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*Review*

# Use of elicitors as an approach for sustainable agriculture

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**Plant pathogens are responsible for large declines in agricultural production. Their control is carried out mainly by chemical and frequently proposed biological methods to reduce their environmental impact. On the other hand, plant-pathogen or microbe interactions generate multiple signals within plants activating defense mechanism, some of which can also be induced by elicitors (protective molecules). Elicitor-induced plant signaling serves as a guide to a series of intracellular events that end in activation of transduction cascades and hormonal pathways triggering induced resistance (IR) and consequently activation of plant immunity to environmental stresses. So, it is necessary to understand where and how elicitors act in cellular defense mechanism of crops, to improve protection and management for sustainable crop. Therefore this review focused on main topics that guide induced resistance and therefore activation of plant immune response.**

**Key words:** Elicitors, defense mechanism, Immune response, Induced resistance, MAPK.

## INTRODUCTION

Pathogens are responsible for much decline in agricultural production and their fight is done primarily by chemical and frequently proposed biological control methods as alternatives to pesticides to reduce their environmental impact (Agrios, 2005; Suzuki et al., 2005; Verhagen et al., 2006; Buonaurio et al., 2009). Significant progress has been made in understanding the molecular mechanisms governing resistance to plant diseases and therefore could reduce pesticide use, which would conserve energy and provide farmers with new opportunities for sustainable disease control (Hammond-Kosack and Parker, 2003). Various practical applications, such as use of transgenic crops, tissue culture, seed treatment, etc, have allowed exploiting these intrinsic resistance mechanisms (many of them dependent on the generation of active oxygen species) to reduce pesticide applications and synthetic regulators (Benavides-Mendoza, 2002).

However, modern approaches to agricultural

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**Abbreviations: SAR,** Systemic acquired resistance; **ISR,** induced systemic resistance; **SA,** salicylic acid; **JA,** jasmonic acid; **ET,** ethylene; **MAPK,** mitogen-activated protein kinase; **MAPKK,** MAPK kinase; **MAPKKK,** MAPK kinase kinase; **ETI,** effector-triggered immunity; **HR,** hypersensitive response; **PR,** pathogenesis related.

