Microbiome approaches provide the key to biologically control postharvest pathogens and storability of fruits and vegetables

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Submitted to: FEMS special issue on "Sustainable Agriculture"

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ABSTRACT

Microbes play an important role in plants and interact closely with their host starting from sprouting seeds, continuing during growth, and after harvest. The discovery of their importance for plant and postharvest health initiated a biotechnological development of various antagonistic bacteria and fungi for disease control. Nevertheless, their application often showed inconsistent effects. Recently, high-throughput sequencing-based techniques including advanced microscopy reveal fruits and vegetables as holobionts. At harvest, all fruits and vegetables harbor a highly abundant and specific microbiota including beneficial, pathogenic and spoilage microorganisms. Especially, a high microbial diversity and resilient microbial networks were shown to be linked to fruit and vegetable health, while diseased products showed severe dysbioses. Field and postharvest handling of fruits and vegetables was shown to affect the indigenous microbiome and therefore has a substantial impact on the storability of fruits and vegetables. Microbiome tracking can be implemented as a new tool to evaluate and assess all postharvest processes and contribute to fruit and vegetable health. Here we summarize current research advancements in the emerging field of postharvest microbiomes and elaborate its importance. The generated knowledge provides profound insights into postharvest microbiome dynamics and sets a new basis for targeted, microbiome-driven and sustainable control strategies.

Keywords: Biocontrol, Biopreservation, postharvest decay, High-throughput sequencing, fruit microbiome

1. Introduction

Over the past millions of years plants closely evolved in an environment dominated by microorganisms (Cordovez et al., 2019). This close interaction resulted in co-evolved, host-specific plant microbiomes, which are also influenced by the surrounding microbiota from soil and aboveground environments (Berg and Smalla, 2009). The impact of both factors, plant genotype and soil quality facilitates plasticity and response to changing environmental conditions (Bergna et al., 2018). Studying the structure and function of plant microbiomes in detail, enlightened our understanding of the dynamics of plant associated microbes and their importance for plant health (Berg et al., 2014a; Philippot et al., 2013). Starting from the seed, microbes efficiently colonize the plant’s rhizosphere, phyllosphere and carposphere (Adam et al., 2016; Berg and Raaijmakers, 2018; Mitter et al., 2017). Recent studies have shown a plant species and genotype specificity as well as transfer of the microbiota to the next plant generation via seeds and fruits (Berg et al., 2014a; Bergna et al., 2018; Sánchez-Cañizares et al., 2017). This transfer connects the field microbiome with postharvest fruit stability and widens the impact of field disease control measures on fruit quality.

The issue of food loss and waste represents a major challenge worldwide. Nearly half of the cultivated fruits and vegetables are lost between production and consumption, according to the Food and Agriculture Organization of the United Nations (FAO, 2011) (Fig. 1). Postharvest food loss can either be a direct quantitative loss *e.g.* during harvest, or a result from losses in food quality *e.g.* water and sugar content loss, physiological disorders, or undesired sprouting (Aulakh and Regmi, 2013). Despite the substantial waste during processing and transport, a major loss in fruits and vegetables occurs also during storage. Here, the main causes are mold and bacterial contaminations (Bourne, 1977; Buchholz et al., 2018; Padmaperuma et al., 2020). Various fungi, mainly belonging to the genera *Alternaria*, *Aspergillus*, *Botrytis*, *Colletotrichum*, *Fusarium*, *Monilia*, *Penicillium* and *Rhizopus* as well as bacteria such as *Clostridium*, *Clavibacter, Streptomyces, Xanthomonas, Erwinia*, *Listeria, Salmonella* and *Escherichia* were found to cause the highest proportion of spoilage or harmful contamination that can affect consumers (Boudon et al., 2005; Perez Pulido et al., 2016; Snowdon, 1990). To overcome these problems, production is increased to compensate losses, innovative packaging technologies are developed as well as control measures primarily relying on physical measures or synthetic chemicals are applied. Chemical postharvest treatments include wax coatings, applications of growth regulators and diverse pesticides. However, due to health and environmental concerns, greater restrictions are being imposed especially on the use of synthetic fungicides by the society and regulatory agencies. In this regard, finding safe and effective alternatives to synthetic chemical fungicides in order to reduce losses has been the focus of many studies over the past years. Even though numerous biological approaches have been developed during the past 30 years, biological products have never reached broad usage, due to their limited applicability in the current postharvest processes (Droby et al., 2009, 2016; Sharma et al., 2009).

