



## Review article

# Decrypting the multi-functional biological activators and inducers of defense responses against biotic stresses in plants

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## ABSTRACT

Plant diseases are still the main problem for the reduction in crop yield and a threat to global food security. Additionally, excessive usage of chemical inputs such as pesticides and fungicides to control plant diseases have created another serious problem for human and environmental health. In view of this, the application of plant growth-promoting rhizobacteria (PGPR) for controlling plant disease incidences has been identified as an eco-friendly approach for coping with the food security issue. In this review, we have identified different ways by which PGPRs are capable of reducing phytopathogenic infestations and enhancing crop yield. PGPR suppresses plant diseases, both directly and indirectly, mediated by microbial metabolites and signaling components. Microbial synthesized anti-pathogenic metabolites such as siderophores, antibiotics, lytic enzymes, hydrogen cyanide, and several others act directly on phytopathogens. The indirect mechanisms of reducing plant disease infestation are caused by the stimulation of plant immune responses known as initiation of systemic resistance (ISR) which is mediated by triggering plant immune responses elicited through pathogen-associated molecular patterns (PAMPs). The ISR triggered in the infected region of the plant leads to the development of systemic acquired resistance (SAR) throughout the plant making the plant resistant to a wide range of pathogens. A number of PGPRs including *Pseudomonas* and *Bacillus* genera have proven their ability to stimulate ISR. However,

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there are still some challenges in the large-scale application and acceptance of PGPR for pest and disease management. Further, we discuss the newly formulated PGPR inoculants possessing both plant growth-promoting activities and plant disease suppression ability for a holistic approach to sustaining plant health and enhancing crop productivity.

## 1. Introduction

In diverse scenery plants bear the characteristic of incantation amount by uncountable microbes, which threatens their presence. Still, many of them are shortened innocuous owed to subservient as well as dynamic protector blockades exist in the floras and work for the wellbeing of floras [1]. For an extended period, plants are preserved with many plant extracts and artificial synthetic compounds, which are waged for cell wall wreckages, and induction of resistance to successive pathogen spells [2]. This tempted resistance infrequently initiate towards the whole pathogen regulator, subsequent as an alternative to a decrease in laceration scope and/or amount [3]. In a comprehensive manner, persuaded resistance can be divided into two main kinds: systemic acquired resistance (SAR) and induced systemic resistance (ISR). SAR can be persuaded by action with various chemical agents, together with necrotizing pathogens and certain chemicals which is interceded by salicylic acid (SA)-dependent process [4]. Positive plant growth-promoting rhizobacteria (PGPR) colonize plant roots through ISR developments, it is arbitrated by pathways of jasmonate and ethylene (ET) [5]. Initiation of confrontation has a straight role in the initiation of defenses, the same time can lead to the cells priming, subsequent in other barricades, succeeding attacks by disease-causing agents [6]. It appears probable that maximum persuaded resistance phenomena are founded on an amalgamation of direct initiation and priming [7]. One of the greatest notable plant variations approaches to abiotic stresses was to trigger manifold multifaceted responses that elaborate physiological, biochemical, cellular, and molecular procedures with numerous dissimilar pathways at the whole-plant side by side [8]. Based on the above points, in the present review, we are focusing on beneficial PGPR and their part in plant-pathogen interface, ISR, a spectrum of protection by PGPR, synergistic effect of PGPR strain combinations, the durability of ISR, PGPR-mediated ISR under field conditions, and biotic stress management.

## 2. Plants and stresses

The growing population of humans drives the need for sufficient food with high-quality yields in agricultural sectors [9]. Plant developments are greatly inclined by abiotic and biotic stresses [10] for instance viruses, bacteria, fungi, nematodes [11], insects, and herbivores [12] are considered as biotic stress, and while the abiotic stress includes heat, flooding [13], drought, salinity [14], allelochemicals, metal toxicity, ozone, UV radiations, and herbicides that caused losses developments in plants [15]. Stresses can

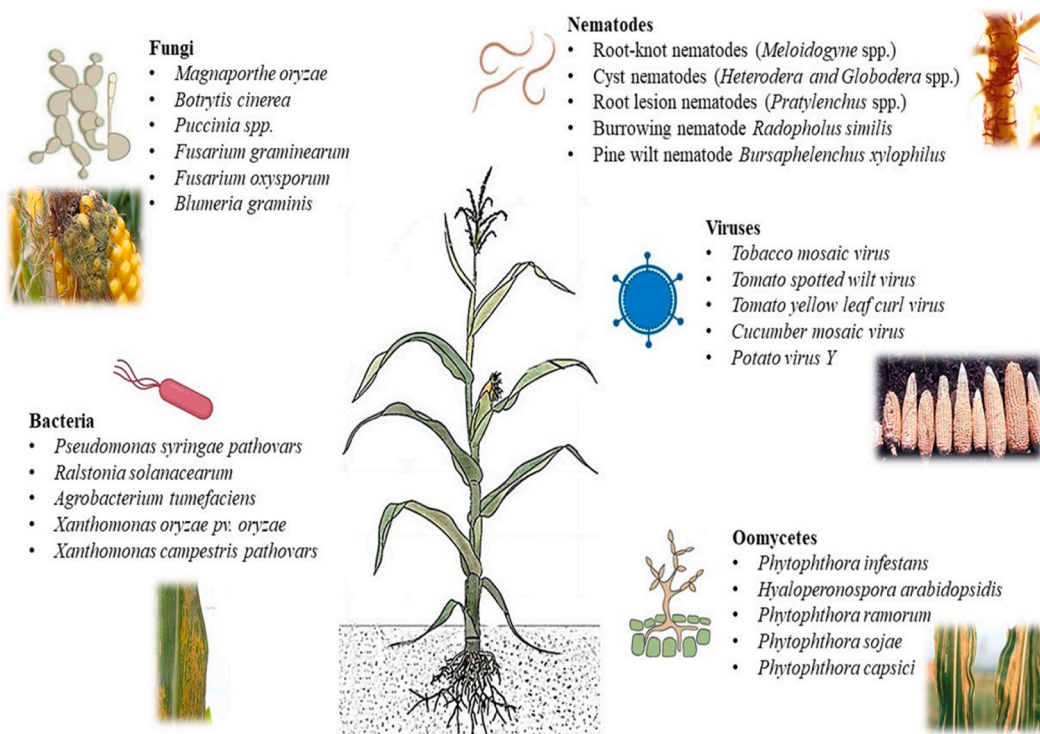


Fig. 1. Representative list of phytopathogens causing vast economic damages globally.

create imperative economic losses in agricultural and forestry systems by decreasing in quantity and quality of yields. Global data shows the major effects of biotic agents (*i.e.*, pathogens, pests, and weeds) on harvesting [16,17].

### 3. Biotic stress

Biotic stress comprises the living organisms such as pathogenic viruses, bacteria, fungi, nematodes, pests, and weeds [14,18,19]. These biotic agents can significantly affect development, vigor, mortality, and yields in pre- and post-harvest periods in plants [20]. In different reviews, main pathogens were referred to worldwide that have done a lot of damage to plants. A brief schematic diagram of major plant pathogens is shown in Fig. 1. These pathogens included fungi *e.g.*, *Magnaporthe oryzae*; *Botrytis cinerea*; *Puccinia* spp.; *Fusarium graminearum*; *F. oxysporum*; *Blumeria graminis*; *Mycosphaerella graminicola*; *Colletotrichum* spp.; *Ustilago maydis*; and *Melampsora lini* [21,22]. Oomycetes *e.g.*, *Phytophthora infestans*; *P. sojae*; *P. capsica*; *P. ramorum*; *P. cinnamomic*; *P. parasitica*; *Hyaloperonospora arabidopsidis*; *Plasmopara viticola*; *Pythium ultimum*; and *Albugo candida* [23,24]. Further, pathogenic bacteria are also reported *Eudomonas syringae* pathovars; *Ralstonia solanacearum*; *Agrobacterium tumefaciens*; *Xanthomonas oryzae* pv. *Oryzae*; *X. campestris* pathovars; *X. axonopodis* pathovars; *Erwinia amylovora*; *Xylella fastidiosa*; *Dickeya (dadantii and solani)* [25,26]. Likewise, viruses *e.g.*, Tobacco mosaic virus, Tomato spotted wilt virus, Tomato yellow leaf curl virus, Cucumber mosaic virus, Potato virus Y, Cauliflower mosaic virus, African cassava mosaic virus, Plum pox virus, Brome mosaic virus and Potato virus X [27] and nematodes *e.g.*, root-knot nematodes (*Meloidogyne* spp.); cyst nematodes (*Heterodera* and *Globodera* spp.); root lesion nematodes (*Pratylenchus* spp.); the burrowing nematode (*Radopholus similis*); *Ditylenchus dipsaci*; pine wilt nematode (*Bursaphelenchus xylophilus*); reniform nematode (*Rotylenchulus reniformis*); *Xiphinema index*; *Nacobbus aberrans*; and *Aphelenchoides besseyi* also reported as pathogens [28,29].

These pathogens create the most losses on agricultural and forestry plants and play essential roles as the main agents in biotic stress in the world. Due to created losses by biotic stresses, utilizing PGPR as an eco-friendly technique for controlling phytopathogens and enhancing crop yield. PGPR overwhelms pathogens by producing antagonistic compounds, and by inducing the plant immune system [30,31].

#### 3.1. Plant defense responses against biotic stresses

Different networks of signals and responses create plant tolerance against stress, and these networks provided an intricate mechanism to help plants for prevention of pathogen attacks [32] (Fig. 2). The DNA and histone levels can alter by biotic stress in the epigenetic process in which different changes in resistance and signal adjustment are affected by DNA methylation, histone modification, and small non-coding RNAs (sncRNAs) [33]. Defense mechanisms of plants in contrast to pathogens carried out by different methods *i.e.*, reactive oxygen species (ROS) production [34], agglomeration of  $H_2O_2$  [35], suberization and lignification of cell walls at the infected sites [33], and expression of pathogenesis-related (PR) protein genes [36]. For instance, defense-related proteins that were identified in sugarcane in response to biotic stress included  $\beta$ -1,3-glucanase (PR-2), chitinases (PR-3, PR-4, PR-8, and PR-11), thaumatin (PR-5), proteinase inhibitors (PR-6), peroxidase (PR-9), ribonuclease-like (PR-10), defensin (PR-12), lipid-transfer protein (PR-14), NBS-LRR protein, glycoproteins, catalases, and WRKY proteins [37]. Furthermore, plants encompass an innate immune system or inducible defense mechanism contained in pathogen/microbe-associated molecular patterns (PAMPs/MAMPs) [38] that cause activation of pattern-triggered immunity (PTI) [39], as well as effector-triggered immunity (ETI) activated nucleotide-binding domain leucine-rich repeat-containing receptors (NLRs) [40]. For example, the immunity system of the rice plants has been indicated a vital

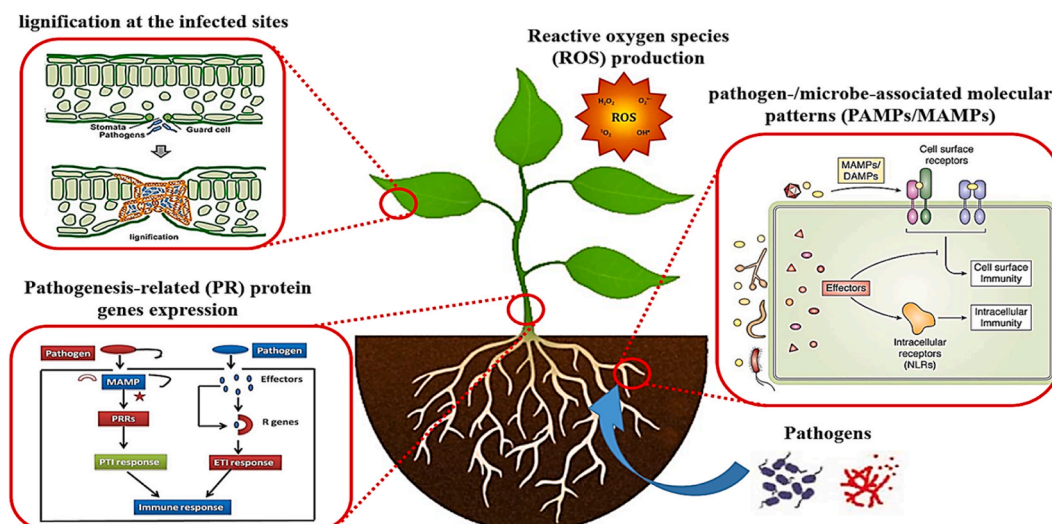


Fig. 2. Defense mechanisms of plants in contrast of pathogens.

role against *Magnaporthe oryzae* with PTI and ETI [41]. About plant defense, induced systemic resistance (ISR) responses will increase healthy plant defense with activation of PTI and ETI in plant defense. In addition to ISR, there is another systemic resistance in plants that enhance plant defense against different pathogens named systemic acquired resistance (SAR) [5]. In addition, MicroRNAs (miRNAs), i.e., non-coding RNAs, can play essential roles in plant immune responses with physiological processes against pathogens and herbivores [42]. Details about pathogenesis-related protein and genes and their application in plant defense are given in Table 1.

### 3.2. Agents that induce resistance against biotic stresses

Countless dissimilar organic and inorganic complexes have been exposed to trigger and encourage confrontation in the floras. Through the use of salicylic acid (SA) as a crucial endogenous sign for systemic acquired resistance (SAR), a rigorous exploration was started in the direction to recognize mock chemicals intelligent enough to impersonate SA in SAR initiation. 2, 6-dichloroisonicotinic acid (INA) and its methyl radical phenylacetate were the initial mock complexes testified to trigger the successful response of SAR in the plants [4,63]. Far ahead, benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester (BTH) developed as a striking mock SAR activator. SA, INA and BTH are expected to trigger SAR by similar pathways for signaling [64,65]. Some common chemical activators are included in Fig. 3.

#### 3.2.1. Acibenzolar-S-methyl (ASM)

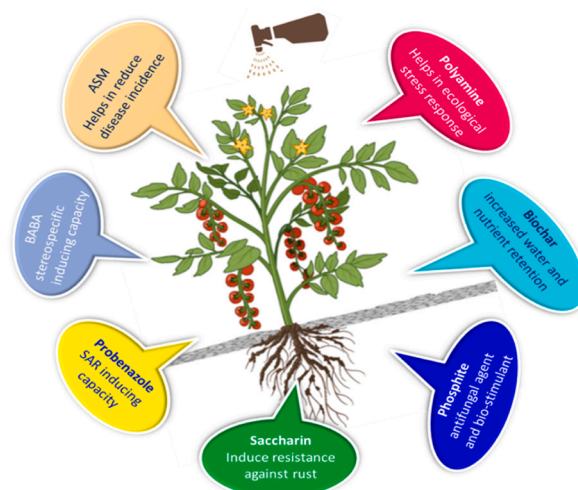
ASM is utmost operative and effective activator for treating downy mildew, microbial spot, and blue mold of vegetable crops. Its performances almost equal as a salicylic acid in SAR process [66]. Numerous pre-harvest bids of ASM were responsible to decrease latent infections instigated by *Alternaria alternata* and *Fusarium* spp. On muskmelons [67]. ASM similarly revealed to decrease contagion of muskmelon fruits by *Trichothecium roseum* and to decrease disease occurrence on fruits at the time of packing and loading at room temperature [68]. ASM induced resistance was connected with improved activities of defense-related enzymes and phenolic resin, lignin and flavonoids content [69].

#### 3.2.2. $\beta$ -Aminobutyric acid (BABA)

BABA has a stereospecific persuading power since only the R enantiomer is active in plants [70,71]. BABA does not depend on salicylic acid, jasmonic acid and ethylene signaling pathways, but it augments ailment protection contrary to late blight of tomato, downy mildew of grapevine and phytophthora blight of pepper [72]. Since the unearthing of BABA, the wide-ranging resistance-inducing capacity of BABA mutual with its aptitude is leading a large arrangement of plants for improved protection contrary to stressors [73,74]. Exogenous usage of BABA can inspire confrontation against viruses, bacteria, fungi, oomycetes, nematodes, and

**Table 1**  
Examples of some genes and their application in plant defense.

Protein/genes	Plants	Biological application	References
MicroRNAs (miRNAs),	<i>Oryza sativa</i>	Plant immune responses with physiological processes against pathogens and herbivores	[42]
Pn-PR like genes	<i>Panax notoginseng</i>	Provides defense against the root rot pathogen	[43]
PR proteins	<i>Triticum</i> sp.	Providing resistance in non-race specific high temperature	[44]
VpPR10.1	<i>Vitis vinifera</i>	Reducing the disease caused by downy mildew caused by <i>Plasmopara viticola</i>	[45]
BjPR proteins	<i>Brassica juncea</i>	Proteins showed important cis-regulatory elements related to biotic, abiotic, and hormonal stresses.	[46]
LrPR10-5	<i>Lilium regale</i>	Antifungal activity, RNase activity plays important role during response to <i>F. oxysporum</i> infection.	[47]
PR10 proteins	Transgenic <i>Arabidopsis thaliana</i>	Exhibits resistance to salt stress	[48]
Thaumatococin-like protein (TLP)	<i>Vitis vinifera</i>	Enhancing the salicylic acid and jasmonic acid/ethylene signaling pathways.	[49]
PR10 proteins	Moss	Ribo-nuclease activity	[50]
JIOsPR10 proteins	Transgenic <i>Oryza sativa</i>	Modulation of biotic and abiotic stresses tolerance probably by activation of stress related proteins	[51]
GmPRP	<i>Glycine max</i>	Defense of against <i>Phytophthora sojae</i> infection.	[52]
PR-4b	<i>Theobroma cacao</i>	RNase activity, Ca <sup>2+</sup> and Mg <sup>2+</sup> dependent-DNase activity and antifungal action on <i>Moniliophthora perniciosa</i> .	[53]
PR10-1 gene	<i>Gossypium herbaceum</i>	Antifungal activity against wilt fungi	[54]
PR2	<i>Arabidopsis thaliana</i>	Induces abscisic acid (ABA) production and mediate pathogen-induced callose deposition	[55]
JcPR-10	<i>Jatropha curcas</i>	Exhibit RNase and have antifungal activity	[56]
PgPR10-1	<i>Arabidopsis thaliana</i>	Provides resistance against fungal and bacterial infection	[57]
PR4 proteins	<i>Triticum</i> sp.	Antifungal activity	[58]
LrPR4	<i>Lycoris radiata</i>	Antifungal activity against <i>Magnaporthe grisea</i>	[59]
PR4 proteins	<i>Triticum</i> sp.	Ribo-nuclease activity	[60]
Rab28 gene	<i>Zea mays</i>	ABA inducing ability in embryos and vegetative tissues	[61]
5' region of <i>cor15a</i> between nucleotides -305 and +78	<i>Arabidopsis thaliana</i>	Helps in imparting cold-, drought- and ABA-regulated gene expression	[62]



**Fig. 3.** Schematic diagram showing chemical activators that induce resistance. [Acibenzolar-S-methyl (ASM);  $\beta$ -Aminobutyric acid (BABA), and systemic acquired resistance (SAR)].

arthropods, as well as against abiotic stressors like cold, heat, drought, and salt [75]. Furthermore, upsurge in confrontation persuaded by BABA can also be conveyed to the offspring of BABA-treated plants, which exist mutually for increasing resistance to pathogen and as well for sensitization to its action [76].

### 3.2.3. Probenazole

Probenazole and its active metabolite 1,2-benzisothiazole-1,1-dioxide encourage SAR in Arabidopsis by thought-provoking a site upstream of the theme of buildup of SA in the SAR-signaling pathway [77]. This activator has been extensively cast off contrary to rice blast, caused by *Magnaporthe grisea*, and leaf blight, instigated by *Xanthomonas oryzae* pv. *Oryzae* [78]. Contempt of its widespread usage, expansion of confrontation in the target pathogens has not been detected [79]. Usage of probenazole seems constrained to rice, even though this capacity alteration occurs in the upcoming time. Few investigations established operative regulation of southerly corn leaf blight on maize, instigated by *Cochliobolus heterostrophus*, deprived of harmful possessions on plant development [80]. Meanwhile southern corn leaf blight is presently meticulous by usage of several applications of the antifungal agent i.e., maneb, the prepared obtainability and less poisonousness of probenazole might verify valuable as a substitutional regulator for controlling significant disease of maize [81].

### 3.2.4. Saccharin

Saccharin is one of the metabolites of probenazole (PBZ) in plants and perform as activator. It can be used as a root saturate which was generally extraoperative than the leaf treatment at persuading defense [82]. Alike retort has been also detected by others in numerous plant species [83]. Saccharin is same time induces SAR in rice contrary to *M. grisea* and *X. oryzae* [1]. Similarly, it is too tempting confrontation against rust on broad bean [83], and powdery mildew and *Rhynchosporium commune* on barley [1]. Saccharin was also exposed to defend soybeans counter to rust (*Phakospora pachyrhizi*), with root-drench action showing further operative action than foliar bids. Moreover, systemic protection seeming 15 days after subsequent usage of saccharin as a root saturate [84].

### 3.2.5. Phosphite

Phosphate (Pi) is most important element in the soil and its reduced form is Phosphite (Phi). It is developing as an innovative bio-stimulator in numerous agricultural practices [85]. However, there is no consent on its physical purpose as a P-source for plant nourishment, investigational indication has shown that Phi can performance as a biocide and distress plant manufacture and efficiency [86]. Phi is effortlessly engrossed and spread with the help of the xylem and phloem to entirely parts of the plant [87]. Phi is normally used as an antifungal agent and bio-stimulant in existing agronomic practices. It is regularly articulated as a liquid, which upsurges its agility in loam, mud, and different tissues of plant [86,88]. Phi reported killing agricultural fungal diseases, mostly those belonging to the oomycetes (*Phytophthora* spp., *Pythium* spp.) and the Downy Mildew pathogen that affect different agronomically significant crops and non-crops [86,88–90].

### 3.2.6. Biochar

Biochar is formed by the thermal alteration of organic substances in an oxygen-limited situation. Biochar concurrently recovers a wide range of soil possessions and thus intensifies agronomic harvests [91], its free radicals hinder seed germination and saplings growth by rising the pH. Alkaline biochars lighten Al and substantial metal venomousness that can decrease root development in acidic loams and muds [92,93]. Additionally, at higher biochar concentrations, solubilization levels of salts are also high which leads to osmotic stress (OS), this stress hinders sprouting, propagation, and seedling growth [94]. Furthermore, free radicals linked with

biochar have remained found to damage certain carbon-based and mineral impurities [95]. Yet, carbon-based particles released can be phytotoxic in nature, consequently smearing biochar a few days before spreading rope-up sprout development through the expansion of an advantageous rhizosphere microbiome [96].

### 3.2.7. 4.1.7. Polyamine

Polyamines (PAs) are aliphatic nitrogenous bases having low molecular weight, they contain 2 or extra amino groups. They are byproducts of numerous organisms during metabolic processes and exist in practically all cells. They also play significant parts in varied plant progress and developmental procedures and ecological stress responses, they are measured as a novel kind of plant bio-stimulant [97]. In higher plants, PAs are mostly present in their permitted form. Putrescine, spermidine, and spermine are the chief PAs in plants, and they are intricate in the parameter of varied physical procedures [98], e.g., fruits and flower growth, embryogenesis, organogenesis [99], senescence, and fruit ripening. They are also intricate as rejoinders for the stresses i.e., biotic and abiotic [98].

## 3.3. Effective phenotypic characteristics of plants to cope with biotic stress

### 3.3.1. Root system architecture

The complete longitudinal planning of the separate parts of the root system architecture (RSA) is subtle to edaphic and endogenous gestures that provide detail on the health management standing of soil and plant, microbe interaction, and impacts grain yield [100]. Throughout, dissimilar growing stages of *Arabidopsis thaliana*, RSA changes for extensive variety of nutrient insufficiencies, which is related with the cause that not all nutrients have the identical accumulation pattern and thus ask for a different response [101]. In beans and maize root phenotypes such as crown roots, differential production of root cortical parenchyma and hypocotyl-borne roots are play important role in large quantity of nitrogen and phosphorus gaining from soil and suppress the metabolic costs implicated in soil investigation [102]. Plant development hormones (auxin and cytokinin) and carbohydrates are vital for both intrinsic root growth, and modulating RSA in diverse growth conditions, and thus providing the optimization of root growth in difficult, and heterogeneous environment [103].

