



Epiphytic Bacteria and their uses in Sustainable Agriculture: A Review

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Abstract

Agriculture plays a pivotal role in the Indian economy, contributing to ~ 17% of the total GDP, providing employment to ~58% of the population. With a growing population of over 8 billion people, demand for food is rising. This demand for food needs to be mandated with restrictions to safely operate within the planetary boundaries (i.e., *biogeochemical flows, land-system change, freshwater-use and ocean acidification*). This can be achieved by using biological plant growth promoting agents as natural alternatives. Epiphytic bacteria harboured by surfaces of plants such as leaves, stems and roots show a potential in sustainable agriculture. They have the potential to gradually replace chemical fertilisers due to their ability to promote plant growth through phytohormones and suppress phytopathogens. They do this through mechanisms such as competitive exclusion and nutrient solubilisation, as discussed in this review. Epiphytic bacteria can solubilise essential nutrients such as zinc, potassium and phosphorus making them bioavailable to plants. Certain bacterial species can fix nitrogen from the atmosphere, which provide additional symbiotic benefits to plants. Additionally, epiphytic bacteria can produce some phytohormones like auxin, cytokinin and gibberellin which the plant use for growth and development. They also secrete antimicrobial compounds making them less susceptible to disease causing pathogens. However, some species of epiphytic bacteria can be harmful to plants and therefore their pathogenicity could be used to produce biological herbicides providing natural alternatives. These bacteria can also be used in bioremediation methods to prevent eutrophication. Despite their promising potential, further research is required to understand the underlying pathology and mechanisms by which they offer plant promoting benefits. Identifying specific environmental conditions, crop / soil types where these bacteria can operate at optimal capacity needs to be investigated.



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Abbreviations

UN	United Nations
IPM	Integrated Pest Management
ATP	Adenosine Triphosphate
IAA	Indole-3-Acetic Acid
ABA	Absciscic Acid
GA	Gibberellic Acid
ACC Deaminase	1-Aminocyclopropane-1-carboxylic acid deaminase
N ₂	Nitrogen Gas
NH ₃	Ammonia
TCP	Tri-Calcium Phosphate
DCP	Di-Calcium Phosphate
pH	Potential of Hydrogen
BOD	Biological Oxygen Demand
CF	Chemical Fertiliser

Introduction

The human population continues to rise every year and with problems such as global warming, we are pushed to find solutions to increase food production without harming the environment. The global population is predicted to reach 10 billion people by 2050.¹ With an increase in population, a 60% increase in food production is expected by the United Nations (UN).² This is where the concept of sustainable agriculture comes into the picture - producing food while protecting the environment.

There are many ways to practice sustainable agriculture such as crop rotation, agroforestry, organic farming and integrated pest management (IPM).³ IPM is an interesting method used in sustainable agriculture where biological, cultural or mechanical techniques prevent disease and the spread of pests.^{4,5} In this review, we will be focusing on the biological methods in IPM.

Microbes, for instance, can be used in the place of harmful chemical pesticides to promote plant growth and prevent disease.^{6,7} One such type of microbe is epiphytic bacteria.⁸ Epiphytic bacteria live on the surface of plants which includes leaves, roots, and stems. Leaves especially can host bacterial populations of up to 10 million microbes per square centimetre.^{9,10} Most epiphytes are rod-shaped, gram-negative, pigmented and fermentative bacteria.^{11,12} They act as mutually beneficial organisms and don't affect the plant negatively. The bacteria promote plant growth and in exchange, the plants provide

essential nutrients. Hence, plants and epiphytic bacteria have a mutualistic relationship where two species live in close association with each other.¹³ In the marine environment, for instance, epiphytic bacteria reside on macroalgae and in return provide the algae with necessary nutrients and protection from pathogens.^{14,15}

Another example of mutualistic interaction between species includes the biosurfactants produced by the bacteria *Pseudomonas syringae* and its benefits for plants.^{16,17} These substances can alter cuticle permeability allowing the plant to retain water and nutrients on leaf surfaces. This not only improves bacterial growth but also allows the plant to survive harsh conditions when essential nutrients need to be retained.^{18,17}

However, sometimes if bacterial populations grow significantly, it can harm the plant. Bacteria like *Pseudomonas* sp., *Stenotrophomonas* sp., and *Achromobacter* sp. increase water permeability in plants such as *Hedera* (ivy) and *Prunus* (cherry).^{19,17} If water availability on leaf surfaces increases excessively, it provides an ideal environment for harmful microbes to thrive, which can potentially inhibit plant growth or even kill the plant. This can be used strategically in sustainable agriculture to get rid of plants such as weeds and other invasive species.