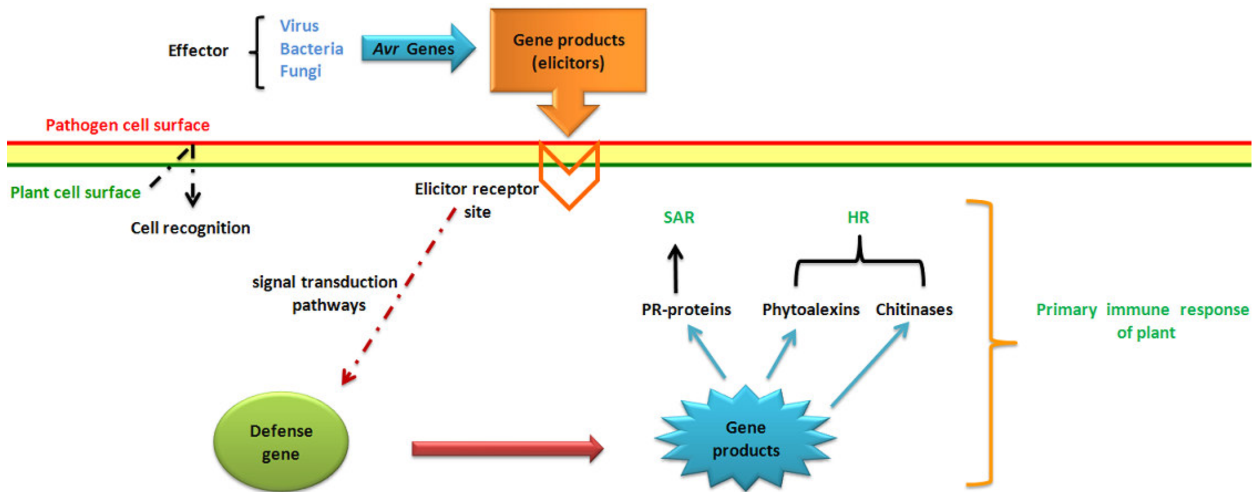


**Figure 1.** Primary immune response of plant in plant-pathogen interaction

production include application of signaling mechanisms of stress as a strategy to increase tolerance of plants against various environmental factors (Walters et al., 2007; Takatsuji et al., 2010). These new control strategies arise because environmental stress is a serious constraint to increase productivity and expansion of crops, since it is estimated that only 10% of the arable land area is free of stress (Benavides-Mendoza, 2002; Verhagen et al., 2006; Buonaurio et al., 2009).

## IMMUNE SYSTEM OF PLANTS

Most of the microorganisms associated with plants are pathogens that impair plant growth and reproduction of same, so plants usually respond to infection using innate immune system (Jones y Dangl, 2006). Plants recognizes and respond to common molecules of various kinds of microorganisms, including non-pathogenic and pathogenic avirulence factors that are recognized directly or through their effects on host (Jones y Dangl, 2006). However, resistance often differs in speed and intensity of defense response according to the microorganism which concerned (Taiz and Zeiger, 2006). In general, "immunity" refers to physiological state of having sufficient biological defenses to avoid infection, disease or unwanted biological invasion. This definition applies to all multicellular eukaryotic systems, and is appropriate to describe ability of plants to cope with microbial infections as "immune" response (Jones y Dangl, 2006; Zipfel et al., 2008; Castro-Mercado y García-Pineda, 2009). Therefore, plant primary immune response is defined as immunity triggered by recognition of invariant structures of microbial surface called pathogen or microbes-associated molecular patterns (PAMPs / MAMPs) through receptor proteins called pattern recognition receptors (PRRs), which are important to guide immunity to microbial infection in all plant species (Chisholm et al., 2006; Jones y Dangl, 2006; Bittel and Robatzek, 2007; Castro and García, 2009; Boller and Felix, 2009; Postel and Kemmerling, 2009). PAMPs are typically essential components of whole classes of pathogens, such as bacterial flagellin or fungal chitin. Plants also respond to endogenous molecules released by pathogen invasion, such as cell wall or cuticular fragments called danger-associated molecular patterns (DAMPs) (Lotze et al., 2007; Matzinger, 2007; Zipfel et al., 2008; Postel and Kemmerling, 2009). Stimulation of PRRs leads to PAMP-triggered immunity (PTI) (Dodds and Rathjen, 2010). Intracellular responses associated with PTI include rapid ion fluxes across the plasma membrane, MAP kinase activation, production of reactive-oxygen species, rapid changes in gene expression and cell wall reinforcement (Zipfel, 2008). Besides PTI, a second class of perception involves recognition by intracellular receptors of pathogen virulence molecules called effectors, this recognition induces effector-triggered immunity (ETI) (Postel and Kemmerling, 2009; Dodds and Rathjen, 2010).

This mode of recognition leads to co-evolutionary dynamics between plant and pathogen that are quite different from PTI as, in stark contrast to PAMPs, effectors are characteristically variable and dispensable (Dodds and Rathjen, 2010). Generally, PTI and ETI give rise to similar responses, although ETI is qualitatively stronger and faster and often involves a form of localized cell death called the hypersensitive response (HR) (Zipfel, 2008). PTI is generally effective against non-adapted pathogens in a phenomenon called non-host resistance, whereas ETI is active against adapted pathogens (Figure 1). However these relationships are not exclusive and depend on elicitor molecules present in each infection (Zipfel, 2009; Boller and Felix, 2009; Dodds and Rathjen, 2010). Recent studies indicate that this system can be activated by elicitors, besides already known systems of plant defense in which also participate (Postel and Kemmerling, 2009).

