

# Plant grafting: Maximizing beneficial microbe-plant interactions

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## ABSTRACT

Grafting, a traditional agricultural technique, holds significant potential for increasing productivity by harnessing the plant microbiome. The microbiome provides adaptability and metabolic diversity, increasing plant capacity to cope with challenging conditions. Although grafting effects on the composition and structure of microbiome on the root endosphere and, consequently, on the aerial endosphere have been reported, the impact on potential functionalities for plant traits remains to be elucidated. Beneficial microbes assembled by plant grafting have significant biotechnological potential to increase plant performance against biotic and abiotic stressors. In view of the optimal use of rootstock-scion combinations, in this review, we focused on recent grafting studies with plant-microbiome underlying mechanisms related to growth promotion, nutrient accessibility, and protection against abiotic and biotic environmental stresses. We provide significant first-hand information to guide future directions and prospects in shaping plant and core microbiome interactions, which helps in sustainable agriculture.

## 1. Plant grafting

Grafting is an ancient practice developed to overcome the challenges associated with propagating horticultural crops such as apple, pear, plum and cherry through cuttings (Mudge et al., 2009). This technique connects the shoot portion of a plant, known as the 'scion', with the root system of another plant, referred to as the 'rootstock' allowing them to grow together (Warschefsky et al., 2016; Yang et al., 2022). Grafting has been applied from fruit trees to vegetable crops, combining genotypically distinct plants for asexual plant propagation (Goldschmidt, 2014; Turnbull, 2010). The successful union between the scion and the rootstock in plant grafting depends on intraspecific or interspecific compatibility (Goldschmidt, 2014).

The grafting compatibility means the formation of vascular connections between the rootstock and the scion with the development of canopy and new roots (Aloni et al., 2010). A variation in the degree of compatibility may happen due to genetic and anatomic differences between rootstock and scion (Edelstein et al., 2004). Compatible species establish a successful graft union with the proper functioning of the combined grafted plant (Goldschmidt, 2014). Therefore, the long-time survival of an intraspecific or interspecific rootstock-scion connection is

dependent on plant genotype, englobing anatomical and physiological attributes that allow for the biophysically stable union of the vascular tissues and the healing of the cuts and wounds (Aloni et al., 2010; Goldschmidt, 2014; Thomas et al., 2023).

Grafting is also applied to native and cultivated tree species from tropical regions (de Oliveira Castro et al., 2021; Mendes et al., 2020; Trueman et al., 2014; Wendling et al., 2017), and fruit and vegetable crops such as citrus, grapes, coffee, tomato, and others (de Andrade et al., 2013; de Lima et al., 2021; Leão et al., 2020; Lopes and Mendonça, 2016; Meneses et al., 2020). As grafting has been used for centuries, it has proven an effective tool for trait improvements of different plants around the world where it was not previously possible (Colla et al., 2006; McAdam et al., 2016; Rivard and Louws, 2008). However, only in the last decades, the discovery of physiological and molecular mechanisms involved in rootstock and scion interactions brought new possibilities for improving horticulture and agriculture (Albacete et al., 2015; Gregory et al., 2013).

As a research tool, grafting provides relevant advances to plant biology (Gaion and Carvalho, 2018). With advanced knowledge about root-shoot communication, grafting may be expanded globally toward the enhancement of vegetable production and to combat environmental

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challenges (Gaion et al., 2017; Santos et al., 2021; Torres et al., 2021; Williams et al., 2021). Combining desired traits in the scion and rootstock can improve fruit quality (Legua et al., 2018) and provide vigor to scions, resulting in increased fruit production, biomass, and overall yield by augmenting the resource efficiency of vegetable crops (Álvarez-Hernández et al., 2015; Kumbar et al., 2021; Sabatino et al., 2022). Furthermore, grafting plays a crucial role in addressing nutrient limitations, as the vigorous root system of rootstock enhances nutrient uptake and accumulation (Nawaz et al., 2016). It has also been used to avoid or reduce losses in production caused by alkalinity (Colla et al., 2010), salinity (Estañ et al., 2005), drought (França et al., 2018), organic pollutants (Schwarz et al., 2010), and high levels of toxic elements (Edelstein et al., 2017; Guimarães et al., 2009). Grafting allows us to understand the several mechanisms involved in the enhanced resistance to water stress (Kumar et al., 2017; Yang and Chen, 2022; Rodríguez-Gamir et al., 2011; Opazo et al., 2020), as it enables us to study hormonal signaling between shoots and roots (Guillermo et al., 2021; Silva et al., 2018). At the same time, the improved tolerance to flooding in grafted plants is facilitated by the development of adventitious roots and aerenchyma, for example (Yetisir et al., 2006).

In addition to preventing abiotic stress, grafting is also applied to manage soil-borne pathogens (Miguel et al., 2004; Ramesh et al., 2022), foliar pathogens (Zhang et al., 2012), and nematode infestation (Freitas et al., 2014; Thies et al., 2010; Phani et al., 2023) addressing many biotic stresses. For example, grafting scions of susceptible cultivars onto resistant rootstocks, developing disease-resistant germplasm lines for use as rootstocks or introgressing genes provided effective control against pathogens into cultivars (Cohen et al., 2012; Douhan et al., 2011; Rivard and Louws, 2008).

