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Physiological Response and Resistance of Plants to Disease and Pest Stress

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Abstract This paper outlines the physiological responses of plants to pathogenic microbial infection and pest feeding stress, as well as the resistance characteristics of plants to diseases and pests, and proposes new directions for future research on crop resistance to diseases and pests. The objective of this paper is to provide a reference framework for the breeding of crops with enhanced resistance to diseases and pests, the utilization of natural immunity in crops, and the efficient prevention and control of diseases and pests. This framework is intended to facilitate the healthy and sustainable development of the agricultural industry.

Key words Pathogenic microorganism; Pest; Disease resistance; Pest resistance; Resistance breeding; Defensive response

1 Introduction

A primary cause of yield reduction in the production of agricultural and forestry crops is the occurrence of plant diseases and pests. Throughout the production process, crops are consistently exposed to significant damage from a variety of diseases and pests. Consequently, chemical control has consistently been the most effective method for managing diseases and pests. The prevailing agricultural and forestry production practices continue to rely predominantly on chemical pesticide measures to control plant diseases and pests. However, the use of chemical control can result in the development of resistance to diseases and pests, the killing of natural enemies of diseases and pests, the accumulation of excessive agricultural residues, and the pollution of the environment. As the general public's expectations regarding environmental quality and food safety continue to rise, it becomes increasingly important to reduce or eliminate the use of pesticides in agricultural production. It is therefore of great importance to investigate the physiological responses and resistance of plants to disease and pest stress, as well as to develop green and sustainable prevention and control technologies for diseases and pests.

Plant stress resistance is a critical factor for plants to flourish in the natural environment. Insect feeding and disease infection are the primary external stresses on plants. In response to these stresses, plants synthesize a range of defense substances, enabling them to resist diseases and pests. One of the green prevention and control technologies for diseases and pests is breeding for plant resistance to diseases and pests. Research on plant response to disease and pest stress and their resistance can provide a theoretical basis for breeding for plant resistance to diseases and pests and for the utilization of plant natural immunity. This paper presents an overview of the current state of research on the physiological responses of plants to pathogenic microbial infection and insect feeding stresses, as well as their resistance to diseases and pests.

2 Plant response to pathogenic microbial infection stress

2.1 Plant structural characteristics and disease resistance

Plants can provide a direct defense against disease infection when stressed by pathogenic microorganisms by altering structural features. These alterations may include thickening of xylem cell walls, an increase in lignin content, and an increase in leaf wax content.

The cell wall represents the initial mechanical barrier that separates plants from pathogens[1]. The cross-linking of the cell wall is a consequence of the plant's response to external stimuli, including environmental stress, pathogen interactions, and mechanical damage. Peroxidase plays a pivotal role in the cross-linking process of the cell wall. Hydrogen peroxide (H_2O_2) is a necessary component in the oxidative cross-linking of cell wall phenolics. Peroxidase, an oxidizing enzyme, catalyzes the oxidation of coupled lignin-like compounds, which are then utilized in the synthesis of plant cell walls and the regulation of the intracellular concentration of H_2O_2[2]. Furthermore, lignin is regarded as a crucial factor to resist the infection and dissemination of pathogenic bacteria. In contrast, both acid and alkaline peroxidases are involved in the synthesis of lignin[3]. It has been demonstrated that an enhanced peroxidase activity is associated with the accumulation of suberin and lignin[4]. Plants strengthen their cell walls through a series of defense reactions, including lignification and suberification. The production and accumulation of lignin analogs in different parts of the cell wall, intercellular layer, and cytoplasm are the main manifestations of lignification. These processes can restrict and impede the further invasion and expansion of pathogens

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to varying degrees[1].

Furthermore, the waxy layer represents a significant barrier to plant resistance to pathogens. For instance, Feng Lizhen *et al.* [5] discovered that the leaf waxy content of the highly resistant asexual line *Eucalyptus* 9224 was considerably higher than that of the highly susceptible line *Eucalyptus* 5. This indicates that the waxy layer of eucalyptus leaves serves as the outermost line of defense against pathogenic bacteria, preventing their invasion and delaying the onset of infection. The removal of the wax results in the transformation of the resistant varieties into susceptible varieties. *Ginkgo biloba* resistant varieties exhibit a considerable quantity of wax deposits in their leaves. Inoculation of *G. biloba* leaves with *Neurospora* and *Stemphylium* revealed that both pathogens were unable to penetrate the cuticle with its waxy covering. Conversely, the removal of the wax from the leaves of resistant varieties demonstrated that both pathogens could penetrate the leaf blades[6-7]. The waxy layer not only resists and delays the invasion of pathogens but also affects the germination and branching of pathogens, thus reducing their ability to infect disease-resistant varieties. For instance, Li Haiying *et al.* [8] observed that the mycelium of *Cercospora sojina* exhibited a greater diversity of forms and a higher frequency of germination and branching on susceptible varieties than on resistant ones.

