LUMEN ET VIRTUS
ISSN: 2177-2789

UNDERSTANDING THE EFFECTS OF ELICITORS ON SECONDARY METABOLITES BIOSYNTHESIS IN PLANTS

COMPREENDENDO OS EFEITOS DOS ELICITADORES NA BIOSSÍNTESE DE METABÓLITOS SECUNDÁRIOS EM PLANTAS

COMPRENDIENDO LOS EFECTOS DE LOS ELICITADORES EN LA BIOSÍNTESIS DE METABOLITOS SECUNDARIOS EN PLANTAS

https://doi.org/10.56238/levv17n58-073

Submitted on: 02/27/2026 **Publication date:** 03/27/2026

Rafael Salgado Garciglia[1], Braulio Edgar Herrera Cabrera[2], Luis Germán López Valdez[3], Hebert Jair Barrales-Cureño[4]

ABSTRACT
Plant stress is defined as any unfavorable condition or substance that affects or blocks the metabolism, development or growth of a plant. The factors that cause stress in plants are classified as internal factors, which come from within the plant, and external factors that exist outside the plant. Plants are exposed to different stress factors that limit yield, growth and quality. With respect to their origins, the factors can be separated into biotics, for example, pathogenic microorganisms and insects; and abiotic, such as extreme temperatures, salinity, radiation, drought, etc. The impact of stress factors is not only controlled by the dose, but also by their duration. The balance between plant response (yield, growth, quality, defense or tolerance) and sensitivity determines whether a stressor has a positive (eustress) or negative (stress) effect on plant metabolism and thus impacts growth. Therefore, the objectives of the present research are to mention the different types of endogenous and exogenous elicitors, the mechanism of elicitation and the elucidation of the possibilities offered by elicitors (eustresses of biological origin) to improve plant production at pre- and post-harvest levels).

Keywords: Distres. Eustress. Euxogenous Elicitors. Plant Immunity.

RESUMO
O estresse vegetal é definido como qualquer condição ou substância desfavorável que afeta ou bloqueia o metabolismo, o desenvolvimento ou o crescimento de uma planta. Os fatores que causam estresse nas plantas são classificados em fatores internos, que se originam no interior da planta, e fatores externos, que existem fora dela. As plantas estão expostas a diferentes fatores de estresse que limitam o rendimento, o crescimento e a qualidade. Quanto à sua origem, os fatores podem ser divididos em bióticos, como microrganismos patogênicos e insetos, e abióticos, como temperaturas extremas, salinidade, radiação, seca, entre outros. O impacto dos fatores de estresse não é determinado apenas pela intensidade,

[1] Instituto de Investigaciones Químico-Biológicas. Universidad Michoacana de San Nicolás de Hidalgo. Mexico.
[2] Colegio de Postgraduados. Mexico.
[3] Laboratorio de Productos Naturales, Universidad Autónoma Chapingo. Mexico.
[4] Universidad Intercultural Indígena de Michoacán. E-mail: hebert.jair@uiep.edu.mx

mas também pela sua duração. O equilíbrio entre a resposta da planta (rendimento, crescimento, qualidade, defesa ou tolerância) e sua sensibilidade determina se um agente estressor terá um efeito positivo (eustresse) ou negativo (distresse) sobre o metabolismo vegetal, influenciando, assim, o crescimento. Portanto, os objetivos da presente pesquisa são apresentar os diferentes tipos de elicitores endógenos e exógenos, o mecanismo de elicitação e a elucidação das possibilidades oferecidas pelos elicitores (eustresses de origem biológica) para melhorar a produção vegetal nos níveis pré e pós-colheita.

Palavras-chave: Distresse. Eustresse. Elicitadores Exógenos. Imunidade Vegetal.

RESUMEN

El estrés vegetal se define como cualquier condición o sustancia desfavorable que afecta o bloquea el metabolismo, el desarrollo o el crecimiento de una planta. Los factores que causan estrés en las plantas se clasifican en factores internos, que provienen del interior de la planta, y factores externos, que existen fuera de ella. Las plantas están expuestas a diferentes factores de estrés que limitan el rendimiento, el crecimiento y la calidad. En cuanto a su origen, los factores pueden dividirse en bióticos, como microorganismos patógenos e insectos, y abióticos, como temperaturas extremas, salinidad, radiación, sequía, entre otros. El impacto de los factores de estrés no solo está determinado por la intensidad, sino también por su duración. El equilibrio entre la respuesta de la planta (rendimiento, crecimiento, calidad, defensa o tolerancia) y su sensibilidad determina si un agente estresante tendrá un efecto positivo (eustrés) o negativo (distrés) sobre el metabolismo vegetal, influyendo así en el crecimiento. Por lo tanto, los objetivos de la presente investigación son mencionar los diferentes tipos de elicitores endógenos y exógenos, el mecanismo de elicitação y la elucidación de las posibilidades que ofrecen los elicitores (eustrés de origen biológico) para mejorar la producción vegetal a nivel pre y poscosecha.

