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Review

Decoding the fruit microbiome: A climate smart strategy to manage postharvest decays

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ABSTRACT

There is an urgent necessity to shift our diets toward those rich in fruits and vegetables and at reduce postharvest losses of perishables. Approximately 20%–50% of fruits and vegetables are lost due to poor postharvest handling and pathogen infections in developing countries while it was estimated as 5%–35% in developed countries. Fresh fruits have evolved with a plethora of microorganisms having important roles in maintaining fruit health. However, little information is available on the dynamics, structure, and functional capacities of underpinning fruit microbiomes. The present review discussed environmental conditions favoring fruit-harbored antagonists and their different modes of action for suppressing postharvest pathogens in fruits. It also provides information on omics technologies such as next-generation sequencing (NGS), metaproteomics, metatranscriptomic, and metabolomics studies to characterize fruit microbiomes. With the advent of NGS and meta-omics technologies, microbiome research could bring remarkable development and understanding in succeeding biological treatments. In addition, they may provide us with a fundamental understanding of microclimate requirements for fruit microbiome establishment and microbiome shifts during post-harvest storage, which would be advantageous in developing composite biocontrol treatments for post-harvest decay management.

Keywords: Biological control; Food loss; Fruit microbiome; Meta-omics; Microclimate; Postharvest decay

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1. Introduction

The demand for fruit is increasing in parallel with population growth. The requirement for fresh produce to meet aesthetic standards in terms of color, shape, size, and variability is equally prioritized by consumers (Romanazzi et al., 2016). Despite the remarkable progress made in increasing food production globally, 27%–50% of total agriculture production (McKenzie et al., 2017) failed to reach the consumption stage either due to food losses taking place at production, postharvest, and processing stages or wasted at the end of the food supply chain (Parfitt et al., 2010). Short shelf life is the main drawback of fruit, during the producer-to-consumer market chain, and it depends on their distinct properties, environmental conditions, microbial contaminations,

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physiological disorders, mechanical damages, and post-harvest treatments (Kusumaningrum et al., 2015). Dukare et al. (2019) described fruit infections caused by several fungi such as *Aspergillus*, *Alternaria*, *Fusarium,* and *Penicillium* sp. which lead to post-harvest decay of the fruit. Such infections produced mycotoxins that might represent an imminent risk to human health. Several prevailing methods such as hot water and hot air treatment (Jin et al., 2016), proper packing methods (Osman et al., 2009), storage in controlled and modified atmospheric conditions (Yahia, 2011; Oliveira et al., 2015), irradiation methods (Dhall, 2013), edible coating (Bordoh et al., 2020), microwave treatments (Karabulut and Baykal, 2002), application of GRAS (Generally Regarded As Safe) compounds (El-Ramady et al., 2015; Ong and Ali 2015; Palou, 2018), usage of ozone and 1-Methyl cyclopropane (Paltrinieri, 2014; Ong and Ali, 2015), and exposure to pulse light to reduce postharvest losses at cold storage conditions (Wang et al., 2022), have been succeeded to minimize post-harvest losses. Fungicide application is used for controlling post-harvest diseases in fruit, especially those that are ready to be stored for an extended period or undergo distance transportation. However, restrictions have been implemented by many countries for the importation and exportation of fresh produce which exceeded the minimum percentage of the residual limit of synthetic pesticides (Palou, 2018). Therefore, it is necessary to identify eco-friendly, economical, and safe alternative methods to reduce post-harvest damages caused by microbial infections.

Microbes are innate constituents of fruit and vegetables, commonly known as epiphytes and endophytes which reside on the surface and within the host tissues respectively (Preto et al., 2017; Droby and Wisniewski, 2018). Several studies explored the taxonomic and functional behavior of most microorganisms harbored on fruits (Bartuv et al., 2023). However, they captured only a limited portion of existing microbial diversity using traditional culture-dependent approaches, never covered slow-growing and uncultured microbes in environmental samples. Therefore, it is crucial to understand how microbiota impacts each other and their different ecosystem to create a sustainable biocontrol package. Past research studies provided details on the evolutionary process approaching the metabarcoding system to investigate the hidden microbial world (Abdelfattah et al., 2018). Most of these microbial functions involved bacteria belonging to the phyla Proteobacteria, Bacteroidetes, and Firmicutes (Zarraonaindia et al., 2015), whereas, Ascomycota and Basidiomycota were prominent phyla for antagonistic fungal species (Abdelfattah et al., 2018). Nevertheless, their importance in maintaining fruit health, quality, and disease management has been identified but detailed knowledge about microbial ecology, the contribution to pathogenesis, microbe–microbe interactions, mode of action and secondary metabolites are still unexplored.

The recent developments and understanding of the microbiome provide the opportunity to explore new perspectives in the post-harvest biocontrol of fruit and vegetables. Droby and Wisniewski (2018) elucidated that studies of the epiphytic and endophytic microbiome of fruit offer a cutting-edge possibility to use in post-harvest biocontrol. The quality maintenance of perishables must be prioritized but is a difficult task. It is crucial to minimizing post-harvest losses in an eco-friendly manner. Therefore, this review concisely addresses the importance of fruit residing beneficial microbiome to maintain and extend the post-harvest life of fruit comprising their ecological requirements, mode of action and the contribution of omics technologies in the identification of fruit holobiont to create a biological package.

