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PIF transcription factors-versatile plant epigenome landscapers

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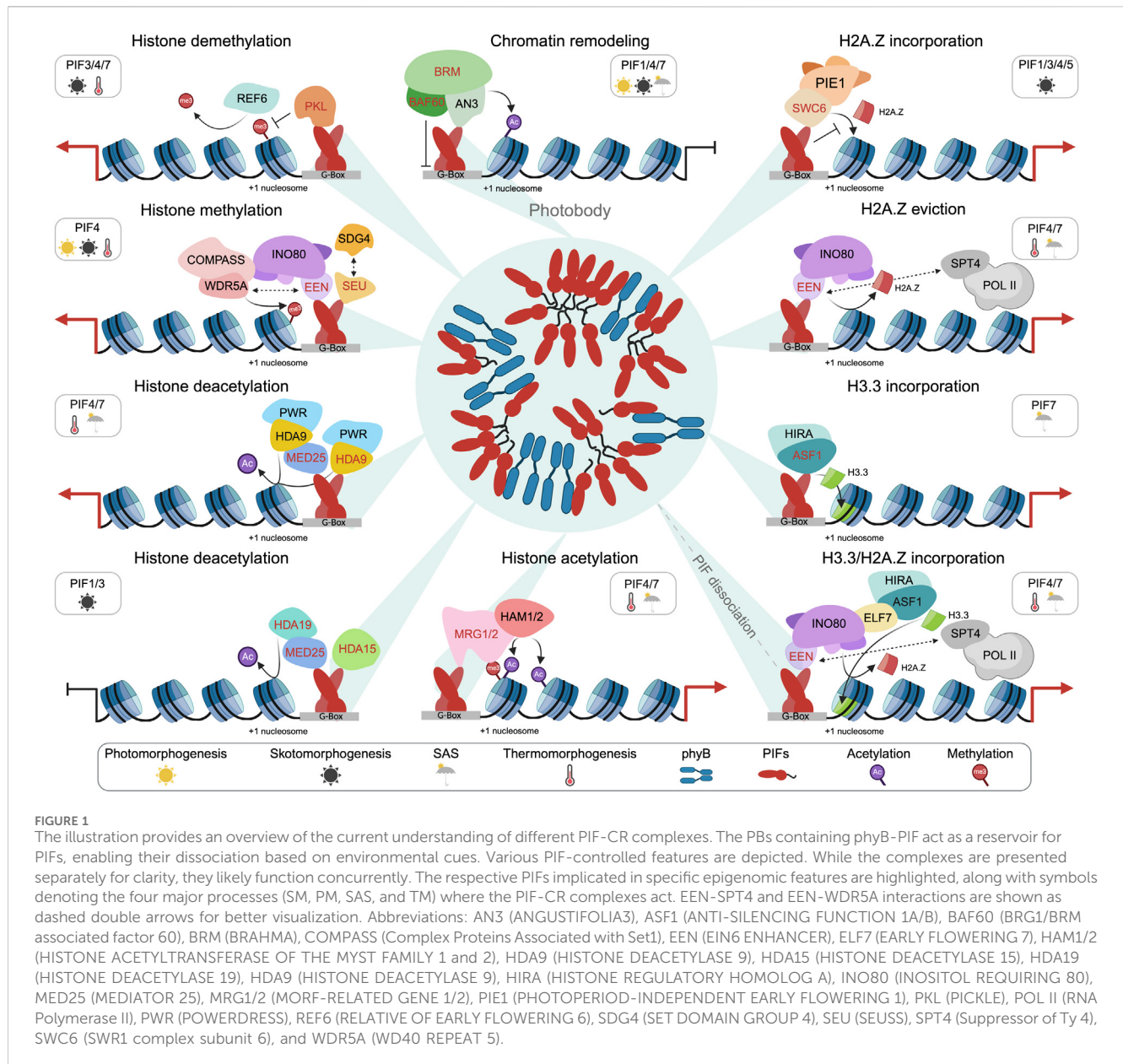
Plants are exquisitely responsive to their local light and temperature environment utilizing these environmental cues to modulate their developmental pathways and adjust growth patterns. This responsiveness is primarily achieved by the intricate interplay between the photoreceptor phyB (phytochrome B) and PIF (PHYTOCHROME INTERACTING FACTORS) transcription factors (TFs), forming a pivotal signaling nexus. phyB and PIFs co-associate in photobodies (PBs) and depending on environmental conditions, PIFs can dissociate from PBs to orchestrate gene expression. Until recently, the mechanisms governing epigenome modifications subsequent to PIF binding to target genes remained elusive. This mini review sheds light on the emerging role of PIFs in mediating epigenome reprogramming by recruiting chromatin regulators (CRs). The formation of numerous different PIF-CR complexes enables precise temporal and spatial control over the gene regulatory networks (GRNs) governing plant-environment interactions. We refer to PIFs as epigenome landscapers, as while they do not directly reprogram the epigenome, they act as critical sequence-specific recruitment platforms for CRs. Intriguingly, in the absence of PIFs, the efficacy of epigenome reprogramming is largely compromised in light and temperature-controlled processes. We have thoroughly examined the composition and function of known PIF-CR complexes and will explore also unanswered questions regarding the precise of locations PIF-mediated epigenome reprogramming within genes, nuclei, and plants.

KEYWORDS

plant epigenomics, chromatin dynamics, transcription factors, chromatin remodeling complexes, light and temperature signaling

Introduction

The major sensor of red (R), far-red (FR) light as well temperature in *Arabidopsis* is the photoreceptor phyB (Quail et al., 1995; Rockwell et al., 2006; Jung et al., 2016; Legris et al., 2016). After photoactivation, phyB translocates from the cytosol to the nucleus where it compartmentalizes into PBs through liquid-liquid phase separation (LLPS) (Sakamoto and Nagatani, 1996; Kircher et al., 1999; Chen et al., 2003; Chen et al., 2022). PBs function as regulatory light and temperature modules, housing a variety of signaling components that interact directly or indirectly with phyB (Van Buskirk et al., 2012; Jung et al., 2016; Legris et al., 2016; Hahm et al., 2020; Pardi and Nusinow, 2021; Kim et al., 2023; Kwon et al., 2024; Willige et al., 2024). One of the most critical PB component are the PIFs, a family of basic helix-loop-helix (bHLH) TFs which acts a transcriptional activators or repressors (Ni et al., 1998; Huq and Quail, 2002; Huq et al., 2004; Oh et al., 2004; Castillon et al., 2007; Leivar et al., 2008; Shen et al., 2008; Leivar and Quail, 2011; Leivar and Monte, 2014). The *Arabidopsis* genome encodes eight PIFs (PIF1-PIF8), which integrate phyB's environmental input into GRNs underlying light and temperature responses (Leivar and Quail, 2011; Jeong



and Choi, 2013; Leivar and Monte, 2014; Pham et al., 2018; Bian et al., 2022; Han et al., 2023). PIF1/3/4/5 control the transition from skotomorphogenesis (SM) to photomorphogenesis (PM) by repressing light-responsive gene expression in the dark until light exposure initiates their phytochrome-mediated phosphorylation, ubiquitination and subsequent proteasomal degradation (Leivar and Quail, 2011; Leivar and Monte, 2014; Pham et al., 2018). Furthermore, PIF7 functions as the major regulator alongside PIF1/3/4/5 in orchestrating the shade avoidance syndrome (SAS) (Willige et al., 2021). This syndrome is induced by low R:FR light ratios (referred to as shade) resulting from nearby vegetation, prompting elongation of hypocotyls and petioles, early flowering, and upward leaf positioning (Franklin and Whitelam, 2005; Franklin, 2008; Casal, 2012; Sessa et al., 2018; Casal and Fankhauser, 2023). A phenotypically similar response to SAS is thermomorphogenesis (TM) which refers to the profound effect of

elevated ambient temperature (EAT) (up to 28°C, below the heat stress range) on plant growth, development, and immunity (Casal and Balasubramanian, 2019; Burko et al., 2022). In *Arabidopsis*, TM regulation primarily involves PIF4 and PIF7 (Koini et al., 2009; Kumar et al., 2012; Gangappa et al., 2017; Chung et al., 2020; Fiorucci et al., 2020) whereas TM under shade (low R:FR light) conditions is mainly regulated by PIF7 alone (Burko et al., 2022).

The detailed complex mechanisms governing PIFs at both the transcriptional and protein levels along the crosstalk with other signaling pathways have been extensively discussed in several excellent reviews (Leivar and Quail, 2011; Jeong and Choi, 2013; Shin et al., 2013; Leivar and Monte, 2014; Paik et al., 2017; Pham et al., 2018; Favero, 2020). Additionally, readers are encouraged to explore superb reviews that delve into the exciting connection between light/temperature signaling and chromatin dynamics (Perrella and Kaiserli, 2016; Bourbousse et al., 2019; Jing and Lin,

2020; Perrella et al., 2020). We aim to provide a brief introduction to PIF7, which serves as a partial representation of other PIFs and highlights crucial regulatory aspects such as posttranslational modifications (PTMs), condensate formation, and DNA binding among PIF proteins. In white light (WL) PIF7 is phosphorylated and unlike other PIFs relatively light-stable (Leivar et al., 2008; Huang et al., 2018; Willige et al., 2021; Zhou et al., 2021). PIF7 undergoes LLPS to form biocondensates under WL conditions which subsequently associate with phyB condensates in photobodies (PBs) (Leivar et al., 2008; Willige et al., 2021; Chen et al., 2022; Xie et al., 2023). Upon exposure to shade, PIF7 gets rapidly dephosphorylated and dissociates from PBs to bind to G-boxes (CACGTG) within *cis*-regulatory elements (CREs) of its targets (Chung et al., 2020; Willige et al., 2021; Xie et al., 2023). PIF7 regulates an extensive GRN encompassing multiple biosynthesis genes for the growth-promoting plant hormone auxin, along with numerous transcription factors (TFs) such as *ATHB2* (*ARABIDOPSIS THALIANA* HOMEODOMAIN PROTEIN 2) (Chung et al., 2020; Willige et al., 2021). A similar signaling mechanism operates during TM (Chung et al., 2020; Fiorucci et al., 2020; Burko et al., 2022), where PIF7 mRNA also serves as a direct thermosensor (Chung et al., 2020).

