Bioinoculants for Bioremediation Applications and Disease Resistance: Innovative Perspectives

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Abstract Soil microbial species that act as PGPR or bioinoculants have the capability of improving plant health and promoting its growth. They facilitate plants for uptake nutrients from their surroundings. They provide resistivity to pathogenic pests and also play many roles in the bioremediation process. Bioremediation is the biological approach for the elimination of toxic contaminants by the approach of beneficial microbes. By the consortium of beneficial microbes and plant, a large number of heavy metal and organic contaminants can be controlled. With this advancement of bioremediation, microbial species that act as bioinoculants also help in the enhancement of induced systemic resistance (ISR) and their consortium triggers it by controlling SA, JA, ET and hormonal signaling pathways. Here, this review discusses the progress made on these areas and how the beneficial microbes that act as bioinoculants towards triggering bioremediation and ISR mechanism.

Keywords Bioinoculants · Induced systemic resistance (ISR) · Bioremediation · Phytohormones · Signaling pathway

Introduction

Microbial species that act as bioinoculants have the capability of promoting plant growth by colonizing within the plant root system. They show the various type of relationship viz. free-living or symbiosis [5]. Particularly in the soil, plants play a crucial role in maintaining complex food web by utilizing useful microbes. Various principle and mechanism are studied for a plant-bioinoculants relationship. In this type of relationship, the root system of the plant is the chief host due to deposition of photosynthetic carbon in plant roots. The supreme rich zone is the rhizospheric zone in the ecosystem. PGPR (Plant growth promoting rhizobacteria) and PGPF (Plant growth promoting fungi) are the most beneficial and useful microbiota for the health improvement of plants. Basically, those PGPR that acts as bioinoculant performs their function in different ways: by the uptake of nutrients and lessening or reducing plant from diseases [16, 43, 45]. The increase in the modernization leads to fateful effects on the world by the discharge of toxic wastes. According to the EPA report in 2004, more than 35,000 contaminated sites present in developed countries like the U.S. and in European countries. Hence, for the elimination of pollutants in soil, mostly chemical, physical and biological methods are used.

Bioremediation is the beneficial biological process which is used for the removal and reduction of toxic pollutants from the contaminated soil and environment [11, 12, 50]. This process is convenient, cost-effective and causes complete degradation of toxic pollutants. The widespread use of bioinoculants for the remediation process shows much potential for the reduction of toxic pollutants by enhancing controlled studies. Various toxic contaminants like PAHs (polycyclic aromatic hydrocarbons), PCBs (Polychlorinated Biphenyls), PCTs (polychlorinated

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terphenyls), PCE (perchloroethylene), atrazine and TPHs (trichloroethylene) can exist for a long time and cause a lot of threat for a living being [51]. Hence, for their bioremediation, bioinoculants that are used as PGPR are used. In addition to the bioremediation process, bioinoculants also improve the health of plants by enhancing their defense system by the mechanism of ISR (Induced Systemic Resistance) [40, 42]. This mechanism is activated by JA (Jasmonic acid)/ET (ethylene) and SA (Salicylic acid), dependent-independent pathways. It is reported that SA-dependent pathways are enhanced by the establishment and activation of PR proteins [21, 59]. *P. fluorescens* can induce resistance against several pathogens viz. *Spo-doptera exigua* and *P. syringae*. Many molecular and hormonal pathways are reported for the defense stimulation process. SA (Salicylic acid), ABA (Absciscic acid), ET (ethylene), GA (Gibberellic acid) and JA (Jasmonic acid), Volatile organic compounds (VOC's) and phytohormones play much better coordination signaling pathways during stress condition and against the various pests [54]. These phytohormones trigger ISR and mediate another symbiotic process by the interaction between plants and beneficial microbes [22, 30]. In addition to this, the tri-trophic interaction level also has been studied. This present review describes both the application of bioinoculants, i.e., the bioremediation process and the hormonal mechanism implicated in ISR defense mechanism by the beneficial microbes.

