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Microbiome-based biotechnology for reducing food loss post harvest

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Microbiomes have an immense potential to enhance plant resilience to various biotic and abiotic stresses. However, intrinsic microbial communities respond to changes in their host's physiology and environment during plant's life cycle. The potential of the inherent plant microbiome has been neglected for a long time, especially for the postharvest period. Currently, close to 50% of all produced fruits and vegetables are lost either during production or storage. Biological control of spoilage and storage diseases is still lacking sufficiency. Today, novel multiomics technologies allow us to study the microbiome and its responses on a community level, which will help to advance current classic approaches and develop more effective and robust microbiome-based solutions for fruit and vegetable storability, quality, and safety.

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Introduction

Many discoveries of microorganisms and their entire community, the microbiome, changed the view on life in general [12]. Each higher organism, including plants, is now considered as a holobiont, which describes a mutually dependent and coevolved biocoenosis of a eukaryotic host and its microbiome [64]. Nowadays, next-generation sequencing technologies such as metagenomics, metaproteomics, metabolomics are the drivers of microbiome research. Together with advanced cultivation and microscopy technologies, those technologies allow us not only to capture the microbiota's general presence but also the potential and actual functions they perform in a certain environment and at a certain timepoint. However, microbiomes are highly specific and complex, consisting of hundreds of species of different microbial lineages, including bacteria, archaea, fungi, and protists [12]. Moreover, especially in interconnected, open environments, the microbiome's dynamics are poorly constrained and the responses to environmental changes, biotic or abiotic, are still hardly predictable.

Compared with open environments, postharvest storage facilities represent rather-controlled systems, and one would assume that here, pathogens and pests are easier to combat. However, spoilage and storage rot caused by pathogens is still a major global problem in addition to postharvest food loss due to technical constraints in harvesting and handling, and undesired sprouting or loss of sugar and water content. Even though packaging technologies as well as physical and chemical control treatments are being optimized continuously, the relative amount of postharvest food loss has not decreased much during the past 40 years [14,51]. Currently, close to 50% of all produced fruits and vegetables are lost either during production or in the postharvest period [22].

In addition to the limited efficiency of current control approaches, huge amounts of chemicals applied in the postharvest sector, such as growth regulators and pesticides, can exert negative impacts on the environment and human health [39]. Moreover, the plant microbiome has already been negatively affected by all these anthropogenic activities [10]. Finally, the energy consumption in storage facilities is particularly high, which is not only costly, but simply no longer sustainable in view of planetary health issues and climate change. Using the microbiome is becoming a promising aspect for biotechnological applications, from both ecologic and economic perspectives [31]. Microbial applications do not require extreme conditions or energy intake, the products are environmentally degradable, and the functional potential for plant health, quality, and resilience to diverse stresses is almost infinite [16].

In the following, we review current microbiome-based knowledge and practices and their limitations, present innovative ideas, for example, prediction of produce storability already in the field, and discuss the potential of microbiome modulation for sustainability along the food chain. The indigenous plant microbiome will play a decisive role for any effective future application. Thus, we start our conceptional review at how the plant microbiome is being initially assembled.

The plant microbiome is a highly dynamic community subjected to various assembly strategies

Understanding the plant microbiome relies heavily on considering the plant and its microbiome as a continuous line of temporally and spatially dynamic communities of which the propagative material, that is, seed or vegetative parts, represents the starting point. The propagative material harbors a subset of the plant microbiome that is transmitted to the offspring, referred to as the inherited microbiome [56,65]. Environmental microorganisms that colonize the plant subsequently are termed horizontally acquired microorganisms that represent a substantial fraction of the plant microbiome [15]. After the dynamic processes of microbial migration and assembly, rhizosphere, phyllosphere, and especially plant endosphere patterns of healthy plants remain surprisingly stable. Yet, the community composition varies significantly between those plant compartments, which was recently summarized by Trivedi et al. [62]. In terms of microbial diversity and abundance, a general decline from rhizosphere to phyllosphere and endosphere can be stated [62].

The phyllosphere encompasses all aboveground organs, including leaves and fruits. These tissues have inherently major differences in their nutrient composition, morphology, and anatomy [26], which results in significant variations in the associated microbial diversity and community composition. Variation in the microbiome extends to even different fruit compartments. The core of apple fruits was reported to contain the highest bacterial abundance but lowest bacterial diversity ($\sim 10^8$ bacteria, Shannon H′: ~4), whereas peel and pulp showed the reverse pattern ($\sim 10^4$ bacteria, Shannon H′: ~6.5) [4,70]. Those communities are furthermore influenced by the plant genotype, the geographical location, including soil conditions, the management practice, as well as the plant's age [1,46,70]. Yet, despite these variations, few members of the apple microbiome can be considered as the core. The fungal genera *Aureobasidium*, *Cladosporium*, *Alternaria*, *Filobasidium*, *Vishniacozyma*, and *Sporobolomyces* and the bacterial genera *Sphingomonas* and *Methylobacterium* were found to be present in 75% of the apples collected from 21 locations in eight countries across the world [1].

After harvest, fruit and vegetable microbiomes can be significantly affected by storage treatments and time. In apple fruits, for instance, species richness and abundance were found to remain relatively stable, whereas the community composition changed drastically [3,71]. Here, especially an increase of Enterobacteriales abundance was repeatedly observed [3,69,70]. In addition, storage and transport were shown to provoke a shift in the antimicrobial-resistance gene (ARG) composition of apple fruits toward higher ARG diversity [71]. Specifically, ARG counts associated with multidrug, quinolone, rifampicin, Fosfomycin, and aminoglycoside resistance increased after storage, independent of the cultivar. While a versatile resistome is a regular feature of plant microbiomes [49], complex food systems, including intercontinental transport, might further the transmission of ARGs globally. The surveillance of postharvest-resistance emergence was highlighted as critically important in view of One and Planetary health concepts [28].

Finally, the microbiome composition of postharvest fruits and leaves depends largely on their health status. Diseased fruits or leaves tend to have a lower microbial diversity than healthy ones, which is mainly due to higher abundance of pathogenic fungi or bacteria in the affected tissues, resulting in both reduction in species richness and community evenness [36,69,74,76]. The development of novel and robust disease-control strategies relies on understanding the dynamics of disease emergence on the level of plant-microbiome interaction, in the field, and post harvest.

