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Biological control of postharvest fungal rots of rosaceous fruits using microbial antagonists and plant extracts – a review

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This article aims to give a comprehensive review on the use of microbial antagonists (fungi and bacteria), botanicals and compost extracts as biocontrol agents against different pathogenic fungi causing postharvest fungal rots in rosaceous fruits which shows that they can play an important role in the biomanagement of fungi causing rot diseases. Plant extracts reported in the literature against pathogenic fungi indicate that they can act as a good biological resource for producing safe biofungicides. However most of the work has been done under experimental conditions rather than field conditions. There is still a need for research to develop suitable formulations of biofungicides from these microbial biocontrol agents and plant extracts. The review reveals that extensive ecological research is also required in order to achieve optimum utilisation of biological resources to manage various postharvest diseases of fruits.

Key words: biological control, postharvest diseases, microbial pesticides, rosaceous fruits.

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Cílem článku je poskytnout komplexní přehled o využití mikrobiálních antagonistů (hub a bakterií) a extraktů z rostlin a kompostu jako prostředků biologické kontroly, úcinných proti patogenním houbám způsobujícím posklizňové hniloby plodů růžovitých; tyto prostředky mohou hrát důležitou roli v biomanagementu houbových původců hnilob. Jak je popsáno v literatuře, rostlinné extrakty úcinné proti patogenním houbám mohou být dobrým zdrojem pro výrobu bezpečných biofungicidů, nicméně práce, které to dokládají, byly většinou prováděny v experimentálních podmínkách spíše než v terénu. Stále je třeba vyvíjet vhodné biofungicidy z uvedených mikrobiálních agens a rostlinných výtažků a – jak vyplývá z uvedeného přehledu – je také třeba zkoumat dostupné možnosti v ekologických souvislostech. Tak lze dosáhnout optimálního využití biologických zdrojů pro zamezení posklizňového poškození ovoce.

Introduction

Rosaceous fruits such as apple, pear, peach, cherry and plum are of great economic importance but their production is affected by several diseases especially rot-causing fungi and bacteria developing after harvest. Fruits are highly perishable products during the postharvest phase, when considerable losses due to fungi and bacteria occur. Postharvest losses in fruits in developing countries have been estimated in the range of 10 to 30% or more (Kader 2002, Agrios 2005). In India, postharvest diseases of fruits are responsible for causing losses up to 30% during harvest, subsequent handling and consumption (Parpia 1976). Postharvest diseases of fruits mainly spread during sale, transport and storage (Pierson et al. 1971, Snowdon 1990, Barkai-Golan 2001, Janisiewicz & Korsten 2002) and result in reduced food supplies, products of poorer quality, economic hardships for growers and ultimately higher prices (Agrios 1997, Monte 2001).

Several management practices, viz. physical, chemical, regulatory (control by regulatory agencies, plant quarantine and certification agencies), cultural and biological control methods have been used to manage postharvest diseases of rosaceous fruits. Some of these methods, in particular the use of pesticides, cause hazardous effects on humans and the environment. Hence strong regulatory actions have been imposed on their use. Additionally, the continued use of chemicals have resulted in the appearance of pathogens which are resistant to fungicides (Spotts & Cervantes 1986) and have resulted in various iatrogenic diseases (Griffiths 1981). These health and environmental concerns have stimulated the development of beneficial microorganisms as microbial pesticides (Droby 2006). Microbial pesticides are products used to control plant diseases consisting of beneficial microorganisms or the metabolites they produce. Biological control is defined as the reduction of inoculum density or disease producing activities of a pathogen or parasite in its active or dormant state, by one or more organisms accomplished naturally or through manipulation of the environment or host or antagonist or by mass introduction of one or more antagonists (Baker & Cook 1974). Biological control would appear to have a significant potential in terms of both environmental and economic issues for incorporation into organic and conventional fruit production systems. Various biocontrol agents such as fungi and bacteria have been identified for the control of postharvest diseases of many fruits and have been marketed worldwide and obviously play an important role in sustainable agriculture and management of plant pathogens (Wisniewski & Wilson 1992, Ragsdale & Sisler 1994, Montesinos 2003, Sobowale et al. 2008, Montesinos & Bonaterra 2009, Junaid et al. 2013). The effectiveness of antagonistic microorganisms depends on their ability to colonise fruit surfaces and adapt to various environmental conditions (Wilson & Wisniewski 1989, Droby et al. 2002, Sharma 2014). Wilson & Wisniewski (1994) indicated the following characteristics of an ideal antagonist: genetic stability, efficacy at low concentrations and against a wide range of pathogens on various fruit products, simple nutritional requirements, survival in adverse environmental conditions, growth on cheap substrates in fermenters, lack of pathogenicity to the host plant and no production of metabolites potentially toxic to humans, resistant to the most frequently used pesticides and compatible with other chemical and physical treatments. Thus, biological control has been suggested as an effective, non-hazardous strategy to control major postharvest decays of fruits and to improve crop production (Janisiewicz & Korsten 2002, Dalal & Kulkarni 2013). Postharvest biocontrol is feasible especially because harvested fruits are readily accessible to treatment with antagonists and many postharvest pathogens infect fruits through wounds after harvest (Janisiewicz & Jeffers 1997, Nunes et al. 2001).

In the current review, a brief overview of research that has led to comprehensive understanding of various filamentous fungi, yeasts and bacteria which have been used for postharvest biological control of rosaceous fruits is presented. This review also gives information about various medicinal plants that have been screened for their antifungal activity and can act as a good source for the biomanagement of fungi causing postharvest rot diseases.

