Phytohormone and Chromatin Crosstalk: The Missing Link For Developmental Plasticity?

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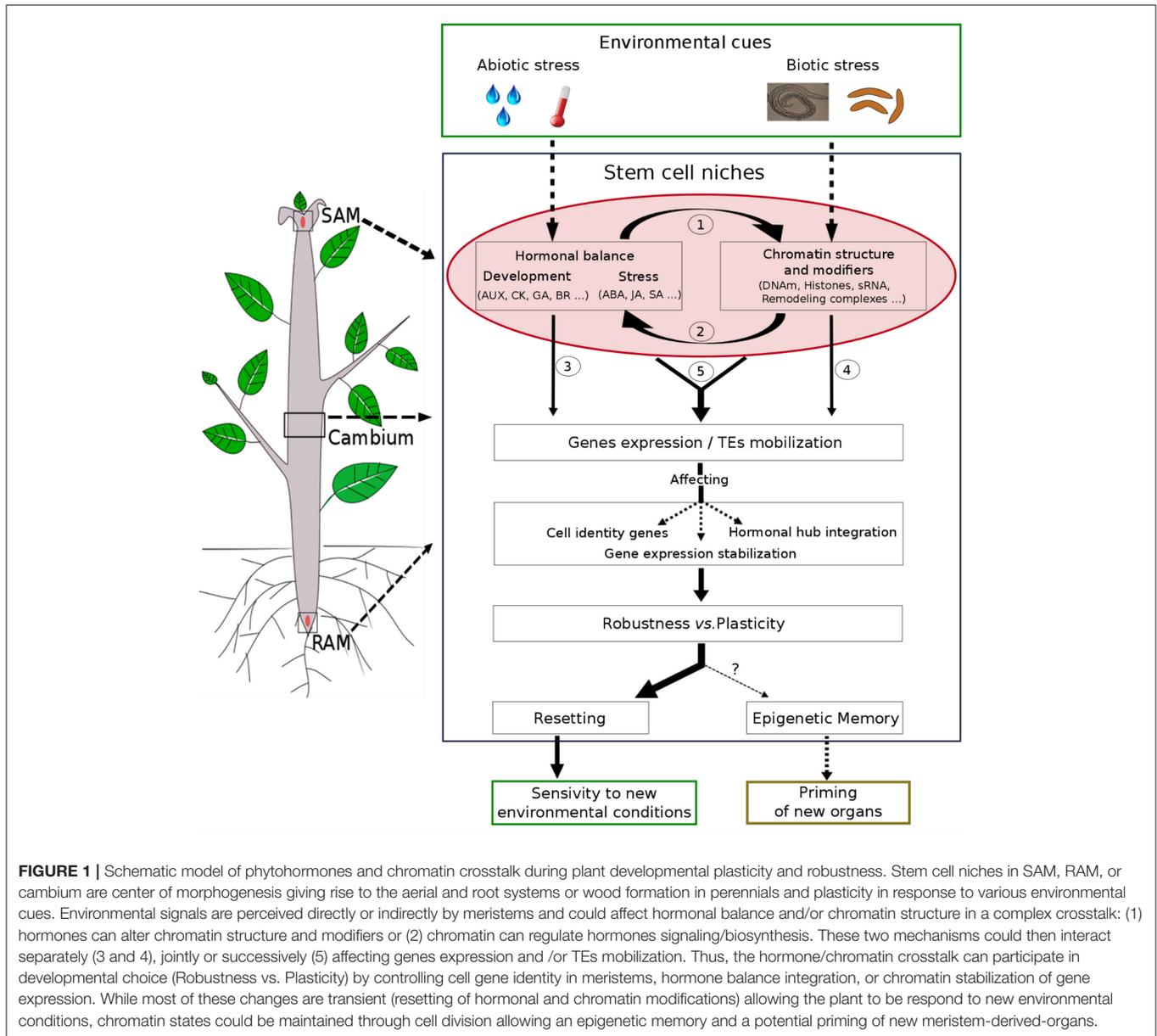
Plants grow continuously, forming new meristem-derived organs and tissues throughout their post-embryonic life. As sessile organisms, plants need to constantly integrate and reflect environmental fluctuations in their growth and development, which can translate into high level of developmental plasticity in response to environmental changes (Gaillochet and Lohmann, 2015). Alternatively, variable environments can select for robustness, where organisms function across a wide range of conditions with little change in phenotype. Plant growth is then governed by complex interplay of phytohormone signaling, chromatin structure remodeling and gene expression reprogramming. How these regulatory levels are interconnected remains largely enigmatic, but mechanistic evidence of crosstalk between phytohormone signaling and chromatin organization is emerging.

