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Review

Role of Pathogen-Related Protein 10 (PR 10) under Abiotic and Biotic Stresses in Plants

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Abstract: Members of the Pathogenesis Related (PR) 10 protein family have been identified in a variety of plant species and a wide range of functions ranging from defense to growth and development has been attributed to them. PR10 protein possesses ribonuclease (RNase) activity, interacts with phytohormones, involved in hormone-mediated signalling, afforded protection against various phytopathogenic fungi, bacteria, and viruses particularly in response to biotic and abiotic stresses. The resistance mechanism of PR10 protein may include activation of defense signalling pathways through possible interacting proteins involved in mediating responses to pathogens, degradation of RNA of the invading pathogens. Moreover, several morphological changes have been shown to accompany the enhanced abiotic stress tolerance. In this review, the possible mechanism of action of PR10 protein against biotic and abiotic stress has been discussed. Furthermore, our findings also confirmed that the *in vivo* Nitric oxide (NO) is essential for most of environmental abiotic stresses and disease resistance against pathogen infection. The proper level of NO may be necessary and beneficial, not only in plant response to the environmental abiotic stress, but also to biotic stress. The updated information on this interesting group of proteins will be useful in future research to develop multiple stress tolerance in plants.

Keywords: Pathogenesis-related (PR); PR10; abiotic stress; biotic stress; ribonuclease; stress tolerance; nitric oxide

1 Introduction

Plant growth and development are affected by both abiotic and biotic stresses and they have the potential to significantly reduce agricultural productivity. Biotic stresses are caused by plant pathogens and abiotic stresses due to extremes in temperature, drought, salinity and heavy metals. However, plants have developed various mechanisms that enable them to adapt to such stress conditions, including high light stress [1,2]. In plants, response to pathogens (bacteria, fungi, and viruses) is accompanied by increased synthesis of defense-related proteins, often referred to as Pathogenesis Related (PR) proteins. PR proteins

are localized into the vacuolar compartment, cell walls or intercellular spaces [3] and have been shown to be expressed in response to pathogens [4,5], and in response to abiotic stresses [6–8]. Conversely, study related to the expression of PR genes confirmed its involvement in both abiotic and biotic stresses, which makes PR genes, one of the key candidates for future research in the development of multiple stress tolerance plants [1,8,9].

Pathogen attack is destructive to plants, and the plant copes up with such an attack by inducing defense mechanisms and even genetic regulation. In this process plant hormone signaling pathways contribute to plant defense [10]. The induction of several PR-10 genes upon infection of strawberry plants with fungal pathogen infection and consequently increases in production of phytohormones, suggests the interplay between PR10, pathogen infection and phytohormones [11]. This was further confirmed, when the expression of PR 10 was increased by the external application of phytohormone like JA, ABA, and SA [4,12]. During a pathogenic attack, pathogen release elicitors which trigger the plant defense system to fight against the pathogenic infection that includes the formation of reactive oxygen species (ROS) along with the nitric oxide (NO), protein kinases, Ca^{2+} signaling, and ultimately transcriptional reprogramming [1,13,14]. NO plays an important role in the regulation of biotic and abiotic stress in plants. The role of NO in plants linked to a broad spectrum of physiological processes, metabolism and disease responses have been extensively studied in the last decades. The effects of NO can be protective and harmful (toxic) to cells depending on the concentration and site of production [15–17]. It was earlier reported that NO employ beneficial effects on modulating several physiological processes, including nutrient stress [14,18], overcoming a water deficit [19], mitigating Cd toxicity [20], salt stress [21], alleviating heavy metal toxicity [22] and tolerance to chilling and freezing [23,24]. Earlier results suggest that, NO formed due to Cd toxicity is useful in plant adaptation against Cd toxicity stress [25,26]. NO formed during Cd toxicity leads to the upregulation of genes involved in iron uptake which ultimately reducing root elongation and growth [25,26]. Heavy metal-induced accumulation of NO also appears to be responsible for heavy metal toxicity. The relationship between heavy metal toxicity and NO production is still not clear. However, NO can inhibit Cd translocation from root to shoot and protect plants from Cd toxicity [15,27]. The two possible mechanisms of action of NO are proposed, first, it can neutralize the excess ROS production by behaving as an antioxidant which is produced as a result of stresses [28]. Secondly, it can work as a signaling molecule to regulate the expression of stress-responsive genes [29]. The researcher supports that, NO play dual role in barley microspore culture, it involved in programmed cell death (PCD) as well as helping in the initiation of microspore division which helps in reprogramming of microspore embryogenesis [30,31]. This review summarizes current knowledge on a specific group of PR proteins, PR10, in relation to their known structure, ligand binding characteristics, ribonuclease activity, possible biological functions and how those biological roles may be crucial in mediating plant responses to abiotic and biotic stresses, as well as during normal growth and development.

