



The fruit microbiome: A new frontier for postharvest biocontrol and postharvest biology

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ABSTRACT

Microorganisms are an integral part of the composition of fruits and vegetables and are found as epiphytes on the surface or as endophytes within tissues. The realization that fruit surfaces harbor beneficial microorganisms fostered the field of biological control using epiphytic microorganisms which led to the development of several commercial biocontrol products. Advances in DNA sequencing and “omics” technologies have enhanced our ability to characterize the diversity and function of microbial communities (microbiome) present in and on plant tissues. Microbiome studies have the potential of providing knowledge that will lead to a fundamental paradigm shift in the way we think about biocontrol strategies, biocontrol products, and postharvest biology, as well as the health attributes of fruits and vegetables. Fruit microbiome research will enhance our understanding of harvested commodities as an ecosystem in which the microbiome plays an essential role in the health and physiology of fruit after it is harvested. Meta-omic (metagenomics, metatranscriptomics, metaproteomics, and metametabolomics) technologies are only beginning to be applied to postharvest studies and will revolutionize our understanding of postharvest biocontrol systems, foodborne pathogens, and postharvest physiology. The role of the microbiome in plant health, productivity, and cultivar development should be considered as much as the plant itself. Plant breeding or genetic modification of plants could be used to intentionally modulate the composition of the microbiome and its function, recruiting disease antagonists and plant-growth promoters that enhance plant health and the quality of the harvested products. Increased knowledge of microbial community systems will lead to the development of natural or synthetic consortia that can be used to prevent postharvest diseases and mitigate physiological disorders in harvested commodities.

1. Introduction

Microorganisms are an integral part of the composition of fruits and vegetables and are found as epiphytes on the surface or as endophytes within tissues. The majority of these microorganisms are not pathogenic, however, their role and function in fruit health, quality, and disease resistance before and after harvest is largely unknown. Information about their ecology, colonization, survival, and growth on and in harvested commodities is also lacking. The realization that fruit surfaces harbor beneficial microorganisms fostered the field of biological control using epiphytic microorganisms and led to the development of several commercial biocontrol products, and numerous scientific publications (Droby et al., 2016). Rapid developments in exploring and understanding the microbiome, now offer the opportunity to develop new approaches to postharvest biocontrol that are more effective. It is our opinion that studies of the microbiome in and on fruit offer a

new frontier that will greatly change our understanding of postharvest biocontrol and postharvest biology.

Droby et al. (2009) reviewed twenty-years of postharvest biocontrol research, providing a brief history, and their ideas about the concepts underlying the science of postharvest biocontrol and the limitations experienced by postharvest biocontrol products in the marketplace. They suggested that it was time to develop new paradigms about the biology and functional application of biocontrol agents if biocontrol was going to reach its' full potential. They emphasized the need to view the postharvest biocontrol as a system as an integrated whole, composed of the biocontrol agent, the pathogen, the host, and the environment. While such an approach represented distinct challenges, they indicated that it was necessary if problems related to the efficacy and consistent performance of biocontrol products were to be overcome. The role of fruit microbiome in the biocontrol system, however, was not raised at that time since the technologies to study the

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microbiome were not yet readily available.

In 2016, two articles in a Special Issue of Postharvest Biology and Technology were devoted to reviewing alternative approaches in general and biocontrol in particular (Wisniewski et al., 2016; Droby et al., 2016). Advances in the science and development of biocontrol agents were described, especially in regard to our understanding of the interaction between microbial antagonists and their hosts, target pathogens, and the resident microflora. Wisniewski et al. (2016) and Droby et al. (2016) noted that the interest in biological approaches to postharvest disease control, and biologically-based products in general, continues to grow and discussed the drivers underlying the sustained interest in biocontrol products. Droby, et al. (2016) noted that the approach utilized to identify and select postharvest biocontrol agents had not changed much since the original approach was discussed by Wilson and Wisniewski (1989) and a selection method was described by Wilson et al. (1993). The commonly-used approach involves the identification of a single antagonist possessing properties that allow it to develop rapidly in wounded fruit tissue, thus preventing pathogens from becoming established. This approach, however, neglects the fact that the introduced antagonist is not the only player in the system, and in general neglects the interactions antagonists experience as part of a microbial network and as a component of a biological system (Droby et al., 2016). One aspect of microbial ecology that has the potential to revolutionize our understanding of plant pathology and biology is the technological advances that have been made in the use of next-generation-sequencing (NGS) and meta-omic technologies to characterize the diversity and function of the microbial communities present in and on host tissues (Abdelfattah et al., 2017). NGS technologies are opening a new frontier in exploring the role of microbes in our environment and their interaction with various hosts (Berg et al., 2016). It is our opinion that microbiome studies will provide information that will result in a fundamental paradigm shift in the way we think about biocontrol strategies, biocontrol products, and postharvest biology, as well as the health attributes of fruits and vegetables. Investigations of the fruit microbiome will enhance our understanding of harvested commodities as an ecosystem in which the microbiome plays an essential role in the health and physiology of fruit before and after it is harvested. The current contribution, rather than serving as a comprehensive review, discusses various aspects of microbiome research and highlights how they can serve as a foundation for studies on postharvest biocontrol and biology. A comprehensive review of the application and the tools used for microbiome research on biocontrol of plant diseases was recently provided by Massarat et al. (2015) and Abdelfattah et al. (2017).

