA, Lee SH, Patel D, *et al*. 2011. Phytochrome-interacting factor 4 (PIF4) regulates auxin biosynthesis at high temperature. Proceedings of the National Academy of Sciences, USA **108**, 20231–20235.

Franklin KA, Toledo-Ortiz G, Pyott DE, Halliday KJ. 2014. Interaction of light and temperature signalling. Journal of Experimental Botany **65**, 2859–2871.

Gibcus JH, Dekker J. 2013. The hierarchy of the 3D genome. Molecular Cell **49**, 773–782.

Godoy Herz MA, Kubaczka MG, Brzyżek G, *et al*. 2019. Light regulates plant alternative splicing through the control of transcriptional elongation. Molecular Cell **73**, 1066–1074.

Greer EL, Shi Y. 2012. Histone methylation: a dynamic mark in health, disease and inheritance. Nature Reviews. Genetics **13**, 343–357.

Grob S. 2019. Three-dimensional chromosome organization in flowering plants. Briefings in Functional Genomics **19**, 83–91.

Grob S, Schmid MW, Grossniklaus U. 2014. Hi-C analysis in Arabidopsis identifies the KNOT, a structure with similarities to the flamenco locus of Drosophila. Molecular Cell **55**, 678–693.

Groves NR, Biel AM, Newman-Griffis AH, Meier I. 2018. Dynamic changes in plant nuclear organization in response to environmental and developmental signals. Plant Physiology **176**, 230–241.

Horton JE, Elgar SJ, Khan SI, Zhang X, Wade PA, Cheng X. 2007. Structure of the SANT domain from the Xenopus chromatin remodeling factor ISWI. Proteins **67**, 1198–1202.

Hu B, Wang N, Bi X, Karaaslan ES, Weber AL, Zhu W, Berendzen KW, Liu C. 2019. Plant lamin-like proteins mediate chromatin tethering at the nuclear periphery. Genome Biology **20**, 87.

Huai J, Zhang X, Li J, Ma T, Zha P, Jing Y, Lin R. 2018. SEUSS and PIF4 coordinately regulate light and temperature signaling pathways to control plant growth. Molecular Plant **11**, 928–942.

Hyun KG, Noh YS, Song JJ. 2017. Arabidopsis FRIGIDA stimulates EFS histone H3 Lys36 methyltransferase activity. Plant Cell Reports **36**, 1183–1185.

Koini MA, Alvey L, Allen T, Tilley CA, Harberd NP, Whitelam GC, Franklin KA. 2009. High temperature-mediated adaptations in plant architecture require the bHLH transcription factor PIF4. Current Biology **19**, 408–413.

Kumar SV, Lucyshyn D, Jaeger KE, Alós E, Alvey E. 2016. Transcription factor PIF4 controls the thermosensory activation of flowering. Nature **484**, 242–245.

Kumar SV, Wigge PA, Centre JI, Lane C, Nr N. 2010. H2A.Z-containing nucleosomes mediate the thermosensory response in Arabidopsis. Cell **140**, 136–147.

Lau OS, Deng XW. 2012. The photomorphogenic repressors COP1 and DET1: 20 years later. Trends in Plant Science **17**, 584–593.

Laugesen A, Højfeldt JW, Helin K. 2019. Molecular mechanisms directing PRC2 recruitment and H3K27 methylation. Molecular Cell **74**, 8–18.

Leemans C, van der Zwalm MCH, Brueckner L, Comoglio F, van Schaik T, Pagie L, van Arensbergen J, van Steensel B. 2019. Promoter-intrinsic and local chromatin features determine gene repression in LADs. Cell **177**, 852–864.e14.

Leivar P, Monte E. 2014. PIFs: systems integrators in plant development. The Plant Cell **26**, 56–78.

Liu C, Cheng Y-J, Wang J-W, Weigel D. 2017. Prominent topologically associated domains differentiate global chromatin packing in rice from Arabidopsis. Nature Plants **3**, 742–748.