2 PR Proteins and Its Classification

Pathogenesis related (PR) proteins are low molecular weight, either acidic, basic, or neutral, cysteine-rich plant proteins which include a diverse array of proteins such as chitinase, glucanases, thaumatin, endoproteinases, peroxidases, defensins, thionins and Lipid Transfer Proteins (LTPs) reviewed in [32]. Even though PR proteins are induced by both abiotic and biotic factors, all of them are still referred to as "pathogenesis-related" proteins. On the basis of their biological properties and characteristics, PR proteins have been classified into 17 different families (PR1-17) and are implicated in defense responses, as well as in various physiological and developmental processes [33,34]. In addition, the accumulation of PR proteins has been shown to increase following pathogen invasion [5,35,36], and during the abiotic stresses [1,23,36–39]. Several PR proteins involved in antimicrobial activity, developmental programs, including leaf senescence and abiotic factors, including cold, osmotic stress and light [4,23,32]. Earlier

study; clearly suggest a broad spectrum of roles of PR proteins in plant defense and influencing different plant traits. The stability and solubility of PR proteins under acidic conditions and their resistance to extracellular and intracellular proteolytic enzymes enable their survival under harsh conditions thereby protecting them against degradation [40]. Also, the localization of major PR proteins in the intracellular space enables contact with invading fungi or bacteria, resulting in elicitation of defense response. Moreover, the majority of PR proteins have conserved cysteine residues which have been reported to be involved in antimicrobial activity against phytopathogens [41,42].

2.1 PR10 Protein and Its Homologs

Homologs of PR10 such as Bet v1 and the Major Latex Proteins (MLPs) are also small, acidic proteins with amino acid sequence similarities with PR10. MLPs have been identified from a variety of plant species, including Arabidopsis and ginseng [14,17,43] and are found to have similar biological functions as of PR10 e.g., growth and development [44]. MLPs from peach [45] and cucumber [46] are highly expressed during fruit development and MLP transcript from *Arabidopsis* was shown to be expressed during seed germination and seedling development [43]. These functional similarities as well as their similarities in size and isoelectric point, possibly indicate a common origin and conserved structure, particularly the P-loop motif [32,47]. An earlier study on MLPs suggests that, it might play a role in different stress responses, including abiotic stress [48,49]. However, further studies are necessary to understand the function of MLPs in plant growth and development or in plant defense [50] in order to validate their similarities to the PR family of proteins.

2.2 Structure and Amino Acid Sequence and RNase Activity of PR10

PR10 proteins are relatively small molecules with a molecular weight ranging from (6–43 kDa) with a theoretical isoelectric pH (pI) in the acidic range (4.75–6.65) Liu et al. [32]. Alignment of deduced amino acid sequences of PR10 proteins from different plant species (Fig. 1) was performed using COBALT (constraint-based multiple protein alignment tools) from NCBI. Typical PR10 protein contain the P-loop motif (consensus sequence; aa 46–54, GNGGNGTIK), as well as the conserved amino acids (E103, E102, E149, E150 and Y 152) which are required for the RNase activity [50]. Besides the P loop motif, PR10 proteins also possess the Bet v1 signature motif, which is also a characteristic feature of PR proteins [50].

