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Review paper

Multiple defense layers in plant-pathogen interactions

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Abstract: Biotic stresses always impact the yield of plants, and understanding the interaction between plants and pathogens is crucial for disease control. Plants' defense mechanisms against pathogens have various complex layers. As pathogens evolve to have more complicated and efficient effector systems during plant-pathogen coevolution, plants develop more sophisticated defense systems. The complexity of plant defense systems can be explored at different levels, including reactive oxygen species (ROS) scavenging, changes in transcription factor (TFs) expression, increased activity of PRs, and accumulation of lignin. Additionally, systemic acquired resistance (SAR) and induced systemic resistance (ISR) induction pathways play a significant role in how plants respond to biotic stresses. *ERF* and *NPR1* genes activate SAR and ISR pathways. Various protein families associated with the plant defense system, such as pathogenesis-related proteins (PRs), regulate a wide range of responses to pathogens, hindering pathogen penetration. The accumulation of certain metabolites, like lignin, helps prevent pathogen penetration and the spread of disease in plants, serving as part of the defense system. This review provides a brief overview of the diverse and essential layers of the plant's defense system against pathogens, aiding in the understanding of plant-pathogen interactions.

Keywords Biotic stress, molecular aspect, induced resistance, plant defense strategies.

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Introduction

Plants can recognize microbe-associated molecular patterns (MAMP) or damage-associated molecular patterns (DAMP) by pattern recognition receptors (PRR) and sense the presence of pathogens (Schwessinger and Ronald, 2012). Some subsequent events that cause the activation of the immune system include ion flux changes in the plasma membrane, oxidative burst, activation of the MAPK cascade, expression of defense genes, and callus deposition. This level of immunity, called (MAMPs/DAMPs)-triggered immunity (MTI) or pattern triggered immunity (PTI), is the first layer of the immune system ((Jones and Dangl, 2006); (Zipfel, 2009)). Some pathogens have developed different effectors during evolution to disrupt MTI (Dangl et al., 2013). During the co-evolution of plant and pathogen, plants developed intracellular receptors and resistance proteins (PR) to detect the presence of effectors and activate effector-induced immunity (ETI). This level of defense is considered the second layer of protection (Spoel and Dong, 2012). These two layers of immunity are usually known as the innate immunity of plants (Schwessinger and Ronald, 2012). Activating the plant's innate immunity in a specific tissue (infected tissue) leads to the transmission of defense signals to other tissues (without contamination) systemically. It promotes long-term resistance against a wide range of disease agents. This acquired immunity is known as systemic acquired resistance (SAR) (Zhou and Wang, 2018). In addition to pathogens, some chemical compounds such as salicylic acid, nitric oxide, N-hydroxy pipecolic acid, and azelaic acid can activate the SAR and, or other defense-related systems ((Chen et al., 2018); (Haghpanah et al., 2021), (Haghpanah et al., 2024); (Jung et al., 2009); (Park et al., 2007); (Wang et al., 2014)).