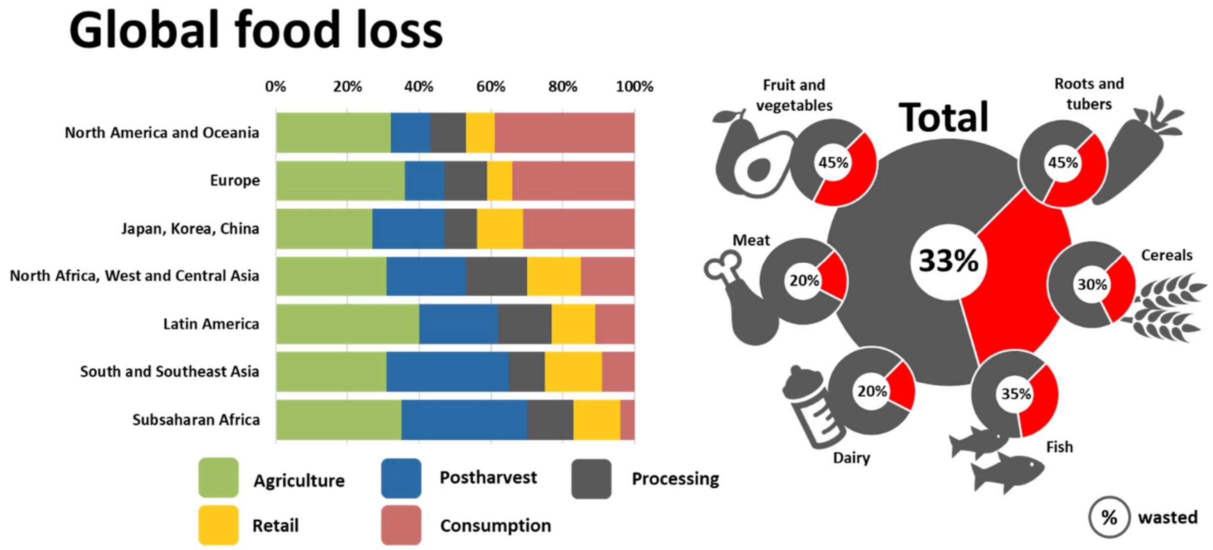

Figure 1: Analysis of global food loss for different regions and products. The visualization is based on data provided by the Food and Agriculture Organization (FAO) of the United Nations (FAO, 2011).

Naturally occurring microorganisms, that are either found as epiphytes on the surface or as endophytes in plant tissues, are highly diverse and comprise a great variety of microbial lineages. Although some are known to be plant pathogens, a larger fraction of these microbes are hypothesized to play a key role in fruit health, quality and disease resistance (Berg et al., 2014b; Droby and Wisniewski, 2018; Leff and Fierer, 2013). This gave rise to the first biocontrol approaches that were established in the late 1980s (Pusey and Wilson, 1988; Wilson and Wisniewski, 1989). Since then, relatively few changes in the general development of new biocontrol agents were made and adapted selection methods first described by Wilson and colleagues are still state of the art (Wilson et al., 1993). The commonly used approach involves the isolation and screening of antagonistic single strains that carry the ability to establish quickly in wounded fruit tissue to prevent pathogenic infections. However, the impact of the introduction of these biocontrol strains into a versatile host microbiome was often neglected (Droby and Wisniewski, 2018; Droby et al., 2016). The technological advances in the past years starting from high-throughput sequencing methods to meta-omics technologies provide tools for a deeper understanding of microbial interactions with the environment, various plant hosts, diversity changes due to diseases, and biocontrol-microbiome interactions (Abdelfattah et al., 2018a; Berg et al., 2016). In addition, cutting edge bioinformatic tools and predictive modeling enables substantially improved interpretation of the data generated (García-Jiménez et al., 2018). New approaches to track changes in the microbiome during growth and storage of different fruits provide a deeper understanding of microbial interplay in disease development than classical methods (Abdelfattah et al., 2016a; Kusstatscher et al., 2019a).

This review provides an overview from the beginning of microorganism-based biocontrol to the currently integrated approach of biocontrol with the host microbiome. Furthermore, we highlight the advances brought by modern technology in exploring the postharvest microbiome and their compatibility with classical methods. By discussing the present research progress in this field, we address its impact on modern agriculture and provide future perspectives and hurdles for microbiome-driven application technologies.

2. Developments and products in classical microbe-based biocontrol

Postharvest food quality loss and waste due to microbial infections is a major global problem in an increasing globalized, intense agricultural and horticultural production (FAO, 2011). The research on microbial antagonists as postharvest biocontrol agents has a long history and started with the first few studies published in the late 70s and 80s (Pusey and Wilson, 1988; Tronsmo and Raa, 1977). However, after the prohibition of several existing fungicides in the past years, the research interest in new biological alternatives gradually increased and hundreds of research papers and reviews were published (Droby et al., 2009; Sharma et al., 2009; Spadaro and Droby, 2016). Despite the potential of microbial antagonists to control several postharvest pests, the market for biological products is still small and only a few products found their niche whereas others were discontinued after a short period (Wisniewski et al., 2016). Facilitated by new regulations and an increased consumer awareness, the market is estimated to grow constantly in the next years (Glare et al., 2012).

Table 1: Overview about the most studied antagonistic strains that were implemented in commercialized postharvest products.