### 3.3.2. Leaf pubescence

Further down the stress or favorable circumstances, the transpiration rate dramas a vital part in the plant retort to a stress stimulus. The rate of transpiration is influenced by the different leaf characteristics traits for example, root-to-leaf ratio, leaf area, leaf shape, leaf orientation, leaf thickness, and delivery and density of stomata in a leaf. Amongst these, the most essential features are the leaf surface physical features (pubescence/gloriousness) [104]. Leaf pubescence plays a crucial biological character in confrontation against pests and reworking to the different environment conditions and demonstrated wide phenotypical disparity [105]. Under the drought stress condition plants species having lower leaf absorbance values. While lower leaf absorbance minimizes the water consumption after closing the stomata under drought condition and maintained leaf longevity during different growing stages [106]. But in case of wheat plants leaf pubescence is often controlled by two genes *H11* on chromosome 4 B and *H12* on chromosome 7 B [107].

### 3.3.3. Leaf water potential regulation

Leaf water potential regulation is indispensable mechanism in which the entire plants and bionetwork contribute and performed pointedly. Most of the time, the majorly open stomatal pores are inducing low water level in plants, which same time also connected with higher CO<sub>2</sub> and a large water fluidity [108]. Other factor which are influencing the leaf water potentials are potential of soil water. The water potential regulation is significant not lone for of its function in amplification plant retorts to drought and other stress but also for the reason that of it effect the pathways for different metabolic processes [109]. Water stress had noteworthy consequence on grain and dry stuff harvest as well as crop water stress index and leaf water potential of quinoa cv. *Titicaca* [110]. Furthermore, plant morphology, photosynthetic adaptability, and ultimately better chilling tolerance are extremely influenced and improved by high leaf water potential [111].

### 3.3.4. Cuticular wax

Cuticular wax is complex formation and chemical arrangement varied per different plant species, while, cuticular wax continually assists a serious part in confining nonstomatal liquid damage, plant abiotic and biotic stress tolerance [112], and has been concerned in protection machineries counter to extreme UV radiation, high temperature, bacterial and fungal pathogens, insects, high salinity, and low temperature [113]. It is composed on the plants external surface and the whole amount is delimited in retort to the severity of drought stress, which is ultimately performed by waxy genes [114]. Thus, variations in the biogenesis and build-up outline of cuticular wax, in retort to altering environmental circumstances, working as a key part in plant defense against stress [30]. Drought stress treatments significantly increased cuticular wax capacity in some important crops such as wheat [115]; some fruits viz. Mango [116]; orange [117]; bayberry [118], and pear [119].

### 3.3.5. Canopy temperature

During the initiation of crop water resistance, canopy temperature has been working as an indicator, meanwhile a lessening in plant accessible water consequences in inferior transpiration tariffs and subsequently higher canopy temperatures arrives [120]. The major resin behind increase in canopy temperature is engrossment of solar radiation, but temperature goes down when that energy is cast-off for evaporating water rather than solar heating of plant surfaces [121]. It is also usually following a diurnal curve, means temperature will rise in daytime because of upsurges in solar radiation and temperature. Further, a water stressed plant will decrease transpiration

and will characteristically have a higher temperature than the non-stressed crop [122].

### 3.4. Host genotype

Host genotype has well established evidence to mediate the induced resistance expression [123]. For instance, plant genotype is a prime factor of how the associated microbial community will behave. A wide range of *Arabidopsis* accessions in hydroponic system demonstrated support towards *Pseudomonas fluorescens* growth in wider scale [124], Samain et al. [125] tested the influence on induced resistance by *Paenibacillus* sp. Strain B2 against *Septoria tritici* blotch causing *Mycosphaerella graminicola* in wheat genotype dependent. There was a substantial variation in protection efficiency among the cultivars upon PB2 induced resistance. In another study by Mora-Romero et al. [126], three distinct common beans (A-55, Az Reg87, and Az Hig) and two tomato (Missouri and Micro-Tom) genotypes were colonized with *Rhizophagus irregularis*, an arbuscular mycorrhizal fungi, to check the induced disease protection against *Sclerotinia sclerotiorum* and *Xanthomonas campestris* pv. *Vesicatoria*, respectively [127]. Smaller necrotic lesions found in genotype A-55 and Az Reg87 than Az Hig, and significant variability in lesion numbers perceived between two tomato genotypes, which helped understanding the impact of host genotype in induced resistance against pathogens. Again, different host genotypes demonstrated varying levels (e. g. incomplete, partial, and complete) of resistance towards pathogenicity of the same pathogen [128]. Attack of identical pathogens in hosts of diverse genotypes face differential resistance. Lakkis et al. [129] inoculated *Pseudomonas fluorescens* in two different cultivars of grapevine, with susceptible resistance against downy mildew and partial resistance against grey mold diseases. Both cultivars displayed well distinguished basal level defense, photosynthetic efficiency, and phenotypic susceptibility against the two diseases. In addition, *P. fluorescens* introduction induced systemic resistance against those diseases based on their basal genotypic immunity. Such dissimilarity in induced resistance among host genotypes has been reported in other studies as well [130,131].

### 3.5. Effect of light on plant–pathogen interaction

Light, a prime source of energy, is essential for almost all realms of life. From plant physiology to microbial physiology, light plays a pivotal role. Cyanobacteria, a group of phototrophic bacteria, is one such group of bacteria where the light dependency of bacterial processes for energy production were first reported [132]. Besides phototrophic bacteria, light also significantly shapes the lifestyle of non-phototrophic bacteria. Photoreceptors in non-phototrophic bacteria regulate their decisions regarding their location, biofilm formation or inhibition, surface attachments, stress situation sensing, and switching between environmental and pathogenic behavior [133]. Microbes inhabiting plant leaf surfaces come across the complete solar radiation, however, those found inside plant tissues comparatively receive modified radiation upon absorption and passing among cell walls and remaining intercellular air gaps [134, 135]. Different photosensory proteins (for example, UVA/blue light sensitive LOV, BLUF proteins) present in plant pathogenic bacteria contribute to their pathogenicity. *Pto* phytochrome present in bacterial speck disease causing *Pseudomonas syringae* pv. *Tomato DC3000* (*Pto*) associates with light and controls the bacterial capability of entering plant apoplast along with regulating other functions like motility, adhesion to surface, and formation of biofilms [136]. Significant differences observed when *Ralstonia pseudosolanacearum*, a soil-borne plant pathogen, wild type (LOV present) and a designed mutant (LOV absent) were compared *in vitro* in terms of their pathogenicity processes under white light and dark conditions [137]. Absence of photosensory LOV protein decreased the motility, adhesion ( $p < 0.0059$  and  $p < 0.00001$  under darkness and white light, respectively), and production of thinner biofilm in the mutant *R. pseudosolanacearum* compared to wild type one. Bacteriophytochrome *BphP1*, capable of sensing red light, signal transduction pathway present in *P. syringae* B728a configures crucial stages of their life cycle like colonization, motility, and regulation of virulence [138]. Kahl et al. [139] correlated *Pseudomonas aeruginosa* biofilm matrix inhibition with the low-level activity of cyclic di-GMP (*c-di-GMP*), when exposed to low-intensity blue light for extended periods. Formation of *c-di-GMP* phosphodiesterases under prolonged exposure to low-intensity blue light contributed to biofilm inhibition in *P. aeruginosa*. Rajalingam and Lee [140] inoculated *P. cichorii* JBC1 in tomato plants under various light conditions for verifying the effect of different light in plant-pathogenic disease severity. Seedlings grown in red and green light conditions showed substantial induction of defense contributing genes like phenylalanine ammonia-lyase (*PAL*) compared to seedlings grown in white light and dark conditions. In further study, they also reported significantly lower involvement of genes for phytotoxic lipopeptides, iron acquisition, type 1 and type 6 secretion system, however, the expression of bacteriophytochrome (*bphP*) and heme-oxygenase (*bphO*) were upregulated [141].

### 3.6. Reactive oxygen species (ROS) accumulation in biotic stress

Numerous pathogens and parasites infect plants and incite biotic stress. Plants possess or produce signal molecules (e. g., reactive oxygen species or ROS) that interlink sensory mechanisms to detect any biotic invasion, which help them to mitigate the harmful effects in order to survive. ROS are derived from molecular oxygen ( $O_2$ ), produced either spontaneously by specific oxidases or passively as byproduct of plant aerobic metabolism in different cell components like mitochondria, chloroplasts, and peroxisomes [142–144]. Hydrogen peroxide ( $H_2O_2$ ), superoxide ( $O_2^-$ ), and the hydroxyl radical ( $HO^\bullet$ ) are some major ROS formed commonly in different plant cells. These molecules are an interplay between beneficial and harmful molecules that occur within a plant cell. They are canonical signal molecules to various abiotic and biotic stresses to plants which upregulates defense-related genes and interact with other signaling molecules [145], contrastingly, responsible for irreparable DNA damage and even cell death. Because, production site, distinct reactivity levels, concentration, and capability to penetrate biological membranes orchestrate the role of ROS in the cell [146]. Redox status of infected plant cells shifts upon accumulation of ROS, a crucial primary event inside cells after pathogen attack. The

accumulation pattern is distinct between abiotic and biotic stresses. Again, oxidative burst - occurs in plant cells immediately during pathogen attack, associates microbe/pathogen-associated molecular patterns (MAMPs/PAMPs) perception during hypersensitive reactions [147]. Perception of MAMPs/PAMPs induces signaling phenomena such as ion fluxes, protein kinase formation ( $\text{Ca}^{2+}$ -dependent), cell wall lignification, and ROS assembly [148]. During pathogen attack,  $\text{O}_2^-$  and  $\text{H}_2\text{O}_2$  are produced in the apoplast considering oxidases (e.g., respiratory burst oxidase homologues or RBOH) activation [149]. In chloroplasts, ROS build up due to imbalance and interference in metabolic pathways [150]. During avirulent pathogen infection, plants accumulate ROS in two steps; a low-level transient first stage prior to a more permanent ROS accumulation in second stage [149]. Researchers over the decades have identified genes that regulate ROS productivity and functionality when encounter biotic stress stimulus in different crops like NAC56 and TaRar1 gene in oilseed rape and wheat, respectively [151,152].

### 3.7. Root exudates in biotic stress

Root exudates are a group of metabolites secreted by plants to their adjacent soils. Plants release a substantial portion (11–40% [153]) of their assimilated carbon as primary and secondary metabolites, though the exudation process is still elusive [154,155]. Composition of exudates depend on various factors like species, growth stage, root morphology, genotype, mineral nutrient accessibility, and environmental circumstances [156]. Secreted metabolites act as the regulator of plant-soil feedbacks in case of plant growth and defense against biotic stresses by reshaping the soil microbial composition [157]. Exudates from roots act as attractant for microorganisms for building up symbiotic relationships with plants, where microbes use these secreted metabolites as their carbon source. Beneficial microbes solubilize insoluble nutrients (e.g., zinc, phosphorus, potassium, iron) for easier root uptake, which were inaccessible for roots previously [47,158–160]. Besides contributing in nutrient acquisition, root exudates also helps in biotic stress management or disease suppression [161]. Healthy plant roots are often habitat for heterogeneous microbial consortia that enhances plant survival ability by defending against pathogens and pests [162]. Plant immune signaling system and rhizosphere microbial community composition are sophisticatedly linked [163]. Root exudates serve in plant defense upon adopting some strategies. Beneficial microbes may contribute to defense signaling pathways activation and/or antibiotics secretion to mitigate virulence and severity of pathogens [164]. Another common strategy is “cry for help”- where plants manipulate their root exudates in such a way that these bioactive molecules attract specific groups of microbes who will play the defensive role [163]. Maize root exudates can engage *B. amyloliquefaciens* OR2-30 for protecting them against *Fusarium graminearum* infection, where difference was evident between pre- and post-infection root exudates and the post-infection exudates supported more effective colonization of OR2-30 strain [165]. Yuan et al. [166] inoculated *P. syringae* pv *tomato* in *A. thaliana* and showed that infected plants have substantial increase in amino acids, long chain organic acids, and nucleotides exudation. On the other hand, lower secretion of sugars, alcohols, and short chain organic acids was observed. They also found that introduction of a pathogen reshaped the soil bacterial composition in both adjacent rhizosphere and bulk soil, which is conclusive about the recruitment of beneficial microbial communities by plants under pathogen invasion.

### 3.8. Role of phytohormones in plant response to biotic stress

Phytohormones are biomolecules synthesized in plants from secondary metabolism. In parallel to enhancing plants growth and development, phytohormones also support plants under abiotic and biotic conditions. Auxin, gibberellin, and cytokinin assist plants in development responses while abscisic acid (ABA), ethylene, salicylic acid (SA) and jasmonic acid (JA) help plants overcoming abiotic and biotic stresses [167,168]. In general, SA is employed in defense response activation of against biotrophic pathogens, since JA response against necrotrophic pathogens and herbivorous insects [169–171]. When plant cells detect phytopathogens, the SA synthesis is activated, which triggers defense response in other unharmed cells to be prepared for defense. Plants synthesize SA using the isochorismate and the phenylalanine ammonia-lyase pathways [172]. Enhanced SA level give rise to different proteins with antimicrobial activity in the cells upon inducing pathogenesis related genes [173]. Thus, SA provides augmented defense towards several pathogens. Alongside biotic stress reduction, SA also facilitates plants in abiotic stress tolerance, DNA damage repair, seed germination and some other agronomic aspects [172]. Applications of SA in rice were effective in reducing disease incidence and severity occurred by *F. oxysporum*, *X. oryzae*, and *Oebalus pugnax* [174–176]. The JA is another most important signaling molecule against insect attacks in plants [169]. Level of JA increased when plants are damaged by insects, and the enhanced JA level can induce polyphenol oxidase, a defensive enzyme, production and thereby protect plants against herbivores [177]. The methyl ester derivative of JA (Me-JA) application was successful in combating *Ostrinia furnacalis* moth in maize, where Me-JA induced toxic protein production [178]. Like SA, JA is also involved in different plant developmental processes like plant growth, seed germination, fruit ripening, and senescence besides biotic stress mitigation [179].

Use of nanotechnology for crop production improvement is becoming a trend in agriculture. Nanoparticles can modulate a wide array of physiological and biochemical processes in plants and therefore considered as regulatory molecules [180]. Thus, the activity regulation of different phytohormones can provide additional defense against phytopathogens. Several studies reported that the activity of SA and JA are also affected when exposed to nanoparticles in plants. Vankova et al. [181] reported the elevation of ABA and SA when ZnO nanoparticles were introduced in model plants *A. thaliana*, however, the JA synthesis went down. Upregulated SA synthesis and enhanced disease resistance were observed in a close relative species (*Nicotiana benthamiana*) of tobacco plants, against *Tobacco mosaic virus*, when Fe-oxide nanoparticles ( $\text{Fe}_3\text{O}_4$ ) were foliar applied [182]. Soria et al. [183] found down regulation in JA when *A. thaliana* was treated with copperoxide (CuO) nanoparticles, though some of the JA precursors were upregulated. Again, foliar application of copper sulfide (CuS) nanoparticles in different copper and sulfur mixture ratio in rice (*Oryza sativa* L.) upregulated shoot SA



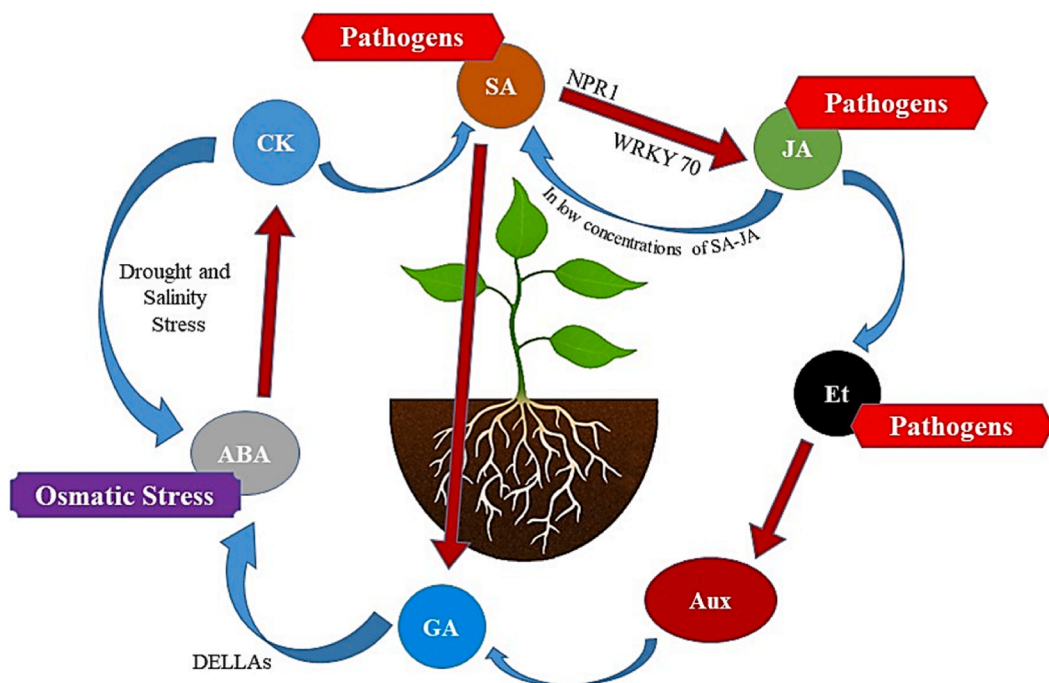
and JA production and decreased disease incidence by 15–32.5% [184].

### 3.8.1. Hormonal crosstalk in plant's resistance under stress conditions

The interactions of ABA, SA, JA, and ET signaling pathways are known to regulate the plant's defense response but the determining factor and the critical feature in stress conditions is the complete adaptation of the plant and its stable growth [152,185]. Therefore, the interaction of ABA, SA, JA, and Et with the main growth-stimulating hormones, Auxins, GAs (gibberellin), and CKs (cytokinins) play an important role in mediating the stress response [186]. The type of interference (positive or negative) between the signaling pathways of different hormones determines the defense responses activated in plants in response to different stresses, not just the individual contributions of each hormone [187]. For example, GA interacts with ABA, mediated by DELLAs, in regulating the balance between seed dormancy and germination, a key mechanism for escaping early abiotic stress conditions [188]. It has also been found that the signaling pathways of SA and JA cross at different points because SA and JA regulate biotic stress responses oppositely [189]; have shown that NPR1 is a key player in the antagonistic interaction of SA and JA [190]. Another critical component is the transcription factor WRKY 70, which mediates the antagonistic interaction between these two hormones [191]. Some studies have observed synergistic interactions at low concentrations of SA-JA and with simultaneous induction of both defences [192,193]. A review of plant hormone signaling networks and their interaction shows that ABA, SA, JA, and Et have major roles in stress response, ABA mainly regulates osmotic stress [194]. SA, JA, and Et are involved in biotic stress responses [195]. Several transcription factors have opposing regulatory effects on the SA and JA pathways [196]. JA-Et have a synergistic effect with each other [197]. Auxins, GAs, and CKs participate in biotic stress responses through the SA signaling pathway [198]. Auxins interact with ethylene in plant stress conditions to regulate growth and root architecture, which is the key point in plant tolerance to drought and salinity [97]. The negative regulation of lateral root formation and the positive regulation of unwanted root formation by ethylene through the modulation of auxin transport provide another example of auxin-ethylene interaction in the modification of root architecture [186]. Studies have shown that most of the auxin-related genes are repressed after SAR induction, which clearly shows that auxin increases disease susceptibility and therefore suppression of auxin signaling is essential in increasing disease resistance [97]. CKs, also interact with ABA and act in abiotic stress responses such as drought and salinity [199].

## 4. Induction of systemic resistance (ISR)

Any induced plant reaction that leads to increased resistance and protection, including local and systemic induced resistance against diseases, is generally called induced resistance (IR) [201]. SAR is one form of IR that reacts to the endogenous gathering of



**Fig. 4.** The plant hormones and their crosstalk in stress responses. Abbreviations: ABA: abscisic acid, SA: salicylic acid, JA: jasmonic acid, Et: ethylene, Aux: auxin, GA: gibberellin, CK: cytokinin, WRKY70: WEKY DNA binding protein 70, DELLAs: DELLA proteins constitute a small clade within the GRAS family of loosely defined plant specific nuclear proteins. Their name was coined on the basis of a short stretch of amino acids (D-E-L-L-A) in their *N*-terminal region, which is tightly conserved among all higher plant species [200]. Note: blue arrows indicate positive regulation and red arrows indicate negative regulation.

salicylic acid and is measured by the signaling pathway [202] (Fig. 4). SAR can be activated against pathogens or elicitors and protect the plant against a wide range of pathogens [203]. A promising result on plant health and control of plant pathogens is that plant systemic resistance can be induced against pathogens. For the first time were presented reports of a strategy in addition to SAR in cucumber against *Colletotrichum orbiculare* [204], in common bean against *Pseudomonas syringae* pv. *Phaseolicola* [205], and in carnation against *Fusarium oxysporum* f. sp. *Dianthi* [206]. In these reports, the reasons of ISR were stated that some PGPR are able to encourage systemic resistance of the plant against other pathogens (Fig. 4).

#### 4.1. Induction of systemic resistance by PGPR

Bacteria that are situated in the rhizosphere, rhizosphere, and phyllosphere of the plants and have beneficial and growth-stimulating properties (directly or indirectly) on their host plants are generally called PGPR [207–214]. In addition to direct effects, PGPR can reduce plant pathogens and indirectly improve plant growth and development through competition for nutrients, production of antibiotics, production of lytic enzymes, ISR, etc. [215–217]. Unlike SAR, ISR occurs when plant roots are colonized by PGPR and the ISR pathway can be mediated by jasmonate or ethylene [218,219]. In both SAR and ISR modes, the plant is prepared to face the next challenge (generally pathogen invasion) by a previous treatment (microorganisms or chemical elicitors). To primed plants to deal with infection and activate the ISR, increasing the expression of JA- and Et-regulated genes is performed [220].

Before the introduction of ISR, the abilities of PGPR to control plant pathogens were mainly attributed to mechanisms such as antibiotic production, competition for nutrients, siderophore production (to compete for iron supply), production of lytic enzymes, hydrogen cyanide production, etc. [221]. The existence of PGPR-mediated ISR has been proven in several plant species, and its effect against a variety of plant pathogens such as bacteria, fungi, and viruses has been reported [218]. ISR leads to a decrease in the speed of disease development as a result of the infection affected by the pathogen, and the severity of the disease in the infected plant decreases. In fact, ISR leads to an increase in the plant's defense capacity to deal with various pathogens [222]. As mentioned earlier, SAR is dependent on SA, and ISR is dependent on JA and Et signaling in plants [223] (Fig. 5). Unlike other plant defense mechanisms, ISR induction does not require extensive root colonization by microbes, and ISR is not specific, unlike R gene-mediated resistance, and is activated against a wide range of pathogens as well as insects and nematodes [224,225]. After induction, ISR leads to plant protection for a significant part of its lifetime and has a relatively stable state [226].

##### 4.1.1. Spectrum of protection by PGPR

The PGPR are soil-borne microorganisms that actively colonize plant roots and provide several advantages to the plant. In many parts of the world, PGPR significantly improves the quality of the soil, plant growth of the plant, and agricultural output [227–229]. While they have negative impacts on the destructive microbial process, they have beneficial impacts on the nutrition of the plant and root growth. Several PGPR strains may exhibit a major role in the management of various diseases of the plant. These strains secrete various chemicals, including pyoluteorin, phenazine, DAPG, tensin, and viscosinamide, which are commonly shown to have disease-reducing action. *Pseudomonas*, *Azotobacter*, *Paenibacillus*, *Azospirillum*, *Enterobacter*, *Streptomyces* and *Bacillus* are examples of these important bacteria in question [230]. Numerous phytopathogens can be inhibited by rhizobacteria in a variety of ways, including by competing with them for nutrient sources and available space and by releasing bacteriocins, lytic enzymes, siderophores and antibiotics [231].