ROS system

The signaling network related to reactive oxygen species (ROS) is highly conserved among aerobic organisms. It controls a wide range of biological processes, such as growth, development, and response to biotic or abiotic stimuli ((Mittler et al., 2011)). In plants, the enzyme complexes generating ROS at the cell surface are still unknown, However, evidence shows that the activity of a set of enzymes, including NADPH oxidase (NOX), class III peroxidases, oxalate oxidases, amine oxidases, lipoxygenases, quinone reductase, causes the production of ROS in plant cells (Camejo et al., 2016). Additionally, cell organelles such as chloroplasts, mitochondria, and peroxisomes are important potential sources of ROS during response to biotic and abiotic stresses (Kohli et al., 2019). It is known that the production of H_2O_2 (hydrogen peroxide) and $O_2^{\bullet-}$ (superoxide) is part of the plant's defense process against pathogens. One of the first defense reactions of the plant against pathogen attack is oxidative burst, which causes the temporary production of ROS and seems to be a common feature of the plant response. ROS production during oxidative burst is associated with pathogen recognition related to the Perception of microbe/pathogen-associated molecular patterns (MAMPs/PAMPs). This process also occurs during HR (Camejo et al., 2016). Excessive production of ROS, is usually seen during the pathogen response process, causes HR or cell death, which is one of the appropriate responses to prevention of pathogen penetration. They also act as local and systemic secondary messengers to create immune responses such as the expression of defense genes or stomatal closure (Gilroy et al., 2014). The biochemical pathway of production and inhibition of oxygen free radicals illustrated that after the formation of free radicals, the activity of the superoxide dismutase (SOD) enzyme causes $O_2^{\bullet-}$ to become H_2O_2. A part of the generated H_2O_2 leaves the cell membrane and acts as a signaling molecule that can regulate cell metabolism involved in growth and response to environmental stimuli (Sagi et al., 2004); (Xia et al., 2009). However, Catalase (CAT) enzyme activity converts a significant part of the produced H_2O_2 into oxygen and water (Oliveira et al., 2016). Other critical enzymes of the ROS pathway include ascorbate peroxidase (APX) and peroxidase (POD), which are involved in the degradation of H_2O_2 and the oxidation of phenolic compounds. Treating the plant with certain chemical inducers, such as potassium phosphite and azelaic acid, stimulates the ROS pathway and triggers a defense response (Haghpanah et al., 2024); (Ramezani et al., 2018).

SAR and ISR pathways

Systemic acquired resistance (SAR) can activated by most pathogens that cause tissue necrosis, either as part of the hypersensitive response (HR) or as a symptom of the disease (Conrath, 2006). When cells detect SAR signals, produce salicylic acid to activate NPR1. The NPR1 activity regulates the transcription of many genes, including pathogenesis-related (PR) genes and endoplasmic reticulum (ER) genes, which contribute to the secretion of PR proteins (Spoel and Dong, 2012); (Wang et al., 2005). As a transcription factor, nuclear NPR1 interacts with TGAs and some TFs (NIMI-interacting) to regulate the expression of downstream defense genes (Kesarwani et al., 2007). TGAs mainly activate NPR1-dependent genes, while NIMIN suppresses the expression of defense genes (Johnson et al., 2003). The SAR pathway primarily regulates the plant's defense for biotrophic pathogens (Santino et al., 2013) (Figure 1).

Induced systemic resistance (ISR) is another form of systemic immunity induced by beneficial non-pathogenic microbes (Pieterse et al., 2014). Although ISR and SAR are both systemic defense mechanisms, they differ from each other in several ways. First, the triggers for ISR and SAR are fundamentally different. SAR is triggered by compatible or incompatible pathogenic interactions, while ISR is initiated by non-pathogenic microbes (Zhou and Wang, 2018). Second, although the biochemical spectrum of both pathways is broad, there is little overlap between these two pathways, especially in exposure and impact on pathogens (Ton et al., 2002). Third, the presence and accumulation of salicylic acid are necessary for the SAR pathway. In contrast, ISR is less dependent on salicylic acid and is more regulated by jasmonic acid and ethylene (Pieterse et al., 2014) (Figure 1). Jasmonic acid and its derivatives provide immunity against necrotrophic pathogens and herbivores (Santino et al., 2013). Some inducers can activate SAR (salicylic acid, azelaic acid (Djami-Tchatchou et al., 2017); (Jung et al., 2009)) or ISR (methyl jasmonate) pathways. The type of pathogen (necrotrophic or biotrophic) can also affect the induction of the type of defense induction system. Results of a recent study showed that the use of azelaic acid can unexpectedly induce defense systems associated with jasmonic acid challenging to necrotrophic types such as *Alternaria solani* as a necrotrophic pathogen (Haghpanah et al., 2024).

