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Quality Retention of Dessert Banana and Other Tropical Fruits by Controlling Postharvest Diseases using Non-Chemical Methods

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ABSTRACT

Banana and other major tropical fruits (i.e. citrus, mango, avocado, pineapple and papaya) are of economic, social and political significance to countries where they are grown worldwide. The inherent perishable nature of these fruits causes serious qualitative and quantitative yield losses at the postharvest phase. Types and magnitudes of postharvest losses are highly case-specific and vary significantly with the type of fruit, processing channel through which the produce travels, infrastructural facilities available and the attitude of consumers towards the final quality of the produce. Among different types of losses, fungal diseases at the postharvest stage contribute substantially to yield reductions of fruits as latent- and/or wound infections. Details of host-pathogen interactions involving *Colletotrichum*, which is a widely-established pathosystem causing latent infections, are discussed in this review. Even though application of synthetic fungicides is the common practice for controlling postharvest diseases at the commercial level, environmental and health hazards associated with them are well known. Hence, alternative non-chemical approaches are emerging rapidly. Potential use of physical, chemical, biological and genetic engineering methods, either solely or as combinations, have proved to be effective in controlling both wound- and latent infections when used as pre- or postharvest treatments. Limitations associated with individual methods could be mitigated by modification of application methods, improvement of formulations, management of the postharvest environment and manipulation of gene expression either in fruits or in biological control agents. Public perception towards microbial pesticides and potential to promote microbial pesticides for the control of postharvest diseases in the future has also been discussed.

Keywords: anthracnose pathosystems, genetic manipulation, microbial antagonists, quiescent infections, wound infections

CONTENTS

TROPICAL FRUITS AND THEIR ECONOMIC SIGNIFICANCE

Banana (*Musa acuminata*) and many other fruits grown specifically in tropical regions of the world are economically-significant in numerous ways. Among a spectrum of tropical fruits, banana (*Musa acuminata*), citrus (*Citrus* spp.), mango (*Mangifera indica*), avocado (*Persea americana*), pineapple (*Ananas comosus*) and papaya (*Carica papaya*) are considered as major tropical fruit crops because of their predominance in production while rambutan (*Nephelium lappaceum*), mangosteen (*Garcinia mangostana*), longan (*Dimocarpus longan*), carambola (*Averrhoa carambola*), lychees (*Litchi chinensis*), passion fruit (*Passiflora edulis* or *P. flavicarpa*) and guava (*Psidium guajava*) are considered as minor tropical fruits (FAO 2005). These fruits are grown in the tropical and subtropical regions (i.e. 11½° north of the Tropic of Cancer and south of Tropic of Capricorn) or in a belt from 35° N to 35° S latitudes. Tropical fruits are blessed with a unique blend of agroecological, climatic and soil conditions prevalent in the tropics. Accordingly, they possess attractive appearances, textures and

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Invited Review

Table 1 Contribution of different types of banana to total production during 1998-2008*.

Type of banana	% Contribution to the total production
Cavendish	47
Gross Michel + Other dessert banana	12
Plantain AAB	17
Highland banana + ABB + other cooking banana	24

* Source: CIRAD-FLHOR

Table 2 Production of Cavendish banana by country (percentage average values 1998-2000)*.

Country	% average values
India	19
Ecuador	12
China	10
Colombia	6
Costa Rica	5
Brazil	5
Philippines	4
Mexico	4
Others	35

* Source: CIRAD-FLHOR

unforgettable flavours and tastes. This review is mainly focused on postharvest quality retention of banana and the major tropical crops. Banana and other tropical fruit crops are valuable agricultural commodities. They contribute to food security, generation of income and employment, especially in developing countries. In addition to the monetary contribution, these fruits add colour, taste and flavour to the diet. Also due to the nutritional and medicinal properties, these fruits are used in pharmaceutical, cosmetic and food industry in addition to the local and international fresh fruit market.

Banana is the world's fourth most valuable food after rice, meat and milk (FAO 2001) and also ranks as the fourth most important food crop used globally after rice, wheat and maize. Banana has an annual production of 100 million tons out of which a major component is used as the starch staple across the Asian, African and American tropics (Heslop-Harrison and Schwarzacher 2007). Because of the specific climatic conditions required for its cultivation, 98% of the world banana production is confined to developing countries which have the environmental and soil conditions required for banana. Out of the total banana production, 15% is exported as dessert banana and serves as the major cash crop in many developing countries in Latin America, Caribbean, Far East and Africa (FAO 2007; Heslop-Harrison and Schwarzacher 2007; **Table 1**).

Among tropical fruit crops, citrus reported a total global production of 105.4 million tons in 2004-2005 (including citrus juice and products) (Talon and Gmitter 2008). Whether it is produced for the processed or fresh fruit market, citrus is an important commodity in the global trade with a high economic impact (Talon and Gmitter 2008). Like banana, pineapple is another tropical fruiting monocot. It is considered as the third most important tropical fruit, after banana and citrus in terms of the world production and contributes 20% of the world production of tropical fruits after banana (Rohrbach *et al*. 2002). Avocado reported a worldwide production of 2.4 million tons of fruits in 2002. Although most of the production is consumed in developing countries, a very attractive national and international market exists for the fruit (Menge and Ploetz 2003). Among all the economically-significant fruit crops, mango is considered as the world's fifth most important fruit crop. 50% of the world mango production comes from India and only 2% of the total harvest is exported as fresh fruits. Papaya or papaw has reported an annual production of 5.47 million metric tons in 2001 (FAO 2001) as a tropical fruit with an emerging worldwide interest. According to papaya production statistics given by Persley and Ploetz (2003), a majority of papaya growing countries are developing countries, with Brazil, Nigeria and India being the major producers.

Production and export statistics of banana and some other major tropical fruits

It is unfortunate that exact production statistics are lacking for most fruit crops. For example, 85% of the production of banana comes mainly from home gardens or small-scale farmers worldwide, whose main target is self-consumption or local-consumption. Moreover, 70% of pineapple produced in the world is consumed as fresh fruit in the country of origin (Loeillet 1997). Hence, although these productions play a crucial role in ensuring food security and improving the family income of the countries where these fruits are grown, recorded data about their importance are lacking. According to Rohrbach *et al*. (2002), especially with reference to pineapple, available statistics sometimes do not give a clear picture between the fresh fruits and processed products or do not differentiae the local consumption from exports. However, given below are the production and export statistics of banana and other major tropical fruits worldwide extracted from various sources of information to create an image of their economic significance.

It is evident from **Tables 2-4** that the majority of countries which produce and export banana and other tropical fruits are the developing countries scattered around the tropics. The export earnings of these countries from banana exports are considerable. According to FAO (1998) records, Ecuador, Costa Rica, Colombia, Philippines, Panama, Italy, USA, France and Guatemala together have earned US$ 3,127.00 million in total, by exporting banana. Mexico is the leading exporter of fresh mangoes, currently worth

Table 3 Production statistics of some other major tropical fruits

Avocado (1997)*		Mango (1998)#		Pineapple (2001)†		Citrus (2004-05)‡		Papaya (2004)**	
Country	**%**	**Country**	**%**	**Country**	**Million tons**	**Country**	**(X1000t)**	**Country**	**%**
Mexico	39.8	India	49.7	Brazil	18.9	Thailand	2300	Brazil	25
USA	7.4	China	9.7	USA	10.49	Philippines	1572	Nigeria	15
Dominican republic	6.9	Thailand	6.4	China	15.22	Brazil	1442	India	12
Indonesia	4.8	Mexico	5.5	Mexico	6.91	China	1284	Mexico	11
Brazil	4.2	Indonesia	4.6	Spain	6.18	India	1100	Indonesia	10
Israel	3.5	Other	24.1	India	4.66	Nigeria	881	Ethiopia	4
Colombia	3.3			Italy	3.32	Mexico	535	Congo	4
Other	30.1			Egypt	2.70	Costa Rica	475	Peru	3
						Colombia	360	Venezuela	3
						USA	293	China	2
						Kenya	280		

*FAOSTAT 1997
FAOSTAT 1998
†Anon, 2002 (includes countries producing more than 250 MT)
‡FAO 2006
** FAO 2004

Table 4 World's leading exporters of fresh fruits.

Banana (average on 2002-2005)†		Citrus (2003)*		Mango (2003-2005)#		Papaya (2004) #		Avocado (2003)‡	
Country	**%**	**Country**	**%**	**Country**	**%**	**Country**	**X1000 t**	**Country**	**%**
Ecuador	29	Spain	25	Mexico	22.64	Mexico	75	Mexico	22.09
Costa Rica	13	USA	14	India	20.25	Malaysia	70	Chile	17.78
Philippines	12	South Africa	11	Brazil	13.18	Brazil	40	Israel	12.65
Colombia	10	Turkey	5	Pakistan	6.94			Spain	12.23
Guatemala	7	Argentina	5	Netherlands	6.42			South Africa	9.07
Rest of the world	29	Greece	4	Peru	5.71			France	5.38
		Netherlands	4	Ecuador	4.31			Netherlands	4.95
		Mexico	4	Philippines	3.61			USA	2.89
		Rest of the world	28	Thailand	1.55			Others	18.34
				China	1.31				
				Others	14. 08				

* Source – UNCTAD from FAO data
# FAOSTAT 2007
†Source - UNCTAD secretariat from FAO statistics
‡Source – APROAM 2003

approximately US$ 160 million annually. The value of mango exports from Mexico to the USA and Canada alone is estimated to be approximately US$ 138 million annually. Mangoes are also important exports of Brazil, South Africa, Pakistan, Philippine and India with an estimated annual value of US$ 346 million (Litz and Gomez-Lim 2002). Therefore, it is clear that banana and other tropical fruits are of significant economic, social and political importance and have an intimate relationship with the livelihoods of the people of tropical countries.

POSTHARVEST LOSSES OF TROPICAL FRUITS

Fruits are delicate horticultural commodities by nature. Hence, they are prone to an array of qualitative and quantitative yield losses from farm gate to the dining table. These are known as postharvest losses. In comparison to other agricultural commodities, fruits possess a higher moisture content (i.e. 70-80%), a large unit size, a very high respiration rate, generating a considerable amount of heat in the range of 5 to 70 MJ t^{-1} d^{-1} at 20°C, and a comparatively shorter shelf-life. Therefore, fruits are of highly perishable nature and are susceptible to postharvest losses of different types. Being live produces even after the harvest, physical, chemical and physiological changes occur within the fruits during the postharvest stage. Reductions of fruit peel thickness, firmness of the fruit pulp and the amount of phenolic and antifungal compounds, changing of nutrient contents and the pH level and breakdown of chemical compounds of the fruits are some of the changes that occur at the postharvest stage. All these changes increase the susceptibility of fruits to postharvest losses. For example, the amount of antifungal compound 1-acetoxy-2-hydroxy-4oxo-heneicosa-12,15 diene, which is present in the skin and the flesh of avocado degrades as the fruit ripens (Everett 1997). pH of the fruit pulp of different dessert banana varieties reduced from a range of 4.8-5.9 to 4.5-3.8 during the course of the ripening process (De Costa *et al.* unpublished data). Moreover, the fruit peel exudates of different banana varieties also showed a decrease in their pH from 6.77-6.25 to 6.9-4.9 during ripening from the fully-matured stage (light green stage in colour scale) (De Costa *et al.* unpublished data).

Reductions of fruit quality in terms of external or internal appearance, texture, flavour, nutritional value and food safety or reduction of quantity from harvesting to consumption are considered as postharvest losses. Nature and the degree of postharvest losses experienced by a particular commodity varies considerably depending on the type of fruit, the type of its production process and the infrastructural facilities available to the producers. As the quality standards differ from country to country and is highly specific to attitudes of the consumers of a given country, recorded postharvest losses show a wide variation, worldwide (Kader 2005) ranging postharvest losses of tropical fruits from 10-80% both in developing and developed countries. The agriculturally-developed countries such as Japan, The Republic of Korea and Taiwan, where infrastructural facilities are developed experience an average of 10% postharvest loss of fruits. In contrast, the average postharvest losses of fruits such as mango, banana, papaya, citrus and pineapple in the Philippines range from 15 to 35%. Moreover, when it comes to more delicate fruits such as papaya, the average postharvest losses range from 30-60% (Arshad *et al.* 2003). According to a survey by Food and Fertilizer Technology Center, Taiwan in 1993, in Thailand, postharvest loss due to fruit rot of mango was as high as 60%. Therefore, it is clear that postharvest losses vary significantly depending on the type and nature of the fresh produce. These losses occur along the production line starting from the harvesting and continuing through grading, packing, transportation, storage, retailing and consumption. Therefore, fruits which target the foreign market with longer destinations and transit times experience higher magnitudes of postharvest losses.