Based on the amino acid substitution studies by Zhou and co-workers where Glycine 51 was substituted with Alanine and Lysine 55 with Asparagine (both in the P-loop region), as well as Glutamic acid 97 (away from the P-loop) with Lysine, a 50%–60% reduction was observed in the RNase activity. These authors concluded these amino acids are not essential for the catalytic activity as the ribonuclease activity was not totally abolished [51]. However, in our opinion, the substantial reduction in activity would strongly indicate a very positive correlation between the presence of these amino acids in the structural motif and the relationship between structural perturbations and reduction of activity. Krishnaswamy et al. [52] provided additional evidence to support the importance of conserved amino acids for the RNase activity of PR10 proteins. Site-directed mutagenesis of H69L and E148A of pea PR10 protein (ABR17) showed altered RNase activity, with the H69L substitution resulting in little or no RNase activity, while E148A substitution resulted in increased activity, demonstrating the importance of these amino acids for the catalytic function of this PR10 protein [52].

The three-dimensional structure of a few PR10 proteins and their homologs such as L1PR10-1A and L1PR10-1B proteins from yellow lupine [53], Bet v1, from birch pollen [53] and major allergen from cherry Pru av1 [54], have been determined using X-ray diffraction and nuclear magnetic resonance (NMR) spectroscopy. Based on the deduced 3D structures, a major feature observed in all these proteins is a seven-stranded antiparallel β-sheet (β1 to β7), surrounding a long C-terminal helix α3 and two short

Figure 1: Deduced Amino acid sequence alignment study of pathogenesis-related protein (PR10) from different plant species. Dashes indicate gaps that were introduced to optimize alignment. The conserved regions are shown in boxes along with P-loop motif (46–54) and Bet v1 motifs. The conserved amino acid H69, E103, E149, E150, Y 152 and L153 are indicated with the asterisks (*)

N-terminal helices (α1 and α2) with a large hydrophobic cavity between the two structural elements [55]. This hydrophobic cavity is presumed to have a crucial role in the biological activity of PR10 proteins [53,55], through its involvement in the intracellular transport of ligands like cytokinins, flavonoids and brassinosteroids [56,57]. All these studies clearly illustrate the detailed structure of PR10 proteins, P-loop and the importance of amino acids responsible for its biological function.

To understand the evolutionary relationship between different PR10 proteins, the amino acid sequence alignment of PR10 proteins from a diverse group of plants ranging from gymnosperms, monocots, and dicots were performed using Constraint-based Multiple Alignment Tool (COBALT) from National Center for Biotechnology Information, NCBI. The dendrogram (Fig. 2) showed two major clades, similar to the one reported previously [34]. All the monocot PR10s included for analysis formed a separate clade which interestingly also contained PR10 protein from yellow lupin. Most of the legumes, on the other hand,

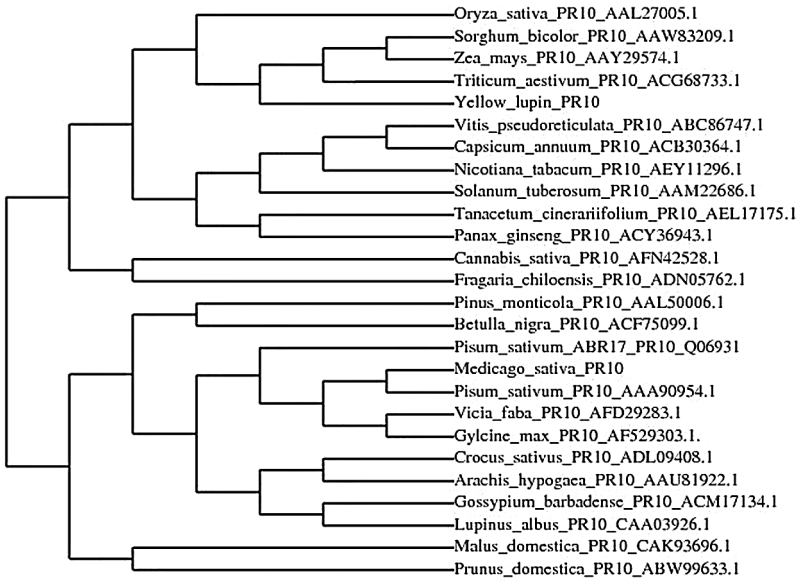

Figure 2: Phylogenic analysis of PR10 proteins from different plant species including monocots, dicots, and gymnosperm

clustered in a separate clade, as did *Solanaceous* PR10s. PR10 proteins from apple and plum were present in a distinct clade of their own, possibly indicating early divergence during the evolution of flowering trees. The structural and functional similarities between PR10 proteins from a diverse array of plant species possibly indicate that they may have originated from a common ancestral gene, which underwent structural divergence during evolution [58].

