



The Art of Amalgamation: Advancing Crop Productivity with PGPR Consortia Solutions

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Abstract

Rhizobacterial communities that colonize the plant roots, known to have a plant-specific influence that can aid the plant with growth enhancement or eliminate pathogens or improve production is known as the Plant Growth Promoting Rhizobacteria (PGPR). Consortia i.e. mixture of two or more microorganisms, remain the lesser-known territory of PGPR till the recent decade, is now open with opportunities. PGPR consortia offer a sustainable approach to boost agricultural productivity by enhancing plant growth, increasing crop yields by 15–30%, and improving nutrient uptake efficiency, with up to 90% for nitrogen and approximately 70% for phosphorus. They also provide biocontrol against pathogens and increase crop stress tolerance under adverse conditions like drought, salinity, and heavy metal contamination by 20–40%. These benefits, mediated by the secretion of exopolysaccharides, ACC deaminase and other bioactive metabolites, are driven by key rhizobacterial species such as *Pseudomonas*, *Bacillus*, *Enterobacter*, *Azotobacter* etc. which promote plant health, enhance soil quality and support sustainable farming practices. A microbial consortium strengthens the capability of partner and also accomplishes the challenging task with the aid of beneficial relationship with their counterpart in consortia which could be potentially impossible to achieve using monocultures. These results can be enhanced by the use of a pertinent combination of rhizobacteria in consortia wherein individual bacteria is involved in the synergistic relationship with each other that ultimately reflecting in overall efficiency. PGPR consortia improve soil health by enriching nutrient cycling, fostering beneficial microbial activity, suppressing pathogens, and enhancing



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resilience to environmental stresses. Therefore, much of recent research on PGPR is inclining towards consortia for its vast possibilities of applicability in the agriculture field. In this chapter, we advocate experimenting on a diverse range of PGPR to produce more and more efficient consortia that possibly could produce manifold results than the traditional monoculture PGPR. This chapter also highlights plant growth-promoting microbial consortia as a tool for orchestration of crops for improved production and outstanding yield.

Introduction

As we can see in today's emerging world, the demand for food is increasing briskly. An estimation made by United Nation's Population Division stated that there would be 9.5 billion people on earth by the end of 2050, which is roughly 30% more than today.¹ While in proportion to population, the demand for agricultural products is increasing simultaneously. According to the Food and Agriculture Organization of the United Nations (FAO), the gap of increment will be filled 80% by increasing the crop yield from the same land and only 20% is expected to result from new land procured for farming purposes.² As the soil resource is limited, the only option is to increase production without losing the fertility of the existing arable land and by making the agricultural practices sustainable. This has become more challenging in the situation of climate change. Most of the agriculture world is developing unsustainably on the basis of rotten wood rather than on the concrete, i.e. sustainability. The extensive use of chemical fertilizers and pesticides make the land polluted and food poisonous. Chemical fertilizers may promote eutrophication, acidification of soil, reduce minerals and vitamins in the food and they may contribute to global warming and climate change by releasing carbon dioxide and nitrous oxide into the environment.³ More than that, climatic change and soil pollution occurred due to chemicals used in agriculture, plant-microbe interaction is weakening mainly due to disruption of a chemical communication network. Besides chemical fertilizers, pesticides are also very harmful to both human health and the environment. Various studies have shown that pesticides are frequently found in cereals, wheat, rice, maize, tea, as well as fruits like apples, grapes, oranges, lemons, peaches, etc. which include chlorpyrifos, aldrin, dichloran, dieldrin, endrin, endosulfan, heptachlor epoxide, dichlorodiphenyl-trichloroethane, lindane, methoxychlor, mirex and

many more.⁴ These may then get bio-accumulated into various animals, plants and even humans and may cause health threats in the long term.⁵ Furthermore, loss of soil quality, the harmful effect of climatic changes such as elevated CO₂ level or rise in temperature and accumulation of hazardous chemicals in the soil are the major factor hampering agriculture productivity around the world. To deal with these issues, increase crop yield, increment in the nutritional value of the food crop and improvement of soil quality should be put on the priority by directing modern agriculture to sustainable agriculture practices.

Sustainable development is the key to balanced growth and the rhizosphere (narrow zone around the plant's roots) becomes the center of attraction among the researchers as it comprises the diverse microbial community. The Rhizospheric microbial community has positive, negative and neutral impacts on the plant's productivity. Hence, the rhizosphere associated microbial community plays a key role in plants and soil health.

In the field of agriculture, Plant Growth Promoting Rhizobacteria (PGPR) gave hope for increased growth and promising yield in an eco-friendly manner. These plant growth-promoting rhizobacteria are indigenous to soil and able to colonize the plant roots and has great potential to improve the soil fertility via circulating the various chemicals like phytohormones, antibiotics, enzymes secreted by them, which ultimately helps to improve the seed germination, yield production, protection against the fungal, bacterial and viral pathogens.⁶ Though, the PGPR is being the most acceptable alternative for sustainable agronomy, the application of a single PGPR to the field faces trouble regarding their shelf life, inconsistency and survival in a natural environment.

With the increasing interest in sustainability, the application of combined microbes proved to be a more relevant strategy that gives better yield and quick results. In recent times, PGPR consortia are getting attention because of their vast applicability and broad possibilities. The symbiotic existence of two or multiple microbial species is known as "Microbial Consortia".⁷ Since the beginning of life on earth, the microbial population has been prevalent in nature and thrives in association with each other. The natural occurrence of microbial consortia is observed in the terrestrial ecosystems, aquatic ecosystems and also other sites like the mammalian gut, biological wastes, etc.⁸ Borrowing this concept from nature, researchers have demonstrated that microbial consortia can reduce chemical fertilizer use by 20–50%, significantly lowering production costs and environmental impact.^{6,9} This has been broadly investigated in various fields of science as a part of the green revolutionary concept. Global studies estimate that widespread adoption of microbial consortia could reduce agricultural greenhouse gas emissions by up to 30%, aligning with global sustainability goals.^{10,11} This chapter will exclusively focus on the concept and possibilities hidden behind this little-known territory of sustainable agricultural practices.

