Emerging microbial biocontrol strategies for plant pathogens

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ABSTRACT

To address food security, agricultural yields must increase to match the growing human population in the near future. There is now a strong push to develop low-input and more sustainable agricultural practices that include alternatives to chemicals for controlling pests and diseases, a major factor of heavy losses in agricultural production. Based on the adverse effects of some chemicals on human health, the environment and living organisms, researchers are focusing on potential biological control microbes as viable alternatives for the management of pests and plant pathogens. There is a growing body of evidence that demonstrates the potential of leaf and root-associated microbiomes to increase plant efficiency and yield in cropping systems. It is important to understand the role of these microbes in promoting growth and controlling diseases, and their application as biofertilizers and biopesticides whose success in the field is still inconsistent. This review focusses on how biocontrol microbes modulate plant defense mechanisms, deploy biocontrol actions in plants and offer new strategies to control plant pathogens. Apart from simply applying individual biocontrol microbes, there are now efforts to improve, facilitate and maintain long-term plant colonization. In particular, great hopes are associated with the new approaches of using "plant-optimized microbiomes" (microbiome engineering) and establishing the genetic basis of beneficial plant-microbe interactions to enable breeding of "microbe-optimized crops".

1. Introduction

It is a persistent issue worldwide that an enormous number of plant pathogens, varying from the smallest viroid consisting solely of a single strand of RNA, to more complex pathogens such as viruses, bacteria, fungi, oomycetes and nematodes, cause many important plant diseases and are responsible for major crop losses. Although there are many causes that can be attributed to the decrease in crop productivity, the loss due to pests and pathogens plays a crucial role in the damages worldwide. Every year, plant diseases cause an estimated 40 billion dollars losses worldwide [1], either directly or indirectly. At least 20–40% of losses in crop yield are caused by pathogenic infections [2]. The consequences of plant diseases range from major devastations to minor nuisances. Some plant diseases can be highly destructive and catastrophic on a large scale. In the 1840s, the potato late blight pathogen *Phytophthora infestans* caused a major destructive disease that had tremendous effects on human history, as it caused food shortages resulting in a million deaths and migration of 1.5 million people from Ireland [3]. Potato is the fourth largest food crop, providing more food on a per hectare basis than any other crop and serving as an important substitute to the major cereal crops for the world population [4]. The annual losses of potato crops due to late blight are conservatively estimated at US$6.7 billion per year [5–7].

Another historic example, brown leaf spot of rice caused by *Helminthosporium oryzae*, had been reported in Asia, Africa, South America and USA. It was not only ranked as one of the major rice fungal diseases, but also one of historical interest [8]. It caused severe devastation by reducing rice yields which caused the death of two million people in Bengal in the 1940s as the direct result of calamitous famine [9,10]. *Helminthosporium maydis* was the causal agent of a severe epidemic of southern corn leaf blight in 1970 in the USA which caused economic hardship that destroyed 15% of the USA corn crop with losses estimated at US$1 billion [9,10]. There are many more historic examples; refer to references [11–15] for a review of the top 10 fungal, oomycete, bacterial and viral plant pathogens, and plant-parasitic nematodes, respectively, that are considered most significant for Molecular Plant Pathology.

Most alarming is the unprecedented recent trend of new fungal and fungal-like plant pathogen alerts that have increased by more than 7-fold since 2000 [16]. This cannot solely be attributed to improved detection methods, but rather agricultural practices, in particular monocultures, increased international trade and the use of only a few cultivars. These practices promote the evolution of more virulent strains, often with increasing pesticide tolerance that not only affect

agricultural crops but many indigenous wild species.

The control of plant diseases is crucial for the production of food, fibre and biomaterials. As global food production must be increased by at least 70% until 2050, there is growing concern for global food security, which has become one of the most important international issues in recent times [17,18]. It is estimated that the demand for food and global food security will continue to increase for the coming 40 years with the growing human population and consumption. Already at present, food systems are responsible for 60% of global terrestrial biodiversity loss, and around 25% of the global greenhouse gas emissions, hence, sustainable solutions for future food security are urgently needed [19]. The worldwide attempt to expand food production to answer the need for food has become serious [20,21]. The growing world population requires an efficient management and control of diseases in crop production. Crop protection plays a significant role in defending crop productivity against competition from pathogens [22]. The following paragraph introduces *Phytophthora cinnamomi* as an example that has gained global significance for both, food security (crop production) as well as biodiversity of wild species.

Phytophthora cinnamomi, a soil-borne oomycete holds a special interest due to its broad host range, mostly of woody species [23]. Several studies showed that chestnut and oaks are the main species affected in Europe [24–26] as well as ornamental crops and nursery plants such as coniferous and broadleaf plants [27,28]. It is considered as one of the most highly destructive forest pathogens globally [29], and is responsible for severe crop diseases [30]. *P. cinnamomi* is native to Southeast Asia, but it was later found in most temperate to tropical areas [31]. Its global spread has led to devastating consequences. For example, in Australian soils, *P. cinnamomi* is now widely distributed and causes major devastation in horticultural crops such as macadamia, pineapple and avocado [32,33]. It has also been listed as an important threat to the Australian environment and biodiversity by the Federal Government [34]. Depending on the environmental conditions and plant susceptibility, several plant species are at risk of extinction [35,36]. Infected plants exhibit root, collar, and sometimes stem necrosis as the primary symptoms, resulting in declines and stem cankers [23]. Being predominately soil-borne, this pathogen is particularly hard to control.

Beneficial biocontrol microbes may be one of the few options that show potential. These can provide benefits by competing with pathogens or by directly antagonising plant pathogens (e.g. by production of antimicrobial compounds; [37]). The local infection with plant pathogens can lead to systemic acquired resistance (SAR; [38,39]) but of significant interest is also the ability of beneficial non-pathogenic rhizobacteria to prime plants for induced systemic resistance (ISR) against pathogens [40]. This priming offers a better preparedness to plants that are able to respond faster and stronger to pathogen attack. Organic mulches colonized with *Gliocadium virens* (KA 2301) and *Tricoderma harzianum* (KA 159.2), termed "bioenhanced mulches" were found efficient in suppressing *P. cinnamomi* in avocado roots when used as surface mulch [41]. In another study, disease severity and stem lesion length of *Phytophthora capsici* root and crown rot of bell pepper significantly reduced and total microbial population and the biocontrol activity was enhanced when soil was incorporated with compost containing chitosan, crab shell waste, and citrus pulp with molasses [42].

2. Plant disease management

2.1. Resistant varieties

Breeding for resistant varieties is one of the successful options and most reliable management tools for controlling plant diseases [43]. It is one of the most attractive approaches and can be considered as an ideal method if good quality plants are adapted to the growing regions with sufficient levels of tolerance and durable resistance [44]. Resistant varieties were introduced via systematic plant breeding by choosing

varieties of high disease resistance level of the same species or genus [45]. The control of plant diseases by means of resistant varieties has been used in many crops and is relatively inexpensive compared to the cost of pesticides [46] but these varieties often take decades to develop and GM-plants suffer from extremely high regulatory approval cost and consumer acceptance. Mixtures of two varieties by the combination of a range of positive characters in a single crop genotype often result in the reduction of yield loss and provide a better disease management [47]. In the USA, disease-resistant plant varieties make up 75% of the land used in crop production [48]. For example, the control of stem rust caused by *Puccinia graminis* f. sp. *tritici* using resistant wheat plants has contributed to the suppression of that disease, whose infection is mainly found on stems and leaf sheaths, as well as on leaf blades and glumes [49–53]. In spite of all the advantages, in many countries the problems began after the breakdown of new varieties' resistance within several years of their release due to several causes, such as mutations of the pathogens toward virulence, sexual and asexual recombination events, issues with variety uniformity in genetics, and decreasing field resistance. Cases of resistance breakdown were observed in many crops, such as blast resistance in rice, cotton leaf curl disease, grapevine downy mildew and yellow wheat of rust [54]. New promising approaches to disease resistant varieties come from genome editing using CRISPR/Cas9 [55] and other intragenic technologies that may be deregulated and considered in par with classical breeding approaches.

2.2. Chemical control

With the growing human population, the need for food has increased as well, resulting in extensive use of agrochemicals targeted to increase crop yields by protecting them from pests and pathogens. Chemicals are one of the main components in Integrated Pest Management (IPM) as they are crucial in preventing losses and damages caused by plant diseases, as demonstrated with the increase in the number of fungicide specifications since the 1960s [56]. It is undeniable that pesticides have brought improvements in crop quality and agricultural output, in terms of market opportunities and facilitation of farm work [57]. However, regardless of the significant importance of chemicals for pest and disease management, fungicide resistance has been one of the unavoidable problems [58,59]. As a result, every year higher costs for fungal disease control applies and higher dosages and new chemicals are introduced to protect crops and plants. As a consequence, this has caused undesirable side effects, such as food contamination, environmental dispersal and higher costs of food production [59]. Many chemicals used in agriculture possibly also destroy the beneficial microbes, such as beneficial endophytic fungi and bacteria [60]. Chemical fungicides are often lethal to beneficial insects and fungi inhabiting the soil and may also enter the food chain [61]. For example, the use of Oryzalin and Trifluralin has been found to inhibit the growth of certain species of mycorrhizal fungi that aid in nutrient uptake in plants roots [62]. Furthermore, Triclopyr, a common landscape herbicide inhibits beneficial ammonia-oxidizing bacteria [63]. Glyphosate, commonly used as weed killer, also greatly reduces the growth and activity of beneficial free-living heterotrophic bacteria that aid in nitrogen fixation [64].

Chemicals used to control pests and diseases are deposited on the crops and their harvests. Reports from FAO-WHO and data provided by the US Food and Drug Administration indicate that persistent organic pollutants (POPs) are present in virtually all types of food, including fruits, vegetables, poultry and dairy products [65]. With the greater concern on the negative effects and continued dependence on toxic chemicals for plant diseases and pest control, more attention should be given to find and develop alternative inputs of less toxic and less disruptive methods to facilitate plant growth in agriculture in controlling pests and pathogens in general and fungal-diseases in particular.

