The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses

**Abstract**

One of the most represented group of Pathogenesis Related (PR) genes are those of the PR-10 class. PR-10 proteins are members of multi gene family, and they often occur in clusters at specific loci following gene duplication and amplification events. To date, large number of PR-10 genes have been cloned and characterized in different species in response to abiotic and biotic stress. This review is focused on recent studies that have described the role, distribution and structure of PR-10 genes in plant genomes. Recent findings have provided insights into the functional roles of PR-10 proteins as ribonuclease, as cytokinin-specific binding proteins, a mammalian lipid transport and plant abscisic acid (ABA) receptor proteins, or as enzyme, (S)-norco claurine synthase. PR-10 proteins are differentially expressed in the presence of different signaling molecules, biotic stresses such as fungal, viral and bacterial pathogens and a number of abiotic stresses. The possibility to use this knowledge for genetic improvement of plant resistance to pathogens through classical breeding approach or transgenic technology is discussed.

**Keywords:** pathogenesis related proteins, ribonucleases, multigene, rnase, abiotic, biotic, agrobacterium

**PR-10 proteins: an overview**

The PR-10 class of PR proteins was first described in parsley and referred as ‘classic’ PR-10 proteins. PR-10 proteins are ubiquitous proteins that have been identified in a number of dicot and monocot plant species. They are small, slightly acidic and resistant to proteases. PR-10 proteins are classified as intracellular PR (IPR) proteins and are present in cytoplasm because they lack signal peptide. They are closely related to a group of major tree pollen allergens and food allergens based on sequence homology to classic PR-10 proteins (~50% identity). The common allergens found in birch pollen, celery, apple, peanut and tomato are included in the PR-10 class. Most PR-10 genes share an open reading frame (ORF) from 456 to 489bp (154-163 amino acids) which is interrupted by an intron of 76-359bp at a highly conserved position.

Amino acid sequence alignments of PR-10 proteins clearly show the most divergent and most conserved segments (Figure 1). This ORF codes for a small protein with conserved sequence features such as a Glycine-rich loop or GXGXXGXXK motif (aa 47-55), a signature motif of PR-10 proteins which is conserved even in distant homologs. This motif has remarkable sequence similarity to P-loop, the Bet v 1 motif (IPR000916) characteristic of proteins from the Bet v 1 super family and three amino acids E96, E148 and Y150 (as positioned in Bet v 1) are possibly involved in ribonucleasic activity. P-loop, is a phosphate-binding loop found in nucleotide binding proteins. However, PR-10 proteins do not have affinity for ATP and the glycine-rich loop is conformationally different from the P-loop.

Interestingly, the glycine-rich loop is the most rigid structural element in the PR-10 fold despite being glycine rich. A characteristic START-like domain (IPR023393), an alpha/beta sandwich structural domain is found in a wide variety of PR protein families. Bet v 1 and PYR/PYL/RCAR domains typically bind phytohormones such as brassino steroids, cytokinins and abscisic acid. Superposition of
the PR-10 structures reveals very significant structural differences, mainly at the C-terminal helix a3, displaying different axial shifts as well as a variable degree of deformation at the center and at its N-terminal connection with loop L9. The internal cavity formed with the participation of a3, displays a remarkable variability in terms of the volume.

Figure 1 Aligned amino acid sequences of 56 PR-10s. Multiple sequence alignment was performed using ClustalW algorithm. Conserved amino acids are marked with asterisk are glycine-rich loop. Bet v 1 domain is highlighted with open boxes. Conserved residues Glu163 and Tyr165 are marked with dots and possibly involved in ribonuclease activity/phosphorylation.

PR-10 genes are multi gene families having low intra specific variation but higher inter specific variation which makes them interesting phylogenetic markers. For example, at least five PR-10 genes in pea, eighteen Mal d 1 genes in apple, ten Bet v 1 genes in birch, eight Fra a 1 genes in strawberry, six PR-10 genes in Solanum suarentense, eight in yellow lupine, five in rice, and eight Pru p 1 and Pru d 1 genes in peach and almond, respectively, have been identified.

They also tend to form physical clusters on specific chromosomes, e.g. in apple, peach and poplar PR-10 genes. Lebel et al., found that thirteen out of the seventeen Vitis vinifera PR-10 sequences are present on the chromosome in direct orientation suggesting that most copies were produced by unequal crossing over events, as described in Arabidopsis and rice. Gene duplication events in the genome evolution process make new copies of a gene which may undergo modifications resulting in functional diversification. These kinds of events are significant source of evolution in plants, however, most of the times gene copies produced by duplication are rapidly lost through pseudo genisation. Therefore, only a part of numerous homologous sequences coexisting in a genome are functional genes.

Another important aspect of PR-10 evolution is evident from differential patterns of expression among the different plant organs, i.e. root, leaf, stem and peduncle, indicating that the transcripts may represent functionally divergent genes. Furthermore, some PR-10 proteins are constitutively expressed in plants while some are induced only under biotic stress, abiotic stress or during plant development, emphasizing functional diversification. The silencing of MtPR-10-1 from Medicago truncatula led to the induction of a new set of PR proteins after infection with Aphanomyces euteiches, suggesting that there is a relationship between PR-10 and other PR proteins.

Structural and functional diversity: decoy strategies to fine tune the defense

PR-10 proteins are involved in many aspects of plant development, growth and defense but their molecular function is still unclear. Various roles for PR-10 proteins have been inferred, such as involvement in enzymatic processes, secondary metabolite biosynthesis, antimicrobial processes, storage, membrane binding, transport, phyto hormone and other hydrophobic ligand binding. However, most of the studies exploring PR-10 functions were conducted in vitro. A protein with ribonuclease activity was isolated from callus cell culture of Panax ginseng showing ~60–70% sequence identity with two intracellular PR proteins from parsley, but did not show any homology with other known ribo nucleases. The RNase activity of PR-10 proteins was also detected in Bet v 1 and BpPR-10c from birch. LaPR-10 from white lupin, LIPR-10.1B from yellow lupine, BpPR-10c from birch, GaPR-10 from cotton, SPE16 from...
The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses

Pachyrhizus erosus, CaPR-10 from hot pepper, SsoPR-10 from Solanum surattense, AhPR-10 from peanut, and PsPR-10.4 from pea. PR-10 proteins exhibit RNase activity and take part in virus resistance via binding to viral RNAs. Structural analysis of PR-10 indicated that it has quite diverse sequences as well as highly conserved sequences. PR-10 family has highly conserved regions including a specific domain (KAXEYL), and the glycine-rich motif (GXGGXGXXXK), which is known as a RNA binding site, but whether these sites have specific binding affinity to target RNA is not clear as PR-10 is also known to be involved in defense functions during a variety of abiotic and biotic stresses. PR-10 proteins have been reported to have several functions but there is no general function common to all members of this class. It is likely that the post translational modifications such as phosphorylation of the protein provide specificity for target RNAs, which in turn delimit potentially dangerous unspecific RNase activity.

