



Review

# Augmenting the Sustainability of Vegetable Cropping Systems by Configuring Rootstock-Dependent Rhizomicrobiomes that Support Plant Protection

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**Abstract:** Herbaceous grafting is a propagation method largely used in solanaceous and cucurbit crops for enhancing their agronomic performances especially under (a)biotic stress conditions. Besides these grafting-mediated benefits, recent advances about microbial networking in the soil/root interface, indicated further grafting potentialities to act as soil environment conditioner by modulating microbial communities in the rhizosphere. By selecting a suitable rootstock, grafting can modify the way of interacting root system with the soil environment regulating the plant ecological functions able to moderate soilborne pathogen populations and to decrease the risk of diseases. Genetic resistance(s) to soilborne pathogen(s), root-mediate recruiting of microbial antagonists and exudation of antifungal molecules in the rhizosphere are some defense mechanisms that grafted plants may upgrade, making the cultivation less prone to the use of synthetic fungicides and therefore more sustainable. In the current review, new perspectives offered by the available literature concerning the potential benefits of grafting, in enhancing soilborne disease resistance through modulation of indigenous suppressive microbial communities are presented and discussed.

**Keywords:** solanaceae; cucurbitaceae; defense mechanisms; soilborne pathogen; genetic resistance; microbial communities; grafting; soil/root interface

## 1. Introduction

Modern agriculture needs innovative strategies inspired by the principles of agroecology, aimed to guarantee soil conservation and fertility, to face the adversities that affect crop productivity and, generally, to increase the sustainability of intensive systems. One of the most important challenges for sustainability concerns the control of soil-borne diseases being considered a major limitation to crop production. The massive use of chemicals against plant pathogens is no longer a viable practice for environmental risks and human health care. The most commonly applied eco-friendly approaches include solarisation, biofumigation, crop rotation, tillage management practices, residue management and organic amendments [1]; additional strategies such as applications of plant growth promoting rhizobacteria (PGPRs), endo- and ectomycorrhizal fungi, cyanobacteria and other organisms can also improve plant resistance to soilborne pathogens. Several studies reported that plants can recruit a specific beneficial rhizosphere microflora which can contribute to reduce the activity of plant pathogens

and to make plants more resistant to environmental stressors [2,3]. Investigations on rhizosphere microbiome carried out by next-generation sequencing technologies allowed to identify and quantify microorganisms associated with the root apparatus of vegetable crops highlighting an evolutionistic mechanism of microbial recruiting adopted by plants.

Vegetable grafting is a propagation method largely used in solanaceous and cucurbit crops to increase plant resistance to soilborne pathogens as well as other environmental stresses, and to enhance crop productivity and fruit quality [4]. In soils infected by highly destructive plant pathogens, the use of resistant grafted plants represents the main biological-based method that allows cultivation of the highly susceptible cultivars [5]. In the latest years, increasing studies on the ecological role of the grafting revealed new interesting opportunities of this technology to contrast and limit the activity of soilborne pathogens and their damages on vegetable crops, by modifying the presence of beneficial root-associated microbes. For instance, Poudel et al. [6] used a grafted tomato system to study the effect of rootstock genotypes and grafting on soil bacteria communities and their results highlighted an effect of rootstock genotype on bacterial diversity and composition in the rhizosphere. Moreover, Duan et al. [7] reported that some pepper grafting combinations significantly increased the populations of fungi and actinomycetes in the rhizosphere enhancing the activities of peroxidase, catalase, phosphatase, invertase, urease, and nitrate reductase in root rhizosphere soil. Similar results were also reported in grafted eggplants [8]. Besides plant species, additional environmental factors such as soil type can also affect the microbial communities in the rhizosphere indicating the need to evaluate the rootstock-mediated effects on rhizosphere microbiome under different environmental conditions [9,10]. The above findings indicate the potential of using plant rootstocks as a mean to recruit specific soil beneficial microorganisms for biotic stress management.

This review offers a novel perspective on the potentialities of vegetable grafting as sustainable practices to enhance crop resistance to environmental stresses through the modulation of microbial community structure in the rhizosphere.