Taxonomic group	Studied antagonistic strains	Product name	Disease/Pathogen	Fruit/ Vegetable	Reference
Bacteria	*Bacillus subtilis*	Serenade® (Bayer, Leverkusen, Germany)	*Cercospora, Colletotrichum*	stone fruit, pome fruit, tomato, strawberry	(Wilson, 1985)
	Bacillus amyloliquefaciens	Amylo-X® (Biogard CBC, Grassobbio, Italy)	*Botrytis, Sclerotinia*	Different fruits	(Arrebola et al., 2010)
	Pseudomonas syringae	BioSafe® (Jet Harvest Solutions, Longwood, FL, USA)	*Botrytis, Penicillium, Mucor*	Citrus fruit, cherry, Potato, sweet potato	(Bull et al., 1997)
	Pantoea agglomerans	Pantovital® (Domca, Granada, Spain)	*Penicillium, Botrytis, Monilinia*	Different fruits	(Usall et al., 2008)
Yeasts	*Candida oleophila*	Nexy® (BioNext, Paris, France)	*Botrytis, Penicillum*	Pome fruit	(Lassois et al., 2008; Lima et al., 1997; Liu et al., 2012; Sui et al., 2020)
	Candida sake	Candifruit® (IRTA, Leida, Spain)	*Penicillium, Botrytis, Rhizopus*	Pome fruit	(Vinas et al., 1998)
	Cryptococcus albidus	Yield Plus® (Anchor Bio-Technologies, South Africa)	*Botrytis*	Pome fruit, Strawberry	(Kowalska et al., 2012)
	Metschnikowia fructicola	Shemer® (Koppert, The Netherlands)	*Botrytis, Penicillium, Mucor*	Table grape, strawberry, sweet potato	(Kurtzman and Droby, 2001; Piombo et al., 2018)
	Aureobasidium pullulans	BoniProtect® (Bio-ferm, Tulln, Austria)	*Penicillium, Botrytis, Monilinia*	Pome fruit	(Leibinger et al., 1997; Lima et al., 1997; Mari et al., 2012)

Biocontrol strains are usually isolated from the natural epiphytic microflora of fruits and vegetables (Droby et al., 2009; Liu et al., 2013). Some of the best-studied biocontrol bacteria are *Bacillus subtilis* (Wilson, 1985), *B. amyloliquefaciens* (Arrebola et al., 2010), *B. megaterium* (Kong et al., 2010), *Pseudomonas syringae* (Bull et al., 1997), *Erwinia herbicola* (Bryk et al., 1998) and *Pantoea agglomerans* (Usall et al., 2008). Several products using these strains were commercialized including BioSafe® (Jet Harvest Solutions, Longwood, FL, USA) based on *Pseudomonas syringae* for the control of potato and sweet potato diseases; Serenade® (Bayer, Leverkusen, Germany), using *B. subtilis* against diseases in stone and pome fruit, tomato and strawberry; Pantovital® (Domca, Granada, Spain), containing *P. agglomerans* and used on different fruits; and Amylo-X® (Biogard CBC, Grassobbio, Italy) using *B. amyloliquefaciens* also used on different fruit varieties (Table 1).

In addition, numerous yeast strains were studied for their disease control ability (Droby et al., 2009; Liu et al., 2013). Investigated strains including *Pichia guilliermondii* (Wilson et al., 1993), *Pichia anomala* (Haïssam, 2011), *Cryptococcus laurentii* (Filonow, 1998), *Candida oleophila* (Lima et al., 1997; Liu et al., 2012), *Candida sake* (Nunes et al., 2001), *Metschnikowia fructicola* (Kurtzman and Droby, 2001; Piombo et al., 2018), and *Aureobasidium pullulans* (Leibinger et al., 1997; Lima et al., 1997; Mari et al., 2012) showed promising biocontrol potential. Several products using those strains were commercialized: Candifruit® (IRTA, Leida, Spain) using *Candida sake*; Nexy® (BioNext, Paris, France) based on *Candida oleophilia*, BoniProtect® (Bio-ferm, Tulln, Austria) based on *Aureobasidium pullulans* and Shemer® (Koppert, The Netherlands) containing *Metschnikowia fructicola* (Table 1).

Approaches of combining biocontrol agents with conventional treatments were also shown to be a promising solution to reduce the input of chemicals (Droby et al., 2009; Lima et al., 2008). Lima and colleagues showed the potential of integrating biocontrol yeasts with pesticides to lower the levels of fungicide residues while maintaining comparable control of disease on apples (Lima et al., 2011). Similarly, the combination of hot water treatment and biocontrol was shown to be highly effective on peaches (Zhang et al., 2010) and on apples (Wassermann et al., 2019a). The elucidation of the modes of action of biological treatments permitted a greater focus on research pertaining to microbial volatile organic compounds (mVOCs), to which the observed effects were often shown to be attributed. The use of mVOCs as well as the exploitation of induced systemic resistance for postharvest biocontrol applications are therefore gaining more interest in the last years (Bailly and Weisskopf, 2017). New concepts, combining microbial with conventional treatments and the use of synthetic consortia are predicted to be of great research interest in the future (Droby et al., 2016).

Currently postharvest biological treatments are still struggling with limited markets and short lifespan of developed products (Wisniewski et al., 2016). Extension of product shelf life and adaption of the storage conditions will be one of the most important challenges in the future. Moreover, treatment processes themselves must become easier to integrate into the available infrastructure of processing facilities. At the moment biocontrol products are mainly applied in liquid form by dipping and drenching methods applied after harvest, which is not always implementable in the present postharvest processes (Droby et al., 2016). Further improvements, including formulation, are necessary to increase efficiency, range and usability of the products. One recent development is the study of fruit and vegetable microbiomes which could both increase our understanding of the ecology of postharvest microbial communities and promote the substitution of chemical fungicides with natural solutions (Droby and Wisniewski, 2018). Moreover, the technology could start new directions for biocontrol application and development.