Palabras clave: Distrés. Eustrés. Elicitadores Exógenos. Inmunidad Vegetal.

1 INTRODUCTION

Plant stress is defined as any unfavorable condition or substance that affects or blocks the metabolism, development or growth of a plant. The factors that cause stress in plants are classified as internal factors, which come from within the plant, and external factors that exist outside the plant. Plants are exposed to different stress factors that limit yield, growth and quality. With respect to their origins, the factors can be separated into biotic, for example, pathogenic microorganisms and insects; and abiotic, such as extreme temperatures, salinity, radiation, drought, etc. The impact of stress factors is not only controlled by the dose, but also by their duration. The balance between plant response (yield, growth, quality, defense or tolerance) and sensitivity determines whether a stressor has a positive (eustress) or negative (stress) effect on plant metabolism and thus impacts growth. From an ecological point of view, secondary metabolites have an important function in plants acting as a defense system against herbivores and pathogens by triggering repellency, attraction or toxicity in other organisms.

They also play a very important role in the reproduction of angiosperms (flowering plants) by attracting pollinators through volatile compounds that give off characteristic aromas to the flowers and allow chemical communication with pollinating insects or mammals. These compounds also act as allelochemicals, that is, as molecules that when released by plants into the environment affect the growth and/or development of other plants around them, thus competing for resources of interest for their survival. In this way, the production of secondary metabolites in plants is fundamental from the ecological context by providing protection, increasing the possibilities of reproduction and perpetuation of the species and, granting adaptive advantages in the competition for resources such as nutrients against other plants, space and light (Nobler et al. 2018). The biosynthesis of these compounds is a function of the genetic characteristics of the species and the activation of the genes involved in their production, generally caused in response to a stimulus that generates some type of stress, whether biotic, such as physical damage to plant tissues caused by pathogens, or abiotic, such as drastic changes in temperature, pH or light.

These stimuli are perceived at the cellular level by receptors found in the plasma membrane and cytosol, triggering the activation of messengers that amplify the signal and stimulate gene expression leading to the accumulation of secondary metabolites. These compounds can be produced and accumulate in different plant organs depending on their interactions with the environment (e.g., in flowers for insect attraction or in leaves for defense against herbivores) and, at specific times that may depend on the circadian rhythm of the species or its phenology (Kessler and Kalske, 2018).

Among the strategies used to increase the production of secondary metabolites, elicitation is the most widely used and explored at the laboratory level and in field and greenhouse trials. Elicitation refers to the induction of metabolite biosynthesis using compounds or environmental conditions that trigger secondary metabolite production pathways. Elicitors can be biological, such as enzymes, cell wall fragments or polysaccharides; chemical, such as inorganic salts and heavy metals; or physical factors, such as ultraviolet radiation, extreme temperatures, high pressures or mechanical injury. Most elicitors trigger signaling pathways in plants that depend on the type of stimulus and act by triggering the expression of defense genes, originating the production of secondary metabolites. Elicitors reprogram the expression of genes related to secondary metabolites and manifest themselves as differential patterns in the level of chemical compounds between elicited and non-elicited plants. One of the most widely used exogenous elicitors is methyl jasmonate, which has been evaluated in Catharanthus roseus (Apocynaceae), a species of great medical interest because it produces indole terpene alkaloids (TIAs) such as serpentine and ajmalicine, important hypertensive agents, and vinblastine and vincristine, natural anticancer compounds of great use against leukemia.

Due to the increase in demand for some of the metabolites produced by this species, several investigations are being carried out to increase their yield through the use of biotechnological tools (Guo et al. 2011). Zhou et al. (2015) evaluated in this species the production of metabolites in cambium meristematic cell cultures finding that MeJA at a concentration of 150 μM in combination with 10 mM β-cyclodextrin generated a high production of vindoline, catharanthin and ajmalicin, in concentrations 799, 654 and 426% higher respectively when compared to the culture of CMCs in Erlenmeyer flasks without elicitors. Salicylic acid is another of the most commonly used elicitors, which is found naturally in plants and plays the role of a signaling molecule to activate plant defense mechanisms against pathogens.

This elicitor was able to increase the production of taxol (alkaloid used in solid tumor cancer) 5.1 times, with respect to the control, in callus of Taxus baccata; in addition, its use increased the production of anthocyanins up to two times more, with respect to the control, in cultures of Vitis vinifera; and, ginkgolides a and b (sesquiterpenes) were increased 6.1 times, with respect to the control, in cultures of Vitis vinifera; and, ginkgolides a and b (sesquiterpenes) were increased 6. 1-fold, relative to the control, in suspensions of Gingkgo biloba (Oraei et al. 2019). Therefore, the objectives of the present research are to mention the different types of exogenous elicitors, the mechanism of elicitation and the elucidation of the possibilities offered by elicitors (eustresses of biological origin) to improve plant production at pre- and post-harvest levels).