## 2. Soil Microorganisms for Biological Control of Plant Diseases

Rhizosphere and bulk soil around growing plants constitute the habitat for a large number of microbial species with different lifestyles, interacting with one another, with the soil and plants. The culturable bacteria and fungi associated with rhizosphere can contain up to  $10^{11}$  microbial cells per gram of roots [11]. Some microorganisms have a neutral effect on the plant, but many known microorganisms are beneficial to the plants for nutrient and carbon cycling, soil organic matter formation and stabilization, so influencing agricultural productivity. They are symbiotic nitrogen-fixing bacteria (*Rhizobium leguminosarum*), endo- and ectomycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR) and other fungi [12]. Many of these microorganisms are even investigated for their ability to prevent or limit soil-borne plant pathogens (fungi and oomycetes are the most important) through mechanisms as hyperparasitism, antibiosis and competition for ecological niches and nutrients [13].

Microbial hyperparasites have a predatory behavior: they enter host cells of fungi and oomycetes helped by secreting cell-wall lytic enzymes (as chitinases, cellulases and proteases) and feed on the pathogen as long as it dies. Parasitic activity is quite common, and well documented for *Trichoderma* and *Gliocladium* against fungal pathogens as *Rhizoctonia*, *Sclerotinia*, *Verticillium* and *Gaeumannomyces* [14–16]. Even *Coniothyrium minitans* [17] and *Sporidesmium sclerotivorum* [18] are effective in controlling diseases caused by sclerotia-forming fungi. Chitinolytic activity of *Pseudomonas* spp. is responsible of antagonistic activity towards *R. solani* [12].

Antibiosis results from the release of low-molecular weight compounds produced by microorganisms in the surrounding environment which are deleterious to the metabolism or growth of plant pathogens [19,20]. Fluorescent *Pseudomonas* spp., *Bacillus* spp., *Streptomyces* spp. and *Trichoderma* spp. produce antibiotic molecules (phenazines, 2,4-diacetylphloroglucinol, pyoluteorin, and pyrrolnitrin) affecting the electron transport chain, metalloenzymes, membrane integrity, or cell membrane and zoospores [20–22].

With the competition for space, pathogens are prevented from accessing root surface and plant tissue whereas the competition for nutrients, especially for carbon released as root exudates, affect the saprophytic phase of pathogens, and may cause lacking spore germination and microbiostasis [11]. Siderophore-producing *Pseudomonas* spp. are involved in the competition for iron, a micronutrient essential for growth and activity of the pathogens and are able to reduce disease incidence or severity of pathogenic fungi [23].

Literature survey reveals many pivotal examples of rhizosphere-competent microbial biocontrol agents of plant pathogens. Fungi belonging to *Trichoderma* genus, for example, have antagonistic properties towards a plethora of plant pathogens relying on all of the antagonist modes [24]. *T. harzianum* and *T. asperellum* showed antagonistic effects against *Fusarium oxysporum* of tomato [25–27] and melon [28] under field conditions. Gava et al. [28] tested different *Trichoderma* species (*T. harzianum*, *T. viride*, *T. koningii*, and *T. polysporum*) in a naturally infested soil and obtained the highest control of melon wilt using *T. polysporum*.

Malolepsza [29] observed a significant stimulation of systemic defenses (activation of antioxidant enzymes and enhancement of phenols) by *T. virens* inoculation of tomato plants, leading to lowered *Rhizoctonia solani* infection. Some authors verified the involvement of the proteins Sm1 and Epl1 in the systemic protection of tomato plants mediated by *Trichoderma* spp. [30]: in presence of these proteins it was observed an increase in disease resistance against *Alternaria solani*, *Botrytis cinerea*, and *Pseudomonas syringae* due to the increased expression of peroxidase and  $\alpha$ -dioxygenase encoding genes [30], the elicitation of the salicylic acid pathway [31,32] and the ethylene pathway [31]. Even the accumulation of phenolic acids, flavonoids and *de novo* synthesis of catechins, enhanced by *T. atroviride* inoculation, is supposed to contribute to cucumber protection against *R. solani* [33]. In cucumber seedlings inoculated with *T. harzianum* inoculations, Chen [34] found alterations in nuclear DNA content and cell cycle-related genes expression that might maintain a lower ROS accumulation and higher root cell viability counteracting *Fusarium* disease in open field. Quantitative proteomics studies on black pepper plants primed with *T. harzianum* confirmed the plant defense response against the pathogen *Phytophthora capsicum* through an increase of ethylene synthesis and activating both the isoflavanoid pathway and lignin synthesis [35].

