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

Postharvest diseases of fruits and vegetables cause major losses in food production. It is estimated that in the United States, approximately 24% of harvested fruits and vegetables is lost to postharvest spoilage (23). Such estimates are conservative, since they are generally based on assessments made at one point in the food system. No one has evaluated the accumulative postharvest losses of fruits and vegetables that occur during harvesting, processing, storage, transportation, on the grocery shelf, and in homes. In addition, we have no estimates of postharvest losses that occur during food preparation in restaurants and fast-food outlets. In developing countries, where sanitation and refrigeration are lacking or minimal, postharvest losses are even greater, amounting in many cases to over 50% of the harvested crop (2).

Despite the magnitude of the problem, plant pathologists have not given postharvest diseases the priority they warrant, in part because an abundant food supply in developed countries has masked the severity of postharvest losses. Most research has been directed toward improving and protecting crops in the field or greenhouse. This lack of attention is reflected in graduate programs at many universities where little consider-

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ation is given to postharvest pathology.

Until recently, there have been a number of effective fungicides for the control of postharvest diseases of fruits and vegetables. Some of these, such as the systemic fungicide benomyl, are effective at reducing postharvest decay and extending the shelf life of produce. However, these fungicides are becoming less effective because postharvest pathogens are developing resistance to them. Also, recent health concerns over pesticide contamination of food have precipitated the complete withdrawal of a number of key fungicides from the market (19). These developments have lessened our ability to control postharvest diseases and have stimulated exploration for alternative technologies. To address this problem, researchers from the USDA-ARS Appalachian Fruit Research Station in Kearneysville, West Virginia; Laval University, Quebec, Canada; Tuskegee University, Tuskegee, Alabama; and the Volcani Center, Bet Dagan, Israel have formed a working collaboration. This paper describes our cooperative research on utilizing induced resistance to control postharvest diseases.

Alternatives to Fungicide

Antagonistic microorganisms were recently developed as "living fungicides" for the control of postharvest diseases (27,28). Some have been patented, shown to be effective in large-scale tests, and targeted by industry for commercialization (27). However, it appears that control of postharvest diseases with antagonists often is not as consistent as control with synthetic fungicides. Therefore, it

may be necessary to combine antagonistic microorganisms with other forms of biological control such as natural fungicides and elicitors of defense responses (25).

Plant resistance has been the cornerstone of control strategies for plant diseases. However, in harvested commodities, we have only recently started to explore resistance as a means of controlling postharvest diseases. Ironically, breeding programs aimed solely at the selection of harvested fruits and vegetables for tenderness and lack of astringency may have inadvertently depleted these commodities of phenolic compounds and cellular structures that impart resistance. Furthermore, unlike vegetative plant tissue, harvested commodities are senescing rather than developing. The senescence process generally reduces resistance responses in harvested commodities. These negative factors may have contributed to a lack of emphasis on disease resistance in harvested fruits and vegetables.

In our experience, induced resistance holds promise as a new technology for the control of postharvest diseases. Both physical and biological agents can elicit resistance responses in harvested fruits and vegetables. Heat treatment, wounding, gamma radiation, UV-C light, antagonists, attenuated strains, and natural compounds have all been suggested as elicitors of resistance in harvested crops (Fig. 1). In this article, we discuss the use of low-dose UV light, natural compounds, and antagonistic microorganisms as elicitors of resistance responses in fruits and vegetables.

Low-dose UV light. The UV light present in sunlight is generally designated UV-C (wavelength below 280 nm), UV-B (280–320 nm), and UV-A (320–390 nm). All types of UV radiation can damage plant DNA and physiological processes (17,21). However, we have found that low doses of UV-C may induce resistance in harvested commodities (1,3,13–16,18,22).

It was shown initially at Tuskegee University that low-dose UV-C light and gamma radiation treatments of onions (16) and sweet potatoes (22) reduced storage rots and extended the shelf life of these commodities. Because UV-C light treatments showed potential as an alternative to synthetic fungicides for the control of postharvest diseases, cooperative studies were undertaken at Tuskegee University with the USDA Appalachian Fruit Research Station, the Volcani Center in Israel, and Laval University in Canada to further explore this technology. This cooperative effort demonstrated that low-dose UV light will also protect citrus fruit (Fig. 2) (1,3), apples (Fig. 3) (15), peaches (14,15), peppers (Fig. 4), carrots (Fig. 5) (18), tomatoes (13), and sweet pototoes (22) against postharvest storage rots and extend their shelf life.

We were surprised that UV-C light induced resistance in such a wide array of commodities. We are examining the fundamental changes that occur in UV-light-treated tissues to account for the resistance. In our study of citrus fruits, the onset of UV-induced resistance coincided with the induction of activity by phenylalanine ammonia lyase (PAL) (a key enzyme in the phenylpropanoid pathway) and peroxidase (1,3). PAL activity in the peel of grapefruit increased within 24 hours after UV treatment and remained elevated for 72 hours, while peroxidase activity reached its maximum 72 hours after treatment. Both enzymes are considered to play a role in inducible resistance in plants against pathogens.