2.3. Biological control

Among the alternatives, biological control of plant pests and pathogens appears to the best option for the development of low cost, eco-friendly and sustainable management approaches for protecting plants and crops. Biologicals, including biocontrol microbes, are now accepted as significant tools for the control of plant diseases in sustainable agriculture [66]. A number of biological control options are available. However, a better understanding of the complex interaction between plants, environment and pathogens is necessary for further exploration on this topic because it may easily fail if plants are already under high disease pressure [67]. In plant pathology, biocontrol can be referred to as the interrelationship of many environmental factors, aiming to diminish the unfavourable effects of detrimental organisms and enhance the growth of useful organisms, such as crops, beneficial insects, and microorganisms [68]. It often results in multiple interactions, such as suppressing the pest organism using other organisms or the application of antagonistic microorganisms to suppress diseases and the introduction of host-specific pathogens. The application of natural products and chemical compounds extracted from different sources, such as plant extracts, natural or modified organisms or gene products are other examples of biological control [68,69]. The primary idea of conducting research on biocontrol is to reduce the reliance on agrochemical use and the risks for human health and the environment [70]. It was developed 20–25 years ago when plant pathology research and education attracted more interest in the application of useful microorganisms for the management of plant diseases, including plant parasitic nematodes [70]. The different types of interactions between the populations are referred to as mutualism [71], protocooperation [72], commensalism [73], neutralism [74], competition [75], amensalism [76], parasitism [77], and predation [78]. All these biological control interactions between plants and microbes occur naturally at a macroscopic and microscopic level [68].

Throughout their life cycle, plants are vulnerable to the various environmental challenges of abiotic and biotic stresses, such as drought, herbivores and potentially pathogenic fungi, oomycetes, nematodes, bacteria and viruses. In response, plants have evolved a broad range of strategies to counter-attack and ward off attackers [79]. Plant defense mechanisms can be categorized as passive defenses; non-host resistance, physical and chemical barriers, rapid active defenses and delayed active defenses. Rapid active defenses involve the changes in membrane function, the initial oxidative burst, cell wall reinforcement, hypersensitive response (HR), resulting in programmed cell death (PCD) and phytoalexins [80]. Delayed active defenses include pathogen containment and wound repair, pathogenesis-related (PR) gene expression and systemic acquired resistance (SAR). Plant defense signaling molecules include salicylic acid (SA), which is generally considered necessary for defense against biotrophic pathogens and SAR, as well as jasmonic acid (JA) and ethylene (ET), both of which are involved in defense against necrotrophic pathogens as well as in beneficial plant-microbe interactions, including priming and induced systemic resistance (ISR) [81]. The latter two terms define a state of higher alertness of the plant that enables a faster and stronger response to pathogen attack. Fig. 1 provides an overview of the various plant-microbe interactions, defense signaling and systemic resistance.

3. Types of pathogens and how some successful pathogens are able to trick plants

Plants are infected by pathogens with different modes of nutrient uptake [82]. These have direct consequences to how the plant needs to respond. Host-pathogen relationships generally comprise three groups according to their mode of infection on plant: necrotrophs, biotrophs, and hemibiotrophs [83]. If this is not recognized early enough, the plant may respond in the wrong manner which can aggravate the damage. A good understanding of the pathogen's lifestyle is therefore important if we wish to assist plants to defend themselves.

3.1. Biotrophic pathogens

Biotrophic pathogens grow, reproduce and obtain nutrients from living plant tissue by engaging in an intimate relationship with living plant cells. Examples are the tomato leaf mold causal agent, *Cladosporium fulvum* and *Ustilago maydis* which is the causal agent for corn smut. Some of them coevolved into obligate biotrophs, and cannot be grown on artificial media, for instance, rusts and powdery mildews [84,85]. On the other hand, the non-obligate biotrophs which limit the damage of host cells can be cultured on artificial media; however, they cannot grow as saprophytes. Biotrophs have a restricted number of host ranges where these pathogens are only fitted to particular types of plants. These pathogens have evolved specialized structures such as nutrient-absorbing haustoria that penetrate into the plasma membrane of the host cells and take up the nutrient sap and release effector molecules that let them grow invasively on particular host genotypes [85–88]. However, the pathogen is unable to initiate a parasitic relationship if the host cells die in advance of invasion by the pathogen. Hence, ROS production, HR, PCD and SAR are the most effective defense responses against biotrophs and in *Arabidopsis* these responses are generally associated with SA signaling.

3.2. Necrotrophic pathogens

Necrotrophic pathogens feed on dead plant tissues by killing the cells before parasitizing the plants. Necrotrophs usually invade the host cell through wound sites or dead cells and secrete toxins and cell wall-degrading enzymes to destroy the host tissue. They can also live as saprophytes outside the host cells and can be grown on synthetic media [89]. The pathogens are unable to kill the host cell if the host genotype is unresponsive to the toxins or the toxins are derivatized, compartmentalized or not released at the right time, place or concentration. Examples of fungal necrotrophs are species of *Cochliobolus, Alternaria* and *Botrytis* [82,85]. It is essential that plants recognize necrotrophs early to counteract the initial oxidative burst and prevent HR and PCD. This role is attributed to JA signaling in *Arabidopsis* that acts as antagonistic pathway to SA signaling in this respect.

3.3. Hemibiotrophic pathogens

Hemibiotrophs such as *Magnaporthe grisea,* the causal agent for rice blast, are pathogens that have an intermediate lifestyle, where they initially have a biotrophic relationship with the host but consequently cause the death of host cells, at which point they switch their lifestyle to necrotrophic nutrient acquisition [90]. *Phytophthora*, *Pythium* and *Fusarium* species have a similar lifestyle as well as some species in the genera *Colletotrichum* and *Venturia* and the well-studied bacterium *P. syringae* [85,91]. Many agronomically important pathogens belong to this group as often crops are not able to respond with plant defense in an appropriate and timely manner.

3.4. How successful pathogens trick plants

According to the feeding behavior of the pathogen, plants activate different post-invasive lines of defense, mediated by phytohormones [92]. When attacked by biotrophs, typically SA activates an HR leading to localized PCD that limits pathogen spread, together with the production of PRs, ROS detoxifying enzymes and antioxidants which exhibit antimicrobial properties and provide protection against oxidative stress, respectively, in the surrounding tissues [92]. SAR can then be triggered in healthy systemic tissues of locally infected plants. Alternatively, necrotrophs and herbivorous insects typically activate the JA defense signaling pathway [92]. This prevents localized cell death and leads to the production of chemical and physical defenses against the
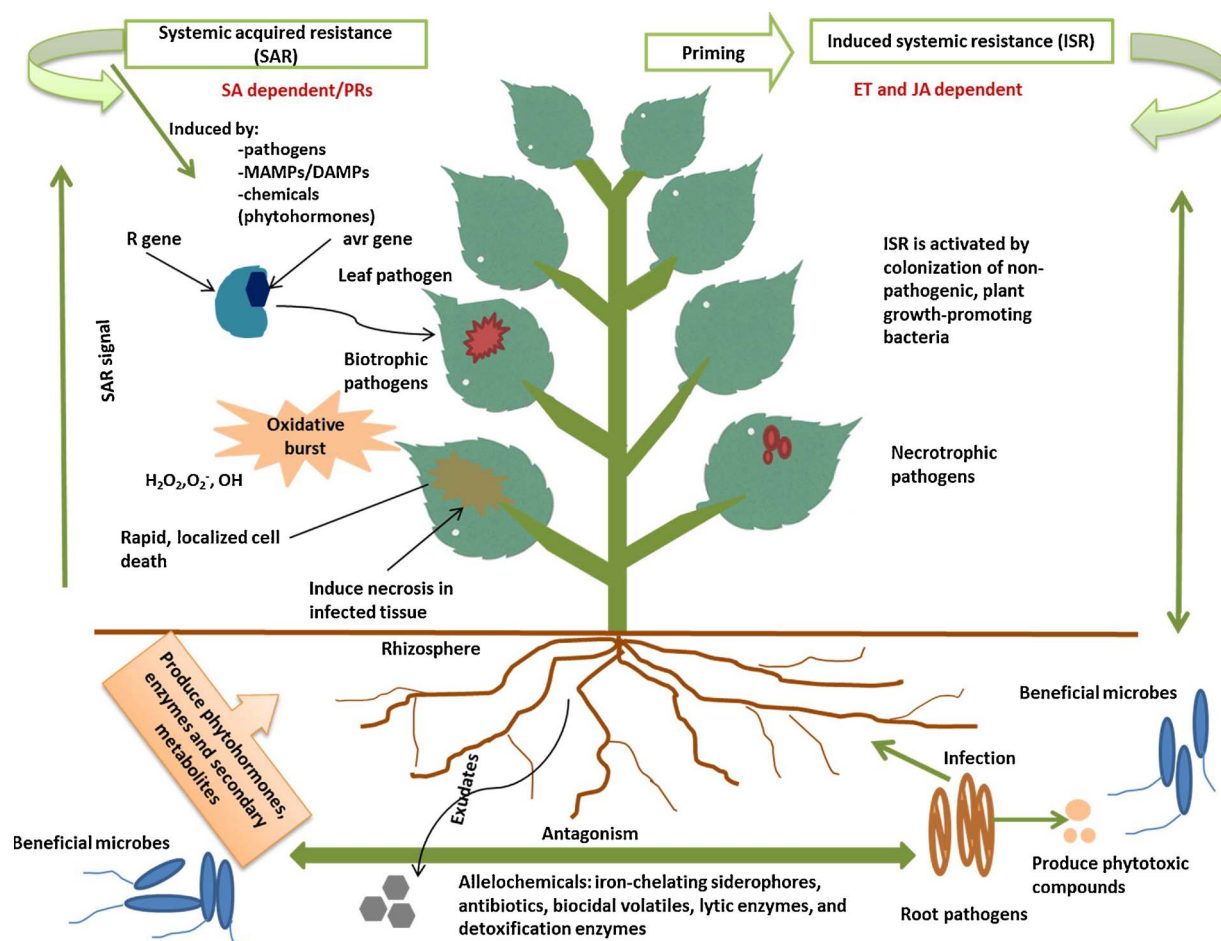
Fig. 1. Schematic diagram showing two different types of systemic resistance in plants. SA-dependent systemic acquired resistance (SAR) is activated upon pathogen attack, foliar treatments of plants with microbe- or damage-associated molecular patterns (MAMPs, DAMPs), phytohormones or certain xenobiotics (e.g. some pesticides). SA-independent induced systemic resistance (ISR) is directed primarily by jasmonic acid (JA) and ethylene (ET). Both SAR and ISR are crucial in plants for defense against biotic and abiotic stresses.

pathogen. However, recently it has become clear (including findings from our own work, [93]) that many severe pathogens hijack the wrong pathway, leading to a further weakening of plants. For example, hemibiotrophs, such as *Fusarium* spp.,

Phytophthora spp., and *P. syringae* as well as plant viruses can suppress the SA pathway by early activation of the antagonistic JA pathway that prevents HR and cell death. This can also be interpreted as pathogens disguising themselves as beneficial microbes. By comparison, root-colonizing beneficial microbes activate ISR that is also mediated by JA and ET signaling. Some of the available microbial products developed for agricultural applications include these microbes in their formulation [94].