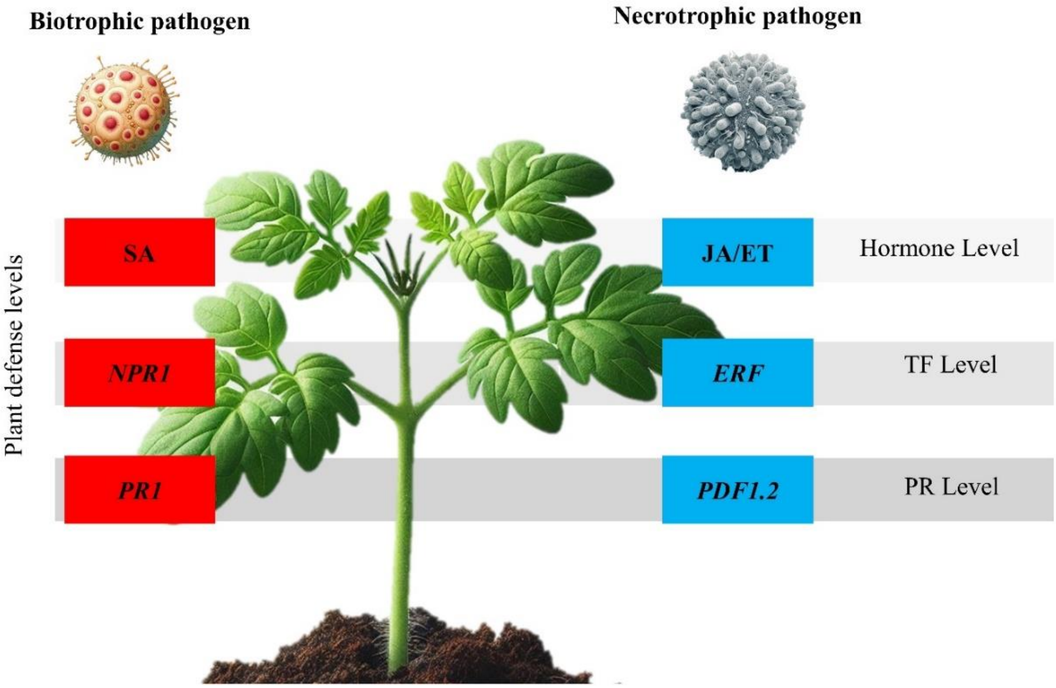

Figure 1. Plant response to biotrophic and necrotrophic pathogens.

Transcription factors

Transcription factors (*TFs*) are crucial regulators that control gene expression in all living organisms and play a significant role in plant growth, the cell cycle, signaling, and stress responses. TFs alter gene expression by binding to the cis-elements of the target gene, and in plants, TFs are encoded by approximately ten percent of genes (Inukai et al., 2017). Large *TF* families, such as *WRKY*, *NAC*, and *ERF* serve as critical regulators of various stress-related genes, aiding in the selection of genetic engineering to enhance plant resistance against various stresses (Wang et al., 2016). Studies show that inducers stimulate the defense system in plants by affecting TFs.

The WRKY family is a unique transcription factor family found in higher plants and algae, playing a crucial role in numerous biological processes, particularly in response to biotic and abiotic stresses. The structure of *WRKY* protein consists of two main parts, N-terminal DNA binding domain and C-terminal zinc-finger structure (Li et al., 2020). Based on the diversity within the structures of these parts, *WRKY* is divided into different classes (Eulgem et al., 2000). *WRKY* family members have diverse regulatory mechanisms. In summary, *WRKY* protein can efficiently combine with W-box elements and activate or inhibit the transcription of downstream genes. Additionally, it can bind to other active elements and form protein complexes, which increases the binding activity of transcription (Phukan et al., 2016). The W-box is found in the promoter regions of many defense genes, and studies show that *WRKY* causes the expression of these defense genes by binding to this region and providing resistance to pathogens (Shinde et al., 2018). The expression of the WRKY gene in tomato plants was observed to increase after inoculation with *A. solani* (Haghpanah et al., 2023).

NAC proteins constitute a large family of plant-specific transcription factors with more than 100 members in Arabidopsis and rice. *NAC* TFs are characterized by the presence of a conserved N-terminal region known as the NAC domain, which acts as a DNA-binding domain (Yuan et al., 2019). NACs play a significant role in the plant's immune system. (Rabiei et al., 2022) showed that hexanoic acid treatment increases the expression of *NAC1* and induces resistance to early blight disease in tomato plants (Rabiei et al., 2022).

