DOI: 10.13926/j.cnki.apps.2004.05.001
植物病理学报
ACTA PHYTOPATHOLOGICA SINICA 34(5): 385-394(2004)

专题评述

Potential of Induced Resistance in Postharvest Diseases Control of Fruits and Vegetables

TIAN Shi-ping, CHAN Zhu-long

(Key Laboratory of Photosynthesis and Environmental Molecular Physiology, Institute of Botany, Chinese Academy of Science, Beijing 100093, China)

Abstract The phenomenon of induced resistance to postharvest disease in fruits and vegetables has been studied intensively in recent years. Biotic and abiotic inducers, including microbial agents, chemical compounds, physical treatment and nature substance, have been used in fruits and vegetables. The mechanism of resistance has been studied on cell structure, physiological and biochemical changes of host. In this paper, some of the strategy and defense expressed in postharvest fruits and vegetables will be discussed in relation to how the induced plants may restrict disease development.

Key words induced resistance; postharvest disease; fruits; vegetables

诱导抗性在果蔬采后病害防治中的研究与应用 田世平, 产祝龙 (中国科学院植物研究所 光合作用与环境分子生理重点实验室, 北京 100093)

摘要: 近年来,有关果蔬产品采后诱导抗性的研究较多,生物和非生物因子(如微生物、化学物质、物理因素以及天然物质等)都能够诱导果蔬产品采后的抗性。生物因子研究较多的是拮抗菌,许多生物拮抗菌都具有自生和诱导果实产生抗病相关酶活性的作用,可以有效抑制病原菌的生长。物理诱导主要包括V射线、离子辐射、紫外光照和热水处理等,热水浸泡柑橘果实能有效控制贮藏期间的腐烂;低剂量紫外光照射桃、芒果、草莓、葡萄和甜椒等果蔬产品可明显减轻采后病害。用于果蔬产品的化学诱导剂主要有β氨基丁酸(BABA),苯丙噻重氮(ASM),水杨酸(SA),茉莉酸(JA)和茉莉酸甲酯(MJ)等。将SA与生物拮抗菌配合,可诱导甜樱桃果实过氧化物酶(POD),苯丙氨酸裂解酶(PAL)和β-1,3葡聚糖酶的活性,提高果实贮藏期间的抗病性;ASM在开花前处理哈密瓜也具有一定的抗病诱导效果;用BABA处理葡萄柚后,能刺激果实伤口附近PAL活性增加,增强了果实对绿霉病菌侵染的抵抗力;作为植物生长调节剂的JA及其酯化物MJ,对植物抗病性也具有明显的诱导作用,JA和MJ被认为是植物在病原菌侵染防御反应中细胞信号转导的一种关键物质;用MJ处理采后的苹果和桃果实能增强贮藏期间的抗病性,其诱导强度与果实的成熟度密切相关;将钙盐与生物拮抗菌配合使用,也显著提高拮抗菌的抑病效果。另外,在自然抗病物质中壳聚糖的使用较多,用它处理柑橘果实可提高贮藏期间绿霉病的防治效果。这些生物和非生物因子的诱导抗性机理主要涉及到寄主的细胞结构变化和生理生化反应。本文较详细地论述了诱导果蔬产品采后抗性的因子及其可能的诱导机理。

关键词: 诱导抗性; 采后病害; 水果; 蔬菜

中图分类号: S609.3 文献标识码: A 文章编号: 0412-0914(2004)05-0385-10

Received date 2004-02-06; **Revised date** 2004-06-08

Foundation items This study was supported by grants from the National Science Fund for Distinguished Young Scholars of China (30225030); the National Natural Science Foundation of China (30170663)

Biography Tian Shi-ping (1957-), female, Chongqing, Ph D, Professor, studies on biological control of postharvest diseases in fruits and the antagonistic mechanism.

1 Introduction

Fresh fruits and vegetables are highly perishable products, especially during the postharvest phase, when considerable losses can occur due to microbiological diseases, disorders, transpiration and senescence. Although quality deterioration of fresh postharvest fruits and vegetables is the result of a number of different factors, microbial activity is by far the single most important one[1]. Some reported values for disease losses showed in the developed countries, approximately 10% – 30% of harvested fruits and vegetables is lost to postharvest spoilage, and in the developing countries the losses are over 30% – 50% annually due to lacking sanitation and refrigeration[2].

