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From non-coding to chromatin regulators: *VIVIPary* and the rise of lncRNAs in plant biology

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In the current era of molecular biology, where the major components of transcription, translation, and chromatin regulation have been extensively described, attention has shifted toward identifying fine regulators that confer spatial and temporal specificity to gene expression. Among the most intriguing of these are long non-coding RNAs (lncRNAs). Once defined by their lack of coding potential and considered transcriptional noise, lncRNAs are, for the last decades, emerging as critical regulators with unique structural and functional versatility: they can fold into complex conformations, scaffold protein complexes, interact with DNA or other RNAs, guide chromatin remodelers, or act as molecular decoys. As such, they are increasingly recognized not merely as byproducts of transcription but as central players in gene regulation (Yang et al., 2023).

This conceptual transformation is particularly compelling in plants. Although animals have provided a wealth of functional lncRNA studies, plants offer an even more diverse and specialized transcriptional machinery, including two additional DNA-dependent RNA polymerases (Pol IV and V) largely devoted to non-coding RNA production (Wierzbicki et al., 2021). Yet, systematic functional characterization of lncRNAs in plants remains in its early stages, and many questions persist: are lncRNAs universal regulators or specific modulators? Do their functions converge mechanistically, or is their diversity analogous to the versatility we accept in proteins? And, crucially, what defines the limits of their regulatory potential—especially regarding chromatin architecture, transcriptional control, and responses to environmental cues?

A growing number of case studies have begun to address these questions, particularly in chromatin remodeling, where lncRNAs have emerged as versatile regulators (Figure 1). While this represents only a subset of known lncRNAs, it is rich in mechanistic insight. Several lncRNAs have been shown to recruit Polycomb Repressive Complexes (PRC1 and PRC2) to modify chromatin states: *COLD AIR* and *COLD WRAP* facilitate H3K27me3 deposition at the *FLC* locus in *Arabidopsis*, acting in concert with *COOL AIR*, which also shapes chromatin through transcriptional interference (Wierzbicki et al., 2021). Similarly, *AG-lncRNA4* silences *AGAMOUS* via PRC2 recruitment (Wu et al., 2018). Other lncRNAs influence the genome's three-dimensional structure: *APOLO* promotes chromatin loop formation at auxin-responsive loci by interacting with LHP1 and forming R-loops (Ariel et al., 2020), while *MARS* mediates spatial reorganization of a metabolic gene cluster in response to abscisic acid (ABA), in part by decoying chromatin regulators (Roulé et al., 2022). In rice, *LAIR* modulates H3K4me3 levels at the *LRK1* locus by recruiting epigenetic complexes, enhancing grain yield (Wang et al., 2018). And in immunity, *SABC1* adjusts salicylic acid biosynthesis by targeting chromatin repressors. These and other examples support the idea that lncRNAs act as molecular integrators of several cellular processes, fine-tuning gene expression in developmentally or environmentally sensitive contexts (Chorostecki et al., 2023).

The recent study by Yang et al. (2025) exemplifies the kind of mechanistic depth and physiological impact that positions lncRNA study at the frontier of plant molecular biology. The

authors identify *VIVIparry*, a previously uncharacterized lncRNA in rice, as a key regulator of seed dormancy and pre-harvest sprouting—two traits of agronomic relevance. What makes this work particularly compelling is not just the identification of a functional lncRNA, but the depth of mechanistic insight and the direct link to a phenotypic outcome. *VIVIparry* is specifically expressed in rice embryos and regulates ABA signaling pathway by acting at the chromatin level. It binds to OsMSI1, a chromatin-associated protein, and facilitates its interaction with OsHDAC1, a histone deacetylase. This complex represses the ABA receptor gene OsPYL10 by reducing chromatin accessibility at its promoter, thereby modulating dormancy. As a result, overexpression of *VIVIparry* leads to premature sprouting, while silencing delays germination.