## 2. Modulation of the root microbiome by plants

Plants actively modulate root and shoot microbiome through root exudation (Hartmann et al., 2009). Plant species and genotype within a species, phenology, physiology, as well as edaphic and climatic conditions, are factors that influence the composition of the diversified elements released from the roots (Chaparro et al., 2013, 2014; Dietz et al., 2020; Micallef et al., 2009; Edwards et al., 2023). Root-shoot communication also plays a role in the type and amount of root-derived compounds, which encompass exudates, metabolites, and organic and chemical compounds (Aloni et al., 2010). The significant variation in space and time of the exudation and rhizodeposition creates specific niches surrounding the roots, which drives the microbiome recruitment of unique microbial populations that actively interact with the plant in the rhizosphere (Cardarelli et al., 2020; Pascale et al., 2020; Philippot et al., 2013).

Plants establish interactions with rhizosphere microbiomes either by recruiting beneficial microbes or repelling pathogens (Pérez-Jaramillo et al., 2016), which may have either negative or positive effects on their host (Mansfield et al., 2012; Martin et al., 2017; Mendes et al., 2013). While some microorganisms in the rhizosphere can be pathogenic, numerous microbes, such as symbiotic nitrogen-fixing bacteria, plant growth-promoting bacteria (PGPB) and mycorrhizal fungi, benefit their host, thereby improving plant fitness (Bossolani et al., 2020; De Oliveira et al., 2022; de Souza et al., 2015).

Those microorganisms colonizing plant roots are a source for endophytic microbial communities inside plant organs (Andrade et al., 2023; Trivedi et al., 2020). While host genotype partly drives the structure of the rhizobiome (Sousa et al., 2020; Van Overbeek and Van Elsas, 2008), the rhizospheric microbial community has a significant impact on plant performance and soil physicochemical processes that are essential for proper plant functioning (Berendsen et al., 2012; Haichar et al., 2008; Moe, 2013).

The large biodiversity of soil microorganisms is filtered into a rhizobiome assembly (Girvan et al., 2003; Mendes et al., 2014). The microbial recruitment is initiated with signals emitted by plant roots,

which are recognized by soil microbial communities and lead to root colonization (Bais et al., 2006). Specific microorganisms selected from bulk soil to the rhizosphere influences the structure and function of microbial populations associated with the plant (Berg et al., 2006). For agricultural applications, enriching the rhizosphere with beneficial microbes can improve plant growth, health, and quality (Andreote et al., 2014; Santos and Olivares, 2021).

## 3. Plant-associated microbiomes assembled by plant grafting

Grafting influences the microbiota of below-ground compartments (roots, rhizosphere) and above-ground compartments (leaves, phyllosphere) (Ling et al., 2015; Marasco et al., 2022; Toju et al., 2019). Multiple studies have demonstrated that host genetic factors, both from rootstock and scion, play a crucial role in shaping the microbial communities associated with the roots, rhizosphere and endosphere of grafted plants (Marasco et al., 2018; Poudel et al., 2019; Song et al., 2020). In addition, the connection between the shoot and the root systems of distinguish plants differently affects the attraction of microorganisms that will integrate the host microbiome (Ling et al., 2015; Marasco et al., 2018; Poudel et al., 2019; Swift et al., 2021).

Experiments in fruit crops showed grafting effects on plant-associated microbiomes (Berlanas et al., 2019; Ruan et al., 2020). Grafting in watermelon changes the rhizobacterial diversity and, induces increased network complexity and strengthens the structural robustness of the bacterial network in the rhizosphere, providing a potential mechanism that protects plants from soil-borne diseases (Ruan et al., 2020). In grapevines, the selection of root-associated microbial communities by rootstock may be influenced by factors such as plant's genetic background, physiological responses modifying the physical and chemical properties of the surrounding soil environment, niche modulation, root system and architecture, plant-bacteria cross-talk mediated by the rhizodeposition of metabolites and consequences of wounding stress in the grafting process (D'Amico et al., 2018; Marasco et al., 2018; Poudel et al., 2019).

Interactive effects of scion and rootstock genotypes have also been shown to influence the rhizospheric bacterial diversity and the relative abundance of microbial communities of grafted grapevines. However, those effects need to be further understood to unravel the relations between grapevine genomes that might influence their root exudation patterns and, consequently, the root microbiome (Vink et al., 2021; Marasco et al., 2022). The type of rootstock, independently of the scion cultivar, is a factor determining the specificity of microbial community in grape root system compartments (Marasco et al., 2018) and evidence of distinct rhizosphere bacterial community was found when apple scion varieties were grafted into the same rootstock with the different photosynthetic efficiencies between scion cultivars being a plausible explanation to an indirect influence on rhizosphere microbic community (Chai et al., 2022).