Traditionally, postharvest disease is often controlled by the application of synthetic fungicides[3]. However, due to problems related to fungicide toxicity, development of fungicide resistance by pathogens, and potential harmful effects on the environment and human health, alternatives to synthetic chemicals have been proposed[4,5]. The use of biologically based fungicides in conjunction with induced resistance was suggested as a feasible approach for reducing postharvest disease in harvested fruits and vegetables[6,7].

Induced resistance (IR) is a plastic response, which diverts carbon and nitrogen resources from plant growth and reproduction to provide a long lasting and systemic resistance to a broad spectrum of pathogens and pests[8]. Two types of IR are well characterized. Systemic acquired resistance (SAR) is dependent on salicylic acid-mediated signaling and associated with the production of PR proteins. Induced systemic resistance (ISR), which develops after colonization by some biocontrol rhizobacteria, is dependent on the sequential action of jasmonic acid and ethylene and does not involve expression of PR proteins[8]. In many experiences, induced resistance holds promise as a new technology for the control of postharvest diseases and has been proven to be effective in the laboratory and in a few field cases[9,10]. This review describes potential strategies to induce the resistance and illustrates possible mechanisms of IR of fruits and vegetables against postharvest diseases.

2 Inducing agents

2.1 Microbial biological agents

In recent years, considerable attention has been placed on postharvest application of BCAs (biological control agents) for the inhibition of plant disease[11,12]. Treatment with antagonistic yeasts[8,12] suggested that intensification of defense mechanisms had potential in reducing postharvest decay.

Antagonistic yeasts induce several biochemical defense responses in surface wounds, including 1) the accumulation of the phytoalexin (scoparone and scopoletin)[10]; 2) the deposition of structural barriers (papillae)[9]; 3) an increase in β-1, 3-glucanase, chitinase[13], and 4) biosynthesis of ethylene[10]. Latterly, El-Ghaouth *et al*. further found that, along with the induction of a systemic protection in fresh apples, *Candida saitoana* caused a rapid accumulation of chitinase and β-1, 3-glucanase activities locally in the treated wound site and systemically in tissues distant from the initial wound[12]. Of course, wounding also triggered increases in β-1, 3-glucanase, chitinase, and peroxidase activity, but the increases were markedly less than those detected in yeast-treated wounds[13,14]. On the other hand, other evidences showed that no qualitative differences in phenolic profile of water-treated and yeast extract treated apple leaves, both of which have phloridzin and phloretin present[15].

In our research, appealing results had also been achieved. More than 10 strains of antagonists which can effectively control postharvest disease of fruits were screened out from antagonists stored or isolated from surface and wound of peach fruits[16]. Further experiments indicated that β-1, 3-glucanase and chitinase of *Pichia membranefaciens* and *Candida guilliermondii* could be significantly induced both *in vitro* and *in vivo*. *P. membranefaciens* was able to produce significantly higher levels of chitinase (exochitinase and enochitinase) *in vitro* than *C. guilliermondii* grown in Czapeck minimal medium[17]. The same induced effects were recently obtained in jujube fruits immersed with antagonists or other elicitors[18]. Moreover, researches in postharvest peach fruits suggested that the activation of peroxidase (POD), polyphenol oxidase (PPO) and phenylalanine ammonia lyase (PAL) was involved in the action of *P. membranefaciens* against *Rhizopus stolonifer*[19].

2.2 Physical agents

Curing[20], V-radiation[21], hot water brushing (HWB)[22, 23] and UV-C light[24] have recently been reported to be effective in reducing postharvest rots of fruit and vegetables, such as kiwifruit, peaches and strawberries.

2.2.1 HWB A new hot water brushing (HWB) treatment, which sprays hot water on fruit as they move along a belt of brush-rollers, induced resistance against postharvest diseases. Garcia *et al*. found that a hot water treatment of 45℃ for 15 min significantly reduced postharvest losses of strawberry fruit by delaying the onset of decay[22]. Unfortunately, the fruit displayed shrivel and loss of shine because effective heat treatments against pathogens are often close to the level of tolerance of the commodity. Recently, a short duration heat treatment (10- 30 s) at very high temperatures (56- 62℃) has shown promising results for citrus decay control without damage to the fruit[25]. This treatment is believed to sanitize the fruit as well as induce resistance to pathogens in some cases.

The HWB treatment induced the accumulation of some proteins that cross-reacted with an antibody raised against bovine heat shock protein (HSP). On the other hand, the increases in the accumulation of the 21, 22 and 25 kDa chitinase proteins and of the 38 and 43 kDa β-1, 3-glucanases proteins, which were observed 1 and 3 d after the HWB treatment when the fruit appeared to be more resistant to *Penicillium digitatum*, may be part of the complex fruit disease resistance mechanisms induced by the heat treatment[23].

