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Review

Biological control of postharvest diseases of fruits and vegetables by microbial antagonists: A review

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ABSTRACT

Postharvest diseases cause considerable losses to harvested fruits and vegetables during transportation and storage. Synthetic fungicides are primarily used to control postharvest decay loss. However, the recent trend is shifting toward safer and more eco-friendly alternatives for the control of postharvest decays. Of various biological approaches, the use of antagonistic microorganisms is becoming popular throughout the world. Several postharvest diseases can now be controlled by microbial antagonists. Although the mechanism(s) by which microbial antagonists suppress the postharvest diseases is still unknown, competition for nutrients and space is most widely accepted mechanism of their action. In addition, production of antibiotics, direct parasitism, and possibly induced resistance in the harvested commodity are other modes of their actions by which they suppress the activity of postharvest pathogens in fruits and vegetables. Microbial antagonists are applied either before or after harvest, but postharvest applications are more effective than preharvest applications. Mixed cultures of the microbial antagonists appear to provide better control of postharvest diseases over individual cultures or strains. Similarly, the efficacy of the microbial antagonist(s) can be enhanced if they are used with low doses of fungicides, salt additives, and physical treatments like hot water dips, irradiation with ultraviolet light etc. At the international level, different microbial antagonists like *Debaryomyces hansenii* Lodder & Krejer-van Rij, *Cryptococcus laurentii* Kufferath & Skinner, *Bacillus subtilis* (Ehrenberg) Cohn, and *Trichoderma harzianum* Rifai, are being used. Biocontrol products like Aspire, BioSave, and Shemer etc., have also been developed and registered. Although the results of this technology are encouraging, we need to continue to explore potential uses on the commercial scale in different corners of the world.

1. Introduction

Postharvest decays of fruits and vegetables account for significant levels of postharvest losses. It is estimated that about 20–25% of the harvested fruits and vegetables are decayed by pathogens during postharvest handling even in developed countries (El-Ghaouth et al., 2004; Droby, 2006; Zhu, 2006; Singh and Sharma, 2007). In developing countries, postharvest losses are often more severe due to inadequate storage and transportation facilities. Synthetic fungicides are primarily used to control postharvest diseases of fruits and vegetables (El-Ghaouth et al., 2004; Korsten, 2006; Singh and Sharma, 2007; Zhu, 2006). However, the global trend appears to be shifting towards reduced use of fungicides on produce and hence, there is a strong public and scientific desire to seek safer and eco-friendly alternatives for reducing the decay loss in the harvested commodities (Mari et al., 2007). Among different biological approaches, use of the microbial antagonists like yeasts, fungi, and bacteria is quite promising and gaining popularity (Eckert and Ogawa, 1988; Droby et al., 1991; Wisniewski and Wilson, 1992; Droby, 2006; Korsten, 2006). This review deals with the use of microbial antagonists for controlling postharvest diseases of fruits and vegetables.

2. Basic approaches for using the microbial antagonists

There are two basic approaches for using the microbial antagonists for controlling the postharvest diseases of fruits and vegetables: (1) use of microorganisms which already exist on the produce itself, which can be promoted and managed, or (2) those that can be artificially introduced against postharvest pathogens.

2.1. Natural microbial antagonists

Natural occurring antagonists are those, which are present naturally on the surface of fruits and vegetables, and after isolation,

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antagonists are used for the control of postharvest diseases (Janisiewicz, 1987; Sobiczewski et al., 1996). Chalutz and Wilson (1990) found that when concentrated washings from the surface of citrus fruit were plated out on agar medium, only bacteria and yeast appeared while after dilution of these washings, several rot fungi appeared on the agar, suggesting that yeast and bacteria may be suppressing fungal growth. Thus, it indicates that when fruits and vegetables are washed, they are more susceptible to decay than those, which are not washed at all.

2.2. Artificially introduced microbial antagonists

Although the first reported use of a microbial antagonist was the control of Botrytis rot of strawberry (*Fragaria x ananassa* Duch.) with *Trichoderma* spp. (Tronsmo and Denis, 1977), the first classical work was the control of brown rot of stone fruits by *Bacillus subtilis* (Pusey and Wilson, 1984). Since then, several antagonists have been identified, and used for controlling postharvest diseases of different fruits and vegetables. Artificial introduction of microbial antagonists is more effective in controlling postharvest diseases of fruits and vegetables than other means of biological control.

Several microbial antagonists have been identified and artificially introduced on a variety of harvested commodities including citrus, pome, and stone fruits, and vegetables for control of postharvest diseases (Table 1). For instance, effective control of fruit rot decay of citrus was observed with yeasts such as *Pichia guilliermondii* Wiskerham, *Candida oleophila* Montrocher, *Candida sake* Saito and Ota, *Candida formata* Meyer & Yarrow, *Candida saitona* Nakase & Suzuki, *Debaryomyces hansenii* Lodder & Kre-Van Rij, *Aureobasidium pullulans* (de Bary) Arnaud, *Pantoea agglomerans* (Ewing & Fife) Gavini et al. *Saccharomyces cerevisiae* Hansen and *Metschnikowia fructicola* Kurtzman & Droby and *M. pulcherrima* Pittes & Miller (El-Ghaouth et al., 1998, Wilson and Chalutz, 1989; Chalutz and Wilson, 1990; Droby et al., 1991; Arras, 1996; Ippolito et al., 2000; Nunes et al., 2001a,b; Teixido et al., 2001; Karabulut et al., 2003; Spadaro et al., 2004; Lahlali et al., 2005; Droby, 2006; Long et al., 2006, 2007; Torres et al., 2007; Morales et al., 2008). Control of decay of citrus fruit caused by *Penicillium digitatum* (Pers.:Fr.) Sacc., and *Penicillium italicum* Wehmer was also reported with bacterial antagonists such as *Bacillus subtilis* (Ehrenberg) Cohn, *Burkholderia* (*Pseudomonas*) *cepacia* Palleroni & Holmes, and *Pesudomonas syringae* Van Hall (Singh and Deverall, 1984; Smilanick and Denis-Arrue, 1992; Huang et al., 1995; Bull et al., 1997; Singh, 2002; Long et al., 2007). Fungal antagonists including *Myrothecium roridum* Tode.:Fries (Appel et al., 1988) and *Trichoderma viride* Persoon.:Fries, (Borras and Aguilar, 1990; De-Matos, 1983; Kota et al., 2006) were also shown to reduced decay of citrus fruit. *Trichoderma harzianum* Rifai has been effective in controlling anthracnose in banana (Devi and Arumugam, 2005) and rambutan (*Nephelium lappaceum* L.) (Sivakumar et al., 2000), and gray mold in grapes, kiwifuits and pears (Batta, 2007).

The biocontrol potential of microbial antagonists was also reported on pome and stone fruits. On apples and pears, control of decay caused by *Botrytis cinerea* Pers.:Fr. and *Penicillium expansum* Link was reported with bacterial antagonists *Pseudomonas cepacia* Burkh, *Pseudomonas syringae* Van Halt and *Pseudomonas fluorescens* Migula (Janisiewicz et al., 1991; Mikani et al., 2008). Decay of apple was also controlled by antagonistic yeasts such as *Candida sake* Saito & Ota (Janisiewicz and Roitman, 1988; Teixido et al., 1999; Vinas et al., 1996; Usall et al., 2001; Zhou et al., 2002; Torres et al., 2006), *Candida oleophila* Montrocher (El-Neshawy and Wilson, 1997; Wisniewski et al., 1995), *Candida saitona* Nakase & Sutuki (El-Ghaouth et al., 1998). Chand-Goyal and Spotts (1997) have observed that *Cryptococcus infirmo-miniatus* (Okanuki) Phaff & Fell and *Cryptococcus laurentii* (Kufferath) Skinner were effective in controlling decay of apple and pear caused by *Botrytis cinerea* Pers.: Fries and *Penicillium expansum* Link. On stone fruits, different microbial antagonists have reduced postharvest diseases like brown rot, gay mold, Rhizopus rot and Penicillium rots (Pusey and Wilson, 1984; Wilson et al., 1987; Tian et al., 2002; Lin et al., 2003; Singh, 2004, 2005; Karabulut et al., 2005; Yao and Tian, 2005; Demoz and Korsten, 2006; Zhang et al., 2007a,b). The biocontrol potential of several other microbial antagonists has also been demonstrated in several fruits such as banana (Utkhede and Sholberg, 1986; Qin et al., 2004; Tian et al., 2004; Costa and Erabadupitiya, 2005 Devi and Arumugam, 2005), mango (*Mangifera indica* L.) (Pathak, 1997; Govender et al., 2005), litchi (*Litchi chinensis* Sonn.) (Jiang et al., 1997, 2001), papaya (*Carica papaya* L.) (Gamagae et al., 2003), guava (*Psidium guajava* L.) (Majumdar and Pathak, 1995), pineapple (Tong and Rohrbock, 1980), grapes (Chalutz et al., 1988; Karabulut et al., 2003), strawberry (Tronsmo and Denis, 1977; Batta, 2007; Zhang et al., 2007b; Zhao et al., 2007), avocado (Demoz and Korsten, 2006), kiwi fruit (*Actinidia deliciosa* Ber.) (Batta, 2007), jujube (Qin and Tian, 2004; Tian et al., 2005) and vegetables like tomatoes (Chalutz et al., 1988; Saligkarias et al., 2002; Xi and Tian, 2005), cabbage (*Brassica oleracea* var. *capitata* L.) (Adeline and Sijam, 1999), chillies (*Capsicum fruitsecence* L.) (Chanchaichaovivat et al., 2007) and potato (Colyer and Mount, 1984) (Table 1). The success of some of these microbial antagonists in laboratory studies and pilot tests conducted in packing houses have generated interest by several agrochemical companies in the development and commercialization of bioproducts containing microbial antagonists for control of postharvest diseases of fruits and vegetables. Several microbial antagonists have been patented and evaluated for commercial use, of which, ASPIRE, YieldPlus, and BIOSAVE-110 are used worldwide for controlling postharvest diseases of fruits and vegetables effectively.

3. Mode of action of microbial antagonists

A significant amount of research on the use of the microbial antagonists has been reviewed by several workers (Droby et al., 1989; Wisniewski et al., 1991; Filonow et al., 1996; Chand-Goyal and Spotts, 1997; Korsten et al., 1997; Filonow, 1998; Calvente et al., 1999; Janisiewicz et al., 2000; El-Ghaouth et al., 2004). However, the mechanism(s) by which microbial antagonists exert their influence on the pathogens has not yet been fully understood. It is important to understand the mode of action of the microbial antagonists because, it will help in developing some additional means and procedures for better results from the known antagonists, and it will also help in selecting more effective and desirable antagonists or strains of antagonists (Wilson and Wisniewski, 1989; Wisniewski and Wilson, 1992).