Phytohormonal Effects in Induced Systemic Resistance

Phytohormones such as ethylene, salicylic acid, JA, cytokinins, IAA (Indole acetic acid), gibberellins and absciscic acid are the main phytohormones for regulating ISR throughout tri-trophic interactions [15, 23, 47]. These phytohormonal dependent pathways can control a lot of defense response in various ways. JA signaling is the key ISR pathway which is associated with rhizospheric microbes against many insect pests. ET and JA dependent genes, PDF 1.2, HEL and LOX2 enhance the ISR mechanism by the treatment of rhizobacteria against insect pests in *Arabidopsis* roots [38]. Rhizobacterial colonization of *P. simiae* evokes privileged expression of ET/JA dependent signaling and cause ISR activation. PGPR enhances the level of resistance and JA (defense associated and octadecanoid-derived phytohormone) by root colonization in cotton plants. By using various mechanisms, *B. subtilis* induces resistance against whitefly insect in *Solanum lycopersicum* by the expression of JA dependent genes viz. proteinase and protease inhibitor encoding genes and JA independent genes viz. terpenoid and photosynthetic genes

[36]. Root colonization by *Pseudomonas fluorescens* increased the weakness of *Myzus persicae* (phloem-feeding) by the expression of PDF1.2 and LOX2. These studies demonstrate that various rhizobial species including *Pseudomonas* and *Bacillus* have dissimilar effects against insect pests. Most of the rhizobial strains assist ISR through ET and JA dependent pathways, but *P. fluorescens* facilitate ISR by SA dependent pathway. It is also reported that mechanism triggered by PGPR dependent on both SA and ET/JA signaling pathways. It is reported that MAMPs (microbe-associated molecular pattern) of various useful microbes predictable by phytoceptors that leads to specific hormonal signals that produced in plant roots. Molecular pattern of useful microbes like secondary metabolites, flagellin and LPS can activate immunity and phytohormonal signals that are triggered by MAMPs [42, 44]. Expression of the defense-associated genes LOXF and LOXD are enhanced by *B. amyloliquefaciens* for the induction of ISR in tomato plants by the production of lipopeptide. It is reported many other endophytic lipopeptide producing strains of *B. amyloliquefaciens* like Blu-v2 that helps in the induction of ISR against armyworms pest. ISR expression against insect pest requires receptiveness to the ET/JA and SA signaling pathways which depend upon 'non-expressor of pathogenesis-related genes1'. Organization of various signal within plant system activate ISR in leaves by concurrently activation of ET, SA and JA dependent signaling pathways. This type of signaling pathway ahead of the expression of genes that encodes NPR1 for ISR against pathogens (shown in Fig. 1). Additional studies are required for the clarification of MAMPs

Fig. 1 Signaling pathway ahead of the expression of genes that encodes NPR1 by ISR against pathogens

that affect phytohormonal signals. Moreover, phytohormones produced by beneficial microbes also stimulate plant cell division and also their growth under environmental stress condition [10]. The phytohormonal activity of bioinoculant during stress condition is shown in Table 1.

Specific strains like *B. subtilis*, *B. amyloliquefaciens*, *B. pasteurii*, *B. pumilus*, *B. mycoides*, *B. cereus* and *Trichoderma* bring out the significant reduction of various disease by inducing systemic resistance [6]. A snapshot of enhanced defense strategies of *Trichoderma* induced resistance is shown in Fig. 2. It has been reported that beneficial microbial inoculants protect plants against bacterial and leaf-spotting fungal pathogens, root-knot nematodes, blue mold, damping off and systemic viruses [27]. Microtitre plate assays developed to find out elicitation of ISR by *Bacillus* and compared it with the results of pot trials in the greenhouse. *Peronospora tabacina* that cause blue mold of tobacco has been removed by applying *Bacillus* spp. [1]. Actinobacteria also act as bioinoculants and colonizing the rhizospheric roots of leguminous plants [19, 46]. *Micromonospora* strain of Actinobacteria isolated from root nodules of Alfalfa promotes plant growth by inducing plant resistance. By in-vitro antagonistic assay, it was reported that *Micromonospora* strain had an inhibitory effect against the pathogenic fungal strain by producing antitumorals substances and enzymes like proteases, chitinases and lytic enzyme. Secondary metabolites produced by *Actinobacteria* also had an antibiotic effect against pathogenic fungi [19]. Rhizobial inoculants induce a different kind of defense mechanism against pathogenic bacteria, viruses and fungi. Induce systemic resistance (ISR) utilizes phytohormones (ethylene, salicylic acid and jasmonic acid) and organic acid in plants signaling and stimulates the host plant defense response against a variety of plant pathogens [4, 44]. The response of bioinoculants to the ISR is felt by the enhanced mechanical and physical

