Phytochemistry xxx (2014) xxx–xxx

Contents lists available at ScienceDirect

Phytochemistry

journal homepage: www.elsevier.com/locate/phytochem

Review

Roles of cell wall peroxidases in plant development

Edith Francoz, Philippe Ranocha, Huan Nguyen-Kim, Elisabeth Jamet *, Vincent Burlat, Christophe Dunand *

Université de Toulouse, UPS, UMR 5546, Laboratoire de Recherche en Sciences Végétales, BP 42617, F-31326 Castanet-Tolosan, France
CNRS, UMR 5546, BP 42617, F-31326 Castanet-Tolosan, France

ARTICLE INFO

Article history:
Available online xxxx

Keywords:
Arabidopsis thaliana
Class III peroxidase
Gene expression
Loosening
Plant cell wall
Proteomics
Stiffening

ABSTRACT

Class III peroxidases (CIII Prxs) are plant specific proteins. Based on *in silico* prediction and experimental evidence, they are mainly considered as cell wall localized proteins. Thanks to their dual hydroxylic and peroxidative cycles, they can produce ROS as well as oxidize cell wall aromatic compounds within proteins and phenolics that are either free or linked to polysaccharides. Thus, they are tightly associated to cell wall loosening and stiffening. They are members of large multigenic families, mostly due to an elevated rate of gene duplication in higher plants, resulting in a high risk of functional redundancy between them. However, proteomic and (micro)transcriptomic analyses have shown that CIII Prx expression profiles are highly specific. Based on these omic analyses, several reverse genetic studies have demonstrated the importance of the spatio-temporal regulation of their expression and ability to interact with cell wall microdomains in order to achieve specific activity *in vivo*. Each CIII Prx isoform could have specific functions *in muro* and this could explain the conservation of a high number of genes in plant genomes.

Contents

1. Introduction

Plant primary cell walls (CWs) mainly contain carbohydrate polymers and proteins. The polysaccharide part is composed of cellulose microfibrils interlaced with hemicellulose cross-linking glycans. This network is embedded within a gel matrix of pectic polysaccharides (Carpita and Gibeaut, 1993). The arabinoxylan content of primary cell walls of commelinid monocots is relatively high when compared with dicots and non-commelinid monocots and also these polymers can be cross-linked through phenolic substitutions on the polysaccharides. In commelinid monocots, arabinoxylan-linked ferulic and *p*-coumaric acids replace xyloglucans and extensins as cross linkers. Plant CWs can be thickened in specialized cell types to form secondary walls strengthened with

* Corresponding authors at: Université de Toulouse, UPS, UMR 5546, Laboratoire de Recherche en Sciences Végétales, BP 42617, F-31326 Castanet-Tolosan, France. Tel.: +33 534 32 38 01; fax: +33 534 32 38 02.
E-mail addresses: jamet@lrsv.ups-tlse.fr (E. Jamet), dunand@lrsv.ups-tlse.fr (C. Dunand).

http://dx.doi.org/10.1016/j.phytochem.2014.07.020
0031-9422/

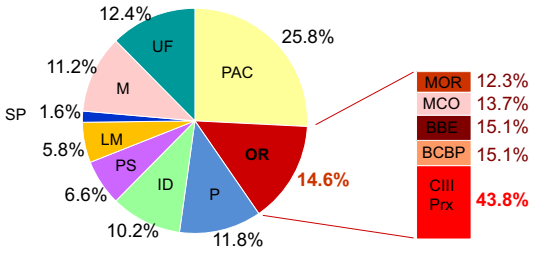

Fig. 1. Distribution of the 500 *A. thaliana* CWPs within nine functional classes. PAC: proteins acting on carbohydrates; OR: oxido-reductases; P: proteases; ID: proteins with interacting domains; PS: proteins possibly involved in signaling; LM: proteins related to lipid metabolism; SP: structural proteins; M: miscellaneous proteins; UF: proteins of yet unknown function. ORs constitute the second most enriched functional class and are subdivided as follows: MOR: miscellaneous oxido-reductases (among which only 1 laccase); MCO: multicopper oxido-reductases; MCO: multicopper oxido-reductases; BBE: berberine bridge oxido-reductases; BCBP: blue copper binding proteins; CIII Prxs: class III peroxidases. Note that CIII Prxs represent about one half of the identified ORs.

additional hydrophobic polymers (e.g., lignins in xylem or suberin and lignins in endodermis Casparian strips). This extracellular matrix is a dynamic structure that plays numerous roles in the physical control of growth, the establishment of cell shape and the maintenance of structural integrity of the plant body in response to environmental cues. Cell wall proteins (CWPs) also play an important role in all these processes. More than 20 proteomics studies have been performed on various *Arabidopsis thaliana* CW-enriched fractions. Around 500 different CWPs have been identified and distributed in nine functional classes (Fig. 1, Albenne et al., 2013; Jamet et al., 2008). The most abundant category contains proteins modifying carbohydrates (25.8% of the identified CWPs). Among other things, the proteins belonging to this class may contribute to CW polysaccharide disassembly and re-assembly processes. The second most abundant category of CWPs is that of oxido-reductases (OR) (14.6%) with about one half of these ORs belonging to the green plant-specific heme class III peroxidases (CIII Prxs).