Here, we will discuss the emerging role of PIFs as epigenome landscapers by recruiting various chromatin regulators (CRs) to shape the epigenome at their target genes (Figure 1). The plant epigenome plays a crucial role as a regulatory framework, integrating both developmental signals and environmental cues into spatiotemporal-specific GRNs (Lloyd and Lister, 2022). In a broad sense, the epigenome encompasses not only all chemical modifications of DNA and histone proteins but also other features that control gene expression, including DNA binding of TFs and CRs, chromatin accessibility, 3D chromatin conformation, nucleosome positioning, and long non-coding RNAs (Rivera and Ren, 2013). We utilize the term CR to encompass all regulatory factors capable of modifying the epigenome, chromatin remodeling complexes (CRCs), histone acetyltransferases/deacetylases (HATs/HDACs), histone methyltransferases/demethylases (KMTs/KDMs), and many others. To enhance comprehension, we discuss various epigenome feature dynamics separately, although it is crucial to recognize their intricate interconnections. Finally, we outline some unresolved questions for further exploration.

H2A.Z and H3.3 dynamics

Histone variants are histone proteins that differ from canonical histones in their amino acid sequence, structure, and functions (Yi et al., 2006; Borg et al., 2021). One of the best studied histone variants in *Arabidopsis* is H2A.Z that confers gene responsiveness to environmentally-responsive genes (Coleman-Derr and Zilberman, 2012). The *Arabidopsis* genome encodes three functionally redundant H2A.Z genes (*HTA8*, *HTA9*, *HTA11*) whose mutations leads to pleiotropic effects such as early flowering, enhanced disease resistance and DNA hypermethylation (Choi et al., 2007; March-Diaz et al., 2008; Coleman-Derr and Zilberman, 2012; Nie et al., 2019). H2A.Z exerts a repressive influence on transcription, and its eviction is a common characteristic of transcriptional activation in plant-environment

interactions (Kumar and Wigge, 2010; Kumar et al., 2012; Boden et al., 2013; Cortijo et al., 2017; Sura et al., 2017; Zander et al., 2019; Willige et al., 2021; Xue et al., 2021).

The discovery of H2A.Z's involvement in PIF-regulated processes occurred with a forward genetic screen aiming to identify temperature sensors in *Arabidopsis* (Kumar and Wigge, 2010). This screen revealed ARP6 (ACTIN-RELATED PROTEIN 6), a subunit of the SWR1 (SWI2/SNF2 (SWITCH/SUCROSE NONFERMENTABLE)-related 1) chromatin remodeler (Choi et al., 2005; Martin-Trillo et al., 2006; Choi et al., 2007), as a negative TM regulator (Kumar and Wigge, 2010). Other key components of the multi-subunit plant SWR1 complex (SWR1-C) are the ATPase PIE1 (PHOTOPERIOD-INDEPENDENT EARLY FLOWERING 1) and accessory units such as SWC6 (SWR1 COMPLEX 6) and SEF (SERRATED LEAVES AND EARLY FLOWERING) (Noh and Amasino, 2003; Choi et al., 2007; March-Di et al., 2007; Luo et al., 2020). Consistent with SWR1-C's role in incorporating H2A.Z into chromatin (Deal et al., 2007), *arp6* mutants have reduced H2A.Z levels resulting in the elevation of thermo-responsive gene expression and longer hypocotyls and petioles even without an EAT stimulus (Kumar and Wigge, 2010). As PIF4 governs the expression of EAT-induced genes (Koini et al., 2009), it was suggested that H2A.Z-containing nucleosomes occlude PIF4 from binding to its target genes. This hindrance is lifted in *arp6* mutants, thereby facilitating higher thermo-responsive gene expression (Kumar and Wigge, 2010).

The first direct connection between H2A.Z and PIFs was shown for PIF4-dependent EAT-induced flowering in *Arabidopsis* (Kumar et al., 2012). EAT-induced expression of *FT* (*FLOWERING LOCUS T*) requires direct PIF4 binding at *FT* which is facilitated by EAT-induced eviction of H2A.Z nucleosomes (Kumar et al., 2012). To elucidate the PIF-H2A.Z interplay in more detail, PIF7 DNA binding as well as H2A.Z occupancy in wildtype and *pif457* mutants were tracked simultaneously during SAS over time using ChIP-seq (Chromatin immunoprecipitation followed by sequencing) (Willige et al., 2021). PIF7 initiates shade-induced H2A.Z eviction at its target genes through the association with the INO80 (INOSITOL REQUIRING 80) chromatin remodeling complex (INO80-C) via direct interaction with its essential subunit EEN (EIN6 ENHANCER) (Zander et al., 2019; Willige et al., 2021). Strikingly, this PIF-INO80-C regulatory module is also operational with PIF4 during TM (Figure 1) (Sureshkumar and Balasubramanian, 2021; Xue et al., 2021).

INO80-C belongs to the INO80-type subfamily of SWI2/SNF2 chromatin remodeler (Clapier and Cairns, 2009; Han et al., 2015) and it was shown in various species that INO80-C can facilitate H2A.Z eviction to regulate gene expression (Papamichos-Chronakis et al., 2011; Alatwi and Downs, 2015; Brahma et al., 2017; Zhao et al., 2022). In plants, INO80-C's role in H2A.Z eviction was shown for ethylene-, low R:FR light-, and EAT-induced genes (Zander et al., 2019; Willige et al., 2021; Xue et al., 2021). INO80-C additionally acts as a platform for recruiting other CRs, thereby potentially expanding the functional capabilities of the PIF-INO80-C regulatory module (Shang et al., 2021; Xue et al., 2021; Zhao et al., 2023). Its subunit EEN interacts with WDR5a (WD40 REPEAT 5), an integral component of the COMPASS (Complex Proteins Associated with Set1) histone H3K4 methyltransferase complex, to facilitate trimethylation of histone 3 lysine 4 (H3K4me3) at PIF4 target genes (Figure 1)

(Xue et al., 2021). The association of INO80-C with other major COMPASS histone H3K4 methyltransferase complex components was independently shown (Shang et al., 2021). In addition, EEN interacts with the transcription elongation factors (TEFs) SPT4 (Suppressor of Ty 4)-1 and SPT4-2 to mediate RNA Polymerase II (RNAPII) elongation during TM (Figure 1) (Xue et al., 2021). Interestingly, PIF1/3/4/5 can also associate with SWR1-C via SWC6 during PM to inhibit H2A.Z deposition (Figure 1) (Chen H. et al., 2023). Under this scenario, PIFs inhibit SWR1-C activity at auxin-responsive genes in the dark through an unknown mechanism (Chen H. et al., 2023). All these findings indicate that PIFs can use multiple strategies to alter the H2A.Z landscape at their target genes thereby fine-tuning their expression in an environmental stimulus-dependent manner.

The histone variant H3.3 forms together with the replicative H3.1/H3.2, and the centromeric CenH3 the H3 (Histone 3) family (Henikoff and Ahmad, 2005; Borg et al., 2021). H3.3 is incorporated during transcription and rapid upregulation of environmentally-responsive genes is compromised in *h3.3* knockdown mutants (Wollmann et al., 2017). The deposition of H3.3 is in part mediated by the histone chaperones ASF1A (ANTI-SILENCING FUNCTION 1A) and ASF1B in conjunction with the histone chaperone HIRA (HISTONE REGULATORY HOMOLOG A) (Tagami et al., 2004; Zhu et al., 2011; Nie et al., 2014; Duc et al., 2015; Zhong et al., 2022). During SAS, PIF7 recruits ASF1A/B and HIRA to facilitate H3.3 deposition at shade-responsive genes (Figure 1) (Yang et al., 2023). In addition, *asf1ab* and *hira* mutants show also reduced hypocotyl elongation under EAT (Yang et al., 2023; Zhao et al., 2023) which suggest that the PIF-ASF1A/B-HIRA module is also operational during TM. Although a PIF4-ASF1A/B interaction has not been confirmed, ASF1A/B could also be indirectly recruited by PIF4 through the INO80 ATPase that associates with ASF1A/B through the TEF PAF1c (Polymerase-Associated Factor 1 complex) subunit ELF7 (EARLY FLOWERING 7) (Figure 1) (Zhao et al., 2023). These findings highlight again the prominent role of PIFs in initiating epigenomic reprogramming through the recruitment of functionally diverse CRs.

Histone acetylation dynamics

One of the most extensively studied PTM of histones is acetylation, which plays a crucial role in numerous gene regulatory processes (Jiang et al., 2020; Shvedunova and Akhtar, 2022; Chen Y. et al., 2023). Acetylation occurring at various lysine residues of histones H3 and H4, such as H3K9ac or H3K27ac, typically corresponds to gene activation, whereas deacetylation is associated with gene repression (Pandey et al., 2002). The balance of histone acetylation is regulated by the interplay between HATs and HDACs (Eberharther and Becker, 2002). The *Arabidopsis* genome encodes for 12 HATs and 18 HDACs (Pandey et al., 2002; Hollender and Liu, 2008), and although no direct interactions between PIFs and HATs have been documented, an active role of HATs in PIF-mediated chromatin reprogramming can be inferred (Martínez-García and Moreno-Romero, 2020). During SAS, H3K9ac levels rapidly increase at gene bodies of shade-responsive genes in a PIF4/5/7-dependent manner (Willige et al., 2021). Furthermore, levels of

H4K5ac, H3K9ac, and H3K27ac increase in response to shade and EAT at *YUC8* in a PIF4/7-dependent manner (Peng et al., 2018; Zhou et al., 2024).