This comprehensive review paper will investigate the functions of epiphytic bacteria and how they can be harnessed in the field of sustainable agriculture.

Competition between Epiphytic Bacteria and Plant Pathogens for Resources

Pathogens on plants must compete with epiphytic bacteria for nutrients and space- both essential to survival.^{20,21} Microbes need carbon, nitrogen, hydrogen, oxygen, sulphur and phosphorus to grow efficiently. Carbon, hydrogen and oxygen are mainly used as energy sources. Nitrogen, sulphur and phosphorus are involved in the production of essential substances such as amino acids and carbohydrates. Nitrogen especially is important in the production of amino acids, purines, pyrimidines and some carbohydrates and lipids. Phosphorus is present in phospholipids, nucleic acids and nucleotides like Adenosine Triphosphate (ATP). Finally, sulphur is required for the synthesis of certain amino acids such as cysteine and methionine. It is also important to produce vitamins like vitamin B7.²²

Marine epiphytic bacteria residing on macroalgae obtain carbon and polysaccharides by producing enzymes capable of breaking down the cell walls of the algae.²³ Epiphytic bacteria on plants primarily reside near the stomata, on the veins, or even the epidermal grooves of the leaves. This is because these areas are rich in nutrients such as sugars and water.²⁴ The presence of such epiphytic bacteria can increase competition for these nutrients between pathogenic organisms resulting in the competitive exclusion of the harmful pathogens. This reduces the likelihood of infection and colonization by pathogens.²¹ For instance, *Pseudomonas fluorescens* A506 competes with other pathogens for sugars present on the surface of bean leaves. Sugar concentration on these leaves decreased by 10% after the colonization of *P. fluorescens* A506.^{25,21} Additionally, sugars on leaves are already scarce as permeability is limited between the apoplast and the leaf surface. For instance, fructose and sucrose are available in limited quantities on leaf surfaces.^{24,21} The limited quantity of sugars available leads to increased competition which can potentially eliminate populations of harmful pathogens.²¹ Similarly, populations of phytopathogen *Erwinia amylovora* reduce due to competitive exclusion after the colonization of epiphyte *Pantoea agglomerans* E325 on apple flowers.^{26,21} The stigma of the apple flower is the primary area where bacterial colonization occurs. The E325 strain of epiphyte *Pantoea agglomerans* colonized this area first, making it harder for the pathogen to grow in the same space. This strain

can also produce antibiotics that directly suppress the growth of *E. amylovora*. This was seen after research from a study found that mutants of the same strain are incapable of producing antibiotics, proving that the E325 strain is crucial in the suppression of pathogens present in apple flowers. This reduces the likelihood of the fire blight disease caused by *Erwinia amylovora*.²⁶

Antimicrobial Agents Produced by Epiphytic Bacteria

In addition to competition for resources, some epiphytic bacterial species produce antimicrobial agents which prevent the growth of pathogens and parasites. Marine epiphytic bacteria specifically, can produce antiviral, antibacterial and antifungal bio-compounds and bioagents. Common phyla of epiphytic bacteria present in marine algae include *Proteobacteria*, *Firmicutes*, *Bacteroidetes*, *Actinobacteria*, *Cyanobacteria*, *Planctomycetes*, *Verrucomicrobia*, and *Deinococcus*.^{27,23} However, epiphytic bacteria on marine algae may not be suitable for direct use in fertilizers and sustainable agriculture due to their high salt content. Nevertheless, the beneficial secondary metabolites and enzymes that they produce can be extracted for use in sustainable agriculture. Epiphytic bacteria on macroalgae produce violacein, macro-lactines M and G, haliangicin, korormicin, chlorophyll d, and oligomycin A, all of which are secondary metabolites with antiprotozoal, antibiotic, antifungal, and antifouling properties.^{28,15}

Streptomyces, a genus of actinobacteria, are gram-positive aerobic bacteria²⁹ that produce antimicrobial substances which prevent other pathogens from colonizing the surface of leaves, microalgae or macroalgae.^{30,15} Table 1 below shows a few *Streptomyces* species and how they can be used in sustainable agriculture.