1.1 ELICITORS

Lichtenthaler (1996) defines plant stress as any unfavorable condition or substance that affects or blocks the metabolism, development or growth of a plant.Factors that cause stress in plants are classified as internal factors, which come from within the plant and external factors that exist outside the plant (Kranner et al, 2010). In horticultural and agricultural practices worldwide, plants are exposed to different stress factors that limit yield, growth and quality. Regarding their origins, the factors can be separated into biotic, e.g. pathogenic microorganisms and insects; and abiotic, such as extreme temperatures, salinity, radiations, drought, etc. The impact of stress factors is not only controlled by the dose, but also by their duration (Lichtenthaler, 1996). Therefore, the balance between plant response (yield, growth, quality, defense or tolerance) and sensitivity can determine whether a stressor has a positive (eustress) or negative (distres) effect on plant metabolism and thus growth (Kaciene et al. 2015).

1.2 CLASSIFICATION OF ELICITORS

Elicitors are very varied although their purpose is the same, and they have two classifications based on their characteristics: a) According to their origin: Endogenous (endoelicitors): they are produced or originate naturally within the plant when the need to create defenses is detected. Exogenous (exoelicitors): they are created by external elicitors that are applied to induce the production of defenses in the plant preventing an attack, for example: fosetyl-Al, potassium phosphite, silicon, etc. b) According to their nature: Biotic: they are molecules of pathogenic origin that can induce defense responses (such as accumulation of phytoalexins or hypersensitive response) in the plant tissue.Mostly organic compounds produced by the stressor (carbohydrates, lipids, microbial enzymes, salicylic acid). Abiotics: generated by abiotic factors such as environmental conditions (cold, UV light, heavy metals, detergents).

Schwarz et al. (2010) mention that low temperatures below freezing cause stress to vegetative tissues of vascular plants and are lethal to many plant species; while Kalberer et al. (2006), mentions that low temperatures for a brief period in the morning (morning cold pulse) induces hardening and tends to enhance growth in favor of growers' objectives.

According to this approach, a stress factor is called eustress if the plant response in terms of yield, growth, quality and disease/pest resistance or tolerance to abiotic factors is positive eustress, or distressor if the response is negative. The eustress approach is reminiscent of the concept of hormesis published in toxins when applied at low doses in medicine (Calabrese, 2004).

Plants are sessile organisms, which have evolved a defense system based on pre-existing and inducible responses to cope with different types of biotic and abiotic environmental stressors (Cardenas-Manriquez et al. 2016). A variety of stressors of biological origin trigger inducible defense responses after being recognized by the plant, providing efficient resistance against non-adapted pathogens (Wiesel et al. 2014).

Such eustressors are called: elicitors and can be derived from a plant, a microbe or generated synthetically. Currently, there is a proposed classification of eustressors based on their nature of origin (Vázquez Hernández et al. 2019).

Elicitors are classified as biogenic (elicitors) being eustress factors yeast extract, hydrogen peroxide, polysaccharides, oligosaccharides, nucleic acids (RNA, DNA), complete cells (mycorrhizae, PGPBs), cell extracts (bacterial, viral and fungal), phytohormones (jasmonic acid, salicylic acid, ethylene, etc.);and abiogenic (eustressors) classified into physical ones such as: temperature, water stress, magnetic fields, acoustic waves, tigmomorphogenesis, and radiations (VIS/UV); as well as chemical ones: salicylic acid analogues (benzothiadiazole), nanostructures (silicon, silver, carbon nanotubes), gases (methanol, nitric oxide, ozone, CO2), mineral salts (NaCl, sulfates, phosphates) and beneficial elements (Al, Co, Na, Se, Si, heavy metals). It should be noted that each eustress factor in higher doses can behave as stress factors.

The use of some elicitors additionally improves plant growth, development and production (Yakhin et al. 2017) Various non-biological stress factors of chemical or physical origin induce a positive plant response resulting in growth or quality improvement (Demkura and Ballaré, 2012) Most reports evaluating the effects of these physical and chemical eustressors on plant performance confirm their potential and positive role in horticulture and agriculture to improve production (Li and Kubota, 2009) Elicitors (eustressors of biological origin), as a new type of plant production activators, should be monitored under the regulations of a national and international legal framework similar to the legal aspects of biostimulants and agronomic fertilizer additives in the European Union (EU), which proposes adequate data requirements and efficient administrative procedures to be able to assess the risks as well as the efficacy of these (Traon et al. 2014).