Several modes of action have been suggested to explain the biocontrol activity of microbial antagonists (Table 2). Still, competition for nutrient and space between the pathogen and the antagonist is considered as the major modes of action by which microbial agents control pathogens causing postharvest decay (Droby et al., 1992; Wilson et al., 1993; Filonow, 1998; Ippolito et al., 2000; Jijakli et al., 2001). In addition, production of antibiotics (antibiosis), direct parasitism, and possibly induced resistance are other modes of action of the microbial antagonists by which they suppress the activity of postharvest pathogens on fruits and vegetables (Janisiewicz et al., 2000; Barkai-Golan, 2001; El-Ghaouth et al., 2004).

3.1. Competition for space, and nutrients and space

Competition for nutrition and space between the microbial antagonist and the pathogen is considered as the major mode of action by which microbial antagonists suppress pathogens causing

Table 1
Microbial antagonists used for the successful control of postharvest diseases of fruits and vegetables.

Antagonists	Disease (pathogen)	Fruits/ vegetables	Reference(s)
Acremonium brevae(Sukapure& Thirumulachar) Gams	Gray mold (*Botrytis cinerea*)	Apple	Janisiewicz (1988)
Aureobasidium pullulans	Monilinia rot (*Monilinia laxa*)	Banana	Wittig et al. (1997)
	Penicillium rots (*Penicillium* spp.)	Citrus	Wilson and Chalutz (1989)
	Botrytis rot (*Botrytis cinerea*)	Grape	Schena et al. (2003)
	Soft rot (*Monilinia laxa*)	Grape	Barkai-Golan (2001)
Bacillus subtilis	Brown rot (*Lasiodiplodia theobromae*)	Apricot	Pusey and Wilson (1984)
	Stem end rot (*Botryodiplodia theobromae* Pat.)	Avocado	Demoz and Korsten (2006)
	Botrytis rot (*Botrytis cinerea*)	Cherry	Utkhede and Sholberg (1986)
	Green mold (*Penicillium digitatum*)	Citrus	Singh and Deverall (1984)
	Sour rot (*Geotrichum candidum* Link)	Citrus	Singh and Deverall (1984)
	Stem end rot (*Botryodiplodia theobromae, Phomopsis citri* Fawc., *Alternaria citri* Ell.& Pierce)	Citrus	Singh and Deverall (1984)
	Alternaria rot (*Alternaria alternata* (Fr.) Keissler)	Litchi	Jiang et al. (1997, 2001)
	Brown rot (*Lasiodiplodia theobromae*)	Nectarine	Pusey and Wilson (1984)
	Brown rot (*Lasiodiplodia theobromae*)	Peach	Pusey and Wilson (1984)
	Brown rot (*Lasiodiplodia theobromae*)	Plum	Pusey and Wilson (1984)
	Gray mold (*Botrytis cinerea*)	Strawberry	Zhao et al. (2007)
	Alternaria rot (*Alternaria alternata*)	Muskmelon	Yang et al. (2006)
Bacillus licheniformis (Weigmann) Verhoeven	Anthracnose (*Colletotrichum gloeosporioides*) and stem end rot (*Dothiorella gregaria* Sacc.)	Mango	Govender et al. (2005)
Bacillus pumilus	Gray mold (*Botrytis cinerea*)	Pear	Mari et al. (1996)
Burkholderia cepacia	Anthracnose (*Colletotrichum musae*)	Banana	Costa and Erabadupitiya (2005)
	Blossom end rot (*Colletotrichum musae*)	Banana	Costa and Erabadupitiya (2005)
Brevundimonas diminuta (Leifson & Hugh) Segers	Anthracnose (*Colletotrichum gloeosporioides*)	Mango	Kefialew and Ayalew (2008)
Candida guilliermondii	Gray mold (*Botrytis cinerea*)	Nectarine	Tian et al. (2002)
	Gray mold (*Botrytis cinerea*)	Peach	Tian et al. (2002)
	Gray mold (*Botrytis cinerea*)	Tomato	Saligkarias et al. (2002)
Candida membranifaciens Hansen	Anthracnose (*Colletotrichum gloeosporioides*)	Mango	Kefialew and Ayalew (2008)
Candida oleophila	Penicillium rot (*Penicillium expansum*)	Apple	El-Neshawy and Wilson (1997)
	Penicillium rots (*Penicillium digitatum and Penicillium italicum*)	Citrus	El-Neshawy and El-Sheikh (1998), Lahlali et al. (2004, 2005)
	Crown rot (*Colletotrichum musae*)	Banana	Lassois et al. (2008)
	Anthracnose (*Colletotrichum gloeosporioides*)	Papaya	Gamagae et al. (2003)
	Gray mold (*Botrytis cinerea*)	Peach	Karabulut and Baykal (2004)
	Gray mold (*Botrytis cinerea*)	Tomato	Saligkarias et al. (2002)
Candida sake (CPA-1)	Penicillium rot (*Penicillium expansum*)	Apple	Vinas et al. (1996), Usall et al. (2001), Torres et al. (2006), Morales et al. (2008)
	Gray mold (*Botrytis cinerea*)	Apple	Vinas et al. (1998)
	Rhizopus rot (*Rhizopus nigricans* Ehrenberg)	Apple	Vinas et al. (1998)
	Blue mold (*Penicillium expansum*)	Pear	Torres et al. (2006)
Cryptococcus laurentii	Bitter rot (*Glomerella cingulata*)	Apple	Blum et al. (2004)
	Brown rot (*Monilinia fructicola*)	Cherry	Karabulut and Baykal (2003), Tian et al. (2004), Qin et al. (2006)
	Alternaria rot (*Alternata alternata*) and Penicillium rot (*Penicillium expansum*)	Jujube	Qin and Tian (2004), Tian et al. (2005)
	Rhizopus rot (*Rhizopus stolonifer*)	Peach	Zhang et al. (2007c)
	Gray mold (*Botrytis cinerea*)	Peach	Zhang et al. (2007c)
	Brown rot (*Monilinia fructicola*)	Peach	Yao and Tian (2005)
	Blue mold (*Penicillium expansum*)	Peach	Zhang et al. (2007c)
	Mucor rot (*Mucor piriformis* Fischer)	Pear	Roberts (1990b)
	Gray mold (*Botrytis cinerea*)	Pear	Zhang et al. (2005)
	Blue mold (*Penicillium expansum*)	Pear	Zhang et al. (2003)
	Rhizopus rot (*Rhizopus stolonifer*)	Strawberry	Zhang et al. (2007b)
	Gray mold (*Botrytis cinerea*)	Tomato	Xi and Tian (2005)
Cryptococcus flavus	Mucor rot (*Mucor piriformis*)	Pear	Roberts (1990b)
Cryptococcus albidus (Saito) Skinner	Mucor rot (*Mucor piriformis*)	Pear	Roberts (1990b)
	Gray mold (*Botrytis cinerea*)	Apple	Fan and Tian (2001)
	Blue mold (*Penicillium expansum*)	Apple	Fan and Tian (2001)
Cryptococcus spp.	Blue mold (*Penicillium expansum*)	Apple	Chand-Goyal and Spotts (1997)
Debaryomyces hansenii	Green and blue mold (*Penicillium digitatum* and *Penicillium italicum*)	Citrus	Singh (2002)
	Blue mold (*Penicillium italicum*)	Citrus	Chalutz and Wilson (1990)
	Sour rot (*Geotrichum candidum*)	Citrus	Chalutz and Wilson (1990)
	Rhizopus rot (*Rhizopus stolonifer*)	Peach	Mandal et al. (2007), Singh (2004, 2005)
Enterobacter aerogenes Hormaeche & Edwards	Alternaria rot (*Alternaria alternata*)	Cherry	Utkhede and Sholberg (1986)
Enterobacter cloacae	Rhizopus rot (*Rhizopus stolonifer*)	Peach	Wilson et al. (1987)
Kloeckera apiculata(Rees) Janke	Botrytis rot (*Botrytis cinerea*)	Cherry	Karabulut et al. (2005)
	Penicillium rots (*Penicillium* spp.)	Citrus	Long et al. (2006, 2007)
	Green (*Penicillium digitatum*) and blue mold (*Penicillium italicum*)	Citrus	Long et al. (2006, 2007)
Metschnikowia fructicola	Botrytis rot (*Botrytis cinerea*)	Grape	Karabulut et al. (2003)

(*continued on next page*)

Table 1 (*continued*)