2. Ecological factors influencing microbiome on the phyllosphere and fruit

Many intrinsic and extrinsic factors are involved in microbial biomass production and propagation. Intrinsic factors are substrate-dependent factors such as pH, moisture content (water activity), and nutrient composition of the substrate, whereas relative humidity, oxygen, carbon dioxide concentration, and temperature are extrinsic and substrate-independent factors (Kusumaningrum et al., 2015).

According to Schlechter et al. (2019), permeation at the leaf surface allows the leaching of water and compounds to the phyllosphere, making nutrients available for microorganisms, resulting in densely colonized microbial communities such as a niche. Meanwhile, glandular trichomes can release a broad spectrum of exudates, especially polysaccharides, salts, lipids, volatile compounds, and proteins which are associated with plant–microbe interactions. The growth of intercellular bacteria is supported by a high content of carbohydrates, amino acids, and inorganic nutrients in intercellular places of plants (Bacon and Hinton, 2006). Most microorganisms can hydrolyze complex carbohydrates and convert them into simple forms to facilitate nutrient absorption and pathogenesis. Fruit, phloem sap, fruit juices, and plant exudates are the most prominent habitats of pathogenic and beneficial microorganisms (Lievens et al., 2015).

The phenomena of distribution of microorganisms on fresh fruit are equal to fast-spread weed species on freshly exposed fertile soil in plant biology. Such an ecosystem was termed an open habitat that was rich in nutrients required by microorganisms. However, these open habitats could be converted into closed habitats which contain derivatives of microbial secretions and changes of physicochemical parameters of the substrate due to the dominance of one or few microbial species; hence diversity will not be in a perpetual manner (Lievens et al., 2015). Furthermore, the microbial community was not stable due to drastic changes in stress factors in such a niche, especially in sugar-based substrates. Glushakova and Kachalkin (2017) elucidated that the seasonal dynamics manipulate the secretion of plant substrates, and they have suggested the different yeast species and their relative abundance on the surface of pear and apple fruit. A high density of bacteria is harbored on the lower surfaces of plants due to the high density of stomata and trichomes. Bacteria were capable of entering through stomata and trichomes and performing as a niche for proliferation (Beattie and Lindow, 1999). However, the ecological factors dealt with microorganisms of the phyllosphere and their shaping of the eco-evolutionary process with abiotic and biotic factors are still not clear. At present, DNA barcoding represents an advanced molecular method to identify fruit microbiomes. Meanwhile, informative metagenomic studies fostered by metabarcoding with supporting analytical software are important in identifying the whole microbiome in environmental samples.

3. Factors for post-harvest disease development

The post-harvest disease development can be analyzed using the 'Disease triangle' concept which is similar to the plant disease triangle but with a variation. The disease triangle is greatly influenced by biotic and abiotic factors such as host factors, environmental factors, and microbiome interactions (Fig. 1). Generally, virulent pathogens lead to disease development, and it is dominated by altering the beneficial microbiome. This is accelerated often due to biotic and abiotic stresses such as ripening, harvesting, mechanical injuries, way of transportation, and storage conditions. The integrated disease management, including physical, biological and chemical methods is practised for sustainable post-harvest disease.

In the host, fungal pathogens remain quiescent without any symptoms until favorable situations such as ripening and senescence (Bass et al., 2019). The physiological stress created during the harvest and packing serves as the major gateway for the pathogen entry. Further, the progression of the disease depends on the enzymatic and growth requirements of the pathogen and the physiological resistance of the fruit. Similarly, the wounded or cut surfaces are hotspots that may be minute and microscopic, but sufficient to invade and readily colonized by post-harvest pathogens. For example, the grey mold-causing pathogen *Botrytis cinerea* has a wide range of hosts, which invade in the pre-harvesting stage and exist on fruit symptomless until storage conditions (Feliziani and Romanazzi, 2016). Most of the fungal pathogens enter the latent stage when the infection happens in the early stages of the fruit harvest. As the fruit ripens, fruit gradually loses its resistance and the pathogens resume their growth. For example, *Diplodia*, *Phomopsis*, and *Alternaria* establish latent infections in the stern ends of citrus fruits because this part is vulnerable to attack when the fruits are very small (Eckert and Ratnayake, 1983).

The stored fruits are accomplished by water loss. Cold storage is the most common method of storing fruits (Mitchell and Crisosto, 1995; Mohammed et al., 2022). The lower temperature reduces the microbial activity on the fruits and also the vapor pressures between the product and the outer atmosphere delay the ripening process (Palipane and Rolle, 2008). The most critical

