

Biological control of post-harvest diseases of fruits and vegetables: alternatives to synthetic fungicides

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Abstract

Spoilage of fruits and vegetables after harvest often causes losses as great as 25–50% of the harvested crop. Much of this is due to rot micro-organisms which are currently controlled by refrigeration and fungicides. A number of bacterial and fungal antagonists have been found that can effectively control post-harvest rots of peaches, citrus, apples, grapes and tomatoes. These antagonists have various modes of action that include antibiosis and /or competition for nutrients and space. The commercialization of some of these antagonists to control post-harvest decay of fruits and vegetables appears to be feasible and may present an alternative to synthetic pesticides.

Keywords

Biological control; post-harvest diseases; antagonists

Introduction

Withdrawal of a number of fungicides used to control post-harvest diseases of fruits and vegetables has caused alternative disease control methods to be sought. Biological control presents an attractive option. This paper examines the prospects for biological control of post-harvest diseases of fruits and vegetables and recommends future research directions.

Environmental concerns in the 1960s over pesticides, raised by Rachel Carson's book, *Silent Spring*, focused on the environmental impact of insecticides. Subsequent events led to the withdrawal of DDT and other insecticides from the market. During this period, fungicides and herbicides were perceived by the public and scientific community as relatively safe.

Use of fungicides world-wide is variable, comprising 26% of the pesticide market in Europe and Asia and only 6% in the United States (Jutsum, 1988). However, as most fungicides are applied to fruits and vegetables (*Table 1*), man is more subject to direct exposure to fungicides than to other pesticides applied to protect foliage.

In 1980, the Environmental Protection Agency (EPA) asked the National Academy of Sciences (NAS) to study the issue of pesticide residues on our food. It was particularly interested in the Delaney Clause under section 409 of the Federal Food, Drug and Cosmetic (FDC) Act, which stipulates a zero tolerance of any potentially oncogenic pesticide used on processed food.

In 1987, the NAS published its report (National Research Council, 1987) which contained a number of revelations. The report states that, as a class, the fungicides present special difficulties because nine oncogenic compounds account for about 90% of all fungicide sales. The NAS study concludes that fungicides constitute 60% of the oncogenic risk among all the pesticides used on food. The report further states: 'for certain crops in certain regions, the loss of all oncogenic compounds – particularly fungicides – would cause severe short-term adjustments in pest control practices because of the lack of economically viable alternatives'.

We face an urgent need for alternatives to fungicides for the control of plant diseases. As fungicides are used primarily on fruits and vegetables, alternatives are especially needed for these commodities.

Prospects for biological control in the post-harvest environment

Baker (1987) defines biological control of plant disease as 'the decrease of inoculum or the disease-producing activity of a pathogen accomplished through one or more organisms, including the host plant, but excluding man'. Using this broad definition, a number of potential biological control avenues are open for controlling post-harvest diseases of fruits and vegetables (Wilson and Wisniewski, 1989). Among these are: (1) the use of antagonistic micro-organisms; (2) the use of plant-derived fungicides from secondary plant metabolites; and (3) the manipulation of resistance responses in harvested commodities.

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Table 1. Global sales of fungicides used on the world's major crops*

Сгор	End-use value $(US\$ \times 10^{-6})$	Use (%)
Fruits and vegetables	1290	46
Rice	430	15
Wheat	380	14
Soya	55	2
Maize	40	1
Sugar beet	40	Ī
Cotton	40	1
Other	_	20

[&]quot;Adapted from Jutsum, 1988

Antagonistic micro-organisms

Researchers have explored the use of antagonistic microorganisms to control a variety of plant pathogens. The history of this research has been largely successful in the laboratory and a failure in the field. A few notable exceptions exist, such as the control of the crown gall bacterium, Agrobacterium tumefaciens, through the use of an antagonistic bacterium (Kerr, 1980) and the use of Trichoderma for the control of a number of soil-borne pathogens (Lewis and Papavizas, 1984).