Plant Growth Promoting Rhizobacteria in Agriculture

Plant growth promoting rhizobacteria are a well-recognized group of the rhizospheric community that plays a significant role in the improvement of plant health and their productivity. The rhizosphere is the hotspot of intense microbial interactions as it comprises most diverse microbial populations like bacteria, fungi, algae, actinomycetes, and protozoa. Since the rhizospheric region has high nutritional value, it provides the platform to the microbial community, and thus, the interaction takes place among the soil, plant, and microbial population which influences the crop productivity. The bacterial community, however, is the most abundant microbial community found in the rhizospheric region.¹² Bacteria that are able to colonize the plant roots and excrete the beneficial effects on the plants through multitudinous mechanisms are known as 'Plant Growth Promoting Rhizobacteria'. The wide range of symbiotic as well as free-living rhizobacteria comes out as an attractive PGPR candidate that mainly belongs to diverse bacterial taxa like

Acinetobacter, *Burkholderia*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Erwinia*, *Flavobacterium*, *Rhizobium*, *Serratia*, *Xanthomonas*, *Proteus*, *Micrococcus* and *Pseudomonas* exhibit successful colonization in rhizosphere.¹³ The potent PGPR tends to harbour the plant growth-promoting [PGP] traits like nitrogen fixation, solubilization of mineral nutrients, production of phytohormones, antibiosis, siderophore production, antibiotic production, lytic enzyme production, production of hydrogen cyanide [HCN], production of ammonia, and other secondary metabolites.¹³

During the last couple of decades, scientists have proven the numerous PGPR as successful bio-inoculants as they are able to facilitate the enhanced plant growth and yield and they encourage the use of biofertilizers instead of synthetic inputs. Since the late 20th century, PGPR has been gaining momentum as prominent bio-inoculants for sustainable agriculture. PGPR is known to have a crucial role in the increment of soil fertility, nutrient cycling, and augment plant growth and yield. Hence, there are many commercial bio-fertilizers like Cell-Tech®, Accomplish®, Nodulator®, Bioboot®, Nitrofix®, etc. are available in the market today.¹⁴

Though PGPR community directs towards secure global agriculture, there are certain limitations of single bio-inoculants. As the rhizospheric region remains the most resourceful and active site due to the secretion of various organic compounds by the roots of plants, numerous biochemical interactions take place among the rhizobacteria and the host plants. The participating bacterial genera are usually very specific to the host plant and they could be antagonistic, synergistic, or neutral towards the host plants. When a single PGPR is applied to the field, it may face competition for nutrients and the space to colonization, and eventually, their survival becomes difficult. At the field level, various biotic and abiotic factors and the continuous change in the environment may affect the optimal functionality of single bio-inoculants. The inconsistent performance and specificity of PGPR, thus, limit their applicability at the broad spectrum as the chemical inputs.

Recently, the changing scenario of agricultural practices and increased environmental awareness has raised the demand for a more significant,

innovative attitude for enhanced crop production which will provide global food security in an eco-friendly manner. To accomplish this goal, modern agriculture has switched over to the application of 'Microbial Consortia'.

Plant Growth Promoting Microbial Consortia (PGPC): Amalgamation of Beneficial rhizobacteria Consortium (or consortia) evolved from the Latin word and it is derived from "Consorts" which refers to the partnership, association, or community that works together for a common purpose.⁷ From the microbiological aspect, the microbial consortium comprises the compatible microbial population of diverse groups. Despite using the monocultures, the consortium treatment ensures the increased activity and better viability of PGPR.³ Therefore, there is considerable interest in exploiting the plant growth promoting microbial consortia for improved crop production. Microbial assemblage within a natural community proved to be more buoyant when faced with the challenging condition compared to a single microbe as diverse biochemical reactions in consortia that may reduce the accumulation of toxic by-products.⁶ Survival of microbial consortium

has been in adverse conditions mainly due to the communication through metabolites via some signalling molecules such as N-acylhomoserine lactones (AHL), volatile organic carbons (VOCs) and other similar molecules such as aryl-HSL or dialkylresorcinols, among the partners. The communication through metabolites determines the nature of the interaction, population dynamics, and functions to be carried out by each partner in evolving that encourages the stable formation of microbial consortia.¹⁴

Formulation of Consortia

A step towards a greener economy led to the application of combined microbes as a promising strategy to give efficient yield and quick results. Construction of plant growth promoting microbial consortia is achieved by isolating microbes from the natural habitat mainly from rhizosphere and they are evaluated for the desired traits and ability for coexistence in the lab as well as on the host plant (figure 1). The mutual partners of microbial consortia may vary based on its specific application, purpose and also on host plant specificity.

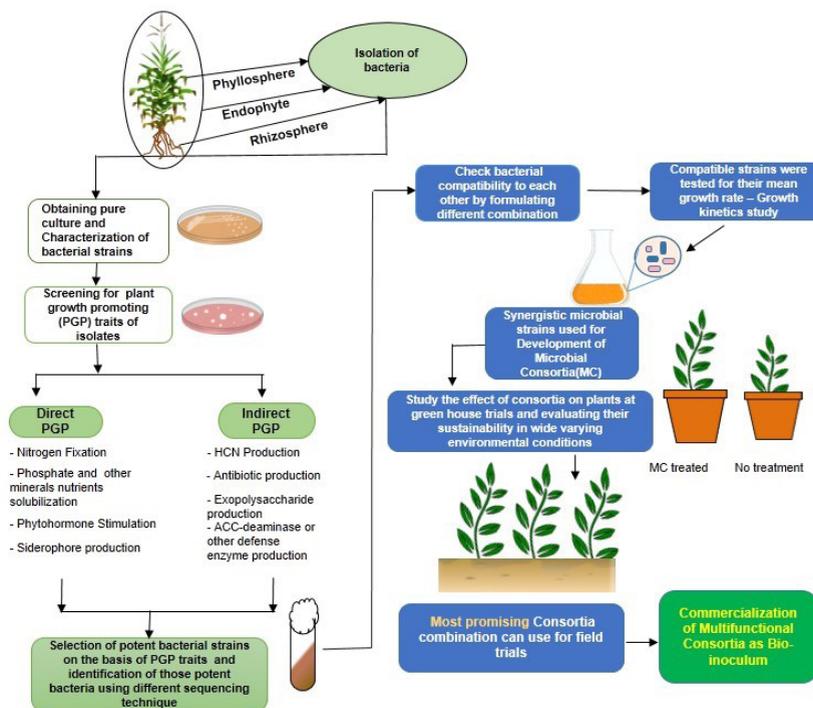


Fig. 1: Framework for Development of Consortia

Ideal Characteristics of PGPR Consortia

Here are some ideal characteristics of the PGPR Consortia.

