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Induced resistance to control postharvest decay of fruit and vegetables

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1 **Induced resistance to control postharvest decay of fruit and vegetables**

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22 **Highlights**

23

- 24 - Several treatments applied to fruit and vegetables can trigger host defenses
- 25 - Induced resistance can be systemic acquired resistance or induced systemic resistance
- 26 - Biocontrol agents, physical means, and natural compounds elicit host defense system
- 27 - Induced resistance is a strategy that contributes to control of postharvest decay
- 28 - Induced resistance can increase amounts of beneficial antioxidant compounds

29

30

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73 **Abstract**

74

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

99

100 **Keywords:** biostimulants, elicitors, induced systemic resistance, resistance inducers, systemic
101 acquired resistance

102

103

104 **1. Introduction**

105

106 Recent investigations have shown that more than one third of harvested fruit and vegetables are lost
107 (FAO, 2011; USDA, 2014; OECD, 2014). Most losses occur due to pathogen infections in the field
108 or after harvest, which lead to postharvest decay, when fruit ripen and vegetables senesce. Moreover,
109 during the last decade, several postharvest fungicides that often had wide spectra of targets have been
110 withdrawn from the market, due to: (i) selection of resistant fungal isolates; (ii) toxicity to humans
111 and the environment; (iii) increasing consumer concern toward risk of pesticide residues on products,
112 with the consequent strict requirements from several major supply chains for the quantity and number
113 of active ingredient(s) on foodstuffs, as percentages of maximum residue limit; and (iv) increasing
114 costs of registration and re-registration (Romanazzi et al., 2016a). Therefore, there is growing interest
115 in finding cheap, safe, and eco-friendly alternatives to synthetic fungicides for the control of
116 postharvest decay of fresh produce. Induction of plant resistance by biological, chemical, or physical
117 means is considered a sustainable strategy to manage postharvest decay of fruit and vegetables. This
118 approach has gained increasing interest during recent years, in which we can see a high trend in papers
119 dealing with induced resistance, from few ones recorded 30 years ago to more than 800 recorded
120 yearly in 2013-2015 (Fig. 1), and due to new tools, further knowledge has been obtained on host
121 responses to various methods of control (Hershkovitz et al., 2013; Gapper et al., 2014).

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

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

138

139 **2. Mechanisms involved in induced resistance**

140

141 Various biotic inducers (e.g., fungi, bacteria, viruses, phytoplasma, insects) and abiotic stresses (e.g.,
142 chemical and physical inducers) can trigger resistance in plants, which is known as ‘induced
143 resistance’ (Pieterse et al., 2012; Walters et al., 2013; Pieterse et al., 2014). These can produce rapid
144 expression of defense responses (Conrath et al., 2002; Fu and Dong, 2013). Examples of treatments
145 able to induce resistance in host tissues and of representative mechanisms involved are reported in
146 Fig. 2. We can imagine induced resistance as produced by an array of treatments that elicit a cloud of
147 defense responses. There are two types of induced resistance in plants: systemic acquired resistance
148 (SAR) and induced systemic resistance (ISR). Both of these mechanisms can induce defenses that
149 confer long-lasting protection against a broad spectrum of microorganisms, and are mediated by
150 phytohormones, such as salicylic acid (SA), jasmonic acid (JA), and ethylene (ET). SAR requires the
151 signal molecule SA and is associated with accumulation of pathogenesis-related (PR) proteins, which
152 are believed to contribute to resistance (Durrant and Dong, 2004). Instead, the ISR pathway functions
153 independently of SA, while it is dependent on JA and ET (van Wees et al., 1999).

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

161

162 **2.1. Systemic acquired resistance (SAR)**

163 The mechanisms of SAR are based on SA-mediated defense. The transcription factor Nonexpressor
164 of pathogenesis-related genes 1 (NPR1) is considered to be the master regulator of SA and SAR.
165 Here, biotic, abiotic, chemical, and physical inducers can trigger defense responses locally, and can
166 also induce the production of suggested mobile immune signals, including SA, methyl salicylic acid
167 (MeSA), azelaic acid (AzA), glycerol 3-phosphate, and abietane-diterpenoid-dehydroabietinal (Park
168 et al., 2007; Chaturvedi et al., 2012). One or more of these signals can lead to systemic defense
169 ‘memory’ that can last for weeks to months, to protect the plant from future infection (Jung et al.,
170 2009).

171 Cellular redox and reactive oxygen species (ROS) are modified during SAR. Both primary
172 and secondary oxidative bursts are required for the onset of SAR (Alvarez et al., 1998). Furthermore,
173 cellular redox has been shown to be modified during SAR, as initially oxidized, and then reduced.
174 NPR1, a master regulator of SA and SAR, was shown to be reduced by thioredoxin. The NPR1
175 oligomer is disrupted and its monomers enter the nucleus, and activate SA-mediated defense (Tada
176 et al., 2008). The transcription factor NPR1 and the activated SA-mediated defense response result in
177 SAR and the activation of approximately 10% of the plant transcriptome (Fu and Dong, 2013). This
178 defense response includes direct targets of the WRKY domain transcription factor family, and
179 synthesis and secretion of various PR proteins, with activation of the mitogen-activated protein kinase
180 (MAPK) cascade, the DNA repair machinery, histone modifications, and a whole arsenal of defense-
181 related transcripts (Fu and Dong, 2013).

182

183 **2.2. Induced systemic resistance (ISR)**

184 Induced systemic resistance is known to reprogram plant-induced mechanisms based on JA and ET
185 defenses that alleviate physiological, abiotic, and biotic stresses. Elicitors and effectors known as
186 ‘microbe-associated molecular patterns’ can be identified by plant receptors (Bent and Mackey,
187 2007). This recognition has a key role in activation of innate immunity. The ISR responses to biotic
188 or abiotic stresses are diverse and can elicit plant defense responses. These responses include: MAPK
189 signaling, generation of ROS, the octadecanoic pathway (which synthesizes oxidized fatty acid
190 signals known as oxylipins), the phenylpropanoid pathway (which is involved in terpenoid and
191 phytoalexin biosynthesis), increased levels of phenolic compounds, lignification at the site of
192 pathogen infection, and cell-wall metabolism (Shoresh et al., 2010; Lloyd et al., 2011). ISR activates
193 hydrogen peroxide producers on the one hand, such as oxalate oxidase and glucose oxidase, and
194 antioxidants on the other hand, such as peroxidase (POD) and superoxide dismutase (SOD) (Shoresh
195 et al., 2010). The balance between these two determines the ROS levels, and high ROS levels can
196 lead to lipid peroxidation (Mittler, 2002). Additionally, several key transcripts, such as lipoxygenase
197 (LOX1), phenylalanine ammonia lyase (PAL), and heat-shock proteins (HSPs), have been shown to
198 be induced during ISR (Bi et al., 2007; Shoresh et al., 2010).