4. Microbial biocontrol options

Weller [95] predicted that a big challenge will be faced by microbiologists and plant pathologists who are trying to search for and develop environmentally friendly control agents against plant diseases, to limit the use of large amounts of chemical pesticides. Alternatively, using beneficial microorganisms as biopesticides is one of the most effective methods for safe crop-management practices that works under low to medium disease pressure [69]. For over 65 years, studies on soil-borne pathogens have been conducted by introducing microorganisms into the rhizosphere [70]. Generally, the interest in this research area has gradually increased, evidenced by a number of early books [70,96,97] and reviews that have been published on this topic [98–100]. In the backdrop of food security issues and the alarming increase in recent pathogen alerts [16], there is now significant

renewed interest in this topic and all of the large Agbiotech companies are now investing in the development of biological applications [101,102]. It was suggested by the researchers that biological control will continue its significance and play a major role in modern agriculture in the future and present.

4.1. Microbial antagonisms

The microbes that are considered ideal for use as biological control agents are the ones that can grow in rhizospheres, where the soil is described to be microbiologically suppressive to pathogens, as this area provides a frontline defense for the roots against various pathogenic attacks. Root colonization by beneficial microbes delivers their pathogen-antagonising metabolites into the root system where they directly suppress pathogenic bacterial growth [103]. This antagonistic relationship between microbes and pathogens mostly leads to significant disease control, where the established populations of metabolically active beneficial microbes initiate protection either by direct antagonistic activity of pathogens, by outcompeting pathogens or by stimulation of host plant defenses (priming) [104]. It also involves antibiosis which is the secretion of diffusible antibiotics, volatile organic compounds, and toxins, as well as the development of extracellular cell wall degrading enzymes such as chitinase, β-1,3-glucanase, beta-xylosidase, pectin methylesterase and many more [103,105].

4.2. Plant-microbe interactions that assist in biocontrol

Plant roots offer an ecological habitat for the growth of soil bacteria

that thrive on root exudates and lysates as nutrients. The mutualistic interaction between plants and beneficial microbes that commonly occurs in nature often leads to either an improvement in plant nutrition and/or enhancement of the plant's ability to prevail over biotic and abiotic stress. In all cases, this provides a competitive advantage leading to improved growth and plant proliferation [101].

A variety of endophytic bacteria and free-living rhizobacteria on the root surface and rhizosphere utilize the nutrients released from the host, as well as secrete metabolite substances to the soil that aid in controlling plant diseases caused by fungi or bacteria [106,107]. This indirect interaction between the microbes and plants causes an increase in the supply of minerals and other nutrients that have an influence on plant growth, for example by atmospheric nitrogen fixation or phosphorous solubilization [108]. The interaction between plants and a group of biocontrol microorganisms also indirectly enhance plant growth by suppressing pathogens' growth and activity [109,110]. Furthermore, microorganisms can be directly involved in plant growth promotion, by acting as agents for stimulation of plant growth and management of soil fitness, for example through the production of auxin [111]. This may also include mitigation of abiotic stress. Despite their different ecological rhizosphere niches, some of the beneficial microbes apply the same mechanisms to stimulate plant growth and suppress deleterious pathogens [112–114]. The following sections provide examples how certain plant-microbe interactions assist in biocontrol against pathogens.

4.3. Production of antimicrobial compounds

The colonization of the rhizosphere niche by plant growth-promoting bacteria (PGPR) is assisted by the production of allelochemicals such as iron-chelating siderophores, antibiotics, biocidal volatiles, lytic enzymes (chitinases and glucanases), and detoxification enzymes [113–115]. For example, rhizobacteria include antibiotic-producing strains such as *Bacillus* sp. producing iturin A and surfactin, *Agrobacterium* sp. producing agrocin 84, *Pseudomonas* spp. producing phenazine derivatives, pyoleutorin and pyrrolnitrin, and *Erwinia* sp. producing herbicolin A [169,170], that are persistent in the rhizosphere [171,172]. The mycoparasitism of phytopathogenic fungi of the *Trichoderma* and *Streptomyces* genera have important roles in secretion of chitinases and glucanases [173]. A common feature of successful biocontrol strains and a crucial factor for plant root pathogen suppression is the production of antibiotic compounds and fluorescent siderophores that enable effective competition for iron [174]. Allelochemicals as secondary metabolites are generated directly or indirectly by plants and secreted into the root zone through abiotic or biochemical reactions [116], but can also be produced by associated fungi and bacteria. Numerous non-pathogenic *Pseudomonas* rhizobacteria have the capability of inducing systemic resistance in plants to protect against a wide range of plant pathogenic fungi, bacteria, and viruses [81]. In addition, they also produce siderophores to suppress soil-borne plant pathogens [117,118]. Bacterial siderophores inhibit plant pathogens by competing for copper, zinc, manganese [119] and especially iron [120]. Solubilization and the competitive acquisition of ferric iron under iron-limiting conditions limit the availability of iron to other soil inhabitants and subsequently limits their growth [121,122]. The scarcity of essential trace elements in the soil ecology results in harsh competition between the soil inhabitants [121].

Pseudomonas is a genus of which many species have been identified to produce antifungal metabolites, such as phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol (DAPG), and pyoluteorin [123]. Numerous studies on the plant growth inducer of fluorescent *Pseudomonas* [99,124] have described it as the most promising class of PGPR for biocontrol of plant diseases [125]. This is due to their ability of rapid and aggressive colonization in which this indirectly prevents the invasion of deleterious pathogens from the root surface [126].

Many studies have reported members of the *Bacillus* genus as

elicitors of ISR, as well as plant growth promoters. It was indicated that the mechanisms of elicitation are related to the cytochemical alterations and ultrastructural changes in plants during pathogen attack [127]. Some strains of *Bacillus* spp. were found to elicit ISR against *Cucumber mosaic virus* (CMV) on tomato with severity reduction of 32–58% for PGPR-treated plants [128]. Murphy et al. [129] reported the elicitation of systemic protection against CMV by two-strain combinations of *Bacillus* spp. incorporated into the potting mix, resulting in a significant reduction of disease severity and significant increases in plant fresh weight and number of fruits and flowers. Several strains of *Bacillus* sp. have demonstrated an efficacy in reducing disease and promoting plant growth under field conditions. The application of PGPR *Bacillus subtilis* IN937b, *Bacillus pumilus* SE34 and *Bacillus amyloliquefaciens* IN937a as seed treatments for ISR against CMV on tomato has significantly increased the yield and plant height and reduced the disease severity and incidence [128]. Similarly, field trials conducted on cucumber have confirmed the elicitation of systemic protection against cucurbit wilt by *Bacillus* strain INR7 [128].

4.4. Priming and induced systemic resistance (ISR)

Rhizobacteria-induced systemic resistance or ISR, also referred to in its early stage as priming, was first discovered by Van Peer et al. [130]. It is described as an enhanced defensive capacity of the whole plant to multiple pathogens induced by beneficial microbes in the rhizosphere [131] or elicited by specific environmental stimuli which lead to potentiation of the plant's innate defense against biotic challenges [132]. This higher state of alertness then enables the plant to respond faster and stronger against subsequent pathogen attacks. Some selected strains of non-pathogenic PGPR and fungi are able to activate plant defenses in plants to reduce the activity of deleterious microorganisms, and then initiate ISR that is mediated by JA and ET signaling [81,132]. Non-pathogenic rhizobacteria are capable of activating defense mechanisms in plants in a similar way to pathogenic microorganisms, including reinforcement of plant cell walls, production of phytoalexins, synthesis of PR proteins and priming/ISR [133].

The complex ISR system has been partially elucidated in several model plants including *Arabidopsis*, with three general pathways being recognized. Two of the recognized pathways are involved in the direct production of PR proteins with alternate mechanisms for induction. In one of the pathways, PR proteins are produced as the result of pathogen attack while in the other pathway, production of PR proteins are initiated due to wounding or necrosis-inducing plant pathogens. In the pathogen-induced pathway, SA is produced by plants, contrary to the wounding pathway which relies on JA as the signaling molecule [40]. Both pathways antagonize each other, possibly to enable the plant to finely tune its defense response depending on the attacker encountered [92]. The third pathway of induced resistance which leads to systemic resistance is referred to as rhizobacteria-induced systemic resistance (ISR) which is provoked by non-pathogenic root-associated bacteria, and is dependent on the plant hormones JA and ethylene.