- Have compatibility among co-inoculated microbial strains.
- Have a lack of competition (*i.e.*, having different nutritional and habitat requirements) within consortia.
- Have a cross-feeding mechanism (that increases the chances to survive as well as to thrive in rhizosphere).
- Have rhizosphere competence.
- Have a faster growth rate.
- Be able to stimulate plant growth.
- Express a broad spectrum of action.
- Be compatible with indigenous rhizoflora.
- Survive in stress conditions like drought, high salinity, heat or cold, high heavy metal concentration.^{15,16}

The use of combined strains proved superior to single inoculants, as these mixed inoculants mutually work together with multiple benefits for the betterment of crop and yield.

Need of Plant growth promoting consortia (PGPC)

Monoculture has a major drawback of not remaining viable in the natural environment or not performing in natural habitat as it performed in the laboratory.¹⁵ While well-designed consortia may perform the same in the natural habitat because the consortium is mimicking the natural microbial communities as well as it can use less refined substrates that are difficult for a monoculture to utilise.¹⁷ Designed consortia are generally more efficient than monoculture¹⁸ mainly because of the elimination of the metabolic burden on one strain by dividing labour and ruling out competition.¹⁹ Thus, there are increased chances of the same output as it has given in the laboratory in the case of consortia than the monoculture and so, consortia can create more possibilities in the field of agriculture.

Consortia are not only better than the monoculture commercially but consortia as the living system

are backed up by the ecological theories as well. Resource Ratio Theory (RRT) and Maximum Power Principle (MPP) are ecological theories that support the consortia over monoculture evidenced the fact that consortia has better chances of not only surviving but thriving in the natural environment.^{6,13}

Resource Ratio Theory (RRT)

This theory formulated by David Tilman in 1980 hypothesized that the likelihood of a living system to survive depends on the capacity of the living system to deplete the resources in the most competitive manner. This theory led to either coexistence of the species and/or the exclusion of competitors. In consortia, one bacteria excretes compound(s) creates a resource base for other bacteria. This type of interaction makes a super-competitor unit. This unit allows the consortia to deplete the environmental resources effectively, increment productivity, and can even perform the metabolism of the substrate that usually cannot be metabolized by monoculture.²⁰ Thus, consortia are more likely to survive the competition in the natural habitat than monoculture.

Maximum Power Principle (MPP)

Maximum power principle was first formulated by Alfred Lotkawho stated that fitness of the living system, *i.e.*, the likelihood of survival and evolution is linked to its capacity to capture energy from surroundings measured in a unit of power $J s^{-1}$. Consortia that utilize multiple substrates in the parallel would have higher fitness than the monoculture that utilizes resources sequentially.²¹ This theory also supports the scope of survival of the consortia in the field are more than the monoculture. Both RRT and MPP not only provide a solid theoretical framework for designing and examining consortia but also provide clarity that consortia are more favourable in natural habitat than the monoculture bacteria.²⁰

In table 1 below, there are some studies that give significant results of plant growth and its productivity in a more sustainable manner by using microbial consortia that supports that the consortia are more effective as biofertilizers than the monoculture.

Table 1: Comparison of monoculture and consortia treatment on crops

No	Plant	PGPR as Monoculture	Results of Monoculture treatment	PGPR as Consortia	Results of consortia treatment	Reference
1.	<i>Oryza sativa</i> L.	<i>Bacillus licheniformis</i>	11% increment in plant biomass under drought stress	<i>B. paraliche-niformis</i> + <i>B. licheniformis</i> + <i>B. haynesii</i>	Highest plant biomass (14%) increment under drought stress	22
2	<i>Triticum aestivum</i> L	<i>Providencia sp.</i>	43% Increment in total biomss	<i>Bacillus sp.</i> + <i>Providencia sp.</i> (AW1+AW5)	55% Increment in total biomass	23
3	<i>Pisum sativum</i>	<i>Pseudomonas aeruginosa</i> PJHU15	Around 50% mortality rate observed against <i>Sclerotinia sclerotiorum</i>	<i>P. aeruginosa</i> PJHU15 + <i>B. subtilis</i> BHHU 100	About 20%-30% mortality rate observed against <i>Sclerotinia sclerotiorum</i>	24
4	<i>Zea mays</i> (Blue maize)	<i>Acinetobacter sp.</i> EMM02	Between 10% to 30% increment in shoot dry weight	<i>P. putida</i> KT2440 + <i>A. brasilense</i> Sp7 + <i>Acinetobacter sp.</i> EMM02 + <i>Sphingomonas sp.</i> OF178	About 75% increment in shoots dry weight	25
5	<i>Pisum sativum</i>	<i>B. thuringiensis</i>	Enhanced chlorophyll – a content than control but lower than consortia	<i>Azotobacter chroococcum</i> + <i>B. thuringiensis</i>	Highest chlorophyll -a content observed.	26
6	<i>Solanum lycopersicum</i>	<i>Klebsiella pneumoniae</i>	Lowest seedling vigour index among the treated tomato plants.	<i>B. subtilis</i> , <i>P. aeruginosa</i> , <i>K. pneumonia</i> and <i>Citrobacter youngae</i>	Highest seedling vigour index observed in tomato plants.	27
7	<i>Triticum aestivum</i>	<i>Aeromonas sp.</i> WBC4	73.3% seed germination rate was seen.	<i>Aneurinibacillus sanerini</i> lyticus WBC1 + <i>Aeromonas sp.</i> WBC4 + <i>Pseudo monas sp.</i> WBC10	93.3% seed germination rate and highest biomass observed.	28

Classification of Microbial Consortia

While discussing consortia, it is very important to delve deeper into the type of consortia which include two species consortia, three species consortia, and multispecies consortia. Here we will discuss the different applicability of two species, three

species, and multi-species (*i.e.*, more than three species) consortia. Some studies have revealed that bacteria will interact with each other synergistically, supply nutrients, eliminate inhibitory chemicals and advantageously help one another to improve their physiology.²⁹ This was further adapted for the plant

growth promoting rhizobacteria (PGPR) to improve the performance and effectiveness of the individual plant growth promoting rhizobacteria.