Current postharvest biocontrol approaches and limitations

Postharvest biocontrol is being investigated for more than 30 years, and several products have been commercialized. A summary of products, based on bacteria and fungi as control agents, and their target pathogens, was published recently [35]. The mode of action of a bacterial or fungal biological control agent (BCA) is often diverse and includes competition for nutrients and space, mycoparasitism, the formation of biofilms that inhibit growth of pathogens, competition for iron and other elements, the production of ‘killer toxins’, hydrolytic enzymes, reactive oxygen species, mycotoxins, and antimicrobial substances, including volatile organic compounds [23,41,58,66]. In addition, most of the BCAs induce the host plant's systemic resistance by either enhancing defensive enzyme activity or by upregulating pathogenesis-related gene expression [30,68].

Previous research that decoded these modes of action was fundamental for current postharvest biocontrol, and nowadays, besides applications of single strains, microbial consortia, or microbial volatile organic compounds (mVOCs), other concepts integrate bio-safe-considered chemical compounds or physical treatments to enhance the performance of BCAs. The combination with, for example, $CaCl_2$, methyl jasmonate, or UV protectants as well as heat treatments or gamma radiation were proven to be successful in addressing consistency for pathogen loads, temperature fluctuations, and sanitation processes at different storage facilities [27,37,40,47,48,54,63,69,77]. Bacteriophages for biopreservation and food safety represent a promising approach as well. Especially if a high target specificity is given, phages exert low risks for human consumption and the environment [75]. Phage endolysins, the enzymes that are responsible for the final lysis step of bacteria, have a future potential because they are even safer, more specific, and more efficient than whole-phage application [55].

Yet, microbial treatments at storage still lack broad applications. The reasons are competition to existing chemicals, the difficulties to implement them into current postharvest processes, lack of industry and consumer acceptance, hurdles for registration, and problems in formulation [73]. Additionally, most of biocontrol products showed inconsistent effects, which is, for instance, due to their confined host range and the dependency on specific conditions for successful disease control. But also the interaction between the BCA-introduced and the indigenous plant microbiome as well as the dynamics and evolution of those communities in response to plant's physiological state and to abiotic factors play a critical role [19,33,59].

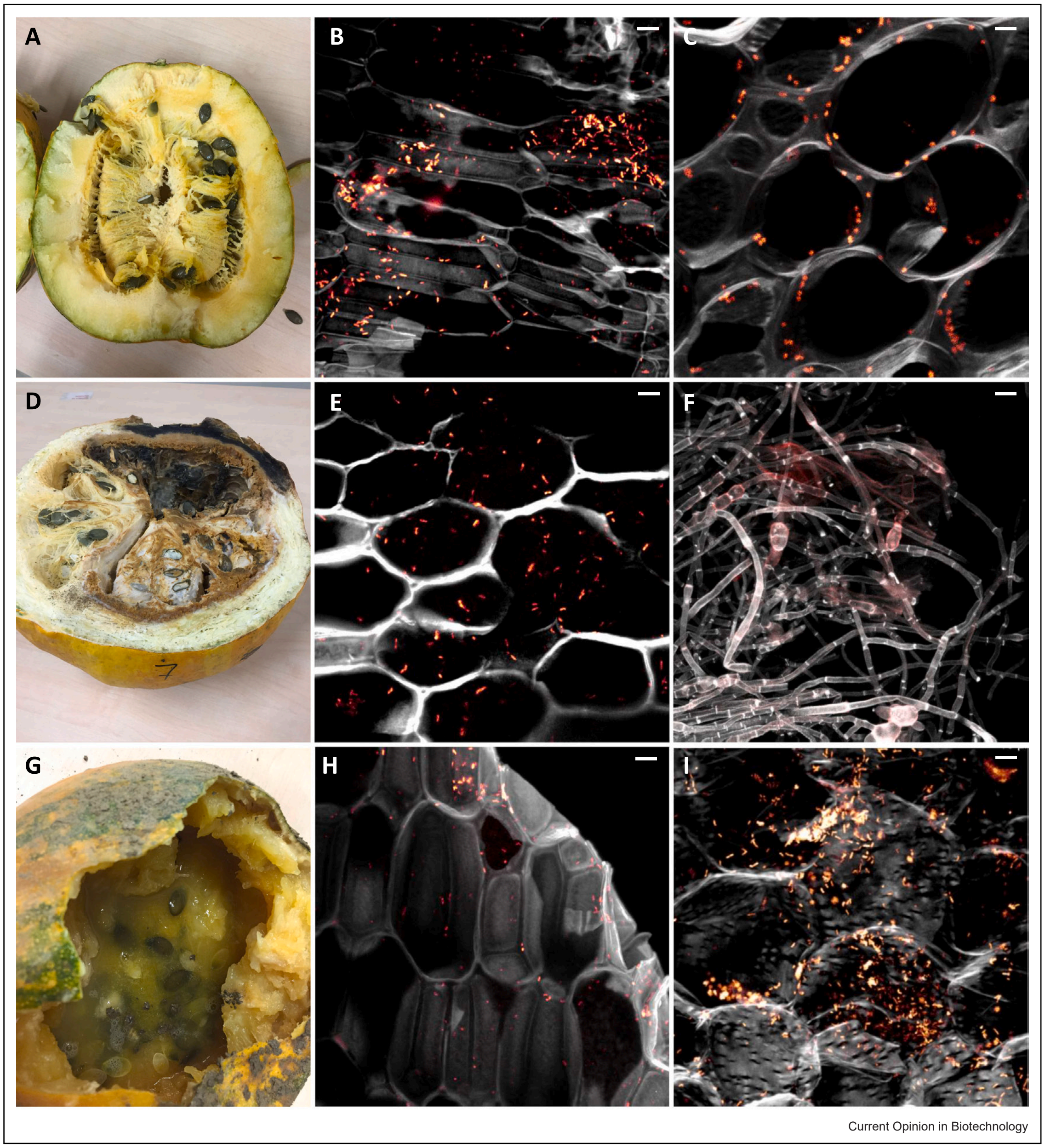
The development of a postharvest disease is complex, and infestation can occur at different stages of a plant's life cycle. Microbial pathogens are primarily field diseases where symptoms accelerate after harvest on infected fruits (e.g. bacterial soft rots and fungal gray molds) but they can also infect the fruit after harvest, for example, through wounded tissues. Overall, the condition in which fresh produce including its microbiota arrives at the storage facility is decisive for fruit and vegetable health, quality, and safety at later storage timepoints [1,50]. Already in the field, next-generation sequencing-based measures can be taken to predict produce storability, for example, by identifying microbial-indicator taxa for health and disease [36].

Microbial indicators for health and disease: can we predict and improve the storability of produce?