Mechanical, biological, microbiological, physiological and biochemical losses are the most common among the different types of postharvest losses which occur across the supply channel of fruits. Interestingly, most of these damages are accelerated not only by the activities and conditions prevailing at the postharvest phase, but also by the activities and conditions that had prevailed during the preharvest stage. This shows the gravity of the problem of postharvest losses and the amount of effort and precautions that needs to be taken to minimize postharvest losses. Hence, a generalized value cannot be assigned for postharvest losses of fruits occurring worldwide. However, the universal reality for postharvest losses of horticultural commodities is that the economic impact of these losses is much more than we realize at first glance.

Punctures by insects, wind damage, improper harvesting methods, overpacking and overloading of fruits, use of improper containers and carriers for transporting, poor transport facilities and roads are some factors which lead to mechanical (physical) damages of fruits at the postharvset stage. Biological losses cause quantitative and qualitative losses of the harvest due to the consumption of fruits by macroorganisms and also due to contamination of fruits with excretory material of the macroorganisms. In general, fungi are the predominant type of microorganisms causing microbiological losses of fruits while bacteria dominate the pathogenicity in vegetables. These fungal pathogens infect fruits either at pre- or post-harvest stages. Different types of infections caused by such fungal pathogens will be discussed in detail elsewhere in this text.

Horticultural commodities are prone to physiological losses after harvest. Loss of moisture and the resulting loss of turgour pressure of the cells through evaporation will lead to shriveling and wilting of tissues and undesirable textural changes. An increase in water loss together with the leakage of electrolytes across cell membranes causes chilling injury (Whitaker 2002). Due to respiration at the postharvest stage, the produce becomes more perishable. Shelf life of a horticultural produce has an inverse relationship with the rate of respiration. Therefore, when a commodity is having a higher respiration rate it becomes more perishable. Moreover, due to continuous respiration at the postharvest stage, substances such as sugars will be depleted resulting in eventual loss of taste, especially the sweetness (Kader and Saltveit 2002). Heat and moisture generated due to respiration have a positive influence on microbial growth on stored products. Heat or chilling injuries due to extreme environmental conditions and early senescence and death of tissues due to storage at temperatures below or above the optimum are some more examples of physiological losses experienced by fruits at the postharvest stage. Because the fruits are alive even after harvest, several biochemical reactions are being activated in fruits at the postharvest stage. These include changes of enzymes, hormones, carbohydrates, phenolic and antifungal compounds and pigments. Degradation of diene during ripening is carried out by the enzyme lipoxygenase (Everett 1997). A pronounced increase of ethylene just before the increase in respiration can be seen in climacteric fruits. Increase of ethylene leads to physiological and biochemical changes such as loss of chlorophyll, softening of tissues, accumulation of sugar and aromatics and decline of organic acids (Ludford 2002). Even though ethylene is essential for fruit ripening, it brings consequences that promote postharvest losses. Based on the above scenario, it is evident that postharvest losses are part and parcel of the horticultural commodities until they reach the dining table though their magnitude is case specific.

CAUSATIVE FACTORS OF POSTHARVEST LOSSES IN TROPICAL FRUITS

The wide range of factors causing postharvest losses of tropical fruits can be broadly categorized as environmental and socio-economic factors.

Environmental factors

The quality of tropical fruits is a blend of the uniqueness of their germplasms and environmental conditions that prevail in the tropical regions where they are grown. Unfortunately, the same environmental conditions that contribute to the high quality of tropical fruits, influence the development of postharvest losses. Some of the climatic factors that are found in the tropical regions such as heavy rains, intense solar radiation and high relative humidity favour colonization, infection and survival of pathogenic microorganisms. Development of anthracnose by *Colletotrichum* spp. in different tropical fruits is heavily influenced by rainy weather. Presence of a film of water on the fruit surface is a prerequisite for spore germination of *Colletotrichum* spp. According to de Lapeyre de Bellaire *et al.* (2000) and Everett (1997), the main source of inoculum for the development of banana and avocado anthracnose, is rain-borne. A very clear relationship has been observed between anthracnose severity and frequency of rainfall in avocado grown in Australia (Peterson 1978) and South Africa (Darvas and Kotze 1987) and banana in the French West Indies (de Lapeyre de Bellaire *et al.* 2000). Anthracnose severity could be reduced either by covering bunches of banana with plastic sheets or by growing the crop under rain shelters (de Lapeyre de Bellaire *et al.* 2000). Rainfall and prolonged wet periods after rainfall have been highlighted as pre-requisites for dispersal of conidia of *Colletotrichum* spp. in citrus canopies (Denham and Waller 1981).

Relatively high ambient temperatures (20-30°C) are prevalent in the tropics throughout the year (Dodd *et al.* 1992). The effect of temperature on postharvest disease development often interacts with other microenvironmental factors such as leaf surface wetness, leaf surface temperature and relative humidity which have direct influences on spore germination, infection and growth of fungal pathogens on tropical hosts. On the other hand, exposure of the fruit to high temperatures particularly close to or at harvest may induce tolerance of the fruit to low temperatures at the postharvest stage (Ferguson *et al.* 1999). Moreover, heat shock proteins synthesized in the fruits as a result of exposure to high temperatures may induce tolerance to subsequent high or low temperatures (Sabehat *et al.* 1996).

Socio-economic factors

Apart from the climatic conditions, poor infrastructure facilities and logistics, farm practices and storage facilities, lack of awareness of the physiological aspects of the perishable nature of horticultural commodities, lack of knowledge on postharvest handling and unorganized marketing systems that exist in the majority of developing tropical countries contribute to their high postharvest fruit losses (FAO 2005). Kader (2005) also highlighted the inadequate marketing systems, lack of communication facilities between producers and receivers, lack of market information, inadequate transport facilities, government regulations and legislations and poor maintenance of available facilities as the factors contributing to the postharvest losses in developing countries. Most of these countries still do not have proper road systems to reach the farmer fields and collection points which are in remote areas. The available roads are not smooth enough to reduce vibration and mechanical damage. Well-designed containers, with power supply to maintain low temperature storage during transportation are not available either. Furthermore, proper extension systems are not available to disseminate knowledge, expertise and training on correct postharvest handling techniques and practices to farmers and people involved in the supply chain. Very often, the supply chain between the farmer and the consumer involves a large number of intermediaries, with substantial postharvest losses at every stage. Except for banana cultivations which are operated by large scale companies, most of the other tropical fruits are handled by small- or medium-scale growers. Therefore, refrigerated storage facilities and organized marketing systems are not available to most of the fruits produced in many tropical countries. Due to the socio-economic factors, postharvest losses of fresh produces experienced by developing countries have been estimated to be much higher than those in developed countries. Based on the very limited actual survey data published, the estimated cumulative posthavest losses of fresh produces in developed countries range from 7-53% in comparison to 7-70% in developing countries (Kader 2005). Kantor *et al.* (1997) estimated the total retail, foodservice and consumer food losses in the United States for fruits to be 23% in 1995. According to data of the National Academy of Sciences report in 1978, the estimated percentage losses of banana, papaya, avocado and citrus ranged from 20-80, 40-100, 43 and 20-95%, respectively in less-developed countries.

Ferguson *et al.* (1999) and Korsten (2006) have highlighted how pre- and postharvest cultural practices, handling practices and storage conditions influence different types of postharvest losses. Out of the many causal factors, fungal pathogens act as a significant contributing factor on postharvest losses. **Table 5** shows the most commonly-occurring postharvest diseases of banana and other major tropical fruits.

POSTHARVEST FUNGAL INFECTIONS

Fungal infections are a major cause of quality deterioration in tropical fruits. Among different types of postharvest pathogens, fungi are the predominant group causing postharvest diseases in fruits. Growth of fungi is promoted in acidic growing environments and media. The slightly acidic nature of fruits, especially at the unripe stage, could be responsible for the higher incidence of fungal infections on fruits as compared to other horticultural produces. Successful infection by fungal pathogens consists of several indis-

Table 5 Most commonly-occurring postharvest diseases of banana and other major tropical fruits and the causal organisms recorded.

Fruit	Postharvest disease	Causal organisms recorded
Banana	Crown rot	*Fusarium* spp.[1] *Colletotrichum* spp.[1, 2] *Cladosporium* spp.[1] *Verticillium* spp.[1] *Lasiodiplodia theobromae*[3] *Verticillium theobromae*[3] *Colletotrichum musae*[3] *Fusarium pallidoroseum*[3] *Ceratocystis paradoxa*[3]
	Anthracnose	*Colletotrichum musae*[1, 2] *Colletorichum* spp.[1]
	Blossom end rot	*Colletotrichum* spp.[1, 2] *Fusarium* spp.[1]
	Ripe rot	*Fusarium* spp.[1]
	Finger rot	*Lasiodiplodia theobromae*[3]
	Johnson spot	*Magnaporthe grisea*[3]
	Squirter disease	*Nigrospora sphaerica*[3]
	Cigar-end rot	*Trachysphaera fructigena*[3] *Verticillium theobromae*[3]
Mango	Anthracnose	*Colletotrichum gloeosporioides* (teleomorph: *Glomerella cingulata*)[2, 4, 5]
	Stem end rot	*Lasiodiplodia theobromae*[4, 5] *Pestalotiopsis mangiferae*[4, 5]
	Botryodiplodia fruit rot (stem end rot)	*Botryodiplodia theobromae*[4, 5]
	Dorthiorella fruit rot	*Dothiorella dominicana*[4, 5] *Dothiorella mangiferae*[4, 5] *Dothirella* spp.[4, 5]
	Phomopsis fruit rot	*Phomopsis mangiferae*[4, 5]
	Aspergillus rot	*Aspergillus niger*[4, 5]
	Black spot	*Alternaria alternata*[5]
Pineapple	Black rot (soft rot/stem end rot/water rot/ water blister/ Thielaviopsis fruit rot)	*Thielaviopsis paradoxa* (teleomorph: *Ceratocystis paradoxa*)[2, 6]
	Fruitlet core rot (black spot)	*Fusarium subglutinans*[6] *Penicillium funiculosum*[6]
	Pink disease	*Erwinia herbicola*[6] *Acetobacter liquefaciens*[6]
	Marbel disease	*Acetobacter peroxydans*[6]
Citrus	Stem end rot	*Diplodia* spp.[7] *Phomopsis* spp.[7]
	Black rot/stem end rot	*Alternaria alternata*[7]
	Brown rot	*Phytophthora* spp.[7]
	Botrytis rot	*Botrytis* spp.[7]
	Anthracnose	*Colletotrichum* spp.[7]
	Green mold	*Penicillium digitatum*[7]
	Blue mold	*Penicillium italicum*[7]
	Sour rot	*Geotrichum* spp.[7]
	Trichoderma rot	*Trichoderma* spp.[7]
Avocado	Anthracnose	*Colletotrichum gloeosporioides*[2, 8]
	Stem end rot	*Thyronectria pseudotrichia*[8] *Colletotrichum gloeosporioides*[2, 8] *Dothiorella aromatica*[8] *Phomopsis persae*[7] *Fusarium decemcellulare*[8] *Pestalotiopsis versicolor*[8] *Botryodiplodia theobromae*[2, 8] *Rhizopus stolonifer*[8] *Fusarium sambucinum*[8] *Fusarium solani*[8] *Drechslera setariae*[8]
	Dothiorella and Colletotrichum complex fruit rot	*Dothiorella aromatica*[8] *Colletotrichum gloeosporioides*[8]

[1]Ramma *et al.* 1999; [2] De Costa *et al.* 2008; [3] Ploetz 1998; [4] Sangchote 1987; [5] Ploetz 2003; [6] Rohrbach and Johnson 2002; [7] Eckert and Eaks 1989; [8] Darvas and Kotzé 1981

pensable steps occurring in a sequential manner, namely, deposition of conidia on the host surface, germination of conidia and penetration of the host tissues and finally colonization. Depending on the fungal pathogen, mode of penetration is two-fold, i.e. through openings existing on the host surface and direct penetration of the intact plant cuticle (Bailey *et al.* 1992).

Postharvest fungal pathogens exploit three different routes of entry during the infection process: (1) Through entry points created by biotic and/or abiotic agents (i.e. due to damages caused by insects and wind and mechanical factors) during growth, development and storage; (2) through natural openings such as stomata, lenticels, stem ends and pedicel-fruit interfaces and (3) by direct penetration of the intact host cuticle at any time of the growth period of the fruit (Prusky and Lichter 2007). After penetration, these fungal pathogens show two main modes of parasitism: (a) biotrophy, in which nutrients are obtained from the living cells of the host and (b) necrotrophy, in which the nutrients are obtained from dead host cells (Perfect *et al.* 1999). In addition to the route of entry and mode of parasitism, fungal infections at the postharvest stage vary depending on the duration required by different pathogens to establish a successful host-pathogen interaction following initial infection. While some fungal pathogens show rapid colonization and parasitism immediately after entering host tissues, some other fungal pathogens show quiescent or latent infections. Here, the pathogen is unable to germinate or develop beyond any subsequent stage as result of a ‘temporary resistance’ exerted by the host. This short-term resistance to the pathogen could be due to adverse physiological conditions temporarily imposed by the host, either directly on the pathogen or indirectly, by modification of its pathogenic capability (Swinburne 1983). This temporary arrest of the infection process can happen at any of its stages from the initiation of conidia germination to penetration and colonization of host tissue. Postharvest diseases originating from such quiescent pathogen infections cause substantial reductions in the quality of tropical fruits.

