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 km², 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. 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. 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. 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. 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. 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. 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.

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. 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. 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.

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. 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.\textsuperscript{22,23} Bacteria defective in flagellar motility hinder the colonization of plant roots. For example, \textit{Pseudomonas} mutant strains defective in flagella-driven chemotaxis (\textit{cheA} or \textit{pilA}) could not successfully colonize the root.\textsuperscript{24,25} Kost et al.\textsuperscript{26} reported the role of root exudates such as oxalate in root colonization by \textit{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 \textit{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.\textsuperscript{17,27-29} Hallmann et al.,\textsuperscript{30} reported that \textit{Enterobacter asburiae} enter the host plant by hydrolyzing cellulose of plant cell wall. Phytophthora bacteria also enter plant tissue through stomata, particularly on leaves and, also through wounds and cracks generated by wind, insect and pathogen attacks.\textsuperscript{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, \textit{Bacillus subtilis} colonized \textit{Arabidopsis thaliana} by producing subtilomycin that binds to flagellin, thereby reducing the induction of plant defence mechanisms. \textit{Bacillus subtilis} also colonize the host plant \textit{Amorphophallus konjac} by producing subtilomycin.\textsuperscript{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.\textsuperscript{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 \textit{Bacillus megaterium} in maize and rice plant.\textsuperscript{37} Mcinroy and Kloepper\textsuperscript{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, Nongklaw and Joshi\textsuperscript{39} observed the transverse sectioned of roots and leaves for colonization of endophytes within \textit{Centella asiatica}, \textit{Houttuynia cordata} and \textit{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.\textsuperscript{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
| Endophytic isolate                  | Host plant                        | Growth inhibition                                      | Cell wall degrading enzymes | Ref. |
|------------------------------------|-----------------------------------|--------------------------------------------------------|----------------------------|------|
| Streptomyces olivaceus, Rhynchotoechum ellipticum | Fusarium oxysporum, Fusarium proliferatum | 4                                                      |                            |      |
| Streptomyces sp.                    | Mussaenda roxburghii              | Sclerotium rolfsi, Sclerotinia sclerotiorum            | 6                          |      |
| Acinetobacter sp., Pseudomonas sp. | Litsea cubeba                     | Fusarium oxysporum, Emericella nidulans                | 41                         |      |
| Bacillus siamensis                 | Centella asiatica                 | Fusarium oxysporum Emericella nidulans                | 41                         |      |
| Bacillus subtilis                  | Centella asiatica                 |                                                        |                            |      |
| Serratia marcescens                | Centella asiatica                 |                                                        |                            |      |
| Bacillus mycoides                  | Rubia cordifolia                  |                                                        |                            |      |
| Streptomyces anulatus, Schima wallichi | Fusarium culmorum, Fusarium proliferatum | 51                                                      |                            |      |
| Streptomyces sampsonii,            | Mikania micranth Kunth, WI        | Fusarium oxysporum, Fusarium rolferatum                | 52                         |      |
| Streptomyces sp.                   | Clerodendrum colebrookianum Walp. | Rhizoctonia solani, Fusarium species, Colletotrichum capsici | 53                         |      |
| Bacillus sp., Paenibacillus sp.    | Acorus calamus                    | Rhizoctonia solani, Helminthosporium oryzae, Fusarium oxysporum | 54                         |      |
| Ochrobactrum intermedium           | Achyranthes aspera L.             | Rhizoctonia solani                                     | 55                         |      |
characteristics of endophytic bacteria isolated from ethnomedicinal plants of NEIHR are shown in Table 1.

Nongkhlaw and Joshi\textsuperscript{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., \textit{Centella asiatica}, \textit{Litsea cubeba}, \textit{Rubia cordifolia}, \textit{Zingiber montanum}, \textit{Acmella oleracea}, \textit{Houttuynia cordata}, \textit{Aloe vera} and \textit{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 \textit{Bacillus siamensis} isolated from \textit{Litsea cubeba} and \textit{Bacillus subtilis} from \textit{Centella asiatica} exhibits antagonistic activity against \textit{Fusarium oxysporum} and \textit{Emericella nidulans}. \textit{Serratia marcescens} and \textit{Bacillus subtilis} strains obtained from \textit{Centella asiatica} produce cell wall degrading enzymes such as chitinase and cellulase. Strains \textit{Bacillus mycoides}, \textit{Pseudomonas baetica}, \textit{Bacillus sp.} and \textit{B. licheniformis} isolated from \textit{Rubia cordifolia}, \textit{Zingiber montanum}, \textit{Houttuynia cordata} and \textit{Potentilla fulgens} produced cell wall degrading enzymes such as chitinase and cellulase that can act as biocontrol agents against fungal pathogens.