Predicting the storability of plant-based products would not only facilitate the reduction of economic losses worldwide but also reduce agricultural waste and land use in general. Targeted microbiome approaches enable the identification of indicator taxa that can be later quantified, for example, by molecular approaches (e.g. qPCR), as a sophisticated proxy for the storability of harvested produce [36]. Such indicator taxa must not only include typical postharvest pathogens but can on the contrary also include certain taxa that are indicative for enhanced storability as previously shown for sugar beets [36]. The potential of preharvest microbiome profiling was also highlighted by Ref. [25]. Based on the pathosystem tomato–*Ralstonia solanacearum*, the authors showed that the binary outcome of health and disease of plant individuals growing under homogeneous conditions and in the presence of a soilborne pathogen, results from an early and rapid divergence of the rhizosphere microbiome. Those differences were found to significantly predict health and disease even before disease outbreak. In addition, bacteria isolated from persistent healthy plants reduced disease severity by up to 100% after being reintroduced into the pathosystem [25]. Such findings provide the basis for the implementation of targeted postharvest biotechnological treatments that may be coupled with preharvest microbiome diagnostics for plant diseases, analogous to precision agriculture, which mainly relies on artificial intelligence [78].

Current research is often focused on the identification of pathobionts in host-associated microbiota. Pathobionts are microorganisms that can occur under specific genetic or environmental conditions as a harmless symbiont in their respective hosts [34]. However, when these conditions change, the same microorganisms can cause specific diseases in their host. Recent studies that analyzed postharvest losses on microbiome level, found that several of the prominent storage pathogens, such as *Penicillium* spp., *Neofabrea* spp., *Aspergillus* spp., *Botrytis* spp., *Sclerotinia* spp., *Erwinia* spp., and *Agrobacterium* spp., are usually present in natural environments as well and can be even found in healthy fruits after storage [3,7,24,32,36,53,69,76]. In natural and healthy environments, the functionally highly diverse microbiota can, in case of disturbance (e.g. pathogen attack), intervene and take supportive action. In contrast, during storage, certain abiotic parameters might favor the growth of specific microbes, and at the same time, downregulate the native functions of the indigenous microbiome, which is consequentially not able to compensate the caused dysbiosis. Figure 1 shows microbial colonization of seeds and fruit pulp of healthy and diseased pumpkins. In the included example, the pulp of diseased pumpkins clearly shows high abundances of *Fusarium* hyphae (Figure 1f) and *Erwinia amylovora* cells (Figure 1i). In contrast, the microbiota of the seeds apparently remained unchanged under all health conditions (Figure 1b, e, and h). Such observations support the idea that all plant tissues, including seeds, are natively colonized by diverse microbial communities and it is not the general presence of a certain potentially pathogenic microbial species, but rather a shift in the microbiome, and especially a significant decrease in microbial diversity and evenness, that affects the storability of fresh produce [11,20].

Figure 1



Microbial colonization of healthy and diseased Styrian oilseed pumpkin seeds and pulp. Panel A shows a healthy bisected pumpkin and panels B and C visualize fluorescent *in situ* hybridization–confocal laser scanning micrographs of the respective seed endosphere **(b)** and pulp **(c)**. Panels D, E, and F visualize a pumpkin and its seed and pulp affected by *Fusarium*. Please note that in seeds **(e)**, only bacteria were observed, whereas no intact plant cells and only fungal hyphae were detected in the pulp **(f)**. Panels G, H, and I visualize the whole fruit, seed endosphere, and pulp of a pumpkin affected by *Erwinia amylovora*. Here, seeds **(h)** showed regular bacterial colonization, while, compared with healthy tissues, higher numbers of bacterial cells were observed in the pulp **(i)**. Scale bars indicate 10 μm.

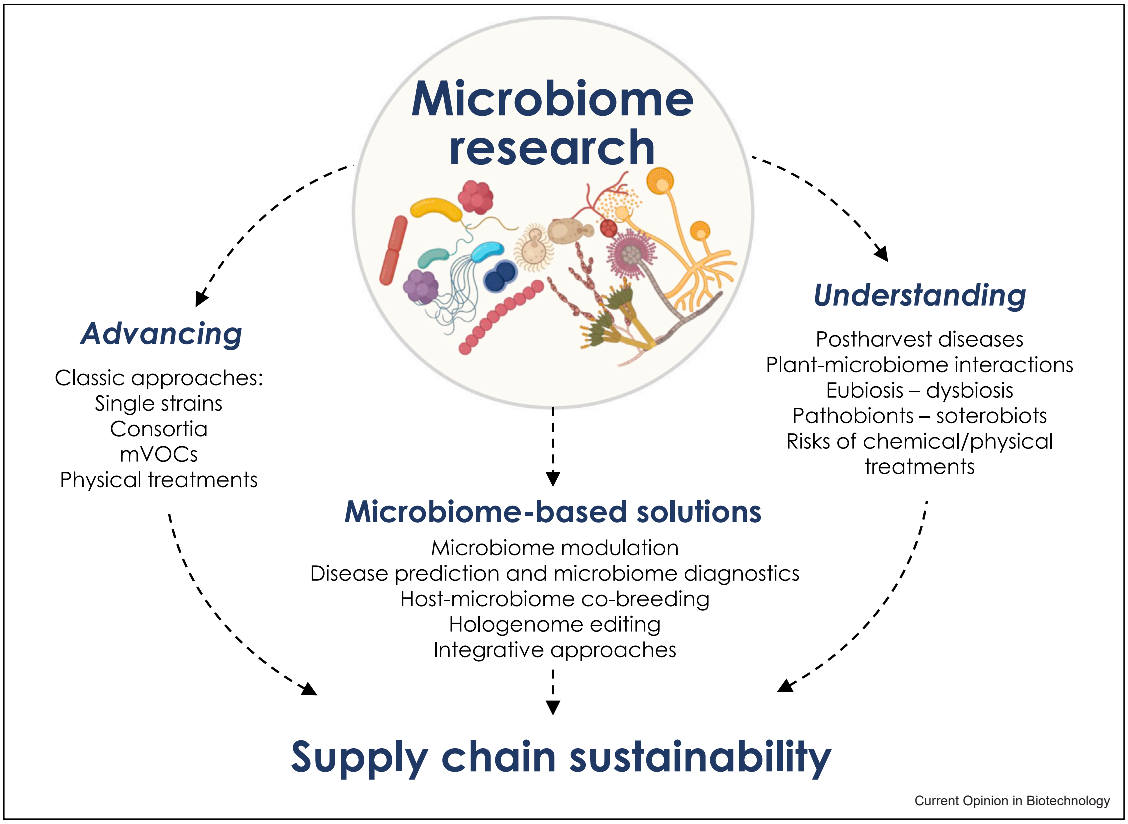
Preventive strategies to counteract common postharvest pathogens already in the field were established and successfully applied in the past [38]. Such applications would greatly benefit from targeted predictions via microbiome tracking if microorganisms are present that could cause disease. This would allow to specifically apply biotechnological products, such as formulated antagonistic microorganisms, that can counteract certain phytopathogens that are naturally occurring during plant growth. Another promising strategy would be the targeted application of so-called soterobionts that specifically prevent the outbreak of postharvest diseases. Soterobionts were only recently described [17] as distinct microorganisms that can holistically protect their hosts from disease. However, so far, no soterobionts that are specific for postharvest diseases were described. Their identification and transfer into biotechnological applications will benefit from microbiome-guided predictive approaches that have the potential to reveal pathogens that require countermeasures to avoid disease emergence.