2.2 Plant chlorophyll and disease resistance Photosynthesis is a vital process in the growth of plants, providing them with the organic matter they require for optimal development. Chlorophyll is the foundation of plant photosynthesis, and the presence of pathogens in plants can impair the function of their chloroplasts. Pathogens that infect plants impede the synthesis of chlorophyll by the plant, thereby inhibiting photosynthesis and reducing the plant's ability to resist disease. Upon infection of the plant by the pathogen, the pathogen interacts with the chloroplasts, resulting in their disintegration and subsequent blockage of chlorophyll synthesis. This process ultimately leads to the manifestation of pathologic symptoms, including leaf chlorosis, yellowing, and mottled leaf[9]. In the absence of inoculation with the powdery mildew pathogen, the chlorophyll content of leaves from susceptible alfalfa varieties did not differ significantly from that of moderately susceptible and resistant varieties. However, following inoculation with the pathogen, there were significant differences in chlorophyll content among susceptible, moderately susceptible, and resistant varieties. Furthermore, the chlorophyll content exhibited a notable decline with the prolongation of the inoculation period and the degree of disease incidence. Nevertheless, the reduction in chlorophyll content of susceptible varieties was considerably more pronounced than that of disease-resistant varieties[10-11].

2.3 Plant symbiotic bacteria and disease resistance The plant rhizosphere represents an active interface for material exchange between plants and soil. Plant rhizosphere microorganisms are regional microorganisms that are in close contact with plant roots. The plant rhizosphere symbiotic bacteria play a pivotal role in maintaining soil fertility, promoting plant growth and development, and enhancing plant disease resistance. For instance, *Aspergillus terreus* strains in the rhizosphere demonstrate robust antagonistic effects against three pathogenic fungi, including *Fusarium oxysporum*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum*[12]. Bacterial wilt is a disease that has a significant impact on eucalyptus plantation forests. Research has demonstrated that ectomycorrhizal fungi exhibit antagonistic activity against *Ralstonia solanacearum*, and mycorrhiza can secrete growth-regulating substances and a variety of phytohormones, thus enhancing eucalyptus' resistance to the disease[13]. Fifteen strains of *Bacillus* spp. isolated from the rhizosphere by Wang *et al.* [14] exhibited robust resistance to tobacco black shank. Furthermore, both ectomycorrhiza (ECM) and arbuscular mycorrhiza (AM) or a combination of the two mycorrhizal types demonstrated efficacy in reducing the prevalence of soil-borne diseases.

The symbiotic bacteria that are present in the plant may compete with pathogenic bacteria for nutrients or space. Alternatively, they may induce resistance in plants to inhibit the growth of pathogenic bacteria. For instance, *Pseudomonas* strains can elicit induced systemic resistance (ISR) responses in *Dianthus caryophyllus* stems against wilt, while *Bacillus subtilis* can enhance the activity of host disease defense enzymes (POD, PPO, and SOD) and stimulate the synthesis of various hormones to enhance host resistance to early and late blight in tomato seedlings[15-16]. Furthermore, plants can utilize antimicrobial substances secreted and produced by symbiotic bacteria to enhance their disease resistance. This phenomenon is known as the antagonistic effect of plants on pathogenic microorganisms. *Bacillus cereus* UW85 secretes two antimicrobial substances: amido-polyols and aminoglycosides. The antibiotic pyrrolnitrin was isolated from the *Pseudomonas fluorescens* BL915 strain. These antimicrobial substances have been shown to antagonize *R. solani* of alfalfa[17-18].