1.3 ELICITORS AND BIOSTIMULANTS

1.3.1 Elicitors

Biostimulants and elicitors come from a clear biological origin (du Jardin, 2015). Elicitors are compounds of biological origin, which activate chemical defenses in plants (Thakur and Singh, 2013). Elicitors, can be external to the plant, such as: Microorganism-Associated Molecular Patterns, Pathogens (MAMPs and PAMPs), as well as Herbivore-Associated Molecular Patterns (HAMPs), or internal to the plant, such as Damage-Associated Molecular Patterns (DAMPs) (Vega-Muñoz et al. 2018).

1.3.2 Biostimulant

A biostimulant is a formulated product of biological origin that improves plant productivity by novel or emergent properties of the complex of its constituents, and not as a sole consequence of the presence of known essential plant nutrients, plant protective compounds or plant growth regulators (Yakhin et al. 2017).

Therefore, biostimulants have a growth-promoting effect that may, or may not, be accompanied by a chemical defense-enhancing effect on plants (Colla and Rouphael, 2015).

Thus, elicitors share recognized properties in plant biostimulants that have or do not have inducing activity according to the European Biostimulants Industry Council (EBIC, 2011). Biostimulants include various formulations of compounds, substances and other products that are applied to plants or soils to regulate and enhance crop production, improving crop vigor, yields, quality, post-harvest shelf life and conservation by increasing the efficiency of different physiological pathways Their applications in horticultural crops have been widely tested (Mejía-Teniente et al. 2010). Based on these definitions, other types of eustressors of non-biological origin cannot be considered as biostimulants.

1.3.3 General examples of the application of elicitors in plants

Plants evolved a complex and robust adaptation to recognize and/or perceive both self and exogenous signals to activate defense mechanisms. The activation of defense responses depends on the specific recognition of the type of pathogen, by means of molecular dialogue between the organisms involved. Two main levels of defense have been described.

Levels of defense. The first involves the perception and recognition of highly conserved molecules or elicitors specific to pathogenic microorganisms, generally referred to as PAMPs (Pathogen-associated molecular patterns), through PRR receptors (Pattern recognition receptors), and of plant-specific molecules released after attack by the phytopathogen, called

DAMPs (Damage-associated molecular patterns), including cutin monomers and/or cell wall fragments; These activate the defense mechanism called PTI (PAMP-triggered immunity) (Macho and Zipfel, 2014).

A second level of defense can originate with pathogens that evade PTI and typically occurs in a plant-pathogen specific manner, in which virulence proteins produced by the pathogen (called effector) are recognized by intracellular Nucleotide-binding leucine-rich repeat (NLR) receptors and trigger effector-triggered immunity (ETI). Intracellular recognition of effectors is often associated with programmed cell death (PCD), known as hypersensitive response (HR), and subsequent induction of systemic acquired resistance (SAR) (Hacquard et al. 2017).

Immediately following the perception of PAMPs/DAMPs/effectors, an early response is the production of reactive oxygen species (ROS), followed by signaling cascades involving Ca2+ fluxes and MAP kinase cascades, MAPK (Mitogen-Activated Protein Kinases), deposition of the cell wall-strengthening polysaccharide callose, and phytoalexin production. All these signals converge in the production of plant hormones, including ethylene (ET), jasmonic acid (AJ), salicylic acid (AS) and abscisic acid (ABA), which trigger transcriptional reprogramming of defense-related genes (Dodds and Rathjen, 2010).

Elicitors are formulated from: a) whole cells, b) extracts of microorganisms (MAMPs, PAMPs, NAMPs), c) herbivores (HAMPs), d) plant extracts (DAMPs), or e) specific-individual compounds. Some general examples of their effects on plants depending on the type of elicitor based on the above-mentioned classification of their origin for their formulation are presented below.

a) Whole cells

Plants inoculated with beneficial microorganisms, such as plant growth-promoting bacteria (PGPB), induce morphological and biochemical modifications that result in increased tolerance to abiotic stress defined as ISR (induced systemic response). PGPBs increase plant growth and resistance to abiotic stress through various mechanisms, such as ACC (1-aminocyclopropane-1-carboxylate) deaminase production, reducing ethylene stress production, additional phytohormone modifications, induction of plant antioxidant enzyme synthesis, enhanced uptake of essential mineral elements, production of extracellular polymeric substances (EPS), decreased uptake of excess nutrients/heavy metals and induction of abiotic stress resistance genes (Etesami and Maheshwari, 2018).

b) Microbe-associated molecular patterns (MAMPs, PAMPs, NAMPs)

Among the elicitors derived from extracts of microorganisms are those from fungi, which provide fungal cell wall degradation products containing a mixture of chitin, mannoproteins and β-glucans, which elicit a variety of defense and sometimes biostimulatory responses in plants (Wiesel et al. 2014).

Bacterial-derived elicitors are extracellular polysaccharides (EPS), lipopolysaccharides (LPS), flagellin and elongation factor Tu (EF-Tu), or mixtures of them and other bacterial cell molecular compounds (Deslandes and Rivas, 2012).