Simple Consortia

Two species consortia are the simplest form of consortia which pruned the complexity in natural microbial community unveiling one-to-one interaction among the subject species and eliminate the undesirable third party interference. These binary communities are helpful in the understanding of ecological principles that existed in nature which are strenuous to perceive using higher organisms. It is also helpful in the elucidation of evolutionary relationships in natural communities. While talking in terms of economical applications, two-species consortia have a wide range of applicability. Two-species consortia are well studied with regards to economical applications. It's reported that microbial co-culture carries out functions more efficiently than single ones.³⁰ There are many studies evidenced this fact. Consortia including PGPR and *rhizobium/bradyrhizobium spp.* tend to shoot up root and shoot length and weight, nitrogen fixation abilities as well as crop yield in leguminous plants.³¹ Another study, reported that root and shoot length and weight enhanced when inoculated with consortia.³²

Complex Microbial Consortia

Three species consortia are far more complex than two species consortia due to the formation of complex relations between member species. Three species and multispecies consortia require not only cooperative interactions but also suppressive interaction in order to get stability.³³ Thus, a compatible three species or multi-species consortia tend to exhibit complex types of relationships to maintain integrity. From an economical point of view, three species consortia have many applications. *Withania somnifera* (Ashwagandha- a medicinal plant of Indian origin)treated with *Azospirillum spp.*, *Azotobacter chroococcum*, *Pseudomonas fluorescens* and *Bacillus megaterium* show an increase in plant height, root length as well as withaferin-A content, which is a root alkaloid.³⁴ Likewise, a notable increment in plant height and dry weight was observed in the plant of oilseed (*Salicornia bigelovii*) with the use of consortia containing *Azospirillum halopraeferens*, *Bacillus licheniformis*, and *Phyllobacterium sp.*²⁹ There are many more to come but as of now the field of three species as well as multispecies consortia is largely unfathomed and has lots of scopes in the future for young researchers.

Table 2: Crop improvement by different types of plant growth promoting microbial consortia

Types of Consortia	Strains of Consortia	Tested Plant	Significance	References
Simple Consortia				
Two Species Consortia	1 <i>Burkholderia sp.</i> MSSP + <i>Sinorhizobium meliloti</i> PP3.	<i>Cajanus cajan</i>	IAA Production and Phosphate Solubilization	35
	2 <i>Bacillus brevis</i> (MS1) + <i>Acinetobacter calcoaceticus</i> (MS5)	<i>Jatropha curcas</i>	Production of ACC deaminase	32
	3 <i>Pseudomonas putida</i> + <i>B. amyloliquefaciens</i>	<i>Cicer arietinum</i> L.	Drought resistance	36
	4 <i>B. aryabhatai strain</i> B8W22 + <i>B. cereus strain</i> IAM 12605	<i>Solanum lycopersicum</i>	Wilt disease management	37
	5 <i>B. megaterium</i> + <i>Serratia spp.</i>	<i>Zea mays</i>	Increased N,P, K uptake	38
Complex Consortia				
Three Species Consortia	1 <i>B. brevis</i> (MS1)+ <i>B. licheniformis</i> (MS3) and <i>A. calcoaceticus</i> (MS5)	<i>Jatropha curcas</i>	Solubilize inorganic Phosphate	32
	2 AW1 (<i>Bacillus sp.</i>)+ AW5 (<i>Providencia sp.</i>) and AW7 (<i>Brevundimonas sp.</i>)	<i>Triticum aestivum</i> L	Micronutrient uptake	23

	3	<i>Pseudomonas</i> sp.+ <i>Azospirillum brasilense</i> + <i>Burkholderia</i> sp	<i>Bacopa monnieri</i>	Promote plant shoot growth and its total protein content.	39
	4	<i>Pseudomonas aeruginosa</i> + <i>Serratia</i> spp. + <i>Pseudomonas fluorescens</i>	<i>Zea Mays</i>	Increase the growth of maize in Fusarium infested soil.	38
	5	<i>B. cereus</i> AR156 + <i>B. subtilis</i> SM21 + <i>Serratia</i> sp. XY21	<i>Lycopersicon esculentum</i>	Protects under low temperature stress	40
Multispecies Consortia	1	<i>Brevibacillus brevis</i> (MS1)+ <i>B. licheniformis</i> (MS3)+ <i>Micrococcus</i> sp. (MS4) and <i>A. calcoaceticus</i> (MS5)	<i>Jatropha curcas</i>	Solubilize inorganic P, Production of ACC deaminase and siderophore.	32
	2	<i>Pseudomonas</i> sp. DN 13–01 + <i>Sphingobacterium suaeda</i> T47+B. <i>pimilus</i> X22 and <i>B. cereus</i> 263AG5	<i>Solanum lycopersicum</i>	Enzyme production	41
	3	<i>P. aeruginosa</i> strain A1K319) +EX-5 (<i>B. subterraneus</i> strain CF1.9) +KNL-1 (<i>B. subtilis</i> strain JMP-B)+ CTR-4 (<i>Enterobacter cloacae</i> strain VITKJ1) and ANT-4 (<i>B. subtilis</i> strain SBMP4)	Arachis hypogaea	Biocontrol	42
	4	<i>S. nematodiphila</i> strain DZ0503SBS1+ <i>B. toyonensis</i> strain BCT-7112 + <i>B. aryabhattai</i> strain B8W22 + <i>B. cereus</i> strain IAM 12605	<i>Solanum lycopersicum</i>	Biocontrol	37
	5	<i>Achromobacter</i> sp. clone ADCNI + <i>Bacillus</i> sp. clone ADCNE + <i>B. sonorensis</i> clone ADCNF + <i>Bacillus</i> sp. clone ADCNJ + <i>Delftia</i> sp. clone ADCNK + <i>Enterobacter</i> sp. clone ADCNP	<i>Solanum lycopersicum</i>	Salt tolerance	43
	6	<i>Azotobacter chroococcum</i> + <i>B. subtilis</i> + <i>P. aeruginosa</i> + <i>B. pumilis</i>	<i>Cicer arietinum</i>	Increased germination index and chlorophyll content.	44

Interaction Among Bacterial Consortia

It is extremely important to understand the interaction between bacteria existing in the plant rhizosphere or phyllosphere before the formulation of consortia. The plant rhizosphere is full of bacterial diversity that has the potential to promote plant growth. The ability of bacterial consortia to promote the growth of plants is largely dependent on the bacteria-bacteria interaction among the consortia.

