JOJ Horticulture & Arboriculture
ISSN: 2641-8215

Mini Review
Volume 2 Issue 5 - June 2020
DOI: 10.19080/JOJHA.2020.02.555600

JOJ Hortic Arboric

Elicitors and Plant Defence

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Submission: May 21, 2020; **Published:** June 15, 2020

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Abstract

Pest and disease control in agricultural crops include the use of chemicals which could be hazardous for people and environment. The obtainment of resistant genotypes as well as development of new strategies more environmentally friendly, seems to be of high priority in a sustainable agriculture. The use of elicitors to induce a faster and stronger defence response in plants seems to be a promising alternative. In this review, the different type of elicitors according to nature (physical or chemical), origin (biotic or abiotic) or structure (complex or well defined) are indicated. An insight into the complexity of the action mechanism, from perception at plasma membrane to the appearance of defence related products (phytoalexins and PR proteins, among others), as well as the evaluation of factors determining the success of elicitation are included. Finally, the priming process and its epigenetic basis, cross-factor priming and its possible use to improve disease management on commercial fruit orchards and the possibilities that transgenerational priming offers as a breeder´s tool, are discussed.

Keywords: Disease control; Improved plant response, Stress exposure, Priming,

Abbreviations: AVR: Avirulent Gen; BABA: β-Aminobutyric Acid; CGMP: Cyclic Guanosine Mono Phosphate; cADPR: Cyclic Adenosine Diphosphate-Ribose; MeJA: Methyl Jasmonate; NAC domain: N-terminal 160 Aminoacids domain; NPR1: Non-Expressor of Pathogenesis-Related gene 1; PR: Pathogenesis Related gene; PR1: Pathogenesis Related 1 gene; qRT-PCR: quantitative Reverse Transcription Polymerase Chain Reaction; R: Resistance gene; RD1 & RD2: Rice Drought responsive genes 1 and 2; SA: Salicylic Acid; SAR: Systemic Acquired Resistance; StWRKY1: *Solanum tuberosum* WRKY 1; UV-B: Ultraviolet-B radiation

Introduction

Plants are continually exposed to different stress factors which could be either biotic (bacteria, fungi, viruses, insects, herbivores and oomycetes) [1,2] or abiotic (heavy metals, salinity, ozone, UV-B radiation, extreme temperature, excess or lack of nutrients, drought) in nature [3]. These factors cause general damage in plants and economically important losses in cultivated land [4]. To counteract these problems, several approaches are being undertaken including the use of physical (solarization, culture rotation) chemical (pesticides or fungicides) or biological control (antagonist microorganisms) methods as well as development of resistant genotypes [5]. Moreover, damage caused by the use of previous approaches on people, plants, animals and environment is of great concern to general public; ca. use of pesticides is linked to residues accumulation in water and soil, harmful to human health and environment while use of physical methods such as tillage is linked to erosion problems [6]. In this scenario, there exists an increasing demand for alternative approaches, more environmentally friendly, and the use of elicitors appears as an interesting biological alternative.

Elicitors

Elicitors are either molecules or compounds which upon application to the plant induce important physiological changes; ca. similar mechanisms to those appearing in plant responses to pathogens or environmental stress are initiated, affecting plant metabolism and enhancing the biosynthesis of secondary metabolites [7,8]. According to Zheng [6] use of elicitors has several advantages over other approaches, e.g., they are non-toxic and environmentally friendly, and more important, small amounts are enough to provide the plants with long time protection to a wide range of pathogens.

Classification

There are different ways to classify elicitors. In accordance to Radman [9] they could be divided into physical or chemical, biotic or abiotic and complex or well defined, considering nature, origin or molecular structure. Vasconsuelo & Boland [1] when studying elicitation to increase production of secondary metabolites under *in vitro* conditions and Baenas [7], in their review of elicitation as tool to increase content of bioactive compounds, emphasize the importance of origin and classify elicitors into biotic (exogenous, those of biological origin appearing as result of fungal, bacterial or virus infections, or endogenous, produced by the plant as result of pathogen attack) or abiotic (physical or chemical) and plant hormones. Another way of classification would be considering the relation between plant and elicitor, considering general elicitors as those inducing unspecific defence mechanisms in different crops and specific elicitors only affecting a determinate host [1,7]. An overview of elicitors classification can be found in (Figure 1).