Investigators at Laval University found the induction of 6-methoxymellen (a phytoalexin) in carrot slices by UV-C increased the resistance of tissue to *Botrytis cinerea* and *Sclerotinia sclerotiorum* infection (18). UV-induced resistance in carrot was expressed only after 1 week of storage, when the concentration of 6-methoxymellen in the tissue reached inhibitory levels. The content of 6-methoxymellen in UV-treated carrot slices stored at 1 and 4 C remained elevated for up to 35 days after treatment. Implication of another phytoalexin (scoparone) in UV-induced resistance was also reported in UV-treated lemon fruit (20).

Recently, UV-C treatment was shown to stimulate antifungal hydrolases in apples (25), bell peppers, and tomato fruit (4). In addition, we have shown that UV-treatments retarded ripening of several postharvest commodities (13–15). A consequent decrease in their susceptibility to infection could be anticipated. In many harvested commodities, notably climacteric-type fruits, susceptibility of the tissue to infection and ripening are closely linked.

A number of lines of evidence from citrus and apple indicate that the UV-C effect is due to its ability to induce
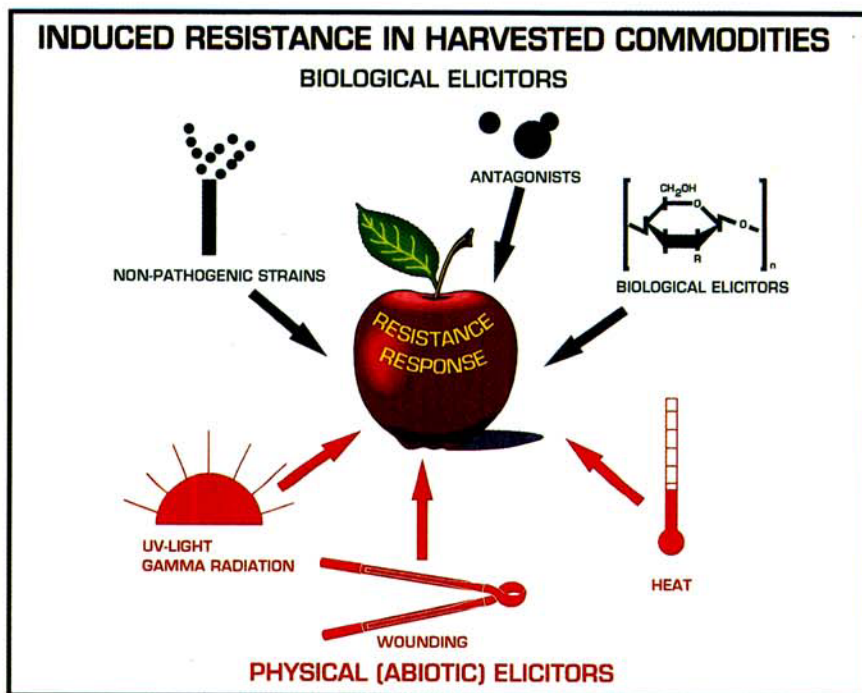

Fig. 1. Physical and biological agents that have been suggested to elicit resistance responses in harvested fruits and vegetables.
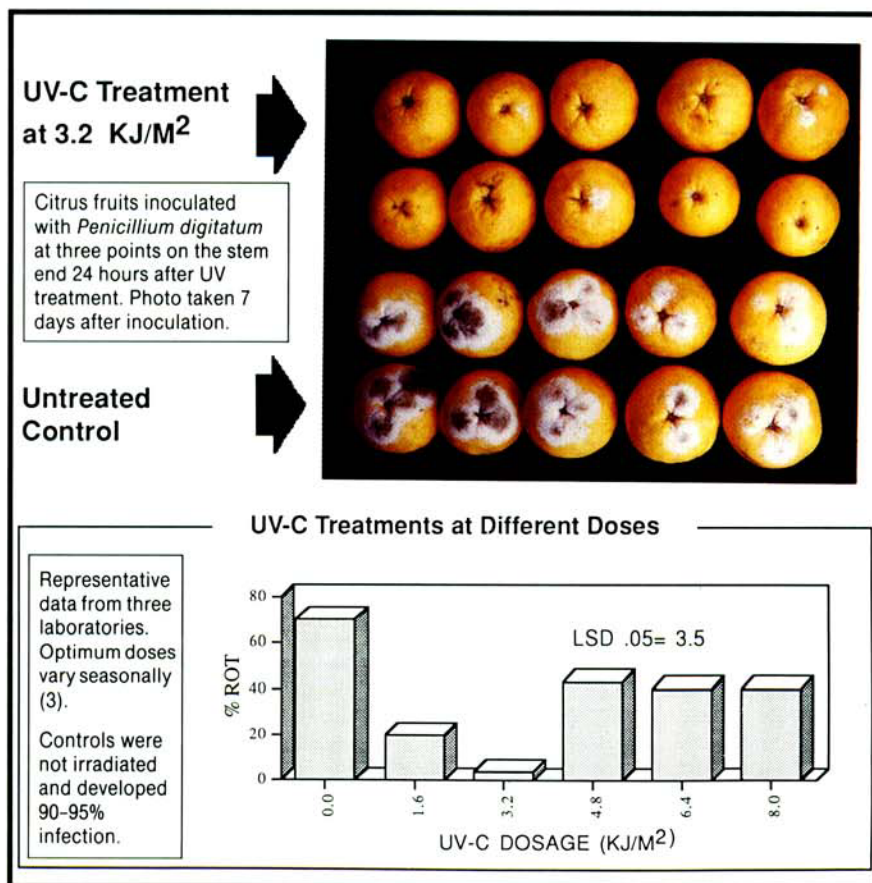