PIF4/7 directly associate with MRG1/2 (MORF-RELATED GENE 1/2) which are histone methylation readers that bind to H3K4/H3K36 trimethylation (H3K4me3/H3K36me3) and can interact with the HATs HAM1/2 (HISTONE ACETYLTRANSFERASE OF THE MYST FAMILY 1 and 2) (Xu et al., 2014). The recruitment of HAM1/2 through the PIF4/7-MRG1/2 module is the current model of PIF4/7-driven histone acetylation dynamics during SAS and TM (Figure 1) (Peng et al., 2018; Zhou et al., 2024). However, additional experimental support is needed because no direct association of HAM1/2 with PIF target genes has been shown so far (Latrasse et al., 2008).

HDA9 (HISTONE DEACETYLASE 9) was found to positively regulate hypocotyl elongation during TM and SAS (Tasset et al., 2018; van der Woude et al., 2019; Nguyen et al., 2023). HDA9's positive role is still puzzling since expression of *PIF4* and *YUC8*, both essential regulators of EAT-induced hypocotyl elongation (Koini et al., 2009; Franklin et al., 2011; Sun et al., 2012; Proveniers and van Zanten, 2013; Bellstaedt et al., 2019), requires HDA9-mediated H3K9ac/14ac deacetylation at its +1 nucleosome (van der Woude et al., 2019). Interestingly, mutation of the HDA9-interacting SANT-domain containing protein PWR (POWERDRESS), phenocopies *hda9* mutants regarding reduced *PIF4/YUC8* expression due to higher H3K9ac levels (Tasset et al., 2018). EAT-induced H2A.Z eviction was also compromised in *hda9* mutants (van der Woude et al., 2019), however, the mechanism of how HDA9 regulates H2A.Z eviction is still unclear. Although PIF4 was not found to interact with HDA9 (van der Woude et al., 2019), PIF7 was recently identified as an interactor of HDA9 (Nguyen et al., 2023). Given PIF7's critical role in TM and its capacity to heterodimerize with PIF4 (Kidokoro et al., 2009; Fiorucci et al., 2020), it's possible that a PIF7/PIF4 heterodimer recruits the HDA9-PWR module to its target genes (Figure 1). The hypothesis of HDA9 recruitment to shade-induced genes via PIF7 has also been proposed for SAS (Nguyen et al., 2023).

During SM, HDA15 (HISTONE DEACETYLASE 15) is recruited by PIF3 to repress the expression of photosynthesis genes through H4 deacetylation (Liu et al., 2013). In addition, PIF1 also interacts with HDA15 to repress genes via histone deacetylation (H3ac) during seed germination in the dark (Figure 1) (Gu et al., 2017). In contrast to HDA9's positive role, HDA15 is a negative TM regulator directly associating at thermo-responsive genes potentially through HFR1 (LONG HYPOCOTYL IN FAR-RED) (Shen et al., 2019). A current hypothesis that elucidates the contradictory functions of HDA9 and HDA15 proposes that at higher temperatures, the HFR1-HDA15 complex is displaced by PIF4, possibly forming a complex with HDA9 and PWR (Shen et al., 2019). HDA19 is an additional PIF1/3-interacting HDAC that represses PM via H3 deacetylation at the PM genes *BBX21* (*B-BOX CONTAINING PROTEIN 21*) and *GLK1* (*GOLDEN2-LIKE1*) (Guo et al., 2023). Another possible route of connecting PIFs with HDACs is HOS1 (HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE 1), a RING E3 ligase which can directly interact with PIF4 but also with HDA6 (HISTONE DEACETYLASE 6) and HDA15 (Jung et al., 2013; Kim et al., 2017).

An additional functional link between PIFs and HDACs are the subunits MED25 (MEDIATOR 25) and MED14 (MEDIATOR 14) of the Mediator complex (Bajracharya et al., 2022; Guo et al., 2023; Shapulatov et al., 2023), which is an evolutionary conserved large multi-subunit protein complex regulating RNAPII function on various levels (Allen and Taatjes, 2015; Soutourina, 2018). MED25 or PFT1 (PHYTOCHROME AND FLOWERING TIME 1) was first discovered as a SAS regulator and can interact with PIF4 in *Arabidopsis* and tomato to recruit RNAPII (Sun et al., 2020; Shapulatov et al., 2023). During TM, MED25 can associate with HDA9, thereby potentially facilitating the PIF4-mediated recruitment of HDA9 for histone deacetylation at the *PIF4* and *YUC8* gene (Figure 1) (Shapulatov et al., 2023). Moreover, PIF1 and PIF3 also interact with MED25 and HDA19 to down-regulate the expression of positive the positive PM regulators *BBX21* and *GLK1* via histone deacetylation and reducing chromatin accessibility (Figure 1) (Guo et al., 2023). Intriguingly, MED25 also undergoes LLPS to form biomolecular condensates with PIF1/3 and HDA19 (Guo et al., 2023). Moreover, PIF4 as well as its coactivator HMR (HEMERA) interact with MED14 to positively regulate thermo-responsive genes (Bajracharya et al., 2022).

Also noteworthy is the recently resolved protein composition of PBs, which has identified the Groucho/Tup1-type co-repressors TPL (TOPLESS) and TPR1 (TOPLESS-RELATED 1) as PB components (Kim et al., 2023). TPL and TPRs putatively exert their repressive function through the direct association with various HDACs such as HDA6 and HDA19 (Long et al., 2006; Krogan et al., 2012; Wang et al., 2013; Plant et al., 2021). The confirmation of whether PIFs indeed interact with TPL/TPRs at their target genes remains uncertain at this point. However, the spatial proximity of PIFs and TPL/TPRs in PBs implies a potential functional connection (Kim et al., 2023). In addition, an interaction of PIF1 with LUH (LEUNIG_HOMOLOG), another member of the Groucho/Tup1-type co-repressor family, was shown to regulate expression of PIF1 target genes during seed germination through an unknown mechanism (Lee et al., 2015; Kim et al., 2023).

Histone methylation dynamics

Methylation of various lysine (K) residues of histones H3 and H4 can occur in plants and depending on the modified lysine residue and degree of methylation (mono-, di-, and/or tri), gene expression is instructed differently (Liu et al., 2010; Xiao et al., 2016; Cheng et al., 2020). H3K4me3 on the +1 nucleosome is a critical epigenome feature indicating active genes, and assessing H3K4me3 occupancy is commonly employed as an indicator of an active chromatin state (Bernstein et al., 2002). Mutants in PIF-interacting CRs frequently exhibit altered levels of H3K4me3 at PIF target genes (Huai et al., 2018). However, whether this alteration is regulatory in nature or merely a consequence of transcriptional changes remains unclear. Until very recently, the exact function of H3K4me3 remained elusive. Using an elegant acute depletion method, all SET1/COMPASS complexes were eliminated from mouse embryonic stem cells, unveiling the critical involvement of H3K4me3 in regulating RNAPII pausing, elongation, and eviction (Wang et al., 2023).

The dark-to-light transition at the beginning of PM leads to a PIF-dependent rapid upregulation of gene expression and

H3K4me3 levels (Calderon et al., 2022). How this achieved in a PIF-dependent manner is not clear but the PIF4 interacting transcriptional co-regulator SEU (SEUSS) might provide a link between PIFs and active H3K4me3 regulation (Figure 1) (Huai et al., 2018). SEU is a negative PM regulator under red, far-red, and blue light conditions, but interestingly a positive TM regulator (Huai et al., 2018). It has been demonstrated for SEUSS that it controls H3K4me3 deposition at *WOX5* (*WUSCHEL-RELATED HOMEODOMAIN 5*) targets genes by associating with the H3K4 methyltransferase SDG4 (SET DOMAIN GROUP 4) (Zhai et al., 2020). Therefore, it is plausible to hypothesize the existence of an operational PIF-SEU-SDG4 complex. Additionally, PIFs regulate the local H3K4me3 environment at their target genes by associating with INO80-C/COMPASS complexes during TM (Figure 1) (Shang et al., 2021; Xue et al., 2021).

Removal of histone methylation marks is facilitated by jumonji domain-containing histone demethylases (Lu et al., 2008; Mosammaparast and Shi, 2010). The primary demethylase in *Arabidopsis* is REF6 (RELATIVE OF EARLY FLOWERING 6) whose mutation causes ectopic gain of H3K27me3 at thousands of genes (Lu et al., 2011; Zander et al., 2019). REF6 was found to cooperatively regulate EAT-induced gene expression with PIF4 via H3K27me3 demethylation (Figure 1) (He et al., 2022). Whether REF6 can interact with PIFs is unknown but it can interact with INO80-C (Smaczniak et al., 2012), suggesting a potential regulatory pathway through which PIFs could influence the H3K27me3 landscape. During SM, PIF3 interacts with the SWI/SWF chromatin-remodeler (PKL/EPP1) (PICKLE/ENHANCED PHOTOMORPHOGENIC1) to repress H3K27me3 deposition at PIF3 target sites (Figure 1) (Zhang et al., 2014). How PKL inhibits the H3K27me3 deposition is not understood since PKL acts cooperatively with the SWR1-C ATPase PIE1 and the H3K27 methyltransferase CLF (CURLY LEAF) to establish and maintain the H3K27me3 landscape in *Arabidopsis* (Carter et al., 2018).