2. Microbiome theory and concepts

Microbial communities have an essential role in ecosystem processes, including nutrient cycling, primary production, litter decomposition, and disease resistance (Delgado-Baquerizo et al., 2015). Unfortunately, a complete description of the microbial diversity present in an ecosystem cannot be obtained by standard culturing methods alone. This is also true for identifying the diversity of microbes that inhabit the internal and external portions of an organism. Regarding postharvest diseases, biocontrol of postharvest diseases, and postharvest biology in general, this shortcoming has greatly limited our understanding of the impact that whole microbial communities and their genetic material (the microbiome) potentially play in the physiology of a plant and its interactions with the environment and other organisms (Berg et al., 2016; Abdelfattah et al., 2017).

The use of amplicon sequencing and metagenomics (shotgun sequencing), have provided a fundamental breakthrough in our ability to describe, compare, and discover new microbial communities (Ursell et al., 2012). Various studies have demonstrated that the composition of the microbiota inhabiting an organism (both endo- and epiphytically) can have a profound effect on the physiology of their hosts, including disease resistance responses (Hardoim et al., 2015). In general,

however, the role of the microbiota in postharvest pathology and physiology is poorly understood, and how the resident microflora impacts biocontrol efficacy is simply not known.

Meta-omic (metagenomics, metranscriptomics, metaproteomics, and metametabolomics) technologies are only beginning to be applied to postharvest studies. Microbiome theory suggests that species, due to their close relationship and interaction with microbial assemblages, should be viewed as metaorganisms, defined as an organism plus its associated microbiome. The “holobiont” theory further suggests that microbial assemblages and their associated hosts have co-evolved and resulted in stable microbiome-organism relationships (Zilber-Rosenberg and Rosenberg, 2008). Berg et al., (2016) have indicated that it is critical to consider the role of the microbiome in experimental botany and breeding strategies. How the concept of the metaorganism relates to postharvest biocontrol systems and postharvest biology, in general, remains to be determined. Importantly, Douglas and Werren (2016) have suggested that the holobiont or hologenome concept is too rigid and will need to be adjusted as more data on the relationship between hosts and their associated microbiota become available.

3. The fruit microbiome

An increasing number of studies have documented the microbial diversity present on a variety of fruit species (Abdelfattah et al., 2017). These studies have examined the impact of management practices on the composition of the microflora, temporal changes in the microbiome over the course of a growing season, and the composition of the microbiota after harvesting, processing, shipping, and distribution to a local supermarket. Studies documenting the effect of the application of biocontrol agents on the resident microflora have been comprehensively reviewed by Massart et al. (2015), however, most of the reported studies were not postharvest studies.

Abdelfattah et al. (2016) demonstrated that the alpha and beta diversity of the fungal microflora of harvested apples differed significantly between fruit parts (Fig. 1). PCoA analysis indicated that the microbiota of samples clustered distinctly based on the part of the fruit from which they were obtained, such as peel, wound, calyx-end, or stem-end tissues. This strongly indicates that the microflora associated with different portions of the apple fruit need to be considered when designing biocontrol systems for the management of postharvest diseases. Significantly different populations of fungi were present on fruit obtained from organic vs. conventional orchards, and the presence of several unique taxa in the organically-produced fruit may have been related to the management practice used to grow the fruit. In their study, *Penicillium* was dominant in peel samples, while *Alternaria* was dominant in the calyx- and stem-end samples. *Ascomycota* accounted for over 90% of the observed species, followed by *Basidiomycota* (8%), and *Chytridiomycota* (0.1%). No significant temporal changes in the microbiome were observed over a two-week storage period at room temperature.

Additional studies are presently being conducted to determine the impact of waxing and storage on the resident microbiome of harvested apples, and the impact of waxing on the specific survival of the food-borne pathogen, *Listeria monocytogenes*. Temporal changes in the wound-related microbiome of apple and citrus fruit and their effect on biocontrol agents in the wound are also being investigated. Preliminary findings indicate the presence of a wide spectrum of bacteria in wounds and that their presence and abundance is influenced by inoculation of the wound with a pathogen or the application of a biocontrol agent (unpublished data). The effect of wound-colonizing endophytic bacteria on infection and the development of decay, as well as the efficacy of biocontrol agents are still largely unknown. A major question that needs to be resolved is how unique and stable is the core microbiome (as defined by taxa) of fruit across different climates, growing regions, and cultivars. While one would predict a stable, predictable microbiome based on the holobiont theory, previous research in grape has indicated

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