3. The potential of microbiome-level postharvest monitoring using high-throughput sequencing tools

Current developments in DNA and RNA sequencing techniques provide a novel toolkit to improve postharvest treatments (Fig. 2). In the past years several high-throughput sequencing approaches were developed to study plant-microbe interactions as well as host-associated microbial community dynamics in general (Knief, 2014; Schlaeppi and Bulgarelli, 2015). Currently, the most used technology, barcoded amplicon sequencing or metabarcoding, involves the amplification of specific marker gene regions (e.g. 16S and 18S rRNA gene fragments; ITS region, etc.) to study the microbial community associated with distinct samples. Other techniques, based on shotgun sequencing of total community DNA/RNA, assess the whole metagenome or the metatranscriptome of the microbial community. For metagenomics-based approaches, the total DNA of a sample is extracted and fragmented. After sequencing, common workflows include reassembly of contigs, taxonomic binning, and annotation with reference databases (Kuczynski et al., 2011). Metatranscriptomic approaches are based on similar workflows on the mRNA level. Following *in vitro* or *in silico* rRNA removal, the remaining RNA is re-transcribed to cDNA and sequenced on a high-throughput sequencing platform. This approach provides information about genes that are activated in a microbial community under certain conditions (Massart et al., 2015). Additional information can be gained using other -omics techniques such as metaproteomics, targeting the proteins in complex communities (Schneider and Riedel, 2010) or metabolomics, which is applicable to study metabolites in microbial communities and the plant (Cevallos-Cevallos et al., 2009).

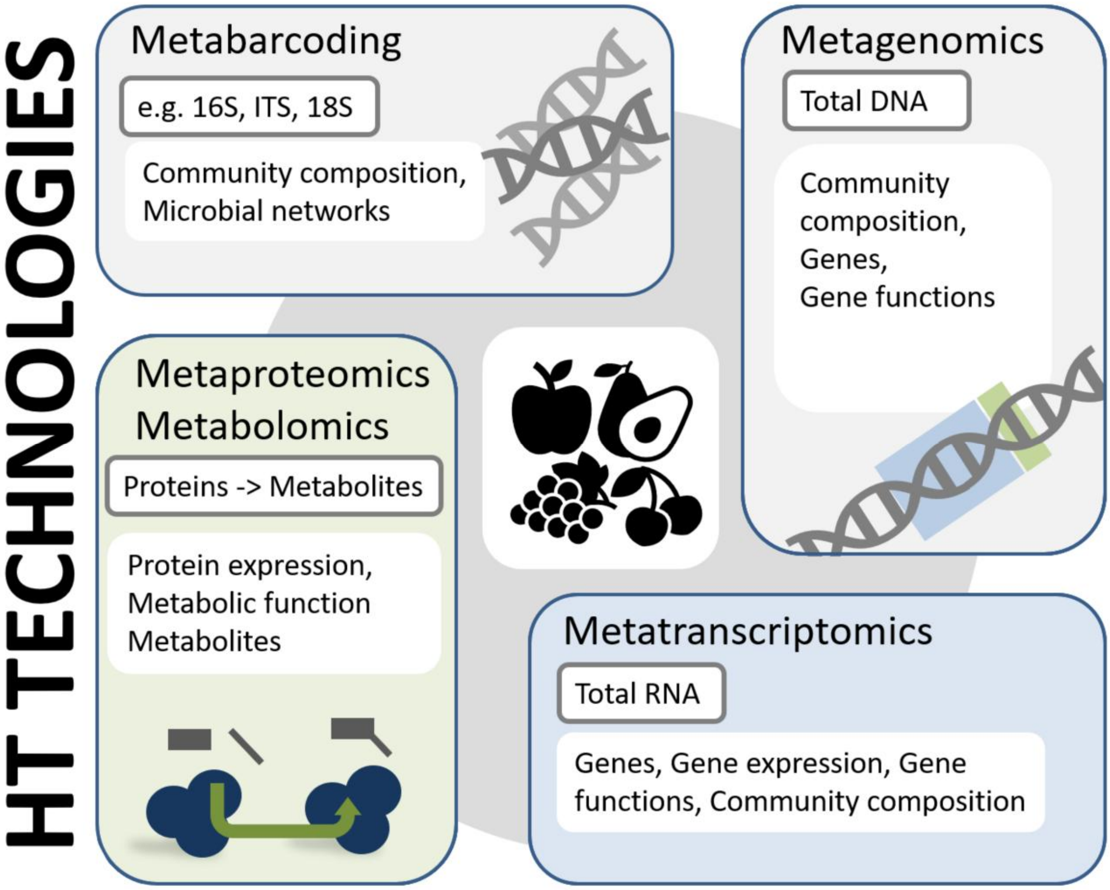

Figure 2: Overview of available high-throughput (HT) methods to study the postharvest microbiome, its genes and its functions. Studied sequences or molecules as well as possible observations are mentioned for each technology.