Chromatin remodeling

Chromatin remodeling is a key process in genome organization, transcriptional regulation, DNA repair and replication (Clapier and Cairns, 2009). Of particular importance for gene expression is the accessibility of *cis*-regulatory elements and incorporation/eviction of histone variants which is regulated by multi-subunit ATP-dependent SWI2/SNF2 CRCs (Clapier and Cairns, 2009). Besides the interaction of PIFs with the INO80-type remodelers SWR1-C and INO80-C (Willige et al., 2021; Xue et al., 2021; Chen H. et al., 2023), PIFs also interact with various SWI/SNF-type remodelers (Zhang et al., 2017; Hussain et al., 2022). The SWI/SNF-type family consists of the BRM (BRAHMA)-, SYD (SPRAYED)-, and MINU1/2 (MINUSCULE1/2)-associated SWI/SNF (BAS, SASc (to avoid confusion with SAS), and MAS) complexes (Guo et al., 2022). PIF1 recruits BRM to photosynthesis genes in the dark to repress their expression though mechanism that remains unidentified (Zhang et al., 2017). Moreover, PIF7 interacts with AN3 (ANGUSTIFOLIA3), a subunit of either the BAS or SASc complex (Guo et al., 2022) to regulate leaf cell proliferation during shade (Hussain et al., 2022). Shade-stabilized

PIF7 outcompetes AN3 at its target genes and represses their expression (Hussain et al., 2022). An additional antagonism between PIFs and a SWI/SNF subunit was shown for PIF4 and BAF60 (BRG1/BRM associated factor 60) (Jegu et al., 2017). BAF60 can be a subunit of the BAS, SASc, and MAS complex but because of a reported direct interaction between PIF4 and BRM, an association within the BAS complex is likely (Zhang et al., 2017; Guo et al., 2022). BAF60 target sites overlap with PIF4 DNA binding sites and strikingly BAF60 antagonizes PIF4 binding through the diurnal regulation of DNA accessibility at PIF4 binding sites (Figure 1) (Jegu et al., 2017).

Discussion

Where in the gene, where in the nucleus, and where in the plant do the PIF-CR complexes act? For PIFs and their respective CRs to interact, they must be brought into proximity. Unlike CRs, which typically occupy gene bodies, PIFs span a wide spectrum, ranging from proximal to distal, intronic, and 3' CRE binding (Chung et al., 2020; Willige et al., 2021). Most CRE-promoter communications are established by chromatin loops where TF-bound distal CREs or enhancers make direct physical contact with the proximal promoter/gene body region (Panigrahi and O'Malley, 2021). Indeed, a COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1)-controlled phyB-PRC2 (POLYCOMB REPRESSIVE COMPLEX 2)-mediated chromatin loop has been identified at the positive SAS regulator *ATHB2* (Steindler et al., 1999; Kim et al., 2021; Wang et al., 2024), which is one of the most prominent shade and EAT-induced PIF7 targets, possessing an unusually large CRE with five PIF7 binding peaks 3–9 kb (kilobase) upstream of its transcription start site (Chung et al., 2020; Willige et al., 2021; Burko et al., 2022). Notably, the PIF interactor MED25 facilitates chromatin looping during active jasmonic acid (JA) signaling through interaction with the JA master TF MYC2 (Wang et al., 2019). Like MYC2 which can form tetramers to support loop formation (Lian et al., 2017), PIF4 can also form tetramers suggesting the potential of PIF4 to form loops (Gao et al., 2022).

This leads us to the nuclear 3D space and our second question: where precisely within the nucleus do the PIF-CR complexes act? We pose this question due to the rapid nature of shade-induced PIF7 DNA binding, which occurs at a few hundred genes within 5 min of shade exposure (Willige et al., 2021), potentially even earlier. Since we lack information regarding the DNA scanning speed of PIF7, we cannot ascertain whether the swift DNA targeting of PIF7 is attributable to PIF7's search throughout the entire nucleus, or as previously speculated, solely in proximity to PBs (Van Buskirk et al., 2012). Various nuclear bodies in mammals are known to directly regulate chromatin activities (Shan et al., 2023), and intriguingly, a temperature-dependent chromatin association has been demonstrated for phyB (Jung et al., 2016). Moreover, recent findings have unveiled an active role of phyB in chromatin loop formation at the PIF target *ATHB2* (Kim et al., 2021; Wang et al., 2024). To further explore this exciting scenario of PB-associated chromatin structures, future research necessitates 3D chromatin conformation analyses as well as single locus imaging technologies.

All findings presented here stem from bulk-level analyses, which may obscure crucial spatial information (Cole et al., 2021). It has been demonstrated that for EAT-induced hypocotyl elongation, it is crucial for PIF4 to function within the epidermis (Kim et al., 2020), in conjunction with the DOF TF CDF2 (CYCLING DOF FACTOR 2) (Gao et al., 2022). Similarly, epidermal phyB plays a pivotal role in regulating most light responses, including SAS (Kim et al., 2016). Recent advancements in single-cell (sc) technologies, such as single-cell RNA sequencing (scRNA-seq), now facilitate the capturing of gene expression profiles at the single-cell level (Han et al., 2023). Thus far, only one scRNA-seq study has been reported for a *pif* mutant revealing that expression levels of *PIF1/3/4/5* remain relatively uniformly across cells in wildtype aerial tissues, but interestingly, the expression of PIF target genes varies among different cell types in *pifq* mutants (Han et al., 2023). This suggests that the cell-type specificity of PIF signaling may stem from cell type-specific epigenome disparities at PIF target genes (Han et al., 2023). Considering that PIFs initiate epigenome reprogramming at their target genes by recruiting various CR complexes, we hypothesize the existence of cell type-specific PIF-CR complexes to establish gene expression patterns unique to each cell type.

Highlighting these discoveries underscores the pivotal role of PIFs as epigenome landscapers. From our viewpoint, three key elements of PIFs' epigenome landscaping abilities are particularly noteworthy. Firstly, binding of PIFs to CREs at their target genes is the starting point of stimulus-induced epigenome reprogramming. Secondly, most epigenome features can be directly and simultaneously governed by functionally diverse PIF-CR complexes. Thirdly, several PIF-CR modules, such as PIF-INO80-C, PIF-MRG1/2, and PIF-ASF1-HIRA are operational in multiple response pathways like SAS and TM (Shang et al., 2021; Willige et al., 2021; Yang et al., 2023; Zhao et al., 2023; Zhou et al., 2024), indicating that these complexes belong to the general repertoire of PIF-mediated transcriptional regulation.