3 Biological Functions of PR10 Protein

3.1 Ligand Binding Activity

Structural studies have revealed that PR10 proteins contain an internal cavity that could function as a binding site, as well as a reservoir for hydrophobic ligands [52]. Several studies have indicated the ability of PR10 proteins to bind to steroids, cytokinin, fatty acids and flavonoids [33,57,59]. The crystal structure of two homologous PR proteins from yellow lupine (LIPR-10.1A, B) identified the ligand-binding site between the glycine-rich loop and the junction between α1 and α2 proximal to the internal cavity [56]. Furthermore, the X-ray crystallography of a PR10 protein from yellow lupine (LIPR-10.2B) indicated the interaction of a cytokinin (*trans*-Zeatin) within the hydrophobic cavity [56]. Subsequent studies [60] confirmed the ligand binding interaction of PR10 protein with the synthetic cytokinin *N, N′-diphenylurea (N, N′-DPU)*, and the ligands were found in the internal hydrophobic cavity [60], although the interaction was weaker than those compared to the natural cytokinin-Zeatin. Interestingly, the physiological relationship between ligand binding activity and enzymatic activity was shown by Zubini et al. [59], where they demonstrated that the two (Pru p 1.01 and Pru p 1.06D) isoforms of PR10 protein from peach (*Prunus persica*) behave differently, and the rate of hydrolysis of RNA by Pru p1.01 was diminished due to binding with Zeatin. There was no effect on RNAse activity of Pru p 1.06D due to Zeatin binding [59]. This possibly indicates that the RNA hydrolysis activity of PR10 could be regulated through sensing endogenous cytokinin concentration and could form a part of the negative feedback regulation of cytokinin homeostasis. It has also been hypothesized that the modulation of endogenous cytokinin levels may be involved in plant defense signaling [61,56], in particular, there must be a correlation between ligand binding and enzymatic activity. The RNase activity of PR10 has been shown

to modulate the CK abundance, probably through the degradation of tRNAs with CK moiety [62], possibly leading to increase in endogenous CK levels [63]. However, it is conceivable that the active site on PR10 binds both CKs and tRNAs, and competition could arise for the binding site in the presence of both these molecules which need to be demonstrated by performing enzyme kinetic studies in future.

3.2 RNase Activity

Several PR10 proteins have been shown to possess RNase activity which might play a role in the defense mechanism against abiotic and biotic stresses in plants. Ribonucleases are involved in the hypersensitive response (HR) of plants, which has been implicated in programmed cell death or apoptosis [64]. The HR constitutes a coordinated plant response to pathogen attack which involves the oxidative burst [38], and release of local and systemic signals for defense reaction in near and distant cells, resulting in the death of plant cells shortly after pathogen infection in the immediate vicinity of the infection site. This localized cell death is thought to contribute to the resistance of the plant to different diseases [65]. Another possible mechanism of enhanced tolerance is through the degradation of the RNA of invading pathogens which helps in limiting the growth of fungal, bacterial and viral invaders [6,64].