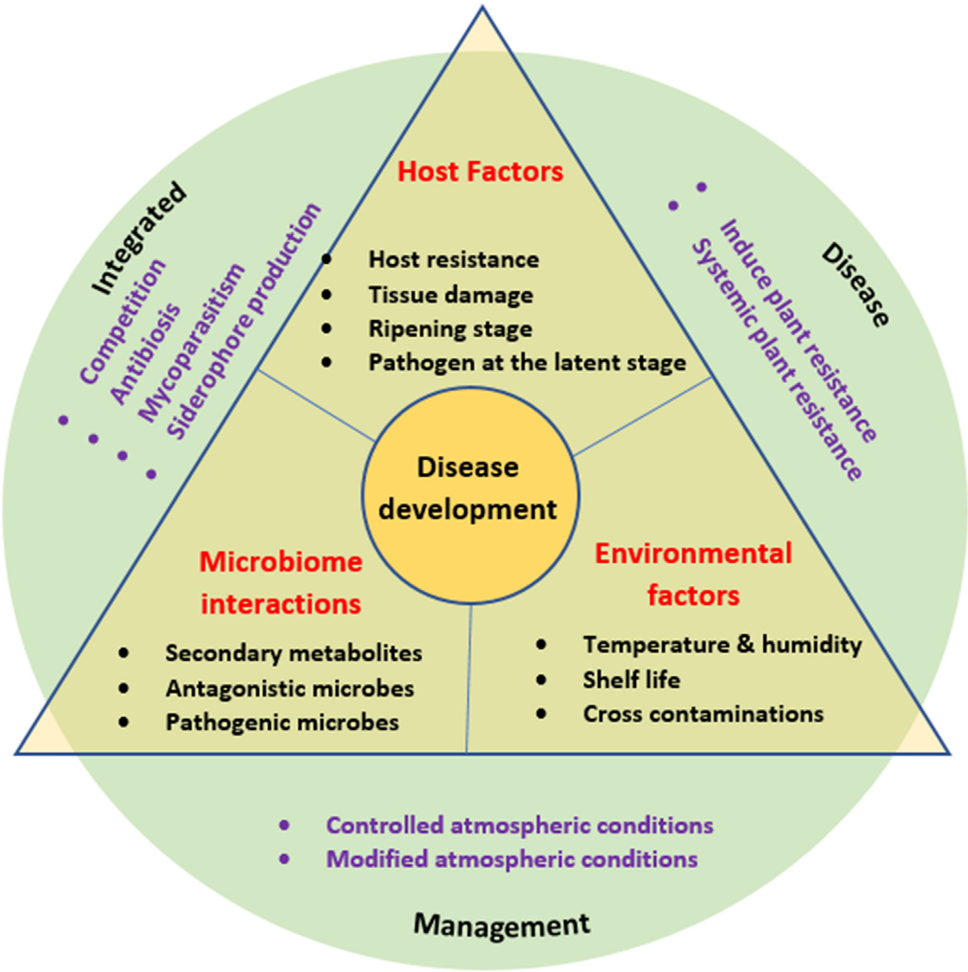

Fig. 1 Disease triangle including the three key factors that contribute towards the disease development and their interaction in developing an integrated disease management

factors in cold storage are temperature and relative humidity. Generally, cold stores are maintained in highly humid conditions to prevent water loss and maintain fruit physiology. As most fungi cease to grow under relative humidity (RH) conditions of less than 90% and a few fungi can grow at 85% RH, the RH of 90% is usually the most suitable for fruit storage (Palipane and Rolle, 2008). Cabbage also seems to be more resistant to pathogens when stored at very high humidity which delays the onset of senescence of the outer leaves (Van den Berg and Lentz, 1973). The microbiome interaction and its effect on disease development is an intrinsic and unexplored factor in postharvest science. The fungi residing in the carposphere secrete some volatile compounds thought to play an important role in forming and maintaining the ecology on the fruit surface that in turn influences postharvest disease development (Bartholomew et al., 2021). The host, pathogen and microbiome interaction involves many other compounds such as plant hormones, elicitors, cell wall degrading enzymes, quorum sensing molecules, and antimicrobial compounds. The plant hormones, signaling molecules, and volatile organic compounds (VOCs) not only play a significant role in altering the microbiome but also has a direct effect on plants (Pusztahelyi et al., 2015; Schulz-Bohm et al., 2017). Hence understanding how these compounds fluctuate in biological and environmental interactions and how the manipulation of these compounds alters the host, pathogen, and microbiome dynamics could lead to an innovation in postharvest disease management.

4. Fruit microbiome and their role in post-harvest decay management

Recently the concept of the pathobiome has been elaborated which has deviated from Koch's postulate. This concept describes a consortium of microbial species associated with a relevant host and their interaction to foster pathogenesis and disease development. Post-harvest diseases of banana crown rot, and stem end rot in avocado, papaya, pineapple, mango and apple are involved with multiple causal agents such as *Colletotrichum* sp., *Lasiodiplodia* sp. and *Neofabraea* sp. (Wenneker and Thomma, 2020). However, the pathobiome concept is a relatively new insight for researchers working with plant pathology, while culture-dependent traditional diagnosis methods cannot emphasize this conceptual shift and stimulate novel techniques for postharvest disease management. The important milestones in the plant microbiome studies have been listed in Table 1.

Harvested commodities followed the holobiont concept which describes the assembly, dynamics, composition, and functions of residing microbes (Saminathan et al., 2018). Liu and Brettell (2019) discussed that plants serve as a community or holobiont that performs as an ecological unit comprising the host and all the symbiotic microbes to enhance plant immunity through a "crying for help strategy". This strategy not only employs environment-derived microbiomes to inhibit pathogens and modulate their immune system but also can attract beneficial microbes from the environment to cope with abiotic and biotic stresses.

