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REVIEW ARTICLE

The Function of Like Heterochromatin Protein 1 (LHP1) as an Epigenetic Regulator of Plant Development

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Abstract

Plants have the fascinating ability to regulate their genetic expression through epigenetic mechanisms. Polycomb group (PcG) proteins in Polycomb repressive complexes (PRC1 and PRC2) especially regulate cellular and developmental processes in eukaryotes through epigenetic mechanisms. *Arabidopsis thaliana* has a fascinating name, LIKE HETEROCHROMATIN PROTEIN 1 (LHP1), called TERMINAL FLOWER 2 (TFL2). This protein was initially recognized as the plant equivalent of animal HP1 due to the presence of a chromo domain and a chromo shadow domain. It can bind to the trimethylated lysine 27 of histone H3 (H3K27me3) mark spread throughout the genome and regulate gene expression. This is crucial for the plant PcG system, which PRC2 establishes for epigenetic control. Although LHP1 has been found to perform diverse functions, it is still unclear whether these functions are carried out through similar mechanisms and whether it regulates the same target genes. This highlights the need for further research on LHP1 to better understand its mechanisms and functions. The following review provides detailed information about LHP1, which is closely linked to histone marks and the regulation of gene expression and explores how LHP1 influences flower timing and root development to improve crop traits. Recent progress in tomato and soybean production highlights the crucial role of LHP1 in shaping crop characteristics. The review suggests that LHP1 may control H3K27me3 in different plant species by regulating specific genes through epigenetic mechanisms. In summary, it emphasizes the importance of understanding LHP1's role in plant development for breeding purposes.

Keywords Histone modification · LIKE HETEROCHROMATIN PROTEIN 1 · Polycomb repressive complex 2 · Plant development

Introduction

DNA in eukaryotes is packaged around histone octamers to form nucleosomes (Feng and Lu 2017). These nucleosomes collectively form a structural framework known as chromatin, which comprises DNA, RNA, histones, and non-histone protein nucleosomes (Feng and Lu 2017). Histone octamers comprise four core histones, H2A, H2B, H3, and H4, around which DNA is wrapped (Lugar et al. 1997). Each histone has a tail that can undergo various modifications, such as acetylation, methylation, ubiquitination, and phosphorylation (Shi et al. 2015; Feng and Lu 2017). These modifications are essential for controlling the chromatin structure and regulating gene expression by altering its shape and compactness, ultimately affecting the three-dimensional structure of the genome (Mozgova and Hennig 2015; Feng and Lu 2017).

Polycomb group (PcG) proteins play essential roles in the development of eukaryotic organisms by regulating gene expression (Li et al. 2016). This process involves the silencing of specific genes through transcriptional regulation (Li et al. 2016). The PcG protein was initially discovered in Drosophila and has since been found in both plants and animals (Lewis 1978; Margueron and Reinberg 2011; Calonje 2014). PcG proteins are divided into two primary complexes, Polycomb repressive complexes (PRC1 and PRC2), responsible for mediating epigenetic repression through histone changes (Moltor and Shen, 2013; Xiao and Wagner

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2015). PRC1 is required for histone H2A monoubiquitination (H2Aub) at lysine 119, which inhibits gene expression and nucleosome contraction (Sanchez-Pulido et al. 2008; Xiao and Wagner 2015). In contrast, PRC2 is responsible for histone H3 lysine-27 trimethylation (H3K27me3) (Di Croce and Helin 2013; Faivre et al. 2024). Studies have shown that PRC1 and PRC2 can independently bind to chromatin or form binding sites (Di Croce and Helin 2013; Xiao and Wagner 2015).

