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REVIEW ARTICLE

STRATEGIES OF PLANT BIOCHEMICAL DEFENSES TO PATHOGENS AND INDUCTION OF PLANT DEFENSE APPLIED TO AGRICULTURE: A REVIEW

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ABSTRACT

The current competitive agriculture drives the plant breeders to select genotypes with greater yield potential and responsive to environmental improvements. This targeted selection often does not prioritize the resistance of genotypes against pathogens as the main factor, but agronomic traits that influence greater yield potential. This targeting on the most yield potential of plants is sustained largely by the use of fungicides. However, the frequent use of fungicides causes the selection of pathogens with great aggression potential, endangering agricultural production and creating the necessity of strategies that enable reducing the fungicide use dependence. Genetic resistance, pyramiding resistance genes, and plant defense that involves the activation of defense mechanisms are strategies that help the plant defense against pathogens attack. The objective of this review was to address some of the principal biochemical plant defense mechanisms against pathogens and report some agronomic strategies that are currently reported in the literature to provide plant defense support facing pathogens. Among alternatives to fungicide use, induced systemic resistance in crops is a feasible alternative and current studies are contributing to this new reality.

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INTRODUCTION

Plants are often exposed to biotic and abiotic stresses. Abiotic stress conditions correspond to drought, heat, cold, and salinity, while biotic stress corresponds to the action of bacteria, fungi, viruses, nematodes, and insects. Plants adapting to adverse conditions evolved developing defense mechanisms managed by phytohormones, which allow an adequate stress response (Verma *et al.*, 2016).

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Plant hormones act in growth, development, and reproduction of plants as keys in defense regulation to microbial pathogens. The signaling among these hormones provides plant adaptation to their biotype environment, allowing the use of the necessary resources for growth and survival, taking into account the cost and efficiency in activating the immune system to combat the attack of pathogens and herbivores (Pieterse *et al.*, 2012). In response to the attack of pathogens and pests, plants activate a signaling cascade leading to accumulation of endogenous hormones involved in the defense mechanism. In a wide variety of species, jasmonic acid and ethylene are specific hormones involved in signal communication (Rojo *et al.*, 2003). Moreover, some enzymes are related to plant defense to pathogens, among them the SOD, CAT, POX, PPO, LOX, and

PAL defense proteins (Motallebi *et al*., 2016). Ethylene performs a critical role inplant defense activation against various biotic stresses, participating in complex networks with jasmonic acid, salicylic acid, and abscisic acid (Adie *et al.*, 2007). In general, plants are constituted with a family of enzymes known as superoxide dismutase (SODs), which protect cells against possible consequences caused by O_2cytotoxic reaction, i.e. SODs are the first line of plant defense facing stress(Gill *et al*., 2015).Plants perform constant monitoring regarding the identification of possible microorganism presence, aiming to present an adaptive response to their attack. Generally plants use pattern recognition receptors (PRRs), seeking identification of microorganisms-associated and pathogen-associated molecular patterns (MAMPs/PAMPs). The PRRs are kinases or receptor proteins located in the plasma membrane. The MAMP detection provides a defense program known as MAMP-triggered immunity (Trdá *et al*., 2015). Understanding some basic processes of plant defense mechanisms against pathogens has great importance to develop adequate defense strategies, such as the alternative use of defense strategies aiming to reduce the dependency on fungicide use. Thus, the objective of this review was to address some of the principal biochemical plant defense mechanisms against pathogens and report some agronomic strategies that are currently reported in the literature to provide plant defense support facing pathogens.