Another instance is the production of secondary metabolites from *Bacillus* spp. This bacterium produces 2-n-pentyl-4-quinolinol and 4-hydroxy-benzaldehyde which are secondary metabolites with anti-algal, anti-microbial and anti-peronosporomycetal effects. Additionally, specific bacteria act against specific microorganisms. For instance, *Pseudoalteromonas tunicate* produces secondary metabolites that protect plants from parasites such as *Caenorhabditis elegans*.^{37,15} Similarly, Filho *et al*

proved that *Paenibacillus macerans* and *Bacillus pumilus* can decrease the effects of bacteria - *Xanthomonas vesicatoria* and fungi - *Alternaria solani* that affect tomato plants. Experiments conducted in the laboratory revealed that these epiphytic bacteria produce antimicrobial compounds

that form inhibition zones around pathogens, preventing their growth. This process is referred to as antibiosis.³⁸ Another study by Halfeld-Vieira *et al* showed that the epiphytic bacterium *Bacillus cereus* can defend against pathogens like *Phytophthora infestans*.^{39,40}

Table 1: Secondary metabolites produced by Streptomyces species

Streptomyces Species	Secondary Metabolites	Bioactivity	Pathogen and Disease	Mechanism of Action	References
<i>Streptomyces avermitilis</i> , <i>Streptomyces cinnamomensis</i> , and <i>Streptomyces canus</i>	No specific secondary metabolites	Siderophores, chitinase and lignocellulolytic activity	<i>Cerotocystis fimbriata</i> - causes black rot disease <i>Fusarium oxysporum</i> - causes fusarium wilt disease	Siderophores deprive the pathogens of iron. Chitinase breaks down chitin in fungal cell walls. Lignocellulolytic activity breaks down lignocellulose resulting in the death of the pathogens.	31,32
<i>Streptomyces rochei</i>	Palmitic acid, (Z)-hexadec-11-enoic acid, pentadecanoic acid, and oleic acid	Antifungal	<i>Fusarium graminearum</i> - causes fusarium head blight	Competitive inhibition	33,32
<i>Streptomyces globosus</i>	No specific secondary metabolite	Antifungal	<i>Thielaviopsis punctulata</i> - causes black rot disease in date palm plants.	Inhibition zones which suppress the pathogen's growth.	34,32
<i>Streptomyces vinaceusdrappus</i>	Chitinase	Antifungal	<i>Rhizoctonia solan</i> - causes root rot disease in tomato plants	Chitinase hydrolyses chitin which breaks the fungal cell wall	35,32
<i>Streptomyces sindeneusis</i>	No specific secondary metabolite	Antifungal	<i>Magnaporthe oryzae</i> - causes rice blast disease	Creates inhibition zones.	36,32

Blight and leaf spot diseases are common in many plants such as cotton and maize. These infections can be countered using a species of epiphytic gram-negative bacteria called *Pseudomonas fluorescens*. It is capable of fighting leaf spot disease-causing pathogens like *Alternaria*, *Helminthosporium*, and *Myrothecium*.⁴¹ Isolates of these epiphytic bacteria

can also be sprayed on grass infected with a genus of fungi called *Drechslera*.⁴² Another study by Pujol *et al* showed that *P. fluorescens* can grow into a large population on apple and pear trees, protecting them from *Erwinia amylovora*.^{43,40} *P. fluorescens* produces siderophores, molecules that bind to iron, reducing its availability to *E. amylovora*, and thereby limiting its

growth.⁴⁴ Similarly, a study by Sartori *et al* revealed that a common disease in maize plants, northern leaf blight, caused by *Exserohilum turcicum* can be treated using the genera *Bacillus* and *Pantoea*. Not only do these bacteria prevent disease using the process of antibiosis, but they also prevent the pathogen from attaching itself to the plant by creating a physical barrier on the leaf surface.^{18,45}