One of the member of PR-10 family, CaPR-10 isolated from hot pepper (Capsicum annuum), showed phosphorylation. Phosphorylation lead to enhanced ribonucleolytic activity against viral RNAs upon Tobacco Mosaic Virus (TMV) infection showing its direct involvement in plant defense. Some PR-10 proteins from Arachis hypogaea were shown to be phosphorylated but their role in RNase activity was not shown. A report shows that phosphorylation of CaPR-10 is enhanced by leucine-rich repeat 1 (LRR1) protein. However, Punagarnik et al., demonstrated no effect of phosphorylation on the RNase activity or substrate specificity in the cacao TcPR-10 protein.

The PR-10 protein from Theobroma cacao, TcPR-10 showed both antifungal activity against Moniliophthora perniciosa, and in vivo ribonuclease activity. Although non-specific effects of the PR-10 family were observed, the possibility of helper proteins for specific binding of target RNAs, such as viral or host RNAs of PR-10 proteins, cannot be overruled.

Recently, Choi et al., investigated a cytosolic interaction of CaPR-10and LRR1, an innate immune receptor recruited in response to pathogen attack. Compromised cell death mediated-defense signaling as observed in transgenic pepper infected with avirulent Xanthomonas campestris pv. Sesicatia after suppression of cytosolic PR-10/LRR1 interaction.

On the contrary, enhanced resistance to P. syringae pv. Tomato and Hyaaloperonospora arabidopsis was noticed under heterologous overexpression of PR-10/LRR1 in transgenic Arabidopsis, thus, corroborating the role for PR-10 proteins in conjunction with LRR1 during HR. However, the mechanism of CaPR-10-LRR1 interaction-mediated defense and how CaPR-10 recognizes the host RNAs are still unclear. On a similar note, the interaction between another family of PR proteins (PR40) and LRR1 was demonstrated in hypersensitive cell death and defense response in pepper by Hwang et al. To investigate the role of three conserved residues Glu96, Glu148 and Tyr150 (ginseng ribonuclease sequence) in the RNase activity, site-directed mutagenesis of those residues was performed including some positions within the glycine-rich loop. The RNase activities of SPE16 and GaPR-10 are affected to a greater extent when residues of the C-terminal helix are substituted, while in the case of AhPR-10 major effects are seen with mutagenesis at the glycine-rich loop. An elevated level of PsPR-10.4 activity is observed when Glu148 is mutated to alanine and a decreased level is observed with an H69L mutation.

Site directed mutagenesis of the peanut AhPR-10 protein deteriorated the RNase activity and antifungal activities without any discernible effect on protein internalization by fungal mycelium of Fusarium oxysporum and Rhizoctonia solani in a hyphal extension inhibition assay. However, Biessiakda et al., reported that despite having a high level (76.8%) of identity and sequence conservation at the RNase-relevant positions in two yellow lupine LIPR-10.1A and LIPR-10.1B proteins, only LIPR-10.1B showed RNase activity. Therefore, it is presumed that RNase activity is found in some PR10 proteins, but this is not a general property of this class of PR proteins.

Cytokins, a class of plant growth phytohormones, have also been accepted as integral components of plant defense repertoire and abiotic stress responses. A subclass of PR10 proteins has been structurally confirmed as cytokinin-specific binding proteins (CSBPs) despite having marginal (<20%) sequence identity. Some of the classic PR-10 proteins were found to form complexes with brassinosteroid analogs, flavonoids and cytokins. Constitutive expression of a ribonuclease-active pea PR-10 protein (PR-10.1) gene in Brassica napus seedlings endedogenous endogenous cytokinin pool while promoting seedling germination and growth rates under saline conditions. Krishnavammy et al., suggested that PR-10 proteins may modulate cytokinin levels through an uncharacterized mechanism, which may include the degradation of tRNAs containing cytokinin moieties. Interestingly, an evolutionary ancient and versatile polyketide cyclase/dehydrase-like signature domain (polyketide_cyc, Pfam: PF03364) is found in PR-10 proteins, which may be involved in the binding of cytokinins, flavonoids and steroids across cellular aqueous environments. Zubini et al., have investigated the possible role of the two Pru p 1 isoforms in the defense response of peach to the fungal pathogen Monilinia spp. The RNase activity is different for the two proteins, and only that of Pru p 1.01 is affected in the presence of the cytokinin zeatin, suggesting a physiological correlation between Pru p 1.01 ligand binding and enzymatic activity. The difference in binding activity pointed towards the differences in the binding pockets based on homology modeling.

PR-10 proteins have structural and sequence homology with mammalian lipid transport and plant abscisic acid receptor proteins and are predicted to have cavities for ligand binding. A large internal Y-shaped hydrophobic cavity, as determined by three-dimensional structure of PR-10 proteins could be liable for transport of a polar ligand such as fatty acids, flavonoids, cytokinins or brassino steroids in the intracellular spaces. The diverse roles predicted for PR-10 proteins in the plant immune system should have consideration of discernable modifications of the structure and shape of this cavity allowing to bind different ligands.
In a recently study, three new members of the PR-10 family, the Fra a proteins, have been identified in strawberry in response to the flavonoid biosynthesis pathway, which is essential for the development of color and flavor in fruits and it was suggested that Fra a proteins could act as transporters or “chemical chaperones” binding to flavonoid intermediates so that they are available to processing enzymes. Furthermore, structural comparisons of the apo forms of Fra a 1E and the Fra a 3-catechin complex indicates that Fra a proteins show significant flexibility in the loop regions surrounding the cavity (loops L3, L5, and L7) and ligand-binding induces important conformational changes suggesting an important role of PR-10 proteins in control of secondary metabolic pathways.

The discovery of a PR-10 homolog with unique organ/tissue-specific expression in the tapetal cells during anther development suggests a potential role in the sporo pollen in pathway for these proteins. An enzyme (S)-norcoauraline synthase (NCS) which is involved in benzoyl iso-quinoline alkaloid biosynthesis, catalyzing a Pictet–Spangler condensation of dopamine and 4-hydroxy phenyl acetaldehyde to (S)-norcoauraline share 28%–38% sequence identity with classic PR-10 proteins. Four NCS enzymes namely Tf NCS from Thalictrum flavum, Ps NCS1 and Ps NCS2 from Papaver somniferum, and Cj PR10A from Coptis japonica share substantial identity with PR10 and Bet v1 proteins. Similarly, the phenolic oxidative coupling protein (Hyp-1) from Hypericum perforatum which catalyze the condensation of two emodine molecules to the bioactive naphtha dianthrone hypericin, shows approximately 40% sequence identity with classic PR-10 proteins.