2.2.2 Ionizing radiation: Ionizing radiation is used as a means of extending the shelf life of produce. Dosages of 1.5 to 2 kilogray (kGy), and some cases 3.0 kGy (300 krad), had been effective in controlling decay in several products[26]. Strawberry and peach shelf life could be extended with treatments in the range of 2 to 3 kGy[27]. Research conducted since that time suggests that irradiation can be an important treatment to enhance safety of other types of produce. However, commercial application of ionizing a radiation is limited due to the cost and size of equipment needed for the treatment and to uncertainty about the acceptability of irradiated foods to the consumer[28].

2.2.3 Curing: Curing of fruit inoculated with one pathogen could induce resistance against other pathogens; this resistance was mainly localized in the area of pathogen invasion[20]. Manipulating the postharvest environment of citrus to enhance the natural resistance to stress by curing/conditioning had also shown to lessen peel injury induced by regulatory cold treatments[29].

2.2.4 Low-dose UV light: A relatively recent concept in postharvest disease control is the use of hormetic doses of ultraviolet light to elicit resistance[21]. In this case, the low dose ultraviolet light treatments had two effects on brown rot development: reduction in the inoculum of the pathogen and induced resistance in the host. It has been proved that low doses of UV-C irradiation, which stimulate several biological processes such as respiration, biosynthesis of flavonoids and phytoalexin, and elicitation of pathogenesis-related proteins[30]. For this reason, UV-C could be envisaged as an alternative to fungicides for the control of post-harvest diseases.

Recent works have shown that the application of UV-C at low doses reduced post-harvest decay, extended the shelf life, improved quality and delayed maturity of sweet pepper[31], table grapes[32], peaches[33], mango[34], strawberry[24] and carrot roots[35]. Furthermore, Stevens *et al*. observed a possible synergistic effect between the yeast and UV-C in controlling postharvest disease[36]. However, UV light has not become a practical postharvest treatment as yet and requires more research.

2.3 Chemical agents

Resistance can also be induced with chemicals such as DL-3-amino butyric acid (BABA), 1,2,3-benzothiadiazole-7-carbothioic acid S-methyl ester (ASM), salicylic acid (SA), ethylene, Harpin, 2,6-dichloroisonicotinic acid, jasmonic acid (JA), methyl jasmonate (MJ), potassium and phosphates. These compounds were shown to control several fungal, bacterial, or viral diseases on both mono-and dicotyledons[37,38]. Further experiments indicated that the inducing agents reduced disease incidence but not disease severity[39].

2.3.1 Salicylic acid (SA): Salicylic acid (SA) is a natural phenolic compound present in many plants and is an important component in the signal transduction pathway[40]. Exogenous application of SA at nontoxic concentrations to susceptible plants could enhance resistance to pathogens[41]. These induced defense responses by SA are probably involved in the expression of a range of defense genes, especially those encoding the pathogenesis related (PR) proteins such as chitinase, β-1,3-glucanase, and peroxidase[40].

Recently, a significant increase in polyphenoloxidase, phenylalanine ammonia-lyase, and β-1,3-glucanase activity in cherry fruits treated by SA combination with antagonistic yeast was observed in our experiment[42]. Therefore, the mechanism by which SA enhanced biocontrol efficacy of antagonistic yeast may be related to its ability to induce biochemical defense responses in sweet cherry fruit rather than its fungi toxicity effects on the pathogens[42].

2.3.2 Ethylene: It has been proposed that ethylene plays an important role in controlling defense responses of plants to microbial pathogens. In plant defense mechanisms, one would predict that treatment of plants with exogenous ethylene would enhance resistance to subsequent challenge with microorganisms or, conversely, that treatment with ethylene inhibitors would adversely affect their resistance level.

Ethylene can induce the synthesis of the antifungal diene in idioblasts and export of this compound to the pericarp of the fruits. Moreover, exogenous application of ethylene to plants can result in the activation of genes encoding antimicrobial pathogenesis-related (PR) proteins[43], cell wall-strengthening glycoproteins, or enzymes involved in the synthesis of phenylpropanoids[44].