Here we review (1) evidences of molecular mechanisms that mediate the crosstalk between phytohormone signaling, chromatin structure and gene expression (2) how this crosstalk may link to plant developmental plasticity and robustness and finally (3) why meristems may represent central places for this crosstalk allowing plasticity and environmental memory.

CROSSTALK MECHANISMS: A CHICKEN-AND-EGG SITUATION

Phytohormone and epigenetic regulation can interact on multiple levels (**Figure 1**): (1) phytohormone signaling directly affects expression or activity of key chromatin modifiers, (2) chromatin machinery target genes of the phytohormone metabolic/signaling pathways, (3) both players interact on genes involved in developmental or stress responses.

Several examples show that components of phytohormone signaling pathways directly control the activity of key chromatin modifiers such as POLYCOMB REPRESSIVE COMPLEX (PRC) 1 and 2 with histone-methyltransferase activity playing a major role in transcriptional regulation during development (Bratzel et al., 2010; Chen et al., 2010, 2016; Ikeuchi et al., 2015; Mozgová et al., 2017). For example, the brassinosteroid (BR) signaling TFs BRASSINAZOLE-RESISTANT 1 (BZR1) recruits the H3K27me3-demethylase EARLY FLOWERING (ELF) 6 to antagonize the H3K27me3-activity of PRC2, a chromatin modifier, at the flowering repressor *FLOWERING LOCUS C* (*FLC*), preventing precocious floral transition (Yu et al., 2008; Li et al., 2018). Additionally, chromatin complexes can be post-translationally modified by components of phytohormone signaling pathways that influence their activity. For example, abscisic acid (ABA) signaling induces SnRK-mediated phosphorylation of the chromatin remodeling ATPase BRAHMA (BRM), inhibiting its repressive activity at ABA-responsive genes (Peirats-Llobet et al., 2016). These examples demonstrate that activity of chromatin modifiers can be directed to specific loci or directly modulated by phytohormone signaling cascades.

FIGURE 1 | Schematic model of phytohormones and chromatin crosstalk during plant developmental plasticity and robustness. Stem cell niches in SAM, RAM, or cambium are center of morphogenesis giving rise to the aerial and root systems or wood formation in perennials and plasticity in response to various environmental cues. Environmental signals are perceived directly or indirectly by meristems and could affect hormonal balance and/or chromatin structure in a complex crosstalk: (1) hormones can alter chromatin structure and modifiers or (2) chromatin can regulate hormones signaling/biosynthesis. These two mechanisms could then interact separately (3 and 4), jointly or successively (5) affecting genes expression and /or TEs mobilization. Thus, the hormone/chromatin crosstalk can participate in developmental choice (Robustness vs. Plasticity) by controlling cell gene identity in meristems, hormone balance integration, or chromatin stabilization of gene expression. While most of these changes are transient (resetting of hormonal and chromatin modifications) allowing the plant to be respond to new environmental conditions, chromatin states could be maintained through cell division allowing an epigenetic memory and a potential priming of new meristem-derived-organs.

Another possibility is that changes in chromatin structure control phytohormone biosynthesis, signaling and response. Variation in DNA methylation in response to water availability in poplar or among Arabidopsis epigenetic recombinant inbred lines (epiRILs) is associated with changes in jasmonic (JA), salicylic acid (SA) and ethylene responses (Latzel et al., 2012; Lafon-Placette et al., 2018). Similarly, rice plants with reduced H3K27me3 exhibit significant differences in the auxin indole-3-acetic acid (IAA), gibberellin (GA), ABA, JA, and SA content (Liu et al., 2016). Nevertheless, these effects may be pleiotropic and may reflect altered general physiological states. As more direct evidence, PRC2 activity in Arabidopsis seed coat is downregulated by fertilization-dependent auxin, and is required for repressing GA production prior to fertilization, mediating the crosstalk between two phytohormonal pathways

(Figueiredo et al., 2015, 2016; Figueiredo and Köhler, 2018). PRC2 also represses auxin biosynthesis and signaling genes in the SAM and leaves of Arabidopsis (Lafos et al., 2011). Conversely, in the RAM, the expression of the auxin efflux carrier-encoding *PIN-FORMED* (*PIN*) genes is positively regulated by BRM establishing local auxin maxima and stimulating the expression of the RAM-specifying *PLETHORA* genes *PLT1* and *PLT2* (Yang et al., 2015). BRM also binds to GA-related genes to stimulate GA biosynthesis and signaling (Archacki et al., 2013).