REVIEW

Biological control using fungi

Considerable research effort has been devoted to identifying yeasts and other fungi which effectively control postharvest diseases of fruit, vegetables, and grains (Wilson et al. 1996, Droby et al. 2002, Zhang et al. 2004, Sharma et al. 2009, Mishra et al. 2013, Sharma 2014). Postharvest decay of fruits occurs either between flowering and fruit maturity or during harvesting, handling and storage (Eckert & Ogawa 1988). Preharvest infections remain latent upto fruit maturity and storage, such as infection of peaches, cherries, plums and apricots by *Monilinia* sp. The majority of postharvest pathogens infect the fruit through wounds that occur during harvest or subsequent handling (Eckert & Ogawa 1988). Most postharvest rots of several fruits could be reduced considerably by spraying with spores of antagonistic fungi at different stages of fruit development, or by dipping the harvested fruit in their suspensions. Experiments have shown that several antagonistic unicellular fungi have the ability to protect many fruits from *Botrytis cinerea*, *Penicillium expansum*, *Monilinia fructicola* and *Rhizoctonia* rots (Agrios 1997, Karabulut & Baykal 2003). Once the antagonistic fungal cells come into contact with the fruit surface, they also occupy the wounds and affect the germination of pathogenic fungal spores mainly by niche exclusion and competition for nutrients (Liu et al. 2012). Strains of *Candida* *guilliermondii* have been studied for the biological control of grey and blue moulds of apple (McLaughlin et al. 1990, McLaughlin 1991). Control by *Candida guilliermondii* is directly related to the spore concentration of the pathogen and cell concentration of the antagonistic fungi (Droby et al. 1989, McLaughlin et al. 1990). *Candida oleophila* was approved for postharvest decay control in citrus and apples under the trade name Aspire® (Agrios 1997, Droby et al. 1998, Lahlali et al. 2004, Wisniewski et al. 2007). It is used for the biological control of grey mould caused by *Botrytis cinerea* (Mercier & Wilson 1994), *Penicillium* rot caused by *Penicillium expansum* (El-Neshawy & Wilson 1997, Lahlali & Jajakli 2009) and *Penicillium digitatum* (Lahlali et al. 2004). *Kloeckera apiculata* has been used as a biocontrol agent in controlling rots caused by *Penicillium expansum*, *Botrytis cinerea* (McLaughin et al. 1992, Karabulut & Baykal 2003, Long et al. 2005) and *Rhizopus* rot of peaches (McLaughlin et al. 1992, Qing & Shiping 2000). Another species of *Candida*, namely *Candida sake*, was approved for the control of *Penicillium expansum*, *Botrytis cinerea* and *Rhizopus nigricans* under the trade name Candifruit (Viñas et al. 1998, Janisiewicz 2010).

Cryptococcus albidus has been found effective against *Mucor* rot caused by *Mucor piriformis* (Roberts 1990b), blue mould caused by *Penicillium expansum* (Chand-Goyal & Spotts 1996) and grey mould caused by *Botrytis cinerea* (Fan & Tian 2001). It is approved under the trade name Yield Plus in South Africa (Mari et al. 2014). Another species of *Cryptococcus*, namely *Cryptococcus laurentii*, have been studied for the postharvest biological control of grey mould rot of apples (Roberts 1990a), *Mucor* rot of pears (Roberts 1990b), grey and blue mould rot of pears (Zhang et al. 2003, 2005), *Rhizopus* rot of strawberries and peaches (Zheng et al. 2004, Zhang et al. 2007), as well as postharvest diseases of other fruits such as strawberries, kiwi fruits and table grapes (Lima et al. 1998). According to Zhang et al. (2007), *Cryptococcus laurentii* is effective in the control of a wide range of pathogens and can be used in combination with cold storage to enhance disease control. Another yeast strain, *Leucosporidium scottii*, has been found effective against blue mould and grey mould of apple caused by *Penicillium expansum* and *Botrytis cinerea*, respectively (Vero et al. 2013).

Metschnikowia pulcherrima has been reported to occur commonly on apple and in apple cider (Clark et al. 1954, Beach 1958, 1993) and is known to control various postharvest decays on pome fruits and grapes (De Curtis et al. 1996, Piano et al. 1997, Nigro et al. 1999, Janisiewicz et al. 2001, Spadaro et al. 2002). Another strain, *Metschnikowia fructicola*, is effective against rots caused by *Botrytis* sp., *Penicillium* sp., *Rhizopus* sp., and *Aspergillus* sp. It is marketed in Israel under the trade name 'Shemer' (Liu et al. 2011a). A fungal antagonist, *Pichia membranifaciens*, isolated from wounds of peach fruits, was evaluated for its biocontrol capability against *Rhizopus stolonifer*, *Monilinia fructicola* and *Penicillium expansum* (Chan & Tian 2005). *Rhodotorula glutinis* was found effective against apple fruit decay caused by *Penicillium expansum* and *Botrytis cinerea* (Zhang et al. 2009). It has been reported by many researchers that a mixture of different fungal antagonists used in combination proved more effective in controlling postharvest rots of many fruits than any antagonist applied alone (Calvo et al. 2003, Janisiewicz et al. 2008). Calvo et al. (2003) reported that the mixture of *Rhodotorula glutinis* and *Cryptococcus albidus* was more effective against grey mould of apples. Janisiewicz et al. (2008) reported that the mixture of antagonists *Metschnikowia pulcherrima* and *Cryptococcus laurentii*, originally isolated from apples, exhibit better biocontrol against blue mould of apple than either antagonist applied alone. Many other yeasts, viz. *Clonostachys rosea*, *Candida saitoana*, *Cystofilobasidium infirmominiatum*, *Rhodosporidium paludigenum*, *Pichia caribbica*, *P. fermentans*, *P. guilliermondii* and *P. membranifaciens*, have been found effective against various postharvest rot causing pathogens of fruits (El-Ghaouth et al. 2003, Chan et al. 2007, Liu et al. 2011b, Fiori et al. 2012, Wang et al. 2010a, Xu et al. 2013).

