Phytochemistry Letters 15 (2016) 152–158

Contents lists available at ScienceDirect

Phytochemistry Letters

journal homepage: www.elsevier.com/locate/phytol

Mini review

Induced resistance during the interaction pathogen x plant and the use of resistance inducers

M.D.M. Oliveira*, C.M.R. Varanda, M.R.F. Félix

Laboratório de Virologia Vegetal, Instituto de Ciências Agrárias e Ambientais Mediterrânicas, Universidade de Évora, Apartado 94, 7002-554 Évora, Portugal

ARTICLE INFO

Article history:
Received 9 June 2015
Received in revised form 28 October 2015
Accepted 30 December 2015
Available online xxx

Keywords:
Exogenous resistance inducers
Plant defence
Pathogens

ABSTRACT

Plants react to aggressions through different defence responses. Mechanical barriers consist in the increase of production and deposition of substances capable of containing pathogen invasion. Chemical barriers consist in the increase of concentration or activity of defence proteins and synthesis of phenolic compounds and phytoalexins. Elicitor substances have been widely used in plant disease control showing impressive results and a low impact to the environment and man. This review contains information about plant defence mechanisms and shows the use of inducers of resistance in the control of pathogens and prospects of advance towards sustainable agriculture.

Contents

1. Introduction

During the evolutionary process, plants have developed mechanisms to respond to different types of stress, either abiotic, such as drought, salinity and high temperature (Shah et al., 2014), or biotic, such as pathogens (Shah and Zeier, 2013). These defence mechanisms remain inactive or latent until they are activated after exposure and/or contact with inducing agents (Mandal, 2010).

Plants have several defence mechanisms against pathogens. The octadecanoid pathway is one of the best known mechanisms in plant defence, and its final product, the jasmonic acid is a plant hormone that induces the expression of several genes related to defence against stress (Shah et al., 2014). Additionally, this pathway induces the production of H_2O_2, a reactive oxygen species (ROS) that can act as a first defence signalling molecule in plants. A number of other reactive species, as well as several antioxidant enzymes, are constantly modulated in the presence of a certain stress in order to overcome it (Vandenborre et al., 2011; O'Brien et al., 2012; Davar et al., 2013; Raoni and Pratyusha, 2013).

The infection caused by a pathogen may induce dramatic changes in the activity of plant cells around the site of invasion and may lead to the induction of resistance, known as the hypersensitive response (HR), characterised by rapid cell death at the site of infection (Durrant and Dong, 2004). Although this reaction is known for almost a century, it is not yet clear whether cell death has any direct role in resistance or if it is a consequence of signalling mechanisms that lead to events that inhibit pathogen action (Thakur and Sohal, 2013).

Systemic acquired resistance (SAR) and induced systemic resistance (ISR) designate the mechanisms by which plants activate defence mechanisms not just in the induction site but also at other places, after being exposed to an inducing agent (Conrath et al., 2006).

* Corresponding author.
E-mail address: monicadmportella@hotmail.com (M.D.M. Oliveira).

http://dx.doi.org/10.1016/j.phytol.2015.12.011

Advances in research involving ISR in plants have been accompanied by the emergence of new commercial products with higher efficiency, stability and with less impact on the environment than existing ones. These new products are able to increase agricultural productivity not only by reducing the losses caused by pathogens but also by increasing vegetative growth (Farouk and Osman, 2011).

Acibenzolar-S-methyl (ASM) was the first SAR inductor released for commercial use (Lyon and Newton, 2007). Since then, several other products have become available on the market or are currently being researched (Graham and Myers, 2011). Secondary compounds present in medicinal plants have also been used as resistance inducers due to their important roles in plant-pathogen interactions, either by direct antimicrobial action or by the induction of defence mechanisms in other plants (Garcia-Brugger et al., 2006). This review provides an updated summary of plant defence responses and describe some resistance inducers that are used to induce systemic responses in plants as well as the associated oxidative metabolism.

2. Defence mechanisms

Plants have natural resistance mechanisms for defending themselves against pathogenic organisms that are characterised by the resistance ability of the plant to decrease or avoid the establishment of certain populations of pathogens (Farouk and Osman, 2011).

The better understanding of plant signalling pathways has led to the discovery of natural and synthetic compounds called resistance inducers that induce defence responses in plants similar as the ones induced by pathogen infection (Gómez-Vásquez et al., 2004). Different types of resistance inducers have been characterised, including carbohydrate polymers, lipids, glycopeptides, and glycoproteins. In plants, a complex array of defence responses is induced after detection of microorganism via recognition of elicitor molecules released during plant-pathogen interaction. Following elicitor perception, the activation of signal transduction pathways generally lead to the production of reactive oxygen species, phytoalexin biosynthesis, reinforcement of plant cell wall associated with phenyl propanoid compounds, deposition of callose, synthesis of defence enzymes, and the accumulation of pathogenesis-related (PR) proteins, some of which with antimicrobial properties (Van Loon and Van Strien, 1999; Madhusudhan et al., 2008; Aryal et al., 2011; Thakur and Sohal, 2013). ROS lead to hypersensitive response (HR) (Agrios, 2005) in plants which is a rapid death of one or few cells at the infection site to delimit the pathogen growth. Following the activation of HR, uninfected distal parts of the plant may develop resistance to further infection, a phenomenon known as systemic acquired resistance (SAR). SAR is effective against diverse pathogens, including viruses, bacteria, and fungi (Heil and Bostock, 2002; Graham and Myers, 2011; Elsharkawy et al., 2013).