Component bacteria of the consortia can have three types of interactions, i.e. (i) Positive or beneficial (ii) Negative or harmful, or (iii) Neutral. Positive interaction occurs in three possible scenarios, i.e., Mutualism, Commensalism, and Protocooperation. Mutualism occurs when each member needs the other to survive or to add any benefit and both will benefit from the interaction e.g. when *Pseudomonas* spp. Interact with arbuscular mycorrhizal fungi (AMF), AMF is

known to increase the plant resistance to pathogens while *Pseudomonas spp.* Can produce hydrogen cyanide (HCN), enzymes and phytohormones that inhibits pathogenic microbes.^{12,45} Protocooperation is similar to mutualism but its member species do not need other species to survive. *Arthrobacter spp.* and *Strptomyces spp.* Can degrade organophosphate pesticide and degrade diazinon by producing degradative enzymes.⁴⁶ While in commensalism, one member of the consortia will get benefits and another one will remain unaffected, plant-microbe interaction itself is in many cases provide an example of commensalism where plant provides nutrients and other compounds via root exudates that PGPR such as *Helicobacter pylori* can use while the plant remains unaffected by the PGPR.⁴⁷ Negative interaction includes predation, parasitism, amensalism, and competition. Predation and parasitism are the phenomenon wherein one species consumes the other species often harming or diminishing the other species. While competition occurs when two or more members of the consortia have the same requirement whether it is of nutrients or space. In amensalism, toxins produced by one species of the consortia suppress the growth of other members of the consortia. These types of interactions are useful in the case of biocontrol e.g. *Pseudomonas Fluorescens* can suppress the growth of plant pathogen *Pythium spp.* Neutral interaction occurs while both the species have different nutritional needs in order to survive or not produce substances that are not inhibitory effects on one other. Many examples are available in nature for the neutral interaction where bacteria can grow together without affecting each other.⁴⁸ Here, in the case of PGP consortia we only need positively or neutrally interactive bacteria because we need a long-term co-existing entity to harness the beneficial effect on the plant. Consortia members should interact positively where mutualistic interaction is preferable to gain maximum beneficial effect when applied to the field.⁴⁸ But when it comes to multi-species consortia, interaction gets complicated as there are examples that showed negative interaction in standard laboratory conditions but when host factor, i.e., specific compound secreted from the host, is introduced, the very same bacteria can coexist within the same.⁴⁹ Thus, bacteria-bacteria interaction into consortia does not follow a defined set of rule and have a vast scope for exploration.

Hence, the interaction studies need to go further than theoretical boundaries.

Though many have written about the beneficial effects of consortia, there is very little known about how they are interacting or how they are communicating with one other. Bacteria with the ability of quorum sensing release chemical signal molecules known as auto-inducers. A minimum threshold concentration of auto-inducers can be detected by the bacteria that stimulate a specific gene expression and ultimately alter behaviour. With the help of this system bacteria population follows a particular behaviour on a community scale and functions like a multi-cellular organism.⁵⁰ As quorum sensing is used to communicate within and between species, it is crucial to create compatibility within consortia as well as with the plant.⁵⁰ The shape and size of the bacterial consortia depend on the absence or presence or quantity of extracellular signalling molecules, i.e., auto-inducers, which may make the beneficial bacteria more relevant and make them grow in synergy.⁴⁹ Acyl homoserine lactone (AHL) and volatile organic compounds (VOCs) are the most popular signalling molecules among all.⁵¹ AHLs are low molecular weight containing compounds that can freely diffuse in and out of the cell.⁵² AHL producing *Serratia liquefaciens*, and *S. phymuthica* proved to enhance root growth and plant biomass in *Oryza sativa* and *Phaseolus vulgaris*.⁴⁸ VOCs are low molecular weight organic compounds with the characteristic to evaporate at normal temperature and pressure. There are many studies that suggest that VOCs have an inhibitory effect on *pathogenic bacteria*. A study showed that VOCs produces by *Pseudomonas fluorescence* have a strong inhibitory effect on *Agrobacterium tumefaciens* a causative agent of crown gall disease in plants.⁵³ *Pseudomonas chlororafis* and *S. proteamaculans* also have an inhibitory effect on the same. AHLs and VOCs are also known to have plant-promoting and pathogen resisting characteristics other than functioning as signalling molecules.^{53,54}

Applications of PGPR's in Agriculture

The multifunctional aspects of synergistic microbes play a significant role in maximal plant productivity. It may utilize as the unrealized alternative of chemical fertilizers which proved to be eco-friendly without any harmful effect on human as well as animal consumers.

Here, we highlighted some applications of consortia with respect to raised quality and quantity of crops.

Plant Growth Stimulation

The quality and quantity of plant growth and yield mainly rely on the availability of nutrients in the soil which may affect mainly due to the overdosing of chemical fertilizers, pesticides, and other synthetic inputs. Till today, crops nutritional demand mainly depends on the supply of the chemical fertilizers but it has its own adverse effect on soil such as deterioration of soil fertility and pH imbalance or some compound such as nitrosamine known to have carcinogenic and toxic properties and so make it uneconomical for applicability in the long term.⁵⁵ To prevent or limit the environmental and economic challenges the world has to move forward to the application of microbial bio-resource which emerged as a budding perspective. Beneficial microbes are being linked intimately to plant roots that promotes the nutrient availability for the uptake of plants. How consortia can give better results than the monoculture? The main hypothesis to answer this question is the member bacteria of consortia have a synergistic effect on each other making them more efficient for uptake of nutrients like nitrogen, phosphorus, potassium, controlling the pathogenic organisms, coping up with stress and in the end, all of it make consortia more efficient for promoting the plant growth and improve the nutrient content.^{56,57} Though the enormous potential of the consortia in plant growth promotion, it is not fully understood that how consortia can have an impact to such an extent.