Rakotoniriana et al.\textsuperscript{42} isolated endophyte \textit{Bacillus subtilis} and \textit{Pseudomonas fluorescens} from leaves of \textit{Centella asiatica} collected from Madagascar that demonstrated antagonistic activity against \textit{Colletotrichum higginsianum}. Foliar application of bioactive strain \textit{Bacillus subtilis} reduced the incidence and severity of anthracnose disease. Endophytic bacteria associated with \textit{Litsea cubeba} grown in Vietnam have been reported to exhibit antimicrobial activity.\textsuperscript{43,44} Actinobacterial strain associated with \textit{Houttuynia cordata} collected from Japan also possesses antifungal activity against \textit{Alternaria brassicicola} and \textit{Fusarium oxysporum}. Treatment of strain to Chinese cabbage seedlings suppresses the disease caused by \textit{Alternaria brassicicola}.\textsuperscript{45} Chen et al.\textsuperscript{46} reported 2-pyrrol formic acid, a compound produced by endophyte \textit{Streptomyces} sp. K15 of \textit{Houttuynia cordata}, having good antifungal activity against \textit{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 \textit{Alstonia scholaris}, \textit{Centella asiatica}, \textit{Clerodendrum colebrookianum}, \textit{Curcuma longa}, \textit{Eupatorium adoratum}, \textit{Mirabilis jalapa} and \textit{Musa superba}. Majority of the isolates belong to the genus \textit{Streptomyces} followed by \textit{Microbacterium}. Of these, 22 isolates showed an inhibitory effect against at least one tested phytopathogen. Fourteen isolates exerted significant inhibitory activity against \textit{Rhizoctonia solani}, \textit{Fusarium graminearum} and \textit{F. oxysporum}. Promising endophytic strains \textit{Microbacterium} sp., \textit{Leifsonia xyli} and \textit{Streptomyces} sp. demonstrated significant inhibitory against all the test pathogens viz.; \textit{Rhizoctonia solani}, \textit{Fusarium oxysporum} f. sp. \textit{ciceri}, \textit{F. proliferatum}, \textit{F. oxysporum}, \textit{F. graminearum} and \textit{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.\textsuperscript{47}

\textit{Carnobacterium gallinarum} and \textit{C. maltaromaticum} isolated from root and leaves of \textit{Alstonia scholaris}, a native of Indonesia, inhibit the growth of \textit{Fusarium sp.} and \textit{Colletotrichum} sp. The two strains promoted the growth of chilli plant and protected from \textit{Colletotrichum} fruit rot and \textit{Fusarium} wilt disease.\textsuperscript{48} Investigation of endophytic bacteria \textit{Pseudomonas aeruginosa} isolated from \textit{Curcuma longa} L. rhizome collected from Karnataka, India displays good antagonistic effect against \textit{Pythium aphanidermatum} and \textit{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 \textit{Curcuma longa} plant.\textsuperscript{49} Ramanuj and Shelat\textsuperscript{50} also observed inhibition of \textit{Alternaria alternata} and \textit{Aspergillus niger} growth by chitinase producing \textit{Beijerinckia fluminensis}, an endophyte associated with \textit{Curcuma longa}.

Out of 22 \textit{Streptomyces} isolates obtained from medicinal plant \textit{Schima wallichi} collected from Dampa Tiger Reserve, Mizoram, 15 strains exhibited antagonistic activity against one or more of the test pathogens viz.; \textit{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.\textsuperscript{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, Scoparia dulcis and Senecio scandens Buch.-Ham. Seven strains belonging to genus Streptomyces viz.; Streptomyces somalensis, 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.\textsuperscript{52}

Of 73 endophytic bacterial isolates derived from Clerodendrum colebrookianum Walp. by Passari et al.\textsuperscript{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. BPSCAC3, Bacillus sp. BPSCAC6 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. BPSCAC6 demonstrated 57.1% disease suppression while, Bacillus sp. BPSCAC3 and Paenibacillus sp. showed 45.5% and 38% respectively.

Passari et al.\textsuperscript{4} isolated 169 actinobacteria from the endemic medicinal plant Rhynchotoeochium 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. BPSCAC121 showed maximum antagonistic activity against Fusarium oxysporum. Antifungal antibiotics, ketoconazol, fluconazole, rifampicin and miconazole were detected in Streptomyces sp. BPSCAC101 and Streptomyces thermocarboxydyus. The concentration of ketoconazol produced by Streptomyces sp. BPSCAC101 and Streptomyces thermocarboxydyus 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 \textit{in vivo} conditions. Singh et al.\textsuperscript{54} isolated 21 endophytic bacteria from the rhizomes of Acorus calamus collected from different habitats of Manipur. Isolate \textit{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 \textit{Pseudomonas aeruginosa} isolated from leaves and stems of Achyranthes aspera L. display mycelial growth inhibition to Rhizoctonia solani.\textsuperscript{55}

\textsuperscript{51} Tamreihao et al. | J Pure Appl Microbiol | 16(2):747-762 | June 2022 | https://doi.org/10.22207/JPAM.16.2.05
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. Five bacterial endophytes associated with endemic medicinal plant Garcinia lancifolia Roxb. of Assam showed antimicrobial activity against Aspergillus niger and Alternaria alternata. Pandey et al. 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. Endophytic actinobacterial isolates from Emblica officinalis also exhibited antifungal, antibacterial and PGP activities. Actinobacteria isolated from Rauwolfia 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.