Trichoderma is among the most common saprotrophic fungi. Many *Trichoderma* strains have been identified as having potential applications in biological control, being effective against a wide range of plant pathogenic fungi (including wood-rot fungi) or fungus-like organisms: *Armillaria*, *Botrytis*, *Colletotrichum*, *Dematophora*, *Endothia*, *Fulvia*, *Fusarium*, *Chondrostereum*, *Fusicladium*, *Macrophomina*, *Monilia*, *Nectria*, *Phoma*, *Phytophthora*, *Plasmopara*, *Pseudoperonospora*, *Pythium*, *Rhizoctonia*, *Sclerotinia*, *Sclerotium*, *Venturia* and *Verticillium* (Sawant et al. 1995, Agrios 1997, Monte 2001, Batta 2004, Wani et al. 2009, Mishra et al. 2013, Motlagh & Samimi 2013). Many recent studies have demonstrated the effect of various *Trichoderma* species on postharvest rot diseases caused by many fungal pathogens (Batta 2001, 2004, Odebode 2006, Patale & Mukadam 2011, Hafez et al. 2013). *Trichoderma harzianum* is used to control the fungal diseases caused by *Alternaria alternata*, *Penicillium expansum* (blue mould on apples), *Botrytis cinerea* (grey mould on apples), damping-off diseases caused by *Pythium* species, and *Rhizoctonia* sp. (Agrios 1997, Batta 1999, 2003, Biswas 1999, Harman & Kubicek 1998, Dutta & Das 1999, Omarjee et al. 2001). Other strains of *Trichoderma*, namely *T. pseudokoningii*, *T. koningii*, *T. hamatum*, *T. gamsii*, *T. atroviride*, *T. virens* and *T. viride*, are also used as biological control agents to suppress the growth of various pathogenic fungi (Tronsmo & Raa 1977, Odebode 2006, Ngullie et al. 2010, Jagtap et al. 2013, Shaikh & Nasreen 2013). Several commercial biocontrol products and their formulations have been developed and approved, e.g. Trichodermil, Bio-tricho, Supresivit, Eco-77, Trichodex (*Trichoderma harzianum*), Trichdermax EC, Ecohope, Quality WG, Trichotech (*T. asperellum*), Trichospray, Trichopel, Trichodry, Vinevax (*T. atroviride*), Remedier WP (*T. gamsii*), Biocure F, Bio-shield, Binab T (*T. viride*), BW 240 G, BW 240 WP, G-41 technical (*T. virens*), Floragard (*T. hamatum*) (Kabaluk et al. 2010, Bettiol et al. 2012, Woo et al. 2014).

Tab. 1. Fungi used as biological control agents.

Biocontrol agent	Disease	References
Candida guilliermondii	Blue mould (*Penicillium expansum*)	McLaughlin et al. (1990)
	Grey mould (*Botrytis cinerea*)	McLaughlin et al. (1992)
Candida oleophila	*Penicillium* rot (*Penicillium expansum*)	El-Neshawy & Wilson (1997)
	Grey mould (*Botrytis cinerea*)	Mercier & Wilson (1994)
Candida saitoana	Grey mould of apple (*Botrytis cinerea*)	El-Ghaouth et al. (2003)
Candida sake	*Penicillium* rot (*Penicillium expansum*)	Viñas et al. (1996)
	Grey mould (*Botrytis cinerea*)	Viñas et al. (1998)
	Rhizopus rot (*Rhizopus nigricans*)	Viñas et al. (1998)
	Botrytis bunch rot (*Botrytis cinerea*)	Calvo-Garrido et al. (2013)
Clonostachys rosea	*Fusarium* dry rot (*Fusarium avenaceum, Fusarium caeruleum*)	Jima (2013)
	Grey mould (*Botrytis cinerea*)	Reeh (2012)
Cryptococcus albidus	*Mucor* rot (*Mucor piriformis*)	Roberts (1990b)
	Grey mould (*Botrytis cinerea*)	Fan & Tian (2001)
	Blue mould (*Penicillium expansum*)	Chand-Goyal & Spotts (1996), Calvo et al. (2003)
Cryptococcus flavus	*Mucor* rot (*Mucor piriformis*)	Roberts (1990b)
Cryptococcus laurentii	Bitter rot (*Glomerella cingulata*)	Blum et al. (2004)
	Mucor rot (*Mucor piriformis*)	Roberts (1990b)
	Grey mould (*Botrytis cinerea*)	Chand-Goyal & Spotts (1997), Zhang et al. (2005), Zhang et al. (2007)
	Blue mould (*Penicillium expansum*)	Zhang et al. (2003), Zhang et al. (2007)
	Rhizopus rot (*Rhizopus stolonifer*)	Zhang et al. (2007)
Cystofilobasidium infirmominiatum	*Penicillium* rot of apple (*Penicillium expansum*)	Liu et al. (2011b)
Epicoccum nigrum	Brown rot of stone fruits (*Monilinia laxa*)	Madrigal et al. (1994), Foschi et al. (1995)
Kloeckera apiculata	Grey mould (*Botrytis cinerea*)	McLaughlin et al. (1992)
	Rhizopus rot (*Rhizopus stolonifer*)	McLaughlin et al. (1992), Qing & Shiping (2000)
Leucosporidium scottii	Blue mould of apple (*Penicillium expansum*)	Vero et al. (2013)
	Grey mould of apple (*Botrytis cinerea*)	Vero et al. (2013)
Metschnikowia fructicola	Apple rot (*Penicillium expansum*)	Liu et al. (2011a)
Metschnikowia pulcherrima	Blue mould (*Penicillium expansum*)	Spadaro et al. (2002), Janisiewicz et al. (2001)
	Grey mould (*Botrytis cinerea*)	Spadaro et al. (2002)
Penicillium roqueforti and *Penicillium viridicatum*	Black rot disease (*Aspergillus niger*)	Khokhar et al. (2013)
Pichia caribbica	*Rhizopus* rot of peach (*Rhizopus stolonifer*)	Xu et al. (2013)
Pichia fermentans	Apple and peach decay (*Monilinia fructicola* and *Botrytis cinerea*)	Fiori et al. (2012)