Antagonists	Disease (pathogen)	Fruits/ vegetables	Reference(s)
Metschnikowia pulcherrima	Blue mold (*Penicillium expansum*) and Gray mold (*Botrytis cinerea*)	Apple	Spadaro et al. (2002, 2004)
Pantoea agglomerans	Penicillium rot (*Penicillium expansum*)	Apple	Nunes et al. (2002a), Morales et al. (2008)
	Green (*Penicillium digitatum)* and blue mold (*Penicillium italicum*)	Citrus	Teixido et al. (2001), Torres et al. (2007)
	Penicillium rots (*Penicillium* spp.)	Citrus	Plaza et al. (2001)
	Rhizopus rot (*Rhizopus stolonifer*)	Pear	Nunes et al. (2001a,b)
Penicillium sp. (Attenuated strains)	Penicillium rot (*Penicillium* sp.)	Pineapple	Tong and Rohrbock (1980)
Penicillium frequentans Westling	Brown rot (*Monilinia* sp.)	Peach	Guijarro et al. (2007)
Pestalotiopsis neglecta (Thuemen) Steyaert	Anthracnose (*Colletotrichum gloeosporioides*)	*Apricot*	Adikaram and Karunaratne (1998)
Pichia anomala (Hansen) Kurtzman	Penicillium rots (*Penicillium* spp.)	Citrus	Lahlali et al. (2004)
	Crown rot (*Colletotrichum musae*)	Banana	Lassois et al. (2008)
Pichia guilliermondii	Blue mold (*Penicillium expansum*)	Apple	McLaughlin et al. (1990)
	Gray mold (*Botrytis cinerea*)	Apple	Janisiewicz et al. (1998), McLaughlin et al. (1990)
	Green mold (*Penicillium digitatum*)	Citrus	Chalutz and Wilson (1990), Wilson and Chalutz (1989)
	Rhizopus rot (*Rhizopus stolonifer*)	Grape	Chalutz et al. (1988)
	Gray mold (*Botrytis cinerea*)	Grape	Chalutz et al. (1988)
	Anthracnose (*Colletotrichum capsici* (Syd.) Butler & Bisby	Chillies	Chanchaichaovivat et al. (2007)
	Gray mold (*Botrytis cinerea*)	Tomato	Chalutz et al. (1988)
	Alternaria rot (*Alternata alternata*)	Tomato	Chalutz et al. (1988)
	Rhizopus rot (*Rhizopus nigricans*)	Tomato	Zhao et al. (2008)
Pseudomonas aeruginosa (Schroter) Migula	Bacterial soft rot (*Erwinia carotovora* sub sp. *Carotovora*	Cabbage	Adeline and Sijam (1999)
Pseudomonas cepacia	Blue mold (*P. expansum*)	Apple	Janisiewicz and Roitman (1988)
	Mucor rot (*Mucor piriformis*)	Apple	Janisiewicz and Roitman (1988)
	Gray mold (*Botrytis cinerea*)	Pear	Janisiewicz and Roitman (1988)
	Blue mold (*Penicillium expansum*)	Pear	Janisiewicz and Roitman (1988)
	Green mold (*Penicillium digitatum*)	Orange	Huang et al. (1993)
	Brown rot (*Monilinia fructicola*)	Nectarine	Smilanik et al. (1993)
	Brown rot (*Monilinia fructicola*)	Peach	Smilanik et al. (1993)
Pseudomonas corrugata Roberts & Scarlett	Brown rot (*Monilinia fructicola*)	Peach	Smilanik et al. (1993)
	Brown rot (*Monilinia fructicola*)	Nectarine	Smilanik et al. (1993)
Pseudomonas fluorescens Migula	Gray mold (*Botrytis mali* Ruehle)	Apple	Mikani et al. (2008)
Pseudomonas glathei	Green mold (*Penicillium digitatum*)	Citrus	Huang et al. (1995)
Pseudomonas putida (Trevisan) Migula	Soft rot (*Erwinia carotovora* sub sp. *carotovora*)	Potato	Colyer and Mount (1984)
Pseudomonas syringae	Blue mold (*Penicillium expansum*)	Apple	Janisiewicz (1987), Zhou et al. (2002)
	Green and blue mold (*Penicillium digitatum* and *P. italicum*)	Citrus	Wilson and Chalutz (1989)
	Gray mold (*Botrytis cinerea*	Apple	Zhou et al. (2001)
	Brown rot (*Monilinia laxa*)	Peach	Zhou et al. (1999)
Pseudomonas sp.	Crown rot (*Colletotrichum musae*)	Banana	Costa and Subasinghe (1998)
Rahuella aquatilis	Gray mold (*Botrytis cinerea*)	Apple	Calvo et al. (2003, 2007)
	Blue mold (*Penicillium expansum*)	Apple	Calvo et al. (2007)
Rhodotorula glutinis	Blue mold (*Penicillium expansum*)	Apple	Zhang et al. (2009)
	Gray mold (*Botrytis cinerea)*	Apple	Zhang et al. (2009)
	Alternaria rot (*Alternata alternata*)	Jujube	Tian et al. (2005)
	Penicillium rot (*Penicillium expansum*	Jujube	Tian et al. (2005)
	Blue rot (*Penicillium expansum*)	Pear	Zhang et al. (2008b)
	Gray mold (*Botrytis cinerea)*	Pear	Zhang et al. (2008b)
	Gray mold (Botrytis cinerea)	Strawberry	Zhang et al. (2007a)
Trichoderma harzianum	Anthracnose (Colletotrichum musae)	Banana	Devi and Arumugam (2005)
	Gray mold (*Botrytis cinerea*)	Grape	Batta (2007)
	Gray mold (*Botrytis cinerea*)	Kiwifruit	Batta (2007)
	Gray mold (*Botrytis cinerea*)	Pear	Batta (2007)
	Anthracnose (*Colletotrichum gloeosporioides*)	Rambutan	Sivakumar et al. (2000)
	Brown spot (*Gliocephalotrichum microchlamydosporum* (Mey) Wiley & Simmons	Rambutan	Sivakumar et al. (2002a,b)
	Stem end rot (*Botryodiplodia theobromae*	Rambutan	Sivakumar et al. (2001)
	Gray mold (*Botrytis cinerea*)	Strawberry	Batta (2007)
Trichoderma viride	Green mold (*Penicillium digitatum*)	Citrus	De-Matos (1983)
	Stem-end rot (*Botryodiplodia theobromae*)	Mango	Kota et al. (2006)
	Gray mold (*Botrytis cinerea*)	Strawberry	Tronsmo and Denis (1977)
Trichoderma spp.	Sour rot (*Geotrichum candidum*)	Citrus	De-Matos (1983)
	Fruit rots caused by *Lasiobasidium theobromae*, *Phomopsis psidi* and *Rhizopus* spp.	Guava	Majumdar and Pathak (1995)
	Fruit rots (*Lasiobasidium theobromae* and *Rhizopus* spp.)	Mango	Pathak (1997)
Trichosporon pullulans (Lindner) Didlens & Lodder	Alternaria rot (*Alternata alternata*)	Cherry	Qin et al. (2004)
	Gray mold (*Botrytis cinerea*)	Cherry	Qin et al. (2004)

Table 2
Suggested modes of action of some microbial antagonists for controlling postharvest diseases of fruits and vegetables.

Commodity	Postharvest disease	Antagonist	Reference(s)
1. Antibiotic production			
Apple	Blue mold	*Pseudomonas cepacia*	Janisiewicz and Roitman (1988), Janisiewicz et al. (1991)
	Mucor rot	*Pseudomonas cepacia*	Janisiewicz and Roitman (1988)
	Gray mold	*Pseudomonas syringae*	Bull et al. (1998)
Apricot	Brown rot	*Bacillus subtilis*	Pusey et al. (1988)
Cherry	Brown rot	*Bacillus subtilis*	Utkhede and Sholberg (1986)
	Alternaria rot	*Enterobacter aerogenes*	Utkhede and Sholberg (1986)
Citrus	Sour rot	*Bacillus subtilis*	Singh and Deverall (1984)
	Green mold	*Bacillus subtilis*	Singh and Deverall (1984), Smilanick and Denis-Arrue (1992)
	Green mold	*Pseudomonas syringae*	Bull et al. (1998)
	Stem-end rot		Singh and Deverall (1984)
	Sour rot	*Trichoderma spp.*	De-Matos (1983)
Nectarine	Brown rot	*Bacillus subtilis*	Pusey et al. (1988)
	Brown rot	*Pseudomonas corrupta*	Smilanik et al. (1993)
Peach	Brown rot	*Bacillus subtilis*	Pusey et al. (1988)
	Brown rot	*Pseudomonas cepacia*	Smilanik et al. (1993)
Pear	Blue mold	*Pseudomonas cepacia*	Janisiewicz and Roitman (1988)
	Gray mold	*Pseudomonas cepacia*	Janisiewicz and Roitman (1988)
Plum	Brown rot	*Bacillus subtilis*	Pusey et al. (1988)
II. Nutritional competition (N) and/or Induction of host resistance (HR)			
Apple	Blue mold	*Pseudomonas cepacia* (HR)	Janisiewicz (1987)
	Gray mold	*Acremonium brevae* (HR)	Janisiewicz (1988)
	Gray mold	*Debaryomyes hansenii* (N + HR)	Wisniewski et al. (1988), Roberts (1990a),
	Gray mold	*Cryptococcus humicola* Fricke (N)	Filonow et al. (1996)
	Gray mold	*Aureobasidium pullulans* (N + HR)	Ippolito et al. (2000), Castoria et al. (2001)
	Blue mold	*Aureobasidium pullulans* (N + HR)	Ippolito et al. (2000), Castoria et al. (2001)
	Blue mold	*Aureobasidium pullulans* (N)	Bencheqroun et al. (2007)
Citrus	Green mold	*Debaryomyces hansenii* (N + HR)	Chalutz and Wilson (1990), Droby et al. (1992)
	Blue mold	*Debaryomyces hansenii* (N + HR)	Droby et al. (1989), Chalutz and Wilson (1990),
	Sour rot	*Debaryomyces hansenii* (N + HR)	Chalutz and Wilson (1990)
Grapes	Gray mold	*Debaryomyces hansenii* (N)	Chalutz et al. (1988)
	Rhizopus rot	*Debaryomyces hansenii* (N)	Chalutz et al. (1988)
	Gray mold	*Aureobasidium pullulans* (N + HR)	Castoria et al. (2001)
	Blue mold	*Aureobasidium pullulans* (N + HR)	Castoria et al. (2001)
	Rhizopus rot	*Aureobasidium pullulans* (N + HR)	Castoria et al. (2001)
Peach	Rhizopus rot	*Enterobacter cloacae* (N)	Wisniewski et al. (1988)
Strawberry	Gray mold	*Cryptococcus laurentii* (N)	Castoria et al. (1997)
	Gray mold	*Rhodotorula glutinis* (N)	Castoria et al. (1997)
Tomato	Rhizopus rot	*Debaryomyces hansenii* (N)	Chalutz et al. (1988)
	Gray mold	*Debaryomyces hansenii* (N)	Chalutz et al. (1988)
	Alternaria rot	*Debaryomyces hansenii* (N)	Chalutz et al. (1988)

decay in harvested fruits and vegetables (Droby et al., 1989; Wilson and Wisniewski, 1989). To compete successfully with pathogen at the wound site, the microbial antagonist should be better adapted to various environmental and nutritional conditions than the pathogen (Barkai-Golan, 2001; El-Ghaouth et al., 2004).