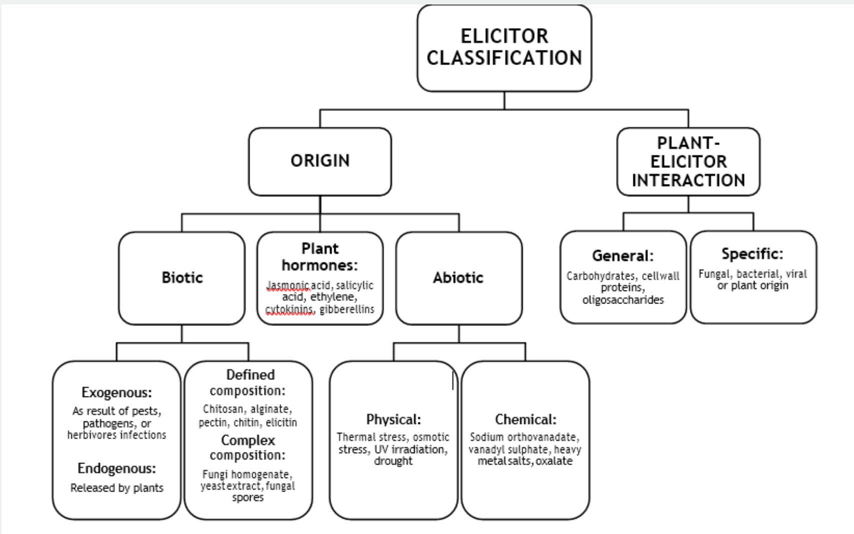

Figure 1: Elicitor classification in accordance to origin or the interaction plant-elicitor. Adapted from Vasconsuelo & Boland [1], Baenas [7] and Radman [9].

Mechanisms of action

Generally, the first step in elicitor signaling would be its detection by receptors located in plasma membrane: moreover, since elicitors can have very different chemical structures, they will show rather different effects depending upon the species in question [1]. Various receptors for elicitors with different structures have been identified so far; it appears that the interaction between plant resistance genes products acting as receptors for AVR (pathogen avirulent gen) merits special consideration to understand response to elicitors [10]. At the same time, a given elicitor could induce responses in different plants, indicating that common receptors should exist in different systems [11]. Signal transduction does not follow a simple model but rather a heavily branched one, where different secondary messengers (free calcium, active oxygen species, cytosolic pH, nitrogen oxide, cGMP and cADPR, among others) interact in each branch. Appearance of profound changes in pentose phosphate pathway and Krebs cycle are indications of serious effects on cell behavior; ca. triggering defence response is often associated with induction of abiotic stress in the cell [10,11]. In any case, activation of signal transduction pathways results in production of phytoalexins, strengthening of cell wall through callose deposition as well as accumulation of pathogenesis related proteins (PR) [2,5,8], with specificity of the response relying on the role played by different secondary messengers and the appearance of targeted proteins at specific times and places [10]. Complexity of the integrated response, cumulative data from the different signaling pathways and their occurrence in different plant species, requires use of computer analysis to integrate at cell level the role played by specific components [10,12].

Although elicitors were initially used to activate plant defence mechanisms, it was observed that, in many cases, elicitation was linked to accumulation of secondary metabolites of great interest in pharmaceutical, cosmetic and agro-food industries [13]. In a recent review, Giri & Zaheer [14] reported that metabolite accumulation could increase in the range 1-2230-fold following elicitor application to *in vitro* cultures (callus, cell suspensions, roots, shoots). Moreover, in postharvest treatments, elicitors can increase nutritional value in grapes (enhanced antioxidant properties) [15] or shelf life, in horticultural crops [16, 17] as well as in ginseng roots [18].

Factors affecting the elicitation process

Plant-elicitor interaction is a rather complex phenomenon and its success will depend upon numerous factors [1,13]. Initially, elicitor specificity merits to be considered, ca. a plant can show positive responses to different elicitors while a given elicitor could induce defence reactions in different plants. Elicitor concentration

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is another important factor to be taken into account; ca. Jesús [19] found that foliar treatments with Salicylic Acid (SA) (0,75-5 mM) increased drought tolerance in *Eucalyptus globulus* and this effect was dependent on the dosage applied, highest dosage being more effective. Similar effects had previously been observed by Singh & Usha [20] in wheat seedlings, where decreased transpiration rate and improved photosynthesis were linked to improved behaviour under water stress conditions. A decrease in transpiration rate was also observed following applications of chitosan to basil plants, improving behaviour under drought stress [21]. Time and frequency of application are also key factors to be considered when optimizing elicitor effects in plant response, with application frequency being linked to persistence of the response. Culture type and growing conditions will determine the most appropriate application method. In accordance to Rohwer & Erwin [22], Methyl Jasmonate (MeJA) could be applied as a gas [23], mixed with lanolin paste [24], in liquid form [25] or, most commonly, as spray with a surfactant agent [26].