In addition to its well-defined mechanism—from lncRNA–protein interaction to physiological phenotype—*VIVIparry* lies within a conserved genomic region spanning several neighbouring genes. Although no cis-regulatory effects were detected on adjacent loci, the conservation of the entire cluster suggests it may form part of a broader regulatory landscape. *VIVIparry* could therefore act not in isolation, but within a chromatin context that coordinates gene expression in a developmental or environmental framework. Supporting this possibility, the authors note that *VIVIparry* is more highly expressed in cultivated rice (*O. japonica*) compared to wild relatives, raising the hypothesis that lncRNAs contributed to traits selected during domestication. This raises a compelling question: how many phenotypic traits inadvertently selected during crop domestication are controlled by non-coding RNAs? Exploring this hidden regulatory layer may not only provide evolutionary insight, but also open new routes for crop improvement. Traits long considered genetically intractable could be re-evaluated through the lens of RNA-mediated regulation.

The expanding catalog of plant lncRNAs highlights a wide range of molecular mechanisms, including chromatin regulation, transcription initiation, alternative splicing, post-transcriptional processing, and small RNA biogenesis. While it is now broadly accepted that lncRNAs don't follow a universal mechanistic model, an emerging question is whether certain organizing principles or functional patterns can still be discerned within this diversity. Interestingly, many characterized lncRNAs tend to have subtle quantitative effects, suggesting they often function as fine-tuners or modulators of protein activity, rather than as primary effectors. Yet, their biological significance may reside precisely in this dynamic role: the ability to act in structurally

flexible and context-dependent ways, tailored to specific genomic loci or stimuli. This notion gains strength from the closing remarks of Yang et al., who speculate that lncRNA-mediated chromatin changes could function as rapid expression switches under environmental stress. Such plasticity—if verified—would position lncRNAs as both sensors and effectors of environmental response. Because lncRNA structure is highly sensitive to physical cues such as temperature, these transcripts may rapidly alter their protein or nucleic acid partners, reshaping regulatory networks in real time. In support of this idea, several plant lncRNAs have already been shown to mediate environment-sensitive processes (Traubenik et al., 2024): *COOLAIR*, *COLD AIR*, and *COLDWRAP* integrate temperature perception with chromatin regulation of flowering; *IPS1* and *PILNCR1* modulate phosphate homeostasis via miRNA target mimicry; and *SABC1* and *ELENA1* fine-tune immune responses through chromatin remodeling and transcriptional coactivator recruitment. These cases underscore how lncRNAs can dynamically interface with chromatin or RNA pathways to adjust gene expression in response to external cues—highlighting their potential as molecular nodes of environmental adaptation. *VIVIPARY*, which controls ABA responsiveness, becomes a prime candidate for investigating this dynamic layer of regulation, potentially opening new routes for breeding stress-resilient cultivars.

The implications for agriculture are substantial. While the role of RNAs as regulators is well established in human biotechnology (Zhu et al., 2022)—e.g., in RNA therapeutics—their use in crops remains underdeveloped. The functional dissection of lncRNAs like *VIVIPARY* not only deepens our understanding of gene regulation but also opens the door to RNA-based crop improvement strategies. Such approaches could target lncRNAs to modulate key traits like dormancy or stress tolerance, with high specificity and minimal off-target effects.

In sum, *VIVIPARY* exemplifies the growing recognition of lncRNAs as regulatory molecules with tangible physiological outcomes. Studies like this challenge the traditional boundaries of functional genomics and highlight the potential of non-coding regions as reservoirs of regulatory innovation. The mechanism characterized for *VIVIPARY* fits within a broader regulatory logic increasingly observed across plant systems, especially in epigenetic control (Figure 1). Although these examples highlight shared regulatory themes, the mechanistic diversity of plant lncRNAs underscores the importance of studying them in individual and contextual detail. As we move

forward, a better understanding of lncRNA biology will be essential—not only to answer questions of mechanism and generality, but also to harness their power in sustainable agriculture.