Chromatin comprises DNA, RNA, and proteins, forming a chromosome, and is divided into two types: heterochromatin and euchromatin (Landberg 2007). Euchromatin is less condensed and contains the most actively transcribed genes (Landberg 2007). In contrast, heterochromatin remains condensed throughout the cell cycle, contains repetitive DNA sequences, and contains fewer genes that can be transcribed (Landberg 2007). Heterochromatin is crucial for proper chromosome segregation and is found in the centromeric and telomeric regions (Landberg 2007). The Heterochromatin protein 1 (HP1) family is a conserved group of non-histone chromosomal proteins involved in nuclear processes and transcriptional regulation (Schoelz and Riddle 2022). HP1 was first identified in Drosophila and is involved in stable and heritable transcriptional silencing, which is required for position effect variation (PEV) (James and Elgin 1986; Landberg 2007). PEV occurs when genes normally found in euchromatin move to areas near heterochromatin, leading to transcriptional silencing (Eissenberg et al. 1992). The HP1 protein can have different functions depending on various factors, such as post-translational modifications, the proteins it interacts with, and its location on the chromosome (Landberg 2007). The HP1 protein in plants, known as TERMINAL FLOWER2 (TFL2), LIKE HETEROCHROMATIN PROTEIN1 (LHP1), or TU8, has been identified in Arabidopsis (Gaudin et al. 2001a; Landberg 2007; Chen et al. 2020). However, studies on LHP1 have mainly focused on differences in protein expression profiles rather than on an in-depth analysis of gene expression, function, and evolution of plant LHP1. LHP1 was originally identified as TFL2 and stands out in genetics due to its unique characteristics. Despite its structural similarity to Heterochromatin Protein 1 (HP1) found in animals, LHP1 is a single-copy gene that encodes a functional Polycomb (Pc) homolog (Gaudin et al. 2001b; Kotake et al. 2003). In Arabidopsis, the LHP1 gene is located on chromosome 5 (AT5G17690) and is composed of six exons and five introns, with a protein size of approximately 45 kDa and 445 amino acids. The structure of the LHP1 protein has been highly conserved throughout evolution and bears a resemblance to that of HP1, which has two primary structural domains: a chromodomain (CD) and a chromoshadow domain (CSD) (Gaudin et al. 2001a; Feng and Lu 2017). However, LHP1 differs from HP1 in that it is usually localized to euchromatin and is necessary for maintaining gene silencing in euchromatin (Feng and Lu 2017). HP1 binds to H3K9me2/3, whereas LHP1 does not bind to H3K9me3 or H3K27me3 marks in the genome (Nakahigashi et al. 2005; Feng and Lu 2017). LHP1 contains five nuclear localization signals (NLSs): four at the N-terminal end and one at the C-terminal end (Feng and Lu 2017). The LHP1 protein requires both CD and CSD domains, which have potential protein-protein interaction sites (Cowieson et al. 2000; Exner et al. 2009). Consequently, LHP1 is efficiently and reliably imported via redundant mediation by importins α-1, α-2, and α-3 (Chen et al. 2020). Multiple LHP1 homologs have been identified in various plant species (Zemach et al. 2006; Mimida et al. 2007a; Hennig and Derkacheva 2009). Hecker et al. (2015) demonstrated that BPC6 actively recruits LHP1 to the GAGA DNA motif. Disrupting the RNA-binding hinge region eliminates LHP1-mediated epigenetic repression (Berry et al. 2017). According to Feng and Lu (2017), LHP1 both activates and represses transcription in plants. Our review has revealed compelling evidence that firmly establishes the critical role of LHP1 in plant growth and development. Therefore, this review aims to summarize these findings and emphasize the importance of understanding the function of LHP1 in plant development.

Epigenetic Regulation in Plants

Plants have unique mechanisms for mastering epigenetic regulation (Pikaard and Scheid 2014; Wang et al. 2024). Plants have complex gene regulation mechanisms to survive environmental changes (Thiebaut et al. 2019; Wang et al. 2024). Plants sense ecological signals that are transmitted through a series of signal transduction pathways (Thiebaut et al. 2019). When facing environmental challenges, a process is triggered that causes the accumulation of transcription factors, activating gene expression and leading to adaptation (Mirouze and Paszkowski 2011; Wang et al. 2024). Epigenetic regulation is another important mechanism of gene regulation in stress response, involving covalent modifications of DNA and histones that affect the transcriptional activity of chromatin (Pikaard and Scheid 2014; Wang et al. 2024). Unlike genetic mutations, epigenetic modifications do not alter DNA sequences (Thiebaut et al. 2019). Chromatin comprises nucleosomes containing histone proteins and DNA. The process allows the DNA to be compactly packaged into the nucleus (Thiebaut et al. 2019). Since gene expression depends on access to DNA, chromatin condensation is crucial for gene regulation (Thiebaut et al. 2019). Euchromatin is often associated with transcriptionally active regions, whereas heterochromatin