3 Plant response to insect feeding stress

3.1 Plant structural characteristics and insect resistance Similarly, plants may utilize their own structural characteristics or undergo structural alterations to provide a direct defense against feeding by phytophagous insects. Plants defend themselves against insect feeding damage primarily through structural characteristics, including water content, unit weight, waxiness, and the thickness of the plant's leaves. A plant's resistance to insects is inversely proportional to its water content. This was demonstrated in a study of five species of *Dalbergia* spp. and the insect *Plecoptera oculata*[19]. The results indicated that as the water content of the leaves decreased, the plant's resistance to insects also decreased. *Leptocybe invasa* has been identified as a significant pest affecting eucalyptus trees. By comparing the water content of the leaves of different eucalyptus asexual lines, Chen Hanzhang *et al.* [20] observed that *Eucalyptus urophylla* × *E. grandis* DH 32-28 exhibited low water content and high resistance to the insect. Zhang Yili *et al.* [21] observed that the greater the number of layers of collenchyma, including spongy tissues, palisade tissues, and the leaf lower epidermis, the greater the resistance to *Empoasca vitis*. A comparable phenomenon was observed in the *Erythrina variegata* species[22]. The greater the thickness of the palisade tissue, spongy tissue, vascular bundle sheath, and upper and lower epidermis of *E. variegata* leaves, the greater the resistance to *Quadrastichus erythrinae*. *E. variegata* with high resistance exhibits a cellular structure comprising small gaps between cells, arranged in a tightly packed manner. This cellular arrangement makes it difficult for *Q. erythrinae* to cause harm to *E. variegata*. In addition to preventing water loss, plant leaf surface waxes can also influence egg laying and feeding by phytophagous pests. For example, the leaf surface wax content of asparagus varieties with high resistance to thrips is significantly higher than that of insect-susceptible or highly-susceptible varieties[23].

3.2 Plant nutrients and insect resistance The nutritional composition of plants exerts a significant influence on the behavior of phytophagous insects, including their host selection and population dynamics[24]. The category of plant nutrients encompasses a diverse range of substances, including soluble sugars, polysaccharides, proteins, lipids, vitamins, free amino acids, and inorganic salts. In response to insect feeding stress, plants undergo significant alterations in their nutrient composition, enabling them to withstand the detrimental effects of pests. The soluble protein and soluble sugar contents of 24 eucalyptus asexual lines demonstrated an increase following damage by *Leptocybe invasa*. A negative correlation was observed between soluble protein content and resistance strength, while a positive correlation was evident between soluble sugar content and resistance strength[25]. A comparable phenomenon has been observed in crops such as rape, cotton, and chili[26-28]. In addition, there are other plant nutrients that affect the insect resistance of plants. For instance, the content of amino acids in plants increases with the degree of insect feeding, and the content of amino acids in tea increases with the prolongation of the feeding time of *Empoasca flavescens*[29]. A number of free amino acids undergo significant changes following insect feeding or mechanical damage. For instance, glutamic acid, theanine, and other major free amino acids in tea tree leaves exhibited a declining trend after three weeks of feeding[30-31]. Li Tiantian *et al.*[32] indicate that the higher the content of soluble sugars, proline, and soluble proteins in cucumber leaves, the stronger the aphid resistance. Conversely, the lower the content of free amino acids, the stronger the aphid resistance.

3.3 Plant secondary metabolites and insect resistance Secondary metabolites, which are volatile compounds inherent in plants, can be utilized by phytophagous insects for host localization. In addition to this function, these metabolites also serve to naturally repel pests, a process known as constitutive defense. For instance, camphor, which is released by *Cinnamomum camphora*, has a repellent effect on a multitude of pests[33]. A second group of volatile secondary metabolites is induced to be synthesized at the affected site after the plant has been harmed by phytophagous insects. This phenomenon, known as induced defenses, can significantly increase resistance to insects. The production of linalool monoterpenoids and (E)-β-farnesene sesquiterpenes by plants serves to counteract the feeding damage caused by phytophagous insects[34]. The composition and content of secondary metabolites in eucalyptus trees damaged by *L. invasa* have undergone a significant transformation, with the emergence of a multitude of novel substances, including terpinolene and 3-phenyl-2-propenyl phenylpropanoate[35]. Furthermore, plants are prompted to synthesize and release volatile secondary metabolites following feeding by phytophagous insects. For instance, as the tea tree is harmed by *Ectropis oblique*, it will release volatiles to attract natural enemies for the prevention and control of the insect pest[36]. The volatile diendiol released from tea trees infected with *E. oblique* demonstrated a strong attraction activity towards the predatory natural enemy, *Evarcha albaria*[37].

