Trends in Food Science & Technology 47 (2016) 39–49

Contents lists available at ScienceDirect

Trends in Food Science & Technology

journal homepage: http://www.journals.elsevier.com/trends-in-food-science-and-technology

Review

Development of biocontrol products for postharvest diseases of fruit: The importance of elucidating the mechanisms of action of yeast antagonists

Davide Spadaro [a, *], Samir Droby [b]

[a] Dept. Agricultural, Forestry and Food Sciences (DISAFA) and AGROINNOVA, Centre of Competence for the Innovation in the Agroenvironmental Sector, University of Torino, Largo Braccini 2, 10095 Grugliasco, TO, Italy
[b] Department of Postharvest Science, ARO, The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel

ARTICLE INFO

Article history:
Received 29 April 2015
Received in revised form
17 November 2015
Accepted 21 November 2015
Available online 23 November 2015

Keywords:
Biofungicide
Biological control
Fruit
Omics
Rots
Yeast

ABSTRACTS

Background: Impressive progress was made in the last decade in development, registration and commercialization of biocontrol products based on yeast to manage postharvest pathogens of fruit. To successfully inhibit the pathogen infection and development, several possible mechanisms operate in a tritrophic host-pathogen-antagonist interaction system.

Scope and Approach: The current reviews focuses on the recent knowledge on the mechanisms by which yeast biocontrol agents (BCAs) interact with pathogens and fruit tissues. The main mechanisms of action explored include antibiosis, mycoparasitism, production of lytic enzymes, induced resistance, competition for limiting nutrients and space, and the role of oxidative stress. Omics techniques can provide a powerful tool to study complex fruit host-pathogen-antagonist-native microflora interactions.

Key Findings and Conclusions: Various aspects relevant to mechanisms of action of yeast antagonists have been discussed, including unique environment of surface wounds, iron competition, biofilm formation, cell wall degrading enzymes, and involvement of oxidative stress. Outstanding advancement in molecular and omics technologies revolutionized the research about the physiological status of BCAs and the global effect of the application of BCAs on the transcriptome and/or proteome of fruit. Microbial communities on plant surfaces could impact disease control through their interactions with host plants, pathogens, and BCAs, in a quadritrophic interaction system, hence microbiome research opens new research opportunities. The complex modes of action make antagonistic performance and efficacy more dependent on production, formulation, packing, application, and storage. A deep understanding of the mode of action is essential to develop appropriate formulation and methods of application.

1. Introduction

Postharvest fungal pathogens are considered the main cause of losses of fresh fruits and vegetables at the postharvest, distribution, and consumption levels. While reports on the level of these losses are conflicting, a report by the Food and Agriculture Organization (FAO, 2011) indicated that global average loss in Europe, North America and Oceania is about 29%, compared to an average of about 38% in industrialized Asia, South East Asia, Africa and Latin America. Efforts have been made to minimize these losses through developing a better understanding of the biology and aetiology of postharvest diseases, as well as by developing adequate postharvest handling technologies and control strategies (Prusky & Gullino, 2010). While several approaches were suggested for managing postharvest decay, chemical control of postharvest diseases, applied in orchard or after harvesting, is still the most widely used method. Increasing concerns, however, regarding residues of fungicides in the fruit, development of resistant biotypes of the pathogens, as well as risks associated with their continuous use have prompted the search for safe and effective alternative strategies. Among these strategies, biological control based on naturally occurring microorganisms, has been the most studied (Liu, Sui, Wisniewski, Droby, & Liu, 2013).

In the past thirty years, there have been extensive research activities to explore and develop strategies based on microbial

---

* Corresponding author.
E-mail address: davide.spadaro@unito.it (D. Spadaro).

http://dx.doi.org/10.1016/j.tifs.2015.11.003
0924-2244/© 2015 Elsevier Ltd. All rights reserved.

antagonists to biologically control postharvest pathogens (Droby, Wisniewski, Macarisin, & Wilson, 2009; Sharma, Singh, & Singh, 2009; Spadaro & Gullino, 2004). By using the key words "biocontrol" OR "biological control" AND "postharvest" OR "post-harvest" in the Scopus search engine, 879 documents were retrieved (search performed on April 3, 2015), most of them (609; 69%) published in the last ten years. Impressive progress was made in development, registration and commercialization of biocontrol products to manage key postharvest pathogens, such as *Penicillium expansum, Penicillium digitatum, Penicillium italicum, Fusarium sambucinum*, *Rhizopus stolonifer* and *Botrytis cinerea*. Different products reached advanced stages of development and commercialization (Table 1). Biosave™ (*Pseudomonas syringae* Van Hall) was originally registered in the USA for postharvest application on pome and citrus fruits, and it was later extended to cherries, potatoes and sweet potatoes (Janisiewicz & Peterson, 2004). Among the first products based on yeasts, Aspire™(based on *Candida oleophila*) (Liu et al., 2013) and Yieldplus™ (based on *Cryptococcus albidus*) (Janisiewicz & Korsten, 2002) were commercialized for some years but they were withdrawn due to various reasons, including low and inconsistent efficacy under commercial conditions, low profitability and difficulties in market penetration and perception of the customers/industry, and small size companies with low available resources to maintain development and commercialization. Other products have been more successful, including Shemer™, based on the yeast *M. fructicola* (Droby et al., 2009), initially registered in Israel for both pre- and postharvest application on various fruits and vegetables, including apricots, citrus fruit, grapes, peaches, peppers, strawberries, and sweet potatoes. Shemer™ was later acquired by Bayer CropScience (Germany) and recently sublicensed to Koppert (Netherlands). A commercial formulation of *Candida sake* has been developed for use on pome fruit and grapevine and registered in Spain under the name Candifruit™ (Calvo-Garrido et al., 2014), however, it is not yet used due to constrains of the distribution company. In South Africa, Avogreen™ has been introduced for the control of Cercospora spot, a postharvest disease of avocado, but its use has been limited due to inconsistent results (Demoz & Korsten, 2006). Furthermore, Nexy, based on another strain of *C. oleophila* was developed in Belgium and is now registered throughout the European Union (Lahlali, Raffaele, & Jijakli, 2011). Finally, BoniProtect™, developed in Germany and based on two antagonistic strains of *Aureobasidium pullulans,* is used as preharvest application to control wound pathogens developing on apples during storage.

