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REVIEW ARTICLE OPEN ACCESS

Phytostimulating Potential of Endophytic Bacteria from Ethnomedicinal Plants of North-East Indian Himalayan Region

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Abstract

North-East Indian Himalayan Region has a humid subtropical climate having diverse ecosystems. The majority of the population of the region depends on agriculture for sustainable livelihood. However, it can produce only 1.5% of the country's food grains, thereby importing from other parts of the country for consumption. To feed the increase in the population of the region, there is an urgent need to augment the agricultural and allied products to sustain the population and uplift the economic conditions. Plant beneficial endophytes isolated from ethnomedicinal plants of North-East India play an important role as a plant growth promoter by the production of phytohormones, solubilization and mobilization of mineral nutrients. It also indirectly promotes growth by protecting the plants from diseases through the production of antibiotics, enzymes and volatile compounds. The bacteria also have the potential to induce systemic resistance against various abiotic stresses. Since the region has various agro-climatic conditions, the plants are continuously affected by abiotic stress particularly, acidity, drought and waterlogging, there is a need to explore the indigenous endophytes that can mitigate the stress and enhance the sustainable development of agricultural products.

Keywords: Medicinal plants, endophytic bacteria, antifungal, plant growth promotion, abiotic stress

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INTRODUCTION

North-East Indian Himalayan Region (NEIHR), with a landmass of 262,230 km^2, contributing 8% of the total geographical area of the country and comprises of eight states is located between 87°32'E to 97°52' E longitude and 21°34'N to 29°50'N latitude. The region can be geographically divided into the Eastern Himalayan, the Patkai Naga Hills and, the Brahmaputra and the Barak valley plains. The region has a humid subtropical climate endowing with diverse ecosystems such as evergreen, tropical, temperate and alpine vegetation. The region is regarded as one of the last remaining rainforests of the Indian subcontinent's supporting different flora and fauna and several agricultural crop species.

About 70% of the population of the region depends on agriculture for sustainable livelihood.[1] However, the region contribute only 1.5% of the country's food grains production and is one of the major importers of food grain from other parts of the country for consumption.[2] The population of the region (excluding Assam) is projected to increase by 24% from 14.5 million in 2011 to 18.09 million in 2036.[3] There is an urgent need to augment the agricultural and allied products to sustain the population and uplift the economic conditions. The region, endowed with a range of diversity of climate, soil and vegetation, has the potential of achieving a much higher level of sustainable development if resources are properly and effectively managed.

Investigation on the bioactivity of medicinal plants is still ongoing, since, it represents a promising resource for production of unique secondary compounds for application in pharmaceutical, agricultural and other industries. Despite the importance of ethnomedicinal plants for human health for treating different diseases, a study on plant growth-promoting activity of their associated endophytes is scanty. The plant endosphere represents a multifaceted micro-environment hosting indigenous microbes that contribute to the growth of plants.[4] Plant beneficial endophytes reside inside the plant tissue without causing a negative effect to the host plants or the environment. They play an important role as plant growth regulators, induction of defence system, and protect the host from various biotic and abiotic stresses.[5] They augment the growth of plants by enhancing nutrient availability through nitrogen fixation, production of phytohormones, 1-aminocyclopropane-1-carboxylate (ACC) deaminase and siderophore, and also solubilization and mobilization of mineral nutrients.[6-10] Endophytic bacteria can also indirectly promote the growth of host plants by the production of antimicrobial compounds, cell wall degrading enzymes, low molecular weight volatile compounds and induction of systemic resistance.[11-15]

This review aims to elaborate on the plant growth-promoting (PGP) potential of the endophytic bacteria associated with the ethnomedicinal plants of NEIHR. Since the hilly region often faces water scarcity and soils are highly acidic and frequent occurrences of waterlogging in the plain valleys, the review also focuses on exploring important endophytes for application in diverse agro-climatic conditions of the NEIHR towards sustainable development of the agricultural sector.

Invasion, colonization and translocation of endophytic bacteria

Since plants and bacteria have co-evolved for millions of years, some bacteria possessed a necessary quality to invade, colonize and translocate to different tissue of plants.[16] Some bacteria from the plant rhizosphere invade and become endophytes as the latter may have an advantage over rhizospheric bacteria in accessing more nutrients without competing with other microorganisms and, better protected from various biotic and abiotic stresses. Endophytic bacteria may in turn exert direct or indirect beneficial effects to host plants.[7,17] Endophytic bacteria are generally believed to be originated from the rhizosphere and phylloplane bacterial communities, while some may be vertically transferred from endophyte-infected seeds or planting materials.[18]

The entry of endophytic bacteria into the host plant particularly in roots occurs in several steps. The first step for the entry of bacteria into host tissue is the chemotaxis-induced motility that recruits bacterial to colonize plant roots.[19-21] The exudates rich in organic substrate released from roots serve as chemo-attractants that facilitate the communication between roots and microbes, ultimately helping in recruiting bacterial communities from the rhizosphere to start colonization of the root.[22,23] Bacteria defective in flagellar motility hinder the colonization of plant roots. For example, *Pseudomonas* mutant strains defective in flagella-driven chemotaxis (*cheA* or *pilA*) could not successfully colonize the root.[24,25] Kost et al.,[26] reported the role of root exudates such as oxalate in root colonization by *Burkholderia* strains. The plant beneficial strains were able to metabolize oxalate as a carbon source but pathogenic fails to degrade the oxalate. Similarly, the mutant strain *Burkholderia phytofirmans* defect in utilizing oxalate fails to colonize the maize root.

The next step is the entry of bacteria into the root through several mechanisms such as passive penetration at the root tip, primary and lateral root cracks, pathogen entry sites, or tissue wounds occurring as a result of plant growth. While others gain entry through active penetration by producing cell wall degrading enzymes, such as cellulase, glucanase, lipase, etc.[17,27-29] Hallmann et al.,[17] reported that *Enterobacter asburiae* enter the host plant by hydrolyzing cellulose of plant cell wall. Phyllospheric bacteria also enter plant tissue through stomata, particularly on leaves and, also through wounds and cracks generated by wind, insect and pathogen attacks.[31,32]

Successful colonization of endophytes into host tissue also occurs when bacteria can reduce or evade plant defence machinery since; plant defence responses may restrict endophytic colonization. For example, *Bacillus subtilis* colonized *Arabidopsis thaliana* by producing subtilomycin that binds to flagellin, thereby reducing the induction of plant defence mechanisms. *Bacillus subtilis* also colonize the host plant *Amorphophallus konjac* by producing subtilomycin.[33] After entering the root tissue, some endophytes can translocate to different tissue of the host plants such as stem, flowers, fruits and seeds. Translocation occurs through the vascular system especially xylem of the host plants facilitated by flagella movement.[29,34-36]

The population of endophytes in the root and stem starts to decline as the host plant continues to grow and reach a mature stage. The steady advance from roots towards stems and leaves, thereby reducing the population in roots and stems, was observed during colonization by *Bacillus megaterium* in maize and rice plant.[37] Mcinroy and Kloepper[38] also observed the decline in the bacterial population in the stem tissue of sweet corn after 10 weeks. The authors concluded that the decline in the population of bacteria, from the base of the plant to the top might be due to travelling of bacteria along with the water/nutrient in the vascular system during plant development. Colonization, multiplication and distribution of endophytic bacteria from ethnomedicinal plants of NEIHR were studied by Nongklaw and Joshi, and Devi et al. Using transmission electron microscopy, Nongkhlaw and Joshi[39] observed the transverse sectioned of roots and leaves for colonization of endophytes within *Centella asiatica, Houttuynia cordata* and *Potentilla fulgens* tissues. The endophytes were observed in the aerenchyma and intercellular spaces of the epidermis and the outer cortex as single, double cell, or the form of a colony. A population of the endophytes was fewer in the leaves as compared to the root.

Devi et al.[40] studied the multiplication and distribution of endophytic bacteria with respect to the inoculation time of host plant grown in a greenhouse. They injected the bacteria into stem tissue and observed the increase in population and distribution at different plant tissue after 3rd and 5th days of incubation (DAI). The authors reported that the bacterial population significantly increase between 3rd and 5th DAI. Bacteria were not detected in leaves till 3rd DAI; however, after 5th DAI, it was recovered from the leaves of host plants.