Author contributions

MA: Conceptualization, Data curation, Visualization, Writing—original draft. KM: Conceptualization, Data curation, Writing—original draft. MZ: Conceptualization, Data curation, Funding acquisition, Visualization, Writing—original draft, Writing—review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Alatwi, H. E., and Downs, J. A. (2015). Removal of H2A.Z by INO80 promotes homologous recombination. *EMBO Rep.* 16 (8), 986–994. doi:10.15252/embr.201540330
- Allen, B. L., and Taatjes, D. J. (2015). The Mediator complex: a central integrator of transcription. *Nat. Rev. Mol. Cell Biol.* 16 (3), 155–166. doi:10.1038/nrm3951
- Bajracharya, A., Xi, J., Grace, K. F., Bayer, E. E., Grant, C. A., Clutton, C. H., et al. (2022). PHYTOCHROME-INTERACTING FACTOR 4/HEMERA-mediated thermosensory growth requires the Mediator subunit MED14. *Plant Physiol.* 190 (4), 2706–2721. doi:10.1093/plphys/kiac412
- Belstaedt, J., Trenner, J., Lippmann, R., Poeschl, Y., Zhang, X. X., Friml, J., et al. (2019). A mobile auxin signal connects temperature sensing in cotyledons with growth responses in hypocotyls. *Plant Physiol.* 180 (2), 757–766. doi:10.1104/pp.18.01377
- Bernstein, B. E., Humphrey, E. L., Erlich, R. L., Schneider, R., Bouman, P., Liu, J. S., et al. (2002). Methylation of histone H3 Lys 4 in coding regions of active genes. *Proc. Natl. Acad. Sci. U. S. A.* 99 (13), 8695–8700. doi:10.1073/pnas.082249499
- Bian, Y., Chu, L., Lin, H., Qi, Y., Fang, Z., and Xu, D. (2022). PIFs- and COP1-HY5-mediated temperature signaling in higher plants. *Stress Biol.* 2 (1), 35. doi:10.1007/s44154-022-00059-w
- Boden, S. A., Kavanova, M., Finnegan, E. J., and Wigge, P. A. (2013). Thermal stress effects on grain yield in *Brachypodium distachyon* occur via H2A.Z-nucleosomes. *Genome Biol.* 14 (6), R65. doi:10.1186/gb-2013-14-6-r65
- Borg, M., Jiang, D., and Berger, F. (2021). Histone variants take center stage in shaping the epigenome. *Curr. Opin. Plant Biol.* 61, 101991. doi:10.1016/j.pbi.2020.101991
- Bourbousse, C., Barneche, F., and Laloi, C. (2019). Plant chromatin catches the Sun. *Front. Plant Sci.* 10, 1728. doi:10.3389/fpls.2019.01728
- Brahma, S., Udugama, M. I., Kim, J., Hada, A., Bhargava, S. K., Hailu, S. G., et al. (2017). INO80 exchanges H2A.Z for H2A by translocating on DNA proximal to histone dimers. *Nat. Commun.* 8, 15616. doi:10.1038/ncomms15616
- Burko, Y., Willige, B. C., Seluzicki, A., Novak, O., Ljung, K., and Chory, J. (2022). PIF7 is a master regulator of thermomorphogenesis in shade. *Nat. Commun.* 13 (1), 4942. doi:10.1038/s41467-022-32585-6
- Calderon, R. H., Dalton, J., Zhang, Y., and Quail, P. H. (2022). Shade triggers posttranscriptional PHYTOCHROME-INTERACTING FACTOR-dependent increases in H3K4 trimethylation. *Plant Physiol.* 190 (3), 1915–1926. doi:10.1093/plphys/kiac282
- Carter, B., Bishop, B., Ho, K. K., Huang, R., Jia, W., Zhang, H., et al. (2018). The chromatin remodelers PKL and PIE1 act in an epigenetic pathway that determines H3K27me3 homeostasis in *Arabidopsis*. *Plant Cell* 30 (6), 1337–1352. doi:10.1105/tpc.17.00867
- Casal, J. J. (2012). Shade avoidance. *Arabidopsis Book* 10, e0157. doi:10.1199/tab.0157
- Casal, J. J., and Balasubramanian, S. (2019). Thermomorphogenesis. *Annu. Rev. Plant Biol.* 70, 321–346. doi:10.1146/annurev-arplant-050718-095919
- Casal, J. J., and Fankhauser, C. (2023). Shade avoidance in the context of climate change. *Plant Physiol.* 191 (3), 1475–1491. doi:10.1093/plphys/kiad004
- Castillon, A., Shen, H., and Huq, E. (2007). Phytochrome Interacting Factors: central players in phytochrome-mediated light signaling networks. *Trends Plant Sci.* 12 (11), 514–521. doi:10.1016/j.tplants.2007.10.001
- Chen, D., Lyu, M., Kou, X., Li, J., Yang, Z., Gao, L., et al. (2022). Integration of light and temperature sensing by liquid-liquid phase separation of phytochrome B. *Mol. Cell* 82 (16), 3015–3029.e6. doi:10.1016/j.molcel.2022.05.026
- Chen, H., Wang, W., Chen, X., Niu, Y., Qi, Y., Yu, Z., et al. (2023a). PIFs interact with SWI2/SNF2-related 1 complex subunit 6 to regulate H2A.Z deposition and photomorphogenesis in *Arabidopsis*. *J. Genet. Genomics* 50 (12), 983–992. doi:10.1016/j.jgg.2023.04.008
- Chen, M., Schwab, R., and Chory, J. (2003). Characterization of the requirements for localization of phytochrome B to nuclear bodies. *Proc. Natl. Acad. Sci. U. S. A.* 100 (24), 14493–14498. doi:10.1073/pnas.1935989100
- Chen, Y., Guo, P. G., and Dong, Z. C. (2023b). The role of histone acetylation in transcriptional regulation and seed development. *Plant Physiol.* 194, 1962–1979. doi:10.1093/plphys/kiad614
- Cheng, K., Xu, Y., Yang, C., Ouellette, L., Niu, L., Zhou, X., et al. (2020). Histone tales: lysine methylation, a protagonist in *Arabidopsis* development. *J. Exp. Bot.* 71 (3), 793–807. doi:10.1093/jxb/erz435
- Choi, K., Kim, S., Kim, S. Y., Kim, M., Hyun, Y., Lee, H., et al. (2005). *SUPPRESSOR of FRIGIDA3* encodes a nuclear ACTIN-RELATED PROTEIN6 required for floral repression in *Arabidopsis*. *Plant Cell* 17 (10), 2647–2660. doi:10.1105/tpc.105.035485
- Choi, K., Park, C., Lee, J., Oh, M., Noh, B., and Lee, I. (2007). *Arabidopsis* homologs of components of the SWR1 complex regulate flowering and plant development. *Development* 134 (10), 1931–1941. doi:10.1242/dev.001891
- Chung, B. Y. W., Balcerowicz, M., Di Antonio, M., Jaeger, K. E., Geng, F., Franaszek, K., et al. (2020). An RNA thermoswitch regulates daytime growth in *Arabidopsis*. *Nat. Plants* 6 (5), 522–532. doi:10.1038/s41477-020-0633-3
- Clapier, C. R., and Cairns, B. R. (2009). The biology of chromatin remodeling complexes. *Annu. Rev. Biochem.* 78, 273–304. doi:10.1146/annurev.biochem.77.062706.153223
- Cole, B., Bergmann, D., Blaby-Haas, C. E., Blaby, I. K., Bouchard, K. E., Brady, S. M., et al. (2021). Plant single-cell solutions for energy and the environment. *Commun. Biol.* 4 (1), 962. doi:10.1038/s42003-021-02477-4
- Coleman-Derr, D., and Zilberman, D. (2012). Deposition of histone variant H2A.Z within gene bodies regulates responsive genes. *PLoS Genet.* 8 (10), e1002988. doi:10.1371/journal.pgen.1002988
- Cortijo, S., Charoensawan, V., Brestovitsky, A., Buning, R., Ravarani, C., Rhodes, D., et al. (2017). Transcriptional regulation of the ambient temperature response by H2A.Z nucleosomes and HSF1 transcription factors in *Arabidopsis*. *Mol. Plant* 10 (10), 1258–1273. doi:10.1016/j.molp.2017.08.014
- Deal, R. B., Topp, C. N., McKinney, E. C., and Meagher, R. B. (2007). Repression of flowering in *Arabidopsis* requires activation of *FLOWERING LOCUS C* expression by the histone variant H2A.Z. *Plant Cell* 19 (1), 74–83. doi:10.1105/tpc.106.048447
- Duc, C., Benoit, M., Le Goff, S., Simon, L., Poulet, A., Cotterell, S., et al. (2015). The histone chaperone complex HIR maintains nucleosome occupancy and counterbalances impaired histone deposition in CAF-1 complex mutants. *Plant J.* 81 (5), 707–722. doi:10.1111/tpj.12758
- Eberharter, A., and Becker, P. B. (2002). Histone acetylation: a switch between repressive and permissive chromatin - second in review series on chromatin dynamics. *Embo Rep.* 3 (3), 224–229. doi:10.1093/embo-reports/kvf053
- Favero, D. S. (2020). Mechanisms regulating PIF transcription factor activity at the protein level. *Physiol. Plant.* 169 (3), 325–335. doi:10.1111/pp.13075
- Fiorucci, A. S., Galvao, V. C., Ince, Y. C., Boccacini, A., Goyal, A., Allenbach Petrolati, L., et al. (2020). PHYTOCHROME INTERACTING FACTOR 7 is important for early responses to elevated temperature in *Arabidopsis* seedlings. *New Phytol.* 226 (1), 50–58. doi:10.1111/nph.16316
- Franklin, K. A. (2008). Shade avoidance. *New Phytol.* 179 (4), 930–944. doi:10.1111/j.1469-8137.2008.02507.x
- Franklin, K. A., Lee, S. H., Patel, D., Kumar, S. V., Spartz, A. K., Gu, C., et al. (2011). PHYTOCHROME-INTERACTING FACTOR 4 (PIF4) regulates auxin biosynthesis at high temperature. *Proc. Natl. Acad. Sci.* 108 (50), 20231–20235. doi:10.1073/pnas.1110682108
- Franklin, K. A., and Whitelam, G. C. (2005). Phytochromes and shade-avoidance responses in plants. *Ann. Bot.* 96 (2), 169–175. doi:10.1093/aob/mci165
- Gangappa, S. N., Berriri, S., and Kumar, S. V. (2017). PIF4 coordinates thermosensory growth and immunity in *Arabidopsis*. *Curr. Biol.* 27 (2), 243–249. doi:10.1016/j.cub.2016.11.012
- Gao, H., Song, W., Severing, E., Vayssieres, A., Huettel, B., Franzen, R., et al. (2022). PIF4 enhances DNA binding of CDF2 to co-regulate target gene expression and promote *Arabidopsis* hypocotyl cell elongation. *Nat. Plants* 8 (9), 1082–1093. doi:10.1038/s41477-022-01213-y
- Gu, D. C., Chen, C. Y., Zhao, M. L., Zhao, L. M., Duan, X. W., Duan, J., et al. (2017). Identification of HDA15-PIF1 as a key repression module directing the transcriptional network of seed germination in the dark. *Nucleic Acids Res.* 45 (12), 7137–7150. doi:10.1093/nar/gkx283
- Guo, J., Cai, G., Li, Y. Q., Zhang, Y. X., Su, Y. N., Yuan, D. Y., et al. (2022). Comprehensive characterization of three classes of *Arabidopsis* SWI/SNF chromatin remodelling complexes. *Nat. Plants* 8 (12), 1423–1439. doi:10.1038/s41477-022-01282-z
- Guo, Q., Jing, Y. J., Gao, Y., Liu, Y. T., Fang, X. F., and Lin, R. C. (2023). The PIF1/PIF3-MED25-HDA19 transcriptional repression complex regulates phytochrome signaling in *Arabidopsis*. *New Phytol.* 240 (3), 1097–1115. doi:10.1111/nph.19205

