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REVIEW

The Polycomb Complex PRC1: Composition and Function in Plants

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ABSTRACT

Polycomb group (PcG) proteins are crucial epigenetic regulators conferring transcriptional memory to cell lineages. They assemble into multi-protein complexes, e.g., Polycomb Repressive Complex 1 and 2 (PRC1, PRC2), which are thought to act in a sequential manner to stably maintain gene repression. PRC2 induces histone H3 lysine 27 (H3K27) trimethylation (H3K27me3), which is subsequently read by PRC1 that further catalyzes H2A monoubiquitination (H2Aub1), creating a transcriptional silent chromatin conformation. PRC2 components are conserved in plants and have been extensively characterized in *Arabidopsis*. In contrast, PRC1 composition and function are more diverged between animals and plants. Only more recently, PRC1 existence in plants has been documented. Here we review the aspects of plant specific and conserved PRC1 and highlight critical roles of PRC1 components in seed embryonic trait determinacy, shoot stem cell fate determinacy, and flower development in *Arabidopsis*.

KEYWORDS: Epigenetics; Chromatin; Histone modifications; Polycomb; PRC1; *Arabidopsis* development

INTRODUCTION

In several organisms, Polycomb group (PcG) proteins were identified as subunits of multi-protein complexes that control the establishment and the maintenance of post-translational histone modifications. Nonetheless, most of the current knowledge on PcG function mechanisms is based on studies in metazoans. The PcG founding member is Polycomb (Pc), which was first discovered in *Drosophila* as a repressor of homeotic (*Hox*) genes. The loss of Pc function leads to strong developmental defects, namely homeotic conversions (Lewis, 1978; Jürgens, 1985). Later on, fly PcG proteins were identified as products of a group of genes the mutations of which cause similar or enhanced *pc* phenotypes. In metazoans, the PcG silencing pathway involves at least three distinct multimeric complexes: Polycomb Repressive Complex 1 (PRC1), PRC2 and the evolutionarily less conserved PHO Repressive Complex (PHORC; Schwartz and Pirrotta, 2007; Schuettengruber and Cavalli, 2009; Margueron and Reinberg, 2011). PRC2 is the most extensively studied complex. It is composed of four core subunits, i.e., Enhancer of zeste (E[z]), Suppressor of zeste 12 (Su[z]12), Extra Sex Combs (ESC) and Multicopy Suppressor of IRA1 (MSI1), and is responsible for histone H3 lysine 27 (H3K27) trimethylation (H3K27me3; Margueron and Reinberg, 2011). Genome-wide mapping studies demonstrated that PRC1 and PRC2 complex members as well as H3K27me3 co-occupy many target loci in metazoans (Wang et al., 2004b; Bracken et al., 2006; Lee et al., 2006; Tolhuis et al., 2006; Ku et al., 2008). This co-localization and the biochemical evidence that H3K27me3 constitutes a PRC1 docking site (Fischle et al., 2003) are commonly interpreted as a consequence of PRC1 recruitment by PRC2 marked loci, the so-called "PcG paradigm". This paradigm proposes that the PRC complexes act in a sequential manner: first the "initiation complex", PRC2, sets H3K27me3; next the "maintenance complex", PRC1, recognizes the mark and mediates downstream H2A monoubiquitination (H2Aub1; Schwartz and Pirrotta, 2007; Schuettengruber and Cavalli, 2009).

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The first reported plant PcG proteins are CURLY LEAF (CLF) and MEDEA (MEA), which are *Arabidopsis* homologs of the PRC2 component E[z] (Goodrich et al., 1997; Grossniklaus et al., 1998). Nowadays it becomes clear that the PRC2 silencing is conserved, at least to a certain degree, in terms of composition and catalytic activity from unicellular green algae to higher plants (Chen et al., 2009; Mosquna et al., 2009; Shaver et al., 2010). In contrast, the extent of the evolutionary conservation of the PRC1 counterpart remained enigmatic for a long time. In mammals and *Drosophila*, early genetic and biochemical evidence indicated that the PRC1 complex is implicated in transcriptional silencing; however in plants and worms, PRC1 function was long thought to be absent, because obvious subunit homologs were not apparent at first (Whitcomb et al., 2007). In addition, H2Aub1 could not be detected in a large proteomic analysis in *Arabidopsis*, reinforcing doubts regarding the PRC1 function conservation in plants (Zhang et al., 2007a). Only more recently, PRC1-like activity has been reported in *Arabidopsis*. This review focuses on the current knowledge of PRC1 complex composition and function mechanism, and highlights crucial roles of PRC1 associated proteins in several key processes of plant development.

PRC1 COMPLEX COMPOSITION AND ASSOCIATED BIOCHEMICAL FUNCTIONS

The core PRC1 members can be classified according to their biochemical function: either they catalyze histone post-translational modifications and thus are classified as writer proteins, or they recognize specific histone modification marks and then are termed reader subunits (Fig. 1).