**Signaling nodes: PR-10 in response to signaling pathways**

Phytohormones such as abscisic acid (ABA), ethylene (ET), jasmionic acid (JA) and salicylic acid (SA) are major signaling molecules in plants during the stress response, and their involvements during induction of PR10 proteins has been investigated in various studies. In general, SA is an important signal for general defense responses and especially for attack by bio trophic pathogens in so-called systemic acquired resistance (SAR) and the JA/ET signaling pathway is involved in responses to wounding and abiotic stresses such as drought and high salinity and also in the defense signaling against necrotrophic pathogens. ABA has a crucial role in responses to plant growth and development as well as in wide range of abiotic stresses, including drought, salt and cold. A diagrammatic representation of the expression of defense related proteins and transcription factors in response to signaling molecules are shown in Figure 2.

Expression of a rice PR10 protein, RSOsPR10 is regulated antagonistically by JA/ET and SA signaling pathways in response to environmental stresses. Accumulations of JIOPR10 and OsPR10 transcripts were observed on application of JA and SA in rice leaves. The folding canon of PR-10 proteins is found in the ABA receptor family known as PVR/PYL/RCA (pyrabactin resistance/PYR-like/regulated component of ABA response). Over-expression of a rice transcription factor, OsWRKY30, activates the expression of LOX, AOS2, PR3 and PR10 genes, increases endogenous JA levels and confers resistance to the rice fungal pathogens *Rhizoctonia solani* and *Magnaporthe grisea*. Following ethylene treatment enhanced levels of accumulation of PR10 transcripts were observed in OsPR10a from rice and *Pg*1 from ginseng.

Two alfalfa PR10 genes, MsPR10.1A and MsPR10.1B, were responsive to ethylene and ABA. Analysis of the root proteome of moderate susceptible *Medicago truncatula* in response to infection by the oomycete root pathogen *Aphanomyces euteiches* and the abundance levels of one group of ABA-responsive proteins (ABR17) of the PR-10 class were observed indicating that ABA-mediated signaling is involved in PR protein induction for disease resistance. Therefore, despite the fact that the mechanism of interaction between signaling molecules and PR-10 proteins remains largely unknown, the results of a number of studies suggest that PR10 expression is triggered by the application of signaling molecules and that this response is important in host resistance.

**Abiotic and biotic stresses: PR-10 response**

Plants are responsive to environmental factor and may adapt to certain amount of abiotic and biotic stresses by activating their survival strategies through changes in biochemical and physiological pathways. Activation of the plant immune system that allows survival of plants in response to these extreme stress regimes is important. The PR-10 genes are one of the important components of the plant growth and developmental system and are differentially regulated by various environmental stimuli such as pathogen attack and/or abiotic stresses. Some PR-10 proteins are shown to possess antifungal activity such as, AhPR-10 of *Arachis hypogaea* and TcPR-10 of *Theobroma cacao* through RNAase activity and internalization of fungal mycelium. Other PR-10 proteins that possess antifungal activity are SsPR10 from *Solanum surattense*, maize PR-10 proteins, *CsPR-10* from *Crocus sativus* and JcPR-10a from *Jatropha curcas*.

A study by Soh et al., also demonstrated enhanced expression and longevity of PR-10 gene transcripts in a disease-resistant pepper cultivar in response to the fungal pathogen *Colletotrichum acutatum*. In a recent study by Fan et al., a novel PR-10 Protein *Gly m 4l*, was found to increases resistance upon *Phytophthora sojae* infection in soybean (*Glycine max* [L.] Merr). *Gly m 4l* transcripts were increased by SA stress, but relatively low under MeJA and ET treatments, and
almost decreased with ABA and GA, treatments, therefore it was speculated that Gly m 4l might play a key role in soybean plants resistance to P. sojae mainly depending on SA signaling.

Some PR-10 proteins also show antibacterial and antiviral activity. Ocatin inhibits the growth of phytopathogenic bacteria, such as Agrobacterium tumefaciens, Agrobacterium radiobacter, Serratiamarcescens and Pseudomonas aurofaciens.33 The PR-10 proteins from maize, ZmPR-10 and ZmPR-10.1 have antibacterial activity against bacteria P. syringae.31 Antiviral activity of pepper CalPR-10 was shown to degrade viral RNA of tobacco mosaic virus.44

Antinematode activity has been reported for PR-10 proteins. The CpPRI from Crotalaria pallid roots shows nemato static and nematicide effects against root-knot nematode Meloidogyne incognita by inhibiting the papa in-like enzymes present in the digestive tube and the cuticles of the pathogens.54 In addition to papa in inhibition, CpPRI was observed to internalize and diffuse over the entire body of juvenile M. incognita nematodes in fluorescence based assay.64 In another study, transcripts of genes encoding PR-10 (SAM22) were increased 5- to 10-fold after 12 days of infection and remained high even 10 weeks after infection.51 Similarly, PR-10 expression was higher in resistant pine trees than in susceptible pine trees at 7 and 14 days post inoculation with the pine wood nematode (PWN) Bursaphelenchus xylophilus.65 Synchronized expression of PR-10 with peroxidase in resistant trees indicates this gene may be induced by reactive oxygen species (ROS) such as H2O2 or it may act as a protease against some enzymes such as cellulases, beta-1,3-glucanase, and pectate lyases which are secreted from PWN.87

PR-10 proteins have been shown to be transcriptionally responsive across a large range of abiotic stress environments such as drought, salinity, low and high temperatures, heavy metals, wounding and UV exposure.52,53 Several proteins with similarities to the PR-10 family members were identified through two dimensional gel electrophoresis, which were up-regulated in peanut callus cultures subjected to salt stress.49 Transgenic overexpression of one peanut salinity-induced PR-10 gene (ALSIPR10) in tobacco exhibited enhanced tolerance to salt, heavy metal (ZnCl2) and mannitol-induced drought stress.58 The expression of CcPR-10 transcripts was induced by wounding and jasmonic acid treatments as well as by armyworm (Spodoptera littura), which suggested that CcPR-10 may be involved in cross-tolerance to abiotic and biotic stresses.89 The abundance of two PR-10 proteins from maize (ZmPR-10 and ZmPR-10.1) was increased by multiple abiotic stresses including SA, CuCl2, H2O2, coldness, darkness and wounding and biotic stresses such as Erwinia lactucae and Aspergillus flavus infection.89