- Hahm, J., Kim, K., Qiu, Y., and Chen, M. (2020). Increasing ambient temperature progressively disassembles Arabidopsis phytochrome B from individual photobodies with distinct thermostabilities. *Nat. Commun.* 11 (1), 1660. doi:10.1038/s41467-020-15526-z
- Han, S. K., Wu, M. F., Cui, S., and Wagner, D. (2015). Roles and activities of chromatin remodeling ATPases in plants. *Plant J.* 83 (1), 62–77. doi:10.1111/tpj.12877
- Han, X., Zhang, Y., Lou, Z., Li, J., Wang, Z., Gao, C., et al. (2023). Time series single-cell transcriptional atlases reveal cell fate differentiation driven by light in Arabidopsis seedlings. *Nat. Plants* 9 (12), 2095–2109. doi:10.1038/s41477-023-01544-4
- He, K. X., Mei, H. L., Zhu, J. P., Qiu, Q., Cao, X. F., and Deng, X. (2022). The histone H3K27 demethylase REF6/JMJ12 promotes thermomorphogenesis in Arabidopsis. *Nat. Sci. Rev.* 9 (5), nwab213. doi:10.1093/nsr/nwab213
- Henikoff, S., and Ahmad, K. (2005). Assembly of variant histones into chromatin. *Annu. Rev. Cell Dev. Biol.* 21, 133–153. doi:10.1146/annurev.cellbio.21.012704.133518
- Hollender, C., and Liu, Z. (2008). Histone deacetylase genes in Arabidopsis development. *J. Integr. Plant Biol.* 50 (7), 875–885. doi:10.1111/j.1744-7909.2008.00704.x
- Huai, J., Zhang, X., Li, J., Ma, T., Zha, P., Jing, Y., et al. (2018). SEUSS and PIF4 coordinately regulate light and temperature signaling pathways to control plant growth. *Mol. Plant* 11 (7), 928–942. doi:10.1016/j.molp.2018.04.005
- Huang, X., Zhang, Q., Jiang, Y. P., Yang, C. W., Wang, Q. Y., and Li, L. (2018). Shade-induced nuclear localization of PIF7 is regulated by phosphorylation and 14-3-3 proteins in Arabidopsis. *Elife* 7, e31636. doi:10.7554/elife.31636
- Huq, E., Al-Sady, B., Hudson, M., Kim, C. H., Apel, K., and Quail, P. H. (2004). PHYTOCHROME-INTERACTING FACTOR 1 is a critical bHLH regulator of chlorophyll biosynthesis. *Science* 305 (5692), 1937–1941. doi:10.1126/science.1099728
- Huq, E., and Quail, P. H. (2002). PIF4, a phytochrome-interacting bHLH factor, functions as a negative regulator of phytochrome B signaling in Arabidopsis. *EMBO J.* 21 (10), 2441–2450. doi:10.1093/emboj/21.10.2441
- Hussain, E., Romanowski, A., and Halliday, K. J. (2022). PIF7 controls leaf cell proliferation through an AN3 substitution repression mechanism. *Proc. Natl. Acad. Sci. U. S. A.* 119 (5), e2115682119. doi:10.1073/pnas.2115682119
- Jegu, T., Veluchamy, A., Ramirez-Prado, J. S., Rizzi-Paillet, C., Perez, M., Lhomme, A., et al. (2017). The Arabidopsis SWI/SNF protein BAF60 mediates seedling growth control by modulating DNA accessibility. *Genome Biol.* 18 (1), 114. doi:10.1186/s13059-017-1246-7
- Jeong, J., and Choi, G. (2013). Phytochrome-interacting factors have both shared and distinct biological roles. *Mol. Cells* 35 (5), 371–380. doi:10.1007/s10059-013-0135-5
- Jiang, J. J., Ding, A. B., Liu, F. Q., and Zhong, X. H. (2020). Linking signaling pathways to histone acetylation dynamics in plants. *J. Exp. Bot.* 71 (17), 5179–5190. doi:10.1093/jxb/eraa202
- Jing, Y., and Lin, R. (2020). Transcriptional regulatory network of the light signaling pathways. *New Phytol.* 227 (3), 683–697. doi:10.1111/nph.16602
- Jung, J. H., Domijan, M., Klose, C., Biswas, S., Ezer, D., Gao, M., et al. (2016). Phytochromes function as thermosensors in Arabidopsis. *Science* 354 (6314), 886–889. doi:10.1126/science.aaf6005
- Jung, J. H., Park, J. H., Lee, S., To, T. K., Kim, J. M., Seki, M., et al. (2013). The cold signaling attenuator HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENE1 activates FLOWERING LOCUS C transcription via chromatin remodeling under short-term cold stress in Arabidopsis. *Plant Cell* 25 (11), 4378–4390. doi:10.1105/tpc.113.118364
- Kidokoro, S., Maruyama, K., Nakashima, K., Imura, Y., Narusaka, Y., Shinwari, Z. K., et al. (2009). The phytochrome-interacting factor PIF7 negatively regulates DREB1 expression under circadian control in Arabidopsis. *Plant Physiol.* 151 (4), 2046–2057. doi:10.1104/pp.109.147033
- Kim, C., Kwon, Y., Jeong, J., Kang, M., Lee, G. S., Moon, J. H., et al. (2023). Phytochrome B photobodies are comprised of phytochrome B and its primary and secondary interacting proteins. *Nat. Commun.* 14 (1), 1708. doi:10.1038/s41467-023-37421-z
- Kim, J., Bordiya, Y., Kathare, P. K., Zhao, B., Zong, W., Huq, E., et al. (2021). Phytochrome B triggers light-dependent chromatin remodeling through the PRC2-associated PHD finger protein VIL1. *Nat. Plants* 7 (9), 1213–1219. doi:10.1038/s41477-021-00986-y
- Kim, J., Song, K., Park, E., Kim, K., Bae, G., and Choi, G. (2016). Epidermal phytochrome B inhibits hypocotyl negative gravitropism non-cell-autonomously. *Plant Cell* 28 (11), 2770–2785. doi:10.1105/tpc.16.00487
- Kim, J. H., Lee, H. J., Jung, J. H., Lee, S., and Park, C. M. (2017). HOS1 facilitates the phytochrome B-mediated inhibition of PIF4 function during hypocotyl growth in Arabidopsis. *Mol. Plant* 10 (2), 274–284. doi:10.1016/j.molp.2016.11.009
- Kim, S., Hwang, G., Kim, S., Thi, T. N., Kim, H., Jeong, J., et al. (2020). The epidermis coordinates thermoresponsive growth through the phyB-PIF4-auxin pathway. *Nat. Commun.* 11 (1), 1053. doi:10.1038/s41467-020-14905-w
- Kircher, S., Kozma-Bognar, L., Kim, L., Adam, E., Harter, K., Schafer, E., et al. (1999). Light quality-dependent nuclear import of the plant photoreceptors phytochrome A and B. *Plant Cell* 11 (8), 1445–1456. doi:10.2307/3870974
- Koini, M. A., Alvey, L., Allen, T., Tilley, C. A., Harberd, N. P., Whitelam, G. C., et al. (2009). High temperature-mediated adaptations in plant architecture require the bHLH transcription factor PIF4. *Curr. Biol.* 19 (5), 408–413. doi:10.1016/j.cub.2009.01.046
- Krogan, N. T., Hogan, K., and Long, J. A. (2012). APETALA2 negatively regulates multiple floral organ identity genes in Arabidopsis by recruiting the co-repressor TOPLESS and the histone deacetylase HDA19. *Development* 139 (22), 4180–4190. doi:10.1242/dev.085407
- Kumar, S. V., Lucyshyn, D., Jaeger, K. E., Alos, E., Alvey, E., Harberd, N. P., et al. (2012). Transcription factor PIF4 controls the thermosensory activation of flowering. *Nature* 484 (7393), 242–245. doi:10.1038/nature10928
- Kumar, S. V., and Wigge, P. A. (2010). H2A.Z-containing nucleosomes mediate the thermosensory response in Arabidopsis. *Cell* 140 (1), 136–147. doi:10.1016/j.cell.2009.11.006
- Kwon, Y., Kim, C., and Choi, G. (2024). Phytochrome B photobody components. *New Phytol.* 242, 909–915. doi:10.1111/nph.19675
- Latrasse, D., Benhamed, M., Henry, Y., Domenichini, S., Kim, W., Zhou, D. X., et al. (2008). The MYST histone acetyltransferases are essential for gametophyte development in Arabidopsis. *BMC Plant Biol.* 8, 121. doi:10.1186/1471-2229-8-121
- Lee, N., Park, J., Kim, K., and Choi, G. (2015). The transcriptional coregulator LEUNIG_HOMOLOG inhibits light-dependent seed germination in Arabidopsis. *Plant Cell* 27 (8), 2301–2313. doi:10.1105/tpc.15.00444
- Legris, M., Klose, C., Burgie, E. S., Rojas, C. C., Neme, M., Hiltbrunner, A., et al. (2016). Phytochrome B integrates light and temperature signals in Arabidopsis. *Science* 354 (6314), 897–900. doi:10.1126/science.aaf5656
- Leivar, P., and Monte, E. (2014). PIFs: systems integrators in plant development. *Plant Cell* 26 (1), 56–78. doi:10.1105/tpc.113.120857
- Leivar, P., Monte, E., Al-Sady, B., Carle, C., Storer, A., Alonso, J. M., et al. (2008). The Arabidopsis phytochrome-interacting factor PIF7, together with PIF3 and PIF4, regulates responses to prolonged red light by modulating phyB levels. *Plant Cell* 20 (2), 337–352. doi:10.1105/tpc.107.052142
- Leivar, P., and Quail, P. H. (2011). PIFs: pivotal components in a cellular signaling hub. *Trends Plant Sci.* 16 (1), 19–28. doi:10.1016/j.tplants.2010.08.003
- Lian, T. F., Xu, Y. P., Li, L. F., and Su, X. D. (2017). Crystal structure of tetrameric Arabidopsis MYC2 reveals the mechanism of enhanced interaction with DNA. *Cell Rep.* 19 (7), 1334–1342. doi:10.1016/j.celrep.2017.04.057
- Liu, C., Lu, F., Cui, X., and Cao, X. (2010). Histone methylation in higher plants. *Annu. Rev. Plant Biol.* 61, 395–420. doi:10.1146/annurev-arplant.043008.091939
- Liu, X., Chen, C. Y., Wang, K. C., Luo, M., Tai, R., Yuan, L., et al. (2013). PHYTOCHROME INTERACTING FACTOR3 associates with the histone deacetylase HDA15 in repression of chlorophyll biosynthesis and photosynthesis in etiolated Arabidopsis seedlings. *Plant Cell* 25 (4), 1258–1273. doi:10.1105/tpc.113.109710
- Lloyd, J. P. B., and Lister, R. (2022). Epigenome plasticity in plants. *Nat. Rev. Genet.* 23 (1), 55–68. doi:10.1038/s41576-021-00407-y
- Long, J. A., Ohno, C., Smith, Z. R., and Meyerowitz, E. M. (2006). TOPLESS regulates apical embryonic fate in Arabidopsis. *Science* 312 (5779), 1520–1523. doi:10.1126/science.1123841
- Lu, F., Cui, X., Zhang, S., Jenuwein, T., and Cao, X. (2011). Arabidopsis REF6 is a histone H3 lysine 27 demethylase. *Nat. Genet.* 43 (7), 715–719. doi:10.1038/ng.854
- Lu, F., Li, G., Cui, X., Liu, C., Wang, X. J., and Cao, X. (2008). Comparative analysis of JmjC domain-containing proteins reveals the potential histone demethylases in Arabidopsis and rice. *J. Integr. Plant Biol.* 50 (7), 886–896. doi:10.1111/j.1744-7909.2008.00692.x
- Luo, Y. X., Hou, X. M., Zhang, C. J., Tan, L. M., Shao, C. R., Lin, R. N., et al. (2020). A plant-specific SWR1 chromatin-remodeling complex couples histone H2A.Z deposition with nucleosome sliding. *EMBO J.* 39 (7), e102008. doi:10.15252/embj.2019102008
- March-Diaz, R., Garcia-Dominguez, M., Florencio, F. J., and Reyes, J. C. (2007). SEF, a new protein required for flowering repression in Arabidopsis, interacts with PIE1 and ARP6. *Plant Physiol.* 143 (2), 893–901. doi:10.1104/pp.106.092270
- March-Diaz, R., Garcia-Dominguez, M., Lozano-Juste, J., Leon, J., Florencio, F. J., and Reyes, J. C. (2008). Histone H2A.Z and homologues of components of the SWR1 complex are required to control immunity in Arabidopsis. *Plant J.* 53 (3), 475–487. doi:10.1111/j.1365-313x.2007.03361.x
- Martinez-Garcia, J. F., and Moreno-Romero, J. (2020). Shedding light on the chromatin changes that modulate shade responses. *Physiol. Plant.* 169 (3), 407–417. doi:10.1111/ppl.13101
- Martin-Trillo, M., Lazaro, A., Poethig, R. S., Gomez-Mena, C., Pineiro, M. A., Martinez-Zapater, J. M., et al. (2006). EARLY IN SHORT DAYS 1 (ESD1) encodes ACTIN-RELATED PROTEIN 6 (AtARP6), a putative component of chromatin remodelling complexes that positively regulates FLC accumulation in Arabidopsis. *Development* 133 (7), 1241–1252. doi:10.1242/dev.02301
- Mosammaparast, N., and Shi, Y. (2010). Reversal of histone methylation: biochemical and molecular mechanisms of histone demethylases. *Annu. Rev. Biochem.* 79, 155–179. doi:10.1146/annurev-biochem.78.070907.103946
- Nguyen, N. H., Sng, B. J. R., Chin, H. J., Choi, I. K. Y., Yeo, H. C., and Jang, I. C. (2023). HISTONE DEACETYLASE 9 promotes hypocotyl-specific auxin response under shade. *Plant J.* 116 (3), 804–822. doi:10.1111/tpj.16410