## BIOTIC STRESS IN THE PLANT

Stress is usually defined as an external factor that exerts an alteration in plant homeostasis initiating a set of biochemical or physiological responses that define a particular state of the organism different to that observed under a range of optimal conditions (Benavides-Mendoza, 2002; Peters et al., 2004; Susuki et al., 2005; Taiz and Zeiger, 2006). Therefore biotic stress is defined as stress that occurs as a result of damage done to plants by other living organisms, such as bacteria, viruses, fungi, parasites, harmful insects and weeds (Peterson and Higley, 2001; Fujita et al., 2006). Stress response is initiated when plants recognize stress at cellular level, activating signal transduction pathways that transmit information within individual cell and throughout plant, leading to changes in expressing of many gene networks (Gorovits and Czosnek, 2007). Biotic stress is a main factor that prevents extend range of crops in certain species as well as increase yields and crop quality, so adaptation and acclimation to environmental stresses result from integrated events occurring at all levels of organization, from anatomical and morphological level to cellular, biochemical, and molecular level (Benavides-Mendoza, 2002; Taiz and Zeiger, 2006).

At cellular level, interactions of plant cells with both symbiotic and pathogenic organism trigger a range of highly dynamic plant cellular response. This include reorganization of cytoskeleton, organelle translocation, vesicle trafficking and alterations in subcellular protein localization. Besides changes in cell cycle and cell division, changes in cell wall architecture, endomembrane system and vacuolization of cells, lead to enhanced stress tolerance of cells (Lipka and Panstruga, 2005). At biochemical level, plants alter metabolism in various ways to accommodate environmental stresses, including producing osmoregulatory compounds such as proline and glycine betaine (Taiz and Zeiger, 2006). The molecular events linking perception of a stress signal with the genomic responses leading to tolerance have been intensively investigated in recent years (Lipka and Panstruga, 2005; Susiki et al., 2005).

## BIOTIC STRESS TOLERANCE

The concept of stress is closely associated with stress tolerance; that is, an ability of the plant to cope with some success to unfavorable environment and remain under a particular state of stress without suffering significant changes in their phenotype (Benavides-Mendoza, 2002; Fujita et al., 2006; Mittler, 2006; Taiz and Zeiger, 2006). Under this context, agricultural research has focused in recent years to study relationship between induction of signaling pathways and response of plant defense to environmental stress. This due to relationship between biotic stress and plant yield affects directly in economic decisions as well as practical development (Roberts et al., 2002; Suzuki et al., 2005; He et al., 2007; Gorovits and Czosnek, 2008). The impact of biotic injury on crop yield impacts population dynamics, plant-stressor coevolution and ecosystem nutrient cycling (Peterson and Higley, 2001).

## ELICITORS

Plants treated with elicitors generally develop resistance to host, because application of elicitors on plant surface activates multiple signaling pathways of intracellular defense (Odjacova and Hadjiivanova, 2001; Garcia-Brugger et al., 2006; Bent and Mackey, 2007; Holopainen et al., 2009). Elicitors are very stable molecules that induce an immune defense response in plants, they have low molecular weight and synthesized as such or released from polymeric precursors during infection (Ozeretskovskaya and Vasyukova, 2002; Zhao et al., 2005; Boller and Felix. 2009; Holopainen et al., 2009). In a broad sense, “elicitors”, for a plant refer to chemicals from various sources that can trigger physiological and morphological responses and phytoalexin accumulation. Their variability is less than the rest pathogens, which have been "chosen" by plants and animals as "telltale signs" of different groups of pathogens (Somssich and Hahlbrock, 1998; Ozeretskovskaya and Vasyukova, 2002; Zhao et al., 2005; Dodds and Rathjen, 2010). Elicitor needs to be recognized on plant by a receptor (protein), which activates the expression of defense genes. There are two groups of elicitors, the biogenic and abiogenic. On one hand, Biogenic Elicitors are divided into two groups, exogenous and endogenous. The exogenous are isolated from pathogens or culture medium, while endogenous tissue are isolated from same plant (Ozeretskovskaya and Vasyukova, 2002; Zhao et al., 2005; Bent and Mackey, 2007). On the other hand, the abiogenic elicitors are heavy metal ions, inhibitors of certain metabolic stages, UV radiation, some kinds of antibiotics and fungicides (Ozeretskovskaya and Vasyukova, 2002). Compared with biogenic, abiogenic elicitors induce defense reactions of plant when given in relatively high doses. In turn, the biogenic elicitors are active at very low doses. When applied, they cause no symptoms of demand and stress accumulation of toxic compounds that sensitize the plant tissue and improve their resistance to subsequent infections (Ozeretskovskaya et al., 1994; Ozeretskovskaya and Vasyukova, 2002; Bent and Mackey, 2007; Boller and Felix. 2009).