Biocontrol agent	Disease	References
Pichia guilliermondii	Grey mould (*Botrytis cinerea*)	Wisniewski et al. (1991a)
Pichia membranifaciens	*Penicillium expansum* (peach)	Chan et al. (2007)
	Apple fruit decay (*Penicillium expansum*, *Monilinia fructicola*, *Rhizopus stolonifer*)	Chan & Tian (2005)
Rhodosporidium paludigenum	Pear fruit decay (*Alternaria alternata*, *Penicillium expansum*)	Wang et al. (2010a)
Rhodotorula glutinis	Apple fruit decay (*Penicillium expansum*, *Botrytis cinerea*)	Zhang et al. (2009)
Trichoderma atroviride	*Phomopsis* sp.	Das et al. (2014)
Trichoderma hamatum	Fungal diseases (*Phytophthora palmivora*, *Rhizoctonia solani*, *Fusarium* spp., *Sclerotium rolfsii*, *Pythium* sp.)	Ha (2010), Ngullie et al. (2010)
Trichoderma harzianum	Grey mould (*Botrytis cinerea*)	Batta (1999, 2003)
	Blue mould (*Penicillium expansum*)	Batta (2004)
Trichoderma koningii	*Alternaria* diseases (*Alternaria alternata*)	Odebode (2006), Shaikh & Nasreen (2013)
Trichoderma pseudokoningii	Brown rot (*Monilinia laxa*)	Tronsmo & Raa (1977)
Trichoderma viride	Fruit rots (*Colletotrichum gloeosporioides*)	Ngullie et al. (2010), Jagtap et al. (2013)

Biological control using bacteria

Several bacteria have been identified to play an important role as biological control agents in controlling disease caused by many plant pathogenic fungi (Pusey & Wilson 1984, Pratella et al. 1993, Smilanick et al. 1993, Frances et al. 2006, Pal & Garderner 2006, Sreevidya & Gopalakrishnan 2012, Mishra et al. 2013). Among different bacteria used as biological control agents, an isolate of *Burkholderia cepacia* provided biological control of blue mould and grey mould of Golden Delicious apples (Janisiewicz & Roitman 1988). A saprophytic strain of *Pseudomonas syringae* marketed under trade name Biosave™, provided biological control against grey mould, blue mould and *Mucor* rot on pear and apple (Janisiewicz & Marchi 1992, Jeffers & Wright 1994, Mari et al. 2014). On pears it was reported to be the most effective postharvest treatment against various diseases in an integrated management programme (Sugar 2006). Another species of *Pseudomonas*, namely *Pseudomonas fluorescens*, has been reported to control grey mould caused by *Botrytis* sp. (Mikani et al. 2008). Strains of *Pantoea agglomerans* were reported to be effective against rots caused by *Botrytis cinerea*, *Rhizopus stolonifer*, *Penicillium expansum*, *Penicillium digitatum* and *Penicillium italicum* (Nunes et al. 2001, Teixidó et al. 2001, Frances et al. 2006, Kotan et al. 2009, Trias et al. 2010). *Bacillus subtilis* applied to wounded apples reduced fruit rot caused by *Botrytis cinerea*, *Alternaria alternata*, *Penicillium expansum* and *P. malicorticis* (Leibinger et al. 1997, Wang et al. 2010b). It has been reported that the postharvest brown rot of stone fruits can also be controlled by the application of *Bacillus subtilis* and *Pseudomonas* sp. (Pusey & Wilson 1984, Smilanick et al. 1993). *Bacillus pumilus* and *Bacillus amyloliquefaciens* are reported to control grey mould in pears and tomatoes caused by *Botrytis cinerea* (Mari et al. 1996). Another species of *Bacillus*, namely *Bacillus licheniformis*, has been reported to control grey mould caused by *Botrytis mali* (Jamalizadeh et al. 2008). *Rahnella aquatilis* has been studied as a possible biocontrol agent against plant pathogenic fungi, viz. *Penicillium expansum*, *Botrytis cinerea* and *Alternaria alternata*, which produce postharvest spoilage in apple fruits (Nunes et al. 2001, Calvo et al. 2007).