Priming

Following elicitation or plant exposure to a stress situation induces physiological changes in such a way, that plant will show a faster and stronger response when exposed to subsequent stress conditions (priming). Stress exposure or elicitor treatments generally induce modifications in histone proteins at defence related genes, suggesting an epigenetic base of the priming mechanism [27,28]. Along this line, investigations being carried out by our group within the pathosystem *Persea americana* (avocado) and the soilborne pathogen *Rosellinia necatrix* (causal agent of White Root Rot), have shown that application of either SA or MeJA (5mM) to plants prior to fungal inoculation induced a 15 day delay, in plant death. Moreover, qRT-PCR quantification of the defence protease inhibitor gene, showed a 4- and 5-fold increases following elicitation with salicylate and jasmonate, respectively, in root samples after 12 hours (Clara Pliego, IFAPA-Málaga, unpublished results, May, 18, 2020). Previous investigations, also in avocado plants, had shown that exposure to mild water stress improved plant response to White Root Rot (cross-factor priming) [29]; the improved performance of avocado plants was linked to a general increased expression of plant defence genes, in particular those coding for NPR1 protein and NAC domain containing protein 72, leading these authors to conclude that adequate irrigation management could be an useful strategy to control fungal infections in commercial avocado orchards. In rice, Samota [30] observed that seed elicitation with methyl jasmone induced changes in expression of drought responsive genes RD1 and RD2 and plants derived from the elicited seeds would respond better to water stress than those from control seeds. It has also been shown that stress-induced epigenetic changes occurring during the seed formation process could be transmitted to the progeny (transgenerational stress memory) [27, 31, 32]. Along this line, Slaughter [33] observed that seed progeny of *Arabidopsis* plants, treated with an avirulent strain of *Pseudomonas syringae* pv tomato, showed an enhanced resistance to a virulent strain while Luna [34] found a higher expression of SAR genes in *Arabidopsis* plants exposed to a virulent strain of the same bacteria, *Pseudomonas syringae* pv tomato DC3000. Seed progeny showed enhanced tolerance to this bacterial strain and to the hemi biotrophic fungus *Hyaloperonospora arabidopsidis* while it was more susceptible to the necrotrophic pathogen *Alternaria brassicicola* In the woody perennial *Quercus ilex*, seedlings derived from acorns collected from trees infected with *Phytophthora cinnamomi* under field conditions, showed a better response following artificial inoculation with the oomycete [35]. The tuber or seed progeny from β-Amino Butyric acid (BABA) elicited potato, showed an enhanced resistance to *Phytophthora infestans*, linked to methylation changes in the R3a resistance gene as well as other SA dependent genes (NPR1, StWRKY1, PR1) [36]. Similar results were obtained by Ramirez-Carrasco [37], also with the BABA elicitor in *Phaseolus vulgaris*, ca. seed progeny showed enhanced resistance to *Pseudomonas syringae* pv. phaseolicola. In this case, increased resistance was linked to an enhanced expression of *Phaseolus vulgaris* PR1, a highly responsive gen to elicitation. These results led Ramirez-Carrasco [37] to recommend elicitation as a tool to be used for breeders by priming plants in the field and selecting induced heritable states in the progeny.

Conclusions

Use of elicitors have become an important tool to gain knowledge on defence responses in plants; at the same time, they can be used to improve plant response to stress situations in an environmentally friendly way. Moreover, the occurrence of cross-factor priming offers an interesting alternative to manage pest and diseases in commercial plantings while transgenerational priming appears as an important tool to be used by plant breeders for increasing resistance to biotic and abiotic factors through selection of induced heritable states in the progeny of primed plants.

Acknowledgments

C Pliego is currently supported by an INIA-CCAA contract, co-financed by INIA 16 (20%) and FEDER (80%). A. Moreno-Pérez is financed by a PhD FPI-INIA (RTA2017-00040-00) contract cofinanced by FSE. Part of the results included in this review have been carried out in the frame of projects RTA2017-00040-00 and AVA2019.008.

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How to cite this article: Moreno-Pérez A, Martínez-Ferri E, Pliego-Alfaro F, Pliego C. Elicitors and Plant Defence. JOJ Hortic Arboric. 2020; 2(5): 555600. DOI:10.19080/JOJHA.2020.02.555600.

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How to cite this article: Moreno-Pérez A, Martínez-Ferri E, Pliego-Alfaro F, Pliego C. Elicitors and Plant Defence. JOJ Hortic Arboric. 2020; 2(5): 555600. DOI:10.19080/JOJHA.2020.02.555600.

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