A biocontrol product called *B. amyloliquefaciens* (SN13) works against *R. solani* by extending tolerance through improved plant

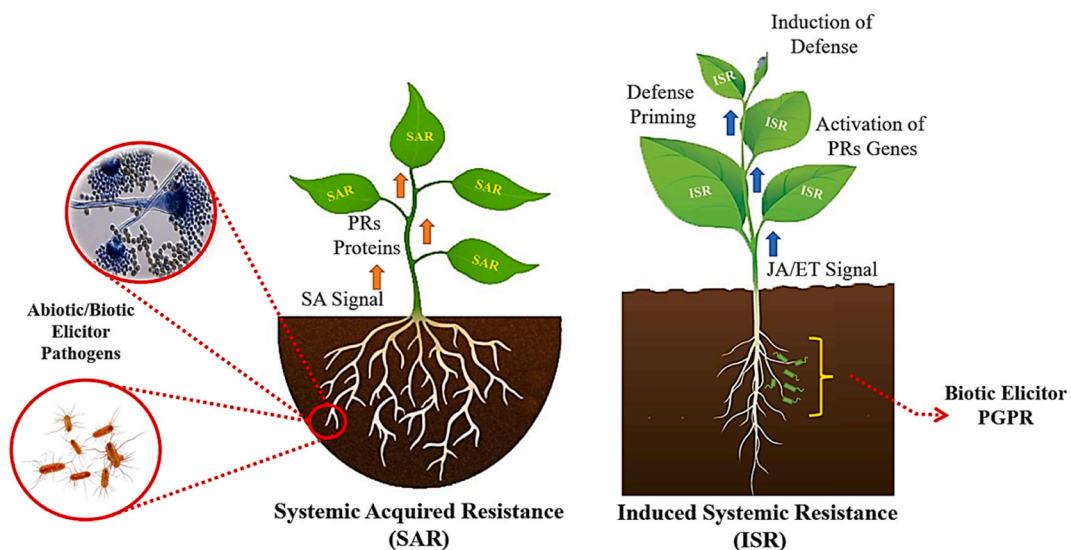


Fig. 5. The difference between SAR and ISR as plant systemic resistances.

defense mechanisms. The colonized plants have altered phytohormone signaling, persistent elicitor maintenance, secondary metabolite secretion, and a balance between ROS and scavengers that produce reactive oxygen species [232]. Increased jasmonic acid and gossypol production was observed in *G. hirsutum* plants infected with *Bacillus* species, which inhibited *S. exigua* larval feeding. Inoculated plants had increased gene transcript levels notable in the production of jasmonates and allelochemicals and the pest was suppressed more [233]. By boosting the expression of antioxidant enzymes and defense-related genes, such as peroxidase, phenylalanine ammonia lyase, superoxide dismutase, and catalase, *E. asburiae* BQ9 promoted inhibition against the yellow leaf curl virus (TYLCV) in tomato in plants [234]. The concentration of the RNA cucumber mosaic virus (CMV) in *N. tabacum* cv was reduced after *P. lentimorbus* B-30488 was inoculated in the soil which showed a 91% reduction in the white burley leaf disease. This suggested increased resistance to the virus since it was accompanied by an increment in pathogenesis and stress-related gene expression as well as enzymes involved in antioxidant activity. Plants with PGPR colonization had better tissue health and physiology, which led to more seeds and flowers being produced [235]. Additionally, the bacteria generate ACCd and promote tolerance to the *Sclerotium rolfsii*-caused southern blight disease of tomato plants. The antioxidant enzyme and ethylene pathway activities were modulated in the inoculated plants, and pathogen-related gene expression analyses supported systemic tolerance [236]. ISR was induced in *S. lycopersicum* against *Alternaria alternata* by producing acyl-homoserine lactones (AHL). *S. liquefaciens* MG1 and *P. putida* IsoF, whereas AHL-null mutant strains of the two rhizobacteria PGPR resulted in decreased ISR [237]. Chemicals mimicking AHL signals have been discovered in root exudates, which promote beneficial rhizosphere interactions while suppressing harmful bacterial growth [238]. Additionally, its exhibited biocontrol potentials, PGPR shields plants against infections by triggering internal molecular and biochemical defensive mechanisms [215]. To prepare plants for potential pathogen assault, PGPR can elicit ISR in plants, which activates genes relevant to pathogenesis through defense regulatory proteins and phytohormone signaling pathways [239]. The induction of ISR in plants is modulated by bacterial signal molecules and chemical triggers connected to microbes, including chitin oligomers. ISR is induced by pathogen cell-surface components such the lipopolysaccharides O-antigen and flagellins, whereas analogs of JA and SA cause Et to be released, which causes plants to develop NPR1-mediated SAR [240].

#### 4.1.2. Mechanism of ISR-mediated by PGPR

PGPRs similar to phytopathogenic microbes might provoke inducible defense mechanisms in the plants. These mechanisms could involve fortification of cell walls, phytoalexin (low molecular weight antimicrobial compounds) production, synthesis of pathogenesis-related proteins (PRs) [211,213,241,242], also an augmented potential to induce these defense responses after exposed with a phytopathogen that defined as “sensitization”, “priming,” or “potentiation” [73,243]. With considering defense motivations, sometimes the beneficial rhizobacterium might recognize as potential threat and cause to making compounds with resistance-eliciting efficiencies in which act similar to phytopathogen (bacteria and fungi) elicitors. The kingdoms of plant have special mechanisms for perceiving of fungi and bacteria elicitors that these are usually mentioned to as pathogen-associated molecular patterns (PAMPs) [244]. In carnation and radish hosts, the outer membrane LPS with the O-antigenic side chain (strain WCS417r) is the momentous determinant for the activation of ISR against wilt disease caused by *Fusarium* spp [5,245]. Also, it is confirmed that mutated bacterium cannot induce resistance without O-antigenic side chain, but LPS-involving cell walls and purified LPS of WCS417r can induce ISR similar to living bacteria. Furthermore, siderophores and SA are the other determinants to ISR induction in bacteria [246]. Fluorescent *Pseudomonas* spp. Have different pathway for ISR induction in *Arabidopsis*, as well as, it was from the results of LPS of WCS417r in carnation and radish. The LPS of WCS417r shown that not only had a slight role for induction of ISR in *Arabidopsis*, but also signifying that WCS417r had more than a single ISR-inducing determinant [247]. WCS417r in high temperature or low density could induce host resistance against wide range of phytopathogens [248] which contain complex or multiple resistance response. In another study verified that *P. fluorescens* WCS374r-elicited ISR in rice (*Oryza sativa*) against blast fungus (*Magnaporthe oryzae*) is founded on Pseudobactin-mediated priming for a SA-repressible with having many facets in defense responses [249]. PGPRs apply different mode actions for disease prevention in plants with include siderophore competition for iron, antibiosis, lytic enzyme production, and ISR [245,250]. The rhizobacteria and endophytic bacteria can contribute and help to ISR in induction of plant responses in multi-trophic interactions between plant-PGPR-pathogen [251] with producing components in which induce ISR with flagella, lipopolysaccharides (LPS), SA, and siderophores [223]. Also, other components have been shown that induce ISR against various phytopathogens that including, cyclic lipopeptides [252], the antifungal factor 2,4-diacetyl phloroglucinol (Phl) [253], the signal molecule *N*-acyl homoserine lactone (AHL) [254], pyochelin and pyocyanin [225], volatile blends, volatiles acetoin and 2,3-butanediol in *B. subtilis* [255]. In grapevine plant, *P. fluorescens* CHA0 and *P. aeruginosa* 7NSK2 induced ISR against grey mold (*B. cinerea*) with oxidative burst and phytoalexin agglomeration in host cells that SA, pyochelin, and/or pyoverdine play essential roles in priming phytoalexin [256, 257].

Ferric iron competition that considered as action mode of *P. putida* WCS358 [258], cannot induce ISR in carnation [259] or radish [260], but it triggers ISR in *A. thaliana* [247], *E. urophylla* [248], bean, and tomato [261]. In root colonization by *P. fluorescent* with microarray analysis confirmed that transcription factor gene activated and triggered ISR against diseases including brown-black leaf spots (*P. syringae* pv. tomato), downy mildew (*Hyaloperonospora parasitica*), Black spot (*Alternaria brassicicola*), and grey mold (*B. cinerea*) [262]. *Bacillus* strains with production of cyclic peptides, aminopolyols, and aminoglycosides play a role on ISR activation [225]. PGPRs with secretion of volatile organic compounds (VOCs) has essential role in ISR process [263]. For instance, VOC secreted by *B. subtilis* and *B. amyloquefaciens* had a potential for suppression of soft-rot disease (caused by *E. carotovora* ssp. *carotovora*) in *Arabidopsis* seedlings by ISR activation [264]. In another study shown that L-malic acid secretion increased in artificial inoculation of *A. thaliana* seedlings with causal agent of brown-black leaf spots (*P. syringae* pv. tomato) that this L-malic acid activate ISR response with taking help from *B. subtilis* [265]. One study on fengycin indicated that it had ISR activation potential with inducing the synthesis of plant phenolics with deriving from the defense-related phenylpropanoid metabolism [266,267]. In addition, surfactin can induce

biochemical pathways with defense-related events in tobacco cell with recognition of amphiphilic lipopeptides from *Bacillus* spp. And perception of elicitors by host cells [268].

**4.1.2.1. Biofilm production.** Microbial aggregates and self-organized and cooperative communities that are composed of single or multiple species and have the ability to adhere to living or non-living surfaces are known as biofilms [269]. The requirement for the formation of the matrix of extracellular polymers around the microbial consortium is close contact with each other and quorum sensing [270]. Physiological changes in microbial cells followed by increased cell stress tolerance are among the benefits of exopolysaccharides (EPS) formation [271]. It has been reported that one of the important strategies used by bacterial strains under different stress conditions is the formation of biofilms that lead to their successful survival in the plant rhizosphere [272]. Bacteria with mucus colonies have a high capacity in biofilm formation, and the pattern of root colonization in the rhizosphere of plants is largely similar to biofilm formation in non-living surfaces [273]. Biofilms are composed of carbohydrates, oligos and polysaccharides, protein, lipid and extracellular DNA, and due to their high microbial and enzyme diversity, they play different roles in the interaction between rhizobacteria and plants, such as improving water and nutrients availability in the rhizosphere [274]. Due to the positive effect of biofilm formation on plants under stress conditions, there is great interest in the isolation of biofilm-forming PGPR [275]. Studies have shown that biofilm formation by PGPR plays an important role in protecting plants against abiotic and biotic stresses, for example, strains of *Pseudomonas putida* have been reported to colonize root surfaces and produce biofilm-like structures that protect the plant from drought stress [276]. It has also been reported that the formation of biofilm by *Bacillus amyloliquefaciens* has led to an increase in the salinity stress tolerance threshold in barley plants [272]. Studies have also shown that the biofilm formed by *Bacillus subtilis* protects against tomato wilt disease [277]. The ability to form a biofilm in *Paenibacillus polymyxa* has helped the wheat plant to tolerance biotic and abiotic stresses [278]. It has been reported that the gene encoding EPS plays a vital role in *Bacillus amyloliquefaciens* FZB42 to increase stress tolerance of *Arabidopsis thaliana* [279]. Biofilm formation under in-vitro conditions by *B. amyloliquefaciens* was positively correlated with stress tolerance in tomato plants [280].

**4.1.2.2. Volatile organic compounds.** Volatile organic compounds (VOCs) are a foremost part in plant communication where they arbitrate above- and below-ground interactions between plants and microorganisms and faunas (i.e., other plants, pollinators, microorganisms, herbivores, seed dispersers, and their natural hosts) [281]. Microbes generate a broad range of info chemicals, secondary metabolites (SMs), most of soluble and volatile. VOC profiles shaped by microorganisms are consistent, linking to cultural conditions, environment and inputs, and so to population density and function procedures [282]. In recent years, there has been rising confirmation that microbial volatile organic compounds (mVOC) play an important role in microorganism and plant interactions. Various studies were performed to analyses the impact of microbial volatile organic compounds (mVOC) released by diverse microorganism on the biosynthesis of SMs and the antioxidant status in key plant species [263]. Santoro et al. [283] reported that *Pseudomonas fluorescens* and *Bacillus subtilis* are two main microorganisms those were responsible for enhancement of pulegone, menthone, menthol, and menthofuran bioactive compounds in *Mentha piperita* plant species. Similarly, an odoriferous *Streptomyces albidoflavus*

**Table 2**

Volatile organic compounds and antimicrobial compounds reported from the biological activators or plant growth regulator.

Microorganisms	Source/Plant/Rhizosphere	Secondary metabolites	References
<b>Volatile organic compounds</b>			
<i>Pseudomonas fluorescens</i> , <i>Bacillus subtilis</i>	<i>Mentha piperita</i>	Pulegone, menthone, menthol, menthofuran	[283]
<i>Bacillus subtilis</i>	<i>Arabidopsis thaliana</i>	3-hydroxy-2-butanone (acetoin), (2R,3R)-butanediol.	[294]
<i>Bacillus subtilis</i> GB03	<i>Ocimum basilicum</i>	R-terpineol, eugenol	[295]
<i>Pseudomonas chlororaphis</i>	Tobacco	2,3-butanediol	[296]
<i>Pseudomonas fluorescens</i>	<i>Nicotiana tabacum</i>	13-O-Tetradecadien-1-ol, 2-Methyl- <i>n</i> -1- tridecene	[297]
<i>Glomus mosseae</i>	<i>Triticum aestivum</i>	Antioxidant enzymes, ascorbic acid	[298]
<i>Glomus</i> spp.	<i>Saccharum arundinaceum</i>	Phenolics, ascorbic acid, glutathione, antioxidant enzymes	[299]
<i>Glomus deserticola</i>	<i>Antirrhinum majus</i>	Proline	[300]
<i>Pseudomonas putida</i> BW11M1	Banana roots	Putidacin	[301]
<i>Streptomyces albidoflavus</i>	Corn seeds	Albaflavenone	[284]
<b>Antimicrobial compounds</b>			
<i>Plasmopara viticola</i>	<i>Bianca</i>	Farnesene, nerolidol, ocimene, valencene	[302]
<i>Sclerotinia sclerotiorum</i>	<i>Phaseolus vulgaris</i>	2-methyl-1-butanol, 3-methyl-1-butanol	[292]
<i>B. amyloliquefaciens</i> , <i>B. thuringiensis</i>	<i>Bambara groundnut</i>	Dimethylfuvene	[293]
<i>Hypoxyylon anthochroum</i>	<i>Bursera lancifolia</i>	Phenylethyl alcohol, eucalyptol	[303]
<i>Escherichia coli</i> , <i>Salmonella enteritidis</i> , <i>Staphylococcus aureus</i> , <i>Bacillus cereus</i>	<i>Centaurium erythraea</i>	Thymol, carvacrol	[304]
<i>Pseudomonas fluorescens</i>	<i>Medicago truncatula</i>	Dimethylhexadecylamine	[305]
<i>Pseudomonas syringae</i>	<i>Arabidopsis thaliana</i>	(E)-b-caryophyllene	[306]
<i>Rossellomorea vietnamensis</i>	<i>Rhizophora apiculata</i>	Ethyl acetate	[307]
<i>Fusarium oxysporum</i> , <i>Sclerotium oryzae</i>	<i>Cymbopogon flexuosus</i> , <i>Cymbopogon winterianus</i> , <i>Cymbopogon martini</i>	Citral, neral, citronellal, $\delta$ -limonene, geraniol	[308]
<i>Pythium ultimum</i> , <i>Verticillium dahliae</i>	<i>Eucryphia cordifolia</i>	1-butanol, 3-methyl-, phenylethyl alcohol, acetic acid, 2-phenylethyl ester	[309]

isolate from corn seeds was shown to produce a novel sesquiterpene, named albaflavenone, with antibacterial properties [284]. Such plant–microorganism interaction release phytohormones, molecules or volatile compounds, which may act directly or indirectly either to trigger plant immunity or to regulate plant morphogenesis and growth [285,286]. Some studies and reported volatile organic compounds are given in Table 2.

**4.1.2.3. Production of antimicrobial compounds.** Volatile organic compounds (VOCs) generally have high vapor pressure and low molecular weight. They are active at very small concentrations and fit in to numerous chemical groups, such as aldehydes, alcohols, esters, ketones, terpenes, lactones and sulfur compounds [287]. Due of their volatility, these compounds can pass through large distances in a heterogeneous environment composed of liquids, solids and gases [287], which is a foremost improvement for this variety of antimicrobial agents. Plant growth promoting bacteria produce VOCs in response to environmental signals (info-chemicals) for the period of their interactions with other organisms to influence microbial population density and communities. For instance, plant growth promoting bacteria can release VOCs as biocontrol factors or prevention beside plant pathogenic fungi and extra competing bacteria species to guard the host plant [288,289]. Among diverse biocontrol traits, the capability to inhibit pathogens (antimicrobial and antifungal), encourage defense responses, and promote plant growth can result from the production of VOCs [290, 291]. For instance, the 2-methyl-1-butanol and 3-methyl-1-butanol VOCs produced from *Phaseolus vulgaris* to inhibited the growth and spore germination of *Sclerotinia sclerotiorum* [292]. Similarly, Ajilogba and Babalola [293] reported the antibacterial activity of VOCs (Dimethylfufvene) extracted from the plant species *Bambara groundnut* towards the *B. amyloliquefaciens*, and *B. thuringiensis* microorganisms. Some studies and reported antimicrobial compounds are given in Table 2.

**4.1.2.4. Antioxidant activities of PGPR.** One of the effects of stress on living organisms eg. plants, is the production and accumulation of reactive oxygen species (ROS) i.e., superoxide ( $O_2^-$ ), singlet oxygen ( $O_2$ ), hydroxyl ( $OH^\cdot$ ), and hydrogen peroxide ( $H_2O_2$ ), which can have destructive effects on vital biomolecules such as proteins, nucleic acids and, lipids, therefore, these harmful compounds for cells must be neutralized [306,310]. One of the damaging effects of ROS is the peroxidation of membrane lipids, and malondialdehyde (MDA) has been used as an important and widely used indicator to evaluate the degree of damaging effects caused by ROS on membrane lipids to reduce membrane stability [311]. There are reports that show that PGPR reduces the MDA content of plants under stress conditions [312,313]. It has been reported that *B. amyloliquefaciens* 54 protects the cell membrane against ROS by forming a biofilm, reduces cell membrane damage, and increases stress tolerance in plants [314]. To prevent oxidative damage, plants under stress produce ROS-inhibiting enzymes, including superoxide dismutase (SOD), peroxidase (POD), glutathione reductase (GR), catalase (CAT), and ascorbate peroxidase (APX) [315,316]. It has been reported that plants inoculated with *B. amyloliquefaciens* 54 showed relatively higher activity of SOD, POD, CAT and APX enzymes than the control groups, and biofilm producing strains also showed higher activity of antioxidant enzymes [317]. It has also been reported that the use of PGPR with the ability of ACC deaminase activity, by increasing ROS inhibiting enzymes, has led to an increase in seed germination, chlorophyll content and growth of okra plants under environmental stress conditions [318]. Potato plants inoculated with PGPR under biotic stress had increased activities of various ROS inhibiting enzymes [319].

#### 4.1.3. PGPR determinants in ISR

SAR and ISR, which are caused by pathogenic and non-pathogenic microorganisms, respectively, can be used to classify plant systemic resistance [225]. Beneficial microbial colonization causes the plant host to enter a physiological condition known as “priming.” As a typical characteristic of systemic resistance established by helpful microbes, plants exhibit greater and quicker defensive responses upon activation of “priming” against the ensuing invasion of pathogens [73]. SAR was known as a SA-dependent plant defense in 1961, characterized by SA accumulation and a stimulation of the expression of genes linked to pathogens [320]. Three research teams separately and convincingly demonstrated in 1991 that such helpful microorganisms improved plant immunity through ISR [321,322].

PGPR was among these three types, and it has been discovered that they might increase the systemic resistance of cucumber to *Fusarium* wilt, angular leaf spot caused by bacteria, root-knot nematode, and cucumber mosaic cucumovirus [204,225,323]. In 1996, Pieterse et al. revealed for the first time that the distinction between SAR and ISR was that systemic resistance generated by PGPR was independent of SA and PR proteins in *A. thaliana*, but reliant on Et and JA pathway [324]. However, several subsequent studies showing that both the Et/JA and SA signaling pathways in ISR were activated by advantageous microorganisms highlighted the intricacy and variety of ISR signal pathways [225,325,326].

Many PGPR secrete auxins, which have particularly potent impacts on root development and architecture [327,328]. The auxin generated by PGPR known as IAA is the most researched auxin [329,330]. The amounts of endogenous IAA in plants are necessary for exogenous IAA to work. Bacterial IAA application may exhibit negative, neutral, and positive, effects on plant development at optimum IAA concentrations in plants [331]. According to Spaepen and Vanderleyden [331], auxin producing PGPR has been demonstrated to generate root biomass increment, longer roots, stomata density and size reduction, as well as activate genes involved in auxin response that promote plant development [332,333]. Most PGPR secretes gibberellins and cytokinins [327,330], however, it is still unclear how these hormones function in plants and how bacteria synthesize them [334]. Other PGPR strains may stimulate comparatively high gibberellin concentrations, which improves the development of plant shoot [328]. These hormonal interactions with auxins often change the structure of roots [335]. According to Ruzzi et al. [332], the generation of cytokinins by PGPR can also increase the plant's ability to produce root exudate, consequently leading to an increment in increasing the PGPR presence that is connected to the plant. As evidenced by the fact that its concentration rises in response to numerous biotic and abiotic stressors, Et is a

gaseous hormone that is active at incredibly low concentration. It is known as a “stress hormone.” Stress-related ethylene buildup may improve tolerance of the plant or aggravate senescence and other indications of the stress response [336]. Both unstressed and stressed environments have been researched for PGPR function, and the latter frequently stimulates growth more when the former is present, as in the case of drought stress [337]. According to Nadeem et al. [338], certain PGPR release ACCd, which decreases the synthesis of ethylene in plants, and therefore limits the plants’ ability to withstand stress [330,339]. Many studies have demonstrated that inoculating plants with PGPR, which produces ACC deaminase, increases their ability to withstand stress. It has been shown that PGPR can prevent ethylene levels from rising to a point where they can inhibit plant development in *C. sativa* [329,340].

#### 4.1.4. PGPR formulation and methods of application

Multipurpose bacteria such as PGPR can be useful in commercial agriculture and are important to the bioeconomy. Numerous economically significant plants are produced in monoculture and need supplements for the best development and production as well as defense against pathogens [330,341]. Crop output is inconsistently affected by the use of bacterial consortiums [342]. The combination of *B. amyloliquefaciens* and *T. virens* is commercially available and increases crop yields, including those of tomatoes and maize plants [343,344]. Both products are commercially accessible; Excalibre-SA (ABM) mixes *Bradyrhizobium* with *Trichoderma* to boost soybean growth, while BioGrow Endo (Mycorrhizal Applications) combines AM fungi with *Trichoderma* to increase growth and remove diseases found in the soil.

Increased sesame oil quality and seed production were achieved with the inoculation of *N*-fixing bacteria and *N*-fertilizer (*Azotobacter* and *Azospirillum*) [345]. *Brassica carinata* cv. *Peelaraya* infected with *A. vinelandii* had similar results [346]. In addition to increasing fruit output to about 39% and quality (titratable acids, vitamin C, and soluble sugars), a group of bacteria (*B. subtilis* SM21, *Serratia* sp. XY2 and *B. cereus* PX35) decreased the prevalence of the root-knot nematode (*M. incognita*) in tomatoes [347]. To avoid interfering with food production, advanced biofuels are made from non-food biomass and materials made from lignocellulose [348]. The long-term objective is to provide sustainable fuels and advanced bioproducts of importance to mitigate the atmospheric carbon dioxide emissions caused by fossil fuels [349].