Antifungal activities of endophytic bacteria isolated from ethnomedicinal plants of NEIHR

Numerous studies on the bioactivity of medicinal plants are still underway since they constitute a rich source for production of compounds having important ecological functions, protecting from pests, diseases and other environmental stresses. Recently endophytic bacteria isolated from medicinal plants received significant importance in the hunt for novel bioactive compounds having important ecological functions. Endophytic bacteria from ethnomedicinal plants have also demonstrated a broad range of bioactivity against many important pathogenic microorganisms. Antifungal

Table 1. Fungal growth inhibition characteristics of the endophytic bacteria from medicinal plants of NEIHR

Endophytic isolate	Host plant	Growth inhibition	Cell wall degrading enzymes	Ref.
Streptomyces olivaceus, Streptomyces sp.	*Rhynchotoechum ellipticum*	*Fusarium oxysporum, Fusarium proliferatum*		4
Acinetobacter sp., *Pseudomonas* sp.	*Mussaenda roxburghii*	*Sclerotium rolfsii, Sclerotinia sclerotiorum*		6
Bacillus siamensis	*Litsea cubeba*	*Fusarium oxysporum, Emericella nidulans*		41
Bacillus subtilis	*Centella asiatica*	*Fusarium oxysporum Emericella nidulans*	Chitinase, cellulase	41
Serratia marcescens	*Centella asiatica*		Chitinase, cellulase	41
Bacillus mycoides	*Rubia cordifolia*		Chitinase, cellulase	41
Streptomyces anulatus, Streptomyces sampsonii, Streptomyces tempisquensis, Streptomyces sp.	*Schima wallichi*	*Fusarium culmorum, Fusarium proliferatum*		51
Streptomyces sp.	*Mikania micranth* Kunth, WI	*Fusarium oxysporum, Fusarium roliferatum*		52
Bacillus sp., *Paenibacillus* sp.	*Clerodendrum colebrookianum* Walp.	*Rhizoctonia solani, Fusarium species, Colletotrichum* capsici	Cellulase, amylase, protease	53
Ochrobactrum intermedium	*Acorus calamus*	*Rhizoctonia solani, Helminthosporium oryzae, Fusarium oxysporum*	Chitinase, protease, lipase	54
Pseudomonas aeruginosa	*Achyranthes aspera* L.	*Rhizoctonia solani*		55

characteristics of endophytic bacteria isolated from ethnomedicinal plants of NEIHR are shown in Table 1.

Nongkhlaw and Joshi[41] collected 10 ethnomedicinal plants from the forests of 4 districts of Meghalaya to study the antifungal against plant pathogens and PGP activities of endophytic and epiphytic bacteria. Of these, endophytes from 8 plants i.e., *Centella asiatica, Litsea cubeba, Rubia cordifolia, Zingiber montanum, Acmella oleracea, Houttuynia cordata, Aloe vera* and *Potentilla fulgens* revealed antimicrobial activities. The researcher found that endophytic bacteria demonstrated antifungal whereas, epiphytic bacteria failed to exhibit the same result. Endophytic bacteria also showed better PGP traits. The crude extract of *Bacillus siamensis* isolated from *Litsea cubeba* and *Bacillus subtilis* from *Centella asiatica* exhibits antagonistic activity against *Fusarium oxysporum* and *Emericella nidulans. Serratia marcescens* and *Bacillus subtilis* strains obtained from *Centella asiatica* produce cell wall degrading enzymes such as chitinase and cellulase. Strains *Bacillus mycoides, Pseudomonas baetica, Bacillus* sp. and *B. licheniformis* isolated from *Rubia cordifolia, Zingiber montanum, Houttuynia cordata* and *Potentilla fulgens* produced cell wall degrading enzymes such as chitinase and cellulase that can act as biocontrol agents against fungal pathogens.

Rakotoniriana et al.[42] isolated endophyte *Bacillus subtilis* and *Pseudomonas fluorescens* from leaves of *Centilla asiatica* collected from Madagascar that demonstrated antagonistic activity against *Colletotrichum higginsianum.* Foliar application of bioactive strain *Bacillus subtilis* reduced the incidence and severity of anthracnose disease. Endophytic bacteria associated with *Litsea cubeba* grown in Vietnam have been reported to exhibit antimicrobial activity.[43,44] Actinobacterial strain associated with *Houttuynia cordata* collected from Japan also possesses antifungal activity against *Alternaria brassicicola* and *Fusarium oxysporum.* Treatment of strain to Chinese cabbage seedlings suppresses the disease caused by *Alternaria brassicicola.*[45] Chen et al.[46] reported 2-pyrol formic acid, a compound produced by endophyte *Streptomyces* sp. K15 of *Houttuynia cordata*, having good antifungal activity against *Botrytis cinerea*.

Search on the biocontrol activities of the bacterial endophytes derived from ethnomedicinal plants of Mizoram has been extensively done by Passari et al. and other research groups. A total of 42 endophytic actinomycetes were isolated from the 7 ethnomedicinal plants *Alstonia scholaris, Centella asiatica, Clerodendrum colebrooklanum, Curcuma longa, Eupatorium odoratum, Mirabilis jalapa* and *Musa superba.* Majority of the isolates belong to the genus *Streptomyces* followed by *Microbacterium.* Of these, 22 isolates showed an inhibitory effect against at least one tested phytopathogen. Fourteen isolates exerted significant inhibitory activity against *Rhizoctonia solani, Fusarium graminearum* and *F. oxysporum.* Promising endophytic strains *Microbacterium* sp., *Leifsonia xyli* and *Streptomyces* sp. demonstrated significant inhibitory against all the test pathogens viz.; *Rhizoctonia solani, Fusarium oxysporum* f. sp. *ciceri, F. proliferatum, F. oxysporum, F. graminearum* and *Colletotrichum capsici.* Among the 22 endophytic actinobacterial strains showing inhibition to fungal growth, 19 and 15 isolates were found to be positive for chitinase and hydrogen cyanide (HCN) production.[47]

Carnobacterium gallinarum and *C. maltaromaticum* isolated from root and leaves of *Alstonia scholaris*, a native of Indonesia, inhibit the growth of *Fusarium* sp. and *Colletotrichum* sp. The two strains promoted the growth of chilli plant and protected from *Colletotrichum* fruit rot and *Fusarium* wilt disease.[48] Investigation of endophytic bacteria *Pseudomonas aeruginosa* isolated from *Curcuma longa* L. rhizome collected from Karnataka, India displays good antagonistic effect against *Pythium aphanidermatum* and *Rhizoctonia solani.* The strain also produced cell wall degrading enzymes such as protease and cellulase. The strain reduced the leaf blight and rhizome rot disease of *Curcuma longa* plant.[49] Ramanuj and Shelat[50] also observed inhibition of *Alternaria alternate* and *Aspergillus niger* growth by chitinase producing *Beijerinckia fluminensis,* an endophyte associated with *Curcuma longa.*

Out of 22 *Streptomyces* isolates obtained from medicinal plant *Schima wallichi* collected from Dampa Tiger Reserve, Mizoram, 15 strains exhibited antagonistic activity against one or more of the test pathogens viz.; *Fusarium* *culmorum, F. proliferatum, F. oxysporum, F. graminearum, F. oxysporum* f. sp. *ciceri, Alternaria* sp. and *Colletotrichum* sp. All 15 bioactive strains demonstrated antifungal activity against *Fusarium culmorum* and *F. proliferatum* whereas, 4 isolates exhibited positive antagonistic effect against all the selected test pathogens. Of 22 isolates, 9 strains were positive for the biosynthetic genes cluster PKSI and 11 strains were positive for NRPS.[51]

A 17 actinobacteria were isolated from root, stem, petiole, flower and rhizome of 6 medicinal plants of Mizoram viz., *Ageratum conizoides* L., *Costus speciosus* Sm., *Mikania micranth* Kunth. WI, *Scopariadulcis* and *Senecio scandens* Buch.-Ham. Seven strains belonging to genus *Streptomyces* viz.; *Streptomyces somaliensis, Streptomyces* sp. BPSEAC7, *Streptomyces* sp. BPSEAC8, *Streptomyces* sp. BPSEAC16, *Streptomyces* sp. BPSEAC18, *Streptomyces* sp. BPSEAC23 and *Streptomyces* sp. BPSEAC33 associated with *Mikania micranth* Kunth. WI, *Senecio scandens, Cassia fistula* L. and *Scoparia dulcis* demonstrated antagonistic activity against *Fusarium oxysporum* f. sp. *ciceri* and *F. proliferatum.* The majority of the antagonist isolates were isolated from the root except one from the petiole.[52]

Of 73 endophytic bacterial isolates derived from Clerodendrum colebrookianum Walp. by Passari et al.[53,52] isolates showed inhibition against three out of five fungal phytopathogens viz; *Rhizoctonia solani, Fusarium oxysporum, F. proliferatum, F. graminearum* and *Colletotrichum capsici.* Ten isolates demonstrated strong inhibition action against all the pathogens. Forty five, 52 and 47 isolates were found to be positive for cellulase, amylase and protease production. All the 52 isolates were able to produce HCN. Three potent strains i.e., *Bacillus* sp. BPSAC3, *Bacillus* sp. BPSAC6 and *Paenibacillus* sp. that exhibit good antimicrobial activities were studied for disease suppression caused by *Fusarium oxysporum* in tomato plants under greenhouse conditions. Treatment of tomato seedlings in the form of soil drenching significantly reduced the disease incidence. Bioactive isolates *Bacillus* sp. BPSAC6 demonstrated 57.1% disease suppression while, *Bacillus* sp. BPSAC3 and *Paenibacillus* sp. showed 45.5% and 38% respectively.