In practice, however, the acceptance and widespread use of postharvest biocontrol products is still limited. This can be attributed to several shortcomings related to reduced and inconsistent performance when biocontrol agents (BCAs) are used under commercial conditions, as well as to limited market and small size companies involved in their development and commercialization. Host, pathogen and environment variables affecting the decreased efficacy of postharvest BCAs and strategies for their improvement were the subject of several reviews (Droby et al., 2009; Janisiewicz & Korsten, 2002).

Among the antagonistic microorganisms used as BCAs against postharvest pathogens, a relatively high number of yeast was reported (Table 1) and this is related to their features that make them effective as BCAs on fresh agricultural commodities as well as other foods. Yeasts are tolerant to extreme environmental conditions prevailing before and after harvest (low and high temperatures, desiccation, wide range of relative humidity, low oxygen levels, pH fluctuations, UV radiation). Furthermore, yeast are uniquely adapted to the fruit micro-environment (high sugar concentration, high osmotic pressure and low pH). Yeast can grow rapidly on inexpensive substrates in fermenters and are therefore easy to produce in large quantities (Spadaro, Ciavorella, Zhang, Garibaldi, & Gullino, 2010). In addition, they do not produce allergenic spores or mycotoxins, in contrast to filamentous fungi, and they have simple nutritional requirements that enable them to colonize dry surfaces for long periods of time.

The current review focuses on presenting recent knowledge on the mechanisms by which postharvest yeast BCAs interact with the pathogen and fruit tissue while discussing the importance of these interactions to effectively explore new antagonists, improve efficacy, develop effective formulations and proper application of the commercial products.

2. Fruit surface and wound environment

Interactions between the antagonist, the pathogen, the host and the fructoplane resident microflora have been extensively studied and suggested to play critical role in various biocontrol systems (Chan, Qin, Xu, Li, & Tian, 2007; Hershkowitz et al., 2013; Jiang, Zheng, & Chen, 2009; Kwasiborski, Bajji, Renaut, Delaplace, & Jijakli, 2014). In this regard, the wound site, the court of infection of most necrotrophic postharvest pathogens, is of particular interest when exploring the mechanisms of action of microbial antagonists.

In general, at the initial stages of the bitrophic plant–pathogen interaction (Fig. 1), the fungal pathogen can release pathogen-associated molecular patterns (PAMPs) that can be recognized by specific plant recognition receptors, leading to trigger the first innate immunity response associated with a slight oxidative burst (Jones & Dangl, 2006). The response of the fruit is depending on the fruit species and/or cultivar and on its physiological/senescent stage (Cantu et al., 2009; Prusky, Alkan, Mengiste, & Fluhr, 2013). The pathogen can then overcome this first line of defence by releasing effectors to supress further plant defence mechanisms, making the tissue susceptible to infection. In case the pathogen is unable to manipulate fruit defences to its advantage, the fruit can respond by triggering a stronger oxidative burst (Heller & Tudzynski, 2011), accompanied by the biosynthesis of

Table 1
Commercially available biofungicides, based on microorganisms, for the control of postharvest diseases.

Microorganism	Product name	Target pathogens	Fruit	Country
Aureobasidium pullulans	Boniprotect	*Penicillium, Botrytis, Monilinia*	Pome fruit	EU (preharvest)
Bacillus subtilis	Avogreen[a]	*Cercospora, Colletotrichum*	Avocado	South Africa (preharvest)
Candida oleophila	Nexy	*Botrytis, Penicillium*	Pome fruit	Belgium, EU
Candida oleophila	Aspire[a]	*Botrytis, Penicillium*	Citrus fruit, pome fruit	United States
Candida sake	Candifruit	*Penicillium, Botrytis, Rhizopus*	Pome fruit	Spain
Cryptococcus albidus	Yield plus	*Botrytis, Penicillium, Mucor*	Pome fruit	South Africa
Metschnikowia fructicola	Shemer	*Botrytis, Penicillium,Rhizopus, Aspergillus*	Table grape, strawberry, sweet potato	Netherlands
Pantoea agglomerans	Pantovital	*Penicillium, Botrytis, Monilinia*	Citrus fruit, pome fruit	Spain
Pseudomonas syringae	Biosave	*Penicillium, Botrytis, Mucor*	Pome, citrus fruit, cherry, potato, sweet potato	United States

[a] Biofungicides not currently commercialized.