### 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., Bacillus sp., Serratia marcescens, Bacillus subtilis, Serratia marcescens, Bacillus mycoides, Bacillus siamensis, Lysinibacillus xylanilyticus Streptomycyes thermocarboxydus Bacillus sp., Paenibacillus sp., Pseudomonas sp. Ochrobactrum intermedium Pseudomonas aeruginosa Streptomyces spp. | Mussaenda roxburghii Centella asiatica Houttuynia cordata Achyranthes aspera L Costus speciosus Sm. Houttuynia cordata Thumb, Solanum khasianum C.B. Clarke, Zanthoxylum armatum DC | IAA and siderophore production, P solubilization, N fixation ACC deaminase IAA and siderophore production, P solubilization, N fixation P solubilization, N fixation ACC deaminase P solubilization, N fixation IAA and ammonia production, P solubilization IAA and ammonia and siderophore production, P solubilization IAA and siderophore production, P solubilization, N solubilization, N fixation IAA, ACC deaminase and siderophore production, P solubilization | 6 39, 41 40 41 41 41 52 53 54 55 54 64 |

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.\textsuperscript{62} PGP activities of endophytic bacteria isolated from ethnomedicinal plants of NEIHR are shown in Table 2.

Passari et al.\textsuperscript{53} investigate the PGP potential of the 52 endophytic isolates associated with \textit{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 92 mg/100 mL. Siderophore production of 16 and 5 isolates were chosen for studying plant growth promotion under greenhouse conditions. The treatment of chilli plants with a mixture of two promising strains showed further enhancement in growth as compared to inoculation with the individual strain.\textsuperscript{47}

Patel et al.\textsuperscript{63} documented that \textit{Bacillus} sp., \textit{Enterobacter} sp., \textit{Klebsiella} sp. and \textit{Microbacterium} sp. associated with \textit{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 \textit{Pseudomonas aeruginosa} associated with \textit{Curtis longa} rhizome significantly promote the growth and rhizome yield of host plant under greenhouse conditions.\textsuperscript{49} \textit{Carnobacterium gallinarum} and \textit{C. maltaromaticum} isolated from root and leaves of \textit{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.\textsuperscript{48}

Nongkhlaw and Joshi\textsuperscript{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., \textit{Centella asiatica}, \textit{Litsea cubeba}, \textit{Rubia cordifolia}, \textit{Zingiber montanum}, \textit{Acmella oleracea}, \textit{Houttuynia cordata}, \textit{Aloe vera} and \textit{Potentilla fulgens} display antimicrobial activities. \textit{Serratia marcescens} and \textit{Bacillus subtilis} strains obtained from \textit{Centella asiatica} could solubilize P and fix atmospheric N. Similarly, \textit{Bacillus siamensis} and \textit{Lysinibacillus xylanilyticus} isolated from \textit{Litsea cubeba} have PGP traits such as soluble P and N fixing. Bioactive isolates \textit{Pseudomonas baetica}, \textit{Pseudomonas paleroniana}, \textit{Herminimonas saxobsidens} and \textit{Bacillus licheniformis} isolated...
Barman and Dkhar sp. PAK9 were able to grow on N-free medium. Pandey et al. evaluated the endophytic bacteria isolated from Mussaenda roxburghii of Arunachal Pradesh for PGP activity and demonstrated that Pseudomonas sp. PK2, Klebsiella sp. PK3, Acinetobacter sp. PK6, and Pseudomonas sp. could solubilize inorganic P and displayed N fixation. ACC deaminase gene was detected in Bacillus sp. and Bacillus mycoides.

Pandey et al. evaluated the 7 endophytic bacteria isolated from Mussaenda roxburghii of Arunachal Pradesh for PGP activity and demonstrated that Pseudomonas sp. PK2, Klebsiella sp. PK3, Acinetobacter sp. PK6, 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. PK1 and Acinetobacter sp. PK9 were able to produce siderophore. Similarly, strains Pseudomonas sp. PK2, Pseudomonas sp. PK7, Pseudomonas sp. PK8 and Acinetobacter sp. PK9 were able to grow on N-free medium.

Barman and Dkhar investigated the PGP traits of the endophytic actinobacterial communities associated with 6 medicinal plants of Meghalaya viz., Clerodendrum colebrookiunum 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 Scoparia dulcis of Mizoram were able to solubilize P and, produce IAA and ammonia. Similarly, 5 strains isolated from Garcinia lancifolia Roxb. could produce IAA and ammonia, and solubilize tricalcium P. Devi et al. 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.

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. 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.

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.\(^{58,66}\) 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.

**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.\(^{83,84}\) 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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