is usually transcriptionally silent, with hypermethylation of DNA and specific histone modifications (Vaillant and Paszkowski 2007; Thiebaut et al. 2019). Three epigenetic markers have been identified as important for gene regulation: (a) DNA methylation, (b) histone modifications, and (c) non-coding RNAs: small RNAs (Fig. 1) (Thiebaut et al. 2019). DNA methylation adds a methyl group to cytosine's fifth carbon atom, critical for gene regulation (Takeda and Paszkowski 2006). In plants, methylation can occur at three sites: CG, CHG, and CHH, where H represents A, C, or T (Law and Jacobsen 2010). Studies have indicated that distinct enzymes are responsible for methylation at each site (Law and Jacobsen 2010; Thiebaut et al. 2019). The MET1, CMT3, and DRM1/2 or CMT2 methyltransferases are responsible for CG, CHG, and CHH methylation, respectively (Ronemus et al. 1996; Du et al. 2012). DNA methylation affects gene expression in the gene-coding regions (Thiebaut et al. 2019). In Arabidopsis, 1/3 of methylated genes are in transcribed areas, whereas 5% of genes in promoter regions show methylation, suggesting epigenetic regulation through DNA methylation (Zhang et al. 2006). The process of histone modification involves "writers" who add modifications (such as acetyltransferases, methyltransferases, and ubiquitin-ligases) and "erasers" who remove them (including deacetylases, demethylases, and deubiquitinases) (Kang et al. 2022). These modifications are recognized by "readers" to assemble transcriptional machinery and chromatin-remodeling complexes (CRCs) (Kang et al. 2022). PcG proteins easily form two powerful Polycomb repressive complexes, PRC1 and PRC2, which play crucial roles in repressing epigenetic gene expression through histone modification (Bemer and Grossniklaus 2012; Grossniklaus and Paro 2014; Xiao and Wagner 2015; Feng and Lu 2017). Arabidopsis FLOWERING LOCUS D (FLD) definitively encodes an LSD1-family HKDM responsible for removing H3K4me1/2 and is essential for responding to SAR signals, directing the accumulation of SA, and significantly enhancing disease resistance (Kang et al. 2022). Furthermore, the histone demethylase SlJMJ6 promotes tomato fruit ripening by facilitating H3K27me3 demethylation and overexpressing SlJMJ6 activates ripening-related genes and accelerates the ripening process (Fang et al. 2023). sRNAs can trigger DNA methylation and chromatin modification, making them particularly important in many cases (Matzke and Mosher 2014). siRNAs (Short-interfering RNAs) guide the RNA-directed DNA Methylation (RdDM) pathway (Matzke and Mosher 2014). Further, RNA Polymerase IV transcribes long double-stranded RNAs within the nucleus that DICER-LIKE 3 (DCL3) processes to form siRNAs (Matzke and Mosher 2014). siRNAs integrate with ARGONAUTE (AGO4) protein in the cytoplasm's RNA-induced silencing complex (RISC) (Matzke and Mosher 2014). siRNA-AGO4 complex transported to the nucleus aligns with scaffold transcript from RNA Polymerase V (Thiebaut et al. 2019). The RNA-directed DNA Methylation pathway is completed when siRNA aligns with its target

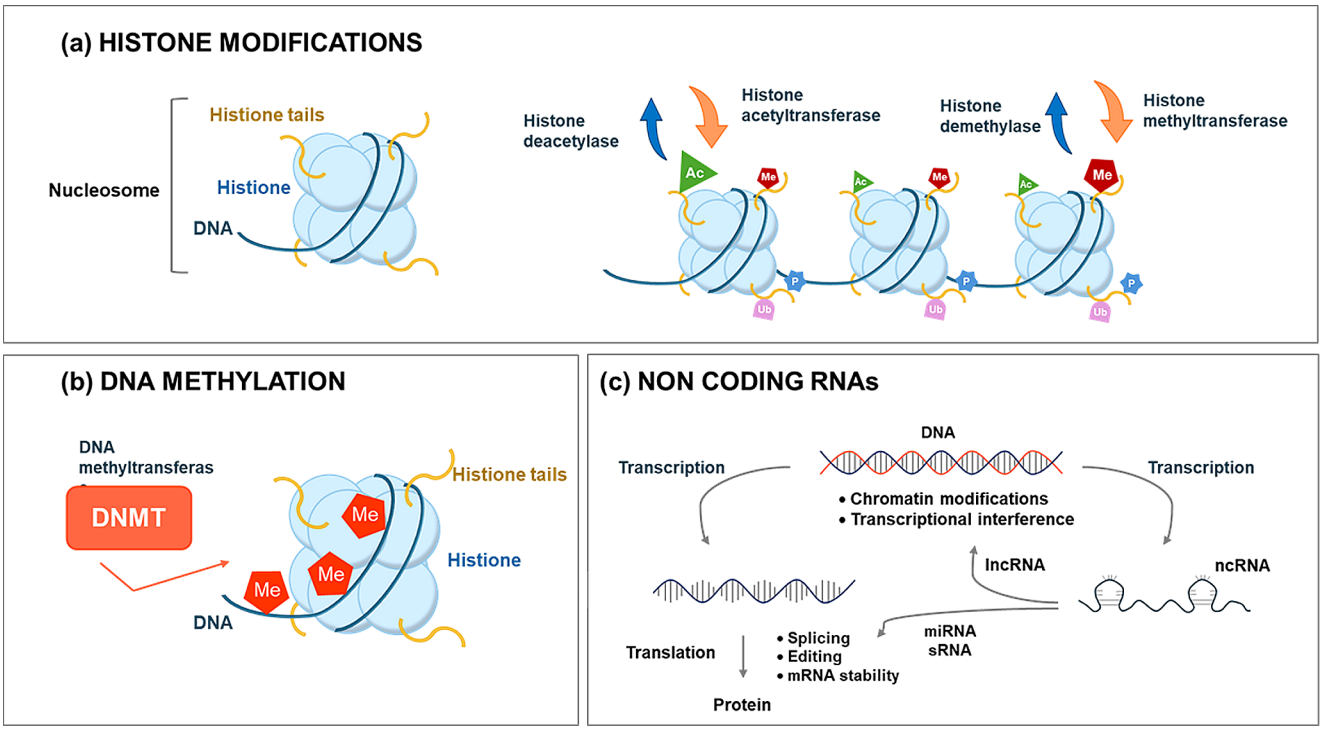

Fig. 1 Epigenetics regulates gene expression without altering the DNA sequence. This process includes. **a** histone modification, **b** DNA methylation, and **c** non-coding RNA