Microbiome engineering: exploiting the full potential of microbiome biotechnology for sustainability along the food chain

Changes in microbial diversity and composition can be expected to influence the host phenotype and thus determine between health and disease. Microbiome engineering is based on the implementation of microbial populations that perform specific functions for the host plant and contribute to a desired phenotype. Microbiome modulation is a term that summarizes the modes of action of microbial inoculants, that is, formulated single strains or microbial consortia, to pointedly influence the indigenous plant microbiome temporarily or constantly with health benefits for the host [11]. The potential of microbiome research to find biotechnological solutions for postharvest applications is presented in Figure 2.

In general, microbiome management comprises applying (i) microbiome transplants, (ii) microbes with beneficial properties, or (iii) microbiota-active metabolites to shift microbiota structure and function from dysbiosis into a healthy state. Biocontrol by microbial inoculation is a classical strategy. However, classic microbial inoculants continue to face significant obstacles, restricting their application in agricultural contexts due to a lack of reproducibility and efficacy under field conditions [61]. Recent advances in multiomics approaches have provided a more comprehensive picture of intermicrobial and plant–microbial interactions and led to the

Figure 2



Supply-chain sustainability can be achieved by incorporating the microbiome at all levels, from field to fork. Microbiome research will substantially advance current postharvest approaches (*left arrow*), increase our understanding of disease development, and help to assess impacts and risks of current and novel postharvest treatments (*right arrow*). Definitions: Pathobionts: host-associated, disease-causing (micro-)organisms with a distinct pathogenic potential under certain genetic and environmental conditions. Soterobionts: host-associated, disease-preventing microorganisms that are transferable to disease-susceptible hosts to confer disease resistance. Microbiome modulation: mode of action of single strains or microbial consortia to pointedly modulate the indigenous plant microbiome temporarily or constantly with health benefits for the host. Hologenome editing: application of microbes that provide a functional trait to support plant health. Integrative approaches: changing the environmental conditions to modulate the microbiome on a community level.

identification of 'health conferring' agents (soterobionts) with high efficiency [17]. An example was recently provided by Ref. [44], which used a combination of high-throughput amplicon sequencing, gene mutagenesis, and molecular-interaction assays that allowed the identification of the underlying mode of action of *Sphingomonas melonis*, a seed-endophytic bacterium that is transmitted across generations and that differentiates between rice seedling blight-resistant and -susceptible phenotypes of the same rice cultivar. Inoculation of the isolated strain into disease-susceptible rice phenotypes resulted in resistance due to the production of anthranilic acid that interferes with the sigma factor RpoS, a protein that is needed for virulence-factor biosynthesis by the seedborne pathogen [44]. Considering the indigenous plant microbiome in disease-preventing strategies is pivotal to design more targeted microbial inoculants.

Host–microbiome cobreeding is another strategy to improve disease resistance and other beneficial traits in crops. It is well-documented that plant-associated microbial communities are partly influenced by host genetics [2,67]. Since the selection of these specific taxa is strongly driven by the host, they may provide beneficial functions. For example, the microbiome of *Fusarium oxysporum*-resistant cultivars of common bean was shown to present higher gene-expression rates for nutrient metabolism and biosynthesis of the antifungal compounds compared with nonresistant cultivars [42]. In another study, *indica* varieties of rice were found to utilize nitrogen more effectively than *japonica* varieties because they can attract a more diverse microbiome, including strains that carry nitrogen-metabolism functions [79]. Genome-wide association studies have emerged as a useful tool for breeding programs to investigate the genetic complexity of plant phenotypes [18,29]. Another study highlighting the importance of host–microbiome cobreeding was published by Adam et al. [5]: the seed microbiome in pumpkin, especially the intraspecific diversity of *Enterobacteriaceae*, was correlated with healthy pumpkins in the field. These findings represent the first steps into microbiome-driven breeding for plant-beneficial microbes.

Hologenome editing, an idea recently designated by Ravanbakhsh et al. [52], relies on the application of microbes that provide a functional trait to support plant health. Based on a simplified holobiont model with *A. thaliana* and *Pseudomonas putida*, the authors demonstrated that the plant nutritional value can be increased by either targeted mutations of the microbiome or alterations of the plant genome. Both, altering the plant ethylene-synthesis gene ETO1, or the microbial gene acdS, yielded in increased ethylene production and thus, similar plant phenotypes [52]. Similar approaches can also be applied at postharvest by modulating the indigenous microbiota that can protect harvested products from postharvest pathogens. This can also include gene editing of biocontrol strains, for example, *Trichoderma* virens mutants carrying a mitogen-activated protein kinase-encoding gene (Δ*tvk1)* showed improved biocontrol ability against *Rhizoctonia solani* due to increased expression of genes associated with mycoparasitism and overproduction of lytic enzymes [43]. Similarly, silencing of *ace1* gene in *Trichoderma atroviride*, increased the synthesis of antibiotics and other secondary metabolites that significantly enhanced its potential as a biocontrol agent against *Fusarium oxysporum* and *R. solani* [21]. CRISPR-based technologies belong also to the genome-editing technologies. This was recently applied to regulate microbial activity by altering the genetic content within a species of interest from a complex microbial population [9]. Thereby, new avirulent strains can be produced that compete directly with virulent ones or trigger plant immune responses [45]. The authors furthermore suggested that CRISPR–Cas can be introduced via engineered phage particles or extracellular vesicles into spoilage microorganisms to target specific genes, that is, virulence, antibiotic resistance, and toxin genes, to specifically impair survival and colonization rates [9].