RNases, like the defense-related protein chitinases, are usually sequestered in plant vacuoles and increase in abundance during pathogen attack leading to degradation of the pathogen cell wall [66]. Several members of PR10 protein have been reported to hydrolyze RNA [33]. PR10 protein from *Capsicum annuum* showed RNase activity which was found to be directly associated with its antiviral function [67]. The heterologous expression of recombinant protein ABR17, a member of PR10 protein, showed RNase activity [68] and was found to be involved in response to biotic and abiotic stresses [4]. The recombinant SsPR10 from yellow–fruit nightshade (*Slanumsurattense*) also possesses RNase activity and inhibits the hyphal growth of *Pyriculariaoryzae* [69]. Chadha et al. (2006) demonstrated that recombinant protein (AhRP10) from *Arachis hypogaea* L. possesses ribonuclease activity as well as *in vitro* antifungal activity against the peanut pathogen (*Fusarium oxysporum* and *Rhizoctonia*) [70]. Furthermore, it was found that phosphorylation of CaPR10 (from *Crocus sativus*) protein, increased its ribonuclease activity which subsequently cleaved the invading viral RNA, suggesting that phosphorylation may be an important mechanism for the regulation of RNase activity of PR10 proteins [67]. To elucidate the role of the catalytic important amino acids involved in the RNase activity of pea ABR17, two variants of ABR17 protein, His69Leu and Glu148Ala were generated which exhibited decreased and elevated RNase activity, respectively, providing evidence that both H69 and E148 are important residues for the RNase activity of pea ABR17 protein [52] (Fig. 3). However, recently through a biochemical assay, it was revealed that the Mg^{2+} was required for maintaining the RNase activity of OsPR10a [71]. The RNase activity of OsPR10a was diminished in the presence of the reducing agents β-ME and DTT. Huang et al. proposed that cysteine residues might play a role in maintaining RNase activity in OsPR10a [71]. The above facts, therefore, suggest a comprehensive link between the amino acids, RNase function and ligand binding activity. Further research on PR10 protein and ligand binding interaction could also provide additional information on the control of gene expression during plant defense response as well as normal growth and development.

3.3 Involvement of PR10 Proteins in Abiotic Stress Tolerance

Several lines of evidence implicate the role of PR10 proteins in plant defense mechanism when they are exposed to different abiotic stress conditions. Under drought stress, increased accumulation of the PR10 protein was reported in Banana, Arabidopsis and tobacco [72–74] and in maritime pine [75]. PR10 homologs are also induced by other abiotic factors such as cold, oxidative stress [23,73,63,76], and ultraviolet radiation [77]. Furthermore, transcriptomic analysis of *Oxytropis* (Fabaceae) species revealed

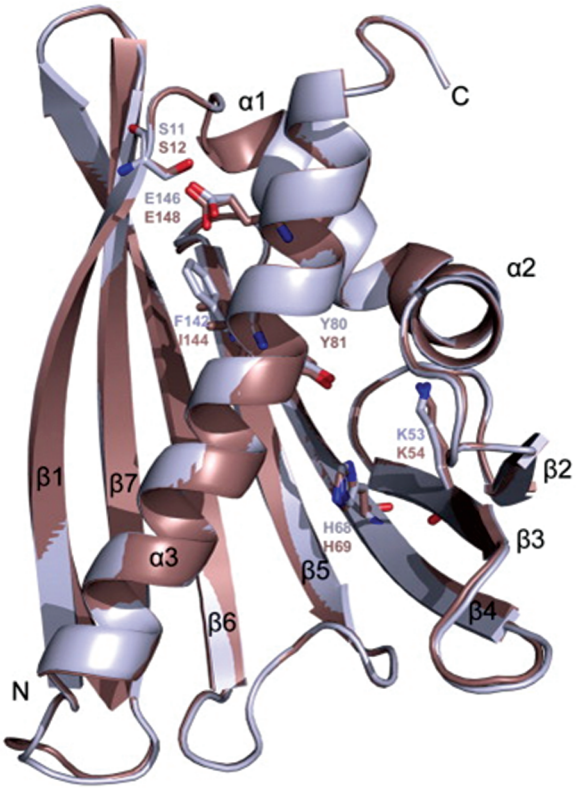

Figure 3: Comparative modeling showing the 3-D structure of pea ABR17 and chain A of *Lupinus luteus* PR10 protein (lIFVA) superimposed. Blue color indicates lIFVA whereas magenta indicates the pea ABR17 protein. The conserved amino acid residues include His 69, E148, Y81 and K64 as shown in brown color. (Reprinted with permission from Krishnaswamy et al. [52])

the enhanced expression of a PR10 gene family of cold stress, suggesting that members of the PR10 gene family may be involved in long-term adaptation to arctic adverse conditions [78].

