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# A Dynamic Signaling Path to Chromatin-Level Control of Plant Drought Response

As sessile organisms, plants display a high capacity for phenotypic adaptations allowing them to meet the constraints of a changing local environment. This plasticity notably originates from the aptitude of plants to adjust their development and physiology throughout their lifetime to reach an optimal trade-off between growth and fitness. As in all eukaryotes, dynamic control of plant gene expression in different cell types is dependent on multiple regulatory layers that often converge onto chromatin-based mechanisms. Dynamic control of chromatin composition and organization has a strong impact on the cellular transcriptional program, notably contributing to selective modulation of gene expression in a reversible manner. Chromatin state changes generally involve remodeling of nucleosome positioning, incorporation of nucleosomal and linker histone variants, and DNA and histone modifications recognized by cognate readers. Together, these processes modulate the access and activity of *trans*-acting factors such as transcription factors and RNA polymerases. Temporary shifts between transcriptionally permissive and repressive chromatin states rely on various mechanisms, among which is the rapid reversion of a “responsive” chromatin status through active erasure of newly established features.

## INTEGRATION OF ENVIRONMENTAL SIGNALS ONTO CHROMATIN BY SIGNAL TRANSDUCTION

Targeted regulation of chromatin responses within the genome in response to developmental and external signals is likely involved in a large panel of transduction pathways that fine-tune gene responsiveness and modulate plant developmental and physiological status. Recent studies have unveiled that in several instances the signaling components are themselves associated with chromatin. Consequently, the identification of direct interplays between signal transduction pathways, transcription factors, and chromatin modifying/remodeling machineries has been an area of intense study (Xiao et al., 2017). A recent study by Ma et al. (2019) unveils how a transcription factor, OsbZIP46 in rice (*Arabidopsis* ABI5 homolog), is at the nexus of an elaborate chromatin regulatory process modulating plant capacity to cope with drought stress. The system involves histone H2B monoubiquitination (H2Bub) at OsbZIP46-targeted genes by an associated E3 ligase, the evolutionarily conserved HUB1/HUB2 complex, which allows for efficient inducibility of abscisic acid (ABA)-sensitive genes. As other chromatin marks, histone H2Bub can actively be removed through the proteolytic activity of specific histone deubiquitinases (DUBs).

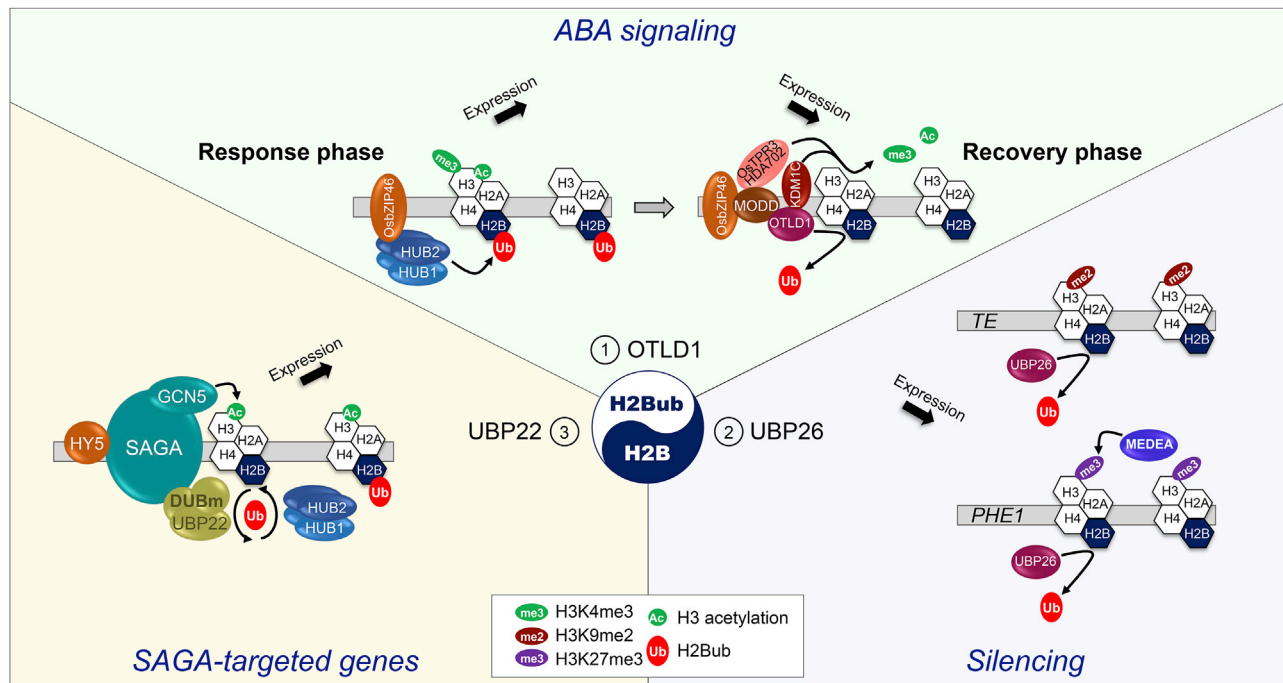
## HISTONE H2Bub AND THE ESTABLISHMENT OF TRANSCRIPTIONALLY PERMISSIVE CHROMATIN