Several antagonists were evaluated by deMatos (1983) for the biocontrol of Penicillium digitatum green mould on citrus. He was able to reduce mould incidence from 35% to 8% when the antagonist Trichoderma viride was inoculated with the pathogen into lemon peel. Colyer and Mount (1984) have shown that the post-harvest soft rot potential in potatoes can be reduced by 15% through treatment of seed pieces with the antagonistic bacterium, Pseudomonas putida. Seed pieces of the potato cultivar 'Superior' were dipped in a suspension of the antagonistic bacterium before planting.

Tong-Kwee and Rohrback (1980) were able to reduce the incidence of disease in pineapple fruit caused by Penicillium funiculosum by spraying the fruit with nonpathogenic strains of the pathogen. Tronsmo and Dennis (1983) were able to reduce the Botrytis responsible for preand post-harvest rotting of strawberries by applying sprays of Trichoderma species.

The post-harvest environment appears to present a better milieu for biological control than do field conditions. In the post-harvest environment, it is often possible to control temperature and humidity. In addition, the postharvest environment is an artificial 'ecological island' separated from the buffering effect of natural microbial ecosystems. Such conditions favour the use of introduced antagonists for biological control.

Several antagonistic micro-organisms have been found that exercise control over a number of different postharvest pathogens of stone fruits (Pusey and Wilson, 1984, 1988; Pusey et al., 1986, 1988), pome fruits (Tronsmo and Ystaas, 1980; Janisiewicz, 1987, 1988; Janisiewicz and Roitman, 1988), citrus fruits (Singh and Deverall, 1984; Wilson and Chalutz, 1989; Chalutz and Wilson, 1988a, 1990), and various other fruits and vegetables. Patents have been issued or are pending on a number of these antagonistic micro-organisms. Attempts are being made to commercialize some of these antagonists. Bacillus subtilis has been patented for the control of brown rot of stone fruit (Pusey and Wilson, 1988). Patents have been issued on Pseudomonas cepacia and Acremonium breve for the control of Botrytis and Penicillium rots of pome fruit (Janisiewicz, 1987, 1988; Janisiewicz and Roitman, 1988), and yeasts (Pichia guilliermondi, strain US-7 and Hanseniaspora uvarum, strain 138) for the control of a wide variety of rots of citrus, stone fruit, pome fruit and tomato (Wilson and Chalutz, 1989; Chalutz and Wilson, 1990).

The antagonist inhibits the pathogen directly by secretion of antibiotics. This is a common phenomenon in nature which may have an important role in protecting commodities against diseases before or after harvest. In screening tests for naturally occurring microbial antagonists of post-harvest diseases of citrus and deciduous fruits (Wilson and Chalutz, 1989), a large proportion of the epiphytic microbial population isolated from the surface of these fruits showed inhibition against fungal pathogens in culture. Bacillus subtilis exhibits potent antibiotic activity in culture against several important pathogens of fruits and vegetables (Pusey, 1989). The identity of the active substance (iturin) involved in this inhibition has been elucidated recently (Gueldner et al., 1988). Pseudomonas cepacia also controls a number of fruit rot pathogens and produces an antibiotic, pyrrolonitrin (Janisiewicz and Roitman, 1988).

The antagonist successfully competes with the pathogen for nutrients and/or space. Antagonists of this group are often better adapted than the pathogen to adverse environmental conditions. The antagonist may exhibit a rapid growth rate. It may be able to utilize effectively nutrients at low concentrations and survive and develop on the surface of the commodity or at the infection site under temperature, pH, or osmotic conditions which are unfavourable for the growth of the pathogen. Typically, such an antagonist will inhibit, but not kill the pathogen.

Yeast or yeast-like micro-organisms that exhibit antagonistic action against post-harvest pathogens fall into this category. An example is the yeast antagonist US-7. Its antagonistic activity against the citrus pathogen, Penicillium digitatum, can be reduced markedly by the addition of nutrients to the interaction site between the yeast and the pathogen (Droby et al., 1989). Effective competition for nutrients with the pathogen was demonstrated by this yeast also in culture, when both the antagonist and the pathogen were co-cultured in a minimal synthetic medium or in wound leachate solutions (Droby et al., 1989). Similarly, Enterobacter cloacae, a bacterium, inhibited germination of Rhizopus stolonifer through nutrient competition (Wisniewski, Wilson and Hershberger, 1989).