strength of the cell wall and their biochemical and physical reaction to abiotic and biotic stress. ISR could be triggered by several bacterial compounds like lipopolysaccharides, siderophores production, salicylic acid, N-acyl homoserine lactone, and antibiotics [8, 48, 49]. Microbes involved in ISR are *Pseudomonas* and *Bacillus pumilus*. Zehnder reported that bioinoculant had improved the ISR against *Colletotrichum lagenarium*, *Pseudomonas syringae* and *Erwinia tracheiphila* that causes anthrax in cucumber, angular leaf spot and bacterial wilt [57].

Bioinoculants Activity Towards Bioremediation

Microbes that are used as bioinoculants enhance the degradation of toxic contaminants and pesticides present in soil [53, 56]. Even though, plant growth promoting rhizobial species were earliest used for the control of plant growth and diseases. They convert toxic organic compounds into harmless compounds. Microbial species have the capability of degrading both mineralize organic compounds and inorganic compounds by a consortium with plants. Therefore, the knowledge of effectual pathways for the mineralization and degradation of toxic organic compounds can play a key role nearby future. Thus far, microbes with the capability of degrading various organic compounds like PCBs (polychlorinated biphenyls) have been isolated from different places and also their encoding genes pathways have been studied. Through enzymatic activity, microbes can effectively remove contaminants such as TPHs (Total petroleum hydrocarbons), Polychlorinated biphenyls, Zinc, Lead and organophosphates, organochlorines and carbamates [41, 49]. Toxic contaminants degradation capabilities of some notable bioinoculants are described in Table 2. Fungi used as bioinoculants such as *Agrocybe semiorbicularis*, *Phanerochaete*

Table 1 Phytohormonal activity of bioinoculant towards stress condition

Bioinoculants	Plant species	Effect	References
<i>Azospirillum</i> sp.	<i>Triticum aestivum</i>	Increased uptake of nutrients and water under drought stress and lateral root formation	[2]
<i>B. subtilis</i>	<i>Platycladus orientalis</i>	Increased also cytokinins production in shoots	[26]
<i>B. thuringiensis</i>	<i>Lavandula dentate</i>	Decreased ascorbate peroxidase, glutathione reductase and IAA production	[28]
<i>R. leguminosarum</i>	<i>Triticum aestivum</i>	Consortia produced IAA and improved biomass and drought tolerance	[20]
<i>P. putida</i>	<i>Glycine max</i>	Increased secretion of gibberellin that improved plant growth	[25]
<i>P. brassicacearum</i>	<i>Arabidopsis thaliana</i>	Secretes abscisic acid content that results in decreased leaf transpiration	[57]
<i>B. licheniformis</i>	<i>Piper nigrum</i>	Expressed genes i.e. VA, Cadhn, sHSP and CaPR-10	[31]
<i>Bacillus thuringiensis</i> AZP2	<i>Triticum aestivum</i>	Higher photosynthesis and reduction of volatile organic compounds	[32]

Fig. 2 A snapshot of enhanced defense strategies of *Trichoderma* induced systemic resistance