Proteomic investigation of pea under salinity stress revealed a significant increase in the levels of several members of PR10 proteins, which led to the speculation that PR10 proteins may be important in mediating responses to salinity [79]. The constitutive expression of PR10 (*ABR17*) protein resulted in enhanced tolerance against salt stress in *B. Napus* (80) and multiple abiotic stresses in *Arabidopsis thaliana* [63]. Furthermore, the proteome analysis of rice roots under different abiotic stresses including salinity and drought, also demonstrated the induced expression of PR10 proteins [4]. Overexpression of the PR10 protein from *Panax ginseng* in *Arabidopsis* provided salinity tolerance with increased root length [81], while ectopic expression of *AhSIPR10* from callus cell lines of peanut in tobacco provided tolerance to salt, heavy metal and drought stresses in transgenic tobacco plants [82]. Earlier studies have also revealed enhanced germination and early seedling growth in *PR10.1* transgenic *B. napus* [63]as well as in *ABR17*-transgenic *A. thaliana* [68]. These transgenic plants showed elevated endogenous concentrations of cytokinins (CKs) and may be related to the observed RNase activity of the PR10 proteins studied. It is possible that endogenous CK concentrations are modulated through the possible degradation of tRNAs which contain CK moieties [83]. However, this hypothesis needs to be tested.

Additional studies on the transcriptional analysis of transgenic *Arabidopsis* lines overexpressing pea PR10 (*ABR17*) when subjected to salinity stress, revealed the possible roles of many ABA- and

CK- responsive genes including plant defensins, heat shock proteins and several transcription factors such as RAP2.6L, RAP 2.6, DREB19 and DREB26 [61]. Overexpression of these transcription factors (RAP2.6L, DREB19) also resulted in enhanced plant growth and development of *Arabidopsis* plants under salt and drought stress [52]. Further studies by transforming cDNAs encoding PR10 proteins with altered RNase activities variants in *Arabidopsis*, combined with CK analysis of the transformed lines, will be useful in confirming whether the observed RNase activity is crucial for mediating resistance to abiotic stresses or, if abiotic stress responses are the result of an, as of yet, uncharacterized biological function of PR10 proteins.

3.4 Role of PR10 Protein in Mediating Responses to Biotic Stress

PR10 proteins are induced by pathogen attack in a wide variety of plant species (Tab. 1). Overexpression of cDNA encoding *JIOsPR10* from the rice was shown to be involved in the up-regulation of signaling components of defense-related pathways, including jasmonate, salicylate, and H_2O_2 [96,98]. Induction of PR10 proteins has also been observed in response to viruses [98], bacteria [37,67]; and fungi [88,96,81,37]. PR10 protein from western white pine has been found to be significantly induced upon wounding, further supporting the role of PmPR10 protein in the defense response [84] Also, Liu and colleagues demonstrated the role of PR10 protein from *Pinus monticola* against white pine blister rust caused by *Cronartium ribicola* [95]. Additional support for an important role played by PR10 proteins in mediating biotic stress responses is provided by studies where expression of PR10 has resulted in increased disease tolerance. For example, constitutive expression of the pea PR10 in potato has been shown to confer resistance to *Verticullium dahlia* disease in potato [99], while *Zea mays* (*ZmPR10*) cDNA over-expressed in *E. coli* possessed ribonuclease activity and inhibited the growth of *Aspergillus flavus* [100]. Subsequently, overexpression of cDNA encoding *ZmPR10* and *ZmPR10.1* in *Arabidopsis* resulted in enhanced tolerance also against the bacteria *Pseudomonas syringae* as well as the fungi *Aspergillus flavus*, indicating an important role of PR10 protein in plant defense response [101]. In a recent study, the heterologous expression of PR10 cDNA from ginseng (*PgPR10-1*) in transgenic *Arabidopsis* also provided increased resistance against fungal (*Fusarium oxysporum* and *Botrytis cinerea*) and bacterial (*Pseudomonas syringe*) pathogens [81].