Non-volatile chemicals are divided into two categories: those inherent in the plant itself and those induced by insect feeding stress. The first group encompasses a suite of intrinsic, non-volatile, toxic secondary metabolites, including glucosinolates, phenols, nicotine, and furocoumarins. These compounds possess the capacity to directly repel phytophagous pests[38]. The second group is the induced synthesis of non-volatile secondary metabolites. The induced secondary metabolites include flavonoids, tannins, total phenols, and Dimboa, which can be developed as antibiotic substances, repellents, or anti-feedants for use in plant insect resistance[39]. Following insect feeding, eucalyptus leaves undergo an induced defense response, resulting in the synthesis of a number of defense chemicals, including benzenetriol compounds, flavonoids, and tannins[40]. Acylphloroglucinol derivatives derived from eucalyptus can be classified into four distinct groups. The genus *Eucalyptus* contains 38 flavonoids, which are structured as flavones or flavonols and their glycosides, flavanones or flavanonols and their glycosides[41-42]. The leaves of *E. urophylla* × *E. grandis* were found to contain a number of flavonoids, including chlorogenic acid, quercetin-3-O-glucuronide, hyperin, guaijaverin, and quercetin-3-O-α-arabinose-2-gallate[43]. Tannin is one of the more prevalent chemical constituents in Myrtaceae plants. The structural type of tannin is dominated by hydrolysable tannins, with minor contributions from condensed and mixed tannins[44]. The degree of damage, pupation rate, quality of the pupa, and emergence rate of the corn pest *Pyrausta nubilalis* exhibited a positive correlation with the reduction in the content of Dimboa in different corn varieties[45]. Qin Huanju *et al.*[46] revealed that the alkaloid content in tobacco plants exhibited a notable increase following the feeding of tobacco aphids. The aforementioned insect-resistant secondary metabolites have been demonstrated to exert a significant inhibitory effect on insect feeding[25, 47].

3.4 Plant defense enzymes and insect resistance In response to insect stress, plants often exhibit alterations in the activity of relevant defense enzymes, as well as changes in the composition of nutrients within their bodies and the production of secondary metabolites, which collectively initiate defense responses. The primary common defense enzymes are superoxide dismutase (SOD), peroxidase (POD), polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), catalase (CAT), *etc*.

SOD represents the initial and most significant antioxidant enzyme within the plant reactive oxygen species (ROS) scavenging system. When plants are subjected to adversity stress, the excessive accumulation of free radicals in the body will lead to an increase in the level of membrane lipid peroxidation, an increase in the permeability of the membrane, damage to the membrane structure and its function, and ultimately harm to the plant body. SOD is an antioxidant enzyme that can scavenge free radicals in the body. Zhang Jinfeng *et al.* [48] observed an increase in SOD activity and pests resistance in rice plants following infection by *Sogatella furcifera* Lignin, which is synthesized by POD, is the main component of the cell wall and serves as an important barrier against the invasion of pathogenic bacteria. Furthermore, the lignin content is related to insect resistance. A notable surge in the activity of the cassava protective enzyme POD following mite damage can effectively mitigate oxidative damage and thus facilitate mite resistance in cassava[49]. The enzyme PPO, which plays a crucial role in plant resistance, is an important defense enzyme that synthesizes and catalyzes phenolics. Yang Shiyong *et al.* [50] observed that elevated PPO activity in cotton leaves enhanced insect resistance in cotton seedlings. The PAL activity of tobacco leaves infected with tobacco aphids exhibited a rapid increase in activity within a short period of time, indicating the production of defense mechanisms against the aphids[51]. A variety of defense enzymes also interact to work together against insect damage. For example, An Yu *et al.* [52] found that the three antioxidant enzyme activities of SOD, CAT, and POD in poplar showed a significant upward trend after insect feeding.

4 Signal transduction and plant defense against diseases and pests

Insect feeding and infection by pathogenic microorganisms will secrete a considerable quantity of secretions to the area in contact with the plant. These substances contain signaling molecules that will stimulate the plant to produce a series of signaling pathways, stimulate the interlocking reaction of protein kinase and phosphatase, and induce the expression of relevant defense genes, thereby inducing a defense response against diseases and pests. These defensive processes consume a considerable quantity of energy and metabolic substances, thereby establishing a balance between the plant's resistance to diseases and pests and its own growth and development. The cross-interaction of phytohormone signaling pathways represents a crucial mechanism for the fine-tuning of the balance between disease resistance and growth and development. Plant defense signaling molecules include salicylic acid (SA), jasmonic acid (JA), methyl jasmonate (MeJA), and ethylene (ET).