Coating of tomato seeds with *T. asperellum* and *Bacillus subtilis* decreased the susceptibility of plants to *Pythium aphanidermatum* [36]. Frequently the combination of different antagonists in microbial consortia improves their effectiveness for the involvement of diverse biocontrol mechanisms [37]. In watermelon, a systemic acquired resistance against *F. oxysporum* f.sp. *niveum* was related to the inoculation with a consortium of *T. harzianum*, *Paenibacillus polymyxa* and other antagonistic microorganisms that activated defense-related enzymes [38]. *T. harzianum* and *Bacillus amyloliquefaciens* together inhibited the growth and production of mycelia and sclerotia protecting over 80% of tomato, squash and eggplant seedlings against *Sclerotinia sclerotiorum* [39]. Similarly, to *T. asperellum*, even the arbuscular mycorrhizal fungus *Rhizophagus irregularis* (previously known as *Glomus intraradices*) lowered disease incidence of *Fusarium* wilt in tomato plants [40]. Both these agents increased plant height, chlorophyll content and Ca, Mg, S, Mn, B and Si uptake. *T. harzianum* combined with *Glomus intraradices* induced a plant basal resistance attenuating the hormone (ethylene and abscisic acid) disruption induced by *F. oxysporum* in melon [41] whereas associated with *Glomus mossae* is useful in cucumber against *Phytophthora melonis* increasing the transcription level of defensive genes as phenylalanine ammonia-lyase, cucumber pathogen-induced 4, lipoxygenase and galactinol synthase [42]. In field experiment the consortium mycorrhizae, *Trichoderma* and plant growth-promoting bacteria enhanced the pepper yield and modulated the activities of defense enzymes as polyphenol oxidase, peroxidase, superoxide dismutase, and catalase [43]. Even arbuscular mycorrhizal fungi alone can control plant soil-borne diseases [44,45] activating a systemic plant immune response. Mycorrhizal fungi reduced the disease severity index of eggplant *Verticillium* wilt [46]; the disease tolerance was related to a lower proline content and relative electrical conductivity in leaves, and to higher activity of browning related enzymes (phenylalanine ammonia-lyase, polyphenol oxidase and peroxidase). Panda et al. [47]

found that pre-colonization of tomato roots with mycorrhizal fungus *Piriformospora indica* systemically induced resistance against early blight by *Alternaria solani*; after pathogen attack *P. indica* induced a rapid activation of jasmonic acid/ethylene-mediated basal defenses against pathogen infection by altering the expression of JA/ET related genes. *Glomus mossae* suppresses *F. oxysporum* development in the roots and rhizosphere of watermelon and modulates the composition of root exudates. Bacterial species of the *Bacillus* and *Pseudomonas* genus control plant disease by producing antibiotics or stimulating the host resistance [48]. Tomato plants inoculated with *Bacillus amyloliquefaciens* exhibited significantly low *F. oxysporum* f. sp. *lycopersici* infection compared with the control [49]. *Clonostachys rosea* counteracted gray mold disease not only by suppressing development and sporulation of *Botrytis cinerea* but also by inducing the resistance of tomato plants against *B. cinerea* [50].