Recently, a class of small molecules that is formed only by nematodes, and functions as pheromones in these organisms, was shown to be recognized by a wide range of plants. In the presence of these molecules, termed Nematode Associated Molecular Patterns (NAMPs), plants activate innate immune responses and show enhanced resistance to a broad spectrum of microbial and nematode pathogens (Choi and Klessig, 2016).

c) Herbivore-associated molecular patterns (HAMPs)

Herbivores, during their feeding, cause damage to plants by depositing a range of molecules on plant organs, such as fatty acid conjugates that plants can sense and activate their defense response. These signals may be present in saliva, oral and oviposition secretions, and feces in the herbivore, and are referred to as herbivore-associated molecular patterns (Acevedo et al. 2015).

Mechanical damage to tissues caused by various herbivore feeding strategies will trigger a series of reactions by activating signaling pathways extremely similar to those occurring in vertebrates under pain stimulus in which prostaglandins are synthesized from arachidonic acid; impressively in plants the analogous process is carried out by a chemically very similar compound, jasmonic acid (JA). To prove the great importance of jasmonates against insect attack, mutant plants (unable to express genes involved in the accumulation of jasmonates) have been developed in the laboratory and shown not only to be able to respond to insect attack, but also possess a specialized metabolism that regulates growth while activating defenses, mediates wound tolerance and symbiotic relationships, participates in pollen production, tuberization, trichome development on leaves, root and leaf growth and morphogenesis, as well as bud and flower formation, among others (Schluttenhofer, 2020).

Under normal conditions, jasmonate synthesis in plants is inhibited by a repressor complex that binds jasmonate ZIM domain (JAZ) proteins and MYC transcription factors, preventing the interaction of these genes and the RNA polymerase II machinery required to initiate jasmonate transcriptional reprogramming. The JAZ-MYC repressor complex recruits the adaptor protein NINJA, the TOPLESS general co-receptor (TPL) incorporating histone deacetylase 6 and 19 (HDA6 and HDA19). After rupture of the chloroplast cell membrane by herbivory, α-linolenic acid is released by phospholipase A1 enzymes; then, with the help of two other enzymes (allene oxide synthase and allene oxide cyclase), it leads to the formation of OPDA within the chloroplast. OPDA is a precursor of jasmonic acid that requires passage to the peroxisome, where it undergoes three cycles of beta-oxidation; this gives rise to jasmonic acid that in the cytoplasm by the action of the enzyme JAR1 is conjugated with an amino acid, preferably isoleucine, which originates jasmonic acid isoleucine (AJ-Isoleucine), the active form of the hormone (Giménez-Ibáñez et al. 2016). In the nucleus, high concentrations of AJ-Isoleucine are sensed by the JAZ-SCFCOI1 repressor complex.The SCFCOI1 protein is a ubiquitin ligase that will mark the JAZ protein to be degraded by the 26S proteasome; therefore, the JAZ-MYC repressor complex releases transcription factors (TFs) to begin expression of previously suppressed genes (Wasternack and Strnad, 2019).

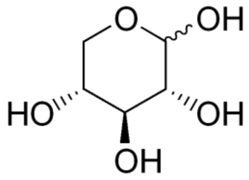
d) Damage-associated molecular patterns (DAMPs).

Plants evolutionarily evolved a repertoire of signal perception systems (exogenous and endogenous) that regulate various developmental processes and adaptive responses to pathogen infections and environmental changes. Among these perception systems are plasma membrane receptor proteins such as the so-called Pattern Recognition Receptors (PRRs). PRRs perceive ligands derived from the plant itself, such as peptides or wall glycans, known as Damage-Associated Molecular Patterns (DAMPs), or molecules of diverse nature derived from microorganisms (Microbe-Associated Molecular Patterns, MAMPs). DAMPs function as 'danger' warning signals that trigger plant immunity through signaling mechanisms that appear to be similar to those activated by MAMPs, which modulate plant resistance to disease. The identification of PRR-DAMP/PRR-MAMP couples will contribute to understanding the functions of plant immunity and could allow the design of strategies that improve crop resistance to diseases and pests and contribute to the development of a more sustainable agriculture.

DAMPs are currently considered the most recently discovered category of elicitors as internal indicators of plant injury (Quintana-Rodriguez et al. 2018). Plant-derived elicitors can be breakdown products of plant cell walls, including β-glucans, oligogalacturonides (OG), xylose (Figure 1), and phenylpropanoid-containing compounds produced by herbivores attacking plants (Ferrari et al. 2013).

Figure 1

Xylose (C5H10O5, 150.13 g/mol).



e) Group of specific compounds

This group includes phytohormones, volatile organic compounds, as well as extracellular ATP and conspecific DNA (Vega-Muñoz et al. 2018). The are molecules produced by plants that regulate plant growth and development. Even recently, volatile compounds of microbial origin have been shown to be plant growth inducers (Fincheira and Quiroz, 2018).