Microbiome research, enabled by modern high-throughput sequencing and –omics tools, has highlighted the importance of microorganisms during the whole lifecycle of plants. A broad range of microorganisms from various taxonomic groups were found to play an important role in both plant health and productivity (Berg et al., 2014a; Bulgarelli et al., 2013). Additionally, the plant microbiome was also shown to contribute to phenotypic and epigenetic plasticity as well as evolution (Partida-Martinez and Heil, 2011). The plant associated microbiome is highly plant-specific, especially in the rhizosphere (Smalla et al., 2001). Plant root exudates, which are integral chemo-attractants as well as repellants, attract specific bacterial species from the surrounding soil (Berg et al., 2014a). Metabolomic analysis of fruit surfaces have additionally demonstrated an ability to produce exudates that promote enteric pathogen growth, albeit without direct infection of the plant (Han and Micallef, 2016). In the context of the applicability for postharvest treatments, plant-associated bacteria not only contribute to the health of a plant during growth, but are also involved in fruit and plant part stability after harvest (Droby and Wisniewski, 2018). Although numerous microorganism-based products were developed over the past years, only a few studies investigated the establishment and impact on the native microbiome of the antagonistic strains after the harvest (Droby et al., 2009; Massart et al., 2015). So far, we know that the interplay of antagonistic bacteria with the host microbiome, in addition to environmental conditions, plant species and physiological state, plays an important role in biocontrol efficiency on the field and postharvest (Massart et al., 2015; Scherwinski et al., 2008; Schreiter et al., 2018). It will become increasingly important to implement these tools in the development of novel products for postharvest applications due to the new insights for their impact on the native microbiome.

The available high-throughput sequencing and -omics tools can provide a deeper insight into the numerous fruit/vegetable-microbiome interactions during postharvest storage and assist in the development and monitoring of postharvest treatments. Even though, cultivation dependent techniques are still necessary to identify new biocontrol strains, high-throughput sequencing can facilitate the detection of promising candidates, be implemented as a monitoring tool and guide the improvement of promising strains and their application. Studying the community dynamics and shifts over the storage period as well as the establishment of biocontrol agents within the community is not only of value for obtaining deeper insights into the microbial community but also a complementary supplement for product monitoring and registration (including risk assessment). Additionally, the knowledge about community dynamics combined with external abiotic factors such as temperature, moisture etc. could strengthen the understanding of the most crucial parameters during postharvest storage.

4. The current knowledge base in postharvest fruit and vegetable microbiome research

So far, the importance of the postharvest microbiome was highlighted in several reviews (Droby and Wisniewski, 2018; Massart et al., 2015; Wisniewski and Droby, 2019); however, there is only a handful of studies implementing high-throughput sequencing methods in the development of novel postharvest solutions. Nevertheless, the pioneering studies have indicated a high potential and exploitability of this technology for novel approaches to increase postharvest storability. One of the major findings relates to changes in microbial diversity during storage, which is also an important indicator for plant and human health (Berendsen et al., 2012; Hooper and Gordon, 2001) (Table 2).

Table 2: Overview of microbiome studies investigating fruit and vegetables after harvest using high-throughput sequencing.

Fruit/ Vegetable	Aim of the study	Targeted organisms and region	Key findings	Reference
Apple	Effect of hot water treatment and postharvest disease on the fruit microbiome	Bacteria (16S) and fungi (ITS1)	- Postharvest hot water treatment had no significant effect on the fruit microbiome - Significant microbiome changes with postharvest disease and diversity loss was observed	(Wassermann et al., 2019a)
	Microbiome changes during cold storage	Fungi (ITS1)	- Stored apples harbored higher diversity compared to before storage - Significant taxonomic changes were identified	(Shen et al., 2018)
	Microbial differences of fruit parts depending on managing practice	Fungi (ITS2)	- Fruit parts showed a significant different microbiome composition - Managing practice (organic, conventional) had significant influence on the microbiome of all fruit parts	(Abdelfattah et al., 2016a)
	Microbial differences of apple microhabitats depending on managing practice	Bacteria (16S)	- Significant differences were found between fruit parts and managing practice - Highest abundance of bacteria was in fruit pulp and seeds	(Wassermann et al., 2019b)
	Metagenomic approach on the apple epiphytic microbiome	Metagenome	- High bacterial and fungal diversity was found - Pathogens and biocontrol agents are found naturally in the community	(Angeli et al., 2019)
Brassica sp.	Microbial composition of raw eaten vegetables	Bacteria (16S)	- Plant type specific compositional differences were found - Myrosinase activity was found to be enriched in the microbiome of *Brassica* plants	(Wassermann et al., 2017)
Date	Fungal community	Fungi (ITS2)	- *Penicillium*, *Cladosporium*, *Aspergillus*, and *Alternaria* were the most abundant genera	(Piombo et al., 2020)