POSTHARVEST DISEASES ORIGINATING FROM QUIESCENT INFECTIONS

Fungal pathogens such as *Colletotrichum*, *Monilinia*, *Botrytis* and *Alternaria* show long quiescent periods in fruits and subsequently show necrotrophic development at ripening and senescence (Prusky and Lichter 2007). Among these genera of fungi, *Colletotrichum* and *Alternaria* are predominantly associated with quiescent infections of tropical fruit species, while *Monilinia* and *Botrytis* are mainly associated with temperate fruits. Quiescent infections caused by *Colletotrichum*, *Monilinia*, *Botrytis* and *Alternaria* in fruits are generally termed as anthracnose, brown rot, gray mold and alternaria rot, respectively (Barkai-Golan 2001; Prusky and Lichter 2007). Furthermore, decay of apple by *Nectria galligena*, stem-end-rots of citrus by *Diplodia natalensis* and *Phomopsis citri* and stem-end-rot of avocado by *Dorthiorella gregaria* and *Phomopsis* spp. have also been reported as quiescent infections (Barkai-Golan 2001).

Colletotrichum, *Botrytis*, *Monilinia*, *Alternaria*, *Nectria* and the other fungi have long quiescent periods, starting the infection when fruits are at early developing stages (Barkai -Golan 2001; Fourie and Holz 1995; Pezet *et al.* 2003; Prusky and Lichter 2007). In most *Colletotrichum* species, the quiescent stage starts after the appressorium formation or after the initial penetration of the host cuticle by the penetration peg (Muirhead and Deverall 1981; Prusky and Plumbley 1992). Chakravarty (1957) has reported the presence of subcuticular hyphae of *C. musae* in unripe fruits just after infection while Muirhead and Deverall (1981) have observed melanized and unmelanized appressoria on the unripe fruit surface. In avocado, anatomical studies have revealed the presence of appressoria of *C. gloeosporioides*, in some cases even with a short infection peg, in the peel of unripe fruits (Binyamini and Schiffmann-Nadel 1972; Prusky *et al.* 1991). Daykin and Milholland (1984) also have reported the presence of subcuticular hyphae on unripe blueberry fruits infected with *C. acutatum*. According to Holliday (1995), the latency of *C. musae* can even be longer than five months.

Prusky (1996) highlighted three possible reasons for the temporary arrest of the pathogen's activity in quiescent infections: (1) deficiency in the host nutritional resources required for pathogen development; (2) presence of preformed or inducible fungistatic antifungal compounds in resistant unripe fruits and (3) an unsuitable environment in the fruit for the activation of fungal pathogenicity factors. In addition to the above reasons, production of phytoalexins by unripe fruits could also be responsible for short-term arresting of the infection process and delaying of disease development (Jeffries *et al*. 1990).

Biochemical changes that occur during the ripening stage of the fruit have a significant influence on the activation of the pathogens that are in a quiescent phase. One of the major changes that occur in fruits during ripening is the conversion of storage carbohydrates to soluble sugars, which provide the nutrients and energy needed for the reactivation of growth of the pathogen. Evidence for this possibility is provided by the observed relationship between resistance to fungal diseases and the sugar content of fruits (Horsfall and Diamond 1957). Moreover, higher levels of soluble solids and ascorbic acid in fruit tissues have been reported with higher resistance against *Glomerella cingulata* (anamorph: *C. gloeosporioides*) in fruits such as guava (Sing and Sharma 1981). Increase or decrease in glucose: sucrose ratio of fruits at the postharvest phase influence the signal transition from quiescent (biotrophic) to necrotrophic phases. Expression of the *pel*B gene, which encodes for pectate lyase, is a factor essential for pathogenicity of *C. gloeosporioides.* For example, expression of this gene is significantly enhanced by glucose as a carbon source (Drori *et al*. 2003) whereas low glucose levels lead to derepression of polygalacturonase (PG) activity.

Pre-formed antifungal compounds in the fruits could be another factor responsible for activation of a quiescent phase in the pathogen. For example, reduction of the level of 1-acetoxy-2-hydroxy-4-oxo-heneicosa12,15-diene (i.e. antifungal diene, AFD) in ripe avocado fruits in comparison to unripe fruits, could re-activate the quiescent infection of *C. gloeosporioides* when the fruit ripens (Prusky *et al*. 1983; Prusky 1996). Cojocaru *et al*. (1986) have reported antifungal compounds (i.e. 5-(12-*cis*-heptadecenyl)-resorcinol and 5-pentadeclylresorcinol) in unripe mango fruits. Such antifungal compounds have shown an inhibitory effect on germ tube elongation of *Alternaria alternata* and *C. gloeosporioides* under *in vitro* conditions when exposed to an ED50 of about 120 µg/ml, a concentration which was similar to that present in fruits when symptoms begin to develop. Such antifungal compounds present in the mango fruit peel have been reduced to non-toxic concentrations at the time of expression of symptoms. Furthermore, it has been reported that the rate of reduction of antifungal compounds towards non-toxic concentrations is faster in susceptible mango varieties as compared to resistant varieties (Prusky and Plumbley 1992).

Biochemical changes that occur in the fruit tissues during ripening have an impact on the activation of fungal virulence genes that are needed to affect the switch from the quiescent to the necrotrophic phase. Majority of the fruit tissues become alkaline during ripening and senescence. For instance, pH of the avocado fruit increases from 5.2 to 6.0 during ripening (Yakoby *et al*. 2000b). In contrast, our investigations on different banana varieties have reported an acidification of the fruit peel and fruit pulp due to ripening and some varieties (e.g. variety Embul) recorded a pH of 3.79 at the edible stage (i.e. at a maturity index of 7, the full yellow stage) (De Costa *et al*. unpublished data).

Contrary to what is observed in other fruits, banana shows higher levels of organic acids as the ripening process progresses (Yañez *et al*. 2004). The observation by Yañez *et al*. (2004) that the pH of banana pulp at the pre-climacteric stage changed from 5.4 ± 0.4 to 4.5 ± 0.3 in the post-climacteric pulp agrees with our observations of pH reduction of dessert banana during ripening (De Costa *et al*. unpublished data). Expression of genes which are essential for the necrotrophic phase of several pathogens having a quiescent stage is influenced by alkaline conditions in the fruit pulp, increasing levels of sugars in the ripening fruit and increasing ammonia concentration in the fruit tissue (Denison 2000; Yakoby *et al*. 2000a; Eshel *et al*. 2002; Drori *et al*. 2003). For example, expression of the endoglucanase gene AaK1 of *Alternaria alternata* occurs at pH levels above 6.0 while expression of *pel*B gene of *C. gloeosporioides* occurs at pH levels above 5.7. These coincide with the pH values of decaying fruit tissue, when the infections are highest. Similarly, there are some postharvest pathogenic fungi such as *Penicillium expansum* (*pepg*1 gene at pH 4.0) and *Sclerotinia sclerotiorum* (*pg*1 gene) of which pathogenicity genes are regulated in acidic environments.

ANTHRACNOSE PATHOSYSTEMS

Among a large number of *Colletotrichum* species, *C. gloeosporioides* (teleomorph: *Glomerella cingulata*), *C. acutatum* (teleomorph: *Glomerella acutata*) and *C. musae* play prominent roles as postharvest pathogens of banana and the other tropical fruits. *C. gloeosporioides* has been reported as the prominent causal organism of anthracnose of avocado, mango, papaya and citrus worldwide. However, *C. acutatum* have been reported to cause anthracnose of avocado only in New Zealand (Menge and Ploetz 2003) and anthrac-

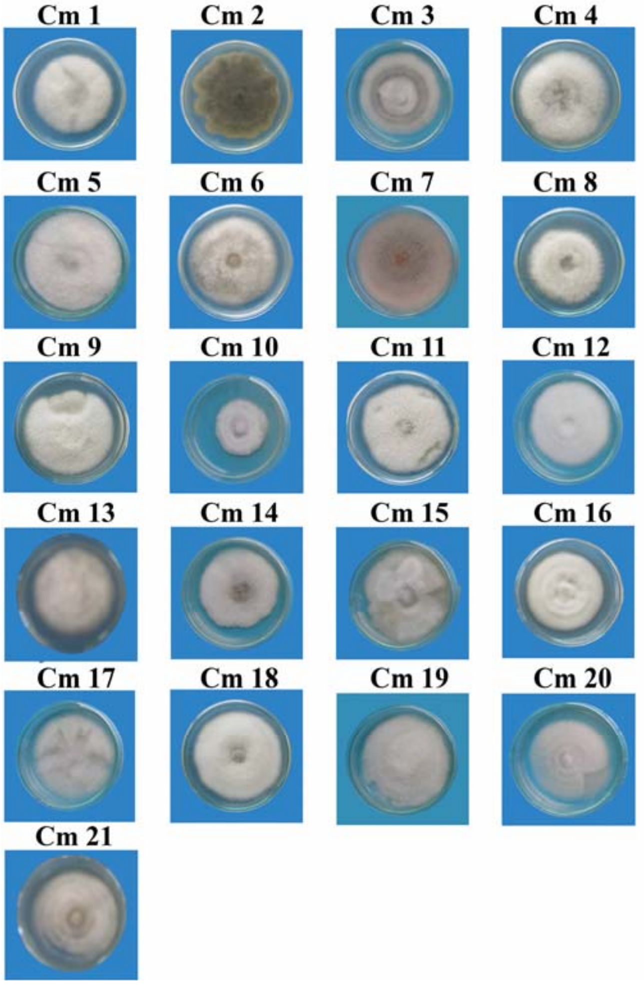

Fig. 1 Diversity of colony morphology of different isolates of *Colletotrichum* obtained from different banana varieties collected from different locations of Sri Lanka - (front side) when grown on PDA medium. From **De Costa and Kalpage** (2006) Differential response of *Colletotrichum* isolates infecting banana to synthetic fungicide and a biological control agent. *Sri Lankan Journal of Agricultural Sciences* **43**, 50-65, with kind permission from Editor-in-Chief, Sri Lankan Journal of Agricultural Sciences.

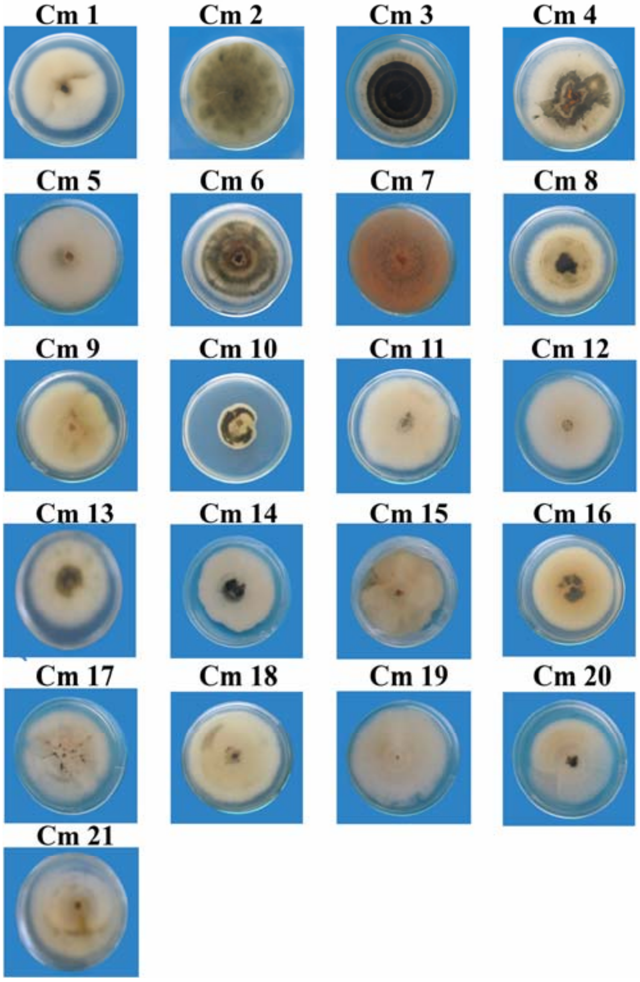

Fig. 2 Diversity of colony morphology of different isolates of *Colletotrichum* obtained from different banana varieties collected from different locations of Sri Lanka - (lower side) when grown on PDA medium. From **De Costa and Kalpage** (2006) Differential response of *Colletotrichum* isolates infecting banana to synthetic fungicide and a biological control agent. *Sri Lankan Journal of Agricultural Sciences* **43**, 50-65, with kind permission from Editor-in-Chief, Sri Lankan Journal of Agricultural Sciences.