Passari et al.[4] isolated 169 actinobacteria from the endemic medicinal plant *Rhynchotoechum ellipticum.* Of these, 72 isolates showed significant mycelial growth inhibition against *Fusarium proliferatum, F. oxysporum* f. sp. *ciceri* and *F. oxysporum.* Among them, *Streptomyces olivaceus* exhibited the maximum percentage of inhibition against *Fusarium proliferatum* and *F. oxysporum* f. sp. *ciceri* whereas; *Streptomyces* sp. BPSAC121 showed maximum antagonistic activity against *Fusarium oxysporum.* Antifungal antibiotics, ketoconazol, fluconazole, rifampicin and miconazole were detected in *Streptomyces* sp. BPSAC101 and *Streptomyces thermocarboxydus.* The concentration of ketoconazol produced by *Streptomyces* sp. BPSAC101 and *Streptomyces thermocarboxydus* were 276 µg/g and 289 µg/g respectively.

Endophytic bacteria obtained from ethnomedicinal plants of Manipur have been reported to demonstrate the antifungal activity to phytopathogens and suppress the development of fungal disease *in vivo* conditions. Singh et al.[54] isolated 21 endophytic bacteria from the rhizomes of *Acorus calamus* collected from different habitats of Manipur. Isolate *Ochrobactrum intermedium* was selected as a promising strain since the strain demonstrated good antagonist activity. Isolate display mycelial growth inhibition against *Rhizoctonia solani, Helminthosporium oryzae, Fusarium oxysporum, Aspergillus niger* and *Curvularia oryzae* showing the highest inhibition against *Rhizoctonia solani.* Isolate also showed positive results for fungal cell wall degrading enzymes such as chitinase, protease and lipase. Soil and foliar spray treatment of the bioactive strain suppressed the disease lesion caused by *Rhizoctonia solani* in rice plants under nethouse conditions. Bioinoculant treated plant challenged with *Rhizoctonia solani* also demonstrated significant growth and grain yield production of rice plant over control and pathogen alone treated plant. The authors concluded that the disease suppressing ability may be due to the various antifungal attributing factors of the strain. Similarly, non-pathogenic strain *Pseudomonas aeruginosa* isolated from leaves and stems of *Achyranthes aspera* L. display mycelial growth inhibition to *Rhizoctonia solani.*[55]

Table 2. PGP characteristics of the endophytic bacteria from medicinal plants of NEIHR

Endophytic isolate	Host plant	PGP activities	Ref.
Acinetobacter sp., *Klebsiella* sp., *Pseudomonas* sp.,	*Mussaenda roxburghii*	IAA and siderophore production, P solubilization, N fixation	6
Bacillus sp.	*Houttuynia cordata*	ACC deaminase	39, 41
Serratia marcescens	*Achyranthes aspera* L	IAA and siderophore production, P solubilization, N fixation	40
Bacillus subtilis,	*Centella asiatica*	P solubilization, N fixation	41
Serratia marcescens	*Centella asiatica*	P solubilization, N fixation	41
Bacillus mycoides	*Rubia cordifolia*	ACC deaminase	41
Bacillus siamensis, Lysinibacillus xylanilyticus	*Litsea cubeba*	P solubilization, N fixation	41
Streptomyces thermocarboxydus	*Costus speciosus* Sm.	IAA and ammonia production, P solubilization	52
Bacillus sp., *Paenibacillus* sp., *Pseudomonas* sp.	*Clerodendrum colebrookianum* Walp.	IAA, Siderophore and NH_3 production, P solubilization	53
Ochrobactrum intermedium	*Acorus calamus*	IAA, ammonia and siderophore production, P solubilization	54
Pseudomonas aeruginosa	*Achyranthes aspera* L	IAA and siderophore production, P solubilization, N-fixation	55
Streptomyces spp.	*Clerodendrum colebrookianum* Walp., *Costus speciosus, Houttuynia cordata Thumb, Solanum khasianum C.B. Clarke, Zanthoxylum armatum* DC	IAA, ACC deaminase and siderophore production, P solubilization	64

Of 76 putative actinomycetes from 6 medicinal plants viz.; *Azadirachta indica, Emblica officinalis, Murraya koenigii, Rauwolfia serpentine, Terminalia chebula* and *Terminalia arjuna* of Assam, 7 strains showed antifungal activity against *Rhizoctonia solani.*[56] Five bacterial endophytes associated with endemic medicinal plant *Garcinia lancifolia* Roxb. of Assam showed antimicrobial activity against *Aspergillus niger* and *Alternaria alternata.*[57] Pandey et al.[6] studied the antifungal activity of endophytic bacteria isolated from *Mussaenda roxburghii* of Arunachal Pradesh. Of the 7 isolates, *Pseudomonas* sp. PAK1, *Pseudomonas* sp. PAK2, *Acinetobacter* sp. PAK6, *Pseudomonas* sp. PAK7 and *Acinetobacter* sp. PAK9 inhibited the mycelia growth of *Sclerotium rolfsii.* Isolates *Acinetobacter* sp. PAK6, *Pseudomonas* sp. PAK7, *Pseudomonas* sp. PAK8 and *Acinetobacter* sp. PAK9 inhibited *Sclerotinia sclerotiorum.* Isolates *Pseudomonas* sp. PAK2 and *Acinetobacter* sp. PAK9 were able to produce HCN.

Endophytic bacteria belonging to *Streptomyces* sp., *Nocardia* sp. and *Streptosporangium* sp. associated with *Azadirachta indica* collected from other parts of India have been reported to have antimicrobial effect against fungal pathogens.[58,59] Endophytic actinobacterial isolates from *Emblica officinalis* also exhibited antifungal, antibacterial and PGP activities.[60] Actinobacteria isolated from *Rauvolfia serpentine* have also been reported to exhibit antifungal against plant fungal pathogens and PGP activities. Bioactive microbial strains were also found to promote growth and reduce the mortality caused by pathogens in chickpea plants.[61]

PGP activities of endophytic bacteria isolated from ethnomedicinal plants of NEIHR

To feed the increasing population in NEIHR in the future, there is a need to augment the production of agricultural and allied sectors. The production can be enhanced with the use of synthetic chemicals and fertilizers which in turn affect health, environment and disrupt the ecological balance. An intensive search for PGP bacteria (PGPB) is undergoing that can act as biocontrol and biofertilizing agents. However, most of the PGPBs show inconsistent efficacy in field conditions. Surveys for PGPBs from NEIHR that are suited to local agro-climatic conditions become important for sustainable food production.[62] PGP activities of endophytic bacteria isolated from ethnomedicinal plants of NEIHR are shown in Table 2.

Passari et al.[53] investigate the PGP potential of the 52 endophytic isolates associated with *Clerodendrum colebrookianum* Walp. that demonstrated antimicrobial activities. Of these, 44 isolates were found to be promising for solubilization of tricalcium P in the range of 8.2 to 92 mg/100 mL. Forty-eight isolates could produce IAA ranging from 14.2 to 80.6 µg/mL. Fifty-one isolates were found to be positive for the production of ammonia ranging from 12.8 to 68.3 mg/100 mL. Siderophore production was detected with 41 isolates. Of 10 isolates belonging to 3 *Bacillus* species, 2 *Staphylococcus* species, *Paenibacillus* sp., *Bacillus thuringiensis, Lysinibacillus sphaericus, Pseudomonas* sp., and *Pseudomonas stutzeri* showing multiple PGP traits were screened for their ability to colonize on the root surface. All the bioactive strains were able to excessively colonize on the root surface of a tomato plant. Three beneficial isolates *Bacillus* sp. BPSAC3, *Bacillus* sp. BPSAC6 and *Paenibacillus* sp. were chosen for studying plant growth promotion under greenhouse conditions. The treatment of seedlings with the bioinoculant significantly enhances the growth of tomato plants. Among the 3 bacteria, strain *Bacillus* sp. BPSAC6 which displays better PGP traits and antifungal properties also demonstrated better growth promotion in tomato plants.