When resistant plants recognize resistance inducers, intracellular signal transduction pathways are activated. These pathways ultimately result in the derepression of a battery of genes called defence response genes. These latter genes encode various pathogenesis related (PR) toxic proteins such as chitinases, glucanases, lysozyme-active proteins, or cell wall strengthening proteins such as hydroxyproline rich glycoproteins. Response proteins may also be enzymes that act in biosynthetic pathways for lignification of cell walls or production of phytoalexins, low molecular weight toxic chemicals that antagonize the invader. In the following section, the biochemical response of plant defence mechanism related to PR-proteins including chitinase and glucanase, as well as plant lignin content will be explained (Ebrahim et al., 2011).

The production and accumulation of PR proteins in plants in response to invading pathogen and/or stress situation is very important (Liu and Ekramoddoullah, 2006). Phytoalexins are mainly produced by healthy cells adjacent to localized damaged and necrotic cells, but PR proteins accumulate not only locally in the infected and surrounding tissues but also in remote uninfected tissues. Production of PR proteins in the uninfected parts of plants can prevent the affected plants from further infection (Ryals et al., 1996; Delaney, 1997; Ebrahim et al., 2011). PR proteins in plants were first discovered in tobacco plants infected with *Tobacco mosaic virus* (Van Loon and Van Kammen, 1970). At present, these proteins have been found in many plants. Most plant PR proteins are acid-soluble, have low molecular weight, and are protease-resistant (Leubner-Metzger and Meins, 1999; Neuhaus, 1999). PR proteins depending on their isoelectric points may be acidic or basic proteins but they have similar functions. Most acidic PR proteins are located in the intercellular spaces, whereas, basic PR proteins are predominantly located in the vacuole (Legrand et al., 1987; Niki et al., 1998; Van Loon and Van Strien, 1999). PR proteins have been classically divided into 5 families (Sels et al., 2008) based on molecular mass, isoelectric point, localization and biological activity (Van Loon, 1985). Currently PR-proteins are categorized into 17 families according to their properties and functions, including β-1,3-glucanases, chitinases, thaumatin-like proteins, peroxidases, ribosome-inactivating proteins defences, thionins, nonspecific lipid transfer proteins, oxalate oxidase, and oxalate-oxidase-like proteins (Van Loon and Van Strien, 1999). Among these PR proteins, chitinases and β-1,3-glucanases are two important hydrolytic enzymes that are abundant in many plant species after infection by different type of pathogens. They play a main role on defence reactions against fungal pathogens by degrading their cell walls, of which chitin and β-1,3-glucan are major structural components. β-1,3-glucanases appear to be coordinately expressed along with chitinases after fungal infection. This co-induction of the two hydrolytic enzymes has been described in many plant species, including pea, bean, tomato, tobacco, maize, soybean, potato and wheat (Mauch et al., 1988a; Mauch et al., 1988b; Vogelsang and Barz 1993; Jach et al., 1995; Bettini et al., 1998; Lambais and Mehdy, 1998; Petruzzelli et al., 1999; Cheong et al., 2000; Li et al., 2001; Ebrahim et al., 2011).

Constituent chemical and anatomical factors such as cuticles and preformed cell walls and inhibitors, may be sufficient to prevent colonization of plant tissues. However, if penetration occurs, the induced defence system is activated. This includes the rapid generation of reactive oxygen species, changes in cell wall polymers, synthesis of low molecular weight metabolites such as phytoalexins, production of new classes of proteins related to the defence and a hypersensitivity response followed by programmed cell death (Thakur and Sohal, 2013). Collectively, these systems first prevent the pathogen entrance and then inhibit the pathogen establishment (Shewry and Lucas, 1997; Thakur and Sohal, 2013).

The induced resistance (IR) can be activated by a number of substances, preventing or delaying the entry or subsequent activity of the pathogen in their tissues (Abdel-Kader et al., 2013; Shah et al., 2014). Several agents can induce the production of "signs" in plant tissues, triggering reactions that culminate in a lasting protection against a wide range of pathogens. The perception occurs when the inducing agent molecules bind to receptor molecules that are probably located in the plasma membrane of the plant cell. These reactions trigger the activation of several defence mechanisms (Graham and Myers, 2011). The IR can be divided into two categories, systemic acquired resistance and induced systemic resistance (Van Loon et al., 1998). In SAR, resistance develops systemically in response to a pathogen that causes necrotic lesions or through exogenous application of salicylic acid or synthetic compounds such as ASM and