The effects of rootstock and scion genotype on the composition of root endophytic microbiome were evident in fruit crops such as apples, citrus, peach, and grapevine. For example, in grafted grapes, the genetic characteristic of rootstocks was shown to be the primary driver of specific bacterial and fungal OTUs associated with the rhizosphere, shaping the colonization and composition of AMF in the roots (Berlanas et al., 2019; Moukarzel et al., 2021). The significant differences in the composition and diversity of AMF communities suggest the potential for the beneficial use of AMF to enhance grapevine production and sustainability (Moukarzel et al., 2021).

In citrus and avocado plants, the structure and composition of AMF community were mainly influenced by scion varieties, selectivity recruiting members of the genus *Glomus* among other arbuscular mycorrhizal fungal (AMF) genera to colonize the roots (Shu et al., 2017; Song et al., 2015). However, the rootstock genotype in citrus cultivars may impact the AMF community more than the scion genotype (Song et al., 2020). Moreover, improving microbial diversity and enriching

beneficial bacterial and fungal taxa associated with the watermelon roots by grafting shaped a protective root-associated microbiome against *Fusarium* wilt in continuous cropping soils (Ge et al., 2022).

The influence of rootstock genotypes on the microbiome of endophytic microbiome in roots was observed in apple orchards, with significant differences in the composition, diversity and structure of bacterial and fungal communities between apple rootstocks (van Horn et al., 2021; Wang et al., 2022), increasing the plant resistance to *Valsa mali*, a destructive disease of apple (Wang et al., 2022). Interestingly, in grafted tomatoes, there are cases where the bacterial communities within roots (in the endosphere) are more responsive to specific rootstock than in the rhizosphere surrounding the roots (Poudel et al., 2019).

Because grafting influences the microbial properties of the root and rhizosphere, grafting can change the microbiota diversity and composition of above-ground compartments (Tian et al., 2009; Toju et al., 2019). For example, the endophytic microbiome of apple scion differs when grafted with different rootstock-scion combinations (Liu et al., 2018). In tomato plants, grafting combinations have increased the diversity of leaf endophytic bacterial communities under high saline conditions (Bai et al., 2020). Furthermore, different tomato rootstocks were found to have an impact on the diversity and composition of bacterial communities in both the root and shoot endosphere, with the above-ground microbiome structure being preferentially associated with particular rootstock genotypes (Poudel et al., 2019; Toju et al., 2019). Moreover, bacterial and fungal endophyte groups regulated by scion genotype differed between apple cultivars resistant or susceptible to canker caused by *Neovectria ditissima* (Olivieri et al., 2021).

Similarly, studies also found that rootstock genotypes are associated with the diversity and composition of shoot system microbiota in grapevine and tomato (Moukarzel et al., 2021; Swift et al., 2021; Toju et al., 2019). The influence that grafting exerts on microbial communities surrounding scion-rootstock and living in close association with the host can make plants more resistant to environmental stressors (Cardarelli et al., 2020; Ge et al., 2022). For example, compared to ungrafted plants, rootstock and scion combinations result in more diversity and amount of root exudates attracting diverse microbial taxa that increase the interaction of microbes and confer resistance to soil-borne diseases (Ruan et al., 2020). Moreover, the variety of exudate composition in grafted plants can contribute to inhibiting soil-borne disease (Liu et al., 2009; Ge et al., 2022). However, an experiment with grapevines showed that even when bacterial diversity is influenced by rootstock or scion, the potential functionality of those groups may not be changed (Marasco et al., 2018). This can happen when many microbial species have highly redundant metabolisms, by using the same substrates and performing the same function (Hester et al., 2019).

#### 4. Exploring grafting traits through signaling and core microbiome

The plant-microbe communications, also called interkingdom signaling between microbes and plants, happens in the rhizosphere, where there is lower diversity but higher abundance of microorganisms compared to the bulk soil (Andreote et al., 2014). The selection process for microbiota by plant-derived metabolites and exudates shapes the rhizobiome by modifying the environment surrounding the roots (Zhang et al., 2014). The plant-microbiome interaction is highly complex and happens through chemical signals emitted in response to specific conditions that involve biotic and abiotic factors, activating regulatory mechanisms that can be either positive or negative (Bais et al., 2006).

Bacteria and fungi constitute the major portion of microbes in the rhizosphere, and they undergo chemical signaling with the plant host via low-molecular-weight compounds that induce symbiotic interactions with the plant and can trigger changes in plant transcriptome (Jamil et al., 2022). The main signaling in plant-rhizomicrobiome interactions is related to nutrient acquisition and abiotic and biotic stress control (Jamil et al., 2022). The factors of signaling include the

production of organic molecules such as phytohormones, siderophores, and enzymes for abiotic stress control (Aslantaş et al., 2007; Toju et al., 2019); induced systemic resistance (ISR), including systemic acquired resistance (SAR), for biotic stress control (Durrant and Dong, 2004; Pieterse et al., 2014); and, signal-mediated symbiosis of nodulation and mycorrhizal colonization for resource use efficiency (Foo et al., 2016; Lohar and VandenBosch, 2005).