### 3. How Plants Recruit Antagonist Microbes to Prevent the Infection by Pathogens

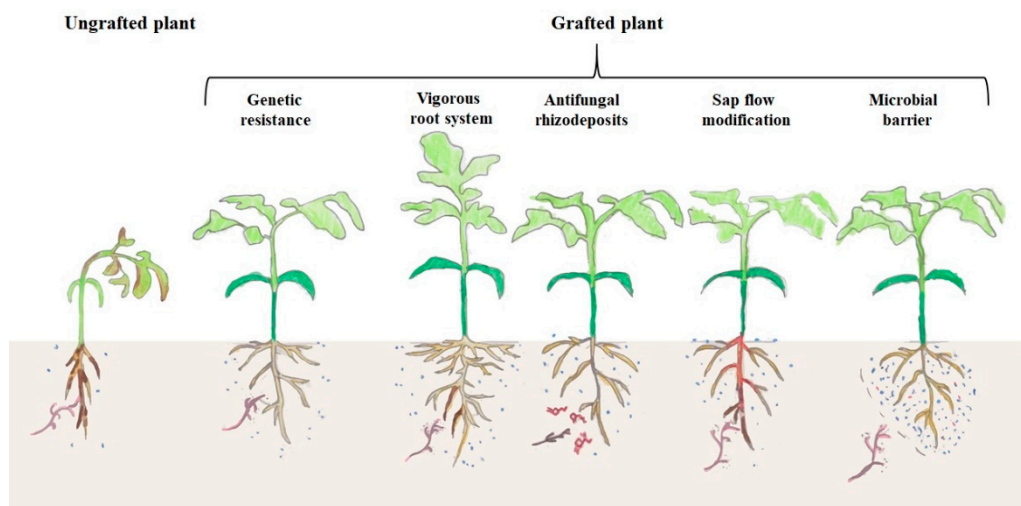
The rhizosphere microbiome has been recognized as the second genome of the plants [11], and it may reveal the greater ability of the plant in adapting to the external environment, including the protection degree against pathogenic agents. Plants through their roots are in dynamic communication with the surrounding bulk soil microbial communities [51]. Roots exudates are a main food source for microorganisms and a driving force for their assembling and activities. Carbon and nitrogen are exudates as simple molecules (sugars, organic acids, secondary metabolites) or complex polymers (mucilage) but their composition varies with the plant genotype, developmental stage, and the presence of (a)biotic stresses [52]. It has been seen that microbial communities in the rhizosphere of different plant species growing on the same soil are often different and vice versa [53,54] thus demonstrating that plants modulate exudates profile (alteration of biosynthesis and transport of molecules) and immune system activities to recruit specific beneficial microbes. Moreover, plants can detect communication signals between bacteria in the rhizosphere (quorum sensing signals) and produce molecules that stimulate or deactivate these signals so influencing the outcome of microbe-microbe and/or plant-microbe interactions [55]. L-malic acid is the small signalling molecule exudated from tomato plant roots that is responsible for biofilm formation and root colonization of the antagonistic *Bacillus subtilis* [56]. Similarly, Tan et al. [57] confirmed the important role of malic and citric acids in tomato root surface colonization of *Bacillus amyloliquefaciens*. Moreover, different organic acids in watermelon and cucumber roots exudates stimulate the beneficial *Paenibacillus polymyxa* [58] and *Trichoderma harzianum* [59], respectively. Glucose, succinic acid, *p*-hydroxybenzoic acid, *p*-coumaric acid and glutamic acid in cucumber root exudates recruit *Trichoderma* with the most relevant effect from glucose [60].

Recent advances reveal that multiple signals operate in the establishment and the maintenance of arbuscular mycorrhizal symbiosis including calcium spiking, reactive oxygen species and phytohormones [61,62]. The plant hormones strigolactones are actively exuded into rhizosphere as ex-planta signalling molecules that attract arbuscular mycorrhizal fungi affecting both pre-symbiotic and symbiotic phases [63]. Other important hormones involved in the onset of the AM symbiosis are jasmonates [64], gibberellins [65], ethylene [66], and auxins [67]. A possible crosstalk between auxin and strigolactones is also postulated in tomato plants [68]. Martínez-Medina et al. [69] studied the interaction between tomato roots and the AM fungus *Rhizophagus irregularis* showing a regulatory role of nitric oxide mediated by a specific phytohemoglobin during the symbiosis.

