



Pathogenesis-related proteins and peptides as promising tools for engineering plants with multiple stress tolerance



Sajad Ali^{a,b}, Bashir Ahmad Ganai^b, Azra N Kamili^b, Ajaz Ali Bhat^c, Zahoor Ahmad Mir^a, Javaid Akhter Bhat^d, Anshika Tyagi^a, Sheikh Tajamul Islam^e, Muntazir Mushtaq^d, Prashant Yadav^a, Sandhya Rawat^a, Anita Grover^{a,*}

^a National Research Centre on Plant Biotechnology, Pusa Campus, New Delhi, India

^b Centre of Research for Development, University of Kashmir, Jammu and Kashmir, India

^c Govt Degree College Boys Baramulla, Jammu and Kashmir, India

^d School of Biotechnology, SKAUST Jammu, Jammu and Kashmir, India

^e Department of Bioresource, University of Kashmir, Jammu and Kashmir, India

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ABSTRACT

Pathogenesis-related (PR) proteins and antimicrobial peptides (AMPs) are a group of diverse molecules that are induced by phytopathogens as well as defense related signaling molecules. They are the key components of plant innate immune system especially systemic acquired resistance (SAR), and are widely used as diagnostic molecular markers of defense signaling pathways. Although, PR proteins and peptides have been isolated much before but their biological function remains largely enigmatic despite the availability of new scientific tools. The earlier studies have demonstrated that PR genes provide enhanced resistance against both biotic and abiotic stresses, which make them one of the most promising candidates for developing multiple stress tolerant crop varieties. In this regard, plant genetic engineering technology is widely accepted as one of the most fascinating approach to develop the disease resistant transgenic crops using different antimicrobial genes like PR genes. Overexpression of PR genes (chitinase, glucanase, thaumatin, defensin and thionin) individually or in combination have greatly uplifted the level of defense response in plants against a wide range of pathogens. However, the detailed knowledge of signaling pathways that regulates the expression of these versatile proteins is critical for improving crop plants to multiple stresses, which is the future theme of plant stress biology. Hence, this review provides an overall overview on the PR proteins like their classification, role in multiple stresses (biotic and abiotic) as well as in various plant defense signaling cascades. We also highlight the success and snags of transgenic plants expressing PR proteins and peptides.

1. Introduction

Plants being sessile are constantly challenged by various pathogenic microorganisms (e.g., fungi, oomycetes, bacteria and viruses) that compromise plant survival and their fitness (Cramer et al., 2011). These pathogens lead to significant reduction in annual crop yield as well as pose serious threat to the future food security. Plants defend these enemies by using an array of defense mechanisms in order to survive or retain their fitness (Roux et al., 2014). There are two modes of plant immunity namely, pathogen-associated molecular pattern-triggered immunity (PTI) and effector-triggered immunity (ETI). Pathogen-associated molecular patterns (PAMPs) generally consists of microbial or pathogen structures like flagellins, lipopolysaccharides and fungal cell wall components (chitins and glucans), and these are recognised by

special plant receptors called pattern recognition receptors (PRRs) that further activates PTI (Zipfel and Felix, 2005). On the other hand, microbial pathogens secrete effector proteins which are recognised by a special group of resistance (R) proteins that stimulates the activation of induced defense response so called ETI (Dangl and Jones, 2001). These effector proteins are key elements produced by fungal pathogen for its virulence against plants and are particularly important during the biotrophic phase of infection (Sonah et al., 2016). However, the significance of PR proteins during plant–fungal pathogen interactions has been widely recognised, and there is a growing list of identified pathogen effector proteins that directly interact with PR proteins during infection (Breen et al., 2017). The complexity and efficiency of plant defense system to combat pathogen attack varies within the plant species (Jones and Dangl, 2006).

* Corresponding author at: National Research Centre on Plant Biotechnology, Pusa Campus, New Delhi, India.
E-mail address: anitagrover@hotmail.com (A. Grover).

Plants use both preformed (structural and biochemical) as well as inducible defense responses to combat various biotic stresses (Slusarenko et al., 2000). Preformed defense system includes cutin, waxes, rigid lignin deposition on cell walls and production of antimicrobial molecules like phytoanticipins, and are generally considered as first line of defense to prevent further invasion of pathogens (VanEtten et al., 1994; Osbourn, 1996). However, many pathogens cross this first defense barrier and they must possess an alternative defense approach to counter these pathogens. One such defense mechanism is pathogen inducible defense response which includes hypersensitive response followed by generation of reactive oxygen species (ROS), cell wall cross-linking, synthesis of antimicrobial molecules like phytoalexins, and eventually the production of PR proteins (Van Loon et al., 1994; Van Loon and Van Strien, 1999; Van Baarlen et al., 2007). Among them are PR proteins which are the key ingredients of SAR, an inducible plant immune response that prevents further infection to noninfected parts of the host.