Biological inducers trigger the ISR and protect the parts of the plant that are not infected by activating defense mechanisms that can be expressed locally at the site of induction and systemically, enhancing the level of protection against a broad spectrum of attackers (Pieterse et al., 2014). In the case of SAR, the alarm signal produced and released from the host-pathogen interaction is graft-transmissible. Scions grafted onto infected rootstocks are capable of developing protection in response to the systematic signal of SAR that is translocated through the vascular system after grafting union and sensitize the plant defense mechanisms to protect the scion (Dean and Kuć, 1986). The SAR confers enhanced resistance against a broad spectrum of pathogens and is characterized by increased levels of the hormone salicylic acid (Pieterse et al., 2014).

Plants recognize microbial signals as microbe-associated molecular patterns (MAMPs) that trigger a local defense through a hormonal signaling network, which in turn produces immune responses (Pieterse et al., 2014). For example, phytohormones produced by PGPR, such as auxin, abscisic acid, salicylic acid, cytokinin, gibberellin, and strigolactones can regulate plant resistance against abiotic and biotic stresses. The influence of microbial communities associated with plants on important plant functionalities has been well established (Berendsen et al., 2012; Marasco et al., 2022; Ruan et al., 2020; Wang et al., 2022).

Therefore, it is plausible to hypothesize that plant performance can be enhanced with the optimization of microbial community assembly that develops with adequate grafting combinations (Bai et al., 2020; Gao et al., 2015; Ge et al., 2022; Rolli et al., 2015), and this includes understanding the grafting effects on the core microbiome, i.e. the commonly occurring organisms that appear in all assemblages of a particular habitat and that are critical to the function of that type of community (Shade and Handelsman, 2012). In plants, the concept of core microbiome also relies on essential microorganisms' interactions within plant organs (rhizosphere, endosphere, phyllosphere) that may include arbuscular mycorrhizal fungus, growth-promoting microbes, and other beneficial microbes whose functions benefit plant growth or protect the host from pathogens (Darriaut et al., 2022; Santos and Olivares, 2021; Tian et al., 2017; Toju et al., 2018; Vincent et al., 2022).

Grafting-mediated recruitment of beneficial plant microbiomes combined with improvement of grafting efficiency may augment the sustainability of food production. Although it remains out of reach the assumption that grafting will select only beneficial taxa, plant-beneficial microbes recruited by rootstock can increase plant nutrient availability and nutrient use efficiency. However, efforts to understand the microbiomes recruited by grafting are necessary to explore the mechanisms by which grafting may increase plant fitness to biotic and abiotic stresses (Busby et al., 2017; Ruan et al., 2020; Sabatino et al., 2022; Sabir, 2013).

Genetic resistance to soil-borne pathogens, rootstock-mediate recruitment of microbial antagonists, exudation of antifungal rhizodeposits, and high microbial diversity in the rhizosphere as a microbial barrier are some defense mechanisms that grafted plants can provide (Cardarelli et al., 2020; Ruan et al., 2020). Understanding those mechanisms will facilitate the development of future strategies for making crop production less prone to the use of synthetic or chemical pesticides and, therefore, more sustainable. Besides, identifying specific bacterial and fungal genera with known beneficial functionality or potential biocontrol activity against plant pathogens may be used to develop biological control technologies (Olivieri et al., 2021).

#### 5. Nutritional benefits of grafting

Rootstock × scion combinations are investigated to assess their



compatibility and ability to optimize plant–microbial partnerships for resource-use-efficiency, including biological nitrogen fixation (BNF). Symbiotic and non-symbiotic nitrogen-fixing bacteria have a key role in increasing plant yield, and their importance is highlighted in several studies conducted under several experimental conditions, such as in aseptic *in vitro* culture, under greenhouse and field conditions (Bhattacharjee et al., 2008). Grafting can be applied to improve N use efficiency of plants through the vigorous root system of specific rootstocks that enhance the uptake and accumulation of N and other nutrients in scions or through the increased expression of genes, such as nitrate reductase and nitrite reductase that are responsive to grafting and improve N uptake and assimilation (Nawaz et al., 2017).

Grafting potential to improve N accumulation can be tuned by microbial communities. The BNF by the colonizing bacteria and the plant growth-promoting substances produced by the rhizobacteria can be promoted using rootstocks that are tolerant to low nitrogen levels in soils. Yet, the leaf nitrogen concentration can be increased by rootstocks that shape their rhizobacteria community structure with bacterial genera such as *Pseudomonas* and *Bacillus*, growth-promoting rhizobacteria, as observed in apple rootstocks (Chai et al., 2019; Vessey, 2003).

Still, in the context of grafting, there is a shoot-derived factor associated with nodule formation (Lohar and VandenBosch, 2005), with the rootstock genotype influencing the BNF (Vougeleka et al., 2023). For example, in grafts involving garden pea (*Pisum sativum*) and blue lupin (*Lupinus angustifolius*), both of which are capable of nodulating, it was observed that nodulation was promoted in pea rootstocks grafted to lupin scions. This promotion of nodulation occurred because peptide signals derived from pea roots were only partially recognized by lupin shoots in the autoregulation of nodulation (AON) pathway, leading to a reduction in a shoot-derived inhibitor and increased nodulation. The induction of root exposure to rhizobial bacteria was involved in this process (Foo et al., 2016). AON signaling elements are conserved in tropical and temperate legumes, such as soybean and *Medicago truncatula* (Ferguson et al., 2014; Osipova et al., 2012).