3.1.1. Space

Rapid colonization of fruit wound by the antagonist is critical for decay control, and manipulations leading to improved colonization enhance biocontrol (Mercier and Wilson, 1994). Thus, microbial antagonists should have the ability to grow more rapidly than the pathogen. Similarly, it should have the ability to survive even under conditions that are unfavorable to the pathogen (Droby et al., 1992). The biocontrol activity of microbial antagonists with most harvested commodities increased with the increasing concentrations of antagonists and decreasing concentrations of pathogen. For example, *Candida saitona* was effective at a concentration of 10^7 CFU/ml for controlling *Penicillium expansum* on apples (McLaughlin et al., 1990). In an another study, El-Ghaouth et al. (1998) reported that for *Candida saitona*, a concentration of 10^8 CFU/ml was better in controlling blue mold (*Penicillium expansum*) on apples. This qualitative relationship, however, is highly dependent on the ability of the antagonists to multiply and grow at the wound site. This was demonstrated by using a mutant of *Pichia guilliermondii*, which lost its biocontrol activity against *Penicillium digitatum* on grapefruit and against *Botrytis cinerea* on apples, even when applied to the wounds at concentrations as high as 10^{10} CFU/ml (Droby et al., 1991). The cell population of this mutant remained constant at the wound sites during incubation period, while that of the wild type increased 10- to 20-fold, within 24 h.

3.1.2. Attachment

Attachment by microbial antagonist to the pathogen hyphae appears to be an important factor necessary for competition for nutrients as shown by the interactions of *Enterobacter cloacae* (Jordon) Hormaeche & Edwards and *Rhizopus stolonifer* (Ehrenberg: Fries) Lind (Wisniewski et al., 1989), and *Pichia guilliermondii* Wickerham and *Penicillium italicum* Wehmer (Arras et al., 1998). In vitro studies conducted on such interactions revealed that due to direct attachment, antagonistic yeasts and bacteria take nutrients more rapidly than target pathogens and thereby prevent spore germination and growth of the pathogens (Droby et al., 1989, 1998; Wisniewski et al., 1989).

In contrast, direct physical interaction did not appear to be required for the antagonistic activity of *Aureobasidium pullulans* (de Bary) Arnaud against *Botrytis cinerea* Pers.: Fries, *Penicillium expansum* Link, *Rhizopus stolonifer*, and *Aspergillus niger* van Tieghem infecting table grapes (*Vitis vinifera* L.) and *Botrytis cinerea* and *Penicillium expansum* on apple (*Malus domestica* Borkh.) fruit (Castoria et al., 2001). In these examples, antagonism was not the result of direct attachment of the microbial antagonist(s) with hyphae of the pathogens, but other mechanisms like antibiosis might have played a significant role for antagonism.

3.1.3. Nutrient competition

Research work conducted on this mode of action of microbial antagonists supports the hypothesis that competition for nutrients plays a major role in the mode of action of *Pichia guilliermondii* against *Penicillium digitatum* Pers.: Fries) Sacc., in citrus (Droby et al., 1992; Arras et al., 1998), *Enterobacter cloacae* against *Rhizopus stolonifer* on peach [*Prunus persica* (L.) Batsch] (Wisniewski et al., 1989), *Cryptococcus laurentii* against *Botrytis cinerea* on apple (Roberts, 1990a), and *Rhodotorula glutinis* (Fresenius) Harrison and *Cryptococcus laurentii* against *Penicillium expansum* and *Botrytis cinerea*, respectively (Castoria et al., 1997) and *Metschnikowia pulcherrima* Pitt & Miller on apples (Kim et al., 1997). *M. pulcherrima* out competes pathogens like *Botrytis cinerea* and *Penicillium expansum* in apple through iron depletion (Saravanakumar et al., 2008). As a result of its ability for suppressing postharvest diseases, Kurtzman and Droby (2001) and Grebenisan et al. (2008) have recommended it as potential yeast for controlling fruit rots. Biocontrol of gray mold (*Botrytis cinerea*) on apple by *Metschnikowia pulcherrima* was reduced or totally suppressed by the addition of several nutrients suggesting that competition for nutrients plays a role in the biocontrol capability of *Metschnikowia pulcherrima* against *Botrytis cinerea* (Piano et al., 1997). Further, non-pathogenic species of *Erwinia*, such as, *E. cypripedii* (Hori) Bergey, showed antagonistic activity against various isolates of *Erwinia caratovora sub sp. caratovora* (Jones) Bergey, the causal agent of soft rot of many vegetables like carrot, tomatoes (*Lycopersicon esculentum* L.) and pepper (*Capsicum annuum* L.), primarily by competing for nutrients (Moline, 1991; Moline et al., 1999). It has been demonstrated through in vitro studies that microbial antagonists take up nutrients more rapidly than pathogens, get established and inhibit spore germination of the pathogens at the wound site (Wisniewski et al., 1989; Droby and Chalutz, 1994; Droby et al., 1998).

3.1.4. Populations of the microbial antagonist

The level of control provided by the microbial antagonists is also highly dependent on the initial concentration of the antagonists applied on the wound site and the ability of the antagonist to rapidly colonize the wound site (Janisiewicz and Roitman, 1988; Wisniewski et al., 1989; McLaughlin et al., 1990). In general, microbial antagonists are most effective in controlling postharvest decay on fruits and vegetables when applied at a concentration of 10^7–10^8 CFU/ml (McLaughlin et al., 1990; El-Ghaouth et al., 2004), and rarely, higher concentrations are required.

Currently, there is only fragmented data regarding the antagonist-pathogen interaction in terms of competitions for limiting nutrients essential for pathogenesis. Once more information regarding the specificity of competition between antagonistic and pathogens in fruit wounds is available and genes responses of antagonism of biocontrol agents have been characterized, it will be possible to develop antagonistic stains with a higher rate of transport and/or metabolism of limiting nutrient essential for pathogenesis. This may allow us to circumvent some of the limitations of microbial antagonists.

3.2. Production of antibiotics

Production of antibiotics is the second important mechanism by which microbial antagonists suppress the pathogens of harvested fruits and vegetables. For instance, bacterial antagonists like *Bacillus subtilis* and *Pseudomonas cepacia* Burkh are known to kill pathogens by producing the antibiotic iturin (Gueldner et al., 1988; Pusey, 1989). The antagonism so produced by *Bacillus subtilis* was effective in controlling fungal rot in citrus (Singh and Deverall, 1984) and *Monilinia fructicola* (Winter) Honey in peaches and cherries (Pusey and Wilson, 1984; Utkhede and Sholberg, 1986). Further, *Pseudomonas cepacia* inhibited the growth of postharvest pathogens like *Botrytis cinerea* and *Penicillium expansum* in apple by producing an antibiotic, pyrrolnitrin (Janisiewicz and Roitman, 1988; Janisiewicz et al., 1991). *Pseudomonas cepacia* was also effective in controlling green mold (*Penicillium digitatum*) in lemon (*Citrus limon* L.) by producing antibiotics (Smilanick and Denis-Arrue, 1992). Similarly, the bacterial antagonist, *Pseudomonas syringae* Van Hall, controlled green mold of citrus and gray mold of apple, by producing an antibiotic syringomycin (Bull et al., 1998). However, the production of this antibiotic was never detected on the fruit and vegetables despite extensive efforts, raising a doubt on the role of the antibiosis in postharvest diseases control and suggesting the operation of a different mechanism not dependent on the production of syringomycin (Bull et al., 1998).

Although, antibiosis might be an effective tool for controlling postharvest diseases in a few fruits and vegetables, at present emphasis is being given for the development of non-antibiotic producing microbial antagonists for the control of postharvest diseases of fruits and vegetables (El-Ghaouth et al., 2004; Singh and Sharma, 2007). Researchers are aiming to isolate, evaluate or to develop those antagonistic microorganisms that control postharvest diseases of harvested commodities by the mechanism of competition for space and nutrient, direct parasitism or induced resistance (Droby, 2006).

3.3. Direct parasitism

In the literature, very little information is available on direct parasitism of the microbial antagonists in controlling postharvest diseases of fruits and vegetables. However, Wisniewski et al. (1991) observed that while *Pichia guilliermondii* cells had the ability to attach to the hyphae of *Botrytis cinerea* and *Penicillium*. After yeast cells were dislodged from the hyphae, the hyphal surface appeared to be concave and there was partial degradation of the cell wall of *Botrytis cinerea* at the attachment sites. In contrast, co-culturing *Botrytis cinerea* with non-antagonistic yeast elicited only a loose attachment to the fungus with no pitting in the hyphae (Wisniewski et al., 1991). Similarly, *Candida saitona* Nakase & Suzubi attached strongly to the hyphae of *Botrytis cinerea* and caused swelling (El-Ghaouth et al., 1998).

Microbial antagonists also produce lytic enzymes such as gluconase, chitinase, and proteinases that help in the cell wall degradation of the pathogenic fungi (Lorito et al., 1993; Castoria et al., 1997, 2001; Jijakli and Lepoivre, 1998; Kapat et al., 1998; Mortuza and Ilag, 1999; Chernin and Chet, 2002). Bonaterra et al. (2003) reported that direct parasitism was a major factor that permitted *Pantoea agglomerans* (Ewing & Fife) Gavini et al. to control *Monilinia laxa* (Aderh. & Ruhl.) Honey or *Rhizopus stolonifer* decay on stone fruits. Thus, strong attachment of microbial antagonist with enhanced activity of cell wall degradation enzymes may be responsible for enhancing the efficacy of microbial agents in controlling the postharvest diseases of fruits and vegetables (Wisniewski et al., 1991). And, attachment of the microbial antagonists to a site enhances their potential activity for the utilization of nutrients at the invasion site; it partly affects the access of the pathogen to nutrients as well (El-Ghaouth et al., 2004).

3.4. Induced resistance

Induction of defense responses in the harvested fruits and vegetables by the microbial antagonists has been suggested and shown as another mode of action of microbial antagonists for controlling postharvest decay in them (Arras, 1996; El-Ghaouth et al., 1998; Ippolito et al., 2000). For example, *Cryptococcus saitona* induced chitinase activity and formed structural barrier (papillae) on host cell walls in apple against *Penicillium expansum* (El-Ghaouth et al., 1998). Similarly, *Aureobasidium pullulans* caused a transient increase in the activity of 1,3-gluconase, peroxidase, and chitinase enzymes in apple wounds which stimulated wound healing processes and induced defense mechanisms against *Penicillium expansum* (Ippolito et al., 2000). Induction of disease resistance responses was also reported in pineapple, avocado, and citrus fruits (Tong and Rohrbock, 1980; Prusky et al., 1994; Rodov et al., 1994; Arras, 1996).