Plant Defense Signaling

Hormones and signaling

Plant hormones are the principal signaling components that regulate cell development and function of plants. Furthermore, current research demonstrated the role of hormones in signaling networks that control mitochondrial function and its biogenesis. Mitochondria play an important role in plant metabolism via ATP energy source through oxidative phosphorylation synthesis and other metabolic reactions. These energy blocks generated in the mitochondria provide fuel for the plant responses to biotic and abiotic stresses (Berkowitz *et al*., 2016). Ethylene, jasmonic acid, and salicylic acid are the featured hormonesthat interact in the defense metabolism of superior plants against pathogen attack. The jasmonic acid (JA) and ethylene (ET) act together for the regulation and activation of plant defense mechanisms against pathogens, insects, and herbivores (Lorenzo *et al*., 2002; Does *et al*., 2013; Kazan, 2015). Likewise, salicylic acid (SA) is associated with activation of proteins that assist in plant defense (Glazebrook *et al*., 2005) and acts as a key signaling in response of superior plants. Moreover, JA has importance in response to pathogens diversity in local and systemic (Zheng *et al*., 2012; Kang *et al*., 2014). The levels of JA and AS present variation in levels among plants and also in different tissues within the same plant (Cho *et al*., 2013). Ethylene has controlling action regarding the responses of other plant hormones, such as JA, SA, abscisic acid, auxin, and cytokinin (Guo and Ecker, 2005). The ET in combination with JA is required for the activation of many plant defense genes, particularly with respect to necrotrophic microorganisms. However for biotrophicmicro organisms, ethylene production generally increases plant response to pathogen attack. In addition, ET has a direct relation with leaf senescence (Taiz and Zeiger, 2013). In general, the AS, JA, and ET signaling pathways are very integrated. In some cases, there is the necessity of joint action of AS and JA signaling and in other cases such interaction is negative, where the presence of one hormone inhibits the other. Studying Arabidopsis mutants, Glazebrook *et al.* (2005) found results indicating that in responses of plant defense to pathogens, SA acts against biotrophic microorganisms and JA and ET act in dependence against necrotrophic microorganisms.

Superoxide dismutase (SOD)

If there is nometabolization of reactive oxygen species (ROS), it can occur damage to DNA, proteins, lipids, and other macromolecules until the cell metabolism detention. The superoxide dismutase (SOD) are a family of enzymes that protect cells against possible consequences caused by cytotoxic O_2, catalyzing its conversion into H_2O_2constitutingthe first line of plant defense (Gill *et al.*, 2015). In a study with stress induced by drought and aluminum excess, Pandey *et al.* (2016) indicated that higher levels of SOD, CAT, and GPX oxidizing enzymes occur in tolerant cultivars, showing their activation as a function of time of stress.

Stages of Plant Defense

Responses of hypersensitivity, nitric oxide, and calcium

Plants evolutionarily have developed resistance mechanisms to diseases, such as the production of antimicrobial agents and a type of programmed cell death, known as hypersensitivity response. The hypersensitive response has as a principle the host cells death. This process occurs rapidly, depriving the pathogen from access to nutrients and reducing its spread. This response is in most cases preceded by the production of nitric oxide (NO). Moreover, NO may act as a contributor to hypersensitivity response or directly in the pathogen death. Besides that, calcium enters the cell by the membrane permeability, after potassium exit by activating the R gene, which has an important role regarding the presence of NO. Furthermore, cytosolic calcium is necessary to activate the NO synthase enzyme, since nitric oxide and calcium are required for hypersensitivity response activation (Taiz and Zeiger, 2013).

Biotrophic and Necrotrophic organisms

Throughout its evolution, plants developed perceptual mechanisms tomicro organism attack, which corresponds the recognition in adaptive responses, where the first defenses begins with the activation of antimicrobial compounds at cuticle level. The pathogens that attack plants are divided into pathogens that kill the host (necrotrophic) and those that use the host to complete their life cycle (biotrophic). The necrotrophic pathogens are often followed by the toxin production and biotrophicpathogens are regulated by specific interactions among the pathogen virulence and the host specific gene (Dangl and Jones, 2001).

Phytoalexins and plant defense

Phytoalexinsare secondary metabolites with low molecular weight and antimicrobial activity. They are synthesized following the stress occurrence and are used by plants against pathogens (Ahuja *et al*., 2012). Current and growing researches are aiming to identify the phytoalexin metabolism directed to improve the protection of agricultural crops (Grobkinsky *et al*., 2012).

Lines of plant defense

The plant protection can be divided into two defense lines. Thus, the first line of defense is provided by a system which recognizes large groups of pathogens, where plant receptors recognize the general molecular patterns associated with microorganisms. These MAMPs molecules are recognized by specific receptors and activate a defense response, such as the largephytoalexin production. In a second phase, (second line of defense), an interaction occurs among the gene and the pathogen, which is very specific and referred to as gene-by-gene resistance. In this case, the R plant gene (resistance gene) interacts with derivative products from the pathogen (virulence gene) (Taiz and Zeiger, 2013).

et al., 2012; Dallagnol *et al*., 2015).The host microorganism composition influences the host health and can also be a response from the microorganisms according to the host plant genetic makeup. In a study with *Arabidopsis thaliana*, Haney *et al.* (2015) suggested that small changes mediated by the host may have great effect on the host sanity.