Grafting also modulates soil phosphorus cycling processes mediated by microorganisms. In grafted navel orange, the influence of rootstock on phosphorus immobilization and plant phosphorus acquisition efficiency (PAE), being the efficiency of phosphorus absorption of the rootstock and transport to the shoot, was associated with phosphatase activity in the rhizosphere (Raiesi and Moradi, 2021). Similarly, in grafted grapevines, changes in potential nutrient uptake were induced by rhizosphere bacteria's ability to produce siderophores and solubilize inorganic phosphate (Marasco et al., 2018). Since plants have different PAE mechanisms, grafted plants' nutrient efficiency depends on the rootstock's genetic potential for nutrient acquisition (Raiesi and Moradi, 2021). Thus, screening for highly efficient rootstocks in nutrient uptake can effectively promote sustainable agriculture development (Nawaz et al., 2017).

Similar to nitrogen, plants' phosphorus requirements can also be met with the help of a core microbiome, when different microbial species share functions related to nutrient acquisition (Neu et al., 2021). For instance, strigolactones are compounds that play a crucial role in AMF symbiosis by acting as signals that activate fungal spore germination and hyphal branching, thereby increasing contact with the host root (Besser et al., 2008). Strigolactones have the potential to indirectly promote the establishment of AMF symbioses or even *Rhizobium*-legume symbioses. They can be perceived as exogenous signals or plant endogenous compounds regulating shoot and root architecture (Kowalczyk and Hryniewicz, 2018). Grafting experiments revealed that mycorrhizal effects are related to enhanced nutrient absorption, growth performance, and plant stress tolerance (Camprubí et al., 2008; Navarro et al., 2014; Shu et al., 2017).

However, the responsiveness of grafted or ungrafted plants to signals that regulate the development of AMF symbiosis depends on the features of the scion and the rootstock used in grafting (Graham and Syvertsen, 1985; Nakaho et al., 2000). For example, shoot-derived factors of

non-AM host legume can suppress AM formation in pea roots, which typically host AMF, by downregulating strigolactone exudation (Foo et al., 2016). Moreover, adding strigolactone alone cannot induce AM symbiosis in non-AM species (Illana et al., 2011). The ability of specific rootstock to harbor a high percentage of AMF species colonizing the roots, as observed in apple replant orchard soils, is another condition that can be exploited or manipulated to improve apple nutrition but also other species of tree fruit (van Horn et al., 2021).

Promoting rootstock-selected microbiomes that regulate potassium absorption by plants can be beneficial as well. Using rootstocks that select potassium-solubilizing microorganisms overcomes potassium deficiency in *Vitis vinifera* varieties by increasing the diversity and abundance of microbes with similar traits in root-associated communities (D'Amico et al., 2018). In addition, exploring the use of rootstocks able to absorb higher amounts of potassium from soils (uptake efficiency) can enhance plant tolerance to low potassium stress and mitigate its negative effects on plant performance, as observed for grafting watermelon (Huang et al., 2013).

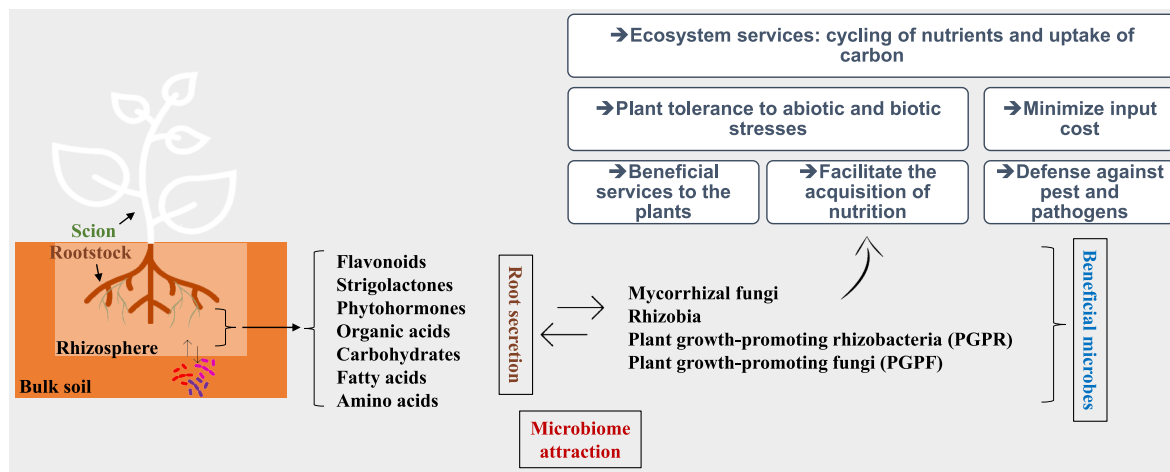
New grafting combinations with enhanced ability to recruit beneficial rhizobiome, including potassium-solubilizing microbes, mycorrhiza, plant growth-promoting rhizobacteria, and rhizobia, which result in beneficial outcomes such as FBN, nutrient availability, and protection against stresses, may be promising to improve plant nutrient uptake in general (Aslantaş et al., 2007; Vessey, 2003; Zhang et al., 2019). Moreover, discovering chemical mediators that orchestrate the conversation between plants and beneficial associated microbiota opens perspective to a knowledge-based chemical modulation of plant microbiomes that can sustain plant health and productivity (D'Amico et al., 2018).