Inclusive reports on post-harvest biocontrol dealing with the ideas, the concept of post-harvest biocontrol, and the shortcomings in the implementation of the methods and the biocontrol products have been documented (Droby et al., 2009; Massart et al., 2015; Abdelfattah et al., 2018). Droby et al. (2009) emphasized the urgency to view post-harvest biocontrol as an integrated whole system to overcome the issues related to the efficacy and consistent performance of biocontrol products. Also, they highlighted the importance of developing new models about the biology and functional application of biocontrol agents.

Plant microbiomes consist of potentially mutualistic, commensal, and pathogenic microbes colonizing the same niches in plants. Based on behavioral patterns and microbial activity, they can be classified into several functional groups. Besides, a clear difference between plant-beneficial or pathogenic microorganisms may not always be drawn (Hentschel et al., 2000).

Recently, a new paradigm on post-harvest biocontrol dealing with fruit microbiome research has gained popularity. The general approach involves identifying microbial diversity on the fruit (non-pathogenic); the microbes possessing antagonistic potential can multiply on the fruit surface, inhibiting the pathogen establishment. Generally, competition for nutrients and space, inducing plant resistance and antimicrobial substances are main biocontrol mechanisms. However, the introduced antagonist(s) is not the only contributor to suppression; the interactions experienced by antagonists as a part of the microbial network and as a component of a biological system are neglected (Abdelfattah et al., 2016a). High-throughput sequencing approaches such as next-generation-sequencing (NGS) and meta-omics technologies revolutionized our understanding of characterizing the microbial ecology and functioning of the microbial community (Bai et al., 2015; Abdelfattah et al., 2018). In McKenzie et al. (2017), metagenomic DNA was sequenced to understand the attributes of healthy and diseased kiwifruit microbiomes. The healthy fruit was generally colonized with higher microbial diversity with distinct microbiome composition compared to diseased fruit. The fungal pathogens, namely, *Neofusicoccum parvum* and *Diplodia seriata* dominated the diseased fruit, whereas bacteria belonging to the family Methylobacteriaceae, Sphingomonadaceae, Nocardioidceae, and fungi in Pleosporaceae were prominent in healthy fruit. Furthermore, they identified genes associated with ABC transporters (defense genes), a two-component system, bacterial chemotaxis, and bacterial secretion system in healthy fruit. Several studies relied on antimicrobial compounds mainly produced by non-ribosomal peptide synthetases and polyketide synthetases (Levy et al., 2018). The high relative abundance of ABC transporter genes reflects an increased tolerance to antimicrobial compounds (Wu et al., 2018), whereas the two-component system contributes to biofilm formation in bacteria (Tiwari et al., 2017), this probably enhances the biofilm formation by bacteria on the fruit surface, minimizing the availability of microsites and increasing nutrient competition between microbes and pathogens.

On the contrary, the genes related to polycyclic aromatic hydrocarbon (PAH) degradation, amino, and nucleotide sugar metabolism are prevalent in diseased fruit. These indicated that microbes in diseased fruit are involved in energy conversion and carbohydrate digestion (Yang et al., 2014), and biodegradation of toxic compounds on fruit surfaces to use PAH as a carbon and energy source (Hamann et al., 1999). These findings depicted that infections caused by post-harvest pathogens shift the diversity of the fruit microbiome and regulate the predicted microbiome functioning.

Table 1 The important milestones in the plant microbiome studies

Important milestones	References
The recommendations for selection method of antagonistic microorganisms	Wilson et al., 1998
Holobiont theory for describing microbial assemblages and their associated hosts	Zilber-Rosenberg and Rosenberg, 2008
The utilization of amplicon and short sequencing to explore microbial community	Ursell et al., 2012
Disease management through identifying microbial assemblages of microbial networks	Poudel et al., 2016
The role of endophytic microorganisms in plant tissues to tolerate biotic and abiotic stresses	Kaul et al., 2016
NGS have potential to use as a new frontier in exploring microbes in our environment and their interactions	Berg et al., 2016
Significant differences of apple microbiome were observed in between organic and conventional practices	Abdelfattah et al., 2016a
Olive leaves are the niche of available higher microbiome than flowers and fruits while, ripen fruits harbored high fungal diversity and it may change with infection of disease	Abdelfattah et al., 2016b
The most common taxa of grapes were found as Bacillales, Pseudomonadales, Lactobacillales and Enterobacteriales	Mezzasalma et al., 2017
Microbiome in mango fruits are influenced by storage duration, temperature and peel colour	Diskin et al., 2017
Significantly higher microbial diversity in apple was reported in cold stored fruits with taxonomic changes than before storage	Shen et al., 2018
Metagenomic technologies like NGS were used to characterize the diversity and function of microbial networks with host tissues	Abdelfattah et al., 2018
Both significantly higher pathogenic and antagonistic microbiome presence in natural environment	Angeli et al., 2019
Significant taxonomic changes and different functions were reported in healthy and diseased Kiwi fruits	Wu et al., 2019
Bacterial and fungal diversity changed with different varieties of grapes	Zhang et al., 2019
Berries harboured less microbiome with comparing to bark and significant taxonomic changes occur with management practices and the locations in grapes cultivations	Vitulo et al., 2019
Ozone treatment has significant influence on the microbiome on grapes	Cravero et al., 2016