and recruits DNA methyltransferase, effectively silencing the target (Matzke and Mosher 2014; Thiebaut et al. 2019). Plant epigenetic regulations play a crucial role in growth, development, reproduction, and resistance to pathogens (Abdulraheem et al. 2024). They also help plants adapt to environmental stressors such as temperature, salinity, and nutrient scarcity (Abdulraheem et al. 2024). Regulating epigenetic processes requires significant effort to improve crop yield, growth, quality, and productivity (Abdulraheem et al. 2024). These improvements contribute to sustainable agriculture, as epigenetic mechanisms regulate important agronomic traits in crops through DNA methylation, histone modifications, and small RNAs, affecting gene expression and impacting growth, seeding, germination, and fruit development (Ashapkin et al. 2020). The impact of these epigenetic mechanisms is readily evident in crop productivity, yield, and quality. Long-term changes are crucial in evolution, providing a stable genetic foundation for adapting traits (Tu et al. 2022). Recent studies show that plants can adjust gene expression through DNA methylation patterns to help them survive tough conditions (Duarte-Aké et al. 2023; Abdulraheem et al. 2024). Understanding how epigenetic changes influence plant adaptability is crucial for improving crop productivity in challenging conditions (Ferrari et al. 2020; Abdulraheem et al. 2024). There is still no direct evidence linking epigenetic changes to the adaptability of plants in different environments or under various types of stress.

Role of LHP1 in Plant Development

LHP1 Regulates Flowering Time

Plants require precise timing for reproduction, and multiple factors regulate flowering (Takada and Goto 2003; Feng and Lu 2017). In Arabidopsis, long days, gibberellins, and vernalization promote flowering. However, it can also occur without environmental cues, known as autonomous promotion (Simpson and Dean 2002). Recent studies have shown that temperature also plays a role in regulating flowering in Arabidopsis (Blazquez et al. 2006; Takada and Goto 2003). Therefore, both promoting and repressive factors are important for controlling the flowering process (Fig. 2) (Takada and Goto 2003). The *FLOWERING LOCUS T* (*FT*) gene is regulated by multiple genes that converge at the leaf vein and play a critical role in promoting flowering (Feng and Lu 2017). This convergence is crucial for precisely regulating the expression of *FT* mRNA (Turck et al., 2008). Loss-of-function mutants of *lhp1* display an early flowering phenotype completely independent of the photoperiod compared to the wild-type (Feng and Lu 2017). The overexpression of LHP1 (35 S: LHP1) significantly decreases flowering time, and the early flowering of *lhp1* is fully inhibited by ft mutations (Feng and Lu 2017). Molecular analysis of the mutants has indicated that LHP1 controls the timing of flowering by recognizing and binding to H3K27me3 and directly interacting with *FT* chromatin to repress *FT* expression (Feng and Lu 2017). Several studies have shown a strong correlation between LHP1 and H3K27me3 deposition (Turck et al. 2007; Veluchamy et al. 2016; Feng and Lu 2017). Furthermore, the deposition of H3K27me3 decreases globally in the *lhp1* background (Feng and Lu 2017). However, increasing *LHP1* expression did not affect the timing of floral transition in wild-type Arabidopsis (Takada and Goto 2003; Feng and Lu 2017). LHP1 mRNA is expressed in all tissues of wild-type organisms. However, its expression in mature leaves is confined to vascular tissue only (Kotake et al. 2003; Feng and Lu 2017). According to Wang et al. (2014), a specific PcG complex is formed by EMF1, LHP1, and histone H3 lysine-4 demethylases, which is known as EMF1c. This complex is responsible for directly repressing the expression of *FT* in vascular tissue before dusk and at night. Takada and Goto (2003) proved that CO (CONSTANS) activates *FT* expression and significantly disrupts EMF1 binding to *FT* chromatin in leaf veins, particularly during dusk. The EMF1-PcG complex integrates multiple flowering-regulatory pathways to synchronize phloem *FT* expression with environmental cues (Takada and Goto 2003). LHP1 is critical for vernalization and the autonomous pathway and creates a multiprotein complex with PRC2 that represses *FLC* expression by re-establishing H3K27me3 (Feng and Lu 2017). Chen et al. (2020) found that the importin triple mutant reduced nuclear targeting of LHP1, resulting in the de-repression of target genes *AG, AP3, SHATTERPROOF 1*, and *FT*. This highlights the critical role of IMPα-1, 2, and 3 proteins in importing LHP1 into the nucleus (Chen et al. 2020).