## 6. Plant health benefits of grafting

Grafting also influences the recruitment of microbial communities in the rhizosphere, which can contribute to plant disease tolerance. For example, the influence of rootstocks on the severity of apple replant disease (ARD), a frequent soil-borne disease that affects young apple trees in replanted orchards, is involved with changes in the population of the root-zone microbial community determined by genotype (Laurent et al., 2010). Similarly, the resistance or susceptibility of apple cultivars to canker, a severe disease caused by *Neonectria ditissima*, is associated with the composition of endophytic bacterial and fungal communities in apple woody tissues (Olivieri et al., 2021). At the same time, the incidence of apple Valsa canker is related to the enrichment of specific species of bacteria and fungi assembled by rootstock types (Wang et al., 2022).

The root microbiota expands the capacity of plants by fostering processes such as defense responses to prevent diseases or reduce their severity, as well as enhancing growth and nutrient acquisition (Backer et al., 2018; Chowdhury et al., 2022; Liu et al., 2020). Recent research has demonstrated the reciprocal interaction between plants and root microbiome. For instance, suppressing plant immunity via the PHR1-RALF-FERONIA pathway allows the recruitment of specialized microbes that help alleviate phosphate starvation responses in *A. thaliana* (Tang et al., 2022). Bacterial-derived molecules, which are chemically and functionally diverse, are typically exo-metabolites readily accessible to the plant and other components of the biological community. These molecules may induce plant signaling pathways, leading to appropriate responses to environmental challenges (Fig. 1).

Grafted plants can also recruit a higher diversity and abundance of certain microbes that actively suppress pathogens or occupy the same niche in the rhizosphere (Ling et al., 2015; Ogundeji et al., 2021). In watermelon, the combined effect of grafting and root-associated microbiomes shaped a protective environment around plant roots against *Fusarium* wilt disease (Wang et al., 2022). Alternatively, in cases where grafted plants do not naturally harbor specific beneficial microbes for disease control, the rootstocks can recruit abundant and more diverse



**Fig. 1.** Schematic illustration showing how the microbiome is modulated by root exudation. Soil factors influence plant roots and microorganisms reshape the environment through a dynamic exchange of chemical responses and living and non-living stimuli. Plant-rhizomicrobiome signaling improves plant performance by optimizing microbial community assembly that develops with appropriate graft combinations. The benefits of grafting include plant growth, nutrient use efficiency, stress tolerance, disease resistance, and sustainable enhancement of cropping systems.

microbial communities that help suppress pathogens (Ling et al., 2015; Liu et al., 2009; Wang et al., 2022). Even foliar diseases can be controlled by root secretions triggered by pathogen infection, which recruit beneficial rhizobacteria and induce defense responses and disease resistance (Rudrappa et al., 2008).

Selecting rootstocks that attract effective antagonistic microorganisms can be a suitable approach to improving agriculture with sustainable disease control methods and enhancing plant resistance against pathogens (Wang et al., 2022). In addition, inoculating the soil with indigenous AMF is also effective in enhancing the resistance of common rootstock under pathogenic conditions by increasing the activity of defense-related enzymes and the accumulation of defense-related substances (Wang et al., 2021). Using specific grafting combinations and beneficial microbiome recruiting or inoculation to improve plant defense mechanisms may open new opportunities for disease risk management, reducing the need for chemical control in cropping systems and making it more sustainable (Cardarelli et al., 2020).

The mechanisms developed by grafted plants to recruit their microbiomes, either by the scion, rootstock or both compartments, as well as the interactions between them is challenging and yet could be a relevant field of study to contribute to plant adaptation in the context of changing climatic conditions (Darriaut et al., 2022).

## 7. Conclusion and future prospects

Integrating agricultural techniques that optimize plant and soil microbiomes can reduce the reliance on chemical fertilizers and pesticides by harnessing the beneficial microbiota of below-ground and above-ground compartments. Grafting offers the potential to enhance crop performance by combining adequate rootstock-scion that can modulate beneficial interactions between microbial communities and plant hosts (Cardarelli et al., 2020). Advances have been made to develop suitable rootstock-scion combinations for modern agriculture, managing diverse abiotic and biotic stresses in a more sustainable approach (Vougeleka et al., 2023; Yang et al., 2022). Gene editing system in plants by grafting was demonstrated to be an efficient method of transgene-free plant production that could be applied to a wide range of breeding programs and crop plants (Yang et al., 2023). Another advancement includes studying the vast diversity of bacteria and fungi in the rhizosphere and their interaction with grafted plants as an emerging field of science to understand its role in improving plant adaptation in the face of environmental challenges and pathogenic prevention (Gramaje et al., 2022; Darriaut et al., 2022; van Horn et al.,

2021). These advances support the interest in harnessing plant microbiome through grafting to enhance agricultural sustainability.