In vitro cryo protective activity was exhibited by PR-10 suggesting the role of some PR-10 proteins in frost-tolerance mechanisms.60 Another PR-10 homolog i.e. vegetative storage protein (VSP) from white clover (Trifolium repens L.), also accumulates under autumn and winter conditions, and thus may endow the plants with tolerance to chilling.91 Moreover, PR-10 proteins are over expressed in Oxytopis (Fabaceae) species adapted to the Arctic as opposed to temperate species.92 In a study by Vaas et al.,92 overexpression of PR-10a in suspension cultures of Solanum tuberosum causes an enhanced osmotic tolerance, which in turn leads to enhanced ability for cryo preservation. Abiotic stress-induced Zea mays PR-10 genes (ZmPR-10 and ZmPR-10.1) were also up-regulated following infection with pathogenic bacteria Erwinia caratii and fungus Aspergillus flavus in young maize leaves and immature kernels, respectively.9

**PR-10 proteins: A resource for crop improvement**

The development of resistant cultivars with high yields and excellent quality is the most efficient, cost effective and environment friendly approach to prevent the losses caused by abiotic and biotic stress. Although some plants have remarkable ability to cope with extreme environmental onslaughts, however these stresses nevertheless represent a primary cause of crop-loss worldwide. Understanding the molecular process regulating these metabolic adaptations and untangling the network of interconnected signal pathways is important for developing stress-resistant plants. Figure 3 displays different methods which can be applied to develop plants using PR-10 mediated resistance. An approach to transfer PR-10 mediated resistance in commercial cultivars is use of classical methods of plant breeding.

The steps needed for developing stress tolerant plants through traditional breeding approach are

i. Screen the germplasm in order to identify preexisting sources of resistance and their phenotypic evaluation

ii. Introgression of the resistance traits in elite lines through hybridization

iii. Assess the performance of newly developed cultivars under field conditions.

However, the experiments needed here are very time consuming and laborious. Recent developments in genomics have potential to facilitate engineering for stress tolerance in plants.48 Advances in high-throughput sequencing and phenol typing platforms have potential to transform conventional breeding to genomics-assisted breeding and will address the challenge of increasing food yield, quality and stability of production through advanced breeding techniques. Next generation sequencing can help in the identification of the numerous PR-10 gene family members in the plant genome, and in the characterization of the associations with resistant phenotypes.

---

**Citation:** Jain S, Kumar A. The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses. Adv Plants Agric Res. 2015;2(7):305-314.

DOI: 10.15406/apar.2015.02.00077
However, exploitation of the increasing knowledge of PR-10 proteins to enhance abiotic and biotic stress tolerance in the field should be exercised with caution. Sequence similarity of PR-10 with known allergens is a major setback in this area. Another less unexplored area is that manipulation of a PR-10 proteins might increase resistance to one pathogen or pest, but as an unwanted side effect might increase susceptibility to other pathogens or pests since induction or silencing of PR10 may affect the expression of other defense relates genes. Transgenic technologies have enormous potential to improve important crops by introduction of gene of interest often by Agrobacterium-mediated transformation or direct DNA transfer by particle bombardment method. Characterization of PR-10 proteins and development of transgenic plants overexpressing PR-10 proteins is important step in this direction. Table 1 lists the PR-10 genes which have been used to develop transgenic plants in different crop species. Multi-location field trials of transgenic plants expressing PR-10 will likely be next step for further evaluation.

| Transgenic plant | Source of transgene | Host resistance | Gene symbol | Reference |
|------------------|----------------------|-----------------|-------------|-----------|
| Tobacco          | Asparagus officinalis| Oxidative stress| AoPR1       | 95,96     |
| Arabidopsis      | A. officinalis        | Oxidative stress| AoPR10 (AoPR1) | 97 |
| Arabidopsis      | Pinus monticola      | Cronartium ribicola, Wounding | PmPR10-1.13 | 98 |
| Brassica napus   | Pea                   | Salinity        | PR 10.1     | 99 |
| Arabidopsis      | Pea                   | Salinity, cold and heat | ABR17 | 46 |
| Maize            | Maize                | Aspergillus flavus and Aflatoxins | PR10 | 100 |
| Faba bean        | Potato               | Drought and Salt | PR10a | 101 |
| Tobacco          | Peanut               | Salt and drought | AhSIPR10 | 88 |
| Arabidopsis      | Western white pine   | Cold            | PmPR10-1.10 | 102 |
| Rice             | Soybean              | Salt            | GmPR10      | 103 |
| Arachis hypogaea | Arachis hypogaea     | A. flavus       | ARAhPR10    | 104 |
| Arabidopsis      | Maize                | A. flavus, Pseudomonas syringae | ZmPR10, ZmPR10.1 | 9 |
| Tobacco          | Panax ginseng        | Colletotrichum gloeosporioides, Alternaria solani, SA, H2O2, JA, ABA, salt | PgPR10-2 | 35 |
| Potato           | Potato               | Salinity, Osmotic stress | PR-10a | 105 |
| Nicotiana benthamiana | Alfalfa            | Wounding        | MsPR10.1A | 78 |
| Vitis vinifera   | Vitis pseudoreticulata | Plasmopara viticola | VpPR10.2 | 106 |
| Arabidopsis      | Pepper               | P. syringae pv. tomatoand Hyaloperonospora arabidopsid | PR-10/LRR1 | 10 |
| Arabidopsis      | Panax ginseng        | Salt stress     | PgPR10      | 107 |
| Soybean          | Soybean, tobacco     | Phytophthora sojae | GmPR10 | 108 |
| Soybean          | Soybean              | Phytophthora sojae | Gly m 41 | 82 |
| Banana           | A. hypogaea          | Salt and Drought | AhSIPR10 | 109 |

Conclusion

Our global food supply is threatened by multitude of abiotic and biotic stresses and advance molecular research techniques are trying to fill the gaps through understanding of plant resistance mechanism. PR-10 proteins are induced in response to pathogen and abiotic stimuli. Despite widespread reports on PR-10 involvement in combating a stress conditions sensed by plants, their functional mechanism is still unclear. However, many successful attempts were made to show the role of PR-10 proteins in stress resistance mechanism through transgenic approach in many species. Given the importance of the PR-10 proteins for abiotic and biotic stress tolerance, better understanding of these metabolic pathways involving PR-10 gene will be an exciting and rewarding process for plant scientists in the years to come.