To make materials from lignocellulose economically competitive, the process of converting it into fuel must become simpler and cheap [350]; also, the biomass availability in the specially cultivated biomass crops (such as Sorghum, switchgrass, miscanthus) must be improved [351,352]. Switchgrass has been used as an example to show how PGPR inoculation might enhance the development and productivity of crops developed specifically for biofuels [353–355]. In order to prevent disputes over food vs energy crops, marginal and polluted sites can be used to cultivate biofuel crops. The biofuel crops might be utilized effectively for phytoremediation and to lower high levels of pesticide residues in agricultural areas with the usage of PGPR that include inherent capacity to deal with soil pollutants [356].

An alternate approach to battling plant diseases is biological techniques, and there are commercial products in this regard [357]. Antibiotics and other substances that are harmful to plant pathogens may be secreted by beneficial rhizobacteria. One of the more prevalent biocontrol measures is the production of antibiotics [251]. Examples of this commercially accessible bioagents are available [357]. Antibiotics and other biocontrol methods are frequently ineffective against pathogens because they acquire resistance to them. As a result, they cannot be permanently controlled. Hence, when dealing with infections, a comprehensive strategy with a variety of regulating techniques is typically preferable to excessive reliance on a single remedy. Long-term changes in the pathogens’ mechanism of action will also be made by bacteria that are hostile to them. Additionally, PGPR creates antimicrobial metabolites such as polyketides, metabolites from fungi that inhibit infections and lipopeptides [330].

**4.1.4.1. Criteria to suitable PGPR candidate selection.** Though scores of bacteria reside in soil in proximity of plants, not all of them are PGPR. There is no hard and fast rule for tagging any bacteria isolate as PGPR. If any bacteria strain can provide any kind of plant growth enhancing support upon inoculation, that strain can be regarded as a PGPR. According to Vejan et al. [358], an appropriate PGPR strain should be efficient in the root rhizosphere, should substantially colonize in roots, capable of plant growth promotion (PGP), can demonstrate wide range of action, should have compatibility with other microbial inhabitants in the rhizosphere, can withstand numerous physicochemical factors, and compete better with other rhizobacteria. Most of the PGPR selection were based on one or more of the earlier mentioned criteria, which is inefficient. Because these criteria are based on the knowledge of mechanisms adopted by different PGPR rather than considering the complex interplay between plants and their associated microbes [359]. Again, there is lack of comparative studies for evaluating PGPR performance in controlled environment (e.g., laboratory, greenhouse) and natural conditions, where these PGP mechanisms may face new challenges [360,361]. Therefore, researchers are recently looking for more specific and reliable PGPR selection criteria on the basis of microbial phenotypes and metabolic activities [359,362]. Since well correlated PGP traits and microbial phenotypes help isolate efficient bacterial strains. In three *Rhizobium* sp. Amaya-Gómez et al. [362] correlated bacterial colonization phenotypes (i.e., surface spreading, H<sub>2</sub>O<sub>2</sub> resistance, and biofilm formation) with their two PGP traits-phosphorus solubilization ability and siderophores production. Again, metabolic use of 11 nutrient substrates, commonly found in root exudates, showed both positive (e.g., β-methyl-D-glucoside, D-cellobiose) and negative (L-aspartic acid, α-keto-glutaric acid) correlation with PGP traits like mineral phosphate solubilization, chitinase activity, and siderophore production [359].

#### 4.1.5. Synergistic effect of PGPR strain mixtures

PGPR reside in multi-species assemblages in plant or soil rhizosphere in their native environments [335]. Given that PGPR is found in communities, it is suggested that they be mixed with PGPR from different species to increase the effectiveness and dependability as a biocontrol agent in various agricultural sites, with the understanding that the combination will confer synergistic control of the

pathogens targeted. In a field trial, only co-inoculation of *P. fluorescens* F113 and *S. maltophilia* W8 stopped the suppress sugar beet's damping-off disease by the extracellular proteolytic activity and DAPG synthesis, respectively [363]. When PGPR was co-inoculated on maize plants, *Fusarium* spp. infection was significantly reduced as compared to control and a single bacterial treated plant. This is because both *Bacillus* sp. MRF and *P. fluorescens* sp. M23 produce siderophores and antifungal metabolites, as well as being effective in the colonization of the rhizosphere [364].

Similar to this, the combination of *B. pumilus* IN937b and *B. amyloliquefaciens* IN937a induced systemic resistance, resulting in more reliable broad-spectrum control of pathogen in different crops on the field [365], and this mixture of *Bacillus* strain had 25–30% increased peroxidase and superoxide dismutase as compared with the control [366]. Similar to this, combining *P. putida* strains RE8 and WCS358 decreased the incidence of *Fusarium* wilt in radish by about 50% as opposed to the 30% decrease from each strain alone [367]. When two separate disease-suppressive processes (producing pseudobactin for WCS358 to compete for iron and establishing systemic resistance for RE8) were combined in this case by using the strain combination, illness suppression was enhanced. It was also conceivable that the 2 strains occupied distinct niches, hence reducing competition for iron between them [368]. In contrast to single inoculation and control, *Burkholderia* spp. RTH12 and RHT8 both demonstrated the production of the siderophore, as well as 1,3-glucanase and chitinase, and their co-inoculation reduced the effects of *F. oxysporum*, resulting in the increment in yield and growth of fenugreek in both field and *in vitro* conditions [369]. In these situations, improved suppression of disease in a bacterial mixture may emerge from interactions between two or more strains of PGPR introduced, which may have a favorable impact on the bacterial strains' proliferation, colonization of the roots, and activity of pathogen.

#### 4.1.6. PGPR-mediated ISR under field conditions

Non-pathogenic bacteria called PGPR, which colonize the surface of the root of plants, have positive effects on plant growth and health. They also protect plants from unfavorable environmental effects, phytopathogens suppression, and hasten the assimilation and availability of nutrients [370,371]. The usage of PGPR is an eco-friendly substitute for managing the diseases of plants frequently brought on by harmful pathogens. Using noxious chemicals and disease-resistant plants, plant diseases are often managed. The chemical application to induce resistance or promote the growth of the plant is limited due to the side effects of chemical treatment as well as the challenge of determining the best concentrations that will benefit the plants [215]. Resistance is not always effective against many diseases, and resistant plant production may take some years [372]. The use of PGPR is regarded as a beneficial strategy to improve plant immunity and prevent plant diseases. Direct antibiosis, nutritional competition, and ISR are only a few of the many mechanisms that PGPR uses to prevent diseases [373]. ISR refers to enhanced resistance that is expressed across the entire plant, not limited to locations where the rhizobacteria have colonized [321].

ISR and SAR share phenotypic characteristics, which is evident from the direct antibiosis between the causing bacteria and the pathogen. When the inducing organism induces necrosis, the highest degree of SAR is produced, but ISR induced by rhizobacteria often does not result in any necrotic signs on the host plants [223]. Under field experiments, using SAR-inducing organisms has not proven effective, and generally speaking, the length of protection after pathogen induction as compared with the ISR-mediated rhizobacteria [204]. Additionally, a variety of bacterial, viral and fungal plant diseases can be controlled by ISR mediated by PGPR [31].

ISR is induced by a variety of specific PGPR components, including flagellin, a cell wall component and lipopolysaccharides [5, 372]. The secondary metabolites 4-aminocarbonyl phenylacetate, butyl 2-pyrrolidone-5-carboxylate and *N*-alkylated benzylamine derivative [374], and have all been identified to cause ISR in specific strains of PGPR. Some PGPR strains emit VOCs that are active in ISR, such as 2-butanediol and acetoin [372]. The metabolites from PGPR have drawn a lot of interest as a component of agricultural practices that offer a substitute for synthetic pesticides for the control of disease [374]. Therefore, it is of great importance to agriculture to discover novel metabolites from microbes having ISR action against plant diseases.

#### 4.2. Durability of ISR

The majority of studies that have revealed conflicting findings regarding the negative and positive interactions between IRH and ISR have concentrated on distinct pathway levels and/or have employed various techniques, with "biological" induction leading to chemical elicitation and cross-resistance primarily producing trade-offs. There are already several variations between naturally and chemically induced resistance [375]. Research that applies elicitors externally may suffer greatly from elicitor-resistant concentrations and spatial distributions that are physiologically unrealistic.

When resistance is evoked chemically, the mechanisms that control how resistance pathways interact in response to natural elicitation are likely disregarded. To rule out the dependencies between physiological and molecular events alongside the phenotypical resistance and to proffer a broad pattern in the communications among resistance pathways, studies integrating the physiological, biological and molecular aspects of resistance are necessary. These studies must take into account multiple resistance at the same time [376]. To fully realize the prospects of inducible resistance techniques in the control of agricultural pests, studies which will systematically examine signaling synergies and conflicts in plant-pathogen and plant-herbivore interactions are required [377].

### 5. Biotic stress management

Plants' survival in different ecosystems rely on their defensive attributes against stress situations. Sometimes plants do self-defense and sometimes with the help of beneficial microbes. Plants employ induced resistance after receiving appropriate signals of pathogen attacks, which is called induced systemic resistance (ISR) [378]. ISRs include a set of defense mechanisms triggered by root inhabiting beneficial rhizobacteria [379–381]. Plants recruit beneficial microbial communities with "cry for help" strategy as mentioned earlier.

When pathogen-stricken host plants come in contact with beneficial microbes, they redefine their defense signaling process related metabolic pathways moderately or completely [382]. Application of *B. amyloliquefaciens* and *P. fluorescens* upregulated withanolide biosynthetic pathway in *Withaniasomnifera* substantially during *Alternaria alternata* pathogenicity [383].

Again, plant cell organelles take part in defense against biotic stress by inducing signal molecules, disrupting their own functionalities, and programmed cell death. Incompatible plant-pathogen interactions disrupt mitochondrial homeostasis and leads to production of mitochondrial ROS, which causes graded dysfunction of mitochondrion and initiates cellular responses like induction of defense genes and programmed cell death [384]. In addition, there are some elicitors which also contribute to biotic stress management. Elicitors are molecules that mainly induce any defense system in the host [385]. These elicitor molecules differ from each other based on their synthesis sources, chemical structures, and nature of molecules [386]. There are two main types of elicitors: exogenous-pathogen derived and endogenous-produced by host in response to exogenous elicitor [387]. Acetoin produced by *B. subtilis* instigates systemic resistance in model plant *A. thaliana* when infected by *P. syringae* pv. *Tomato* DC3000 [388]. Wang et al. [389] showed systemic acquired resistance promotion against tobacco mosaic virus (TMV) in tobacco plants upon upregulating SA biosynthesis related genes when introduced Reticine A synthesized in *Citrus reticulata* fruit peel.

## 6. Conclusion and future prospects

This assessment elaborates not only the supply of the most important biotic stress agents, but also illuminate diverse features of the plant immunity responses and PGPR effects on plant health with different mechanisms. Our review show that the plants are exposed to various agents with complex interactions for adapting and responding in environment. Although different groups of rhizobacteria applied for plant growth promoting, but different regions with various plants must be investigate for finding new rhizobacteria with better efficiencies. Furthermore, these rhizobacteria's can formulated and tested with effective compounds to measure of their efficiencies in biotic and abiotic stresses and promoting plant development and growth. It is interesting to note that new findings with new PGPRs will help to sustainable agriculture in future years and will be a good substitution for chemical pesticides and manures. While there is insufficient food for 800 million people in the world, it has been proven that at tiniest 10% of global plant products are mislaid owing to plant diseases, and therefore this is a hazard to global food security. According to the FAO report, the cost of damage caused by plant diseases was 33 billion dollars per year. This fact reveals why plant diseases are as important and significant as wars and human diseases throughout history. In the past decades, it has been common to use chemical including fungicides to control plant pathogens, and despite reducing the development of plant diseases, it has had many negative effects on the environment and humans. In addition, the strict regulation of the use and disposal of fungicides and the appearance of fungicide-resilient strains of pathogens, make it logical that the use of chemical controllers should be reduced. Therefore, the need for an alternative to chemical controller to repel plant diseases is felt more and more in order to prevent negative and side effects on human well-being and the atmosphere.

In a new perspective, ISR is an effective strategy for an extensive variety of plant pathogens that can be grasped with full scientific support in dealing with the menace caused by plant disease. In this regard, using the potential of PGPR living in the rhizosphere, which produce secondary metabolites and suppress plant pathogens in the soil, can be very valuable because, as an environmentally friendly approach, it has no negative side effects for humans and the environment [390]. Significant progress has been made in various dimensions of ISR and although only 20 years have passed since its discovery, there are countless scientific encounters for investigate in the area of ISR by PGPR and additional beneficial plant microbes. Using molecular techniques to investigate the genome of rhizosphere microbes (helpful and harmful) and biodiversity also gives useful results. Despite many research efforts related to the identification of ISR-inducing factors, especially PGPR, there are still many unclear points about ISR-inducing factors. Deciphering microbial signals is another important factor that, in addition to molecular techniques, can help in understanding ISR occurrence.

### Author contribution statement

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### Data availability statement

This is a review article and no data was generated during its preparation.

### Declaration of interest's statement

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



## Additional information

No additional information is available for this paper.

## References

- [1] D.R. Walters, J. Ratsep, N.D. Havis, Controlling crop diseases using induced resistance: challenges for the future, *J. Exp. Bot.* 64 (5) (2013) 1263–1280.
- [2] D.R. Walters, J.M. Fountaine, Practical application of induced resistance to plant diseases: an appraisal of effectiveness under field conditions, *J. Agric. Sci.* 147 (2009) 523–535.
- [3] Q. Du, W. Zhu, Z. Zhao, X. Qian, Y. Xu, Novel benzo-1,2,3- thiadiazole-7-carboxylate derivatives as plant activators and the development of their agricultural applications, *J. Agric. Food Chem.* 60 (2012) 346–353.
- [4] D.F. Klessig, H.W. Choi, D.M.A. Dempsey, Systemic acquired resistance and salicylic acid: past, present, and future, *Mol. Plant Microbe Interact.* 31 (9) (2018) 871–888.
- [5] C. Zhou, L. Zhu, J. Huang, X. Lu, Development of plant systemic resistance by beneficial rhizobacteria: recognition, initiation, elicitation and regulation, *Front. Plant Sci.* 4 (2022) 288–295.
- [6] K. Goellner, U. Conrath, Priming: it's all the world to induced resistance, *Eur. J. Plant Pathol.* 121 (2008) 233–242.
- [7] S. Ahmad, R. Gordon-Weeks, J. Pickett, J. Ton, Natural variation in priming of basal resistance: from evolutionary origin to agricultural exploitation, *Mol. Plant Pathol.* 11 (2010) 817–827.
- [8] N.J. Atkinson, P.E. Urwin, The interaction of plant biotic and abiotic stresses: from genes to the field, *J. Exp. Bot.* 63 (2012) 3523–3543.
- [9] N. Nonthakaew, W. Panbangred, W. Songnuan, B. Intra, Plant growth-promoting properties of *Streptomyces* spp. isolates and their impact on mung bean plantlets' rhizosphere microbiome, *Front. Microbiol.* 3113 (2022).
- [10] G. Pal, R. Bakade, S. Deshpande, V. Sureshkumar, S.S. Patil, A. Dawane, S. Agarwal, V. Niranjana, M.K. PrasannaKumar, R.S. Vemanna, Transcriptomic responses under combined bacterial blight and drought stress in rice reveal potential genes to improve multi-stress tolerance, *BMC Plant Biol.* 22 (1) (2022) 1–20.
- [11] E. Gimenez, M. Salinas, F. Manzano-Agugliaro, Worldwide research on plant defense against biotic stresses as improvement for sustainable agriculture, *Sustainability* 10 (2) (2018) 391.
- [12] I. Kovalchuk, Transgenerational genome instability in Plants, in: *Genome Stability*, Academic Press, 2021, pp. 659–678.
- [13] J. Venegas-Molina, S. Proietti, J. Pollier, W. Orozco-Freire, D. Ramirez-Villacis, A. Leon-Reyes, Induced tolerance to abiotic and biotic stresses of broccoli and *Arabidopsis* after treatment with elicitor molecules, *Sci. Rep.* 10 (1) (2020) 1–17.
- [14] M.D. Mashabela, L.A. Piater, I.A. Dubery, F. Tugizimana, M.I. Mhlongo, Rhizosphere tripartite interactions and PGPR-mediated metabolic reprogramming towards ISR and plant priming: a metabolomics review, *Biol.* 11 (3) (2022) 346.
- [15] M.M. Vaughan, A. Block, S.A. Christensen, L.H. Allen, E.A. Schmelz, The effects of climate change associated abiotic stresses on maize phytochemical defenses, *Phytochemistry Rev.* 171 (2018) 37–49.
- [16] S. Savary, L. Willocquet, S.J. Pethybridge, P. Esker, N. McRoberts, A. Nelson, The global burden of pathogens and pests on major food crops, *Nat. Ecol. Evol.* 3 (2019) 430.
- [17] D.T. Teshome, G.E. Zharare, S. Naidoo, The threat of the combined effect of biotic and abiotic stress factors in forestry under a changing climate, *Front. Plant Sci.* (2020) 1874.
- [18] D. Goswami, J.N. Thakker, P.C. Dhandhukia, Portraying mechanics of plant growth-promoting rhizobacteria (PGPR): a review, *Cogent. Food Agric.* 2 (2016), 1127500.
- [19] H. Etesami, Can interaction between silicon and plant growth-promoting rhizobacteria benefit in alleviating abiotic and biotic stresses in crop plants? *Agric. Ecosyst. Environ.* 253 (2018) 98–112.
- [20] J. Singla, S.G. Krattinger, C.W. Wrigley, J. Faubion, H. Corke, K. Seetharaman, Biotic stress resistance genes in wheat, *Curr. Trends Nat. Sci.* 8 (2016) 388–392.
- [21] 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, G.D. Foster, The Top 10 fungal pathogens in molecular plant pathology, *Mol. Plant Pathol.* 13 (4) (2012) 414–430.
- [22] A.B. Kutawa, K. Ahmad, A. Ali, M.Z. Hussein, M.A. Abdul Wahab, A. Adamu, A.A. Ismaila, M.T. Gunasena, M.Z. Rahman, M.I. Hossain, Trends in nanotechnology and its potentialities to control plant pathogenic fungi: a review, *Biol.* 10 (9) (2021) 881.
- [23] 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, D. Cahill, The Top 10 oomycete pathogens in molecular plant pathology, *Mol. Plant Pathol.* 16 (4) (2015) 413–434.
- [24] A. Geiger, Z. Karácsony, R. Golen, K.Z. Váczy, J. Geml, The compositional turnover of grapevine-associated plant pathogenic fungal communities is greater among intraindividual microhabitats and terroirs than among healthy and esca-diseased plants, *Phytopathology* 112 (5) (2022) 1029–1035.
- [25] J. Mansfield, S. Genin, S. Magori, V. Citovsky, M. Sriariyanum, P. Ronald, M.A.X. Dow, V. Verdier, S.V. Beer, M.A. Machado, I.A.N. Toth, Top 10 plant pathogenic bacteria in molecular plant pathology, *Mol. Plant Pathol.* 13 (6) (2012) 614–629.
- [26] Y. Liu, T.C. Helmann, P. Stodghill, M.J. Filiatrault, Complete genome sequence resource for the necrotrophic plant-pathogenic bacterium *Dickeyadanthicola* 67-19 isolated from New Guinea Impatiens, *Plant Dis.* 105 (4) (2021) 1174–1176.
- [27] K.B.G. Scholthof, S. Adkins, H. Czosnek, P. Palukaitis, E. Jacquot, T. Hohn, B. Hohn, K. Saunders, T. Candresse, P. Ahlquist, C. Hemenway, Top 10 plant viruses in molecular plant pathology, *Mol. Plant Pathol.* 12 (9) (2011) 938–954.
- [28] 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, R.N. Perry, Top 10 plant-parasitic nematodes in molecular plant pathology, *Mol. Plant Pathol.* 14 (9) (2013) 946–961.
- [29] S. Leontopoulos, P. Skenderidis, I.K. Vagelas, Potential use of polyphenolic compounds obtained from olive mill waste waters on plant pathogens and plant parasitic nematodes, *Plant Defence: Biol. Control* (2020) 137–177.
- [30] S. Singh, S. Das, R. Geeta, Role of cuticular wax in adaptation to abiotic stress: a molecular perspective, in: *Abiotic Stress-Mediated Sensing and Signaling in Plants: an Omics Perspective*, Springer, Singapore, 2018, pp. 155–182.
- [31] X. Jiao, Y. Takishita, G. Zhou, D.L. Smith, Plant associated rhizobacteria for biocontrol and plant growth enhancement, *Front. Plant Sci.* 12 (2021), 634796.
- [32] A. Schneider, M. Leibman-Markus, R. Gupta, I. Marash, D. Rav-David, Y. Elad, M. Bar, Immunity priming uncouples the growth-defense tradeoff in tomato, *bioRxiv* 4 (2022) 49–62, <https://doi.org/10.1101/2022.07.24.501304>.
- [33] C. Garcion, O. Lamotte, J.L. Cacas, J.P. Métraux, Mechanisms of defence to pathogens: biochemistry and physiology, *Induced Resistance for Plant Defense* (2014) 106–136.
- [34] J. Dumanović, E. Nepovimova, M. Natić, K. Kuća, V. Jačević, The significance of reactive oxygen species and antioxidant defense system in plants: a concise overview, *Front. Plant Sci.* 11 (2021), 552969.
- [35] L. Feng, J. Sun, Y. Jiang, X. Duan, Role of reactive oxygen species against pathogens in relation to postharvest disease of papaya fruit, *Horticulturae* 8 (3) (2022) 205–214.
- [36] M. Alizadeh, Y. Vasebi, M. Chauhan, A. Rani, Bioprimering: a prospective techniques for crop improvement, *Innovations* 66 (2021) 1035–1058.
- [37] T.P. Souza, R.O. Dias, M.C. Silva-Filho, Defense-related proteins involved in sugarcane responses to biotic stress, *Genet. Mol. Biol.* 40 (2017) 360–372.
- [38] G. Benjamin, G. Pandharikar, P. Frendo, Salicylic acid in plant symbioses: beyond plant pathogen interactions, *Biol.* 11 (6) (2022) 861.
- [39] Z. Yang, P. Zhi, C. Chang, Priming seeds for the future: plant immune memory and application in crop protection, *Front. Plant Sci.* 13 (2022).
- [40] I. Saur, R. Panstruga, P. Schulze-Lefert, NOD-like receptor-mediated plant immunity: from structure to cell death, *Nat. Rev. Immunol.* 21 (2021) 305–318.
- [41] X. Chen, P.C. Ronald, Innate immunity in rice, *Trends Plant Sci.* 16 (8) (2011) 451–459.