Myriads of histone post-translational modifications acting in combination or sequentially can contribute to adjusting tran-

scriptional activity by establishing a repressive context, such as *Polycomb*-group modifications, or by favoring RNA polymerase II (RNPII) and RNA processing. This is typically the case of histone H2B monoubiquitination, which in this context plays a non-degradative role. From yeast to metazoans and plants, H2Bub deposition by Bre1, Rnf20, or HUB E3 ligase homologs, respectively, and subsequent deubiquitination by the so-called SAGA complex are part of a transcription-coupled process occurring over most, if not all, active genes. This co-transcriptional cyclic activity is thought to facilitate RNPII processivity through nucleosomes by affecting DNA accessibility, helping to recruit the histone chaperone FACT, and ensuring nucleosome reassembly upon RNPII passage. Despite being part of the fundamental process of transcription-coupled chromatin dynamics, the machineries controlling histone H2Bub levels have now been found to be targeted by several specific signaling pathways and to influence a wide range of plant responses to environmental cues. For example, HUB is required for efficient gene inducibility during plant adaptive responses, such as during plant defense and photomorphogenesis (reviewed in Feng and Shen, 2014) or during drought stress response as shown in the study of Ma et al. (2019).

## AN H2Bub-MEDIATED REGULATORY SWITCH DURING PLANT ADAPTIVE RESPONSES TO DROUGHT STRESS

The “chromatin response” to moderate drought stress described by Ma and colleagues is reversible, as shown by the recovery of normal H2Bub levels upon return to non-inductive conditions. Strikingly, this phase also relies on the OsbZIP46 transcription factor. OsbZIP46 mediates the recruitment of MODD and of the associated ubiquitin protease OTLD1, previously known to act as a histone DUB on several genes, including *ABI5* itself (Keren and Citovsky, 2016). MODD, also known as ABI5-binding protein in *Arabidopsis*, is a suppressor of ABA signaling and drought resistance that represses the expression of OsbZIP46 target genes via the recruitment and concerted action of additional players. In addition to OTLD1 recruitment, MODD brings a TOPLESS co-repression complex that decreases histone acetylation levels and the OsPUB70 E3 ubiquitin ligase that triggers OsbZIP46 degradation (Tang et al., 2016). In this scenario, gene targeting of the H2Bub E3 ligase by OsbZIP46 transcription factor followed by OTLD1 recruitment, and subsequent degradation of OsbZIP46, would allow for a concerted and dynamic regulatory switch between functionally contrasted chromatin states (Figure 1).