The word “PR proteins” indicates a group of diverse proteins that are induced by phytopathogens as well as defense-related signaling molecules. After pathogen challenge, activation of defense signaling pathways viz., salicylic acid (SA) and jasmonic acid (JA) take place which further leads to the accumulation of PR proteins that minimises pathogen load or disease onset in uninfected plant organs. In general, there are two types of pathogens viz., biotrophic and necrotrophic, the first one activates the SA pathway that stimulates the transcription of NPR1 (non-expressor of pathogen-related gene 1) which in turn leads to activation as well as accumulation SA signature gene (PR1, PR2 & PR5) products locally as well as systematically leading to systemic acquired resistance (SAR). The second i.e., necrotrophic pathogen stimulates JA pathway that induces the activation JA signature genes (PR3, PR4 & PR12) and leads to accumulation of their product locally, and hence provides only local acquired resistance (LAR) (Fig. 1) (Ali et al., 2017b). The SAR provides enhanced resistance to a wide range of pathogens (Sticher et al., 1997; Van Loon et al., 2006; Fu and Dong, 2013). Moreover, PR proteins are widely distributed in plant domain and are present in all plant organs being particularly rich in the leaves, and forms 5–10% of total leaf proteins (Van Loon et al., 1994). These proteins have been successfully isolated from diverse plant species belonging to different families (Takeda et al., 1991). Based on

biochemical features PR proteins largely differ from each other. They are generally low-molecular weight proteins approximately 6–43 kDa, thermo stable, resistant to proteases and remain soluble at low pH (< 3) (Van Loon et al., 1994). The PR proteins have two subgroups namely acidic PR protein that is usually secreted to the extracellular space, and second subgroup is basic PR protein which is generally transported to the vacuole by a signal sequence located at the C-terminal end (Takeda et al., 1991). Pathogenesis-related proteins predominantly accumulate in the apoplastic region however they are also vacuolar (Van Loon et al., 1994). Transcriptomic studies have revealed that PR genes are significantly induced by both biotic and abiotic stresses, and makes them one of the most promising candidates for developing multiple stress tolerant crop varieties (Seo et al., 2008; Fountain et al., 2010; Archambault and Strömvik, 2011; Gupta et al., 2013; Jiang et al., 2015; Dai et al., 2016; Ali et al., 2017a,b, 2018).

Some of the PR proteins are so called antimicrobial peptides (AMPs) which are usually cysteine rich molecules possess potential and broad range of antimicrobial activity. They include PR6 protein family (protease inhibitors), PR12 protein family (plant defensins), PR13 protein family (plant thionins) and PR 14 protein family (lipid transfer proteins) respectively. Generally, AMPs are ubiquitous in nature and forms an important part of host defense against a broad range of microbial pathogens and pests in different living forms ranging from microbes to plants (Egorov et al., 2005).

Therefore, the present review has been drafted to provide an overview on the PR proteins like their classification, role in multiple external stresses as well as in plant defense signaling cascades, and also highlights the success and snags of transgenic plants expressing PR proteins and peptides.

2. History and classification of PR proteins and peptides

Pathogenesis-related proteins were first discovered in tobacco plants infected by tobacco mosaic virus (TMV) (Van Loon and Van Kammen, 1970; Bol et al., 1990). Initially, only five major classes of PR proteins viz., PR1, PR2, PR3, PR4 and PR5 were reported in tobacco plants based on the biochemical and molecular approaches (Bol et al., 1990). However, in later studies many new PR proteins have been isolated and identified in various plants. In 1994, a proper nomenclature technique was employed to group PR proteins into different families based on different criteria like molecular, biochemical, serological and other biological or enzymatic activity. Later on, PR proteins were grouped into 11 families in tobacco and tomato plants which serve as a platform for isolating the homologs of PR proteins in other plant species including both monocots and dicots (Van Baarlen et al., 2007). There are two fundamental features for adding newly isolated protein in the PR protein family viz, first, it must show basal level expression in tissues but significantly increased expression upon pathogen exposure, and the second one is this increased expression should be confirmed in various plant pathological labs or must occur in similar fashion during different plant pathogen interactions. Presently, PR proteins are grouped into 17 families that are mainly based on their protein sequence similarities, enzymatic activities and other biological features which are shown in (Table 1) (Sels et al., 2008). Interestingly, PR proteins show diverse functions such as α -1, 3-glucanase (PR2), chitinases (PR3), thaumatin like (PR5), peroxidases (PR9), plant defensins (PR12) and thionins (PR13) (Van Loon and Van Strien, 1999).

3. PR proteins as antifungal agents

Fungi are rated as one of the most detrimental phytopathogens causing significant yield losses in most agriculturally important crops across the globe (Dean et al., 2012). Based on their lifestyle, plant fungal pathogens are grouped into three categories viz, biotrophs, hemibiotrophs and necrotrophs. To gain access, fungal pathogens generally produce a blend of hydrolytic enzymes like cutinases,

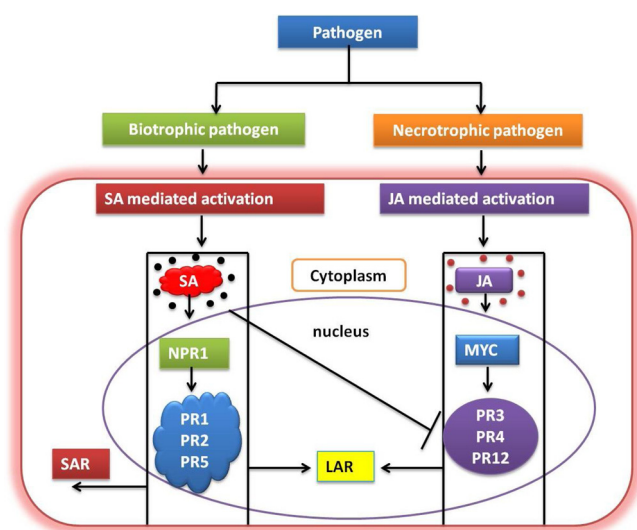


Fig. 1. An overview of activation of signaling cascades in plants after biotrophic and necrotrophic pathogenic infection. Accumulation of plant defense hormones like SA and JA further activates PR genes through selective transcription factor dependent pathways. SA accumulation also leads the activation SAR pathway. Increased expression of PR1 and PR2 genes have routinely been used as a molecular marker of SAR.

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