	during fruit development		- Severe changes during fruit development were observed	
Different raw vegetables	Accessing the vegetable microbiome throughout the supply chain	Bacteria (16S)	- Unique microbiomes were found for each plant - Postharvest treatments, packaging and manufacturing stage influences the microbiome	(Jarvis et al., 2018)
Grapes	Bacterial community on different grape varieties	Bacteria (16S)	- *Bacillales*, *Pseudomonadales*, *Lactobacillales* and *Enterobacteriales* were the most common bacterial taxa - Grape variety, vineyard origin and geographic location influenced the microbiome	(del Carmen Portillo et al., 2016)
	Grape microbiome from different locations	Bacteria (16S) and fungi (ITS1)	- Shared core microbiomes of grapes from the same variety were found - Different sampling locations changed specific taxonomic compositions	(Mezzasalma et al., 2017)
	Impact of the location and managing practice on the bark and grape microbiome	Bacteria (16S)	- Grape berries harbored a lower bacterial diversity compared to bark - Geographic location and managing practice both influenced the microbiome	(Vitulo et al., 2019)
	Fungal community of grapes, plant and surrounding air	Fungi (ITS2)	- Grape microbiome mostly was shared between plant parts and less with the air - The plant microbiome was found to be the main influencing factor of the surrounding airborne fungal community.	(Abdelfattah et al., 2019)
	Microbial community on different grape varieties	Bacteria (16S) and fungi (ITS1)	- Grape variety played a significant role in shaping the bacterial and fungal community - Varieties were distinguished by the abundance of several key bacterial and fungal taxa	(Zhang et al., 2019)
	Effects of ozone on the fungal community	Fungi (18S)	- Ozone treatments with best sterilizing effects were identified - Ozone treatments changed the fungal community on the grapes	(Gao et al., 2020)
Kiwifruit	Microbiome changes due to postharvest disease	Metagenome	- Comparing healthy and diseased fruits a severe loss in diversity as well as significant taxonomic change was observed - Significant different functions were found between the microbiomes of the two groups	(Wu et al., 2019)
Mango	Microbiome changes with stem end rot of mango	Bacteria (16S) and fungi (ITS1)	- *Alternaria alternata* and *Lasiodiplodia theobromae* were identified as the main causal agents of stem end rot - Microbiome changes depending on storage duration, peel color and storage temperature were found	(Diskin et al., 2017)
Olive	Investigating the fungal diversity of olive	Fungi (ITS2)	- Leaves harbored a higher diversity compared to flowers and fruits - Fungal pathogens were found in all samples, however enriched in ripe fruits - Disease was correlated with reduction in the fungal diversity	(Abdelfattah et al., 2015)
	Impact of the olive fruit fly on the fungal fruit community	Fungi (ITS2)	- Fruit fly infestation reduced fungal diversity, however, did not change fungal composition	(Abdelfattah et al., 2018b)

Onion	Microbiome associated with onion bulb rot	Bacteria (16S) and fungi (ITS2)	- Significant change of bacterial and fungal taxa with disease, including diversity loss - Pathogenic taxa were also widely found in the microbiome of healthy bulbs	(Yurgel et al., 2018)
Orange	Effect of postharvest drenching on microbial communities	Bacteria (16S) and fungi (ITS1-2)	- Postharvest drenching had a severe effect on fungal communities, however, not on bacteria. - Pathogen survival during the treatment was shown	(Gomba et al., 2017)
Strawberry	Microbial composition of leaves, flowers and fruits depending on managing practice	Fungi (ITS2)	- *Botrytis* and *Cladosporium* were the most abundant genera - Different plant locations harbored significant different communities - Chemical treatment had a significant impact on the fruit and phyllosphere microbiome	(Abdelfattah et al., 2016b)
Sugar beet	Microbiome changes due to postharvest rotting	Bacteria (16S) and fungi (ITS1)	- Significant change of the microbiome and diversity loss due to postharvest disease were found - Microbial indicators were linked to sugar loss	(Kusstatscher et al., 2019a)
Watermelon	Fruit associated microbiome and involvement in carbohydrate metabolism	Bacteria (16S) and Metatranscriptome	- Cultivar differences in the microbiome were observed - Links between the host and the fruit-associated microbiome in carbohydrate metabolism were found	(Saminathan et al., 2018)

By assessing the findings of several studies in the field of postharvest microbiomes, our understanding of the microbial dynamics and their complex involvement in health and diseases become evident. Several studies have highlighted the severe changes in the microbiome due to postharvest disease. The analysis of microbial communities associated with stored onions, mango and kiwi showed clear changes in the microbiome between healthy and diseased samples. Between health states, the diversity, function and abundance of the microbial community drastically shifted when affected by storage diseases. Interestingly, the prevalence of specific fungal and bacterial taxa, associated with the occurrence of rot was also found in healthy samples (Diskin et al., 2017; Wu et al., 2019; Yurgel et al., 2018). Shen and colleagues (2018) characterized the surface fungal communities of apple fruits from the point of harvest throughout cold storage and revealed fungi species associated with postharvest deterioration on the surface of stored apples in a higher diversity (Shen et al., 2018). Moreover, some of the detected fungal species were reported to exhibit pathogenic features and have been associated with fruit decay and aflatoxin contamination. The metagenome generated from freshly harvested apples acquired from an organically managed orchard further indicated the natural occurrence of plant pathogens in healthy fruit (Angeli et al., 2019), supporting amplicon-based investigations. A related study on strawberries compared different managing practices and further highlighted the presence of pathogenic fungal taxa in the natural microbiome of fruits (Abdelfattah et al., 2016b).

In a recent approach that included large high-throughput sequencing libraries from multiple locations, a distinct correlation between microbial community compositions and the health status of sugar beets on fields and in storage was shown. Microbial diversity as well as composition of the communities substantially differed when healthy and decaying sugar beets were compared. In addition to the general observations related to microbiome responses, disease predictive taxa were identified (Kusstatscher et al., 2019b, 2019a). When the origin of microbiome changes was investigated, Abdelfattah and colleagues (2018b) showed specific microbiome changes induced by fruit flies in olives (Abdelfattah et al., 2018b). Fruit fly infection caused diversity reduction and taxonomical shifts within the community.