The antagonist induces resistance processes in the host. Documented evidence to support this possible mode of action is lacking. However, during the interaction of some biocontrol agents with the host, processes common to the wound healing response and the development of resistance have been noted. For example, when a cell suspension of the antagonistic yeast US-7 was placed on surface wounds of grapefruit, ethylene production increased, a phenomenon not observed when a non-effective yeast isolate was applied to the wounds (E. Chalutz, unpublished data). In citrus and in other commodities, ethylene induces activity of phenylalanine ammonia-lyase (PAL), an enzyme which catalyses the branch point step reaction of the shikimic acid pathway, leading to the biosynthesis of phenols, phytoalexins and lignins - all associated with induced resistance to diseases (Kuc, 1982). In citrus fruit, PAL activity was induced after the application to the peel of an effective yeast antagonist (E. Chalutz, unpublished data), possibly leading to increased resistance. An effective antagonist could also provide resistance to the host indirectly by changing the chemical and/or osmotic environment at the wound site to favour the antagonist over the pathogen (McLaughlin et al., 1990).

The antagonist directly interacts with the pathogen. Antagonistic fungi such as Trichoderma attack pathogens by direct parasitism or by the production of antibiotics. Results of light and electron microscopy illustrate the attachment of the antagonist yeast US-7 to the mycelium of the Botrytis pathogen (Biles et al., 1990). The possible production of glucanases or chitinases by the antagonist during such interactions is indicated by the apparent dissolution of mycelial cell walls at the point of attachment.

Plant secondary metabolites in biocontrol

Secondary metabolism consumes a considerable part of the plant's energy. Tens of thousands of compounds are produced that appear to be involved in plant fitness through their ability to 'repel or attract' other organisms (Rosenthal and Jansen, 1979). A number of effective insecticides have been derived from plants, but at present no fungicides of plant origin are available commercially. This is not because of a lack of effective fungicidal compounds in plants. Ark and Thompson (1959) showed that aqueous and organic solvent extracts of garlic contained very potent fungicidal and bactericidal activity against a variety of plant pathogens. They were able to control post-harvest brown rot of peaches effectively by dipping the fruit in an odourless garlic extract. Wilson, Franklin and Otto (1987) found that volatile compounds naturally produced by ripening peaches were highly fungicidal. Three of the compounds (benzaldehyde, methyl salicylate, ethyl benzoate) completely inhibited growth of two major rot fungi, Monilinia fructicola and Botrytis cinerea. A number of essential oils are produced by plants that have fungicidal activity and may have potential for the control of post-harvest diseases of fruit (Maruzzella et al., 1960). Homeopathic drugs of plant origin have also been shown to control certain post-harvest diseases (Khanna and Chandra, 1976).

It is estimated that < 2% of the described higher plant species have been screened for pesticide activity (Grainge and Ahmed, 1988). Most of this screening has been for insecticides: <1% of the plants have been observed for antimicrobial activity. This leaves a large untapped source for future fungicides. In the screening of plant extracts for fungicidal activity, $\approx 5\%$ of the plants exhibited fungicidal activity (C. L. Wilson, unpublished data).

Manipulation of resistance in harvested commodities

Resistance to pathogens in plants is the rule and susceptibility is the exception. Most of our understanding of resistance comes from studies of the vegetative plant. Resistance in harvested fruits and vegetables has been identified in only a few systems.