199

200 **2.3. Other mechanisms of induced resistance**

201 While the main induced resistance mechanisms are SAR and ISR, some processes of induced
202 resistance combine these two resistance mechanisms in various ways. For example, β -aminobutyric
203 acid (BABA)-induced resistance involves both SA-dependent and abscisic acid (ABA)-dependent
204 defense mechanisms (Buonaurio et al., 2009; Pieterse et al., 2009). The relative importance of these

205 phytohormone-dependent defenses varies according to the nature of the challenge pathogen. Indeed,
206 BABA-induced resistance against *Botrytis cinerea* resembles SAR and requires SA accumulation
207 (Zimmerli et al., 2000), while the ABA-dependent pathway, which is associated to callose deposition,
208 is necessary against *Hyaloperonospora parasitica* and *Plectosphaerella cucumerina* (Zimmerli et al.,
209 2000; Ton and Mauch-Mani, 2004).

210

211 **3. Induced resistance by biocontrol agents**

212

213 Numerous reports have indicated that biocontrol agents, such as antagonistic yeast, can increase fruit
214 resistance against postharvest diseases (Ippolito et al., 2000; Tian et al., 2006; Janisiewicz et al., 2008;
215 Droby et al., 2016; Spadaro and Droby, 2016) (Tab. 1). As defense responses in plants are complex
216 and involve both biochemical and structural barriers, the mechanisms of biocontrol agents are usually
217 multiple. One is the secretion of extracellular lytic enzymes, as for *Pichia membranifaciens* and
218 *Cryptococcus albidus*, where these can attach and degrade the hyphae of *Monilinia fructicola*,
219 *Penicillium expansum* and *Rhizopus stolonifer*, both in vitro and in vivo (Chan and Tian, 2005). The
220 second is the accumulation of host PR proteins (Jijakli and Lepoivre, 1998). These are strongly
221 induced in response to wounding or infection by pathogens, and they accumulate abundantly at the
222 site of infection, to contribute to SAR (Ryals et al., 1996). Treatment with *Cryptococcus laurentii*
223 noticeably stimulated expression of the β -1,3-glucanase (*Glu-1*) gene in jujube fruit (Tian et al.,
224 2007), which suggested that *Glu-1* has a role in defense responses to fungal pathogens. *C. laurentii*
225 and *P. membranifaciens* have been shown to reduce disease incidence in pears (Tian et al., 2006),
226 peaches (Xu et al., 2008a), and table grapes (Meng and Tian, 2009), via enhancement of defense-
227 related enzyme activities, such as chitinase (CHT), β -1,3-glucanase (GLU) and PAL. *Aureobasidium*
228 *pullulans* induced the production of CHT, GLU and POD in apple tissues starting 24 h after treatment,
229 which reached maximum levels 48 h and 96 h after treatment (Ippolito et al., 2000). Then, the
230 induction of host antioxidant enzymes and specific proteins has a relevant role. *P. membranifaciens*
231 can induce host hydrogen peroxide metabolism, to enhance the resistance of sweet cherry against blue
232 mold by *P. expansum* (Chan and Tian, 2006). Additionally, four antagonistic yeasts (*P.*
233 *membranifaciens*, *C. laurentii*, *Candida guilliermondii*, *Rhodotorula glutinis*) can stimulate catalase
234 (CAT) and POD activity, and reduce the levels of protein carbonylation in response to ROS caused
235 by *M. fructicola* in peach fruit (Xu et al., 2008b). These results suggest that yeast treatments can
236 alleviate protein carbonylation and pathogen-induced oxidative damage, which implies that the
237 antioxidant defense response is involved in the mechanisms of microbial biocontrol agents against
238 fungal pathogens. Other yeasts, such as *P. membranifaciens*, *C. guilliermondii*, and *R. glutinis*, have

239 also been shown to stimulate the expression of both PR proteins and redox enzymes (e.g., CHT, GLU,
240 CAT, POD) in peach fruit during all storage periods (Xu et al., 2008b). *Candida saitoana* induced
241 postharvest systemic resistance in apple fruit against *B. cinerea*, with increased activities of CHT and
242 GLU reported (El Ghaouth et al., 2003b). *Candida intermedia* induced strawberry fruit defense
243 mechanisms, which included β -1,3-exoglucanase, and was effective in postharvest control of *B.*
244 *cinerea* (Huang et al., 2011a). Higher PAL, CHT and GLU activities were observed when *Pichia*
245 *guilliermondii* and *C. laurenti* were applied to harvested tomatoes (Zhao et al., 2008).

246

247 **4. Induced resistance by physical means**

248

249 Several physical means, such as ultraviolet-C (UV-C) light, heat, hypobaric and hyperbaric treatments
250 are known to be effective in controlling postharvest decay of fruit and vegetables (Usall et al., 2016).
251 The advantage of most of these relies on direct effects on the pathogen without leaving residues on
252 the fruit (Sanzani et al., 2009a). Moreover, these can induce several changes in host tissues, including
253 increased resistance to abiotic and biotic stress (Tab. 2).

254

255 **4.1. UV-C irradiation**

256 The eliciting effects of UV-C irradiation have been studied for different fruit and vegetables (Charles
257 and Arul, 2007). The first studies on the effects of UV-C irradiation on host tissues were carried out
258 with carrots, the phytoalexin content of which was increased by the treatment (Mercier et al., 1993).
259 Strawberries exposed to UV-C at 0.50 kJ m⁻² and 1.00 kJ m⁻² increased their PAL activity 12 h after
260 treatment (Nigro et al., 2000). Peach fruit treated with UV-C showed increases in PAL, CHT and
261 GLU activities (El Ghaouth et al., 2003a). Tomatoes exposed to UV-C and later inoculated with *R.*
262 *stolonifer* showed 40% reduction in polygalacturonase (PG) activity, as compared to the control 72 h
263 after the challenge (Stevens et al., 2004). The application of UV-C to harvested table grape berries
264 increased the content of trans-resveratrol and catechin in the skin (Cantos et al., 2000; Romanazzi et
265 al., 2006). A higher production of both compounds occurred when the berries were treated with
266 chitosan 48 h before harvest and later exposed to UV-C irradiation (Romanazzi et al., 2006).

267

268 **4.2. Heat treatment**

269 Temperature (both high and low) is one of the oldest means to control postharvest diseases of fruit
270 and vegetables. In particular, the use of low temperature is the most diffuse means of control, and
271 nowadays imperfect management of this cold chain can cause heavy losses of fresh produce
272 (Romanazzi et al., 2016a). The physiological changes in host tissues induced by heat treatment were

273 well described by Lurie and Pedreschi (2014). In peaches exposed to hot water treatment, cell-wall
274 genes involved in ripening, such as β -galactosidase, pectin lyase, PG, and pectin methyl esterase,
275 showed general decreased expression, while ROS scavenging genes and PAL, CHT, and HSP70
276 showed increased expression (Spadoni et al., 2014). A microarray analysis run on apples treated at
277 45 °C for 45 min and inoculated with *P. expansum* showed up-regulation of HSP, HS cognate protein,
278 and HS transcription factor genes, which were linked to resistance of the fruit to the heat stress
279 (Spadoni et al., 2015). Thus, this short hot water treatment has been shown to induce resistance to
280 chilling and pathogens in various fruit (Fallik, 2004; Lurie and Pedreschi, 2014).