Table 2 Toxic contaminants degrading capabilities of some notable bioinoculants

Bioinoculants	Plant	Contaminant	Bioinoculants role	References
<i>Pseudomonas putida</i> (PML2)	<i>Arabidopsis thaliana</i>	Polychlorinated biphenyls	1. Degradation of PCBs 2. Utilization of secondary metabolites of plants	[34]
<i>Azospirillum lipoferum</i> and <i>Azospirillum brasilense</i>	<i>Triticum aestivum</i>	Crude oil	Enhancing the development of wheat root system and level of oil degradation	[39]
<i>Enterobacter cloacae</i>	<i>Festuca arundinacea</i>	TPHs (Total petroleum hydrocarbons)	Promotion of plant growth in the presence of TPHs	[13]
<i>Pseudomonas fluorescens</i>	(<i>Medicago sativa</i>) Alfalfa	PCBs (Polychlorinated biphenyls)	metabolized PCBs with bph gene	[52]
<i>Mesorhizobium huakuii</i>	<i>Astragalus sinicus</i>	Cadmium	Expression of PCSAtgene	[53]
<i>Azotobacter chroococcum</i>	<i>Brassica juncea</i>	Zinc and Lead	Stimulation of plant growth	[35]
<i>Bacillus subtilis</i>	<i>Brassica juncea</i> (Indian Mustard)	Nickel	Ni accumulation	[1]
<i>Kluyvera ascorbata</i>	<i>Brassica juncea</i>	Lead and Nickel	Plant growth inhibition due to heavy metals	[35]

chrysosporium, *Phanerochaete sordida*, *Auricularia auricular*, *Hypholoma fasciculata*, *Coriolus versicolor*, *Pleurotus ostreatus*, and *Cyathus bulleri* have been reported to degrade a wide range of pesticide groups like lindane, phenylurea, phenylamide, chlorinated, triazine and organophosphorus compounds. It was reported that when *Burkholderia cepacia* PCL3, immobilized on a corn cob,

resulted in 94.5% removal of carbofuran [14, 43, 44]. *Serratia marcescens* DT-1P degraded 15 ppm of DDT and their further increase in concentration to 45 ppm resulted in complete loss of the degradative capacity of *S. marcescens* DT-1P [9, 36 37].

A large number of plants that can accumulate and tolerate heavy metals concentration are described as

hyperaccumulators. Due to the sequestration and high sensitivity ability of microbes, heavy metals and organic compounds are used for the bioremediation process. Microbial species including PGPR have been proved more effective for removal of contaminants. These microbial species facilitate the growth of plants by degradation of heavy metals. The consortium of PGPR increased the degradation of toxic organic pollutants like creosote and aromatic hydrocarbon by the enhancement of plant survival and germination in contaminated soil. It was reported that remediation technology for the TPHs (petroleum hydrocarbons) is not so effective. Hence, the consortium of PGPR and the contaminant degrading of a specific strain of bacterial species were found more effectual. Recently, it is reported that for the degradation process, the MPPS (multi-process phytoremediation system) was developed [44, 55]. In this system, both specific pollutant-degrading bacteria and PGPR used for the treatment of TPHs and this specific strain is selected according to the contaminants properties. These strains easily and fastly metabolize these pollutants and help in plant growth promotion by enhancing the tolerance capability to pollutants.

Rhizosphere Metabolomics-Driven and Genetically Engineered Approach

As discussed above, rhizobial species that play key role in the mineralization and degradation of organic compounds but their metabolic efficiency is not very high. This may be due to less solubility, high pressure and little microbial biomass. For this problem, plant exudates are employed to enhance microbial degradation. While PCB-degrading microbe that acts as PGPR are found everywhere, but most of them are not efficient for the degradation of PCBs due to lack of underneath nutrients. It has been reported that various plants have the capability of releasing structural analogs of Polyaromatic hydrocarbons, such as phenol for the promotion of the growth of PAHs degrading-microbes. The approach for enhancing microbial biomass via secondary metabolites that are discharged by plants [34]. By the foundation of *Pseudomonas*-*Arabidopsis* spp. rhizospheric model, secondary metabolites were discharged for the establishment of that rhizosphere that are specific to rhizobial strain for metabolizing phenylpropanoids. By using genetic-engineering methods, characteristics for using secondary metabolites by pollutant degrading were also introduced [3, 17, 29]. It has been shown that switchgrass and canarygrass degraded Aroclor 1248 (type of PCB) by enhancing the activity of microbial dehydrogenase. Some researchers reported that various bacterial species are inoculated into rhizosphere for the degradation of pesticides and chlorobenzoates [33, 58]. But their