Microbial antagonists induced disease resistance in the harvested commodities by the production of antifungal compounds, as in avocado (*Persea americana* Mill) fruit (Prusky et al., 1994; Yakoby et al., 2001), and accumulation of phytoalexins, like scoparone and scopoletin in citrus fruit (Rodov et al., 1994; Arras, 1996). Production of such antifungal compounds by microbial antagonists in the host cells help in inducing defense mechanism and hence provide biocontrol on the harvested commodities. Although a causal connection between the accumulation of host defense responses and bioprotection by antagonistic yeasts has not yet been clearly established, the occurrence of high levels of host antifungal compounds in protected tissue suggests their implication in diseases resistance. Detailed studies regarding the implications of induced defense responses in the bioprotection by microbial antagonists are needed. In fruit wounds, some microbial antagonists often produce a large amount of extra-cellular mucilage along host cell walls. This extra-cellular mucilage is believed to be implicated in cell adhesion and may well contain active chemical elicitors that provides signals for recognition and subsequent responses, providing defense mechanism (Wisniewski et al., 1991; Castoria et al., 1997; El-Ghaouth et al., 1998). Further, oligosaccharide fragments of yeast cell wall polysaccharides are known to be active elicitors of host defense responses (Base et al., 1992).

4. Introduction of microbial antagonists

Many factors are involved for the introduction of a microbial antagonist for effective control of postharvest diseases of fruits and vegetables. Various studies have indicated that microbial agent should be introduced to wound site before the arrival of the pathogen (Smilanick, 1994; Barkai-Golan, 2001; El-Ghaouth et al., 2004; Droby, 2006; Singh and Sharma, 2007). For instance, *Trichoderma viride* Pers.: Fries antagonist was only effective in controlling *Lasiodiplodia theobromae* (Pat.) Griffith & Maubl in banana (*Musa* spp.) fruit when it was introduced 4 h prior to the inoculation of the pathogen (Mortuza and Ilag, 1999); otherwise it was not effective at all. Another factor, which is equally important for the effectiveness of a microbial antagonist, is the presence of moisture in the wound sites. For example, antagonistic yeast *Candida oleophila* Montrocher was effective in controlling *Botrytis cinerea* in apple only when it was applied to fresh wounds but when moisture dried in the fruit wound later, it became a limiting factor for yeast growth and hence for the control (Mercier and Wilson, 1995). In addition, a microbial antagonist should have certain desirable characteristics to meet the basic requirements of the biological control as reported hereunder.

4.1. Criteria for an ideal antagonist

A potential microbial antagonist should have certain desirable characteristics to make it an ideal bioagent (Wilson and Wisniewski, 1989; Barkai-Golan, 2001): The antagonist should be: (a) genetically stable; (b) effective at low concentrations; (c) not fastidious in its nutritional requirements; (d) capable of surviving under adverse environmental conditions; (e) effective against a wide range of the pathogens and different harvested commodities; (f) resistant to pesticides; (g) a non-producer of metabolites harmful to human; (h) non-pathogenic to the host; (i) preparable in a form that can be effectively stored and dispensed; and (j) compatible with other chemical and physical treatments. In addition, a microbial antagonist should have an adaptive advantage over specific pathogen (Wilson and Wisniewski, 1989). For example, *Rhizopus stolonifer* is more sensitive to low temperature than many other pathogens. Thus, for its effective control, a microbial antagonist should have the ability to grow, multiply, and suppress the pathogen at low temperature. Similarly, *Candida oleophila* was effective along with dicloran to reduce the incidence of *Penicillium expansum* and *Rhizopus* rot in nectarine even under controlled atmosphere storage conditions (Lurie et al., 1995). Most of the pome fruits are stored in cold storage. Thus, for controlling their postharvest diseases to a satisfactory level, a microbial antagonist should have the ability to survive under cold stored conditions as well. Considering these factors, research work on the use of microbial antagonists for the control of postharvest diseases of fruits and vegetables has been re-oriented in many countries. Accordingly, a new strain of *Candida sake* Saito & Ota was isolated, which controlled *Penicillium expansum*, *Botrytis cinerea*, and *Rhizopus stolonifer* even under various storage conditions (Vinas et al., 1996). However, even if an antagonist has all the desirable characteristics, economic factor decides whether it has to be commercialized or not. If there is no potential market for the product, then it cannot be commercialized.

4.2. Antagonistic preparations

Only a few of the microbial antagonists reported to control postharvest diseases of fruits and vegetables under laboratory

Table 3
Biocontrol products developed for control of postharvest diseases of fruits and vegetables.

Product	Microbial agent	Fruit/vegetables	Target disease(s)	Manufacturer/distributor
AQ-10 bio-fungicide	*Ampelomyces quisqualis* Cesati ex Schlechtendahl	Apples, grapes, strawberries, tomatoes and cucurbits	Powdery mildew	Ecogen, Inc., USA
Aspire	*Candida oleophila* strain 1–182	Apple, pear and citrus	Blue, gray, and green molds	Ecogen, Inc., USA
Biosave 10LP, 110	*Pseudomonas syringae*(strain 10 LP, 110	Apple, pear, citrus, cherries and potatoes	Blue and gray mold, mucor, and sour rot	Eco Science Corporation, USA
Blight Ban A 506	*Pseudomonas fluorescence* A 506	Apple, pear, strawberries and potatoes	Fire blight and soft rots	Nu Farm, Inc., USA
Contans WG, Intercept WG	*Coniothyrium minitans* Campbell	Onion	Basal and neck rots	Prohyta Biologischer, Germany
Messenger	*Erwinia amylovora* (Burrill) Winslow et al.	Vegetables	Fire blight	EDEN Bioscience Corporation, USA
Rhio-plus	*Bacillus subtilis* FZB 24	Potatoes and other vegetables	Powdery mildew and root rots	KFZB Biotechnick, Germany
Serenade	*Bacillus subtilis*	Apple, pear, grapes and vegetables	Powdery mildew, late blight, brown rot and fire blight	Agro Quess Inc., USA

conditions were commercialized (Table 3). There could be many reasons for this, but two primary barriers, which prevented this, are: (a) the relative ineffectiveness of the antagonists compared to chemical control procedures; and (b) a lack of economic incentives (Wilson and Wisniewski, 1989). However, once effective antagonist is identified, search starts for its preparation, storage and application methodology. For instance, *Bacillus subtilis* (strain B-3) was the first organism patented as a postharvest biocontrol agent for stone fruits in the USA (Pusey and Wilson, 1984). Pusey et al. (1988) conducted a pilot test applying *Bacillus subtilis* under simulated commercial conditions for the control of brown rot of peaches, in which bioagent was effectively incorporated into wax normally used on the packing line. Botrytis rot was effectively controlled by this procedure, but considerable variation was found in the control rendered by the different preparations of the antagonists. However, industrial experience is needed to develop preparations of the microbial antagonists (Sher and Castagno, 1986). Several commercial products have been were developed and commercialized. For example, 'BioSave' has been developed from a saprophytic strain of *Pseudomonas syringae* by 'EcoScience' Corp., Orlando, USA, which is highly useful for controlling blue and gray mold on apples and pears (*Pyrus communis* L.) (Janisiewicz and Jeffers, 1997; Janisiewicz and Korsten, 2002). 'EcoScience' Corp., USA tested its final formulation in a pilot test. To build confidence in the product within the fruit industry, these pilot tests were conducted in commercial packinghouses (Jeffers and Wright, 1994; Koomen and Jeffrics, 1993). Further, extensive technical support and quality control have been instrumental in the success of this product. The commercial use of 'Biosave' is increasing day-by-day for controlling postharvest diseases in different corners of the world (Droby, 2006). Ecogen-Israel Partnership Ltd. has developed the 'Aspire' from the yeast, *Pichia guilliermondii* previously designated as *Debaryomyces hansenii* (McLaughlin et al., 1990; Janisiewicz and Korsten, 2002). The earliest research on this product (Wilson and Chalutz, 1989; Chalutz and Wilson, 1990) and a pilot test (Droby et al., 1993) conducted in a commercial packingline indicated that it in a combination with a 10-fold-diluted thiobendazole (200 $\mu g\ ml^{-1}$) provided 100% control of postharvest diseases of citrus.

Similar research has been conducted with the yeast antagonist *Candida oleophila* (Mercier and Wilson, 1994; Wisniewski et al., 1995), which had been previously described as *Candida sake* (Wilson et al., 1993; Mercier and Wilson, 1994; Wisniewski et al., 1995). Tests conducted in commercial citrus packinghouses gave satisfactory control of green and blue molds and sour rot only in combination with 10-fold diluted thiobendazole (Droby et al., 1998). The research and commercial development of 'YieldPlus' for biocontrol of fruit decays follows the same pattern as described for 'Aspire' or *Candida oleophila*. The development of 'Avogreen' from this *Bacillus* followed a slightly different path in that it was tested in the field for biocontrol. It was prepared from *Bacillus subtilis* and used in South Africa for the control of *Cercospora* species and anthracnose of avocado (Korsten et al., 1997; Janisiewicz and Korsten, 2002). More recently years, other products like 'Shemer' that is effective against some postharvest diseases of fruits have been developed (Droby, 2006).

4.3. Yeast: As potential microbial antagonists

Many types of yeast are regarded as potential microbial antagonists and deserve special mention. Janisiewicz (1987), Chalutz et al. (1988) and Janisiewicz (1988) have made several positive points in recommending yeasts as potential microbial agents for controlling the postharvest diseases of fruit and vegetables, including (a) yeasts can colonize the surface for long period even under dry conditions; (b) yeasts produce extra-cellular polysaccharides, which enhance their survivability and restrict the growth of pathogen propagules; (c) they can use nutrients rapidly and proliferate at a faster rate; and (d) they are the least affected by the pesticides. Of the various yeasts, *Debaryomyces hansenii* has exhibited a wide spectrum of biological activity against many pathogens (Wisniewski et al., 1988; Wilson and Chalutz, 1989; Karabulut and Baykal, 2003). However, recent research has been focused on the use of several other yeasts for controlling postharvest diseases of fruits and vegetables.

5. Application methods for microbial antagonists

Once an effective and potential antagonist is identified or selected, it is necessary to search a method which applies it effectively for controlling or suppressing the pathogen. In general, microbial antagonists are applied by two different ways i.e., preharvest application, and postharvest application.