Plants with ISR exhibit stronger and/or faster activation of defense mechanisms after a subsequent pathogen or insect attack or as a response to abiotic stress, when inoculated with rhizobacteria [81]. Beneficial microbes play an important role in defense priming of ISR for applied plant protection. Few studies have been conducted on the potential of priming using beneficial microbes in the rhizosphere to induce systemic immunity to airborne pathogens under glasshouse and field conditions. The inducing biocontrol strain *P. fluorescens* WCS374 was found to suppress *Fusarium* wilt and increase radish yield [134]. Similarly, root colonization by the beneficial fungus *Piriformospora indica* increased growth and yield of the medicinal plants *Spilanthes calva* and *Withania somnifera* under field conditions [135]. It was also found to systematically prime barley for tolerance against biotic and abiotic stress [135]. Enhancement in the plant's defense capability by priming is associated with defense gene expression, *de novo* synthesis of PR

Table 1

Some early examples of successful priming of plants by beneficial microbes for ISR-mediated defense mechanisms.

Treatments	Response	References
Tomato roots colonized with mycorrhizal fungus *Glomus mossae*	Fungus systemically safeguards plants against *Phytophthora parasitica*	[140]
Cucumber plants previously inoculated with PGPF *Trichoderma asperellum* T203, then infected with *Pseudomonas syringae* pv. *Lachrymans*	Priming induced in plants triggering expression of PR genes	[166]
Carnation (*Dianthus caryophyllus*) inoculated with *Pseudomonas* sp. WCS417r followed by *Fusarium oxysporum* f. sp. *dianthi* attack	Phytoalexin levels were increased compared to control plants	[130]
ISR induced by *Bacillus pumilus* SE34 against the root-rot fungus *F. oxysporum* f. sp. *pisi* in bean (*Phaseolus vulgaris*)	Appositions of phenolic material and fungal entry successfully prevented by rapid strengthening of root cell wall at penetration site	[167]
ISR triggered by *Pseudomonas fluorescens* WCS417r in *Arabidopsis*	Effective against different types of pathogens without activation of *PR* genes	[168]
Endophytic colonization of *Vitis vinifera* L by plant growth promoting bacteria *Burkholderia phytofirmans* strain PsJN	Accumulation of phenolic compounds and cell walls in the exodermis and cortical cell layers	[169]
ISR activated by *P. fluorescens* EP1 against red rot of sugarcane caused by plant PGPR *Colletotrichum falcatum*	Higher levels in the defenses related enzymes such as chitinase and peroxidase in the treated sugarcane tissue	[170]
Pseudomonas denitrificans and *Pseudomonas putida* evaluated against *Ceratocystis fagacearum* on oak	Oak wilt pathogen significantly reduced crown loss in inoculated containerized live oaks	[171]

Table 2

Examples of bioactive signaling compounds that lead to beneficial plant-microbe interactions.

Exudate/Compound	Beneficial microbe(s) attracted	Function/Benefit to plant/Reference
Flavonoids	Rhizobia	N-fixation to legumes and other plants when free-living; leads to increased yields [144,145]
JA defense signaling-specific exudates (after MeJA treatment)	*Bacillus thuringiensi, Bacillus cereus, Planococcaceae; Paenibacillus amylolyticus; Lysinibacillus sphaericus; Lysinibacillus fusiformis*	Antifungal, antibacterial; antioomycete; insecticidal; assist in defense against root pathogens and herbivorous insects; reduced yield losses [142]
Arabinose, glucose, fructose, ribose, inositol; erythritol (during P deficiency)	To be determined	P solubilization; leads to increased yields [172]
Strigolactone	Mycorrhizae, *Burkholderia, Frateuria, Sphingomonas, Legionella, Talaromyces, Peziza*	P solubilization, water supply, defense; leads to increased yields and resilience against abiotic and biotic stresses (unpublished)
Malate, succinate, fumarate	*Pseudomonas fluorescens*	Suppresses pathogens *Pythium ultimum, Gaeumannomyces graminis, Fusarium oxysporum*; reduced yield losses from pathogen attacks [173]

proteins and antimicrobial compounds in uninfected tissue as a reaction to the first infection. It has been reported that activation of the inducible resistance and defenses in plants incur a major cost for plant reproduction and growth [136]. However, in other studies, it has been reported that the cost of priming in *Arabidopsis* is much lower than the cost of directly inducing defense against pathogens [137]. Considering the protection priming offers when disease occurs, one can conclude that the benefits of priming outweigh the cost involved during activation.

The first report of ISR being observed was in carnation roots treated with *Pseudomonas* sp. WCS417r which exhibited resistance when inoculated with *Fusarium oxysporum* f. sp. *dianthi* on the stem [130]. In another study, seeds treated with *Pseudomonas fluorescens* caused a reduction in incidence of foliar lesions of *Pseudomonas syringae* pv. *phaseolicola* on bean [138]. A similar incident of induced resistance was observed when *Colletotrichum orbiculare* was inoculated into emerging leaves when PGPR was previously applied to cucumber seeds [139].

Priming is a well-known common feature of induced resistance responses to challenge pathogenic infections by beneficial microorganisms [140]. Table 1 shows some of the first examples of successful priming of plants for defense mechanisms with beneficial microbes. Tomato roots colonized with mycorrhizal fungi showed a similar interaction when systemically protected after infection with *P. parasitica* [140].

5. Emerging biocontrol strategies

Deciphering the "plant-microbiome language" could be a good approach to develop new biocontrol strategies. Plants may have their own language that allows them to communicate with their associated microbiomes by releasing a broad variety of chemicals through their leaves and roots. This language could be what helps the plant to attract and select specific microbes in the rhizosphere and phyllosphere that can provide specific benefits that are needed [141]. In turn, this microbiome will influence plant health and growth, via different mechanisms. Similar like individual plant beneficial microbes, rhizosphere soil microbiomes contain a wide variety of microbes that promote plant growth through direct mechanisms by increasing the availability of nutrients to plants, or by the production of various phytostimulators (modulating plant hormone levels) or through indirect mechanisms by acting as biocontrol agents.

Understanding how plants communicate will give us ideas and may help us fight diseases without the application of chemicals. The attraction of specific microbes in the rhizosphere is associated to the signaling molecules and hormones [142] and specific root exudates [143] secreted by the plants to match their needs. The vast and well-studied symbiosis interaction of legume-rhizobia is a good example of chemical language where secretions of specific compounds by the plants attract specific rhizobacteria [144,145]. Table 2 provides some examples of known plant exudate-microbe interactions that lead to beneficial outcomes.

Comprehensive study of the individual bioactive exudates in the rhizosphere is required to understand the attraction of individual microbes within microbiomes to enable more accurate manipulation of soil microorganisms before it can be adapted into agricultural practices. The following paragraphs outline new promising approaches that may lead to improved crop yields and potentially more resilient plants (Fig. 2).

5.1. Use of exudates as a way to attract beneficial biocontrol microbes

Root exudates are one of the major factors that influence composition and function of rhizosphere microbial populations. Specific root exudates attract specific beneficial microbes that match their specific

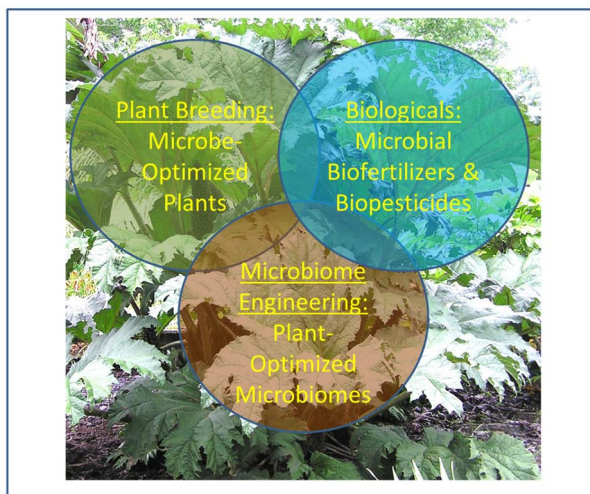## Integrated microbial approaches to increase crop production

Fig. 2. Proposed integrated strategies for improved crop yields by making use of the plant's microbiome. While the use of microbial biofertilizers and biopesticides for disease control are advancing rapidly in recent years, crop breeding programs have yet to incorporate amenity to beneficial plant-microbe interactions to breed "microbe-optimized plants". Similarly, efforts towards microbiome engineering can in the future lead to microbial consortia that are better suited to support plants. The combination of all three approaches may be integrated to achieve maximum benefits and potentially significantly improved crop yields to address food security.

needs (Table 2). An abundance of evidence has shown that plants provide benefits for the microbes by attracting and maintaining specific microbiomes using chemical exudates. For example, flavonoids released from legumes attract specific nitrogen-fixing rhizobacteria [145] and some beneficial rhizobacteria were found to activate the plant defense responses to prevent foliar diseases [146]. By gathering all these information, we are able to apply this knowledge to use exudates as an approach to attract beneficial microbes to control various plant diseases. The application of soil microbiomes in agriculture has also been practised extensively to improve plant nutrition and/or disease resistance [147,148]. Our recent studies have shown that there is a correlation between hormone-treated plants and defense signaling mutants which resulted in different exudate profiles and an attraction of different microbial populations [142,143]. Furthermore, signaling by the plant hormone strigolactone attracted not only mycorrhiza but also other microbes that aid in phosphate solubilization, water supply and defense (unpublished data). It can be concluded that we can manipulate the rhizosphere microbial population by simply spraying plants with signaling chemicals or altering the genotype (plant breeding) to attract beneficial microbes [143,149].

5.2. Use of substrates to maintain beneficial biocontrol microbes near crops

Beneficial biocontrol microbes can be kept by culturing using substrates as medium of growth. Substrates are the composition of nutrients they require for growth, metabolism and activity of microbial cells. Bai et al. [150] showed that the majority of associated microbes can be cultured by employing systematic bacterial isolation approaches. This can be seen as an advantage to recruit the beneficial microbiomes from the existing soil microbiota as well as adding and maintaining beneficial microbes for the biocontrol of plant diseases by providing the right substrates as media of growth. The nutritional versatility of beneficial microbes, especially bacteria, make them adaptable to different types of habitats and environments.

5.3. Phyllosphere biocontrol

Foliar diseases are a serious problem for many types of crops [151].