In summary, epiphytic bacteria are useful in preventing plant diseases as they utilize mechanisms like antibiosis and competitive exclusion to get rid of phytopathogens. This results in plant growth promotion. Many studies prove the effectiveness of epiphytic bacteria in preventing and fighting against diseases. For instance, *Xanthomonas translucens* cause the leaf streak disease in rice, however, this can be countered by spraying the plant with isolates of *Erwinia* or *Pseudomonas*. Apple leaf scars caused by *Nectria galligena* can be countered using *Bacillus subtilis*. Similarly, specific to peanut or tobacco plants, *Pseudomonas cepacia* counters *Cercospora* and *Bacillus* counters *Alternaria*.⁴²

Plant Growth-Promoting Hormones Produced by Epiphytic Bacteria

In addition to producing antimicrobial compounds and competing for resources, epiphytic bacteria also use phytohormones as a means of plant growth promotion. These bacteria can produce essential hormones like auxins, cytokinins, and gibberellins.^{46,10}

Auxins

All aspects of plant growth and development are controlled by phytohormones. Auxins, for example, control the differentiation and elongation of cells in the root and shoot. The hormone is responsible for processes such as phototropism, where plants grow towards a light source and gravitropism, where roots grow downwards. During phototropism, light falls on one side of the plant causing auxins to migrate to the opposite side of the plant away from light. The presence of auxins in the cells on this side initiates cell elongation causing the plant to grow towards the light source. In the case of gravitropism, when the root is horizontal, auxins migrate to the lower part of the root which inhibits cell elongation in that area. Hence, root cells at the top elongate at a higher rate than the bottom of the root causing the root to grow

downwards.⁴⁷ A species of *actinobacteria* called *Streptomyces hygroscopicus* TP-A0451, found on the stem of *Pteridium aquilinum*, has auxin-like effects as they improved root elongation in *Phaseolus vulgaris* (kidney bean) hypocotyls.^{48,49}

Indole-3-acetic acid (IAA)

Pseudomonas fluorescens can produce a type of auxin called Indole-3-acetic acid (IAA). However, IAA production is influenced by environmental factors such as temperature. Moderate temperatures are optimal to produce the hormone. Too high or too low temperatures negatively impact IAA synthesis. The hormone's production is also heavily dependent on the availability of an amino acid called tryptophan because this molecule is used as a precursor to IAA production.^{50,51} Epiphytic bacteria like *Streptomyces* can produce this hormone.^{52,49} Species such as *Streptomyces atrovirens* ASU14 use tryptophan to produce 22 µg/mL of IAA.^{53,49} Other *Streptomyces* species that can produce this hormone include *S. olivaceoviridis*, *S. rimosus*, and *S. viridis*.^{54,55} The IAA hormone controls cell division, apical dominance, vascular differentiation, lateral root development,⁵⁶ root initiation, cell elongation and cell enlargement. As roots develop better due to the presence of this hormone, they can cover more surface area which allows for greater nutrient and water intake. This directly improves plant growth and development. From the study conducted by War Nongkhlaw *et al*, it was found that *Raoultella ornithinolytica* and *Pantoea eucalypti* are two epiphytic bacterial species that produce high levels of the IAA hormone.⁵⁷ The hormone also enhances plant growth and various plant mechanisms. It improves the plants' defence system through the synthesis of molecules such as phytoalexins, phenylpropanoids, and pathogenicity-related proteins.^{58,55}

Cytokinin

Another major phytohormone responsible for plant growth is cytokinins.⁵⁹ Examples of epiphytic bacteria that produce cytokines are *Bacillus*, *Pseudomonas* and *Methylobacterium*.⁶⁰ Cytokinins are remarkable in increasing the stress tolerance of plants.^{61,59} For instance, during droughts, cytokinins can regulate stomatal closure, hence reducing the rate of transpiration, which in turn prevents water loss.^{62,59} Furthermore, cytokinins have been shown to reverse the effects of abscisic acid (ABA) hence promoting