5.1. Preharvest application

In several cases, pathogens infest fruits and vegetables in the field, and these latent infections become major factor for decay during transportation or storage of fruits and vegetables. Therefore, preharvest application(s) of microbial antagonistic culture are often effective to control postharvest decay of fruits and vegetables (Ippolito and Nigro, 2000; Janisiewicz and Korsten, 2002; Ippolito et al., 2004; Irtwange, 2006). The purpose of preharvest application is to pre-colonize the fruit surface with an antagonist immediately before harvest so that wounds inflicted during harvesting can be colonized by the antagonist before colonization by a pathogen (Ippolito and Nigro, 2000). Although this approach could not become commercially viable, because of poor survival of microbial antagonists in the field conditions, however, it has been quite successful in certain cases. For instance, the antagonists *Cryptococcus infirmo-miniatus* (Okanuki) Phaff & Fell, *Cryptococcus laurentii*, and *Rhodopholus glutinis* (Fresenius) Harrison, applied to 'd Anjou' and 'Bosc' pears in the field 3 weeks before harvest reduced gray mold on 'Bosc' pears from 13% to 4% and on 'd Anjou' pear from 7% to nearly 1% (Benbow and Sugar, 1999). *Candida sake* CPA-1 reduced blue mold by nearly 50% on wounded apples if the apples were inoculated with antagonist 2 days before harvest and inoculation with *Penicillium expansum* and cold storage for 4 months (Teixido et al., 1999). Although it is difficult to control postharvest diseases of strawberry even with preharvest application of fungicides, some success has been achieved with field application(s) of various microbial antagonists like *Gliocladium roseum* Bainier (Sutton et al., 1997), *Trichoderma harzianum* (Tronsmo and Denis, 1977; Kovach et al., 2000) and *Epicoccum nigrum* Link (Larena et al. (2005). The highest levels of control, however, were obtained with application of pyrrolnitrin, a secondary metabolite produced by *Pseudomonas cepacia* (Janisiewicz and Roitman, 1988; Janisiewicz and Korsten, 2002). Near harvest application of *Metschnikowia fructicola* Kurtzman & Droby alone or in combination with ethanol or sodium bicarbonate controlled postharvest diseases of grapes significantly over control (Karabulut et al., 2003). Preharvest spray of *Metschnikowia fructicola* Kurtzman & Droby was also effective in controlling preharvest and postharvest fruit rots in strawberry (Karabulut et al., 2004). Similarly, preharvest application of *Aureobasidium pullulans* reduced storage rots in strawberry significantly (Lima et al., 1997), grapes (Schena et al., 1999, 2003), cherries (Wittig et al., 1997; Schena et al., 2003), and apples (Leibinger et al., 1997). And, the incidence of green mold (*Penicillium digitatum*) on grapefruit was reduced by preharvest spray of *Pichia guilliermondii* (Droby et al., 1992). In citrus, preharvest application of the biocontrol yeast *Pantoea agglomerans* CPA-2 effectively controlled postharvest rots under laboratory conditions. Similarly, preharvest application(s) of *Cryptococcus laurentii* and *Candida oleophila* reduced storage rots in pear (Benbow and Sugar, 1999). Field application of *Epicoccum nigrum* was reported to be effective for controlling postharvest brown rot (*Monilinia* spp.) in peaches. Canamas et al. (2008) have very recently reported that preharvest application of different concentrations of *Pantoea agglomerans* was effective for protecting oranges [(*Citrus sinensis* (L.) Obseck.] against *Penicillium digitatum* during storage. However, it appears that this approach has still many limitations, and in commercial practice, it is used only in avocado.

5.2. Postharvest application

From the available literature, it appears that postharvest application of microbial antagonists is a better, practical and useful method for controlling postharvest diseases of fruits and vegetables. In this method, microbial cultures are applied either as postharvest sprays or as dips in an antagonist's solution (Barkai-Golan, 2001; Irtwange, 2006). This approach has been more effective than preharvest application of microbial antagonists, and has several successes (Table 1). For example, postharvest application of *Trichoderma harzianum, Trichoderma viride*, *Gliocladium roseum* and *Paecilomyces variotii* Bainier resulted in better control of *Botrytis* rot in strawberries and *Alternaria* rot in lemons than preharvest application(s) (Pratella and Mari, 1993). In lemons, postharvest application of *Pseudomonas variotii* was more effective in controlling *Aspergillus* rot than iprodion treatment, and in potatoes (*Solanum tuberosum* L.), postharvest application of *Trichoderma harzianum* controlled Fusarium rot effectively than benomyl dip treatment. However, some *Trichoderma* strains have been pathogenic to the harvested conditions, limiting their possible use to only a few strains. A significant reduction in storage decay was achieved by bringing several yeast species in direct contact with wounds in the peel of harvested fruits. For instance, direct contact of microbial antagonist and infested fruit peel has been quite useful for the suppression of pathogens like *Penicillium digitatum*, *Penicillium italicum* in citrus (Chalutz and Wilson, 1990); *Botrytis cinerea* in apples (Gullino et al., 1992; Mercier and Wilson, 1995; Roberts, 1990a; Wisniewski et al., 1988), *Botrytis cinerea* and *Penicillium expansum* in pears (Chand-Goyal and Spotts, 1996, 1997; Sugar and Spotts, 1999), and *Botrytis cinerea*, *Rhizopus stolonifer* and *Alternaria alternata* in tomatoes (Chalutz et al., 1988). However, all the pathogens do not react in a similar fashion to a given antagonist.

6. Enhancing the bioefficacy of microbial antagonists

Microbial antagonists when applied alone usually do not bring about 100% controls of postharvest diseases of fruits and vegetables. To increase their effectiveness, and to enhance their bioefficacy, following approaches have been useful.

6.1. Manipulations in the physical and chemical environment during storage

Fruits and vegetables are usually stored at pre-determined temperature, relative humidity and in gas combinations for varying periods with the primary objective of maintaining the quality to meet the market demands. Microbial antagonists are screened for their ability to develop rapidly under the required storage conditions and only those microbial antagonists that fulfill the basic requirements are only selected. However, modification in the storage environment can be a useful strategy for enhancing the efficacy of microbial antagonists, as it is possible to manipulate the physical and chemical environment to the advantage of microbial antagonists in storage (Janisiewicz and Korsten, 2002). These manipulations should, however be, such that they should not affect the quality of the produce, and should be well suited for the establishment of the microbial antagonist (Dock et al., 1998; Usall et al., 2000). Fruits and vegetables are often treated and/or handled in water before, during, and after the storage which provides an excellent opportunity to modify the environment. Nitrogen is likely to be a limiting nutrient in the carbon rich environment of apple and pear wounds, which can be increased by the addition of L-asparagine and L-proline to enhance the population of microbial antagonist *Pseudomonas syringae*. This treatment prevented blue mold decay completely as against 50% decay in control (Janisiewicz et al., 1992). The bioefficacy of *Candida sake* against *Penicillium expansum* on apples was enhanced significantly with the addition of L-serine and L-aspartic nitrogenous compounds. In cold storage, addition of ammonium molybdate to *Candida sake* entirely eliminated the incidence of blue mold on pears and reduced the severity and incidence of the disease by more than 80% on apples (Nunes et al., 2001b). Similarly, application of *Candida sake* (2×10^6 CFU/ml) plus ammonium molybdate (5 mM/l) markedly reduced the population of *Penicillium expansum*, *Botrytis cinerea* and *Rhizopus stolonifer* in apples stored at 20 °C for 7 days and reduced the incidence of blue and gray mold by more than 90% in apples stored at 1 °C for 60 days (Nunes et al., 2002c). Preferential stimulation of growth of the biocontrol agent by nutrient analog 2-deoxy-D-glucose (2 DOG) has been demonstrated. The development of the antagonists *Pseudomonas syringae, Sporobolomyces roseus* Kluyver & van Niel and *Candida saitona* was favored by the addition of 2 DOG (Janisiewicz, 1994). The combined application of *Candida saitona* and 2 DOG was as effective as the fungicide imazalil in controlling blue mold of apple and green mold of oranges and lemon (Janisiewicz, 1994; El-Ghaouth et al., 2000b). Spraying suspension of *Candida saitona* (10^8 CFU/ml) plus 2 DOG (0.2%) on 'Rome' and 'Empire' apples reduced decay caused by *Botrytis cinerea* and *Penicillium expansum* more efficiently than with thiobendazole (TBZ). On the other hand, level of control of *Penicillium digitatum* on 'Washington', 'Valencia', and 'Hamlin' oranges was to a desirable extent or lower than imazalil treatment (El-Ghaouth et al., 2001). The efficiency of *Rhodotorula glutinis* against *Penicillium expansum* was enhanced by the addition of siderophores. The addition of siderophores reduces decay by sequestering iron required for germination of some postharvest pathogens (Calvente et al., 1999). The bioefficacy of *Pseudomomas syringae* for the control of crown rot and anthracnose was considerably enhanced by the addition of low doses of thiobendazole or imazalil ($250\ \mu g\ ml^{-1}$), which brought control similar to higher doses of fungicides (Williamson et al., 2008).

6.2. Use of mixed cultures

Biological control of postharvest diseases with microbial antagonists is an alarming field, and it has done much progress during the last two decades. However, it has been difficult to select an individual microbial strain with a broad spectrum of activity against major postharvest pathogens that are effective when used on fruits and vegetables. Hence, compatible strains are needed to provide the necessary spectrum of activity for effective control of postharvest diseases of fruits and vegetables (Janisiewicz, 1988; Barkai-Golan, 2001; El-Ghaouth et al., 2004; Singh and Sharma, 2007). Application of mixtures of microbial antagonists has certain advantages:

1. Widening the spectrum of microbial activity resulting in the control of two or more postharvest diseases.

2. Increasing the effectiveness under different situations such as cultivars, maturity stages, and locations.
3. Enhancing the efficiency and reliability of biocontrol as the components of the mixtures act through different mechanisms like antagonism, parasitism, and induction of resistance in the host.
4. Combination of different biocontrol traits without the transfer of alien genes through genetic transformation.

The enhancement of bio-efficacy of microbial antagonists may be due to: better utilization of substrate, resulting in acceleration of the growth rate; removal of substances inhibitory to one organism by the other microbial agent; production of nutrients by one microbe that may be used by another; and formation of more stable microbial community that may exclude other microbes, including pathogens (Janisiewicz, 1998). Further, while selecting components of antagonistic mixtures, certain attributes have to be considered, including: (1) absence of antagonism between one microbial antagonist against another; and (2) selection of components with positive interactions (mutualism) that allow more effective utilization of resources. The practical approach to select the components of mixtures is to evaluate the biocontrol agents with a mixture of many antagonists and to remove the inefficient or incompatible ones (Fukui et al., 1999).