Among the 22 bioactive endophytic actinobacteria isolated from 7 plants of Mizoram i.e., *Eupatorium odoratum, Musa superba* Roxb., *Mirabilis jalapa, Centella asiatica, Curcuma longa, Clerodendrum colebrooklanum* and *Alstonia scholaris* that showed antagonist against fungi, 14 were able to solubilize inorganic P varying from 3.2 to 32.6 mg/100 mL. Twenty strains could produce IAA in the range of 10 to 32 µg/mL. The hydroxamate and catechol-type siderophores were produced by 16 and 5 isolates ranging from 5.2 to 36.4 and 3.2 to 5.4 µg/mL. All the bioactive strains were positive for the production of ammonia ranging from 5.2 to 54 mg/mL. The majority of the PGP strains belong to *Streptomyces* species. Inoculation of chilli seeds with two promising strains *Streptomyces* sp. and *Leifsonia xyli* showing good antagonistic and PGP traits significantly enhanced the growth of seedlings under greenhouse conditions. Treatment of chilli plants with a mixture of two promising strains showed further enhancement in growth as compared to inoculation with the individual strain.[47]

Patel et al.[63] documented that *Bacillus* sp., *Enterobacter* sp., *Klebsiella* sp. and *Microbacterium* sp. associated with Musa sp. produced IAA and siderophore, and solubilize P. The bioactive strains were able to promote the growth of banana plants grown in the greenhouse. Endophytic bacteria *Pseudomonas aeruginosa* associated with *Curcuma longa* rhizome significantly promote the growth and rhizome yield of host plant under greenhouse condition.[49] *Carnobacterium gallinarum* and *C. maltaromaticum* isolated from root and leaves of *Alstonia scholaris* exhibit antifungal and plant growth activities such as IAA production and solubilization of P. Growth promotion of chilli plants by bioactive strains was also reported by Ulfa et al.[48]

Nongkhlaw and Joshi[41] compared the antimicrobial and PGP activities of endophytic and epiphytic bacteria collected from 10 medicinal plants in Meghalaya. The endophytic bacteria showed better antimicrobial and growth-promoting activities. Of these, endophytes from 8 plants i.e., *Centella asiatica, Litsea cubeba, Rubia cordifolia, Zingiber montanum, Acmella oleracea, Houttuynia cordata, Aloe vera* and *Potentilla fulgens* display antimicrobial activities. *Serratia marcescens* and *Bacillus subtilis* strains obtained from *Centella asiatica* could solubilize P and fix atmospheric N. Similarly, *Bacillus siamensis* and *Lysinibacillus xylanilyticus* isolated from *Litsea cubeba* have PGP traits such as P solubilization and N fixation. Bioactive isolates *Pseudomonas baetica, Pseudomonas palleroniana, Herminiimonas saxobsidens* and *Bacillus licheniformis* isolated from *Rubia cordifolia, Zingiber montanum, Houttuynia cordata* and *Potentilla fulgens* could solubilize inorganic P and displayed N fixation. ACC deaminase gene was detected in *Bacillus* sp. and *Bacillus mycoides.*

Pandey et al.[6] evaluated the 7 endophytic bacteria isolated from *Mussaenda roxburghii* of Arunachal Pradesh for PGP activity and demonstrated that *Pseudomonas* sp. PAK2, *Klebsiella* sp. PAK3, *Acinetobacter* sp. PAK6, and *Pseudomonas* sp. could solubilize inorganic P varying from 3.7 to 5.24 ppm. All the strains produced IAA of 9 to 17 µg/mL. Isolates *Pseudomonas* sp. PAK1 and *Acinetobacter* sp. PAK9 were able to produce siderophore. Similarly, strains *Pseudomonas* sp. PAK2, *Pseudomonas* sp. PAK7, *Pseudomonas* sp. PAK8 and *Acinetobacter* sp. PAK9 were able to grow on N-free medium.

Barman and Dkhar[64] investigated the PGP traits of the endophytic actinobacterial communities associated with 6 medicinal plants of Meghalaya viz., *Clerodendrum colebrookianum* Walp., *Costus speciosus* (J. Koenig), *Houttuynia cordata* Thumb, *Solanum khasianum* C.B. Clarke, *Potentilla fulgens* Wall. Ex Hook and *Zanthoxylum armatum* DC. Of 41 strains studied, 10 produced IAA ranging from 26.38 to 44.70 µg/mL and 11 showed positive results for siderophore production ranging from 56 to 87.95%. P solubilization was detected in 11 isolates which ranges from 155.19 to 361.67 µg/mL and ACC deaminase was shown in 9 isolates. Treatment of rice seedlings with 12 promising actinobacterial strains stimulated the growth of plants under greenhouse conditions. The majority of the PGP isolates belong to *Streptomyces* species.

Endophytic strains *Streptomyces thermocarboxydus, Streptomyces* sp. BPSEAC8, *Streptomyces* sp. BPSEAC14, *Tsukamurella tyrosinosolvens, Streptomyces* sp. BPSEAC33 and *Streptomyces violascens* associated with endemic medicinal plants *Costus speciosus, Mikania micranth, Ageratum conizoides* L. and *Scopariadulcis* of Mizoram were able to solubilize P and, produce IAA and ammonia.[52] Similarly, 5 strains isolated from *Garcinia lancifolia* Roxb. could produce IAA and ammonia, and solubilize tricalcium P.[57]

Devi et al.[40] isolated *Serratia marcescens* from *Achyranthes aspera* L. collected from the different habitats of Manipur for elucidating the potential of the strain for various plant growth parameters. It could produce IAA in the range of 0.8 to 133.2 µg/mL and about 75% units of siderophore. The beneficial strain was able to significantly solubilize P up to 259 µg/mL, able to produce ammonia and fix atmospheric N. Nitrogenase activity was found to be 2.523 nmol ethylene/µg/protein/hour. Priming of *Serratia marcescens* by injecting into the stem of *Achyranthes aspera* L. radically increases shoot length, fresh shoot weight, dry shoot weight, fresh root weight and dry root weight over control under pot trial experiment.[40]

Similarly, non-pathogenic strain *Pseudomonas aeruginosa* associated with leaves and stems of the same medicinal plant produced 114.79 µg/mL of IAA and 72% unit of siderophore. It could also solubilize 383 µg/mL of tricalcium P. Strain could fix N and the nitrogenase activity was found to be 1.8617 nmol ethylene/µg/protein/h. The authors confirmed the N fixing ability by *Pseudomonas aeruginosa* due to the presence of nifH gene. *Pseudomonas aeruginosa* could successfully colonize the internal tissue of *Achyranthes aspera* L seedlings. Priming of Pseudomonas aeruginosa by injecting into the stem of *Achyranthes aspera* L. also showed similar growth promotion as shown by *Serratia marcescens.*[55] Bacteria belonging to genus *Acinetobacter, Citrobacter, Enterobacter, Pseudomonas* and *Serratia* isolated from tissue, rhizoplane and rhizosphere of *Achyranthes aspera* from Rajasthan, India have been reported to solubilized P and produced IAA. The strains also improve the growth of the pearl millet plants under pot condition.[65]

Endophytic bacteria *Ochrobactrum intermedium* isolated from rhizomes of *Acorus calamus,* a medicinal plant used by the ethnic group of Manipur that demonstrated good antagonist activity against phytopathogens was assayed for PGP potential in rice plants. The antagonist strain could produce 29.61 and 112.5 µg/mL of IAA and ammonia, respectively. The strain also produced a significant amount of siderophore (72%) and solubilized inorganic P up to 102 µg/mL. Priming of rice seeds with the bioactive strain significantly enhances seed germination and promotes the growth of rice seedlings under gnotobiotic conditions. Under an agro-shade net, rice plants treated with *Ochrobactrum intermedium* exhibited significant increases in root and shoot length, and number of leaves over control. Bioinoculant treated plant challenged with *Rhizoctonia solani* also demonstrated similar results over control. Bioinoculant treated plants challenged with *Rhizoctonia solani* significantly enhanced the growth of shoot over *Rhizoctonia solani* treated plants. Strain significantly increased the number of filled grains per plant over control. Similar results were shown for treated plants challenged with *Rhizoctonia solani* over plants treated with *Rhizoctonia solani alone.*[54] Similarly, endophyte *Enterobacter cloacae* from the rhizome of *Acorus calamus* collected from Tamil Nadu, India was found to be positive for IAA production, P solubilization and siderophore production. Bioactive strain enhances germination and growth of the host plant.[66] IAA producing *Streptomyces* sp. isolated from the medicinal plant of Meghalaya has also been reported to enhance germination and growth of bean seedlings.[67]

Plant growth promotion by endophytes from ethnomedicinal plants of NEIHR under abiotic stress

Plants are continuously affected by abiotic and biotic stress throughout their life cycle. Abiotic stresses affect microbial functional diversity and soil physicochemical properties contributing to yield losses up to 50% posing a serious challenge for global food production. The most common abiotic stresses affecting plant growth and development are drought, temperature, salinity and heavy metal. However, beneficial bacteria enhance plant growth under abiotic stresses by synthesizing plant hormones that promote plant growth through enhanced root development, increased water uptake and nutrient absorption. It also synthesizes 1-aminocyclopropane-1-carboxylate (ACC) deaminase and rhizobitoxine that reduce the level of stress ethylene, induce production of stress-related enzymes and induce systemic resistance in plants.[68,69] Plant beneficial endophytic bacteria having the prospective to endure abiotic stresses can be used as a promising agent for climate-smart farming.