Apart from biosynthesis and signaling, phytohormone-response genes are under direct control of chromatin modifiers. Initially described as involved in auxin homeostasis (Sorin et al., 2005), the ARGONAUTE protein AGO1, guided by small RNAs and associating with SWI/SNF complexes, was recently described to bind genes activated upon JA, auxin, and SA stimuli in

Arabidopsis (Liu C. et al., 2018). ABA-responsive genes in Arabidopsis are repressed by histone deacetylation (Perrella et al., 2013) through the action of MULTICOPY SUPRESSOR OF IRA (MSI) 1 recruiting the HISTONE DEACETYLASE (HDA)19 (Alexandre et al., 2009; Mehdi et al., 2016) and also by BRM-mediated chromatin remodeling (Han et al., 2012). Significantly, expression of 80% GA–responsive genes relies on the chromatin remodeler PICKLE (PKL) (Park et al., 2017). Consequently, plants with reduced MSI1, HDA19, or BRM levels are more sensitive to ABA, display ABA-dependent growth defects and higher tolerance to drought, and absence of PKL results in GA-reversible root swelling and embryonic lipid accumulation (Ogas et al., 1997) demonstrating the developmental importance of chromatin modifiers in phytohormone-mediated responses.

HORMONE SIGNALING AND CHROMATIN CROSSTALK CAN PARTICIPATE IN PLASTICITY AND ROBUSTNESS

Hormone signaling and chromatin crosstalk can participate in developmental paths by distinct ways: (1) control of cell identity genes in meristems, (2) chromatin-mediated stabilization of gene expression beyond the hormonal initial signal, (3) chromatin-governed integration of separate hormone signaling pathways.

Chromatin-modifying complexes target key phytohormone-regulated genes that specify meristem cell identity and whose ectopic expression can result in cell reprogramming and homeosis (Zuo et al., 2002; Galinha et al., 2007). For example, the SAM-organizing homeobox gene WUSCHEL (WUS) is regulated by cytokinin signaling, DNA methylation, H3K27me, or chromatin remodeling (Kwon, 2005; Dodsworth, 2009; Cao et al., 2015; Liu H. et al., 2018), and loss of DNA methylation in WUS promoter is connected to in-vitro shoot initiation induced by cytokinin (Li et al., 2011). Other stem cell niche-defining TFs such as WOX4, WOX5, PLT1, or PLT2 are potential PRC2 targets (Oh et al., 2008; Lafos et al., 2011). Co-expression of these TFs can be triggered by environmental and hormone cues or ectopically induced in PRC2-depleted plants, resulting in cell reprogramming (Chanvivattana et al., 2004; Barrero et al., 2007; Ikeuchi et al., 2015; Mozgová et al., 2017). Increased or dispersed expression of cell identity-defining TFs and change and/or loss of cell identity also occurs in mutants of chromatin modifiers such as the repressive H2A-ubiquitinase complex PRC1 (Xu and Shen, 2008; Bratzel et al., 2010; Chen et al., 2010, 2016), histone deacetylases HDA6 and HAD19 (Tanaka et al., 2008; Pi et al., 2015), PKL (Ogas et al., 1999) or replication-dependent H3/H4 chaperone CHROMATIN ASSEMBLY COMPLEX (CAF)-1 (Kaya et al., 2001). Thus, chromatin structure appears to restrict expression of developmental genes to retain cell identities. Similarly, repression of ABA response by several chromatin modifiers (MSI1, HDA19, BRM) could act to prevent an ectopic stress response in favorable environmental conditions.

Chromatin structure may stabilize gene expression state beyond the duration of the environmental or phytohormone stimulus. An example is the cold-induced establishment of H3K27me3 at FLC during vernalization that is stable through mitosis, providing an in-cis memory system of FLC repression even after transfer to warmth (Berry et al., 2015; Hepworth and Dean, 2015). Persistent H3K4me2/3, H3/H4ac or local nucleosome depletion are found at genes primed for biotic or abiotic stress responses including priming by phytohormones or their analogs (Jaskiewicz et al., 2011; Lämke and Bäurle, 2017; Laura et al., 2018; Liu H. C. et al., 2018) demonstrating that also "accessible" chromatin structure contributes to mitotic memory (**Figure 1**).

Chromatin-modifying proteins may also serve as integrators defining the final outcome of interplay of various hormone signaling pathways. Phytohormone-induced change of chromatin structure may rely on multiple different chromatin modifiers as is exemplified by modulators of ABA signaling. A single chromatin modifier can also be implicated in responses to different hormones, as is exemplified by BRM (Sarnowska et al., 2016). Chromatin can thus provide a robust hub integrating different incoming cues while potentiating the persistence of the gene expression patterns through its stability during mitotic cell divisions.