The chemical structure of elicitors is comprised of glycoproteins, polypeptides, oligosaccharides, polysaccharides, compounds that contain lipids or other compounds (Odjacova and Hadjiivanova, 2001). Some proteins are elicitors, directly produced by pathogenic bacteria or fungi, while the biologically active oligosaccharides are released from pathogen and plant cell wall hydrolases secreted by both organisms. This method of induced resistance by elicitors is characterized primarily by some advantages: A) Ecological security. B) Has a prolonged systemic effect. C) Participation of multiple defense systems in induced resistance. D) Induction of nonspecific resistance to various pathogens (Ozeretskovskaya and Vasyukova, 2002; Zhao et al., 2005; Dodds and Rathjen, 2010). Therefore, it is important to learn how plants perceive the presence of pathogens and initiate defense.

## SIGNALING EVENTS PRODUCED BY BIOTIC STRESS AND ELICITORS

As described above, both environment and elicitors guide to a series of intracellular events with purpose of triggering and enhance the plant primary immune response and in both cases, molecular recognition is needed to start signaling pathway. Early cellular events associated with both PTI and ETI, such as protein phosphorylation or activation of plasma membrane proteins, mobilize or generate directly or indirectly diverse signaling molecules such as rapid influx of calcium ions from external stores, nitric oxide (NO), burst of active oxygen species (AOS) (Garcia-Brugger, et al., 2006; Castro and Garcia, 2009; Postel and Kemmerling, 2009; Dodds and Rathjen, 2010). All these responses are known essentially as correlative phenomena because it regulates many processes, interconnecting branch pathways that amplify and specify physiological response through transcriptional and metabolic changes (Dodds and Rathjen, 2010). Particularly, the early activation of genes involved in phytohormone biosynthesis modifies the hormonal balance, leading to appropriate transcriptomic changes (Garcia-Brugger, et al., 2006). In addition, mitogen-activated protein kinase (MAPK) pathways are ubiquitous signal transduction components that transfer signals from extracellular receptors to cellular responses in eukaryotes, and serve as highly conserved central regulators of growth, death, differentiation, proliferation and stress responses (Nakagami et al., 2005; Fiil et al., 2009; Dodds and Rathjen, 2010). A MAPK cascade typically consists of a modular complex consisting of a MAPK kinase kinase (MAPKKK), which phosphorylates a MAPK kinase (MAPKK), which phosphorylates a MAPK (Nakagami et al., 2005; Saucedo and Gavilanes, 2005; Garcia-Brugger et al., 2006; Vlot et al., 2009; Dodds and Rathjen, 2010). These pathways regulate activity of various substrates, such as transcription factors and protein kinases. Importantly, MAPK cascades have been implicated in both PTI and ETI and gene expression signatures in the latter are largely similar, suggesting that responses are same overall but vary in magnitude (Tao et al., 2003; Pitzschke et al., 2009).