mechanism of degrading is not defined. *P. savastanoi* and *Pseudomonas aeruginosa* degraded various types of toxic compounds such as 2, 5-dichlorobenzoic acid, 2, 3-dichlorobenzoic acid and 2-chlorobenzoic acid by enhancing their inoculation in *Elymus dauricus* (white rye). It is also found that bioinoculants that have the capability of degrading 3CBA can also have the degradation power of 2CBA and cause no effect on 25diCBA and 23diCBA [24]. By this type of degradation capability, several pathways can be studied. Also, when two or more bacterial strain was inoculated in hydroponic system of plants, then no degradation of contaminants was seen. Hence, it was summarized that phytoremediation of toxic contaminants only affected by the rhizospheric community present in soil. The rhizospheric community shows much potential for the bioremediation of contaminants. With the advancement of mol-bio techniques, genetically-engineered rhizobial strain and the contaminant-degrading gene are formed for the conduction of bioremediation in rhizosphere. For toxic pollutants like PCBs and TCE, the molecular mechanism by genetically engineered rhizobial species has been understood [47]. The selection of appropriate strain for inoculation and gene recombination in the rhizosphere is a vital problem. The subsequent criteria for their selection are considered as (1) Strain must be insensitive or tolerant to pollutant contaminant; (2) strain has a stability nature during expression. Rather than these criteria some other things are also considered. It has been shown that expression of *bph* gene in *Pseudomonas fluorescens* was lesser in a parental strain that restricted the ability for the degradation of PCBs but grows on biphenyl. Hence, the transcription rate of degrading biphenyl activity has been enhanced by changing the promoter region of genes. The endophytic bacteria were genetically engineered for the improvement of the phytoremediation process of volatile, water-soluble and organic pollutants. This type of engineered approach showed much improvement in the degradation of volatile compounds. Phytochelatins (PCs) and metallothioneins (MTs) are natural peptides that show high-affinity binding with heavy metals. Phytochelatins has more binding affinity than metallothioneins towards heavy metals [7]. For phytochelatin synthase, *Arabidopsis thaliana* gene was introduced into *Mesorhizobium huakuii* and then a mutual symbiosis was established between *Astragalus sinicus* and *Mesorhizobium huakuii*. This expressed gene showed the production of PCs and the accumulation of CD2+, under the regulation of specific promoter. Different type of rhizobacteria can be utilized for the remediation process of contaminant soil under legume-rhizobial symbiosis [18].

Conclusion and Future Perspectives

The recent approaches of the interaction between plants and bioinoculants proved an achievement for the successive studies. ISR mechanism and the bioremediation process that is shown by the beneficial microbes play a key role in the defense response and removal of pollutants from plants and soil. Several pathways are activated by the biosynthesis of defense linked compounds, volatile organic compounds, secondary metabolites and enzymes. These pathways are activated by useful microbes when they show the root colonization process. The chemicals that are synthesized by metabolic pathways act as inhibitors for pathogens. The mutual role of specific strain and plant effectively remove pollutants from soil. Genetic-engineering technologies proved a better extension for the bioremediation. This review provided the latest information for the bioremediation and defense system of plants by ISR. The selection of advantageous soil microorganisms, that acts as bioinoculants manage the pathogen more effectively. This advancement adds a sustainable control on the control of pathogens and defense mechanism by ISR.

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