plant growth. The presence of ABA inhibits seed germination and post-germination growth. However, cytokinins can counter this inhibitory effect and promote seed germination as seen in the case of plant species *Arabidopsis thaliana*.⁶³ When higher concentrations of cytokinins are being produced by epiphytic bacteria they can act as plant growth promoters by increasing resistance to environmental stressors and promoting seed germination. In contrast, reducing cytokinin levels can also be good as it results in enhanced root development and growth which increases surface area for water absorption. The advancement in the root system of plants due to limited cytokinins can increase nutrient uptake, which sustains the plant during times of stress and promotes plant growth during normal times.^{64,59} A study conducted by Kilkno and Kutschera showed the potential of Methylo-bacterium species in root growth

and development. The study focused on *Arabidopsis thaliana* as the model plant species and found that under sterile conditions the seedlings showed limited growth. However, in normal conditions where soil is present with beneficial microbes, root development improves. Taking Methylo-bacterium species and adding them to the sterile conditions showed similar levels of growth as in normal conditions. This proved that Methylo-bacterium is a necessary epiphytic microbe that enhances root development. This happened due to the production of phytohormones such as cytokinins and auxins by the epiphytic bacteria. The cytokinins played a crucial role in root elongation while the auxins enhanced root structure. The IAA hormone positively influenced root elongation and branching. Among the five different species tested, *Methylobacterium mesophilicum* had the greatest effect on root elongation.⁶⁵

Table 2: Gibberellin-producing epiphytic bacteria and their associated host plants

Bacteria	Gibberellins produced	Host Plant (Scientific name and common name)	Reference
<i>Bacillus amyloliquefaciens</i>	GA ₄ , GA ₅ , GA ₈ , GA ₉ , GA ₁₂ , GA ₁₉ , GA ₂₀ , GA ₂₄ , GA ₃₆ , GA ₅₃	Scientific Name: <i>Oryza sativa</i> Common Name: Asian rice	72
<i>Bacillus cereus</i>	GA ₁ , GA ₃ , GA ₄ , GA ₇ , GA ₉ , GA ₁₂ , GA ₁₉ , GA ₂₀ , GA ₂₄ , GA ₃₄ , GA ₃₆ , GA ₄₄ , GA ₅₃	Scientific Name: <i>Capsicum annum</i> Common Name: Red bell pepper	73
<i>Bacillus licheniformis</i>	GA ₁ , GA ₃ , GA ₄ , GA ₂₀	Scientific Name: <i>Alnus glutinosa</i> Common Name: Alder	74
<i>Bacillus macroidesmacroides</i>	GA ₁ , GA ₃ , GA ₄ , GA ₇ , GA ₉ , GA ₁₂ , GA ₁₉ , GA ₂₀ , GA ₂₄ , GA ₃₄ , GA ₃₆ , GA ₄₄ , GA ₅₃	Scientific Name: <i>Capsicum annum</i> Common Name: Red bell pepper	73
<i>Bacillus pumilus</i>	GA ₁ , GA ₃ , GA ₄ , GA ₂₀	Scientific Name: <i>Alnus glutinosa</i> Common Name: Alder	74
<i>Pseudomonas monteilii</i>	GA ₃	Scientific Name: <i>Triticum aestivum</i> and <i>Cicer arietinum</i> Common Name: Wheat and chana bean	75

Gibberellins

Epiphytic bacteria, especially epiphytic rhizobacteria can produce various types of gibberellic acid (GA). For instance, *Azospirillum lipoferum*^{66,67} or *Acetobacter diazotrophicus*^{68,67} can produce GA₁ and GA₃ while GA₄ and GA₁ are produced by *Rhizobium phaseoli*.^{69,67} Gibberellins can stimulate the production of the

hydrolytic enzyme- alpha-amylase which stimulates seed germination in Barley plants. Alpha amylase breaks down starch into maltose which is further broken down into glucose that can be used by respiring tissue in a germinating Barley seed.⁷⁰ Gibberellins have also been found to improve root development. Marine *Streptomyces* species have the incredible

ability to produce gibberellins, improving the length and weight of the roots of *Solanum melongena* (eggplant).^{71,49} Epiphytic bacteria that produce gibberellins can affect plant growth and seed germination to a certain extent. Table 2 shown below, has a list of the few gibberellins-producing epiphytic bacteria and their host plants.⁶⁷