Heavy metal contamination in soil due to increased industrialization, intensive agricultural practices and other human activities severely affects the growth and yield of crops. Heavy metal contamination is non-degradable and toxic even at low concentration.[69,70] Heavy metals hamper the normal functioning of plants by forming a link with the sulfhydryl of the functional groups, causing structural disintegration of important molecules particularly protein. They compete with the essential metals (trace elements) and obstruct the normal function of enzymes or pigments upsetting the photosynthesis, respiration, and enzymatic activities. It also augments the generation of ROS that disturbs the redox homeostasis of cells resulting in the activation of apoptosis.[71-73] Metal tolerant bacteria mitigate stress by producing siderophore, exopolysaccharide and antioxidants that help in the sequestering, bioremediation of metals, and mitigation of the ROS generated by stress conditions. Phytohormones produced by the bacteria, in turn, promote the growth of plants.[73,74]

Aluminium (Al^{+3}) toxicity causes about 25–80% yield losses in several crops.[75] Endophytic bacterial isolates associated with the ethnomedicinal plants of NEIHR have the potential to promote growth of crops under heavy metal stress. Strains *Pseudomonas* sp. PAK2, *Pseudomonas* sp. PAK7, and *Pseudomonas* sp. PAK8 isolated from *Mussaenda roxburghii* of Arunachal Pradesh were able to tolerate 600 µg/mL of Al^{+3} and all the isolates except *Pseudomonas* sp. PAK1 showed tolerance to 600 µg/mL of Mn^{+2} tested. Heavy metal tolerant endophytic bacteria demonstrated PGP traits such as IAA and siderophore production, P solubilization, and ability to grow on N-free medium.[6]

Soil salinity is also considered as one of the major abiotic stresses globally that adversely affect the growth and yield of higher plants. The majority of the arable land to the tune of 3.6 out of 5.2 billion hectares is affected by salinity problems due to human and natural activities.[70] Salt stress has a detrimental consequence on plant growth due to induced ion toxicity, mineral deficiency, development of ROS, alteration of osmotic potential and elevation of ethylene level. It also reduces nutrient and water uptake, photosynthesis, respiration, nodulation, and nitrogen fixation activities.[69,76] Endophytic bacterial strains *Acinetobacter* sp. PAK6, *Acinetobacter* sp. PAK9, *Klebsiella* sp. PAK3, *Pseudomonas* sp. PAK1, *Pseudomonas* sp. PAK2, *Pseudomonas* sp. PAK7 and *Pseudomonas* sp. PAK8 showed good growth at the level of 2.0–10% NaCl[6].

FUTURE PERSPECTIVES AND CONCLUSION

To increase food production in order to feed the escalating increase in the human population without affecting the environment, there is an urgent need to search for the bacteria that can contain the plant diseases and enhance crops production. Interestingly, there is a great potential for discovering unique endophytic bacteria from plants growing in tropical to temperate rainforests, unusual endemic regions, extreme environments and, oceans.[77,78] The NEIHR falls under two mega-biodiversity hotspots having diverse ecosystems. Moreover, there are several under and unexplored ecosystems and plants endemic to a particular region. The need of the hour is to search for beneficial endophytic bacteria from unexplored or under-explored ecosystems of NEIHR, which can be used as effective phyto-stimulating agents for sustainable production of important crops of the region especially rice, maize and horticultural crops.

Due to heavy rainfall, soils in the mountainous and hilly region of North East India are moderate to high acidic. Heavy rainfall and soil low pH causes a deficiency in the plant essential elements like Na, K, Ca and Mg, on the other hand, increasing the solubility of heavy metals such as Al, Fe and Si resulting in toxicity to plants. Al^{3+} ions bind with phosphoric acid and form an insoluble compound limiting the availability of P to plants.[79] Soil acidity stunted the growth and development of root and plant biomass due to metal toxicity, poor fertility and low water-holding capacity.[80,81] It also contributes to a decline in the neutrophilic beneficial bacteria and on the other hand, increases the population of pathogenic fungi.[82] However, acid-tolerant PGP bacteria can support the growth of plants by the production of siderophore and phytohormones, solubilization of P and K, and production of antibiotics that inhibit the growth of pathogenic fungi.[81,83] There are reports of exhibiting higher antifungal and phytostimulating effect by acid-tolerant than neutrophilic bacterial isolates.[84,85]

In NEIHR of India, nearly 90% of the population lives in hilly rural areas and depends on agriculture for sustainable livelihood. Even though the region receives heavy rainfall annually of about 2000 mm, the hilly region often faces water scarcity since most of the rainwater is lost as runoff leading to moisture stress during lean periods.[86,87] Moreover, drought stress has increased in intensity over the past decades and is expected to adversely affect plant growth in >50% of the world's arable lands by 2050.[81,88,89]

Drought stress is regarded as one of the most severe stress agents that negatively influence the germination, growth and yield of various crops. Drought largely affects the plants during the reproduction or flowering stage and severely reduces the yield.[90,91] Drought stress decreases nutrient diffusion, the mass flow of water-soluble nutrients, and the photosynthetic activity while enhancing the biosynthesis of 'stress ethylene' which is known for inhibiting plant growth. It also results in the generation of ROS negatively affecting membrane function, protein conformation, and induce lipid peroxidation resulting in cell apoptosis.[69,73,92] Drought tolerant bacteria have been reported to improve plant growth by phytohormone production that enhances plant growth through enhanced root development, increased water and nutrient absorption. They also synthesize ACC deaminase that reduces the level of ethylene in plant roots.[69] Frequent recurrence of floods in the valley areas of North East India, especially Assam and Manipur has caused tremendous loss of crops, livestock's and economy. During the year 1953 to 2004, the region suffered a loss of 2 billion rupees due to flood/waterlogging.[93] In the past few decades, waterlogging has caused major damage to the world's crop production to almost two to third; losing a billion dollars.[94] It is predicted to further aggravate in the coming decades posing a big threat to sustainable crop production.[95]

Waterlogging affects the growth of plants by depleting the availability of oxygen and light, disturbing the photosynthesis activity and energy production mechanism. It also leads to the accumulation of ethylene thereby stunting the growth of roots and inhibiting plant growth due to a decrease in the absorption of the nutrients.[95,96] Beneficial bacteria mitigate the stress and promote the growth of plants under waterlogged conditions by the production of IAA and ACC deaminase that stimulate the growth and degrade the stress ethylene. The ammonia and α-ketobutyrate produced by the degradation of ACC precursor of ethylene are used by the plants as N and carbohydrate sources under waterlogged conditions.

As climate change and agriculture are inseparably linked, the crop loss due to a rapidly changing climate is expected to significantly reduce the food reserve and spike up the food price in near future. The global food deficit will force the nations to go for more agricultural intensification, which will, in turn increase the carbon and water footprint. Hence, with a rapid change in the climate and environment owing to uncontrolled anthropogenic activities, there is an urgent need for exploring alternative means for increasing the production of food crops to feed the rising human population. In this context, the researcher needs to explore the indigenous bacteria (endophytic) suited to the local environment that can promote the growth of agri-horticultural crops. Further surveys and bioprospecting for beneficial endophytic bacteria that can mitigate the common abiotic stress especially acidity, drought and waterlogging of the region are the need of the hour for climate-resilient agriculture.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

KT conceived and wrote the manuscript. PK compiled relevant information on bioactivity and helped in editing the manuscript. AKD, PL, HNS, CR, TSS, TL, SKS and MAA assisted in the literature survey. SSR provided critical feedback, guided the manuscript preparation, and assisted in language improvement. All authors read and approved the final manuscript for publication.

