



Induced resistance to control postharvest decay of fruit and vegetables



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ABSTRACT

More than one third of harvested fruit and vegetables are lost and do not reach the customers mainly due to postharvest decay. During the last decade, several postharvest fungicides have been excluded from the market, or their allowed residues have been significantly decreased. Therefore, there is growing interest in eco-friendly and safe alternatives to synthetic fungicides. Induced resistance has gained increasing attention as a sustainable strategy to manage postharvest decay of fruit and vegetables. Their natural resistance can be increased by various means, such as biocontrol agents or their secreted elicitors. Alternatively, physical means, such as UV-C, ozone, and heat treatment, can prime plant resistance through abiotic stress. Moreover, various defense-related phytohormones, biological elicitors, non-organic elicitors, and volatile organic compounds have been shown to induce plant resistance. During the last decades, new technologies have enabled the evaluation of gene expression, such as quantitative real time PCR and the most recent next-generation sequencing, and thus the quantification of physiological changes, which have revealed new knowledge about preharvest and postharvest induced resistance in response to various treatments. These techniques allow optimization of postharvest application of the control means, although these data cannot disregard the evaluation of *in vivo* effectiveness. The elicitation of host defenses prevents the appearance of resistant isolates of pathogens. Induced resistance can lead to increased levels of phenolic compounds in the plant tissues, which often have antioxidant properties that are highly beneficial to humans. Moreover, induced resistance preserves the natural microflora, which is rich in potential biocontrol agents, and which provides a combined approach in the control of postharvest decay that is sustainable and safe for both growers and consumers. This approach meets the requirements of integrated disease management on sustainable use of pesticides that in the EU is implemented through Directive 128/2009. This review summarizes recent achievements and knowledge of the elicitation of host defenses to control postharvest decay of fruit and vegetables, and provides an outlook on the new challenges in this fascinating subject.

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1. Introduction

Recent investigations have shown that more than one third of harvested fruit and vegetables are lost (FAO, 2011; USDA, 2014; OECD, 2014). Most losses occur due to pathogen infections in the field or after harvest, which lead to postharvest decay, when fruit ripen and vegetables senesce. Moreover, during the last decade, several postharvest fungicides that often had wide spectra of

targets have been withdrawn from the market, due to: (i) selection of resistant fungal isolates; (ii) toxicity to humans and the environment; (iii) increasing consumer concern toward risk of pesticide residues on products, with the consequent strict requirements from several major supply chains for the quantity and number of active ingredient(s) on foodstuffs, as percentages of maximum residue limit; and (iv) increasing costs of registration and re-registration (Romanazzi et al., 2016a). Therefore, there is growing interest in finding cheap, safe, and eco-friendly alternatives to synthetic fungicides for the control of postharvest decay of fresh produce. Induction of plant resistance by biological,

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chemical, or physical means is considered a sustainable strategy to manage postharvest decay of fruit and vegetables. This approach has gained increasing interest during recent years, in which we can see a high trend in papers dealing with induced resistance, from few ones recorded 30 years ago to more than 800 recorded yearly in 2013–2015 (Fig. 1), and due to new tools, further knowledge has been obtained on host responses to various methods of control (Hershkovitz et al., 2013; Gapper et al., 2014).

The beneficial effects of induced resistance in the postharvest environment were originally demonstrated about two decades ago. For example, the use of heat treatment to decrease chilling injury and disease incidence in fruit through the induction of host resistance has been extensively studied (Lurie and Pedreschi, 2014). Ultraviolet-C (UV-C) irradiation and exposure to sunlight have been shown to induce resistance to pathogens and chilling tolerance in many harvested commodities (Wilson et al., 1994; Ruan et al., 2015; Sivankalyani et al., 2016). More recently, different inducers, such as cell-wall components, plant extracts, compounds of biological origin, and synthetic chemicals, have been shown to trigger plant resistance to pathogen attack locally and systemically (Walters and Fountaine, 2009). Moreover, biological control agents can induce plant resistance to pathogens (Vallad and Goodman, 2004; Da Rocha and Hammerschmidt, 2005; Lyon, 2007). However, to correctly induce resistance in different plants, it is necessary to know and understand the host–microbe interactions, and the effects on postharvest physiology and handling of the different fruit and vegetables (Da Rocha and Hammerschmidt, 2005).

Here, we review the different biological, physical, and chemical inducers that have been shown to control postharvest diseases of fruit and vegetables, and highlight their proposed mechanisms of action.