MERISTEMS ARE CENTRAL PLACES FOR PHYTOHORMONE CHROMATIN CROSSTALK

The biological significance of the crosstalk in meristems is supported by (1) their central role in postembryonic morphogenesis, plasticity and memory, (2) their particularities for phytohomone signaling and chromatin remodeling, (3) first evidences reported for this crosstalk in SAM.

The meristems represent major sites of stem cell niches in plants (Scheres, 2007; Tucker and Laux, 2007; Aichinger et al., 2012). Apical meristems, together with the secondary meristem, the cambium, have the capacity to maintain and self-renew populations of undifferentiated cells, underlying continuous post-embryonic organ development modulated by environmental conditions (**Figure 1**; Gaillochet and Lohmann, 2015; Pavlovic and Radotic, 2017; Xiao et al., 2017). The SAM is also the place of epigenetic memory as reported for vernalization and some priming effects (Hepworth and Dean, 2015; Lämke and Bäurle, 2017).

Phytohormone and epigenetic pathways play overlapping/complementary roles in meristem functions and developmental plasticity or robustness, laying the basis for a biologically significant crosstalk. Importantly, meristems have been shown to be the place of epigenetic control for stem cell pluripotency, differentiation, and reprogramming (Cao et al., 2015; Gaillochet and Lohmann, 2015; Pi et al., 2015; Morao et al., 2016; Ojolo et al., 2018) whose epigenetic setup may differ from the surrounding tissues (Yadav et al., 2009; Baubec et al., 2014).

Major evidence for phytohormone-chromatin crosstalk was obtained using Arabidopsis mutants, or applying phytohormones or chemical inhibitors of chromatin modifiers in various developmental processes (Yamamuro et al., 2016; Campos-Rivero et al., 2017; Wong et al., 2017; Guo et al., 2018; Ojolo et al., 2018; Wakeel et al., 2018; Zheng et al., 2018).

Only a few reports highlight potential crosstalk directly in the meristems as exemplified by PRC2 repressing particular *PIN* genes (auxin transporters) in the SAM of Arabidopsis *clv3* mutants (Lafos et al., 2011). Recent studies in vernalized sugar beet (Hébrard et al., 2016) and in poplar under drought or cold exposure (Conde et al., 2017; Lafon-Placette et al., 2018; Le Gac et al., 2018) have recently shown that differentially expressed genes under DNA methylation control in SAM correspond to a limited developmental gene network mainly involved in growth and phytohormone pathways such as jasmonate activators and ethylene repressors. Indeed, Le Gac et al. (2018) show that hormone-related epigenome reprogramming in the SAM of poplar hybrids is stable for at least several months after the stress period in winter-dormant SAM providing evidence of an environmental epigenetic memory. Recently, this phenomenon was also described in the SAM of natural populations of black poplar under drought conditions (Sow et al., 2018a). Similarly, support for epigenetic memory of climatic conditions is found in Norway spruce trees grown from somatic embryos produced at different temperatures (Yakovlev et al., 2011, 2016). Considering the absence of post-embryonic organs, the SAM could play a major role in the transmission of the environmentally-established chromatin states during early development.

CONCLUSION AND FUTURE PERSPECTIVES

In conclusion, phytohormone action and chromatin modifiers seem to be tightly interacting but the extent to which they act jointly or independently remains unclear (Ojolo et al., 2018). However, the multi-layered control of local chromatin structure in response to hormonal cues may provide an important hub that integrates the incoming cues, conferring developmental robustness while retaining a sufficient potential for gene transcription change, stabilization and phenotypic plasticity (Lachowiec et al., 2016).

Current knowledge leads to the opinion that this crosstalk in meristems can integrate environmental cues for developmental outcome. Erasure of this signaling may allow continuous adjustment to new environmental conditions. Its maintenance through persistent chromatin states can however stimulate

mitotic memory that could prime later organ formation. How the balance between erasure and memory is achieved remains enigmatic (**Figure 1**).

While the mechanistic events could be more easily deciphered in well-established model annuals such as Arabidopsis, it is important to establish perennial models where the impact of mitotic epigenetic memory is of importance in the context of climate change. In addition to SAM and RAM, cambium, whose activity is crucial for environmentally controlled wood formation, may be an appropriate and highly relevant model (Wang et al., 2016; Oles et al., 2017; **Figure 1**). Deciphering this crosstalk in the meristems requires improving single-cell methodologies to study the dynamics of chromatin structure in response to complex phytohormone-associated environmental and developmental responses and its memory. Exploiting epigenetic variation and the potential to derive primed plants from meristem regeneration or somatic embryos (Achour et al., 2017; Gallusci et al., 2017; Springer and Schmitz, 2017; Sow et al., 2018b) seems also promising.

AUTHOR CONTRIBUTIONS

FUNDING

ACKNOWLEDGMENTS

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