Fig. 2. Photo shows the difference in infection between UV-C-treated citrus and an untreated control. Graph shows the variation in percent rot with dosage of UV-C.

resistance and not solely to its germicidal activity. First, we found that tissue inoculated after UV-treatment was more resistant to invasion by the pathogen (Figs. 2 and 3). Also, the UV-effect was not correlated with increased UV doses. Optimum UV-C doses for induced resistance in the various commodities occurred in a narrow range, which was specific for each commodity (Figs. 2 and 3). The maximum protection provided by UV treatments occurred at varying periods after the treatment and depended on the commodity. Maximum tissue resistance was observed at 48–72 hours after treatment of peaches against *Monilinia fructicola* (14,15) and tomatoes against *Rhizopus stolonifer* (13). In sweet potatoes, maximum protection against Java black rot occurred 1–7 days after treatment (22).

Several factors have been found to influence the effectiveness of UV treatments on various commodities. It was found that grapefruits picked at various times during the growing season responded differently to UV treatments. A UV dose of 4.8 kJ/m² was required in November-picked fruit for maximum response. This declined to 1.6 and 3.2 kJ/m² in December- and January-picked fruit, respectively, and increased to 8 kJ/m² in February-picked fruit. Also, the temperature at which fruits were stored following UV treatment affected the resistance (3).

We are currently studying the management of various factors (visible light, temperature, etc.) that influence the effectiveness of UV-light as a postharvest treatment and "on line" application of UV-C during fruit processing. Treatments combining UV light with other biological control procedures and natural compounds are also underway. It was found that optimum UV doses for postharvest treatment of peaches appear to promote a natural population of antagonistic yeasts on the fruit surface (C. Stevens, *unpublished*).

Natural compounds. Natural plant- and animal-derived fungicides also may offer safe alternatives to synthetic fungicides for the control of postharvest diseases (25). Among these, chitosan (produced by the deacetylation of chitin) has proven particularly effective. Chitosan has the ability to form films that can be used to coat the surface of fruit and vegetables, and regulate gas and moisture exchange. Chitosan has also been shown to be fungicidal and to induce postharvest resistance responses in tissues (Figs. 6 and 7).

When applied as a coating, chitosan delayed ripening, reduced the incidence of decay, and in some instances stimulated several defense responses. Reduction of decay by chitosan was reported in tomato, cucumber, strawberry, and bell pepper fruits, and was attributed in part to its antifungal activity

(5,8). Chitosan reduced the radial growth of major postharvest pathogens (6). It also induced cellular alterations in *R. stolonifer* and *B. cinerea* (6,9). Examination of chitosan-treated bell pepper tissue revealed that chitosan limited the proliferation of *B. cinerea*, reduced the degradation of host cell wall components, and caused fungal damage (7). Invading hyphae often displayed various levels of cellular disorganization that ranged from wall loosening to cytoplasm disintegration, as a result of chitosan treatment (7).

The antifungal and resistance-eliciting properties of chitosan present exciting possibilities for crop protection, and postharvest preservation in particular. Recently, the eliciting property of chitosan was demonstrated with several postharvest commodities. Chitosan treatment induced antifungal hydrolases such as chitinases, β-1,3-glucanases, and chitosanases in strawberry fruit, bell pepper, and tomato fruit (4) (Fig. 7). In chitosan-treated bell peppers and tomatoes, chitinases, β-1,3-glucanases, and chitosanases remained elevated for up to 14 days after treatment. The deliberate induction of lytic enzymes in harvested tissue by prestorage treatment with chitosan could give the tissue a head start

in restricting fungal colonization. This is indirectly supported by the cytochemical results obtained in chitosan-treated bell pepper tissue, in which the induction of chitinase and β-1,3-glucanases was followed by a substantial reduction of chitin labeling of the walls of invading hyphae (4). The systemic nature and persistence of defense enzymes in plant tissue on elicitation by chitosan could be important in retarding the resumption of quiescent infections which typically become active when tissue resistance declines. If this is the case, such treatment could be important, since many postharvest diseases arise from latent infections that become active upon the decline of the biosynthetic potential of the tissue to produce antimicrobial compounds.

Chitosan treatment also stimulates various structural defense barriers in bell pepper and tomato fruit (7). The most common were thickening of host cell wall, formation of papillae, and plugging of some intercellular spaces with fibrillar material partially impregnated with amorphous electron-opaque substances which are presumably antifungal phenolic-like compounds (Fig. 7).

Antagonistic Microorganisms. A number of antagonistic microorganisms serve as alternatives to synthetic fungi-

UV-C Treatment at 7.5 KJ/M²

Golden Delicious apples were treated with UV-C and stored at 24 C for 30 days, and the incidence of natural rot infection was recorded.

Photograph was taken after 30 days of storage.

Untreated Control

UV-C Treatments at Different Dosages

Representative data from two laboratories. Optimum dosages vary with the different rot organisms.