- [42] K. Kumar, S.N. Mandal, K. Neelam, B.G. de Los Reyes, MicroRNA-mediated host defense mechanisms against pathogens and herbivores in rice: balancing gains from genetic resistance with trade-offs to productivity potential, *BMC Plant Biol.* 22 (1) (2022) 1–16.
- [43] S. Li, Z. Wang, B. Tang, L. Zheng, H. Chen, X. Cui, F. Ge, D. Liu, A pathogenesis-related protein like gene is involved in the panax notoginseng defense response to the root rot pathogen, *Front. Plant Sci.* 11 (2021), 610176.
- [44] S. Farrakh, M. Wang, X. Chen, Pathogenesis-related protein genes involved in race-specific all-stage resistance and non-race specific high temperature adult-plant resistance to *Puccinia striiformis* f. sp. *tritici* wheat, *J. Integr. Agric.* 17 (2018) 2478–2491.
- [45] H. Ma, G. Xiang, Z. Li, Y. Wang, M. Dou, L. Su, et al., Grapevine VpPR10.1 functions in resistance to *Plasmopara viticola* through triggering a cell death-like defence response by interacting with VpVDAC3, *Plant Biotechnol. J.* 16 (2018) 1488–1501.
- [46] S. Ali, Z.A. Mir, J.A. Bhat, N. Chandrashekar, P.K. Papolu, S. Rawat, A. Grover, Identification and comparative analysis of *Brassica juncea* pathogenesis-related genes in response to hormonal, biotic and abiotic stresses, *Acta Physiol. Plant.* 39 (2017) 1–15.
- [47] Q. Chen, F. Niu, J. Yan, B. Chen, F. Wu, X. Guo, B. Yang, Y.-Q. Jiang, Oilseed rape NAC56 transcription factor modulates reactive oxygen species accumulation and hypersensitive response-like cell death, *Physiol. Plantarum* 160 (2017) 209–221.
- [48] X. Han, X. He, W. Qiu, Z. Lu, Y. Zhang, S. Chen, et al., Pathogenesis related protein PR10 from *Salix matsudana*Koidz exhibits resistance to salt stress in transgenic *Arabidopsis thaliana*, *Environ. Exp. Bot.* 141 (2017) 74–82.
- [49] X. Yan, H. Qiao, X. Zhang, Analysis of the grape (*Vitis vinifera* L.) thaumatin-like protein (TLP) gene family and demonstration that *TLP29* contributes to disease resistance, *Sci. Rep.* 7 (2017) 4269.
- [50] A. Castro, S. Vidal, I. Ponce de León, Moss pathogenesis-related-10 protein enhances resistance to *Pythium irregulare* in *Physcomitrella patens* and *Arabidopsis thaliana*, *Front. Plant Sci.* 7 (2016) 580.
- [51] S.G. Wu, K.Y. Kim, J.G. Kang, S.R. Kim, R. Park, S.T. Gupta, Overexpression of a pathogenesis-related protein 10 enhances biotic and abiotic stress tolerance in rice, *The Plant Pathology Journal* 32 (2016) 552.
- [52] L. Jiang, J. Wu, S. Fan, W. Li, L. Dong, Isolation and characterization of a novel pathogenesis-related protein gene (GmPRP) with induced expression in soybean (*Glycine max*) during infection with *Phytophthora sojae*, *PLoS One* 10 (6) (2015), e0129932.
- [53] S. Menezes, E. Silva, E. Lima, A. Sousa, B. Andrade, L. Lemos, et al., The pathogenesis-related protein PR-4b from *Theobroma cacao* presents RNase activity, Ca<sup>2+</sup> and Mg<sup>2+</sup> dependent-DNase activity and antifungal action on *Moniliophthoraperniciosa*, *BMC Plant Biol.* 14 (2014) 161.
- [54] L. Chen, N. Sun, J. Wang, H. Ling, L. Zhang, K. Zuo, Functional analysis of a wilt fungus inducible PR10-1 gene from cotton, *Am. J. Sci.* 4 (2013) 417–426.
- [55] S. Oide, S. Bejai, J. al, N. Guan, M. Kaliff, C. Dixelius, A novel role of PR2 in abscisic Acid (ABA) mediated, pathogen-induced callose deposition in *Arabidopsis thaliana*, *New Phytol.* 200 (2013) 1187–1199.
- [56] P. Agarwal, V. Bhatt, R. Singh, M. Das, S.K. Sopory, J. Chikara, Pathogenesis-related gene, JcPR-10a from *Jatropha curcas* exhibit RNase and antifungal activity, *Mol. Biotechnol.* 54 (2012) 412–425.
- [57] O.R. Lee, Y.J. Kim, S.R.D. Balusamy, A. Khorolragchaa, G. Sathiyaraj, M.K. Kim, et al., Expression of the ginseng PgPR10-1 in *Arabidopsis* confers resistance against fungal and bacterial infection, *Gene* 506 (2012) 85–92.
- [58] L. Bertini, C. Caporale, M. Testa, S. Proietti, C. Caruso, Structural basis of the antifungal activity of wheat PR4 proteins, *FEBS Lett.* 583 (2009) 2865–2871.
- [59] X. Li, B. Xia, Y. Jiang, Q. Wu, C. Wang, L. He, A new pathogenesis-related protein, LrPR4, from *Lycoris radiata*, and its antifungal activity against *Magnaporthe grisea*, *Mol. Biol. Rep.* 37 (2009) 995–1001.
- [60] C. Caporale, I. Berardino, L. Leonardi, L. Bertini, A. Cascone, V. Buonocore, et al., Wheat pathogenesis-related proteins of class 4 have ribonuclease activity, *FEBS Lett.* 575 (2004) 71–76.
- [61] M. Pla, J. Vilardell, M.J. Guiltinan, et al., The cis-regulatory element CCACGTGG is involved in ABA and water-stress responses of the maize gene *rab28*, *Plant Mol. Biol.* 21 (1993) 259–266.
- [62] S.S. Baker, K.S. Wilhelm, M.F. Thomashow, The 5'-region of *Arabidopsis thaliana* cor15a has cis-acting elements that confer cold-, drought-and ABA-regulated gene expression, *Plant Mol. Biol.* 24 (1994) 701–713.
- [63] A.B. da Rocha, R. Hammerschmidt, History and perspectives on the use of disease resistance inducers in horticultural crops, *HortTechnology* 15 (2005) 518–529.
- [64] G. Lyon, Agents that can elicit induced resistance, in: D. Walters, A. Newton, G. Lyon (Eds.), *Induced Resistance for Plant Disease Control: a Sustainable Approach to Crop Protection*, Blackwell Publishing, Oxford, 2007, pp. 9–29.
- [65] P. Frackowiak, H. Pospieszny, M. Smiglak, A. Obrepalska-Stepulska, Assessment of the efficacy and mode of action of benzo (1, 2, 3)-thiadiazole-7-carbothioic acid S-methyl ester (BTH) and its derivatives in plant protection against viral disease, *Int. J. Mol. Sci.* 20 (7) (2019) 1598.
- [66] J.C. Sillero, M.M. Rojas-Molina, C.M. Avila, D. Rubiales, Induction of systemic acquired resistance against rust, ascochyta blight and broomrape in faba bean by exogenous application of salicylic acid and benzothiadiazole, *Crop Protect.* 34 (2012) 65–69.
- [67] S. Zhang, W. Raza, X. Yang, J. Hu, Q. Huang, Y. Xu, X. Liu, W. Ran, Q. Shen, Control of *Fusariumwilt* disease of cucumber plants with the application of a bioorganic fertilizer, *Biol. Fertil. Soils* 44 (8) (2008) 1073–1080.
- [68] Y. Ren, Y. Wang, Y. Bi, Y. Ge, Y. Wang, C. Fan, D. Li, H. Deng, Postharvest BTH treatment induced disease resistance and enhanced reactive oxygen species metabolism in muskmelon (*Cucumis melo* L.) fruit, *Eur. Food Res. Technol.* 234 (2012) 963–971.
- [69] E. Barilli, E. Prats, D. Rubiales, Benzothiadiazole and BABA improve resistance to *Uromyces pisi* (Pers.) Wint. in *Pisum sativum* L. with an enhancement of enzymatic activities and total phenolic content, *Eur. J. Plant Pathol.* 128 (2010) 483–493.
- [70] Y. Cohen, A.E. Rubin, G. Kilfin, Mechanisms of induced resistance in lettuce against *Bremia lactucae* by DL-β-aminobutyric acid (BABA), *Eur. J. Plant Pathol.* 126 (2010) 553–573.
- [71] D. Thevenet, V. Pastor, I. Baccelli, A. Balmer, A. Vallat, R. Neier, G. Glauser, B. Mauch-Mani, The priming molecule β-aminobutyric acid is naturally present in plants and is induced by stress, *New Phytol.* 213 (2) (2017) 552–559.
- [72] J. Wang, S. Cao, L. Wang, X. Wang, P. Jin, Y. Zheng, Effect of β-aminobutyric acid on disease resistance against *Rhizopus* rot in harvested peaches, *Front. Microbiol.* 9 (2018) 1505.
- [73] U. Conrath, G.J.M. Beckers, C.J.G. Langenbach, M.R. Jaskiewicz, Priming for enhanced defense, *Annu. Rev. Phytopathol.* 53 (2015) 97–119.
- [74] X. Ren, J. Wang, F. Zhu, Z. Wang, J. Mei, Y. Xie, T. Liu, X. Ye, β-aminobutyric acid (BABA)-induced resistance to tobacco black shank in tobacco (*Nicotianatabacum* L.), *PLoS One* 17 (6) (2022), e0267960.
- [75] D. Thevenet, V. Pator, I. Baccelli, A. Balmer, A. Vallat, R. Neiern, G. Glauser, B. Mauch-Mani, The priming molecule β-aminobutyric acid is naturally present in plants and is induced by stress, *New Phytol.* 213 (2) (2016) 552–559.
- [76] A. Slaughter, X. Daniel, V. Flors, E. Luna, B. Hohn, B. Mauch-Mani, Descendants of primed *Arabidopsis* plants exhibit resistance to biotic stress, *Plant Physiol.* 158 (2012) 835–843.
- [77] M.F. Pye, F. Hakuno, J.D. MacDonald, R.M. Bostock, Induced resistance in tomato by SAR activators during predisposing salinity stress, *Front. Plant Sci.* 4 (2013) 116.
- [78] Q. Liu, J. Yang, S. Yan, S. Zhang, J. Zhao, W. Wang, T. Yang, X. Wang, X. Mao, J. Dong, X. Zhu, The germin-like protein OsGLP2-1 enhances resistance to fungal blast and bacterial blight in rice, *Plant Mol. Biol.* 92 (4) (2016) 411–423.
- [79] Z. Wu, G. Wang, B. Zhang, T. Dai, A. Gu, X. Li, X. Cheng, P. Liu, J. Hao, X. Liu, Metabolic mechanism of plant defense against rice blast induced by probenazole, *Metabolism* 11 (4) (2021) 246.
- [80] A.B. Kutawa, K. Ahmad, A. Ali, M.Z. Hussein, M.A.A. Wahab, K. Sijam, State of the art on southern corn leaf blight disease incited by *Cochliobolusheterostrophus*: detection, pathogenic variability and novel control measures, *Bulg. J. Agric. Sci.* 27 (1) (2021) 147–155.
- [81] M. Wang, J. Ma, L. Fan, K. Fu, C. Yu, J. Gao, Y. Li, J. Chen, Biological control of southern corn leaf blight by *Trichoderma atroviride* SG3403, *Biocontrol Sci. Technol.* 25 (10) (2015) 1133–1146.
- [82] S. Mejrri, M. Magnin-Robert, B. Randoux, A. Ghinet, P. Halama, A. Siah, P. Reignault, Saccharin provides protection and activates defense mechanisms in wheat against the Hemibiotrophic pathogen *Zymoseptoriatritici*, *Plant Dis.* 105 (4) (2021) 780–786.

- [83] C. Boyle, D.R. Walters, Saccharin-induced protection against powdery mildew in barley: effects on growth and phenylpropanoid metabolism, *Plant Pathol.* 55 (2006) 82–91.
- [84] P. Srivastava, S. George, J.J. Marois, D.L. Wright, D.R. Walker, Saccharin-induced systemic acquired resistance against rust (*Phakopsora pachyrhizi*) infection in soybean: effects on growth and development, *Crop Protect.* 30 (2011) 726–732.
- [85] F.C. Gómez-Merino, L.F. Gómez-Trejo, R. Ruvalcaba-Ramírez, L.I. Trejo-Téllez, Application of phosphite as a biostimulant in agriculture, in: *New and Future Developments in Microbial Biotechnology and Bioengineering*, Elsevier, 2022, pp. 135–153.
- [86] J.L. Havlin, A.J. Schlegel, Review of phosphite as a plant nutrient and fungicide, *Soil Sys* 5 (3) (2021) 52.
- [87] S. Srivastava, M.K. Upadhyay, A.K. Srivastava, M. Abdelrahman, P. Suprasanna, L.S.P. Tran, Cellular and subcellular phosphate transport machinery in plants, *Int. J. Mol. Sci.* 19 (7) (2018) 1914.
- [88] P.J. Cook, P.J. Landschoot, M.J. Schlossberg, Inhibition of *Pythium* spp. and suppression of Pythium blight of turfgrasses with phosphonate fungicides, *Plant Dis.* 93 (2009) 809–814.
- [89] H.J. Jee, W.D. Cho, C.H. Kim, Effect of potassium phosphonate on the control of *Phytophthora* root rot of lettuce in hydroponics, *Plant Pathol. J.* 18 (2002) 142–146.
- [90] M.A. Mohammadi, X. Han, Z. Zhang, Y. Xi, M. Boorboori, G. Wang-Pruski, Phosphite application alleviates *Phytophthora infestans* by modulation of photosynthetic and physio-biochemical metabolites in potato leaves, *Pathogens* 9 (3) (2020) 170.
- [91] A.I. Osman, S. Fawzy, M. Farghali, M. El-Azazy, A.M. Elgarahy, R.A. Fahim, M.I.A. Maksoud, A.A. Ajlan, M. Yousry, Y. Saleem, D.W. Rooney, Biochar for agronomy, animal farming, anaerobic digestion, composting, water treatment, soil remediation, construction, energy storage, and carbon sequestration: a review, *Environ. Chem. Lett.* (2022) 1–101.
- [92] R. Shetty, C.S.N. Vidya, N.B. Prakash, A. Lux, M. Vaculík, Aluminum toxicity in plants and its possible mitigation in acid soils by biochar: a review, *Sci. Total Environ.* 765 (2020), 142744.
- [93] D. Lauricella, Z. Weng, G.J. Clark, C.R. Butterly, G. Li, C. Gazey, P.W.G. Sale, C. Tang, Biochars and their feedstocks differ in their short-term effects in ameliorating acid soils grown with aluminium-sensitive wheat, *J. Soils Sediments* 21 (8) (2021) 2805–2816.
- [94] T. Sun, B.D. Levin, J.J. Guzman, A. Enders, D.A. Muller, L.T. Angenent, J. Lehmann, Rapid electron transfer by the carbon matrix in natural pyrogenic carbon, *Nat. Commun.* 8 (1) (2017) 1–12.
- [95] X. Ruan, Y. Sun, W. Du, Y. Tang, Q. Liu, Z. Zhang, W. Doherty, R.L. Frost, G. Qian, D.C. Tsang, Formation, characteristics, and applications of environmentally persistent free radicals in biochars: a review, *Bioresour. Technol.* 281 (2019) 457–468.
- [96] A.K. Jaiswal, O. Frenkel, L. Tsechansky, Y. Elad, E.R. Graber, Immobilization and deactivation of pathogenic enzymes and toxic metabolites by biochar: a possible mechanism involved in soilborne disease suppression, *Soil Biol. Biochem.* 121 (2018) 59–66.
- [97] H. Chen, D.A. Bullock Jr., J.M. Alonso, A.N. Stepanova, To fight or to grow: the balancing role of ethylene in plant abiotic stress responses, *Plants* 11 (1) (2021) 33.
- [98] S.H. Mustafavi, H. Naghdi Badi, A. Sčkara, A. Mehrafarin, T. Janda, M. Ghorbanpour, H. Rafiee, Polyamines and their possible mechanisms involved in plant physiological processes and elicitation of secondary metabolites, *Acta Physiol. Plant.* 40 (2018) 1–19.
- [99] L. Xu, The effect of polyamine flower bud differentiation and bud germination of *Chrysanthemum*, *Shandong Agric. Univ.* (2015) 31–36.
- [100] Z. Shahzad, A. Amtmann, Food for thought: how nutrients regulate root system architecture, *Curr. Opin. Plant Biol.* 39 (2017) 80–87.
- [101] B.D. Gruber, R.F.H. Giehl, S. Friedel, N.V. Wires, Plasticity of the *Arabidopsis* root system under nutrient deficiencies, *Plant Physiol.* 163 (1) (2013) 161–179.
- [102] J.P. Lynch, Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture, *New Phytol.* 223 (2) (2015) 548–564.
- [103] P.A. Ingram, J.E. Malamy, Root system architecture, in: *Advances in Botanical Research*, Academic Press, 2010, pp. 55–75.
- [104] B. Ahmad, A. Raina, S. Khan, Impact of biotic and abiotic stresses on plants, and their responses, in: *Disease Resistance in Crop Plants*, Springer, Cham, 2019, pp. 1–19.
- [105] E. Westberg, S. Ohali, A. Shevelevich, P. Fine, O. Barazani, Environmental effects on molecular and phenotypic variation in populations of *Eruca sativa* across a steep climatic gradient, *Ecol. Evol.* 3 (8) (2013) 2471–2484.
- [106] P. Wang, X. Sun, C. Li, Z. Wei, D. Liang, F. Ma, Long-term exogenous application of melatonin delays drought-induced leaf senescence in apple, *J. Pineal Res.* 54 (3) (2013) 292–302.
- [107] M.A. Geneaev, A.V. Doroshkov, T.A. Pshenichnikova, N.A. Kolchanov, D.A. Afonnikov, Extraction of quantitative characteristics describing wheat leaf pubescence with a novel image-processing technique, *Planta* 236 (6) (2012) 1943–1954.
- [108] R. Ratzmann, L. Zakharova, B. Tietjen, Optimal leaf water status regulation of plants in drylands, *Sci. Rep.* 9 (1) (2019) 1–9.
- [109] U. Hochberg, C.W. Windt, A. Ponomarenko, Y.J. Zhang, J. Gersony, F.E. Rockwell, N.M. Holbrook, Stomatal closure, basal leaf embolism, and shedding protect the hydraulic integrity of grape stems, *Plant Physiol.* 174 (2) (2017) 764–775.
- [110] Y.B. Colak, A. Yazar, A. Alghawry, S. Tekin, Evaluation of crop water stress index and leaf water potential for differentially irrigated quinoa with surface and subsurface drip systems, *Irrigat. Sci.* 39 (2021) 81–100.
- [111] J. Lu, F. Shireen, F. Cheng, Z. Bie, High relative humidity improves chilling tolerance by maintaining leaf water potential in watermelon seedlings, *Plant Physiol. Biochem.* 166 (2021) 818–826.
- [112] D. Xue, X. Zhang, X. Lu, G. Chen, Z.H. Chen, Molecular and evolutionary mechanisms of cuticular wax for plant drought tolerance, *Front. Plant Sci.* 8 (2017) 621.
- [113] M. Lewandowska, A. Keyl, I. Feussner, Wax biosynthesis in response to danger: its regulation upon abiotic and biotic stress, *New Phytol.* 227 (3) (2020) 698–713.
- [114] S.B. Lee, M.C. Suh, Advances in the understanding of cuticular waxes in *Arabidopsis thaliana* and crop species, *Plant Cell Rep.* 34 (2015) 557–572.
- [115] T. Li, Y. Sun, T. Liu, H. Wu, P. An, Z. Shui, J. Wang, Y. Zhu, C. Li, Y. Wang, R. Jetter, Z. Wang, TaCER1-1A is involved in cuticular wax alkane biosynthesis in hexaploid wheat and responds to plant abiotic stresses, *Plant Cell Environ.* 42 (11) (2019) 3077–3091.
- [116] J.C. Tafolla-Arellano, Y. Zheng, H. Sun, C. Jiao, E. Ruiz-May, M.A. Hernández-Oñate, A. González-León, R. Báez-Saundo, Z. Fei, D. Domozych, J.K. Rose, Transcriptome analysis of mango (*Mangifera indica* L.) fruit epidermal peel to identify putative cuticle-associated genes, *Sci. Rep.* 7 (1) (2017), 46163.
- [117] J. Wang, L. Sun, L. Xie, Y. He, T. Luo, L. Sheng, Y. Luo, Y. Zeng, J. Xu, X. Deng, Y. Cheng, Regulation of cuticle formation during fruit development and ripening in 'Newhall' navel orange (*Citrus sinensis* Osbeck) revealed by transcriptomic and metabolomic profiling, *Plant Sci.* 243 (2016) 131–144.
- [118] J.P. Simpson, J.B. Ohlrogge, A novel pathway for triacylglycerol biosynthesis is responsible for the accumulation of massive quantities of glycerolipids in the surface wax of bayberry (*Myrica pensylvanica*) fruit, *Plant Cell* 28 (2016) 248–264.
- [119] Y. Wang, M. Dai, S. Zhang, Z. Shi, Exploring candidate genes for pericarp russet pigmentation of sand pear (*Pyrus pyrifolia*) via RNA-seq data in two genotypes contrasting for pericarp color, *PLoS One* 9 (2014), e83675.
- [120] S. Taghvaeian, L. Comas, K.C. Dejonge, T.J. Trout, Conventional and simplified canopy temperature indices predict water stress in sunflower, *Agric. Water Manag.* 144 (2014) 69–80.
- [121] M.A. Rahman, A. Moser, T. Rotzer, P. Stephan, Within canopy temperature differences and cooling ability of *Tilia cordata* trees grown in urban condition, *Build. Environ.* 114 (2017) 118–128.
- [122] A.W. de Jonge, J.G. Wildenbeest, H. Boessenkool, D.A. Abbink, The effect of trial-by-trial adaptation on conflicts in haptic shared control for free-air teleoperation tasks, *IEEE Transact Hap* 9 (2015) 111–120.
- [123] M. Tucci, M. Ruocco, L. De Masi, M. De Palma, M. Lorito, The beneficial effect of *Trichoderma* spp. on tomato is modulated by the plant genotype, *Mol. Plant Pathol.* 12 (2011) 341–354, <https://doi.org/10.1111/j.1364-3703.2010.00674.x>.
- [124] C.H. Haney, B.S. Samuel, J. Bush, F.M. Ausubel, Associations with rhizosphere bacteria can confer an adaptive advantage to plants, *Native Plants* 1 (2015) 1–9.
- [125] E. Samain, T. Aussenac, S. Selim, The effect of plant genotype, growth stage, and *Mycosphaerellagraminicola* strains on the efficiency and durability of wheat-induced resistance by *Paenibacillus* sp. strain B2, *Front. Plant Sci.* 10 (2019) 587.