Finally, we propose integrative approaches to modify the microbiome on community level as most promising. In general, any biotic or abiotic factor can lead to conversions within the microbiome. These conversions are generally not performed by single strains, but by specific ecological units that respond to a certain factor [60]. A targeted conversion of the microbiome, thus, comes down to changing certain environmental conditions that favor a desired ecological unit. Adam et al. [6] suggested, for example, to first clear specific niches by predators within the holobiont and thereby facilitate the establishment of the microbial inoculant. mVOCs, to which the effects of a biocontrol agent are often attributed to, represent another promising tool for integrated measures and to replace hazardous chemicals [8]. Such approaches can be implemented pre-, but especially postharvest, where abiotic conditions can be controlled more precisely.

At the end, we want to highlight the relevance of microbiome research to assess the holistic impact of novel biodecontamination treatments in the postharvest sector. By analyzing the microbiome, [80] showed for instance that cold plasma treatment, which is generally considered as safe for the environment and human consumption [57], reduced overall bacterial diversity and initiated the formation of bacterial spores in wheat grains. Such effects are often not reflected by currently used culture-dependent approaches but may represent a risk to human health.

Conclusion

Management of storage diseases demands on deep understanding of all factors that influence plant–microbiome interactions from the field to the consumer. However, once those factors are disclosed, we will be able to engineer the microbiome on a community level, which will be far more robust and exceed the effectivity of a single-strain application many times over. The future vision is that microbiome-based solutions can be integrated in one's health approaches, and act as human probiotics too.

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Conflict of interest statement

None declared.

Data Availability

No data were used for the research described in the article.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest.

1. Abdelfattah A, Freilich S, Bartuv R, Yeka Zhimo V, Kumar A, Biasi A, Salim S, Feygenberg O, Burchard E, Dardick C, Liu J, Khan A, Ellouze W, Ali S, Spadaro D, Torres R, Teixido N, Ozkaya O, Buehlmann A, Vero S, Mondino P, Berg G, Wisniewski M, Droby S: **Global analysis of the apple fruit microbiome: are all apples the same?** *Environmental Microbiology* (10) 2021 **23**:6038-6055, https://doi.org/10.1111/1462-2920.15469

2. • Abdelfattah A, Tack AJM, Wasserman B, Liu J, Berg G, Norelli J, Droby S, Wisniewski M: **Evidence for host–microbiome co-evolution in apple.** *New Phytol* 2021 **234**:2088-2100, https://doi.org/10.1111/nph.17820.

The study investigated the endophytic microbiome of wild, progenitor and domesticated apple species and concluded that the apple microbiome can be traced back to its ancestors. The authors reported patterns of phylosymbiosis and that apple ancestors have contributed to modern apple in similar proportion as their genes.

3. Abdelfattah A, Whitehead SR, Macarisin D, Liu J, Burchard E, Freilich S, Dardick C, Droby S, Wisniewski M: **Effect of washing, waxing and low-temperature storage on the postharvest microbiome of apple**. *Microorganisms* 2020, **8**:944, https://doi.org/10.3390/microorganisms8060944

4. Abdelfattah A, Wisniewski M, Droby S, Schena L: **Spatial and compositional variation in the fungal communities of organic and conventionally grown apple fruit at the consumer point-of-purchase**. *Hortic Res* 2016, **3**:16047, https://doi.org/10.1038/hortres.2016.47

5. Adam E, Bernhart M, Müller H, *et al*.: **The *Cucurbita pepo* seed microbiome: genotype-specific composition and implications for breeding**. *Plant Soil* 2018, **422**:35-49, https://doi.org/10.1007/s11104-016-3113-9

6. Adam E, Groenenboom AE, Kurm V, Rajewska M, Schmidt R, Tyc O, *et al*.: **Controlling the microbiome: microhabitat adjustments for successful biocontrol strategies in soil and human gut**. *Front Microbiol* 2016, **7**:1079, https://doi.org/10.3389/fmicb.2016.01079

7. Angeli D, Sare AR, Jijakli MH, Pertot I, Massart S: **Insights gained from metagenomic shotgun sequencing of apple fruit epiphytic microbiota**. *Postharvest Biol Technol* 2019, **153**:96-106, https://doi.org/10.1016/j.postharvbio.2019.03.020

8. Bailly A, Weisskopf L: **Mining the volatilomes of plant-associated microbiota for new biocontrol solutions**. *Front Microbiol* 2017, **8**:1638, https://doi.org/10.3389/fmicb.2017.01638

9. Barrangou R, Notebaart RA: **CRISPR-directed microbiome manipulation across the food supply chain**. *Trends Microbiol* 2019, **27**:489-496, https://doi.org/10.1016/j.tim.2019.03.006

10. Berg G, Cernava T: **The plant microbiota signature of the Anthropocene as a challenge for microbiome research**. *Microbiome* 2022, **10**:54, https://doi.org/10.1186/s40168-021-01224-5

11. Berg G, Kusstatscher P, Abdelfattah A, Cernava T, Smalla K: **Microbiome modulation — toward a better understanding of plant microbiome response to microbial inoculants**. *Front Microbiol* 2021, **12**, https://doi.org/10.3389/fmicb.2021.650610

12. Berg G, Rybakova D, Fischer D, Cernava T, Vergès M-CC, Charles T, Chen X, Cocolin L, Eversole K, Corral GH, Kazou M, Kinkel L, Lange L, Lima N, Loy A, Macklin JA, Maguin E, Mauchline T, McClure R, Mitter B, Ryan M, Sarand I, Smidt H, Schelkle B, Roume H, Kiran GS, Selvin J, Souza RSC, de, van Overbeek L, Singh BK, Wagner M, Walsh A, Sessitsch A, Schloter M: **Microbiome definition re-visited: old concepts and new challenges**. *Microbiome* 2020, **8**:103, https://doi.org/10.1186/s40168-020-00875-0

14. Buchholz F, Kostić T, Sessitsch A, Mitter B: **The potential of plant microbiota in reducing postharvest food loss**. *Microb Biotechnol* 2018, **11**:971-975, https://doi.org/10.1111/1751-7915.13252

15. Carlström CI, Field CM, Bortfeld-Miller M, Müller B, Sunagawa S, Vorholt JA: **Synthetic microbiota reveal priority effects and keystone strains in the *Arabidopsis* phyllosphere**. *Nat Ecol Evol* 2019, **3**:1445-1454, https://doi.org/10.1038/s41559-019-0994-z