**Figure 1. Contrasted Roles of Plant Histone H2B Deubiquitination Pathways.**

(1) Rice OTLD1 deubiquitinates histone H2B at ABA-responsive loci during recovery from drought stress. In a first phase, the OsbZIP46 transcription factor recruits the HUB complex to monoubiquitinate histone H2B and favor transcription. In the recovery phase, OsbZIP46 mediates the recruitment of the MODD suppressor of ABA signaling. MODD further allows recruitment of the ubiquitin protease OTLD1 and of a TOPLESS co-repressor complex to deacetylate histones (Tang et al., 2016). OTLD1 may also recruit the KDM1C histone demethylase (Krichevsky et al., 2011). (2) UBP26 deubiquitinates histone H2B to prevent transcription of the *PHERES1* imprinted gene (Luo et al., 2008) and of several transposable elements (TEs) (Sridhar et al., 2007), possibly allowing deposition of repressive chromatin marks on TEs and genes. (3) The UBP22 ubiquitin protease is part of a SAGA-like deubiquitination module (DUBm) (Nassrallah et al., 2018; Pfab et al., 2018) that presumably facilitates RNPII elongation on most genes through ubiquitination/deubiquitination cycles. The SAGA complex also comprises GCN5 that acetylates histones H3, H4, and possibly also H2B, but its link with the DUBm remains uncertain in plants. The master transcription factor HY5 has been proposed to recruit the SAGA complex on light-induced genes (Benhamed et al., 2008).

## TRANSIENT CHANGES IN H2Bub HOMEOSTASIS AS A COMMON THEME IN CHROMATIN RESPONSES TO STRESS CONDITIONS

The chromatin response uncovered in this study is also massive, as a global increase in H2Bub levels was detected in bulk chromatin preparations and over hundreds of ABA-responsive genes upon moderate drought stress. This global change in H2Bub abundance may rely on *OsHUB1* and *OsHUB2* gene upregulation by ABA signaling. The *OTLD1* gene is also subsequently induced, suggesting that regulation of antagonistic and rate-limiting chromatin-modifying activities mediates a stepwise process of responsive and recovery phases. Hence, the study by Ma et al. (2019) exemplifies how the availability of chromatin-modifying machineries can be modulated by an environmental signal to trigger a drastic change in histone mark homeostasis. Recently, we identified how a light-signaling component, the DET1 complex, controls proteolytic degradation of a SAGA histone H2Bub DUB module in darkness (Nassrallah et al., 2018). Consequently, under dark conditions, H2Bub dynamics remain stalled, possibly limiting the expression of light-responsive genes. Taken together, these studies unveil how signaling pathways control the abundance of chromatin-modifying machineries and provide two distinct

mechanisms as to how the cell controls H2Bub homeostasis during cell adaptive responses.

In short, H2Bub capacity is intimately linked with global transcriptional elongation capacity in mammalian cells. Misregulation of H2Bub homeostasis appears to be central in the transcriptional events linked to human oncogenesis, potentially influencing directly cell proliferation processes (Jeusset and McManus, 2017). Hence, determining whether modulation of global H2Bub levels primarily influences a plant cell's capacity for transcription or other processes such as DNA replication and cell cycle progression might constitute interesting additional investigations. Three H2B deubiquitinases have been identified in plants, OTLD1, UBP22 as part of a SAGA-like complex, and UBP26 (Luo et al., 2008; Sridhar et al., 2007). Unlike SAGA-mediated H2Bub deubiquitination that accompanies RNPII elongation, both OTLD1 and UBP26 can have a negative impact on the expression regimes of genes and transposable elements (TEs). These contrasting roles might rely on local pre-existing modifications, on the association with different transcription factors, and possibly also on the extent of H2Bub deubiquitination by distinct DUBs. H2Bub enrichment over most SAGA-targeted genes indicates that co-transcriptional cycles of H2B ubiquitination/deubiquitination result in positive steady-state levels, while in contrast complete erasure of H2Bub on TEs and on genes such as *ABI5*, *PHERES*, and *OSR2p* appears to be part of active

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repressive processes (Figure 1). In the latter case, depletion of H2Bub could be required for establishing a repressive chromatin status and allow for H3K27me3 or H3K9me2 deposition and CHG and CHH methylation on silenced genes and TEs, respectively (Sridhar et al., 2007; Luo et al., 2008). In addition, mechanistic crosstalk between H2Bub removal and *Polycomb*-based activities such as histone H2A ubiquitination/deubiquitination might also be at play, as suggested in mammalian cells (Scheuermann et al., 2010). Given the requirement for HUB in multiple regulatory pathways (Feng and Shen, 2014), the variety of molecular mechanisms underlying H2Bub-dependent chromatin processes and their occurrence during adaptive responses to biotic and abiotic cues will be an interesting aspect to decipher in future studies.

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