JA is a crucial signaling molecule in the plant defense response to diseases and pests, inducing ISR in plants. The JA signaling pathway is the most dominant pathway for plant insect resistance defense. Following infection by *Manduca sexta*, JA is induced to be synthesized in large quantities in tobacco[53]. JA is generally responsible for regulating the defense response against infection by saprophytic pathogens[54]. Phytoalexin is a crucial chemical that elicits disease resistance responses in plants. Additionally, JA has been demonstrated to impede the proliferation of pathogenic microorganisms by stimulating the synthesis of phytoalexins[55]. SA is also an important defense signaling molecule that can stimulate the salicylic acid signaling pathway, thereby improving plant resistance to diseases and pests. The salicylic acid signaling pathway and the jasmonic acid signaling pathway represent the core pathways of the signaling pathway. These pathways play a critical role in regulating the accumulation of downstream secondary products and stimulating a series of defense responses. The genes responsible for the biosynthesis of SA and those involved in the SA-regulated downstream defense response were found to be upregulated and expressed in *Cucurbita pepo* following infection by *Aphis gossypii*[56]. In response to the infection of pathogenic bacteria, plants accumulate SA in high concentrations around the infection site, where it binds to NPRs (non-expressor of pathogenesis-related genes) receptors. This interaction initiates a hypersensitivity reaction that activates the shikimic acid metabolic pathway and synthesizes PRs (pathogenesis-related proteins) to enhance plant resistance[57]. It has been demonstrated that rice steroid hormones can negatively regulate resistance to brown planthopper in conjunction with the SA and JA pathways[58]. ET exhibited a rapid increase in content following infection, which in turn triggered a plant defense response[59]. The release of ethylene is increased in plants that have been infected with pathogenic bacteria, which can regulate the expression of disease resistance genes or proteins. An increase in the ET content of *Medicago truncatula* and overexpression of the ET-regulated defense genes *B-3ERF* and *MtERF1-1* in *M. truncatula* enhanced the resistance of the plant to the fungal pathogen *R. solani*[60]. In addition to its defensive effects as a signaling molecule, ET can also initiate plant defense responses by acting synergistically with JA[61]. ET is known to regulate plant immunity in a synergistic manner with JA. However, there is also antagonism between SA and JA/ET immune pathways at multiple levels. Nevertheless, there is evidence of synergistic regulation. Furthermore, MeJA treatment has been demonstrated to induce plant defense responses to diseases and pests. For instance, the application of MeJA to *Eucalyptus grandis* seedlings resulted in the induction of significant defense responses in the seedlings. The activities of the relevant defense enzymes were found to be related to the concentration of MeJA and the duration of the treatment. Furthermore, the application of MeJA to *E. grandis* seedlings was found to significantly reduce the population fecundity of *L. invasa*[62].

5 Conclusions and prospects

It is inevitable that plants will encounter diseases and pests during their growth cycle. This results in a dynamic process of defense and counter-defense between plants and phytophagous insects or natural enemies of pests, as well as between plants and symbiotic microorganisms or pathogenic microorganisms in nature. Consequently, an understanding of plant resistance to diseases and pests is crucial for the effective, environmentally conscious, and sustainable prevention and control of diseases and pests in crop production practices.

The advent of global environmental change has resulted in the discovery of novel species of diseases and pests, as well as the emergence of novel physiological races of pathogenic microorganisms. Furthermore, the physiological responses of different plant species or the same species to pathogenic microorganisms or pest feeding stresses during different growth periods are not uniform. Consequently, resistance to diseases and pests also varies. The aforementioned developments have resulted in significant challenges in disease and pest control and prevention, necessitating the formulation of more sophisticated strategies for crop protection in the future. The future of crop protection will undoubtedly be shaped by the continued development of existing technologies and the introduction of new ones. This development must be based on a respect for the laws of nature. (i) Plants have evolved in a synergistic manner in response to diseases and pests, acquiring a complex and efficient natural immune system to defend themselves against these threats. The principle of resistance of the plant's natural immune system can be used to inform agricultural production. (ii) It is recommended that plant breeding for disease and pest resistance should be guided by the physiological response and resistance of plants to disease and pest stress. Furthermore, it is necessary to continuously cultivate and screen new plant varieties that are highly resistant to diseases and pests. (iii) It is possible to induce plants to alter their own tissue structure characteristics in order to resist the damage caused by diseases and insects by exploring exogenous compounds. (iv) RNAi-based prevention and control technologies have the potential to be developed and widely applied to crops in order to resist diseases and pests. (v) The biological functions of plant broad-spectrum resistance genes, agglutinin-like receptor kinases, and activators of signaling pathways for disease and pest resistance can be investigated in order to inform the molecular breeding of crop resistance. (vi) The symbiotic biocontrol bacteria, which originate from plants, phyllosphere, or rhizosphere, and are highly effective against pathogenic microorganisms or pests, can be screened and applied. (vii) The application of an exogenous spray can be investigated as a means of inducing a defense reaction. (viii) The identification of additional volatile secondary plant metabolites may be employed to repel pests or attract natural enemies. The advent of these novel technologies offers a promising avenue for the advancement of the nascent global green revolution in agriculture. By enhancing the comprehensive resistance of crops to diseases and pests, these technologies hold the potential to facilitate the healthy and sustainable development of the agricultural industry.

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