Resistance responses have been demonstrated in harvested citrus (Brown, Ismail and Barmore, 1978; Brown and Barmore, 1983; Baudoin and Eckert, 1985), apple (Lakshminarayana et al., 1987; Sommer and Fartlage, 1988) and potato (Austin et al., 1988). Compartmentalization of the pathogen within the plant tissue appears to be an important mechanism. Baudoin and Eckert (1985) showed that lignin-like substances were deposited in the outer peel after wounding. The level of resistance to Geotrichum candidum paralleled the amount of lignin-like deposition. Skene (1981) showed that apples wounded soon after harvest healed quicker and to a greater extent than apples wounded later in storage. This study suggested that wound healing was a cell-mediated reaction that resulted in lignin-like deposits. In potato, wound resistance was highly correlated with lipid and lignin deposits at the wound site (Marvis, Forbes-Smith and Seriven, 1989). As in apples and oranges, the longer the period between wounding and infection, the less disease incidence (Nnodu, Harrison and Workman, 1982). Curing and storage systems have been developed which promote wound-healing reactions in harvested commodities.

Plants have been shown to produce pectinase and proteinase inhibitors (Albersheim and Anderson, 1971; Fielding, 1981; Brown and Adikaram, 1983; Cervone et al., 1989). Albersheim and Anderson (1971) showed that proteins from plant cell walls inhibited polygalacturonases (PG) secreted by plant pathogens. Fielding (1981) found similar inhibitors in extracts of peach and plum fruit. The level of the PG-inhibitor activity was correlated negatively with the rate of fungal rot development in apple fruits. Abu-Goukh, Strand and Labavitch (1983) showed that the PG-inhibitor activity in Bartlett pear fruit decreased as the fruit matured, demonstrating a correlation between developmentally related changes, PG-inhibitor activity, and tissue susceptibility to pathogens. Identification and manipulation of pectinase and proteinase inhibitors in harvested commodities may provide an effective new way to control post-harvest diseases.

Certain resistance responses in plants are 'turned on' or induced (Kuc, 1982). At present there is only a rudimentary understanding of inducible resistance responses in harvested fruits and vegetables and how they might be used for post-harvest disease control. Caruso and Kuc (1979) found that the systemic resistance induced in cucumbers. muskmelon and watermelon by foliar inoculation with pathogens, was transferable to the fruit.

A variety of treatments have been shown to induce resistance responses in fruit. Stevens et al. (1990) and Lu et al. (1987) found that low doses of u.v. irradiation induced resistance in sweet potato and onion to post-harvest rots. Swinburne (1978) demonstrated that proteases from Nectria galligena were able to elicit benzoic acid in apple fruit that was antibiotic to the pathogen. The multiplicity of chemical and physical elicitors that can induce resistance in harvested commodities need to be explored and used for biological control.

Future directions and problems

Antagonists

Antagonistic micro-organisms hold promise as 'living fungicides' for the control of post-harvest diseases of fruits and vegetables. The path from the laboratory to commercial production of these biocontrol agents has several economic and biological obstacles.

The potential market for an antagonistic microorganism must be large enough to justify the research and development necessary for its commercialization. The specificity of an antagonist may prohibit its commercialization on economic grounds, even though it is highly effective. However, with the continued withdrawal of synthetic fungicides from the market, niches for safer alternatives are being created.

Patentability of an antagonist as a biocontrol agent is important. Companies cannot risk the investment needed to develop a product without assurance of a market advantage once it is developed. Patents are pending on antagonists to control post-harvest diseases of citrus, pome fruit, tomato, and other fruits and vegetables (Janisiewicz, 1988; Janisiewicz and Roitman, 1988; Pusey and Wilson,

Commercialization of an antagonist requires special technology that meshes biological control methods with existing commodity processing procedures. Pusey et al. (1986) were able to incorporate the antagonist B. subtilis into the fruit wax normally used to treat peaches on the processing line. In pilot tests, control of brown rot with B. subtilis (B-3) in the commercial wax was equal to that obtained with the wax plus the fungicide benomyl. Integration or minor modification of processing procedures may make biocontrol more attractive and economical as a control procedure. For example, McLaughlin et al. (1990) showed that addition of calcium chloride to yeast suspensions improved the ability of yeasts to control various post-harvest diseases of apples. This modified application method allows significant reduction of the amount of yeast biomass needed for control.