These data represent total rots recorded after 30 days of storage at 24 C.

LSD .05= 3.4

% ROT

UV-C DOSAGE (KJ/M²)
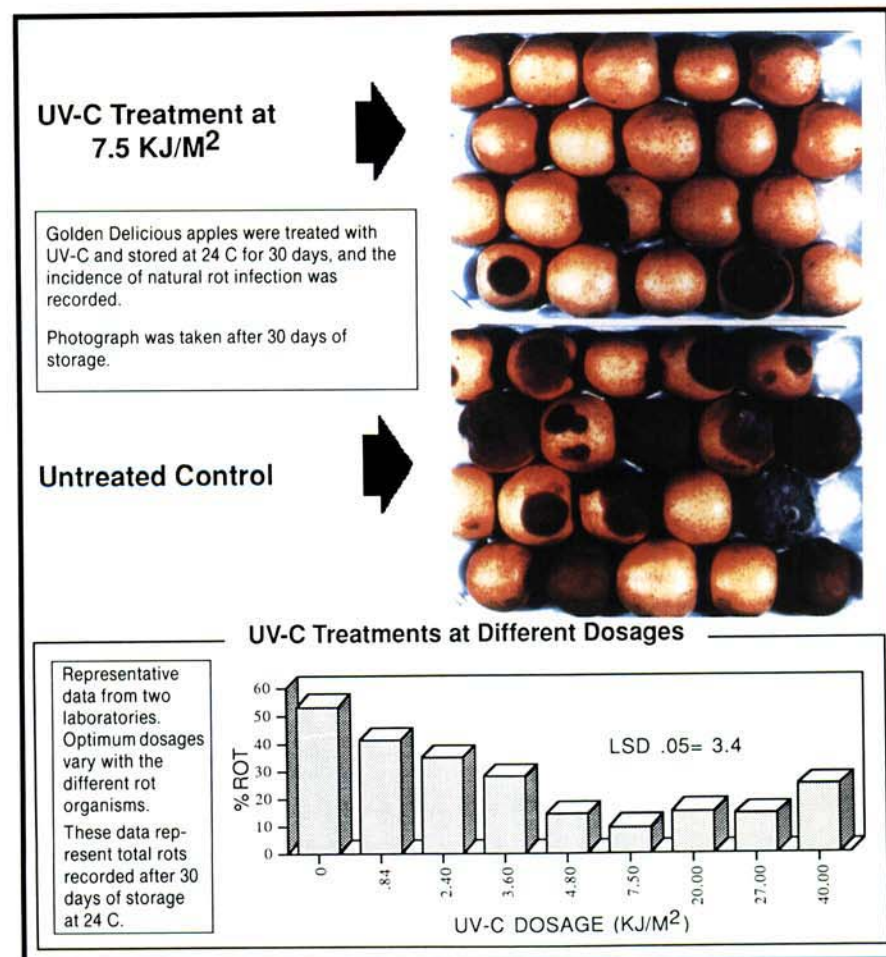0   .84   2.40   3.60   4.80   7.50   20.00   27.00   40.00

Fig. 3. Photo shows the difference in infection between UV-C-treated apples and an untreated control. Graph shows the variation in percent rot with dosage of UV-C.

cides and effectively control postharvest diseases (27,28). Among these, antagonistic yeasts have proved particularly effective (28). Considerable research has been conducted on the mode of action of effective yeast antagonists. These organisms appear to grow rapidly and colonize wound sites where infections occur and out-compete postharvest pathogens for space and nutrients (26, 28). It has also been demonstrated that antagonistic yeasts are capable of inducing resistance responses in the host tissue. The antagonistic yeast *Pichia guilliermondii* (US-7), which is effective in controlling a wide variety of postharvest rots of apples, peaches, and citrus, was shown to induce PAL (28) and the phytoalexin scoparone in citrus fruit peel (20), indicating the induction of a defensive response. Also, the yeast antagonist *Candida saitoana* was found to induce chitinase and cause the deposition of papillae along host cell walls in apple tissue (A. El Ghaouth and C. L. Wilson, *unpublished*).

Induction of resistance by microorganisms was shown to be an effective way to protect vegetative plant tissue (11). Resistance can be induced in plants by a variety of plant pathogens and non-pathogenic microorganisms (11). The use

of nonpathogenic or attenuated strains of postharvest pathogens needs to be explored. Lim and Rohrbach (12) used nonpathogenic strains of *Penicillium funiculosum* in pineapple to protect against pathogenic strains. It was not determined whether the protection resulted from competition, induced resistance, or a combination of both.

The Challenge

Intelligent manipulation of resistance in harvested commodities to extend their shelf life requires fundamental understanding of the nature of constitutive and induced resistance in harvested fruits and vegetables. Our present paradigm for viewing resistance is based on an understanding of resistance in the vegetative plant body. This may be misleading, since the selection pressure for resistance in harvested reproductive organs may be different from that in the vegetative plant.

Resistance in vegetative tissues and organs has been selected to produce plants that are robust enough to form reproductive structures which assure the survival of the species. Resistance in reproductive organs serves to protect the seed until it has been properly dispersed. Selection pressures in the evolution of

resistance in the vegetative plant body and in the reproductive organs have, therefore, been different. We might then expect different forms of resistance in vegetative and reproductive structures. However, since fruit and other reproductive organs evolved as modified leaves, certain vegetative resistance mechanisms may have been conserved in reproductive structures. We should consider the possibility that reproductive structures may have unique resistance mechanisms along with those already encountered in the vegetative plant body.