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REFERENCES

1. Roy A, Dkhar DS, Tripathi AK, et al. Growth performance of agriculture and allied sectors in the North East India. *Economic Affair.* 2014;59:783-795.
2. Jana H, Basu D. Agricultural backwardness analysis of North-east India: a cause of concern for national development. *Int Curr Res.* 2018;10(12):76825-76831. doi: 10.24941/ijcr.33598.12.2018
3. Report of the technical group on population projections, population projection for India and states 2011-2036. National Commission on Population Ministry of Health & Family Welfare, New Delhi, 2019.
4. Passari AK, Mishra VK, Singh G, et al. Insights into the functionality of endophytic actinobacteria with a focus on their biosynthetic potential and secondary metabolites production. *Sci Rep.* 2017;7(1):11809. doi: 10.1038/s41598-017-12235-4
5. Afzal I, Shinwari ZK, Sikandar S, Shahzad S. Plant beneficial endophytic bacteria: mechanisms, diversity, host range and genetic determinants. *Microbiol Res.* 2019;221:36-49. doi: 10.1016/j.micres.2019.02.001
6. Pandey PK, Samanta R, Yadav RNS. Plant beneficial endophytic bacteria from the ethnomedicinal *Mussaenda roxburghii* (Akshap) of Eastern Himalayan province India. *Adv Biol.* 2015;2015:580510. doi: 10.1155/2015/580510
7. Santoyo G, Moreno-Hagelsieb G, del Carmen Orozco-Mosqueda M, Glick BR. Plant growth-promoting bacterial endophytes. *Microbiol Res.* 2016;183:92-99. doi: 10.1016/j.micres.2015.11.008
8. Egamberdieva D, Wirth SJ, Shurigin VV, Hashem A, Allah EFA. Endophytic bacteria improve plant growth, symbiotic performance of chickpea (*Cicer arietinum* L.) and induce suppression of root rot caused by *Fusarium solani* under salt stress. *Front Microbiol.* 2017;8:1887. doi: 10.3389/fmicb.2017.01887
9. Kumar M, Sharma S, Gupta S, Kumar V. Mitigation of abiotic stresses in *Lycopersicon esculentum* by endophytic bacteria. Environmental Sustainability. (2018); 1:71-80. doi: 10.1007/s42398-018-0004-4
10. Erjaee Z, Shekarforoush SS, Hosseinzadeh S. Identification of endophytic bacteria in medicinal plants and their antifungal activities against food spoilage fungi. *J Food Sci Technol.* 2019;56(12): 5262-5270. doi: 10.1007/s13197-019-03995-0
11. Golinska P, Wypij M, Agarkar G, Rathod D,

Dahm H, Rai M. Endophytic actinobacteria of medicinal plants: Diversity and bioactivity. *Antonie van Leeuwenhoek.* 2015;108(2):267-289. doi: 10.1007/s10482-015-0502-7
12. Gos FMWR, Savi DC, Shaaban KA, et al. Antibacterial activity of endophytic actinomycetes isolated from the medicinal plant *Vochysia divergens* (Pantanal, Brazil). *Front Microbiol.* 2017;8:1642. doi: 10.3389/fmicb.2017.01642
13. Beiranvand M, Amin M, Hashemi-Shahraki A, Romani B, Yaghoubi S, Sadeghi P. Antimicrobial activity of endophytic bacterial populations isolated from medical plants of Iran. *Iran J Microbiol.* 2017;9(1):11-18.
14. Mohamad OAA, Li L, Ma J-B, et al. Evaluation of the antimicrobial activity of endophytic bacterial populations from Chinese traditional medicinal plant licorice and characterization of the bioactive secondary metabolites produced by *Bacillus atrophaeus* against *Verticillium dahliae. Front Microbiol.* 2018;9:924. doi: 10.3389/fmicb.2018.00924
15. Bokhari A, Essack M, Lafi FF et al. Bioprospecting desert plant Bacillus endophytic strains for their potential to enhance plant stress tolerance. Scientific Reports. 2019;9:18154. doi: 10.103/s41598-019-54685-y
16. Liu H, Carvalhais LC, Crawford M, et al. Inner plant values: Diversity, colonization and benefits from endophytic bacteria. *Front Microbiol.* 2017;8:2552. doi: 10.3389/fmicb.2017.02552
17. Hallmann J, Quadt-Hallmann A, Mahaffee WF, Kloepper JW. Bacterial endophytes in agricultural crops. *Can J Microbiol.* 1997;43(10):895-914. doi: 10.1139/m97-131
18. Eljounaidi K, Lee SK, Bae H. Bacterial endophytes as potential biocontrol agents of vascular wilt diseases - Review and future prospects. *Biol Control.* 2016;103:62-68. doi: 10.1016/j.biocontrol.2016.07.013
19. You CB, Lin M, Fang XJ, Song W. Attachment of *Alcaligenes* to rice roots. *Soil Biol Biochem.* 1995;27(4-5):463-466. doi: 10.1016/0038-0717(95)98620-4
20. Bacilio-Jimenez M, Aguilar-Flores S, Ventura-Zapata E, Perez-Campos E, Bouquelet S, Zenteno E. Chemical characterization of root exudates from rice (*Oryza sativa*) and their effects on the chemotactic response of endophytic bacteria. *Plant Soil.* 2003;249(2):271-277. doi: 10.1023/A:1022888900465
21. Li X, Hu H-J, Li J-Y, et al. Effects of the endophytic bacteria *Bacillus cereus* BCM2 on tomato root exudates and *Meloidogyne incognita* infection. *Plant Dis.* 2019;103(7):1551-1558. doi: 10.1094/PDIS-11-18-2016-RE
22. Rosenblueth M, Martinez-Romero E. Bacterial endophytes and their interactions with hosts. *Mol Plant Microbe Interact.* 2006;19(8):827-837. doi: 10.1094/MPMI-19-0827
23. Singh M, Kumar A, Singh R, Pandey KD. Endophytic bacteria: a new source of bioactive compounds. *3 Biotech.* 2017;7(5):315.doi: 10.1007/s13205-017-0942-z
24. Camacho Carvajal MM. Molecular characterization of the roles of type 4 pili, NDH-I and PyrR in rhizosphere colonization of *Pseudomonas fluorescens* WCS365. PhD thesis, University Leiden, Leiden, The Netherlands, 2001.
25. De-Weert S, Vermeiren H, Mulders IHM, et al. Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens. Mol Plant-Microbe Interact.* 2002;15(11):1173-1180. doi: 10.1094/MPMI.2002.15.11.1173
26. Kost T, Stopnisek N, Agnoli K, Eberl L, Weisskopi L. Oxalotrophy, a widespread trait of plant-associated *Burkholderia* species, is involved in successful root colonization of lupin and maize by *Burkholderia phytofirmans. Front Microbiol.* 2014;4:421. doi: 10.3389/fmicb.2013.00421
27. Hurek T, Reinhold-Hurek B, Van Montagu M, Kellenberger E. Root colonization and systemic spreading of *Azoarcus* sp. strain BH72 in grasses. *J Bacteriol.* 1994;176(7):1913-1923.
28. Elbeltagy A, Nishioka K, Suzuki H, et al. Isolation and characterization of endophytic bacteria from wild and traditionally cultivated rice varieties. *Soil Sci Plant Nutr.* 2000;46(3):617-629. doi: 10.1080/00380768.2000.10409127
29. James EK, Gyaneshwar P, Mathan N, et al. Infection and colonization of rice seedlings by the plant growth-promoting bacterium *Herbaspirillum seropedicae* Z67. *Mol Plant-Microbe Interact.* 2002;15(9):894-906. doi: 10.1094/MPMI.2002.15.9.894
30. Walitang DI, Kim K, Madhaiyan M, Kim YK, Kang Y, Sa T. Characterizing endophytic competence and plant growth promotion of bacterial endophytes inhabiting the seed endosphere of rice. *BMC Microbiol.* 2017;17(1):209. doi: 10.1186/s12866-017-1117-0
31. Roos IMM, Hattingh MJ. Scanning electron microscopy of *Pseudomonas syringae* pv, *morsprunorum* on sweet cherry leaves. *J Phytopathol.* 1983;108(1):18-25. doi: 10.1111/j.1439-0434.1983.tb00559.x
32. Vorholt JA. Microbial life in the phyllosphere. *Nat Rev Microbiol.* 2012;10(12):828-840. doi: 10.1038/nrmicro2910
33. Deng Y, Chen H, Li C, et al. Endophyte *Bacillus subtilis* evade plant defense by producing lantibiotic subtilomycin to mask self-produced flagellin. *Commun Biol.* 2019;2:368. doi: 10.1038/s42003-019-0614-0
34. Compant S, Reiter B, Sessitsch A, Nowak J, Clement C, Barka E. Endophytic colonization of *Vitis vinifera* L. by plant growth-promoting bacterium *Burkholderia* sp. strain PsJN. *Appl Environ Microbiol.* 2005;71(4):1685-1693. doi: 10.1128/AEM.71.4.1685-1693.2005
35. Compant S, Clement C, Sessitsch A. Plant growth-promoting bacteria in the rhizo- and endosphere of plants: Their role, colonization, mechanisms involved and prospects for utilization. *Soil Biol Biochem.* 2010;42(5):669-678. doi: 10.1016/j.soilbio.2009.11.024
36. Truyens S, Weyens N, Cuypers A, Vangronsveld J. Bacterial seed endophytes: GeNERIa, vertical transmission and interaction with plants. *Environ Microbiol Rep.* 2015;7(1):40-50. doi: 10.1111/1758-2229.12181
37. Liu X, Zhao H, Chen S. Colonization of maize and rice plants by strain *Bacillus megaterium* C4. *Curr*