Rhodopsin

Even though rhodopsin is a protein and not a phytohormone, it has certain plant growth-promoting properties. Certain epiphytic bacteria have been found to produce this protein which activates proton pumps in the bacteria. This allows the bacteria to encounter other light wavelengths that plants don't typically use for photosynthesis. Therefore, competition for light between the bacteria and plant is reduced allowing the plant to grow faster.^{76,17}

1-Aminocyclopropane-1-Carboxylic Acid (ACC) Deaminase

A study conducted in the subtropical forests of Meghalaya, India observed the role epiphytic and endophytic bacteria play in the growth promotion of ethnomedicinal plants. The study's findings showed that plant growth was promoted due to phosphate solubilization and phytohormone production by the epiphytic bacteria. One of the important nutrients plants need for growth is phosphorus. The findings revealed that using acid phosphatase activity, the epiphytic bacteria proficiently broke down phosphorus allowing plants to absorb the nutrient. Enzymes and hormones that promote plant growth like ACC deaminase and IAA were also found to be produced by a few epiphytic bacteria. ACC deaminase reduces ethylene levels in plants hence decreasing the harmful effects of high ethylene concentrations.⁵⁷ High concentrations of ethylene inhibit the hypocotyl growth of eudicot seedlings in the dark hence affecting the seed germination.^{77,78} Hypocotyl is the stem of a germinating seedling.⁷⁹ High ethylene levels also inhibit root development hence affecting the amount of nutrients that plants can obtain from soil.⁸⁰ Additionally, high ethylene levels promote leaf senescence and abscission. Leaf senescence refers to the aging of the plant and abscission refers to the falling of leaves. As plants age faster and leaves fall prematurely, the plant's lifespan also reduces considerably.^{78,81}

ACC deaminase is also capable of enhancing plant fitness during stressful times. *Streptomyces filipinensis* produces ACC deaminase and IAA which improves the plant's resilience to environmental stressors. ACC deaminase breaks down ACC- an ethylene precursor. Hence, ethylene levels are reduced allowing the plant to grow better during stressful conditions.^{54,49} Similarly, *Streptomyces* strain PGPA39 produces ACC deaminase hence alleviating salinity stress in tomato (*Solanum lycopersicum*) plants by increasing the number of lateral roots and plant biomass.^{82,49}

Use of Epiphytic Bacteria in Sustainable Agriculture

Nitrogen Fixation

Our reliance on artificial fertilizer can be reduced using epiphytic bacteria in sustainable agriculture. Epiphytic Cyanobacteria like *Nostoc* and Proteobacteria like *Rhizobium* convert atmospheric nitrogen to soluble nitrate that can be utilized by plants.^{83,84} Firstly, *Rhizobium*, which comes under the phylum of Proteobacteria, fixes nitrogen (N_2) to ammonia (NH_3). The ammonia is converted to nitrite by a genus of chemoautotrophic bacteria called *Nitrosomonas*. Then the nitrite is further converted to nitrate by *Nitrobacter*. *Nitrobacter* and *Nitrosomonas* come under the phylum of Proteobacteria. Only at this point when the nitrogen has been converted to nitrate, can it be used by plants.⁸⁵ Le Chevanton *et al* showed that within the marine environment, epiphytic bacteria from the genera *Muricauda* and *Alteromonas* provide nitrogen to marine algae of the genus *Dunaliella*.^{86,15}

Solubilizing Insoluble Nutrients

Using the process of nutrient solubilization, epiphytic bacteria can also solubilize insoluble nutrients present in the soil like phosphorus, potassium, zinc, and silicon making them available to plants. Potassium, for example, is needed in the transport of food and water through the phloem and xylem. It is also necessary to maintain osmotic and cellular pressures in the plant tissue. Hence, lack of access to potassium results in reduced plant growth. Epiphytic rhizobacteria solubilize potassium and provide it to the plant. Epiphytic rhizobacteria also have the incredible ability to solubilize other materials like zinc and silicon making it available

for roots to absorb. Silicate-solubilizing bacteria not only solubilizes silicon but also makes potassium and potassium silicate more available to plants. Additionally, insoluble phosphorus present in the soil gets solubilized by certain bacteria such as *Pseudomonas*, *Bacillus*, *Aspergillus*, and *Penicillium*. Different forms of insoluble phosphates present in soil include - tri-calcium phosphate (TCP), di-calcium phosphate (DCP), hydroxylapatite and phosphate molecules from rocks. These microorganisms secrete acids that reduce the pH in their surroundings hence breaking down these phosphates and making them soluble for plants. Such useful bacteria existing in the soil decrease our dependence on harmful fertilizers to provide artificial nutrients to plants.⁸⁷