The salicylic acid (SA) and jasmonic acid (JA), ethylene (ET) hormone pathways are important regulators of defense-gene expression (Bari and Jones, 2009). This pathways act antagonistically, SA is involved in resistance to biotrophic pathogens and JA–ET are involved in responses to necrotrophic pathogens and chewing insects. However, although there are substantial differences in gene expression outputs of these pathways, and several genes act as specific markers for the activation of either SA or JA–ET pathways, there is also considerable overlap between them (Vlot et al., 2009; Dodds and Rathjen, 2010). Arabidopsis thaliana, Nicotiana tabacum and Medicago sativum are examples in which plant MAPK pathways components have been suggested to function in different combinations in various biological contexts (Nakagami et al., 2005). Depending on stimulus, a given plant MAPKK can interact and activate several different MAPKs (Cardinale et al., 2002). Zhang and Yang (2001) showed that ectopic expression of SIPK was sufficient to yield active MAPK and induce HR, whereas ectopic WIPK expression yielded neither activated kinase nor HR. On the other hand, Tsuda et al. (2009) showed that salicylic acid and JA–ET pathways act synergistically in PTI to amplify response and even in absence of SA signalling, JA–ET response contributes to maintaining a substantial level of pathogen resistance. Therefore, these compensatory interactions may simply result from higher signal flux in ETI, and probably make this response more robust against pathogen interference (Dodds and Rathjen, 2010). So far, it is known that group A MAPKs of different plant species has been implicated in response to different elicitors (Ortiz-Masia, 2007). In Arabidopsis thaliana there were identified all members of MAP kinase pathway that is activated after receptor FLS2 recognizes elicitor flageline22 (flg22) (Asai et al., 2002).

Treatment of *Arabidopsis thaliana* protoplasts with flg22 resulted in activation of a MAP kinase cascade composed of AtMEKK1, AtMKK4 / 5 and AtMPK3 / 6 resulting in activation of transcription factors WRKY (Asai et al., 2002). On the same system it was found that components MPK4, MPK6 of MAPK cascade are activated by stress to cold, salinity, drought, wounding and touch (Ichimura et al., 2000), and MPK3 can also be activated by osmotic stress (Droillard et al., 2002). On the other hand, ROS and AOS are also versatile signaling molecules that mediate gene responses to developmental cues as well as abiotic and biotic environmental stresses (Apel and Hirt 2004; Laloi et al., 2004). Also lead signal transduction pathways induced by pathogens or elicitors and AOS participated in MAPK activation, generation of $Ca^{2+}$ variations and modifications of the cellular redox state; these last two events usually were monitored after $H_2O_2$ accumulation (Rentel and Knight

**Table 1.** Relationship between the mechanisms of induced resistance.

| | Systemic acquired resistance (SAR) | Systemic induced resistance (ISR) |
|---|---|---|
| Differences | Induced by pathogens and / or chemical Accumulation of SA and PR. | Induced mainly by non-pathogenic biological agents. Do not cause accumulation of SA and PR.<br>Use Regulated Pathways JA, ET.<br>Powered by plant growth promoting rhizobacteria (PGPR). |
| Similarities | Ability to repel cell subsequent attacks. Induction of nonspecific resistance. Systemic and prolonged effect. Activation externally. The strength and stability of the RI for several weeks may be influenced by factors such as climatic conditions and nutrition. | |

**Table 2.** Example of elicitors used in induced resistance for control of plants diseases

| Disease | Causal agent | Crop | Inducer | Reference |
|---|---|---|---|---|
| Fusarium wilt | *Fusarium oxysporum* f. sp. melonis | Melon | Methyl jasmonate | Buzi et al., 2004 |
| Powdery mildew | *Blumeria graminis* f. sp. hordei<br>*Erysiphe necator* | Barley<br>Grape | ASM, Chitosan<br>Chitosan | Faoro et al., 2008<br>Iriti et al., 2008; Vitalini et al., 2009 |
| Blister blight | *Exobasidium vexans* | Tea | ASM, SA | Ajay and Baby, 2010 |
| Pill bugs root-attack | *Armadillium vulgare* | Lettuce | SA, JA | Tierranegra-Garcia et al., 2010 (submitted) |
| Fusarium head blight | *Fusarium graminearum* | Wheat, barley, also colonize *Arabidopsis thaliana*. | SA, JA | Makandar et al., 2010 |

2004).