ERF proteins are a subfamily of the APETALA2 (AP2)/Ethylene-responsive-element-binding protein (EREBP) family of transcription factors, specific to plants (Singh et al., 2002). According to the EST database, 112 families of AP2/ERF have been identified in tomatoes. ERF proteins have a conserved region of 58-59 amino acids (ERF domain) that can bind to two similar cis-elements, such as the GCC box (found in the promoter regions of several PR genes), and cause an ethylene response (Feng et al., 2020). Microarray expression profiling related to sensitive and resistant varieties of tomato under the stress of wave spot disease showed that ERF family transcription factors respond to pathogen attack in resistant plants. ERF transcription factors may play a role in activating PR proteins (Feng et al., 2020).

NPR1 Regulatory Protein

The *NPR1* gene is essential for the activation of the SAR pathway. It was initially discovered in Arabidopsis through the comparison of mutants of this gene, demonstrating that plants lacking *NPR1* can not activate the SAR pathway (Liu et al., 2015); (Shah et al., 1997)). NPR1 activity can be stimulated by the treatment of salicylic acid and its analogs instead of pathogen infection (Wang et al., 2006). Microarray studies have shown that increasing the concentration of salicylic acid in the cell results in the transfer of *NPR1* to the nucleus, leading to changes in the transcription of 2248 genes associated with SAR. Despite not having a second known DNA binding site, *NPR1* is believed to act as a transcriptional cofactor (Withers and Dong, 2016). In addition to its role in the SAR pathway, *NPR1* activity is also crucial for activating the ISR pathway (Pieterse et al., 1998). Nuclear NPR1 is required for the SAR pathway, while cytoplasmic *NPR1* plays a role in ISR pathway activation. Cytoplasmic *NPR1* may regulate the interaction between salicylic acid and jasmonic acid (Ramírez et al., 2010); (Stein et al., 2008).,). Research indicates that the NPR1 protein is important in determining cell death during ETI (Withers and Dong, 2016). When stimulated by salicylic acid, NPR1 regulates and activates the SAR pathway increasing the expression of genes such as

PR1, *PR2*, and *PR5* (Molinari et al., 2014). On the other hand, if jasmonic acid or ethylene stimulates *NPR1*, the ISR pathway is activated, resulting in the expression of defense factors such as *PDF1*.2, *PR3*, and *PR4* (Thomma et al., 1998).

Mitogen-activated protein kinase (MAPK)

MAPKs are signal transduction units that are highly conserved and participate in many signal transduction processes through MAPK cascades. A typical MAPK cascade consists of MAPK (MPK), MAPK kinase (MAPKK, MAP2K, MKK, or MEK), and MAPK kinase kinase (MAPKKK, MAP3K, or MEKK) (Cristina et al., 2010). In a typical MAPK signaling cascade, MAPKKKs are activated by "stimulated plasma membrane receptors" and transmit signals downstream (Cristina et al., 2010). During this molecular cascade, MAPKKK activates MAPKK by phosphorylating specific MAPKK motifs. Then MAPKK activates MAPK by phosphorylating specific areas of MAPK. Finally, MAPK activates downstream kinases, enzymes, transcription factors, and other response factors and transmits extracellular environmental signals to the cell (Cristina et al., 2010); (Zhang et al., 2018). Through step-by-step phosphorylation, the MAPK cascade can amplify signals and transmit them to downstream proteins, causing the expression of resistance genes. The MAPK cascade plays an important role in cell differentiation, cell growth, hormonal activity, and response to biotic and abiotic stresses (Komis et al., 2018). Studies on the interaction between pathogens and tomato plants show that the MAPK family, especially MAPK3, plays a critical role in the response to pathogen attacks (Kandoth et al., 2007); (Melech - Bonfil and Sessa, 2010); (Stulemeijer et al., 2007). Plant treatment with inducers can be effectively stimulate the MAPK cascade (Zheng et al., 2020).

