Physiological and Molecular Plant Pathology 94 (2016) 38–46

Contents lists available at ScienceDirect

Physiological and Molecular Plant Pathology

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

Defense responses of plant cell wall non-catalytic proteins against pathogens☆

Abdur Rashid

USDA-ARS National Small Grains and Potato Germplasm Research, Aberdeen, ID, 83210, United States

ARTICLE INFO

Article history:
Received 25 February 2016
Received in revised form
27 March 2016
Accepted 28 March 2016
Available online 30 March 2016

Keywords:
Plant cell wall
Non-enzymatic proteins
Pathogen
Biological elicitation
Wounding
Defense

ABSTRACT

Plant cell wall (CW) associated non-enzymatic proteins (CWPs) are composed mainly of glycoproteins containing a polypeptide backbone attached with carbohydrate side chains. These CWPs typically include hydroxyproline-rich glycoproteins (HRGPs), proline-rich proteins (PRPs), glycine-rich proteins (GRPs), and arabinogalactan proteins (AGPs). The CWPs have been implicated in plant defense against pathogens. The defense responses appear to be accomplished by several mechanisms. The major mechanisms include: (i) CW hardening through insolubilization and oxidative cross-linking of extensins and PRPs mediated via H_2O_2 and peroxidases, (ii) secretion and agglutination of AGPs at the sites of pathogenic infection, (iii) degradation of the genetic materials of the pathogens by binding of GRPs to the RNA of the pathogens, and (iv) activation of the pathogenesis-related (PR) gene expression using AGPs as a soluble molecular signal. This review summarizes the aforementioned defense responses, provides an update on classification, and explores future research opportunities of CWPs.

Contents

1. Introduction

The plant cell wall (CW) is a dynamic structure that provides plants with structural and mechanical supports, and protection against abiotic and biotic stresses. The components of the CW that play important roles in plant cell include, among others, polysaccharides, phenolics, inorganic ions, catalytic enzymes, and non-catalytic proteins. Numerous reviews are available in the literature on the structure and function of plant CW (for a review, refer to [6,17,18,24,40,51,57,74,122]. However, the current review

☆ Department of Biological Sciences, University of Alberta, Edmonton, AB, TG6 2E9, Canada.
E-mail address: abdur.rashid@ars.usda.gov.

http://dx.doi.org/10.1016/j.pmpp.2016.03.009
0885-5765/

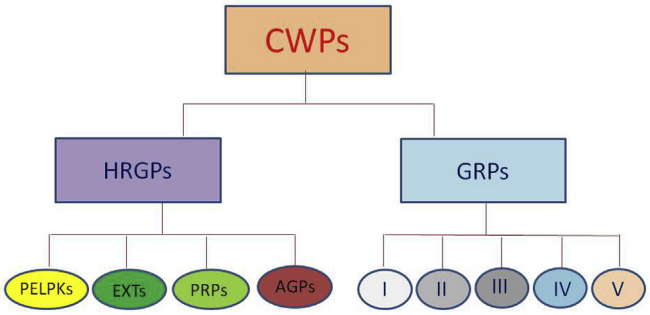

Fig. 1. A schematic diagram showing an updated classification of cell wall non-enzymatic proteins, CWPs. HRGPs: Hydroxyproline Rich Glycoproteins; GRPs: Glycine Rich proteins; AGPs: Arabinogalactan proteins; PRPs: Proline Rich Proteins; EXTs: Extensins; PELPK: Pro-Glu-Leu/Ile/Val-Pro-Lys; I to V: GRP superfamily of protein groups.

concentrates on CW associated non-catalytic proteins, hereafter referred to as CWPs. While multiple detailed reviews were also published on CWPs e.g. [23,50,76,108,114–116], the present review specifically focuses on defense responses of CWPs against pathogenic infection, biological elicitation, and wounding. In addition, this review provides an update on classification and explores research opportunities of CWPs.

2. An updated classification of CWPs

The putative CWPs can be broadly classified into two major groups: hydroxyproline-rich glycoproteins (HRGPs) also referred to as HRGP superfamily of proteins, and glycine-rich proteins (GRPs), often referred to as GRP superfamily of proteins. HRGPs can further be classified into several subfamilies based on number and arrangement of HyPro/Pro repeats and other conserved sequences. The major subfamilies include: extensins and chimeric proteins with extensin-like domains, proline-rich proteins (PRPs), arabinogalactan proteins (AGPs), and solanaceous lectins [23,53,87,114]. In recent years, by extensive bioinformatics and computational analyses, and by sub-cellular protein localization studies, a new subfamily of putative CWPs, designated as PELPK (Pro-Glu-Leu|Ile|Val-Pro-Lys) has been incorporated into HRGP superfamily of proteins [104–106]; TAIR, http://www.arabidopsis.org/). On the other hand, the GRP superfamily of proteins has been divided into five classes based on number and arrangement of Gly-rich repeats, and other conserved motifs [76,129]. An overview of current classification of CWPs is presented in Fig. 1.