### 4. Defense Mechanisms in Grafted Plants against Soilborne Pathogens

Disease control-related mechanisms of grafting may rely on the genetic traits of the rootstock-type. Interspecific grafting, for example, is often secured with the non-host resistance of the rootstock against species-specific soil-borne pathogens, such as the wilting causal agents belonging to *F. oxysporum* group that harbour differentially host-compatible *formae specialis* [70,71]. Limitation in spread of tomato wilting-associated bacteria in resistant cultivars could avoid the generalization of infection to the entire vascular tissues of susceptible scion [72]. Graft-transmissible resistance to airborne disease has been observed for sweet pepper cultivar grafted on a resistant cherry pepper rootstock [73]. In this situation,

the effects of rootstock on the scion is the major determinant of resistance. Disease resistance of grafted plants may also result from the enhanced vigour for which grafted plants grow more fortified and more efficient in resource utilization, as well as developing vigorous root apparatus that allow them to better withstand pathogenic attacks caused by the parenchymatous parasites [74]. For example, reduction of *Verticillium* wilting by effective eggplant grafting on *S. lycopersicum* × *S. habrochaites* rootstock is associated to promotion of plant vigour [75]. Another mechanisms of disease resistance promoted by grafting is the release in the rhizosphere of exudates having antifungal activity on pathogen propagules. Liu et al. [76], for example, found root exudates from grafted eggplants, suppressive against the *Verticillium dahliae* mycelial development, contrarily to those released by the non-grafted ones. Grafting can affect root ability to harbour rhizosphere-competent microbes and to regulate beneficial antagonistic functions by modifying the root-architecture and the exudate profiling [77,78]. Rootstock/scion interaction can modulate regulations of transcripts and metabolites affecting disease susceptibility to fungal pathogens [79]. For instance, rootstock can influence disease resistance of scion by modifying secondary metabolites in the sap flow moving through the vascular system [80]. Shibuya et al. [81] attributed the transient reduction of disease symptoms on cucumber scion to changes in morphology or physiology in response to the modified water relations immediately after grafting onto squash. Defense mechanisms in grafted plants against soil-borne pathogens are summarized in Figure 1.



**Figure 1.** Disease-resistance mechanisms of grafted plants in soil infested by pathogens.

Experimental evidences suggested that the above listed mechanisms act synergistically in the regulation of the disease resistance of grafted roots. Greenhouse trials carried out by Song et al. [77] allowed to define as changes in root exudates from watermelon grafted on *Lagenaria siceraria* and *Cucurbita pepo* rootstocks, have promoted the non-host holobiont resistance to *F. oxysporum* f. sp. *niveum* infections through additional pathogen exclusion effects. In particular, niche chemical shifts around watermelon grafted roots affected the sheltered microbial diversity, increasing, for example, biocontrol-associated bacteria populations, such as *Sphingobacteriia* and *Bacillus* [77]. Biochemical investigations on watermelon/bottle gourd rhizodeposits have allowed to detect the *ex-novo* formation of bioactive proteins associated with plant resistance to biotic and abiotic stresses [82] and the release of chlorogenic and caffeic acids involved in the microbiostasis against propagules of the wilting causal agent [83]. Findings suggesting that the ungrafted watermelon delivery of molecular signals that are normally used as stimuli by pathogens harbouring the rhizosphere [84], with the grafting, likely, it is interrupted. In this light, combining grafting with environmentally friendly soil treatments (e.g., soil solarization) could slow down the recovery of pathogen recrudescence, often observed in conductive soils with the continuous monoculture cropping [84]. Structural

variations of a root-associated microbiome after grafting have been also reported in open field tomato production, where Poudel et al. [6] showed rootstock-specific filtering effects driven by vigorous rooting, on endosphere and rhizosphere microbiomes enriched by representatives of *Firmicutes*, *Verrucomicrobia*, *Planctomycetes*, *Proteobacteria* and *Acidobacteria*. Under greenhouse, the use of *Solanum torvum* as rootstock for eggplant, induced an incremental shift in *Bacteria* and *Actinomycetes* on the root system, and in the responsive rhizosphere soil enzymes were found both associated to the pathogen population lowering and *Verticillium* wilting decrease [85].