Lignin accumulation

Lignin is one of the most important secondary metabolites produced in plant cells through the phenylalanine/tyrosine pathway. This metabolite makes up approximately 30% of the organic carbon content in the biosphere (Ralph et al., 2004). The biosynthesis of lignin is a complex process that can be divided into three main steps: 1) the biological synthesis of lignin monomers, 2) the transport of monomers, and 3) polymerization (Liu et al., 2011). Lignin, as a complex phenolic polymer, increases the stiffness of the plant cell wall, creates a hydrophobic property, and facilitates the transport of minerals through the vascular bundles in the plant (Schuetz et al., 2014). Additionally, lignin is an essential physical barrier against the penetration of pathogens (Ithal et al., 2007); (Liu et al., 2018) . The lignin wall also acts as a reservoir of antimicrobial compounds that are released when the cell wall is destroyed (Miedes et al., 2014). To overcome the plant cell wall barrier, fungi secrete various enzymes, including cellulases, pectinases, hemicelluloses, chitinases, and proteases. These enzymes break down components of the cell wall and potentially trigger plant defense responses. (Yang et al., 2018). Applying certain chemical compounds, such as silica, induces lignin formation in plant tissues. Research indicates that silicic acid (the absorbable form of silica for plants) can interact with pectins and polyphenols in cell walls (Clarkson and Hanson, 1980). Some silicones attached to cell walls likely exist as esters (such as silicic acid derivatives) that function as a link in the structural organization of polyuronides, influencing the content and metabolism of polyphenols in cell walls. Cells are impacted by these changes. Silicon may regulate lignin biosynthesis and enhance the physical barrier against pathogen attack (Song et al., 2016).

Defense genes and proteins (PR)

When plants are attacked by pathogens and herbivores, biochemical and physiological changes occur in plants, such as the physical strengthening of the cell wall through the production of lignin, the production, and accumulation of phenolic compounds, phytoalexins, and an increase in related proteins to the pathogen (PR), which subsequently prevents various pathogen attacks (Bowles, 1990). Meanwhile, the production and accumulation of PR proteins in plants are vital in response to the pathogen. Studies show that some inducers cause rapid expression and significant accumulation of PRs, leading to a stronger defense response to pathogen penetration (Jung et al., 2009); (Ramezani et al., 2017) . In the past, various proteins stimulated during plant-microbe interaction were considered PR proteins, including enzymes such as PAL that exist naturally but their expression increases with plant infection. This definition led to confusion, as a set of antifungal proteins was never considered a part of PRs (van Loon et al., 2006). Recently, 17 protein families (Table 1) have been identified as PRs (Moosa et al., 2018).

PR1 proteins

PR1 proteins are highly conserved among plants in terms of structure and are very similar in some domains, indicating that their general role is in plant response to biotic stresses (Lincoln et al., 2018). Although *PR1* is known as one of the most important members of PR, its biological function is not fully understood and only some of its properties, such as antifungal properties, have been determined (Glazebrook, 2005); (Lincoln et al., 2018). *PR1* mRNA expression has been widely used as a marker of plant disease resistance, while evidence of the protein's presence or direct effect on the disease or pathogen has been reported (Glazebrook, 2005); (Jung et al., 2009) .

Table 1. Characteristics of pathogenesis-related (PR) proteins in plants.