LHP1 Recreates a Dual Role in Transcriptional Regulation and Root Development

Proteins belonging to the PcG family have long been recognized as transcriptional repressors crucial for maintaining gene expression in a silenced state during cell differentiation in animals and plants (Feng and Lu 2017). However, recent studies have suggested that LHP1 may have dual functions as a transcriptional activator. A study was conducted by Veluchamy and colleagues in 2016 to analyze LHP1-target genes in both *lhp1* mutants and wild types. The findings showed a positive correlation between LHP1 and H3K27me3 deposition. On the other hand, a negative correlation was observed between LHP1 and RNA Pol II occupancy (Veluchamy et al. 2016). Additionally, the study found that most of the

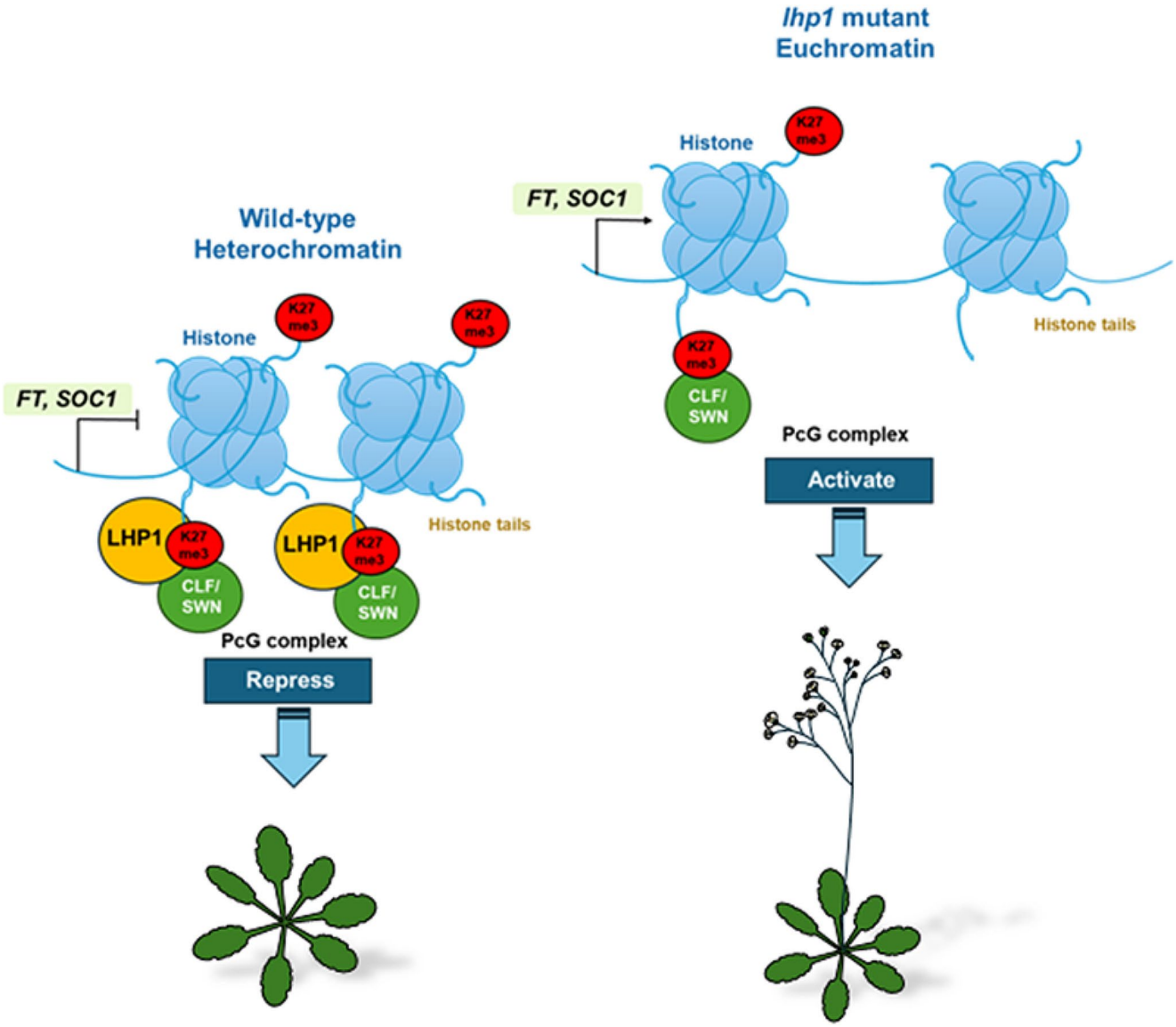

Fig. 2 Schematic model of epigenetic regulation of LHP1 at its target genes. LHP1 and PRC2 complexes bind to H3K27me3. Enriched H3K27me3 mark is necessary for the repressed stated of LHP1 target genes. The decrease in enrichment of H3K27me3 mark causes activate LHP1 target genes in *lhp1* mutant