The usefulness of *Streptomyces*

A particularly useful epiphytic bacteria with tremendous potential in sustainable agriculture is *Streptomyces*. A study found that using the process of acidification, *Streptomyces* break down free phosphate making it available for plants. This is done by the production of malic acid by strain mhcro816 or the production of gluconic acid by mhceo811. The study's findings revealed an increased number of branches and lateral roots, greater shoot length and higher content of iron, manganese, and phosphorus in wheat plants that were inoculated with these particular strains of *Streptomyces*.^{88,49} Another study found that inoculating soil with phosphate-solubilizing *Streptomyces* strains significantly enhanced the levels of iron, manganese, phosphorus, and nitrogen in the shoots of wheat plants.^{52,49} Additionally, *Streptomyces youssoufiensis* can solubilize rock phosphates.^{89,49} *Streptomyces* have also been found to indirectly influence plant growth by improving plant-microbe relationships. A study which utilized the tripartite culture system (plant, *Streptomyces*, beneficial microbes), found that using *Streptomyces* enhanced the function of mycorrhizal fungi and nitrogen-fixing bacteria.^{90,49} *Streptomyces* sp. AcH505, found near the roots of spruce trees (*Picea abies*), increased mycorrhization rate (allowing plants to absorb more nutrients) by supporting the growth of *Amanita muscaria* and *Suillus bovinus*, species of beneficial bacteria. The strain also inhibited the growth of harmful fungi like *Armillaria obscura* and *Heterobasidion annosum*.^{91,49} Additionally, inoculating soil with *Streptomyces lydicus* WYEC108 developed more and larger root nodules in young pea plants (*Pisum sativum*). These

root nodules are home to nitrogen-fixing *Rhizobium*, allowing the plant to fix more nitrogen.^{92,49}

Epiphytic Bacteria against Eutrophication

Freshwater epiphytic bacteria on underwater plantations have shown potential in reducing excess nitrogen levels in water bodies.⁹³ Nutrients such as nitrogen and phosphorus often leach into water bodies from agricultural lands causing eutrophication of lakes and rivers. Nutrient runoff into freshwater ecosystems is caused by rainfall. These nutrients are usually beneficial for the environment, but exorbitant amounts of these substances can have detrimental effects on the underwater ecosystem. Excess nitrogen causes an algal bloom: a rapid increase in the population of freshwater algae due to the increased amounts of nutrients available. The algal bloom prevents sunlight from entering water due to the thick layer it forms on the water's surface. This harms underwater plants causing them to die. As these plants die, microorganisms like bacteria use oxygen to decompose these plants resulting in a lack of oxygen in the water, hence affecting other organisms present. This is known as an increase in the biological oxygen demand (BOD). This destructive chain reaction occurs simply due to an increase in nitrogen levels in freshwater ecosystems.⁹⁴ However, this can be countered by epiphytic bacteria capable of denitrification. They convert nitrates in the water into nitrogen gas that goes back into the atmosphere. A study conducted by Weisner *et al* showed that epiphytic microbes on aquatic plants like *Potamogeton perfoliatus* are effective in denitrifying eutrophic lakes and wastewater reservoirs. Denitrifying activity was significantly higher on the shoots of mature plants with dense layers that host epiphytic organisms. It was also found that older plants hosted larger communities of denitrifying epiphytic bacteria.⁹³ These findings prove the usefulness of epiphytic bacteria in cleaning up lakes, rivers and other freshwater bodies that have high levels of nitrogen.