Resistance in harvested fruits and vegetables is inextricably bound to their stage of maturity and level of senescence. Recent studies, using antisense genetic constructions in tomato to delay ripening and thus control storage decay, clearly show this relationship (10). In general, the more mature and senescent a fruit or vegetable, the more susceptible it is to postharvest decay. This is probably associated with a decline in the tissue's ability to produce defensive compounds and structures. In our studies with UV-C-induced resistance in apple, peach, citrus, and carrot, we found that less mature tissues produced a greater resistance response. Producing consistent results after the application of resistance elicitors to harvested commodities requires fundamental understanding of how the physiological state of the tissue relates to this resistance response.

Energy is required for plant tissue to respond to elicitors and develop resistance responses. Energy flow in harvested commodities differs radically from that in the vegetative plant body. The vegetative plant structure is able to continually replenish its energy requirements by photosynthesis and the translocation of water and nutrients from other plant parts. Once a fruit or vegetable part is harvested, its nutrient supply from the mother plant is severed and its photosynthetic capabilities are greatly diminished. Energy conservation for defensive reactions would seem to be more important in harvested plant parts than in the vegetative plant. Induced resistance, which is an energy-conserving phenomenon (i.e., no resistant response occurs until the tissue is challenged), may be especially important in harvested commodities.

A variety of physical and biological elicitors are capable of inducing resistance responses, but whether each elicitor is stimulating a unique resistance response or they all elicit a similar response in the host tissue is unknown. In tobacco, Ward et al (24) found that a wide variety of elicitors activated the same series of mRNAs, which were encoded for chitinase, peroxidase, β-1,3-glucanase, and other defensive enzymes. Although a wide variety of agents may elicit a resistance response, the agents vary in their effectiveness. It would be
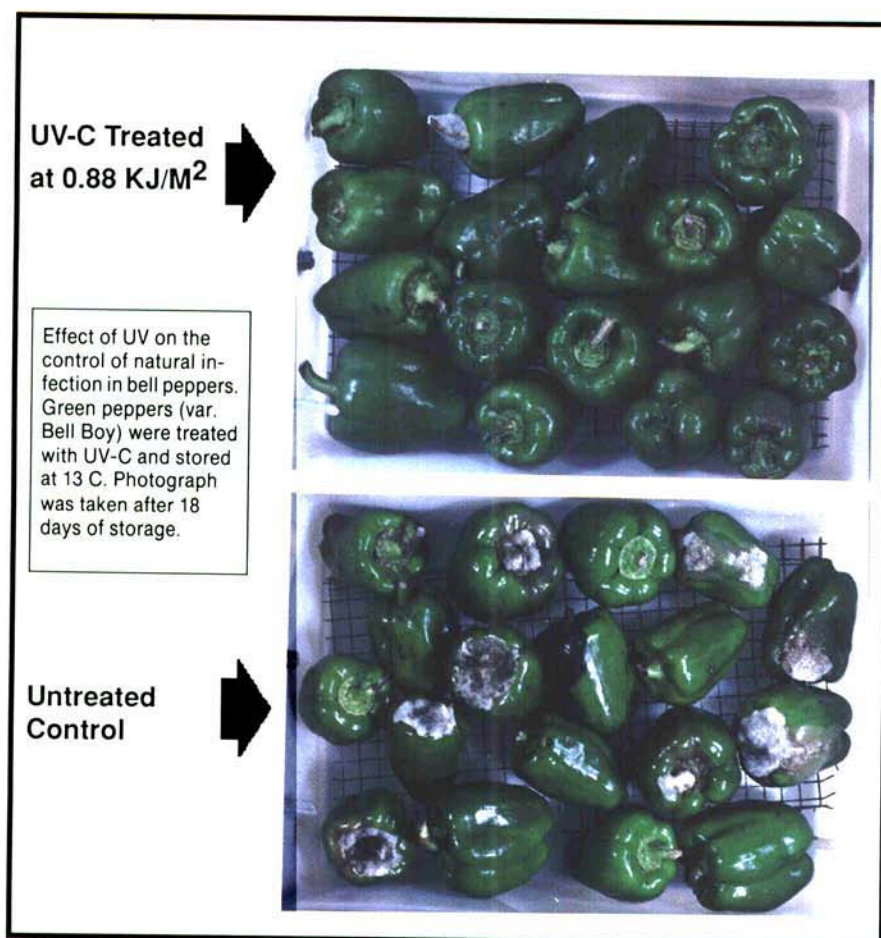

UV-C Treated at 0.88 KJ/M^2

Effect of UV on the control of natural infection in bell peppers. Green peppers (var. Bell Boy) were treated with UV-C and stored at 13 C. Photograph was taken after 18 days of storage.

Untreated Control

Fig. 4. Photos illustrate the difference in infection level between UV-C-treated pepper and an untreated control.

advantageous to select innocuous elicitors that effectively turn on host defenses and interfere with pathogen development.