The molecular mechanisms through which PR10 proteins regulate plant defense responses to pathogens are still not clearly understood. It has been suggested that rice PR10 protein (RSOsPR10) which is rapidly induced against blast fungus infection, could be providing resistance, possibly through activation of the jasmonic acid signaling pathway [4]. Another possibility is the RNase activity of PR10 proteins [67], which could be important in modulating apoptotic processes during pathogen invasion. It has also been reported that *Gossypium arboreum* (GaPR10) in cotton degrades fungal RNA as well as specific plant RNAs induced by the pathogen [51]. Similar studies have demonstrated the induction and subsequent phosphorylation of CaPR10 from hot pepper (*Capsicum annuum*) with exposure to *Xanthomonas campestris*pv Vesicatpria (Xcv) due to increased RNase activity, with the ability to cleave invading fungal RNAs (67). Similarly, the PR10 protein from *Crocus sativus* (CsPR10) with RNase activity has shown to be associated with the inhibition of growth of various fungal pathogens such as *Verticillium dahilae, Penicillium sp*. and *Fusarium oxysporum* [102]. Earlier, PR10 isolated from *Jatropha curcus* (JcPR10), displayed both RNase and antifungal activity [97]. In fact, the transient expression showed up-regulation in response to NaCl, salicylic acid, methyl jasmonate and also in response to the *Macrophomina*, a pathogen causing collar rot in *Jatropha*. In a very recent study, pepper (*Capsicum annuum*) pathogenesis-related protein PR10, a member of the Bet v 1 allergen family, and a leucine-rich repeat (LRR1) interacting partner, was found to be crucial for defense and cell death responses against bacterial pathogen attack [38]. LRR1 promotes the ribonuclease activity and phosphorylation of PR10 and the cytoplasmic localization of the PR10-LRR1 complex and its subsequent secretion into the apoplastic

Table 1: List of PR protein involve in biotic and abiotic stress tolerance

Plants	Biotic/Abiotic tolerance	Gene Symbol	Reference
Arabidopsis	freezing, salinity, and osmotic stresses	*TaPR-1-1*	[8]
Tomato	Chilling	*PR1b1*	[23]
Tobacco	Oxidative stress	*AoPR1*	[76]
Arabidopsis	Wounding	*PmPR10-1.13*	[84]
Brassica napus	Salinity	*PR10.1*	[85]
Arabidopsis	Salinity, cold & heat	*ABR17*	[63]
Maize	*Aspergillus flavus* and Aflatoxins	*PR10*	[86]
Tobacco	Salt and drought	*AhSIPR10*	[74]
Rice	Salt	*GmPR10*	[87]
Arabidopsis	Salt stress	*ABR17*	[80]
Soybean	*Phytophthora sojae*	*GmPR10*, Gly m 41	[81,88]
Potato	Salinity, Osmotic stress	*PR10a*	[89]
Tobacco	*Alternaria solani*, SA, JA, ABA, Salt	*PgPR10-2*	[90]
Grape vine	Plasmoparaviticola	*VpPR10.2*	[91]
Arabidopsis	Salt stress	*PgPR10*	[92]
Banana	Salt and Drought	MaPIP1;1	[93]
Soybean	*Phytophthora sojae*	*GmPRP*	[5]
Rice and Arabidopsis	*Xanthomonas oryzae* Xanthomona campestris	*OsPR10a*	[71]
Rice	Biotic/Abiotic stress	*JIOsPR10*	[36]
Arabidopsis	*Fusarium oxysporum Botrytis cinerea Pseudomonas syringe*	*PgPR10-1*	[81]
Physcomitrella patens Arabidopsis thaliana	*Pythium irregulare*	*PpPR-10*	[94]
Tobacco	*Rhizoctonia solani*	PR Protein*AP24*	[37]
Pinus monticola	*Cronartium ribicola*	PR10	[95]
Rice	Jasmonate	JIOsPR10	[96]
Jatropha curcas	Macrophomina sp.	*JcPR-10a*	[97]

space is essential for cell death-mediated defense signaling [38]. Taken together, all these studies provide convincing evidence for the role of PR10 proteins in biotic stress and defense signaling.