Different yeast species inhibit post-harvest pathogens of fruit crops with a different mode of actions such as competition for nutrients and space, parasitism of the pathogen, secretion of antifungal compounds, induction of host resistance, biofilm formation, and involvement of reactive oxygen species (Matrose et al., 2020). The possibility of using yeast to control post-harvest pathogens is more interesting than bacteria and other antagonistic fungi (Ferraz et al., 2019). As a pivotal mode of action of most abundant yeast species, mycoparasitism was described as glucans consisting of fungal cell walls reacting with yeast secreted *ß* − (1–3) glucanase and forming a strong attachment through a lectin-like interaction. Those reactions were cumulatively affected by the lysis of pathogenic fungal cells (Wisniewski and Wilson, 1992). Exceptionally, some yeast species such as *Pichia membranefaciens* and *Cryptococcus albidus* firmly attach to the hyphae of *Monilinia fructicola*, *Penicillium expansum,* and *Rhizopus stolonifer,* which caused post-harvest deterioration of apple and nectarine (Chan and Tian, 2005). Another effective mechanism has been elucidated as antibiosis, which was performed by epiphytic yeast *Aureobasidium pullulans* secreting antimicrobial compounds such as 2-methyl-1-butanol, 3-methyl -1-butanol, 2-phenethyl alcohol, and 2-methyl-1-propanol and inhibit the growth of postharvest pathogens (Di Francesco et al., 2015).

Candida oleophila and *M. fructicola* produce high levels of superoxide anions around the surface wounds of fruit. ROS produced by yeasts reacts with host-producing ROS resulting in an oxidative burst in the wounded surface and induction of host resistance response (Droby et al., 2009). ROS serves as a signaling component by mediating gene activation such as MAPK cascades, whereas MAPK leads to phosphorylation of transcription factors mediating for expression of defense response genes. Exceptionally ROS produce phytoalexins and secondary metabolites that can arrest invading pathogens (Torres, 2010) or generate physical barriers by oxidative cross-linking precursors to form lignin and suberin polymers (Hückelhoven, 2007). Simultaneously down-regulating SODs (superoxide dismutases), CATs (catalases), and POD contributed to increasing ROS accumulation on wounded tissues and activation of host defense genes. However, the response of the same antagonist applied for some fruit species in different situations relied upon different mechanisms; for example, *Pichia membrnefaciens* treated sweet cherry enhanced POD activity while inhibiting SOD and CAT activities, but it showed an increment of SOD activity while decreasing CAT activity with infection of *P. expansum* (Chan and Tian, 2005). In contrast, Xu et al. (2008) elucidated that *Monilinia fructicola* enhanced the activities and expression of CAT and POD in peach fruit. However, little is known about the molecular basis underlying the induction of host defenses and signaling networks of the antagonists. Meanwhile, peroxidase (POD), superoxide dismutase (SOD), and catalase (CAT) were down-regulated in grapefruit peel treated by *M. fructicola*. It was elaborated that yeast-treated surface wounds contain higher levels of hydrogen peroxide, superoxide anion, and hydroxyl radical production and was correlated with disease suppression Hershkovitz et al. (2012). Macarisin et al.

(2010) reported that *Metchnikowia fructicola* strain 277 and *C. oleophila* strain 182 produce a greater level of superoxide anions even on nutrient-rich or poor fruit surfaces of apple and citrus, these superoxide anions correlated with an increment of hydrogen peroxide around the wounds and perform against brown rot pathogens. Furthermore, they described that existing living yeast cells of *M. fructicola* on fruit surfaces were tolerant to host ROS, and it was a specific intrinsic characteristic of efficient yeast antagonists. Several studies using *A. pullulans*, a yeast like fungus has been succeeded to control postharvest diseases of broad-spectrum fruits such as avocado, citrus, and peach. *A. pullulans* S-2 effectively controlled the postharvest diseases of tomato such as gray mold and black rot disease (Shi et al., 2022a). Moreover, high-throughput sequencing technology witnessed the interaction between *A. pullulans* S-2 and indigenous microorganisms on tomato surface. The high abundance of *Aureobasidium* genus influences tomato microbial diversity and community composition (Shi et al., 2022a). Further, preharvest application of *A. pullulans* S-2 remodeled the fungal and bacterial microbiome of tomato surface (Shi et al., 2022b). The functions and the mechanism of these potentially beneficial taxa need to be explored in depth. Such findings could be helpful for directional regulation of the microbial composition to achieve sustainable disease control.

Antagonistic biocontrol agents suppress plant diseases with diverse modes of action and possibilities to combine with other control measures (Romero et al., 2007). While bacteria (*Bacillus* spp), inhibit pathogenic fungal growth through competition and by producing antimicrobial compounds followed (Ferraz et al., 2019). *Bacillus* spp. and *Pseudomonas* spp. contributed to the well-being of fruit by a different mode of action (Ferraz et al., 2019) such as producing both peptide and non-peptide-originated compounds and cyclic lipopeptides such as fengysin, iturin, and surfactin which can suppress plant pathogens. Ntushelo et al. (2019) mentioned that *Bacillus* produced volatile metabolites and played a pivotal role in activating plant defense mechanisms by triggering and inducing systemic resistance against pathogens. Furthermore, they described *Bacillus* species comprised of fengysin family members have shown specific properties, such as ornithine contain peptide portion act against especially filamentous fungi. Surfactin, a heptapeptide containing β-hydroxy fatty acid, is a potent biosurfactant studied extensively among Bacillus species. It exhibits strong antifungal activity and synergizes with iturin A, forming stable biofilms to suppress pathogens. Beneficial bacteria scavenge iron by forming siderophores and modulating the plant immune system to inhibit pathogenic microbial proliferation. A high number of genes of endophytes in plants are responsible for siderophore production and biosynthesis of proteins by uptaking and storing iron (Sessitsch et al., 2012; Mendes et al., 2014).