281

282 **4.3. Hypobaric and hyperbaric treatment**

283 Hypobaric and hyperbaric treatments rely on the use of pressure different from atmospheric pressure
284 over a short period of time. These treatments do not have direct effects on the pathogen, although
285 they affect the host tissues (Romanazzi et al., 2008). For hyperbaric treatment the occurrence of
286 physiological changes is presumed, but not yet clarified, while the variations in host tissues induced
287 by hypobaric applications have been well known since the middle of the last century, when they were
288 applied to fresh fruit to delay ripening (Burg and Burg, 1966). The reduced pressure affects ET
289 metabolism, which reduces respiration, delays ripening, and makes the fruit less prone to decay
290 (Lougheed et al., 1978). Short hypobaric treatment has been shown to be an effective means of control
291 of postharvest decay of strawberries, sweet cherries, and table grapes (Romanazzi et al., 2001), and
292 increased activities of PAL, CHT, and POD were observed in strawberry exposed to 0.5 atm for 4 h
293 (Hashmi et al., 2013). In contrast, the mechanisms of action of hyperbaric treatments are still not
294 clear. However, this treatment changed lycopene accumulation in tomatoes, as it reduced during
295 storage and increased during ripening (Liplap et al., 2013).

296

297 **5. Induced resistance by natural and synthetic chemicals**

298 **5.1. Phytohormones and chemical elicitors**

299 Phytohormones are well-known in the control of defense responses to pathogens and in the
300 modulation of plant induced resistance (Alkan and Fortes, 2015). A central role in the regulation of
301 plant immune responses has been ascribed to the defense hormones SA, JA, ABA, and ET in the
302 regulation of plant–pathogen interactions (Fujita et al., 2006; Spoel and Dong, 2008). Gibberellic
303 acid, auxin indolacetic acid, brassinosteroids (BR), and cytokinines have recently emerged as
304 important modulators of plant defenses against microorganisms, mostly based on vegetative tissue
305 data and on the lifestyle of the infecting pathogen (Robert-Seilaniantz et al., 2011). The SA and JA
306 signaling pathways are generally considered as antagonistic and are dependent on NPR1 (Spoel et al.,

2007; Spoel and Dong, 2008; Pieterse et al., 2012). This interplay between SA and JA was suggested to optimize the host response to the pathogen lifestyle (Glazebrook, 2005; Spoel and Dong, 2008; Pieterse et al., 2012; Siciliano et al., 2015). In vegetative tissues, it is commonly postulated that effective responses to biotrophic pathogens are typically mediated by SA and programmed cell death, and responses to necrotrophic pathogens, which benefit from host cell death, involve JA and ET signaling (Glazebrook, 2005; Spoel and Dong, 2008). Examples of changes in gene expression or enzyme activities in response to application of natural and synthetic chemicals are reported in Tab. 3.

315

5.1.1. Salicylic acid and its analogs

SA participates in the mechanisms of defense, plant development, fruit ripening, and responses to various abiotic factors. SA application to an active necrotrophic infection with *Colletotrichum gloeosporioides* led to programmed cell death and increased susceptibility (Alkan et al., 2012). Similarly, infection with *C. gloeosporioides* on a ripe *NahG* tomato fruit mutant that lacked SA responses showed increased tolerance to *C. gloeosporioides* (Alkan and Fortes, 2015). Also, preharvest and postharvest treatments with SA for latent infection of *C. gloeosporioides* effectively reduced the occurrence of anthracnose of mango (Zainuri et al., 2001). Application of SA at 0.14 mg/mL by preharvest spraying or soaking before storage induced resistance to gray mold in kiwi fruit (Poole et al., 1998). SA at 0.05 mM in combination with ultrasound induced higher disease resistance to blue mold in peach fruit (Yang et al., 2011). Treatment with 0.5 mM SA reduced incidence and severity of decay caused by *P. expansum* on sweet cherries (Chan and Tian, 2006).

Treatment with SA and its analogs induces the accumulation of ROS, which can kill pathogen cells (Baker and Orlandi, 1995; Mittler et al., 2011). ROS levels are determined by the activities of enzymes, such as NADPH oxidase, that are designated as ‘respiratory burst oxidase homologs’, and antioxidants, such as SOD, ascorbate peroxidase (APX), glutathione reductase (GR), and CAT (Sharma et al., 2012). The induced host resistance was closely related to the levels of hydrogen peroxide and the activities of antioxidant enzymes (Liu et al., 2005; Ren et al., 2012; Dickman and Fluhr, 2013; Ge et al., 2015). On the other hand, activation of NADPH oxidase promotes the SA defense response (Alkan et al., 2012).

SA increased the activities of CHT, PAL, GLU and GR, and reduced the activities of CAT and APX in pears (Cao et al., 2006). A combination of SA and an antagonistic yeast significantly increased the activities of polyphenol oxidase (PPO), PAL, and GLU activities in cherries (Qin et al., 2003). Additionally, in cherry, increases in the activities of CAT, POD, APX, and SOD were observed after application of MeSA (Valverde et al., 2015).

341 Proteome research has shown that antioxidant and PR proteins, as well as enzymes associated
342 with sugar metabolism, are involved in resistance of peach and sweet cherry fruit treated with SA
343 (Chan et al., 2007). Therefore, the induced resistance by SA in fruit and vegetables activates a global
344 defense response, which includes activation of the phenylpropanoid pathway, induction of
345 accumulation of ROS and antioxidants, and production of PR proteins (Liu et al., 2014; Wang et al.,
346 2015b).

347

348 5.1.2. *Benzothiadiazole (BTH)*

349 Benzothiadiazole (benzo(1,2,3)-thiadiazole-7-carbothioic acid S-methyl ester, also known as BTH or
350 ASM) is perhaps the most potent synthetic elicitor discovered to date (Terry and Joyce, 2004; Bi et
351 al., 2007). BTH is a light-insensitive functional analog of SA that induces resistance against a broad
352 range of pathogens through activation of SAR in plants. Preharvest and postharvest BTH treatments
353 have effectively reduced latent infections and induced resistance to diseases in fruit and vegetables,
354 including strawberries (Terry and Joyce, 2004; Mazaro et al., 2008; Cao et al., 2011; Feliziani et al.,
355 2015), pears (Cao et al., 2006), peaches (Liu et al., 2005), melons (Ren et al., 2012; Liu et al., 2014;
356 Li et al., 2015b), and potatoes (Bokshi et al., 2003).

357 Preharvest BTH treatment significantly reduced *Alternaria* rot and blue mold of pears during
358 storage (Cao et al., 2005). The same authors reported that the activities of PR proteins such as POD,
359 CHT, and GLU were significantly enhanced in pears treated with BTH. Similar results were also
360 observed in potatoes (Bokshi et al., 2003), peaches (Liu et al., 2005), and melons (Bi et al., 2006a).

361 Postharvest application of BTH to strawberries induced gene expression and increased activity
362 of a range of enzymes that included several that are linked to biotic stress resistance (Landi et al.,
363 2014). BTH-induced disease resistance enhanced gene expression of PPO and POD, and up-
364 regulation of these genes was related to accumulation of total phenolic compounds, in harvested
365 mango fruit (Lin et al., 2011). Postharvest dipping with BTH at 100 mg/L reduced artificial and
366 natural infections in melons, while concentrations greater than 300 mg/L failed to promote resistance
367 and caused phytotoxicity (Bi et al., 2006a).