Nitrogen

Nitrogen is required to synthesize amino acids and proteins and is the main limiting nutrient in plants. Environmental nitrogen cannot be utilized by the plants directly and it needed to convert into a utilizable form by the process called nitrogen fixation which is carried out by prokaryotic bacteria.⁵⁸ The application of PGPR may lead to better uptake of nitrogen by nitrogen-fixing bacteria which are very popular among rhizobacteria. The process of nitrogen fixation by bacteria is carried out with the help of the nitrogenase enzyme.⁵⁹ There are two types of rhizospheric bacteria functioning to fix the environmental nitrogen (i) symbiotic bacteria eg. *Rhizobium spp.*, *Bradyrhizobium spp.*, and (ii) Free-living bacteria eg. *Azotobacter spp.*, *Beijerinckia spp.*

Symbiotic nitrogen fixers are showing mutualistic interaction with the host plant while free-living bacteria make the synergistic relationship with the host plant. Both types of bacteria make the environmental nitrogen available to plants that lead to better growth of the host plant.⁶⁰ There are many examples regarding growth promotion by nitrogen fixers. Consortia made up of *Pseudomonas putida*, *P. agglomerans*, *Bradyrhizobium sp.* and *Pseudomonas sp.* can increase nitrogen content along with root dry weight, aerial weight, and final yield in *Solanum tuberosum* and *Lupinus luteus* plants.⁴⁸ Treatment of maize seed with the consortium of beneficial bacteria having *Bacillus megaterium*, *Pseudomonas aeruginosa*, *Serratia spp.*, and *Pseudomonas fluorescence* resulted in improved root architecture which enriches the nutrient uptake by the plant.³⁸

Phosphorus

Phosphorus is one of the major growth-limiting nutrients in plants and its deficiency causes a reduction in yield. Although phosphorus is one of the most abundant elements on the earth, it is inaccessible for plant uptake. Soil bacteria are capable to mineralize insoluble phosphate into the soluble mono-basic and di-basic phosphate form utilized by plants.⁶ The bacterial mineralization process involves the secretion of different types of organic acids to lower the pH of the rhizosphere and liberate the phosphorus to make it accessible for plants.⁶¹ Plant inoculated with consortia showed higher phosphorus content than monocultures.²³ Another study suggests that consortia of PGPR along with arbuscularmycorrhizal fungi (AMF) increased the utilization of phosphorus.⁶² Consortia consisting of *Azotobacter*, *P. fluorescens*, and *phosphobacteria* have developed as the biological source of nitrogen and phosphorus marketed as Life® Biomix®, Biozink®, and Biodine®.⁶³

Phytohormones

Rhizospheric the microbial pool is also well known for the secretion of growth-stimulating phytohormones like auxins, gibberellins, cytokinins, ethylene, and abscisic acid. These phytohormones production induces various processes like cell enlargement, division, and extension in symbiotic as well as non-symbiotic roots.⁶⁴ Phytohormones are not only growth stimulators but also functions as growth regulators

which are important for agricultural production, as phytohormones like Indole Acetic Acid (IAA) and ethylene are functioning in the increase root hair formation, stimulate the formation of the lateral root, flower development, and fruit ripening^{65,66} Phytohormones are also known to increase stress tolerance in plants. Cytokinin and abscisic acid are involved in protection against drought stress, salt stress, and toxic metal stress. Ethylene also has a role in plant defence pathways and has an effect on pathogens.⁶⁶ Multispecies consortia of phytohormone producers including *Brevibacillus brevis*, *Bacillus licheniformis*, *Acinetobacter calcoaceticus* encourages the IAA production increased by almost 50% than monoculture treatment.³²

Biotic Stress Management

Nutrient-rich organic compounds of root exudates fascinate some pathogenic microbial communities to colonize the plant roots and negatively affect plant growth. Plants are naturally tainted by heterogeneous pathogenic microbes, which include bacteria, fungi, and viruses, and also by herbivores and insects. In such conditions, an unconventional initiative has been taken to prevent or reduce plant diseases by using PGPR, which is often referred to as a biocontrol agent. In recent times the emphasis has been made towards employing these rhizospheric or endophytic microbes as biocontrol agents, as they possess some attractive features like low developmental cost, environment friendliness, and being able for the inhibition of major disease-causing phytopathogen for sustainable agriculture.⁶⁷ As the PGPR strains are well known for providing a front line of defence against pathogens, many products of them have been commercially available to suppress or prevent the deleterious effect of the pathogen.⁶⁷ The application of beneficial microbes like *B. subtilis* and *P. fluorescens* proved an efficient biocontrol agent against the diseases caused by nematodes.⁶⁷

In response to deleterious effects of phytopathogens, biocontrol agents lessen or prevent the infection via a different mechanism which includes competition for nutrients and space, production of antibiotics, secretion of siderophores that limit the availability of iron to the pathogen, production of lytic enzymes, induce systemic resistance.⁶¹

The combinatorial application of various biocontrol agents may offer an extended level of disease control in crops. Enhanced suppression of *Fusarium* wilt in cucumber was achieved by using a combined application of *Paenibacillus* sp. and *Streptomyces* sp.68 *P. frederiksbergensis* S19 and *P. fluorescens* S49 was effective at controlling fungal as well as zoosporic growth.⁶⁹ Therefore, the use of microbial consortia boosts the level and stability of biocontrol activity by a steadier rhizosphere community and effectiveness over a wide range of phytopathogens.

Abiotic Stress Management

Soil stresses are the principal challenge in the field of agrobiolgy. As the soil stresses make a colossal impact on the growth of the plant and the production of the plant products. Thus, it is very critical to address the issue in the best way possible. If looking over the broad range of this issue, there are mainly three types of soil stresses that make the most of hurdles in agriculture, *i.e.*, drought stress, saline stress, and metal stress. Apart from conservative methods which are sometimes not of much significance, PGPR could provide some out-of-the-box solutions here.

Indian population was facing the drought condition and in general, drought is more common through the Indian peninsula. Other than that, 75% of Indian soil is either saline or sodic. Thus, this makes it very necessary to address this issue economically as well as ecologically. PGPR might give the cure for these stresses but in the right combination, consortia give better results than the individual PGPR.⁷⁰

Stresses are mainly expressed by the presence of ethylene. Many PGPR has 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity led to degradation of ACC -a precursor molecule of ethylene- preventing the production of ethylene molecule that makes the plant free from stress and take over the normal plant growth.⁷¹ The same mechanism rescues plant in stress conditions including drought stress, salt stress or heavy metal stress.^{72,73}