16. Cavicchioli R, Ripple WJ, Timmis KN, Azam F, Bakken LR, Baylis M, Behrenfeld MJ, Boetius A, Boyd PW, Classen AT, Crowther TW, Danovaro R, Foreman CM, Huisman J, Hutchins DA, Jansson JK, Karl DM, Koskella B, Mark Welch DB, Martiny JBH, Moran MA, Orphan VJ, Reay DS, Remais JV, Rich VI, Singh BK, Stein LY, Stewart FJ, Sullivan MB, van Oppen MJH, Weaver SC, Webb EA, Webster NS: **Scientists' warning to humanity: microorganisms and climate change**. *Nat Rev Microbiol* 2019, **17**:569-586, https://doi.org/10.1038/s41579-019-0222-5

17. Cernava T, Berg G: **The emergence of disease-preventing bacteria within the plant microbiota**. *Environmental Microbiology* (8) 2022 **24**:3259-3263, https://doi.org/10.1111/1462-2920.15896

18. Deng S, Caddell DF, Xu G, Dahlen L, Washington L, Yang J, Coleman-Derr D: **Genome wide association study reveals plant loci controlling heritability of the rhizosphere microbiome**. *ISME J* 2021, **15**:3181-3194, https://doi.org/10.1038/s41396-021-00993-z

19. Droby S, Wisniewski M: **The fruit microbiome: a new frontier for postharvest biocontrol and postharvest biology**. *Postharvest Biol Technol* 2018, **140**:107-112, https://doi.org/10.1016/j.postharvbio.2018.03.004

20. Droby S, Zhimo VY, Wisniewski M, Freilich S: **The pathobiome concept applied to postharvest pathology and its implication on biocontrol strategies**. *Postharvest Biol Technol* 2022, **189**:111911, https://doi.org/10.1016/j.postharvbio.2022.111911

21. Fang C, Chen X: **Potential biocontrol efficacy of *Trichoderma atroviride* with cellulase expression regulator ace1 gene knock-out**. *3 Biotech* 2018, **8**:302, https://doi.org/10.1007/s13205-018-1314-z

22. FAO: Global food losses and food waste–extent, causes and prevention. *Save Food An Initiat.* Food Loss Waste Reduct; 2011.

23. Fernandez-San Millan A, Larraya L, Farran I, Ancin M, Veramendi J: **Successful biocontrol of major postharvest and soil-borne plant pathogenic fungi by antagonistic yeasts**. *Biol Control* 2021, **160**:104683, https://doi.org/10.1016/j.biocontrol.2021.104683

24. Gao C, Lin Q, Dong C, Ji H, Yu J, Chen C, Zhu Z-Q, Ban Z, Zhang N, Bao Y: **Effects of ozone concentration on the postharvest quality and microbial diversity of Muscat Hamburg grapes**. *RSC Adv* 2020, **10**:9037-9045, https://doi.org/10.1039/C9RA10479H

25. • Gu Y, Banerjee S, Dini-Andreote F, Xu Y, Shen Q, Jousset A, Wei Z: **Small changes in rhizosphere microbiome composition predict disease outcomes earlier than pathogen density variations**. *ISME J* 2022 **16**:2448-2456, https://doi.org/10.1038/s41396-022-01290-z.

The authors showed that health and disease outcomes of plant individuals grown in homogenous conditions and under pathogen pressure correlate to an early and rapid divergence of the rhizosphere microbiota, and that these differences allow disease prediction.

26. Hawkes CV, Kjøller R, Raaijmakers JM, Riber L, Christensen S, Rasmussen S, Christensen JH, Dahl AB, Westergaard JC, Nielsen M, Brown-Guedira G, Hestbjerg Hansen L: **Extension of plant phenotypes by the foliar microbiome**. *Annu Rev Plant Biol* 2021, **72**:823-846, https://doi.org/10.1146/annurev-arplant-080620-114342

27. He F, Zhao L, Zheng X, Abdelhai MH, Boateng NS, Zhang X, Zhang H: **Investigating the effect of methyl jasmonate on the biocontrol activity of *Meyerozyma guilliermondii* against blue mold decay of apples and the possible mechanisms involved**. *Physiol Mol Plant Pathol* 2020, **109**:101454, https://doi.org/10.1016/j.pmpp.2019.101454

28. Hernando-Amado S, Coque TM, Baquero F, Martínez JL: **Defining and combating antibiotic resistance from One Health and Global Health perspectives**. *Nat Microbiol* 2019, **4**:1432-1442, https://doi.org/10.1038/s41564-019-0503-9

29. Horton MW, Bodenhausen N, Beilsmith K, Meng D, Muegge BD, Subramanian S, Vetter MM, Vilhjálmsson BJ, Nordborg M, Gordon JI, Bergelson J: **Genome-wide association study of *Arabidopsis thaliana* leaf microbial community**. *Nat Commun* 2014, **5**:5320, https://doi.org/10.1038/ncomms6320

30. Huang Y, Sun C, Guan X, Lian S, Li B, Wang C: **Biocontrol efficiency of *Meyerozyma guilliermondii* Y-1 against apple postharvest decay caused by *Botryosphaeria dothidea* and the possible mechanisms of action**. *Int J Food Microbiol* 2021, **338**:108957, https://doi.org/10.1016/j.ijfoodmicro.2020.108957

31. Janisiewicz WJ, Korsten L: **Biological control of postharvest diseases of fruits**. *Annu Rev Phytopathol* 2002, **40**:411-441, https://doi.org/10.1146/annurev.phyto.40.120401.130158

32. Jarvis KG, Daquigan N, White JR, Morin PM, Howard LM, Manetas JE, Ottesen A, Ramachandran P, Grim CJ: **Microbiomes associated with foods from plant and animal sources**. *Front Microbiol* 2018, **9**, https://doi.org/10.3389/fmicb.2018.02540

33. Jijakli MH, Lepoivre P, Grevesse C: **Yeast species for biocontrol of apple postharvest diseases: an encouraging case of study for practical use**. In *Biotechnological Approaches in Biocontrol of Plant Pathogens*. Edited by Mukerji KG, Chamola BP, Upadhyay RK. Springer; 1999:31-49 , https://doi.org/10.1007/978-1-4615-4745-7_2

34. • Jochum L, Stecher B: **Label or concept — what is a pathobiont?** *Trends Microbiol* 2020, **28**:789-792, https://doi.org/10.1016/j.tim.2020.04.011.

The authors discuss the applicability of the pathobiont concept and conclude that it is not universally applicable.