Together with other CWPs, CIII Prxs are assumed to be involved in CW dynamics, (Cosgrove, 2005; Fry, 2004), but they are also supposed to play roles in other biological processes (Passardi et al., 2005). They belong to large multigenic families (e.g., 73 members in *A. thaliana*, 181 in *Eucalyptus grandis*, 138 in *Oryza sativa* and 143 in *Brachypodium distachyon*) (Fawal et al., 2013). The expansion of CIII Prx gene families (large number of genes) and gene duplication events (gene clusters specific to each species) appears to be chaotic (Dunand et al., 2011). Although there is no evidence to date, relationships between land plant emergence and plant CW evolution may exist (Passardi et al., 2004).

CIII Prxs are characterized by conserved key amino acid residues necessary for heme binding, electron transfer or 3D-structure stability (Welinder, 1992). They also contain variable domains (access channel) in relation to their substrate diversity. CIII Prxs are mainly considered as secreted/apoplastic/CW proteins (Welinder, 1992), but vacuolar isoforms also exist (Carter et al., 2004). The complex roles of CIII Prxs could be explained both by the diversity of their substrates and their spatio-temporal regulation of expression. Thus, their functional analysis remains challenging.

During plant growth, cell expansion is tightly associated to CW loosening and stiffening. The balance between these two processes can be precisely controlled by the antagonistic activities of CIII Prxs (Fig. 2). Indeed, they are able to either (i) build a rigid wall by forming bonds by oxidizing aromatic CW compounds (monolignols, cinnamic acids, aromatic amino acids...) in the presence of H_2O_2, or (ii) loosen CWs by regulating the local concentration of H_2O_2 or generating radical oxygen species (ROS) such as hydroxyl radical ($OH^{\cdot}$) which break covalent bonds in cell wall polymers (Schopfer, 2001). CIII Prxs can also control cell elongation through

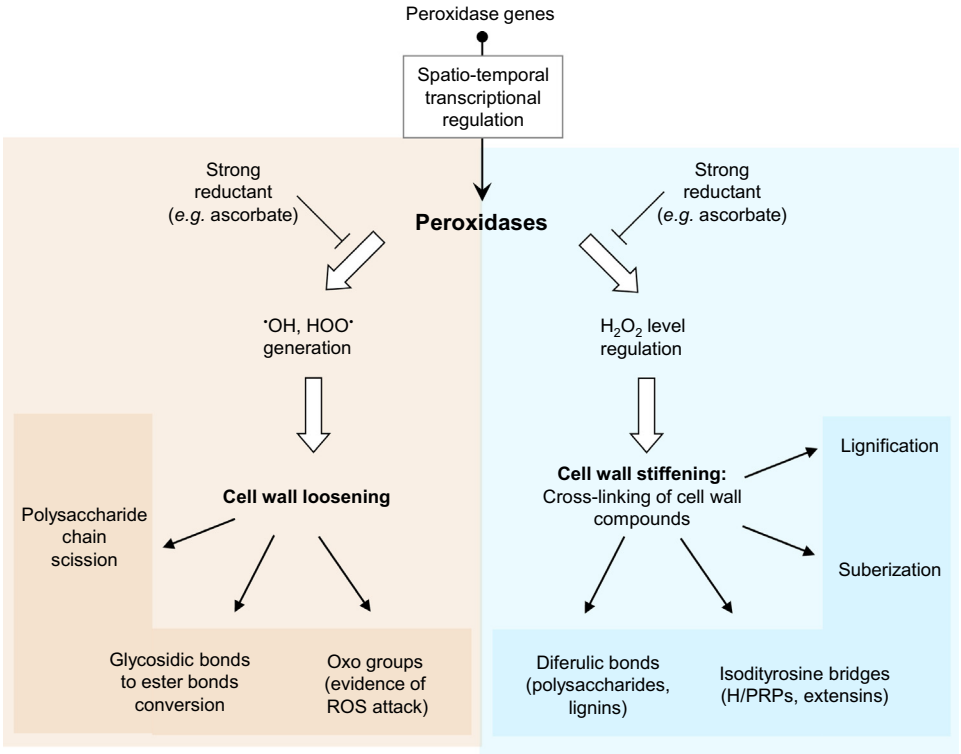

Fig. 2. Dual activity of CW peroxidases. CIII Prxs are capable of generating reactive oxygen species (ROS) such as $^{\cdot}OH$ and $HOO^{\cdot}$, but can also regulate the level of hydrogen peroxide (H_2O_2). Therefore, they play a pivotal role in cellular growth by controlling the subtle balance between CW loosening (left part of the figure) and *de novo* cell wall synthesis/cell wall strengthening (right part of the figure). H/PRPs = Hydroxyproline/Proline-Rich Proteins.

Please cite this article in press as: Francoz, E., et al. Roles of cell wall peroxidases in plant development. Phytochemistry (2014), http://dx.doi.org/10.1016/j.phytochem.2014.07.020