Similarly, *Pseudomonas* antagonists show antibiosis by producing low molecular weighed volatile compounds, which directly affect phytopathogen growth. For example, *Pseudomonas cepacia-produced* pyrrolnitrin has the potential to perform as an antifungal peptide compound. They contribute to forming a biofilm and create competition with pathogenic microorganisms (Saul et al., 2019). Exceptionally *Pseudomonas* species can produce amphisin and viscosinas antimicrobial compounds (Raaijmakers et al., 2010; Falardeau et al., 2013). Zin and Badaluddin (2020) elaborated that *Trichoderma harzianum* and *Trichoderma viride* have different modes of action such as competition, antibiotic production, secretion of hydrolytic enzymes and mycoparasitism against a wide range of postharvest pathogens.

For a few decades, considerable achievements in microbial products for postharvest disease management have been developed. For example, several biocontrol strains such as BioSafeR (Jet Harvest Solutions, Longwood, FL, USA) based on *Pseudomonas syringae* for controlling potato and sweet potato diseases, SerenadeR (Bayer, Leverkusen, Germany) based on *B.subtilis* against diseases of stone and pome fruits, tomato and strawberry, PantovitalR (Domca, Granada, Spain) using *P. agglomerans* and Amylo-XR (Biogard CBC, Grassobbio, Italy) based on *Botrytis amyloliquifaciens* used for controlling fruit diseases have been developed. In addition, several yeast-based products such as CandifruitR (IRTA, Leida, Spain) using *Candida sake*; NexyR (BioNext, Paris, France) based on *Candida oleophilia*, BoniProtectR (Bioferm, Tulln, Austria) based on *A. pullulans* and Shemer R (Koppert, Berkel en Rodenrijs, The Netherlands) containing *Metschnikowia fructicola* have been developed (Kusstatscher et al., 2020).

However, these commercialized biocontrol agents are still struggling with limited markets due to their inconsistency, short lifetime, and low adaptability to harsh environmental conditions. Otherwise, most commercialized biocontrol products have to be applied as dipping or drenching of commodities after harvesting, but they are not properly implemented and they require improvements such as preparing formulations with high efficiency and wide usage for different fruit species (Wisniewski et al., 2016). In addition, Wenneker and Thomma (2020) illustrated that no biocontrol product is available for latent infection of fruits and prevailing biocontrol agents cope with their antagonistic activities against a relevant pathogen. However, Ippolito and Nigro (2000) stated that commercial bioproducts should be assessed in field conditions against latent infections, it is also arguable because of the lack of knowledge about the epidemiology of pathogens, thus researchers are unable to identify the precise time to apply them. Hence, it is imperative to conduct advanced studies such as metagenomics, proteomics, meta transcriptomic and metabolomics to determine the shapes and biological functions of fruit microbiomes while culture-based and metabarcoding methods are pioneered to investigate them taxonomically.

5. Application and translation of omic data: a paradigm to underpin the microbial interaction during postharvest

Research studies have provided details of the mechanisms underlying the infection of fruits by postharvest pathogens and host responses to develop decay control strategies. New omics-based technologies are employed to understand the intrinsic networks between the virulence factors, secondary metabolites and metabolic pathways. Infection and colonization of postharvest pathogens in fruits rely on virulence factors such as cell wall degrading enzymes secreted by pathogens, proteinaceous effectors and diverse phytotoxic compounds (Li et al., 2020a). Infection and colonization of postharvest pathogens in fruits is an intricate process containing multiple components like cell wall degrading enzymes, hormones, VOCs, and signaling molecules (Bartholomew et al., 2021).

As an example, cell wall degrading enzymes are key virulence factors in necrotrophic pathogens while cellobiohydrolase (BcCBH) and β-endoglucanase (BcEG) were key virulence factors of *B. cinerea* (Li et al., 2020b). Similarly, two cutinase encoding genes such as AaCut3 and AaCut7 were identified in *Alternaria alternata* which was involved in a synergistic effect in the pathogenicity of *A. alternata* in citrus leaves (Ma et al., 2019). Vilanova et al. (2021) identified *Monilina fructicola* causing brown rot in stone fruits by transcriptomic analysis. About 134 putative protein effectors were identified and out of them, two effectors (MFRU_002g05260 and MFRU_030g00580) were involved in the necrosis-inducing activity in stone fruits. Similarly, the *Colletotrichum* genus conserved CEC3 co-effector was revealed in *Nicotiana benthamiana* (Tsushima et al., 2021).