Chitosan, a biodegradable food fiber, offers great potential as an antifungal preservative for fresh fruit and vegetables. The antifungal and eliciting activities of chitosan present considerable potential for crop protection. Research is needed to establish the mechanism by which this compound exerts its biological activities and to determine its compatibility with other available disease-control methods, especially biological antagonists. Several antagonistic yeasts were found to be compatible with chitosan (A. El Ghaouth and C. L. Wilson, *unpublished*). Chitosan is regarded as safe, as indicated by feeding trials with domestic animals. However, before it can be utilized as an antifungal preservative, its safety for human consumption and its effect on the organoleptic quality of fruits and vegetables needs to be established. Furthermore, extensive postharvest storage tests are necessary to determine the feasibility of using chitosan coatings commercially.

Postharvest treatments combining elicitors for resistance with other control practices for postharvest diseases perhaps hold the greatest promise for on line practices. Our research has demonstrated, for instance, that a natural compound such as chitosan not only elicits resistance responses in the host, but also acts independently as a fungicide. We are also working to combine chitosan with antagonistic yeasts to form a bioactive coating that will be fungicidal and will serve as a carrier for antagonists that inhibit storage rot pathogens. This strategy of combining various biocontrol treatments (multifaceted biological control) has been characterized (25).

Attention will have to be paid to the effects of various resistance-inducing treatments on the quality and safety of the treated commodities. Lu et al (14,15) studied the effect of UV-light and gamma irradiation on the quality of peaches and found that UV-treated peaches had lower sugar concentrations, total phenols, and anthocyanins than the untreated controls. They interpreted this UV effect as a delay in ripening, since these factors generally increase during the ripening process. UV- and gamma-treated fruits were also firmer in texture, further supporting this interpretation.

A variety of biological and technical problems will have to be overcome before we can utilize induced resistance as an on line practice for the control of postharvest diseases. For this technology to be applied effectively, a more fundamental understanding of the nature of induced resistance in fruits and vegetables will have to be established. Also, effective and economical delivery systems for the elicitors of induced-

resistance responses will have to be developed. These systems will vary with the characteristics of the elicitors. Some of our present practices for the control of postharvest diseases, such as hot water

treatment and synthetic fungicides, may already involve induced resistance as an important aspect of their mode of action.

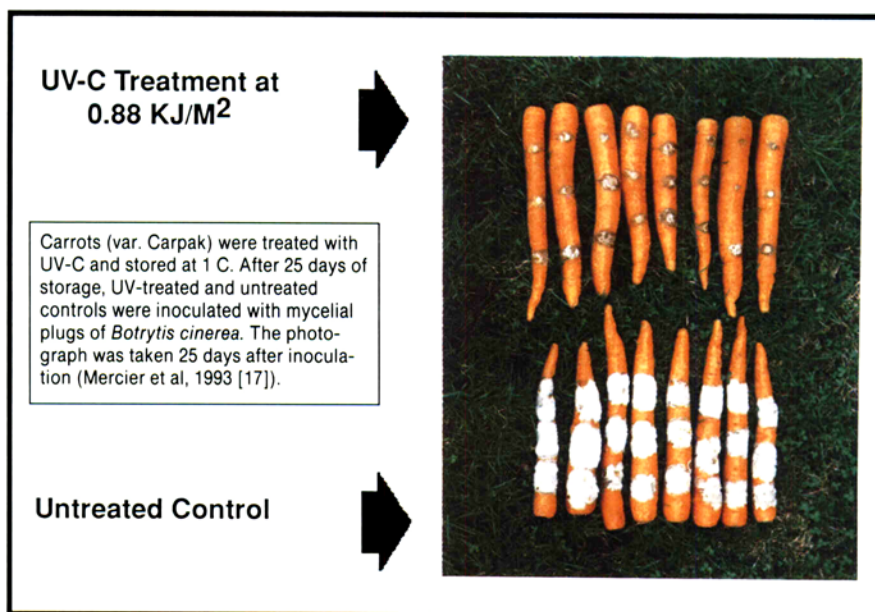Induced resistance in harvested commodities is a greatly underutilized

UV-C Treatment at 0.88 KJ/M^2

Carrots (var. Carpak) were treated with UV-C and stored at 1 C. After 25 days of storage, UV-treated and untreated controls were inoculated with mycelial plugs of *Botrytis cinerea*. The photograph was taken 25 days after inoculation (Mercier et al, 1993 [17]).

Untreated Control

Fig. 5. Photo illustrates the difference in infection level between UV-C-treated carrot and an untreated control.