Tab. 2. Bacteria used as biological control agents.

Biocontrol agent	Disease	References
Bacillus amyloliquefaciens	Grey mould (*Botrytis cinerea*)	Mari et al. (1996)
Bacillus licheniformis	Grey mould (*Botrytis mali)*	Jamalizadeh et al. (2008)
Bacillus pumilus	Grey mould (*Botrytis cinerea*)	Mari et al. (1996)
Bacillus subtilis	Brown rot (*Monilinia* sp.)	Pusey et al. (1986)
	Apple fruit rot (*Botrytis cinerea*, *Penicillium expansum*)	Leibinger et al. (1997)
	Apple ring rot (*Botryosphaeria berengeriana*)	Liu et al. (2009)
	Alternaria diseases (*Alternaria alternata*)	Wang et al. (2010b)
Burkholderia cepacia	Blue mould (*Penicillium expansum*)	Janisiewicz & Roitman (1988)
	Mucor rot (*Mucor piriformis*)	Janisiewicz & Roitman (1988)
	Grey mould (*Botrytis cinerea*)	Janisiewicz & Roitman (1988)
Burkholderia gladioli	Phytopathogenic fungi (*Botrytis cinerea*, *Penicillium expansum*, *Penicillium digitatum*, *Aspergillus flavus*, *Aspergillus niger*, *Phytophthora cactorum*, *Sclerotinia sclerotiorum*)	Elshafie et al. (2012)
Enterobacter cloacae	*Fusarium* dry rot (*Fusarium sambucinum*)	Al-Mughrabi (2010)
Pantoea agglomerans	*Penicillium* rot (*Penicillium expansum)*	Nunes et al. (2001), Teixidó et al. (2001), Frances et al. (2006)
	Rhizopus rot (*Rhizopus nigricans*)	Nunes et al. (2001)
	Brown rot (*Monilinia laxa*)	Bonaterra et al. (2003)
	Soft rot (*Rhizopus stolonifer*)	Bonaterra et al. (2003)
Pantoea vagans	Disease of apple and pears (*Erwinia amylovora*)	Smits et al. (2010)
Pseudomonas fluorescens	Grey mould (*Botrytis* spp.)	Mikani et al. (2008)
Pseudomonas syringae	Blue mould (*Penicillium expansum*)	Janisiewicz (1987), Zhou et al. (2001)
	Grey mould (*Botrytis cinerea*)	Zhou et al. (2001)
	Mucor rot (*Mucor piriformis*)	Janisiewicz & Marchi (1992), Jeffers & Wright (1994)
Rahnella aquatilis	*Penicillium* rot (*Penicillium expansum*)	Calvo et al. (2007)
	Grey mould (*Botrytis cinerea*)	Calvo et al. (2007)

Mechanisms of action of microbial antagonists against postharvest pathogens

Knowledge of the mechanism of action is a key factor to achieve an efficient inhibition of pathogens in their hosts. The mechanisms of action involved in the biocontrol process can permit establishment of optimum conditions for interaction between the pathogen and the biological control agent and is important in implementing a biological control strategy in a particular pathosystem (Cook 1993, Handelsman & Stabb 1996). Several mechanisms have been suggested to operate in postharvest biocontrol, including antibiosis, induced resistance, mycoparasitism, cell-wall degradation, competition for space, and limited resources.

Several strains of antagonistic fungi use a single mechanism to inhibit the growth of pathogenic fungi, while some strains are reported to use multiple mechanisms. The most effective biological control agent studied antagonise a plant pathogen using multiple mechanisms utilising both antibiosis and induction of host resistance to suppress the disease-causing microorganisms, such as in *Pseudomonas* (Janisiewicz & Roitman 1988, Junaid et al. 2013); it is reported that *Pseudomonas* produces antibiotic 2,4-diacetylphloroglucinol and also induces host defences (Iavicoli et al. 2003).

Antibiosis is a direct toxic effect on the pathogen by antibiotic substances released by the antagonist. *Trichoderma harzianum* and *Clonostachys rosea* (formerly *Gliocladium roseum*) control anthracnose of fruits through antibiosis (Živković et al. 2010). Pyrrolnitrin can be the main mode of action of *Pseudomonas cepacia* in controlling *Botrytis cinerea* and *Penicillium expansum* on apples and pears (Janisiewicz & Roitman 1988). *Bacillus subtilis* may control *Monilinia fructicola* by the production of iturine (Pusey & Wilson 1984), grey mould by the production of cyclolipopeptides like fengecins (Ongena et al. 2005). A yeast-like antagonist, *Aureobasidium pullulans*, controls anthracnose caused by *Colletotrichum acutatum* by antibiosis (β-1,3-glucanase and chitinase) and hyperparisitism (Hartati et al. 2015).

Competitive exclusion of the pathogen from sites of infection by better use of nutrients and colonisation than the pathogen is also a common mechanism that can accompany other mechanisms, and is considered as the major modes of action by which microbial agents control pathogens causing postharvest decay of pome fruits (Sharma et al. 2009). Competition for nutrients was suggested to play a role in the biocontrol of *Penicillium digitatum* by *Debaryomyces hansenii* (Droby et al. 1989) and of *Botrytis cinerea* by *Cryptococcus* sp. (Filonow et al. 1996). Preemptive exclusion of fungal infection sites by the antagonist was observed in *Candida oleophila* and *Cryptoccocus laurentii*, which control *Botrytis cinerea* (Roberts 1990a, Mercier & Wilson 1995).