2.3.3 Acibenzolar-S-methyl: Acibenzolar-S-methyl (1,2,3-benzothiadiazole-7-carbothioic acid S-methyl ester, ASM) is a synthetic analogue of SA and has been developed for use as a crop protect through SAR[45]. Huang *et al*. demonstrated that one application of ASM prior to flowering protected rock and Hami melon fruit from several postharvest fungal diseases[46]. ASM may therefore become an important component of an integrated pest management (IPM) approach to reduce viral and fungal disease impact on melons[46].

2.3.4 DL-β-amino butyric acid (BABA): Porat *et al*. found that application of BABA to specific wound sites on the peel surface of grapefruit could induce resistance to *P. digitatum* in a concentration-dependent manner[47]. The effect was local and limited to the vicinity (within 1- 2 cm) of the BABA-treated site. The induction of resistance by BABA was accompanied by the activation of various pathogen defense responses in the fruit peel tissue, including activation of chitinase gene expression and protein accumulation after 48 h, and an increase in phenylalanine ammonia lyase (PAL) activity after 72 h[47].

2.3.5 Jasmonic acid (JA) and methyl jasmonate (MJ): A large body of evidence suggests that jasmonic acid (JA) and its esterified derivative, methyl jasmonate (MJ) are a key component of such intracellular signal in response to pathogen attack, and that its application may, therefore, induce disease resistance in a wide variety of plants[48].

Applications of low concentrations of jasmonic acid (JA) to plants induced proteinase inhibitors, proline-rich cell wall protein, and a range of enzymes involved in plant defense reactions[49]. In this respect, since JA and MJ are regarded as a natural plant growth regulator, it has the advantage of eliciting defense or physiological responses to its exogenous application to plants at low concentrations in a non-destructive manner[50]. Our present researches indicated that methyl jasmonate (MJ) could induce resistance of peach and apple fruit against postharvest disease, and the level of induce resistance is significantly related with maturity degree of the fruit (unpublished data).

2.3.6 Inorganic compound: In combination Ca^{2+} salts with antagonistic yeasts effectively enhanced biocontrol ability of the yeasts against postharvest pathogens in fruit during storage[51]. The infiltration of harvested fruits with several Ca^{2+} salts initially improved the resistance against mechanical damages, some physiological disorders and fruit quality[52]. It has been communicated that these beneficial effects of titanium are due to the intensification of the Fe activity in leaf chloroplasts and fruit chromoplasts, and consequently increased metabolic activity and nutrient absorption[53]. Recently, a new way, that sodium bicarbonate in combination with antagonistic yeasts could significantly enhance biocontrol efficacy of the yeasts to fungal spoilage of pears in storage, was found in our research[54].

2.4 Natural compounds

2.4.1 Chitosan and Margosan-O: Chitosan, a natural compound derived from animals, is known to possess antifungal and resistance-eliciting properties and offers an economically viable option to synthetic chemical control[55]. Likewise, Margosan-O, as a natural compound derived from plants, contains a terpenoid compound called azadirachtin extracted from the neem tree is a known biopesticide. Fajardo *et al*. reported that sweet orange (*Citrus sinensis* cv. ‘Valencia’) treated with chitosan or mangosan-O and challenged by the green mold pathogen (*P. digitatum*) showed a delay in the onset and progression of disease symptoms compared with inoculated fruits not treated with the elicitors[39].

2.4.2 Harpin: Harpin is an acidic, heat-stable, glycinerich, 44 kDa protein, encoded by the *hrpN* gene of the bacterium *Erwinia amylovora*. Dong *et al*. firstly reported that bacterial product was able to elicit the hypersensitive response (HR) in plants[56]. De Capdeville *et al*. also found that harvested Red Delicious apples could elicit systemic acquired resistance (SAR)[57]. The level of resistance depended on harpin concentration, inoculum concentration, and interval between treatment and inoculation[56]. These studies have shown that harpin triggers a variety of cellular responses, such as activation of active oxygen species and cell membrane depolarization, which are known to be involved in resistance response mechanisms of systemic resistance[58]. In addition, Harpin has been produced commercially as “Messenger”, which is currently being suggested for the control of viral and fungal diseases, as well as a plant growth enhancer and a controller of selected insect populations[59].

2.5 Combination treatments

Researchers have been trying to find additives that may enhance the performance of the selected antagonists, or integrating application of combination of antagonists with "physical" treatments, such as pre-treatment of produce with UV-C light, heat or gamma-irradiation[60,61], chemical compounds, such as sodium bicarbonate and ammonium molybdate[16,54], calcium chloride and potassium sorbate[51,62], salicylic acid[42], methyl jasmonate[63], as well as low temperature and controlled atmospheres[11] to enhance the resistance of fruit against pathogenic fungi during storage periods. The biocontrol efficacy of *C. saitoana* could enhance by combining it with either glycochitosan, forming a 'bioactive coating', or with the sugar 2-deoxy-D-glucose[64]. Both approaches increased the protective and curative activity of the yeast in controlling postharvest diseases. Therefore, the use of additives is a useful approach to improve the efficacy of yeast antagonists used for postharvest disease control.