Among the top eight most important fungal plant pathogens worldwide, six of them are the causal agents of serious foliar diseases [11]. It is crucial to gain a better and clear understanding of the role of foliar microbiomes for better insight in crop protection. The application of microbial biocontrol agents is an environmentally friendly and viable alternative method to synthetic chemical control [152]. Biocontrol microorganisms have been tested as spray application on foliar diseases, including powdery mildew, downy mildew, blights and leaf spots [153]. They have also been applied as liquid commercial formulation for controlling stem-end rot pathogen on avocado plants [154]. In another study, several antagonist bacterial was found to inhibit the growth of bacterial stem rot caused by *Erwinia chrysanthemi* on tomato plants under greenhouse condition [155]. The biological products Serenade (*B. substilis* QRD137) suppress floral infection of blueberries and reduces fungal growth in flowers treated with the bacterial strain [156]. Plants defend themselves on the leaf surface by producing antimicrobial compounds or by promoting growth of beneficial microbes through the release of nutrients and/or signals [141]. Scientists have proposed that leaf-colonizing microbes play an essential part in foliar disease progression and prevention in plants [157]. Pre-emptive colonization or niche occupation is suggested as the key factor for development of protection against pathogens [158]. Profiling the phyllosphere microbial [141] and chemical environment, and identifying and making use of important plant-microbe as well as microbe–microbe interactions on the leaf surface will reveal new insights into the shaping of foliar microbiomes by plants and may ultimately lead to new strategies to enhance food security.

5.4. Breeding microbe-optimized plants

Different *Arabidopsis* ecotypes have shown up to 4-fold differences in plant yield when inoculated with *Pseudomonas simiae* WCS417r [149]. This demonstrates that the genetic make-up of the plant plays a major role in the outcome of the beneficial interaction [159]. Hence, the aim of this new approach would be to breed plants that are optimized to attract and maintain beneficial biocontrol microbes. Breeding programs have so far not taken this trait into account, but before this can become a major effort it is essential that we better understand how beneficial microbes are attracted and maintained. Genetic engineering and plant breeding would enable us generate microbe-optimized plant that produce the right exudates to attract and maintain beneficial microbes at the right time, either at the root or on the leaf [160]. Plants design their own rhizosphere environment by the secretion of specific exudates to improve nutrient availability and interaction with specific beneficial microbes [160]. A prerequisite for this is that the targeted microbes are present, so this strategy may need to link with the inoculum of the matching biocontrol microbes.

5.5. Microbiome engineering, plant-optimized microbes and plant-optimized microbiomes

The aim of this new approach is to engineer or breed individual microbes or entire microbial consortia that harbor beneficial microbes and to maintain them for crop plants in different soil types. As a result, we would produce plant/soil-optimized microbes and plant/soil-optimized microbiomes that can be used as inoculum for different crops in different soils. To our knowledge this strategy has not been deliberately applied anywhere, but there is evidence that soil microbiomes adapt to their crops over time leading to improved plant-microbe interactions [161]. A substantial body of evidence supports the major role of the naturally occurring plant microbiome in disease development and progression in plants [162]. Again, it is essential that we better understand how beneficial microbes are attracted and maintained.

5.6. Matching microbe-optimized plant seed with the optimal microbiome and soil amendment practices for each soil type

Scientists are working hard to find the right microbes that help specific crops grow better. Microbe-coating of seeds with promising microbes for the right soil is one of the best options for optimizing plant-microbe interactions. Seeds laced with the right microbiomes would be the best options compared to other applications like sprays or root soaks when considering the transient nature of the microbiomes. The microbiomes potentially act either as inoculants, which help plants to absorb nutrients, or biocontrol products that aid in protecting the plants against pests and diseases, or both. The microbiomes derived from the soil samples are cultured and cryopreserved and stored up before being applied to the seeds. They will ideally become part of the rhizosphere after the seeds germinate and the plant takes root. To make sure that beneficial microbes are maintained, some soil amendments may be required. Maybe it would be possible to identify "probiotics" to maintain healthy plant microbiomes.

Several powerful inoculants formulated from beneficial bacteria (e.g. *Rhizobium*) for treating legume seeds are available in the market. Apart from stimulating the formation of nitrogen fixing nodules on leguminous plant roots for the growth of healthier plants with better yields, they may also help in suppressing the disease-causing microbes, and hasten nutrient availability and assimilation. Kalra et al. [163] demonstrated the effectiveness of vermicompost-based (granular and aqueous extract) bioformulations from natural microbial growth-promoting compounds which improve the stability and life of the bioformulations. Similarly, Rice et al. [164] had shown a successfully commercialized co-culturing of the phosphate solubilizing fungus *Penicillium bilaii* with *Rhizobium* as a legume inoculant. In another study by Liu and Sinclair [165], co-inoculation of soybean with bradyrhizobia and *Bacillus megaterium* enhanced nodulation of soybean.

The integration of microbial biofertilizers, biocontrol microbes, optimized microbiomes, soil amendments and matching microbe-optimized crops for different soil types would be the penultimate goal to benefit most from positive plant-microbe interactions. Clearly, this is a largely untapped area that deserves major research efforts, as it holds the promise to improve crop yields and address food security in an environmentally-friendly and sustainable manner.

Acknowledgements

References

[1] M.J. Roberts, D.E. Schimmelpfennig, E. Ashley, M.J. Livingston, M.S. Ash, U. Vasavada, The Value of Plant Disease Early-warning Systems: a Case Study of USDA's Soybean Rust Coordinated Framework, United States Department of Agriculture, Economic Research Service, 2006.

[2] S. Savary, A. Ficke, J.N. Aubertot, C. Hollier, Crop Losses Due to Diseases and Their Implications for Global Food Production Losses and Food Security, Springer, 2012.

[3] J. Donnelly, Great Irish Potato Famine, The History Press, 2002.

[4] E.C. Oerke, H.W. Dehne, F. Schönbeck, A. Weber, Crop Production and Crop Protection: Estimated Losses in Major Food and Cash Crops, Elsevier, 2012.

[5] J. Guenthner, K. Michael, P. Nolte, The economic impact of potato late blight on US growers, Potato Res. 44 (2001) 121–125.

[6] D. Evers, S. Bonnechère, L. Hoffmann, J.F. Hausman, Physiological aspects of abiotic stress response in potato, Belg. J. Bot. 14 (2007) 141–150.

[7] D. Pimentel, Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species, CRC, Boca Raton, Florida, 2011.

[8] S. Padmanabhan, The great bengal famine, Annu. Rev. Phytopathol. 11 (1973) 11–24.

[9] A. Ullstrup, The impacts of the southern corn leaf blight epidemics of 1970–1971, Annu. Rev. Phytopathol. 10 (1972) 37–50.

[10] L. Tatum, The southern corn leaf blight epidemic, Science 171 (1971) 1113–1116.

[11] R. Dean, J.A. Van Kan, Z.A. Pretorius, K.E. Hammond-Kosack, A. Di Pietro, P.D. Spanu, J.J. Rudd, M. Dickman, R. Kahmann, J. Ellis, The top 10 fungal pathogens in molecular plant pathology, Mol. Plant Pathol. 13 (2012) 414–430.

[12] S. Kamoun, O. Furzer, J.D. Jones, H.S. Judelson, G.S. Ali, R.J. Dalio, S.G. Roy, L. Schena, A. Zambounis, F. Panabières, The top 10 oomycete pathogens in molecular plant pathology, Mol. Plant Pathol. 16 (2015) 413–434.

[13] J. Mansfield, S. Genin, S. Magori, V. Citovsky, M. Sriariyanum, P. Ronald, M. Dow, V. Verdier, S.V. Beer, M.A. Machado, Top 10 plant pathogenic bacteria in molecular plant pathology, Mol. Plant Pathol. 13 (2012) 614–629.

[14] K.B.G. Scholthof, S. Adkins, H. Czosnek, P. Palukaitis, E. Jacquot, T. Hohn, B. Hohn, K. Saunders, T. Candresse, P. Ahlquist, Top 10 plant viruses in molecular plant pathology, Mol. Plant Pathol. 12 (2011) 938–954.

[15] J.T. Jones, A. Haegeman, E.G. Danchin, H.S. Gaur, J. Helder, M.G. Jones, T. Kikuchi, R. Manzanilla-López, J.E. Palomares-Rius, W.M. Wesemael, Top 10 plant-parasitic nematodes in molecular plant pathology, Mol. Plant Pathol. 14 (2013) 946–961.

[16] M.C. Fisher, D.A. Henk, C.J. Briggs, J.S. Brownstein, L.C. Madoff, S.L. McCraw, S.J. Gurr, Emerging fungal threats to animal plant and ecosystem health, Nature 484 (2012).

[17] J. Ingram, A food systems approach to researching food security and its interactions with global environmental change, Food Secur. 3 (2011) 417–431.

[18] A. Keinan, A.G. Clark, Recent explosive human population growth has resulted in an excess of rare genetic variants, Science 336 (2012) 740–743.

[19] H. Westhoek, J. Ingram, S. van Berkum, M. Hajer, Food Systems and Natural Resources, United Nations Environment Programme: United Nations Environment Programme, 2016.

[20] H.C.J. Godfray, J.R. Beddington, I.R. Crute, L. Haddad, D. Lawrence, J.F. Muir, J. Pretty, S. Robinson, S.M. Thomas, C. Toulmin, Food security: the challenge of feeding 9 billion people, Science 327 (2010) 812–818.

[21] L.R. Brown, World population growth, soil erosion, and food security, Science (1981) 995–1002.

[22] E.-C. Oerke, H.W. Dehne, Safeguarding production—losses in major crops and the role of crop protection, Crop Prot. 23 (2004) 275–285.

[23] M. Bergot, E. Cloppet, V. Perarnaud, M. Deque, B. Marcais, M.L. Desprez-Loustau, Simulation of potential range expansion of oak disease caused by *Phytophthora cinnamomi* under climate change, Global Change Biol. 10 (2004) 1539–1552.

[24] T. Jung, H. Blaschke, W. Oßwald, Involvement of soilborne *Phytophthora* species in Central European oak decline and the effect of site factors on the disease, Plant Pathol. 49 (2000) 706–718.