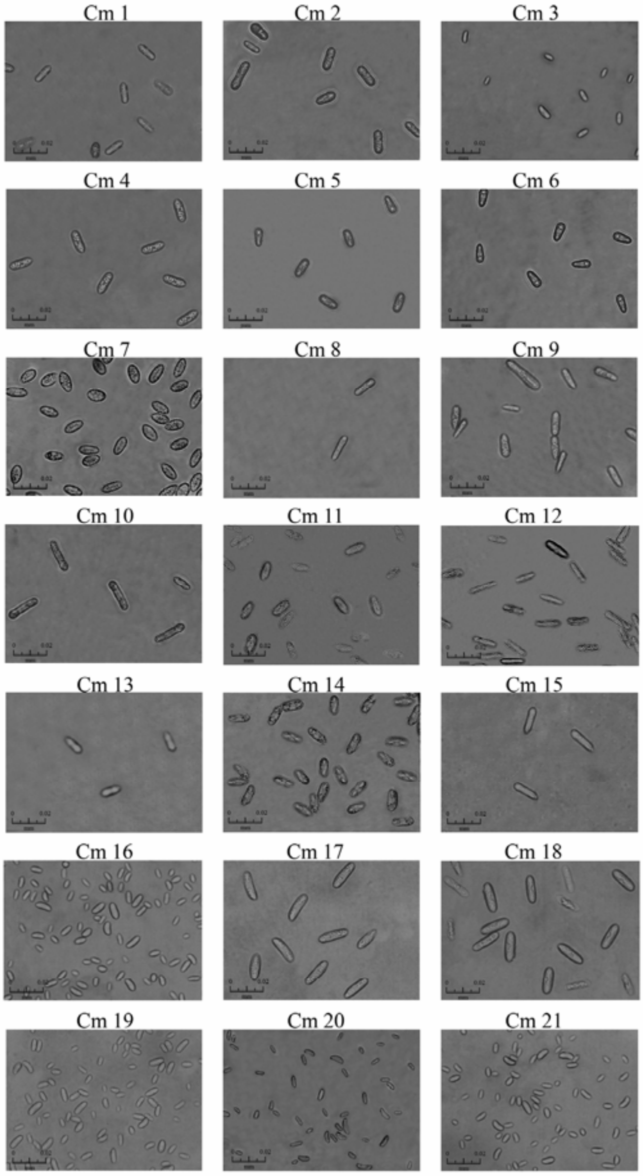

Fig. 3 Spore diversity of *Colletotrichum* spp. isolated from anthracnose-, crown rot- and blossom-end-rot infected banana varieties collected from different locations of Sri Lanka (De Costa *et al.* unpublished data). Observation of the shape of the spores of *Colletotrichum* isolates. The 21 *Colletotrichum* isolates obtained according to De Costa and Kalpage (2006) were maintained as single colony forming units were grown on PDA medium under dark conditions till sporulation. Spore shape was observed and micrographed using light microscope at X400 magnification.

nose of citrus, mango and papaya in many regions of the world (Wharton and Dièguez-Uribeondo 2004). Even though *C. musae* has been reported as the causal organism of banana anthracnose, there are reports on isolations of *C. gloeosporioides* from banana (Mills *et al*. 1992). Furthermore, our investigations revealed a large number of (i.e. 21) morphologically-different *Colletotrichum* isolates from different dessert banana varieties collected from different agroecological regions of Sri Lanka which were infected with anthracnose, crown rot and blossom end rot (De Costa and Kalpage 2006). These isolates showed significant variations of colony morphology, colony growth rate, spore morphology and spore dimensions (**Figs. 1-3**). Similar morphological diversities, both on colony characteristics and spore dimensions, have been shown by *Colletotrichum acutatum,* infecting olive causing olive anthracnose and *C. gloeosporioides* causing anthracnose of avocado and mango (Sanders and Korsten 2003; Talhinhas *et al*. 2005).

In addition to the morphological variations (morphotypes) shown by different isolates of the same species of *Colletotrichum*, these pathosystmes have remarkable features which would be of interest to plant pathologists. For example, genomic and pathogenicity variations have been identified among different isolates of *C. gloeosporioides* (Abang *et al*. 2005) and *C. acutatum* infecting a wide range of hosts (Sreenivasaprasad and Talhinhas 2005). Our investigations have also revealed pathogenicity and genomic variations among the morphologically-different *Colletotrichum* spp. that were isolated from different dessert banana varieties, collected from different agroecological regions and infected with different postharvest diseases (De Costa *et al*. unpublished data). Genomic variations among the *Colletotrichum* isolates have been identified by a range of molecular typing methods including denaturing gradient gel electrophoresis (DGGE) of PCR amplified small subunit (18s) rDNA fragments, microsatellite primed PCR, mitochondrial and ribosomal DNA RFLP (restriction fragment length polymorphism) (Buddie *et al*. 1999), RAPD-PCR (Whitelaw-Wickert *et al*. 2007), arbitrary primed PCR and nucleotide sequence variation of internal transcribed spacer regions of rRNA region (Talhinhas *et al*. 2005).

Infection of *Colletotrichum* spp. also shows interesting features. *Colletotrichum* spp. have the ability to infect intact host surfaces. Moreover, infection of a single host by multiple species of *Colletotrichum* and infection of multiple hosts by a single *Colletotrichum* species are common with many *Colletotrichum* pathosystems (Hayden *et al*. 1994; Freeman *et al*. 1998). Therefore, *Colletotrichum* pathosystems have the cross-infection ability of a range of host species.

FUNGAL INFECTIONS THROUGH NON-INTACT HOST SURFACES

Fungi infect through non-intact host surfaces of fruits via various routes of entry during pre- and postharvest stages (Barkai-Golan 2001). These routes could be natural openings such as stomates, hydathodes and lenticels that exist on fruit surfaces or artificial openings created by mechanical and insect damage. Such mechanical or biological damages could occur at preharvest, harvest or postharvest stages. Fungi and bacterial populations abundant in the aerial and soil microenvironment get the opportunity to invade through these openings and become "wound pathogens". These pathogens, in general, activate their decay development when the fruit is at the ripening stage or at the senescence stage. They also show variations in the procedure of decay development.

As highlighted by Barkai-Golan (2001), air-borne fungal genera such as *Cladosporium*, *Alternaria*, *Stemphylium*, *Penicillium*, *Aspergillus*, *Rhizopus*, *Mucor* and *Botrytis*, and soil-borne fungi such as *Sclerotinia* and *Fusarium* are the predominant "wound pathogens" of fruits. In addition to the above genera of fungi, *Colletotrichum* which has the ability to infect intact host surfaces, also infects through natural or artificial wounds. For example, germ tubes of *C. gloeosporioides* penetrate into young papaya through stomata when the fruit is still at the orchard (Stanghellini and Aragaki 1966) and cause papaya anthracnose. In banana, infection of *C. musae* through wounds is essential to cause crown and finger stalk rot (Krantz *et al*. 1978; Agrios 1988). There are some wound pathogenic fungi which show a latent period after penetrating through a natural or artificial opening. In *Monilinia fructicola*, the germ tubes enter through stomata of stone fruits, in *Dorthiorella gregaria*, through lenticels of avocado, in *Alternaria alternata* through lenticels of mango and persimmon are some examples for such latent infections by wound-invading fungi (Barkai-Golan 2001).

CONTROL OF POSTHARVEST DISEASES OF TROPICAL FRUITS

A number of options, both chemical and non-chemical, are available for the control of postharvest diseases and they can also be either conventional or non-conventional. These control measures can be started when the crop is still in the field (i.e. pre-harvest) or as treatments done after harvesting (i.e. postharvest). Chemical or non-chemical pre-harvest treatments, whether conventional or non-conventional, are of paramount importance in controlling postharvest diseases, as postharvest disease development is heavily influenced by the pre-harvest environment and activities to which the fruits are exposed.

Among the many control measures available, application of pesticides is part and parcel of the production of tropical fruits, especially by large scale commercial growers. Without the use of pesticides, economically-viable yields of many crops would not be achievable and the high quality and the aesthetic value of the products, which is the biggest factor determining consumer demand, cannot be maintained. Moreover, chemical control is widely practiced as the availability and efficiency of chemical control is relatively greater than for the other control measures (Jeger and Plumbley 1988). Potential of chemical methods for the control of postharvest diseases of tropical and subtropical fruits has been reviewed by Eckert and Ogawa (1985). For the control of anthracnose diseases, protectant (i.e. copper oxychloride, metallic dithiocarbamates and chlorothalonil), systemic fungicides (i.e. benzimidazoles, triazole) and eradicant fungicides with multi-site actions (i.e. prochloraz and imazalil) have been widely used either at pre- or postharvest stages (Jeffries *et al*. 1990; Prior *et al*. 1992; Wharton and Dièguez-Uribeondo 2004). Pre- or postharvest application of fungicides is being used for the control of wound-invading fungi which are the main cause of stem end rot of fruits. For example, pre-harvest spray applications with copper compounds or captafol and postharvest spray treatments with procloraz within 24 hours of harvest have been effective in controlling stem end rot of avocado and mango (Darvas and Kotze 1987; Ploetz 2003). Postharvest dips, sprays or recirculating drenches of thiabendazole, imazalil, prochloraz and flusilazole are used for the control of crown and pedicel rot of banana (Jones 1991; Ploetz *et al*. 2003). Furthermore, pre- or postharvest application of benzimidazole is reported to be effective in Diplodia and Phomopsis stem end rot of citrus (Timmer *et al*. 2003).

In addition to the fungicide treatments at the pre-harvest stage, cultural methods, agronomic practices and genetic resistance of the host plant contribute significantly to the reduction of postharvest disease incidence. For example, crown rot and anthracnose incidence of banana can be reduced significantly by agronomic practices such as maintenance of soil fertility and an optimum plant density. Detrashing, removal of leaves rubbing the banana bunches, covering of banana bunches with perforated polythene sleeves, weed control and removal of flower bud from the bunch are some of the effective cultural methods that have been recommended for the control of crown rot and anthracnose of banana (CTAHR publications 2008). It has been reported that wrapping of developing fruits with paper bags, field sanitation and use of resistant varieties have resulted in reduction of severity of mango anthracnose (Arauz 2000).

Despite the wide availability and higher efficiency of pesticides for the control of postharvest diseases, public concern is emerging about the negative effects of the usage of pesticides, especially for horticultural produce, which are eaten raw, mostly without removing the peel and having no time to be kept for a reasonable safety period after the application of fungicides. The possible negative impacts of continuous usage of fungicides are development of resistant strains of postharvest pathogens (Sugar and Powers 1986; Eckert 1990; Jones 1991; Vinas *et al*. 1991; de Lapeyre de Bellaire and Chillet 2000; Mari *et al*. 2003), possible carcinogenic effects (Wharton and Dièguez-Uribeondo 2004), phytotoxicity to fruit (Wharton and Dièguez-Uribeondo 2004) and remaining of visible fungicide residues (i.e. copper) on harvested fruit (Korsten *et al*. 1995). Moreover, though application of fungicides will reduce the incidence or severity of diseases, eradication cannot be achieved (Adaskaveg and Förster 2000). Instead, the situation would become more severe if chemical treatments are stopped and the environmental factors become more conducive for disease development. As a result, alternative non-fungicidal approaches have been tried and tested with varying degrees of success.