Recent research have focused on phytotoxic metabolites produced by pathogens such as *B. cinerea*, *A. alternata*, and *Penicillium* spp. They revealed those pathogenic fungi-producing metabolites such as botryoidal, AM-toxin and organic acid contribute to the best colonization of host tissues (Pontes et al., 2020). *Aspergillus* spp. produces a mycotoxin that belongs to the aflatoxin group. Lately, with the development of omics technologies, researchers identified 27 genes involved in aflatoxin production regulated by AflR and AflS (Scott and Amich, 2022) and suggest that although environmental factors also modulate gene expression, aflatoxin itself was considered to be the causal agent of diseases (Yuan et al., 2018). According to our understanding, metabolomic provides deeper insight into virulence factors of such fungi and infections on hosts, and how they alleviate those pathogens. The production of virulence factors of pathogens is underlying some molecular mechanisms and is controlled by a complex network, but detailed information is still incomplete. Generally, ambient pH is the most important environmental factor regarding the pathogenesis of fungal pathogens. Pac C has been reported as the pH-responsive global transcription factor, mostly involved in the pathogenesis of postharvest fungal pathogens (Rascle et al., 2018; Li et al., 2020a). It regulates the expression of multiple genes to secrete cell wall-degrading enzymes, proteases, and transporters. BcJar1 is a histone H3K4 demethylase in *B. cinerea* and has a pivotal role in fungal development and pathogenesis, while it regulates gene expression for ROS production, stress response, carbohydrate transmembrane transport, and secondary metabolism (Hou et al., 2020).

Comprehensive information on both infection strategies and defense mechanisms is equally essential to the understanding of plant–pathogen interactions (Dodds and Rathjen, 2010). Cre A is well recognized global carbon regulator, which induces the gene expression for virulence factors in fungal pathogens. But mutant

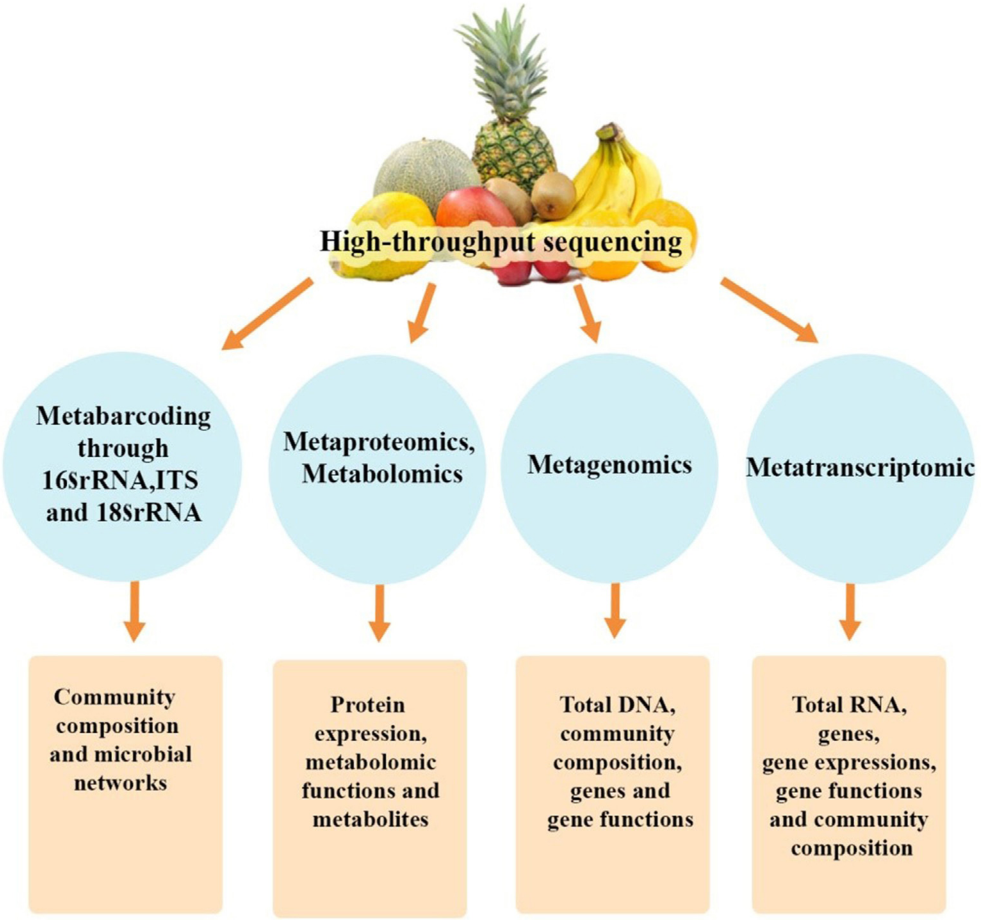

Fig. 2 A schematic diagram of high-throughput sequencing methods to validate post-harvest microbiome in fruit

Cre A has been characterized as an important regulator to induce gene expression in the deprivation of nutrients from the colonizing pathogen through C/N metabolism and transportation. The recognition of the Cre A knockout mutant of *P.expansum* resulted in avirulent apple fruits and it provides new insight into the disease pathway against *P. expansum* (Tannous et al., 2020). High throughput sequencing methods such as dual RNAs sequence and small RNAs sequence may cope to develop RNA fungicides against postharvest pathogens in the future.