4 Conclusions

The pathogenesis-related proteins, PR10s, are widely distributed among the plant kingdom. They have a broad spectrum of roles in plants, ranging from growth and development to defense against invading pathogens and in mediating abiotic stress responses. Expression of PR10 genes is also induced by treatment with phytohormones like JA, ABA, SA and CK, suggesting that PR10 proteins are involved in

phytohormone signaling. The proper concentration of NO is essential, particularly during stress condition, since NO is considered an important signal molecule in plants [103,14]. Excess NO formed during stress responses can fasten the signaling pathways to protect cells from the damage. Structural studies of PR10 proteins have also demonstrated that these proteins bind to a number of molecules such as cytokines, fatty acids, brassinosteroids and flavonoids [33] which may be responsible for the signal transduction following stress imposition.

The exploration of these proteins for improving the agricultural traits may, therefore, open up new avenues towards engineering crops with enhanced tolerance against a variety of stresses. For instance, the constitutive expression of cDNA encoding *PR10* in a variety of transgenic plants has provided resistance to various phytopathogenic fungi, bacteria, and viruses. One possible mechanism of such resistance is through the RNase activity of this protein, which would result in the degradation of the invading pathogenic RNA [4,67]. The involvement of reactive oxygen species, hypersensitive response, and programmed cell death, as well as interactions with leucine-rich repeats, has also been implicated in PR10 mediated pathogen tolerance (Fig. 4). It is possible that the abiotic stress resistance mechanism involves the activation of the defense signaling pathway due to the phytohormone binding ability of this protein, resulting in the modulation of cytokinin levels [63,104] or through the involvement of transcription factor [52]. For instance, the tRNA metabolism leading to possible modulation of CK levels has already been reported [62] and such increases in CK levels may be responsible for the abiotic stress tolerance phenotype of transgenic plants [63]. However, our understanding of their roles *in planta* and the regulation of their expression is far from being complete. Further study on ligand-binding activity of PR10, their competitive inhibitions and its consequent effect on RNase activity can provide additional knowledge on the possible mechanism and mode of action of PR10 protein.

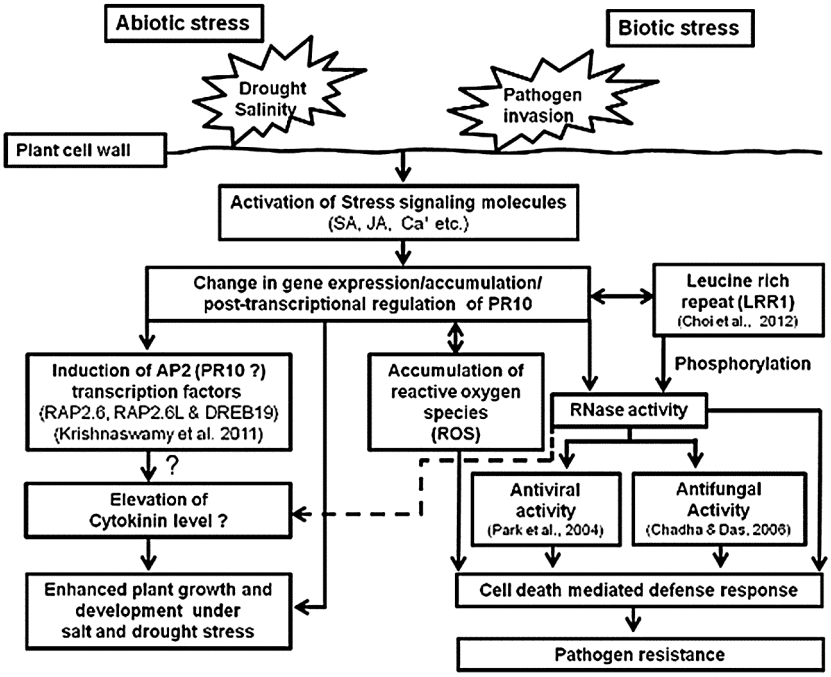

Figure 4: Schematic representation of possible modes of action of PR10 protein against biotic and abiotic stresses in plants

Authors Contribution: SSV and RKS discussed the idea. RKS and SSV have drafted the manuscript, RKS, SSV, and AR edited the manuscript for its improvement.

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Conflicts of Interest: The authors declare that they have no conflicts of interest to report regarding the present study.

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