The use of *Trichoderma* spp .in symbiotic relation with plants could cause changes in metabolism by increasing plant growth and plant defense activation to several diseases (Abdelrahman *et al*., 2016). Biological control with microorganisms is a reality, with increasing acceptance in recent years, as an example of the biological control of powdery mildew in cucurbits with the utilization of the UMAF6639 *Bacillus subtilis* antagoniststrain. This antagonist action is based on the production of antifungal compounds, occurring the activation of jasmonate, where defense responses depends on SA, which include the ROS production and strengthening the cell wall (García-gutiérrez *et al*., 2013). The plant defense mechanisms are activated after plant exposure to the induction agent, where the systemic resistance is induced when the agent is beneficial, symbiont, or abiotic (Barro *et al*., 2010). Induced resistance is activated by substances which may prevent or delay the entry of pathogens into body tissues (Costa *et al*., 2010).

Table 1. Strategies for induction of induced systemic resistance against pathogens in several agricultural crops

Agricultural Crops	Pathogens	References
Passifloraedulis	*Xanthomonasaxonopodis* pv. *passiflrae*	Boro *et al*., 2011
Oryzasativa	*Magnaportheoryzae*	Chern *et al*., 2014
Theobromacacao	*Moniliophthoraperniciosa*	Costa J. de *et al*., 2010
Phaseolusvulgaris	*Colletotrichumlindemuthianum*	Freitas M.B. de and Stadnik*et al*., 2012
Brassica rapapekinensis	*Xanthomonascampestris* pv. *campestris*	Liu *et al*., 2016
Zeamays	*Aspergillusflavus* and *A. parasiticus*	Mahapatra *et al*., 2015
Solanumlycopersicum	*Botrytiscinerea*	Martínez-Hidalgo, *et al*., 2015
Solanumlycopersicum	*Botrytiscinerea*	Mehari *et al*., 2015
Glycinemax	*Phakosporapachyrhizi*	Mehta *et al*., 2015
Glycinemax	*Macrophominaphaseolina* and *Phytophthorasojae*	Pawlowski *et al*., 2016
Loliumperenne	*Magnaportheoryzae*	Rahman *et al*., 2015
Triticum spp	*Gaeumannomycesgraminis* var. *tritici.*	Yang *et al*., 2015

Induction of plant defense and its use in agriculture

At present, there is a constant demand for environmentally acceptable alternatives to the excessive use of chemicals for disease control. Thereby, the use of induced resistance can be considered a strategy to boost natural plant immunity (Burketova *et al.*, 2015). Based on the induced systemic resistance, the presence of bacteria and fungi in the rhizosphere privileges the whole plant, improving the plant defenses against attack by bacteria and fungi. Based on mutualistic system, some microorganisms such as *Pseudomonas*, *Bacillus*, *Trichoderma*, and mycorrhiza sensitize the plant defense system without triggering expensive defenses (Pieterse *et al.*, 2014). When plants receive signals caused by injury or abiotic stress, they recognize its potential adversaries and strengthen their defenses against invading pathogens. This process occurs naturally, however these defenses can also be induced by natural or synthetic chemical products (Conrath *et al*., 2015). As a possibility of induced resistance, the use of JA can have positive results for resistance to pathogens (Awang *et al.*, 2015), as well as the use of silicon may ultimately provide resistance by hypersensitivity reaction (Arsenault-labrecque Furthermore, it can also occur by the induction of organic or inorganic compounds or by using microbial products. Several studies on induction of induced systemic resistance in many agricultural crops are found in the literature, as the example of those reported below (Table 1).

Conclusion

Understanding metabolic processes and biochemical pathways related to plant defense strategies to the attack of pathogenic microorganisms has great importance, supporting the development of strategies that reduce or control the causal agent. The use of induced systemic resistance can occur by the induction of organic and inorganic compounds and microbial products acting as an alternative or in an auxiliary way to the fungicide use. Studies for the development of plant defense alternatives to pathogenic organisms associated with constant pursuit of durable genetic resistance, occasioned by the constant pyramiding of pathogen resistance genes, are considered the principal ways to reduce the risk of epidemics caused by high virulence pathogens. Those studies should be constantly performed in order to provide food security to the global population.

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