Non-chemical (non-pesticidal) approaches to control postharvest diseases of tropical fruits

Use of physical and biological methods, natural antimicrobial substances, substances generally regarded as safe (GRAS) and sanitizing products and implementation of genetically-manipulated approaches are the non-chemical methods which have emerged in the recent past for the control of postharvest fruit diseases (Wisniewski *et al*. 2001; Larrigaudiere *et al*. 2002; Mari *et al*. 2003; Korsten 2006). Hot water (i.e. hot water immersion, hot water rinsing and brushing) or heat shock treatments, radiation (i.e. gamma and UV-C), modified atmosphere storage and controlled atmosphere storage are common physical means that are used for the improvement of postharvest quality of fresh produce by reducing disease incidence and intensity at the postharvest stage (Wisniewski *et al*. 2001; Marquenie *et al*. 2002; Fallik 2004a, 2004b; De Costa and Erabudupitiya 2005; Irtwange 2006; Korsten 2006; Cia *et al*. 2007). Short duration (few minutes) exposure to higher temperatures (44-55°C) or long duration exposure (hours) to slightly lower temperatures (38-46°C) has been effective in controlling latent and wound infections of banana, mango, citrus, papaya, pineapple and many other fruits (Barkai-Golan 2001; De Costa and Erabadupitiya 2005; Wilson Wijeratnam *et al*. 2005; Korsten 2006; Irtwange 2006). These heat treatments can be in the form of hot water dips, vapour heat, hot dry air or hot water rinsing and brushing (Fallik 2004a, 2004b; Irtwange 2006). Immersion of citrus in 50-53°C hot water is recommended for control of *Penicillium* spp. or *Alternaria* spp. which cause rots in oranges, lemons or grapefruit (Couey 1989; Schirra *et al*. 1997; Nafussi *et al*. 2001). Moreover, hot water treatments of 40 and 41°C for 25-30 min reduced Colletotrichum body rots of avocado fruit (Fallik 2004b). Beneficial effects of heat treatments are of many types: (a) inhibiting biochemical pathways involved in ripening and other processes in many fruits and vegetables (Paull and Chen 2000); (b) inhibiting pathogen spread by inducing defense mechanisms in outer layers of the fruit (Ben-Yehoshua *et al*. 1997); (c) sealing the mechanical injuries and surface cracks of the fruit by redistributing the wax layer and developing a physical barrier against the entry of pathogens (Schirra and D'Hallenwin 1997), (d) increasing the accumulation of glucanase and chitinase proteins (Pavoncello *et al*. 2001) and (e) enhancing the accumulation of phytoalexins such as scoparone and scopolitin (Nafussi *et al*. 2001). Furthermore, there are additional advantages of heat treatment (Fallik *et al*. 1999). These include significant reduction of weight loss, maintenance of fruit firmness even after prolonged storage periods and reduction of the sites of fungal penetration into fruit. All these advantages are due to the sealing of surface cracks and natural openings by redistributing the wax layer on the fruit. Additional advantages of hot water treatment are the slowing of ripening of climacteric fruits to achieve a longer storage period, reducing susceptibility to chilling injury, controlling infestation of insect pests and thereby reducing pesticide usage (Fallik 2004b). Nonetheless, development of off-flavours, probably due to increased ethanol level and deterioration of surface appearance have been observed at higher temperatures in citrus subjected to heat treatment (Irwange 2006). Similarly, in view of the limitations of other physical methods, scald on fruits has been reported in papaya treated with UV-C for the control of anthracnose (Cia *et al*. 2007).

Biological control of postharvest diseases of tropical fruits

Use of naturally-derived fungicides, induced host resistance and use of microbial antagonists have been considered as biological control approaches of fruit and vegetable diseases (Chalutz and Droby 1998). As naturally-derived fungicidal substances, the potential *in vitro* use of essential oils of *Cinnamomum zeylanicum*, *Syzygium aromaticum*, *Ocimum basilicum* and some major components derived from essential oils (i.e. eugenol and citral a + b) has been reported for the control of *Colletotrichum musae* and *Fusarium proliferatum*, the crown rot pathogens of banana (Ranasinghe *et al*. 2002; Herath and Abeywickrama 2008).

In this review, attention is specifically focused on the use of microbial antagonists as biological control agents. A large body of information is available on the potential use of microbial antagonists that dwell naturally on host plant surfaces (i.e. phylloplane or fructoplane) for the control of postharvest diseases of tropical fruits. Among the epiphytic antagonists, several bacteria and yeast species have shown promise for the control of latent and wound infections either as pre- or postharvest applications when applied solely or in combinations. For example, control of stem-end rot, anthracnose and Dorthiorella and Colletotrichum fruit rot complex of avocado has been more successful by preharvest application of bacterial antagonists than the standard commercial application programmes of copper oxychloride (Korsten *et al*. 1989). The same bacterial antagonists (i.e. *Bacillus licheniformis* and *B. subtilis*) have been successful in controlling the same diseases of avocado when applied as a packhouse treatment (Korsten *et al*. 1989). Moreover, a pre-harvest application of *Pseudomonas fluorescens* (FP7) with chitin formulation at monthly spray intervals through aerial spray has reported a significant control of the pre- and post-harvest incidence of mango anthracnose (Vivekananthan *et al*. 2004) and pre-harvest application of *Bacillus licheniformis* controlled the incidence of mango anthracnose more consistently (Silimela and Korsten 2007). Success of pre-harvest application of a yeast antagonist, *Pantoea agglomerans* CPA-2 together with formulation strategies to improve the survival of cells under unfavourable environmental conditions, for the control of postharvest diseases of citrus has been reported by Cañamás *et al*. (2008). Potential use of a range of bacterial and yeast antagonists as postharvest treatments for the control of latent and wound infections of many tropical fruits has also been described by Droby (2001), Janiseiwicz and Korsten (2002), Reyes *et al*. (2004) and Korsten (2006). For example, control of wound infections caused by *Penicillium expansum* and *Botrytis cinerea* by combined application of *Pseudomonas syringae* and yeast antagonists (i.e. *Sporobolomyces roseus*, *Kloeckera apiculata*, *Metschnikowia fructicola*) (Janisiewicz and Bors 1995; Karabulut *et al*. 2005) has been reported. Moreover, the efficiency of several other yeasts such as *Rhodotorula glutinis* (LS-11), *Cryptococcus laurentii* (LS-28), *Candida famata* (21-D) and *Pichia guilliermondii* (29-A) and the yeast-like fungus *Aureobasidium pullulans* (LS-30) for the control of postharvest pathogens of fruits (Lima *et al*. 1999) have been reported. Favourability of the postharvest environment on the success of the applied antagonists has been clearly highlighted by several authors (Janiseiwicz and Korsten 2002; Wharton and Dièguez-Uribeondo 2004).

Different biological control agents may have different modes of operation. Competition with the pathogen for nutrients and space (Mari *et al*. 1996), production of antifungal metabolites (Janisiewicz *et al*. 1991), suppression, hypovirulence, predation (Haggag and Mohamed 2007) direct parasitism and induced resistance, sometimes associated with reduction of enzyme activity of the pathogen (Zimad *et al*. 1996), have been reported as possible modes of antagonism of biological control agents against postharvest pathogens. Eventhough the use of antibiotic-producing bacteria as biocontrol agents has been abandoned (Wisniewski and Wilson 1992), several commercial products containing epiphytic yeasts and non-antibiotic-producing bacteria are available to control postharvest diseases. For example, Aspire (Ecogen, Langhorne, PA, USA) and Bio-Save 110 (EcoScience, Worcester, MA, USA) contain yeast *Candida oleophila* strain I-182 and a saprophytic strain of bacterium *Pseudomonas syringae* respectively.

However, several drawbacks of biocontrol agents have also been reported. Inconsistency of field performance, susceptibility to stress factors of the environment, short storage life, inefficiencies of colonization ability are some of the drawbacks associated with biological control agents even when they perform effectively under *in vitro* conditions. Therefore, enhancing the efficiency of the biological control agents is essential. Screening of more promising antagonists, use of mixtures of antagonists with different modes of antagonism, integration of biological control with low doses of fungicides or with other chemicals which are not pesticides are some approaches emerging at present as alternatives to synthetic fungicides (Janiseiwicz and Korsten 2002; Mari *et al*. 2003; Janisiewicz *et al*. 2008). Combining antagonists with chitosan and with additives such as sodium bicarbonate, calcium chloride, EDTA, potassium sorbate, calcium propionate and Tween have been attempted to mitigate the drawbacks and also to improve the efficiency of biological control agents (Wisniewski *et al*. 2001; Janiseiwicz and Korsten 2002; Mari *et al*. 2003; Gamagae *et al*. 2004; De Costa and Erabadupitiya 2005; De Costa *et al*. 2008). Above all, genetic manipulation of biological control agents is a novel approach to enhance their efficiency with a consistent performance. Moreover, the required level of postharvest disease control is often extremely high (i.e. 95-98%) compared to the levels of field- and soil-borne diseases. Also, food safety considerations are very strict with regard to the addition of microorganisms directly to the food product and the potential market for the use of biofungicides is not so satisfactory (Chalutz and Droby 1998). Hence, postharvest biological control is a challenging task.

Integrated approaches in controlling postharvest diseases of tropical fruits

Despite their potential drawbacks and challenges, biological agents when integrated with one or few other control methods have been successful either additively or synergistically in controlling many postharvest fruit diseases (Janiseiwicz and Korsten 2002). Possible options to enhance the biocontrol efficiency of the biological agents are addition of low levels of fungicides, salt additives such as EDTA, calcium chloride, sodium bicarbonate which are considered as GRAS compounds, sugar and nitrogenous nutrients and chitosan with the biological agents, integration of physical measures such as hot water treatment and UV-C radiation and use of mixtures of biological control agents (Droby 2001). A large body of research information is available to support the additive and/or synergistic effect of either physical, chemical or cultural control methods when integrated with biological control at pre- or postharvest stages (Janiseiwicz and Korsten 2002; Korsten 2006). A commercial formulation of *Bacillus licheniformis* (mangogreen) has shown promising results in controlling anthracnose and stem end rot of mango and retaining the marketability of the fruits when integrated with quarter-strength fungicide dip (prochloraz) and hot water treatment at 45°C for 5 min (Govender *et al*. 2005). De Costa *et al*. (2008) have reported the success of a postharvest dip treatment of a bacterial antagonist (i.e. *Burkholderia spinosa*, a member of *Burkholderia cepacia* complex) in controlling anthracnose, crown rot and blossom end rot of banana when integrated with Tween 20 and Tween 20 and hot water treatment (De Costa and Erabadupitiya 2005) (**Fig. 4**). Combination of two yeast strains (*Pichia anomala* (E.C. Hansen) Kurtzman, strain K and *Candida oleophila* Montrocher, strain O) against the parasitic complex responsible for banana crown rot (Lassois *et al*. 2008) and also combination of antagonists with GRAS substances such as sodium carbonate, sodium bicarbonate and ethanol, physical treatments such as hot water treatments and UV-C irradiation, chemical substances such as chitosan and its derivatives and Ca for improved biological control efficiencies have been well highlighted against a range of pathogens causing postharvest decay (Janiseiwicz and Korsten 2002; Korsten 2006).

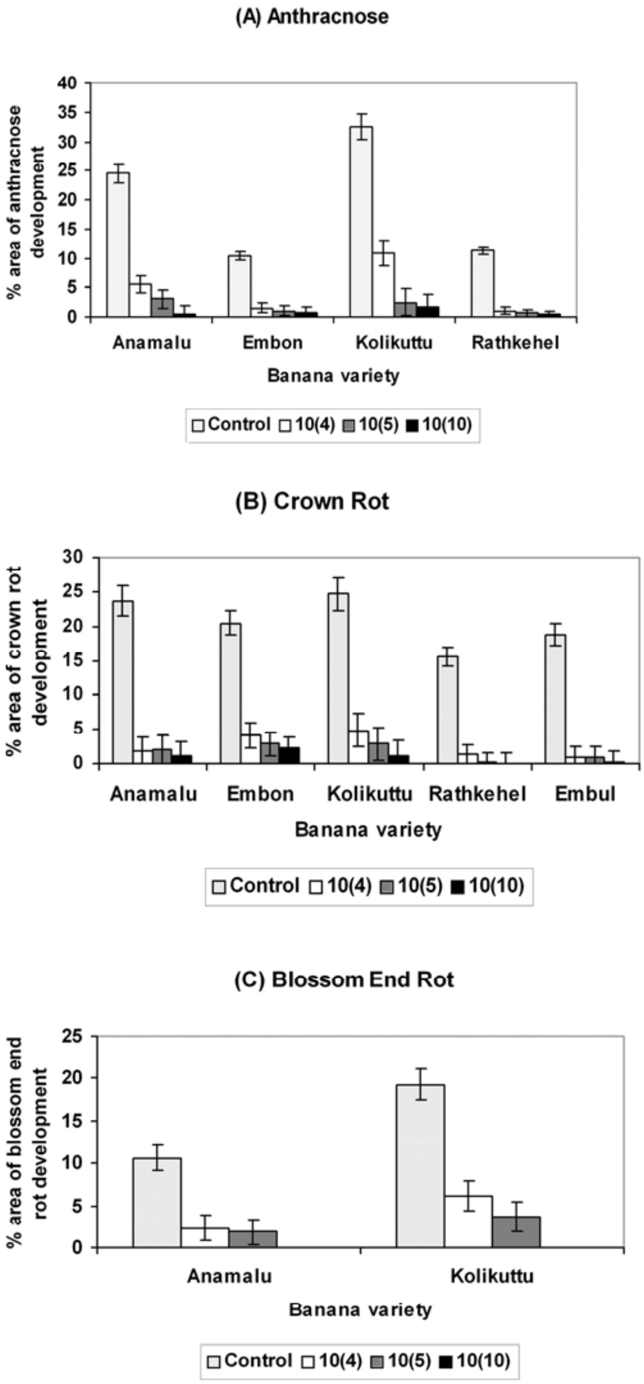

Fig. 4 Percentage anthracnose (**A**), crown rot (**B**) and blossom end rot (**C**) development on four different banana varieties when treated with three different concentrations (i.e. 10^4, 10^5 and 10^{10} cfu/ml) of bacterial antagonists containing 0.02% Tween 20. Each bar is a mean of ten replicates. Vertical bars indicate the Least Significant Difference to compare treatment means within each banana variety. (Modified from De Costa *et al*. 2008).