Registration and labelling of 'living fungicides' for the control of post-harvest diseases poses unique problems for pesticide regulators. The potential toxicity and pathogenicity of the antagonists will have to be evaluated. As these biocontrol preparations will be applied to food, any added carriers will have to be safe for consumption, as well as the antagonist. Those antagonists that are normal

inhabitants of fruit and vegetable surfaces are already consumed by man and may pose less potential risk than 'exotic' ones.

How will the public accept the application of 'living fungicides' to their food? Such an idea is really not new. From ancient times, pickling and fermentation by microorganisms has been an important form of food preservation. The deliberate addition of micro-organisms in the processing of bread and dairy products has long been accepted. The public, therefore, should accept microbial fungicides if they can be shown to be safe and effective alternatives to synthetic fungicides.

Fungicides of plant origin

Although plant pathologists have long recognized the importance of secondary metabolites in plant resistance, not much effort has gone into utilizing these compounds in plant disease control. This has been mainly because a number of very effective synthetic fungicides have been available that were thought to be safe for man and the environment. Recent withdrawal of some of these synthetic compounds makes the utilization of 'natural' fungicides in plants more appealing.

The argument has been made that 'natural' plant pesticides are no safer than synthetic ones (Ames, Magan and Gold, 1987). The coevolution and cohabitation of man with plants may have diminished the impact of toxic plant metabolites through the process of natural selection. Furthermore, it would seem that 'natural' plant metabolites might be more biodegradable than synthetic ones. Basson (1987), in studying poisoning of wildlife in southern Africa found that 'wherever coevolution with toxic plants existed, antelopes usually showed some superior detoxifying mechanisms or innate resistance'.

The use of natural volatiles to control post-harvest diseases has appeal. Commodities could be fumigated with the volatile or it could be incorporated into sprays or packaging. Prasad and Stadelbacker (1973) controlled Botrytis cinerea and Rhizopus stolonifer rots of strawberry and raspberry with acetaldehyde vapour. Acetaldehyde has also been used as a fumigant to control the green peach aphid on head lettuce (Stewart et al., 1980a); however, phytotoxicity from the fumigant has been reported (Stewart et al., 1980b).

Resistance in post-harvest commodities

If resistance in harvested fruits and vegetables is to be manipulated, a more fundamental understanding of the nature of the resistance is needed. Are resistance responses in the harvested commodity the same as those in the vegetative plant? Can resistance be induced in harvested fruits and vegetables? At this point, answers to these questions are incomplete.

Few attempts have been made to select and breed plants for resistance to post-harvest diseases. Breeders, in selecting fruits and vegetables for desirable horticultural characteristics, may have inadvertently selected for greater susceptibility to post-harvest diseases: commodities are selected for reduced tannin content (reduced bitterness) and thin cell walls (greater tenderness); high tannin content and thick cell walls are characteristics associated with resistance (Robertson, Meredith and Scorza, 1988).

Naturally occurring epiphytic micro-organisms on the surfaces of fruits and vegetables may impart resistance to harvested crops. In some instances an epiphytic antagonistic population may be under the genetic control of the host plant (Wilson, 1989). If such is the case, microbialimparted resistance could be manipulated in fruits and vegetables by gene manipulation. Genes that promote epiphytic antagonists could, perhaps, be identified and their expression enhanced or moved to other commodities.

Discussion

The abrupt withdrawal of synthetic fungicides from the market will cause short-term economic hardships to growers, pesticide manufacturers and the public. Longterm effects, however, may be favourable in that a greater effort will be put into finding safer alternatives to synthethic fungicides. In waging war against pests, as diverse an armamentarium as possible is needed.

A variety of biological control strategies are available as alternatives to the use of synthetic fungicides for the control of post-harvest diseases of fruits and vegetables. Development and implementation of this new technology will require greatly accelerated research. Co-operative research among state, federal and industrial laboratories is needed to develop products and procedures that are effective, safe and profitable.

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