Major phytohormones such as auxins, cytokinins, gibberellins, ethylene, abscisic acids and strigolactones are shown to induce tolerance to water and osmotic stress in several plant species (Ruíz-Lozano et al. 2015).

Volatile organic compounds from plants such as limonene (Figure 2), methyl jasmonates (Figure 3), methyl salicylate (Figure 4), trans-2-hexenal (Figure 5), carvacrol (Figure 6), nonanal (Figure 7), methanol, and nitric oxide from lettuce, beans and tobacco show antimicrobial effects and protect plants against biotic stress (Quintana-Rodriguez et al. 2015).

Figure 2

Limonene (C10H16, 136.238 g/mol)

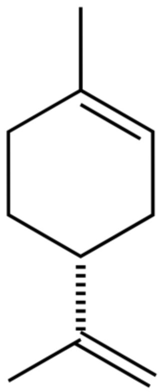


Figure 3

Methyl jasmonate (C13H20O3, 224.3 g/mol)

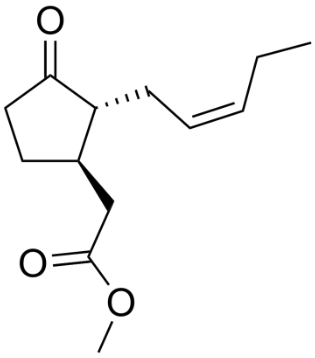


Figure 4

Methyl salicylate (C8H8O3, 152.149 g/mol)

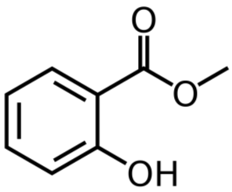


Figure 5

Trans-2-hexenal (C6H10O, 98.14 g/mol)

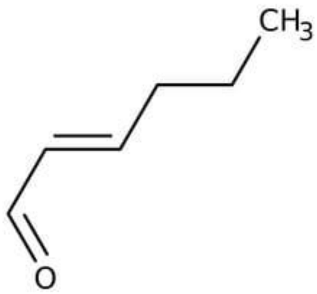


Figure 6

Carvacrol (C10H14O, 150.217 g/mol)

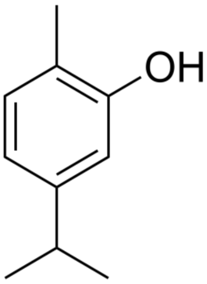
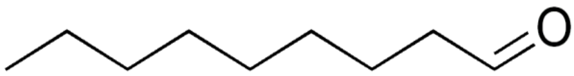


Figure 7

Nonanal (C9H18O,142.24 g/mol)



Successful use of elicitors and biostimulants in horticulture and agriculture will depend on understanding their effects not only on plant defense, but also on other aspects related to plant development and environmental responses to alleviate biotic and abiotic stress and increase plant production in an environmentally friendly manner (Yakhin et al. 2017).

Formulation of elicitor-based products and their legal regulation

Most manufacturers of elicitor and biostimulant formulations do not disclose data on how they produce them given trade secrets (Traon et al. 2014) In general, the formulation of the product depends on the chemical nature of the active ingredient including adjuvants (substance which, when added to another substance, enhances its main effect), surfactants (is an element that acts as a detergent, emulsifier or wetting agent and reduces the surface tension of a fluid) and other co-formulants, as well as the form of application (spray, liquid, powder) (Reglinski et al. 1994).

As any product for use in plant production, specialized legislation is needed for them to allow their commercialization and control. Elicitors could be subject to the legal framework established for biostimulants (du Jardin, 2015), following national/local regulations according to EBIC (European Biostimulants Industry Council), AAPFCO (American Association of Feed Control Officials), USDA (United States Department of Agriculture) or EPA (Environmental Protection Agency).

On the other hand, other chemicals (of non-biological origin) and physical eustressors should be clearly considered in future legislation for horticultural and agricultural applications. This is necessary to avoid misconceptions, establishing guidelines for their commercialization and, therefore, generate greater sustainability and more environmentally friendly agronomic activities (Malusa and Vasileev, 2014) Such legislation should consider a serious characterization and evaluation of their effects on plant metabolism and yield, as well as an assessment of the potential health hazard for consumers.

Mechanism of elicitation

The mechanism of action of elicitors starts from the early infection stage of the pathogen, the recognition of the pathogen is very important for the plant to defend itself. It is assumed that recognition of the elicitor by the plant is mediated by specific receptors in the plant cell, initiating signaling processes and activating plant defenses. A general mechanism for biotic elicitation in plants can be summarized on the basis of elicitor-receptor interaction

When a plant or plant cell culture is challenged by the stimulant, a series of biochemical activities occur; some biochemical activities that are triggered by elicitor application in the plant are generation of reactive oxygen species (ROS), structural changes in the cell wall (cell wall lignification), accumulation of pathogenesis-related proteins such as chitinases and gluconases, cell death at the site of infection (hypersensitive response), transcriptional activation of the corresponding defense response genes, synthesis of plant defensive molecules such as tannins and phytoalexins, synthesis of jasmonic and salicylic acids as secondary messengers, and finally systemic acquired resistance.