Bioremediation using Epiphytic Bacteria

Seaweed-associated epiphytic bacteria is also capable of protecting its *algae* hosts from substances such as crude oils.^{95,23} Epiphytic bacteria can also be used in bioremediation methods to get rid of pollutants such as phenols,^{96,15} metals^{97,15} and hydrocarbons.^{98,15}

Use of Epiphytic Bacteria in Herbicides

Sometimes, secondary metabolites produced by epiphytic bacteria are not always plant growth promoters but are inhibitors. In other cases, the bacteria itself is detrimental towards plants. This happens when the colonization of epiphytic bacteria interferes with the photosynthetic processes of the plant causing it to be more susceptible to disease-causing pathogens.^{99,23} Such bacteria and their secondary metabolites can be utilized in the production of herbicides to suppress the development of unwanted plants. In harsh conditions, epiphytic bacteria do not need to work hard for survival. However, when conditions worsen, certain epiphytic bacteria like *Pseudomonas syringae* tend to go deeper into the leaf surface for protection. When this happens, there is a higher likelihood that the plant catches a disease.^{100,101} This can be used to our advantage by spraying a culture of *Pseudomonas syringae* on unwanted plants during harsh weather conditions. As the bacteria penetrate the leaf to find shelter, it causes a disease to the plant which will either inhibit growth or kill the plant itself. Certain epiphytic bacteria also produce high levels of auxins. Normally, auxins are responsible for the growth of plants. However, high auxin concentrations inhibit seed germination as they improve the function of abscisic acid.^{102,103} High auxin levels can also decrease the production of salicylic acid hence causing the plant to be more susceptible to disease. This is because salicylic acid is one of the primary defence hormones in a plant.^{104,105} Therefore, some epiphytic bacteria that produce high levels of auxins can be used in herbicides to inhibit the seed germination and growth of unwanted plants.

Certain bacteria can also damage plants due to their ice-nucleating properties. For instance, *Pseudomonas syringae* can form ice crystals on leaf surfaces using a protein complex present on its outer membrane. The protein complex acts as an ice nucleating site and causes ice formation to occur at lower temperatures than it normally would. This temperature usually ranges between -2°Celsius and -5°Celsius.¹⁰⁶ This causes frost damage to plants which can injure or possibly even kill them. The affected plant tissue and cells start releasing nutrients that the bacteria use to their advantage. Therefore, spraying cultures of *Pseudomonas syringae* on unwanted plants can help in getting rid of them.

The environment is negatively affected due to the detrimental ingredients in conventional herbicides. Large quantities of these chemicals are found in the soil and water bodies because they take several years to decompose. The chemicals affect the underwater ecosystem as well, impacting marine life. There is also a chance that they harm humans if ingested indirectly. To curb the use of these dangerous herbicides, epiphytic bacteria can be used against unwanted plants.

Other uses of Epiphytic Bacteria

Apart from the use of epiphytic bacterial enzymes and secondary metabolites in sustainable agriculture, they are also widely used in the medical and pharmaceutical industries.²³ For instance, marine epiphytic bacteria on *Halodule uninervis* (a species of seagrass) such as *Bacillus*, *Oceanimonas*, *Paeni bacillus*, and *Planomicrobium* have antibacterial properties. *Oceanimonas* specifically are useful against *Staphylococcus aureus*, a pathogen that resides in the respiratory tract and skin of humans.^{107,108} Such bacteria serve a key role in the future of biotechnological applications in various industries.

Conclusion

Harnessing the diverse capabilities of epiphytic bacteria in sustainable agriculture can prove to be a promising solution to the rising population's food demand while being environmentally aware. Due to their natural ability to promote plant growth, enhance nutrient uptake and suppress phytopathogens using mechanisms like antibiosis or competitive exclusion, these microorganisms can be used instead of chemical fertilisers and pesticides. Their inhibitory effects on plant growth also show potential in producing chemical-free, natural herbicides to get rid of unwanted plants. Furthermore, epiphytic bacterial applications extend beyond agriculture, contributing to bioremediation and combating eutrophication. Even though these microbes have tremendous potential for the future, further research is required to increase their efficiency in varying environmental conditions and identify the crops that specific species are compatible with. Integrating epiphytic bacteria in agricultural practices brings us one step closer to achieving a sustainable world that can feed its growing population and take care of the environment.

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Author Contributions

- **Rishabh Aachath:** Conceptualization, Writing – Original Draft
- **Zeenat Rupawalla:** Critical Review, Supervision and Final Approval

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