Moreover, the study of plant grafting can also have economic relevance since the technique can be applied to assess beneficial root and shoot combinations between species that are economically important, leading to the knowledge about the taxonomic and anatomic limits behind graft compatibility and to the guidance of great choices to explore graft mechanisms (Thomas et al., 2023), which may include the ones related to microbiome assemblage.

Identifying the mechanisms that underlie beneficial grafting-induced traits can contribute to the development of breeding and genetic engineering of new genotype combinations with superior performance (Williams et al., 2021). The a vast area to be explored regarding the plant-driven selection of microbes might provide new opportunities to stimulate potential microbial functionalities to enhance plant performance (Gopal and Gupta, 2016). Thus, grafting may facilitate new discoveries as a research tool to: investigate the signalling mechanisms behind microbiomes effects on plant health; discover new beneficial plant-microbe interactions; identify core microbial strains and compounds with biotechnological applications to enhance crop performance; select desired rootstock and scion traits for practical use in agriculture and breeding programs; and configure scion-rootstock-mediated microbiomes to the development of more efficient grafted plants (Guan et al., 2012; Liaqat and Eltem, 2016; Sabir et al., 2012; Schwarz et al., 2010).

A more sustainable system for plant production may consider embracing microbial-based approaches that promise to improve plant nutrition, increase yield, and mitigate adverse impacts of pests, diseases, and extreme climatic events on crop production (Santos and Olivares, 2021; Toju et al., 2018). The development of microbial-based approaches for crop improvement strategy includes grafting-mediated modulation of plant microbiomes that play a role as regulators of nutrient absorption, including the recruitment of AMF organisms that facilitate the uptake of water and mineral nutrients (D'Amico et al., 2018; Song et al., 2020). Similarly, protective root-associated microbiomes can also be shaped by root exudates, offering plants greater disease resistance (Ge et al., 2022; Liu et al., 2009).

Culture-independent surveys (such as high-throughput sequencing technologies) for bioprospecting are helping to identify plant-associated microbes that should be prioritized for further research. This technological approach could be followed up by selective culturing of candidate core microbiota, and manipulative experiments for the development of biofertilizers or biopesticides out of potent beneficial

microorganisms (Busby et al., 2017; Kumar and Dubey, 2020; Liaquat and Eltem, 2016). There might be a great portion of microbes with critical roles in the microbiome that can be isolated, formulated, and become new biological products with potential biocontrol activity and stimulatory compounds with growth-promoting effects, improving plant resilience to climate stresses in agriculture (Gramaje et al., 2022; Hartmann et al., 2009; Lakshmanan et al., 2014; Santos and Olivares, 2021). The inoculation of plant growth-promoting rhizobacteria (PGPR), engineered microbial consortia that combine complex functions, and synthetic communities on crop species is another management strategy that can be applied to improve microbial ecosystem services for crop yield and resilience (Arif et al., 2020; Cardoso et al., 2021; Vorholt et al., 2017). These kinds of findings imply that PGPR and other beneficial organisms can be employed in food production and point to the replacement of synthetic inputs by microbial-based ecological treatment (Sabir, 2013) (Fig. 2).