Inhibition of plant pathogens by *Pantoea agglomerans* is dependent on the strain and has been attributed to production of an acidic environment (Riggle

& Klos 1972, Beer et al. 1984), competition for nutrients (Goodman 1967), production of herbicolin or other antibiotics (Ishimaru et al. 1988, Vanneste et al. 1992, Kearns & Hale 1996), preemptive colonisation (Wilson et al. 1992, Kearns & Hale 1996), parasitism of the pathogen (Bryk et al. 1998) and induction of plant defense response (Slade & Tiffin 1984).

Attachment alone or in combination with secretion of cell-wall degrading enzymes has been proposed as the viable mechanism operating in the biocontrol of *Botrytis cinerea* by *Pichia guilliermondii* (Wisniewski et al. 1991a). It is reported that *Pichia guilliermondii* and *Candida saitoana* cells have the ability to attach to the hyphae of *Botrytis cinerea* and cause degradation of the cell wall at the attachment sites (Wisniewski et al. 1991b, El-Ghaouth et al. 1998). The antagonistic activity of *Aureobasidium pullulans* against *Botrytis cinerea*, *Rhizopus stolonifer*, *Penicillium expansum* and *Aspergillus niger* was found to be the result of antibiosis in conjugation with attachment of microbial antagonist to the hyphae of pathogenic fungi (Castoria et al. 2001).

Several hyperparasites, especially abundant among fungi like *Pichia* and *Trichoderma*, interact directly and degrade the fungal cell or exert antagonism through antimicrobial compounds, develop hyperparasitism [involving trophic growth of the biocontrol organism towards the pathogenic fungi, causes coiling, attack and dissolution of the cell wall and membrane of the pathogenic fungi by the activity of enzymes (Tewari 1996)], or directly attach to the pathogen cells, interfere with pathogen signals, or induce resistance in the plant host (Harman 2006).

Some bacteria and fungi are able to induce defense responses in plants, by producing either elicitors (e.g. cell-wall components) or messenger molecules (e.g. salicylic acid) (Spadaro & Gullino 2004). Induction of host defence reactions was proposed to be the mechanism in the biocontrol of *Botrytis cinerea* by *Candida saitoana* (El-Ghaouth et al. 1998) and of *Penicillium digitatum* by *Verticillium lecanii* (Benhamou & Brodeur 2000).

Biological control using botanicals

Much work has been carried out to evaluate the antimicrobial efficacy of various medicinal plant extracts against phytopathogenic fungi. It has been reported that they play an important role in controlling diseases of plants caused by these fungi (Hossain et al. 1993, Anwar et al. 1994, Jacob & Sivaprakasan 1994, Arya et al. 1995, Karade & Sawant 1999, Datar 1999, Anwar & Khan 2001, Lin et al. 2001, Okemo et al. 2003, Choi et al. 2004, Mares et al. 2004, Khalil et al. 2005, Abd-El-Khair & Haggag 2007, Ogbebor et al. 2007, Perez-Sanchez et al. 2007, Baka 2010, Znini et al. 2011, Raji & Raveendran 2013, Parveen et al. 2013, 2014, Ekwere et al. 2015, Nweke 2015). Dababneh & Khalil (2007) studied the effect of five different medicinal plant extracts, viz. *Crupina crupinastrum*, *Teucrium polium*, *Achillea santolina*, *Micromeria nervosa* and *Ballota philistaea*, against four pathogenic fungi, viz. *Fusarium oxysporum*, *Rhizoctonia solani*, *Penicillium* sp. and *Verticillium* sp. Webster et al. (2008) screened 14 plants for their antifungal activity against various pathogenic fungi and concluded that *Fragaria virginiana*, *Epilobium angustifolium* and *Potentilla simplex* show a promising antifungal potential. Bobbarala et al. (2009) reported the antifungal activity of 49 different plant extracts against *Aspergillus niger*. Among the 49 plants used, 89% showed antifungal activity, while 11% were not effective. Satish et al. (2009) reported the antifungal potential of 46 plants against eight species of *Fusarium*, viz. *F. equiseti*, *F. moniliforme*, *F. semitectum*, *F. graminearum*, *F. oxysporum*, *F. proliferatum*, *F. solani* and *F. lateritium*. Taskeen-Un-Nisa et al. (2010, 2011) reported the antimycotic activity of some plant extracts including onion *(Allium cepa*), garlic (*Allium sativum*) and mint *(Mentha arvensis*), against *Alternaria alternata*, *Rhizopus stolonifer* and *Fusarium oxysporum*. Gatto et al. (2011) studied the in vitro and in vivo activity of extracts from nine herbaceous species, viz. *Borago officinalis*, *Orobanche crenata*, *Plantago lanceolata*, *Plantago coronopus*, *Sanguisorba minor*, *Silene vulgaris*, *Sonchus asper*, *Sonchus oleraceus* and *Taraxacum officinale*, against some postharvest fungal rot causing pathogens (*Monilinia laxa*, *Botrytis cinerea*, *Penicillium expansum*, *Penicillium digitatum*, *Penicillium italicum*, *Aspergillus carbonarius* and *Aspergillus niger*) and reported that the extract of *Sanguisorba minor* completely inhibited the spore germination of *Monilinia laxa*, *Penicillium digitatum*, *Penicillium italicum* and *Aspergillus niger*. Parveen et al. (2013, 2014) reported the antifungal activity of five different plant extracts, viz. *Artemisia absinthium*, *Rumex obtusifolius*, *Taraxacum officinale*, *Plantago lanceolata* and *Malva sylvestris*, against some rot-causing fungal pathogens, *Alternaria alternata*, *Penicillium expansum*, *Aspergillus niger* and *Mucor piriformis*. Essential oils have been extracted from various plants and evaluated for their efficacy against a number of pathogenic fungi causing postharvest rots of rosaceous fruits (Pandey et al. 1982, Edris & Farrag 2003, Nakamura et al. 2004, Chuang et al. 2007, Tzortzakis & Economakis 2007, Soylu et al. 2010, Znini et al. 2011, 2013). Znini et al. (2013) extracted an essential oil from the plant *Warionia saharae* and reported its antifungal activity against three apple phytopathogenic fungi, viz. *Alternaria* species (*Alternaria* rot), *Penicillium expansum* (blue mould), and *Rhizopus stolonifer* (*Rhizopus* rot). The extracts of these plants used by different researchers against pathogenic fungi show promising antifungal activity which indicates that these plants can act as a good biological resource for producing safe biofungicides.