368

369 5.1.3. *2,6-Dichloronicotinic acid (INA)*

370 2,6-Dichloronicotinic acid (INA) is a synthetic compound that is a structural and functional analog
371 of SA, and it has been reported to mediate resistance against a broad spectrum of pathogens and its
372 induced resistance has been suggested to have long-lasting effects (Lucas, 1999).

373 Preharvest foliar spray of INA at 50 mg/L significantly reduced postharvest diseases of melons
374 (Bokshi et al., 2006). The resistance against *C. gloeosporioides* in mango was noticeably enhanced

375 by preharvest treatment with INA (Santiago et al., 2006). INA at 0.5 g/L also effectively reduced the
376 disease spot sizes on the peel of banana fruit when inoculated with *C. musae* (Huang et al., 2011b).

377

378 5.1.4. Jasmonic acid (JA) and methyl jasmonate (MeJA)

379 Application of JA and methyl jasmonate (MeJA) can control decay incidence of several fruit.
380 Postharvest JA treatment at 0.01 mM reduced green mold of grapefruit and orange (Porat et al., 2002).
381 The optimal concentration of JA or MeJA varies for different fruit, and for different diseases on the
382 same fruit. The effective concentration of MeJA to control tomato anthracnose was 0.0448 mM
383 (Tzortzakis, 2007), while it was 10 mM for the control of tomato gray mold (Zhu and Tian, 2012).
384 When applied by infiltration, the concentration of MeJA was reduced to 0.1 mM (Yu et al., 2009).

385 JA stimulated production of signaling molecules related to resistance and accumulation of
386 antimicrobial compounds, and strengthened the structural barriers that restrict pathogen infection
387 (Tian et al., 2007). MeJA treatment promoted higher PAL activity and increased total phenolics,
388 flavonoids, and anthocyanins (Wang et al., 2009b). MeJA treatment promoted early accumulation of
389 hydrogen peroxide, and increased gene expression of Cu-Zn SOD, CAT, and APX, at the same time.
390 MeJA treatment also enhanced the contents of ascorbic acid and glutathione, which can scavenge
391 excess ROS to alleviate protein oxidation injury (Zhu and Tian, 2012). MeJA treatment induced
392 resistance against *Penicillium citrinum* by priming defense responses, and up-regulated the hydrogen
393 peroxide burst and enhanced translation levels of defense-related proteins and the contents of
394 antimicrobial compounds in Chinese bayberries (Wang et al., 2014).

395

396 5.1.5. Other chemical elicitors

397 Brassinosteroids (BRs) are a group of phyto-steroidal hormones that have crucial roles in a wide
398 spectrum of biochemical, physiological, growth, and developmental processes in plants. A
399 remarkable feature of BRs is their potential to increase resistance to a wide spectrum of stress in
400 plants (Krishna, 2003). BRs at 5 μ M effectively inhibited development of blue mold rot and enhanced
401 the activities of defense-related enzymes in jujube fruit. BRs did not show in vitro antimicrobial
402 activity against *P. expansum* (Zhu et al., 2010).

403 Although BABA is only rarely found naturally in plants, it has been shown to be a potent
404 inducer of acquired resistance and has a broad spectrum of activity against many pathogens (Conrath
405 et al., 2001). BABA induced resistance of mango fruit to postharvest anthracnose caused by *C.*
406 *gloeosporioides*, and enhanced the activity of fruit defense mechanisms (Zhang et al., 2013). BABA
407 caused short-lasting activation of CHT and POD after a first spray, and a boost after a second spray,
408 although to a lower level than that caused by INA (Bokshi et al., 2006).

409 The application of oxalic acid has been shown to induce systemic resistance against
410 postharvest diseases (Zheng et al., 2005). Oxalic acid induced defense-related enzymes and priming
411 of defense responses, enhanced the contents of antimicrobial compounds and modulated antioxidant
412 enzymes in muskmelon (Deng et al., 2015). Oxalic acid at 5 mM increased antioxidant levels and
413 PPO activity, which was beneficial for delayed ripening and enhanced disease resistance in peach
414 fruit during storage at low temperature (Zheng et al., 2005).

415 L-arginine induced disease resistance via its effects on nitric oxide (NO) biosynthesis and
416 defensive enzyme activity in tomato fruit (Zheng et al., 2011).

417 Riboflavin at 1.0 mM inhibited development of *Alternaria* rot, enhanced the activities of
418 defense-related enzymes, such as PAL, PPO and POD, and increased accumulation of flavonoids,
419 phenolics, and lignin (Li et al., 2012b).

420 1-Methylcyclopropene induced resistance against postharvest decay in jujube fruit, and
421 increased PAL, PPO, CAT, and SOD activities (Zhang et al., 2012).

422

423 **5.2. Biological elicitors**

424 *5.2.1. Bacterial effectors*

425 5.2.1.1. Harpin

426 Harpin is an acidic, heat-stable, glycine-rich, 44-kDa protein encoded by the *hrpN* gene, and it was
427 first described in *Erwinia amylovora*, which causes fire blight of *Rosaceae*. Bacterial harpin has been
428 shown to elicit the hypersensitive response and to induce SAR in plants (Baker and Orlandi, 1995).
429 This elicitor has also been shown to induce resistance in some postharvest fruit and vegetables (Bi et
430 al., 2007). Postharvest treatment with harpin at 0.04 mg/L to 0.16 mg/L inhibited incidence of blue
431 mold in apple (De Capdeville et al., 2003). Field spraying with harpin at 50 mg/L reduced latent
432 infections in muskmelons caused by *A. alternata* and *Fusarium* spp., with reductions proportional to
433 the levels of applied harpin, up to 90 mg/L (Wang et al., 2011b). However, harpin higher than 90
434 mg/L failed to promote resistance in melons (Bi et al., 2005). Harpin reduced lesion diameter in both
435 treated and untreated halves of the same melon, which indicated that SAR was induced by harpin (Bi
436 et al., 2005). Some of the defense reactions in melons elicited by harpin were identified as alterations
437 in the levels of preformed antifungal substances, such as phenols and flavonoids, accumulation of PR
438 proteins, such as CHT and GLU, induction of enzyme activities, such as PAL and POD, modulation
439 of metabolism of ROS, such as SOD, CAT, and hydrogen peroxide, and reinforcement of cell walls
440 and lignin (Bi et al., 2005; Wang et al., 2011b; Zhu and Zhang, 2016).

441

442 5.2.1.2. Oligandrin

443 Oligandrin is an elicitor-like protein with molecular mass of >10 kDa that has been shown to be
444 secreted by *Pythium oligandrum*. Oligandrin is known to induce resistance against a number of plant
445 diseases. The treatment of tomato fruit with oligandrin at 10 µg/mL significantly reduced incidence
446 and severity of gray mold, increased the activities of the defense-related enzymes, like PAL, PPO,
447 and POD, and the mRNA levels of the genes encoding PR proteins, and activated the ET-dependent
448 signaling pathway (Wang et al., 2011a).