Genetic manipulation of biological control agents to control postharvest diseases

For more effective performances of the biological control agents either improvements of the environment to favour the biocontrol agent or genetic improvement of the agent is possible (Hornok 2000). Genetic improvements to the biological control agents are possible to increase their effectiveness as 'hyperparasitic' microorganisms (Haggag and Mohamed 2007). As described by Haggag and Mohamed (2007), genetic improvement of the biological control agents can be achieved through molecular tools and techniques such as chemical and physical mutation, sexual hybrids, homokaryons and genetic manipulation through directed mutagenesis, protoplast fusion, recombination, and transformation. In addition to the genetic manipulation of antagonists to overexpress antagonism, foreign genes can be transferred to antagonists to increase tolerance to environmental stresses or to produce antifungal substances and thereby, increase their efficiency (Janisiewicz *et al*. 2008). For example, genes such as defensins, which are isolated from edible plant parts are of high interest in genetic manipulation of antagonists. Plant defensins are small peptides, consisting of 45-54 amino acids, and are not toxic to plants. They inhibit a range of fungi in micromolar concentrations (Janisiewicz *et al*. 2008). Mode of antagonism of the peptides against plant pathogens is believed to be through interaction of the amphipathic cationic peptide with phospholipids on the target cell membrane, followed by either channel formation or simple membrane disruption (Shai 1995). As an example, *Pichia pastoris*, a yeast transformed with *Ps*d I, a defensin obtained from pea seeds (*Pisum sativum*) has become a promising biological control agent for the control of apple decay caused by *Penicillium expansum* (Janisiewicz *et al*. 2008). The same approach has been used to control postharvest decay of tomato caused by *Colletotrichum coccodes* by genetically-modifying *Saccharomyces cerevisiae* using a gene for cecropin production which is an antifungal defensin isolated from insects (Jones and Prusky 2002). Furthermore, successfull control of grey mold of strawberries by using an antifungal peptide obtained from Pacific oyster (*Crassostrea gigas*) (Liu *et al*. 2007) and control of *Botrytis cinerea* and *Penicillium expansum* using a defensin gene originally isolated from the bark of peach tree (Wisniewski *et al*. 2005) have been reported. Antimicrobial peptides (AMPs) are an extremely diverse group of small proteins that are considered together because of their native antimicrobial activity. Antimicrrobial peptides (AMPs) as highlighted by Liu *et al*. (2007) have desirable attributes as biocontrol agents of postharvest diseases due to their broad spectrum activity on a range of microorganisms including bacteria, fungi, viruses and tumor cells; they have not, to date, induced pathogen resistance; and AMPs are generally non-toxic, and can meet food safety requirements. Moreover, reduced-pathogenicity mutants of the *Colletotrichum gloeosporioides* that have been generated by insertional mutagenesis has been reported to be effective in controlling avocado anthracnose caused by the wild type pathogen if pre-inoculated on the fruit surface (Yakoby *et al*. 2001).

Even though there is public concern about using genetically-modified organisms in crop protection, genetically-transformed *Pichia* systems have the potential to become successful biological control agents. The *Ps*d I gene has been isolated from pea seeds that have been part of the human diet for several centuries. Hence, toxic or allergic reactions to humans or other mammals are less likely. Genetically-manipulated *Pichia* systems have additional appeal as this yeast has been approved as a dietary supplement to feed animals. Moreover, yeasts are suitable as biocontrol agents as they rapidly colonize and survive on fruit surfaces for long periods under different environmental conditions, use available nutrients to proliferate rapidly by limiting the nutrient availability to the pathogen and are generally unaffected by commercial fungicides (Jones and Prusky 2002).

Apart from the manipulation of genetic make-up of biological control agents, genetic engineering can be employed to manipulate structural and functional properties of fruits in order to control postharvest diseases. Transcription and translation of many ripening-related genes are affected by ethylene (Giovannoni 2001). Attempts have been made to modify the genes responsible for ethylene production and other features of the ripening process and thereby create a fruit that will have a longer shelf life (Klee 2005). Biotechnological approaches can also be directed towards either indirect control of pathogens through wounding or senescence or direct integration of pathogen resistance genes (Hererra-Estrella 2000; Pech *et al*. 2005; Janisiewicz *et al*. 2008). For example, *Nr*, a tomato mutant impaired in ethylene perception has significant reduction in symptom development to bacterial (i.e. *Xanthomonas campestris* and *Pseudomonas syringae*) and fungal (i.e. *Fusarium oxysporum*) infections (Lund *et al*. 1998). Moreover, ethylene-inhibiting melon plants are resistant to powdery mildew (Bower *et al*. 2002) and antisense ACO tomato fruits are more resistant to artificially-inoculated *C. gloeosporioides* than wild type fruits (Cooper *et al*. 1998). Longer shelf life through biotechnology has been commercially-successful so far with tomato and has a greater potential for increasing postharvest life of other tropical fruit crops (Hererra-Estrella 2000).

Public perception of non-chemical control strategies and their potential for promotion

Public interest in the use of non-chemical strategies for plant protection is increasing rapidly. Numerous advantages of new-era biopesticides such as their greater effectiveness when used in IPM systems, provision of a greater margin of safety to applicators and users, absence of risks to many or to all non-target pests, higher biodegradability, lower probability of resistance development to target pests, allowance of shorter pre-harvest intervals after application, very short restricted-entry intervals, environmental friendliness and increased sustainability are possible reasons for greater interest in biopesticides by the present day stakeholders, especially the consumer (Marrone 2007). Therefore, the 2.4% share of biological pesticides in the current pesticide market is projected to be doubled by 2010 (Marrone 2007). However, socio-economic and attitudinal barriers against biopesticides have been highlighted by Marrone (2007). Among them are very high competitiveness with the synthetic pesticide market, risk averseness of the consumer, unwillingness of the consumers to change from familiar synthetic chemicals, complex selling channels and negative perceptions, especially on the efficacy of biopesticides. Such limitations associated with the usage of biopesticides can be mitigated by promoting research support on biopesticides, demonstrating the benefits of biopesticides and the profits that can be achieved by biopesticides, showing resistance and residue management by the application of biopesticides and most importantly by educating the users and customers (Marrone 2007). The public should be educated to appreciate the presence of slight blemishes which may be left behind due to non-pesticide control measures rather than spotless horticultural commodities, in view of the environmental and health risks associated with synthetic pesticides which are used to enhance the external appearance. Provision of incentives for the users of biopesticides and implementation of reasonably firm rules and regulations during the registration of biopesticides are some other policies for encouraging the use of biopesticides. Nevertheless, two yeast species, namely *Candida oleophila* and *Cryptococcus albidus*, two strains of *Pseudomonas syringae*, *Bacillus subtilis* and *Bacillus licheniformis* are commercially available as ASPIRE, YieldPlus, BIOSAVE, Avogreen and Mangogreen, respectively for the control of a range of post-harvest pathogens (Korsten *et al*. 1998; Droby 2001; Govender *et al*. 2005). Therefore, several more biopesticides for the control of postharvest diseases could be expected in the future, in view of the candidates emerging continuously as prospective biocontrol agents for the control of postharvest pathogens.

Similar limitations are associated with biotechnological applications towards the reduction of crop losses, especially in the developing world due to lack of technology, lack of capital investment and also due to interventions by the developed world (Hererra-Estrella 2000). In addition, non-chemical control measures that can be practiced by small scale growers and retailers should be promoted through proper extension services. Especially, the personnel who deal with horticultural commodities at different levels of the marketing channel should be made aware of the delicate and lively nature of the horticultural produce that they handle.

REFERENCES

Abang MM, Fagbola O, Smalla K Winter S (2005) Two genetically distinct populations of *Colletotrichum gloeosporioides* Penz. causing anthracnose disease of yam (*Dioscorea* spp.). *Journal of Phytopathology* **153**, 137-142

Adaskaveg JE, Förster H (2000) Occurrence and management of anthracnose epidemics caused by *Colletotrichum* species on tree fruit crops in California. In: Prusky D, Freeman S, Dickman MB (Eds) *Colletotrichum: Host Specificity, Pathology and Host-Pathogen Interaction*, The American Phytopathological Society, St. Paul, MN, USA, pp 317-336

Agrios GN (1988) *Plant Pathology* (3rd Edn), Academic Press, London, 803 pp

Anon (2002) FAOSTAT database. Food and Agriculture Organization of the United Nations, Rome, Italy

Arauz LF (2000) Mango anthracnose: Economic impact and current options for integrated management. *Plant Disease* **84**, 600-611

Arshad FM, Radam A, Mohamed Z (2003) An economic analysis of the Malaysian fruits industry. *Proceedings of an International Seminar on Postharvest Handling and Processing of Tropical and Subtropical Fruits*, TFNet General Assembly Kuala Lumpur, Malaysia, 2003, pp 22-28

Bailey JA, O'Connell RJ, Pring RR, Nash C (1992) Infection strategies of *Colletotrichum* species. In: Bailey JA Jeger MJ (Eds) *Colletotrichum: Biology, Pathology and Control*, CABI Publishing, Wallingford, UK, pp 88-120

Barkai-Golan R (2001) *Postharvest Diseases of Fruits and Vegetables: Deve-*

lopment and Control, Elsevier, The Netherlands, 418 pp

Ben-Yehoshua S, Rovov V, Peretz J (1997) The constitutive and induced resistance of citrus fruit against pathogens. In: Johnson GI, Highly E, Joyce DC (Eds) *Disease Resistance in Fruit*, ACIAR Proceedings, No. 80. Canberra, Australia, pp 78-92

Binyamini N, Schiffmann-Nadel M (1972) Latent infections in avocado due to *Colletotrichum gloeosporioides. Phytopathology* **62**, 592-594

Bower J, Holford P, Latchè A, Pech JC (2002) Culture conditions and detachment of fruit influence the effect of ethylene on the climacteric respiration of melon. *Postharvest Biology and Technology* **26**, 135-146

Buddie AG, Martínez-culebras P, Bridge PD, Carcía MD, Auerol A, Cannon PF, Monte E (1999) Molecular characterization of *Colletotrichum* strains derived from strawberry. *Mycological Research* **103**, 385-394

Cañamás TP, Viñas I, Usall J, Casals C, Solsona C, Texidó N (2008) Control of postharvest diseases on citrus fruit by preharvest application of the biocontrol agent *Pantoea agglomerans* CPA-2: Part I. Study of different formulation strategies to improve survival of cells in unfavourable environmental conditions. *Postharvest Biology and Technology* **49**, 86-95

Cia P, Sérgio F, Pascholati SF, Benato EA, Camili EC, Santos CA (2007) Effects of gamma and UV-C irradiation of postharvest control of papaya anthracnose. *Postharvest Biology and Technology* **43**, 366-373

Chakravarty T (1957) Anthracnose of banana (*Gloeosporium musarum* Cke et Massee), with special reference to latent infection in storage. *Transactions of the British Mycological Society* **40**, 337-345

Chalutz E, Droby S (1998) Biological control of postharvest disease. In: Boland GJ, Kuykendall LD (Eds) *Plant-Microbe Interactions and Biological Control*, CRC Press, Boca Raton, FL, USA, pp 157-171

Cojocaru M, Droby S, Glotter E, Goldman A, Gottlieb HE, Jacoby B, Prusky D (1986) 5-(12-Heptadecenyl)-resorcinol, the major component of the antifungal activity in the peel of mango fruit. *Phytochemistry* **25**, 1093-1095

Cooper W, Bouzayen M, Hamilton A, Barry C, Rossall S, Grierson D (1998) Use of transgenic plants to study the role of ethylene and polygalacturonase during infection of tomato fruit by *Colletotrichum gloeosporioides. Plant Pathology* **47**, 308-316

Couey HM (1989) Heat treatment for control of postharvest diseases and insect pests of fruit. *HortScience* **24**, 198-202

CTAHR publications (2008) http://www.ctahr.hawaii.edu/freepubs

Darvas JM, Kotzé (1981) Post-harvest diseases of avocados. *South African Avocado Grower' Association Year Book* **4**, 63-66

Darvas JM, Kotze JM (1987) Avocado fruit diseases and their control in South Africa. *South African Avocado Grower's Association Yearbook* **10**, 117-119

Daykin ME, Milholland RD (1984) Infection of blueberry fruit by *Colletotrichum gloeosporioides. Plant Disease* **68**, 948-950