Tab. 3. Biological control of rot causing fungal pathogens by using botanicals.

Plant extract	Fungal pathogens	References
Aframomum melegueta	*Botryodiplodia theobromae*, *Fusarium oxysporum*, *Aspergillus niger*	Okigbo & Ogbonnaya (2006)
Allium cepa	*Aspergillus niger*, *Fusarium oxysporum*, *Rhizopus stolonifer*, *Penicillium chrysogenum*	Taskeen-Un-Nisa (2010, 2011)
Allium sativum	*Penicillium* sp., *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*, *Fusarium oxysporum*, *Rhizopus stolonifer*, *Penicillium chrysogenum*	Magro et al. (2006), Taskeen-Un-Nisa (2010, 2011), Hadi & Kashefi (2013)
Annona reticulata	*Rhizopus stolonifer*, *Colletotrichum gloeosporioides*	Bautista-Baños et al. (2000)
Anthemis nobilis (currently *Chamaemelum nobile*)	*Penicillium* sp., *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*	Magro et al. (2006)
Artemisia absinthium	*Alternaria alternata* (*Alternaria* rot), *Penicillium expansum* (*Penicillium* rot), *Mucor piriformis* (*Mucor* rot), *Aspergillus niger* (Black mould rot)	Parveen et al. (2013, 2014)
Borago officinalis	*Monilinia laxa*, *Botrytis cinerea*, *Penicillium expansum*, *Penicillium digitatum*, *Penicillium italicum*, *Aspergillus carbonarius*, *Aspergillus niger*	Gatto et al. (2011)
Cinnamomum verum	*Penicillium* sp., *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*	Magro et al. (2006)
Curcuma longa	*Colletotrichum gloeosporioides* (anthracnose diseases of fruits)	Imtiaj et al. (2005)
Datura innoxia and *Datura stramonium*	*Alternaria solani*, *Fusarium oxysporum*	Jalander & Gachande (2012)
Dittrichia viscosa	*Penicillium digitatum*, *Penicillium expansum*, *Botryotinia fuckeliana*, *Aspergillus* sp., *Monilinia laxa*, *Monilinia fructigena*	Mamoci et al. (2011)
Ferula communis	Identical to the pathogens of *Dittrichia viscosa*	Mamoci et al. (2011)
Hypochaeris radiata	*Paecilomyces lilacinus*, *Mucor* sp., *Trichoderma viride*, *Verticillium lecanii*, *Candida albicans*, *Fusarium* sp., *Penicillium* sp., *Aspergillus fumigatus*, *Aspergillus niger*	Senguttuvan et al. (2013)
Lavandula stoechas	*Penicillium* sp., *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*	Magro et al. (2006)
Malva sylvestris	*Alternaria alternata*, *Penicillium expansum*, *Mucor piriformis*, *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*	Magro et al. (2006), Parveen et al. (2013, 2014)
Mentha arvensis	*Aspergillus niger*, *Fusarium oxysporum*, *Rhizopus stolonifer*, *Penicillium chrysogenum*	Taskeen-Un-Nisa (2010, 2011)
Mentha cordifolia	*Colletotrichum gloeosporioides* (anthracnose disease)	Bussaman et al. (2012)

Plant extract	Fungal pathogens	References
Mentha piperita	*Penicillium* sp., *Aspergillus candidus*, *Fusarium culmorum*, *Aspergillus niger*, *Fusarium oxysporum*	Magro et al. (2006), Hadi & Kashefi (2013)
Ocimum gratissimum	*Botryodiplodia theobromae*, *Fusarium oxysporum*, *Aspergillus niger*, *Rhizopus oryzae*	Amandioha (2001), Okigbo & Ogbonnaya (2006)
Orobanche crenata	Identical to the pathogens of *Borago officinalis*	Gatto et al. (2011)
Piper sarmentosum	*Colletotrichum gloeosporioides* (anthracnose disease)	Bussaman et al. (2012)
Plantago coronopus	Identical to the pathogens of *Borago officinalis*	Gatto et al. (2011)
Plantago lanceolata	Identical to the pathogens of *Artemisia absinthium*	Parveen et al. (2013, 2014)
Rumex obtusifolius	Identical to the pathogens of *Artemisia absinthium*	Parveen et al. (2013, 2014)
Sanguisorba minor	Identical to the pathogens of *Borago officinalis*	Gatto et al. (2011)
Silene vulgaris	Identical to the pathogens of *Borago officinalis*	Gatto et al. (2011)
Sonchus asper and *Sonchus oleraceus*	Identical to the pathogens of *Borago officinalis*	Gatto et al. (2011)
Taraxacum officinale	*Alternaria alternata* (*Alternaria* rot), *Penicillium expansum* (*Penicillium* rot), *Mucor piriformis* (*Mucor* rot), *Aspergillus niger* (Black mould rot), *Monilinia laxa*, *Botrytis cinerea*, *Penicillium italicum*, *Penicillium digitatum*	Gatto et al. (2011), Parveen et al. (2013, 2014)
Tagetes erecta	*Colletotrichum gloeosporioides* (anthracnose diseases of fruits)	Imtiaj et al. (2005)
Warionia saharae	*Alternaria alternata* (*Alternaria* rot), *Penicillium expansum* (*Penicillium* rot), *Rhizopus stolonifer* (*Rhizopus* rot)	Znini et al. (2013)
Zingiber officinale	*Colletotrichum gloeosporioides* (anthracnose diseases of fruits)	Imtiaj et al. (2005)