- [126] G.A. Mora-Romero, R.G. Cervantes-Gómez, H. Galindo-Flores, M.A. González-Ortiz, R. Félix-Gastélum, I.E. Maldonado-Mendoza, R. Salinas Pérez, J. León-Félix, M.C. Martínez-Valenzuela, M. López-Meyer, Mycorrhiza-induced protection against pathogens is both genotype-specific and graft-transmissible, *Symbiosis* 66 (2015) 55–64.
- [127] S.P. Singh, C. Keswani, S.P. Singh, E. Sansinenea, T.X. Hoat, *Trichoderma* spp. mediated induction of systemic defense response in brinjal against *Sclerotinia sclerotiorum*, *Curr. Res. Microb. Sci.* 2 (2021), 100051, <https://doi.org/10.1016/j.crmicr.2021.100051>.
- [128] M.K. Chitara, C. Keswani, K.G. Varnava, H. Birla, H. Dilnashin, S.P. Singh, V. Sarojini, J. Sperry, H.B. Singh, Impact of the alkaloid colletotrichumine A on the pathogenicity of *Colletotrichum capsici* in *Capsicum annum* L, *Rhizosphere* 16 (2020), 100247, <https://doi.org/10.1016/j.rhisph.2020.100247>.
- [129] S. Lakkis, P. Trostel-Aziz, F. Rabenoelina, A. Schwarzenberg, E. Nguema-Ona, C. Clément, A. Aziz, Strengthening grapevine resistance by *Pseudomonas fluorescens* PTA-CT2 relies on distinct defense pathways in susceptible and partially resistant genotypes to downy mildew and gray mold diseases, *Front. Plant Sci.* 10 (2019) 1112.
- [130] Z.A. Awan, A. Shoaib, K.A. Khan, Variations in total phenolics and antioxidant enzymes cause phenotypic variability and differential resistant response in tomato genotypes against early blight disease, *Sci. Hortic.* 239 (2018) 216–223.
- [131] A. VanWallendael, G.M.N. Benucci, P.B. da Costa, L. Fraser, A. Sreedasyam, F. Fritschi, T.E. Juenger, J.T. Lovell, G. Bonito, D.B. Lowry, Host genotype controls ecological change in the leaf fungal microbiome, *PLoS Biol.* 20 (2022), e3001681.
- [132] I. Kraiselburd, L. Moyano, A. Carrau, J. Tano, E.G. Orellano, Bacterial photosensory proteins and their role in plant–pathogen interactions, *Photochem. Photobiol.* 93 (2017) 666–674.
- [133] M. Gomelsky, W.D. Hoff, Light helps bacteria make important lifestyle decisions, *Trends Microbiol.* 19 (2011) 441–448.
- [134] T. Ichiro, O. Hiroki, F. Takashi, O. Riichi, Light environment within a leaf. II. Progress in the past one-third century, *J. Plant Res.* 129 (2016) 353–363.
- [135] T.C. Vogelmann, H.L. Gorton, Leaf: light capture in the photosynthetic organ, in: M.F. Hohmann-Marriott (Ed.), *The Structural Basis of Biological Energy Generation, Advances in Photosynthesis and Respiration*, Springer Netherlands, Dordrecht, 2014, pp. 363–377.
- [136] L. Moyano, A. Carrau, S. Petrocelli, I. Kraiselburd, W. Gärtner, E.G. Orellano, Bacteriophytochromes from *Pseudomonas syringae* pv. *tomato* DC3000 modulate the early stages of plant colonization during bacterial speck disease, *Eur. J. Plant Pathol.* 156 (2020) 695–712.
- [137] J. Tano, M.B. Ripa, M.L. Tondo, A. Carrau, S. Petrocelli, M.V. Rodriguez, V. Ferreira, M.L. Siri, L. Piskulic, E.G. Orellano, Light modulates important physiological features of *Ralstonia pseudosolanacearum* during the colonization of tomato plants, *Sci. Rep.* 11 (2021), 14531.
- [138] R. McGrane, G.A. Beattie, *Pseudomonas syringae* pv. *syringae* B728a regulates multiple stages of plant colonization via the bacteriophytochrome BphP1, *mBio* 8 (2017) e01178, 17.
- [139] L.J. Kahl, A. Price-Whelan, L.E.P. Dietrich, Light-mediated decreases in cyclic di-GMP levels inhibit structure formation in *Pseudomonas aeruginosa* biofilms, *J. Bacteriol.* 202 (2020) e00117–e00120.
- [140] N. Rajalingam, Y.H. Lee, Green and red light reduces the disease severity by *Pseudomonas cichorii* JBC1 in tomato plants via upregulation of defense-related gene expression, *Phytopathology* 105 (2015) 412–418.
- [141] N. Rajalingam, Y.H. Lee, Effects of green light on the gene expression and virulence of the plant pathogen *Pseudomonas cichorii* JBC1, *Eur. J. Plant Pathol.* 150 (2018) 223–236.
- [142] K.-J. Dietz, I. Turkan, A. Krieger-Liszka, Redox and reactive oxygen species-dependent signaling into and out of the photosynthesizing chloroplast, *Plant Physiol.* 171 (2016) 1541–1550.
- [143] S. Huang, O. Van Aken, M. Schwarzländer, K. Belt, A.H. Millar, The roles of mitochondrial reactive oxygen species in cellular signaling and stress response in plants, *Plant Physiol.* 171 (2016) 1551–1559.
- [144] R. Mittler, S.I. Zandalinas, Y. Fichman, F. Van Breusegem, Reactive oxygen species signalling in plant stress responses, *Nat. Rev. Mol. Cell Biol.* (2022) 1–17.
- [145] Y.-J. Chen, M.F. Lyngkjær, D.B. Collinge, Future prospects for genetically engineering disease-resistant plants, in: *Molecular Plant Immunity*, John Wiley Sons, Ltd, 2012, pp. 251–275.
- [146] G. Miller, N. Suzuki, S. Ciftci-Yilmaz, R. Mittler, Reactive oxygen species homeostasis and signalling during drought and salinity stresses, *Plant Cell Environ.* 33 (2010) 453–467.
- [147] D. Camejo, Á. Guzmán-Cedeño, A. Moreno, Reactive oxygen species, essential molecules, during plant–pathogen interactions, *Plant Physiol. Biochem.* 103 (2016) 10–23.
- [148] Y. Kadota, K. Shirasu, C. Zipfel, Regulation of the NADPH oxidase RBOHD during plant immunity, *Plant Cell Physiol.* 56 (2015) 1472–1480.
- [149] M.A. Torres, J.D.G. Jones, J.L. Dangl, Reactive oxygen species signaling in response to pathogens, *Plant Physiol.* 141 (2006) 373–378.
- [150] R. Liu, T. Chen, X. Yin, G. Xiang, J. Peng, Q. Fu, M. Li, B. Shang, H. Ma, G. Liu, Y. Wang, Y. Xu, A *Plasmopara viticola* RXLR effector targets a chloroplast protein PsbP to inhibit ROS production in grapevine, *Plant J.* 106 (2021) 1557–1570.
- [151] R. Chen, H. He, Y. Yang, Y. Qu, F. Ge, D. Liu, Functional characterization of a pathogenesis-related protein family 10 gene, LrPr10-5, from *Lilium regale* Wilson, *Australas. Plant Pathol.* 46 (2017) 251–259.
- [152] C. Wasternack, S. Song, Jasmonates: biosynthesis, metabolism, and signaling by proteins activating and repressing transcription, *J. Exp. Bot.* 68 (2017) 1303–1321, <https://doi.org/10.1093/jxb/erw443>.
- [153] K. Zhalnina, K.B. Louie, Z. Hao, N. Mansoori, U.N. da Rocha, S. Shi, H. Cho, U. Karaoz, D. Loqué, B.P. Bowen, M.K. Firestone, T.R. Northen, E.L. Brodie, Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly, *Nat. Microbiol.* 3 (2018) 470–480.
- [154] H. Sun, S. Jiang, C. Jiang, C. Wu, M. Gao, Q. Wang, A review of root exudates and rhizosphere microbiome for crop production, *Environ. Sci. Pollut. Res.* 28 (2021) 54497–54510.
- [155] J. Ruparelia, A. Rabari, D. Mitra, P. Pannierselvam, P.K. Das-mohapatra, C.K. Jha, Efficient Applications of Bacterial Secondary Metabolites for Management of Biotic Stress in Plants, *Plant Stress*, 2022, 100125.
- [156] W. Zhang, C. Wang, R. Xue, L. Wang, Effects of salinity on the soil microbial community and soil fertility, *J. Integr. Agric.* 18 (2019) 1360–1368, [https://doi.org/10.1016/S2095-3119\(18\)62077-5](https://doi.org/10.1016/S2095-3119(18)62077-5).
- [157] L. Hu, C.A.M. Robert, S. Cadot, X. Zhang, M. Ye, B. Li, D. Manzo, N. Chervet, T. Steinger, M.G.A. van der Heijden, K. Schlaeppli, M. Erb, Root exudate metabolites drive plant-soil feedbacks on growth and defense by shaping the rhizosphere microbiota, *Nat. Commun.* 9 (2018) 27–38.
- [158] E.M. Hafez, H.S. Osman, U.A.A. El-Razek, M. Elbagory, A.E.D. Omara, M.A. Eid, S.M. Gowayed, Foliar-applied potassium silicate coupled with plant growth-promoting rhizobacteria improves growth, physiology, nutrient uptake and productivity of *Faba bean* (*Vicia faba* L.) irrigated with saline water in salt-affected soil, *Plants* 10 (2021) 894.
- [159] S.I.A. Pereira, D. Abreu, H. Moreira, A. Vega, P.M.L. Castro, Plant growth-promoting rhizobacteria (PGPR) improve the growth and nutrient use efficiency in maize (*Zea mays* L.) under water deficit conditions, *Heliyon* 6 (2020), e05106.
- [160] M.S.I. Rion, A. Rahman, M.J. Khatun, H.M. Zakir, M.H. Rashid, Q.F. Quadir, Screening of zinc solubilizing plant growth promoting rhizobacteria (PGPR) as potential tool for biofortification in rice, *J. Exp. Agric. Int.* 44 (2022) 132–143.
- [161] C. Preece, J. Peñuelas, A return to the wild: root exudates and food security, *Trends Plant Sci.* 25 (2020) 14–21.
- [162] P. Durán, T. Thiérgart, R. Garrido-Oter, M. Agler, E. Kemen, P. Schulze-Lefert, S. Haquard, Microbial interkingdom interactions in roots promote arabidopsis survival, *Cell* 175 (2018) 973–983.
- [163] P.A.H.M. Bakker, C.M.J. Pieterse, R. de Jonge, R.L. Berendsen, The soil-borne legacy, *Cell* 172 (2018) 1178–1180.
- [164] J. Liu, W. Qi, Q. Li, S.-G. Wang, C. Song, X. Yuan, Exogenous phosphorus-solubilizing bacteria changed the rhizosphere microbial community indirectly, *3 Biotech* 10 (2020) 164.
- [165] S. Xie, L. Jiang, Q. Wu, W. Wan, Y. Gan, L. Zhao, J. Wen, Maize root exudates recruit *Bacillus amyloliquefaciens* OR2-30 to inhibit *Fusarium graminearum* infection, *Phytopathology* 112 (2022) 1886–1893.
- [166] J. Yuan, J. Zhao, T. Wen, M. Zhao, R. Li, P. Goossens, Q. Huang, Y. Bai, J.M. Vivanco, G.A. Kowalchuk, R.L. Berendsen, Q. Shen, Root exudates drive the soil-borne legacy of aboveground pathogen infection, *Microbiome* 6 (2018) 156.

- [167] N. Khan, A. Bano, S. Ali, MdA. Babar, Crosstalk amongst phytohormones from planta and PGPR under biotic and abiotic stresses, *Plant Growth Regul.* 90 (2020) 189–203, <https://doi.org/10.1007/s10725-020-00571-x>.
- [168] O. Sytar, P. Kumari, S. Yadav, M. Brestic, A. Rastogi, Phytohormone priming: regulator for heavy metal stress in plants, *J. Plant Growth Regul.* 38 (2019) 739–752, <https://doi.org/10.1007/s00344-018-9886-8>.
- [169] A. Chini, S. Gimenez-Ibanez, A. Goossens, R. Solano, Redundancy and specificity in jasmonate signalling, *Curr. Opin. Plant Biol.* 33 (2016) 147–156.
- [170] C. Wang, Y. Liu, S.-S. Li, G.-Z. Han, Insights into the origin and evolution of the plant hormone signaling machinery, *Plant Physiol.* 167 (2015) 872–886, <https://doi.org/10.1104/114.247403>.
- [171] C. Wasternack, B. Hause, Jasmonates: biosynthesis, perception, signal transduction and action in plant stress response, growth and development. An update to the 2007 review in, *Annals of Botany. Ann Bot.* 111 (6) (2013) 1021–1058.
- [172] D.A. Dempsey, D.F. Klessig, How does the multifaceted plant hormone salicylic acid combat disease in plants and are similar mechanisms utilized in humans, *BMC Biol.* 15 (2017) 23–37.
- [173] V. Verma, P. Ravindran, P.P. Kumar, Plant hormone-mediated regulation of stress responses, *BMC Plant Biol.* 16 (2016) 86, <https://doi.org/10.1186/s12870-016-0771-y>.
- [174] T. Le Thanh, K. Thumanu, S. Wongkaew, N. Boonkerd, N. Teaumroong, P. Phansak, N. Buensanteai, Salicylic acid-induced accumulation of biochemical components associated with resistance against *Xanthomonas oryzae* pv. *oryzae* in rice, *J. Plant Interact.* 12 (2017) 108–120, <https://doi.org/10.1080/17429145.2017.1291859>.
- [175] D.Y.M. Yousif, Effects sprayed solution of salicylic acid to prevent of wilt disease caused by *Fusarium oxysporum*, *J. Phys. Conf. Ser.* 1003 (2018), 012001, <https://doi.org/10.1088/1742-6596/1003/1/012001>.
- [176] T.F. Stella de Freitas, M.J. Stout, J. Sant'Ana, Effects of exogenous methyl jasmonate and salicylic acid on rice resistance to *Oebalus pugnax*, *Pest Manag. Sci.* 75 (2019) 744–752, <https://doi.org/10.1002/ps.5174>.
- [177] C.-W. Tan, S.-Y. Chiang, K.T. Ravuiwasa, J. Yadav, S.-Y. Hwang, Jasmonate-induced defenses in tomato against *Helicoverpa armigera* depend in part on nutrient availability, but artificial induction via methyl jasmonate does not, *Arthropod-Plant Interact.* 6 (2012) 531–541, <https://doi.org/10.1007/s11829-012-9206-3>.
- [178] Y.T. Zhang, Y.L. Zhang, S.X. Chen, G.H. Yin, Z.Z. Yang, S. Lee, C.G. Liu, D.D. Zhao, Y.K. Ma, F.Q. Song, J.W. Bennett, F.S. Yang, Proteomics of methyl jasmonate induced defense response in maize leaves against Asian corn borer, *BMC Genom.* 16 (2015) 224.
- [179] M. Ghorbel, F. Brini, A. Sharma, M. Landi, Role of jasmonic acid in plants: the molecular point of view, *Plant Cell Rep.* 40 (2021) 1471–1494.
- [180] D. Tripathi, M. Singh, S. Pandey-Rai, Crosstalk of nanoparticles and phytohormones regulate plant growth and metabolism under abiotic and biotic stress, *Plant Stress* 6 (2022), 100107, <https://doi.org/10.1016/j.plstress.2022.100107>.
- [181] R. Vankova, P. Landa, R. Podlipna, P.I. Dobrev, S. Prerostova, L. Langhansova, A. Gaudinova, K. Motkova, V. Knirsch, T. Vanek, ZnO nanoparticle effects on hormonal pools in *Arabidopsis thaliana*, *Sci. Total Environ.* (2017) 593–594, <https://doi.org/10.1016/j.scitotenv.2017.03.160>.
- [182] Lin Cai, Liuti Cai, H. Jia, C. Liu, D. Wang, X. Sun, Foliar exposure of Fe3O4 nanoparticles on *Nicotiana benthamiana*: evidence for nanoparticles uptake, plant growth promoter and defense response elicitor against plant virus, *J. Hazard Mater.* 393 (2020), 122415, <https://doi.org/10.1016/j.jhazmat.2020.122415>.
- [183] N.G.C. Soria, M.A. Bisson, G.E. Atilla-Gokumen, D.S. Aga, High-resolution mass spectrometry-based metabolomics reveal the disruption of jasmonic pathway in *Arabidopsis thaliana* upon copper oxide nanoparticle exposure, *Sci. Total Environ.* 693 (2019), 133443, <https://doi.org/10.1016/j.scitotenv.2019.07.249>.
- [184] H. Shang, C. Ma, C. Li, J.C. White, T. Polubesova, B. Chefetz, B. Xing, Copper sulfide nanoparticles suppress *Gibberella fujikuroi* infection in rice (*Oryza sativa* L.) by multiple mechanisms: contact-mortality, nutritional modulation and phytohormone regulation, *Environ. Sci. Nano* 7 (2020) 2632–2643.
- [185] D. Dasgupta, A. Paul, K. Acharya, T. Minkina, S. Mandzhieva, A.V. Gorovtsov, N. Chakraborty, C. Keswani, Bioinoculant mediated regulation of signalling cascades in various stress responses in plants, *Heliyon* 9 (1) (2023), e12953.
- [186] S. Munné-Bosch, M. Müller, Hormonal cross-talk in plant development and stress responses, *Front. Plant Sci.* 4 (2013) 529.
- [187] A. Raza, H. Salehi, M.A. Rahman, Z. Zahid, M. MadadkarHaghjou, S. Najafi-Kakavand, S. Charagh, H.S. Osman, M. Albaqami, Y. Zhuang, K.H. Siddique, Plant hormones and neurotransmitter interactions mediate antioxidant defenses under induced oxidative stress in plants, *Front. Plant Sci.* 13 (2022).
- [188] X. Liu, X. Hou, Antagonistic regulation of ABA and GA in metabolism and signaling pathways, *Front. Plant Sci.* 9 (2018) 251.
- [189] J. Yang, G. Duan, C. Li, L. Liu, G. Han, Y. Zhang, C. Wang, The crosstalks between jasmonic acid and other plant hormone signaling highlight the involvement of jasmonic acid as a core component in plant response to biotic and abiotic stresses, *Front. Plant Sci.* 10 (2019) 1349.
- [190] A.G. Shahriari, A. Tahmasebi, S. Sazegari, Regulatory network identification, promoter and expression analysis of *Arabidopsis thaliana* NPR1 in defense responses against stresses, *Not. Sci. Biol.* 10 (3) (2018) 333–339.
- [191] X. Xiong, S. Sun, Y. Li, X. Zhang, J. Sun, F. Xue, The cotton WRKY transcription factor GhWRKY70 negatively regulates the defense response against *Verticillium dahliae*, *Crops J* 7 (3) (2019) 393–402.
- [192] N. Aerts, M. Pereira Mendes, S.C. Van Wees, Multiple levels of crosstalk in hormone networks regulating plant defense, *Plant J.* 105 (2) (2021) 489–504.
- [193] S. Hou, K. Tsuda, Salicylic acid and jasmonic acid crosstalk in plant immunity, *Essays Biochem.* 66 (5) (2022) 647–656.
- [194] Y. Fujita, M. Fujita, K. Shinozaki, K. Yamaguchi-Shinozaki, ABA-mediated transcriptional regulation in response to osmotic stress in plants, *J. Plant Res.* 124 (4) (2011) 509–525.
- [195] D. Zhao, H. Wang, S. Chen, D. Yu, R.J. Reiter, Phyto-melatonin: an emerging regulator of plant biotic stress resistance, *Trends Plant Sci.* 26 (1) (2021) 70–82.
- [196] Y. Jiang, D. Yu, WRKY transcription factors: links between phytohormones and plant processes, *Sci. China Life Sci.* 58 (5) (2015) 501.
- [197] X. He, J. Jiang, C.Q. Wang, K. Dehesh, ORA59 and EIN3 interaction couples jasmonate-ethylene synergistic action to antagonistic salicylic acid regulation of PDF expression, *J. Integr. Plant Biol.* 59 (4) (2017) 275–287.
- [198] D. Singh, V.K. Dhiman, H. Pandey, V.K. Dhiman, D. Pandey, Crosstalk between salicylic acid and auxins, cytokinins and gibberellins under biotic stress, in: *Auxins, Cytokinins and Gibberellins Signaling in Plants*, Springer, Cham, 2022, pp. 249–262.
- [199] Y. Yu, Y. Li, Z. Yan, X. Duan, The role of cytokinins in plant under salt stress, *J. Plant Growth Regul.* 3 (2021) 1–13.
- [200] A. Briones-Moreno, J. Hernández-García, C. Vargas-Chávez, F.J. Romero-Campero, J.M. Romero, F. Valverde, M.A. Blázquez, Evolutionary analysis of DELLA-associated transcriptional networks, *Front. Plant Sci.* 8 (2017) 626.
- [201] S. Dreischhoff, I.S. Das, M. Jakobi, K. Kasper, A. Polle, Local responses and systemic induced resistance mediated by ectomycorrhizal fungi, *Front. Plant Sci.* (2020) 1908.
- [202] Q.M. Gao, S. Zhu, P. Kachroo, A. Kachroo, Signal regulators of systemic acquired resistance, *Front. Plant Sci.* 6 (2015) 228.
- [203] A.C. Vlot, J.H. Sales, M. Lenk, K. Bauer, A. Brambilla, A. Sommer, Y. Chen, M. Wenig, S. Nayem, Systemic propagation of immunity in plants, *New Phytol.* 229 (3) (2021) 1234–1250.
- [204] H.S. Yi, J.W. Yang, C.M. Ryu, ISR meets SAR outside: additive action of the endophyte *Bacillus pumilus* INR7 and the chemical inducer, benzothiadiazole, on induced resistance against bacterial spot in field-grown pepper, *Front. Plant Sci.* 4 (2013) 122.
- [205] B. Cooper, K.B. Campbell, H.S. Beard, W.M. Garrett, M.E. Ferreira, The proteomics of resistance to halo blight in common bean, *Mol. Plant Microbe Interact.* 33 (9) (2020) 1161–1175.
- [206] J. Santos-Rodríguez, E. Coy-Barrera, H.D. Ardila, Mycelium dispersion from *Fusarium oxysporum* f. sp. *dianthielicis* a reduction of wilt severity and influences phenolic profiles of *Carnation (Dianthus caryophyllus* L.) Roots, *Plants* 10 (7) (2021) 1447.
- [207] A. Gupta, P. Vandana, Effect of PGPR isolates on plant growth promotion in relation to salinity stress, *Bull. Environ. Pharmacol. Life Sci.* 8 (2019) 18–26.
- [208] M.R. Sarikhani, N. Aliasgharzad, B. Khoshru, P. solubilizing potential of some plant growth promoting bacteria used as ingredient in phosphatic biofertilizers with emphasis on growth promotion of *Zea mays* L., *Geomicrobiol. J.* 37 (2020) 327–335.
- [209] M.R. Sarikhani, B. Khoshru, R. Greiner, Isolation and identification of temperature tolerant phosphate solubilizing bacteria as a potential microbial fertilizer, *World J. Microbiol. Biotechnol.* 35 (2019) 1–10.
- [210] M.R. Sarikhani, B. Khoshru, S. Oustan, Efficiency of some bacterial strains in potassium release from mica and phosphate solubilization under in vitro conditions, *Geomicrobiol. J.* 33 (2016) 832–838.