## PLANT DEFENSE MECHANISMS: ISR AND SAR

Generally, plant defense mechanisms are based on prevention, tolerance or resistance (Thakur, 2007). These mechanisms are activated in different ways, depending on the type of pathogens attacking the plant (or biotrophes appearing necrotrophic) (Jalali et al., 2002). Such mechanisms may be constitutive or induced. The first provides protection of initial invasion of a pathogenic agent by physical barriers or preformed biochemical. Whereas induced resistance is only activated as a response to pathogen attack (Cruz-Borruel, et al., 2006). Activation of an effective defense by plant is based on speed with which it can recognize the pathogen (Fornoni et al., 2004). This is achieved through the activation signals induced by non-specific elicitors and specific compounds that are first recognized by the plant to activate signaling cascade and therefore defense response (Ebel and Cosio, 1994).

Timing of these defense responses is critical and can be the difference between being able to cope or to succumb to the challenge of a pathogen or parasite. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are two forms of induced resistance (Table 1). Both SAR and ISR are preconditioned by prior infection or treatment that results in resistance (or tolerance) against subsequent challenge by a pathogen or parasite (Vallad 2004). This phenomenon has been intensively investigated regarding to underlying signaling pathways as well as to its potential use in plant protection. Elicited by local infection, plants respond with a salicylic-dependent signaling cascade that leads to systemic expression of a broad spectrum and long-lasting disease resistance that is efficient against fungi, bacteria and viruses (Heil and Bostock, 2002).

Changes in cell wall composition, de novo production of pathogenesis –related-proteins such as chitinases and glucanases, and synthesis of phytoalexins are associated with resistance, although further defensive compounds are likely to exist but remain to be identified (Heil and Bostock, 2002; Yoder and Scholes, 2010). The protective effects of induced resistance (IR) have been evaluated in both monocotyledonous and dicotyledonous plants. Some examples of IR application for control of plant diseases are given in Table 2, with the most used inducers being AS, chitosan and methyl jasmonate and acibenzolar-S-methyl (ASM), a photostable functional analogue of salicylic acid (SA) that is associated with accumulation of SA and pathogenesis related (PR) proteins, and is dependent from the regulatory protein NPR1 (non-expressor of PR-genes 1) (Durrant and Dong, 2004).