[25] C. Robin, M.L. Desprez Loustau, G. Capron, C. Delatour, First record of *Phytophthora cinnamomi* on cork and holm oaks in France and evidence of pathogenicity, Annales Des Sciences Forestières, EDP Sciences, 1998.

[26] M. Rodríguez-Molina, L. Torres Vila, A. Blanco-Santos, E. Núñez, E. Torres-Álvarez, Viability of holm and cork oak seedlings from acorns sown in soils naturally infected with *Phytophthora cinnamomi*, For. Pathol. 32 (2002) 365–372.

[27] B.S. Crandall, G. Gravatt, M.M. Ryan, Root disease of Castanea species and some coniferous and broadleaf nursery stocks, caused by *Phytophthora cinnamomi*, Phytopathology 35 (1945) 162–180.

[28] A. Ferguson, S. Jeffers, Detecting multiple species of *Phytophthora* in container mixes from ornamental crop nurseries, Plant Dis. 83 (1999) 1129–1136.

[29] G.A. Zentmyer, *Phytophthora Cinnamomi* and the Diseases It Causes, (1980).

[30] B.L. Shearer, J.T. Tippett, Jarrah Dieback: the Dynamics and Management of Phytophthora Cinnamomi in the Jarrah (Eucalyptus Marginata) Forest of Southwestern Australia, Department of Conservation and Land Management Perth: Department of Conservation and Land Management Perth, 1989.

[31] B. Pratt, W. Heather, C. Shepherd, Recovery of *Phytophthora cinnamomi* from native vegetation in a remote area of New South Wales, Trans. Br. Mycol. Soc. 60 (1973) 197–204.

[32] J.E. Rookes, M.L. Wright, D.M. Cahill, Elucidation of defence responses and signalling pathways induced in *Arabidopsis thaliana* following challenge with *Phytophthora cinnamomi*, Physiol. Mol. Plant Pathol. 72 (2008) 151–161.

[33] P. O'Brien, G.S.J. Hardy, *Phytophthora cinnamomi* in western Australia, J. R. Soc. West Aust. 97 (2014) 47–55.

[34] F. Podger, A National Overview of *Phytophthora Cinnamomi* in Australia: Supplementary Information to Accompany the Draft National Threat Abatement Plan, Environmental Australia, Commonwealth Government of Australia Canberra, 1999.

[35] T. Rudman, Interim Phytophthora Cinnamomi Management Guidelines, Biodiversity Conservation Branch, Department of Primary Industries, Water and Environment, 2005.

[36] H.H. Flor, Current status of the gene-for-gene concept, Annu. Rev. Phytopathol. 9 (1971) 275–296.

[37] J. Mansfield, Antimicrobial Compounds and Resistance, in Mechanisms of Resistance to Plant Diseases, Springer, 2000, pp. 325–370.

[38] M.D. Hunt, J.A. Ryals, D. Reinhardt, Systemic acquired resistance signal transduction, Crit. Rev. Plant Sci. 15 (1996) 583–606.

[39] J.A. Ryals, U.H. Neuenschwander, M.G. Willits, A. Molina, H.Y. Steiner, M.D. Hunt, Systemic acquired resistance, Plant Cell 8 (1996) 1809.

[40] D.K. Choudhary, A. Prakash, B. Johri, Induced systemic resistance (ISR) in plants: mechanism of action, Indian J. Microbiol. 47 (2007) 289–297.

[41] J.L.S. Costa d, J.A. Menge, W.L. Casale, Biological control of *Phytophthora* root rot of avocato with microorganisms grown in organic mulches, Braz. J. Microbiol. 31 (2000) 239–246.

[42] K. Kim, S. Nemec, G. Musson, Control of *Phytophthora* root and crown rot of bell pepper with composts and soil amendments in the greenhouse, Appl. Soil Ecol. 5 (1997) 169–179.

[43] O.C. Maloy, Plant disease management, Plant Health Instr. 10 (2005).

[44] S. Kiyosawa, Genetics and epidemiological modeling of breakdown of plant

disease resistance, Annu. Rev. Phytopathol. 20 (1982) 93–117.

[45] R.L. Metcalf, W.H. Luckmann, Introduction to Insect Pest Management, John Wiley & Sons, 1994.

[46] M. Wolfe, The current status and prospects of multiline cultivars and variety mixtures for disease resistance, Annu. Rev. Phytopathol. 23 (1985) 251–273.

[47] W.E. Fry, Principles of Plant Disease Management, Academic Press, 2012.

[48] Y. Jin, L. Szabo, Z. Pretorius, R. Singh, R. Ward, T. Fetch Jr., Detection of virulence to resistance gene Sr24 within race TTKS of *Puccinia graminis* f. sp. *tritici*, Plant Dis. 92 (2008) 923–926.

[49] S. Mansoor, I. Amin, S. Iram, M. Hussain, Y. Zafar, K. Malik, R. Briddon, Breakdown of resistance in cotton to cotton leaf curl disease in Pakistan, Plant Pathol. 52 (2003) 784.

[50] K. Leonard, L. Szabo, Stem rust of small grains and grasses caused by, *Puccinia graminis*, Mol. Plant Pathol. 6 (2005) 99–111.

[51] Y. Jin, L. Szabo, M. Rouse, T. Fetch Jr, Z. Pretorius, R. Wanyera, P. Njau, Detection of virulence to resistance gene Sr36 within the TTKS race lineage of *Puccinia graminis* f. sp. *tritici*, Plant Dis. 93 (2009) 367–370.

[52] Y. Jin, R. Singh, Resistance in US wheat to recent eastern African isolates of *Puccinia graminis* f. sp. *tritici* with virulence to resistance gene Sr31, Plant Dis. 90 (2006) 476–480.

[53] G.S. Khush, K. Jena, Current status and future prospects for research on blast resistance in rice (*Oryza sativa* L.), Adv. Genetics Genomics Control Rice Blast Dis. (2009) 1–10.

[54] E. Peressotti, S. Wiedemann-Merdinoglu, F. Delmotte, D. Bellin, G. Di Gaspero, R. Testolin, D. Merdinoglu, P. Mestre, Breakdown of resistance to grapevine downy mildew upon limited deployment of a resistant variety, BMC Plant Biol. 10 (2010) 147.

[55] K. Belhaj, A. Chaparro-Garcia, S. Kamoun, N.J. Patron, V. Nekrasov, Editing plant genomes with CRISPR/Cas9, Curr. Opin. Biotechnol. 32 (2015) 76–84.

[56] T. Hirooka, H. Ishii, Chemical control of plant diseases, J. Gen. Plant Pathol. 79 (2013) 390–401.

[57] N.N. Ragsdale, H. Alford, Health and Environmental Factors Associated with Agricultural Use Offungicides, (1991).

[58] Z. Ma, T.J. Michailides, Advances in understanding molecular mechanisms of fungicide resistance and molecular detection of resistant genotypes in phytopathogenic fungi, Crop Prot. 24 (2005) 853–863.

[59] F.P. Carvalho, Agriculture pesticides, food security and food safety, Environ. Sci. Policy 9 (2006) 685–692.

[60] G. Berg, Plant–microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture, Appl. Microb. Biotechnol. 84 (2009) 11–18.

[61] S. Budi, D. Van Tuinen, C. Arnould, E. Dumas-Gaudot, V. Gianinazzi-Pearson, S. Gianinazzi, Hydrolytic enzyme activity of *Paenibacillus* sp. strain B2 and effects of the antagonistic bacterium on cell integrity of two soil-borne pathogenic fungi, Appl. Soil Ecol. 15 (2000) 191–199.

[62] W. Kelley, D. South, Effects of herbicides on in vitro growth of mycorrhizae of pine (*Pinus* spp.), Weed Sci. 28 (1980) 599–602.

[63] M. Pell, B. Stenberg, L. Torstensson, Potential denitrification and nitrification tests for evaluation of pesticide effects in soil, Ambio (1998) 24–28.

[64] A. Santos, M. Flores, Effects of glyphosate on nitrogen fixation of free-living heterotrophic bacteria, Lett. Appl. Microbiol. 20 (1995) 349–352.

[65] K.S. Schafer, S. Kegley, Persistent toxic chemicals in the US food supply, J. Epidemiol. Community Health 56 (2002) 813–817.

[66] C. Azcón-Aguilar, J. Barea, Arbuscular mycorrhizas and biological control of soil-borne plant pathogens–an overview of the mechanisms involved, Mycorrhiza 6 (1997) 457–464.

[67] H. Mirzaee, L. Shuey, P.M. Schenk, Transcriptomics of plants interacting with pathogens and beneficial microbes, Genomics, Proteomics and Metabolomics in Nutraceuticals and Functional Foods, Second edition, (2015), pp. 525–536.

[68] K.K. Pal, B.M. Gardener, Biological control of plant pathogens, Plant Health Instr. 2 (2006) 1117–1142.

[69] D. McSpadden Gardener, D. Fravel, Biological control of plant pathogens: research, commercialization, and application in the USA, Plant Health Prog. 10 (2002).

[70] R.J. Cook, K.F. Baker, The Nature and Practice of Biological Control of Plant Pathogens, American Phytopathological Society, 1983.

[71] J.L. Bronstein, Our current understanding of mutualism, Q. Rev. Biol. 69 (1994) 31–51.

[72] G. James, L. Beaudette, J. Costerton, Interspecies bacterial interactions in biofilms, J. Ind. Microbiol. Biotechnol. 15 (1995) 257–262.

[73] H. Yoon, G. Klinzing, H. Blanch, Competition for mixed substrates by microbial populations, Biotechnol. Bioeng. 19 (1977) 1193–1210.

[74] J. Hallmann, Plant Interactions with Endophytic Bacteria, CABI Publishing, New York, 2001.

[75] B. Trenbath, Plant interactions in mixed crop communities, Multiple Cropping (1976) 129–169.

[76] W. Arthur, P. Mitchell, A revised scheme for the classification of population interactions, Oikos (1989) 141–143.

[77] P.W. Price, General concepts on the evolutionary biology of parasites, Evolution 31 (1977) 405–420.