Acknowledgements

The financial support received from North harvest Bean Growers Association is gratefully acknowledged. The authors thank Dr. Berlin Nelson, North Dakota State University for their helpful suggestions in preparing this article.
The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses

Conflict of interest
The author declares no conflict of interest.

References

1. Antonius JF, Pierpoint WS. Purification of a tobacco leaf protein associated with resistance to virus infection. Biochim Biophys Acta. 1978;61(1):248–250.

2. Van Loon LC, Pierpoint WS, Boller T, et al. Recommendations for naming plant pathogenesis related proteins. Plant Mol Biol Rep. 1994;12(3):245–264.

3. Liu JJ, Ekramoddoulah AKM. The family 10 of plant pathogenesis–related proteins: their structure, regulation, and function in response to biotic and abiotic stresses. Physiol Mol Plant Pathol. 2006;68(1–3):3–13.

4. Seeramanan S, Maziah M, Rosli NM, et al. Enhanced tolerance against a fungal pathogen, Fusarium oxysporum f. sp. cubense (Race 1) in transgenic silk banana. Int J Agri Res. 2006(1):342–354.

5. Kovác G, Sági L, Jacson G, et al. Expression of a rice chitinase gene in transgenic banana (‘Gros Michel’, AAA genome group) confers resistance to black leaf streak disease. Transgenic Res. 2012;22(1):117–130.

6. Ghag SB, Shekhawat UKS, Ganapathi TR. Petunia floral defensins with unique prodomains as novel candidates for development of Fusarium wilt resistance in transgenic banana plants. PLoS One. 2012;7(6):e39557.

7. Van Loon LC, Van Strien EA. The families of pathogenesis–related proteins, their activities, and comparative analysis of PR–1 type proteins. Physiol Mol Plant Pathol. 1999;55(2):85–97.

8. Van Loon LC, Rep M, Pieterse CMJ. Significance of inducible defense–related proteins in infected plants. Annu Rev Phytopathol. 2006;44:135–162.

9. Xie YR, Chen ZY, Brown RL, et al. Expression and functional characterization of two pathogenesis–related protein 10 genes from Zea mays. J Plant Physiol. 2010;167(2):121–130.

10. Choi DS, Hwang JS, Hwang BK. Requirement of the cytokinin interaction between PATHOGENESIS–RELATED PROTEIN10 and LEUCINE–RICH PROTEIN1 for cell death and defense signaling in pepper. Plant Cell. 2012;24(4):1675–1690.

11. Soh HC, Park AR, Park S, et al. Comparative analysis of pathogenesis–related protein 10 (PR10) genes between fungal resistant and susceptible peppers. Eur J Plant Pathol. 2012;132(1):37–48.

12. Somssich IE, Schmelzer E, Bollmann J, et al. Rapid activation by fungal elicitor of genes encoding ‘pathogenesis–related’ proteins in cultured parsley cells. Proc Natl Acad Sci USA. 1986;83(3):2427–2430.

13. Breiteneder H, Pettenburger K, Bito A, et al. The gene coding for the major birch pollen allergen Bet v 1, highly homologous to a pea disease resistance response gene. EMBO J. 1989;8(7):1935–1938.

14. Breiteneder H, Hoffmann–Sommergruber K, O’Riordain G, et al. Molecular characterization of Api g 1, the major allergen of celery (Apiumgraveolens), and its immunological and structural relationships to a group of 17–20kDa tree pollen allergens. Eur J Biochem. 1995;233(2):484–489.

15. Vanek–Krebitz M, Hoffmann–Sommergruber K, da Camara L, et al. Cloning and sequencing of Mal d 1, the major allergen from apple (Malus domestica), and its immunological relationship to Bet v 1, the major birch pollen allergen. Biochem Biophys Res Commun. 1995;214(2):538–551.

16. Mittag D, Akkerdaas J, Ballmer–Wедер BK, et al. Ara h 8, a Bet v 1–homologous allergen from peanut, is a major allergen in patients with combined birch pollen and peanut allergy. J Allergy Clin Immunol. 2004;114(6):1410–1417.

17. Wangorsch A, Jamin A, Foetisch K, et al. Identification of Sola L4 as Bet v 1 homologous pathogenesis related–10 allergen in tomato fruits. Mol Nutr Food Res. 2015;59(3):582–592.

18. Saraste M, Sääbald PR, Wittinghofer A. The P–loop – a common motif in ATP– and GTP–binding proteins. Trends Biochem Sci. 1990;15(11):430–434.

19. Koistinen KM, Soininen P, Venalainen TA, et al. Birch PR–10c interacts with several biologically important ligands. Phyto chemistry. 2005;66(21):2524–2533.

20. Biesiadka J, Bujacz G, Sikorski MM, et al. Crystal structures of two homologous pathogenesis–related proteins from yellow lupine. J Mol Biol. 2002;319(5):1223–1234.

21. Fernandes H, Michalka S, Sikorski M, et al. Structural and functional aspects of PR–10 proteins. FEBS J. 2013;280(5):1169–1199.

22. Lebel S, Schellenbaum P, Walter B, et al. Characterization of the Vitis vinifera PR10 multigene family. BMC Plant Biol. 2010;10:184.

23. Tewari S, Brown SM, Kenyon P, et al. Plant defense multigene families:II evolution of coding sequence and differential expression of PR10 genes in Pisum. Populations and Evolution. 2003;1:1–17.

24. Gao ZS, van de Weg WE, Schaart JG, et al. Genomic cloning and linkage mapping of the Mal d 1 (PR–10) gene family in apple (Malus domestica). Theor Appl Genet. 2005;111(1):171–183.

25. Schenk MF, Cordewener JHG, Amedia AHP, et al. Characterization of PR–10 genes from eight Betula species and detection of Bet v 1 isoforms in birch pollen. BMC Plant Biol. 2009;9:24.

26. Musidlovska–Persson A, Aln R, Emanuelsson C. Cloning and sequencing of the Bet v 1–homologous allergen Fru a 1 in strawberry (Fragariaannanassa) shows the presence of an intron and little variability in amino acid sequence. Mol Immunol. 2007;44(4):1245–1252.

27. Liu X, Huang B, Lin J, et al. A novel pathogenesis–related protein (SpPR10) from Solanum surattense with ribonucleolytic and antimicrobial activity is stress– and pathogen inducible. J Plant Physiol. 2006;163(5):546–556.

28. Handsehluh L, Femiak I, Kasperska A, et al. Structural and functional characteristics of two novel members of pathogenesis related multigene family of class 10 from yellow lupine. Acta Bioch Pol. 2007;54(4):783–796.