Table 1
Amino acid composition of CWPs. Values shown are percentage composition for individual protein (PELPK1), or median values for all Arabidopsis extensins and Arabidopsis PRPs (family membership as defined by Ref. [116] and for proteins (PELPK-like) from various plant species that have been assigned by Phytozome (www.phytozome.org) to the same protein family (22878593) as PELPK1 (adapted in modified form from Ref. [103].

AA residues	PELPK1	PELPK-like	Extensins	PRPs
Ala (A)	3	3.4	3.9	3.4
Cys (C)	0.3	0.4	1.0	2.2
Asp (D)	1.1	0.7	2.6	2.0
Glu (E)	15.7	12.6	2.3	2.1
Phe (F)	2.4	2.5	3.3	2.6
Gly (G)	0.5	0.7	3.9	3.3
His (H)	0	2.3	1.6	2.0
Ile (I)	6.2	3.4	3.2	5
Lys (K)	15.9	8.05	4.3	9.2
Leu (L)	12.2	14.2	6.3	7.4
Met (M)	3	2.3	1.1	0.7
Asn (N)	0.3	0.5	3.7	2.2
Pro (P)	**28.6**	**27.5**	**24.2**	**25.4**
Gln (Q)	1.9	1.0	2.2	1.9
Arg (R)	0.5	1.1	2.7	0.9
Ser (S)	1.9	4.5	12.7	5.4
Thr (T)	1.6	3.5	4.1	7.3
Val (V)	4.9	5.6	6.4	8.1
Trp (W)	0	0	0.3	0
Tyr (Y)	0	0.2	3.8	2.6

3. General characteristics of CWPs

The CWPs, including the newly incorporated PELPKs, have been reported to possess more than one common diagnostic features [32,45,52,53,64,68,76,92,104,111,114,116,118,119]. Based on protein structures, CWPs (i) can have a hydrophobic signal peptide on the amino terminal end destined to secretion (e.g., extensins, PRPs, PELPKs, and some GRPs); (ii) can possess highly repetitive sequences/motifs (Fig. 2); (iii) may be rich in one or more amino acid residues (Table 1); (iv) may be weakly to moderately glycosylated (e.g., PRPs), moderately glycosylated (e.g., extensins), and highly glycosylated (e.g., AGPs); and (v) can form either helical structure such as rod (e.g. extensins, PRPs), or beta-pleated sheet (e.g. GRPs) or fasciclin-ike structure (e.g., AGPs).

Functionally, CWPs have been reported to play multiple roles in plants, particularly in the model plant Arabidopsis [5,14,15,23,50,114]. Examples of a few common functions include: participation in growth and developmental processes, providing structural and mechanical supports to plants (e.g., extensins and PRPs), and playing defensive roles against abiotic and biotic stresses and wounding. This review, however specifically deals with defense responses of CWPs against biotic stresses (e.g., pathogenic infection, and biological elicitation), and wounding.

*MGAPMASFLVLAFSLAFVSQTT*ANYFYSSPPPPV
KHYSPPPVYKSPPPPVKHYSPPPVYKSPPPVHYS
PPVYKSPPPPVKYYSPPPVYKSPPPPVYKSPPPP
VKHYSPPPVYKSPPPPVKHYSPPPVYKSPPPPVK
HYSPPVYKSPPPPVKHYSPPPSYTTLHHHRFTTH
LLQSYTTLHHHRFTTHLLQLYTTPHHHPRSTTNTN
LLLLRTPLLTSTPTLPLQITTSSSLLDYLIVSNGVDD
DTQENKESGDIIKDTRSLTGELKRIHMSKEKVSHF
NVFSLFINTLL

MALMKKSLSAALLSSPLLIICLIALLADPFSVGAR
RLLEDPKPEIPKLPELPKFEVPKLPEFPKPELPKL
PEFPKPELPKIPEIPKPELPKVPEIPKPEETKLPDI
PKLELPKFPEIPKPELPKMPEIPKPELPKVPEIQK
PELPKMPEIPKPELPKFPEIPKPDLPKFPENSKP
EVPKLMETEKPEAPKVPEIPKPELPKLPEVPKLE
APKVPEIQKPELPKMPELPKMPEIQKPELPKLPE
VPKLEAPKVPEIQKPELPKMPELPKMPEIQKPEL
PKMPEIQKPELPKVPEVPKPELPTVPEVPKSEAP
KFPEIPKPELPKIPEVPKPELPKVPEITKPAVPEIP
KPELPTMPQLPKLPEFPKVPGTP

Fig. 2. The primary structure of an Arabidopsis *extensin* (*AT1G76930*) on the left, and an Arabidopsis *PELPK1 (AT5G09530)* on the right, with one-letter amino acid code. The amino-terminal signal peptides are italicized and the transmembrane domains are italicized and underlined. The repetitive sequences are highlighted (Adapted in modified form from Ref. [103].