LHP1 targets were hypomethylated in *lhp1* mutants, aligning with LHP1's role as a transcriptional repressor (Veluchamy et al. 2016). According to Veluchamy et al. (2016), LHP1, a protein that regulates gene expression, can act as both a negative and a positive regulator. This study found that over one-third of the genes regulated by LHP1 were down regulated in the mutant, indicating that LHP1 can also positively affect a set of genes. This is supported by the research conducted by Rizzardi et al. (2011), which showed that LHP1 plays a positive role in activating *YUCCA* genes. Plant roots are vital organs that facilitate the absorption and utilization of water and mineral nutrients. Auxins play significant roles in plant growth and development. Changes in auxin levels can rapidly alter gene expression, leading to a change in phenotype or function (Feng and Lu 2017). In the *lhp1* mutant, auxin levels were lower than in wild-type plants (Rizzardi et al. 2011). To investigate this mechanism, researchers have studied the auxin biosynthetic pathways (Rizzardi et al. 2011). A groundbreaking study by Rizzardi et al. (2011) discovered that the *lhp1* mutant had reduced auxin levels due to downregulated *YUCCA* genes, key players in auxin biosynthesis. The study's most significant finding was the direct impact of LHP1 on the genes responsible for the auxin biosynthetic pathway, a discovery that underscores the importance of this research (Rizzardi et al. 2011). This suggests that LHP1 plays a role in auxin biosynthesis by positively regulating the *YUCCA* genes (Rizzardi et al. 2011). Research conducted on Arabidopsis has

revealed that RNA immunoprecipitation (RIP) experiments illustrated the interaction between LHP1 and two lncRNAs, *APOLO* and *MARS*, in vivo (Mansilla et al. 2023). Recent studies have shown that *APOLO* can identify its targets in trans by creating RNA–DNA hybrids (R-loops) at the target locus. Confirmed targets of *APOLO* were categorized based on their colocalization with LHP1-bound regions, with a positive correlation observed between H3K27me3 levels and direct targets. This emphasizes the significance of the *APOLO*-LHP1 interaction (Ariel et al. 2020). For instance, the auxin biosynthesis gene *YUCCA2* (*YUC2*), which is crucial for plant thermomorphogenic responses, is a common target (Mansilla et al. 2023). The SCARECROW (SCR) transcription factor is essential for the initial cell division in Arabidopsis roots (Cui and Benfey 2009). The *lhp1* and *scr* mutants both exhibit a premature middle cortex phenotype. ChIP-PCR with LHP1 and SCR revealed that they work together to prevent premature middle cortex formation (Cui and Benfey 2009). Earlier studies have revealed that the plant hormone gibberellin (GA) is vital in forming the middle cortex. The GA hormone is pivotal in inhibiting the premature middle cortex phenotype formation in the *scr* mutant (Paquette and Benfey 2005). It effectively prevents the development of the middle cortex in both *lhp1* mutant and wild-type roots (Cui and Benfey 2009). Administering Paclobutrazol (Pac) reinforces the former effect, forming the middle cortex solely in *lhp1* mutants (Cui and Benfey 2009). It is crucial to note that both LHP1 and SCR contribute significantly to the suppression of middle cortex formation through a mechanism that GA regulates (Cui and Benfey 2009).

Table 1 The function of Like Heterochromatin Protein 1 in trait improvement in model and various crop plants

Model/Crops plants	Gene Name	Function	Reference
Arabidopsis	*AtLHP1/TFL2*	Regulation of flowering time	Takada and Goto (2003)
Tomato	*AtLHP1/TFL2*	Hypocotyl elongation regulated by YUCCA 2	Rizzardi et al. (2011)
	AtLHP1/TFL2	Facilitating root hair elongation through modulation of RHD6	Mansilla et al. (2023)
	AtLHP1/TFL2	Response to abiotic stress by regulation of ABA-responsive genes	Feng and Lu (2017)
	SlLHP1a, SlLHP1b	Fruit ripening	Liang et al. (2020)
Melon	*CmLHP1A and CmLHP1B*	Control of flower sex determination	Rodriguez-Granados et al. (2022)
Soybean	*GmLHP1*	Response to *P. sojae* by regulation of the SA signaling pathway	Zhang et al. (2021)
Cucumber	*CsLHP1*	Floral transition/ regulate flowering time	Bai et al. (2004)
Sugarcane	*SoLHP1*	Floral transition/ regulate flowering time	Guan et al. (2011)
Maize	*ZmLHP1*	Floral transition/ regulate flowering time	Libault et al. (2005)
Rice	*OsLHP1*	Floral transition/ regulate flowering time	Gaudin et al. (2001a)
Apple	*MdLHP1a, MdLHP1b*	Regulation of flowering time and plant growth	Mimida et al. (2007b)
Chrysanthemum	*CmLHP1*	Regulation of flowering time	Wu et al. (2019)