Microbiol. 2006;52(3):186-190. doi: 10.1007/s00284-005-0162-3

38. Mcinroy JA, Kloepper JW. Survey of indigenous bacterial endophytes from cotton and sweet corn. *Plant Soil.* 1995;173(2):337-342. doi: 10.1007/BF00011472
39. Nongkhlaw FMW, Joshi SR. Microscopic study on colonization and antimicrobial property of endophytic bacteria associated with ethnomedicinal plants of Meghalaya. *J Microsc Ultrastruct.* 2017;5(3):132-139. doi: 10.1016/j.jmau.2016.09.002
40. Devi KA, Pandey P, Sharma GD. Plant growth-promoting endophyte *Serratia marcescens* AL2-16 enhances the growth of *Achyranthes aspera* L., a medicinal plant. *HAYATI J Biosci.* 2016;23(4):173-180. doi: 10.1016/j.hjb.2016.12.006
41. Nongkhlaw FMW, Joshi SR. Epiphytic and endophytic bacteria that promote growth of ethnomedicinal plants in the subtropical forests of Meghalaya, India. *Rev Biol Trop.* 2014;62(4):1295-1308. doi: 10.15517/rbt.v62i4.12138
42. Rakotoniriana EF, Rafamantanana M, Randriamampionona D, et al. Study *in vitro* of the impact of endophytic bacteria isolated from *Centella asiatica* on the disease incidence caused by the hemibiotrophic fungus *Colletotrichum higginsianum. Antonie van Leeuwenhoek.* 2013;103(1):121-133. doi: 10.1007/s10482-012-9791-2
43. Lam PN, Duong DTT, Nguyen VTH, Son CK, Trang VT, Tien PQ. Distribution and antimicrobial activity of endophytic *actinomycetes* isolated from *Litsea cubeba* (Lour.) Pers. In northern provinces of Vietnam. *Vietnam J Sci Technol.* 2017;55(5A):160-168. doi: 10.15625/2525-2518/55/5A/12191
44. Nguyen QH, Nguyen HV, Vu TH-N, et al. Characterization of endophytic *Streptomyces griseorubens* MPT42 and assessment of antimicrobial synergistic interactions of its extract and essential oil from host plant *Litsea cubeba. Antibiotics.* 2019;8(4):197. doi: 10.3390/antibiotics8040197
45. Igarashi Y, Iida T, Sasaki T, Saito N, Yoshida R, Furumai T. Isolation of actinomycetes from live plants and evaluation of antiphytopathogenic activity of their metabolites. *Actinomycetol.* 2002;16(1):9-13. doi: 10.3209/saj.16_9
46. Chen H, Yang C, Ke T, et al. Antimicrobial activity of secondary metabolites from *Streptomyces* sp. K15, an endophyte in *Houttuynia cordata* Thumb. *Nat Prod Res.* 2015;29(23):2223-2225. doi: 10.1080/14786419.2014.1003134
47. Passari AK, Mishra VK, Gupta VK, Yadav MK, Saikia R, Singh BP. *In vitro* and *in vivo* plant growth promoting activities and DNA fingerprinting of antagonistic endophytic *actinomycetes* associates with medicinal plants. *PLoS One.* 2015;10(9):e0139468. doi: 10.1371/journal.pone.0139468
48. Ulfa R, Suryanto D, Munir E. An ability of endophytes from blackboard tree (*Alstonia scholaris*) in increasing chili performance. *J Pure Appl Microbiol.* 2018;12(2):815-825. doi: 10.22207/JPAM.12.2.43.
49. Vinayarani G, Prakash HS. Growth promoting rhizospheric and endophytic bacteria from *Curcuma longa* L. as biocontrol agents against rhizome rot and leaf blight diseases. *Plant Pathol J.* 2018;34(3):218-235. doi: 10.5423/PPJ.OA.11.2017.0225
50. Ramanuj KB, Shelat HN. Plant growth promoting potential of bacterial endophytes from medicinal plants. *Adv Res.* 2018;13(6):1-15. doi: 10.9734/AIR/2018/40014
51. Passari AK, Mishra VK, Gupta VK, Saikia R, Singh BP. Distribution and identification of endophytic Streptomyces species from Schima wallichii as potential biocontrol agents against fungal plant pathogens. *Polish J Microbiol.* 2016;65(3):319-329. doi: 10.5604/17331331.1215611
52. Momin MD, Tripathi SK. Studies of endophytic *actinomycetes* associated with medicinal plants of Mizoram, Northeast, India. *Int J Curr Microbiol Appl Sci.* 2018;7(12):1398-1407. doi: 10.20546/ijcmas.2018.712.167
53. Passari AK, Mishra VK, Leo VV, Gupta VK, Singh BP. Phytohormone production endowed with antagonistic potential and plant growth promoting abilities of culturable endophytic bacteria isolated from *Clerodendrum colebrookianum* Walp. *Microbiol Res.* 2016;193:57-73. doi: 10.1016/j.micres.2016.09.006
54. Singh YR, Khunjamayum R, Khunjamayam R, et al. Plant growth and grain yield production of black rice as influenced by *Ochrobactrum intermedium* AcRz3, an endophyte associated with medicinal plant. *Crop Res.* 2018;53(3-4):183-191. doi: 10.31830/2454-1761.2018.0001.16
55. Devi KA, Pandey G, Rawat AKS, Sharma GD, Pandey P. The endophytic symbiont-*Pseudomonas aeruginosa* stimulates the antioxidant activity and growth of *Achyranthes aspera* L. *Front Microbiol.* 2017;8:1897. doi: 10.3389/fmicb.2017.01897
56. Gohain A, Gogoi A, Debnath R, et al. Antimicrobial biosynthetic potential and genetic diversity of endophytic actinomycetes associated with medicinal plants. *FEMS Microbiol Lett.* 2015;362(19):1-10. doi: 10.1093/femsle/fnv158
57. Doley P, Jha DK. Antimicrobial activity of bacterial endophytes from medicinal endemic plant Garcinia lancifolia Roxb. *Ann Plant Sci.* 2015;4(12):1243-1247.
58. Verma VC, Gond SK, Kumar A, Mishra A, Kharwar RN, Gange AC. Endophytic actinomycetes from A*zadirachta indica* A. Juss.: isolation, diversity, and anti-microbial activity. *Microb Ecol.* 2009;57(4):749-756. doi: 10.1007/s00248-008-9450-3
59. Singh AK, Sharma RK, Sharma V, Singh T, Kumar R, Kumari D. Isolation, morphological identification and *in vitro* antibacterial activity of endophytic bacteria isolated from *Azadirachta indica* (neem) leaves. *Veterinary World.* 2017;10(5):510-516. doi: 10.14202/vetworld.2017.510-516
60. Gangwar M, Kaur N, Saini P, Kalia A. The diversity, plant growth promoting and anti-microbial activities of endophytic actinomycetes isolated from *Emblica officinalis* Gaertn. *Int J Adv Res.* 2015;3(4):1062-1071.
61. Singh SP, Gaur R. Evaluation of antagonistic and plant growth promoting activities of chitinolytic endophytic *actinomycetes* associated with medicinal plants against *Sclerotium rolfsii* in chickpea. *J Apll Microbiol.*