Acknowledgments

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155 **Figure 1. Schematic representation of lncRNA-mediated chromatin regulation at a generic**
156 **gene locus.**

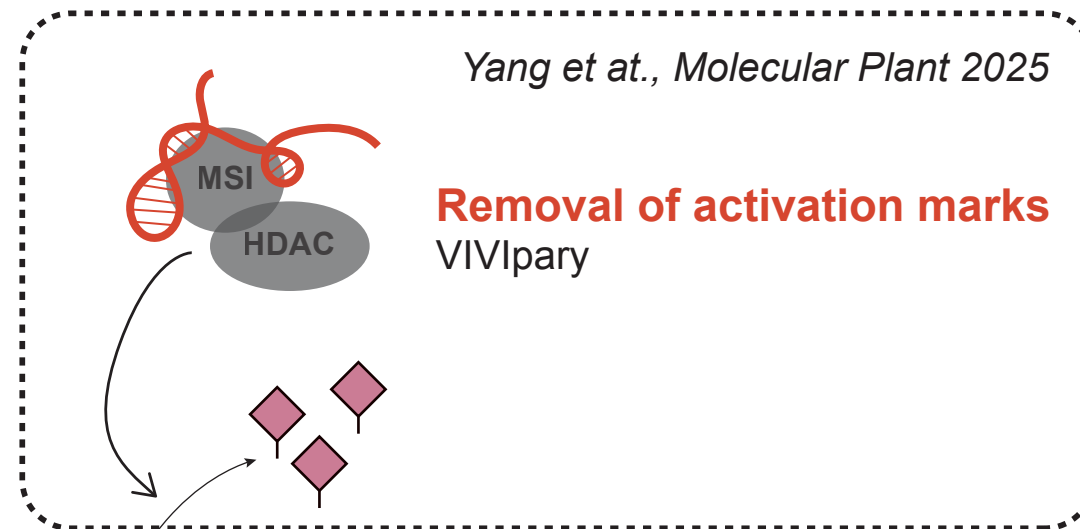
157 Long non-coding RNAs (lncRNAs) regulate gene expression through diverse chromatin-related
158 mechanisms. This conceptual diagram illustrates several known lncRNA strategies acting on a
159 representative gene. These include recruitment of histone-modifying complexes (e.g., LHP1 of
160 PRC1, CLF of PRC2, WDR5, HDACs), DNA methylation proteins, establishments of loops
161 between DNA and RNA (R-loops), and formation of chromatin loops that bring distant
162 regulatory elements into proximity. Many of these processes have been shown to go forward or
163 backward depending on the dose (two-ways arrows). Each lncRNA, represented by a different
164 color, exemplifies a specific regulatory mechanism already described in literature. Some
165 examples of known lncRNAs involved in these pathways are listed below each mechanism. The
166 boxed area highlights the novel *VIVIPARY* mechanism described by Yang et al. (2025). Together,
167 these modes of action highlight the versatility of lncRNAs as scaffolds, guides, or architectural
168 RNAs within the chromatin landscape of plant genomes.

Induction of activation marks

PRC2-mediated repression

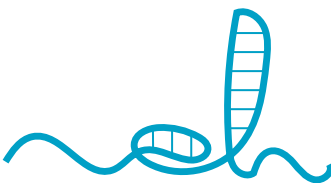
COLDWRAP
COLD AIR
AG-incRNA4
SABC1

MAS
LAIR



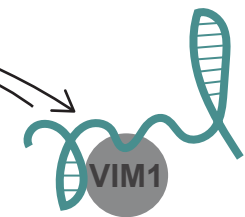
Chromatin loop regulation

APOLO
MARS
COLDWRAP



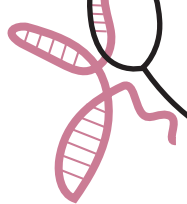
DNA methylation regulation

APOLO



R-loops formation

APOLO



PRC1-mediated regulation

APOLO
MARS



DNA



H3K4me3



H3K27me3



H3K9ac



DNA methylation