Use of mixed strains of microbial antagonists is a challenging work, as microorganisms have different growth habits, and requirements for nutrition and cultural conditions. However, some success has been achieved in this area as well. For instance, a combination of the bacteria *Pseudomonas syringae* and the yeast *Sporobolomyces roseus* proved to have a marked advantage over each of the antagonists in controlling *Penicillium expansum* in apple, both in reducing the incidence of wound infections and in limiting rot diameter (Janisiewicz and Bors, 1995). The advantage of antagonistic pairs over a single antagonist was described by Schisler et al. (1997) in the control of Fusarium dry rot (*Gibberella pulcaris* Hohn & Desjardins) in stored potatoes. The black rot of pineapple [*Ananas comosus* (L.) Merrrill], caused by *Ceratomyces paradoxa* (Dade) Moreau could be controlled by the yeast *Pichia guilliermondii*, its combination with five yeast isolates was still more effective and the level of control was comparable to current industry practice of holding fruit at a low temperature (8–10 °C) (Reyes et al., 2004). With a mixture of *Aureobasidium pullulans* (10^6 CFU/ml) and *Bacillus subtilis* (10^8 CFU/ml), *Penicillium expansum* and *Botrytis cinerea* were controlled to the level provided by a fungicide (Leibinger et al., 1997). The antagonistic mixture consisting of *Candida sake* CPA-1 (2×10^7 CFU/ml) and *Pantoea agglomerans* (2×10^7 CFU/ml) controlled rot diameter completely in 'Blanquilla' pear and brought the maximum control in blue mold rot on 'Golden Delicious' apples (Nunes et al., 2002a). Under natural infection conditions, dipping grapes in a cell suspension culture of *Kloeckera* and *Candida*, was effective in controlling *Rhizopus* decay but had no effect on *Aspergillus* decay caused by *Aspergillus niger* in storage (McLaughlin et al., 1992).

The efficiency of an antagonist is affected both by the concentration of the yeast cells in the wound and by the number of pathogen spores used for inoculation. For example, when wound inoculation was done with a higher concentration of *Botrytis* spores (10^6 spores/ml), a reduced percentage of infection was achieved only by the highest yeast concentration (10^9 cells/ml) and vice versa (Chalutz et al., 1991). Similarly, the best activity of *Trichoderma* spores was achieved at higher concentrations of the antagonist and at lower inoculation levels of pathogen (Elad et al., 1982; Mortuza and Ilag, 1999). On apple, a broader spectrum of pathogens was controlled when microbial antagonists were applied in mixtures than individual microbial strains (Leibinger et al., 1997; Calvo et al., 2003; Conway et al., 2005). In potato, antagonist pairs effectively controlled Fusarium dry rot over their single use (Schisler et al., 1997). Mixed cultures of *Candida sake* and *Pantoea agglomerans* gave better control on blue and gray mold both in apple and pears than their individual use (Nunes et al., 2002b). Very recently, Janisiewicz et al. (2008) reported that mixed cultures of *Metschnikowia pulcherrima* and *Cryptococcus laurentii* exhibited greater biocontrol activity on blue mold (*P. expansum*) than either yeast applied alone, in combination with sodium carbonate or bicarbonate in a pilot test conducted on citrus in controlled atmosphere. Although the use of antagonistic mixtures offers more effective control, the economic viability of this approach appears to be a major obstacle for its adoption, as registration of two microbial antagonists will cause additional burden for the industry.

6.3. Addition of low doses of fungicides in the microbial cultures

Certain fungicides such as imazalil and thiobendazole have been exceptionally effective in controlling postharvest diseases; it is quite difficult to find microbial antagonists that will perform as effective. Hence, special efforts need to be paid to ways of enhancing the efficiency of microbial antagonist (Brown and Chambers, 1996; Droby et al., 1998). One approach has been to combine the microbial antagonists with fungicides. Compatibility between a microbial antagonist and a synthetic fungicide offers the option of using the antagonists in combination with reduced level of the fungicide. As of now, postharvest diseases of fruits and vegetables can also be controlled efficiently by this approach. For example, some biocontrol formulations have been developed which provide nearly 100% control of postharvest diseases if low doses of synthetic fungicides are also added to them (Wisniewski et al., 2001). Applying *Pichia guilliermondii* to citrus fruit in combination with substantially reduced concentration of thiobendazole (TBZ) reduced *Penicillium digitatum* decay to a level similar to that achieved by currently recommended concentration of TBZ application alone (Droby et al., 1993), which helps in maintaining very low level of chemical residue in the fruit (Hofstein et al., 1994). Mixing *Pseudomonas syringae* with low doses of cypronidil brought effective control in decay caused by *Penicillium expansum* on apples, and pear decay in storage was reduced significantly by combining low doses of fungicides with biocontrol agent (Errampalli and Brubacher, 2006; Sugar and Basile, 2008). Chand-Goyal and Spotts (1997) also reported control of blue mold on apple and brown rot on pear when yeasts were used with a low dose of a fungicide. Similarly, fruit decay in citrus was controlled effectively with *Candida oleophila* + thiobendazole as comparable to commercial fungicide treatment (Droby et al., 1998). Zhou et al. (2002) achieved over 90% control in blue and gray mold rots on apples by treating the fruit with cypronidil (20 ppm) and *Pseudomonas syringae* (3×10^7 CFU/ml). Similarly, *Cryptococcus laurentii* + imazalil (25 ppm) treatment was highly effective in controlling storage rots of jujube than applying *Cryptococcus laurentii* or imazalil alone (Qin and Tian, 2004).

6.4. Addition of salt additives in the microbial cultures

Salt additives also improve the bioefficacy of some microbial antagonists in controlling postharvest decay on fruits and vegetables (El-Ghaouth et al., 2004). Among different salt additives, calcium chloride, calcium propionate, sodium carbonate, sodium bicarbonate, potassium metabisulphite, ethanol and ammonium molybdate etc., have been found very successful when used with microbial antagonists for controlling postharvest diseases of fruits and vegetables more efficiently (Janisiewicz et al., 1998, 2008; Plaza et al., 2001; Teixido et al., 2001; Tian et al., 2002; Karabulut et al., 2005; Wan and Tian, 2005; Xi and Tian, 2005; Zhang et al., 2005; Qin et al., 2006; Torres et al., 2007; Cao et al., 2008) (Table 4). However, the effectiveness of microbial antagonists depends

Table 4
Salt additives for enhancing the efficacy of microbial antagonists.

Fruit	Salt additive	Microbial agent	Disease controlled	References
Apple	Calcium chloride	*Candida* spp.	Gray and blue molds	Wisniewski et al. (1995)
	Sodium carbonate	*Metschnikowia pulcherrima*	Blue mold	Conway et al. (2007), Janisiewicz et al. (2008)
	Sodium carbonate	*Cryptococcus laurentii*	Blue mold	Conway et al. (2007), Janisiewicz et al. (2008)
	Calcium propionate	Aspire (*Candida oleophila*)	Blue mold	Droby et al. (2003)
	Sodium bicarbonate	Aspire (*Candida oleophila*)	Blue mold	Droby et al. (2003)
Pear	Sodium carbonate	*Cryptococcus laurentii*	Blue mold and Alternaria rot	Yao et al. (2004)
	Sodium carbonate	*Trichosporon pullulans*	Blue mold and Alternaria rot	Yao et al. (2004)
	Calcium chloride	*Candida saitona*	Gray and blue molds	McLaughlin et al. (1990), Wisniewski et al. (1995)
	Calcium chloride	*Cryptococcus laurentii*	Gray mold rot	Zhang et al. (2005)
	Ammonium molybdate	*Rhodotorula glutinis*	Blue mold	Wan and Tian (2005)
	Ammonium molybdate	*Trochosporon spp.*	Alternaria rot	Wan and Tian (2005)
Peach	Calcium chloride	*Debaryomyces hansenii*	Rhizopus rot	Singh (2004, 2005)
	Calcium propionate	Aspire	Brown rot	Droby et al. (2003)
	Sodium bicarbonate	Aspire	Rhizopus rot	Droby et al. (2003)
Cherry	Ammonium molybdate	*Pichia membranaefaciens*	Brown rot	Qin et al. (2006)
		Crptococcus laurentii	Brown rot	Qin et al. (2006)
	Calcium chloride	*Aureobasidium pullulans*	Brown rot	Ippolito et al. (2005)
	Sodium bicarbonate	*Aureobasidium pullulans*	Brown rot	Karabulut et al. (2005)
	Potassium sorbate	*Candida oleophila*	Postharvest decay	Karabulut et al. (2001)
Grapefruit	Calcium chloride	*Pichia guilliermondii*	Green mold	Droby et al. (1997)
Oranges	Calcium chloride	*Pseudomonas syringae*	Blue mold	Janisiewicz et al. (1998)
	Calcium chloride	*Candida oleophila*	Penicillium rots	El-Neshawy and El-Sheikh (1998)
	Sodium carbonate	*Pseudomonas syringae*	Green mold	Smilanick et al. (1999)
	Sodium bicarbonate	*Pseudomonas syringae*	Green mold	Plaza et al. (2001)
Grape	Sodium bicarbonate	*Metschnikowia fruticola*	Botrytis rot	Karabulut et al. (2003)
Citrus	Sodium carbonate	*Cryptococcus laurentii*	Green mold	Zhang et al. (2004), Usall et al. (2008)
	Sodium bicarbonate	*Bacillus subtilis*	Green and blue molds	Obagwu and Korsten (2003)
	Sodium bicarbonate	*Pantoea agglomerans*	Penicillium rots	Plaza et al. (2001), Teixido et al. (2001), Torres et al. (2007), Usall et al. (2008).
Papaya	Sodium bicarbonate	*Candida oleophila*	Anthracnose	Gamagae et al. (2003)
Loquat	Calcium chloride	*Pichia membranifaciens*	Anthracnose	Cao et al. (2008)
Rambutan	Potassium metabisulphite	*Trichoderma spp.*	Postharvest rots	Sivakumar et al. (2002a,b)
Tomato	Sodium bicarbonate	*Cryptococcus laurentii*	Botrytis rot	Xi and Tian (2005)

upon the concentration of the antagonist, concentration of salt additive(s), their mutual compatibility and duration and time at which they are applied. Usually, the cultures should be applied well before the initiation of infection process (Barkai-Golan, 2001).