35. Kusstatscher P, Cernava T, Abdelfattah A, Gokul J, Korsten L, Berg G: **Microbiome approaches provide the key to biologically control postharvest pathogens and storability of fruits and vegetables**. *FEMS Microbiol Ecol* 2020, **96**:fiaa119, https://doi.org/10.1093/femsec/fiaa119

36. • Kusstatscher P, Zachow C, Harms K, Maier J, Eigner H, Berg G, Cernava T: **Microbiome-driven identification of microbial indicators for postharvest diseases of sugar beets**. *Microbiome* 2019, **7**:112, https://doi.org/10.1186/s40168-019-0728-0.

The study showed that indicator taxa for sugar beet storability can be extracted from microbiome datasets.

37. Lahlali R, Brostaux Y, Jijakli MH: **Control of apple blue mold by the antagonistic yeast *Pichia anomala* strain K: screening of UV protectants for preharvest application**. *Plant Dis* 2011, **95**:311-316, https://doi.org/10.1094/PDIS-04-10-0265

38. Leibinger W, Breuker B, Hahn M, Mendgen K: **Control of postharvest pathogens and colonization of the apple surface by antagonistic microorganisms in the field**. *Phytopathology®* 1997, **87**:1103-1110, https://doi.org/10.1094/PHYTO.1997.87.11.1103

39. Leng J, Yu L, Dai Y, Leng Y, Wang C, Chen Z, Wisniewski M, Wu X, Liu J, Sui Y: **Recent advances in research on biocontrol of postharvest fungal decay in apples**. *Crit Rev Food Sci Nutr* 2022,1-14, https://doi.org/10.1080/10408398.2022.2080638

40. Lima G, Castoria R, De Curtis F, Raiola A, Ritieni A, De Cicco V: **Integrated control of blue mould using new fungicides and biocontrol yeasts lowers levels of fungicide residues and patulin contamination in apples**. *Postharvest Biol Technol* 2011, **60**:164-172, https://doi.org/10.1016/j.postharvbio.2010.12.010

41. Macarisin D, Droby S, Bauchan G, Wisniewski M: **Superoxide anion and hydrogen peroxide in the yeast antagonist–fruit interaction: a new role for reactive oxygen species in postharvest biocontrol?** *Postharvest Biol Technol* 2010, **58**:194-202, https://doi.org/10.1016/j.postharvbio.2010.07.008

42. Mendes LW, Mendes R, Raaijmakers JM, *et al*.: **Breeding for soil-borne pathogen resistance impacts active rhizosphere microbiome of common bean**. *ISME J* 2018, **12**:3038-3042, https://doi.org/10.1038/s41396-018-0234-6

43. Mendoza-Mendoza A, Pozo MJ, Grzegorski D, Martínez P, García JM, Olmedo-Monfil V, Cortés C, Kenerley C, Herrera-Estrella A: **Enhanced biocontrol activity of Trichoderma through inactivation of a mitogen-activated protein kinase**. *Proc Natl Acad Sci* 2003, **100**:15965-15970, https://doi.org/10.1073/pnas.2136716100

44. •• Matsumoto H, Fan X, Wang Y, Kusstatscher P, Duan J, Wu S, Chen S, Qiao K, Wang Y, Ma B, Zhu G, Hashidoko Y, Berg G, Cernava T, Wang M: **Bacterial seed endophyte shapes disease resistance in rice**. *Nat Plants* 2021, **7**:60-72, https://doi.org/10.1038/s41477-020-00826-5.

The study showed that one specific bacterium in plant seeds can confer holistic disease resistance to the host.

45. Muñoz IV, Sarrocco S, Malfatti L, Baroncelli R, Vannacci G: **CRISPR-Cas for fungal genome editing: a new tool for the management of plant diseases**. *Front Plant Sci* 2019, **10**, https://doi.org/10.3389/fpls.2019.00135

46. Morales Moreira ZP, Helgason BL, Germida JJ: **Environment has a stronger effect than host plant genotype in shaping spring *Brassica napus* seed microbiomes**. *Phytobiomes J* 2021, **5**:220-230, https://doi.org/10.1094/PBIOMES-08-20-0059-R

47. Mostafavi AH, Mahyar Mirmajlessi S, Fathollahi H, Shahbazi S, Mohammad Mirjalili S: **Integrated effect of gamma radiation and biocontrol agent on quality parameters of apple fruit: an innovative commercial preservation method**. *Radiat Phys Chem* 2013, **91**:193-199, https://doi.org/10.1016/j.radphyschem.2013.02.020

48. Obagwu J, Korsten L: **Integrated control of citrus green and blue molds using *Bacillus subtilis* in combination with sodium bicarbonate or hot water**. *Postharvest Biol Technol* 2003, **28**:187-194, https://doi.org/10.1016/S0925-5214(02)00145-X

49. Obermeier MM, Wicaksono WA, Taffner J, Bergna A, Poehlein A, Cernava T, Lindstaedt S, Lovric M, Müller Bogotá CA, Berg G: **Plant resistome profiling in evolutionary old bog vegetation provides new clues to understand emergence of multi-resistance**. *ISME J* 2021, **15**:921-937, https://doi.org/10.1038/s41396-020-00822-9

50. Padmaperuma G, Butler TO, Shuhaili FABA, Almalki WJ, Vaidyanathan S: **Microbial consortia: concept and application in fruit crop management**. In *Fruit Crops*. Edited by Srivastava AK, Hu Chengxiao. Elsevier; 2020:353-366.

51. Parfitt J, Barthel M, Macnaughton S: **Food waste within food supply chains: quantification and potential for change to 2050**. *Philos Trans R Soc B Biol Sci* 2010, **365**:3065-3081, https://doi.org/10.1098/rstb.2010.0126

52. Ravanbakhsh M, Kowalchuk GA, Jousset A: **Targeted plant hologenome editing for plant trait enhancement**. *New Phytol* 2021, **229**:1067-1077, https://doi.org/10.1111/nph.16867

53. Saminathan T, García M, Ghimire B, Lopez C, Bodunrin A, Nimmakayala P, Abburi VL, Levi A, Balagurusamy N, Reddy UK: **Metagenomic and metatranscriptomic analyses of diverse watermelon cultivars reveal the role of fruit associated microbiome in carbohydrate metabolism and ripening of mature fruits**. *Front Plant Sci* 2018, **9**, https://doi.org/10.3389/fpls.2018.00004

54. Sare AR, Jijakli MH, Massart S: **Microbial ecology to support integrative efficacy improvement of biocontrol agents for postharvest diseases management**. *Postharvest Biol Technol* 2021, **179**:111572, https://doi.org/10.1016/j.postharvbio.2021.111572

55. Schmelcher M, Loessner MJ: **Bacteriophage endolysins: applications for food safety**. *Curr Opin Biotechnol* 2016, **37**:76-87, https://doi.org/10.1016/j.copbio.2015.10.005