- [211] B. Khoshru, D. Mitra, E. Khoshmanzar, E.M. Myo, N. Uniyal, B. Mahakur, P.K.D. Mohapatra, P. Panneerselvam, H. Boutaj, M. Alizadeh, M.V.T. Cely, Current scenario and future prospects of plant growth-promoting rhizobacteria: an economic valuable resource for the agriculture revival under stressful conditions, *J. Plant Nutr.* 43 (20) (2020) 3062–3092.
- [212] B. Khoshru, D. Mitra, B. Mahakur, M.R. Sarikhani, R. Mondal, D. Verma, K. Pant, Role of soil rhizobacteria in utilization of an indispensable micronutrient zinc for plant growth promotion, *J. Crit. Rev.* 21 (2020) 4644–4654.
- [213] B. Khoshru, S. Moharramnejad, N.H. Gharajeh, B. Asgari Lajayer, M. Ghorbanpour, Plant microbiome and its important in stressful agriculture, in: *Plant Microbiome Paradigm*, Springer, Cham, 2020, pp. 13–48.
- [214] D. Mitra, R. Mondal, B. Khoshru, A. Senapati, T.K. Radha, B. Mahakur, N. Uniyal, E.M. Myo, H. Boutaj, B.E.G. Sierra, P. Panneerselvam, Actinobacteria-enhanced plant growth, nutrient acquisition, and crop protection: advances in soil, plant, and microbial multifactorial interactions, *Pedosphere* (1) (2022) 149–170.
- [215] B. Lugtenberg, F. Kamilova, Plant-growth-promoting rhizobacteria, *Annu. Rev. Microbiol.* 63 (2009) 541–556.
- [216] B. Khoshru, M.R. Sarikhani, Inoculation effect of phosphatic microbial fertilizers containing temperature resistant phosphate solubilizing bacteria on nutritional indices of Zea mays L., *J. Crop Prod.* 12 (2019) 107–122.
- [217] S. Moradi, B. Khoshru, D. Mitra, B. Mahakur, P.K. Das Mohapatra, B. Asgari Lajayer, M. Ghorbanpour, Transcriptomics analyses and the relationship between plant and plant growth-promoting rhizobacteria (PGPR), *Omics Sci. Rhizosphere Biol.* (2021) 89–111.
- [218] H.H. Altinok, H.N. Yildiz, Induced systemic resistance by plant growth-promoting rhizobacteria in control of plant diseases, *Curr. Trends Nat. Sci.* 8 (16) (2019) 125–133.
- [219] B. Khoshru, M.R. Sarikhani, A. Reyhanitabar, S. Oustan, M.A. Malboobi, Evaluation of the ability of rhizobacterial isolates to solubilize sparingly soluble iron under in-vitro conditions, *Geomicrobiol. J.* (2022) 1–12.
- [220] F. Cartieaux, C. Contesto, A. Gallou, G. Desbrosses, J. Kopka, L. Taconnat, J.P. Renou, B. Touraine, Simultaneous interaction of *Arabidopsis thaliana* with *Bradyrhizobium* sp. strain ORS278 and *Pseudomonas syringae* pv. *tomato* DC3000 leads to complex transcriptome changes, *Mol. Plant Microbe Interact.* 21 (2) (2008) 244–259.
- [221] B. Khoshru, M.R. Sarikhani, A. Reyhanitabar, S. Oustan, M.A. Malboobi, Evaluation of the ability of rhizosphere isolates to solubilize low-soluble Zn under in-vitro conditions and their ability to supply Zn to maize, *J. Agri. Sci. Sustain. Prod.* 32 (2022) 183–199, <https://doi.org/10.22034/saps.2022.49165.2776>.
- [222] L.C. Van Loon, P.A.H.M. Bakker, Induced systemic resistance as a mechanism of disease suppression by rhizobacteria, in: *PGPR: Biocontrol and Biofertilization*, Springer, Dordrecht, 2005, pp. 39–66.
- [223] L.C. Van Loon, Plant responses to plant growth-promoting rhizobacteria, in: *New Perspectives and Approaches in Plant Growth-Promoting Rhizobacteria Research*, Springer, Dordrecht, 2007, pp. 243–254.
- [224] F. Kamilova, S. Validov, T. Azarova, I. Mulders, B. Lugtenberg, Enrichment for enhanced competitive plant root tip colonizers selects for a new class of biocontrol bacteria, *Environ. Microbiol.* 7 (11) (2005) 1809–1817.
- [225] Y. Yu, Y. Gui, Z. Li, C. Jiang, J. Guo, D. Niu, Induced systemic resistance for improving plant immunity by beneficial microbes, *Plants* 11 (3) (2022) 386–394.
- [226] M.M. Elsharkawy, F.O. Alotibi, A.A. Al-Askar, M. Adnan, M. Kamran, A. Abdelkhalik, S.I. Behiry, M.H. Saleem, A.A. Ahmad, A.A. Khedr, Systemic resistance induction of potato and tobacco plants against potato virus Y by *klebsiellaoxytoca*, *Life* 12 (10) (2022) 1521.
- [227] S. Gouda, R.G. Kerry, G. Das, S. Paramithiotis, H.S. Shin, J.K. Patra, Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture, *Microbiol. Res.* 206 (2018) 131–140.
- [228] D. Mitra, S. De Los Santos-Villalobos, F.I.P. Cota, A.M.G. Montelongo, E.L. Blanco, A.N. Olatunbosun, B. Khoshru, R. Mondal, P. Chidambaranathan, P. Panneerselvam, P.K.D. Mohapatra, Rice (*Oryza sativa* L.) plant protection by using dual biological control and plant growth-promoting agents—current scenarios and future prospects: a review, *Pedosphere* 17 (1) (2022) 217–237.
- [229] B. Khoshru, E. Khoshmanzar, B.A. Lajayer, M. Ghorbanpour, Soil moisture-mediated changes in microorganism biomass and bioavailability of nutrients in paddy soil, in: *Plant Stress Mitigators*, Academic Press, 2023, pp. 479–494.
- [230] P. Bharti, R. Tewari, Purification and structural characterization of a phthalate antibiotic from *Burkholderia gladioli* OR1 effective against multi-drug resistant *Staphylococcus aureus*, *J. Microbiol. Biotechnol. Food Sci.* 2021 (2021) 207–211.
- [231] M. Tariq, M. Noman, T. Ahmed, A. Hameed, N. Manzoor, M. Zafar, Antagonistic features displayed by plant growth promoting rhizobacteria (PGPR): a review, *J. Plant Sci. Phytopathol.* 1 (1) (2017) 38–43.
- [232] S. Srivastava, V. Bist, S. Srivastava, P.C. Singh, P.K. Trivedi, M.H. Asif, P.S. Chauhan, C.S. Nautiyal, Unraveling aspects of *Bacillus amyloliquefaciens* mediated enhanced production of rice under biotic stress of *Rhizoctonia solani*, *Front. Plant Sci.* 7 (2016) 587.
- [233] S. Zebelo, Y. Song, J.W. Kloepper, H. Fadamiro, Rhizobacteria activates (+)- $\delta$ -cadinene synthase genes and induces systemic resistance in cotton against beet armyworm (*Spodoptera exigua*), *Plant Cell Environ.* 39 (4) (2016) 935–943.
- [234] H. Li, X. Ding, C. Wang, H. Ke, Z. Wu, Y. Wang, H. Liu, J. Guo, Control of tomato yellow leaf curl virus disease by *Enterobacter asburiae* BQ9 as a result of priming plant resistance in tomatoes, *Turk. J. Biol.* 40 (1) (2016) 150–159.
- [235] S. Kumar, P.S. Chauhan, L. Agrawal, R. Raj, A. Srivastava, S. Gupta, S.K. Mishra, S. Yadav, P.C. Singh, S.K. Raj, *Paenibacillus lentimorbus* inoculation enhances tobacco growth and attenuates the virulence of *Cucumber mosaic virus*, *PLoS One* 11 (3) (2016), e0149980.
- [236] R. Dixit, L. Agrawal, S. Gupta, M. Kumar, S. Yadav, P.S. Chauhan, C.S. Nautiyal, Southern blight disease of tomato control by 1-aminocyclopropane-1-carboxylate (ACC) deaminase producing *Paenibacillus lentimorbus* B-30488, *Plant Signal. Behav.* 11 (2) (2016) e1113363.
- [237] R. Schuegger, A. Ihring, S. Gantner, G. Bahnweg, C. Knappe, G. Vogg, P. Hutzler, M. Schmid, F. Van Breusegem, L. Eberl, Induction of systemic resistance in tomato by N-acyl-L-homoserine lactone-producing rhizosphere bacteria, *Plant Cell Environ.* 29 (5) (2006) 909–918.
- [238] O.S. Olanrewaju, A.S. Ayangbenro, B.R. Glick, O.O. Babalola, Plant health: feedback effect of root exudates-rhizobiome interactions, *Appl. Microbiol. Biotechnol.* 103 (3) (2019) 1155–1166.
- [239] 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.
- [240] R. Backer, S. Naidoo, N. Van den Berg, The nonexpressor of pathogenesis-related genes 1 (NPR1) and related family: mechanistic insights in plant disease resistance, *Front. Plant Sci.* 10 (2019) 102.
- [241] O.S. Olanrewaju, B.R. Glick, O.O. Babalola, Mechanisms of action of plant growth promoting bacteria, *World J. Microbiol. Biotechnol.* 33 (11) (2017) 1–16.
- [242] D. Mitra, R. Mondal, B. Khoshru, S. Shadangi, P.K.D. Mohapatra, P. Panneerselvam, Rhizobacteria mediated seed bio-priming triggers the resistance and plant growth for sustainable crop production, *Curr. Res. Microbiol. Sci.* 2 (2021), 100071.
- [243] B. Mauch-Mani, I. Baccelli, E. Luna, V. Flors, Defense priming: an adaptive part of induced resistance, *Annu. Rev. Plant Biol.* 68 (2017) 485–512.
- [244] T. Nürnberger, V. Lipka, Non-host resistance in plants: new insights into an old phenomenon, *Mol. Plant Pathol.* 6 (2005) 335–345.
- [245] P.A. Bakker, C.M. Pieterse, L.C. Van Loon, Induced systemic resistance by fluorescent *Pseudomonas* spp., *Phytopathology* 97 (2007) 239–243.
- [246] C.M. Pieterse, R.L. Berendsen, R. de Jonge, I.A. Stringlis, A.J. Van Dijken, J.A. Van Pelt, S. Van Wees, K. Yu, C. Zamioudis, P.A. Bakker, *Pseudomonas* WCS417: star track of a model beneficial rhizobacterium, *Plant Soil* 461 (1) (2021) 245–263.
- [247] S.C. Van Wees, C.M. Pieterse, A. Trijsenaar, Y.A. Van't Westende, F. Hartog, L.C. Van Loon, Differential induction of systemic resistance in *Arabidopsis* by biocontrol bacteria, *Mol. Plant Microbe Interact.* 10 (6) (1997) 716–724.
- [248] L.X. Ran, L.C. Van Loon, P.A.H.M. Bakker, No role for bacterially produced salicylic acid in rhizobacterial induction of systemic resistance in *Arabidopsis*, *Phytopathology* 95 (11) (2005) 1349–1355.
- [249] N. Kadotani, A. Akagi, H. Takatsuji, T. Miwa, D. Igarashi, Exogenous proteinogenic amino acids induce systemic resistance in rice, *BMC Plant Biol.* 16 (1) (2016) 1–10.
- [250] M. Alizadeh, Y. Vasebi, N. Safaei, Microbial antagonists against plant pathogens in Iran: a review, *Open Agric* 5 (1) (2020) 404–440.
- [251] 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 (9) (2005) 4951–4959.

- [252] M. Ongena, E. Jourdan, A. Adam, M. Paquot, A. Brans, B. Joris, J.L. Arpigny, P. Thonart, Surfactin and fengycin lipopeptides of *Bacillus subtilis* as elicitors of induced systemic resistance in plants, *Environ. Microbiol.* 9 (4) (2007) 1084–1090.
- [253] D.H. Chae, D.R. Kim, M.S. Cheong, Y.B. Lee, Y.S. Kwak, Investigating the induced systemic resistance mechanism of 2, 4-Diacetylphloroglucinol (DAPG) using DAPG hydrolase-transgenic Arabidopsis, *Plant Pathol. J.* 36 (3) (2020) 255.
- [254] C. Hernández-Reyes, S.T. Schenk, C. Neumann, K.H. Kogel, A. Schikora, N-acyl-homoserine lactones-producing bacteria protect plants against plant and human pathogens, *Microb. Biotechnol.* 7 (6) (2014) 580–588.
- [255] M.A. Farag, H. Zhang, C.M. Ryu, Dynamic chemical communication between plants and bacteria through airborne signals: induced resistance by bacterial volatiles, *J. Chem. Ecol.* 39 (7) (2013) 1007–1018.
- [256] K. Wenke, T. Weise, R. Warnke, C. Valverde, D. Wanke, M. Kai, B. Piechulla, Bacterial volatiles mediating information between bacteria and plants, in: *Biocommunication of Plants*, Springer, Berlin, Heidelberg, 2012, pp. 327–347.
- [257] S. Kumar, R. Chandra, C. Keswani, T. Minkina, S. Mandzhieva, M. Voloshina, M. Meena, *Trichoderma viride*-mediated modulation of oxidative stress network in potato challenged with *Alternaria solani*, *J. Plant Growth Regul.* (2022) 1–18, <https://doi.org/10.1007/s00344-022-10669-3>.
- [258] M. Höfte, P.A. Bakker, in: *Competition for Iron and Induced Systemic Resistance by Siderophores of Plant Growth Promoting Rhizobacteria*, *Microbial Siderophores* Springer, Berlin, Heidelberg, 2007, pp. 121–133.
- [259] B.J. Duijff, J.W. Meijer, P.A. Bakker, B. Schippers, Siderophore-mediated competition for iron and induced resistance in the suppression of *Fusarium* wilt of carnation by fluorescent *Pseudomonas* spp., *Neth. J. Plant Pathol.* 99 (5) (1993) 277–289.
- [260] Z. Zhang, Y. Bi, Y. Ge, J. Wang, J. Deng, D. Xie, Y. Wang, Multiple pre-harvest treatments with acibenzolar-S-methyl reduce latent infection and induce resistance in muskmelon fruit, *Sci. Hortic.* 130 (2011) 126–132.
- [261] H. Meziane, I. Van Der Sluis, L.C. Van Loon, M. Höfte, P.A. Bakker, Determinants of *Pseudomonas putida* WCS358 involved in inducing systemic resistance in plants, *Mol. Plant Pathol.* 6 (2) (2005) 177–185.
- [262] S. Mandal, R.C. Ray, Induced systemic resistance in biocontrol of plant diseases, in: *Bioaugmentation, Biostimulation and Biocontrol*, Springer, Berlin, Heidelberg, 2011, pp. 241–260.
- [263] L.D.R. Cappellari, J. Chiappero, T.B. Palermo, W. Giordano, E. Banchio, Volatile organic compounds from rhizobacteria increase the biosynthesis of secondary metabolites and improve the antioxidant status in *Mentha piperita* L. grown under salt stress, *Agro Sur* 10 (8) (2020) 1094.
- [264] E.A. Salem, A. El-Shafea, M. Yasser, Biological control of potato soft rot caused by *Erwinia carotovora* subsp. *carotovora*, *J. Biol. Pest Control.* 28 (1) (2018) 1–5.
- [265] T. Rudrappa, K.J. Czymmek, P.W. Paré, H.P. Bais, Root-secreted malic acid recruits beneficial soil bacteria, *Plant Physiol.* 148 (3) (2008) 1547–1556.
- [266] M. Ongena, P. Jacques, Y. Touré, J. Destain, A. Jabrane, P. Thonart, Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*, *Appl. Microbiol. Biotechnol.* 69 (1) (2005) 29–38.
- [267] Z. Dehghanian, K. Habibi, M. Dehghanian, S. Aliyar, B.A. Lajayer, T. Astatkie, T. Minkina, C. Keswani, Reinforcing the bulwark: unravelling the efficient applications of plant phenolics and tannins against environmental stresses, *Heliyon* 8 (3) (2022), e09094, <https://doi.org/10.1016/j.heliyon.2022.e09094>.
- [268] E. Jourdan, G. Henry, F. Duby, J. Dommes, J.P. Barthelemy, P. Thonart, M.A.R.C. Ongena, Insights into the defense-related events occurring in plant cells following perception of surfactin-type lipopeptide from *Bacillus subtilis*, *Mol. Plant Microbe Interact.* 22 (4) (2009) 456–468.
- [269] M.M. Haque, M.K. Mosharaf, M. Khatun, M.A. Haque, M.S. Biswas, M.S. Islam, M.M. Islam, H.B. Shozib, M.M.U. Miah, A.H. Molla, M.A. Siddiquee, Biofilm producing rhizobacteria with multiple plant growth-promoting traits promote growth of tomato under water-deficit stress, *Front. Microbiol.* 11 (2020), 542053.
- [270] S.K. Nayak, S. Nayak, J.K. Patra, Rhizobacteria and its biofilm for sustainable agriculture: a concise review, in: *New and Future Developments in Microbial Biotechnology and Bioengineering: Microbial Biofilms*, Springer, 2020, pp. 165–175.
- [271] A.K. Abdalla, M.M. Ayyash, A.N. Olaimat, T.M. Osaili, A.A. Al-Nabulsi, N.P. Shah, R. Holley, Exopolysaccharides as antimicrobial agents: mechanism and spectrum of activity, *Front. Microbiol.* 12 (2021), 664395.
- [272] W.A. Kasim, R.M. Gaafar, R.M. Abou-Ali, M.N. Omar, H.M. Hewait, Effect of biofilm forming plant growth promoting rhizobacteria on salinity tolerance in barley, *Ann. Agric. Sci. (Cairo)* 61 (2) (2016) 217–227.
- [273] F.A. Ansari, I. Ahmad, Isolation, functional characterization and efficacy of biofilm-forming rhizobacteria under abiotic stress conditions, *Anton. Leeuw. Int. J. G.* 112 (12) (2019) 1827–1839.
- [274] G. Santoyo, C.A. Urtis-Flores, P.D. Loeza-Lara, M.D.C. Orozco-Mosqueda, B.R. Glick, Rhizosphere colonization determinants by plant growth-promoting rhizobacteria (PGPR), *Biol.* 10 (6) (2021) 475–486.
- [275] F.M. Alaa, Effectiveness of exopolysaccharides and biofilm forming plant growth promoting rhizobacteria on salinity tolerance of faba bean (*Vicia faba* L.), *Afr. J. Microbiol. Res.* 12 (17) (2018) 399–404.
- [276] S.S.K.P. Vurukonda, S. Vardharajula, M. Shrivastava, A. SkZ, Multifunctional *Pseudomonas putida* strain FBK2V from arid rhizosphere soil and its growth promotional effects on maize under drought stress, *Rhizosphere* 1 (2016) 4–13.
- [277] Y. Chen, F. Yan, Y. Chai, H. Liu, R. Kolter, R. Losick, J.H. Guo, Biocontrol of tomato wilt disease by *Bacillus subtilis* isolates from natural environments depends on conserved genes mediating biofilm formation, *Environ. Microbiol.* 15 (3) (2013) 848–864.
- [278] S. Timmusk, S.B. Kim, E. Nevo, I. Abd El Daim, B.O. Ek, J. Bergquist, L. Behers, Sfp-type PPase inactivation promotes bacterial biofilm formation and ability to enhance wheat drought tolerance, *Front. Microbiol.* 6 (2015) 387–395.
- [279] X. Lu, S.F. Liu, L. Yue, X. Zhao, Y.B. Zhang, Z.K. Xie, R.Y. Wang, EpsC involved in the encoding of exopolysaccharides produced by *Bacillus amyloliquefaciens* FZB42 act to boost the drought tolerance of Arabidopsis thaliana, *Int. J. Mol. Sci.* 19 (12) (2018) 3795–3807.
- [280] A.Y. Su, S.Q. Niu, Y.Z. Liu, A.L. He, Q. Zhao, P.W. Paré, M.F. Li, Q.Q. Han, S. Ali Khan, J.L. Zhang, Synergistic effects of *Bacillus amyloliquefaciens* (GB03) and water retaining agent on drought tolerance of perennial ryegrass, *Int. J. Mol. Sci.* 18 (12) (2017) 2651–2664.
- [281] E. Effah, J.K. Holopainen, A.C. McCormick, Potential roles of volatile organic compounds in plant competition, *Perspect. Plant Ecol. Evol. Systemat.* 38 (2019) 58–63.
- [282] B.N. Singh, A. Hidangmayum, A. Singh, S.S. Shera, P. Dwivedi, Secondary Metabolites of Plant Growth Promoting Rhizomicroorganisms, Springer, Singapore, Berlin, Germany, 2019, p. 404.
- [283] M.V. Santoro, J. Zygađlo, W. Giordano, E. Banchio, Volatile organic compounds from rhizobacteria increase biosynthesis of essential oils and growth parameters in peppermint (*Mentha piperita*), *Plant Physiol. Biochem.* 49 (10) (2011) 1177–1182.
- [284] R. Amiri, A. Nikbakht, N. Etemadi, Alleviation of drought stress on rose geranium *Pelargonium graveolens* L. Herit. in terms of antioxidant activity and secondary metabolites by mycorrhizal inoculation, *Sci. Hortic.* 197 (2015) 373–380.
- [285] K.A. El-Tarabily, K. Sivasithamparam, Potential of yeasts as biocontrol agents of soil-borne fungal plant pathogens and as plant growth promoters, *Mycoscience* 47 (1) (2006) 25–35.
- [286] A.E. Richardson, J.M. Barea, A.M. McNeill, C. Prigent-Combaret, Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms, *Plant Soil* 321 (1) (2009) 305–339.
- [287] R. Wheatley, The consequences of volatile organic compound mediated bacterial and fungal interactions, *Antonie Leeuwenhoek* 81 (2002) 357–364.
- [288] H. Calvo, I. Mendiara, E. Arias, A.P. Gracia, D. Blanco, M.E. Venturini, Antifungal activity of the volatile Organic compounds produced by *Bacillus velezensis* strains against postharvest fungal pathogens, *Postharvest Biol. Technol.* 166 (2020), 111208.
- [289] S. Asari, S. Matzén, M.A. Petersen, S. Bejai, J. Meijer, Multiple effects of *Bacillus amyloliquefaciens* volatile compounds: plant growth promotion and growth inhibition of phytopathogens, *FEMS Microbiol. Ecol.* 92 (2016) f1w070.
- [290] A. Korpi, J. Järnberg, A.L. Pasanen, Microbial volatile organic compounds, *Crit. Rev. Toxicol.* 39 (2) (2009) 139–193.
- [291] P. Wonglom, S.I. Ito, A. Sunpapao, Volatile organic compounds emitted from endophytic fungus *Trichoderma asperellum* T1 mediate antifungal activity, defense response and promote plant growth in lettuce (*Lactuca sativa*), *Fungal Ecol* 43 (2020), 1008067.