Chitosan Treated

Mature green tomato fruit were surface-disinfected and air-dried. Fruit stems were carefully excised, and on each stem scar, either 400 μl of chitosan solution (10 mg/ml) or sterile water (control) was applied. After air-drying, fruit were inoculated by pipetting 50 μl of spore suspension of *Botrytis cinerea* onto each stem scar. Inoculated fruit and controls were held at 20 C in plastic containers at 95% RH for 14 days. In chitosan-treated fruit, disease development was not visible until 7 days after inoculation. With the control fruit, signs of infection were evident within 48 hours of inoculation. At the end of the 14-day storage, all inoculated controls reached an advanced stage of decay, whereas less than 10% of chitosan-treated fruit had developed disease. Photo taken 10 days after inoculation.
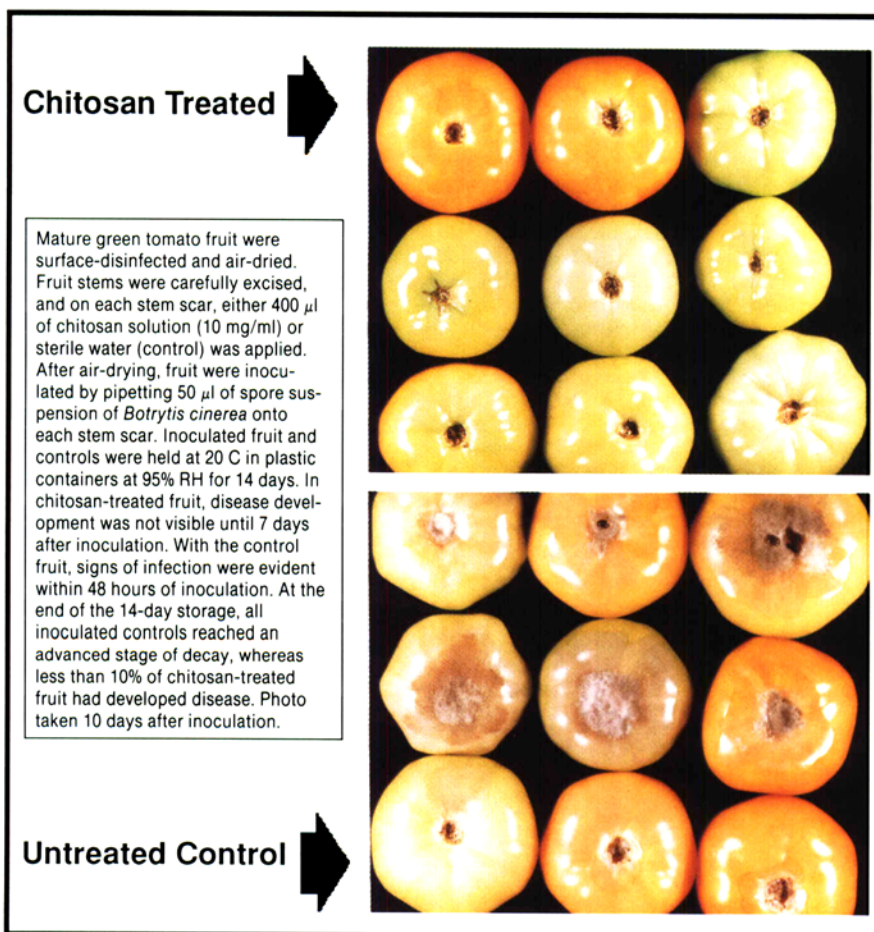
Untreated Control

Fig. 6. Photos illustrate the difference in infection level between tomato treated with chitosan and an untreated control.
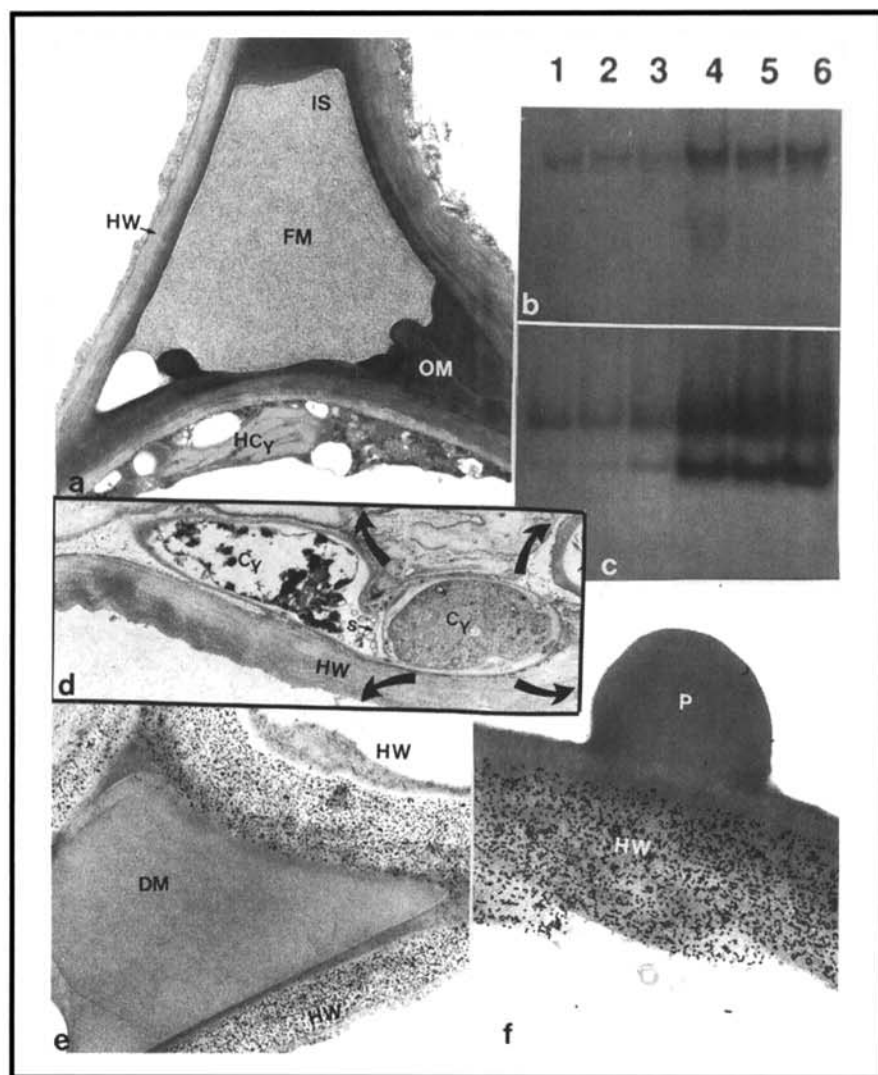
Fig. 7. Defense induction in pepper by chitosan. Transmission electron micrographs of chitosan-treated bell pepper tissue and β-1,3-glucanase and chitinase activities after native gel electrophoresis (PAGE). **(A)** Intercellular spaces filled with fibrillar material. Note the partial deposition of electron-opaque material. Panels **(B)** and **(C)** show acidic β-1,3-glucanase and basic chitinase, respectively. Noninoculated control lanes (1 and 2) and chitosan-treated lanes (4 and 5) stored for 24 and 48 hours. Inoculated control lane (3) and inoculated chitosan-treated lane (6) stored for 48 hours. **(D)** Severely altered fungal cell in contact with host wall. Note the retraction of degenerated protoplasm. Big arrows indicate various host defensive reactions that can further deter the establishment of an active lesion. **(E)** Intercellular spaces filled with fibrillar material. **(F)** Papilla deposition along host cell wall. Bell pepper fruit tissue labeled with the gold complexed exoglucanase for localization of cellulosic β-1,4-glucan. Note the regular and intense cellulose labeling over host walls (E and F). Abbreviations: Cy, cytoplasm; DM, deposited material; FM, fibrillar material; HW, host cell wall; HCy, host cytoplasm; IS, intercellular space; P, papilla; OM, opaque material; and S, septum.