Family	Protein size (KDa)	Reported in plant	Properties	Reference
PR-1	15	Tobacco (PR-1a)	Antifungal	(Antoniw et al., 1980)
PR-2	30	Tobacco (PR-2)	b-1,3-glucanases	(Antoniw et al., 1980)
PR-3	25-30	Tobacco P, Q	Chitinases (I, II, IV, V, VI, VII)	(Van Loon, 1982)
PR-4	15-20	Tobacco R	Chitinases (I, II)	(Van Loon, 1982)
PR-5	25	Tobacco S	Thaumatine-like proteins (TLPs)	(Van Loon, 1982)
RP-6	8	Tomato inhibitor I	Proteinase inhibitor	(Green and Ryan, 1972)
PR-7	75	Tomato P_{69}	Endoproteinase	(Vera and Conejero, 1988)
PR-8	28	Cucumber chitinase	Chitinase (III)	(Metraux et al., 1988)
PR-9	35	Tobacco (lignin-forming peroxidase)	Peroxidase	(Lagrimini et al., 1987)
PR-10	17	Parsley (PR-1)	Ribonuclease-like proteins (RL)	(Somssich et al., 1986)
PR-11	40	Tobacco class-V chitinase	Chitinase (I)	(Melchers et al., 1994)
PR-12	5	Radish RsAFP3	Defensin	(Terras et al., 1995)
PR-13	5	Arabidopsis Thi2.1	Thionin	(Epple et al., 1995)
PR-14	9	Barley LTP4	Lipid-transfer protein (LTP)	(García-Olmedo et al., 1995)
PR-15	20	Barley OxOa (germin)	Oxalate oxidase (OXO)	(Z. Zhang et al., 1995)
PR-16	20	Barley OxOLP	Oxalate oxidase-like (OXO)	(Wei et al., 1998)
PR-17	27	Tobacco PRp27	Antiviral and antifungal	(Okushima et al., 2000)

Chitinase and glucanase are enzymes plants produce to break down molecules of chitin and glucan found in fungi cell walls. Chitin is made up of N-acetyl-D-glucosamine polymers with β-1,4 linkages that are broken down by chitinases, while glucan is composed of β-1,3-glucosidic linkages that are broken down by β-1,3-glucanase. In plants, five classes of chitinases and three classes of glucanases have been identified.

Defensins

Defensins are a crucial family of antimicrobial peptides with a fully conserved structure. These peptides bind to the cell membrane of microbes (which have a negative charge) and interact with them (Parisi et al., 2019). The two main types of defensins are cis-defensins (found in plants and insects) and trans-defensins (found in mammals). Defensin coding genes in plants are known as *PDF1.2* (Sher Khan et al., 2019). Studies have shown that the role of this peptide in creating resistance to necrotrophic pathogens is very important (Mang et al., 2009).

Peroxidases

Peroxidases play a crucial role in multiple biochemical pathways, including scavenging reactive oxygen species (ROS), synthesizing lignin, and plant defense against pathogens (Pandey et al., 2017). Peroxidases are classified into different classes, including:

Class I, includes cytochrome c peroxidase, ascorbate peroxidase, and catalase peroxidase, which are involved in ROS scavenging.

Class II, exclusively contains fungal peroxidases and plays a major role in the biological degradation of lignin.

Class III peroxidase, perhaps the most important class of plant peroxidase, is involved in processes such as cell wall metabolism, ligninization, suberin processes, auxin-related metabolism, wound healing, ROS scavenging, and defense against pathogens (Pandey et al., 2017). In plant-pathogen confrontations, Class III peroxidases strengthen the cell wall to hinder pathogen penetration. These enzymes also participate in the production of phytoalexins and antimicrobial compounds. The effect of inducers on increasing the expression of genes and enzymatic activity of PRs has been discussed in previous studies (Jung et al., 2009); (Ramezani et al., 2017; Ramezani et al., 2018).

Conclusion

In general, the response of plants to pathogen penetration can be investigated in different layers. In the first stage, the plant senses the presence of the pathogen. Plants recognize MAMPs and DAMPs through pattern recognition receptors (PRRs), which activate rapid defense responses such as ion flux changes and oxidative bursts, activating MAPK cascades and defense gene expression. In response to pathogens that weaken MTI, plants produce resistance (R) proteins as intracellular receptors. This secondary defense mechanism enhances local and systemic immunity. SAR involves salicylic acid signaling through the NPR1 gene to orchestrate defenses primarily against biotrophic pathogens. On the other hand, ISR is activated by beneficial microbes and relies on the jasmonic acid and ethylene pathways, protecting against necrotrophic pathogens and herbivores. The role of ROS-related pathways is also important in plant-pathogen interactions. ROS act as signaling molecules and antimicrobial agents. Their production induces protective reactions, including the hypersensitivity response (HR), which increases the overall resilience of the plant. Transcription factors (TFs) such as WRKY, NAC, and ERF families regulate defense gene expression. WRKY proteins respond to various stressors, while NAC and ERF proteins are mainly involved in responding to pathogen attacks.