- Ni, M., Tepperman, J. M., and Quail, P. H. (1998). PIF3, a phytochrome-interacting factor necessary for normal photoinduced signal transduction, is a novel basic helix-loop-helix protein. *Cell* 95 (5), 657–667. doi:10.1016/s0092-8674(00)81636-0
- Nie, W. F., Lei, M., Zhang, M., Tang, K., Huang, H., Zhang, C., et al. (2019). Histone acetylation recruits the SWR1 complex to regulate active DNA demethylation in Arabidopsis. *Proc. Natl. Acad. Sci. U. S. A.* 116 (33), 16641–16650. doi:10.1073/pnas.1906023116
- Nie, X., Wang, H., Li, J., Holec, S., and Berger, F. (2014). The HIRA complex that deposits the histone H3.3 is conserved in Arabidopsis and facilitates transcriptional dynamics. *Biol. Open* 3 (9), 794–802. doi:10.1242/bio.20148680
- Noh, Y. S., and Amasino, R. M. (2003). PIE1, an ISWI family gene, is required for FLC activation and floral repression in Arabidopsis. *Plant Cell* 15 (7), 1671–1682. doi:10.1105/tpc.012161
- Oh, E., Kim, J., Park, E., Kim, J. I., Kang, C., and Choi, G. (2004). PIL5, a phytochrome-interacting basic helix-loop-helix protein, is a key negative regulator of seed germination in *Arabidopsis thaliana*. *Plant Cell* 16 (11), 3045–3058. doi:10.1105/tpc.104.025163
- Paik, I., Kathare, P. K., Kim, J. I., and Huq, E. (2017). Expanding roles of PIFs in signal integration from multiple processes. *Mol. Plant* 10 (8), 1035–1046. doi:10.1016/j.molp.2017.07.002
- Pandey, R., Muller, A., Napoli, C. A., Selinger, D. A., Pikaard, C. S., Richards, E. J., et al. (2002). Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. *Nucleic Acids Res.* 30 (23), 5036–5055. doi:10.1093/nar/gkf660
- Panigrahi, A., and O'Malley, B. W. (2021). Mechanisms of enhancer action: the known and the unknown. *Genome Biol.* 22 (1), 108. doi:10.1186/s13059-021-02322-1
- Papamichos-Chronakis, M., Watanabe, S., Rando, O. J., and Peterson, C. L. (2011). Global regulation of H2A.Z localization by the INO80 chromatin-remodeling enzyme is essential for genome integrity. *Cell* 144 (2), 200–213. doi:10.1016/j.cell.2010.12.021
- Pardi, S. A., and Nusinow, D. A. (2021). Out of the dark and into the light: a new view of phytochrome photobodies. *Front. Plant Sci.* 12, 732947. doi:10.3389/fpls.2021.732947
- Peng, M., Li, Z., Zhou, N., Ma, M., Jiang, Y., Dong, A., et al. (2018). Linking PHYTOCHROME-INTERACTING FACTOR to histone modification in plant shade avoidance. *Plant Physiol.* 176 (2), 1341–1351. doi:10.1104/pp.17.01189
- Perrella, G., and Kaiserli, E. (2016). Light behind the curtain: photoregulation of nuclear architecture and chromatin dynamics in plants. *New Phytol.* 212 (4), 908–919. doi:10.1111/nph.14269
- Perrella, G., Zioutopoulou, A., Headland, L. R., and Kaiserli, E. (2020). The impact of light and temperature on chromatin organization and plant adaptation. *J. Exp. Bot.* 71 (17), 5247–5255. doi:10.1093/jxb/era154
- Pham, V. N., Kathare, P. K., and Huq, E. (2018). Phytochromes and phytochrome interacting factors. *Plant Physiol.* 176 (2), 1025–1038. doi:10.1104/pp.17.01384
- Plant, A. R., Larrieu, A., and Causier, B. (2021). Repressor for hire! The vital roles of TOPLESS-mediated transcriptional repression in plants. *New Phytol.* 231 (3), 963–973. doi:10.1111/nph.17428
- Proveniers, M. C. G., and van Zanten, M. (2013). High temperature acclimation through PIF4 signaling. *Trends Plant Sci.* 18 (2), 59–64. doi:10.1016/j.tplants.2012.09.002
- Quail, P. H., Boylan, M. T., Parks, B. M., Short, T. W., Xu, Y., and Wagner, D. (1995). Phytochromes: photosensory perception and signal transduction. *Science*. 268 (5211), 675–680. doi:10.1126/science.7732376
- Rivera, C. M., and Ren, B. (2013). Mapping human epigenomes. *Cell* 155 (1), 39–55. doi:10.1016/j.cell.2013.09.011
- Rockwell, N. C., Su, Y. S., and Lagarias, J. C. (2006). Phytochrome structure and signaling mechanisms. *Annu. Rev. Plant Biol.* 57, 837–858. doi:10.1146/annurev.arplant.56.032604.144208
- Sakamoto, K., and Nagatani, A. (1996). Nuclear localization activity of phytochrome B. *Plant J.* 10 (5), 859–868. doi:10.1046/j.1365-313x.1996.10050859.x
- Sessa, G., Carabelli, M., Possenti, M., Morelli, G., and Ruberti, I. (2018). Multiple pathways in the control of the shade avoidance response. *Plants (Basel)* 7 (4), 102. doi:10.3390/plants7040102
- Shan, L., Li, P., Yu, H., and Chen, L. L. (2023). Emerging roles of nuclear bodies in genome spatial organization. *Trends Cell Biol.* doi:10.1016/j.tcb.2023.10.012
- Shang, J. Y., Lu, Y. J., Cai, X. W., Su, Y. N., Feng, C., Li, L., et al. (2021). COMPASS functions as a module of the INO80 chromatin remodeling complex to mediate histone H3K4 methylation in Arabidopsis. *Plant Cell* 33 (10), 3250–3271. doi:10.1093/plcell/kob187
- Shapulatov, U., van Zanten, M., van Hoogdalem, M., Meisenburg, M., van Hall, A., Kappers, I., et al. (2023). The Mediator complex subunit MED25 interacts with HDA9 and PIF4 to regulate thermomorphogenesis. *Plant Physiol.* 192 (1), 582–600. doi:10.1093/plphys/kiac581
- Shen, H., Zhu, L., Castillon, A., Majee, M., Downie, B., and Huq, E. (2008). Light-induced phosphorylation and degradation of the negative regulator PHYTOCHROME-INTERACTING FACTOR1 from Arabidopsis depend upon its direct physical interactions with photoactivated phytochromes. *Plant Cell* 20 (6), 1586–1602. doi:10.1105/tpc.108.060020
- Shen, Y., Lei, T. T., Cui, X. Y., Liu, X. Y., Zhou, S. L., Zheng, Y., et al. (2019). Arabidopsis histone deacetylase HDA15 directly represses plant response to elevated ambient temperature. *Plant J.* 100 (5), 991–1006. doi:10.1111/tpj.14492
- Shin, J., Anwer, M. U., and Davis, S. J. (2013). Phytochrome-interacting factors (PIFs) as bridges between environmental signals and the circadian clock: diurnal regulation of growth and development. *Mol. Plant* 6 (3), 592–595. doi:10.1093/mp/sst060
- Shvedunova, M., and Akhtar, A. (2022). Modulation of cellular processes by histone and non-histone protein acetylation. *Nat. Rev. Mol. Cell Biol.* 23 (5), 329–349. doi:10.1038/s41580-021-00441-y
- Smaczniak, C., Li, N., Boeren, S., America, T., van Dongen, W., Goerdal, S. S., et al. (2012). Proteomics-based identification of low-abundance signaling and regulatory protein complexes in native plant tissues. *Nat. Protoc.* 7 (12), 2144–2158. doi:10.1038/nprot.2012.129
- Soutourina, J. (2018). Transcription regulation by the Mediator complex. *Nat. Rev. Mol. Cell Biol.* 19 (4), 262–274. doi:10.1038/nrm.2017.115
- Steindler, C., Matteucci, A., Sessa, G., Weimar, T., Ohgishi, M., Aoyama, T., et al. (1999). Shade avoidance responses are mediated by the ATHB-2 HD-zip protein, a negative regulator of gene expression. *Development* 126 (19), 4235–4245. doi:10.1242/dev.126.19.4235
- Sun, J. Q., Qi, L. L., Li, Y. N., Chu, J. F., and Li, C. Y. (2012). PIF4-Mediated activation of YUCCA8 expression integrates temperature into the auxin pathway in regulating Arabidopsis hypocotyl growth. *Plos Genet.* 8 (3), e1002594. doi:10.1371/journal.pgen.1002594
- Sun, W., Han, H., Deng, L., Sun, C., Xu, Y., Lin, L., et al. (2020). Mediator subunit MED25 physically interacts with PHYTOCHROME INTERACTING FACTOR4 to regulate shade-induced hypocotyl elongation in tomato. *Plant Physiol.* 184 (3), 1549–1562. doi:10.1104/pp.20.00587
- Sura, W., Kabza, M., Karlowski, W. M., Bieluszewski, T., Kus-Slowinska, M., Pawelozek, L., et al. (2017). Dual role of the histone variant H2A.Z in transcriptional regulation of stress-response genes. *Plant Cell* 29 (4), 791–807. doi:10.1105/tpc.16.00573
- Sureshkumar, S., and Balasubramanian, S. (2021). Complexes and complexities: INO80 takes center stage. *Mol. Plant* 14 (11), 1776–1778. doi:10.1016/j.molp.2021.08.012
- Tagami, H., Ray-Gallet, D., Almouzni, G., and Nakatani, Y. (2004). Histone H3.1 and H3.3 complexes mediate nucleosome assembly pathways dependent or independent of DNA synthesis. *Cell* 116 (1), 51–61. doi:10.1016/s0092-8674(03)01064-x
- Tasset, C., Singh Yadav, A., Sureshkumar, S., Singh, R., van der Woude, L., Nekrasov, M., et al. (2018). POWERDRESS-mediated histone deacetylation is essential for thermomorphogenesis in *Arabidopsis thaliana*. *PLoS Genet.* 14 (3), e1007280. doi:10.1371/journal.pgen.1007280
- Van Buskirk, E. K., Decker, P. V., and Chen, M. (2012). Photobodies in light signaling. *Plant Physiol.* 158 (1), 52–60. doi:10.1104/pp.111.186411
- van der Woude, L. C., Perrella, G., Snoek, B. L., van Hoogdalem, M., Novak, O., van Verk, M. C., et al. (2019). HISTONE DEACETYLASE 9 stimulates auxin-dependent thermomorphogenesis in *Arabidopsis thaliana* by mediating H2A.Z depletion. *Proc. Natl. Acad. Sci.* 116 (50), 25343–25354. doi:10.1073/pnas.1911694116
- Wang, H., Fan, Z., Shliha, P. V., Miele, M., Hendrickson, R. C., Jiang, X. J., et al. (2023). H3K4me3 regulates RNA polymerase II promoter-proximal pause-release. *Nature* 615 (7951), 339–348. doi:10.1038/s41586-023-05780-8
- Wang, H., Li, S., Li, Y., Xu, Y., Wang, Y., Zhang, R., et al. (2019). MED25 connects enhancer-promoter looping and MYC2-dependent activation of jasmonate signalling. *Nat. plants* 5 (6), 616–625. doi:10.1038/s41477-019-0441-9
- Wang, L., Kim, J., and Somers, D. E. (2013). Transcriptional corepressor TOPLESS complexes with pseudoresponse regulator proteins and histone deacetylases to regulate circadian transcription. *Proc. Natl. Acad. Sci. U. S. A.* 110 (2), 761–766. doi:10.1073/pnas.1215010110
- Wang, W., Kim, J., Martinez, T. S., Huq, E., and Sung, S. (2024). COP1 controls light-dependent chromatin remodeling. *Proc. Natl. Acad. Sci. U. S. A.* 121 (8), e2312853121. doi:10.1073/pnas.2312853121
- Willige, B. C., Yoo, C. Y., and Saldierna Guzman, J. P. (2024). What is going on inside of phytochrome B photobodies? *Plant Cell*, koae084. doi:10.1093/plcell/koae084
- Willige, B. C., Zander, M., Yoo, C. Y., Phan, A., Garza, R. M., Wanamaker, S. A., et al. (2021). PHYTOCHROME-INTERACTING FACTORS trigger environmentally responsive chromatin dynamics in plants. *Nat. Genet.* 53 (7), 955–961. doi:10.1038/s41588-021-00882-3
- Wollmann, H., Stroud, H., Yelagandula, R., Tarutani, Y., Jiang, D., Jing, L., et al. (2017). The histone H3 variant H3.3 regulates gene body DNA methylation in *Arabidopsis thaliana*. *Genome Biol.* 18 (1), 94. doi:10.1186/s13059-017-1221-3
- Xiao, J., Lee, U. S., and Wagner, D. (2016). Tug of war: adding and removing histone lysine methylation in Arabidopsis. *Curr. Opin. Plant Biol.* 34, 41–53. doi:10.1016/j.pbi.2016.08.002