Drought Stress

Drought stress is when there is not enough water to fulfil the needs of the plants. Solute concentration tends to increase during drought stress and cell

enlargement will show inhibition and leaf expansion may decrease due to loss of turgor pressure.⁷⁴ Eventually, the concentration of Abscisic acid (ABA) will be built up which causes stomata closure,⁷⁵ which ultimately led to CO₂ assimilation during photosynthesis, and create the hindrance in transpiration and gaseous exchange due to the ethylene hormone activity.⁷² Water stress may hinder the photosynthesis process in many ways including reduction in chlorophyll content, inhibition of chloroplast functioning, inhibition of ribulose-1,5-biphosphate carboxylase/oxygenase, and other such enzymes, disturbing electron transport chain, and accumulation of reactive oxygen species (ROS).⁷ Some symptoms also occur due to water stress condition. 'Wilting' is common among them^{72,76}

Some PGPR started the synthesis of osmolytes to impart resistance to plant towards drought stress. PGPR also helps the plant by secreting exopolysaccharides (EPS) which prevent the plant from desiccation and salicylic acid (SA) which functions as a signalling molecule and induces the genes responsible for producing antioxidants, heat shock proteins, enzymes, and some other secondary metabolites to cope up with drought stress⁷⁷⁻⁷⁹

In this condition, drought tolerating PGPR consortia could be proved as the underdog. Common beans (*Phaseolus vulgaris*) when grown under drought condition, treated with *Peanibacillus polymyxa* (DSM 36), *P. Polymyxa Loutit* (L) and *Rhizobium tropici* (CIAT 899) remarkably increase the nitrogen content, nodulation and, thus, the growth of the plant as compared to the plant inoculated with *Rhizobium* only.⁷⁷ Maize plant when inoculated with *P. entomophila* strain BV-P13, *P. stutzeri* strain GRFHAPP14, *P. putida* strain GAP-P45, *P. syringae* strain GRFHYP52, and *P. monteilli* strain WAPP53 under drought condition shows increased biomass, higher RAS/RT (root adhering soil/root tissue) ratio, better mean weight diameter, greater relative water content and aggregate stability.⁸⁰ Consortia of *Bacillus amyloliquefaciens* 5113 and *Azospirillum brasilense* noticed to increase drought tolerance in plants when used as biofertilizers.⁷²

Saline Stress

Salinity is defined as the higher salt level exceeding the requirements of the plants or in terms of

concentration, saline soil is the soil having electrical conductivity 4 dS m⁻¹ or higher.⁸¹ The surfeit concentration of salts makes the nutrients unavailable for plants. It affects the plant by reducing the growth, photosynthetic capacity, nitrogen content, and some of the essential metabolic activities.⁷ Availability of other nutrients is also affected by surplus salt concentration. Leaf water potential and leaf osmotic pressure decrease in higher salt concentration. Symptoms of saline stress include stunted growth, lower fresh weight and dry weight of the plant, and necrosis of leaves.⁸² Salinity has bigger harm on agriculture as it affects almost 5% of the areas worldwide.⁸³

According to some reports, ACC deaminase along with IAA, regulates the K/Na ratio, chlorophyll, and proline level that induces the salt tolerance.¹⁵ Apart from ACC deaminase induction of induced systemic tolerance (IST) is the major way of PGPR to cope up with the salt stress.¹⁶ Some also reported that PGPR produces antioxidants to scavenge ROS.²⁰

The microbial consortia can give growth promoting as well as stress alleviation activity in the saline stress condition.⁷ This is evidenced by various studies. Consortia of *Pseudomonas spp.*, and *Rhizobium spp.* exhibit maximum increase in growth, ion uptake, chlorophyll content in maize plants under saline stress as compared to the single culture.⁸⁴

Metal Stress

Heavy metal can be defined as metals with higher molecular weight including transition elements. Some heavy metals are essential for plants while some are not but plants have the ability to accumulate both. Excess metal concentration inhibits cytoplasmic enzymes and damages cell structure because of oxidative stress.⁸⁵ More than that, heavy metal stress reduces the number of bacteria including bacteria beneficial to plants which led to a decline in soil nutrients due to a decrease in organic matter decomposition in absence of bacteria. Both will lead to serious damage or death of the plant.

Besides an ACC deaminase activity, several PGPRs release metal-chelating compounds such as Siderophore, influencing the uptake of several metals such as zinc, iron, and copper. Acidification of the microenvironment is also executed by PGPR

to cope with heavy metals stress that changes the redox potential of the soil, affecting the bioavailability of metals. Volatilization through Methylation and intracellular sequestration or precipitation as insoluble organic or inorganic compounds are the other mechanisms used to prevent plants from heavy metal stress.⁷⁹

Treatment of some consortia can improve the plant performance in metal stress conditions. Plant treated with *Pseudomonas putida* SGPI32 and *P. Putida* SGPI32b shows significant growth due to higher production of ACC deaminase and IAA formation under heavy metal stress condition. A study on tomato plants where tomato inoculates with *Burkholderia* sp. CMBM40 and *Methylobacterium oryzae* CMBM20 in soil treated with Ni and Cd. The plant shows a reduction in metal uptake and also shows an increase in plant hormone which led to the growth of the plant. Inoculation of *Bacillus*, *Pseudomonas* & *Streptomyces* strains proved as potent metal biosorbents.⁸⁶ The sunflower inoculated with *Ralstonia eutropha* (B1) and *Chryseobacterium humi* (B2) when grown in soil contaminated with Zn²⁺ and Cd²⁺ shows a decrease in metal concentration inside the plant tissues indicating that metal resistant PGPR can be a potential treatment for plants under heavy metal stress situation.⁸⁷ Another example of a PGPR consortium's potential in bioremediation is the reconstitution of *Bacillus* and *Agrobacterium* spp. which exhibited both Cd–Zn resistance. When applied in rice cultivation, this consortium effectively remediated Cd (76%), and Zn (92.2%) in co-contaminated soil within 30 days.⁸⁸

Bioremediation

Fertile soil is a fundamental requirement for a successful intensive cropping system as it is the primary source of the nutritional requirements of crops. Over usage of chemical fertilizers leads to the accumulation of various organic and inorganic pollutants in soil. The implication of microbial inoculants to enhance the toxic degradation of contaminants and pesticides arises as a safer, greener and cleaner approach which is generally known as bioremediation. The recent observations of rhizobacterial strains exhibit the enhanced remediation process of toxic pollutants present in soil.⁸⁹

For bioremediation, PGPR follows various mechanisms for the remediation of different pollutants. To remove polycyclic aromatic hydrocarbons (PAHs), PGPR produces bio-surfactants that may enhance the solubilisation of PAH and promote removal from the environment.⁹⁰