449

450 5.2.2. Fungal effectors

451 5.2.2.1. Chitosan

452 Chitosan (poly-β-(1,4)-N-acetyl-d-glucosamine) is a natural biopolymer with wide antimicrobial
453 properties that can elicit defense responses in fruit and vegetables (El Ghaouth et al., 1992;
454 Romanazzi et al., 2002). This chemical and its derivatives, such as oligochitosan and glycol chitosan,
455 can be used in solution, as powders, and as edible coatings (Romanazzi et al., 2016b). Preharvest and
456 postharvest treatments with chitosan and its derivatives tend to suppress storage rots in many
457 commodities, such as strawberry (El Ghaouth et al., 1992; Reddy et al., 2000), jujube (Yan et al.,
458 2012), sweet cherries (Feliziani et al., 2013a), citrus fruit (Fajardo et al., 1998; Zeng et al., 2010),
459 apples (Felipini and Di Piero, 2009), banana (Meng et al., 2012), table grapes (Romanazzi et al., 2002;
460 Meng et al., 2008), and tomatoes (Liu et al., 2007; Badawy and Rabea, 2009), and for many other
461 vegetables (Miranda-Castro, 2016).

462 Several studies have shown that chitosan has multiple mechanisms of action, with direct
463 antimicrobial properties, film-forming activities, and induction of host defenses (Romanazzi et al.,
464 2016b). There was a significant increase in CHT and GLU activities in banana and jujube treated with
465 oligochitosan (Meng et al., 2012; Yan et al., 2012). Chitosan and oligochitosan treatments induced
466 significant increases in the activities of PPO (Liu et al., 2007), POD (Liu et al., 2007; Yan et al.,
467 2012), and PAL (Romanazzi et al., 2002; Meng et al., 2012; Landi et al., 2014) in several harvested
468 products. Chitosan treatment enhanced the total content of phenolics, flavonoids, and other antifungal
469 substances (El Ghaouth et al., 1992; Yan et al., 2012), and accumulated ROS through regulation of
470 the activity of metabolic enzymes, such as SOD, CAT, and APX (Zeng et al., 2010; Yan et al., 2012;
471 Landi et al., 2014). Spraying with chitosan increased the activities of PPO and PAL in table grapes,
472 thus promoting protection from latent infection of *B. cinerea* (Romanazzi et al., 2002; Meng et al.,
473 2008). Next-generation sequencing with chitosan-treated avocado has defined more genes as up-
474 regulated than down-regulated (Gutiérrez-Martínez et al., 2016). CHT and ROS production in table
475 grape berries varied according to the formulation of chitosan applied (Feliziani et al., 2013b).
476 Structural defense responses, such as preservation of pectin binding sites and the intense and regular

477 cellulose distribution over host cell walls were observed in the first tissue layers beneath the ruptured
478 cells in bell peppers treated with chitosan (El Ghaouth et al., 1997).

479

480 5.2.2.2. Burdock fructooligosaccharide

481 Burdock fructooligosaccharide (BFO) is a fructosan oligomer that effectively inhibited postharvest
482 diseases and reduced incidence of gray mold in tomato. BFO increased mRNA levels of genes
483 encoding PR proteins, such as PR-1a, PR-2a (extracellular GLU), PR-2b (intracellular GLU), PR-3a
484 (extracellular CHT), and PR-3b (intracellular CHT), and induced accumulation of PAL mRNA in
485 tomatoes (Wang et al., 2009a). BFO also effectively controlled postharvest diseases in grapes, apples,
486 banana, kiwi fruit, citrus fruit, strawberries, and pears (Sun et al., 2013).

487

488 5.2.3. Other biological elicitors

489 Peach fruit pretreated with yeast saccharide activated CHT, GLU, PAL, and POD. Moreover, yeast
490 saccharide triggered endogenous NO in peaches during storage (Yu et al., 2012). The flavonoid
491 quercetin significantly reduced blue mold in apples, and genes differentially expressed in quercetin-
492 treated apples revealed high similarities with different classes of PR proteins (i.e., RNase-like PR10,
493 PR8), and with proteins expressed under stress conditions (Sanzani et al., 2009b; Sanzani et al., 2010).
494 The resistance inducer protein hydrolysates were effective against green mold of citrus fruit and gray
495 mold of table and wine grapes (Lachhab et al., 2015, 2016).

496

497 5.3. Inorganic elicitors

498 5.3.1. Silicon (Si)

499 Silicon (Si) is the second most abundant element in the Earth lithosphere, and it is as important as
500 phosphorus and magnesium in the biota (Exley, 1998). Si is also considered to be biologically active
501 and to trigger more rapid and extensive deployment of plant natural defenses. Guo et al. (2007)
502 reported that Si oxide and sodium silicate suppressed pink rot in muskmelons. Sodium silicate at 100
503 mM reduced rots in melons caused by *A. alternata*, *F. semitectum*, and *T. roseum* (Bi et al., 2006b;
504 Li et al., 2012a).

505 Sodium silicate has been shown to be effective for suppression of pathogen growth and for
506 induction of resistance to postharvest diseases in fruit and vegetables. Si treatment did not affect the
507 activities of POD, PPO, PAL, and GLU, or the content of total phenols and flavonoids in potato tuber,
508 although these were significantly accumulated after a challenge with *F. sulphureum* (Li et al., 2009).
509 These results indicated that a priming state was induced by Si in potato tubers (Conrath et al., 2001).
510 In Hami melons, Si treatments caused activation of POD and CHT (Bi et al., 2006b). The effects of

511 Si on postharvest diseases of muskmelons were associated with elicitation of the antioxidant system
512 (Li et al., 2012a).

513

514 5.3.2. Nitric oxide (NO)

515 Nitric oxide (NO) is an important bioactive molecule that serves as a signal in plants, in particular for
516 maturation and senescence (Leshem et al., 1998). Lai et al. (2011) reported that NO treatment
517 activated antioxidant enzymes and induced resistance against gray mold in tomato. NO increased
518 accumulation of phytoalexin rishitin in potato tubers (Niritake et al., 1996), and induced resistance
519 against dry rot in potato tubers (Hu et al., 2014a). Moreover, NO treatment modulated anthracnose
520 levels and induced defense-related enzymes in mangoes (Hu et al., 2014b).

521

522 5.3.3. Sodium carbonate

523 Sodium carbonate and bicarbonate were effective in the control of green mold of citrus fruit (Youssef
524 et al., 2014). These salts exerted direct antifungal effects on *Penicillium digitatum*, and increased the
525 activities of resistance enzymes, such as GLU, POD, and PAL. Moreover, citrus peel extracts showed
526 increased levels of sugars and phytoalexins, with sucrose and scoparone being the most represented.