resource for extending the shelf life of fruits and vegetables. The occurrence of this phenomenon in a wide range of divergent crops augurs well for its usefulness in the control of a large number of postharvest diseases. With the existing critical need for alternatives to synthetic fungicides, it is imperative that we continue to develop new approaches to control postharvest diseases.

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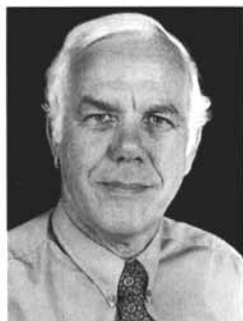
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Dr. Wilson is a research plant pathologist at the USDA-ARS Appalachian Fruit Research Station in Kearneysville, West Virginia. He received his B.A. degree from the University of Virginia in 1953 and his M.S. (1956) and Ph.D. (1958) degrees from West Virginia University. During the early part of his career, Dr. Wilson was a professor at the University of Arkansas, where he conducted research on forest pathogens and weed biocontrol. For the past 15 years, he has conducted research at the USDA-ARS Appalachian Fruit Research Station on alternatives to synthetic fungicides for the control of fruit diseases.

Dr. El Ghaouth, formerly with the Center for Horticultural Research, Laval University, Quebec, is currently a visiting scientist at the USDA-ARS Appalachian Fruit Research Station in Kearneysville, West Virginia. He received his B.A. degree from Kansas State University in 1985 and his M.S. (1988) and Ph.D. (1991) degrees from Laval University. Dr. El Ghaouth conducts research in collaboration with Dr. Wilson on alternatives to synthetic fungicides for the control of fruit diseases. His main research involves the manipulation of defense responses in harvested tissue by bioactive elicitors such as chitosan. Currently, Drs. El Ghaouth and Wilson are developing a bioactive coating for harvested commodities that will make it possible to exploit the antifungal and eliciting properties of the coating as well as the biological activity of the antagonist.

Dr. Chalutz is a senior scientist in the Department of Postharvest Science at the Volcani Center, Bet Dagan, Israel. He received his Ph.D. degree in plant pathology from the University of California at Davis in 1968 and joined the Department of Postharvest Science after spending a postdoctoral year at the Department of Biochemistry, University of Wisconsin, Madison. During subsequent years he headed the Department (1979–1983) as well as the Institute for Technology and Storage of Agricultural Products (1983–1987). Dr. Chalutz has spent three sabbatical years in the United States—in 1976 and 1982 at the University of Maryland and the USDA Plant Hormone Laboratory at Beltsville, Maryland, and in 1990 at the USDA Plant Molecular Biology Laboratory at Beltsville and the USDA Appalachian Fruit Research Station in Kearneysville, West Virginia. His main research interests are in the field of host-parasite interactions in harvested commodities with emphasis on the involvement of ethylene and its biosynthesis, postharvest handling and chilling injuries of citrus, and the development of biological and physical alternatives to synthetic chemical fungicides for the control of postharvest diseases of fruits and vegetables.

Dr. Droby is a senior research plant pathologist in the Department of Postharvest Sciences, Agricultural Research Organization, the Volcani Center, Bet Dagan, Israel. He received his B.Sc.

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