Control using compost extracts

Compost extracts from plant materials have been used as a biological control agent for different postharvest pathogens, such as *Plasmopara viticola*, *Uncinula necator*, *Pseudopeziza tracheiphila*, *Botrytis cinerea*, and *Sclerotium rolfsii* (Weltzien 1989, Zmora-Nahum et al. 2008). Chakroune et al. (2008) found that compost extracts from palm were very effective in managing *Fusarium oxysporum* f. sp. *albedinis*. Exadaktylou & Thomidis (2010) used compost extracts from a seagrass species, *Posidonia oceanica*, and the organic fertiliser Cofuna 3, made from bagasse (fibrous matter that remains after sugarcane or sorghum stalks are crushed to extract their juice) and found them effective against the postharvest fruit rots of peach caused by *Monilinia* sp., *Penicillium* sp. and *Rhizopus* sp. They found that fruits treated with an extract from Cofuna 3 showed relatively fewer symptoms of rotting for all fungi tested than *Posidonia oceanica*. It was shown that compost extracts rich in lignocellulosic substances are most effective in inhibiting the growth of several species of *Fusarium* (Znaidi 2002). There are very few reports on the use of compost extracts to control pathogens that cause postharvest fruit rots. They are mostly used for controlling soil-borne plant pathogens (Mokhtar & El-Mougy 2014).

DISCUSSION AND CONCLUSION

Biological control using microorganisms associated with plants is an efficient and effective approach to control diseases and is considered environmentally friendly. The first step is to screen potential biological control agents (BCA), while the main screening strategy used by many scientists is based on in vitro antagonistic activity.

A successful biocontrol agent is generally equipped with several mechanisms which often work in concert, and may be crucial in controlling disease development. It involves a complex interaction between host, pathogen, antagonists and environment (Droby et al. 2009, Nunes 2012). A bacterial biocontrol agent of the genus *Bacillus* uses nutrient and space competition, induced resistance, production of diffusible antibiotics, volatile organic compounds, toxins, and cell-wall degrading enzymes such as chitinase and β-1,3-glucanase (Nunes 2012). Numerous studies have reported a range of antifungal compounds produced by different biological control agents. Among them, lipopeptides from the fengycin, iturin and surfactin families are regarded as key factors in biological control activity (Santoyo et al. 2012).

Information on the mechanisms of action by which biological control agents suppress postharvest diseases is still not fully known mainly due to difficulties encountered during the study of complex interactions between host, pathogen and biological control. However several possible mechanisms have been mentioned, which include production of antibiotics, lytic enzymes, direct parasitism, induction of resistance in the host tissue, and competition for nutrients and space. Spadaro & Gullino (2004) provided the major characteristics of an efficient antagonist or biological control agent, including genetic stability, efficiency at low levels and against a range of pathogens on various fruits, growth on cheap substrates in fermenters, survival in adverse environmental conditions, lack of pathogenicity on the host, and no production of metabolites toxic to humans. Based on these traits, yeasts seem to be excellent candidates for the biological control of pathogenic fungi. Moreover, characteristics inherent to yeasts, such as fast growth, fruit surface colonisation and the deprivation of nutrients from pathogens (through competition) have placed these organisms among the most suitable biocontrol agents (Richard & Prusky 2002).

Botanicals are also effective in controlling postharvest rot of fruit. Plants provide a wide range of secondary metabolites, i.e. essential oils which have antimicrobic, allelopathic, bioregulatory and antioxidant properties. The family *Brassicaceae* is well documented for their antimicrobial activity and production of glucosinolates.

Since significant progress has been made in different aspects of the biological control of various plant diseases including postharvest rots, but this area still needs more attention to solve the existing problems. In order to have more effective biological control strategies in future, a better understanding of the biocontrol agent and its interaction with the microorganism is needed. Microbial biological control agents have their limitation, which may restrict their use under certain circumstances. Microbial biological control agents have been criticised mainly for not providing such a consistent or broad-spectrum control as synthetic fungicides. Some biocontrol agents can be toxic or cause environmental contamination, so the key success of this technology for disease control is related to the biosafety and environmental impact of biocontrol agents. It is important to carry out more research studies on less known aspects of biological control including development of novel formulations from microbial agents and bioagents of plant origin reported by several researchers, their impact on the environment, and mass production to make new biocontrol products effective, stable, safer and cost effective. The approach would undoubtly encourage environmentally friendly products to reach the market and would lead us towards a sustainable agricultural system in the future.

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