527

528 6. Induced resistance by disinfecting agents

529 6.1. Ozone

530 Since its recognition in 1997 by the US Food and Drug Administration as a safe food disinfectant,
531 both gaseous ozone (O₃) and ozonated water have gained particular attention for the control of
532 postharvest diseases of fruit and vegetables. The most recent examples of its use are those reported
533 for blueberries (Crowe et al., 2012), persimmons (Ikeura et al., 2013), papaya (Ali et al., 2014), and
534 table grapes (Feliziani et al., 2014). Ozone is a strong oxidizing agent; however, as the O₃ disinfecting
535 activity is limited to surface-contaminating microflora, and as various microbes show different
536 susceptibilities (Pascual et al., 2007), further modes of action appear to be involved (Feliziani et al.,
537 2016). Artes-Hernandez et al. (2007) reported that continuous flow of O₃ increased total flavonol and
538 hydroxycinnamates contents in cold-stored 'Autumn Seedless' table grapes. Moreover, it has been
539 reported that O₃ boosts maintained the total polyphenols, and greatly increased the phytoalexin
540 resveratrol content in cold-stored 'Napoleon' table grapes (Artés-Hernández et al., 2003). Similarly,
541 O₃ at 0.1 μmol/mol increased total phenolic content in red bell peppers (Glowacz et al., 2015). A
542 proteomic analysis conducted on O₃-treated kiwi fruit identified 102 differentially expressed proteins
543 that were mainly involved in energy, protein metabolism, defense, and cell structure (Minas et al.,
544 2012). A set of candidate kiwifruit proteins was defined as sensitive to protein carbonylation, which

545 was induced by ripening and depressed by O₃. Moreover, O₃ treatment transiently increased
546 expression of CHT and PAL in ‘Redglobe’ and ‘Sugraone’ table grapes (Duarte-Sierra et al., 2016)
547 (Tab. 4).

548

549 **6.2. Electrolyzed water**

550 Electrolyzed water (EW) is obtained by adding a small amount of an electrolyte to tap water, which
551 is traditionally sodium chloride, and passing an electrical current across an anode and a cathode. EW
552 has high oxidation–reduction potential with strong direct effects against decay causing fungi
553 (Guentzel et al., 2010). However, recently, it has shown resistance inducer potential. In particular, it
554 caused 30% increase in the total phenolic content of broccoli (Navarro-Rico et al., 2014) and
555 maintained fresh-cut cilantro firmness (Hao et al., 2015), thus improving their resistance to pathogen
556 attack. More recently, other electrolytes have been tested to improve EW performance and to avoid
557 production of chlorine by-products. Encouraging results were obtained using NaHCO₃ against
558 postharvest rots of citrus fruit, which also induced host defense responses (Fallanaj et al., 2016). In
559 particular, up-regulation of defense-related genes that encode CHT, POD, and PAL was observed at
560 6 h to 12 h post-treatment, with increased activity of the related enzymes and of GLU (Tab. 4). As
561 this was observed at 12 h post-treatment, this suggested an early host response against *P. digitatum*
562 by limiting tissue colonization.

563

564 **6.3. Ethanol**

565 The effects of ethanol dipping as a surface disinfectant that can reduce pathogen populations without
566 impairing product quality are well known (Lichter et al., 2002; Mlikota Gabler et al., 2004; Lee et al.,
567 2015). However, its mode of action appears to be much more complex. Ethanol induction of
568 resistance to postharvest anthracnose in loquat fruit was demonstrated by Wang et al. (2015a).
569 Ethanol at 300 µL/L inhibited anthracnose caused by *Colletotrichum acutatum*, and maintained
570 overall quality. Moreover, it increased SOD activity, thus resulting in higher levels of hydrogen
571 peroxide, which can activate disease resistance. Meanwhile, ethanol treatment significantly enhanced
572 the activities of defense-related enzymes, including PAL, POD, PPO, CHT, and GLU (Tab. 4).
573 Recently, ethanol treatments were shown to decelerate the ripening process and down-regulate
574 expression of major lipoxygenase-encoding genes involved in melon fruit ripening, thus contributing
575 to its increased resistance to biotic and abiotic stress (Zhang et al., 2015).

576

577 **7. Induced resistance by microbial and plant volatile organic compounds (VOCs)**

578

579 Biotic agents that contribute to plant disease management include PGPR, growth promoting fungi,
580 and fungi that work as biocontrol agents (Lyon, 2007). In addition to the use of microorganisms and
581 chemical compounds in plant protection, there is an important developing area of research in the
582 control of postharvest pathogens in fruit and vegetables based on the use of volatile organic
583 compounds (VOCs), which can be produced by microorganisms (MVOCs) or by plants (PVOCs)
584 (Mari et al., 2016).

585

586 **7.1. Induced resistance by microbial volatile organic compounds (MVOCs)**

587 Microbial volatile organic compounds (MVOCs) are mixtures of carbon-based compounds that are
588 highly volatile or are vapors (Morath et al., 2012). Fungi, yeasts, and bacteria produce MVOCs as
589 primary and secondary metabolites (Jijakli and Lepoivre, 1998; Korpi et al., 2009). MVOCs have
590 shown applicative potential as biofumigants and have motivated great interest, mainly because they
591 occur naturally without chemical synthesis (Li et al., 2015a). MVOCs can be signaling substances for
592 regulation and control of some physiological actions, which include induction of systemic resistance
593 against pathogens (Ryu et al., 2004).

594 Some defense mechanisms activated by biocontrol bacteria are induced in fruit and leaves by
595 MVOCs, including production of phytoalexins, PR proteins, such as CHT and GLU, and protein
596 inhibitors (Conrath et al., 2006; Li et al., 2012c). *Bacillus* spp. VOCs (2-3-butanediol and lipopeptides)
597 induced over-expression of the surfactin and fengicin genes, which caused metabolic changes in host
598 tissues (Ryu et al., 2004; Ongena et al., 2007).

599

600 **7.2. Induced resistance by plant volatile organic compounds (PVOCs)**

601 The eliciting activities of PVOCs, such as MeSA, were reported in section 5.1.1. Citrus fruit produce
602 VOCs that are actively involved in defense systems before pathogen attacks. The presence and
603 variation of VOCs depend on the type of produce and of its development phase. VOCs occur naturally
604 in plant systems and can be associated with the biochemistry of constitutive defense mechanisms
605 (Wightwick et al., 2010). Structures in the petals of citrus flowers, called osmophores, can release
606 more than 60 VOCs, such as phenols, terpenes, and lipophilic compounds, which have been
607 recognized as antifungal agents (Caccioni et al., 1995; Lattanzio et al., 2006). It was reported that
608 limonene and linalool have antifungal actions against *C. acutatum* and are associated with constitutive
609 biochemical responses and can be used in the control of pathogens (Rodrigues Marques et al., 2015).

610 Essential oils produce their activity through vapor, and thyme and cinnamon essential oils
611 increased PPO, PAL, CHT, GLU activities in peach fruit (Cindi et al., 2016). In tomato, it has been
612 reported that VOCs are induced and modified in defense responses, and ripening processes, and by

613 wounding. In a microarray analysis of tomato fruit at different stages of ripening, more than 4,000
614 differentially expressed genes have been reported. Genes related to defense mechanisms were
615 expressed in the early stages of ripening, and genes related to VOCs changed during late maturation.
616 Overall, more than 40 VOCs were detected, and their profiles were characterized along the fruit
617 ripening stages (Baldassarre et al., 2015).