29. Kim ST, Yu S, Kang YH, et al. The rice pathogen–related protein 10 (JJoSPR10) is induced by abiotic and biotic stresses and exhibits ribonuclease activity. Plant Cell Rep. 2008;27(3):593–603.

30. Chen L, Zhang S, Illa E, et al. Genomic characterization of putative allergen genes in peach/almond and their syntenity with apple. BMC Genomics. 2008;9:543.

31. Schenk MF, Gilihisen LJWJ, Esselink GD, et al. Seven different genes encode a diverse mixture of isoforms of Bet v I, the major birch pollen allergen. BMC Genomics. 2006;7:168.

32. Rizzon C, Ponger L, Gaut BS. Striking similarities in the genomic distribution of tandemly arrayed genes in Arabidopsis and rice. PLoS Comput Biol. 2006;2(9):e115.

33. Flagel LE, Wendel JF. Gene duplication and evolutionary novelty in plants. New Phytol. 2009;183(3):557–564.

34. Mohammadi M, Srivastava S, Hall JC, et al. Two wheat (Triticum aestivum) pathogenesis–related 10 (PR–10) transcripts with distinct patterns of abundance in different organs. Mol Biotechnol. 2012;51(2):103–108.

35. Palla RK, Lee OR, In JG, et al. Expression and functional characterization of pathogenesis–related protein family 10 gene, PgPR10–2, from Panax ginseng. Physiol Mol Plant Pathol. 2010;74(5–6):323–329.

Citation: Jain S, Kumar A. The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses. Adv Plants Agric Res. 2015;2(7):305–314.
DOI: 10.15406/apar.2015.02.00077
The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses

36. Colditz F, Niehaus K, Krajinski F. Silencing of PR–10–like proteins in Medicago truncatula results in anTAGonistic induction of other PR proteins and in an increased tolerance upon infection with the oomycete Aphanomyces euteiches. Plant. 2007;22(4):57–71.

37. Moiseyev GP, Beintema JJ, Fedoreyeva LI, et al. High sequence similarity between a ribonuclease from ginseng calluses and fungus elicited proteins from parsley indicates that intracellular pathogenesis–related proteins are ribonuclease. Planta. 1994;193(3):470–472.

38. Bufe A, Spangfort MD, Kahler H, et al. The major birch pollen allergen, Bet v 1, shows ribonuclease activity. Planta. 1996;199(3):413–415.

39. Swoboda I, Hoffmann Sommergruber K, et al. Bet v 1 proteins, the major birch pollen allergens and members of a family of conserved pathogenesis–related proteins, show ribonuclease activity in vitro. Physiol Plant. 1996;96(3):433–438.

40. Baustignies B, Seguin J, Muzac I, et al. Direct evidence for ribonucleolytic activity of a PR–10–like protein from white lupin roots. Plant Mol Biol. 2000;42(6):871–881.

41. Koistinen KM, Koko HJ, Hassinen VH, et al. Stress–related RNase PR–10c is post–translationally modified by glutathione in birch. Plant Cell Environ. 2002;25(6):707–715.

42. Zhou XJ, Lu S, Xu YH, et al. A cotton cDNA (GaPR–10) encoding a pathogenesis related 10 protein with in vitro ribonuclease activity. Plant Sci. 2002;164(4):629–636.

43. Wu F, Yan M, Li Y, et al. cDNA cloning, expression, and mutagenesis of a PR–10 protein SPE–16 from the seeds of Pachyrhizus erosus. Biochem Biophys Res Commun. 2003;312(2):761–766.

44. Park CJ, Kim KJ, Shin R, et al. Pathogenesis–related protein 10 isolated from hot pepper plants as a ribonuclease in an antiviral pathway. Plant J. 2004;37(2):186–198.

45. Chadha P, Das RH. A pathogenesis related protein, AhPR10 from peanut:an insight of its mode of antifungal activity. Planta. 2006;225(1):213–222.

46. Srivastava S, Neil Emery RJ, Kurepin LV, et al. Pea PR10.1 is a ribonuclease and its transgenic expression elevates cytokinin levels. Plant Growth Regul. 2006;49(1):17–25.

47. Srivastava S, Emery RJN, Rahman MH, et al. A crucial role for cytokinins in pea ABR17–mediated enhanced germination and early seedling growth of Arabidopsis thaliana under saline and low temperature stresses. J Plant Growth Regul. 2007;26(2):26–37.

48. Krishnaswamy S, Baral PK, James MN, et al. Site–directed mutagenesis of histidine 69 and glutamic acid 148 alters the ribonuclease activity of pea ABR17 (PR10.4). Plant Physiol Biochem. 2007;49(9):958–962.

49. Filipenko EA, Kochetov AV, Kanayama Y, et al. PR–proteins with ribonuclease activity and plant resistance against pathogenic fungi. Russ J Genet. 2013(3):476–480.

50. Huh SU, Paek K. Plant RNA binding proteins for control of RNA virus infection. Front Plant Biol. 2013;4:397.

51. Jain S, Srivastava S, Sarin NB, et al. Proteomics reveals elevated levels of PR10 proteins in saline–tolerant peanut (Arachis hypogaea) calli. Plant Physiol Biochem. 2006;44(4):253–259.

52. Pungartnik C, da Silva AC, de Melo SA, et al. High–affinity copper transport and Smq2 export permease of Saccharomyces cerevisiae modulate cytotoxicity of PR–10 from Theobroma cacao. Mol Plant Microbe Interact. 2009;22(1):39–51.

53. Hwang IS, Choi DS, Kim NH, et al. Pathogenesis–related protein 4b interacts with leucine–rich repeat protein 1 to suppress PR 4b:triggered cell death and defense response in pepper. Plant J. 2014;77(4):521–533.

54. Chang KM, Igaru K, Uchida N, et al. New perspectives on plants defense responses through modulation of developmental pathways. Mol Cells. 2008;26(2):107–112.

55. Pasternak O, Bujacz GD, Fujimoto Y, et al. Crystal structure of Vigna radiata cytokinin specific binding protein in complex with zeatin. Plant Cell. 2006;18(10):2622–2634.

56. Markovic–Housley Z, Degano M, Lambda D, et al. Crystal structure of a hypoallergenic isoform of the major birch pollen allergen Bet v 1 and its likely biological function as a plant steroid carrier. J Mol Biol. 2003;325(1):123–133.

57. Koffler S, Asam C, Eckhard U, et al. Crystallographically mapped ligand binding differs in high and low IgE binding isoforms of birch pollen allergen bet v 1. J Mol Biol. 2012;422(1):109–123.