Plant domestication privileged the selection of agronomic traits strictly related to the edibility, quantity and quality of the yields, leaving on the way all those alleles that gave to wild relatives the ability to profitably deal with soil microorganisms, reducing the potential of modern cultivars to lead rhizosphere microbiome assembly and functions [86]. In order, to bridge this gap, only recently some breeding programs are including, among the genetic improvement objectives, the enhanced ability of crops in recruiting beneficial host-specific root microbiota too [87]. In the meantime, horticultural experiences indicated that, at the moment, grafting better than others available technologies allows to reach this phenotype more quickly depending on the specific influence of rootstock genotype [84,88]. The metabolic structure of rootstock-recruited microorganisms, for example, has been implemented for managing tree resistance to the apple replant disease complex in replanted orchards [89]. Thereby, also vegetable productions may alleviate detrimental risks hidden into the intensive cropping systems following a holistic approach, in which grafting improves telluric environment adaptation of cultivar through the reinforcement of partnerships with beneficial and biodiverse microbiota and the enhancement of the efficient resource utilization. A summary of the possible directional interactions occurring in the soil environments shared by grafted roots and microbiome aiming at reducing pathogens pressure is reported in Table 1.

**Table 1.** Possible directional interactions occurring in the soil between grafted roots and microbiome aiming at reducing pathogens pressure.

To	Grafted Roots	Microbiota
Grafted roots	Allelopathy Competition for space, water and nutrients	Selection-filtering effects C-food providing Activation of the endophytism
Microbiota	Nutrients availability Growth promotion Induction of resistance to (a)biotic stresses	Antibiosis Hyperparasitism Niche occupying Essential food depletion

Relationships-mediated by rootstock between the vegetable scion and the infected soil open new opportunities for disease risks management in a more environmentally friendly way (Table 2).

**Table 2.** Soilborne disease risk management using ungrafted and grafted plants.

Management Goal	Ungrafted Plants	Grafted Plants
Reduction of disease risks	Cultivation of susceptible cultivars on healthy soils	Grafting of susceptible cultivars on disease resistant rootstocks
Genetic innovation regarding plant protection objectives	New cultivars resistant/tolerant to pathogens	New rootstock genotypes resistant/tolerant to pathogens New grafting combinations with enhanced root ability to recruit protective rhizobiome
Engineering soil microbiome for enhancing its antagonistic structure	Soil conditioning techniques mitigating soil sickness phenomena	Actions for maintenance of ecological bio-barriers proliferating on the rootstock roots
Increased effectiveness of the chemical control means	Wide-spectrum preventive and curative applications of fungicides	Targeted use of active molecules both in time and in dosage
Increased effectiveness of the biological control agents	Mass applications of the bio-based formulates	Coordinating application of the external microbial antagonists, with the naturally present rhizobiome Targeted use of specific microbial strains characterized by grafted-rhizosphere competence

Moreover, the integration of grafting technology with other agronomic, chemical and/or biological control means can allow to further reduce the risks of soilborne diseases especially in a long term. However, the use of chemical inputs must be carefully evaluated to avoid depression of beneficial indigenous soil microflora in the rootstock rhizosphere. Under these boosted agroecological conditions monitoring of plant and soil health status over time is crucial.

## 5. Conclusion and Future Prospects

Grafting represents a relatively recent innovation in the vegetable production systems of Western Countries; this advanced technology allowed to reduce the negative impact of soilborne pathogens in solanaceous and cucurbit crops depending on the disease resistance level of rootstock. Grafting can enhance plant disease resistance through several multiple defense mechanisms in plant. Recent studies demonstrated that rootstock-mediated effects on rhizosphere microbiome can contribute to reduce the soilborne diseases by stimulating indigenous microflora able to compete for food and space with plant pathogens and to reduce their activity through antibiosis and hyperparasitism. Moreover, plant-beneficial microbes recruited by rootstock can enhance soilborne disease resistance indirectly through the increase of plant nutrient availability, the stimulation of plant growth and the induction of resistance to biotic stresses. Despite experimental evidences demonstrated a significant role of rhizosphere microbiome in enhancing soilborne disease resistance in grafted plants, more studies are necessary to better understand the scion-rootstock-rhizosphere microbiome interaction under different environmental conditions. Advanced technologies like metagenomics can help to identify and characterize the microbial strains in the rhizosphere of grafting combinations in order to link the changes in rhizosphere microbial community to enhanced plant resistance to specific soilborne pathogens. This knowledge could allow to develop new disease control strategies based on the combined application of selected microbial inoculants and specific grafting combinations.

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