56. Shade A, Jacques MA, Barret M: **Ecological patterns of seed microbiome diversity, transmission, and assembly**. *Curr Opin Microbiol* 2017, **37**:15-22, https://doi.org/10.1016/j.mib.2017.03.010

57. Siddique SS, Hardy GESJ, Bayliss KL: **Cold plasma: a potential new method to manage postharvest diseases caused by fungal plant pathogens**. *Plant Pathol* 2018 **67**:1011-1021, https://doi.org/10.1111/ppa.12825

58. Sipiczki M: **Metschnikowia strains isolated from botrytized grapes antagonize fungal and bacterial growth by iron depletion**. *Appl Environ Microbiol* 2006, **72**:6716-6724, https://doi.org/10.1128/AEM.01275-06

59. Spadaro D, Droby S: **Development of biocontrol products for postharvest diseases of fruit: the importance of elucidating the mechanisms of action of yeast antagonists**. *Trends Food Sci Technol* 2016, **47**:39-49, https://doi.org/10.1016/j.tifs.2015.11.003

60. Strous M, Sharp C: **Designer microbiomes for environmental, energy and health biotechnology**. *Curr Opin Microbiol* 2018, **43**:117-123, https://doi.org/10.1016/j.mib.2017.12.007

61. Timmusk S, Behers L, Muthoni J, Muraya A, Aronsson A-C: **Perspectives and challenges of microbial application for crop improvement**. *Front Plant Sci* 2017, **8**, https://doi.org/10.3389/fpls.2017.00049

62. Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK: **Plant–microbiome interactions: from community assembly to plant health**. *Nat Rev Microbiol* 2020, **18**:607-621, https://doi.org/10.1038/s41579-020-0412-1

63. Tournas V, Katsoudas E: **Effect of CaCl 2 and various wild yeasts from plant origin on controlling Penicillium expansum postharvest decays in golden delicious apples**. *Microbiol Insights* 2019, **12**:117863611983764, https://doi.org/10.1177/1178636119837643

64. Vandenkoornhuyse P, Quaiser A, Duhamel M, Le Van A, Dufresne A: **The importance of the microbiome of the plant holobiont**. *New Phytol* 2015, **206**:1196-1206, https://doi.org/10.1111/nph.13312

65. Vannier N, Mony C, Bittebiere A-K, Michon-Coudouel S, Biget M, Vandenkoornhuyse P: **A microorganisms' journey between plant generations**. *Microbiome* 2018, **6**:79, ,https://doi.org/10.1186/s40168-018-0459-7

66. Wallace RL, Hirkala DL, Nelson LM: **Mechanisms of action of three isolates of *Pseudomonas fluorescens* active against postharvest grey mold decay of apple during commercial storage**. *Biol Control* 2018, **117**:13-20, https://doi.org/10.1016/j.biocontrol.2017.08.019

67. Walters WA, Jin Z, Youngblut N, Wallace JG, Sutter J, Zhang W, González-Peña A, Peiffer J, Koren O, Shi Q, Knight R, Glavina del Rio T, Tringe SG, Buckler ES, Dangl JL, Ley RE: **Large-scale replicated field study of maize rhizosphere identifies heritable microbes**. *Proc Natl Acad Sci* 2018, **115**:7368-7373, https://doi.org/10.1073/pnas.1800918115

68. Wang Z, Sui Y, Li J, Tian X, Wang Q: **Biological control of postharvest fungal decays in citrus: a review**. *Crit Rev Food Sci Nutr* 2022, **62**:861-870, https://doi.org/10.1080/10408398.2020.1829542

69. Wassermann B, Kusstatscher P, Berg G: **Microbiome response to hot water treatment and potential synergy with biological control on stored apples**. *Front Microbiol* 2019, **10**:2502, https://doi.org/10.3389/fmicb.2019.02502

70. Wassermann B, Müller H, Berg G: **An apple a day: which bacteria do we eat with organic and conventional apples?** *Front Microbiol* 2019, **10**:1629, https://doi.org/10.3389/fmicb.2019.01629

71. Wassermann B, Abdelfattah A, Müller H, Korsten L, Berg G: **The microbiome and resistome of apple fruits alter in the post-harvest period**. *Environ Micro* 2022, **17**:10.

73. Wisniewski M, Droby S: **The postharvest microbiome: the other half of sustainability**. *Biol Control* 2019, **137**:104025, https://doi.org/10.1016/j.biocontrol.2019.104025

74. Wu W: **Structure and function of the fruit microbiome in healthy and diseased kiwifruit**. *Pak J Agric Sci* 2019, **56**:577-585, https://doi.org/10.21162/PAKJAS/19.8820

75. Xu Y: **Phage and phage lysins: new era of bio-preservatives and food safety agents**. *J Food Sci* 2021, **86**:3349-3373, https://doi.org/10.1111/1750-3841.15843

76. Yurgel SN, Abbey L, Loomer N, Gillis-Madden R, Mammoliti M: **Microbial communities associated with storage onion**. *Phytobiomes J* 2018, **2**:35-41, https://doi.org/10.1094/PBIOMES-12-17-0052-R

77. Zhang D, Lopez-Reyes JG, Spadaro D, Garibaldi A, Gullino ML: **Efficacy of yeast antagonists used individually or in combination with hot water dipping for control of postharvest brown rot of peaches**. *J Plant Dis Prot* 2010, **117**:226-232, https://doi.org/10.1007/BF03356365

78. Zhang P, Guo Z, Ullah S, Melagraki G, Afantitis A, Lynch I: **Nanotechnology and artificial intelligence to enable sustainable and precision agriculture**. *Nat Plants* 2021, **7**:864-876, https://doi.org/10.1038/s41477-021-00946-6

79. Zhang J, Liu Y-X, Zhang N, Hu B, Jin T, Xu H, Qin Y, Yan P, Zhang X, Guo X, Hui J, Cao S, Wang X, Wang C, Wang H, Qu B, Fan G, Yuan L, Garrido-Oter R, Chu C, Bai Y: **NRT1.1B is associated with root microbiota composition and nitrogen use in field-grown rice**. *Nat Biotechnol* 2019, **37**:676-684, https://doi.org/10.1038/s41587-019-0104-4

80. Los A, Ziuzina D, Boehm D, Bourke P, *et al.*: **Effects of cold plasma on wheat grain microbiome and antimicrobial efficacy against challenge pathogens and their resistance**. *International Journal of Food Microbiology* 2020, **335**:108889, , https://doi.org/10.1016/j.ijfoodmicro.2020.108889