Consortia consisting of three *Bacillus* sp. strains, two *Pseudomonas aeruginosa* strains, and one *micrococcus* sp. strain can reduce 57% alkanes from diesel contaminated soil as compared to 10% to 30% in general.⁹¹ Once a study showed that 60% of the total petroleum hydrocarbons (TPH) were removed from the soil in the first three months of inoculation when treated with consortia.⁹² Another study reported 45% reduction in lead (Pb) content in rice plants after treatment with the PGPR.⁹³ While a study pointed out that bacterial consortia not only effective on metal contamination but also on hydrocarbon contamination. Study showed improvement of 24%-35% in chickpeas agronomic characteristics while treated with bacterial consortia.⁹⁴

Biopesticides

There is a constant threat of destruction or damage of crops infected by different pests including fungi, insects, weeds, viruses, nematodes, animals and birds which result in a noteworthy loss in yield. Towards an attempt to avoid such losses, the conventional outlook has been employed to eliminate these pests by using chemical pesticides like chlorinated hydrocarbons, organophosphates, carbamates, etc.⁹⁵ Although chemical pesticides are efficient and relatively cheap, the overdependence on chemical pesticides led to a deleterious and hazardous impact on the environment and consumers. Annually about 1 million deaths and chronic diseases are caused due to pesticides. Long-term, low-dose exposure to pesticides can lead to immune suppression, hormone disruption, diminished intelligence, reproductive abnormalities, and cancer in humans, and so pesticides are also known as endocrine disruptors. To overcome the adverse effect of agrochemicals, the utilization of microbes as biopesticides came into existence as an alternative towards the green revolution. Most commonly used microbial biopesticides are derived from bacteria, fungi, viruses, and protozoa.

Biopesticides affect the deleterious organisms by one of the two mechanisms either by (i) secreting some compounds that are toxic to pests and/or pathogens like in the case of *Bacillus thuringiensis* or (ii) by ingestion as agents functioning as biopesticides are pathogenic that cause an infection and being lethal to the unwanted ones e.g. *Metarhizium anisopliae* fungi and *Baculo virus* proved to be lethal to pests when ingested.⁹⁶

Among various bacterial species and subspecies application of *Pseudomonas* sp. and *Bacillus* sp. has been established as an improved biopesticide to control plant diseases like powdery mildew, bacterial spots etc. Out of all *Bacillus thuringiensis* (Bt) transpired as the most successful microbial biopesticide, to suppress the pathogen via secreting crystalline protein have been known for their toxic and inhibitory effect against insect pests like lepidopteron.⁹⁷ A study indicates that the consortia of *Pseudomonas putida*, *Pseudomonas fluorescens* and *Providencia vermicola* fortified with botanical extracts shows the reduction in reproduction of nematode.⁶⁹ Even the commercial products of biopesticides are using the mix of *Pseudomonas fluorescens* and *Bacillus thuringiensis*.⁹⁸ But there is a lot of space waiting to be filled up in the field of commercially available biopesticides. Hence, the application of microbial biopesticide aimed to reduce the constraints induced by chemical pesticides and their high effectiveness has increased the scope for more products which proved to be an asset in sustainable agriculture.

Future Prospects and Economic Benefits of Consortia over Chemical Fertilizers and Monoculture

The Global biofertilizers market was valued at 1.5 billion USD in 2017, which is estimated to reach 3.5 billion USD by 2025. Biofertilizer's market is growing day by day and this demand tend to increase by the time.⁹⁹ In the case of chemical fertilizers on the field, about 60-90% of the chemical fertilizers tends to lose during the application. Only a small percentage i.e. 10-40% of the fertilizers can be actually utilised by the crop. While co-inoculants can supply 70% plus uptake for phosphorus, while this number is even bigger i.e. 90% plus in nitrogen uptake.⁹ This will lower the requirement of fertilizers in the field and make the fertilizers cheaper even on the individual level. PGPR consortia also maintain

the sustainability of various crops production by aiding in soil fertility renovation and the bio-control of pathogens and pests which in turn can give higher and more nutritional crop yield for a long period of time and again consortia proves itself beneficial economically on the individual level. It has shown that phosphorus assimilation in PGPR takes place for their own requirements but it will be available for the plants as well. Unlike chemical fertilizers this makes phosphorus available to plant but that it will not be the cause of eutrophication or any other kind of pollution -if available in the exceed amount- that ultimately harm the environment and causes a big monetary loss in the long term.⁹ As consortia show higher assimilation of phosphorus in general, consortia can make agriculture cheaper for the farmers²³ and it has a bigger impact both economically and environmentally. Due to various practical limitations of current biofertilizers, the advanced biofertilizers i.e. more effective, transportation friendly, easier to use and having longer shelf-life will always be welcomed in the market.⁹⁹ By enhancing the viability and commercial applicability of biofertilizers, consortia can pave the way for sustainable, economically viable agricultural practices that address both current and future challenges.

Conclusion

Sustainable development is essential for humanity's survival, especially as modern agricultural practices contaminate water and food with toxins from chemical fertilizers and pesticides. Shifting to sustainable agriculture is crucial to mitigate these health hazards, but current practices face challenges in meeting global demands for food, fuel, and fiber. Farmers must also see tangible benefits in adopting sustainable practices, as the associated costs, efforts, and efficiency often outweigh the perceived rewards.

Microbial consortia offer a promising solution by replacing chemical fertilizers and pesticides. They promote plant growth and exhibit antagonistic effects against pathogens, addressing rising food demands while minimizing harmful chemical usage. However, challenges include variability in growth rates and cultural requirements of member species, competition among species, environmental instability, and limited understanding of mechanisms driving plant growth promotion.

To ensure successful field application of PGPR consortia, detailed protocols are necessary, including consortia formulation, media preparation specifics, accurate taxonomy of strains, and guidelines to prevent failure. While many questions remain unanswered, microbial consortia hold immense potential for sustainable agriculture. With continued research and global promotion, they could pave the way toward a safer, more sustainable future in agronomy.

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Conflict of Interest

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This research did not involve human participants, animal subjects, or any material that requires ethical approval.

Author Contributions

- **Joshi N.:** Original draft preparation, Visualization.
- **Raval B.:** Original draft preparation, conceptualisation.
- **Jha CK:** Supervised and revised the manuscript.

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