Liu C, Wang C, Wang G, Becker C, Zaidem M, Weigel D. 2016. Genome-wide analysis of chromatin packing in *Arabidopsis thaliana* at single-gene resolution. Genome Research **26**, 1057–1068.

Liu C, Weigel D. 2015. Chromatin in 3D: progress and prospects for plants. Genome Biology **16**, 170.

Lopez-Vernaza M, Yang S, Müller R, Thorpe F, de Leau E, Goodrich J. 2012. Antagonistic roles of SEPALLATA3, FT and FLC genes as targets of the polycomb group gene CURLY LEAF. PLoS One **7**, e30715.

Ma L, Li J, Qu L, Hager J, Chen Z, Zhao H, Deng XW. 2001. Light control of Arabidopsis development entails coordinated regulation of genome expression and cellular pathways. The Plant Cell **13**, 2589–2607.

Méteignier L-V, Lecampion C, Velay F, *et al*. 2019. Topoisomerase VI participates in an insulator-like function that prevents H3K9me2 spreading into euchromatic islands. bioRxiv 829416. [Preprint]

Michaels SD, Amasino RM. 2001. Loss of FLOWERING LOCUS C activity eliminates the late-flowering phenotype of FRIGADA and autonomous pathway mutations but not responsiveness to vernalization. The Plant Cell **13**, 935–941.

Nassrallah A, Rougée M, Bourbousse C, *et al*. 2018. DET1-mediated degradation of a SAGA-like deubiquitination module controls H2Bub homeostasis. eLife **7**, e37892.

Pavet V, Quintero C, Cecchini NM, Rosa AL, Alvarez ME. 2006. Arabidopsis displays centromeric DNA hypomethylation and cytological alterations of heterochromatin upon attack by *Pseudomonas syringae*. Molecular Plant-Microbe Interactions **19,** 577–587.

Pecinka A, Dinh HQ, Baubec T, Rosa M, Lettner N, Mittelsten Scheid O. 2010. Epigenetic regulation of repetitive elements is attenuated by prolonged heat stress in Arabidopsis. The Plant Cell **22**, 3118–3129.

Pedmale UV, Huang S-SC, Zander M, *et al*. 2016. Cryptochromes interact directly with PIFs to control plant growth in limiting blue light. Cell **164**, 233–245.

Peng S, Huang J, Sheehy JE, Laza RC, Visperas RM, Zhong X, Centeno GS, Khush GS, Cassman KG. 2004. Rice yields decline with higher night temperature from global warming. Proceedings of the National Academy of Sciences, USA **101**, 9971–9975.

Perrella G, Kaiserli E. 2016. Light behind the curtain: photoregulation of nuclear architecture and chromatin dynamics in plants. New Phytologist **212**, 908–919.

Petrillo E, Godoy Herz MA, Fuchs A, *et al*. 2014. A chloroplast retrograde signal regulates nuclear alternative splicing. Science **344**, 427–430.

Pham VN, Kathare PK, Huq E. 2018. Phytochromes and phytochrome interacting factors. Plant Physiology **176**, 1025–1038.

Portoso M, Ragazzini R, Brenčič Ž, Moiani A, Michaud A, Vassilev I, Wassef M, Servant N, Sargueil B, Margueron R. 2017. PRC 2 is dispensable for HOTAIR-mediated transcriptional repression. The EMBO Journal **36**, 981–994.

Quint M, Delker C, Franklin KA, Wigge PA, Halliday KJ, Van Zanten M. 2016. Molecular and genetic control of plant thermomorphogenesis. Nature Plants **2**, 1–9.

Rosa S, Duncan S, Dean C. 2016. Mutually exclusive sense–antisense transcription at FLC facilitates environmentally induced gene repression. Nature Communications **7**, 13031.

Rutowicz K, Lirski M, Mermaz B, *et al*. 2019. Linker histones are fine-scale chromatin architects modulating developmental decisions in Arabidopsis. Genome Biology **20**, 157.

Schubert D, Clarenz O, Goodrich J. 2005. Epigenetic control of plant development by Polycomb-group proteins. Current Opinion in Plant Biology **8**, 553–561.