De Costa DM, Erabadupitiya HRUT (2005) An integrated method to control postharvest diseases of banana using a member of the *Burkholderia cepacia* complex. *Postharvest Biology and Technology* **36**, 31-39

De Costa DM, Kalpage MD (2006) Differential response of *Colletotrichum* isolates infecting banana to synthetic fungicide and a biological control agent. *Sri Lankan Journal of Agricultural Sciences* **43**, 50-65

De Costa DM, Zahra ARF, Kalpage MD, Rajapakshe EMG (2008) Effectiveness and molecular characterization of *Burkholderia spinosa*, a prospective biocontrol agent for controlling postharvest diseases of banana. *Biological Control* **47**, 257-267

De Lapeyre de Bellaire L, Chillet M (2000) Alternatives to chemical control for anthracnose in Guadeloupe. *Biocontrol News and Information* **21**, 73-75

De Lapeyre de Bellaire L, Chillet M, Dubois C, Mourichon X (2000) Importance of different sources of inoculum and dispersal methods of conidia of *Colletotrichum musae,* the causal agent of banana anthracnose, for fruit contamination. *Plant Pathology* **49**, 782-790

Denham TG, Waller JM (1981) Some epidemiological aspects of post-bloom fruit drop disease (*Colletotrichum gloeosporioides*) in citrus. *Annals of Applied Biology* **98**, 65-77

Denison SH (2000) pH regulation of gene expression in fungi. *Fungal Genetics and Biology* **29**, 61-71

Dodd JC, Estrada A, Jeger MJ (1992) Epidemiology of *Colletotrichum gloeosporioides* in the tropics, In: Bailey JA, Jeger MJ (Eds) *Colletotrichum: Biology, Pathology and Control*, CABI Publishing, Wallingford, UK, pp 308-325

Droby S (2001) Enhancing biocontrol activity of microbial antagonists of postharvest diseases. In: Vurro M, Gressel J, Butt T, Harman G, Pilgeram A, St. Leger R, Nuss D (Eds) *Enhancing Biocontrol Agents and Handling Risks*, IOS Press, Amsterdam, The Netherlands, pp 77-85

Drori N, Kramer-Haimovich H, Rollins J, Dinoor A, Okon Y, Pines O, Prusky D (2003) External pH and nitrogen source affect secretion of pectate lyase by *Colletotrichum gloeosporioides*. *Applied and Environmental Microbiology* **69**, 3258-3262

Eshel D, Miyara I, Ailing T, Dinoor A, Prusky D (2002) pH regulates endoglucanase expression and virulence of *Alternaria alternata* in persimmon fruit. *Molecular Plant-Microbe Interactions* **15**, 774-779

Eckert JW, Eaks IL (1989) Postharvest disorders and diseases of citrus fruits In: Reuther W, Calavan EC, Carman GE (Eds) *The Citrus Industry* (Vol V), ANR Publication, New York, USA, pp 179-260

Eckert JW (1990) Recent developments in the chemical control of postharvest diseases. *Acta Horticulturae* **269**, 477-494

Eckert JW, Ogawa JM (1985) The chemical control of postharvest diseases: subtropical and tropical fruits. *Annual Review of Phytopathology* **23**, 421-454

Everett KR (1997) Progress in managing latent infections: A review. In: Cutting JG (Ed) *Proceedings from Conference '97: Searching for Quality*, Joint meeting of the Australian Avocado Grower's Federation, Inc. and New Zealand Avocado Growers Association Inc. 23-26 September, pp 55-68

Fallik E, Grinberg S, Alkali S, Yekutieli O, Wiseblum A, Regev R, Beres H, Bar-Lev E (1999) A unique rapid hot water treatment to improve storage quality of sweet pepper. *Postharvest Biology and Technology* **15**, 25-32

Fallik E (2004a) Hot water treatments for control of fungal decay on fresh produce. In: Sapers GM, Gorny JR, Yousef AE (Eds) *Microbiology of Fruits and Vegetables*, CRC Press Inc., Boca Raton, FL, USA, pp 461-478

Fallik E (2004b) Prestorage hot water treatments (immersion, rinsing and brushing). *Postharvest Biology and Technology* **32**, 125-134

FAO (1997) FAOSTAT database. Food and Agricultural Organization of the United Nations, Rome, Italy

FAO (1998) FAOSTAT database. Food and Agricultural Organization of the United Nations, Rome, Italy

FAO (2001) Online database of the Food and Agricultural Organization of the United Nations. Available online: http://apps.fao.org/default.htm

FAO (2004) available online: http://www.uga.edu/fruit/papaya.html

FAO (2005) Committee on commodity problems: intergovernmental group on banana and tropical fruits, fourth session, Ecuador, 19-23 September 2005, postharvest handling losses. Available online: http://www.fao.org/docrep/meeting/009/j5778e.htm#P44_4533

FAO (2006) Citrus fruit. Fresh and processed. Annual statistics, Commodities and Trade division, Food and Agricultural Organization of the United Nations, Rome, Italy

FAO (2007) FAOSTAT database. Available online: http://faostat.fao.org/

Ferguson I, Volz R, Woolf A (1999) Preharvest factors affecting physiological disorders of fruit. *Postharvest Biology and Technology* **15**, 255-262

Fourie JF, Holz G (1995) Initial infection process by *Botrytis cinerea* on nectarine and plum fruit and the development of decay. *Phytopathology* **85**, 82-87

Freeman S, Katan T, Shabi E (1998) Characterization of *Colletotrichum* species responsible for anthracnose diseases of various fruits. *Plant Disease* **82**, 596-605

Gamagae SU, Sivakumar D, Wijesundera RLC (2004) Evaluation of postharvest application of sodium bicarbonate-incorporated wax formulation and *Candida oleophila* for the control of anthracnose of papaya. *Crop Protection* **23**, 575-579

Giovannoni J (2001) Molecular biology of fruit maturation and ripening. *Annual Review of Plant Physiology and Plant Molecular Biology* **52**, 725-749

Govender V, Korsten L, Sivakumar D (2005) Semi-commercial evaluation of *Bacillus licheniformis* to control mango postharvest diseases in South Africa. *Postharvest Biology and Technology* **38**, 57-65

Haggag WM, Mohamed HAA (2007) Biotechnological aspects of microorganisms used in plant biological control. *American-Eurasian Journal of Sustainable Agriculture* **1**, 7-12

Herath H, Abeywickrama K (2008) *In vitro* application of selected essential oils and their major components in controlling fungal pathogens of crown rot in Embul banana (*Musa acuminata* – AAB). *International Journal of Food Science and Technology* **43**, 440-447

Herrera-Estrella LR (2000) Genetically modified crops and developing countries. *Plant Physiology* **124**, 923-925

Hayden HL, Pegg G, Aitken EAB, Irwin JAG (1994) Genetic relationships as assessed by molecular markers and cross infection. *Australian Journal of Botany* **42**, 9-18

Heslop-Harrison JS, Schwarzacher T (2007) Domestication, genomics and the future for banana. *Annals of Botany* **100**, 1073-1084

Holliday P (1995) *Fungus Diseases of Tropical Crops*, Courier Dover Publications, New York, USA, 624 pp

Hornok L (2000) Genetically modified microorganisms in biological control. *Novenyvedelem* **36**, 229-237

Horsfall JG, Diamond AE (1957) Interactions of tissue sugar, growth substances and disease susceptibility. *Zietschrift für Pflanzenkrankheiten und Pflanzenschutz* **64**, 415-419

Irtwange SV (2006) Hot water treatment: A non-chemical alternative in keeping quality during postharvest handling of citrus fruits. *Agricultural Engineering International: The CIGR Ejournal* **5**, 10 pp

Janisiewicz WJ, Yourman L, Roitman J, Mahoney N (1991) Postharvest control of blue mold and grey mold of apples and pears by dip treatment with pyrrolnitrin, a metabolite of *Pseudomonas cepacia. Plant Disease* **75**, 490-494

Janisiewicz WJ, Bors B (1995) Development of a microbial community of bacterial and yeast antagonists to control wound-invading postharveset pathogens of fruits. *Applied and Environmental Microbiology* **61**, 3261-3267

Janisiewicz W, Korsten L (2002) Biological control of postharvest diseases of fruits. *Annual Review of Phytopathology* **40**, 411-441

Janisiewicz WJ, Pereira IB, Almeida MS, Roberts DP, Wisniewski M, Kurtenbach E (2008) Improved biocontrol of fruit decay fungi with *Pichia pastoris* recombinant strains expressing *Ps*dI antifungal peptide. *Postharvest Biology and Technology* **47**, 218-225

Jeffries P, Dodd JC, Jeger MJ, Plumbley RA (1990) The biology and control of *Colletotrichum* species on tropical fruit. *Plant Pathology* **39**, 343-366

Jeger MJ, Plumbley RA (1988) Postharvest losses caused by anthracnose (*Colletotrichum gloeosporioides*) of tropical fruit and vegetables. *Biodeterioration* **7**, 642-646

Jones DR (1991) Chemical control of crown rot in Queensland bananas. *Australian Journal of Experimental Agriculture* **31**, 693-698

Jones RW, Prusky D (2002) Expression of an antifungal peptide in *Saccharomyces*: a new approach for biological control of the postharvest disease caused by *Colletotrichum coccodes*. *Phytopathology* **92**, 33-37

Kader AA, Saltveit ME (2002) Respiration and gas exchange In: Bartz JA, Brecht JK (Eds) *Postharvest Physiology and Pathology of Vegetables* (2nd Edn), CRC Press, Boca Raton, FL, USA, pp 7-30

Kader AA (2005) Increasing food availability by reducing postharvest losses of fresh produce. *Acta Horticulturae* **682**, 2169-2176

Kantor LS, Lipton K, Manchester A, Oliveira V (1997) Estimating and addressing America's food losses. *Food Reviews* **20**, 3-11

Karabulut OA, Arslan U, Ilhan K, Kuruoglu G (2005) Integrated control of postharvest diseases of sweet cherry with yeast antagonists and sodium bicarbonate applications within a hydrocooler. *Postharvest Biology and Technology* **37**, 135-141

Klee H (2005) Transgenes, ethylene and postharvest applications. *Acta Horticulturae* **682**, 291-298

Korsten L, Bezuidenhout JJ, Kotzé JM (1989) Biocontrol of avocado postharvest diseases. *South African Avocado Growers' Association Year Book* **12**, 10-12

Korsten L, De Jager ES, De Villiers EE, Lourens A, Kotzè JM, Wehner FC (1995) Evaluation of bacterial epiphytes isolated from avocado leaf and fruit surfaces for biocontrol of avocado postharvest diseases. *Plant Disease* **79**, 1149-1156

Korsten L, Towsen E, Claasens V (1998) Evaluation of Avogreen as post-harvest treatment for controlling anthracnose and stem-end rot on avocado fruit. *South African Avocado Growers' Association Year Book* **21**, 83-87

Korsten L (2006) Advances in control of postharvest diseases in tropical fresh produce. *International Journal of Postharvest Technology and Innovation* **1**, 48-61

Krantz J, Schmutterer H, Koch W (1978) *Diseases, Pests and Weeds in Tropical Crops*, Wiley and Sons, Chichester, UK, 666 pp

Larrigaudiere C, Pons J, Torres R, Usall J (2002) Storage performance of Clementines treated wit h host water, sodium carbonate and sodium bicarbonate dips. *Journal of Horticultural Science and Biotechnology* **77**, 314-319

Lassois L, de Lapeyre de Bellaire L, Jijakli MH (2008) Biological control of crown rot of bananas with *Pichia anomala* strain K and *Candida oleophila* strain O. *Biological Control* **45**, 410-418

Lima G, Arru S, De Curtis F, Arras G (1999) Influence of antagonist, host fruit and pathogen on the biological control of postharvest fungal diseases by yeasts. *Journal of Industrial Microbiology and Biotechnology* **23**, 223-229

Litz RE, Gomez-Lim MA (2002) Genetic transformation of mango (*Mangifera indica* L.). In: Khachatourians GG, McHughen A, Scorza R, Nip W-K, Hui YH (Eds) *Transgenic Plants and Crops*, CRC Press, Boca Raton, FL, USA, pp 421-436

Liu Z, Zeng M, Dong S, Xu J, Song H, Zhao Y (2007) Effect of an antifungal peptide from oyster enzymatic hydrolysates for control of gray mold (*Botrytis cinerea*) on harvested strawberries. *Postharvest Biology and Technology* **46**, 95-98

Loeillet D (1997) Panorama du marché mondial de l'importance de l'Europe (The world pineapple market: the importance of Europe). *Acta Horticulturae* **425**, 37-48

Ludford PM (2002) Hormonal changes during postharvest, In: Bartz JA, Brecht JK (Eds) In: *Postharvest Physiology and Pathology of Vegetables* (2nd Edn), CRC Press, Boca Raton, FL, USA, pp 31-78