6.5. Addition of nutrients and plant products in microbial cultures

The efficacy of the microbial antagonists can also be enhanced considerably by the addition of some nutritious compounds or natural plant products. For example, additions of nitrogenous compounds like L-aspargine and L-proline, and 2-deoxy-D-glucose, a sugar analog helped in enhancing the bioefficacy of microbial antagonists in controlling the postharvest decay rots in some fruits and vegetables (Janisiewicz, 1994; El-Ghaouth et al., 2000a,b). When applied in fruit wounds, the combination of *Candida saitona* and 2-deoxy-D-glucose (0.2%) controlled fruit decay on apples, oranges and lemons caused by *Botrytis cinerea*, *Penicillium expansum*, and *Penicillium digitatum* (El-Ghaouth et al., 2000a,b) than when either *Candida saitona* or 2-deoxy-D-glucose was applied alone. The treatment of peaches with *Cryptococcus laurentii* (1×10^8 CFU/ml) alone or in combination with methyl jasmonate (200 (µM/l) inhibited the lesion diameter of brown rot and blue mold rots caused by *Monilinia fructicola* and *Penicillium expansum*, respectively (Yao and Tian, 2005). The inhibitory mechanism was mainly because of resistance induced in peach fruit by methyl jasmonate and *Cryptococcus laurentii*. In addition, direct inhibition of methyl jasmonate on *Penicillium expansum* also played a role in controlling blue mold.

6.6. Use of the microbial cultures in association with physical treatments

Integration of microbial antagonists with physical methods such as curing or heat treatments could enhance the bioefficacy of microbial antagonists (Stevens et al., 1997) (Table 5). For example, biocontrol of green mold using *Pseudomonas glathei* Zolg & Ottow was enhanced when heat was applied to citrus fruits to retard conidia germination of *Penicillium digitatum* (Huang et al., 1995). Irradiation of pome, stone, and citrus fruit with ultraviolet (UV) rays along with bioagent were quite successful (Wilson et al., 1993). In such treatments, the role of the UV rays on the fruit is restricted mainly to its phytosanitary effect on reducing the survival of pathogen propagules. Lurie et al. (1995) reported that efficacy of *Pichia guilliermondii* against *Penicillium digitatum* increased when orange fruit were stored at optimum low storage temperature under controlled atmosphere. Further, Karabulut and Baykal (2004) reported that postharvest diseases of peaches could be effectively reduced if fruit are treated with hot water at 55 °C for 10 s, and then inoculated with *Candida oleophila*. Similarly, Singh and Mandal (2006) and Mandal et al. (2007) reported that hot water treated peaches inoculated with *Debaryomyces hansenii* could be stored for longer time than those inoculated alone with *Debaryomyces hansenii*, primarily by reducing the decay loss caused by Rhizopus rot. In apple, integration of yeasts microbial antagonists with hot water dipping or bruising has been applied to check postharvest rots caused by *Penicillium expansum* and *Botrytis cinerea* (Leverentz et al., 2000, 2003; Conway et al., 2004, 2007; Spadaro et al., 2004).

6.7. Use of the microbial cultures with other approaches/additives

Some other useful recommendations have emerged out of the research conducted by the scientists for improving the bioefficacy of microbial antagonists. For example, a bioactive coating consisting of *Cryptococcus saitona* + glycochitosan has been developed to control fruit decay in apple (El-Ghaouth et al., 2000a,c). In laboratory studies, the biocontrol activity of *Candida saitona*, against decay of apple, lemon, and orange, caused by *Botrytis cinerea*,

Table 5
Enhancing the bioefficacy of microbial antagonists with physical treatments.

Crop	Microbial antagonist	Physical treatment	Disease controlled	Reference
Apple	*Pseudomonas syringae*	Heat treatment	*Green mold*	Conway et al. (2005)
	Candida sake	Controlled atmosphere	Blue mold	Usall et al. (2000), Conway et al. (2007), Janisiewicz et al. (2008)
	Yeast	Hot water treatment	*Colletotrichum aculatum* Simmonds and *Penicillium expansum* rots	Conway et al. (2004)
	Metschnikowia pulcherrima	Hot water dip	*Penicillium expansum* and *Botrytis cinerea* rots	Spadaro et al. (2004)
	Pseudomonas syringae	Heat treatment	Postharvest diseases	Leverentz et al. (2000, 2003)
Kiwifruit	Yeast	Fruit curing	*Botrytis cinerea*	Cook et al. (1999)
Citrus	*Bacillus subtilis*	Hot water treatment	Green (*P. digitatum*) and blue mold (*P. italicum*)	Obagwu and Korsten (2003)
Nectarine	*Cryptococcus oleophila*	Controlled atmosphere	*Penicillium* rots	Lurie et al. (1995)
Oranges	*Pseudomonas glathei*	Heat	Green mold	Huang et al. (1995)
Strawberry	*Cryptococcus laurentii*	Hot water dip	Rhizopus rot	Zhang et al. (2007b)

Penicillium expansum, and *Penicillium digitatum* was enhanced markedly by the addition of gylcochitin (El-Ghaouth et al., 2000a). Under semi-commercial conditions, the bioactive coating was superior to *Candida saitona* or glycochitin alone in controlling decay of oranges and lemons, and the control level was equivalent to that with imazalil (El-Ghaouth et al., 2000a). Nisin, a polypeptide antibiotic, enhanced the effectiveness of *Candida oleophila* for controlling apple rots caused by *Botrytis cinerea* and *Penicillium expansum* (El-Neshawy and Wilson, 1997). Similarly, the bioefficacy of microbial antagonists like *Debaryomyces hansenii, Cryptococcus laurentii*, *Rhodotorula glutinis*, *Trichoderma harzianum* etc., can be enhanced for effective control of postharvest rots on different fruits and vegetables by using additives like silicon, methyl jasmonate, salicylic acid, gibberellic acid or dipping fruit in beeswax or lac based formulations (Table 6).

7. Conclusion

Application of synthetic fungicides has been the traditional strategy for the management of postharvest diseases. The increasing concern for health hazards and environmental pollution due to chemical use has necessitated the development of alternative strategies for the control of postharvest diseases of fruits and vegetables. Management of postharvest diseases by employing microbial agents has been demonstrated to be most suitable strategy to replace the chemicals which are either being banned or recommended for limited use.

This review reported the success of some biocontrol agents under laboratory and commercial conditions, and some bioproducts have been developed for commercial use. The continuous increase in the use of BioSave, without an incidence of failure since 1996 indicates that current biological control practices can be cost effective in large packinghouses. However, the quantitative relationship between the populations of the antagonist and resulting control necessitates the presence of high cell densities of the antagonist in product, thereby cutting profit margins. In addition, postharvest practices in the developed nations are different to those adopted in developing countries, and bioproducts like BioSave may be too costly in such regions. However, the biocontrol strategies should be such that these are adapted to practices in different regions of the world.

The issue now in many developed countries is not if or when microbial antagonists will be used, but how broad its use will be and how fast it will expand to different commodities. This strategy has its own limitations that may restrict its use under certain circumstances, but many of those limitations may be effectively addressed; this method is amenable to manipulations, as indicated in many examples mentioned above. It would be inappropriate to equate this strategy with fungicidal treatment without considering

Table 6
Enhancing the efficacy of microbial agents through the addition of different additives.

Fruit	Microbial agent	Additive	Disease controlled	Reference
Apple	*Cryptococcus laurentii*	Gibberellic acid	Blue and gray mold	Yu and Zheng (2007)
	Cryptococcus lauretii	Methyl jasmonate	Blue and gray mold	Yao and Tian (2005)
	Cryptococcus laurentii	Salicylic acid	Postharvest rots	Yu and Zheng (2005)
	Cryptococcus laurentii	Indole-3-acetic acid	Gray mold	Yu et al. (2008b)
	Saccharomyces cerevisiae Meyen ex Hansen	Ethanol	Gray mold	Mari and Guizzardi (1998)
Banana	*Trichderma harzianum*	Bee wax	Anthracnose	Devi and Arumugam (2005)
Cherry	*Rhodotulura glutinis*	Salicylic acid	Blue mold	Qin et al. (2003)
	Cryptococcus laurentii	Salicylic acid	Blue mold and Alternaria rot	Qin et al. (2003)
Grape	*Metschnikowia fruticola*	Ethanol	Botrytis rot	Karabulut et al. (2003)
Jujube	*Cryptococcus laurentii*	Silicon	*Alternaria alternata*	Tian et al. (2005)
	Rhodotorula glutinis	Silicon	*Penicillium expansum*	Tian et al. (2005)
Kinnow	*Debaryomyces hansenii*	Lac based wax emulsion	Penicillium rots	Singh (2002)
Pear	*Cryptococcus laurentii*	Cytokinin	*Penicillium expansum* rot	Zheng et al. (2007)
	Cryptococcus laurentii	Salicylic acid	Blue mold (*Penicillium expansum*) and Gray mold (*Botrytis cinerea*)	Yu et al. (2007)
	Cryptococcus laurentii	Gibberellic acid	Blue mold (*Penicillium digitatum*)	Yu et al. (2006)
	Cryptococcus laurentii	Chitin	Blue mould rot (*Penicillium expansum*)	Yu et al. (2008a)
Peach	*Rhodotorula glutinis*	Salicylic acid	Gray mold (*Botrytis cinerea*)	Zhang et al. (2008a)
	Debaryomyces hansenii	UV rays	Brown rot (*Monilinia fructicola*)	Stevens et al. (1997)
Tangerine	*Debaryomyces hansenii*	UV rays	Green mold (*Penicillium digitatum*)	Stevens et al. (1997)
Tomato	*Debaryomyces hansenii*	UV rays	Rhizopus rot (*Rhizopus stolonifer*)	Stevens et al. (1997)

the advantages and limitations of both methods. Experiments should be designed systematically to expand this use of this strategy, including new areas, e.g., control of food borne pathogens, where new fungicides are ineffective.

The present model of postharvest disease control in fruits and vegetables is based on the knowledge of natural process of the antagonist–pathogen interaction. Although there are several successes but we should move adapt the aspects of biotechnology as a means to improve disease control with even safer and more effective methods. In the well-defined environment of a postharvest system, there are unique opportunities to use microbial antagonists as delivery system. In the future, it may be possible to use only strains adapted to postharvest conditions and introduce genes for biocontrol activity as needed. Development of microbial strains, as in developing new cultivars adapted to our needs, may become common practice in the future.

It appears that this strategy of biocontrol system is still in its infancy compared to fungicidal treatment, but progress made in this area during the last two decades has been remarkable. However, if the same pace continues, the use of microbial antagonists for the control of postharvest diseases of fruits and vegetables will be greatly expanded in the future and will definitely become an internationally adopted practice.

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