618

619 **8. Induced resistance perspectives**

620

621 A large amount of data has been generated during the last few years that are related to the triggering
622 of host defenses during postharvest (see as examples, Tables 1, 2, 3 and 4, and Fig. 1). The elicitation
623 of host defenses has a central role nowadays in integrated disease management strategies, and this is
624 welcome for the reasons summarized in Tab. 5. The effects on plants can last for weeks or months.
625 Induced resistance has a wider spectrum of targets than synthetic fungicides. Induced resistance does
626 not lead to the appearance of resistant strains, due to involvement of various modes of action. Induced
627 resistance is usually applied before the appearance of the symptoms, so there are no side effects on
628 nontarget organisms and on humans, in terms of farmers, people working in the packinghouses,
629 retailers, or consumers. Moreover, induced resistance can lead to increased levels of phenolic
630 compounds in the plant tissues, which often have antioxidant properties that are highly beneficial to
631 humans. However, we cannot forget the weaker points linked to the application of strategies based on
632 induced resistance, such as possible inconsistent results or difficulties in their implementation in
633 packinghouse practices. Recently, a high number of biostimulants have appeared on the market, and
634 are considered as part of the effective treatments. Usually these biostimulants have combinations of
635 direct activities on pathogens and indirect activities on the host. Increasing interest in this novel
636 approach that is based on the triggering of host defenses satisfies consumer demands and the
637 guidelines on sustainable approaches to plant protection, which in European Union is implemented
638 through Directive 128/2009 on sustainable use of fungicides. New tools, such as the -omics sciences,
639 allow better understanding of the changes in host physiology and provide information on gene
640 functions. This information will provide optimization of the application of alternative treatments to
641 control postharvest decay.

642

643

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648

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1149 **Figure captions**

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1151 **Figure 1.** Number of articles available through Scopus over the last 30 years using the search
1152 keywords of “induced resistance postharvest” (accessed on June 16, 2016).

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1154 **Figure 2.** Treatments that can induce resistance in fresh fruit and vegetables, and the mechanisms
1155 or enzymes involved. Images from <http://cliparts.co/free-fruit-pictures>.

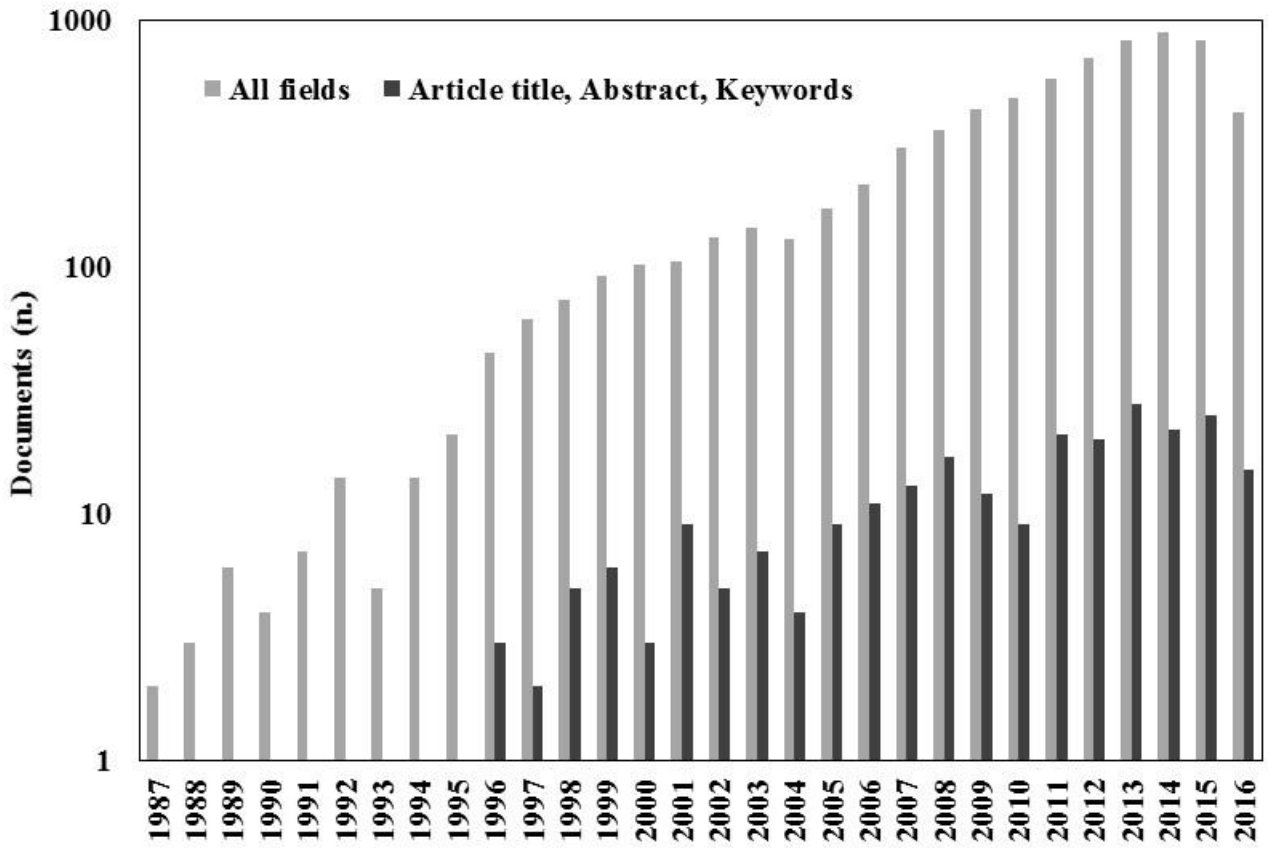
1156 INA, 2,6-Dichloronicotinic acid; HWT, Hot water treatment; GRAS, generally recognized as safe;
1157 JA, jasmonic acid; SA, salicylic acid; MeJa, methyl jasmonate; BFO, Burdock
1158 fructooligosaccharide; BTH, benzothiadiazole; EOW, Electrolyzed oxidizing water; NO, nitric
1159 oxide; UV-C, ultraviolet C irradiation; BCA, biocontrol agents; MVOCs, microbial volatile organic
1160 compounds; Si, silicon; PVOCs, plant volatile organic compounds; EtOH, ethanol; SC, sodium
1161 carbonate; SAR, systemic acquired resistance; PG, polygalacturonase; BABA, β -aminobutyric acid;
1162 GLU, β -1,3-glucanase; PR, pathogenesis related proteins; MAMP, microbe-associated molecular
1163 pattern; LOX, lipoxygenase; ROS, reactive oxygen species; CHT, chitinase; CAT, catalase; ABA,
1164 abscisic acid; PPO, polyphenol oxidase; PAL, phenylalanine ammonia lyase; ISR, induced systemic
1165 resistance; PAMP, pathogen-associated molecular pattern; SOD, superoxide dismutase; NPR1,
1166 nonexpressor of pathogenesis-related genes 1; hsp, heat shock protein.