LHP1 Role in Crop Plants

Over the past few years, there has been growing interest in understanding the role of LHP1 in various crops (Table 1; Fig. 3). Recently, the function of tomato (*Solanum lycopersicum*) LHP1 was explored. It is worth noting that tomatoes have two copies of *LHP1*, *SlLHP1a* and *SlLHP1b* (Liang et al. 2020). *SlLHP1a* was expressed consistently across all tissues, whereas *SlLHP1b* expression was limited to fruits during ripening. Functional experiments aimed at clarifying the role of *SlLHP1b* have demonstrated that this protein plays a role in the initiation of ripening, production of climacteric ethylene, and fruit softening. Downregulation of *SlLHP1b* promotes these events in tomato fruits, whereas its overexpression triggers the opposite effect (Liang et al. 2020). *SlLHP1b* is responsible for directly regulating several genes involved in fruit ripening. These genes include MADS-box transcription factor [RIN], 1-carboxylate synthase 2 and 4 [ACS2, ACS4] and 1-aminocyclopropane-polygalacturonase-2 A [PG2a] (Liang et al. 2020). As members of the PRC1 complex, these genes are marked with the H3K27me3 repressive mark, which indicates their expected behavior (Liang et al. 2020). Furthermore, H3K27me3 enrichment increased when SiLHP1b was overexpressed, resulting in a delay in events related to fruit ripening. Like AtLHP1, SlLHP1 interacts with PRC2 member MSI1 to control fruit ripening genes epigenetically (Liang et al. 2020). It is worth noting that *SiLHP1a* was expressed in all of the analyzed tomato tissues. However, whether both LHP1 proteins found in tomatoes have similar functions is still unclear. The importance of these traits in tomato breeding implies that *SlLHP1b* may play a vital role in optimizing fruit ripening in this important crop.

Soybean is a major protein crop that is severely affected by pathogens, resulting in significant economic losses (Mansilla et al. 2023). *Phytophthora sojae* is one of the most lethal

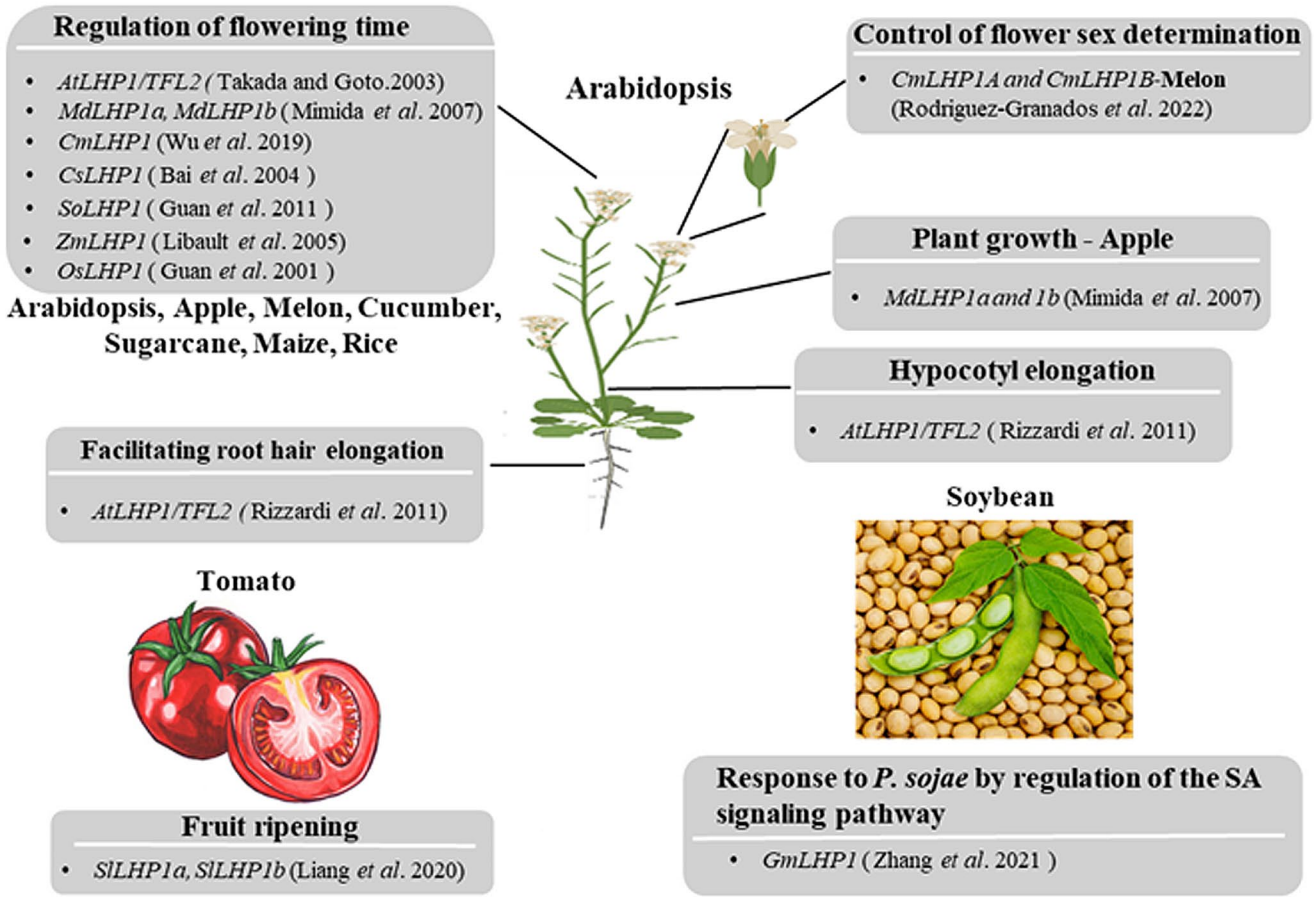

Fig. 3 This figure illustrates the diverse roles of LHP1 and its multifunctional nature in plant development