Lund ST, Stall RE, Klee HJ (1998) Ethylene regulates the susceptible response to pathogen infection in tomato. *Plant Cell* **10**, 371-382

Mari M, Guizzardi M, Pratella GC (1996) Biological control of grey mold in pears by antagonistic bacteria. *Biological Control* **7**, 30-37

Mari M, Bertolini P, Pratella GC (2003) Non-conventional methods for the control of post-harvest pear diseases. *Journal of Applied Microbiology* **94**, 761-766

Marrone PG (2007) Barriers to adoption of biological control agents and biological pesticides. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* **2**, 1-12

Marquenie D, Lammertyn J, Geeraerd AH, Soontjens C, Van Impe JF, Nicolai BM, Michiels CW (2002) Inactivation of conidia of *Botrytis cinerea* and *Monilinia fructigena* using UV-C and heat treatment. *International Journal of Food Microbiology* **74**, 27-35

Menge JA, Ploetz RC (2003) Diseases of avocado. In: Ploetz RC (Ed) *Diseases of Tropical Fruit Crops*, CABI Publishing, Wallingford, UK, pp 35-72

Mills PR, Hodson A, Brown AE (1992) Molecular differentiation of *Colletotrichum gloeosporioides* isolates infecting tropical fruits. In: Bailey JA, Jeger MJ (Eds) *Colletotrichum: Biology, Pathology and Control*, CABI Publishing, Wallingford, UK, pp 269-288

Muirhead IF, Deverall BJ (1981) Role of appresoria in latent infection of banana fruits by *Colletotrichum musae. Physiological Plant Pathology* **19**, 77-84

Nafussi B, Ben-Yehoshua B, Rodov V, Peretz J, Ozer BK, D'Hallewin G (2001) Mode of action of hotwater dip in reducing decay of lemon fruit. *Journal of Agriculture and Food Chemistry* **45**, 3216-3220

Paull RE, Chen NJ (2000) Heat treatment and fruit ripening. *Postharvest Biology and Technology* **21**, 21-38

Pavoncello D, Lurie S, Droby S, Porat R (2001) A hot water treatment induces resistance to *Penicillium digitatum* and promotes the accumulation of heat shock and pathogenisis-related proteins in grapefruit flavedo. *Physiological Plant Pathology* **111**, 17-22

Pech JC, Bernadae A, Bouzayen M, Latchè A (2005) Use of genetic engineering to control ripening, reduce spoilage and maintain quality of fruits and vegetables. In: Ben-Yehoshua S (Ed) *Environmentally Friendly Technologies for Agricultural Produce Quality*, CRC Press, Boca Raton, FL, USA, pp 397-438

Perfect SE, Hughes HB, O'Connell RJ, Green JR (1999) *Colletotrichum:* A model genus for studies on pathology and fungal–plant interactions. *Fungal Genetics and Biology* **27**, 186-198

Persley DM, Ploetz RC (2003) Diseases of papaya. In: Ploetz RC (Ed) *Diseases of Tropical Fruit Crops*, CABI Publishing, Wallingford, UK, pp 373-412

Peterson RA (1978) Susceptibility of Fuerte avocado fruit at various stages of growth to infection by anthracnose and stem-end-rot fungi. *Australian Journal of Experimental Agriculture and Animal Husbandry* **18**, 158-160

Pezet R, Viret O, Perret C, Tabacchi R (2003) Latency of *Botrytis cinerea* Pers.: Fr. and biochemical studies during growth and ripening of two grape berry cultivars, respectively susceptible and resistant to grey mould. *Journal of Phytopathology* **151**, 208-214

Ploetz RC (1998) Banana diseases in the sub tropics: A review of their importance, distribution and management. *Acta Horticulturae* **490**, 263-276

Ploetz RC (2003) Diseases of mango. In: Ploetz RC (Ed) *Diseases of Tropical Fruit Crops*, CABI Publishing, Wallingford, UK, pp 327-364

Ploetz RC, Thomas JE, Slabaugh WR (2003) Diseases of banana and plantain. In: Ploetz RC (Ed) *Diseases of Tropical Fruit Crops*, CABI Publishing, Wallingford, UK, pp 73-134

Prior C, Elango F, Whitwell A (1992) Chemical control of *Colletotrichum* infection in mangoes. In: Bailey JA, Jeger MJ (Eds) *Colletotrichum: Biology, Pathology and Control*, CABI Publishing, Wallingford, UK, pp 326-336

Prusky D, Keen NT, Eaks I (1983) Further evidence for the involvement of a preformed antifungal compound in the latency of *Colletotrichum gloeosporioides* on the unripe fruits. *Physiological and Molecular Plant Pathology* **2**, 189-198

Prusky D, Plumbley RA, Kobiler I (1991) The relationship between the antifungal diene levels and fungal inhibition during quiescent infections of *Colletotrichum gloeosporioides* in unripe avocado fruits. *Plant Pathology* **40**, 45-52

Prusky D, Plumbley RA (1992) Quiescent infections of *Colletotrichum* in tropical and subtropical fruits. In: Bailey A, Jeger MJ (Eds) *Colletotrichum: Biology, Pathology and Control*, CABI Publishing, Wallingford, UK, pp 289-307

Prusky D (1996) Pathogen quiescence in postharvest diseases. *Annual Review of Phytopathology* **34**, 413-434

Prusky D, Lichter A (2007) Activation of quiescent infections by postharvest pathogens during transition from the biotrophic to the necrotrophic stage. *FEMS Microbiology Letters* **268**, 1-8

Ramma I, Beni Madhu SP, Peerthum S (1999) Post-harvest quality improvement of banana. In: Lalouette JA, Bachraz DY, Sukurdeep N (Eds) *AMAS*, Food and Agricultural Research Council, Réduit, Mauritius, pp 187-194

Ranasinghe L, Jayawardena B, Abeywickrama K (2002) Fungicidal activity of essential oils of *Cinnamomum zeylanicum* (L.) and *Syzygium aromatium* (L.). Merr et L.M. Perry against crown rot and anthracnose pathogens isolated from banana. *Letters in Applied Microbiology* **35**, 208-211

Reyes MEQ, Rohrbach KG, Paull RE (2004) Microbial antagonists control postharvest black rot of pineapple fruit. *Postharvest Biology and Technology* **33**, 193-203

Rohrbach KG, Leal F, Coppens d'Eeckenbrugge G (2002) History, distribution and world production. In: Bartholomew DP, Paull RE, Rohrbach KG (Eds) *The Pineapple: Botany, Production and Uses* (1st Edn), CABI Publishing, Wallingford, UK, pp 1-12

Rohrbach KG, Johnson MW (2002) Pests, diseases and weeds. In: Bartholomew DP, Paull RE, Rohrbach KG (Eds) *The Pineapple: Botany, Production and Uses* (1st Edn), CABI Publishing, Wallingford, UK, pp 203- 252

Sabehat A, Weiss D, Lurie S (1996) The correlation between heat-shock protein accumulation and persistence and chilling tolerance in tomato. *Plant Physiology* **110**, 531-537

Sanders GM, Korsten L (2003) A comparative morphological study of South African avocado and mango isolates of *Colletotrichum gloeosporioides. Canadian Journal of Botany* **81**, 877-885

Sangchote S (1987) Postharvest diseases of mango fruits and their losses. *Kasetsart Journal (Natural Science)* **21**, 81-85

Schirra M, Agabbio M, D'Hallewin G, Pala M, Ruggiu R (1997) Response of Tarocco oranges to picking date, postharvest hot water dips, and chilling storage temperature. *Journal of Agricultural and Food Chemistry* **45**, 3216-

3220

Schirra M, D'Hallewin G (1997) Storage performance of Fortune mandarins following hot water dips. *Postharvest Biology and Technology* **10**, 229-237

Shai Y (1995) Molecular recognition between membrane spanning polypeptides. *Trends in Biochemical Science* **20**, 460-464

Silimela M, Korsten L (2007) Evaluation of pre-harvest *Bacillus licheniformis* sprays to control mango fruit diseases. *Crop Protection* **26**, 1474-1481

Singh JP, Sharma SK (1981) Screening and chemical basis of resistance in guava varieties to anthracnose (*Glomerella cingulata*). *Haryana Journal of Horticultural Sciences* **10**, 155-157

Sreenivasaprasad S, Talhinhas P (2005) Genotypic and phenotypic diversity in *Colletotrichum acutatum*, a cosmopolitan pathogen on a wide range of hosts. *Molecular Plant Pathology* **6**, 361-378

Stanghellini ME, Aragaki M (1966) Relation of periderm formation and callose deposition to anthracnose resistance in papaya fruits. *Phytopathology* **66**, 444-450

Sugar D, Powers K (1986) Interactions among fungi causing post-harvest decay of pear. *Plant Disease* **70**, 1132-1134

Swinburne TR (1983) Quiescent infections in postharvest diseases. In: Dennis C (Ed) *Postharvest Pathology of Fruits and Vegetables*, Academic Press, London, UK, pp 1-21

Talhinhas E, Sreenivasaprasad S, Neves-Martins J, Oliveira H (2005) Molecular and phenotypic analyses reveal association of diverse *Colletotrichum acutatum* groups and a low level of *C. gloeosporioides* with olive anthracnose. *Applied and Environmental Microbiology* **71**, 2987-2998

Talon M, Gmitter Jr. FG (2008) Citrus genomics. *International Journal of Plant Genomics* (Vol 2008), 17 pp

Timmer LW, Garnsey SM, Broadbent P (2003) Diseases of citrus. In: Ploetz RC (Ed) *Diseases of Tropical Fruit Crops*, CABI Publishing, Wallingford, UK, 163-197

Vinas I, Usall J, Sanchis V (1991) Tolerance of *Penicillium expansum* to postharvest fungicide treatments in apple packing-houses in Lerida (Spain). *Mycopathologia* **113**, 15-18

Vivekanathan R, Ravi M, Saravanakumar D, Kumar N, Prakasam V, Samiyappan R (2004) Microbially induced defense related proteins against postharvest anthracnose infection in mango. *Crop Protection* **23**, 1061-1067

Wharton PS, Dièguez-Uribeondo J (2004) The biology of *Colletotrihcum acutatum. Anales del Jardìn Botánico de Madrid* **61**, 3-22

Whitaker BD (2002) Chemical and physical changes in membranes. In: Bartz JA, Brecht JK (Eds) *Postharvest Physiology and Pathology of Vegetables* (2nd Edn), CRC Press, Boca Raton, FL, USA, pp 79-110

Whitelaw-Weckert MA, Curtin SJ, Huang R, Steel CC, Blanchard CL, Roffey PE (2007) Phylogenetic relationships and pathogenicity of *Colletotrichum acutatum* isolates from grape in subtropical Australia. *Plant Pathology* **56**, 448-463

Wilson Wijeratnam RS, Hewajulige LGN, Abeyratne N (2005) Postharvest hotwater treatment for the control of Thielaviopsis black rot of pineapple. *Postharvest Biology and Technology* **36**, 323-327

Wisniewski ME, Wilson CL (1992) Biological control of postharvest diseases of fruits and vegetables: Recent advances. *HortScience* **27**, 94-98

Wisniewski M, Wilson C, El Ghaouth A, Droby S (2001) Non-chemical approaches to postharvest disease control. *Acta Horticulturae* **553**, 407-412

Wisniewski ME, Bassett CL, Artlip TS, Janisiewicz WJ, Norelli JL, Droby S (2005) Overexpression of a peach defensin gene can enhance the activity of postharvest biocontrol agents. *Acta Horticulturae* **682**, 1999-2006

Yakoby N, Freeman S, Dinoor A, Keen NT, Prusky D (2000a) Expression of pectate lyase from *Colletotrichum gloeosporioides* in *C. magna* promotes pathogenicity. *Molecular Plant-Microbe Interactions* **13**, 887-891

Yakoby N, Kobiler I, Dinoor A, Prusky D (2000b) pH regulation of pectate lyase secretion modulates the attack of *Colletotrichum gloeosporioides* on avocado fruits. *Applied and Environmental Microbiology* **66**, 1026-1030

Yakoby N, Zhou R, Kobiler I, Dinoor A, Prusky D (2001) Development of *Colletotrichum gloeosporioides* restriction enzyme-mediated integration mutants as biocontrol agents against anthracnose disease in avocado fruits. *Phytopathology* **91**, 143-148

Yañez L, Armenta M, Mercado E, Yahia EM, Guttierrez P (2004) Integrated handling of banana. In: Dris R, Jain SM (Eds) *Production Practices and Quality Assessment of Food Crops (Vol 3) Quality Handling and Evaluation*, Springer, Berlin, Germany, pp 129-168

Zimad G, Elad Y, Chet I (1996) Effect of *Trichoderma harzianum* on *Botrytis cinerea* pathogenicity. *Phytopathology* **86**, 1255-1260