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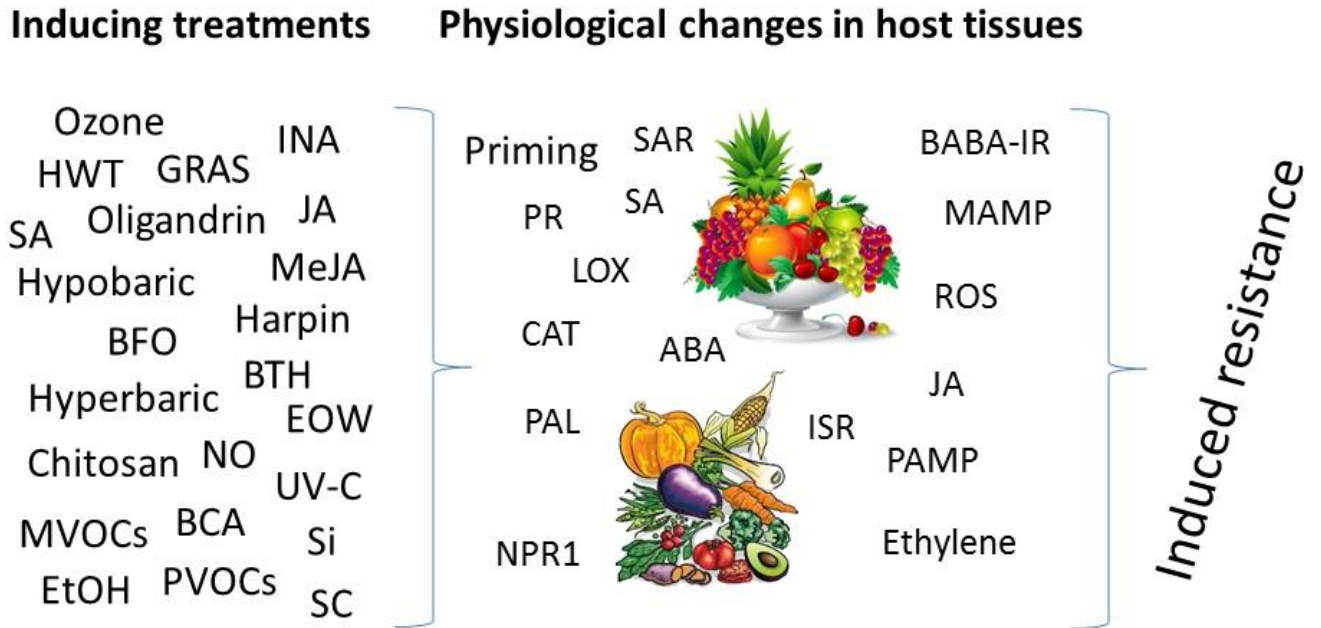
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Fig. 2

Table 1. Examples of differential gene expression or enzyme activities in response to the application of biocontrol agents.

Treatment	Genes and/or enzymes										Reference
	PAL*	CHT	SOD	CAT	SA	LOX	GLU	SURFACTIN	FENGICIN	POD	
<i>Bacillus subtilis</i>						+/++**		+/+++		+/+++	Ongena et al., 2007
<i>Candida saitoana</i>		+/++					+				El Ghaouth et al., 2003b
<i>Cryptococcus laurentii</i>							+				Tian et al., 2007
<i>Pichia membranifaciens, Candida guilliermondii Rhodotorula glutinis</i>		+			+/+++		+/+++			+/++	Xu et al., 2008b
<i>Pichia guilliermondii</i>	+	+	+	-/+			+			-/+	Zhao et al., 2008
<i>Aureobasidium pullulans</i>		+					+			+	Ippolito et al., 2000

*PAL, phenylalanine ammonia lyase; CHT, chitinase; SOD, superoxide dismutase; CAT, catalase; SA, salicylic; LOX, lipoxygenase; GLU, β -1,3-glucanase; POD, peroxidase

**+, overexpressed up to 3-fold; ++, overexpressed from 4-fold to 10-fold; +++, overexpressed more than 10-fold; -, down-regulated up to 3-fold

Table 2. Examples of differential gene expression or enzyme activities in response to application of physical means.

Treatment	Genes and/or enzymes					Reference	
	PAL*	CHT	GLU	POD	<i>Trans-resveratrol</i>		Catechin
UV-C irradiation	***	++/+++	+		++/+++	++	Cantos et al., 2000; Nigro et al., 2000; El Ghaouth et al., 2003a; Romanazzi et al., 2006
Heat treatment	+/-	-					Spadoni et al., 2014, 2015
Hypobaric treatment	+	+		+			Hashmi et al., 2013

*PAL, phenylalanine ammonia lyase; CHT, chitinase; GLU, β -1,3-glucanase; POD, peroxidase

***+, overexpressed up to 3-fold; ++, overexpressed from 4-fold to 10-fold; +, overexpressed more than 10-fold; -, down-regulated up to 3-fold

Table 3 Examples of differential gene expression or enzyme activities in response to application of natural and synthetic chemicals.

Treatment	Genes and/or enzymes							Reference	
	SOD	CAT	POD	APX	CHT	PAL	GLU		PPO
Salicylic acid		-.**	++	-	+	++	+		Cao et al., 2006
Methyl salicylic acid	+	++	++	+					Valverde et al., 2015
Benzothiadiazole	+	+	++		+	+	++		Cao et al., 2005
β -aminobutyric acid			+		+				Bokshi et al., 2006
Riboflavin			++			+		+	Li et al., 2012b
1-Methylcyclopropene	+	+				+		+	Zhang et al., 2012
Harpin			+++		+++				Bi et al., 2005
Oligandrin			+			+		+	Wang et al., 2011a
Chitosan			+	+/+++	+/+++	+/++++	+/++++	+	Romanazzi et al., 2002; Liu et al., 2007; Meng et al., 2012; Yan et al., 2012; Feliziani et al., 2013b; Landi et al., 2014
Yeast saccharide			++		+	+++	+++		Yu et al., 2012
Silicon			+++		+++				Bi et al., 2006b
Sodium carbonate			++		-	++	++		Youssef et al., 2014

SOD, superoxide dismutase; CAT, catalase; POD, peroxidase; APX, ascorbate peroxidase; CHT, chitinase; PAL, phenylalanine ammonia lyase; GLU, β -1,3-glucanase; PPO, polyphenol oxidase

**+, overexpressed up to 3-fold; ++, overexpressed from 4-fold to 10-fold; +++, overexpressed more than 10-fold; -, down-regulated up to 3-fold

Table 4. Examples of differential gene expression or enzyme activities in response to application of disinfecting agents.

Treatment	Genes and/or enzymes						Reference
	PPO*	GLU	PAL	LOX	POD	CHT	
Ozone			***				+ Duarte-Sierra et al., 2016
Electrolyzed water			+		++	+++	Fallanaj et al., 2016
Ethanol				-			Zhang et al., 2015

*PPO, polyphenol oxidase; GLU, β -1,3-glucanase; PAL, phenylalanine ammonia lyase; LOX, lipoxygenase; POD, peroxidase; CHT, chitinase

***+, overexpressed up to 3-fold; ++, overexpressed from 4-fold to 10-fold; +++, overexpressed more than 10-fold; -, down-regulated up to 3-fold

Table 5. Aspects related to the induction of resistance to postharvest diseases of fruit and vegetables

Negative sides	Positive sides
Complete effect is not always reproducible	Long-lasting effects
Does not provide a complete control of decay	Broad range of targets
Not easy to implement as part of farmer and packinghouse practices	Do not cause appearance of resistant isolates of the pathogen
Investigation methods are not standardized	Increasing number of biostimulants on the market
	Low side effects
	Reduction of pesticide use
	Promoted by EU Directive n. 128/2009
	«Sustainable Use of Pesticides» and following National Action Plans
	Increased amounts of beneficial antioxidant compounds