58. Fernandes H, Bujacz A, Bujacz G, et al. Cytokinin–induced structural adaptability of a Lupinus luteus PR–10 protein. FEBS J. 2009;276(6):1596:1609.

59. Krishnaswamy SS, Srivastava S, Mohammadi M, et al. Transcriptional profiling of pea ABR17 mediated changes in gene expression in Arabidopsis thaliana. BMC Plant Biol. 2008;8:91.

60. Zubini P, Zambelli B, Musiani F, et al. The RNA hydrolysis and the cytokinin binding activities of PR–10 proteins are differently performed by two isoforms of the Pru p 1 peach major allergen and are possibly functionally related. Plant Physiol. 2009;150(3):1235–1247.

61. Casanal A, Zander U, Muñoz C, et al. The strawberry pathogenesis–related 10 (PR–10) Fra a proteins control flavonoid biosynthesis by binding to metabolite intermediates. J Biol Chem. 2013;288(49):35322–35332.

62. Radauer C, Lackner P, Breiteneder H. The Bet v I fold:an ancient, versatile scaffold for binding of large, hydrophobic ligands. BMC Evol Biol. 2008;8:286.

63. Neudecker P, Schweimer K, Nerkamp J, et al. Allergic cross–reactivity made visible:solution structure of the major cherry allergen Pru av 1. J Biol Chem. 2001;276(25):22756–22763.

64. Balsamo RA, Wang J–L, Eckard KJ, Wang C–S, et al. Immunogold localization of a developmentally regulated, tapetal–specific, 15 kDa lily anther protein. Proteoplasma. 1995;189(1):17–25.

65. Samanani N, Liscombe DK, Facchini PJ. Molecular cloning and characterization of norcocurarine synthase, an enzyme catalyzing the first committed step in benzylisoquinoline alkaloid biosynthesis. Plant J. 2004;40(2):302–313.

66. Lee EJ, Facchini P. Norcocurarine synthase is a member of the pathogenesis–related 10/Bet v1 protein family. Plant Cell. 2010;22(10):3489–3503.

67. Luk LY, Bunn SL, Liscombe DK, et al. Mechanistic studies on norcocurarine synthase of benzyl isouquinoline alkaloid biosynthesis:an enzymatic Pictet–Spengler reaction. Biochemistry. 2007;46(35):10153–10161.

68. Bais HP, Vepachedu R, Lawrence CB, et al. Molecular and biochemical characterization of an enzyme responsible for the formation of hypericin in St. John’s wort (Hypericum perforatum L.). J Biol Chem. 2007;282(34):32413–32422.

69. Michalska K, Fernandes H, Sikorski M, et al. Crystal structure of Hyp–1, a St. John’s wort protein implicated in the biosynthesis of hypericin. J Struct Biol. 2010;169(2):161–171.

70. Kosuth J, Katokovcova Z, Oleoxva P, et al. Expression of the hyp–1 gene in early stages of development of Hypericum perforatum L. Plant Cell Rep. 2007;26(2):211–217.

71. Agarwal P, Agarwal P. Pathogenesis related–10 proteins are small, structurally similar but with diverse role in stress signaling. Mol Biol Rep. 2014;41(2):599–611
The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses

72. Yamaguchi-Shinozaki K, Shinozaki K. Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annu Rev Plant Biol.* 2006;57:781–803.

73. Takeuchi K, Gyohda A, Tominaga M, et al. ROSOsPR10 expression in response to environmental stresses is regulated antagonistically by jasmonate/ethylene and salicylic acid signaling pathways in rice roots. *Plant Cell Physiol.* 2011;52(9):1686–1696.

74. Jwa NS, Agrawal GK, Rakwal R, et al. Molecular cloning and characterization of a novel jasmonate inducible pathogenesis–related class10 protein gene, JGOSPR10, from rice (*Oryza sativa L.*) seedling leaves. *Biochem Biophys Res Commun.* 2001;286(5):973–983.

75. Rakwal R, Agrawal GK, Yonekura M. Light–dependent induction of OsPR10 in rice (*Oryza sativa L.*) seedlings by the global stress induction molecule jasmonic acid and protein phosphatase 2A inhibitors. *Plant Sci.* 2001;161(3):469–479.

76. Peng X, Hu Y, Tang X, et al. Constitutive expression of rice WRKY30 gene increases the endogenous jasmonic acid accumulation, PR gene expression and resistance to fungal pathogens in rice. *Planta.* 2012;236(5):1485–1498.

77. Jwa NS, Agrawal GK, Tamogami S, et al. Role of defense/stress–related marker genes, proteins and secondary metabolites in defining rice self–defense mechanisms. *Plant Physiol Biochem.* 2006;44(5–6):261–273.

78. Yamasnetskaya EG, Bulgakov VP, Gorbach VI, et al. Ethephon and jasmonate–elicited pathogenesis–related ribonucleases in cultured ginseng cells. *Russ J Plant Physiol.* 2003;50(4):492–497.

79. Bahramnejad B, Goodwin PH, Zhang J, et al. comparison of two class 10 pathogenesis–related genes from alfalfa and their activation by multiple stresses and stress–related signaling molecules. *Plant Cell Rep.* 2010;29(11):1235–1250.

80. Colditz F, Braun HP, Jacquet C, et al. Proteomic profiling unraveling insights into the molecular background underlying increased *Aphanomyces euteiches*–tolerance of *Medicago truncatula*. *Plant Mol Biol.* 2005;59(3):387–406.

81. Gomez–Gomez L, Rubio–Moraga A, Ahrazem O. Molecular cloning and characterization of a pathogenesis–related protein CsPR10 from *Crocus sativus*. *Plant Biol (Stuttg).* 2011;13(2):297–303.

82. Agarwal P, Bhatt V, Singh R, et al. Pathogenesis–related gene, JcPR–10a from *Jatropha curcas* exhibit RNase and antifungal activity. *Mol Biotechnol.* 2013;54(2):412–425.

83. Fan S, Jiang L, Wu J, et al. A Novel Pathogenesis–Related Class 10 Protein Gly m 4I. Increases Resistance upon Phytophthoraeae Infection in Soybean (Glycine max [L.] Merr.). *PloS One.* 2005;10(10):e0140364.

84. Flores T, Alape–Giron A, Flores–Diaz M, et al. Ocatin. A novel tuber storage protein from the Andean tuber crop oca with antibacterial and antifungal activities. *Plant Physiol.* 2002;128(4):1291–1302.

85. Andrade LB, Oliveira AS, Ribeiro JK, et al. Effects of a novel pathogenesis–related class 10 (PR–10) protein from *Crotalaria pallida* roots with papain inhibitory activity against root–knot nematode *Meloidogyne incognita*. *J Agric Food Chem.* 2010;58(7):4145–4152.