pathogens that cause stem and root rot (Zhang et al. 2010; Mansilla et al. 2023). It has been observed that regulating GmLHP1 affects soybeans' response to *P. sojae* by repressing SA signaling (Zhang et al. 2021). GmLHP1 is responsible for suppressing the expression of the *GmWRKY40* gene, which is required for SA signaling through two mechanisms. GmLHP1 binds to the promoter of *GmWRKY40*, repressing its transcription (Zhang et al. 2021). SA induces *GmWRKY40* expression, but GmLHP1 impairs SA accumulation, suggesting an indirect mechanism of repression (Zhang et al. 2021; Mansilla et al. 2023). GmLHP1 degradation via ubiquitination is mediated by the GmBTB/POZ complex, enhancing soybean's defence response against *P. sojae* (Zhang et al. 2021). GmLHP1 also plays a negative regulatory role in SA and a role in soybean stress response through a non-PCR1/2 canonical mechanism (Mansilla et al. 2023). The GmPHD6 (PLANT HOMEODOMAIN FINGER 6) protein binds G-rich elements in target loci promoters and interacts with H3K4me0/1/2 marks. GmPHD6 recruits LHP1 to activate stress-associated genes (Wei et al. 2017). Furthermore, Guan et al. (2011) investigated the conservation and divergence of plant LHP1 protein sequences and their expression patterns in various plant species, including cucumber, sugarcane, maize, and rice. LHP1 regulates plant stress responses, mitigating biotic and abiotic stresses in various crops (Mansilla et al. 2023).

Conclusions and Future Outlooks of LHP1

We have meticulously gathered and analyzed extensive information on the molecular function of the epigenetic remodeler LHP1 in both model and crop plants (Fig. 3). Our review has revealed some common and distinct characteristics regarding its mode of action. LHP1 is a crucial regulator of various developmental and physiological traits in different plant species, and it also plays a critical role in modulating biotic and abiotic stress responses. The structural analysis of LHP1 has revealed a strong preference for H3K27me3 over H3K9me3. This preference has been observed consistently across various plant genomes and has significant implications for our understanding of chromatin biology. However, the exact reasons for LHP1's association with H3K27me3 remain unclear. It's important to note that the structural analyses only focused on crystallizing the CD domain, indicating that other protein domains may also

influence LHP1's preference for histone marks. Additionally, the CDS and Hinge domains play a role in determining LHP1's localization and function. LHP1 can impact chromatin structure, and the genomic and epigenomic context determines its affinity.

Gene and genome duplication significantly impact the evolution of plants, particularly in flowering plants, which have given rise to most domesticated crop plants. In the case of LHP1, duplicated copies may have acquired new, unknown functions that require further investigation. In tomatoes, only one of the two duplicated copies of LHP1 has been studied in terms of its function (Liang et al. 2020), while the role of the other copy is yet to be determined. Although duplicate copies of LHP1 have been identified in various plant species, discovering a duplicate copy with a new function would be a significant breakthrough. Therefore, another exciting aspect to explore from an evolutionary perspective is the function of paralog copies of LHP1.

An important research direction is the molecular and biological role of LHP1 functions in one of the most important groups of flowering plants, the Monocots. This group is highly diverse and includes numerous economically important crops with various uses in the food industry, such as ornaments and medicinal products. Given the importance and diversity of the biological roles of LHP1 in Dicots, we must extend our understanding to Monocots. The only known instance of post-translational regulation affecting LHP1 activity is in a crop species, soybeans, where BTB/POZ ubiquitinates LHP1 for degradation (Mansilla et al. 2023). This finding raises intriguing questions about other potential regulatory mechanisms. Understanding these mechanisms could have significant implications for the biotechnological use of LHP1 in plant development. By effectively blending our in-depth understanding of LHP1's role with cutting-edge biotechnological tools, we can optimize the desired traits for crop improvement. Researchers interested in exploring the mechanisms and applications of LHP1 in agriculture could gain valuable insights from experimental approaches such as functional genomics, biochemical assays, and genome editing techniques. Overall, this review has carefully identified future research directions to explore LHP1's function and potential as a promising target for crop improvement, emphasizing the significance of understanding LHP1 in Monocots.

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Data Availability This statement indicates that the review contains referenced information.

Declarations

Conflict of Interest The authors declare no conflict of interest.

Ethics Approval and Consent to Participate Not applicable.

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