In addition, studies investigating a variety of fruits and vegetables highlighted the uniqueness of each plant microbiome. Studying the microbial taxa associated with different foods such as cucumbers, cilantro and mung bean sprouts, showed the unique composition of each associated microbiome as well as the impact of disease-associated microbes (Jarvis et al., 2018). Wassermann and colleagues (2017) investigated the microbiome of raw eaten *Brassica* vegetables and showed that different genetically related vegetable types carry distinct microbiomes (Wassermann et al., 2017). Postharvest microbiome studies with apples showed that the microbiome differs not only between fruit type and species but also between sampling locations on the fruit. In fact, the spatial variation in the diversity and composition of the fungal and bacterial communities within the fruit (e.g. peel, stem-end, calyx-end, and mesocarp) were identified as the main factor shaping the fruit microbiome. In addition, the influence of managing practices was shown for the fungal and the bacterial community, which can lead to the predictive understanding of diagnoses and future management. (Abdelfattah et al., 2016a; Wassermann et al., 2019b)

All these studies increase the understanding of postharvest microbial community dynamics under different treatment and storage conditions. One of the key findings so far was that storage rot is often not caused by one species but is an interplay of several different factors such as decreased microbial diversity and species pathogenicity. Mainly the observation that potential pathogens can be found in every native microbiome, leads to the conclusion that they should not be seen as contaminants. Rather, microbial shifts within the extant community induced by biotic or abiotic changes has the potential to change their prevalence and pathogenicity. Moreover, postharvest disease is not predictable by the occurrence of potential pathogenic strains within the community, it rather seems that indigenous pathogens can become increasingly prevalent following decreases in community diversity or compositional changes. Furthermore, these changes can be induced by abiotic factors and biophysiochemical interactions. Therefore, those predictions require a holistic approach including biophysiochemical parameters, the whole microbiome analysis and identification of indicator species.

5. Looking into the future: How can we further utilize our current knowledge?

The knowledge provided by postharvest microbiome studies opens a new view on fruits and vegetables – all of them form a unit with their specific microbiota. Various biotic and abiotic parameters were identified to have an impact on the fruit and vegetable microbiome. The fruit and vegetable type as well as the cultivar is crucial; however it is important to mention that the microbiome is strongly linked to the biotic as well as abiotic field conditions before harvest. Management practices, cultivar, rootstock, surrounding vegetation, soil type, health statues, etc. can have a strong impact on the microbiota found on the fruits and vegetables (Abdelfattah et al., 2016a; Vitulo et al., 2019; Wassermann et al., 2019b). With this knowledge of the natural interaction between various microorganisms, microbial communities can be shaped in the field thereby influencing fruit and vegetable quality and storability (Padmaperuma et al., 2020). Additional insights of how microbial communities are influenced by managing practice are required to trigger specific microbial changes, which have an impact on fruit and vegetable yield, quality and taste.

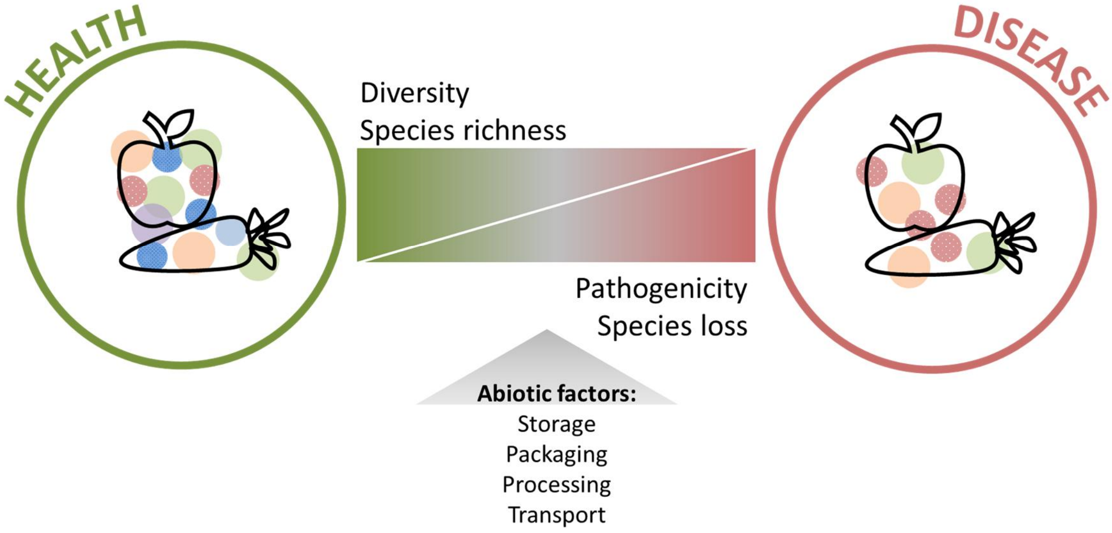

Figure 3. Schematic representation of the impact of different biotic and abiotic factors on the postharvest fruit and vegetables microbiome. Factors that are generally considered as beneficial for postharvest storability and those with negative impacts are shown. Important abiotic factors that can induce shifts in either direction are shown additionally.