[78] P.W. Price, C.E. Bouton, P. Gross, B.A. McPheron, J.N. Thompson, A.E. Weis, Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies, Annu. Rev. Ecol. Syst. 11 (1980) 41–65.

[79] I. Ponce de León, M. Montesano, Activation of defense mechanisms against pathogens in mosses and flowering plants, Int. J. Mol. Sci. 14 (2013) 3178–3200.

[80] A.G. Darvill, P. Albersheim, Phytoalexins and their elicitors-a defense against

microbial infection in plants, Annu. Rev. Plant Physiol. 35 (1984) 243–275.

[81] C.M. Pieterse, C. Zamioudis, R.L. Berendsen, D.M. Weller, S.C. Van Wees, P.A. Bakker, Induced systemic resistance by beneficial microbes, Annu. Rev. Phytopathol. 52 (2014) 347–375.

[82] G.N. Agrios, Plant Pathology, 5th eds., Department of Plant Pathology. University of Florida, United States of America, 2005.

[83] L. Wen, Cell death in plant immune response to necrotrophs, J. Plant Biochem. Physiol. 1 (2013) 1–3.

[84] J. Ellis, A.M. Catanzariti, P. Dodds, The problem of how fungal and oomycete avirulence proteins enter plant cells, Trends Plant Sci. 11 (2006) 61–63.

[85] M. Latijnhouwers, P.J. de Wit, F. Govers, Oomycetes and fungi: similar weaponry to attack plants, Trends Microbiol. 11 (2003) 462–469.

[86] D.R. Walters, N. McRoberts, Plants and biotrophs: a pivotal role for cytokinins? Trends Plant Sci. 11 (2006) 581–586.

[87] H.G. Mang, K.A. Laluk, E.P. Parsons, D.K. Kosma, B.R. Cooper, H.C. Park, S. AbuQamar, C. Boccongelli, S. Miyazaki, F. Consiglio, The *Arabidopsis* RESURRECTION1 gene regulates a novel antagonistic interaction in plant defense to biotrophs and necrotrophs, Plant Physiol. 151 (2009) 290–305.

[88] M. Wiermer, B.J. Feys, J.E. Parker, Plant immunity: the EDS1 regulatory node, Curr. Opin. Plant Biol. 8 (2005) 383–389.

[89] R.N. Trigiano, Plant Pathology Concepts and Laboratory Exercises, CRC press, 2007.

[90] S. Münch, U. Lingner, D.S. Floss, N. Ludwig, N. Sauer, H.B. Deising, The hemibiotrophic lifestyle of Colletotrichum species, J. Plant Physiol. 165 (2008) 41–51.

[91] V. Bhadauria, S. Banniza, Y. Wei, Y.-L. Peng, Reverse genetics for functional genomics of phytopathogenic fungi and oomycetes, Comp. Funct. Genomics (2009) 2009.

[92] C.M. Pieterse, J. Ton, L. Van Loon, Cross-talk between plant defence signalling pathways: boost or burden? AgBiotechNet 3 (2001) 1–8.

[93] Y.C. Chen, B.N. Kidd, L.C. Carvalhais, P.M. Schenk, Molecular defense responses in roots and the rhizosphere against *Fusarium oxysporum*, Plant Signal. Behav. 9 (2014) e977710.

[94] A. Pérez-García, D. Romero, A. De Vicente, Plant protection and growth stimulation by microorganisms: biotechnological applications of *Bacilli* in agriculture, Curr. Opin. Biotechnol. 22 (2011) 187–193.

[95] D.M. Weller, Biological control of soilborne plant pathogens in the rhizosphere with bacteria, Annu. Rev. Phytopathol. 26 (1988) 379–407.

[96] K. Baker, R.J. Cook, Biological Control of Plant Pathogens, WH Freeman and Company, 1974.

[97] G.C. Papavizas, Biological Control in Crop Production in Beltsville Symposia in Agricultural Research, (1981).

[98] M.E. Brown, Seed and root bacterization, Annu. Rev. Phytopathol. 12 (1974) 181–197.

[99] T. Burr, M. Schroth, T. Suslow, Increased potato yields by treatment of seedpieces with specific strains of *Pseudomonas fluorescens* and P. *putida*, Phytopathology 68 (1978) 1377–1383.

[100] T. Suslow, Role of Root-colonizing Bacteria in Plant Growth, (1982).

[101] C.H. Haney, B.S. Samuel, J. Bush, F.M. Ausubel, Associations with rhizosphere bacteria can confer an adaptive advantage to plants, Nat. Plants 1 (2015).

[102] E. Bach, G.D. dos Santos Seger, G. de Carvalho Fernandes, B.B. Lisboa, L.M.P. Passaglia, Evaluation of biological control and rhizosphere competence of plant growth promoting bacteria, Appl. Soil Ecol. 99 (2016) 141–149.

[103] M. Shoda, Bacterial control of plant diseases, J. Biosci. Bioeng. 89 (2000) 515–521.

[104] V. Nihorimbere, M. Ongena, M. Smargiassi, P. Thonart, Beneficial effect of the rhizosphere microbial community for plant growth and health, Biotecnol. Agron. Soc. 15 (2011) 327.

[105] S. Compant, B. Duffy, J. Nowak, C. Clément, E.A. Barka, Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects, Appl. Environ. Microbiol. 71 (2005) 4951–4959.

[106] E. Gray, D. Smith, Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signaling processes, Soil Biol. Biochem. 37 (2005) 395–412.

[107] P. Kiely, J. Haynes, C. Higgins, A. Franks, G. Mark, J. Morrissey, F. O'gara, Exploiting new systems-based strategies to elucidate plant-bacterial interactions in the rhizosphere, Microbiol. Ecol. 51 (2006) 257–266.

[108] G. Bowen, A. Rovira, The rhizosphere and its management to improve plant growth, Adv. Agron. 66 (1999) 1–102.

[109] I. Chet, L. Chernin, Microbial Agents in Soil. In: Bitton G (ed) Encyclopedia of Environmental Microbiology, Willey, New York, USA, 2002, pp. 450–465.

[110] H.P. Bais, T.L. Weir, L.G. Perry, S. Gilroy, J.M. Vivanco, The role of root exudates in rhizosphere interactions with plants and other organisms, Annu. Rev. Plant Biol. 57 (2006) 233–266.

[111] G.E. Welbaum, A.V. Sturz, Z. Dong, J. Nowak, Managing soil microorganisms to improve productivity of agro-ecosystems, Crit. Rev. Plant Sci. 23 (2004) 175–193.

[112] S. Dobbelaere, J. Vanderleyden, Y. Okon, Plant growth-promoting effects of diazotrophs in the rhizosphere, Crit. Rev. Plant Sci. 22 (2003) 107–149.

[113] B.R. Glick, The enhancement of plant growth by free-living bacteria, Can. J. Microbiol. 41 (1995) 109–117.

[114] A. Sturz, B. Christie, Beneficial microbial allelopathies in the root zone: the management of soil quality and plant disease with rhizobacteria, Soil Tillage Res. 72 (2003) 107–123.

[115] H.P. Bais, S.W. Park, T.L. Weir, R.M. Callaway, J.M. Vivanco, How plants communicate using the underground information superhighway, Trends Plant Sci. 9 (2004) 26–32.

[116] C. Tang, K. Komai, R. Huang, Allelopathy and the chemistry of the rhizosphere,

Phytochem. Ecol. 9 (1989).

[117] J.E. Loper, Role of fluorescent siderophore production in biological control of *Pythium ultimum* by a *Pseudomonas fluorescens* strain, Phytopathology 78 (1988) 166–172.

[118] S. Buysens, K. Heungens, J. Poppe, M. Hofte, Involvement of pyochelin and pyoverdin in suppression of *Pythium*-induced damping-off of tomato by *Pseudomonas aeruginosa* 7NSK2, Appl. Environ. Microbiol. 62 (1996) 865–871.

[119] G.V. Bloemberg, B.J. Lugtenberg, Phenazines and their role in biocontrol by *Pseudomonas* bacteria, New Phytol. 157 (2003) 503–523.

[120] J. Leong, Siderophores: their biochemistry and possible role in the biocontrol of plant pathogens, Annu. Rev. Phytopathol. 24 (1986) 187–209.

[121] J.E. Loper, M.D. Henkels, Availability of iron to *Pseudomonas fluorescens* in rhizosphere and bulk soil evaluated with an ice nucleation reporter gene, Appl. Environ. Microbiol. 63 (1997) 99–105.

[122] D. Haas, G. Défago, Biological control of soil-borne pathogens by fluorescent pseudomonads, Nat. Rev. Microbiol. 3 (2005) 307.

[123] G.V. Bloemberg, B.J. Lugtenberg, Molecular basis of plant growth promotion and biocontrol by rhizobacteria, Curr. Opin. Plant Biol. 4 (2001) 343–350.

[124] J. Kloepper, D. Hume, F. Scher, C. Singleton, B. Tipping, M. Laliberte, K. Frauley, T. Kutchaw, C. Simonson, R. Lifshitz, Plant growth-promoting rhizobacteria on canola (rapeseed), Plant Dis. 72 (1988) 42–46.

[125] T. Suslow, Growth and yield enhancement of sugar beets by pelleting seed with specific *Pseudomonas* spp, Phytopathol. News 12 (1980) 40.

[126] T.A. Toussoun, R.V. Bega, P.E. Nelson, Root Diseases and Soil-borne Pathogens, Univ of California Press, 1970.

[127] J.W. Kloepper, C.M. Ryu, S. Zhang, Induced systemic resistance and promotion of plant growth by *Bacillus* spp, Phytopathology 94 (2004) 1259–1266.

[128] G.W. Zehnder, C. Yao, J.F. Murphy, E.R. Sikora, J.W. Kloepper, Induction of resistance in tomato against Cucumber mosaic cucumovirus by plant growth-promoting rhizobacteria, Biocontrol 45 (2000) 127–137.

[129] J.F. Murphy, M. Reddy, C.-M. Ryu, J.W. Kloepper, R. Li, Rhizobacteria-mediated growth promotion of tomato leads to protection against Cucumber mosaic virus, Phytopathology 93 (2003) 1301–1307.