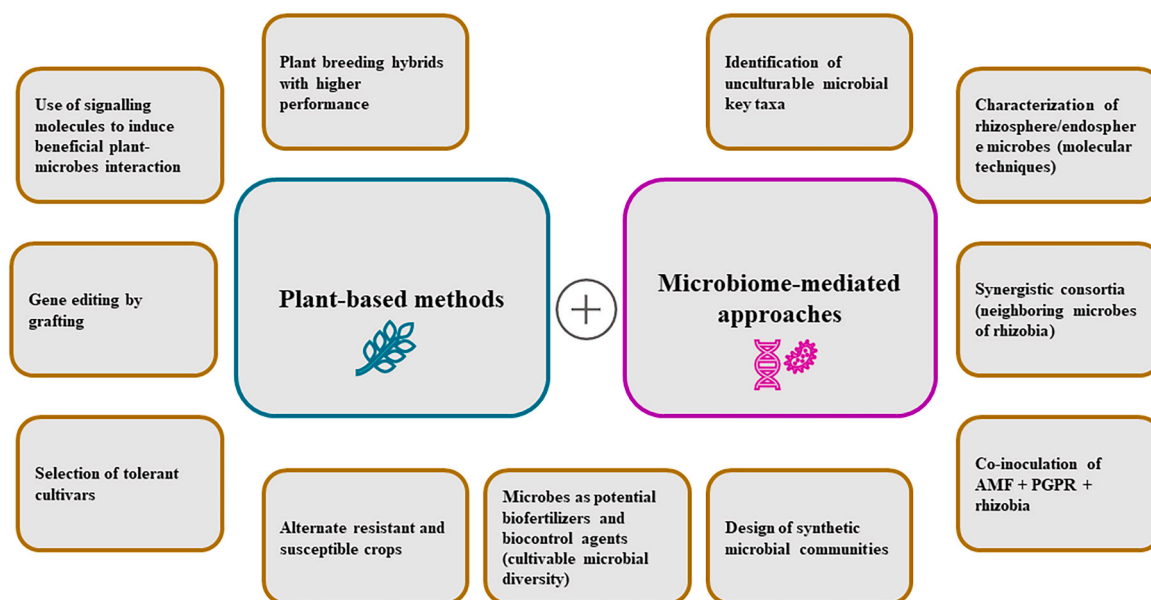
The selection of microbiotas in plant compartments through grafting provides a basis for future applications, such as microbial inocula, biofertilizers, or biostimulants, that favor a better microbiome composition in grafted and non-grafted plants (D'Amico et al., 2018; Marasco et al., 2018). As an alternative to inoculation, grafting allows the manipulation of rhizosphere microbiome to increase plant productivity. The influence of rootstock and plant compartments on microbial communities indicates opportunities for developing designed communities and microbiome-based breeding to improve future crop production (Poudel et al., 2019). Improving microbial selection with functional capabilities, such as antagonistic activity towards the plant pathogens, implicates positive effects on plant fitness, contributing to maintaining soil health and sustaining ecosystems and agricultural lands (Berg et al., 2006).

Many aerial endosphere microbes originate from the soil and migrate to the shoots from the root through the vasculature (Bertin et al., 2003; Marasco et al., 2018; Vives-Peris et al., 2019). Thus, changes in exudate composition resulting from grafting can lead to significant modifications in the taxonomic profile of plant microbiome, fostering beneficial interactions in the rhizospheric and impacting plant productivity and health (Saleem et al., 2018). Plant-associated endophytic bacteria in the root and leaves may have capacities such as biological nitrogen fixation, phosphate solubilization, and siderophores, among other traits (Andrade et al., 2023; James et al., 1997). Enhancing leaf microbiomes

with such functional traits can promote plant growth and stimulate effective components within the host plant, thereby increasing the potential for more sustainable agriculture practices.

Finally, more studies are needed to decipher the causes of rootstock and scion microbiome selection and the mechanisms by which grafted plants can shape their associated microbial community in shoot and root compartments. Understanding the extent to which host genotypes affect root systems, including root architecture and types, as the physiology with potential mechanisms that regulate microbiomes via metabolites and exudates. New research with experiments that deal with unclassified and unculturable taxa that could be important for host performance would also contribute to bioprospecting methods. Advanced metagenomics technologies will be helpful to identify and characterize the microbial strains beneficial to grafted plants. As well as the development of culturing methods to isolate and functionally characterize potentially key taxa candidate as beneficial microbes and test their biological functions, providing direct biological evidence of their impact to support the design of synthetic communities in microbiome-based crop production (Poudel et al., 2023).

However, the limiting factors determining the success of grafting connections must be considered when selecting scion and rootstocks genotypes. It is also important to conduct more studies to better understand the rootstock-scion microbiome interaction under different local environment, considering open-field and greenhouse conditions. The combinations of grafted and non-grafted crops, alternating resistant and susceptible varieties, can also contribute to sustain a more resilient ecosystem for vegetable production (Phani et al., 2023). Despite the advances of genome editing in plants, the application of such technology must ensure genomic stability for its use in food production (Yang et al., 2023). Always, when possible, the adoption of grafting can be optimized to benefit plants when combined with customized approaches to agriculture practices. These include compost application, organic soil amendments, 'microbe-friendly' crop cultivars, stimulating the resident, antagonistic microbial communities and non-tillage systems that increase the diversity of soil microorganisms, improve soil nutrient status and create a more resilient environment for plant growth and health sustaining the vegetable productivity (Gao et al., 2015; Tian et al., 2009; Wang et al., 2017).



**Fig. 2.** Future prospects involving microbiome-mediated approaches combined with plant-based methods, i.e., grafting with genetic improvement and cultivar selection that optimize beneficial microbes functioning. It will also act as an efficient strategy to improve plant performance under pathogenic conditions or in farming systems with limited inputs.



## CRediT authorship contribution statement

**Maristela Calvente Morais:** Investigation, Methodology, Supervision, Writing - original draft, Writing - review & editing. **Luana Ferreira Torres:** Investigation, Writing - original draft, Writing - review & editing. **Eiko Eurya Kuramae:** Conceptualization, Supervision, Validation, Writing - original draft, Writing - review & editing. **Sara Adrián Lopez de Andrade:** Data curation, Supervision, Validation, Writing - original draft, Writing - review & editing. **Paulo Mazzafera:** Conceptualization, Funding acquisition, Project administration, Resources, Validation, Writing - original draft, Writing - review & editing.

## Declaration of competing interest

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.

## Data availability

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

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