Shen Y, Lei T, Cui X, Liu X, Zhou S, Zheng Y, Guérard F, Issakidis-Bourguet E, Zhou D-X. 2019. Arabidopsis histone deacetylase HDA15 directly represses plant response to elevated ambient temperature. The Plant Journal **100**, 991–1006.

Sun J, Qi L, Li Y, Chu J, Li C. 2012. Pif4-mediated activation of yucca8 expression integrates temperature into the auxin pathway in regulating arabidopsis hypocotyl growth. PLoS Genetics **8**, e1002594.

Sura W, Kabza M, Karlowski WM, Bieluszewski T, Kus-Slowinska M, Pawełoszek Ł, Sadowski J, Ziolkowski PA. 2017. Dual role of the histone variant H2A.Z in transcriptional regulation of stress-response genes. The Plant Cell **29**, 791–807.

Swiezewski S, Liu F, Magusin A, Dean C. 2009. Cold-induced silencing by long antisense transcripts of an Arabidopsis Polycomb target. Nature **462**, 799–802.

Tasset C, Singh Yadav A, Sureshkumar S, Singh R, van der Woude L, Nekrasov M, Tremethick D, van Zanten M, Balasubramanian S. 2018. POWERDRESS-mediated histone deacetylation is essential for thermomorphogenesis in *Arabidopsis thaliana*. PLoS Genetics **14**, 1–21.

Tessadori F, van Zanten M, Pavlova P, *et al*. 2009. PHYTOCHROME B and HISTONE DEACETYLASE 6 control light-induced chromatin compaction in *Arabidopsis thaliana*. PLoS Genetics **5**, e1000638.

van der Woude LC, Perrella G, Snoek BL, *et al*. 2019. HISTONE DEACETYLASE 9 stimulates auxin-dependent thermomorphogenesis in *Arabidopsis thaliana* by mediating H2A.Z depletion. Proceedings of the National Academy of Sciences, USA **116**, 25343–25354.

van Steensel B, Belmont AS. 2017. Lamina-associated domains: links with chromosome architecture, heterochromatin, and gene repression. Cell **169**, 780–791.

van Zanten M, Tessadori F, Peeters AJM, Fransz P. 2012. Shedding light on large-scale chromatin reorganization in *Arabidopsis thaliana*. Molecular Plant **5**, 583–590.

Willige BC, Zander M, Phan A, Garza RM, Trigg SA, He Y, Nery JR, Chen H, Ecker JR, Chory J. 2019. PHYTOCHROME INTERACTING FACTORs trigger environmentally responsive chromatin dynamics. bioRxiv 826842. [Preprint]

Wu S-H. 2014. Gene expression regulation in photomorphogenesis from the perspective of the central dogma. Annual Review of Plant Biology **65**, 311–333.

Wu Z, Fang X, Zhu D, Dean C. 2019. Autonomous pathway: FLOWERING LOCUS C repression through an antisense-mediated chromatin silencing mechanism. Plant Physiology **182**, 27–37.

Wu Z, Ietswaart R, Liu F, Yang H, Howard M, Dean C. 2016. Quantitative regulation of FLC via coordinated transcriptional initiation and elongation. Proceedings of the National Academy of Sciences, USA **113**, 218–223.

Yang W, Chen Z, Huang Y, Chang G, Li P, Wei J. 2019. Powerdress as the novel regulator enhances Arabidopsis seeds germination tolerance to high temperature stress by histone modification of SOM locus. Plant Science **284**, 91–98.

Yu C, Liu X, Luo M, Chen C, Lin X, Tian G, Lu Q. 2011. HISTONE DEACETYLASE6 interacts with FLOWERING LOCUS D and regulates flowering in Arabidopsis 1. Plant Physiology **156**, 173–184.

Zhao L, Peng T, Chen C-Y, Ji R, Gu D, Li T, Zhang D, Tu Y-T, Wu K, Liu X. 2019. HY5 interacts with the histone deacetylase HDA15 to repress hypocotyl cell elongation in photomorphogenesis. Plant Physiology **180**, 1450–1466.