The final layers in the plant's response to the pathogen are PR proteins and physical barriers such as lignin accumulation. PR proteins induced during pathogen encounters include different classes with roles in antifungal activity and enzymatic functions. Their structural and functional diversity is vital to strengthen the plant's defense system. Lignin is a physical barrier that strengthens plant tissues and prevents pathogen invasion. Promoting lignin biosynthesis can significantly increase pathogen resistance.

The interconnectedness of these components reveals how plants use a multi-layered defense strategy to combat biotic stresses. A deeper understanding of MTI, ETI, ROS signaling, and the function of TF and PR proteins can inform innovative agricultural practices, including genetic engineering and breeding approaches aimed at increasing plant resilience. Such advances are critical to ensuring sustainable agriculture, allowing crops to grow amid challenges posed by climate change and emerging pathogens. Overall, this multifaceted view of plant immunity enriches our knowledge of plant biology and provides critical insights for future agricultural strategies.

Supplementary Materials

No supplementary material is available for this article.

Author Contributions

Conceptualization; M.H. and A.N., writing original draft, investigation, reviewing and editing; M.H., supervision; M.H. All authors listed have made substantial, direct, and intellectual contributions to the work and have approved it for publication. All data were generated in-house, and no paper mill was used. All authors agree to be accountable for all aspects of work ensuring integrity and accuracy.

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Conflict of Interest Statement

The authors declare no conflict of interest.

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لایه‌های مختلف دفاعی در تعامل گیاه-پاتوژن

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چکیده: تنش‌های بیولوژیکی همیشه بر عملکرد گیاهان تأثیر می‌گذارد و درک تعامل بین گیاهان و پاتوژن‌ها برای کنترل بیماری بسیار مهم است. مکانیسم‌های دفاعی گیاهان در برابر عوامل بیماری‌زا دارای لایه‌های پیچیده مختلفی است. همانطور که پاتوژن‌ها برای داشتن سیستم‌های موثر پیچیده‌تر و کارآمدتر در طول تکامل همزمان گیاه و بیماری زا تکامل می‌یابند، گیاهان نیز سیستم‌های دفاعی پیچیده‌تری را توسعه می‌دهند. پیچیدگی سیستم‌های دفاع گیاهی را می‌توان در سطوح مختلف، از جمله مهارROS ، تغییرات در بیان فاکتورهای رونویسی (TFs)، افزایش فعالیت PRs و تجمع لیگنین بررسی کرد. علاوه بر این، مسیرهای القای SAR و ISR نقش مهمی در نحوه واکنش گیاهان به تنش‌های بیولوژیکی دارند. همچنین *ERF* و *NPR1* مسیرهای SAR و ISR را فعال می‌کنند. خانواده‌های پروتئینی مختلف مرتبط با سیستم دفاعی گیاه مانند PRs، طیف وسیعی از پاسخ‌ها را به پاتوژن‌ها تنظیم می‌کنند و مانع از نفوذ پاتوژن می‌شوند. تجمع برخی متابولیت‌ها مانند لیگنین به جلوگیری از نفوذ بیماری و گسترش آن در گیاهان کمک می‌کند و به عنوان بخشی از سیستم دفاعی عمل می‌کند. این بررسی مروری کوتاه بر لایه‌های متنوع و ضروری سیستم دفاعی گیاه در برابر پاتوژن‌ها ارائه می‌کند و به درک تعاملات گیاه و بیماری‌زا کمک می‌کند.

کلمات کلیدی: القای مقاومت، تنش زنده، جنبه‌های مولکولی، ساز و کارهای دفاعی گیاه.

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