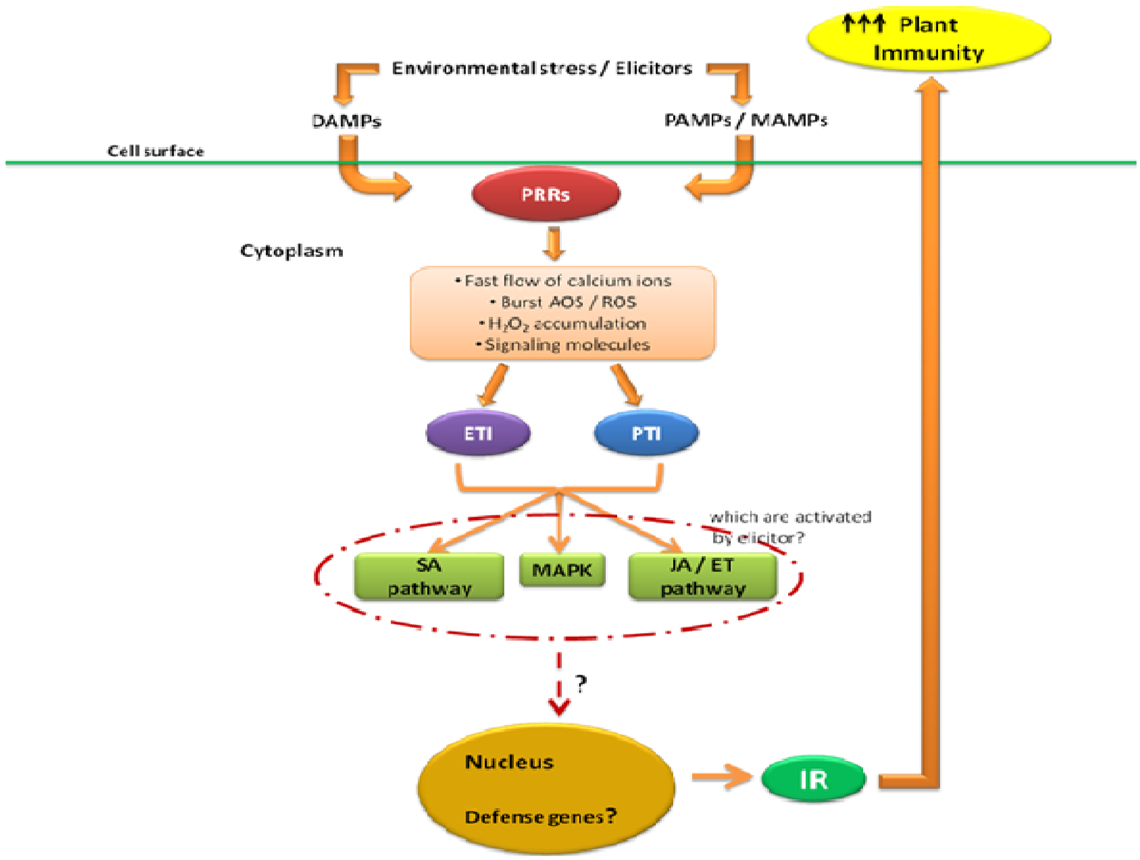


**Figure 2.** Proposed scheme in activation-induced resistance by elicitors in the *Capsicum* spp system.

## CONCLUSION

Plant diseases caused by biotic stress are primarily responsible for considerable losses in the current performance of agricultural production, and control is mainly based on application of agrochemicals and resistance breeding (Verhagen et al., 2006). Control strategies are directed against a single or a small group of plant pathogens, so induced disease resistance is an attractive alternative of plant protection, as it is based on the activation of resistance mechanisms in plant and is effective against a broad spectrum of plant pathogens (Kuc, 2001; Van der Ent et al., 2008; Ajay and Baby, 2010). As mentioned earlier, induced response is mainly activated by elicitors (biotic or abiotic) which guide to multiple plant signaling pathways (Van der Ent et al., 2008; Pieterse et al., 2009; Buonaurio et al., 2009). Pathways such as JA, ethylene and SA regulate defense response against elicitor or various stresses, modulating for instance, biosynthesis of defensive compounds which should be a combined result from multiple signaling actions (Zhao et al., 2005). Induced response is still a relatively new concept and an underestimated resource in plant-disease management. Despite a large number of biotic and abiotic elicitors are now known for IR to pathogen infections in plants, including oomycetes and fungi, only some of these are used for crop protection in practice (Schreiber and Desveaux, 2008). Accordingly the efficacy of IR in field is variable, as it can be influenced by environment, genotype, crop nutrition and extent to which plants have already been induced (Walters and Fountaine, 2009). Plant adaptation to environmental stresses is controlled by cascades of molecular networks. These activate stress-responsive mechanisms to re-establish homeostasis and to protect and repair damaged proteins (Wang et al., 2005). Also, even as it is known in Arabidopsis the site of action of flg22 and inductive response genes that are activated upon recognition of the elicitor to generate IR (Asai et al., 2002). However, it is necessary to understand where and how elicitors act in cellular defense mechanism of crops, as well as which genes are activated in response to SA, peroxide or other elicitors. For example, in studies with Capsicum spp, it has been suggested part of the cellular defense mechanism to enhance the IR involved, but it is necessary more detail in what are the defense genes activated by elicitors and thus generate immunity of the plant (Anaya-Lopez et al., 2005; Barrera-Pacheco et al., 2008; Gasca-Gonzalez et al., 2008) (Figure 2). Therefore, to evaluate efficiency of elicitors in inducing resistance to different biotic and abiotic stress of Capsicum spp in natural environment conditions, it could be elucidated possible answers to the above issues and propose improved sustainable control strategies, as well as reducing agrochemicals in crops of commercial interest, in order to obtain better yields and especially a more economical way for farmers and environmentally friendly agriculture.

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