Commercial plant defense inducing compounds

Potassium phosphites. Phytoalexin synthesis inducers by stimulating PAL (Phospho-amino-lyase) enzyme, key in the production of phenol-like compounds (resveratrol), lignins, suberins and compounds derived from cinnamic acid; all of these are plant defense mechanisms. They have high mobility within the plant and the phytoalexins induced have an effect on fungi of the oomycete family. Their use is recommended when there are no phosphorus deficiencies, since they can have counterproductive effects.

Glutathione. It is formed by the union of glutamic acid, cysteine and glycine.It acts as a reductant in metabolic reactions, is a component of plant resistance to disease and has a detoxifying action in cells.

Oligosaccharins.They are glycoside chains produced by the disintegration of cell walls by the activity of pathogen enzymes. These molecules activate hypersensitivity resistance genes that induce the production of protective compounds.

Saponins. They are located in the supporting tissue of plants, they perform a protective function by disintegrating the membrane of the pathogenic organism that causes stress.

Most elicitors trigger the release of defense compounds, and in turn, are found to have a controlling effect on specific diseases such as Alternaria spp, Fusarium spp, and Phytophthora spp.

2 CONCLUSIONS

Elicitors are molecules that induce any type of defense in the plant and are produced by biotic and abiotic stressors. The application of an elicitor activates the metabolism of the plant and it becomes more resistant to subsequent stress attacks. The use of elicitors has increased due to the excellent benefits that are triggered by their use in agricultural crops, since they act as precursors of secondary metabolites such as phytoalexins; these secondary metabolites prevent or delay the entry of the pathogen into the plants, limiting its activity in the tissue or organ that suffered the infection. Elicitors are natural or mineral substances that, when applied preventively to plants, help reduce or avoid damage caused by insect pests, microorganisms, diseases or adverse abiotic factors. Future studies with respect to elicitors in in vitro crops are emerging as a model of physiological and molecular responses that can be explored and extrapolated to various agricultural crops.

REFERENCES

Acevedo, F. E., Rivera-Vega, L. J., Chung, S. H., Ray, S., & Felton, G. W. (2015). Cues from chewing insects: The intersection of DAMPs, HAMPs, MAMPs and effectors. Current Opinion in Plant Biology, 26, 80–86. https://doi.org/10.1016/j.pbi.2015.05.029

Colla, G., & Rouphael, Y. (2015). Biostimulants in horticulture. Scientia Horticulturae, 196, 39–48. https://doi.org/10.1016/j.scienta.2015.10.044

Choi, H. W., & Klessig, D. F. (2016). DAMPs, MAMPs, and NAMPs in plant innate immunity. BMC Plant Biology, 16, 232. https://doi.org/10.1186/s12870-016-0921-2

Chinnusamy, V., & Zhu, J. K. (2009). Epigenetic regulation of stress responses in plants. Current Opinion in Plant Biology, 12(2), 133–139. https://doi.org/10.1016/j.pbi.2008.12.006

Deslandes, L., & Rivas, S. (2012). Catch me if you can: Bacterial effectors and plant targets. Trends in Plant Science, 17(11), 644–655. https://doi.org/10.1016/j.tplants.2012.06.011

Dodds, P. N., & Rathjen, J. P. (2010). Plant immunity: Towards an integrated view of plant-pathogen interactions. Nature Reviews Genetics, 11, 539–548.

Du Jardin, P. (2015). Plant biostimulants: Definition, concept, main categories and regulation. Scientia Horticulturae, 196, 3–14.

Etesami, H., & Maheshwari, D. K. (2018). Use of plant growth promoting rhizobacteria (PGPRs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. Ecotoxicology and Environmental Safety, 156, 225–246. https://doi.org/10.1016/j.ecoenv.2018.03.013

Ferrari, S., et al. (2013). Frontiers in Plant Science, 4, 49.

Fincheira, P., & Quiroz, A. (2018). Microbial volatiles as plant growth inducers. Microbiological Research, 208, 63–75. https://doi.org/10.1016/j.micres.2018.01.002

Giménez-Ibáñez, S., Chini, A., & Solano, R. (2016). How microbes twist jasmonate signaling around their little fingers. Plants, 5(1), 9. https://doi.org/10.3390/plants5010009

Guo, Z. G., Liu, Y., & Xing, X. H. (2011). Enhanced catharanthine biosynthesis through regulation of cyclooxygenase in cell suspension culture of Catharanthus roseus. Process Biochemistry. https://doi.org/10.1016/j.procbio.2010.10.017

Guevara González, R. G., Villagómez Aranda, A. L., Ferrusquía Jiménez, N. I., & Martínez Reséndiz, M. (2020). Elicitores en la agricultura: Bases teóricas y algunas aplicaciones. Universidad de Almería.