16srRNA gene and Internal Transcribed Spacer of rRNA genomic sequencing methods are usually explicated to investigate the microbial community. The protocol is directly amplified from extracted metagenomic DNA from culturable organisms. Details about their functioning and ecological factors and any recognition of unculturable microorganisms are negligible (Regalado et al., 2020).

The PCR-based well-known methods have limitations such as variability in PCR amplification efficiency, chimaera formation between multiple parental sequences, and potencies of primer-biased PCR (Hao et al., 2011; Brooks et al., 2015). Hao and Chen (2012) suggested that the explosion of sequencing data on environmental samples has not yielded reliable insight through targeted 16srRNA gene sequences. Hence, Brooks et al. (2015) revealed that the observed community composition relied on DNA extraction and PCR amplification. These results have been based on the protocol, which hampered a valid conclusion about the quantities of microorganisms.

Tian et al. (2017) explored the philosopheric microbial communities through different microorganism collection methods. Abdelfattah et al. (2016a) investigated the composition of fungal communities associated with different parts of strawberries by ITS amplicon sequencing and diversity analysis. Different parts of strawberries displayed diverse fungal communities, but the sequence of the ITS amplicon method only reported two genera *Botrytis* and *Cladosporium*. No evidence has been distinguished on microbiota regarding their functions in environments through 16srRNA or Internal Transcribed Spacer gene sequencing methods. However, the impacts of parameters such as cultivar, rootstock, surrounding vegetation, health status, soil types, management practices and climatic changes have been strongly linked with the composition of the microbiome of harvested fruits.

Microarrays are distinct molecular methods to validate the microbial population, especially in terms of environmental samples. As an advent of Dot plot, Southern Blot, qPCR is popularized as microarrays but has some limitations. Some methods were time-consuming and some needed high-cost consumables. These limitations were recovered with the next-generation sequencing, whereas the high capacity of multiplexing gave information about the microbiome of environmental samples (Everett et al., 2010). Omic studies are hot topics regarding microbiome research, a genome-based and high-throughput technique that relied on the relationship between plants and microbiota. Proper sampling and appropriate preparatory steps strongly affected in molecular analysis of plant holobiont (Lucaciu et al., 2019). New approaches to tracking changes in microbiome studies provide deep insights into understanding taxonomical and functional behaviour (Abdelfattah et al., 2016a). The most popular high-throughput technology, metabarcoding through 16srRNA, ITS, and 18srRNA, elaborates only on microbial community composition and microbial networks, but no taxonomic details could be obtained. Interestingly, currently developed metagenomics, metabolomics, and metatranscriptomic high-throughput sequencing techniques provide taxonomic details such as community composition, metabolomic functions, and gene expression (Kusstatscher et al., 2020).

Metagenomics coupled with transcriptomics or proteomics allowed the identification of functional capacity and biochemical activities of the microbial population. They conducted next-generation sequencing (NGS) with two principal approaches, such as single nucleotide polymorphism analysis (SNP) and genomic multi-locus sequence typing (MLST), to obtain concordant results (Jagadeesan et al., 2019).

Metagenomics allows high-resolution genomic analysis of environmental samples, even unculturable microorganisms, microenvironmental factors, and their correlation (Ghosh et al., 2019). The omic studies, including metagenomics, metatranscriptomic, metabolomic, and NGS, open a new vision that could perform as a platform to discover a novel microbial world and explore a new environment on fruit surfaces. This could be used for distinguishing detailed information on fruit microbiomes to manage postharvest diseases through naturally available microbiota. As evident metabarcoding provided information on the epidemiology of *Ramularia mali* which is causing lenticel rot a postharvest disease in the apple as a prediction before visualizing the symptoms (Garello et al., 2023). Although intrinsic microbial communities respond to the well-being of their hosts in stress conditions, the potential of plant microbiome is still underestimated, especially in the postharvest stage of many fruits. In such cases, multi-omic techniques contribute to develop more efficient and robust microbiome-based solutions in the postharvest stage of fruits (Wassermann et al., 2022). The schematic diagram concisely elaborates on the high-throughput sequencing methods to identify post-harvest microbiomes in fruit (Fig. 2).

There are knowledge gaps in the tritrophic interactions, and omic data could bridge the gap. The omic data played an important role in identifying plant disease and postharvest biocontrol agents, such as *Lysobacter* spp. and *P. syringae,* respectively. The latter is formulated as a product sold under the name BioSave^{R}100 and BioSave^{R}110 (Bartholomew et al., 2021). Biosave combats various postharvest pathogens like *P. expansum*, *B. cinerea*, *Penicillium digitatum*, *Penicillium italicum*, *Mucor piriformis*, and *Geotrichum candidum*, and a few other mycotoxins (Bartholomew et al., 2021).

6. Conclusions

Generally, biological controls for postharvest spoilage relied on single antagonists. It could be anticipated that augmenting the efficacy of biocontrol agents for postharvest diseases will utilize a consortium of different bioagents. In this review, we summarized the ecological and microclimatic factors shaping the plant/fruit microbiome and how these factors could alter the dominance of the beneficial microbiome over pathogenic microbes. Moreover, the fundamental basis underlying the protective effect of microbial antagonists against postharvest decay, and the development and application of microbial consortia were also discussed.

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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