- [292] M.B. Fialho, M.H.D.D. Moraes, A.R. Tremocoldi, S.F. Pascholati, Potential of antimicrobial volatile organic compounds to control *Sclerotinia sclerotiorum* in bean seeds, *Pesqui. Agropecu. Bras.* 46 (2011) 137–142.
- [293] C.F. Ajillogba, O.O. Babalola, GC–MS analysis of volatile organic compounds from Bambara groundnut rhizobacteria and their antibacterial properties, *World J. Microbiol. Biotechnol.* 35 (6) (2019) 1–19.
- [294] 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 (3) (2004) 1017–1026.
- [295] E. Banchio, X. Xie, H. Zhang, P.W. Pare, Soil bacteria elevate essential oil accumulation and emissions in sweet basil, *J. Agric. Food Chem.* 57 (2) (2009) 653–657.
- [296] S.H. Han, S.J. Lee, J.H. Moon, K.H. Park, K.Y. Yang, B.H. Cho, K.Y. Kim, Y.W. Kim, M.C. Lee, A.J. Anderson, Y.C. Kim, GacS-dependent production of 2R, 3R-butenediol by *Pseudomonas chlororaphis* O6 is a major determinant for eliciting systemic resistance against *Erwinia carotovora* but not against *Pseudomonas syringae* pv. tabaci in tobacco, *Mol. Plant Microbe Interact.* 19 (2006) 924–930.
- [297] Y.S. Park, S. Dutta, M. Ann, J.M. Raaijmakers, K. Park, Promotion of plant growth by *Pseudomonas fluorescens* strain SS101 via novel volatile organic compounds, *Biochem. Biophys. Res. Commun.* 461 (2) (2015) 361–365.
- [298] B. Rani, Effect of Arbuscular Mycorrhiza Fungi on Biochemical Parameters in Wheat *Triticum aestivum* L. Under Drought Conditions, CGSHAU, Hisar, 2016. Doctoral dissertation.
- [299] P.P. Mirshad, J.T. Puthur, Arbuscular mycorrhizal association enhances drought tolerance potential of promising bioenergy grass *Saccharum arundinaceum* Retz, *Environ. Monit. Assess.* 188 (2016) 425.
- [300] A.A. Asrar, G.M. Abdel-Fattah, K.M. Elhindi, Improving growth, flower yield, and water relations of snapdragon *Antirrhinum majus* L. plants grown under well-watered and water-stress conditions using arbuscular mycorrhizal fungi, *Photosynthetica* 50 (2012) 305–316.
- [301] A.H. Parret, G. Schoofs, P. Proost, R. De Mot, Plant lectin-like bacteriocin from a rhizosphere-colonizing *Pseudomonas* isolate, *J. Bacteriol.* 185 (3) (2003) 897–908.
- [302] V. Ricciardi, D. Marciano, M. Sargolzaei, G. Maddalena, D. Maghradze, A. Tirelli, P. Casati, P.A. Bianco, O. Failla, D. Fracassetti, S.L. Toffolatti, From plant resistance response to the discovery of antimicrobial compounds: the role of volatile organic compounds (VOCs) in grapevine downy mildew infection, *Plant Physiol. Biochem.* 160 (2021) 294–305.
- [303] Á. Ulloa-Benítez, Y.M. Medina-Romero, R.E. Sánchez-Fernández, P. Lappe-Oliveras, G. Roque-Flores, G. Duarte Lisci, T. Herrera Suárez, M.L. Macías-Rubalcava, Phytotoxic and antimicrobial activity of volatile and semi-volatile organic compounds from the endophyte *Hypoxyylonanthochroum* strain Blaci isolated from *Bursera lancifolia* (Burseraceae), *J. Appl. Microbiol.* 121 (2) (2016) 380–400.
- [304] I. Jerković, D. Gašo-Sokac, H. Pavlović, Z. Marijanović, M. Gugić, I. Petrović, S. Kovač, Volatile organic compounds from *Centaurium erythraea* Rafn (Croatia) and the antimicrobial potential of its essential oil, *Molecules* 17 (2) (2012) 2058–2072.
- [305] R. Hernández-León, D. Rojas-Solís, M. Contreras-Pérez, M. del Carmen Orozco-Mosqueda, L.I. Macías-Rodríguez, H. Reyes-de la Cruz, E. Valencia-Cantero, G. Santoyo, Characterization of the antifungal and plant growth-promoting effects of diffusible and volatile organic compounds produced by *Pseudomonas fluorescens* strains, *Biol. Control* 81 (2015) 83–92.
- [306] H. Huang, F. Ullah, D.X. Zhou, M. Yi, Y. Zhao, Mechanisms of ROS regulation of plant development and stress responses, *Front. Plant Sci.* 10 (2019) 800–817.
- [307] T.T.H. Dat, P.T.T. Oanh, L.C.V. Cuong, L.T. Anh, L.T.H. Minh, H. Ha, L.T. Lam, P.V. Cuong, H.L.T. Anh, Pharmacological properties, volatile organic compounds, and genome sequences of bacterial endophytes from the mangrove plant *Rhizophora apiculata* Blume, *Antibiotics* 10 (12) (2021) 1491.
- [308] M.A. Devi, D. Sahoo, T.B. Singh, Y. Rajashekar, Antifungal activity and volatile organic compounds analysis of essential oils from Cymbopogon species using solid-phase microextraction-gas chromatography-mass spectrometry, *J. Agric. Food Res.* 3 (2021), 100110.
- [309] M. Stinson, D. Ezra, W.M. Hess, J. Sears, G. Strobel, An endophytic Gliocladium sp. of *Eucryphia cordifolia* producing selective volatile antimicrobial compounds, *Plant Sci.* 165 (4) (2003) 913–922.
- [310] S. Swanson, S. Gilroy, ROS in plant development, *Physiol. Plantarum* 138 (4) (2010) 384–392.
- [311] C. Mas-Bargues, C. Escrivá, M. Dromant, C. Borrás, J. Viña, Lipid peroxidation as measured by chromatographic determination of malondialdehyde. Human plasma reference values in health and disease, *Arch. Biochem. Biophys.* 709 (2021), 108941.
- [312] J. Pan, F. Peng, X. Xue, Q. You, W. Zhang, T. Wang, C. Huang, The growth promotion of two salt-tolerant plant groups with PGPR inoculation: a meta-analysis, *Sustain. Times* 11 (2) (2019), 378385.
- [313] R. Rani, V. Kumar, P. Gupta, A. Chandra, Potential use of *Solanum lycopersicum* and plant growth promoting rhizobacterial (PGPR) strains for the phytoremediation of endosulfan stressed soil, *Chem* 279 (2021), 130589.
- [314] S.Q. Wang, M.A. Jia, W.A.N.G. Meng, X.H. Wang, Y.Q. Li, C. Jie, Combined application of *Trichoderma harzianum* SH2303 and difenoconazole-plantazolin controlling Southern corn leaf blight disease caused by *Cochliobolusheterostrophus* in maize, *J. Integr. Agric.* 18 (9) (2019) 2063–2071.
- [315] C. Keswani, H. Dilnashin, H. Birla, S.P. Singh, Unravelling efficient applications of agriculturally important microorganisms for alleviation of induced inter-cellular oxidative stress in crops, *Acta Agric. Slov.* 114 (1) (2019) 121–130, <https://doi.org/10.14720/aas.2019.114.1.14>.
- [316] N.K. Denaxa, T. Damvakaris, P.A. Roussos, Antioxidant defense system in young olive plants against drought stress and mitigation of adverse effects through external application of alleviating products, *Sci. Hortic.* 259 (2020), 108812.
- [317] M. Jimenez-Perez, I.I. Morales-Manzo, F.I.T.A. Ana, A. Rodríguez-Burruero, Mitigation of drought stress in solanaceae vegetables through symbiosis with plant growth-promoting bacteria and arbuscular mycorrhizal fungi, *A review*, *Sci. J* 11 (2022) 86.
- [318] N. Bharti, D. Barnawal, Amelioration of salinity stress by PGPR: ACC deaminase and ROS scavenging enzymes activity, in: *PGPR Amelioration in Sustainable Agriculture*, Woodhead Publishing, 2019, pp. 85–106.
- [319] S. Mehmood, M.A. Muneer, M. Tahir, M.T. Javed, T. Mahmood, M.S. Afridi, N.P. Pakar, H.A. Abbasi, M.F.H. Munis, H.J. Chaudhary, Deciphering distinct biological control and growth promoting potential of multi-stress tolerant *Bacillus subtilis* PM32 for potato stem canker, *Physiol. Mol. Biol. Plants* 27 (9) (2021) 2101–2114.
- [320] T. Gaffney, L. Friedrich, B. Vernooij, D. Negrotto, G. Nye, S. Uknes, E. Ward, H. Kessmann, J. Ryals, Requirement of salicylic acid for the induction of systemic acquired resistance, *Science* 261 (5122) (1993) 754–756.
- [321] P. Kannoja, K.K. Choudhary, A.K. Srivastava, A.K. Singh, PGPR bioelicitors: induced systemic resistance (ISR) and proteomic perspective on biocontrol (Pp. 67–84, in: *PGPR Amelioration in Sustainable Agriculture*, Woodhead Publishing, 2019.
- [322] M. Meena, P. Swapnil, K. Divyanshu, S. Kumar, Y.N. Tripathi, A. Zehra, A. Marwal, R.S. Upadhyay, PGPR-mediated induction of systemic resistance and physicochemical alterations in plants against the pathogens: current perspectives, *J. Basic Microbiol.* 60 (10) (2020) 828–861.
- [323] M. Singh, D. Nagar, D.C. Kala, Plant growth promoting rhizo-bacteria (PGPR) and its role in resistance against biotic stresses in plants, *Curr. Res. Innov. Plant Pathol.* 27 (2021) 3–19.
- [324] 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 (8) (1996) 1225–1237.
- [325] M. Yuan, Y. Huang, W. Ge, Z. Jia, S. Song, L. Zhang, Y. Huang, Involvement of jasmonic acid, ethylene and salicylic acid signaling pathways behind the systemic resistance induced by *Trichoderma longibrachiatum* H9 in cucumber, *BMC Genom.* 20 (1) (2019) 1–13.
- [326] A. Samarasinghe, E. Roumeliotis, P. Ntasiou, G. Karaoglaniadis, *Bacillus subtilis* MBI600 promotes growth of tomato plants and induces systemic resistance contributing to the control of soilborne pathogens, *Plants* 10 (6) (2021) 1113.
- [327] G. Gupta, S.S. Parihar, N.K. Ahirwar, S.K. Snehi, V. Singh, Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture, *J. Microb. Biochem. Technol.* 7 (2) (2015) 96–102.
- [328] C.K. Jha, M. Saraf, Plant growth promoting rhizobacteria (PGPR), *J. Agric. Res.* 5 (2015) 108–119.
- [329] M. Ahemad, M. Kibret, Mechanisms and applications of plant growth promoting rhizobacteria: current perspective, *J. King Saud Univ. Sci.* 26 (2014) 1–20.
- [330] R. Backer, J.S. Rokem, G. Ilangumaran, J. Lamont, D. Praslickova, E. Ricci, S. Subramanian, D.L. Smith, Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture, *Front. Plant Sci.* 9 (2018) 1473.



- [331] S. Spaepen, J. Vanderleyden, Auxin and plant-microbe interactions, *Perspect. Biol.* 3 (4) (2011) a001438.
- [332] M. Ruzzi, R. Aroca, Plant growth-promoting rhizobacteria act as biostimulants in horticulture, *Sci. Hortic.* 196 (2015) 124–134.
- [333] R. Çakmakçı, G. Mosber, A.H. Milton, F. Alatürk, B. Ali, The effect of auxin and auxin-producing bacteria on the growth, essential oil yield, and composition in medicinal and aromatic plants, *Curr. Microbiol.* 77 (4) (2020) 564–577.
- [334] S.M. Kang, G.J. Joo, M. Hamayun, C.I. Na, D.H. Shin, H.Y. Kim, J.K. Hong, I.J. Lee, Gibberellin production and phosphate solubilization by newly isolated strain of *Acinetobacter calcoaceticus* and its effect on plant growth, *Biotechnol. Lett.* 31 (2) (2009) 277–281.
- [335] J. Vacheron, G. Desbrosses, M.L. Bouffaud, B. Touraine, Y. Moëgne-Loccoz, D. Muller, L. Legendre, F. Wisniewski-Dyé, C. Prigent-Combaret, Plant growth-promoting rhizobacteria and root system functioning, *Front. Plant Sci.* 4 (2013) 356–367.
- [336] M. Fatma, M. Asgher, N. Iqbal, F. Rasheed, Z. Sehar, A. Sofo, N.A. Khan, Ethylene signaling under stressful environments: analyzing collaborative knowledge, *Plants* 11 (17) (2022) 2211–2227.
- [337] R.L. Rubin, K.J. van Groenigen, B.A. Hungate, Plant growth promoting rhizobacteria are more effective under drought: a meta-analysis, *Plant Soil* 416 (1) (2017) 309–323.
- [338] S.M. Nadeem, M. Ahmad, Z.A. Zahir, A. Javaid, M. Ashraf, The role of mycorrhizae and plant growth promoting rhizobacteria (PGPR) in improving crop productivity under stressful environments, *Biotechnol. Adv.* 32 (2) (2014) 429–448.
- [339] B.R. Glick, Bacteria with ACC deaminase can promote plant growth and help to feed the world, *Microbiol. Res.* 169 (1) (2014) 30–39.
- [340] Z. Heydariyan, M. Yu, M. Gruber, B.R. Glick, R. Zhou, D.D. Hegedus, Inoculation of soil with plant growth promoting bacteria producing 1-aminocyclopropane-1-carboxylate deaminase or expression of the corresponding *acdS* gene in transgenic plants increases salinity tolerance in *Camelina sativa*, *Front. Microbiol.* 7 (2016) 1966.
- [341] P. Vejan, R. Abdullah, T. Khadiran, S. Ismail, B. Nasrulhaq, Role of plant growth promoting rhizobacteria in agricultural sustainability—a review, *Molecules* 21 (5) (2016) 573, <https://doi.org/10.3390/molecules21050573>.
- [342] C.H. Wu, S.M. Bernard, G.L. Andersen, W. Chen, Developing microbe–plant interactions for applications in plant-growth promotion and disease control, production of useful compounds, remediation and carbon sequestration, *Microb. Biotechnol.* 2 (4) (2009) 428–440.
- [343] S.A. Akladios, S.M. Abbas, Application of *Trichoderma harziunum* T22 as a biofertilizer supporting maize growth, *Afr. J. Biotechnol.* 11 (35) (2012) 8672–8683.
- [344] A.H. Molla, M. Haque, A. Haque, G. Ilias, *Trichoderma*-enriched biofertilizer enhances production and nutritional quality of tomato (*Lycopersicon esculentum* Mill.) and minimizes NPK fertilizer use, *Agric. Res.* 1 (3) (2012) 265–272.
- [345] E. Shakeri, S.A.M. Modarres-Sanavy, M. Amini Dehaghi, S.A. Tabatabaei, M. Moradi-Ghahderjani, Improvement of yield, yield components and oil quality in sesame (*Sesamum indicum* L.) by N-fixing bacteria fertilizers and urea, *Arch. Agron Soil Sci.* 62 (4) (2016) 547–560.
- [346] A. Nosheen, A. Bano, H. Yasmin, R. Keyani, R. Habib, S.T. Shah, R. Naz, Protein quantity and quality of safflower seed improved by NP fertilizer and Rhizobacteria (*Azospirillum* and *Azotobacter* spp.), *Front. Plant Sci.* 7 (2016) 104–115.
- [347] D.D. Niu, Y. Zheng, L. Zheng, C.H. Jiang, D.M. Zhou, J.H. Guo, Application of PSX biocontrol preparation confers root-knot nematode management and increased fruit quality in tomato under field conditions, *Biocontrol Sci.* 26 (2) (2016) 174–180.
- [348] I. Ajjawi, J. Verruto, M. Aqwi, L.B. Soriaga, J. Coppersmith, K. Kwok, L. Peach, E. Orchard, R. Kalb, W. Xu, Lipid production in *Nannochloropsis gaditana* is doubled by decreasing expression of a single transcriptional regulator, *Nat. Biotechnol.* 35 (7) (2017) 647–652.
- [349] J.S. Rokem, C.L. Greenblatt, Making biofuels competitive: the limitations of biology for fuel production, *JSM Microbiology* 3 (2) (2015) 1023–1037.
- [350] R.C. Kuhad, R. Gupta, A. Singh, Microbial cellulases and their industrial applications, *Enzym. Res.* (2011) 1–10, <https://doi.org/10.4061/2011/280696>. Article ID 280696.
- [351] L.R. Lynd, M.S. Laser, D. Bransby, B.E. Dale, B. Davison, R. Hamilton, M. Himmel, M. Keller, J.D. McMillan, J. Sheehan, How biotech can transform biofuels, *Nat. Biotechnol.* 26 (2) (2008) 169–172.
- [352] J.P. McCalmont, A. Hastings, N.P. McNamara, G.M. Richter, P. Robson, I.S. Donnison, J. Clifton-Brown, Environmental costs and benefits of growing *Miscanthus* for bioenergy in the UK, *Global Environ. Change* 9 (3) (2017) 489–507.
- [353] D.L. Smith, D. Praslickova, G. Ilangumaran, Inter-organismal signaling and management of the phytomicrobiome, *Front. Plant Sci.* 6 (2015) 722.
- [354] K. Ker, P. Seguin, B.T. Driscoll, J.W. Fyles, D.L. Smith, Switchgrass establishment and seeding year production can be improved by inoculation with rhizosphere endophytes, *Biomass Bioenerg. Res.* 47 (2012) 295–301.
- [355] S. Arunachalam, T. Schwinghameer, P. Dutilleul, D.L. Smith, Multi-year effects of biochar, lipo-chitoooligosaccharide, thuricin 17, and experimental bio-fertilizer for switchgrass, *Agron. J.* 110 (1) (2018) 77–84.
- [356] M. Evangelou, A. Deram, Phytomanagement: a realistic approach to soil remediating phytotechnologies with new challenges for plant science, *Int. J. Plant Biol.* 2 (2014) 1023–1036.
- [357] S.L. Velivelli, P. De Vos, P. Kromann, S. Declerck, B.D. Prestwich, Biological control agents: from field to market, problems, and challenges, *Trends Biotechnol.* 32 (10) (2014) 493–496.
- [358] P. Vejan, R. Abdullah, T. Khadiran, S. Ismail, A. Nasrulhaq Boyce, Role of plant growth promoting rhizobacteria in agricultural sustainability a review, *Molecules* 21 (2016) 573.
- [359] P. Shi, J. Zhang, X. Li, L. Zhou, H. Luo, L. Wang, Y. Zhang, M. Chou, G. Wei, Multiple metabolic phenotypes as screening criteria are correlated with the plant growth-promoting ability of rhizobacterial isolates, *Front. Microbiol.* 12 (2022) 747–762, <https://doi.org/10.3389/fmicb.2021.747982>.
- [360] A.A. Adedeji, M.M. Häggblom, O.O. Babalola, Sustainable agriculture in Africa: plant growth-promoting rhizobacteria (PGPR) to the rescue, *Sci. Afr.* 9 (2020), e00492.
- [361] S. Timmus, L. Behers, J. Muthoni, A. Muraya, A.-C. Aronsson, Perspectives and challenges of microbial application for crop improvement, *Front. Plant Sci.* 8 (2017).
- [362] C.V. Amaya-Gómez, M. Porcel, L. Mesa-Garriga, M.I. Gómez-Álvarez, A Framework for the Selection of plant growth-promoting rhizobacteria based on bacterial competence mechanisms, *Appl. Environ. Microbiol.* 86 (2020) e00760, 20.
- [363] C. Dunne, Y. Moëgne-Loccoz, J. McCarthy, P. Higgins, J. Powell, D. Dowling, F. O'gara, Combining proteolytic and phloroglucinol-producing bacteria for improved biocontrol of Pythium-mediated damping-off of sugar beet, *Plant Pathol.* 47 (3) (1998) 299–307.
- [364] K. Pal, K. Tilak, A. Saxena, R. Dey, C. Singh, Suppression of maize root diseases caused by *Macrophomina phaseolina*, *Fusarium moniliforme* and *Fusarium graminearum* by plant growth promoting rhizobacteria, *Microbiol. Res.* 156 (3) (2001) 209–223.
- [365] N. Konappa, S. Krishnamurthy, U.C. Arakere, S. Chowdappa, N.S. Ramachandrappa, Efficacy of indigenous plant growth-promoting rhizobacteria and *Trichoderma* strains in eliciting resistance against bacterial wilt in a tomato, *J. Biol. Pest. Control.* 30 (1) (2020) 1–13.
- [366] K. Jetiyanon, Defensive-related enzyme response in plants treated with a mixture of *Bacillus* strains (IN937a and IN937b) against different pathogens, *Biol. Control* 42 (2) (2007) 178–185.
- [367] B. Wang, S. An, C. Liang, Y. Liu, Y. Kuz'yakov, Microbial necromass as the source of soil organic carbon in global ecosystems, *Soil Biol. Biochem.* 162 (2021), 108422.
- [368] H. Wang, R. Liu, M.P. You, M.J. Barbetti, Y. Chen, Pathogen biocontrol using plant growth-promoting bacteria (PGPR): role of bacterial diversity, *Microorganisms* 9 (2021) 198.
- [369] H. Kumar, R. Dubey, D. Maheshwari, Seed-coating fenugreek with *Burkholderia* rhizobacteria enhances yield in field trials and can combat *Fusarium* wilt, *Rhizosphere* 3 (2017) 92–99.
- [370] O.O. Babalola, Ethylene quantification in three rhizobacterial isolates from *Striga hermonthica*-infested maize and sorghum, *Egypt. Acad. J. Biol. Sci.* 12 (2010) 1–5.
- [371] M.D.C. Orozco-Mosqueda, A.E. Fadji, O.O. Babalola, B.R.A.S. Glick, G. Santoyo, Rhizobiome engineering: unveiling complex rhizosphere interactions to enhance plant growth and health, *Microbiol. Res.* 263 (2022), 127137.

- [372] M. Sumayo, M.S. Hahm, S.Y. Ghim, Determinants of plant growth-promoting *Ochrobactrum lupini* KUDC1013 involved in induction of systemic resistance against *Pectobacterium carotovorum* subsp. *carotovorum* in tobacco leaves, *Plant Pathol. J.* 29 (2) (2013) 174.
- [373] M. Kamle, R. Borah, H. Bora, A.K. Jaiswal, R.K. Singh, P. Kumar, Systemic acquired resistance (SAR) and induced systemic resistance (ISR): role and mechanism of action against phytopathogens, in: *Fungal Biotechnology and Bioengineering*, Springer, Cham, 2020, pp. 457–470.
- [374] M.R. Park, Y.C. Kim, S. Lee, I.S. Kim, Identification of an ISR-related metabolite produced by rhizobacterium *Klebsiella oxytoca*C1036 active against soft-rot disease pathogen in tobacco, *Pest Manag. Sci.* 65 (10) (2009) 1114–1117.
- [375] M. Yassin, J. Ton, S.A. Rolfe, T.A. Valentine, M. Cromey, N. Holden, A.C. Newton, The rise, fall and resurrection of chemical-induced resistance agents, *Pest Manag. Sci.* 77 (9) (2021) 3900–3909.
- [376] R. Peyraud, U. Dubiella, A. Barbacci, S. Genin, S. Raffaele, D. Roby, Advances on plant–pathogen interactions from molecular toward systems biology perspectives, *Plant J.* 90 (4) (2017) 720–737.
- [377] L. Urban, F. Lauri, D. Ben Hdech, J. Aarouf, Prospects for increasing the efficacy of plant resistance inducers stimulating salicylic acid, *Agro Sur* 12 (12) (2022) 3151.
- [378] G.E. Vallad, R.M. Goodman, Systemic acquired resistance and induced systemic resistance in conventional agriculture, *Crop Sci.* 44 (2004) 1920–1934, <https://doi.org/10.2135/cropsci2004.1920>.
- [379] P. Kumari, M. Meena, P. Gupta, M.K. Dubey, G. Nath, R.S. Upadhyay, Plant growth promoting rhizobacteria and their biopriming for growth promotion in mung bean (*Vigna radiata* (L.) R. Wilczek), *Biocatal. Agric. Biotechnol.* 16 (2018) 163–171.
- [380] P. Kumari, M. Meena, R.S. Upadhyay, Characterization of plant growth promoting rhizobacteria (PGPR) isolated from the rhizosphere of *Vigna radiata* (mung bean), *Biocatal. Agric. Biotechnol.* 16 (2018) 155–162.
- [381] J.A. Lucas, J. Garcia-Cristobal, A. Bonilla, B. Ramos, J. Gutierrez-Mañero, Beneficial rhizobacteria from rice rhizosphere confers high protection against biotic and abiotic stress inducing systemic resistance in rice seedlings, *Plant Physiol. Biochem.* 82 (2014) 44–53.
- [382] A. Singh, A.P. Singh, S.K. Singh, S. Rai, D. Kumar, Impact of addition of biochar along with Pgp on rice yield, availability of nutrients and their uptake in alluvial soil, *J. Pure Appl. Microbiol.* 10 (2016) 2181–2188.
- [383] A. Mishra, S.P. Singh, S. Mahfooz, A. Bhattacharya, N. Mishra, P.A. Shirke, C.S. Nautiyal, Bacterial endophytes modulates the withanolide biosynthetic pathway and physiological performance in *Withaniasomnifera* under biotic stress, *Microbiol. Res.* 212–213 (2018) 17–28.
- [384] S. Amirsadeghi, C.A. Robson, G.C. Vanlerberghe, The role of the mitochondrion in plant responses to biotic stress, *Physiol. Plantarum* 129 (2007) 253–266.
- [385] A. Zehra, N.A. Raytekar, M. Meena, P. Swapnil, Efficiency of microbial bio-agents as elicitors in plant defense mechanism under biotic stress: a review, *Curr. Res. Microb. Sci.* 2 (2021), 100054.
- [386] M. Thakur, B.S. Sohal, Role of elicitors in inducing resistance in plants against pathogen infection: a review, *ISRN Biochem* (2013) 1–10.
- [387] K. Ramirez-Estrada, H. Vidal-Limon, D. Hidalgo, E. Moyano, M. Golenioswki, R.M. Cusidó, J. Palazon, Elicitation, an effective strategy for the biotechnological production of bioactive high-added value compounds in plant cell factories, *Molecules* 21 (2016) 182.
- [388] Y. Shen, J. Li, J. Xiang, J. Wang, K. Yin, Q. Liu, Isolation and identification of a novel protein elicitor from a *Bacillus subtilis* strain BU412, *Amb. Express* 9 (2019) 117–126.
- [389] D.C. Wang, C.H. Jiang, L.N. Zhang, L. Chen, X.Y. Zhang, J.H. Guo, Biofilms positively contribute to *Bacillus amyloliquefaciens* 54-induced drought tolerance in tomato plants, *Int. J. Mol. Sci.* 20 (24) (2019) 6271.
- [390] C. Keswani, H.B. Singh, C. García-Estrada, J. Caradus, Y.W. He, S. Mezaache-Aichour, T.R. Glare, R. Borriss, E. Sansinenea, Antimicrobial secondary metabolites from agriculturally important bacteria as next-generation pesticides, *Appl. Microbiol. Biotechnol.* 104 (2020) 1013–1034, <https://doi.org/10.1007/s00253-019-10300-8>.