[130] R. Van Peer, G. Niemann, B. Schippers, Induced resistance and phytoalexin accumulation in biological control of *Fusarium* wilt of carnation by *Pseudomonas* sp. strain WCS 417 r, Phytopathology 81 (1991) 728–734.

[131] U. Conrath, G.J. Beckers, C.J. Langenbach, M.R. Jaskiewicz, Priming for enhanced defense, Annu. Rev. Phytopathol. 53 (2015) 97–119.

[132] L. Van Loon, Induced resistance in plants and the role of pathogenesis-related proteins, Eur. J. Plant Pathol. 103 (1997) 753–765.

[133] U. Conrath, C.M. Pieterse, B. Mauch-Mani, Priming in plant-pathogen interactions, Trends Plant Sci. 7 (2002) 210–216.

[134] M. Leeman, J. Van Pelt, M. Hendrickx, R. Scheffer, P. Bakker, B. Schippers, Biocontrol of *Fusarium* wilt of radish in commercial greenhouse trials by seed treatment with *Pseudomonas fluorescens* WCS374, Phytopathology 85 (1995) 1301–1305.

[135] M. Rai, D. Acharya, A. Singh, A. Varma, Positive growth responses of the medicinal plants *Spilanthes calva* and *Withania somnifera* to inoculation by *Piriformospora indica* in a field trial, Mycorrhiza 11 (2001) 123–128.

[136] M. Heil, Ecological costs of induced resistance, Curr. Opin. Plant Biol. 5 (2002) 345–350.

[137] M. van Hulten, M. Pelser, L. Van Loon, C.M. Pieterse, J. Ton, Costs and benefits of priming for defense in *Arabidopsis*, Proc. Natl. Acad. Sci. 103 (2006) 5602–5607.

[138] S. Alström, Induction of disease resistance in common bean susceptible to halo blight bacterial pathogen after seed bacterization with rhizosphere pseudomonads, J. Gen. Appl. Microbiol. 37 (1991) 495–501.

[139] G. Wei, J.W. Kloepper, S. Tuzun, Induction of systemic resistance of cucumber to *Colletotrichum orbiculare* by select strains of plant growth-promoting rhizobacteria, Phytopathology 81 (1991) 1508–1512.

[140] U. Conrath, G.J. Beckers, V. Flors, P. García-Agustín, G. Jakab, F. Mauch, M.-A. Newman, C.M. Pieterse, B. Poinssot, M.J. Pozo, Priming: getting ready for battle, Mol. Plant Microbe Interact. 19 (2006) 1062–1071.

[141] J.A. Vorholt, Microbial life in the phyllosphere, Nature Rev. Microbiol. 10 (2012) 828–840.

[142] L.C. Carvalhais, P.G. Dennis, D.V. Badri, G.W. Tyson, J.M. Vivanco, P.M. Schenk, Activation of the jasmonic acid plant defence pathway alters the composition of rhizosphere bacterial communities, PLoS One 8 (2013) e56457.

[143] L.C. Carvalhais, P.G. Dennis, D.V. Badri, B.N. Kidd, J.M. Vivanco, P.M. Schenk, Linking jasmonic acid signaling root exudates, and rhizosphere microbiomes, Mol. Plant Microbe Interact. 28 (2015) 1049–1058.

[144] N. Fierer, M.A. Bradford, R.B. Jackson, Toward an ecological classification of soil bacteria, Ecology 88 (2007) 1354–1364.

[145] J. Cooper, Early interactions between legumes and rhizobia: disclosing complexity in a molecular dialogue, J. Appl. Microbiol. 103 (2007) 1355–1365.

[146] C.-M. Ryu, M.A. Farag, C.-H. Hu, M.S. Reddy, J.W. Kloepper, P.W. Paré, Bacterial volatiles induce systemic resistance in *Arabidopsis*, Plant Physiol. 134 (2004) 1017–1026.

[147] Y. Cao, Z. Zhang, N. Ling, Y. Yuan, X. Zheng, B. Shen, Q. Shen, Bacillus subtilis SQR 9 can control *Fusarium* wilt in cucumber by colonizing plant roots, Biol. Fertil.

Soils 47 (2011) 495–506.

[148] A. Kavoo-Mwangi, E. Kahangi, E. Ateka, J. Onguso, R. Mukhongo, E. Mwangi, J. Jefwa, Growth effects of microorganisms based commercial products inoculated to tissue cultured banana cultivated in three different soils in Kenya, Appl. Soil Ecol. 64 (2013) 152–162.

[149] P.C. Wintermans, P.A. Bakker, C.M. Pieterse, Natural genetic variation in *Arabidopsis* for responsiveness to plant growth-promoting rhizobacteria, Plant Mol. Biol. 90 (2016) 623–634.

[150] Y. Bai, D.B. Müller, G. Srinivas, R. Garrido-Oter, E. Potthoff, M. Rott, N. Dombrowski, P.C. Münch, S. Spaepen, M. Remus-Emsermann, Functional overlap of the *Arabidopsis* leaf and root microbiota, Nature 528 (2015) 364.

[151] L. Madden, F. Nutter Jr., Modeling crop losses at the field scale, Can. J. Plant Pathol. 17 (1995) 124–137.

[152] I. Maksimov, R. Abizgil'Dina, L. Pusenkova, Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens, Appl. Biochem. Microbiol. 47 (2011) 333–345.

[153] A. Heydari, M. Pessarakli, A review on biological control of fungal plant pathogens using microbial antagonists, J. Biol. Sci. 10 (2010) 273–290.

[154] B.T. Demoz, L. Korsten, Bacillus subtilis attachment colonization, and survival on avocado flowers and its mode of action on stem-end rot pathogens, Biol. Control 37 (2006) 68–74.

[155] Y. Aysan, A. Karatas, O. Cinar, Biological control of bacterial stem rot caused by *Erwinia chrysanthemi* on tomato, Crop Prot. 22 (2003) 807–811.

[156] H. Scherm, H. Ngugi, A. Savelle, J. Edwards, Biological control of infection of blueberry flowers caused by *Monilinia vaccinii-corymbosi*, Biol. Control 29 (2004) 199–206.

[157] C.E. Morris, J.-M. Monier, The ecological significance of biofilm formation by plant-associated bacteria, Annu. Rev. Phytopathol. 41 (2003) 429–453.

[158] S.E. Lindow, Competitive exclusion of epiphytic bacteria by Ice-*Pseudomonas syringae* mutants, Appl. Environ. Microbiol. 53 (1987) 2520–2527.

[159] K.P. Smith, J. Handelsman, R.M. Goodman, Genetic basis in plants for interactions with disease-suppressive bacteria, Proc. Natl. Acad. Sci. 96 (1999) 4786–4790.

[160] P. Trivedi, P.M. Schenk, M.D. Wallenstein, B.K. Singh, Tiny Microbes, Big Yields: enhancing food crop production with biological solutions, Microbiol. Biotech. 10 (2017) 999–1003.

[161] R.L. Berendsen, C.M. Pieterse, P.A. Bakker, The rhizosphere microbiome and plant health, Trends Plant Sci. 17 (2012) 478–486.

[162] D. Bulgarelli, K. Schlaeppi, S. Spaepen, E.V.L. van Themaat, P. Schulze-Lefert, Structure and functions of the bacterial microbiota of plants, Annu. Rev. Plant Biol. 64 (2013) 807–838.

[163] A. Kalra, M. Chandra, A. Awasthi, A.K. Singh, S.P.S. Khanuja, Natural compounds enhancing growth and survival of rhizobial inoculants in vermicompost-based formulations, Biol. Fertil. Soils 46 (2010) 521–524.

[164] W. Rice, P. Olsen, M. Leggett, Co-culture of *Rhizobium meliloti* and a phosphorus-solubilizing fungus (*Penicillium bilaii*) in sterile peat, Soil Biol. Biochem. 27 (1995) 703–705.

[165] Z. Liu, J. Sinclair, Enhanced soybean plant growth and nodulation by *Bradyrhizobium* in the presence of strains of *Bacillus megaterium*, Phytopathology 80 (1990) 1024.

[166] M. Shoresh, I. Yedidia, I. Chet, Involvement of jasmonic acid/ethylene signaling pathway in the systemic resistance induced in cucumber by *Trichoderma asperellum* T203, Phytopathology 95 (2005) 76–84.

[167] N. Benhamou, J.W. Kloepper, A. Quadt-Hallmann, S. Tuzun, Induction of defense-related ultrastructural modifications in pea root tissues inoculated with endophytic bacteria, Plant Physiol. 112 (1996) 919–929.

[168] C. Pieterse, S. Van Wees, E. Hoffland, J.A. Van Pelt, L.C. Van Loon, Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression, Plant Cell 8 (1996) 1225–1237.

[169] S. Compant, B. Reiter, A. Sessitsch, J. Nowak, C. Clément, E.A. Barka, Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN, Appl. Environ. Microbiol. 71 (2005) 1685–1693.

[170] R. Viswanathan, R. Samiyappan, Induction of systemic resistance by plant growth promoting rhizobacteria against red rot disease in sugarcane, Sugar Tech. 1 (1999) 67–76.

[171] D.S. Brooks, C.F. Gonzalez, D.N. Appel, T. Filer, Evaluation of endophytic bacteria as potential biological-control agents for Oak Wilt, Biol. Control 4 (1994) 373–381.

[172] L.C. Carvalhais, P.G. Dennis, D. Fedoseyenko, M.R. Hajirezaei, R. Borriss, N. von Wirén, Root exudation of sugars amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency, J. Plant Nutr. Soil Sci. 174 (2011) 3–11.

[173] S. Oku, A. Komatsu, Y. Nakashimada, T. Tajima, J. Kato, Identification of *Pseudomonas fluorescens* chemotaxis sensory proteins for malate, succinate, and fumarate and their involvement in root colonization, Microbes Environ. 29 (2014) 413–419.

[174] D.J. O'Sullivan, F. O'Gara, Traits of fluorescent *Pseudomonas* spp. involved in suppression of plant root pathogens, Microbiol. Rev. 56 (1992) 662–676.