Postharvest treatments and postharvest disease have a substantial impact on the microbial community. Moreover, a higher diversity was generally associated with health and defense against diseases (Fig. 3). Application of these findings to further develop detection, predictive models and potential biocontrol measures has thus far been discussed, however actionable insights are yet to be made. Kusstatscher and colleagues (2019a) have developed a new predictive tool for early detection of postharvest diseases, by focusing on pathogenic taxa, as well as those taxa which indicate an ongoing microbial shift in the community. Such applications, relying on relatively low-cost qPCR tests, could not only prevent storage loss in the future, but also predict the storability of fruits and vegetables and become an important decision-making tool in agriculture. Moreover, the knowledge about predictable microbial shifts associated with postharvest disease can be used for other targeted approaches. Due to the importance of the microbiome for plant health in the whole production chain from seed to produce, microbiome tracking is definitively a future scenario for sustainable horticulture. In comparison to current practice of seed and produce monitoring for selected plant and human pathogens, it would be of value to assess the entire microbiome. Moreover, it allows a cheap, fast and comprehensive discovery of beneficial and risk microbes. Data can be stored in a global database allowing predictive approaches and prescriptive analytics.

Biocontrol strategies can be improved by microbiome insights. Specific treatments with biocontrol agents could shift the microbial community to a healthier and stable state, which prolongs the storability and prevents further microbial shifts. Interestingly, a microbiome shift was recently described as important mode of action of biocontrol agents (Berg et al., 2017; Erlacher et al., 2014); this knowledge can be used for further selection and evaluation strategies. Biocontrol agents could moreover originate from the microbiome of diseased produce, as was successfully demonstrated by using nonpathogenic *Rhizobium rhizogenes* on stone fruit infected with crown gall (Ellis, 2017). Diseased produces can be the source of highly effective biocontrol strains, which could be applied to fruit and vegetables during the early stages of seed and fruit development to increase plant and fruit health and start the biocontrol activity at an earlier stage. Moreover, biocontrol strategies can be embedded in a multi-stage intervention, as promoted by Wenneker and Thomma (2020) for latent postharvest diseases. Currently, the registration procedure is one of the main hurdles for biocontrol products. Microbiome studies can help to understand the risk associated with the release of microorganisms for human and environment. Additionally, understanding the ecology of the biocontrol agents is essential to assess the impact on the indigenous microbiome, and beyond, on inter-linked microbiomes e.g. in humans in frame of the one health concept (Flandroy et al., 2018; Van Bruggen et al., 2019).

6. Conclusion

Postharvest food loss is a severe global problem that requires more sustainable solutions. Various physical, chemical as well as biological treatments to control food loss were developed in the past and provide the basis for integrative approaches. However, a reduction or replacement of chemical treatments is urgently necessary for environmental as well as human health (Cavicchioli et al., 2019). With the advent of novel high-throughput sequencing methods, addressing the challenges in postharvest technologies has propelled a merging of classical postharvest biocontrol with state-of-the-art bioinformatics tools. Different pioneering studies have shown the importance of these developments and provide distinct opportunities to increasingly acquire a wealth of knowledge about the close interactions of microorganisms with fruits and vegetables even after their harvest. This new knowledge has the potential to be integrated in future biological control developments and applications to comprehensively understand the interactions of biocontrol agents with the indigenous microbiome and further to direct microbiome changes.

Overall, microbiome approaches definitively provide a new key to biologically control postharvest pathogens and storability of fruits and vegetables. Summarizing the current knowledge on fruit and vegetable postharvest microbiomes, we suggest the following statements:

1. The microbiome of fruits and vegetables at harvest contain millions of specific microorganisms dominated by bacteria and fungi but comprising also archaea, algae and protists. The microbiota is cultivar-, microhabitat- and niche-specific and additionally reflects the cultivation conditions in the field. Together, fruits and vegetables form functional units (holobiont).
2. At harvest, all fruit and vegetable microbiomes harbor a large proportion of microorganisms, including beneficial microorganisms, potential plant and human pathogens as well as spoilage microorganisms.
3. After harvest, the microbiome changes significantly during the storage into a senescent plant microbiome. This is characterized by decreasing microbial diversity, and by increasing degradation and decomposition by special groups of microorganisms.
4. The microbiome of infected and healthy fruits and vegetables differs significantly. A healthy microbiome is diverse, evenly structured and forms a resilient network. In contrast, disease is characterized by severe dysbioses, which are highly variable from case to case.
5. Microbial indicators at harvest can predict postharvest loss and tools utilizing these indicators are proposed.
6. Abiotic conditions influence the postharvest microbiome as well as postharvest treatments (e.g. chemicals, biologicals, ozone). Moreover, field management strategies (organic/conventional)

are also important drivers. Microbiome tracking can be implemented to evaluate postharvest strategies and assess postharvest processes prior to disease.

7. Strategies to prolong shelf life and avoid diseases of fruits and vegetables during storage should consider the indigenous microbiome and strategies to manage it sustainably.

7. Acknowledgements

The authors gratefully thank Birgit Wassermann and Expedito Olimi (Graz) for the critical review of the article. This project has received funding from the European Union's Horizon 2020 research and innovation program under grant agreement No 817946. Gabriele Berg and Lise Korsten were further supported by the ÖAD: AUSTRIA / SOUTH AFRICA JOINT SCIENTIFIC AND TECHNOLOGICAL COOPERATION (Improving fruit and vegetable health and food safety).

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