PRC1 writer proteins

The ubiquitin ligase activity of PRC1 complex writers relies on the RING-domains, which modify the chromatin state by catalyzing the deposition of monoubiquitin on H2A. All PRC1 writers are characterized by a conserved combination of two domains: an N-terminal RING-domain and a yet poorly characterized C-terminal ubiquitin-like domain named RAWUL (Sanchez-Pulido et al., 2008). Based on sequence similarity, the PRC1 writer proteins can be subdivided into two clades: RING1 and BMI1.

The RING1 subfamily is composed of two members in human: Ring1A/Ring1 (Satijn et al., 1997) and Ring1B/Rnf2, while only one member exists in *Drosophila*, dRING/SCE (Fritsch et al., 2003). Based on sequence homology and protein domain organization, two members belonging to the RING1 subfamily have been identified in *Arabidopsis*: AtRING1a and AtRING1b (Sanchez-Pulido et al., 2008; Xu and Shen, 2008).

The BMI1 subfamily is composed of six members in human: Bmi1/Pcgf4, Mel18/Pcgf2, Nspc1/Pcgf1, Pcgf3, Pcgf5 and MBLR/Pcgf6 (Gao et al., 2012), a single member in *Drosophila*: Polyhomeotic (Psc; Brunk et al., 1991), and three

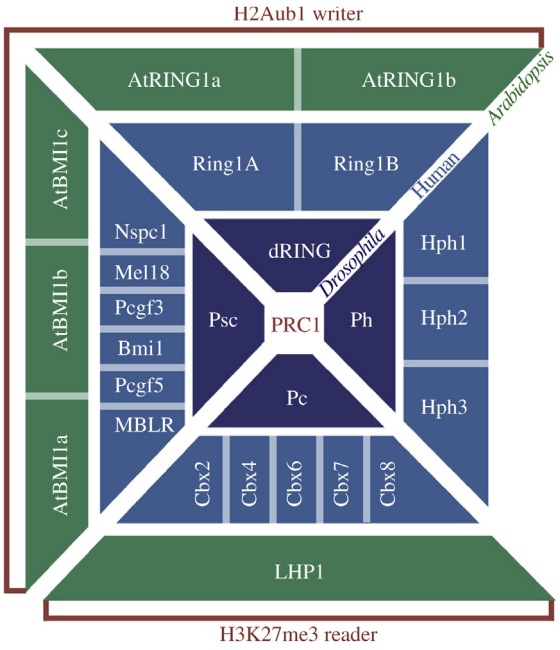

Fig. 1. Schematic representation of PRC1 components in *Drosophila* (inner circle), human (middle circle), and *Arabidopsis* (outer circle).
The known biochemical functions, i.e., catalyzing H2A monoubiquitination (H2Aub1 writer) and binding trimethyl-H3K27 (H3K27me3 reader), are indicated for the responsible components.

members in *Arabidopsis*: AtBMI1a, AtBMI1b and AtBMI1c (Bratzel et al., 2010; Chen et al., 2010; Li et al., 2011).

It is well established in *Drosophila* and mammals that the RING1 subunits (i.e., dRING and Ring1B) deposit monoubiquitin on H2AK119 (de Napoles et al., 2004; Wang et al., 2004a). This enzymatic reaction is strongly enhanced by the addition of other RING-domain subunits of the PRC1 complexes (Buchwald et al., 2006; Li et al., 2006). Recent lines of evidence confirm the H2A monoubiquitination activity of PRC1 writers in plants (Bratzel et al., 2010; Li et al., 2011) and worms (Karakuzu et al., 2009), suggesting that the function of PRC1 RING-domain proteins within the PcG silencing pathway is more widely conserved than originally proclaimed.

Indeed, E3 ligase activity was revealed for all five PRC1 RING-domain proteins in *Arabidopsis*. Levels of monoubiquitinated Flag-H2A.1 proteins were found reduced in *Atbmi1a Atbmi1b* double mutants, and *in vitro* assays confirm E3 ligase activity of AtBMI1a, AtBMI1b, AtRING1a and AtRING1b on a conserved lysine residue of H2A.1 (Bratzel et al., 2010). Consistently, overexpression of *AtBMI1c* is leading to increase H2Aub1 levels in transgenic *Arabidopsis* plants (Li et al., 2011). Notably, the *Atring1a Atring1b*, and *Atbmi1a Atbmi1b* mutants do not exhibit altered H3K27me3 levels (Xu and Shen, 2008; Bratzel et al., 2010), which is in agreement with a PRC1 function downstream of PRC2. In conclusion, since all plant PRC1 writers display typical PRC1 RING-domain protein sequences and stimulate H2Aub1 deposition, they should be considered as homologs of the animal counterparts. Future studies will be required to determine the functional redundancy and the precise number of RING-domain proteins in a plant PRC1 complex unit.