86. Ibrahim HMM, Hosseini P, Alkarharof NW, et al. Analysis of Gene expression in soybean (Glycine max) roots in response to the root knot nematode *Meloidogyne incognita* using microarrays and KEGG pathways. *BMC Genomics.* 2011;12:220.

87. Hirao T, Fukatsu E, Watanabe A. Characterization of resistance to pine wood nematode infection in *Pinus thunbergii* using suppression subtractive hybridization. *BMC Plant Biol.* 2012;12:13.

88. Kikuchi T, Shibuya H, Aikawa T, et al. Cloning and characterization of pectate lyases expressed in the esophageal gland of the pine wood nematode *Bursaphelenchus xylophilus*. *Mol Plant Microbe Interact.* 2006;19(3):280–287.

89. Jain S, Kumar D, Jain M, et al. Ectopic overexpression of a salt stress–induced pathogenesis related class 10 protein (PR10) gene from pepper (*Arachis hypogaea L.*) affords broad spectrum abiotic stress tolerance in transgenic tobacco. *Plant Cell Tiss Organ Cult.* 2012;109(1):19–31.

90. Deng W, Bian WP, Xian ZQ, et al. Molecular cloning and characterization of a pathogen related protein PR10 gene in *physyrum* (*Crysanthemum cinerariaefolium*) flower response to insect herbivore. *Afr J Biotechnol.* 2011;10:19514–19521.

91. Ukaji N, Kuwabara C, Takezawa D, et al. Accumulation of pathogenesis related (PR) 10/Bet v 1 protein homologues in mulberry (*Morus bombycis* Koiz.) tree during winter. *Plant Cell Environ.* 2009;27(11):1112–1121.

92. Goulas E, Richard–Molard C, Le Dily F, et al. A cytosolic vegetable storage protein (TrVSP) from white clover is encoded by a cold–inducible gene. *Physiol Plant.* 2007;129(3):567–577.

93. Archambault A, Stromvik MV. PR–10, defense and cold dehydrin genes are among those over expressed in *Oxystepsis* (*Fabaceae*) species adapted to the Arctic. *Plant Cell Environ.* 2011;14(3):497–505.

94. Vaas LAI, Marheine M, Seufert S, et al. Impact of pr–10a overexpression on the cryopreservation success of *Solanum tuberosum* suspension cultures. *Plant Cell Rep.* 2012;31(6):1061–1071.

95. Kole C, Muthamilarasan M, Henry R, et al. Application of genomics–assisted breeding for generation of climate resilient crops:progress and prospects. *Front Plant Sci.* 2015;6:563.

96. Warner SA, Scott R, Draper J. Isolation of an asparagus intracellular PR gene (AoPR1) wound–responsive promoter by the inverse polymerase chain reaction and its characterization in transgenic tobacco. *Plant J.* 1995;3(3):191–201.

97. Mur LAJ, Brown IR, Darby RM, et al. A loss of resistance to avirulent bacterial pathogens in tobacco is associated with the attenuation of a salicylic acid–potentiated oxidative burst. *Plant J.* 2000;23(5):609–621.

98. Mur LAJ, Sturgess FJ, Farrell GG, et al. The AoPR10 promoter and certain endogenous PR10 genes respond to oxidative signals in Arabidopsis. *Mol Plant Pathol.* 2004;5(5):435–451.

99. Liu JJ, Ekramoddoulah AKM, Piquott N, et al. Molecular cloning of a *pathogen/wound–inducible* PR10 promoter from *Pinus monticola* and characterization in transgenic Arabidopsis plants. *Planta.* 2005;221(2):159–169.

100. Srivastava S, Fristensky B, Kav NNV. Constitutive expression of a PR 10 protein enhances the germination of *Brassica napus* under saline conditions. *Plant Cell Physiol.* 2004;45(9):1320–1324.

101. Chen ZY, Brown RL, Damann KE, et al. PR10 expression in maize and its effect on host resistance against *Aspergillus flavus*infection and aflatoxin production. *Mol Plant Pathol.* 2010;11(1):69–81.

102. Hanafy MS, El–Banna A, Schumacher HM, et al. Enhanced tolerance to drought and salt stresses in transgenic faba bean (*Vicia faba L.*) plants by heterologous expression of the PR10a gene from potato. *Plant Cell Rep.* 2013;32(5):663–674.

103. Liu JJ, Ekramoddoulah AKM, Hawkins B, et al. Overexpression of a western pine white PR10 protein enhances cold tolerance in transgenic *Arabidopsis*. *Plant Cell Tiss Organ Cult.* 2013;114:217–223.

104. Kim H, Baek SH, Shin WC, et al. Development of salt tolerant transgenic rice using soybean PR10 gene. *Korean J Breed Sci.* 2010;42:540–546.

Citation: Jain S, Kumar A. The pathogenesis related class 10 proteins in plant defense against biotic and abiotic stresses. *Adv Plants Agric Res.* 2015;2(7):305–314. DOI: 10.15406/apar.2015.02.00077
105. Xie C, Wen S, Liu H, et al. Overexpression of ARAhPR10, a member of the PR10 family, decreases levels of Aspergillus flavus infection in peanut seeds. *Am J Plant Sci.* 2013;4:602–607.

106. El–Banna A, Hajirezaei MR, Wissing I, et al. Over–expression of PR–10a leads to increased salt and osmotic tolerance in potato cell cultures. *J Biotechnol.* 2010;150(3):277–287.

107. He M, Xu Y, Cao J, et al. Subcellular localization and functional analyses of a PR10 protein gene from *Vitispseu reticulata* in response to Plasmopara viticola infection. *Protoplasma.* 2013;250(1):129–140.

108. Lee OR, Pulla RK, Kim YJ, et al. Expression and stress tolerance of PR10 genes from *Panax ginseng* C. A Meyer. *Mol Biol Rep.* 2013;39(3):2365–2374.

109. Xu PF, Jiang LY, Wu JJ, et al. Isolation and characterization of a pathogenesis–related protein 10 gene (GmPR10) with induced expression in soybean (*Glycine max*) during infection with *Phytophthora sojae*. *Mol Biol Rep.* 2014;41(8):4899–4909.

110. Rustagi A, Jain S, Kumar D, et al. High efficiency transformation of banana (*Musa acuminata* L. cv. Matti (AA)) for enhanced tolerance to salt and drought stress through overexpression of a peanut salinity–induced pathogenesis–related class 10 protein. *Mol Biotechnol.* 2015;57(1):27–35.