- Xie, Y., Liu, W., Liang, W., Ling, X., Ma, J., Yang, C., et al. (2023). Phytochrome B inhibits the activity of phytochrome-interacting factor 7 involving phase separation. *Cell Rep.* 42 (12), 113562. doi:10.1016/j.celrep.2023.113562
- Xu, Y. F., Gan, E. S., Zhou, J., Wee, W. Y., Zhang, X. Y., and Ito, T. (2014). Arabidopsis MRG domain proteins bridge two histone modifications to elevate expression of flowering genes. *Nucleic Acids Res.* 42 (17), 10960–10974. doi:10.1093/nar/gku781
- Xue, M., Zhang, H., Zhao, F., Zhao, T., Li, H., and Jiang, D. (2021). The INO80 chromatin remodeling complex promotes thermomorphogenesis by connecting H2A.Z eviction and active transcription in Arabidopsis. *Mol. Plant* 14 (11), 1799–1813. doi:10.1016/j.molp.2021.07.001
- Yang, C., Zhu, T., Zhou, N., Huang, S., Zeng, Y., Jiang, W., et al. (2023). PIF7-mediated epigenetic reprogramming promotes the transcriptional response to shade in Arabidopsis. *EMBO J.* 42 (8), e111472. doi:10.15252/embj.2022111472
- Yi, H., Sardesai, N., Fujinuma, T., Chan, C. W., Veena, G. S. B., and Gelvin, S. B. (2006). Constitutive expression exposes functional redundancy between the Arabidopsis histone H2A gene HTA1 and other H2A gene family members. *Plant Cell* 18 (7), 1575–1589. doi:10.1105/tpc.105.039719
- Zander, M., Willige, B. C., He, Y., Nguyen, T. A., Langford, A. E., Nehring, R., et al. (2019). Epigenetic silencing of a multifunctional plant stress regulator. *eLife* 8, e47835. doi:10.7554/eLife.47835
- Zhai, H., Zhang, X., You, Y., Lin, L., Zhou, W., and Li, C. (2020). SEUSS integrates transcriptional and epigenetic control of root stem cell organizer specification. *EMBO J.* 39 (20), e105047. doi:10.15252/embj.2020105047
- Zhang, D., Jing, Y., Jiang, Z., and Lin, R. (2014). The chromatin-remodeling factor PICKLE integrates brassinosteroid and gibberellin signaling during skotomorphogenic growth in Arabidopsis. *Plant Cell* 26 (6), 2472–2485. doi:10.1105/tpc.113.121848
- Zhang, D., Li, Y., Zhang, X., Zha, P., and Lin, R. (2017). The SWI2/SNF2 chromatin-remodeling ATPase BRAHMA regulates chlorophyll biosynthesis in Arabidopsis. *Mol. Plant* 10 (1), 155–167. doi:10.1016/j.molp.2016.11.003
- Zhao, F., Xue, M., Zhang, H., Li, H., Zhao, T., and Jiang, D. (2023). Coordinated histone variant H2A.Z eviction and H3.3 deposition control plant thermomorphogenesis. *New Phytol.* 238 (2), 750–764. doi:10.1111/nph.18738
- Zhao, Q., Dai, B. D., Wu, H. Y., Zhu, W. C., and Chen, J. Y. (2022). Ino80 is required for H2A.Z eviction from hypha-specific promoters and hyphal development of *Candida albicans*. *Mol. Microbiol.* 118 (1–2), 92–104. doi:10.1111/mmi.14954
- Zhong, Z., Wang, Y., Wang, M., Yang, F., Thomas, Q. A., Xue, Y., et al. (2022). Histone chaperone ASF1 mediates H3.3-H4 deposition in Arabidopsis. *Nat. Commun.* 13 (1), 6970. doi:10.1038/s41467-022-34648-0
- Zhou, N., Li, C., Xie, W., Liang, N., Wang, J., Wang, B., et al. (2024). Histone methylation readers MRG1/2 interact with PIF4 to promote thermomorphogenesis in Arabidopsis. *Cell Rep.* 43 (2), 113726. doi:10.1016/j.celrep.2024.113726
- Zhou, Y., Park, S. H., Soh, M. Y., and Chua, N. H. (2021). Ubiquitin-specific proteases UBP12 and UBP13 promote shade avoidance response by enhancing PIF7 stability. *Proc. Natl. Acad. Sci. U. S. A.* 118 (45), e2103633118. doi:10.1073/pnas.2103633118
- Zhu, Y., Weng, M., Yang, Y., Zhang, C., Li, Z., Shen, W. H., et al. (2011). Arabidopsis homologues of the histone chaperone ASF1 are crucial for chromatin replication and cell proliferation in plant development. *Plant J.* 66 (3), 443–455. doi:10.1111/j.1365-313x.2011.04504.x