2016;121(2) 506-518. doi: 10.1111/jam.13176
62. Tamreihao K, Ningthoujam DS, Nimaichand S, et al. Biocontrol and plant growth promoting activities of a *Streptomyces corchorusii* strain UCR3-16 and preparation of powder formulation for application as biofertilizer agents for rice plant. *Microbiol Res.* 2016;192:260-270. doi: 10.1016/j.micres.2016.08.005
63. Patel DH, Naik JH, Amaresan N. Synergistic effect of root-associated bacteria on plant growth and certain physiological parameters of banana plant (*Musa acuminata*). *Arch Agron Soil Sci.* 2018;64(7):1021-1031. doi: 10.1080/03650340.2017.1410703
64. Barman D, Dkhar MS. Seasonal variation influence endophytic actinobacterial communities of medicinal plants from tropical decidous forest of Meghalaya and characterization of their plant growth-promoting potentials. *Curr Microbiol.* 2020;77:1689-1698. doi: 10.1007/s00284-020-01988-3
65. Misra N, Gupta G, Jha PN. Assessment of mineral phosphate-solubilizing properties and molecular characterization of zinc-tolerant bacteria. *J Basic Microbiol*. 2012;52(5):549-558. doi: 10.1002/jobm.201100257
66. Prakash P, Karthikeyan B. Isolation and identification of potential diazotrophic endophytic bacteria from sweet flag (*Acorus calamus*) medicinal plant. *Int J Adv Pharma Bio Chem.* 2015;4(3):704-712.
67. Dochhil H, Dkhar MS, Barman D. Seed germination enhancing activity of endophytic *Streptomyces* isolated from indigenous ethno-medicinal plant *Centella Asiatica. Int J Pharm Bio Sci.* 2013;4(1):256-262.
68. Kloepper JW, Ryu C-M. Bacterial Endophytes as elicitors of induced systemic resistance BT - Microbial Root Endophytes. In: Schulz BJE, Boyle CJC, Sieber TN (eds). Springer Berlin Heidelberg, Berlin, Heidelberg, 2006:33-52. doi: 10.1007/3-540-33526-9_3
69. Kumar A, Verma JP. Does plant-Microbe interaction confer stress tolerance in plants: A review? *Microbiol Res.* 2018;207:41-52. doi: 10.1016/j.micres.2017.11.004
70. Goswami M, Deka S. Plant growth-promoting rhizobacteria-alleviators of abiotic stresses in soil: A review. *Pedosphere.* 2020;30(1):40-61. doi: 10.1016/S1002-0160(19)60839-8
71. Sharma P, Jha AB, Dubey RS, Pessarakli M. Reactive oxygen species, oxidative damage, and antioxidative defense mechanism in plants under stressful conditions. *J Bot.* 2012;2012:217037. doi: 10.1155/2012/217037
72. Emamverdian A, Ding Y, Mokhberdoran F, Xie Y. Heavy metal stress and some mechanisms of plant defense response. *Sci World J.* 2015;2015:756120. doi: 10.1155/2015/756120
73. Tiwari S, Lata C. Heavy metal stress, signaling, and tolerance due to plant-associated microbes: An overview. *Front Plant Sci.* 2018;9:452. doi: 10.3389/fpls.2018.00452
74. Mesa V, Navazas A, Gonzalez-Gil R, et al. Use of endophytic and rhizosphere bacteria to improve phytoremediation of arsenic-contaminated industrial soils by autochthonous *Betula celtiberica. Appl Environ Microbiol.* 2017;83(8):e03411-16.doi: doi: 10.1128/AEM.03411-16
75. Singh D, Singh N P, Chauhan SK, Singh P. Developing aluminium-tolerant crop plants using biotechnological tools. *Curr Sci.* 2011;100(12):1807-1814.
76. Gupta S, Pandey S. ACC deaminase producing bacteria with multifarious plant growth promoting traits alleviates salinity stress in French Bean (*Phaseolus vulgaris*) plants. *Front Microbiol.* 2019;10:1506. doi: 10.3389/fmicb.2019.01506
77. Strobel G, Daisy B. Bioprospecting for microbial endophytes and their natural products. *Microbiol Mol Biol Rev.* 2003;67(4):491-502. doi: 10.1128/MMBR.67.4.491-502.2003
78. Strobel G. The emergence of endophytic microbes and their biological promise. *J Fungi.* 2018;4(2):57. doi: 10.3390/jof4020057
79. Ritchie GSP. Soluble aluminium in acidic soils: Principles and practicalities. In: Date RA, Grundon NJ, Rayment GE, Probert ME. (eds) Plant-Soil Interactions at Low pH: Principles and Management. Developments in Plant and Soil Sciences. 1995;64:23-33. Springer, Dordrecht. doi: 10.1007/978-94-011-0221-6_2
80. Haling RE, Simpson RJ, Culvenor RA, Lambers H, Richardson AE. Effect of soil acidity, soil strength and macropores on root growth and morphology of perennial grass species differing in acid-soil resistance. *Plant Cell Environ.* 2011;34(3):444-456. doi: 10.1111/j.1365-3040.2010.02254.x
81. Goswami G, Deka P, Das P, et al. Diversity and functional properties of acid-tolerant bacteria isolated from tea plantation soil of Assam. *3 Biotech.* 2017;7(3):229. doi: 10.1007/s13205-017-0864-9
82. Tamreihao K, Salam N. Ningthoujam DS. Use of acidophilic or acidotolerant actinobacteria for sustainable agricultural production in acidic soils. D. Egamberdieva et al. (eds), Extremophiles in Eurasian Ecosystems: Ecology, Diversity, and Applications, Microorganisms for Sustainability. 2018;8:453-464. doi: 10.1007/978-981-13-0329-6_17
83. Tamreihao K, Nimaichand S, Chanu SB, et al. Acidotolerant *Streptomyces* sp. MBRL 10 from limestone quarry site showing antagonism against fungal pathogens and growth promotion in rice plants. *J King Saud Univ Sci.* 2018b;30(2):143-152. doi: 10.1016/j.jksus.2016.10.003
84. Zakalyukina YV, Zenova GM. Antagonistic activity of soil acidophilic actinomycetes. *Biol Bull.* 2007;34:329-332. doi: 10.1134/S1062359007040036
85. Poomthongdee N, Duangmal K, Pathom-Aree W. Acidophilic *actinomycetes* from rhizosphere soil: Diversity and properties beneficial to plants. *J Antibiot.* 2015;68(2):106-114. doi: 10.1038/ja.2014.117
86. Jain S K, Kumar V, Saharia M. Analysis of rainfall and temperature trends in northeast India. *Int J Climatol.* 2013;33(4):968-978. doi: 10.1002/joc.3483
87. Singh LK, Devi SR. Important traditional soil and water conservation techniques practices for sustainable agricultural in North East India. *Ind J Hill Farming.* 2018;31(2):220-226.
88. Kasim WA, Osman ME, Omar MN, El-Daim IAA, Bejai S, Meijer J. Control of drought stress in wheat using plant-growth-promoting bacteria. *J Plant Growth Regul.* 2013;32(1):122-130. doi: 10.1007/s00344-012-

9283-7

89. Vurukonda SSKP, Vardharajula S, Shrivastava M, Sk ZA. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiol Res.* 2016;184:13-24.doi: doi: 10.1016/j.micres.2015.12.003
90. Zhang J, Zhang S, Cheng M, et al. Effect of drought on agronomic traits of rice and wheat: A meta-analysis. *Int J Environ Res Public Health.* 2018;15(5):839. doi: 10.3390/ijerph15050839
91. Wu LM, Fang Y, Yang H, Bai LY. Effects of drought-stress on seed germination and growth physiology of quinclorac-resistant *Echinochloa crusgalli. PLoS One*. 2019;14(4):e0214480. doi: 10.1371/journal.pone.0214480
92. Ojuederie OB, Olanrewaju OS, Babalola OO. Plant growth promoting rhizobacterial mitigation of drought stress in crop plants: Implications for sustainable agriculture. *Agronomy.* 2019;9(11):712. doi: 10.3390/agronomy9110712
93. Das A, Ghosh PK, Choudhury BU, et al. Climate change in Northeast India: recent facts and events-worry for agricultural management, ISPRS Archives XXXVIII-8/W3 Workshop Proceedings: Impact of Climate Change on Agriculture. 2009;32-37.
94. Food and Agriculture Organization of the United Nations [FAO]. The Impact of Disasters and Crises on Agriculture and Food Security. Rome: FAO. 2017;168.
95. Ravanbakhsh M, Sasidharan R, Voesenek LACJ, Kowalchuk GA, Jousset A. ACC deaminase-producing rhizosphere bacteria modulate plant responses to flooding. *J Ecol.* 2017;105(4):979-986. doi: 10.1111/1365-2745.12721
96. Kim AY, Shahzad R, Kang SM, et al. IAA-producing *Klebsiella variicola* AY13 reprograms soybean growth during flooding stress. *J Crop Sci Biotechnol.* 2017;20(4):235-242. doi: 10.1007/s12892-017-0041-0