3 Defense mechanisms of harvested commodities

The natural defense mechanism in fruits includes such things as morphology changes and biochemical changes (Fig.).

In response to elicitors and stress, fruit produces lignin and resin, which is a compound that strengthens cell walls and chemicals called phytoalexins that inhibit the growth of the pathogen. As the resistance is built up, the activities of certain enzymes also increase, including peroxidase (EC 1.11.1.7), phenylalanine amonia-lyase (EC 4.3.1.5), lipoxygenase (EC 1.13.11.12), β-1,3-glucanase (EC 3.2.1.6), and chitinase (EC 3.2.1.14). These enzymes are needed for the production of new compounds.

4 Conclusion and prospect

Fruits and vegetables can express induced resistance to postharvest pathogens when they are infected by pathogens or treated by other resistance activating. In turn, many experiments have shown that IR can lead to long-lasting, broad-spectrum disease control and be used preventively to bolster general plant health. The availability of this long-lasting, broad-spectrum and potentially stable solution to disease control may have a positive impact on harvested commodities[65]. Therefore, induced resistance may be a worthwhile strategy for postharvest disease control.

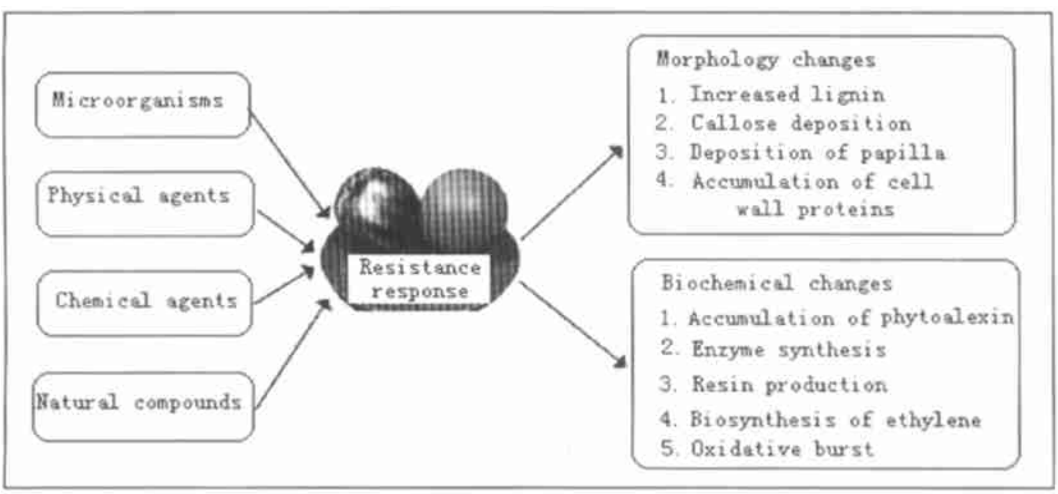

Fig. Induced resistances in harvested commodities

To fully understand the induced resistance phenomenon, future research should focus on critically evaluating the roles of the putative defenses identified thus far in the expression of resistance. Use of transgenic plants that are suppressed in the production of PR proteins is one approach that can be used to evaluate the relative contribution of these proteins in the defense response. In addition, attempts should be made to find mutants that cannot express a specific defense[66], and the usage of RNA blotting methods to detect the expression of genes (peroxidase, phenylalanine amonia-lyase, lipoxygenase, β-1, 3-glucanase, and chitinase etc.) in fruits or vegetables after being challenged with elicitors.

A variety of biocontrol and technical problems will still have to be overcome before induced resistance as an on line practice for the control of postharvest disease are utilized. Therefore, integrative strategy may be the greatest promise in biocontrol of postharvest diseases. The various resistance inducing treatments, especially UV-light and gamma irradiation, will be paid attention to the effects of fruit quality and safety. In addition, further research towards molecular characterization of IR with techniques of conventional mutagenesis (ionizing radiations, mutagenic chemicals, fungicide or antibiotic exposure) or of sexual recombination, through protoplast fusion or genetic transformation, as well as the formulation should be studied further to allow for commercialization of the product[67].

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