Hacquard, S., Spaepen, S., Garrido-Oter, R., & Schulze-Lefert, P. (2017). Interplay between innate immunity and the plant microbiota. Annual Review of Phytopathology, 55, 565–589.

Kessler, A., & Kalske, A. (2018). Plant secondary metabolite diversity and species interactions. Annual Review of Ecology, Evolution, and Systematics, 49, 115–138.

Khan, S., Banu, T., Islam, M., & Das, N. (2017). In vitro regeneration of Piper nigrum L. Bangladesh Journal of Botany, 46(2), 789–793.

Lukens, L. N., & Zhan, S. (2007). The plant genome's methylation status and response to stress: Implications for plant improvement. Current Opinion in Plant Biology, 10(3), 317–322.

Macho, A. P., & Zipfel, C. (2014). Plant PRRs and the activation of innate immune signaling. Molecular Cell, 54, 263–272.

Malusà, E., & Vassilev, N. (2014). A contribution to set a legal framework for biofertilisers. Applied Microbiology and Biotechnology, 98(15), 6599–6607.

Mejía, T. L., Durán, F. F. D., Chapa, O. A., Torres, P. I., Cruz, H. A., González, C. M., & Guevara González, R. G. (2013). Oxidative and molecular responses in Capsicum annuum L. after elicitor applications. International Journal of Molecular Sciences, 14(3), 10178–10196. https://doi.org/10.3390/ijms140510178

Nobler, J. D., Camp, M. J., Crowell, M. M., Shipley, L. A., Dadabay, C., Rachlow, J. L., & Forbey, J. S. (2018). Preferences of mammalian herbivores for mixtures versus individual plant secondary metabolites. Journal of Chemical Ecology. https://doi.org/10.1007/s10886-018-1030-5

Oraei, M., Panahirad, S., Zaare-Nahandi, F., & Gohari, G. (2019). Pre-véraison treatment of salicylic acid to enhance anthocyanin content of grape berries. Journal of the Science of Food and Agriculture. https://doi.org/10.1002/jsfa.9869

Traon, D., Amat, L., Zotz, F., & Du Jardin, P. (2014). A legal framework for plant biostimulants and agronomic fertiliser additives in the EU. Arcadia International.

Mejía-Teniente, L., Torres-Pacheco, I., González-Chavira, M. M., Ocampo-Velázquez, R. V., Herrera-Ruiz, G., Chapa-Oliver, A. M., & Guevara-González, R. G. (2010). Use of elicitors as an approach for sustainable agriculture. African Journal of Biotechnology, 9, 9155–9162.

Quintana-Rodríguez, E., Morales-Vargas, A. T., Molina-Torres, J., Adame-Álvarez, R. M., Acosta-Gallegos, J. A., & Heil, M. (2015). Plant volatiles cause resistance in common bean. Journal of Ecology, 103(1), 250–260.

Reglinski, T., Lyon, G. D., & Newton, A. C. (1994). Assessment of yeast-derived elicitors to control barley powdery mildew. Journal of Plant Diseases and Protection, 101(1), 1–10.

Schluttenhofer, C. (2020). Origin and evolution of jasmonate signaling. Plant Science, 298, 110542. https://doi.org/10.1016/j.plantsci.2020.110542

Vega-Muñoz, I., Feregrino-Pérez, A. A., Torres-Pacheco, I., & Guevara-González, R. G. (2018). Exogenous fragmented DNA acts as a damage-associated molecular pattern. Functional Plant Biology, 45(10), 1065–1072.

Wasternack, C., & Strnad, M. (2019). Jasmonates as signals in biosynthesis of secondary metabolites. New Biotechnology, 48, 1–11. https://doi.org/10.1016/j.nbt.2017.09.007

Wiesel, L., Newton, A. C., Elliott, I., Booty, D., Gilroy, E. M., Birch, P. R. J., & Hein, I. (2014). Molecular effects of resistance elicitors and their potential for crop protection. Frontiers in Plant Science, 5, 1–13.

Yakhin, O. I., Lubyanov, A. A., Yakhin, I. A., & Brown, P. H. (2017). Biostimulants in plant science: A global perspective. Frontiers in Plant Science, 7, 2049. https://doi.org/10.3389/fpls.2016.02049

Zhou, P., Yang, J., Zhu, J., He, S., Zhang, W., Yu, R., & Huang, X. (2015). Effects of β-cyclodextrin and methyl jasmonate on alkaloid production. Applied Microbiology and Biotechnology, 99(17), 7035–7045. https://doi.org/10.1007/s00253-015-6651-9