2. Mechanisms involved in induced resistance

Various biotic inducers (e.g., fungi, bacteria, viruses, phytoplasma, insects) and abiotic stresses (e.g., chemical and physical inducers) can trigger resistance in plants, which is known as ‘induced resistance’ (Pieterse et al., 2012; Walters et al., 2013; Pieterse et al., 2014). These can produce rapid expression of defense responses (Conrath et al., 2002; Fu and Dong, 2013). Examples of treatments able to induce resistance in host tissues

and of representative mechanisms involved are reported in Fig. 2. We can imagine induced resistance as produced by an array of treatments that elicit a cloud of defense responses. There are two types of induced resistance in plants: systemic acquired resistance (SAR) and induced systemic resistance (ISR). Both of these mechanisms can induce defenses that confer long-lasting protection against a broad spectrum of microorganisms, and are mediated by phytohormones, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). SAR requires the signal molecule SA and is associated with accumulation of pathogenesis-related (PR) proteins, which are believed to contribute to resistance (Durrant and Dong, 2004). Instead, the ISR pathway functions independently of SA, while it is dependent on JA and ET (Van Wees et al., 1999).

This induced resistance does not directly activate plant defense responses, but activates the plant to a state of ‘alertness’, so that a future pathogen attack will be strongly and efficiently responded to. This phenomenon is also known as the ‘priming effect’ (Conrath et al., 2006; Jung et al., 2009), and one of the most known priming effects is root colonization by plant-growth-promoting rhizobacteria (PGPR), which induce plant development and ISR-mediated resistance (Vallad and Goodman, 2004; Verhage et al., 2010). While PGPR induces ISR, other inducers can activate SAR or both of these systems.

2.1. Systemic acquired resistance (SAR)

The mechanisms of SAR are based on SA-mediated defense. The transcription factor Nonexpressor of pathogenesis-related genes 1 (NPR1) is considered to be the master regulator of SA and SAR. Here, biotic, abiotic, chemical, and physical inducers can trigger defense responses locally, and can also induce the production of suggested mobile immune signals, including SA, methyl salicylic acid (MeSA), azelaic acid (AzA), glycerol 3-phosphate, and abietane-diterpenoid-dehydroabietinal (Park et al., 2007; Chaturvedi et al., 2012). One or more of these signals can lead to systemic defense ‘memory’ that can last for weeks to months, to protect the plant from future infection (Jung et al., 2009).

Cellular redox and reactive oxygen species (ROS) are modified during SAR. Both primary and secondary oxidative bursts are required for the onset of SAR (Alvarez et al., 1998). Furthermore,

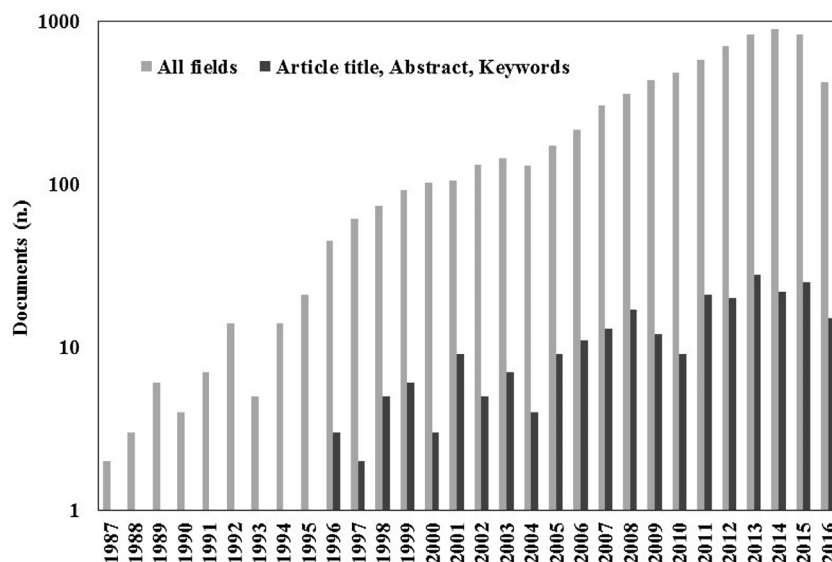


Fig. 1. Number of articles available through Scopus over the last 30 years using the search keywords of “induced resistance postharvest” (accessed on June 16; 2016).

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